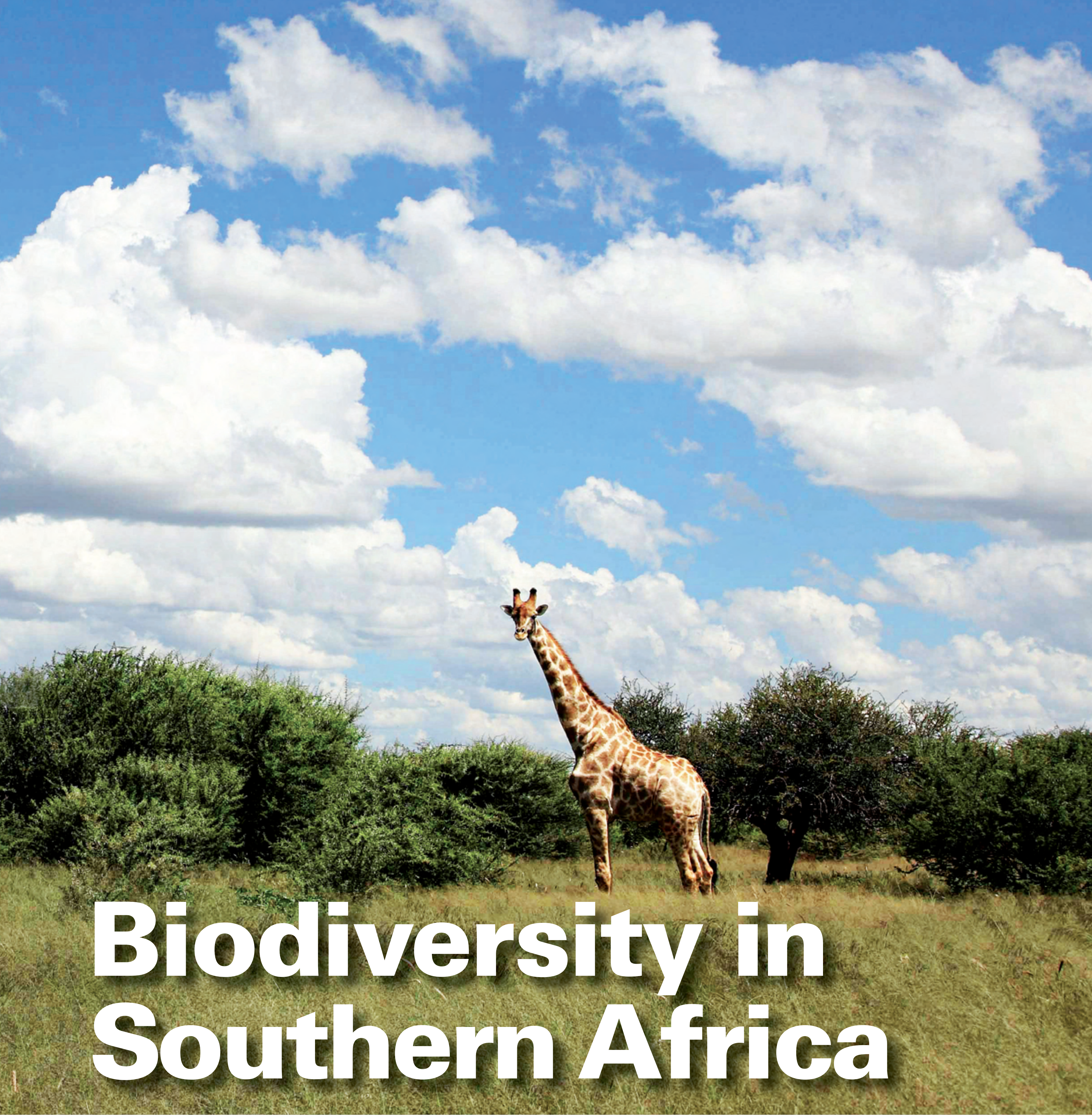

Biodiversity in Southern Africa

Vol. 2

Patterns and Processes at Regional Scale

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BIOTA transect and the Biodiversity Observatories in southern Africa.

Uwe Ulrich Jäschke & Karen Langner • HTW - University of Applied Sciences Dresden

Number, name and respective biome of the BIOTA Biodiversity Observatories.
Page number refers to the description of the Observatory in Volume I.

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Biodiversity in southern Africa

Volume 2:
Patterns and processes at regional scale

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III.1 Reconstruction of historical changes

Climate history of Namibia and western South Africa

Andreas Haensler*, Stefan Hagemann & Daniela Jacob

Summary: The climate characteristics of Namibia and western South Africa as well as observed changes throughout the 20th century are presented in this section. The focus is on observed changes of the temperature and rainfall characteristics. As long-term station data is rather sparse for the southern African region, the analysis focuses on global datasets available at a horizontal resolution of 0.25 to 0.5 degrees.

Climate characteristics of Namibia and western South Africa

The climate of Namibia and western South Africa is characterised by semi-arid to arid conditions with strong rainfall seasonality and a pronounced north-south rainfall gradient (e.g. Schulze 1965). During the summer season (October to March) the western part of southern Africa is generally influenced by a weak heat low (low pressure system induced by regional heating of land surface) located in the north-east, which tends to produce convective rainfall systems over these areas (e.g. Mason & Jury 1997). In winter the situation changes to a predominant anticyclonic circulation system caused by a large single high pressure cell centred further east. In the more humid regions towards the north-eastern part of Namibia, tropical systems sometimes carry a substantial amount of rain during the summer season. The central region around the Namibian–South African border and a large part of the western coastal areas, where the Namib Desert is located, are characterised by arid conditions throughout the year. The lack of rainfall in these regions can mainly be attributed to the cold Benguela upwelling system, which occurs off the western coast and which suppresses rain formation (e.g. Muller et al. 2008). In the arid regions of the western part of southern Africa, coastal fog and dew are important moisture sources. Further south, the climate becomes more humid again but still shows strong rainfall seasonality. Around the Cape Region a Mediterranean climate with a rather dry summer and a wet winter (April to September) season is predominant. This region is characterised by prevailing westerly flows and frontal systems. Only a limited part of the South African south coast receives rainfall throughout the year (e.g. Schulze 1965).

In Fig. 1 mean temperature and rainfall patterns derived from globally available datasets are displayed. Temperature patterns in the region are affected by the relatively cold sea surface temperatures of the South Atlantic. They show a distinct annual temperature cycle in the range of about 8°C in Namibia and about 12°C around the Cape region. Mean annual temperature on the adjacent land, however, ranges from about 15°C in the south up to about 23°C in the north-east of Namibia (Fig. 1a). Seasonal rainfall amounts (Fig. 1b, c) vary from about

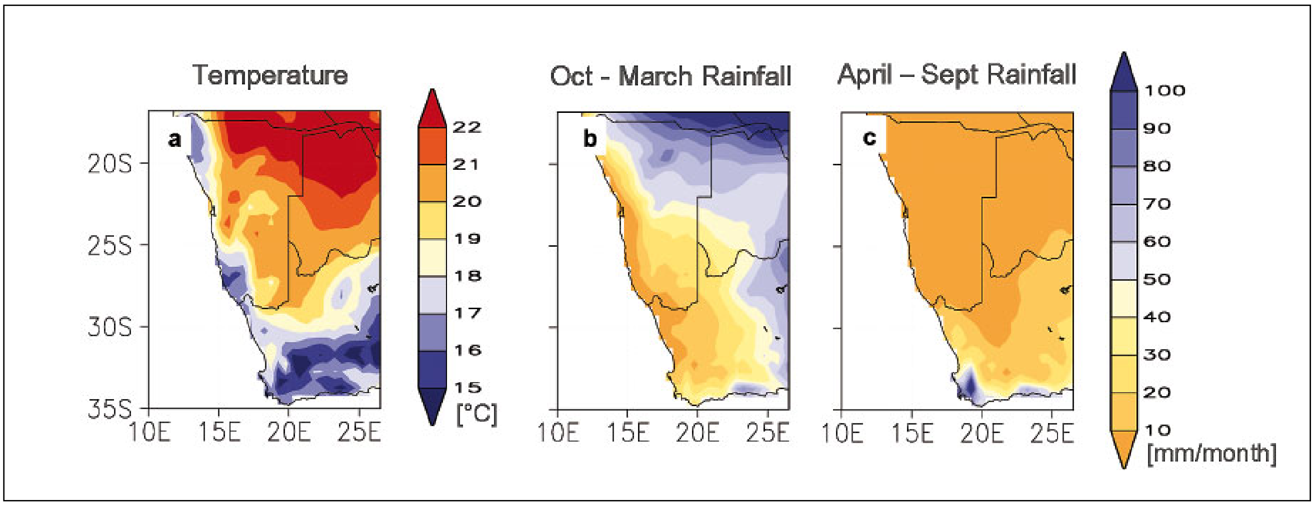

Fig. 1: Observed (Climate Research Unit dataset, Vs. 2.1, CRU Vs. 2.1; New et al. 2002) mean annual temperature (a) and mean seasonal precipitation (Global Precipitation Climatology Centre dataset [GPCC], Schneider et al. 2008) for the summer (b) and winter (c) season for the period from 1951 to 2000.

100 mm/month in the north and around the Cape during the respective rainy seasons to almost no rain in the desert regions. Furthermore, the region is affected by a strong variability in rainfall, often connected to anomalies in the sea surface conditions of the South Atlantic and the adjoining Southern Ocean (e.g. Reason et al. 2002, Rouault et al. 2003, Muller et al. 2008). Rainfall variability is largest in the arid regions along the coast and declines towards the more humid regions. Large scale circulation patterns are frequently superimposed on by local circulation features, induced by the land sea contrast and the complex orography, often leading to locally very different climate states. As a consequence of the unique and extreme climate conditions a specialised flora and fauna has evolved in the region.

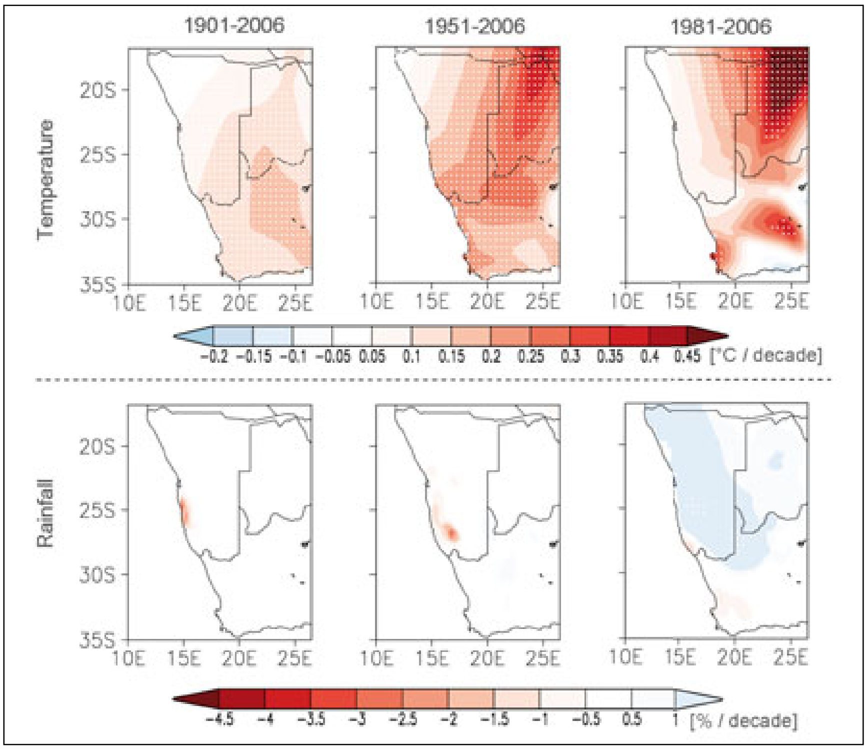

Fig. 2: Observed (CRU3) temperature (upper panels) and precipitation trends per decade for three different periods (1901 to 2006; 1951 to 2006; 1981 to 2006). Statistically significant trends on a 95th level are stippled.

Observed changes in the past

In this section we discuss observed changes of the climate characteristics of Namibia and western South Africa over the last century. However, one has to keep in mind that there are only a limited number of long-term climate observations available for the southern African region. The analysis of long-term trends is therefore based on the most recent version of the globally available dataset of the Climate Research Unit (CRU3), which has a horizontal resolution of 0.5 degree. In the 4th Assessment Report (AR4) of the Intergovernmental Panel on Climate Change (IPCC) a synthesis of observed changes of surface and atmospheric climate characteristics at a global scale was given (Trenberth et al. 2007). They found that the global mean temperature increased in the period from 1906 to 2005 by 0.74°C. In AR4 increasing temperature trends were also reported for the southern African region. Kruger & Shongwe (2004) analysed South African temperature station data for the period 1960 to 2003. For the western part of South Africa, they found a statistically significant temperature increase of about 0.1–0.2°C per decade. In Fig. 2 (upper panels) the observed temperature trend for Namibia and western South Africa for three different time periods (1901 to 2006, 1951 to 2006, 1981 to 2006) are shown for the CRU3 dataset. According to this dataset a warming occurred over the majority of the region for all investigated periods. Furthermore, an increasing warming trend is visible in the second half of the observed period. Maximum warming trends occur in the north-east of the region and with about 0.35°C/decade for the period from 1951–2006 and about 0.5°C/decade for 1981–2006. However, during the last period most of the changes observed in Namibia and western South Africa are not statistically significant.

For precipitation, AR4 indicated that a drying trend is evident over the greater southern Africa region since 1901. The observed decrease in annual rainfall is mainly caused by a decrease in dry season rainfall, as a long-term analysis of mean summer rainfall (December to April) did not show a significant downward trend (Faucherau et al. 2003). Connected to the decrease in annual rainfall is an increase in drought conditions over the region (Trenberth et al. 2007).

For the Namaqualand region MacKellar et al. (2007) investigated rainfall changes that occurred during the 1950–1999 period. They found a rather heterogenic behaviour that somehow seems to be related to topographical patterns. In general, a trend towards more rainfall was observed for the low-lying costal regions, whereas further inland over the higher elevated regions a drying trend was noted. This patchy structure of observed rainfall trends during the second half of the 20th century can also be extended to the whole western part of South Africa (Warburton & Schulze, 2005). In both studies no measure for the statistical significance of the observed trends over the Namaqualand region as well as for the greater western South Africa was provided. An analysis of observed annual precipitation trends for western South Africa and Namibia based on the CRU3 data is presented in Fig. 2 (lower panels). This analysis shows that for the whole region only very small, but statistically insignificant changes occurred during the 20th century.

Analyses of long-term trends on a higher temporal resolution than discussed above are rather sparse for the southern African region. New et al. (2006) analysed daily temperature and

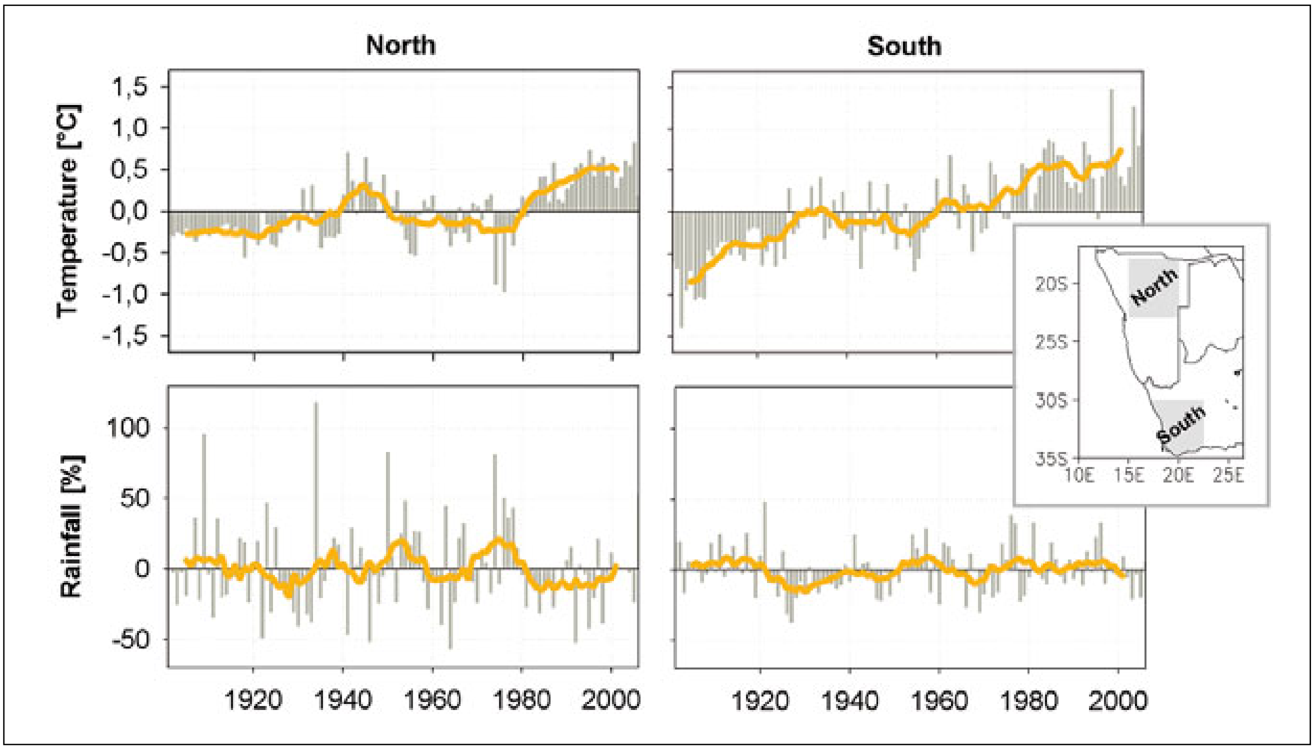

Fig. 3: Observed (CRU Vs. 3) yearly anomalies of the long-term mean (1901–2006) of temperature (in °C, upper panels) and rainfall (in %, lower panels). The orange line depicts a 10-year running mean. Data is an area average over all land points for the region from 15 E to 20 E and 18 S to 23 S in the case of the North region and from 17 E to 22 E and 30 S to 35 S for the South region (indicated in the inlet figure).

precipitation station data for the southern African region for the 1961 to 2000 period. They found a consistent pattern for daily temperature trends, with a statistically significant increase of both, daily maximum and minimum temperatures. For rainfall, the trends found at the stations are less consistent and significant. Averaged for the whole southern African region statistically significant increases of average rainfall intensity, one day maximum rainfall, and extend of the dry spell length were found, but no clear signal for the western part of the southern African region could be identified.

Instead of showing a clear significant trend towards a drier climate, the western part of southern Africa is characterised by strong interannual rainfall variability (Fig. 3; lower panels), which is, as already mentioned, mainly connected to anomalies in the South Atlantic surface characteristics. The interannual rainfall variability shows a cyclic behaviour, which varies for different areas of the southern African region. Around the south-western part of South Africa, Tyson et al. (1975) assigned an oscillation interval of more than 20 years. The oscillation of South African rainfall is related to interdecadal anomalies of the Ocean surface and atmospheric waves (Mason & Jury 1997). The time series of annual rainfall anomalies also confirms that not only does annual rainfall amount show no significant trend, but also the interannual variability remains relatively constant throughout the period covered by the observations. For the central Namibian region, represented by the North area, evidence suggests that the last 25 years of the observation period have been remarkably dry. However, a significant change towards a drier climate can not be seen yet. For temperature (Fig. 3, upper panels), the general warming trend is also visible in the time series of both regions. Generally a gradual warming occurred in the first half of the 20th century, followed by an extended period of cooling. It is only since the mid seventies that a continuous warming trend is observed.

Conclusion

The climate of Namibia and western South Africa is characterised by semi-arid to arid conditions with strong rainfall seasonality. During the 20th century a statistically significant temperature increase was observed for the region. However, the temperature increase was not linear but showed an extended period of cooling in the middle of the 20th century. Since the 1970s temperature has again risen gradually. For annual precipitation no significant trend is visible in the observation record, but a strong interannual variability can be noted throughout the observed period. However in Namibia, the data might indicate a tendency to a drier climate during the last 25 years. To investigate if the observed tendencies are likely to continue in the future, high-resolution climate projections are required. A regional climate projection for the western part of the southern African region is discussed in Article III.3.1. Article III.2.1 further extends the discussion of the projected climate change signal to the greater southern African region.

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Landscape and vegetation change in Namibia since 1876 based on the photographs of the Palgrave Commission

Richard F. Rohde* & M. Timm Hoffman

Summary: Forty-eight repeat photographs of central and southern Namibia first taken in 1876 form the basis for our analysis of vegetation change and allow us to address the following key questions: (a) What have been the major patterns of change in grass, shrub and tree cover since 1876 along an aridity gradient? (b) How have anthropogenic impacts influenced these changes? (c) Are the trajectories of change consistent in direction and magnitude with the projections derived from climate change studies? Each photo site was surveyed for vegetation species and percentage cover change identifying discrete landform units systematically at each location. TWINSPAN was used to group landform units and Reciprocal Averaging ordination displayed the groupings and associated dominant species in two-dimensional space. The results show that there is a significant positive relationship between the % change in tree cover and mean annual precipitation (MAP). Increased grass cover and relative stability in shrub cover within the vegetation units is indicative of a landscape that has not become more degraded since 1876. Sites with less than 275 mm MAP have remained reasonably stable over time. For sites where MAP is > 275 mm, the history of landuse appears to have had a direct bearing on processes of bush encroachment. Our findings do not lend support to future climate change scenarios, nor do we find any verification of a predicted decrease in run-off or increased evaporation as a result of global warming although the increases in tree cover might be partially the result of CO_2 fertilisation.

Introduction

This chapter investigates the environmental history of central and southern Namibia using repeat landscape photography, based on a comprehensive set of archival images taken in 1876. Studies of vegetation change over this timeframe are almost non-existent for this region (Rohde 1997, Heine 2005) and studies of long-term ecological responses to land-use and/or climate change are either site specific or lack historical context (Eitel et al. 2002, Gil-Romera 2007, Chase et al. 2009). Understanding the extent and cause of change, however, is important since degradation in Namibia is commonly blamed on inappropriate land-use practices leading to bush encroachment and desertification (de Klerk 2004, Getzin 2005, DRFN 2008). The causes of both processes are accepted as primarily related to high densities of livestock in the more arid rangelands and fixed stocking rates and fire suppression in commercial cattle farming areas (Wiegand et al. 2005, Joubert et al. 2008). Furthermore, it is anticipated that these ecological processes will be exacerbated by the regional impact of anthropogenic global warming (Midgley et al. 2005). Future climate change scenarios predict an expansion of the desert and arid shrubs into present grassland savannas and a reduction in net primary productivity (Thuiller et al. 2006). Because the rural economy is based on livestock farming across the drier areas of Namibia, climate change that reduces vegetation cover will have severe negative impacts on livelihoods (Reid 2007).

This chapter is based on evidence derived from repeat photography spanning a 133 year period. It describes and analyses vegetation change across several bioclimatic zones that co-occur with the steep west/east rainfall gradient from the Namib Desert to the interior highland savannas and from there south along a more gradual aridity gradient through the dwarf shrub savanna to the desert margin of the Gariep River basin. We address the following key questions: (a) What have been the major patterns of change in grass, shrub and tree cover since 1876 along an aridity gradient in Namibia? (b) How have anthropogenic impacts influenced these changes? (c) Are the trajectories of change consistent in direction and magnitude with the projections derived from climate change studies?

Background

The archival photographs, made during the 1st Commission of William Coates Palgrave to Great Namaqualand and Damaraland in 1876, represent one of the first and certainly the most detailed and comprehensive visual record of central and southern Namibia before the onset of German Colonisation (Silvester et al. 1999). We retraced a 1500 km transect following Palgrave's ox-wagon route from Walvis Bay to Okahandja and south to Windhoek, Keetmanshoop and Warmbad to the Gariep River. Palgrave made this trip during a brief period of peace in the territory. Prior to, and following his five missions in the 1870s, raiding and intermittent conflict between and within groups of Nama, Oorlam, Herero, and Europeans was the order of the day (Gewald 1999). Palgrave's main objective was to broker peace between these various interests and to establish consent for a British protectorate (Stals 1991). It is perhaps partly as a result of Palgrave's photographs depicting a parched, desolate, undeveloped and sparsely populated territory that the British Foreign Office hesitated long enough for a German initiative to succeed.

Under German occupation during the 1890s and early 1900s internecine raiding and localised conflicts escalated into full-scale war. The Rinderpest epizootic decimated native and settler cattle herds while smallpox and prolonged drought leading to famine had catastrophic consequences for the social economy of German South-West Africa (Marquardt 2007). As a consequence of these overlapping natural and man-made disasters, large areas of central Namibia were abandoned by both native and settler populations, only to be re-colonised by white settler farmers during the early decades of the 20th century (Gewald 1996). This succession of human and natural disasters was accompanied by a rapid change in landuse to private commercial cattle farms in the central highlands where bush encroachment has since become a major problem. Many of more marginal arid parts of the southern Namibia were also privatised as commercial farms in the early part of the 20th century leaving confined communal enclaves scattered across the study area (Rohde et al. 1999).

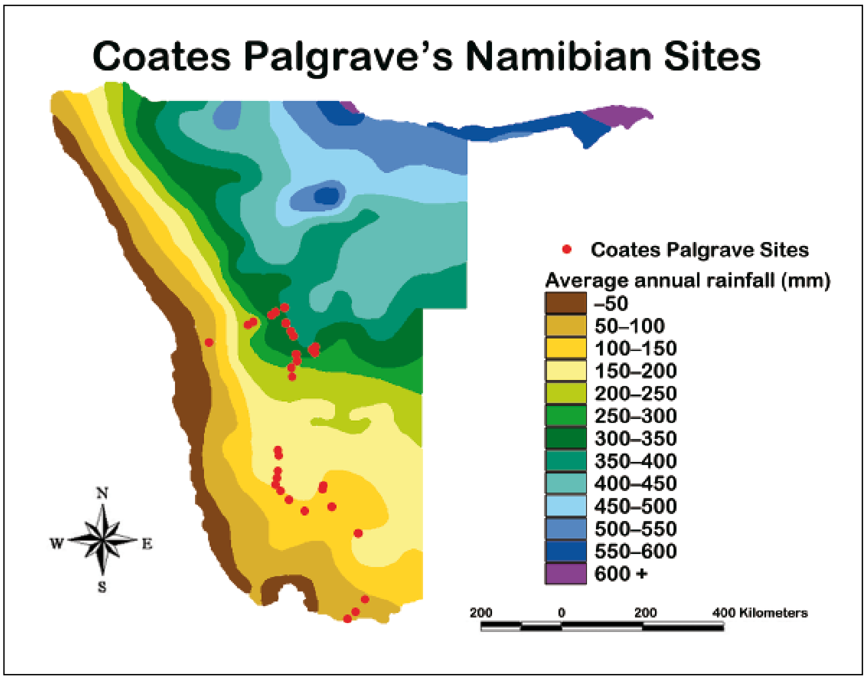


Fig. 1: Average annual rainfall (mm) and the location of 48 repeat photos from 33 sites (red dots) in central and southern Namibia.

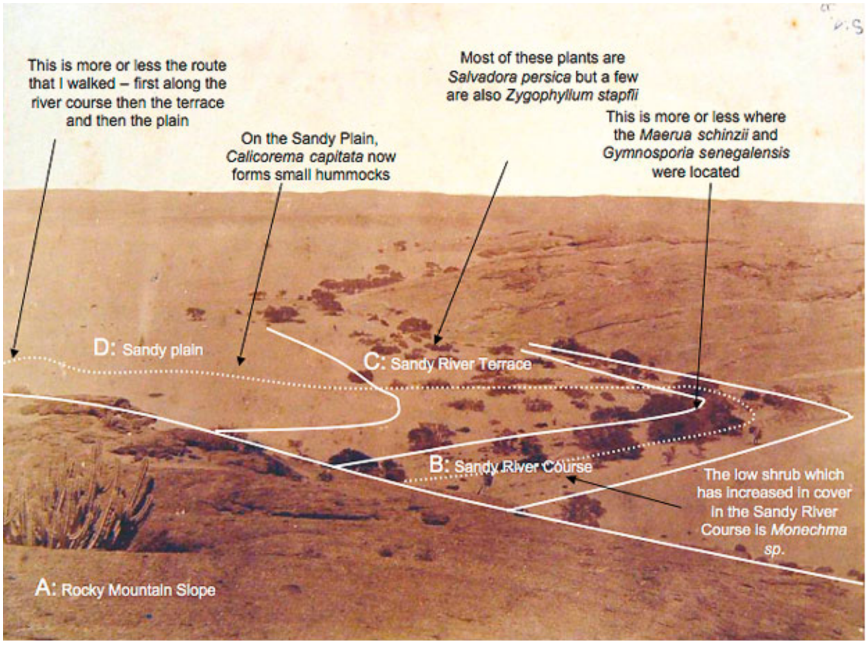


Fig. 2: Demarcation of landform units, notes and survey route at Site No 510. Courtesy of the National Library of South Africa.

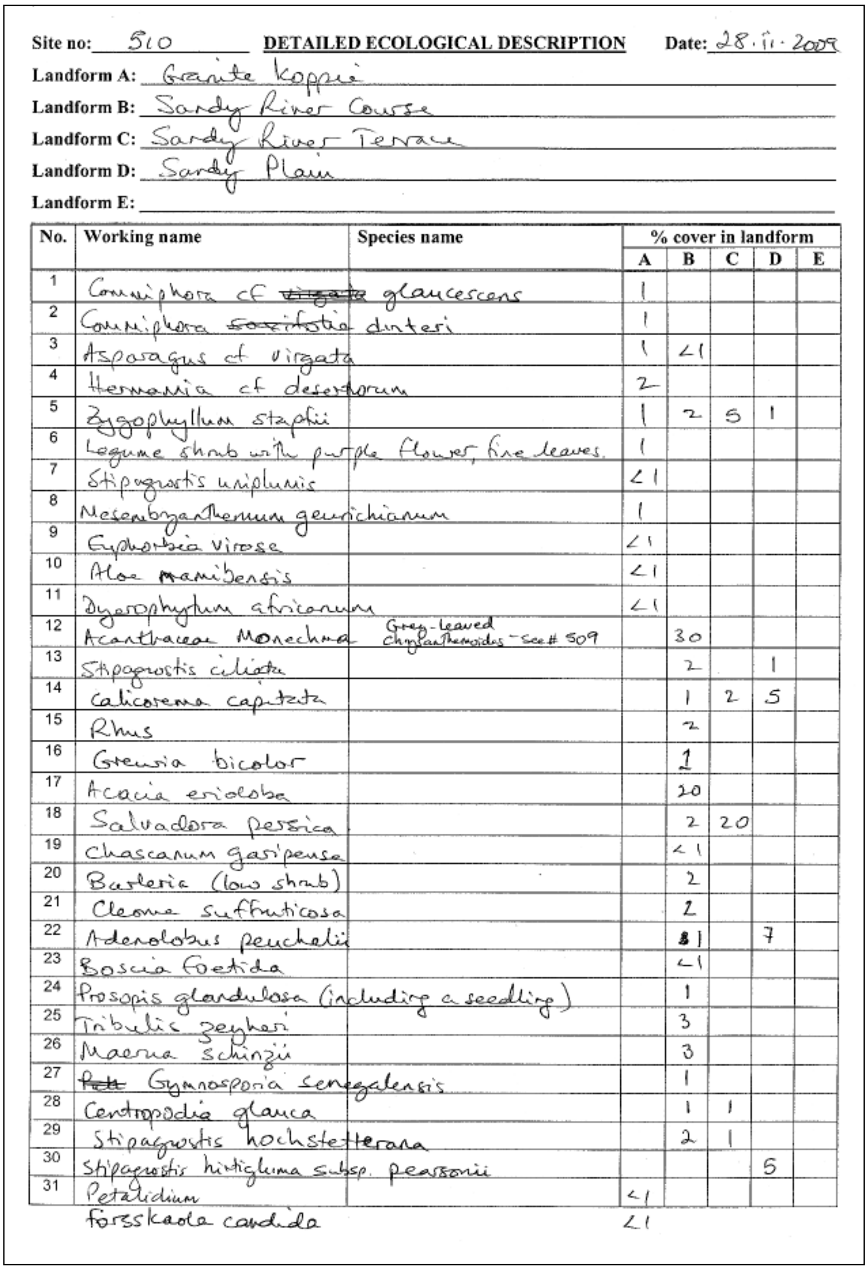
Methodology

Photographic images

Of 78 landscape photographs in the Palgrave album (NLSA 1876), many of which consist of two, three or four photos in panoramic sequences, we were unable to locate 21 images due to either featureless landscapes or highly disturbed urban settings. Nine of the remaining 57 were eliminated due to excessive disturbance or conurbation. The remaining 48 images comprise our sample set of repeat photos and associated site surveys that form the basis for our analysis of change. Where clusters of repeat photo sites were located within 10 km of each other, they were amalgamated to comprise 33 site localities (Fig. 1).

Field notes and surveys

After taking the repeat photographs at each site, the major changes in landuse and vegetation cover evident between the two periods were noted in the field for descriptive and narrative purposes. Where possible, local landusers were consulted for their views on the changes that had occurred in the landscape, and for an explanation of the history of landuse at the location. In addition to the more general description of changes over time at each



Site no: 510 **DETAILED ECOLOGICAL DESCRIPTION** Date: 28.11.2009

Landform A: Granite koppie

Landform B: Sandy River Course

Landform C: Sandy River Terrace

Landform D: Sandy Plain

Landform E:

No.	Working name	Species name	% cover in landform				
			A	B	C	D	E
1	Commiphora cf ~~virgata~~	glaucescens	1				
2	Commiphora ~~saxifolia~~	dinteri	1				
3	Asparagus cf virgata		1	<1			
4	Hermania cf desertorum		2				
5	Zygophyllum stapfii		1	2	5	1	
6	Legume shrub with purple flower, fine leaves.		1				
7	Stipagrostis uniplumis		<1				
8	Mesembryanthemum geurichianum		1				
9	Euphorbia virose		<1				
10	Aloe namibensis		<1				
11	Dyerophytum africanum		<1				
12	Acanthaceae Monechma	Grey-leaved chrysanthemoides – see # 509		30			
13	Stipagrostis ciliata			2		1	
14	Calicorema capitata			1	2	5	
15	Rhus			2			
16	Grewia bicolor			1			
17	Acacia erioloba			20			
18	Salvadora persica			2	20		
19	Chascanum garipense			<1			
20	Barleria (low shrub)			2			
21	Cleome suffruticosa			2			
22	Adenolobus peuchelii			1		7	
23	Boscia foetida			<1			
24	Prosopis glandulosa (including a seedling)			1			
25	Tribulis zeyheri			3			
26	Maerua schinzii			3			
27	~~Rott~~ Gymnosporia senegalensis			1			
28	Centropodia glauca			1	1		
29	Stipagrostis hochstetterana			2	1		
30	Stipagrostis hirtigluma subsp. pearsonii					5	
31	Petalidium		<1				
	Forsskaola candida		<1				

Fig. 3: Detailed species cover survey in four categories of landform unit at Site No. 510 (Gawib 1).

location, we wanted to compare changes in vegetation cover in similar landform units across gradients of rainfall and land use in Namibia. In order to do this we divided the landscape into discrete landform units (sandy river course, rocky river course, sandy river bank/terrace, rocky river bank/terrace, sandy footslope, rocky footslope, sand dune, sandy plain, rocky plain, rocky ridge, saline pan) and by consensus, applied this classification systematically at each location (Fig. 2). We then surveyed each landform unit by walking through it and listing the percentage cover of the dominant species in the unit (Fig. 3).

Data analysis

In order to assess the overall changes in percentage vegetation cover the images were digitised and matched exactly using standard image analysis software. Using the matched images for comparison the authors agreed by consensus on the total percentage cover of vegetation within the Palgrave images and repeat photographs. Where possible the vegetation was also divided into three growth forms viz. grasses, shrubs (< 1.5 m in height) and trees (> 1.5 m in height) and the percentage cover of each growth form estimated for each time period. To determine the extent of change within key species the individuals of a species were counted for the two time periods.

To compare the changes that had occurred more generally across the Namibian landscape TWINSPAN was used to group landform units and Reciprocal Averaging ordination techniques were used to display the groupings and associated dominant species in two-dimensional space. Several landform units were excluded from the final data set either because the unit was 1) not sampled; 2) less than 1 ha; 3) a disturbed settlement; 4) disturbed road verge and/or 5) comprised a unique vegetation unit with little or no replication, leaving a final total of 39 photo sites, 71 landform units and 193 species which were included in the analysis. The percentage change in tree cover was assessed separately for Grassy Shrublands, Thornbush Savanna and Riverine Habitats and correlated with mean annual rainfall. Values for mean annual rainfall were derived from the Worldclim data set (Hijmans et al. 2005).

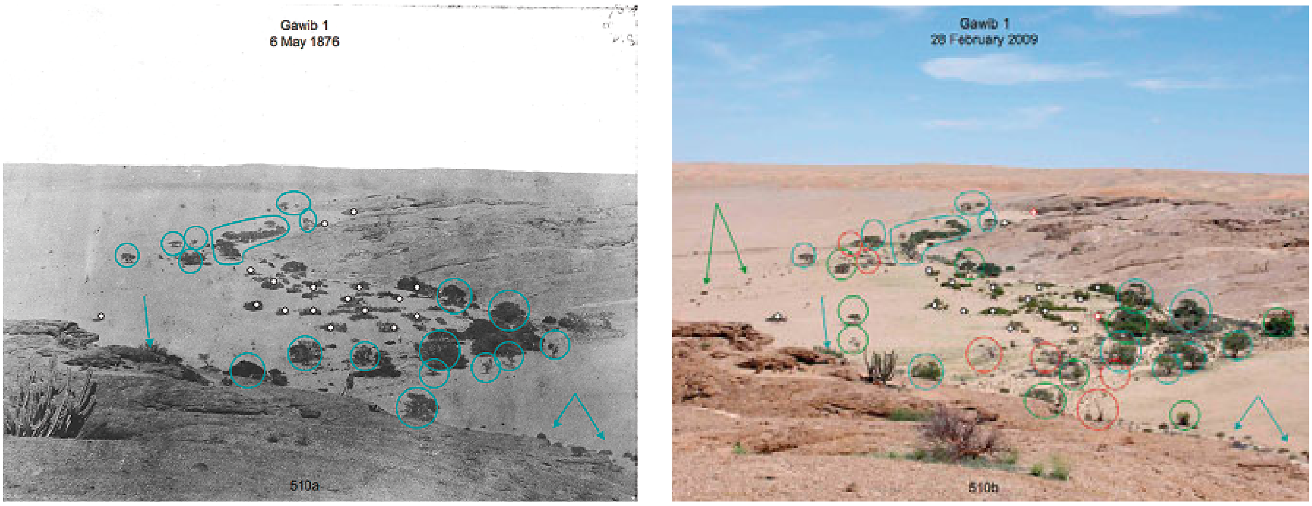
Results

Analysis of individual repeat photographs

Of the 33 site localities identified, 17 depict arid landscapes with a mean annual precipitation (MAP) of < 200 mm; the remainder represent semi-arid landscapes with MAP of between 250 and 375 mm. Ten repeat photos comprise six site localities that document continually inhabited communal landscapes or settlements.

The five repeat photographs that illustrate this chapter are generally representative of the arid (Photos 1–4), riparian (Photos 5 & 6) and semi-arid (Photos 7–10) landscapes across the sample. They are situated in desert, semi-desert savanna transition, highland savanna, camelthorn savanna and dwarf shrub savanna vegetation types (Giess 1971).

The desert landscape of Fig. 4 is situated in what is now a protected area north of the Langer Heinrichberge Uranium Mine on the old ox-wagon route from Walvis Bay to Salem on the lower Swakop River. The ruins of a small house within a kilometer of the photo-station indicate



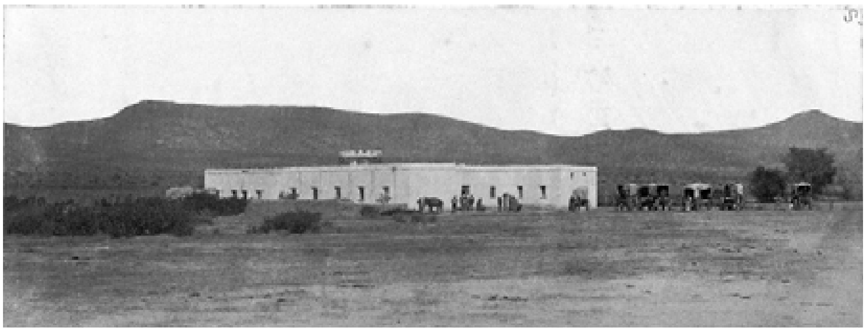
Photos 1 and 2: Looking SSW across a minor tributary of the ephemeral Gawib River, approximately 5 km south of the Swakop River on 6 May 1876 (left) and 28 Feb. 2009 (right). Blue circles indicate *Acacia erioloba* present in both images; red circles indicate *A. erioloba* deaths; green circles indicate *A. erioloba* recruitment. Blue arrows show persistent shrubs (*Adenolobus peuchelii*, *Calicorema capitata*); green arrows show shrub recruits; white dots locate persistent *Salvadora persica* dominated dunes. There has been a slight increase in *A. erioloba* in the sandy river course with a turn-over of approximately 25%. The dune vegetation in the sandy river terrace has remained remarkably stable over 133 years. (Biome: Namib desert; Vegetation type: Central desert; MAP: 51 mm). Photo 1: courtesy of the National Library of South Africa, Photo 2: Rohde & Hoffman.

Photos 3 and 4: Looking WSW to Rooikransberg on Dabis farm in the Karas District. Palgrave's photo was taken on the ox-wagon route about half way between water holes during the dry season following a drier than average rainy season (10 Nov. 1876). The *Acacia erioloba* in the right photo (29 Aug 2008) shows die-back of a very old individual. Nine out of ten *A. erioloba* identified in the original image were found in the repeat as well as several young recruits. Grass cover in 2008 (*Stipagrostis uniplumis* 50% cover; *Eragrostis annulata* 10%; *Enneapogon cenchroides* 8%; *S. ciliata* 5%) occurred during an exceptionally good rainy season. (Biome: Nama-karoo; Vegetation type: Dwarf Shrub Savanna; MAP: 178 mm). Photo 3: courtesy of the National Library of South Africa, Photo 4: Rohde & Hoffman.

that some livestock farming probably did take place here, at least intermittently in the past and the old ox-wagon route is still visible as a gravel track. However, in spite of the evidence of past disturbance, this site shows virtually no change in dominant species composition or cover.

The landscape depicted in Photos 3 and 4 was part of the main southern trek artery for cattle trading with the Cape during the mid 19th century (Andersson 1989). Situated in the Karas Region just north of Helmeringhausen, it became a large (> 10k ha) commercial mixed-livestock farm around 1900 and has been owned by one family since that time. Previous heavy disturbance by very large herds being transported south and subsequent conservative stocking rates within camps has resulted in almost no change in perennial shrub cover or composition.

The village of Otjimbingwe (Photos 5 & 6) was one of the first trading settlements in central Namibia, and remained a communal enclave during and after the colonial period. The authors' collection contains seven more repeat photos of Otjimbingwe taken between 1876 and 1950. In addition we have viewed the earliest image of the village—Chapman's stereoscopic photograph taken in 1862—which shows the river area, the foreground and background plain almost completely devoid of vegetation. Together, these images show 1) a gradual yet significant increase in riparian



Photos 5 and 6: Otjimbingwe Store, on the bank of the Swakop River, 15 May 1876 (top) and 27 Feb. 2009 (below). One of the *Acacia erioloba* trees on the right behind the wagons is still alive. The low *Lycium* spp. to the left of the store have been replaced by *Prosopis glandulosa,* which is widespread in the village and extremely thick nearer the river. This increase in riparian vegetation was observed at all but the driest sites in the study. A survey of the sandy river terrace at site of Palgrave's two panoramic photographs from the roof of the Otjimbingwe Store (Namibia Archive Photo Nos. 2657 & 2658) looking back to the photo station of Photo 6 give the following estimated cover: *Prosopis glandulosa* 28%, *Hyphaene petersiana* 7%, *Phoenix dactylifera* 18%, *Faidherbia albida* 15%. (Biome: Nama-karoo; Vegetation type: Semi-desert savanna transition; MAP: 179 mm). Photo 5: courtesy of the National Library of South Africa, Photo 6: Rohde & Hoffman.

Photos 7 and 8: Stinkwater Farm near Dordabis looking SSE on 14 Oct 1876 (top) and 25 Feb. 2009 (below). The most significant changes include the introduction or increase in *Acacia mellifera* in the foreground sandy river terrace; the invasion of *A. karroo* and *Ziziphus mucronata* in the river course itself, which was previously dominated by scattered *A. erioloba*; and the dramatic invasion of the distant rocky foot-slope by *Dichrostachys cinerea* and *A. mellifera*. (Biome: Tree and shrub savanna; Vegetation type: Camelthorn savanna; MAP: 330 mm). Photo 7: courtesy of the National Library of South Africa, Photo 8: Rohde & Hoffman.

woody vegetation through time; 2) invasion of *Acacia tortilis* and more recently *Prosopis glandulosa* in the village settlement area, and 3) a slight increase in patchiness of woody vegetation on the distant sandy plain. This site illustrates the general trend in the growth of riparian vegetation both within established settlement areas and sparely inhabited livestock farms. The recent invasion of *Prosopis* spp. is most common in highly disturbed landscapes.

Two repeat photos from the highland savanna region illustrate two distinct trends in these wetter landscapes. The Photos 7 and 8 are panoramic photos of a mixed livestock farm in the Dordabis area, 60 km southeast of Windhoek, which has been managed as a commercial enterprise since the early 20th century, having at various times been under the control of Nama pastoralists, European commercial farmers and the Rehoboth Baster Raad. The riverine area in the middle distance has thickened considerably. It appears to have been dominated originally by *Acacia erioloba*, but *Ziziphus mucronata* (30%) and *A. karroo* (20%) now predominate. The most dramatic change, however, is across the rocky foot-slope and the adjoining rocky mountain apronveld, which was sparsely populated by *Boscia albitrunca* in 1876 but which now contains large populations of dense *Dichrostachys cinerea* (25–50%) and *Acacia mellifera* (±15%).

Photos 9 and 10: The Windhoek to Okahandja road at Brakwater, looking NE on 19 Sept. 1876 (left) and 1 Dec. 2006 (right). The valley bottom is intersected by the Klein Windhoek River and marshy depressions around which *Acacia erioloba* (30% cover), *Lycium* spp. (10%) and *Ziziphus mucronata* (5%) have thickened considerably. (Biome: Tree and shrub savanna; Vegetation type: Highland savanna; MAP: 360 mm). Photo 9: courtesy of the National Library of South Africa, Photo 10: Rohde & Hoffman.

The repeat image of the Brakwater valley north of Windhoek (Photos 9 & 10) illustrates a variation on this theme typical of highland savannas with MAP in excess of 300 mm. Here *Acacia erioloba* has increased dramatically (30% cover) across the flat sandy, slightly raised banks of an ephemeral river bed. *Lycium* spp. (10%) appear to have remained more or less stable in terms of its percentage cover whereas *Ziziphus mucronata* (5%) and *A. karroo* (4%) have probably increased slightly. *Prosopis* spp. occur in the most highly disturbed areas at the distant footslope.

General changes across the gradient

The landform units were grouped into three main vegetation units, namely Grassy Shrublands, Thornbush Savanna and Riverine Habitats (Fig. 4).

- The Grassy Shrublands were dominated by grasses such as *Stipagrostis obtusa, S. ciliata*, and low shrubs such as *Rhigozum trichotomum*, *Calicorema capitata* and *Lycium cinereum*.
- The Thornbush Savanna was dominated by a range of spinescent *Acacia* spp. as well as *Dichrostachys cinerea* and the palatable tree *Boscia albitrunca* with an understorey of grasses such as *Panicum maximum* and *Eragrostis lehmanniana*. Dominant low shrubs in this vegetation unit included the spinescent shrub *Phaeoptilum spinosum*.
- Riverine Habitats were dominated by trees such as *Acacia karroo*, *A. erioloba* and *Ziziphus mucronata* with an understory of grasses (*Cynodon dactylon*) and sedges (*Cyperus marginatus*) at some sites.

We used this classification to group our results further and to derive a more general understanding of growth form changes within vegetation units along an aridity gradient in Namibia.

The change in the cover of different growth forms and total vegetation cover within the different vegetation units is shown in Table 1.

- The Grassy Shrublands generally experienced an increase in grass cover although there was considerable variation between sites. Shrub cover declined slightly and together with tree cover rarely comprised a large part of the overall vegetation cover. Although total vegetation cover declined in two of the Grassy Shrubland landform units sampled in our survey it increased by an average of 13.5% within this vegetation unit.
- Thornbush Savanna was characterised by a substantial yet variable increase in grass cover and an even larger but less variable increase in tree cover. Shrub cover changed very little between 1876 and 2009. Total cover increased by nearly a third in this vegetation unit although there was considerable variation between sites.
- The change in the percentage cover of different growth forms within Riverine Habitats showed that grass and tree cover increased at most sites while shrub cover declined on average by 3%. There was a high degree of variation between sites although total cover generally increased within Riverine Habitats between the two time periods.

An analysis of the % change in tree cover between 1876 and 2009 in each vegetation unit in relation to mean annual rainfall (Fig. 5) showed that there was no significant relationship in Grassy Shrubland sites ($N = 8$, $y = 0.0103x - 0.6914$, $R^2 = 0.1046$, $p = \text{NS}$). However, for Thornbush Savanna ($N = 13$, $y = 0.1932x - 37.268$, $R^2 = 0.4566$, $p < 0.05$) and Riverine Habitats ($N = 19$, $y = 0.0803x + 0.4225$, $R^2 = 0.3196$, $p < 0.05$) tree cover increased more at sites with a higher mean annual rainfall than at drier sites. For all sites combined there was also a significant positive relationship between the % change in tree cover and mean annual rainfall ($N = 40$, $y = 0.0993x - 7.0819$, $R^2 = 0.4391$, $p < 0.01$).

Discussion

Our results show a general increase in cover throughout central and southern Namibia since 1876, particularly of trees taller than 1.5 m in height. While grass cover has generally increased this is a relatively ephemeral component in the landscape and can be heavily influenced by seasonal and short-term cycles. Palgrave

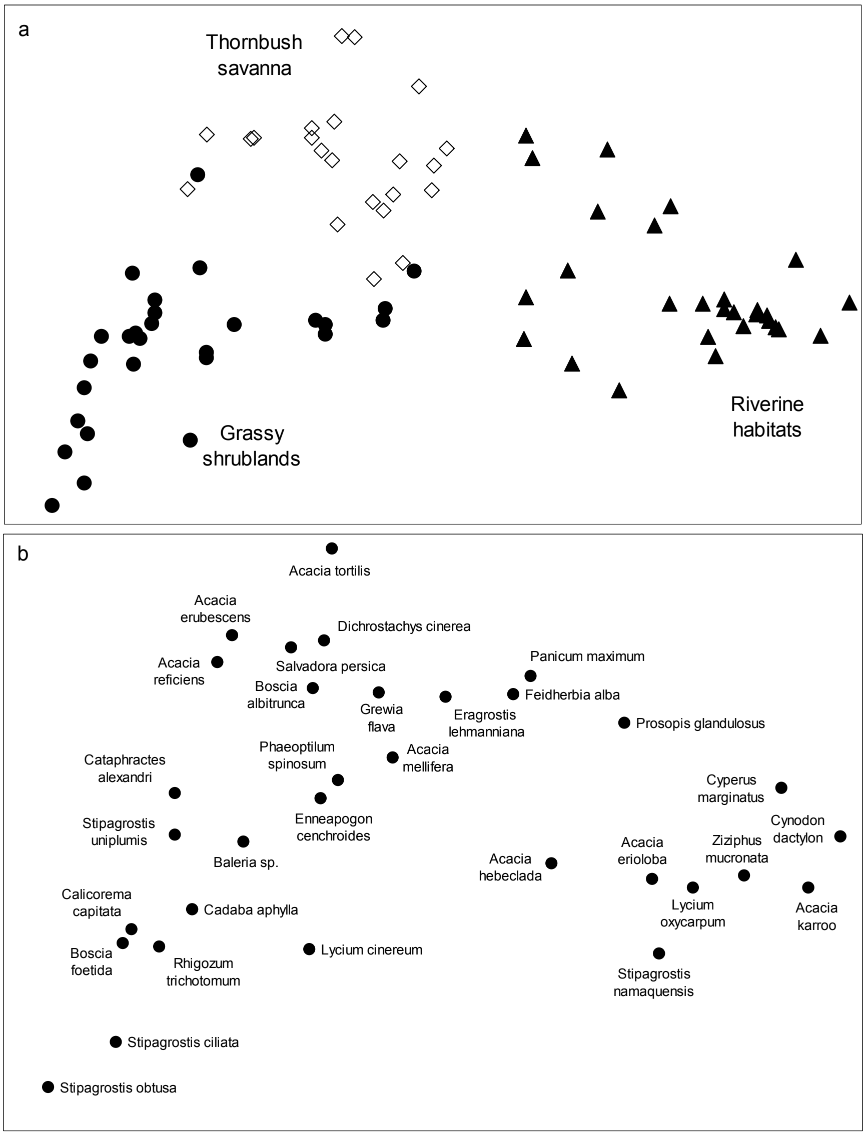


Fig. 4: Reciprocal Averaging ordination of (a) the 71 relatively homogenous landform units derived from 39 repeat photograph sites, which have been grouped according to their species composition within Grassy shrublands (filled circles), Thornbush Savanna (open diamonds) and Riverine habitats (filled triangles) and; (b) the 32 dominant species associated with the landform units.

also makes reference to the dry conditions in southern Namibia at the time of his journey at the end of the dry season (he did not indicate a state of drought) while the 2009 surveys occurred after a relatively benign period in Namibia's climate history.

Despite the ephemeral nature of changes in grass cover we interpret the increased grass cover and relatively stability in shrub cover within the vegetation units as indicative of a landscape, which has not become more degraded with time. The Nama-karoo biome in particular is susceptible to significant changes in shrub and grass cover in response to heavy overgrazing (O'Connor & Roux 1995). Several studies have reported on the widespread increase in, for example *Rhigozum trichotomum* in response to grazing impacts but our analysis suggests that this has not been a widespread occurrence at the sites photographed by Palgrave in 1876.

The increase in tree cover supports the general perception that bush encroachment is widespread in Namibia. What is novel about our analysis, however, is the finding that the increase in tree cover is determined in part by the amount of rainfall expected in an area. For sites with less than 275 mm MAP there has been very little increase in tree cover. This finding has differential implications for landuse planning and environmental policy in arid southern and western regions and the more mesic highland livestock farming areas. Riverine Habitats show the most dynamic response to the MAP gradient primarily because access to stream flow and alluvial aquifers augment the amount of water available to ephemeral river species such as *Ziziphus mucronata* and *Acacia karroo*.

In the study sites where MAP is > 275 mm, the history of landuse has a direct bearing on processes of bush encroachment. In the Highland and Camelthorn savanna areas, even-aged cohorts of *Acacia erioloba* are indications of a widespread recruitment event resulting from the hiatus in landuse occasioned by Rinderpest, war, famine, and disease, which swept the central highlands at the end of the 19th and early 20th centuries (Peters et al. 2006). In the higher MAP sites, the suppression of fire and cattle ranching by settler farmers at constant stocking rates appear to be the main drivers of bush thickening (Hudak 1999, Roques 2001, Joubert et al. 2008). Several of Palgrave's images were taken in or near settlements that have remained under communal tenure throughout this time frame. While landuse intensified within these confined labour reserves and homelands under colonial rule, pastoral practice in communal areas has had as much in common with pre-colonial landuse as with commercial scale settled livestock farming (Rohde et al. 2006). These communal sites are spread across the precipitation gradient and tend to show less increase in tree cover than their commercial counterparts at similar levels of MAP.

The increase in tree cover in the higher rainfall areas could be caused by increased MAP since 1876 (Tews & Jeltsch 2004). However rainfall records from Rehoboth (1913–2008) and Windhoek (1892–2008) show no significant change over this period. While we acknowledge that past climate trends cannot foretell future scenarios, the evidence of vegetation change over the last 133 years (coinciding with the onset of anthropogenic greenhouse gas emissions), indicates the opposite of what GCMs predict. Desert and arid land vegetation is projected to expand at the expense of grassland and savanna vegetation types as well as to suffer some reduction in cover and reduced Net Primary Productivity (Midgley et al. 2005, DRFN 2008). We find no evidence to support these claims, nor do we find any verification of a predicted decrease in run-off or increased evaporation as a result of global warming (DRFN 2008), although the increases we see in tree cover might be partially the result of CO_2 fertilization (Bond & Midgley 2000).

The evidence derived from Palgrave's pre-colonial photographs shows that although regional vegetation change is more nuanced and dynamic than previously assumed, general patterns are evident. We suggest that the vegetation in the more arid parts of Namibia has been remarkably stable since 1876 with little evidence of a decline in either production or species composition. In the central Highlands at locations where MAP is above 275 mm, the region has experienced a significant increase in tree cover. Understanding the key drivers of these general patterns, however, requires a detailed knowledge of local and regional landuse histories as well as an understanding of catchment and site-specific biological processes. These subjects form part of our continued efforts to understand vegetation change in Namibia. We hope that a thorough description of the trajectories of historical vegetation change will help to refine environmental policy and future climate change projections.

Table 1: The difference in the percentage cover of grass, shrub, tree and total vegetation cover between 1876 and 2009 within three different vegetation units in Namibia as determined from repeat photograph pairs (*N* refers to the number of landform units in which it was possible to assess the change in cover of a particular growth form)

		Growth Form		Total cover
Vegetation Unit	**Grass cover**	**Shrub (< 1.5 m) cover**	**Tree (> 1.5 m) cover**	
	%	%	%	%
Grassy Shrublands				
N	9	20	11	21
Average change	31.8	-0.4	0.5	13.5
(±std.dev)	27.0	5.0	1.0	22.4
Range	4–75	-10–5	0–3	-10–21
Thornbush Savanna				
N	6	10	21	21
Average change	21.2	1.5	22.2	29.0
(±std.dev)	28.8	5.4	14.9	19.6
Range	-10–65	-5–15	-5–48	-5–85
Riverine Habitats				
N	4	8	29	29
Average change	14.8	-3.0	19.7	20.9
(±std.dev)	20.8	11.2	17.0	18.9
Range	-5–39	-29–7	0–65	-9–65

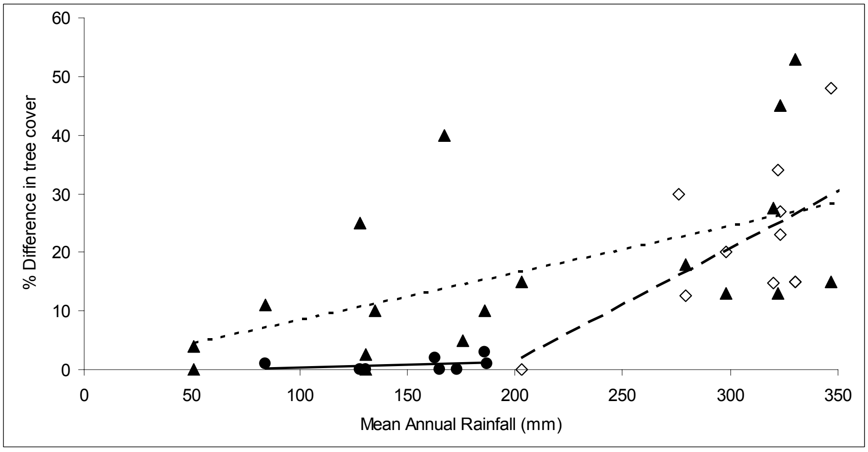


Fig. 5: The relationship between % difference in tree cover between 1876 and 2009 and mean annual rainfall for sites within Grassy Shrublands (filled circles and solid line),Thornbush Savanna (open diamonds and dashed line) and Riverine Habitats (filled triangles and dotted line).

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An analysis of 20th century vegetation change in Namaqualand using repeat photography

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Summary: The extent of change in vegetation cover in Namaqualand, South Africa was investigated using an analysis of 233 historical photographic pairs taken between 1876 and 1971. Each image was divided into different land forms (rivers, sandy pediments, rocky pediments, and slopes) and the extent of vegetation change analysed according to a five point scale, which ranged from –2 (significant decrease in vegetation cover) to +2 (significant increase in vegetation cover). Changes in vegetation cover in communal areas were also compared to changes in vegetation cover in privately owned farms over the time period covered by the matched photograph pairs. For rivers the trend was for an increase in vegetation cover across the region but particularly on privately owned farms. *Acacia karroo* was the most important indigenous riparian species to have increased in cover over time. For the sandy pediments nearly half the sites in the communal areas showed a slight or significant decrease in cover while only 10% of the sites on privately owned farms showed a decrease in vegetation cover. Rocky slopes and pediments appeared better buffered from the impacts of heavy grazing although vegetation cover on privately owned farms increased more than that on communal areas. These findings support the view that landuse, particularly livestock grazing, has had a significant impact on the vegetation of Namaqualand. The influence of landuse, therefore, needs to be considered in any analysis of future potential climate change impacts on the vegetation of the region.

Introduction

The vegetation of Namaqualand is a product of both its evolutionary and historical past and the cover and composition of today's vegetation is determined as much by the soils, topography (Francis et al. 2007) and climate (Desmet 2007) of the region as by landuse influences (Hongslo et al. 2009). It has also changed significantly over time scales of decades to millennia (Hoffman & Rohde 2007) and is currently perceived to be under threat from the twin impacts of heavy grazing (Cowling & Pierce 1999) and future changes in climate (Midgley & Thuiller 2007). Understanding the rate and extent of historical change in the vegetation of Namaqualand in response to different anthropogenic and abiotic influences, such as grazing pressure and climate change, provides the necessary benchmarks against which future changes can be assessed.

However, an accurate determination of the extent of vegetation change in Namaqualand over time is complex. Not only does the region cover a large, bioclimatically-diverse area but the paucity of long-term, scientific records renders accurate reconstruction difficult. Repeat photography is a tool, which has been widely used to bridge the gap between detailed monitoring of change and environmental reconstruction (Turner et al. 2003). We used this approach in an analysis of vegetation change in Namaqualand to ask the following key question: What has been the extent of change in vegetation cover in the region over the course of the 20th century within different land forms and in response to different landuse practices? We address this question in the context of the major land tenure systems, which occur in Namaqualand (communal areas and privately owned farms) and discuss the implications of our findings for the major debates in the region on land degradation and climate change (Hoffman et al. 2007).

Methods

Repeat photography requires both the re-location and re-photographing of an historical image as well as the interpretation of changes visible in the landscape. We re-located 233 historical images of Namaqualand taken between 1875 and 1971 (Fig. 1) and following the approach outlined in Rohde (1997) we re-photographed them between 1998 and 2007. The average number of years between the photograph periods was 60 and ranged between 33 and 128 years. We assessed the extent of change in vegetation cover in three main land forms, namely rivers, sandy pediments and rocky pediments and slopes. Rivers were further divided into perennial and ephemeral rivers while the sandy pediments were divided into those used primarily for cultivation and those used primarily for grazing. All rocky pediments and slopes were used for grazing purposes. In some cases the images contained more than one land form (e.g. an ephemeral river and an adjacent sandy pediment), which were assessed as separate units. In addition to distinguishing between these different land form and landuse categories we also carried out a separate analysis for communal areas and privately owned farms.

For each category within each image we visually assessed the extent of change in vegetation cover using the approach outlined by Nyssen et al. (2009) according

Table 1: A comparison of repeat photograph pairs of the degree of change in different landforms under communal tenure and private management in Namaqualand during the 20th century (areas used for cultivation were assessed separately from areas used primarily for grazing livestock. The values reflect the number of repeat photograph pairs showing the degree of change in vegetation cover in each landform)

Landform, landuse and tenure	No. of photograph comparisons	Assessment of change in vegetation cover				
		Significant decrease	Slight decrease	No change	Slight increase	Significant increase
A: Rivers						
Perennial (communal)	1	0	1	0	0	0
Perennial (Private)	6	0	1	0	1	4
Ephemeral (communal)	6	0	2	0	4	0
Ephemeral (Private)	18	0	1	1	12	4
B: Sandy pediments						
Cultivated (Communal)	15	0	4	5	3	3
Cultivated (Private)	29	1	8	7	8	5
Grazing (Communal)	20	3	6	8	3	0
Grazing (Private)	57	0	5	17	26	9
C: Rocky pediments and slopes						
Grazing (Communal)	49	0	9	27	11	2
Grazing (Private)	77	0	2	58	17	0
All landforms						
Communal	91	3	22	40	21	5
Private	187	1	17	83	64	22

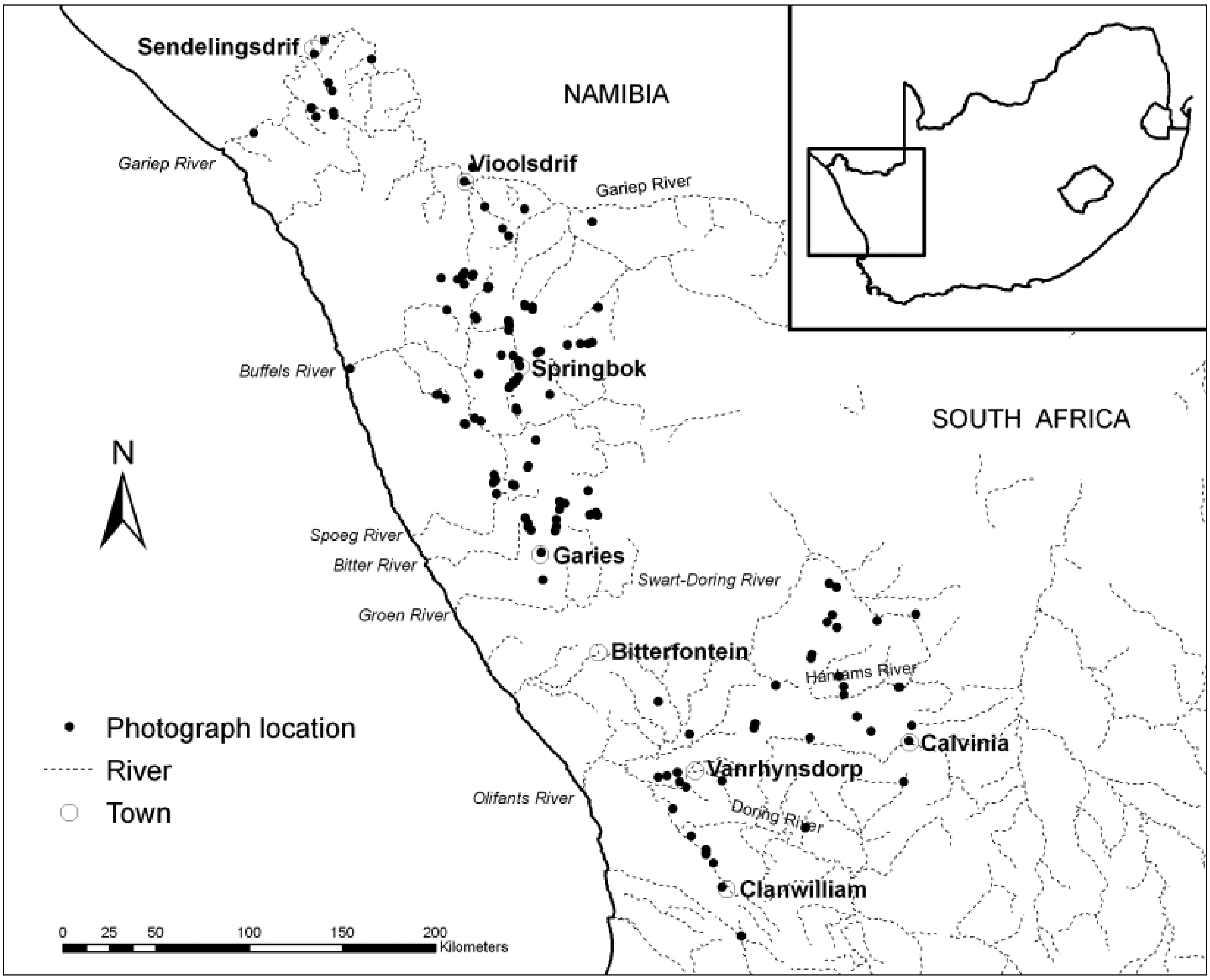

Fig. 1: Map of Namaqualand and the location of repeat photographs used in the analysis shown in Table 1.

Photos 1 and 2: John Acocks took the slightly fogged initial photograph (left) looking northwards and downstream of a flooded Buffels River on 27 October 1957. The right photograph was taken on 25 November 2004 and shows that there has a slight increase in cover on the rocky slope on the left, primarily of the mid-high, succulent shrub *Stoeberia frutescens* while the trees *Acacia karroo* and *Tamarisk usneoides* have also increased slightly in cover and abundance in the river bed itself. Numerous seedlings of *A. karroo* were present in the river bed in 2004 suggesting that no large flood had occurred recently. Photo 1: courtesy of the South African National Biodiversity Institute, Photo 2: Hoffman & Rohde.

to a five point scale as follows: significant decrease in vegetation cover, slight decrease, no change, slight increase, significant increase. A significant decrease or increase was recorded if vegetation cover had declined or increased in the recent photograph by more than 25% relative to the original photograph. A slight decrease or increase was judged to have occurred if the change in vegetation cover was between 5–25% of the original value. A 5% margin of error was allowed on either side for the assessment of 'no change' in the vegetation cover. The number of photograph pairs within each category of change was summed for each land form, landuse and land tenure category and an overall estimate of the trends in vegetation cover over the course of the 20th century for areas managed under communal and private tenure systems was provided.

A detailed description of Namaqualand's communal and private land tenure systems is provided in Rohde & Hoffman (2008). Briefly, the main differences relate to ownership, access and landuse practices. In the communal areas individuals do not hold title to the land (except for clearly-demarcated cultivated areas), which currently rests with the municipalities. Access to the natural resources is granted to all inhabitants of the communal areas, which are characterised by high population densities and high stocking rates. In contrast, privately owned farms are owned by one or a few families who have exclusive access rights to the area's natural resources. Such areas are characterised by low population densities and relatively low stocking rates. These categories are rooted in South Africa's colonial and apartheid past with the communal areas being part of the former Coloured Rural Reserve areas. Most of the farms under private tenure are owned by white land owners.

Results

Rivers

At none of the photo locations with views of either perennial or ephemeral river systems in Namaqualand was there evidence for a significant decrease in vegetation cover (Table 1). Instead the trend was for vegetation cover within river systems to increase, particularly in privately owned areas. *Acacia karroo* was the most important indigenous riverine species to have increased in cover (Photos 1 & 2) while at a number of locations, particularly those associated with southern and south eastern river systems (e.g. Olifants River, Hantams River), a mix of invasive alien species (e.g. *Prosopis* spp., *Eucalyptus* spp., *Nerium oleander*) was responsible for the increase in cover.

Sandy pediments

While there has been some expansion of cultivated lands on sandy pediments and instances of decreased vegetation cover in both communal areas and on privately owned farms the most important trend has been for vegetation cover on cultivated lands to either remain unchanged or to increase slightly (Table 1). At about 20% of sites re-photographed under both communal and private tenure systems there was a significant increase in vegetation cover. This occurred on lands, which have not been cultivated for several decades (Photos 3 & 4). At higher altitude and wetter sites the major species, which re-colonised old lands were *Elytropappus rhinocerotis* and *Lebeckia sericea* while at drier sites *Galenia africana* was the pioneer species, which dominated the early successional colonisation sequence. These species are widespread in the region and are early colonisers of disturbed areas. *E. rhinocerotis* and *G. africana* can form mono-specific, dense stands and are of little forage value. *L. sericea* usually occurs more sparsely in the landscape and is eaten to a limited extent by sheep and goats. There was little proportional difference in the trends in vegetation cover on cultivated lands between communal areas and privately owned farms.

For sandy pediments, where grazing has been the major landuse practice, trends in vegetation cover are very

Photos 3 and 4: This old field on the farm Naries about 27 km west of Springbok was first photographed by John Acocks on 24 September 1957. When it was re-photographed on 27 January 2005 the old field had been lying fallow for several decades and was dominated by *Elytropappus rhinocerotis* and *Galenia africana,* which are both early successional, 1.0–1.5 m high shrubs. Photo 3: courtesy of the South African National Biodiversity Institute, Photo 4: Hoffman & Rohde.

Photos 5 and 6: Situated on the relatively high plateau between Nieuwoudtville and Calvinia this privately owned farm called Soetwater has shown little change in vegetation cover since John Acocks first photographed the site on 20 August 1958. It was re-photographed on 28 October 2005. The site was dominated by a range of dwarf leaf succulent shrubs (*Leipoldtia* sp.) and taller evergreen (*Eriocephalus microphyllous*, *Pteronia incana*) and spinescent, deciduous shrubs (*Lycium cinereum*). Photo 5: courtesy of the South African National Biodiversity Institute, Photo 6: Hoffman & Rohde.

different for communal areas in comparison with privately owned farms (Table 1). Nearly half of the sites rephotographed in the communal areas showed a slight or significant decrease in vegetation cover over time while fewer than 10% of the sites on privately owned farms indicated a decrease in vegetation cover. At only three sites (15%) on sandy pediments in the communal areas where grazing has been the major landuse practice was there a slight increase in vegetation cover and nowhere did this cover increase by more than 25%. In contrast, vegetation cover on sandy pediments used for grazing on privately owned farms increased either slightly (Photos 5 & 6) or significantly on nearly 60% of the sites.

Rocky pediments and slopes

Vegetation cover remained largely unchanged at more than half of the sites on rocky pediments and slopes in Namaqualand's communal areas while 22% of these sites experienced a slight increase in cover with a similar proportion (18%) showing a slight decrease (Table 1). A significant increase in cover was only evident at two sites on rocky pediments and slopes and these were both in communal areas (Photos 7 & 8). For the equivalent sites on privately owned farms more than 75% exhibited no change in cover while the same proportion as for communal areas (22%) showed a slight increase in cover.

General comparisons between communal areas and privately owned farms

About 44% of the sites under both communal and private land tenure showed no change in vegetation cover between the two observation periods (Table 1). The major difference, however, between the communal areas and privately owned farms was that in the former areas the values were distributed more or less equally on either side of the 'No change'

Photos 7 and 8: The profusion of purple colour on this hillslope in the top photograph is probably caused by an abundance of flowering *Drosanthemum hispidum* individuals, which are still present on the hillslope. The site is 19 km north of Springbok in the communal area of Concordia and was first photographed by Frank Steiner in August 1963. It was re-photographed on 10 August 2003 and the dominance of short-lived leaf succulent shrubs has been replaced by a significant increase in the cover of perennial shrubs such as *Tripteris sinuatum*, *Zygophyllum microphyllum* and *Galenia africana*. Photo 7: courtesy of the South African National Biodiversity Institute, Photo 8: Hoffman & Rohde.

score while in the latter, the values were strongly skewed towards a slight or significant increase in vegetation cover. Fewer than 10% of the sites on the privately owned farms showed a decrease in cover while 27% of the sites in the communal areas showed a slight or significant decrease in cover.

Discussion

Major changes in the vegetation of Namaqualand

There were important differences in the extent of vegetation cover change in the different land form units identified in our analysis. The vegetation associated with the perennial and ephemeral river systems of Namaqualand increased in cover more than in other land forms. The widespread increase in the indigenous woody tree, *Acacia karroo*, along even minor drainage lines in Namaqualand is an important change that has taken place during the 20th century. While the species was present in the region in the 17th century (Valentyn 1971) repeat photographs indicate that there has been a widespread recent expansion of the species in Namaqualand. In the southern and south eastern parts of the region, however, the expansion of *A. karroo* is accompanied by an increase in alien species, particularly the woody tree *Prosopis* spp. The slight decline of vegetation cover along the perennial Gariep River reflects the impact of the 1 in 100 to 200-year flood, which occurred at these sites in 1988 (Swart et al. 1988) and the relatively slow recovery of woody elements following such a significant disturbance. The indigenous reed, *Phragmites australis*, however, appears to have increased in cover at most sites. Heavy grazing has also been shown to decrease vegetation cover within ephemeral river courses (Allsopp et al. 2007) and the slight decrease in cover within a few communal area sites has probably occurred in response to this landuse influence.

For the sandy pediments of Namaqualand, which have been extensively cultivated in the past our analysis shows that some areas have been re-colonised by indigenous vegetation while others have been cleared for cultivation. Areas, which have lain fallow for long periods in both communal areas and privately owned farms are located in the drier (< 250 mm per annum) parts of the region (Hoffman & Rohde 2007). In the wetter (> 250 mm per annum) localities the area cultivated has either stayed the same or increased slightly. The impact of cultivation on soil properties is both significant and long-lasting (Allsopp 1999). While some indigenous species are able to colonise abandoned fields successional processes are slow. Even after several decades old fields often remain dominated by one or two disturbance-tolerant species such as *Elytroppaus rhinocerotis* and *Galenia africana* (Rohde & Hoffman 2008) particularly where heavy grazing impacts continue at the site (Honglso et al. 2009).

For non-cultivated sandy pediments, which have been subjected largely to grazing pressures over long time periods there was a major difference in vegetation cover change between communal areas and privately owned farms. The injustices of colonial and apartheid land policies ensured that communal area farmers were under-resourced and confined within relatively small, overcrowded ‘reserves’ (Rohde & Hoffman 2008). This has resulted in a significantly higher grazing pressure in the communal areas, which has been maintained for most of the 20th century (Benjaminsen et al. 2006). In addition, sandy pediments are usually associated with low-lying, relatively flat areas where water points and stock posts are located (Baker & Hoffman 2006, Samuels et al. 2008). The increased impact of livestock trampling and grazing on the vegetation of these areas relative to adjacent, privately owned farms, has been well documented (Anderson & Hoffman 2007, Riginos & Hoffman 2003, Todd & Hoffman 1999, 2009) and is reflected in the repeat photograph analysis of this study. In contrast, vegetation cover on privately owned farms has generally increased over time. This has largely been in response to a reduction in livestock numbers from the 1950s as a result of state intervention in the form of stock reduction and fencing subsidies as well as the shift to a more commercial production system reliant on low stocking rates and rotational grazing management approaches (Hoffman & Rohde 2007). The implication of these differences in cover and composition between communal areas and privately owned farms for livestock production has been explored by Richardson et al. (2007). The loss of vegetation cover in communal areas renders farmers more vulnerable to the impact of even short term droughts in the region although herds rebuild relatively quickly in average or above-average rainfall years (Benjaminsen et al. 2006).

Rocky pediments and slopes in Namaqualand appear better buffered from the impacts of heavy grazing than do sandy pediments (Anderson & Hoffman 2007) and support a significantly higher diversity of plant functional types (Cowling et al. 1994). Our analysis supports this view and indicates that even under heavy grazing pressure, such as occurs in the communal areas, vegetation cover can increase within this land form. It is still not clear why rocky environments should be more resilient than other land forms but the concentration of moisture in small pockets of soil, the protection offered by inaccessible microsites and the reluctance of some animal breeds to negotiate rocky habitats are all important determinants of utilisation patterns and grazing pressure (Petersen et al. 2004). It might also be that rocky slopes and pediments are simply not utilised as heavily as low lying, easily accessible sandy pediments.

Implications of these findings

Our findings have implications for two key debates within the region. Firstly, in terms of the land degradation debate our results support the general view that vegetation cover in communal areas has been more heavily impacted by landuse pressures than the adjacent privately owned farms (Anderson & Hoffman 2007, Hoffman & Ashwell 2001). However, we have also shown that this is by no means universal across all sites and that vegetation cover in many communal areas has remained relatively constant or even increased over time. With greater financial and logistic support and, perhaps more crucially, greater access to land, which has previously been denied to communal area farmers (Cousins et al. 2007), stocking rates are likely to decline in the communal areas with a concomitant increase in cover and improvement in species composition (Hongslo et al. 2009).

Secondly, over the time frames observed in our analysis our results have also demonstrated the significant impact of landuse on vegetation cover. Because of this it is difficult to identify the trajectories of vegetation change imagined by future climate change projections for the region (MacKellar et al. 2007, Midgley et al. 2007). We suggest that over the course of the 20th century changes in cultivation practices and stocking rates as a result of economic pressures (e.g. on the price of machinery, seed, fertilizer, etc.) and state policy (e.g. stocking rate reductions, fencing subsidies) have had a far greater impact on vegetation cover in the region than climate (Hoffman et al. 2009). However, it is important that some of the photographic sites continue to be monitored, perhaps at in increased frequency so that the impacts of climate change can be detected early and in this way they could be used as an early warning system for farming communities. Photographic sites located within ecotonal areas (e.g. between winter and summer rainfall zones) or along an aridity or altitudinal gradient, as well as those with the potential for assessing changes in major plant functional types (e.g. succulent shrubs, grasses, *Rhus* spp., *Aloe dichotoma*) would be particularly useful in this regard.

Repeat photography as a tool for change detection

This analysis shows some of the strengths and weakness of repeat photography as a tool for measuring change. One of its strengths lies in the relatively long time period covered by the images as well as the relatively detailed analysis possible. Individual species and populations can often be assessed in terms of their responses to climate and landuse impacts (Duncan et al. 2006). Repeat photography can also be interpreted and used by a wide range of stakeholders and user groups particularly if they are involved in sharing landuse history details with the researchers. This is an important aspect if local decision makers are to be involved in setting agricultural and landuse policy based on shared experience and evidence (Rohde et al. 2006). However, there are also serious limitations to the technique. These include the choice of sites, which is set entirely by the serendipitous location of historical material as well as the specific nature and idiosyncratic content of the available imagery. Finding a general quantitative method to assess change, which is applicable across space and time, has proven problematic insofar as it allows only a basic indication of change. Our approach, which uses a large number of images, grouped into different land form, landuse and land tenure units, is an attempt to develop a more general synthesis of vegetation change over long time frames following the analytical methodologies that have evolved over the last 45 years (Hastings & Turner 1965, Kull 2005, Munro et al. 2008, Nyssen et al. 2009).

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Part III

III.2 Large-scale patterns and dynamics

Regional climatological patterns and their simulated change

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Summary: In this section, the results of a high-resolution climate projection over the southern African region are presented. The focus of the analysis is on changes in temperature and hydrological conditions. Projected changes in the mesoscale circulation patterns will also be presented. The simulations were performed using the regional climate model (RCM) REMO at a horizontal resolution of approximately 18 km for the period 1960 to 2100, making it the longest high-resolution climate change projection ever to have been conducted for the southern African region. Boundary conditions for the simulation are provided by the global climate model ECHAM5/MPIOM, as described in Article III.3.1, where an overview of previous regional downscaling activities over the southern African region is also provided.

Evaluation of model quality

As an essential first step, model simulations must be compared with observations. Based on this analysis, the ability of a model to reproduce the regions climate characteristics can be quantified. As area-wide station observations are rather sparse over the southern African region, REMO (Jacob 2001) was validated against global datasets. Fig. 1 shows the simulated and observed climatological mean annual temperature and rainfall. The differences between REMO and the respective observation datasets are also depicted. Annual mean temperature ranges from about 286 K around the Drakensberg Mountains in the south-east up to about 296 K in the greater Okavango Delta (Fig. 1b). The spatial temperature patterns are adequately captured by REMO (Fig. 1a), however the model tends to simulate higher temperatures than were observed over most parts of the region (Fig. 1c). Mean warm bias is in the order of about 1 to 1.5 K, although it is even greater over desert regions like the Kalahari and the Namib. The relationship between warm bias and water availability in the REMO model has already been discussed in an earlier study (Haensler et al., submitted). Here, a significant correlation between warm bias and evaporation rate was found, indicating that REMO tends to have a stronger warm bias for regions with lower water availability. It was speculated that this might be due to too low soil moisture in the model. However, the strong warm bias of REMO in the north-west of Namibia might be due to an underrepresentation of the rather cold sea surface temperatures offshore of this region in the model.

The southern African region is mainly characterised by semiarid conditions with precipitation ranging from almost no rainfall in the arid zone along the west coast to more than 1000 mm/year in the humid mountainous region in the south east (Fig. 2e). Rainfall shows a strong seasonality with the majority of the region receiving its rainfall in the summer season from October to March. Exceptions to this are the south-western Cape (SWC) having its rainfall maximum in the winter season and the south coast of South African that receives rainfall throughout the year. Rainfall patterns are influenced by both, tropical systems (mainly in the northern, central and south-eastern parts of the region) and frontal systems with prevailing westerly flows (mainly in the SWC region). Spatial rainfall patterns are accurately simulated by REMO (Fig. 1d), but there is a tendency for the model to simulate higher rainfall than was observed (Fig. 1e).

We also investigated the simulation of the mean circulation patterns in the summer (December to February) and winter (June to August) seasons. Fig. 2 shows the mean sea level pressure and near surface winds for REMO and ERA40 (Uppala et al. 2005) as a 30 year climatological mean for both seasons. Compared with ERA40 reanalysis data, the predominant circulation patterns are satisfactorily captured by the model for both seasons. Nevertheless, REMO tends to slightly overestimate the winter high pressure cell (Figs. 1a & b) and slightly underestimates the summer heat low (Figs. 1c & d). Especially the latter is likely to have an impact on the simulation of precipitation for the region.

Projections of future change over the southern African region

The REMO projections of different variables for the southern African region are depicted in Figures 3–5. In Figs. 3 & 4, the left panels show the simulated mean values for the control period (1961–1990) and the right panels represent the respective mean changes to the control period for three future periods (2011–2040, 2041–2070, and 2071–2100). For the circulation patterns shown in Fig. 5, all plots represent a mean over each respective period. The projected changes for the presented variables are discussed below.

Annual mean temperature (Fig. 3) is projected to gradually increase over the whole domain. In particular, the interior of the southern African region is projected to undergo a significant warming, with a maximum rise in temperature of approximately 6 K by the end of the 21st century. The warming tends to be more moderate

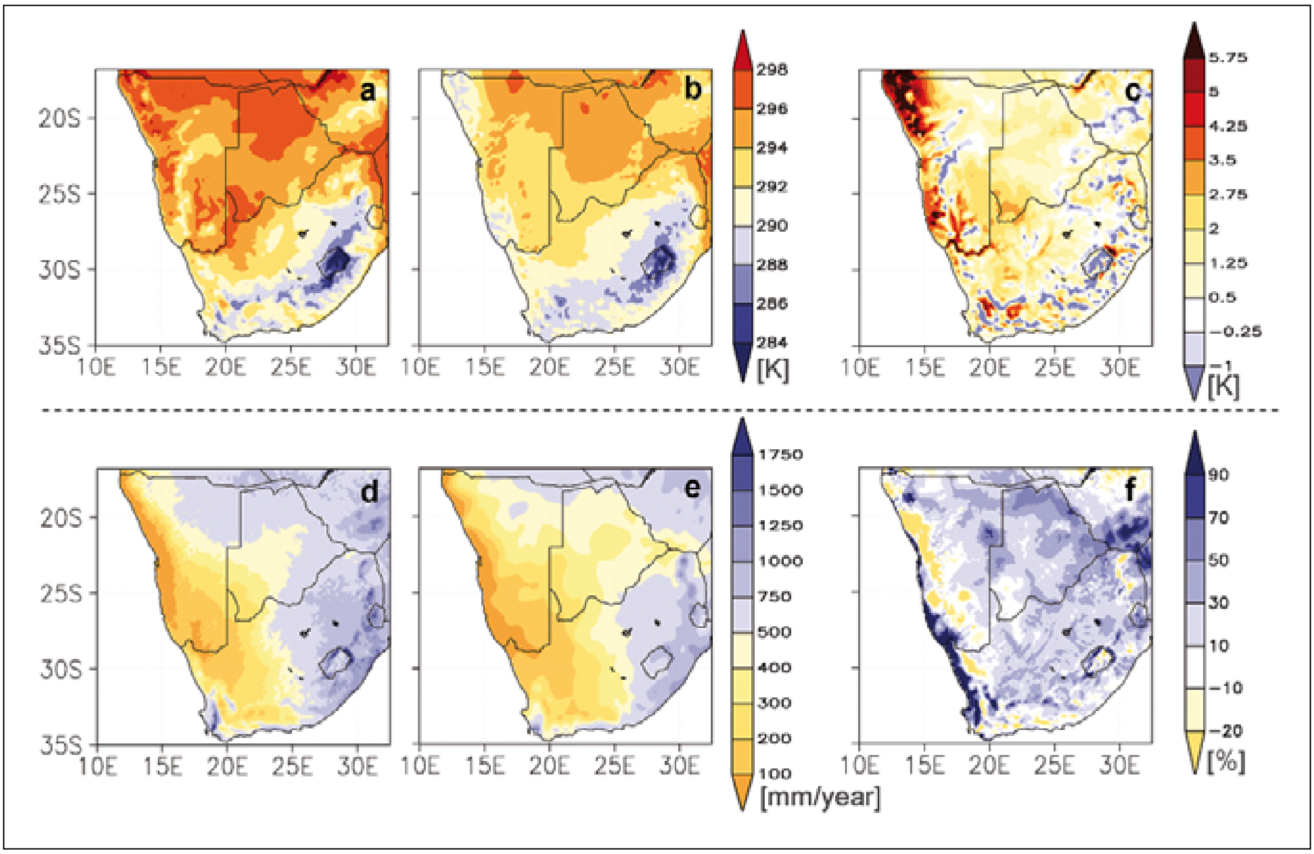

Fig. 1: Annual temperature (upper panels) and rainfall (lower panels) as a climatological mean over the control period (1961–1990). The left panels (a) and (d) indicate the REMO simulations. The central panels show observations. The temperature observations (b) are taken from the CRU dataset (New et al. 2002), and precipitation observations (e) are taken from the GPCC dataset (i.e. Schneider et al. 2008). Fig. 1c depicts the absolute difference between simulated and observed temperature (K), and Fig. 1f depicts the relative difference (%) between simulated and observed rainfall.

in the regions closer to the ocean with a maximum mean temperature rise of approximately 2.5 K compared to the control period.

Annual rainfall (Fig. 3) is projected to decrease in the western and central parts of the southern African region and to increase slightly around the Drakensberg Mountains in the southeast. Relative rainfall decrease at the end of the simulation period is in the order of about 50% compared to the 1961 to 1990 rainfall. However, the **seasonal rainfall** distribution (defined as percentage of annual rainfall falling in the period from April to September; Fig. 3) is projected to stay fairly constant throughout the time, indicating that the drying affects all seasons. Not only is there a projected decrease in rainfall, but there is also a projected increase in **rainfall variability** (the ratio of the annual standard deviation of daily rainfall and the annual mean rainfall; Fig. 3). Rainfall variability is projected to increase over all parts of the domain,

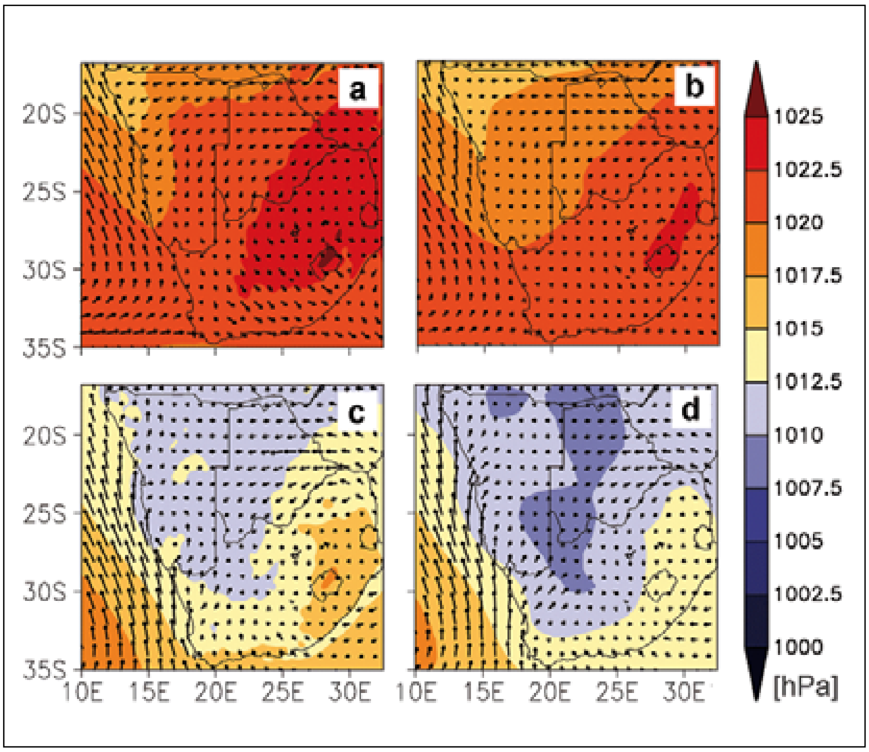

Fig. 2. Simulated REMO (left panels) and ERA40 (right panels) seasonal mean wind vectors and sea level pressure for the winter (June to August; a–b) and summer (December to February; c–d) seasons as a 30 year climatological mean for the 1961 to 1990 control period.

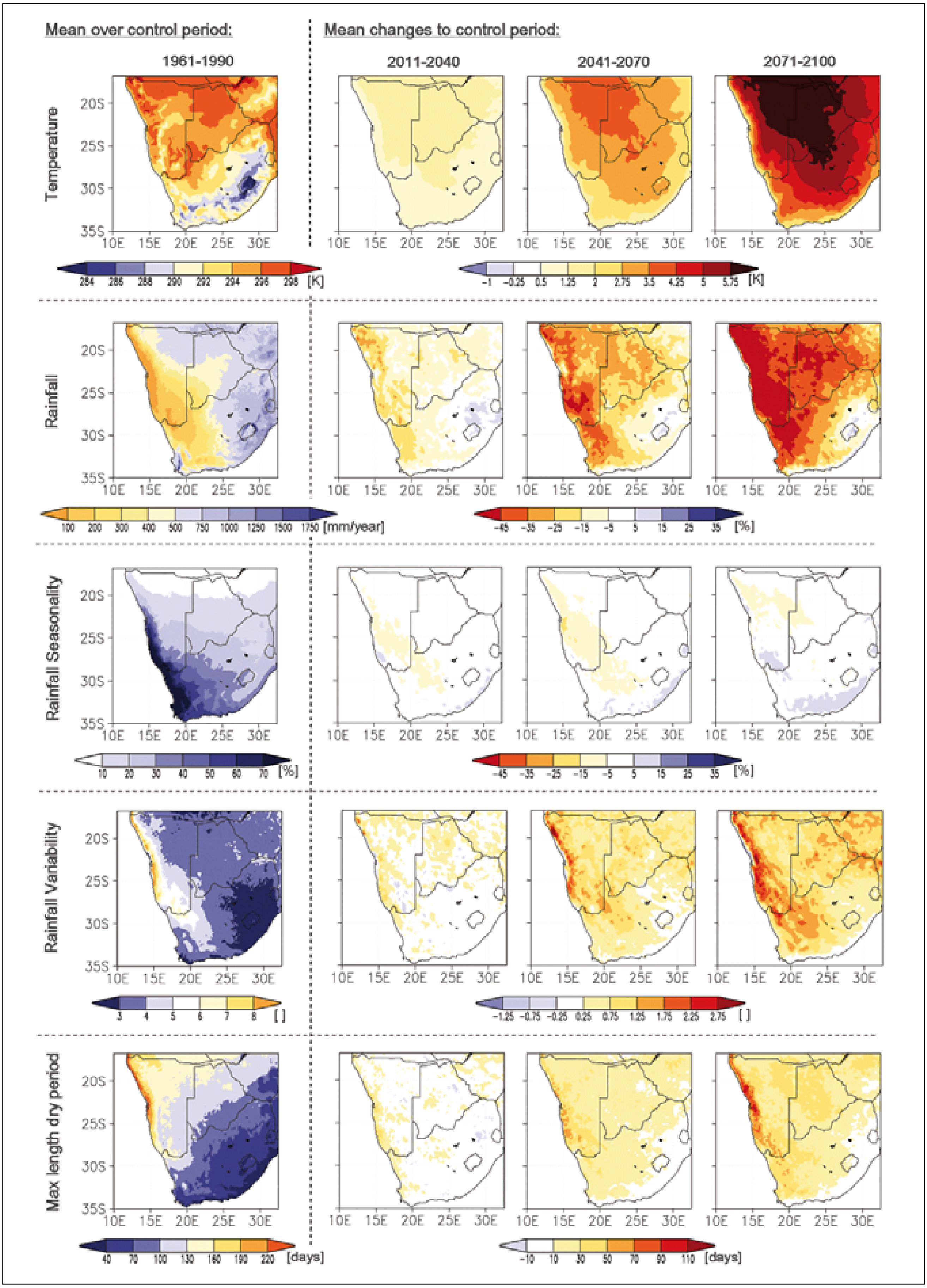

Fig. 3: Climatological mean values for the control period (1961–1990) and their respective changes for three future 30 year periods (2011–2040, 2041–2070, and 2071–2100) for mean annual temperature, annual rainfall, rainfall seasonality (defined as percentage of annual rainfall falling in the period from April to September), rainfall variability and the maximum numbers of consecutive days without rainfall in a year.

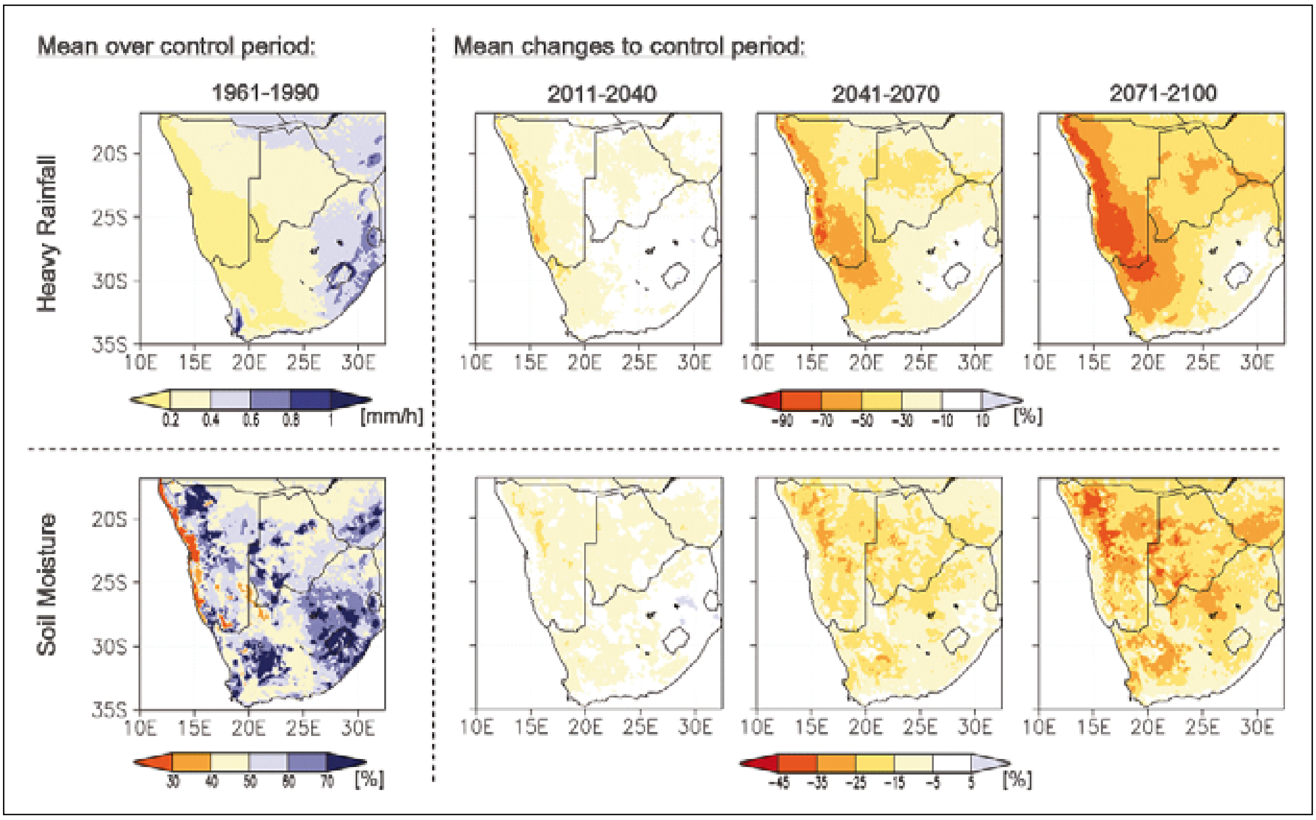

Fig. 4: Climatological mean values for the control period (1961–1990) and their respective changes for three future 30 year periods (2011–2040, 2041–2070, and 2071–2100) for heavy rainfall (95th percentile) and soil moisture.

including the regions where a slight increase in rainfall is projected by REMO. In terms of the **maximum number of consecutive days without rainfall,** the model projects that future rainy seasons will be shorter than at present for most parts of the domain (Fig. 3). Considering the above, it seems likely that future rainfall over the southern African region will be less reliable than it was over the control period.

An increase in atmospheric water content is often connected to a projected warming of the atmosphere, as warmer air can hold more water. In the model, this often leads to increased intensity of torrential rain events. To assess future changes in **heavy rainfall** events we considered the projected changes of the 95th percentile of daily rainfall (Figure 4). For most of the southern African region, REMO projected a decrease in high-intensity daily rainfall events, although there was a slight increase projected around the Drakensberg Mountains.

Soil moisture is closely connected to the biosphere, as changes in soil water availability directly affect the state of ecosystems. Furthermore, it represents an integrated measure, combining changes in rainfall, temperature and evaporation. Assuming a static soil and vegetation distribution, the model projects a remarkable decrease in soil moisture for the whole domain, with a maximum decrease of about 50% in parts of Namibia and Botswana (Fig. 4).

As already mentioned, regional circulation patterns are projected to stay fairly constant over the simulation period (Fig. 5). However, an amplification of the northward flow along the Namibian coastline is visible in the REMO simulation in the summer season but no noteworthy change can be seen for the winter season. This circulation is the major driver of the Benguela upwelling system and this change in the wind fields might therefore trigger a change in the regionally very important upwelling system. However, the REMO version used for the current study does not include feedbacks to the ocean, and it is therefore only possible to speculate on the impacts of these changes.

Final remarks

The REMO projections indicate that the southern part of Africa, which already suffers from a lack of rainfall over large portions of the region, will undergo considerable drying in the future. The drying projected by REMO is substantially greater than the drying projected by the global IPCC models, which projected a rainfall decrease of not more than 20% compared to current climate conditions by the end of the 21st century (Christensen et al. 2007). This strong drying will have a severe impact on the region. The advantages, limitations, and associated uncertainties of the current projection have already been discussed in Article III.3.1. To add to this, the feedback mechanism to the ocean should be taken into account. Furthermore, future changes to the regionally very important moisture input via fog and dew should also be considered. The first studies on this are currently being carried out by the authors.

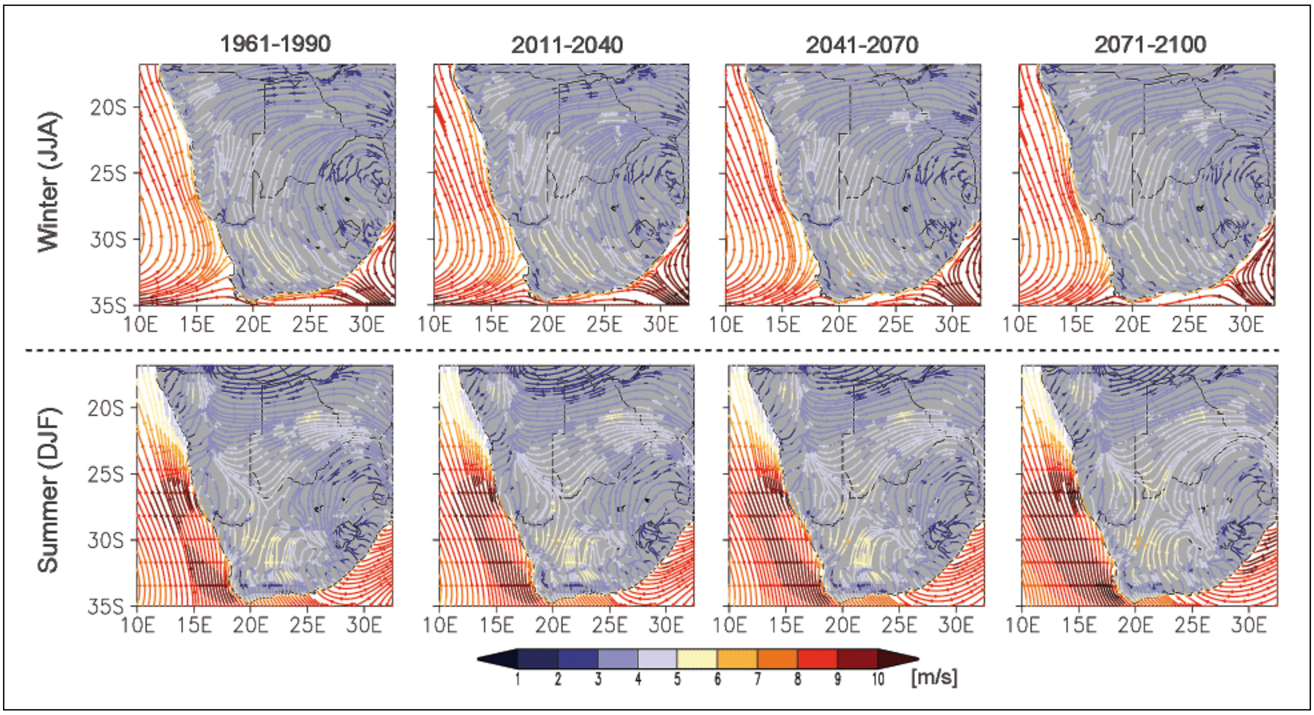

Fig. 5: Climatological mean near surface wind fields in the winter (June to August) and the summer seasons (December to February) for four different time periods.

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Spatial patterns of topography in southern Africa

Manfred Keil*, Ursula Gessner & Christian Hüttich

Summary: The distribution of vegetation types and their specific biogeography are determined to a large extent by the topography and morphology of landscapes. For the BIOTA Southern Africa study area, a harmonised digital elevation model (DEM) was obtained from the Shuttle Radar Topographic Mission (SRTM) of February 2000. Based on this freely available data, with a lateral spatial resolution of about 90 m by 90 m, a colour-shaded relief product was generated by combining an illumination model with information on elevation levels. This product delivered sound information on both the dissected mountainous regions and the smooth landscapes of the basins.

Spatial patterns of topography in the study area of BIOTA Southern Africa

The BIOTA Southern Africa region of investigation comprises Namibia (excluding the Caprivi Strip) and South Africa west of 21° W. An impressive overview of the topographic patterns of this large area is given by the digital terrain model based on the Shuttle Radar Topographic Mission (SRTM). The SRTM data was collected by a single-pass SAR interferometric system during a mission in February 2000. This mission was a result of trilateral cooperation between the US National Aeronautics and Space Administration (NASA), the US National Imaging and Mapping Agency (NIMA), the Italian Space Agency (ASI) and the German Aerospace Center (DLR) (USGS 2008, Rabus et al. 2003). Here, microwave data with a C-band frequency was used for the derivation of the digital elevation model (DEM), which is available to the public with a spatial resolution of about 90 m by 90 m pixel size (i.e. 3 arc-sec by 3 arc-sec, USGS 2007). Fig. 1 shows a colour-shaded relief product, which was generated from the DEM data by combining an illumination model with information on elevation levels. Illumination was assumed to be from the northwest for the generation of the product.

Namibia can be subdivided into four main landscapes from west to east. The Namib Desert extends over a width of about 80 km up to 120 km along the Atlantic Coast in the west. The eastern border of the Namib Desert is formed by the Great Escarpment, stretching parallel to the coast, which swiftly rises to elevations of more than 2000 meters. High differences in elevation are visible especially in the south, in the Tsaris and Naukluft Mountains, but also in the transition zone to the Khomas Highlands and the Central Plateau around Windhoek. While the escarpment is strongly dissected, the Central Plateau is relatively smooth, with a few lone mountains occurring, mainly at elevations between 1000 m and 2000 m above sea level. The highest mountains in Namibia are the Brandberg (2579 m, see the small single mountain range at about 100 km distance from the coast, NW of Windhoek) and the Moltkeblick (2479 m, in the Auas Mountains south of Windhoek). Finally, further to the east, the Central Plateau slopes into the Kalahari Basin, which extends to Botswana and South Africa at altitudes between 900 m and 1200 m.

The escarpment along the coast of Namibia is part of an elevated rim that extends into South Africa to the dissected mountains of the Richtersveld, the Komaggas Mountains and Kamies Mountains of the Northern Cape, and further south to the Bokkeveld Mountains, the Cedar Mountains and other mountain ranges of the Western Cape. The lowlands of the Western Cape are part of the winter rainfall regions with high agricultural landuse. Northeast of the coastal mountain ranges of the Western and Northern Cape, the mountains pass over to the smooth highlands of the Upper Karoo.

The colour-shaded relief provides a good impression of the dissected landscapes of the Great Escarpment and other mountain ranges in the west, and the smooth highland- and basin landscapes in the east. In addition, the western margins of the escarpment, e.g. of Schwarzrand and Weißrand near the BIOTA transect around the Observatories at Niko (S08, S09), in southern Namibia, are clearly visible as well. Prominent landscapes in the north of Namibia are the drainless basins of the Etosha Pan and the Cuvelai Drainage.

The contours of the main drainage systems in the Kavango and in the Kalahari Basin can be easily identified in the northeast and east of Namibia. They are mostly directed towards the northeast (e.g. the Omatako River, flowing into the Kavango River at the Angolan border) or towards the Okavango Delta in the east. Other rivers, like the dry river systems of Nossob at the border between Botswana and South Africa and Anob, drain southeast. Both of these rivers end in the Gariep River, which flows along the southern border of Namibia to South Africa. In the dissected mountainous areas of southern Namibia, the incisions of river systems like the Fish River Canyon west of the Observatory at Karios (S12) are evident.

Even the dune alignments can be identified in the various sand covered regions of the central part of the Namib Desert (south of Gobabeb, Observatory S35), in parts of

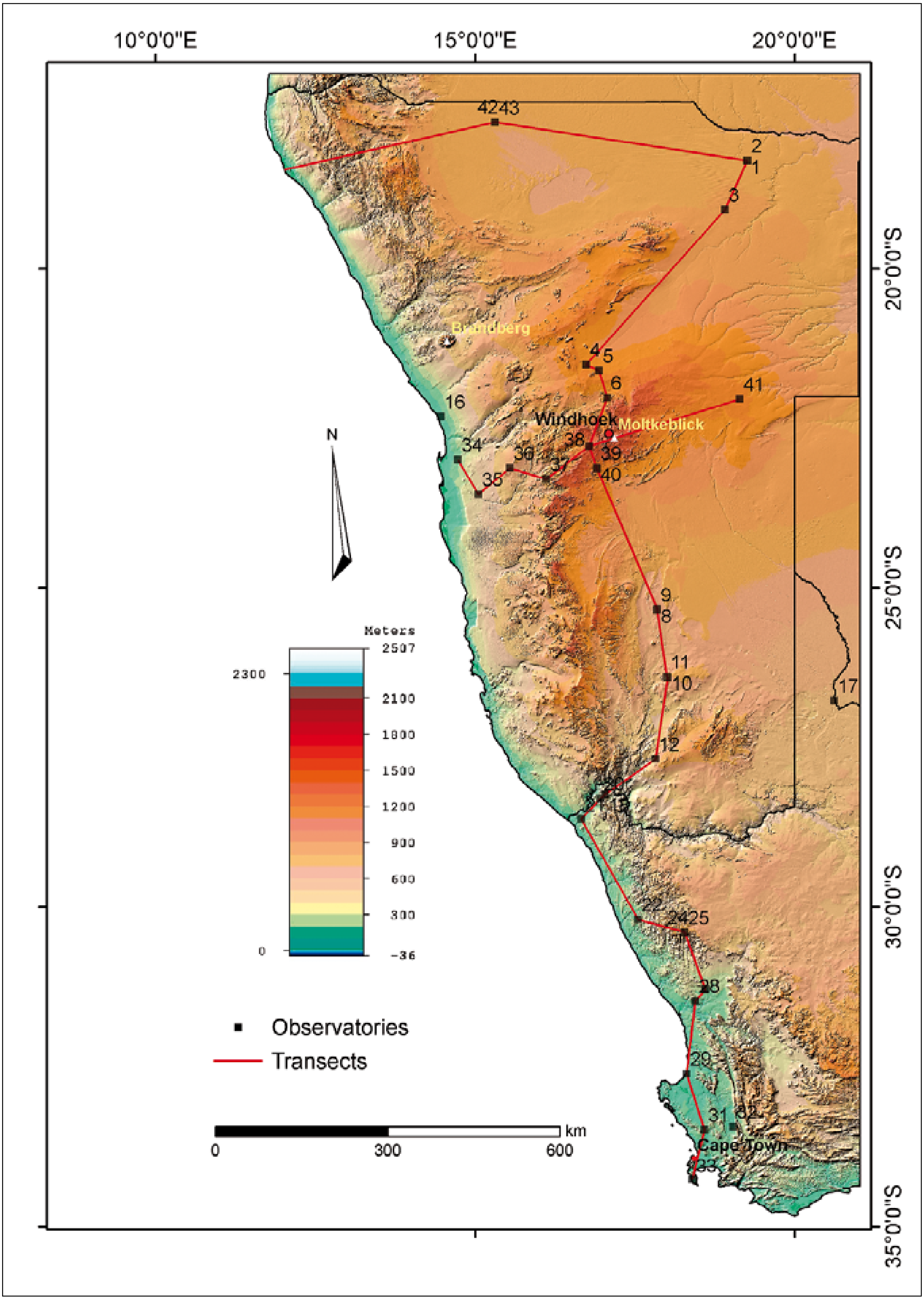

Fig. 1: Digital elevation model with coloured contour levels, overlain by shaded relief information, for the BIOTA Southern Africa study area in Namibia and South Africa.

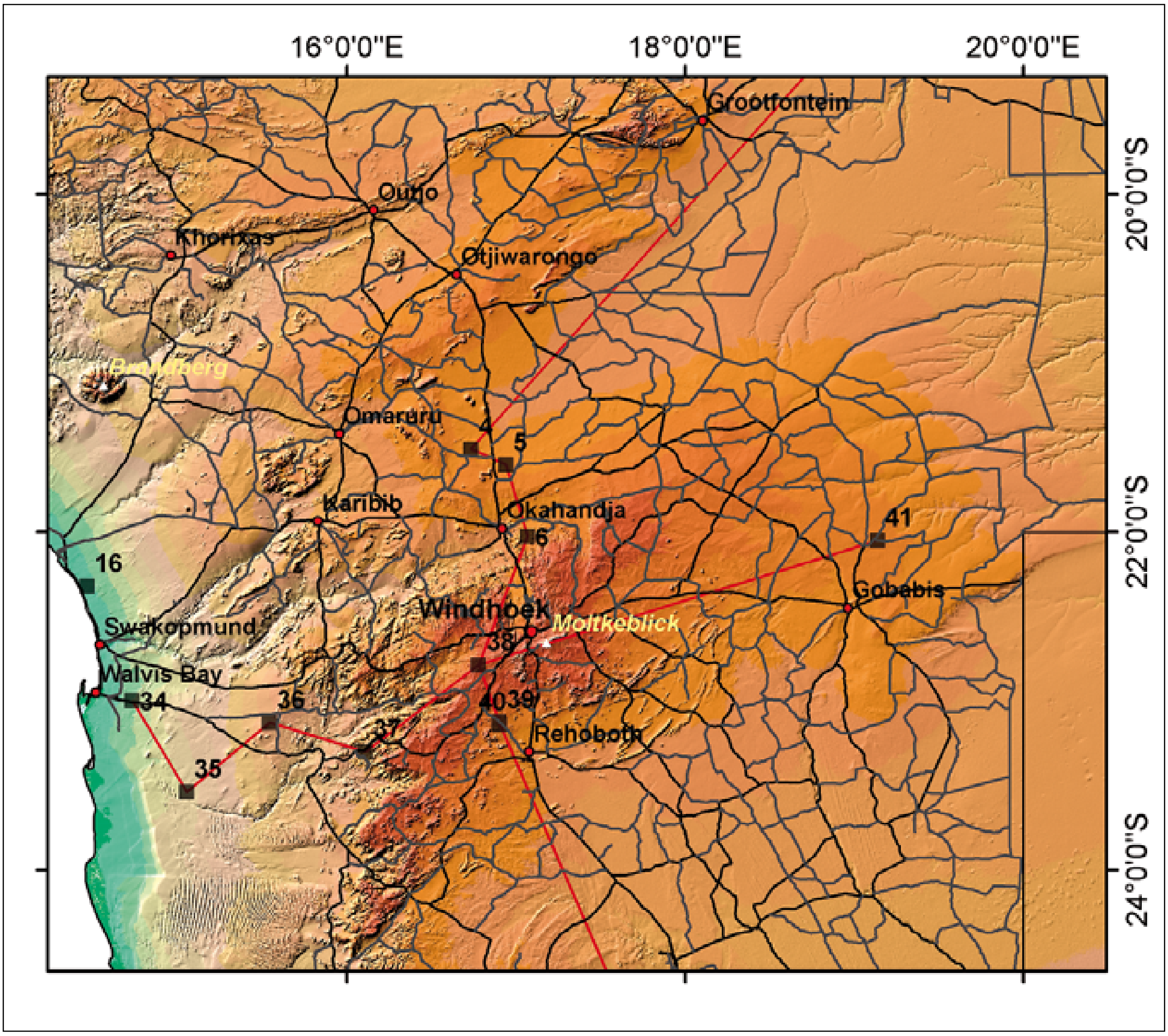

Fig. 2: Digital elevation model of the central part of Namibia with coloured contour levels. The area is overlain by the major roads and settlements and the location of Observatories (black squares with observatory number). The colours represent the same elevations as those in Fig. 1. The Brandberg massive, with the highest peak in Namibia (2579 m), can be identified in the upper left of the Figure. Large dunes with mainly north-south alignment are visible south of Gobabeb (S35).

the Kavango (west and partly east of the Omatako River) and east of the Weißrand Plateau in southeastern Namibia.

Spatial patterns of topography in central Namibia

The central part of Namibia, including the Khomas Highlands, is shown in Fig. 2 at a higher resolution. This sub-scene of the colour-shaded relief covers the gradient from the Namib Desert near the coast up to the Khomas Mountains and further east to the Kalahari basins of Hereroland.

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The authors' general acknowledgements to the organisations and institutions, which supported this work are provided in Volume 1.

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Large-scale vegetation assessments in southern Africa: concepts and applications using multi-source remote sensing data

Manfred Keil*, Ursula Gessner, Christian Hüttich & René R. Colditz

Summary: The interdisciplinary project structure of BIOTA Southern Africa opened the opportunity for applying integrated concepts for the spatiotemporal assessment of arid and semi-arid southern African ecosystems, including the characterisation of inter-annual vegetation dynamics and large-scale land cover mapping. Due to existing high uncertainties in mapping arid and semi-arid environments, the studies on remote sensing-based vegetation mapping aimed to develop and apply land cover classification techniques to derive adapted and standardised maps covering large areas along the BIOTA transects. The application of machine learning classification and regression techniques proved to be useful for both fractional and categorical semi-arid land cover mapping. Key improvements were achieved by mapping vegetation types in Namibia on a national scale using time series data from the Moderate Resolution Imaging Spectroradiometer (MODIS). Synergies of multitemporal remote sensing and botanical field surveys yielded a flexible vegetation type map for the north-eastern Kalahari in Namibia based on the United Nations (UN) Land Cover Classification System (LCCS). The development of fractional land cover maps in north-eastern Namibia showing the percentage cover of woody vegetation, herbaceous vegetation, and bare land surface allowed for a realistic and accurate spatial description of complex and fine-structured semi-arid vegetation types. Time series of MODIS vegetation indices were used to map and analyse annual and inter-annual vegetation dynamics along the BIOTA Observatory transects.

Integrated concepts for semi-arid vegetation mapping using remote sensing

Vegetation mapping as a basis for natural resource management

Spatial information on the distribution and state of plant communities is important for natural resource management and helps to understand the functioning of semi-arid rangeland systems. Consistent, area-wide geo-information on the distribution of plant communities and plant functional types is only available for small parts of the extensive landscapes of southern Africa. Giess (1971) conducted a general descriptive vegetation survey on a national scale for Namibia, based on regional surveys. Approximately 60% of Namibia's surface area has not been analyzed in terms of vegetation composition and community structure (Strohbach, pers. comm. 2009; but see Article III.2.4). The recently available vegetation maps of Namibia (Burke & Strohbach 2000, Strohbach 2001, Strohbach & Petersen 2007) were generated on regional scales. However, the implementation of standardised bottom-up approaches for assessing area-wide vegetation cover is still required for Namibia. This was an objective in the contribution of Strohbach & Jürgens (Article III.2.4). The synergistic use of remote sensing data with in-situ surveys and measurements enhances analyses of spatiotemporal patterns such as large vegetation areas and land cover distribution. Using multi-scale satellite systems, land cover and land cover dynamics can be analysed on different spatial and temporal scales. Data of very high spatial resolution (approx. 1 m) are recorded by satellites such as IKONOS and QuickBird, whereas systems with very high temporal resolution (daily) deliver data of lower spatial resolutions of 250 m to 1 km (e.g. Moderate Resolution Imaging Spectroradiometer, MODIS). The following sections describe and summarise the concepts and results from an integrated mapping framework.

Integrated analysis of environmental data on different scales

In the framework of the BIOTA Southern Africa project, environmental and remote sensing data on different spatial scales were integrated in a mapping framework, where each data type contributed scale-specific land cover information. The two main questions towards the implementation of an integrated ecosystem assessment for the BIOTA Southern Africa focus areas were: Which thematic detail of vegetation (e.g. plant communities or broad structural-physiognomic classes) can be observed, and on which spatial scale can the specific information be derived? Fig. 1 shows the conceptualised relationship of in-situ data, high resolution Landsat data and coarse Moderate Resolution Imaging Spectroradiometer (MODIS) time series data.

In-situ point data from botanical field surveys delivers site-specific information about vegetation cover and composition, life forms, plant species numbers, and soil conditions, and the surveys allow the derivation of information on habitat settings and the status of biodiversity. However, a high manpower effort is required to obtain a representative coverage of this data. High resolution Landsat imagery provides information on vegetation physiognomy at a local scale, with inter-annual data availability. The 16-day composite images of MODIS time series contain information on intra-annual vegetation dynamics, phenology, and land cover type at a coarse spatial resolution (250 m x 250 m). The local site information was used as a reference database and was linked with satellite data at various spatial scales (very high to moderate resolution) to derive the spatial patterns and distribution of vegetation cover and vegetation types, and to extrapolate available field information into larger areas.

Mapping vegetation types in savanna ecosystems involves high uncertainties regarding the detection of the states of different vegetation types, the differentiation of the typical life form composition (coexisting herbaceous and woody vegetation), and the analysis of natural and human-induced land cover and landuse changes. The main limitations originate from dynamic processes, such as the high spatiotemporal variability of the vegetation caused by high spatial and temporal precipitation variability, fire, grazing pressure, and human landuse.

- The key objectives for developing remote sensing applications in the framework of BIOTA Southern Africa were to develop adapted methods for land cover mapping to properly represent the vegetation structure in southern African environments based on multi-scale approaches (fractional cover mapping and categorical classifications),
- develop adapted methods to analyse the spatial extent and magnitude of land cover and landuse change processes. The main focus was on the mapping of human-induced landuse change,
- assess the applicability of a standardised ecosystem assessment concept in semi-arid ecosystems and demonstrate the benefits and limitations for the scientific community related to remote sensing and biodiversity.

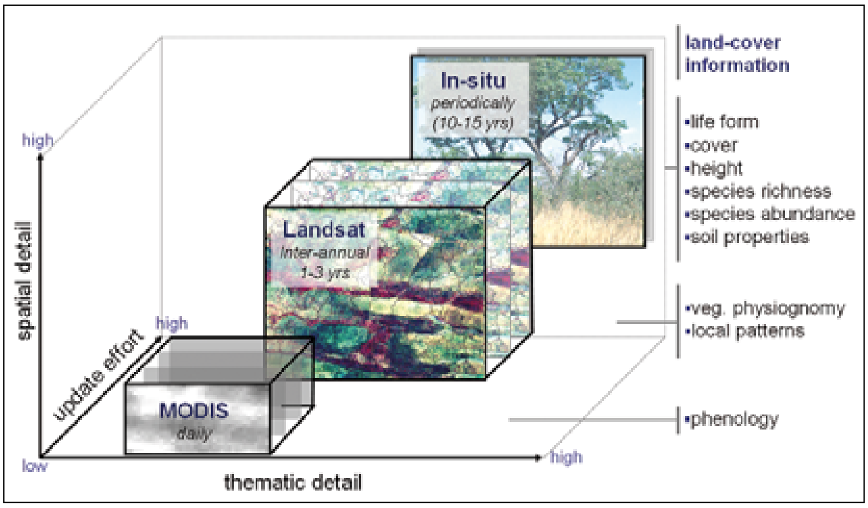

Fig. 1: The integrated concept for ecosystem assessment shows the relationship between thematic and spatial detail and the effort required for updating different data types: In-situ-database, Landsat database and coarse scale MODIS time series data.

Towards the development and application of adapted land cover classification schemes in dry savanna ecosystems

The availability of satellite imagery and derived products has dramatically increased in recent years with the consequence that environmental datasets, such as satellite-based vegetation maps or local plot information, have to be comparable regarding their thematic content. Recent studies emphasise that the highest uncertainties (e.g. overlapping class definition boundaries and mixed pixel problems) in harmonising classification schemes are found in highly heterogeneous landscapes (Herold et al. 2008, Thompson 1996). In terms of land-cover maps, two basic thematic classification concepts were tested. The first conceptual framework was fractional cover mapping, which comprises the estimation of continuous sub-pixel values that indicate the proportional cover of woody vegetation, herbaceous vegetation, and bare soil. The advantage of proportional land cover information is a more realistic representation of the spatial distribution and composition of the vegetation structure in semi-arid environments. Fig. 2 shows the continuous transition between different savanna vegetation types from a human viewing perspective and the top view from a satellite perspective. The second conceptual approach involved the application of the Land Cover Classification System (LCCS; Di Gregorio 2005), which is the most accepted standard internationally for land cover studies. Using LCCS enables retention of the

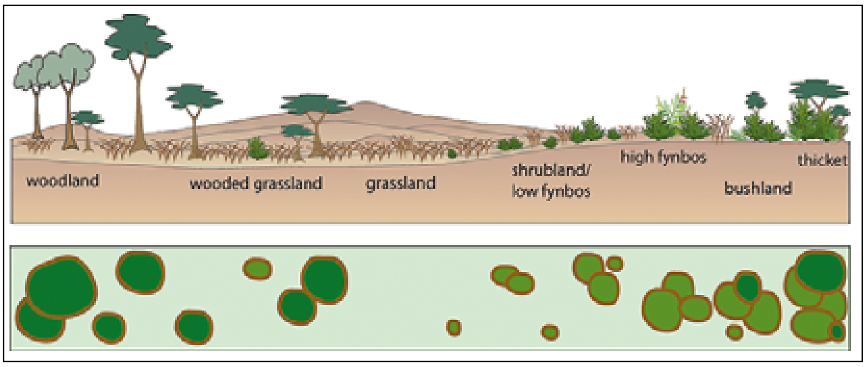

Fig. 2: Schematic illustration of typical savanna vegetation structure and the related classification scheme after Thompson (1996). Note the satellite view of the different savanna vegetation life forms in the bottom part of the illustration.

Table 1: Relationship between the temporal resolution, spatial resolution and land cover information for different environmental datasets

Earth observation data source	Spatial resolution (minimum mapping unit)	Temporal resolution	Land cover information
In-situ point data	Local plots	Annually to periodically	Species composition and diversity, geology, soils, relief, vegetation physiognomy
IKONOS, QuickBird	1–4 m	1–3.5 days (QB), 3–5 days (IK)	Vegetation structure (micro-pattern, life-forms), dynamics (multi-temporal), soils, geology
Landsat, Aster	15–30 m	16 days	Vegetation structure (micro-pattern, life-forms), dynamics (multi-temporal), soils, geology
MODIS time series	250–1000 m	Daily	Phenology, vegetation structure (macro-pattern, life-forms), land surface dynamics

highest thematic detail possible in the resulting vegetation map and provides translation capabilities with other land cover datasets.

Derivation of land surface and land cover characteristics by remote sensing

Besides the derivation of categorical classes of land cover and vegetation types—which are a simplified representation of the ‘real’ vegetation distribution—adapted approaches can yield continuous indicators for analysing the spatiotemporal characteristics of the land surface. Fractional cover maps—a synergistic map product of a multi-scale remote sensing approach—provide subpixel information of the proportional coverage of physiognomic-structural vegetation units. Vegetation indices, such as the Normalised Difference Vegetation Index (NDVI) or the Enhanced Vegetation Index (EVI) represent photosynthetically active vegetation. Time series of vegetation indices contain useful information on the phenological cycle. Leaf Area Index (LAI) data are proxies of the standing biomass of vegetation. Land Surface Temperature (LST) data provide important information on the surface conditions and can indicate natural and human induced land change processes. The Moderate Resolution Imaging Spectroradiometer (MODIS) on board of the satellites TERRA and AQUA is a sensor dedicated for global change research, and many of the above mentioned indicators are available as land surface products in a standardised format (Justice et al. 1998) from NASA’s Land Processes Distributed Active Archive Center (see also USGS LP DAAC 2010).

Multi-scale remote sensing database

Remote sensing for biodiversity applications requires a wide spectrum of environmental information (Table 1). The application of a multi-scale concept requires a database covering a wide range of spatial resolutions in the image database. At the sub-continental scale, the BIOTA transects were covered in full length by satellite time series data from the Moderate Resolution Imaging Spectroradiometer (MODIS). The acquired MODIS data, including assorted biophysical information (e.g. surface reflectances, NDVI and EVI vegetation indices, phenology, Leaf Area Index, Land Surface Temperature, and Albedo; see Huete et al. 2002 and Justice et al. 1998), were available at a spatial resolution from 250 m to 1 km and covered the period from 2000 to 2009. Landsat imagery was acquired for the BIOTA Southern Africa study area to gain a complete spatial coverage. Multiple acquisitions were ordered for a number of focal areas. The spatial resolution of Landsat Thematic Mapper (TM) and Enhanced Thematic Mapper (ETM+) data is 30 m and each scene has a footprint of 180 km x 180 km (for sensor summaries, see e.g. NOAA Coastal Service Center 2010).

Very high resolution (VHR) imagery was integrated for some of the investigation areas in Namibia (Mile 46 S01, Sonop S03, Otjiamongombe S05). VHR imagery from the IKONOS and QuickBird satellites were ordered at a spatial resolution from 0.6 m to 1 m. Besides the disadvantage of high acquisition costs for a small area covered, the main advantage was the very detailed reflection of different life forms. Multi-scale mapping techniques were applied in different regional studies. The fractional cover mapping methodology was developed in the north-eastern Namibian regions, whereas the standard vegetation mapping approach based on multiple remote sensing of local and in-situ data was developed in the north-eastern communal areas of the Kalahari.

Remote sensing based analyses of land cover change

The analysis of land cover and landuse change processes (e.g. deforestation, mining, land degradation, and processes caused by climate change) is important for rangeland management and for understanding the dynamics of semi-arid ecosystems. Remote sensing change detection techniques enable the spatially explicit analysis of land cover dynamics. Changes can be detected by analysing abrupt changes (e.g. fire, deforestation, and expansion of cultivation), but also gradual changes, such as afforestation or land cover transitions associated with slight changes of the vegetation structure.

Examples of remote sensing change detection approaches within BIOTA Southern Africa are given in Volume 3: The assessment of cultivation expansion in the Kavango is described in Chapter IV.1, the assessment of increasing frag-

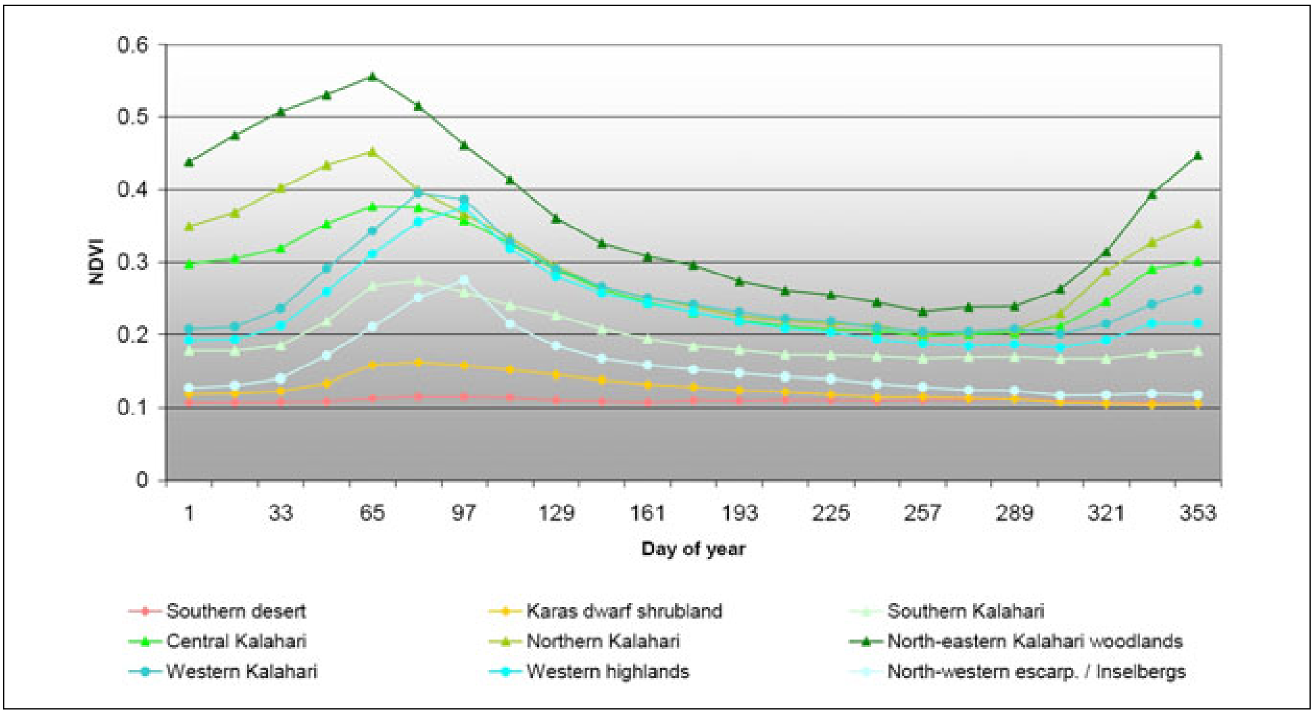

Fig. 3: Time series plots of the normalised difference vegetation index (NDVI) of selected vegetation types in Namibia for the year 2002. NDVI is a measured value of the photosynthetic activity of vegetation and reflects the characteristic phenological cycles of semi-arid vegetation types. Differences in the phenological metrics such as start, end, and length of the growing season become visible for the displayed vegetation types. These phenological characteristics, which are specific to a high degree for different vegetation cover types, were used as features to perform a reclassified large-scale vegetation map covering most of Namibia, by using non-parametric image classification techniques (Colditz et al. 2007, reprinted with permission).

mentation of natural habitats in the Western Cape Lowlands is part of the contribution in Chapter IV.5, and is also discussed by Magidi (2010). Further studies on remote sensing change detection within BIOTA Southern Africa were performed by Vogel (2006) and Shiponeni (2007). Vogel investigated gradual changes in vegetation cover caused by degradation and deforestation processes in Central and North-East Namibia (Vogel 2006, Vogel et al. 2006). Shiponeni investigated fluctuations and directional changes in an ecotone between Bushmanland arid grasslands and Namaqualand shrublands (Shiponeni 2007, Shiponeni et al. 2007).

Mapping the vegetation types of Namibia using MODIS time series: capabilities and improvements

Vegetation maps are usually derived using field-based approaches and botanical knowledge. To extrapolate the results, the textural and spectral characteristics of aerial photographs or high spatial resolution satellite images can be visually interpreted or processed in a semi-automated manner (Nagendra 2001, Turner 2003). Although multispectral approaches are able to distinguish land cover units, their capability to map subtle differences in vegetation units is limited. Time series of multispectral data improve land surface discrimination. Time series of remotely sensed parameters such as vegetation indices, surface reflectance, or thermal emissions show temporal processes both intra- and inter-annually. These differences in phenology between vegetation types (Fig. 3) provide additional information, which is independent of spectral data.

This study employed an automated approach for mapping vegetation structure units in Namibia based on multispectral MODIS time series (Fig. 4). An existing vegetation map of Namibia with 29 vegetation types was used as a base-line dataset (Mendelsohn et. al. 2002). The reference map was compiled from a multitude of vegetation maps including those of Giess (1971), Mendelsohn et al. (2002), and Strohbach (2001). Altogether, 23 vegetation types (for legend see Fig. 5) were remapped using state-of-the-art tree-based classification techniques. The Caprivi Strip and spatially insignificant classes were excluded because they were too small or heterogeneous to be mapped with a 250 m MODIS resolution. The goal of this re-mapping of vegetation types was to detect potential inaccuracies and uncertainties in the boundary definition of field-based studies compared to results from spatially explicit satellite data. Furthermore, ecotones, which can be expected in semi-arid environments with a similar geological background, could be indicated by fuzzy classification results.

Re-mapping vegetation units with remote sensing data provides the possibility for large-scale analysis and can be helpful for rapid change detection, e.g. after fire or for years with phenological changes. The automated approach outlined in this paper can easily be transferred or extended to other regions and provides the opportunity for detailed mapping and detection of ecotones or other transitions.

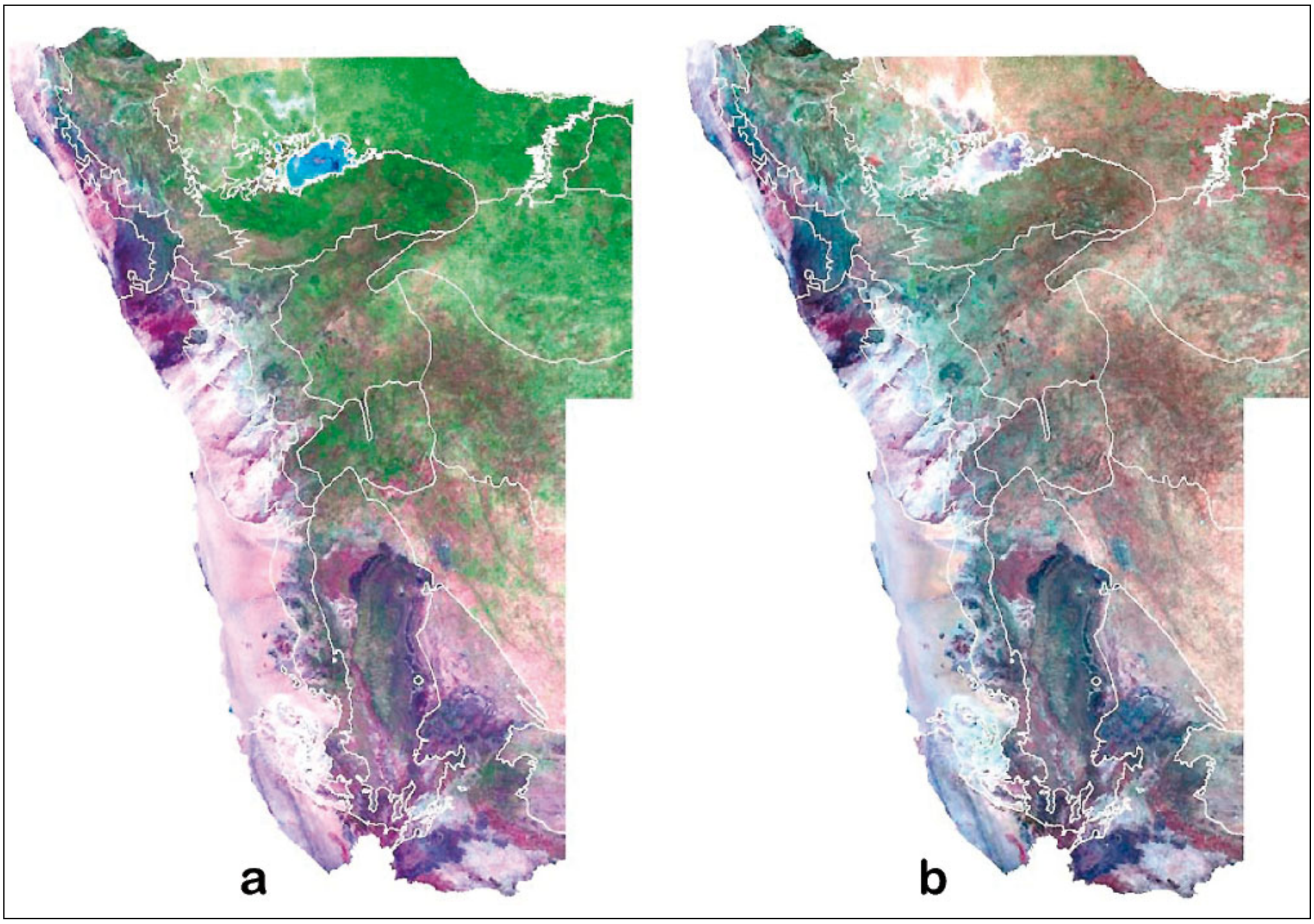

Fig. 4: Multispectral MODIS images with RGB band combination 7 (short-wave infrared), 2 (near infrared), 1 (visible red). White lines indicate the initial mapping of vegetation types of Namibia (Mendelsohn et al. 2002). (a) shows an image from March 6th 2002 (day 65) acquired during the mid-growing season. The near infrared band (displayed in green) depicts the NE-SW gradient of vegetation cover and confirms the rainfall-driven ecosystem functioning of the savanna biome. The North-Eastern Kavango region receives increased precipitation rates compared to the hyper-arid western deserts of the Namib along the Skeleton Coast. Note the flooding of the Etosha Pan depicted in blue. (b) shows an image from September 14th 2002 (day 257), which depicts the peak of the dry season. Compared to the rainy season, the less intensive green colour reflects the dry vegetation condition. The highlighted geological and pedological context (reddish colours) is a key factor influencing the occurrence of plant communities and thus an important feature for the statistical discrimination of broad vegetation type classes. (a) and (b) correspond with the peak and minimum of the NDVI plots in Fig. 3 (Colditz et al. 2007, reprinted with permission).

It produced stable results, with few variations between 2001 and 2003. Moreover, the classification highlighted some areas, which might belong to different vegetation types or are located in broad transition zones for which the assignment of a discrete class is questionable. The limits in spatial resolution of earth observing systems with high temporal resolution, including AVHRR (Advanced Very High Resolution Radiometer) or MODIS, are less important for mapping entire countries with homogeneous units such as Namibia. In contrast to solely field based approaches, results from standardised remote sensing data are less dependent on the analyst and are therefore more objective. However, remote sensing-based mapping cannot replace field-based botanical inventories. The view from space, however, is useful to supplement field-based mapping and to extrapolate ground observations.

Synergies of multitemporal remote sensing and botanical field surveys for vegetation type mapping

Plant communities are the basic natural resource management units in Namibia and give baseline information on ecological processes and ecosystem functioning in semi-arid rangelands for the evaluation of the tendencies of pasture dynamics and grazing capacity (Strohbach 2001). However, there is a lack of consistent geodata for environmental and natural recourses on a national scale in Namibia. In the past, a number of local scale vegetation survey projects were carried out in parts of Namibia. Giess (1971) conducted general descriptive vegetation surveys on a national scale. Nation-wide estimates of biomass and vegetation cover have been calculated using remote sensing techniques. Approximately 60% of Namibia's surface area has not been analyzed in terms of vegetation composition and community structure. This emphasises the need for implementing standardised bottom-up-approaches for assessing vegetation cover in Namibia using synergies of botanical field surveys and large-scale earth observation satellite data (Hüttich et al. 2008). Here, the combination of

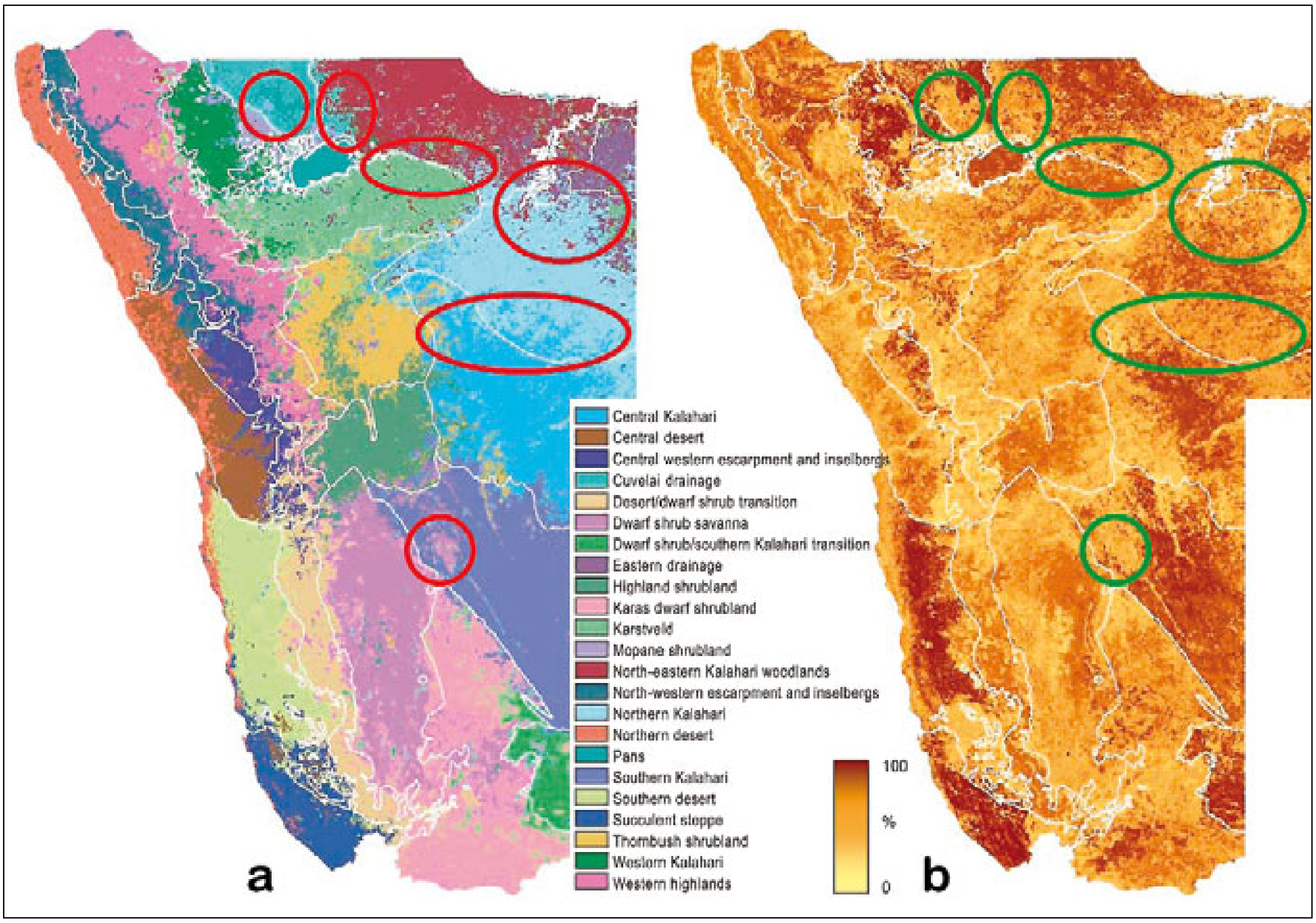

Fig. 5: Classification of vegetation types from time series metrics derived from multispectral data (surface reflectance, NDVI, and land surface temperature) for 2002. White lines indicate the initial mapping of the vegetation types of Namibia (Mendelsohn et al. 2002). (a) shows the class with highest probability. (b) depicts the probability of assigned classes in (a). The classification shows a good agreement with the reference dataset, which was the initial map of the vegetation types of Namibia. However, in North-Western Namibia, the unit “North-Western escarpment and inselbergs” extends further to the east into the “Western highlands”. Large transition zones are mapped between the classes “Central Kalahari” to “Northern Kalahari” and into the “Eastern Drainage”. The transitions are indicated by the “speckle” fading from class A to B and by a decrease in the probability for class assignment, while the probability is comparatively high in the core of the classes (Colditz et al. 2007, reprinted with permission).

botanical field survey data with Landsat satellite images and MODIS time series data allows the mapping of vegetation types over a large area.

In this study, in-situ data from a botanical field survey of the vegetation and soils in the eastern communal areas in Namibia was used to retrieve information on the vegetation structure. The resulting vegetation plots from botanical field surveys were used as reference data for the main savanna vegetation types. For the generation of the training database for image classification, homogeneous landscape patterns derived from Landsat-TM data were used to downscale in-situ data on the coarse MODIS scale. Phenological metrics were derived using MODIS time series from 2000 to 2007. A Random Forest tree-based ensemble classification method was applied by using a hierarchical LCCS-based classification scheme. A detailed description of the remote sensing classification techniques used is provided by Hüttich et al. (2009).

The study region was focussed on the Eastern Communal Areas in the Eastern Kalahari in Namibia. According to Giess (1971), the landscape can be grouped into three main vegetation types: the Central Kalahari along the southern border; the Northern Kalahari, characterised by deep Kalahari sands; and Thornbush shrubland in the western part of the study region (Fig. 6). Land cover characteristics obtained from a reconnaissance survey of soils and vegetation of the Eastern Communal Areas (Strohbach et al. 2004) provide a detailed description of land types, vegetation composition, physiognomy, and habitat settings (see also Photos 1–3). The area is characterised by a subtropical climate with a mean annual rainfall of 350–450 mm, mostly falling in summer and usually with a high variability. The geology of the study area is dominated by aeolian Kalahari sands with sporadic outcrops of sandstone, limestone, schist and dolomite of the Karoo Sequence and the Damara Sequence with a mean altitude of 1,200 m above sea level. Topographically, the transition between the Central Namibian Highlands and the Kalahari Basin is characterised by the southwest/northeast orientated incised omiramba (shallow water courses with no visible gradients or water course, typical of the

Photos 1–3: Photographs taken during the field survey in 2004. The photograph on the left shows the valley floor of an incised omuramba with dominant grass coverage. The middle image depicts the typical coexistence of herbaceous and woody vegetation in the Camelthorn savanna. The photograph on the right displays the typical *Terminalia-Combretum* savannas on deep Kalahari sands near the Botswana border. All Photos: Ben Strohbach.

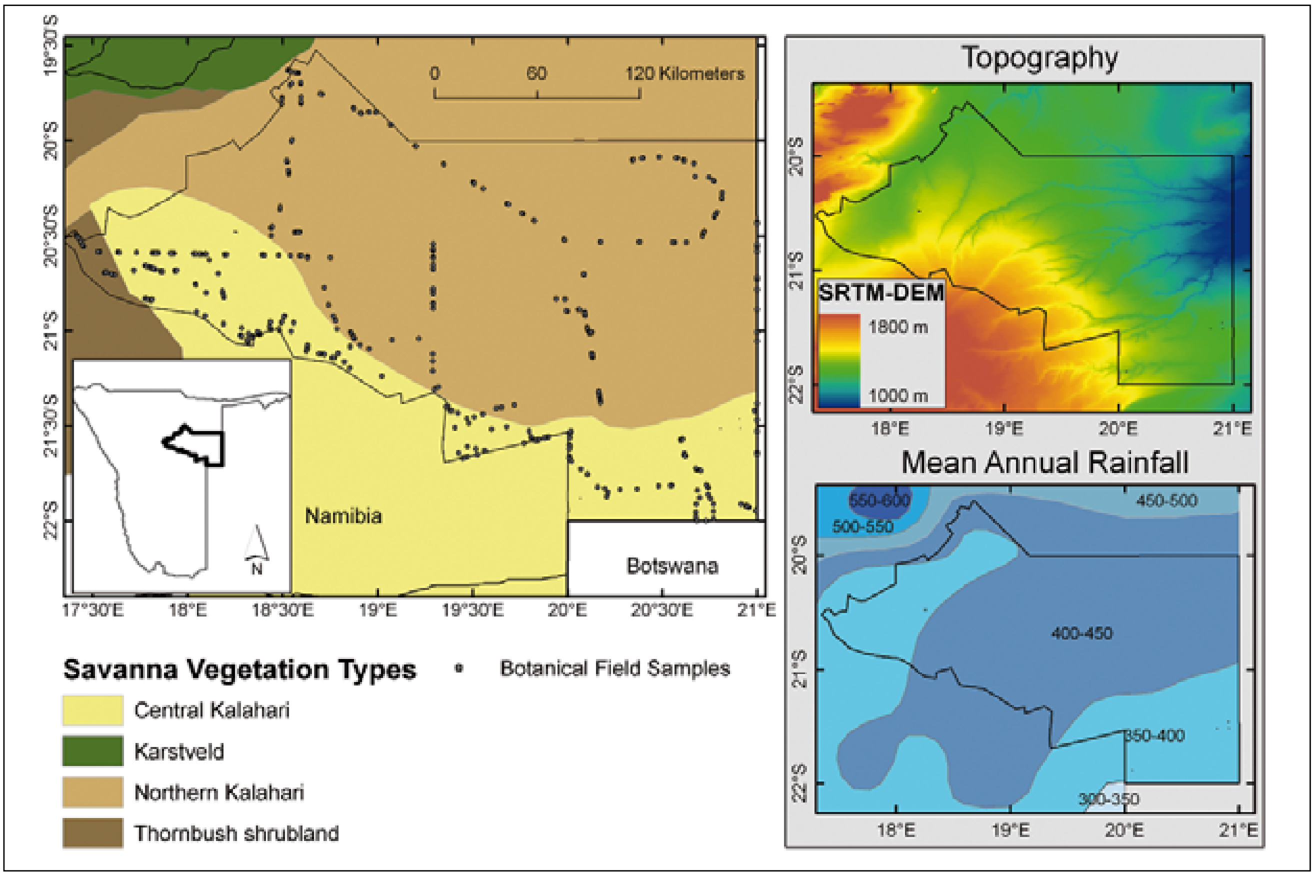

Fig. 6: Overview of the study area comprising the eastern communal areas in the north-eastern part of Namibia.

arid Kalahari sand plateau). The area can be classified into seven Agro-Ecological Zones (AEZ) of common land management practice, e.g. the Southern Omatako and Fringe plains of the Central Plateau, Kalkveld, pans, and stabilised dunes of the Kalahari Sand Plateau (Strohbach et al. 2004). Landuse on all AEZs is characterised by extensive grazing and limited cropping.

The landscapes of the Kalahari in the north-eastern communal areas in Namibia comprise 12 major vegetation types identified from a phytosociological analysis (Strohbach et al. 2004). The major landcover types according to the Food and Agriculture Organisation's (FAO) Land Cover Classification System (LCCS; Di Gregorio 2005) are: broadleaved deciduous woodland with shrubs and herbaceous layer; open [(70–60) –40% shrub coverage] and very open [40– (20–10)% shrub coverage] broadleaved deciduous medium high shrubland with an open

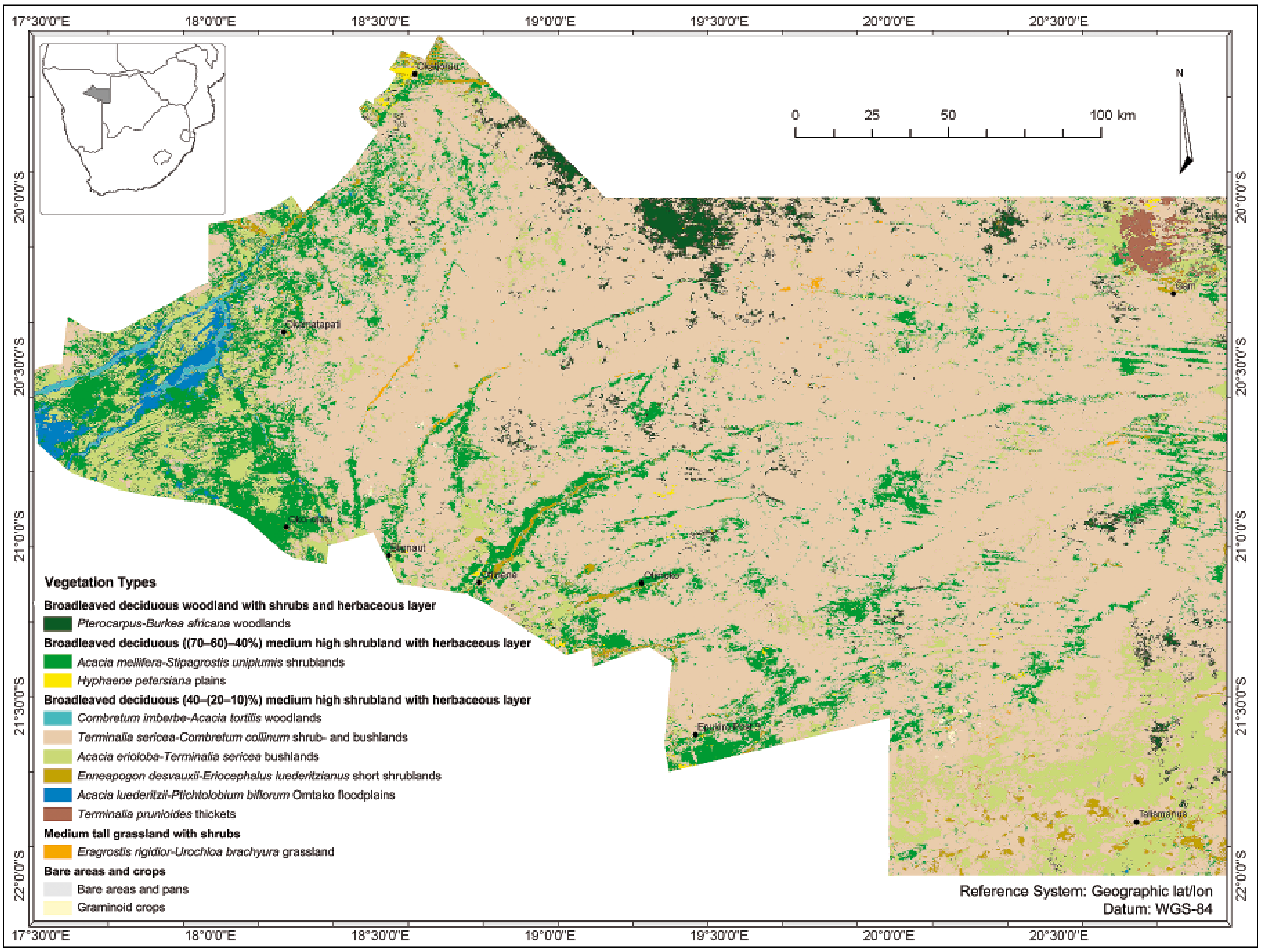

Fig. 7: The dominant structural land cover type in the Kalahari is shrubland, followed by woodland, and grassland. Most of the plant communities, as sampled in the botanical survey, were translated into the LCCS class Open Broadleaved Deciduous Medium to High Shrubland. The map shows the spatial distribution of vegetation types in the north-eastern communal areas of the Kalahari in Namibia using hierarchical land-cover classification. The most dominant vegetation type on the deep Kalahari sands was *Terminalia sericea-Combretum collinum* shrub- and bushlands followed by *Acacietea* vegetation types.

medium to tall herbaceous layer; and medium tall grassland with medium high shrubs (nomenclature on shrub coverage due to LCCS convention, indicating the upper and lower limits of the main life-form layer coverage).

The study showed that bottom-up land cover assessments can be an effective tool to integrate local scale ecological perspectives with coarse scale remote sensing perspectives. With regards to the high confusion between the classification of shrubland and grassland in existing global moderate resolution land cover products, adapted training strategies on these classes could promote increased mapping accuracies at global scales. The integration of inter-annual time series metrics for mapping vegetation types based on satellite-derived phenological metrics and surface reflectance data increases the overall quality of vegetation maps in semi-arid regions. To expand the vegetation type mapping to the whole of Namibia, the most challenging task will be to collect the necessary botanical field data. More than 10,000 botanical field samples are available for Namibia (Article III.2.4) and an interdisciplinary project structure is therefore needed to synergise these data at a landscape scale. The translation of data from the botanical surveys into the Land Cover Classification System (LCCS) of the United Nations (UN) to generate flexible map products will increase the usefulness of land-cover information to the broader user community.

Fractional land cover in north-eastern Namibia derived from remote sensing data

Land cover is a key parameter for any spatial assessment of ecosystems, biodiversity, and biodiversity change. Traditional land cover mapping approaches describe the land surface as categorical classes, such as for example ‘forest’, ‘grassland’ or ‘open woodland’. Savannas are characterised by a high spatial heterogeneity and gradual transitions between a wide range of tree, shrub, and herbaceous compositions—patterns, which cannot be expressed appropriately by discrete classes. For this reason, savannas are not well-suited to the concept of categorical land cover mapping and are represented

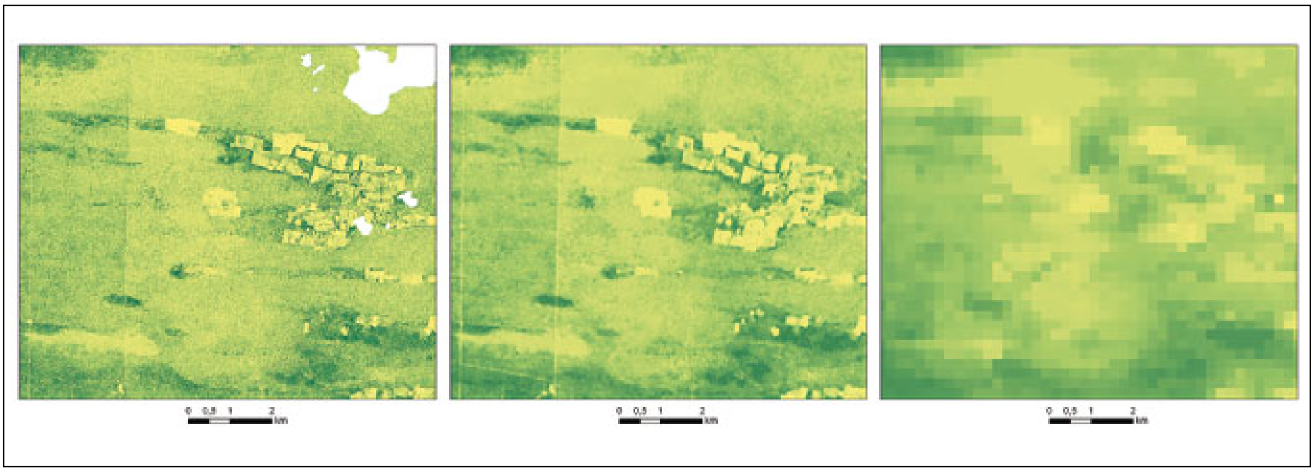

Fig. 8: Percentage woody cover derived from QuickBird, Landsat-5 TM and MODIS time series data for the year 2007. The figure shows an area of approximately 9 km x 9 km including the BIOTA Observatories Mile 46 and Mutompo.

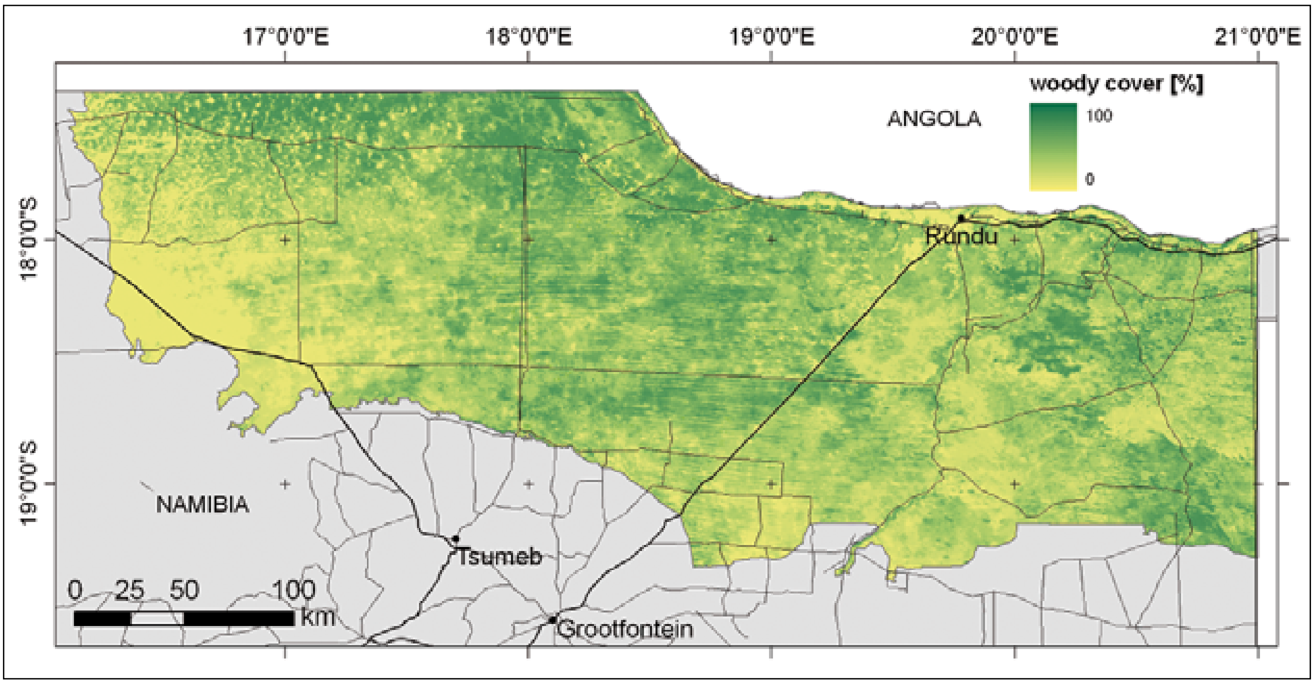

Fig. 9: Percentage cover of woody vegetation in North-Eastern Namibia.

with low accuracy in global discrete land cover maps (Giri et al. 2005, Herold et al. 2008). Realising these shortcomings, researchers have worked with concepts of continuous land cover representation, where land cover characteristics are mapped as continuous distributions at the subpixel level of remotely sensed data.

Here, examples of continuous land cover mapping for the Namibian savanna biome are presented. Subpixel percentage cover of woody vegetation (i.e. shrubs and trees), herbaceous vegetation, and non-vegetated land surfaces were mapped for the Woodland Savanna in north-eastern Namibia. The following vegetation types were included in the analysis: **North-eastern Kalahari Woodland**, **Northern Kalahari**, **Okavango Valley,** and **Omatako Drainage** (according to Mendelsohn et al. 2002). The data basis for these mapping results was 250m-MODIS time series, which were analysed in combination with field surveys and higher resolution IKONOS, QuickBird and Landsat data. Maps of different spatial resolutions could be created according to the different characteristics of these satellite data (see Fig. 8). To derive the continuous surface cover values, ensemble regression tree techniques were applied. Further details on the approach can be found in Gessner et al. (2008, 2009).

The fractional cover maps clearly delineate important vegetation characteristics of the Woodland Savanna in north-eastern Namibia (see Figs. 9–11). The clearing of natural vegetation becomes evident in densely populated areas, especially around the regional centre Rundu and in areas of extensive agricultural cultivation along the Namibian-Angolan

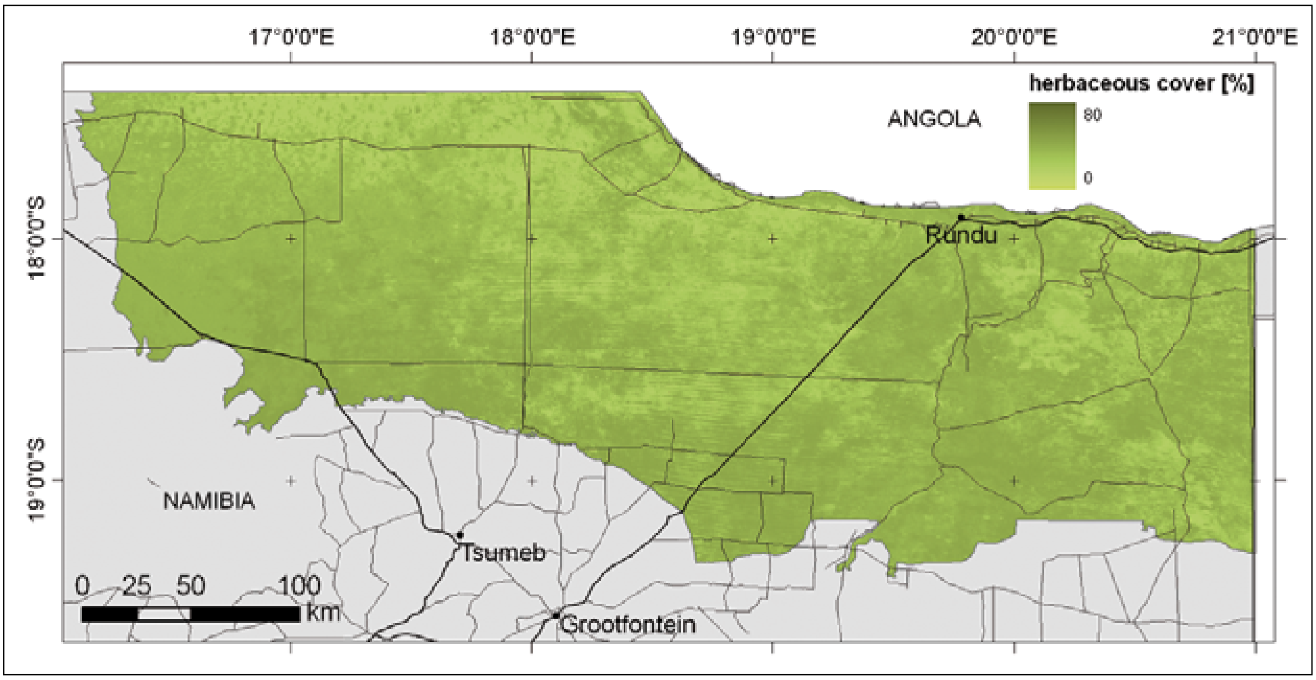

Fig. 10: Percentage cover of herbaceous vegetation in North-Eastern Namibia.

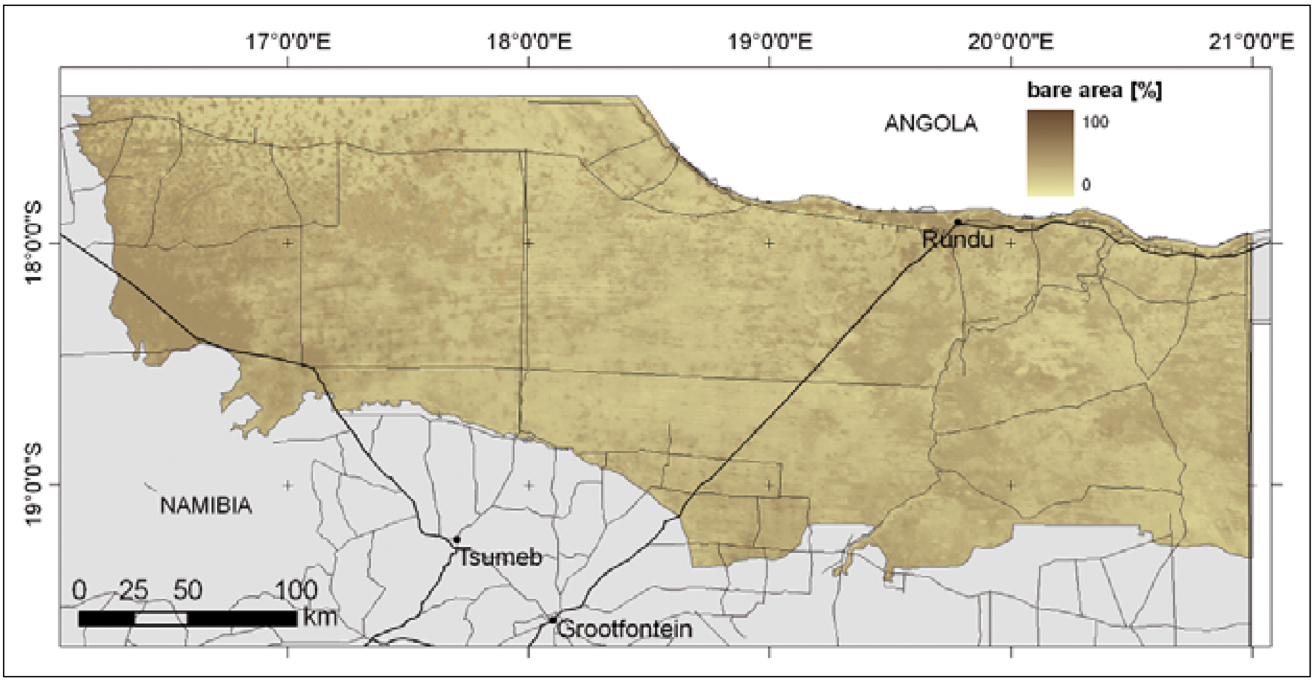

Fig. 11: Percentage cover of bare land surface in North-Eastern Namibia.

border and North-East of the road B8. Frequent fires affect large areas of the region, especially in the eastern parts. These recurrent fires influence vegetation structure, e.g. they diminish understory shrubs and lead to lower woody vegetation coverage in general.

The central part of the Woodland Savanna is characterised by longitudinal dunes formed by Kalahari Sands. The deep sands of the dune crests carry *Burkeo-Pterocarpetea* woodland savanna while the vegetation type *Acacietea* is found on the comparatively heavier soils of interdune areas (Strohbach & Petersen 2007). After Strohbach & Petersen 2007, *Acacietea* frequently form closed thickets whereas the *Burkeo-Pterocarpetea* woodland is more open with higher herbaceous and non-vegetated cover fractions. These vegetation characteristics are also clearly depicted by the fractional cover maps derived from remote sensing.

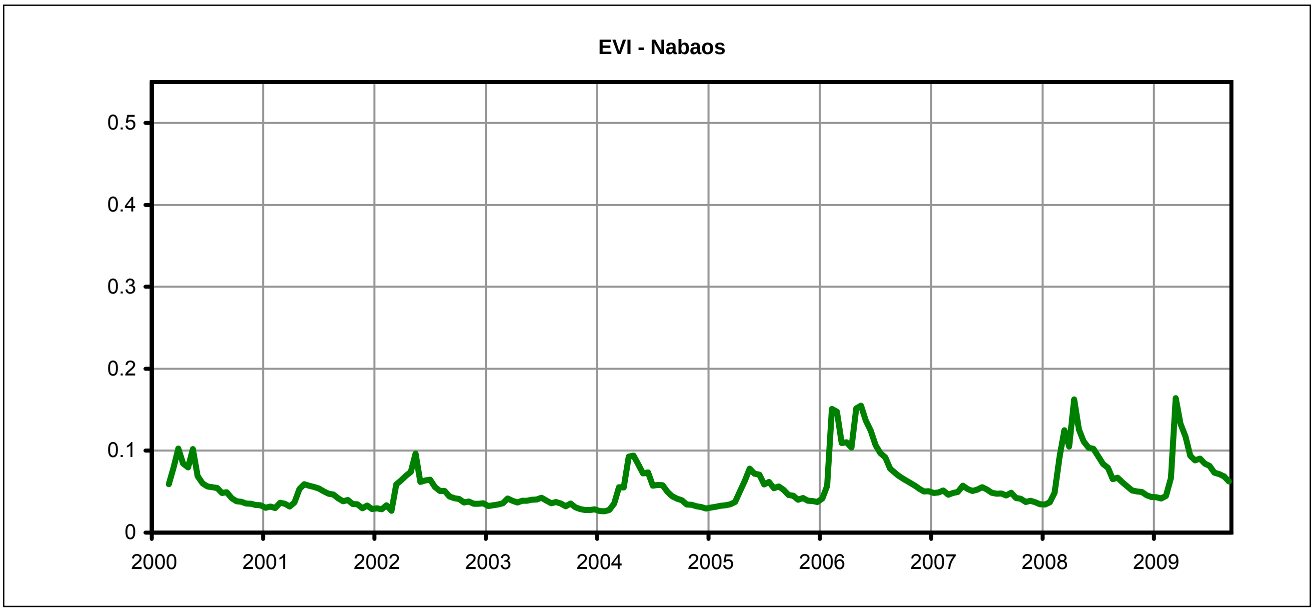

Fig. 12: Example of EVI time series data (16-days composites), here for the observatory of NABAOS.

Vegetation indices derived from MODIS time series

Remotely sensed time series of vegetation indices

Remote sensing techniques provide the opportunity to monitor the land surface and its dynamics over long periods. Different remotely sensed vegetation indices can be used for monitoring vegetation such as NDVI (Normalised Difference Vegetation Index), and EVI (Enhanced Vegetation Index). These indices provide information on vegetation density and productivity.

Vegetation indices are derived from time series of earth observation satellite sensors such as the AVHRR (Advanced Very High Resolution Radiometer), MODIS (MODerate Resolution Imaging Spectroradiometer) and SPOT-4 VEGETATION. These sensors deliver data with high temporal frequency and are therefore able to trace the dynamics of intra-annual growing cycles and inter-annual variability. NDVI time series recorded by AVHRR have been available since 1981, at a spatial resolution of 1 km by 1 km. An important dataset is the global 8 km resolution 10-day composite GIMMS product (Global Inventory Modelling and Mapping Studies), published by the Global Land Cover Facility of the University of Maryland (Tucker et al. 2005). Since 2000, when the BIOTA AFRICA project was initiated, the first MODIS sensor on board the satellite TERRA started to deliver global time series of NDVI and EVI, followed in 2003 by the second MODIS sensor on board AQUA. MODIS vegetation indices are available at a spatial resolution of 250 m by 250 m and at time intervals of 16 days.

NDVI and EVI time series contain information on phenological cycles. In semi-arid environments, they reflect the vegetation response to rainfall cycles and rainfall patterns. These time series and their phenological information content were the basis for remote sensing approaches to derive information on the vegetation composition and vegetation types in Namibian savannas (Gessner et al. 2009, Hüttich et al. 2009). Fig. 12 shows the temporal MODIS-EVI plot for the Observatory of Nabaos near Keetmanshoop in Southern Namibia, with a mean annual rainfall of 147 mm and very low vegetation cover.

The EVI maps shown here are based on MODIS 16-day composites delivered by NASA. During time series generation, additional information on the quality of each dataset was considered and low quality records were removed and smoothed. From these corrected time series, annual means, long-term means and annual anomalies of EVI were calculated.

Map long-term average EVI for the period 2000 to 2009 for the BIOTA Southern Africa study area

The map of the long-term average of the Enhanced Vegetation Index (EVI) for the period 2000 to 2009 shows the spatial distribution of the average photosynthetic activity of vegetation as a proxy for the average production of plant biomass (Fig. 13). The broad patterns of different rainfall regimes are evident as a north-south gradient over the investigation area of the BIOTA transects. The summer rainfall regime enables comparatively higher biomass production for the north-eastern Kavango region in Namibia, forming the open woodland vegetation types. The Fynbos vegetation of the Cape Floristic Region of South Africa is characterised by a distinct winter rainfall regime leading to increased plant biomass production. Lowest biomass productivity is apparent in the very arid western Namib Desert regions and the great salt pans (e.g. the Etosha Pan). Within the transition zones between these two rainfall regimes, dwarf shrub vegetation types, such as the Nama Karoo and Succulent Karoo, are found with comparatively low vegetative activity. Impacts of human landuse on the natural biomass production are visible in the densely populated Cuvelai drainage region in northern Namibia.

Annual maps of mean EVI for the years 2000 to 2009

For presenting the different situations of growing seasons, annual means of EVI were derived.

Fig. 14 shows the annual mean values of MODIS-EVI for the seasons 2000/2001 to 2008/2009. The seasons are defined as the period from 1st October until 30th September in order to cover complete vegetation periods of both the summer rainfall regions in the North and the winter rainfall regions in the South-West of the BIOTA Southern Africa transects.

The mean EVI derived from annual MODIS time series for the growing seasons 2000/2001 to 2008/2009 indicate spatiotemporal variations of the seasonal vegetative activity. The annual maps of vegetation productivity depict the response of biomass production to the actual rainfall conditions of a particular year. A high temporal and geographic variability of precipitation is characteristic for rainfall-driven semi-arid ecosystems. This can be seen for example by comparing the annual mean EVI maps of the very dry growing season experienced during 2002/2003 with the comparatively wet rainy season experienced during 2005/2006. It is apparent that the transitional zones between the summer and winter rainfall regimes,

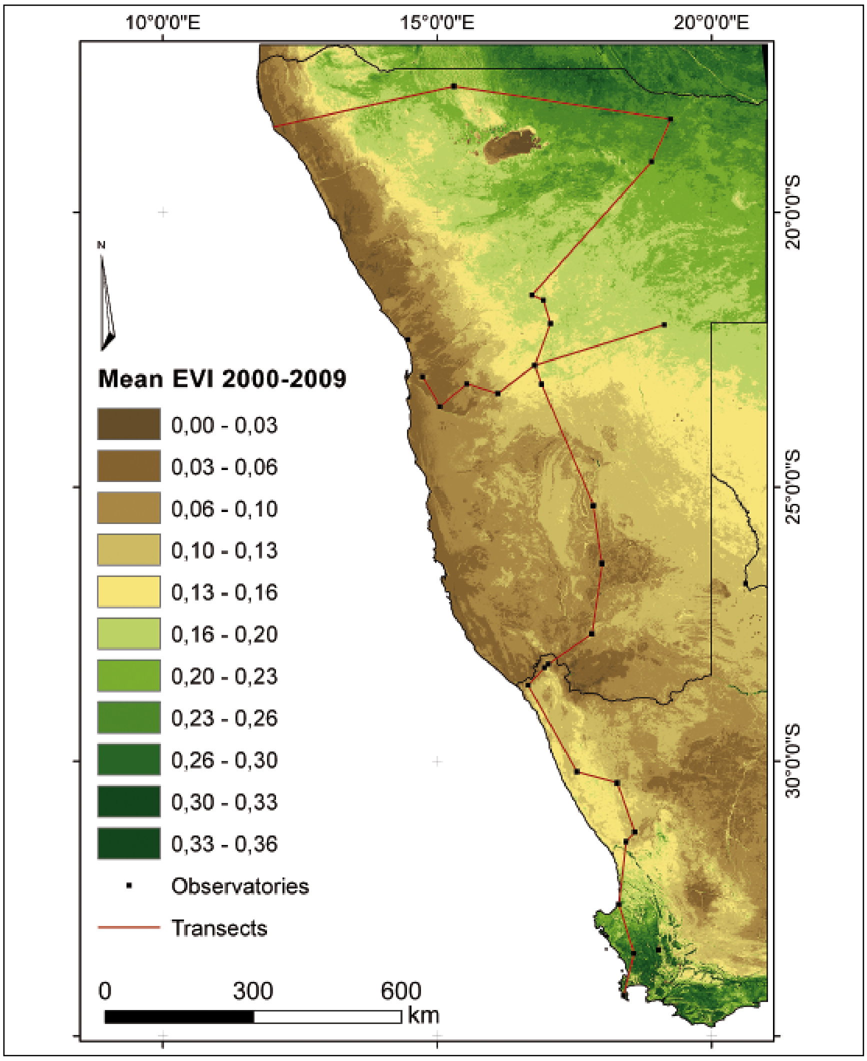

Fig. 13: EVI long-term average (2000–2009).

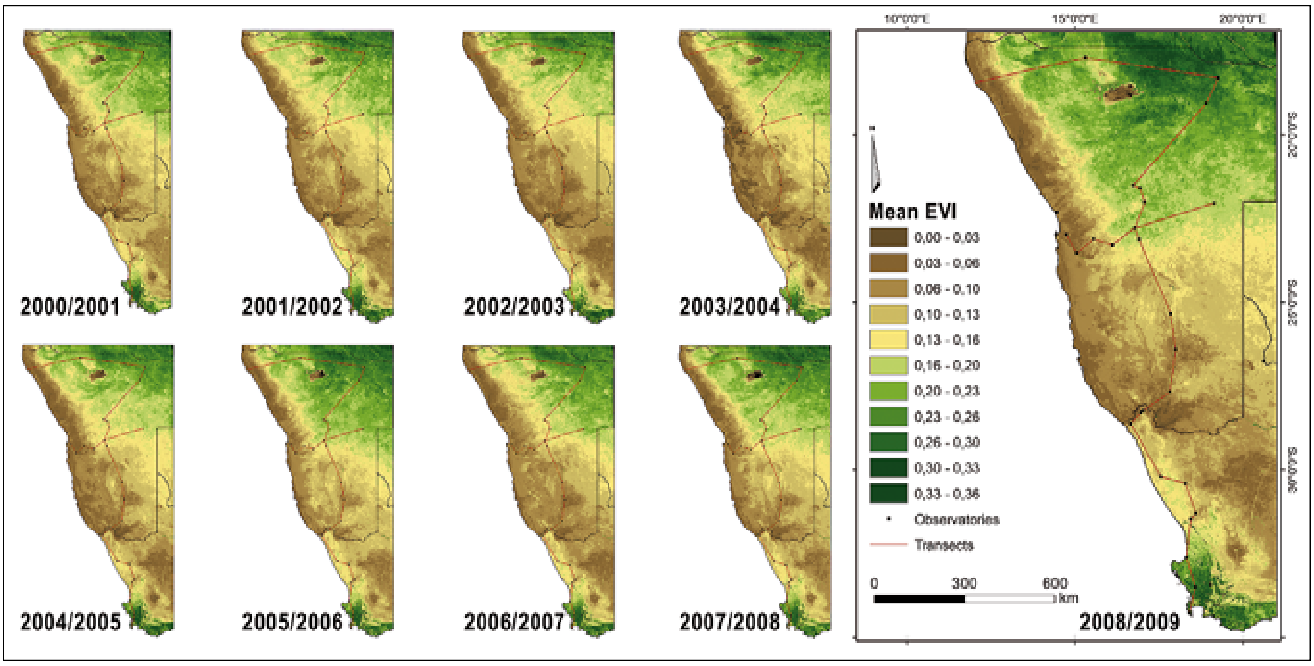

Fig. 14: Annual mean EVI (2000/01–2008/09) showing vegetation productivity in different years over the BIOTA Southern Africa research area.

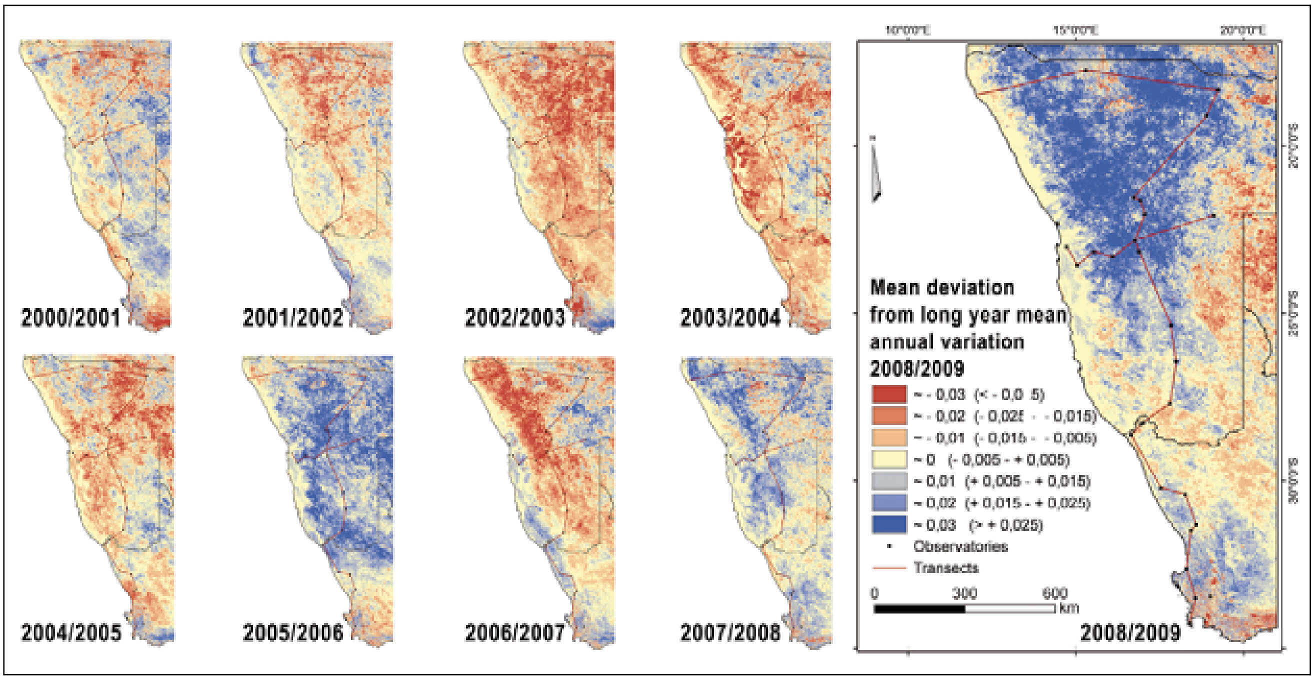

Fig. 15: Annual variation of vegetation activity (2000/01–2007/08) in comparison to the long-term mean EVI (2000 to 2009).

such as the Dwarf Shrub Savanna, Nama Karoo and Succulent Karoo show the highest variations in annual vegetation activity. The southern Cape Floristic Region, northern Kavango woodlands and the western deserts were mapped as ecotypes with comparatively stable vegetation activity.

Annual and inter-annual variation of vegetation activity

The arid and semi-arid desert and savanna ecosystems are characterised by distinct dry and rainy season. As shown above, the timing and intensity of the growing season—depending on the start and duration of the wet season and the amount of precipitation—is characterised by a very high spatiotemporal variability. Geographic location is an important factor for the development of vegetation. Particularly for large-scale rangeland management purposes, the timely availability of map products indicating stable rangelands and anomalies (in terms of vegetative activity per growing season) can be useful for sustainable and predictive rangeland management. The maps in Fig. 15 indicate anomalies of vegetation activity by comparing the annual variation of vegetation activity with the long-term mean. Specific annual precipitation and growing conditions over the sample period from 2000 to 2009 led to different spatial patterns of vegetation anomalies. Negative anomalies (shown in red) indicate lower vegetation activity and lower availability of water, whereas blue colours indicate areas with higher annual EVI values and higher precipitation. For example, the growing season of 2002/2003 was rated as a remarkably dry rainfall year. The impact on the vegetation activity is most pronounced in the vegetation types of the Kavango Woodlands, the Kalahari, and Kalahari-desert transition. The opposite pattern is visible for the growing seasons of 2005/2006 and 2008/2009. These seasons were characterised by high precipitation over most of the region.

Satellite-based earth observation time series allow for the spatially explicit measurement of inter-annual vegetation dynamics. The map in Fig. 16 shows the spatial distribution of areas with constant inter-annual vegetation activity (yellow) and with very high variations of vegetation productivity, derived from the standard deviation of the long-term mean. The very arid deserts as well as the Nama Karoo and Succulent Karoo were mapped as the most stable ecotypes. The highest variability was for the vegetation types of the Cape Floristic Region in the Little Karoo and the lowlands and hilly areas with Renosterveld vegetation near the Cederberg Mountains. The northern woodlands and mountainous regions in Namibia are also characterised by a high variability of rainfall and vegetation activity.

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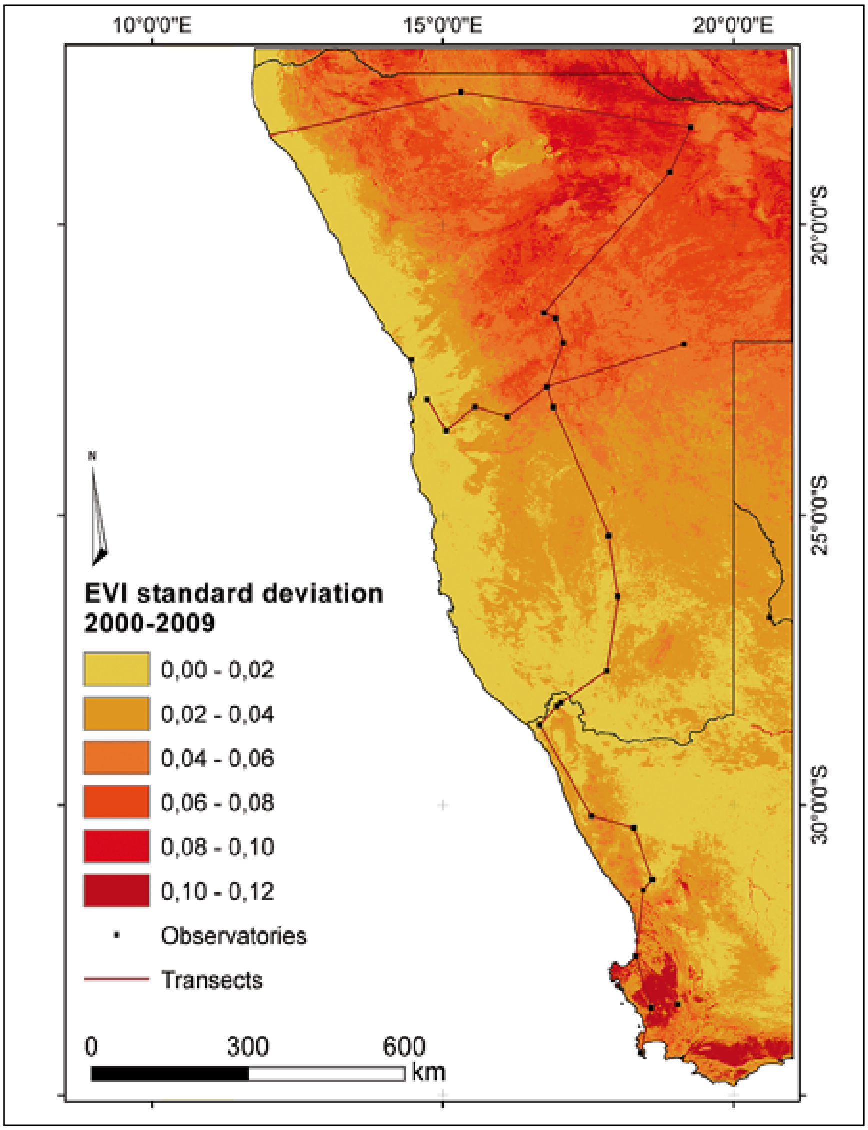

Fig. 16: Standard deviation of the long-term mean EVI (2000–2009).

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Towards a user-friendly vegetation map of Namibia: ground truthing approach to vegetation mapping

Ben J. Strohbach & Norbert Jürgens

Summary: Information regarding the vegetation of Namibia is not readily available, and the few concise sources that are available provide only a broad overview, are sometimes grossly inaccurate and provide very little information that is useful for planning and management purposes. For this reason the Vegetation Survey of Namibia project was initiated in 1996, with progress in the beginning being relatively slow.

During the BIOTA project, more information on the vegetation along the BIOTA transects was needed, prompting collaboration between the two projects. This led to a rapid advancement of the Vegetation Survey of Namibia project, not only in terms of the number of plots, which were surveyed, but also in terms of data- management, processing, mapping and presentation.

A short overview of the project's achievements to date is given in this paper, with some examples of mapping results and information presentation.

Introduction

Plant communities form the basis of all ecological processes. Because vegetation dynamics tend to be uniform within a plant community (veld type), such vegetation (veld) types can be used as management units (Daubenmire 1968, Mueller-Dombois & Ellenberg 1974, Tainton 1981, 1999). For example, extrapolation of any grazing trial result is limited to the plant community in which the trial was conducted, but extrapolation is possible wherever this community is found (even outside the borders of a research station).

Baseline data of the vegetation in Namibia has been sorely lacking (Burke & Strohbach 2000). Two projects were completed during the seventies to try and tackle this problem: the demarcation of Relative Homogeneous Farming Areas (Department Landbou Tegniese Dienste 1979) and the Preliminary Vegetation Map of Namibia (Giess 1971).

Relative Homogeneous Farming Areas were delimited in the 1970s (Department Landbou Tegniese Dienste 1979), and evaluated farming potential and constraints for the commercial farming areas. No baseline data on the vegetation was given, except for an estimation of a fixed grazing capacity. Since then it has been realised that a fixed grazing capacity is misleading, as seasonal variation in rainfall plays a major role in the production of grazable forage in an area (Lubbe 2005, Espach et al. 2006). In order to determine the grazing capacity both at a local and national scale, a number of field and remote sensing based methods have been developed or are still under development (e.g. Bester 1988, Lubbe 2005, Espach 2006, Espach et al. 2006).

This paper briefly describes the progress made in creating an updated vegetation map of Namibia up to the end of the BIOTA Southern Africa project.

Overview of available data

Presently available nation-wide vegetation information

The Giess vegetation map was drawn up in 1971, using basic techniques (Giess 1971, 1998). Although it has been found to be relatively accurate, a number of anomalies have been noted. The description of the vegetation is very basic, giving little baseline data (if any) that can be used for further studies. This map does not compare with John Acocks's Veld Types Map of South Africa, which was first published in 1956, and has seen its 3rd revision (Acocks 1975). Acocks's original field data books are still available, and these sites have recently been proposed as long-term vegetation monitoring sites in South Africa (Westfall & Greeff 1998). In addition, Acocks's map has served as a basis for two further studies on the vegetation of South Africa (Low & Rebelo 1996, Mucina & Rutherford 2006).

The Atlas of Namibia (Mendelsohn et al. 2002) also contains a vegetation map. This map was based on several regional reviews such as the environmental profiles of the Caprivi (Mendelsohn & Roberts 1997), Central North (Mendelsohn et al. 2000) and Kavango (Mendelsohn & el Obeid 2003) regions, some expert opinion and partially based on vegetation data. However, large parts were still based only on the original Giess (1971) map, and little baseline information on the various vegetation types is provided with this map.

In addition to these descriptive data sets, a number of studies on biomass production, as related to the greenness of the vegetation (Sannier et al. 1998, Espach et al. 2006), the biomes (Irish 1994) as well as the biogeography (Craven 2001) have been undertaken on a national basis.

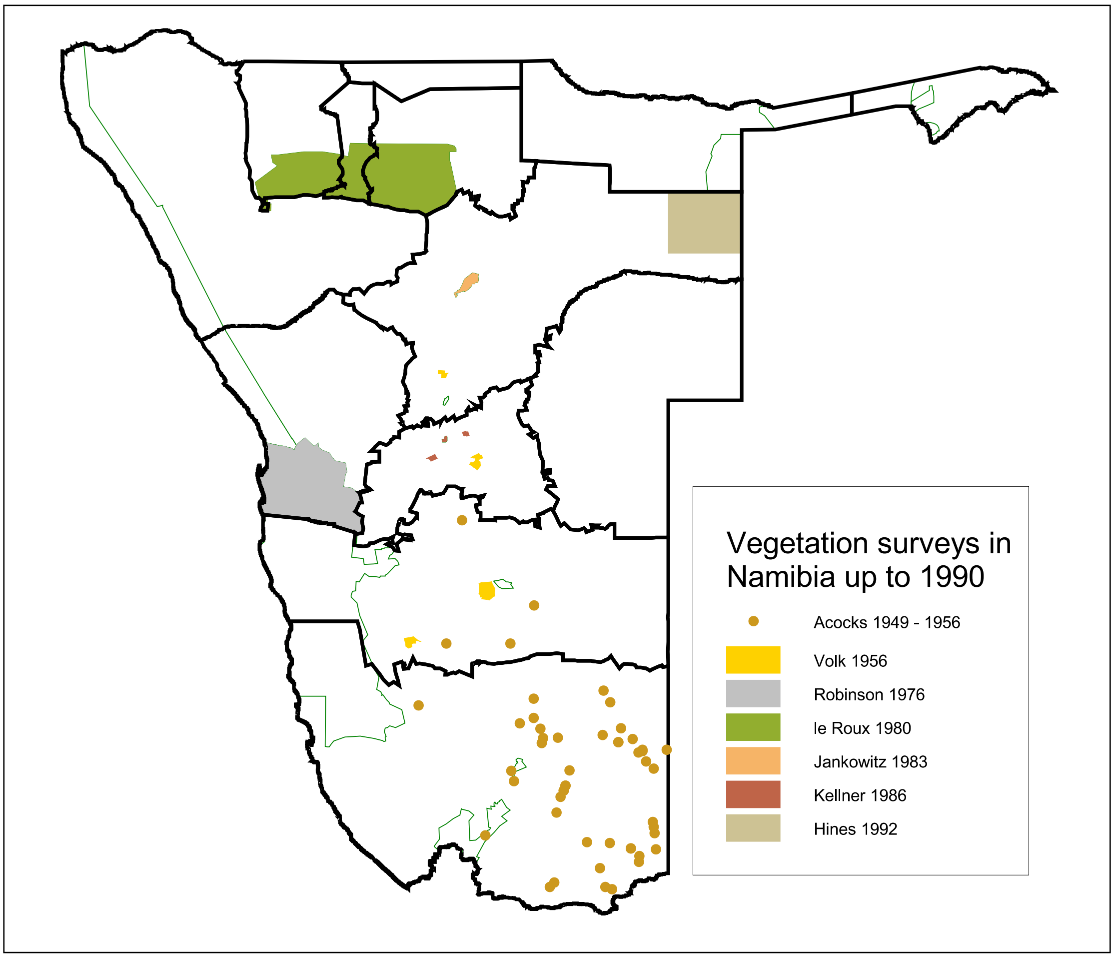

Fig. 1: Vegetation surveys conducted in Namibia before 1990 (1739 plots). Most of the plot positions are unknown, or at best determined from maps presented in various theses, as GPS-technology was not available at the time of surveying.

Regional and small-scale vegetation data

A fair number of regional and small-scale vegetation studies, mostly with the aim of providing management information, have been undertaken in the past:

- Acocks visited southern Namibia on several occasions (1949–1956) during the field work for his epic "Veld Types of South Africa".
- Volk visited a number of farms during 1956, and again in 1963. Some of his data from 1956 are still available, but only one study was published (Volk & Leippert 1971). Apparently he also visited Namibia before World War II in 1936/37, but information and data from this visit is unavailable, and is likely to have been destroyed during the war.
- The Department of Nature Conservation undertook a number of vegetation-related studies in National Parks and conservation areas during the 1970s and 1980s for management purposes: Robinson (1976) in the Central Namib; Le Roux (1980, see also Le Roux et al. 1988) in the Etosha National Park; Jankowitz (1983, see also Jankowitz & Venter 1987 and Jankowitz & van Rensburg 1985) in the Waterberg Plateau Park; Kellner (1986) in Daan Viljoen Nature Reserve, Claratal and Bergvlug; Hines (1985 unpublished) in the Mahangu Game Reserve, as well as in eastern Bushmanland (present-day Tsumkwe district) (Hines 1992); M. Strohbach in the Sperrgebiet (unpublished). During the pre-independence era 1,739 plots were surveyed and their spatial distribution is depicted in Fig. 1.
- Since Independence in 1990, renewed interest in Namibia resulted in the initiation of a number of development projects in the agricultural and environmental sector. Some of these included baseline studies on the vegetation as a natural resource, and a number of purely scientific studies were also initiated on the vegetation of various smaller areas. A list of these studies is presented in Appendix 1 (OOO). It was also decided to include a study on the vegetation of Namibia with the conception of the Agro-Ecological Zoning Programme in 1994. This led to the start of the Vegetation Survey of Namibia project in 1996, with extremely limited resources and manpower. The total number of plots surveyed by the end of 2000, before the start of the BIOTA Southern Africa project, was 3,494 (Fig. 2).
- During the BIOTA project, surveys were initially done only along the BIOTA Southern Africa transects (in addition to the regular continuation of the Vegetation Survey of Namibia project), but were later expanded to include the description of the vegetation in areas adjacent to major Observatory pairs for the purpose of upscaling. This culminated in an attempt to combine the various data sources and start with the development of a single, unified vegetation classification (Fig. 3). With the combined efforts of the Vegetation Survey of Namibia Project, the BIOTA

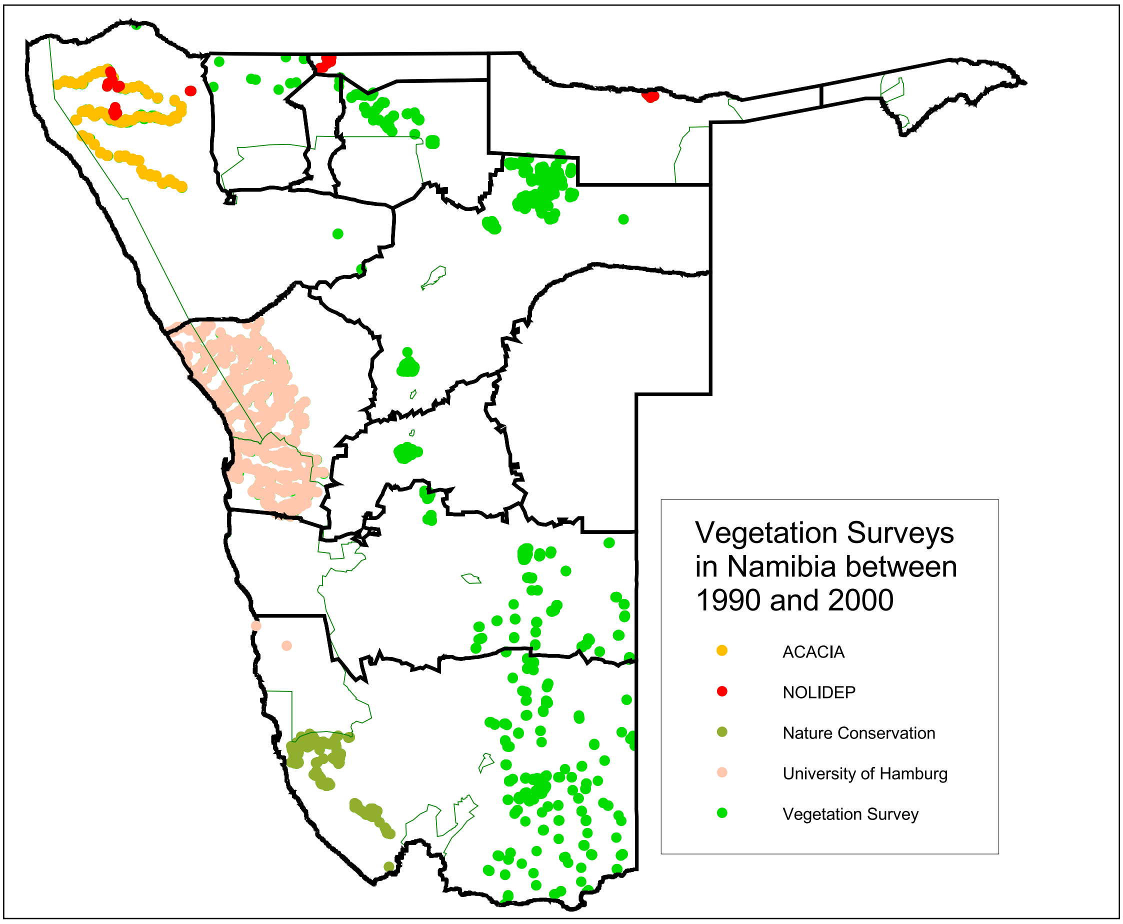

Fig. 2: Vegetation surveys undertaken during the period 1990 and 2000 (3494 plots).

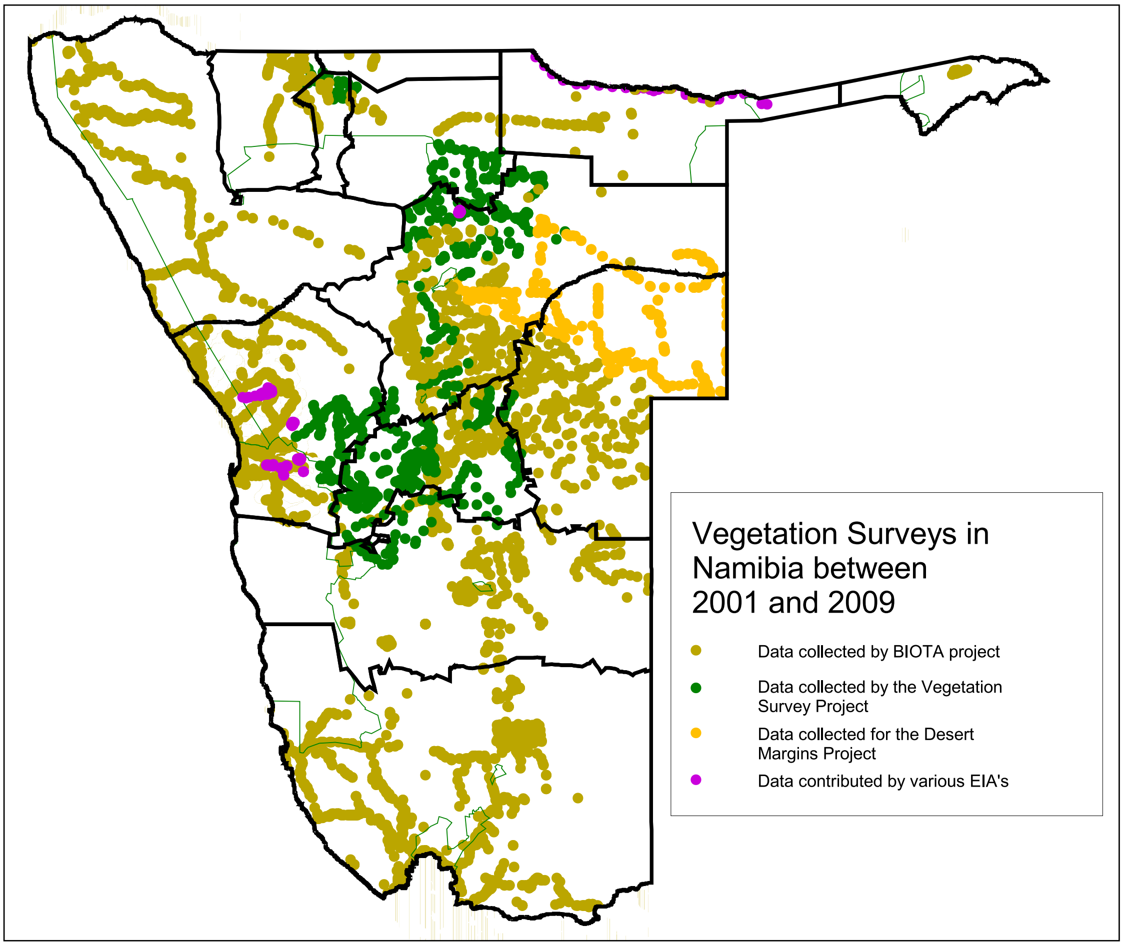

Fig. 3: Vegetation surveys undertaken during the period 2001 and 2009 (8720 plots).

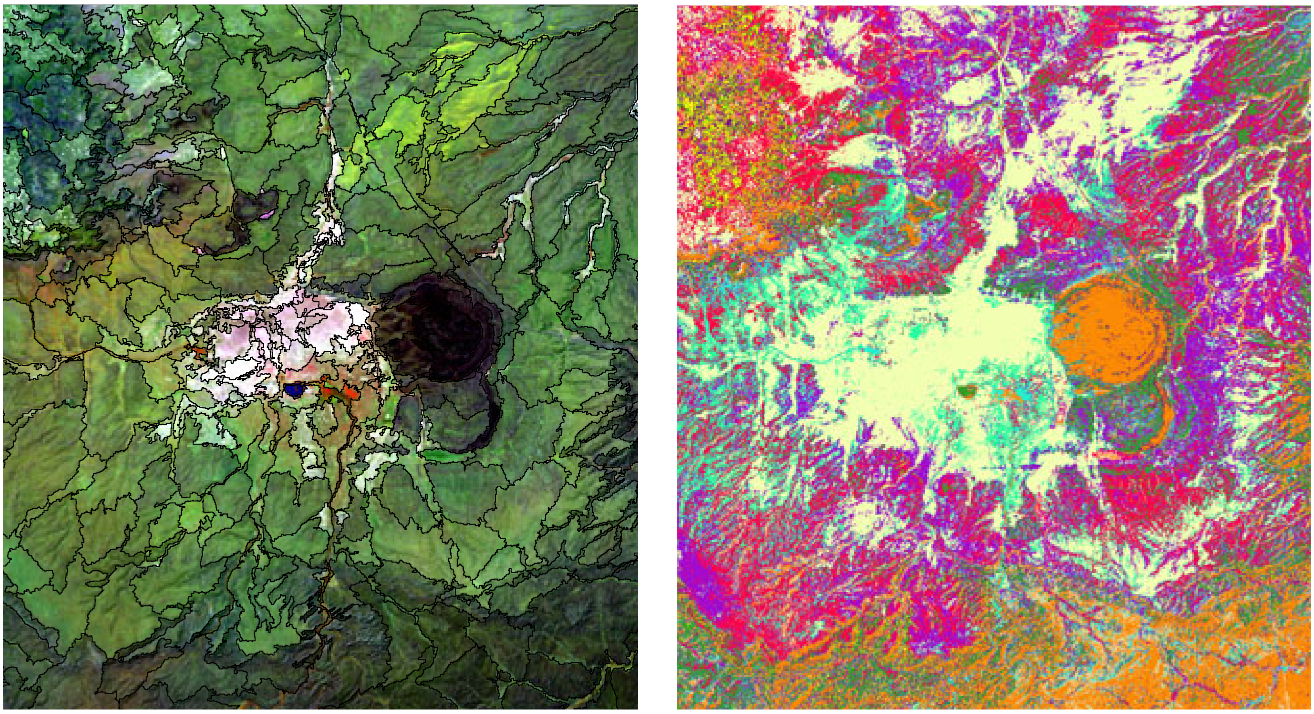

Fig. 4: The pan system at Haribes west of Mariental. a) False colour image of a portion of Landsat ETM scene 177-77, dated 26 March 2001 (left). The superimposed lines are segments of homogenous landscapes created by Definiens Professional 5. This image was used as a field map during surveying. b) Cluster analysis (right). Typical unsupervised classification of the same portion of Landsat ETM scene 177-77. Note the very strong pixelated effect, and the rather confusing colour scheme.

Southern Africa Project, as well as contributions from other projects and environmental impact assessments, a total of 8,720 plots were surveyed during the period 2001 to 2009.

Methods

Approach

The ultimate aim was to produce a vegetation map of Namibia at the scale of 1:1 000 000. Due to the high diversity of habitats (geology, topography, soils and climate—cf. Mendelsohn et al. 2002) a large number of major vegetation types, and an even larger number of minor vegetation types that are typical of niche habitats, were expected. It soon became apparent that small niche habitats and associated vegetation types could not be sampled in detail, but because the purpose of the vegetation map is to serve as a tool for landuse planning, the focus was rather on the mapping of larger vegetation units. The following basic method was applied to achieve this (Strohbach 2001):

Initial stratification

The purpose here was to delimit relatively homogenous mapping units within the study area in order to reduce the sampling effort. The general hypothesis was that plants grow in a specific habitat, and because of that, certain groups of plants (i.e. plant associations) are found in specific habitats.

The Agro-Ecological Zones Map of Namibia (de Pauw 1996, de Pauw & Coetzee 1998/99, de Pauw et al. 1998/99) was used as a baseline map. This map was modified so that the Land Type class ‘R’ (inselbergs and rocky outcrops) was subdivided into 54 units according to geology and secondarily to growing period zones. These agro-ecological zones (AEZ’s) were transferred onto standard 1:250 000 topographic sheets, which were then used in the field. Satellite images became readily available through the Agro-Ecological Zoning project and were used as false colour hardcopies in the field. Only later did Definiens Professional 5 (Definiens AG 2006) become available as a tool for initial stratification. This software delimits relatively homogenous areas in images, based on a group of pixel colour values, forming coherent shapes rather than pixelated unsupervised classifications (Fig. 4). The other advantage over unsupervised classification is that the false colour image can still be displayed as background to the segments.

Field surveying

Plots of 20 m x 50 m (or 1,000 m^2) were placed in the homogenous stratified units (segments) in such a way that each landscape type was adequately covered. In many cases, accessibility led to some bias in the selection of sample sites, in order to minimise travelling time. In cases where the topographic unit would not allow a 20 m wide plot (e.g. narrow streams and riverbeds, and the crests of dunes in the southern Kalahari), a narrower plot of 10 m x 100 m was used. The size of 1,000 m^2 has been found suitable in a wide range of environments within Namibia and has been adopted by other groups working with vegetation in Namibia, e.g. the University of Cologne (ACACIA project). A minimum of 4 to 6 plots was surveyed per mapping unit.

Information gathered at each sampling site. A GPS reading was taken at each plot, preferably in the northwestern corner. Originally the GPS-reference was set to the "Schwarzeck" map datum, but this was later changed to WGS84. Additional locality information included the region, district, farm or locality name, and a short description of the locality.

Habitat information included the slope, the terrain type, aspect, stone cover estimation, lithology (parent material), erosion severity, surface sealing/crusting, disturbances, etc. For this description the SOTER methodology (FAO 1993) was used.

The vegetation information consisted of a full list of species found on the plot, following the standard Braun-Blanquet procedure (Mueller-Dombois & Ellenberg 1974). Geophytes were normally excluded (except if found in flower—i.e. identifiable). Plants, which could not be identified in the field were collected for later identification in the herbarium. Each specimen was accompanied by a standard collection form.

For each species noted, details were provided regarding the plant's growth form (i.e. tree, shrub, dwarf shrub, grass, or herb) following the definitions of Edwards (1983). The abundance of each species was estimated according to its crown cover, more or less following the Domino Scale (Mueller-Dombois & Ellenberg 1974). The abundance was given as percentage cover. Alternatively, methods like the Plant Number Scale (Westfall & Panagos 1988) or the Log scale of McAuliffe (1990) could also be employed.

A photograph was taken at each plot to document the landscape as well as the structure of the vegetation.

Data capture

TurboVeg (Hennekens & Schaminée 2001) is widely used in South Africa and was made available to the National Botanical Research Institute in Namibia by the University of Pretoria. This database is based on a list of species known to occur in southern Africa, prepared and updated by the National Botanical Institute in Pretoria, RSA (Germishuizen & Meyer 2003). It was extensively used to capture vegetation data in Namibia. An elaborate data clean-up procedure was developed. This was generally based on a) a full identification list of collected specimens from the National Herbarium, b) checking the species list generated from the captured data against the identification list, and as a last step, c) painstakingly checking the captured data against the original field data sheets. These original field data sheets were also archived together with a copy of the captured data as hardcopies as well as copies on CD.

At present these data sets are being captured to BIOTABase, in the process updating the captured data with appropriate structural data, more detailed GPS data, photos, and updated identifications.

Data processing

The relevés were classified into vegetation communities following the Braun-Blanquet tabulation method (Mueller-Dombois & Ellenberg 1974, Whittaker 1978). The original TWINSPAN (Hill 1979), as well as a modified version of TWINSPAN (Roleček et al. 2009), Cluster Analysis as part of PC-ORD 5 (McCune et al. 2002) and COCKTAIL (Bruelheide 2000) are all commonly used classification procedures available in the JUICE software package. The output is a typical phytosociological table, from which the community composition and the characteristic plant species for each community can be determined.

The relationships between the various communities, and between the communities and the habitat were further illustrated with ordination techniques. Here again various routines, including Reciprocal Averaging, Canonical Correspondence Analysis as well as Nonmetrical Multidimensional Scaling (NMS) were available in the software package PC-ORD 5 (McCune et al. 2002).

Synopsis

The full diagnostic phytosociological table is rather complicated to read. A synoptic table condenses the information, listing the species in each community, and their relative affiliation to that particular community.

- These data were then used to describe the community in wordsThe characteristic species, i.e. species by which the community could be identified.
- The structure of the community according to the definition of Edwards (1983)—from open woodlands to shrubland vegetation.
- The species diversity—i.e. which species occurred within a particular community, including diversity related statistics such as the number of species observed, the estimated number of species, and various diversity indices (Palmer 1990, 1991, Barbour et al. 1987, Gauch 1982).
- The habitat in which the community was found.
- Species with particular traits—exotics, possible encroachers, possible endemics, rare and endangered plants—were highlighted.
- General management information regarding the vegetation type, including the general suitability for grazing, the sensitivity of the vegetation, as well as the general conservation status. For this purpose a set of indices were developed (Strohbach, in prep.). In terms of general sensitivity, the presence of rare, endemic and/or protected species, the topography as related to erosion hazard, and water flow (following Pringle & Tinley 2003, Pringle et al. 2006) were considered. The utilisation potential was biased towards livestock farming, and took into account the climate (especially annual rainfall and rainfall reliability), the soil and topography (as influencing water availability), the vegetation structure, as well as the species composition (average composition of the grass sward in terms of grazing value as well as presence of toxic plants).

The text was to be accompanied by photographs (if possible). An information sheet for each described association was developed for this purpose, following the idea of Burke (2008; Strohbach, in prep). See Appendix 2 for examples of these information sheets.

Final mapping

This stage was still part of the description stage: the final classification was compared with the original map, and the spatial extent of the communities was defined. This was done using various base maps and remote sensing applications, combined with processed, sorted

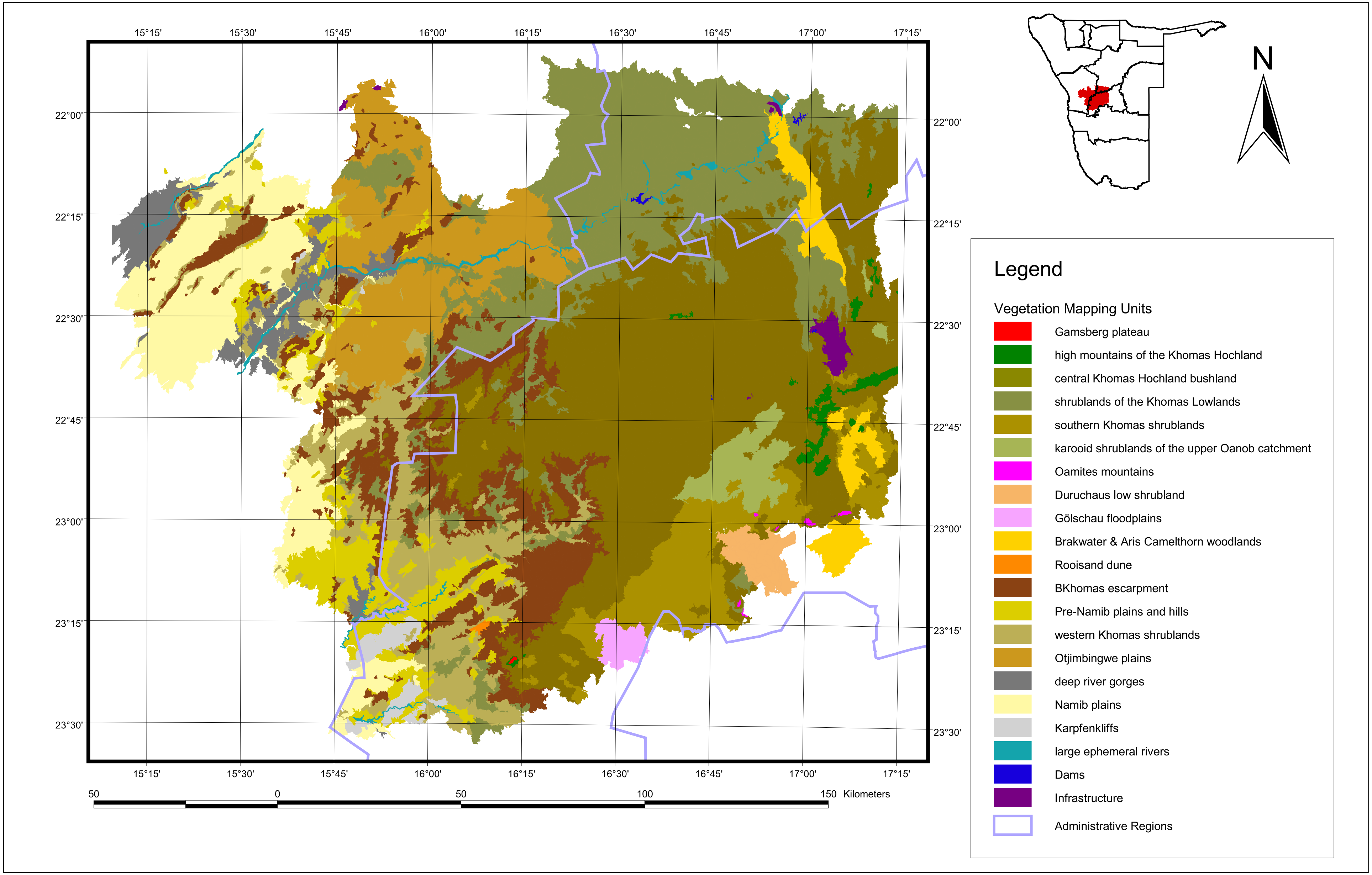

Fig. 5: Example of a completed vegetation map for the Khomas Hochland, based on the classification of segments derived from Landsat ETM scenes 178-75 dated 2000-05-17, 178-76 dated 2001-05-04, 179-75 dated 2001-02-20 and 179-76 dated 2000-04-06 (from Strohbach, in prep).

field data. The generally used approach for classifying satellite images (supervised classification) was found to be unsatisfactory, due to the large areas to be mapped. Therefore, the units identified for the initial stratification were classified with Definiens (Definiens AG 2006), using a nearest neighbour analysis. Sample units were selected based on the position of classified relevés representing a typical mapping unit. Here it should be pointed out that due to the large scale of the final map, it was impossible to map each identified vegetation type. Instead, a vegetation mapping unit was mapped, comprising one (or a few) major vegetation types, but which included several smaller azonal or niche vegetation types (e.g. pans, rivers, etc.). Using Landsat satellite images, the segmentation classification results had a general spatial accuracy of up to 30 m (Fig. 5).

A second approach developed by Hüttich et al. (2009) used a MODIS time series. Here the phenological patterns of the vegetation, displayed over a number of years, was used for classification. This approach was especially promising in large, often very uniform areas like the eastern communal lands (Fig. 6). Here the use of traditional supervised classification of Landsat scenes was found to be highly unsatisfactory, as climatic variation within some scenes caused misclassifications, with up to a 50% error (Strohbach et al. 2004). The cross-border matching between different images scenes was also especially problematic (Fig. 7).

Semi-detailed, small-scale studies of research stations and other areas of interest

In addition to the national survey, semi-detailed studies of various research stations of the Directorate Agricultural Research and Training, as well as other study sites, were undertaken. This was to provide baseline data on these stations and/or farmers associations. In this programme the vegetation of the following areas was described: eastern communal farming areas (Strohbach et al. 2004); a strip transect of the vegetation along the BIOTA transects (Strohbach 2002); Alex Muranda Livestock Development Centre (previously Mile 46 LDC) (Strohbach & Petersen 2007); the Sandveld Research Station (September 2006); the Ogongo Agricultural College (Kangombe 2007); and the Sachinga LDC in Caprivi (Lushetile 2009). Still to be published are accounts of the vegetation of Sonop Research Station, Uitkomst Research Station, Kalahari Research Station, Gellap Ost Research Station, as well as the farms Erichsfelde and Haribes. These latter two accounts are part of a follow-up on historic data collected by Volk in 1956.

The same methodology as above was used, with the exception that more emphasis was placed on smaller vegetation types, including azonal vegetation types. Studies covering slightly larger areas, such as the main and east-west BIOTA transects, or at conservancies, served as “seeding areas” in which vegetation types were described in more detail than could be at a national level. The data of both small-scale and regional studies, and from several Environmental Impact Assessments—if done to standard—were included in the national database.

Way forward

The Vegetation Survey of the Namibia project is not yet completed, although remarkable advances have been made over the past 9 years in close collaboration with the BIOTA project. The National Botanical Research Institute will continue with the task of collecting vegetation data, especially in areas, which have not yet been surveyed, and collating the information in a database. The following steps are envisaged over the next years:

The existing data sets need to be completely transferred to the BIOTABase. In the process, data captured in the field, but not in the TurboVeg data base (e.g. structural data) needs to be captured. The reason for this is that BIOTABase contains more detailed data compared to TurboVeg, and will form an integral part of a database system together with the South African Plants Photodatabase and an Herbarium database, to be developed during the planned Regional Science Service Centre project.

The existing data sets need to be classified, and the resulting units need to be matched to previously defined vegetation types. For all vegetation types, an information sheet (as per Appendix 2) is to be compiled.

The vegetation types are to be mapped. For the initial scale of 1:1,000,000, it will be necessary to combine various vegetation types into one mapping unit (similar to a landscape type being mapped); as more data becomes available, it will be possible to map smaller areas in more detail, teasing out the various associations.

A web-based vegetation information system is to be developed. The aim is to have the map searchable in a very similar way to Google Earth, and linked to the various mapping units and the appropriate vegetation association information sheet. This will also allow the publication of initial results in areas already well-covered, while data is still to be collected in other areas of the country.

Further studies (from various sources) are to be integrated into the National Phytosociological Database, as well as the database on vegetation types as they become available. The web-based vegetation information system will be updated accordingly, thus making the information available and easily accessible to the broader public.

Acknowledgements
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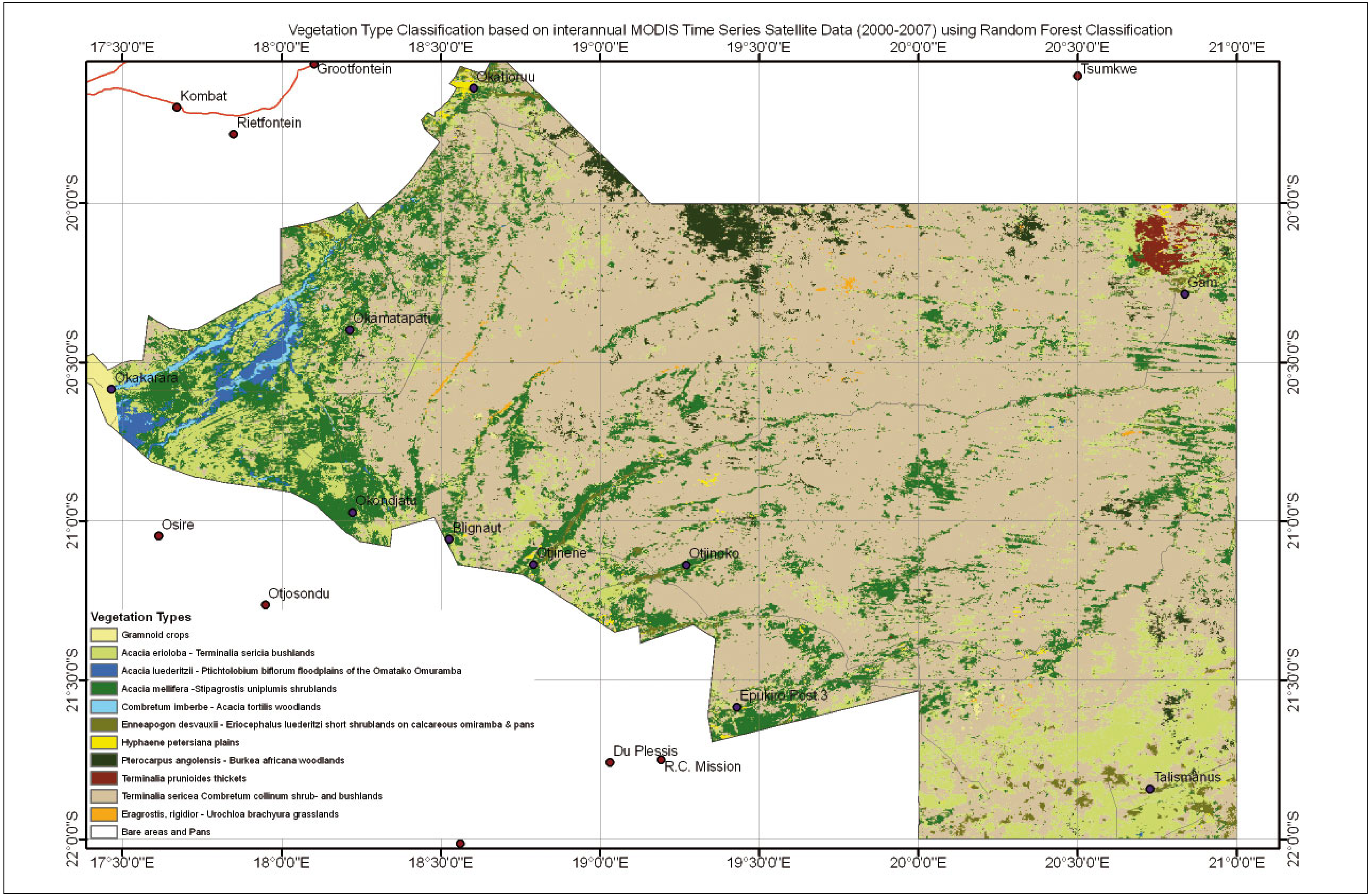

Fig. 6: Vegetation map of the eastern communal areas based on MODIS time series (from Hüttich et al. 2009). Note the simplified legend of the map.

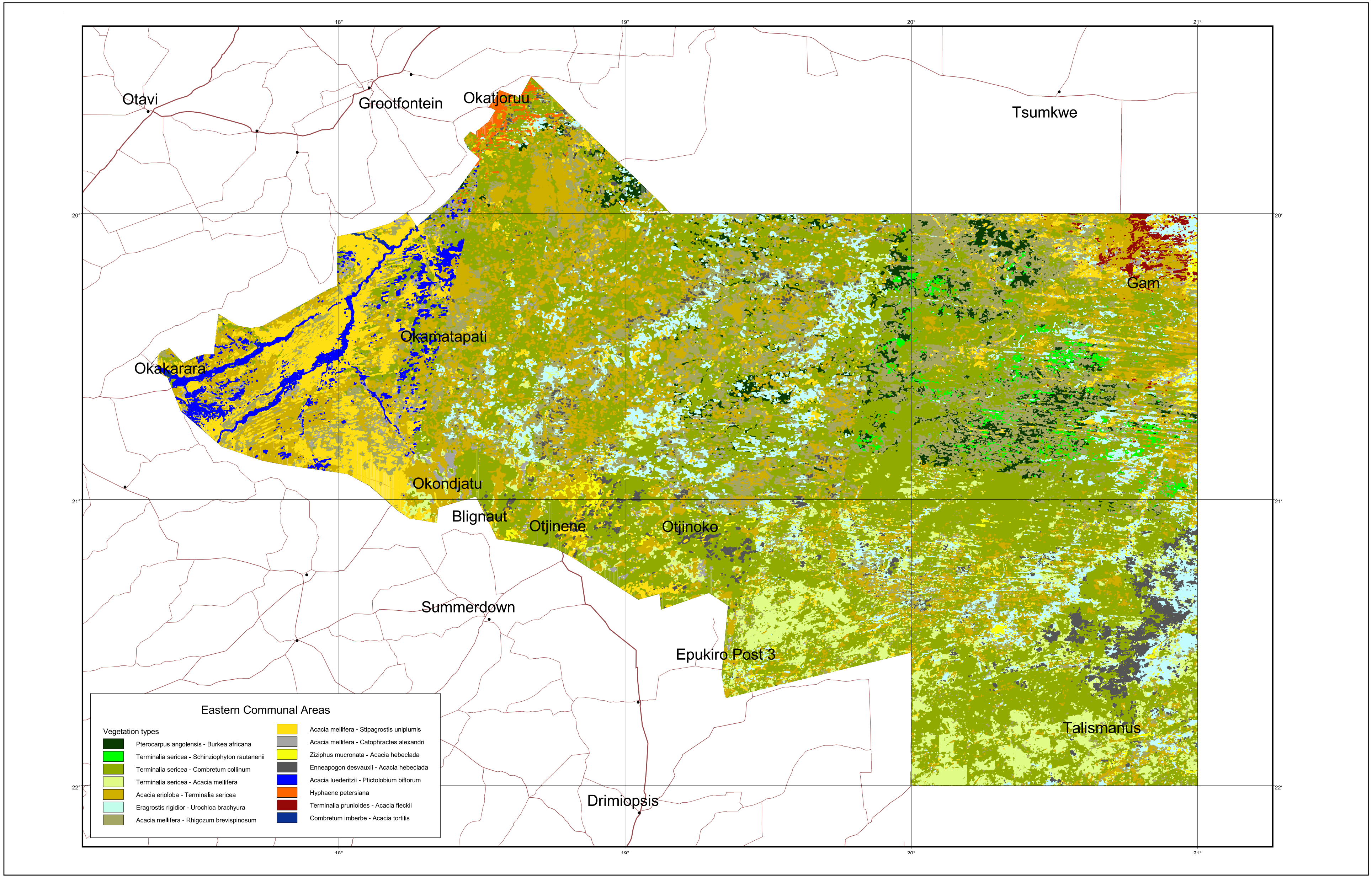

Fig. 7: Original vegetation map of the eastern communal areas based on supervised classification of Landsat TM scenes 177-74, 176-74, 177-75, 176-75 and 178-74. Note the discontinuities between the five different Landsat scenes (especially in the west and the north-east), as well as the very detailed, often confusing map. A mapping accuracy of only 48% was achieved with this procedure (Strohbach et al. 2004).

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Diversity and endemism of true bugs (Heteroptera) in the arid biomes of south-western Africa

Jürgen Deckert

Photo 1: *Broteolus pugnax* (Coreidae), Otjiamongombe.
All Photos: Jürgen Deckert.

Photo 2: *Solenosthedium liligerum* (Scutelleridae), Otjiamongombe.

Summary: Until now, 725 Heteroptera species have been verified for Namibia. 25% (180 species) of these species are endemic to Namibia, the Western- and Northern Cape of South Africa, southern Angola, and Botswana. 14% (103 species) are considered to be endemic to Namibia. The number of species per Heteroptera family in Namibia, and the Northern and Western Cape of South Africa are listed, endemics are pointed out and basic biological information for each family is given.

Methods and sources of information

One main source of information regarding Heteroptera species diversity was the material collected within the BIOTA project over the period 2001 to 2009. The collecting of Heteroptera required the application of different methods due to the different biology and habitat use of species or species groups. One of the best methods to obtain good samples of Heteroptera within acceptable timeframes and with minimal effort was the use of lights and light traps. Because many Heteroptera are crepuscular, the light traps were set up at sundown, but some species, such as certain species of Reduviidae, only appeared later in the night. Heteroptera which were collected at light were trapped using the same methods and were from the same samples as described in detail by W. Mey for light trapping (see Article III.3.12). Net sweeping (net diameter 40 cm) was also used to collected Heteroptera from herbaceous plants and grasses. For woody and thorny plants, net sweeping was not practical and an effective method for collecting insects from these plant types was beating. This method also allowed selective collection of specimens on plants in order to obtain information on host-plant relationships. The simplest method was to use an umbrella with light-coloured covering. Additional collection methods were pitfall- and Malaise trapping.

An overview for Heteroptera of South Africa is given by Jacobs (1985), and in general, the Heteroptera fauna in southern Africa is still poorly known. In the Western and Northern Cape regions of South Africa, only about 700 Heteroptera species have been recorded, based mainly on information from the original description of the species. Hundreds of southern African Heteroptera species are still undescribed, especially within the family Miridae which is known to be species rich, but only about 50 species for instance are known from Namibia. Other families, e.g. Alydidae, Lygaeidae, Reduviidae, and Tingidae, are better known but also require further study.

South Africa and Namibia, as well as the neighbouring countries of Botswana and Angola, and the rest of tropical Africa are far from completely collected. To determine whether or not a species is endemic to a region also requires information about habitat selection and the host-plant relationship.

A short introduction to the biology of Heteroptera

Heteroptera are probably the most abundant and diverse insect group with incomplete metamorphosis. They have successfully colonised every habitat in southern Africa and have a remarkable degree of species richness as well as a high morphological diversity. True bugs may look like other insects such as beetles, ants, or mosquitoes. They are often mimetic to their environment and camouflage themselves by adapting their coloration or shape. The only reliable characteristics that indicate a true bug are their distinctive piercing-sucking mouthparts and the structure of their wings. Only true bugs have stink glands, and a large triangular plate on the dorsal side of the thorax (the "scutellum").

Most heteropterans feed on plants, feeding more or less on all plant parts (pollen grains, seeds, leaves, roots). A number of true bugs prey on other insects, and a few species are hematophagous, living as parasites on birds or mammals.

Heteroptera contains eight higher subgroups, with two of them—Cimicomorpha and Pentatomomorpha—possessing many species of economic importance. However, only a small percentage of Heteroptera species are a serious pest which damage food crops (Schaefer & Panizzi 2000). On the contrary, predatory species of *Geocoris* (Geocoridae) are used for biological control of crop pests in greenhouses or in agricultural fields (Waddil & Shepard 1974).

Heteroptera are known to include a wide range of species which can either be highly specialised or broad generalists. If environmental conditions change, generalists are much more able to adapt than specialists, and specialists tend to become extinct. Species which are highly adapted to their local environment or feed only on one endemic plant species are suitable as indicators for characterising habitats and changes in environmental conditions. Achtziger et al. (2007) summarised the suitability of true bugs for nature conservation and discussed their indicator value.

Many true bug species have good dispersal abilities and they are constantly on the move. This can be observed especially during the rainy season on warm nights when the humidity is high around artificial lights which attract myriads of insects including true bugs. They are able to immediately colonise suitable habitats that develop as they are good flyers. Water bugs can colonise ephemeral water bodies shortly after these water bodies emerge. It is even possible to find water bugs around light in the middle of the desert, far away from the closest water. It is no guarantee that remote habitats only accommodate rare or endemic Heteroptera. Generalists, including predators as well as phytophagous species, may be found there too. For example, the cosmopolitan phytophagous *Nysius ericae* or the Big-eyed Bug *Geocoris phaeopterus* were found at the Observatory Wlotzkasbaken (S16). Both species have vast distributions, spreading far beyond the African continent.

Despite the ability of active flyers to leave unsuitable places to populate new habitats, other species can only survive the unfavourable dry and cold seasons either as eggs or dormant as adults.

Results

725 Heteroptera species are known to occur in Namibia. This number will increase with more detailed studies of the Namibian true bugs. For instance, a study of Tingidae (lace bugs) of Namibia doubled the number of known species from 42 to 85 species, including three newly described species (Deckert & Göllner-Scheiding 2006). As in other insect groups, the richness of Heteroptera species in Namibia is expected to be much higher than is currently known. The total number of insect species in Namibia is between 6400 and 7000 species (Simmons et al. 1998). These authors assume that only about 20% of the insect species are known. I would suspect that, at best, 50% of the Heteroptera species of the region are described, as a conservative estimate. Especially the species rich family Miridae are nearly unknown in Namibia. Less than 50 Miridae species are known from Namibia, but at Otjiamongombe (Observatory S05) more than 120 morphospecies of Miridae were found.

The highest diversity and abundance of Heteroptera species generally occurs within or shortly after the rainy season. Seed-feeders, such as species of the Alydidae, Lygaeidae, or Rhyparochromidae are most abundant when seeds are available, mostly at the end of the rainy seasons.

At Otjiamongombe (Observatory S05) between 2001 and 2009, we collected Heteroptera over a period of 71 days during the months January to May and September to October, with light-, pitfall-, and Malaise traps, as well as by beating on plants and net sweeping. More than 250 Heteroptera species from nearly 2400 specimens were recorded. About 50% of these species were collected only once. This clearly shows the effort needed to bring to light the diversity of Heteroptera in the studied area.

The Heteroptera species of south-western Africa are of heterogenous zoogeographical origin. Two families of Heteroptera (Tingidae and Lygaeidae) illustrate the situation for species found in Namibia (Table 1). Twelve (14%) of the 85 Namibian Tingidae (lace bugs) species are probably endemic to Namibia. 29 species (34%) of the Namibian Tingidae are restricted to the arid parts of south-western Africa (southern Angola, Namibia, and the Western- and Northern Cape Provinces of South Africa). 38 species (45%) of the Namibian Tingidae belong to rather widely distributed Afrotropical species (38 species, 45%), whereas about half of them have eastern- to southern African distribution patterns. Seven species found in Namibia (8%) have a wide distribution range, which includes parts of the southern Palearctic and Oriental regions. Only one species, *Teleonemia scrupulosa*, which is currently found in many tropical areas where it feeds on *Lantana*, was introduced to Namibia from the New World.

The family Lygaeidae is represented in Namibia by 2 endemic species (5%) and 7 species restricted to south-western Africa. One species (3%) is cosmopolitan, 10 are widely distributed (27%) and found also in other parts of the Old World, and only a few are distributed only in southern Africa. The largest portion of Namibian Lygaeidae

Photo 3: *Phricodus hystrix* (Pentatomidae), Otjiamongombe.

Photo 4: *Nariscus cinctiventris* (Alydidae), Otjiamongombe.

Photo 5: *Paromius gracilis* (Rhyparochromidae), Mutompo.

Photo 6: *Carbula abacta* (Pentatomidae), Otjiamongombe.

Photo 7: Broad-headed Bug *Nemausus sordidus* (Alydidae), Sandveld.

Photo 8: *Dieuches herero* (Rhyparochromidae), Karios.

Photo 9: *Teracrius namaquensis* (Pachygronthidae), Waterberg Namibia.

Photo 10: Big-eyed Bug *Geocoris phaeopterus* (Geocoridae), Wlotzskasbaken.

(15 species, 41%) have an Afrotropical distribution.

The preliminary information regarding general species richness and endemism of Heteroptera in the arid biomes of south-western Africa is summarised in Table 2 and is based on the literature on southern African Heteroptera, on data obtained from our own collecting between 1992 and 2009 (Koch et al. 1995), and on the study of museum collections in South Africa, Namibia and Europe. The numbers of Heteroptera species in Namibia, and the Northern- and Western Cape are listed according to their families. The endemics are mentioned separately, and basic biological information for the families is given.

The known endemism of true bugs in Namibia is about 14% (*n* = 103) of the currently known species. By including data from southern Angola, the western parts of Botswana and the Northern Cape Province of South Africa, this percentage increases by only 2% to nearly 16%. 25% of all Heteroptera species found in Namibia are endemic to the south-western African region (this includes Namibia, southern Angola, the Western- and Northern Cape, and Botswana). This corresponds roughly to the results that Simmons et al. (1998) found for Namibian insects in general, i.e. that about 25% of all known insects are endemic to the biomes occurring in Namibia, Northern Angola and the Northern Cape Province of South Africa.

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Table 1: Percentages of the number of species of Tingidae (after Deckert & Göllner-Scheiding 2006) and Lygaeidae occurring in Namibia with respect to their overall distribution patterns

	Type of Distribution						
Taxon	Introduced	Cosmopolitan	Afrotropical, including southern Palearctic and Oriental region	Afrotropical	Southern African	South-western African	Namibian
Lygaeidae (*N* = 37)	–	3%	27%	41%	5%	19%	5%
Tingidae (*N* = 85)	1%	–	8%	45%	12%	20%	14%

Table 2: List of all higher taxa of Heteroptera showing currently known species numbers and endemics in Namibia and the Northern- and Western Cape Provinces of South Africa

Higher taxa of Heteroptera	Namibia	Northern and Western Cape Province	Notes
ENICOCEPHALOMORPHA			
Enicocephalidae (gnat bugs)	At present only one southern African species known	At least six species endemic in the Cape region	Predators of other insects and arthropods, nocturnal; group insufficiently known
DIPSOCOROMORPHA			
Ceratocombidae, Dipsocoridae, Hypsipterygidae, Schizopteridae	One unidentified species in Otjiamongombwe	No records	Probably predatory, insufficiently known; only one species in South Africa collected, more undescribed species existing; smaller than 3 mm, in particular moss or at wet places
GERROMORPHA (semiaquatic bugs)			
Gerridae (true water striders)	Two species	Four species in Western Cape, at least two in Northern Cape	Predatory; all species of large distribution in Africa, and not restricted to south-western Africa; living on surface of standing water
Hebridae (velvet water bugs)	One widely distributed African species in Northern Namibia (Poisson 1956)	At least four species in Western Cape (one endemic to Table Mountains)	Predatory on small arthropods; species living on floating vegetation and wet moss
Hydrometridae (water striders)	Two species	Two species in Western and Northern Cape	Predatory; associated with marginal vegetation near water; no endemic species in the region
Mesoveliidae (pondweed bugs)	One species, widely distributed in Africa		Predatory; associated with aquatic vegetation, near permanent water, e.g. in the Table Mountain National Park, Namib Naukluft, Richtersveld (Gariep river)
Paraphrynoveliidae	Not represented in Namibia	Two endemics in Western Cape and southern Lesotho	Predatory; scarcely collected endemic South African family with two species; after Andersen (1978) on wet rocks covered with water-soaked moss in wet debris
Veliidae (water crickets)	Two species (one subspecies in the Kaokoveld)	10 species, some of them endemic	Predatory; group insufficiently known in southern Africa; some more species expected
NEPOMORPHA (water bugs)			
Aphelocheiridae (river bugs)	No records		Predatory; Aphelocheiridae living submerged below the water surface in the benthos of lakes and permanent streams; in South Africa presently unknown
Belostomatidae (giant water bugs)	Three species in Northern Namibia	Two species in Western Cape, one with South African distribution	Predatory on small fish, tadpoles, molluscs and insects; in standing water or slow flowing part of streams
Corixidae (water boatman)	About 12 species with wider distribution in Africa, and four probably endemic species	At least 12 species in Western and Northern Cape, some endemic	Feeding habits varying; aquatic bugs, occupying wide range of habitats, often numerous and fast colonizers of new water bodies
Gelastocoridae (toad bugs)	Two widely distributed African species		Predatory; semi-aquatic on muddy or sandy shores
Helotrephidae (beetle backschwimmers)	No records	One species in South Africa incl. Cape Regions (Papácek & Zettel 2004)	Predatory; in rock pools, hot springs, water tanks, etc., in arid zones
Naucoridae (creeping water bugs)	Only one widely distributed species	A few species in Western Cape	Predatory; in standing and fast-flowing water
Nepidae (water scorpions)	Two species, not endemic and widely distributed in Africa		Predatory; in water bodies with aquatic plants
Notonectidae (back swimmers)	12 species, one species is endemic	More than 12 species in Western Cape, two species probably endemic to Western Cape	Predatory: in water bodies, pans, pools, dams
Ochteridae (velvet shore bugs)	At least one non-endemic species, widely distributed in Africa		Predatory; littoral, adjacent to shallow water
Pleidae (pygmy backschwimmers)	Two species, not endemic to the region.		Predatory mainly on small crustaceans; among aquatic vegetation.

Higher taxa of Heteroptera	Namibia	Northern and Western Cape Province	Notes
LEPTOPODOMORPHA			
Leptopodidae (spiny shore bugs)	One species	One widely distributed African species in Western Cape	Predatory, associated often with fast flowering rivers, also on dry rocks, far away from water
Saldidae (shore bugs)	Two species	Three species in Western Cape, including one endemic	Predatory: in the littoral zone, in marshes and often on the spray covered rocks of fast flowing streams
CIMICOMORPHA			
Anthocoridae (minute pirate bugs)	At least three species		Predatory; all species known to the region of wider distribution, group insufficiently known
Lyctocoridae	No records	Three species in Western Cape, one probably endemic in Northern Cape (Port Noloth)	Predatory; closely related to Anthocoridae
Cimicidae (bed bugs)	Five species, no one known to be endemic	At least one species	Bloodsucking ectoparasites of man, other mammals (e.g. bats) and birds; in southern Africa about 10 species
Microphysidae (minute bladder bugs)	Not recorded in the region but at least one undescribed species from Namaqualand (Schuh & Stys 1991)		Predatory
Miridae (plant bugs)	Less than 50 described species known, about 25% endemic.	Poorly known, more than 200 species known, several hundred species at least.	The majority phytophagous; hundreds of species undescribed, whereas a high percentage endemic; more than 1000 species estimated for the region
Nabidae (damsel bugs)	Four species	About five species in Western and Northern Cape, one species probably endemic to the Cape Region	Predatory
Pachynomidae	A few species from Africa described, no records in southern Africa		Predatory
Polyctenidae	No records; only one species known in the north-eastern part of South Africa		Bloodsucking ectoparasites on bats
Reduviidae (assassin bugs)	At least 129 species are present, about 38 are endemic.	In Western and Northern Cape currently at least 68 species known, probably 1/3 endemic to the region.	Predatory, some species specialists, several hundreds of species occuring in southern Africa, several endemics
Thaumastocoridae (eucalyptus bugs)	Not recorded	One species in South Africa including Western Cape	The species originated in Australia and introduced with Eucalyptus, its host plant.
Tingidae (lace bugs)	84 species, including 12 endemic species (Deckert & Göllner 2004)	More than 50 species are known from Western and Northern Cape, including endemic species	Phytophagous, often very host specific
PENTATOMOMORPHA			
Acanthosomatidae	One afrotropical species	Rare, five endemic species in the Western Cape Region	Phytophagous
Alydidae (broad headed bugs)	23 species in Namibia, no one endemic	At least eight species in Western Cape, three species in Northern Cape, no species endemic	Phytophagous, often associated with Fabaceae
Aradidae (bark bugs)	Four species, including on endemic species	In Western and Northern Cape only a few species known, in between endemic species	Fungus feeding species, uncommon and rarely collected
Artheneidae	One species on Brandberg (Deckert 2000)	No record for South Africa	The species migrated in recent times into North America and also into tropical Africa, associated with Typha, Salix and Phragmites (Péricart 1998)
Berytidae (thread bugs)	Two species, probably endemic	In the Cape Region at least one species	Phytophagous or partly predatory
Blissidae (chinch bugs)	10 species, including one endemic	In Western Cape more than 30 species, including endemic ones, from Northern Cape no records	Phytophagous, on monocotyledonous plants
Coreidae (twig wilter bugs)	48 species,10 are endemics	In Western and Northern Cape about 20 species known, several species endemic	Phytophagous
Cymidae	Two species	About four species, probably one endemic to western parts of South Africa and Namibia	Phytophagous

Higher taxa of Heteroptera	Namibia	Northern and Western Cape Province	Notes
PENTATOMOMORPHA [continued]			
Cydnidae (burrower bugs)	18 species presently known, three endemic	More than 20 species in Western and Northern Cape, seven or more endemic at least to arid south western parts of southern Africa	Phytophagous
Dinidoridae	In Namibia two species, no endemics	A few species found in the Cape Region, especially in Western Cape	Phytophagous
Geocoridae (big eyed-bugs)	11 species known, at least one species endemic	About five species in Western and Northern Cape	Predatory
Heterogastridae	Seven non-endemic species	One or two species in the Cape Region	Phytophagous, often associated with Ficus
Largidae	One widely distributed African species	Not known from South Africa	Phytophagous, afrotropical species, known especially from Central Africa.
Lygaeidae (seed bugs)	38 species, two species endemics	Five species endemic to arid south western parts of southern Africa	Phytophagous, seed feeders, Melanotelus and Haemobaphus endemic to southern Africa
Ninidae	No records for Namibia and the Cape Region, one species should occur in the North-Eastern parts of Namibia		Phytophagous
Oxycarenidae (cottonseed bugs)	Only four species known	At least 10 species in the Western and Northern Cape Region, one species endemic to Western Cape	Phytophagous, mainly on Malvaceae
Pachygronthidae	Three species	Four species in Western and Northern Cape	Phytophagous, no endemic species known from the region
Pentatomidae (shield bugs)	94 species known, eight restricted to arid south western parts of southern Africa, and four found in Namibia	In the whole Cape Region about 130 species known, and probably at least 30 endemic species in the Western and Northern Cape Province	The majority phytophagous, species of the subgroup Asopinae predatory
Piesmatidae (ash-grey leaf bugs)	At least one common species	Three species in the Western and Northern Cape, one species endemic to the succulent Karoo	Phytophagous
Plataspidae (pill bugs)	Only three species known, one probably endemic	In Western Cape two species, one endemic	Phytophagous
Pyrrhocoridae (cotton stainers)	12 species, endemic species not known	Only three species known from Western and Northern Cape	Phytophagous
Rhopalidae (scentless plant bugs)	17 species, a few endemic to south-western Africa	18 species in the Cape Provinces	Phytophagous
Rhyparochromidae	46 species, two endemic to Namibia, two endemic to western part of South Africa	In the Cape Provinces at least 34 species known, more than 20 endemic to the Western Cape Region	Several more species actually present, but still not identified
Scutelleridae (shield-backed bugs)	16 species, two species probably endemic to Namibia, and two restricted to southern Africa south of the Zambesi river	In South Africa about 18 species known, in the Cape Provinces region only about five, no one known to be endemic	Phytophagous
Stenocephalidae	Three species, one probably endemic	In the Cape Provinces five species found, two of them endemic to the Western Cape Region	Phytophagous on Euphorbiaceae
Termitaphidae	No species known from the region		Mycophagous, in termite nests
Tessaratomidae (inflated stink bugs)	Four species	In Western and Northern Cape one or two species	Phytophagous
Thaumastellidae	One species endemic for southern Namibia and Northern Cape	Two species in the Northern Cape Province, one endemic	Phytophagous, Thaumastellidae consisting of three species, the third species occurring in North Africa

Dragonfly diversity from the Cape to the Kavango

Frank Suhling*, Michael J. Samways, John P. Simaika, Otto Richter, Eugène Marais, Andreas Martens & Jens Kipping

Summary: Dragonflies are amongst the most well-studied and most recognised insects and there is an ongoing worldwide initiative in which the diversity and conservation status of all species are being assessed. In Africa, where about 900 species of Odonata occur, the southern part of the continent is currently the best surveyed for Odonata. In this chapter we analyse and depict biodiversity distribution patterns in the BIOTA transect area, from the Cape in the south to the Okavango River in the north, using Odonata databases for Botswana, Namibia and South Africa. We counted species numbers in each WWF Terrestrial Ecoregion and freshwater basin. Species numbers were highest in the Zambezian ecoregions followed by the Cape ecoregions, whereas the drier ecoregions had fewer species, except for a few outstanding localities. The proportions of range-restricted species were highest in the Cape and Zambezian ecoregions accounting for at least one third of the species, whereas all other ecoregions were almost exclusively populated by widespread species.

Introduction

There is evidence and it is widely recognised that human impacts are causing a severe loss of biodiversity globally (Brooks et al. 2001). However, most biodiversity remains undetected, since many ecosystems are largely unexplored, particularly in the tropics where biodiversity is supposed to be highest (Gaston 2000). Biodiversity hotspot analyses are based on only a few taxonomic groups (Myers et al. 2000), which have been more widely explored, such as mammals, birds, amphibians and vascular plants. For prioritising conservation areas, multitaxonomic rather than single-taxon approaches are critical for identifying areas likely to promote the persistence of most species (Kremen et al. 2008). Estimates suggest that biodiversity loss is most severe in freshwater ecosystems, particularly in Africa (Thieme et al. 2005). A recent attempt at surveying freshwater biodiversity on a larger taxonomic scale is the Pan-Africa Freshwater Biodiversity Assessment (Darwall et al. 2009). This has included the Odonata, which have proved to be of good value for conservation assessment (Simaika & Samways 2009a, b, see also Box 1).

Odonata are amongst the most well-studied groups of insects and freshwater organisms (Box 1) and it is therefore not surprising that Odonata are the first insect group for which global conservation status has been assessed (Clausnitzer et al. 2009). In southern Africa, research on Odonata has a long tradition. The first overview was compiled by Ris (1921), followed by Barnard (1937) who published a comprehensive survey of the dragonfly fauna of the Cape region. Later, it was Elliot Pinhey in particular, who contributed to the knowledge about the Odonata of the region (e.g. Pinhey 1951, 1984b, 1985). To date, about 300 species have been recorded in southern Africa (Suhling et al. 2009a), and checklists have been published for most countries, including Botswana (Pinhey 1976), Mozambique (Pinhey 1981), Namibia (Martens et al. 2003, Suhling & Martens 2007), South Africa (Samways 1999, 2008), Zambia and Zimbabwe (Pinhey 1984a). Field guides have also been

Box 1
Dragonfly biodiversity and conservation

Odonata have aquatic larvae (with a few exceptions) and terrestrial adults and are obligate predators. From a global perspective, Odonata are amongst the best-known insect groups with respect to taxonomy and distribution (Corbet 1999, Kalkman et al. 2008). Not many other insect groups receive so much attention from the general public and have so many organisations devoted to their study, for instance the Worldwide Dragonfly Association. This makes the Odonata a good agent for freshwater conservation, true “guardians of the watershed” (Clausnitzer & Jödicke 2004). At present 5,680 species of Odonata have been described, although the actual number of species may total 7,000. The rate of new descriptions is currently approximately 200 Odonata species per decade (Kalkman et al. 2008). The majority of species occur in the tropics, with the highest diversities in the Neotropical and Oriental regions, which harbour about 1,650 species each, while in the Afrotropics the diversity is lower with 890 species (Kalkman et al. 2008). According to IUCN criteria, only 10% of the globally assessed Odonata species are threatened, which is a relatively low figure compared with 31% for amphibians and 20% for mammals (Clausnitzer et al. 2009).

published (Tarboton & Tarboton 2002, 2005, Samways & Wilmot 2003, Suhling & Martens 2007, Samways 2008), which will surely improve the dragonfly survey in the region.

Brinck (1955) was the first to systematically analyse the patterns of dragonfly diversity of southern Africa from a biogeographical perspective. Based on generalised knowledge of dragonfly distribution patterns at the time, the author assumed that dragonfly species diversity is correlated with average annual precipitation. This led to the prediction that areas with higher rainfall would have higher dragonfly diversity than those with lower rainfall. This pattern was recently corroborated during the southern Africa freshwater assessment initiated by IUCN (Suhling et al. 2009a). More detailed analyses of diversity distribution in South Africa and Namibia have been presented by Simaika & Samways (2010) and Suhling et al. (2009b).

The aim of this contribution was to illustrate patterns of Odonata diversity for the region in which the BIOTA Southern Africa transects falls. The area stretched broadly from the Cape of Good Hope in South Africa, across Namibia to the Okavango River in Botswana, with branches into the Kalahari and Namib Deserts. For this we extracted the point locality distribution data from the Odonata species databases of Botswana, Namibia, and South Africa. The Namibia Odonata database was compiled as part of the BIOTA Southern Africa subproject S08. We analysed species numbers for WWF Terrestrial Ecoregions and freshwater basins, and summarised the conservation status of species according to IUCN criteria.

Databases and analysis

The analysis presented here is based on the Odonata records assembled by the authors from the databases of Botswana (J. Kipping), Namibia (F. Suhling) and South Africa (M. J. Samways & J. P. Simaika). Recently, all data from these three databases, in total ca 25,000 records, was transferred into the Africa Odonata database (administered by J. Kipping), which currently includes about 80,000 records. Thus, the three countries considered in

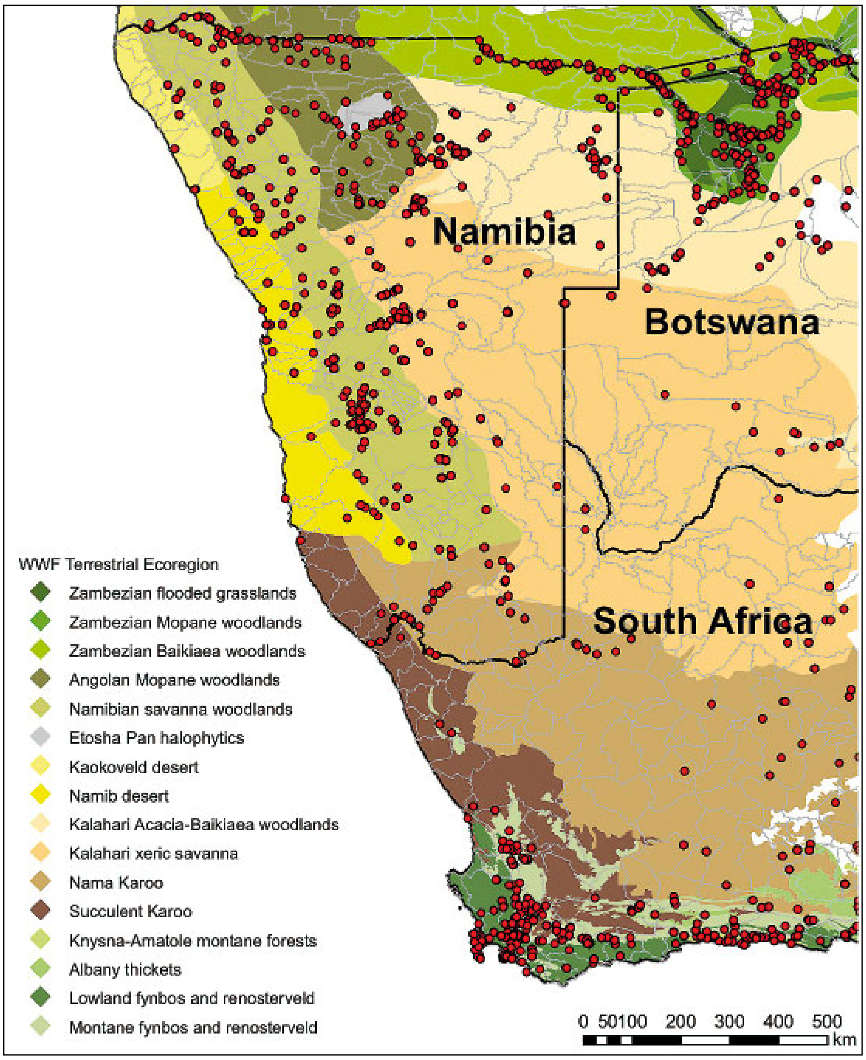


Fig. 1: Distribution of dragonfly records (red dots) in southwestern Africa overlaid on a map of the WWF Terrestrial Ecoregions. The thin grey lines indicate river basins.

Table 1: Overview of numbers of point locality records and numbers of species observed in the major WWF Terrestrial Ecoregions of southwestern Africa

WWF terrestrial ecoregion	Large ecoregion*	No. of species	No. of records
Albany thickets	Cape	31	109
Knysna-Amatole montane forests	Cape	26	149
Lowland fynbos and renosterveld	Cape	63	419
Montane fynbos and renosterveld	Cape	71	1,378
Nama Karoo	Karoo	53	333
Succulent Karoo	Karoo	33	94
Namib desert	Namib	23	167
Kaokoveld desert	Namib	11	31
Namibian savanna woodlands	Savanna	71	2,306
Etosha Pan halophytics	Savanna	21	85
Angolan Mopane woodlands	Savanna	48	275
Kalahari Acacia-Baikiaea woodlands	Kalahari	51	480
Kalahari xeric savanna	Kalahari	70	1,492
Zambezian Mopane woodlands	Zambezian	100	2,195
Zambezian Baikiaea woodlands	Zambezian	102	1,818
Zambezian flooded grasslands	Zambezian	112	3,383
Total		171	14,720

* for later analyses (see Figs. 3, 4) the ecoregions were combined to larger regions.

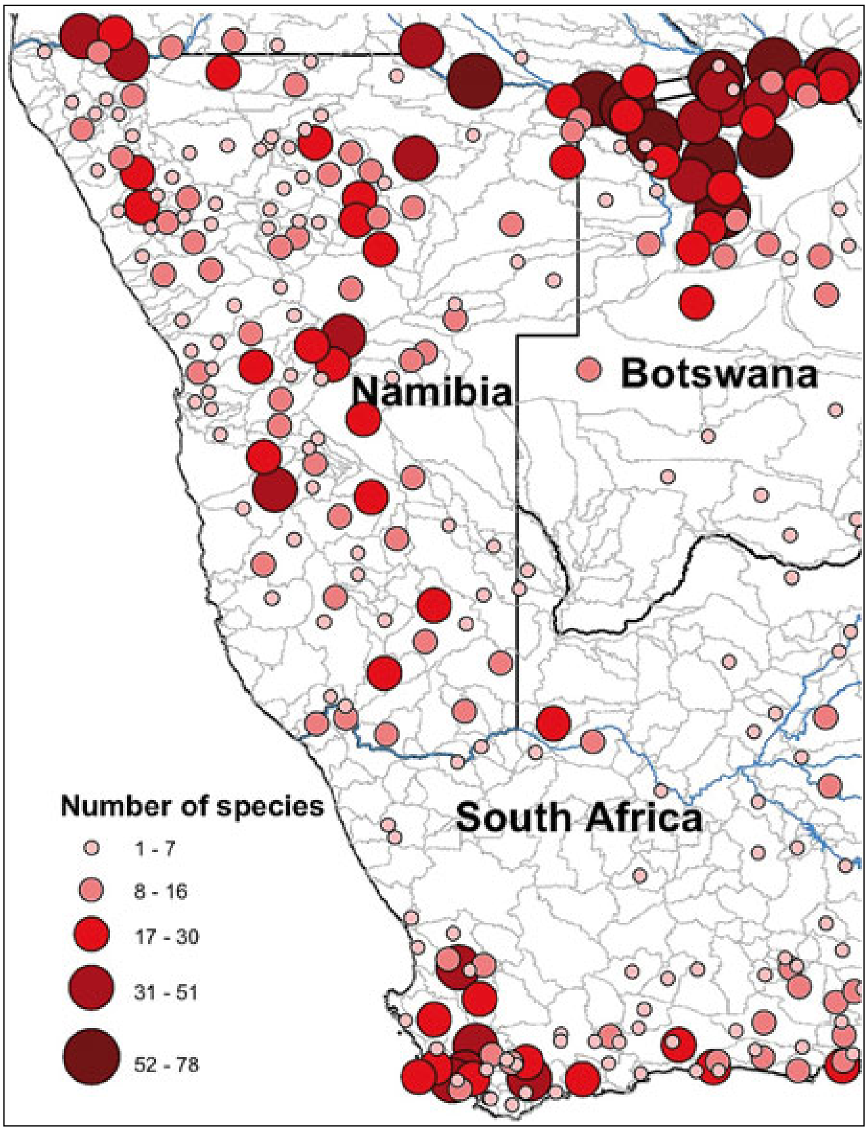


Fig. 2: Dragonfly species numbers per river basin. Basins intersected by ecoregions are represented by more than one dot. Basins with dots absent represent areas where the numbers of records were not sufficient for analysis.

this study have amongst the best records for the whole of Africa. All geographic analyses described below were carried out using ArcGIS 9.

For the purpose of this study we considered only the western part of southern Africa from the Cape of Good Hope in the south to the Okavango River in the north, and extending from the coastline in the west to 26° longitude (roughly a line from Kasane in Botswana to Port Elizabeth in South Africa) in the east (Fig. 1). We assigned all records to the 16 WWF Terrestrial Ecoregions (Olson et al. 2001) that were well represented in the region (Fig. 1). Records from marginal ecoregions were not considered (cf. white areas in Fig. 1). The numbers of records and the numbers of species per ecoregion were counted (Table 1) to identify broad scale patterns of species diversity. A more detailed spatial analysis of species diversity was carried out by counting species numbers in each river basin in the study area according to Darwall et al. (2009). However, certain river basins crossed more than one ecoregion (see Fig. 1). Therefore, in order to obtain polygons of subbasins that were only represented in one ecoregion, we intersected the shapes of the WWF Terrestrial Ecoregions with the river basins shapes (cf. Thieme et al. 2005). This procedure generated 1,077 polygons (subbasins), of which 282 had species records. Species numbers were then counted for those polygons, which had species records.

We also analysed the spatial diversity of range-restricted species in the region. In certain parts of the study area, namely the Cape and the Okavango Delta regions, the WWF ecoregions form comparatively small-scaled mosaics. Therefore, almost no species were identified that were restricted in occurrence to just one of the ecoregions. In order to analyse the diversity of range restricted species we therefore combined the ecoregions to form larger complexes (Table 1).

Spatial distribution of species diversity

A total of 171 species have until now been recorded in the study area (for species names cf. Electronic Appendix). The Zambezian ecoregions possessed the highest species diversities (Tab. 1), with 100 or more species records per ecoregion. In the drier parts of the study area and in the Cape, a maximum of 71 species per ecoregion occurred. The lowest species diversities were found in the Namib Desert and in the Etosha halophytic ecoregion.

On the subbasin scale, a maximum of 78 species was recorded. Highest species diversities occurred along the Okavango, Kwando and Zambezi Rivers (Fig. 2). However, relative high values of 3–51 species were also recorded in some subbasins along the Kunene River in the northwest and the Cape in the south. In addition, at two localised subbasins in Namibia, namely in the Otavi Mountains and the upper Swakop River catchment around a large impoundment, relatively high species numbers were also recorded.

Range restricted and widespread species

Range-restricted species were only recorded in the Zambezian and Cape ecoregions (Fig. 3). The only exception was the Gariep River endemic *Pseudagrion vaalense*, which was restricted to the Karoo in the region considered. All of the species restricted to the Cape were true endemics. By contrast, most of the

Zambezian range restricted species also occur outside the region, particularly in the Palaeo-Chambeshi-Katanga-Region, to which the Okavango and Kwando River swamps belong. The proportion of range-restricted species was 37% in the Cape and 33% in the Zambezian ecoregions.

Seven groups of species were categorised from their biogeographical backgrounds (Fig. 4). Besides the range restricted species mentioned above, we observed patterns of distribution, which suggest that several species entered the other ecoregions mainly from the Zambezian or the Cape ecoregions. Hence, these species had their centre of occurrence in either the Zambezian or the Cape ecoregions. Other species occurred in most ecoregions and these we considered to be widespread species (Fig. 4).

Which environmental variables govern the different patterns identified?

The diversity of dragonflies in the region is influenced by two major determinants. Firstly, two biogeographical realms converge in the region, which both contribute assemblages that differ in their radiation history. Although the Cape is not zoologically recognised as a realm on its own, relatively high numbers of endemic dragonflies occur (Grant & Samways 2007), i.e. 16.5% of the species in the region. This includes, for example, most species of the family Synlestidae, the genus *Syncordulia* among the Corduliidae, and others (Samways 2009). For instance, *Syncordulia* is likely to have diverged in the region 60 million years ago (Ware et al. 2009). Moreover, some other species, which are more widespread in the region, such as *Aeshna minuscula*, are likely to have originated from the Cape (Fig. 4; cf. Suhling et al. 2009). However, the majority of species are of Afrotropical origin of which a high number are restricted to the Zambezian ecoregions.

Secondly, the diversity of dragonflies, being dependent on freshwater habitats, corresponds broadly with humidity gradients, as suggested by Brinck (1955).

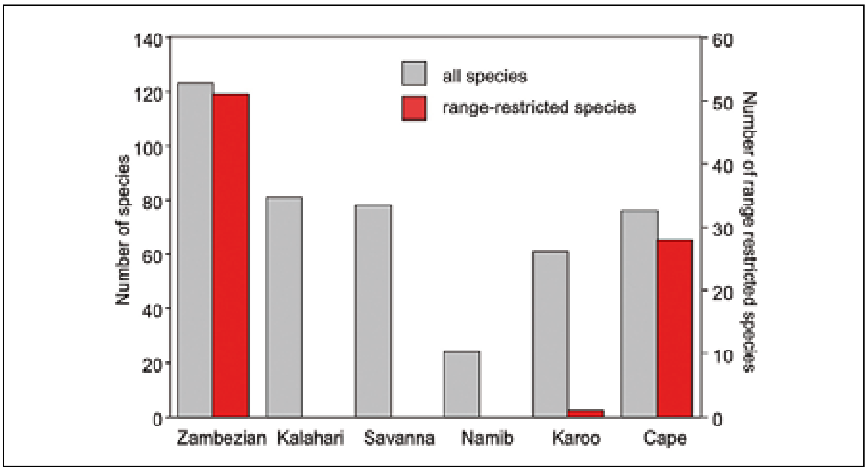


Fig. 3: Numbers of dragonfly species restricted to ecoregion complexes compared to total species numbers. Note that a high proportion of restricted species occur in the Zambezian and Cape complexes, whereas only one restricted species, the Gariep River endemic *Pseudagrion vaalense*, occurs in the other regions.

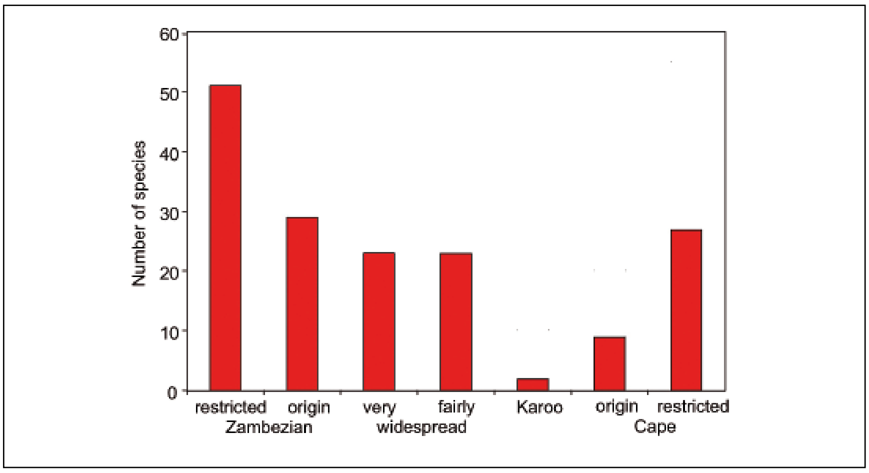
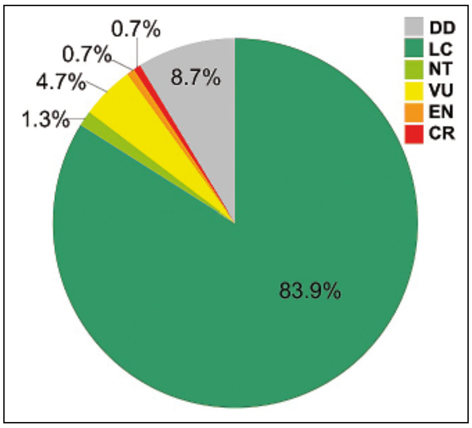


Fig. 4: Biogeographical classification of the dragonfly species occurring in the study area. The number of restricted species matches those in the ecoregion complexes depicted in Fig. 3. Those of Zambezian and Cape origin are mainly recorded in either of these regions but also occur in the drier ecoregions. Thus, their origin has been assumed from a distribution gradient. They broadly match species of category 4 and most of category 6 of Suhling et al. (2009). The widespread species occur in most or all ecoregions, and the fairly widespread species at least in each of the larger ecoregion complexes, although they are less common (categories 1–3 and 5). The two species classed under 'Karoo' are one range restricted species and *Pseudagrion salisburyense*, of which most records are from the Karoo ecoregions.

Fig. 5: The proportions of dragonfly species in each Red List category (CR = Critically Endangered, EN = Endangered, VU = Vulnerable, NT = Near Threatened, LC = Least Concern, DD = Data Deficient) in the study area according to the regional southern African IUCN Red List (cf. Suhling et al. 2009).



Highest diversities occur in the humid northeast of the region, particularly along the large perennial rivers, such as the Okavango, Kwando and Zambezi. Other centres of diversity are in the Cape winter rainfall area and along the Kunene River. The lower species diversity in the arid regions can broadly be explained by the increasing sparseness of freshwater habitats with increasing aridity. However, species numbers in the arid regions are still surprisingly high. Suhling et al. (2009b) tried to explain why so many species occur in the Namibian deserts. They identified six categories of species occurring in the arid landscape:

1. widespread desert-biased Namibian species regularly breeding in the desert;
2. widespread non-desert-biased Namibian species regularly breeding in the desert;
3. widespread species that have been observed entering the desert seasonally;
4. species, which immigrate from neighbouring regions and sometimes breed in the desert locally;
5. species with highly localised breeding populations in the desert (usually at streams), which are widely isolated from potential source populations;
6. species restricted to one of the allochthonous perennial rivers, with no breeding populations away from the river.

Many species of dragonfly are highly mobile and distances of several hundred kilometers can be covered within a few days (cf. Corbet 1999). This applies, in particular, to species belonging to categories 1–4 and especially to members of the family Libellulidae, which make up almost 60% of the species in the desert (Suhling et al. 2009b). These mobile species are able to enter the desert from different neighbouring regions rapidly, and may reproduce if the conditions allow. Such immigration occurs annually during seasonal long-distance mass-migration events at the beginning of the rainy season as with *Pantala flavescens* and some other dragonflies known as obligate migrants (cf. Anderson 2009, see also Article III.2.7). Other species may expand their ranges into the desert during wetter years and contract their ranges again in dry years. In addition, species that have relict populations dating back to wetter periods (category 5) contribute to the diversity. These species have developed mechanisms to avoid intraguild predation by the immigrants (see Article III.2.7). Finally, a few species may have evolved under arid conditions. The late Miocene ancestors of the genus *Trithemis* may have bred in temporary pools (Damm et al. 2010) and *Trithemis kirbyi*, a typical dragonfly of the Namib Desert, may have evolved with ongoing aridification of the continent.

Besides the two major Odonata diversity 'hot spots' in the region (Zambesian and Cape regions), a few local 'hot spots', where relatively high species diversity was recorded in one subbasin, can be identified in the arid ecoregions (Fig. 2). Two of these local 'hot spots' are along the Kunene River, which hosts several species restricted to large perennial rivers, and which therefore enter the otherwise highly arid landscape along the river line. Three more similar local 'hot spots' are scattered over Namibia. One in the northeast is in the Otavi Mountains, which receives the highest rainfall in Namibia, and thus conforms with the general humidity-species richness gradient. Another is in central Namibia at the S. von Bach dam, a large impoundment supplying Windhoek with water, where 46 species of dragonfly have been recorded. Leaks in the dam have formed a swampy wetland colonised by several species, including some otherwise confined to swamps along large tropical rivers, such as *Acisoma panorpoides* and *Hemistigma albipunctum* (cf. Suhling et al. 2009b). The habitat is obviously suitable and still within reach for those species likely dispersing there from the Okavango River. The last 'hot spot' is in the Naukluft Mountains, where at least 32 species occur close to the Namib Desert. Here several small perennial streams originate, which host a set of stream species. In addition, not only has this area been colonised by species from the Cape such as *Aeshna minuscula* and *Trithemis stictica*, possibly during wetter periods, but also by widespread desert species and by those originating from the Zambezian ecoregions.

The conservation status of southwest African dragonflies

The conservation status of Odonata in the region is relatively good with only 6.1% of all species listed as either critically endangered, endangered, or vulnerable on the IUCN regional southern Africa Red List (Fig. 5), in comparison to approximately 10% of dragonflies globally (Clausnitzer et al. 2009). However, all of the threatened species are Cape endemics (cf. Samways 2004, 2006, Suhling et al. 2004) and, compared to the species numbers in the Cape ecoregions, the proportion of threatened species in this subregion is comparatively high (14.1%). The major threats to dragonfly diversity in southern Africa are deforestation, habitat destruction due to water extraction and damming of large rivers, and invasion of alien plants and fish, while pollution is currently only a local problem (Suhling et al. 2009a). In particular, invasive alien plants are a major cause of the red listed Cape endemics, which have been negatively affected as a result of shading of their stream habitats (Samways & Taylor 2004). In the more tropical parts of the region, however, deforestation causes habitat loss of forest-adapted species. For instance, along the Okavango River in Namibia, felling of riverine forests has likely caused local extinctions of species that spend most of their adult life in the shade, such as *Phaon iridipennis*. Habitat destruction due to water extraction is an important factor in the arid ecoregions where certain species are regionally threatened and locally extinct in Namibia (Suhling et al. 2006).

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The relevance of perennial springs for regional biodiversity and conservation

Andreas Martens*, Otto Richter & Frank Suhling

Summary: Natural perennial surface water in the interior parts of Namibia only occurs at widely separated springs around mountains. These waters host a very diverse and unique Odonata assemblage, which is threatened due to the habitat restriction of several species, as well as by recent habitat loss and degradation. Species occurring permanently at these waters, including *Crocothemis sanguinolenta, Orthetrum julia*, and *Trithemis stictica* differ significantly in seasonality, dispersal and life cycle characteristics from species colonising temporary waters. Their larvae grow slowly and they are present in these habitats as larvae throughout the year. This presence is the key factor why invaders with rapid development, which are dominant elsewhere, do not outcompete these species in these unique habitats. There is significant potential for stream dragonfly species to act as indicators for threatened freshwater wetlands in arid Namibia and they may also serve as an indication of the sustainable use of water resources, including the evaluation of measures to rehabilitate environments.

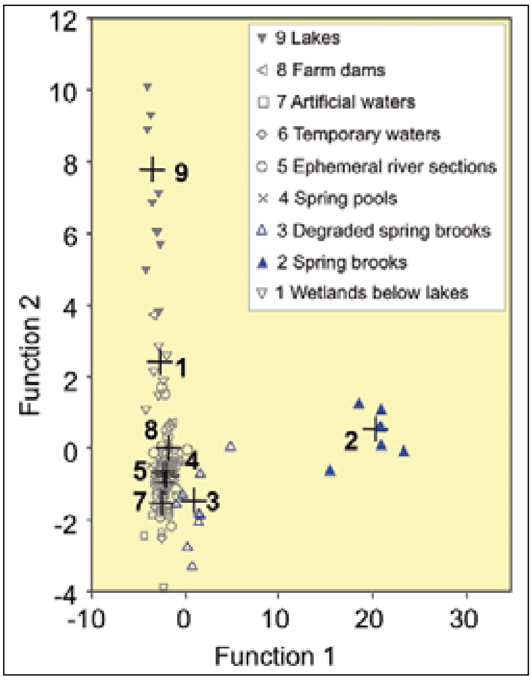
Introduction: permanent springs in Namibia

Namibia is the most arid country in the Afrotropical region south of the Equator. Perennial rivers occur only along the northern and southern borders of the country. Water is therefore one of the most relevant, and limited, resources in Namibia (Heyns et al. 1998, Christelis & Struckmeyer 2001). Natural permanent surface water in the interior parts of Namibia only occurs at widely separated springs around mountains and at certain places along ephemeral river courses.

Development and changes in human lifestyle during the last century have affected the way in which water has been managed (Stern & Lau 1990, Seely 1998). Large impoundments have been built to ensure a reliable water supply, which has altered flood regimes and destroyed perennial wetlands in ephemeral rivers. Large-scale extraction of groundwater has caused a fall in water tables, a loss of spring habitats (Jacobson et al. 1995, Seely 1998), and changes in vegetation structure, especially the loss of large trees, which tap the aquifers. Some large-scale water transfer schemes have also been established, channelling or piping water over long distances to major urban and industrial centres to meet the increasing demand for water.

An analysis of the odonate assemblages in the western ephemeral river catchments of Namibia shows that permanent springbrooks have a unique odonate assemblage (Fig. 1; Suhling et al. 2006). These habitats are marked by the presence of *Crocothemis sanguinolenta*, *Orthetrum julia*, *Trithemis stictica* (for their distribution in Namibia see Fig. 2), *Pseudagrion kersteni*, *Aeshna minuscula,* and *Anax speratus.* These are all perennial stream dwellers being naturally rare in Namibia (Suhling & Martens 2007). Many of these species are declining due to degradation of their natural habitats. For instance, despite intensive surveying, *C. sanguinolenta* has not been recovered at sites in the Otavi Mountains and at the Waterberg where it previously occurred. The likely reason is that many springs are either overutilised or piped. However, even at the remaining running springs this species and others are extinct. In this study we aim to discuss the mechanisms behind this decline in biodiversity in Odonates.

Fig. 1: In the western ephemeral river catchments of Namibia permanent springbrooks have a unique odonate assemblage (group 2). Sorted according to the first two Canonical Discriminance Functions, which together explained 78.4 and 8.9% of the variance, these localities (blue triangles) are well separated from all other freshwater habitats. The symbols depict nine different habitat types and the group centroids (indicated by the crosses) (redrawn after Suhling et al. 2006). Note that anthropogenically disturbed springs (group 3) in most cases do not differ in their assemblages from all kinds of temporary and artificial waters.



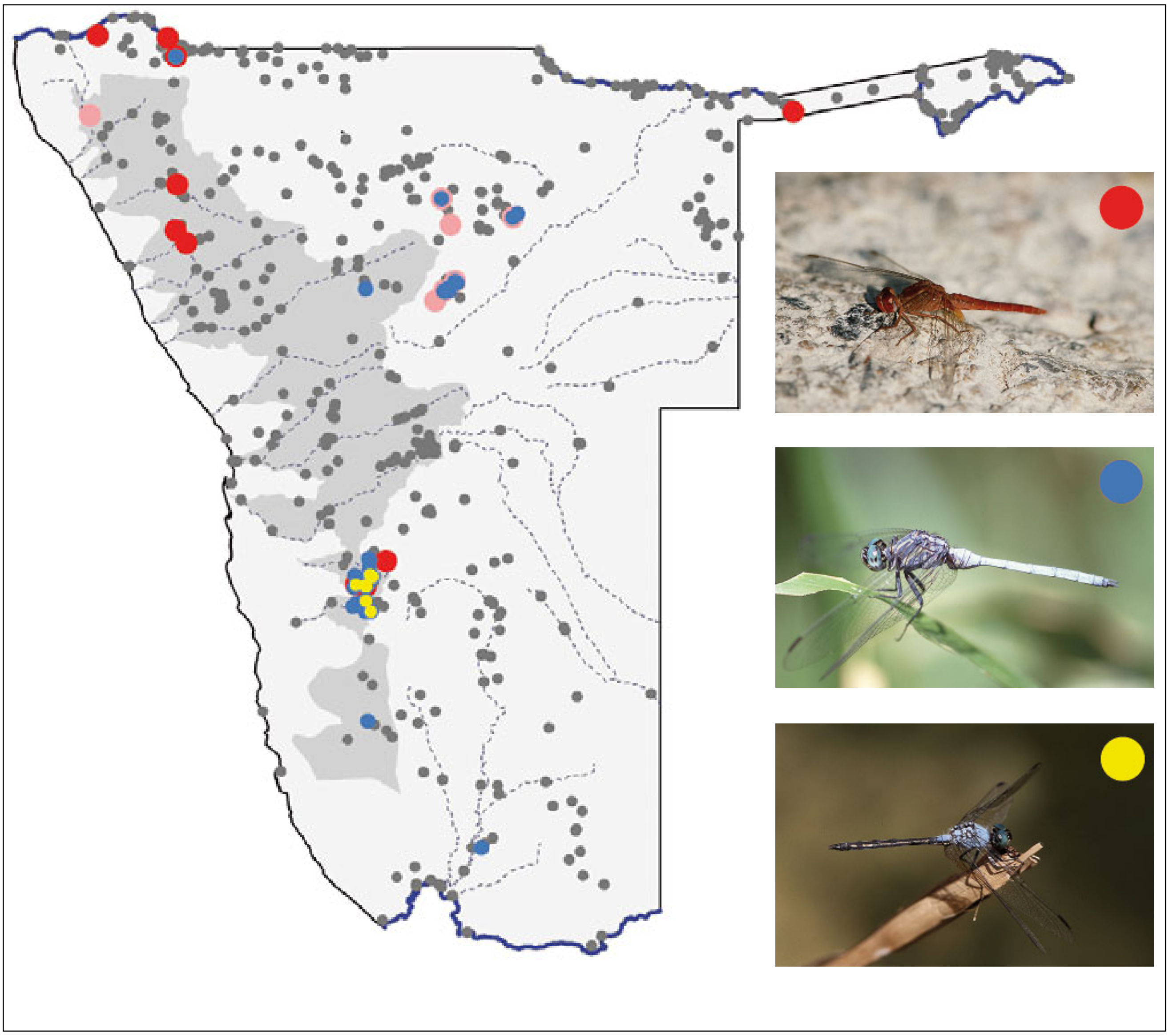


Fig. 2: Distribution of *Crocothemis sanguinolenta* (red dots), *Orthetrum julia* (blue dots) and *Trithemis stictica* (yellow dots) in Namibia. The light red dots indicate records of *C. sanguinolenta* before 2000 that could not be recovered despite intensive surveying, and these populations are likely to be locally extinct. The grey dots depict all dragonfly records in Namibia.

Larval growth and intraguild predation

The composition of dragonfly and other freshwater communities is governed by a set of biotic and abiotic factors (see review of Johnson 1991). A well known example is illustrated by North American species of the genus *Lestes*, which occur along a gradient from short duration temporal to perennial waters (Stoks & McPeek 2003). Species occurring at the one end of the gradient, i.e. in vernal ponds, are constrained by the brief period of availability of their habitat. They need life history traits allowing them to successfully reproduce in such habitats, particularly short development times. At the other end of the gradient, in perennial lakes, species have to deal with fish as top predators and, thus, need traits to survive predation, particularly inconspicuous behaviour (Stoks & McPeek 2003). Species living in intermediate habitats, i.e. longer lasting temporary waters and fish-free perennial waters have mainly to deal with predation by larger invertebrate predators as well as with intraguild predation (Johansson 1993, Wissinger 1992, Wissinger & McGrady 1993, Stoks & McPeek 2003). The result of intraguild predation—as well as of cannibalism—in dragonflies depends particularly on size differences between larvae (e.g. Anholt 1990, Wissinger 1992, Wissinger & McGrady 1993), with larger larvae eating the smaller ones. Success in such interactions can be achieved if the larvae of one species grow faster than those of another (Suhling & Lepkojus 2001). Another successful tactic is for a species to enter the habitat earlier than another so that the larvae have time to develop before the second species arrives (so-called priority effect; Fincke 1999).

We found that both these factors play a role in odonate communities of Namibia (Padeffke & Suhling 2003). Larvae of *Sympetrum fonscolombii,* a species belonging to the category of seasonal invaders (see below) grow faster than those

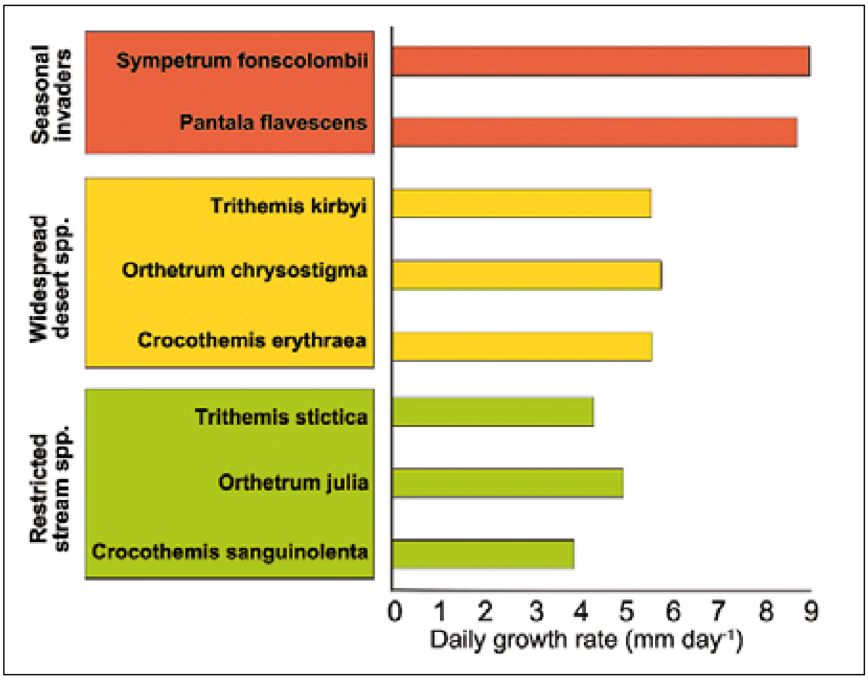


Fig. 3: Growth rates (mm head width/day) of different species of the family Libellulidae, which occur in Namibian deserts. The eight species belong to different ecological groups according to Suhling et al. (2009a, b). Seasonal invaders usually enter the desert with the onset of the rainy season and are absent during the rest of the year. Widespread desert dwellers are found in the desert habitats for most of the year. Restricted stream species occur locally at a few perennial springs. Data modified from Johansson & Suhling (2004), Suhling et al. (2004b), and Suhling et al. (2005).

of *Trithemis kirbyi,* a widespread desert dweller (Fig. 3). Thus, when both species colonise a pond at the same time, *T. kirbyi* (and other similar species) suffer high predation from species like *S. fonscolombii*, which in turn benefit from the interaction by obtaining an elevated food supply (i.e. the larvae of the other species). *T. kirbyi* is only able to reproduce successfully if it colonises ponds earlier. A simulation model of these interactions indicated that a second coloniser of similar growth rate may be completely eradicated if it is delayed by more than four days behind the first coloniser, if the second coloniser has a faster growth rate the than the initial coloniser then this delay period may be longer it may catch up even more days (O. Richter, unpublished). In the experiment conducted by Padeffke & Suhling (2003) *T. kirbyi* was 11 days earlier and win the interaction over *S. fonscolombii*. Although both species had comparatively fast development rates allowing both to develop successfully in temporary waters, the difference in development rate mattered.

The growth rate of a species depends on the habitat in which it predominantly occurs. Species that are able to develop in rain-pools that have a short existence require much faster growth rates than those species living in longer lasting temporary waters (Johansson & Suhling 2004). In arid Namibia such pools are typical of ephemeral rivers. Species inhabiting temporary waters, in turn, have faster growth rates than most species that are restricted to perennial springbrooks (Suhling et al. 2005). The differences in growth rates between species inhabiting these different types of water bodies are depicted in Fig. 3. Beside these differences, the larvae of seasonal invaders also forage more actively than other species (Johansson & Suhling 2004), providing them with the added advantage of gaining more food resources.

Permanent breeding helps to defend against fast growing competitors

During dragonfly surveys of Namibian freshwaters (see Article III.2.6) we were able to monitor the phenology of several species. We observed that species occurring at springbook habitats were present as adults throughout the year. In contrast, other Namibian desert odonates had at least short gaps in their flight season or were even highly seasonal (Fig. 4). A permanent adult flight season is reflected in the continuous presence of aquatic stages. We observed this in particular during sampling at Ongongo Falls near Sesfontein. On each sampling occasion many different larval size classes, including final stadium larvae, of *Crocothemis sanguinolenta* were present. The permanent presence of such large larvae guarantees that at least some offspring survive even if seasonal invaders, which have rapidly growing larvae (see above), colonise. The presence of large stream species larvae may even control the abundance of invaders. If so, permanent breeding is the key factor that allows survival of localised stream species in perennial habitats, and therefore governs the community structure in these habitats.

A single disturbance may result in permanent community loss

As discussed above, stream species are able to coexist with invaders and widespread species as long as the continuity of the habitat for larvae is maintained. Even when parts of a stream dry up, stream species populations can recover quite rapidly as long as some water still remains. We observed this first-hand at the Naukluft River where the populations of several species were continuously shrinking since our first visit in January 2001. During the rainy season of 2005/06 the stream expanded due to exceptional rainfall and the populations recovered within the same season.

However, what happens when the disturbance is more severe, as is the case when a stream completely dries up for a longer period of time due to severe drought or human activities? The larvae of stream species are not likely to survive if a stream is dry for more than a few days (cf. Suhling et al. 2003) and surviving adults may be forced to abandon such streams in search of more favourable habitats. Thus, after drought when streams start flowing again, recolonisation is necessary, like in typical temporary habitats. In such cases, all species start the recolonisation at the same time. The widespread species and particularly the invaders are much better adapted to such conditions. Due to their rapid growth rates they are able to prey on the slower growing larvae of the stream species and thus tend to eradicate these species.

During our surveys we observed several flowing streams fed by large springs, where no stream species occurred. Since these habitats looked perfectly suitable for the stream species we wondered why they were not present. It appears that the explanation lies in the history of these habitats. For instance, in the area of Grootfontein many springs have been completely piped, so that the stream habitats have been lost. At one spring, the outflow was altered several decades ago, resulting in a severe disturbance. Since then it has begun flowing again, but has lost most of its stream fauna. The only remaining species is *Orthetrum julia*, which has a relatively fast growth rate and is the only species that colonises completely shaded habitats.

Beside over-extraction of water, other factors might have the same effect. For example, there is anecdotal evidence from a spring in the Kuiseb valley. This spring appears to provide optimal habitat for spring dwelling species but, in this case, all characteristic species were missing. A plausible explanation materialised during an interview with the farmer who recounted that about 100 years ago the founder of the farm stayed at the spring over a summer with a large herd of cattle while he was on honeymoon. It is possible that the animals may have severely damaged the stream site during this time, and there is no evidence of a recolonisation by spring dragonflies since then.

In the past, perennial spring brook breeders may have been more widespread than today (Martens et al. 2003), but many springs and streams (e.g. at the Waterberg in the Otavi Mountains) have been destroyed by extraction of groundwater for irrigation (e.g. Barnard 1998, Suhling et al. 2004a). No historical data are available for the once large springs of Windhoek and Grootfontein, around which these towns were founded, but an estimation of the former size and permanence of these habitats suggests that they were prime locations for springbrook breeders too.

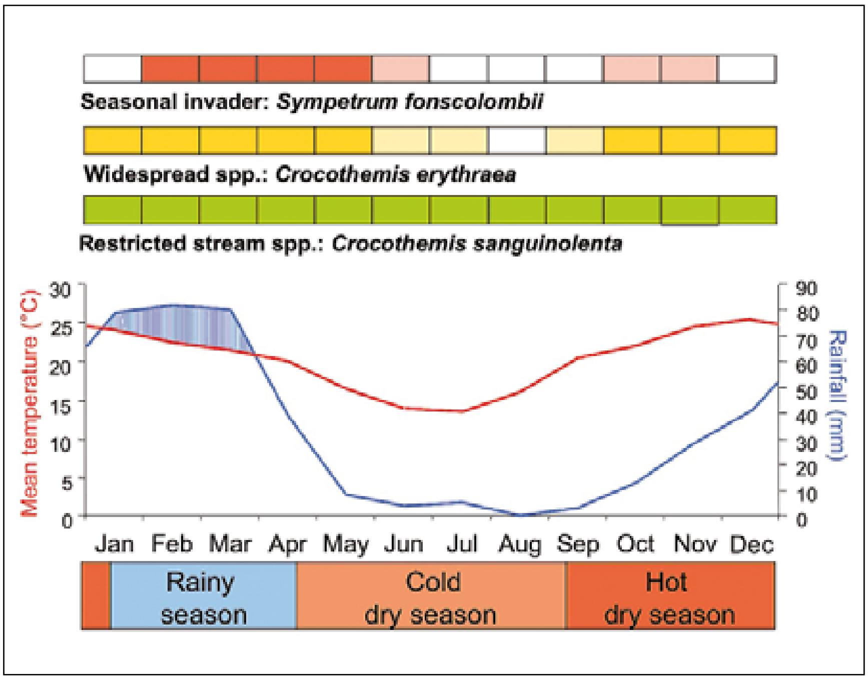


Fig. 4: Adult phenology of the three categories of odonate species occurring at spring habitats in Namibian deserts. Dark colours represent months when a species was common and shaded colours months with only a few records. *Sympetrum fonscolombii* is an invader reaching the desert mainly during the rainy season. *Crocothemis erythraea* belongs to a group of widespread desert species being more or less present during all seasons. *Crocothemis sanguinolenta* is a specialist of permanent spring habitats.

Consequences

Considering the above, several springbrook species of dragonfly are extremely sensitive to habitat alteration. In Namibia this includes *Crocothemis sanguinolenta*, *Orthetrum julia*, *Trithemis stictica*, *Pseudagrion kersteni*, *Aeshna minuscula,* and *Anax speratus.* Sites still colonised by these species, for instance in the Naukluft and Baynes Mountains, are high priority conservation areas for the protection of dragonfly habitats. These springs are unique in that human impacts over the last hundred years have not affected them drastically. Besides dragonflies, these springs host several other rare and endemic species (Curtis et al. 1998). We suggest that the above mentioned dragonfly species, which are easy to observe and identify, should be used as bioindicators of undisturbed, and therefore highly valuable, perennial spring habitats in Namibia.

Acknowledgements
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Part III

III.3 Patterns and dynamics along the BIOTA transects

Surface climate and its simulated change along the BIOTA transects

Andreas Haensler*, Stefan Hagemann & Daniela Jacob

Summary: The southern African region is known to be a biodiversity hotspot but future climate change is likely to have a major influence on this biodiversity. To estimate the impacts of climate change on the biosphere, high resolution climate information is needed for both current and future conditions. This data was generated by applying the regional climate model (RCM) REMO over the southern African region. The model is integrated for a transient climate change simulation over the time period 1960 to 2100 at 18 km horizontal resolution. This study presents the projected climate change signal of this high resolution RCM along the BIOTA transects, focusing on changes in temperature and rainfall.

Introduction

Meteorological and climatological conditions, together with geological and morphological features, define the distribution of natural habitats. It is therefore expected that future climate change will have an impact on the biodiversity patterns in a region (Midgley et al. 2003). In the fourth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC), a severe warming and drying was projected for the southern African region. However, this projection was based solely on coarse scale general circulation models (GCMs). For impact studies on a regional to local scale, as required for biodiversity assessments, it is essential to have projections of the future climate at a higher horizontal resolution. To quantify the magnitude of future climate change along the BIOTA North-South transect, the Max Planck Institute for Meteorology (MPI-M) applied its regional climate model (RCM) REMO (Jacob 2001) over the southern African region. A transient climate change simulation was performed with REMO for the time period 1960 to 2100 at a horizontal resolution of about 18 km. This simulation is thus far the first long-term climate projection for southern Africa conducted at such a high horizontal resolution.

Previous studies (e.g. Haensler et al., submitted, Hagemann et al. 2009) have pointed out that the better description of surface patterns and surface processes by RCMs leads to added value in the representation of the climate characteristics compared to global climate models. The resulting advantage of high-resolution RCM simulations as climate input for impact studies on a regional scale has been recognised (e.g. Fowler et al. 2007). However, although long-term RCM projections exist for many regions of the globe, they are rather sparse for the southern African region. The available high-resolution climate projections for the region consist of statistically downscaled time slices of GCM climate projections (e.g. MacKellar et al. 2007, Hewitson & Crane 2006, Zhao et al. 2005). RCMs have also been applied in time slice experiments over the southern African region, ranging from 10-year simulations of current and future climates (Tadross et al. 2005) up to a 30-year simulation in the case of Hudson & Jones (2002). Engelbrecht et al. (2009) used a variable resolution GCM at a horizontal resolution of about 50 x 50 km for a 30-year time slice experiment to project future climate change.

An RCM has to be forced on its boundaries with large scale meteorological input fields because it only covers a limited area of the globe. In the present study we applied the double nesting setup to achieve the high-resolution 18 km climate change projection (the coordinates of the simulation domain are: 15,75 S to 36 S and 5 E to 35.25 E). The transient boundary forcing for the 18 km simulation was generated by dynamical downscaling of a global simulation of the general circulation model ECHAM5/MPIOM (Roeckner et al. 2003, Jungclaus et al. 2006) with REMO to a horizontal resolution of 50 km (domain boundaries: 15 N to 40 S and 20 W to 52.5 E) The global simulation assumed a greenhouse gas (GHG) emission path following the SRES-A1B (representing an intermediate increase in GHG-emissions) scenario as described by Nakicenovic et al. (2000). Details of the simulation setup are beyond the scope of this chapter and can be found in Haensler et al. (submitted).

Comparison to observations and added value

In order to quantify the skill of a model in representing the climatological near surface characteristics of a region it has to be validated against observations. A short description of the region's climate characteristics can be found in Article III.1.1. Fig. 1 depicts a comparison between observation data and REMO results along the BIOTA North-South transect for the time period 1961 to 1990. REMO is a climate model and is not supposed to identify each single rainfall event at an observed position. Therefore, the data has to be integrated over a larger area and over several years. In the case of the BIOTA transect, the displayed values represent a zonal mean of 3 degrees (see inlet Fig. 1d). General-

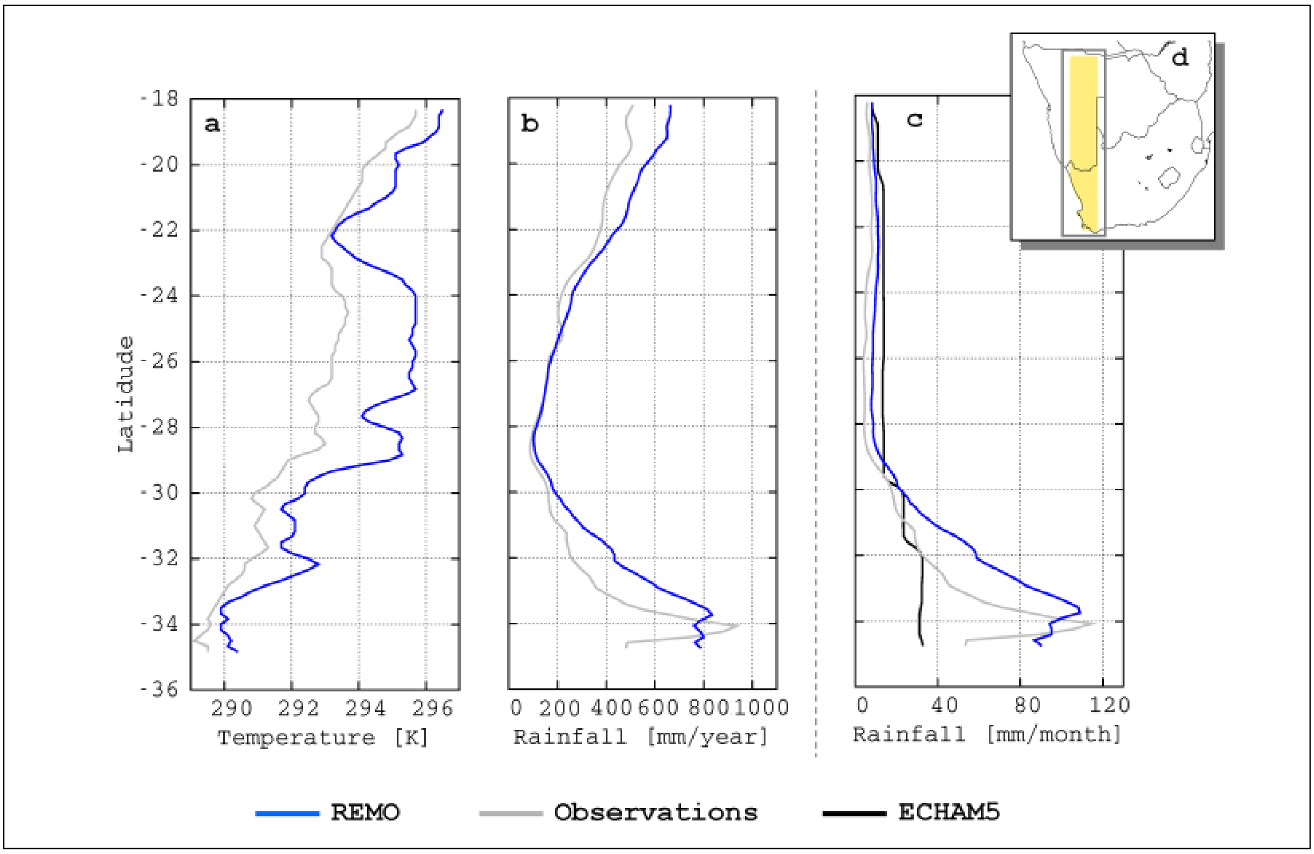

Fig. 1: Simulated and observed mean annual temperature (a), annual rainfall (b) and mean seasonal winter rainfall (c) for the control period (1961–1990) as zonal mean over the BIOTA South transect region (d). The temperature observations are taken from the CRU dataset (New et al. 2002) and the precipitation observations are taken from the GPCC dataset (Schneider et al. 2008).

ly REMO reproduces the mean temperature and rainfall characteristics along the transect very well. However, the model simulates slightly warmer mean annual temperatures than observed, especially in the dry central region, where a warm bias of about 2 K is persistent (Fig. 1a). Rainfall distribution along the transect, with a very dry central region and more humid parts towards the north and south, is adequately captured by REMO (Fig. 1b).

When comparing the simulated rainfall of REMO to that of the horizontally coarse resolved global model ECHAM5/MPIOM, a better representation of the amount of rainfall generated in the winter period (April to October) for the southern regions is obvious for the RCM (Fig. 1c). As already mentioned, this improvement can mainly be attributed to the better representation of the orography and surface characteristics by the RCM, which has a high spatial resolution. The correct representation of absolute rainfall amounts is especially important when climate model data are used as input in impact models (e.g. ecosystem models; hydrology models) as it directly influences the results of these studies.

Future changes along the BIOTA transect

In the future, temperature along the North-South transect of BIOTA is projected to rise gradually until the end of the 21st century (Fig. 2a). Absolute warming is projected to be strongest in the North, were REMO simulates an increase of more than 6 K over the 140 years. In the southern part, where the influence of the South Atlantic Ocean is stronger, the projected warming is more moderate, with a 2 K increase over the simulation period. Annual rainfall is projected to decrease along the whole transect, with a rather uniform relative decrease compared to the 1961 to 1990 base period of about 10 to 20% towards the middle of the 21st century and of about 40 to 50% at the end (Fig. 2b & c). This drying seems to affect all seasons, as the seasonal rainfall distribution is projected to stay fairly constant in the future (Fig. 2d). Furthermore, modelled future water storage in the soil layer is shown in Fig. 2e. Even though the absolute numbers of the simulated soil moisture might not reflect reality, they do relate important information as it is an integrative variable, combining changes in temperature, rainfall and evaporation. A substantial decrease in soil water content is projected by the model along the transect, showing a greater decrease in the north, where temperature rise is greatest. As available soil moisture impacts on the latent heat flux and therefore directly influences the energy balance, the indicated strong warming in regions with a strong soil moisture decrease seems to be a rather robust feature of the projections. The strongest warming consequently occurs in regions with the greatest soil moisture decrease.

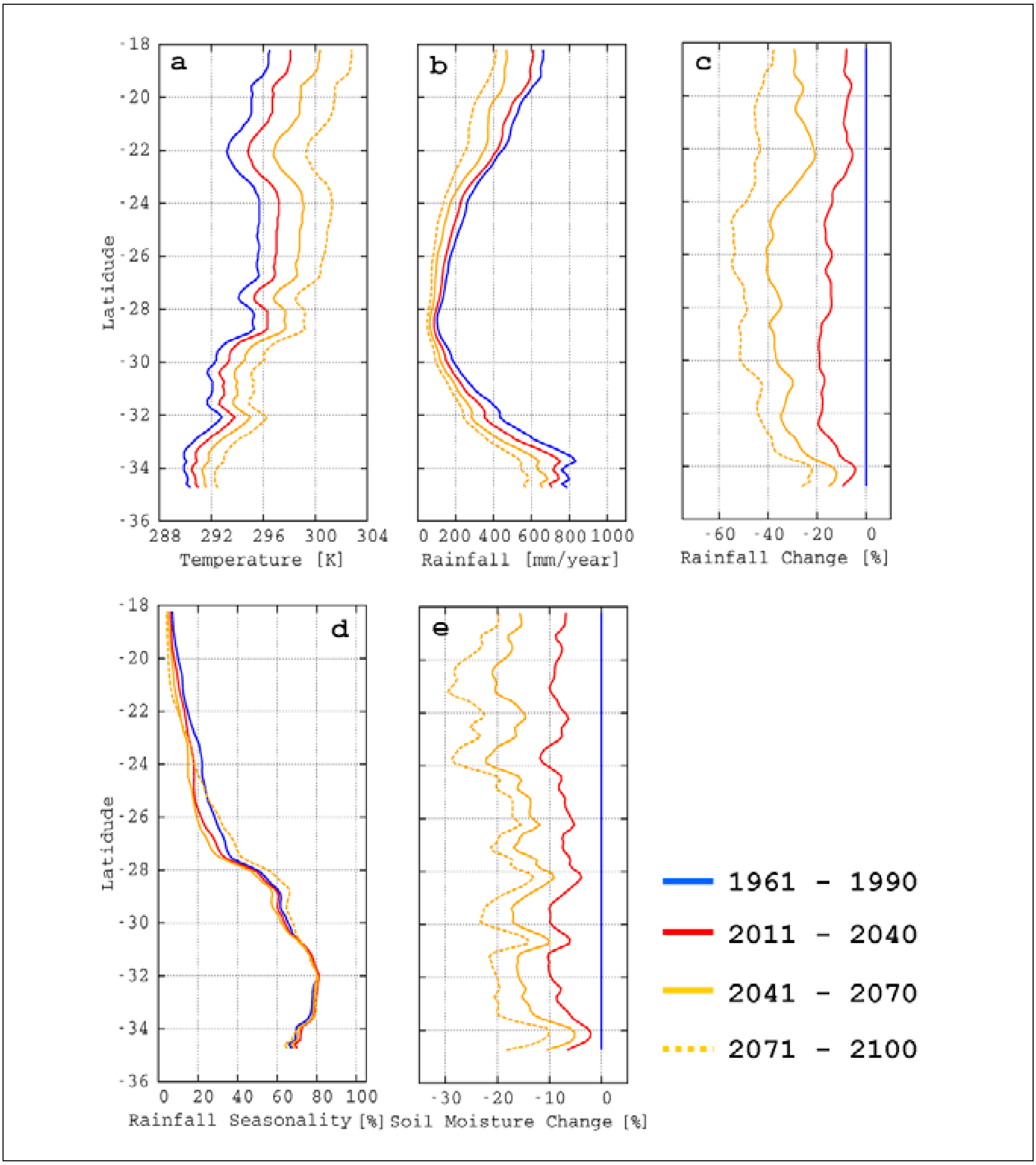

Fig. 2: Projected mean annual temperature (a), annual rainfall (b), relative change in annual rainfall (c), rainfall seasonality indicating the percentage of rainfall falling during the period from April to September (d) and relative soil moisture change (e) for the control period (1961–1990) as well as for three future periods (2011–2040, 2041–2070 and 2071–2100) as a zonal mean over the BIOTA transect region.

Future changes at selected stations

Fig. 3 depicts the temporal evolution of the annual rainfall, the maximum number of consecutive days without rainfall and the rainfall variation coefficient (defined as the ratio of the annual standard deviation of daily rainfall and the annual mean rainfall) for three stations along the transect. The displayed data at each station represents the absolute difference to the mean of the 1961 to 1990 base period as a weighted (inverse distance) mean of REMO output in a radius of about 30 km around the station. A comparison of the annual rainfall for the selected stations reveals the large climate heterogeneity along the BIOTA transect, with Elandsberg and Sonop representing the more humid parts in the North and South, respectively and the Numees station (note the different scaling in Fig. 3) representing the arid central region. All three

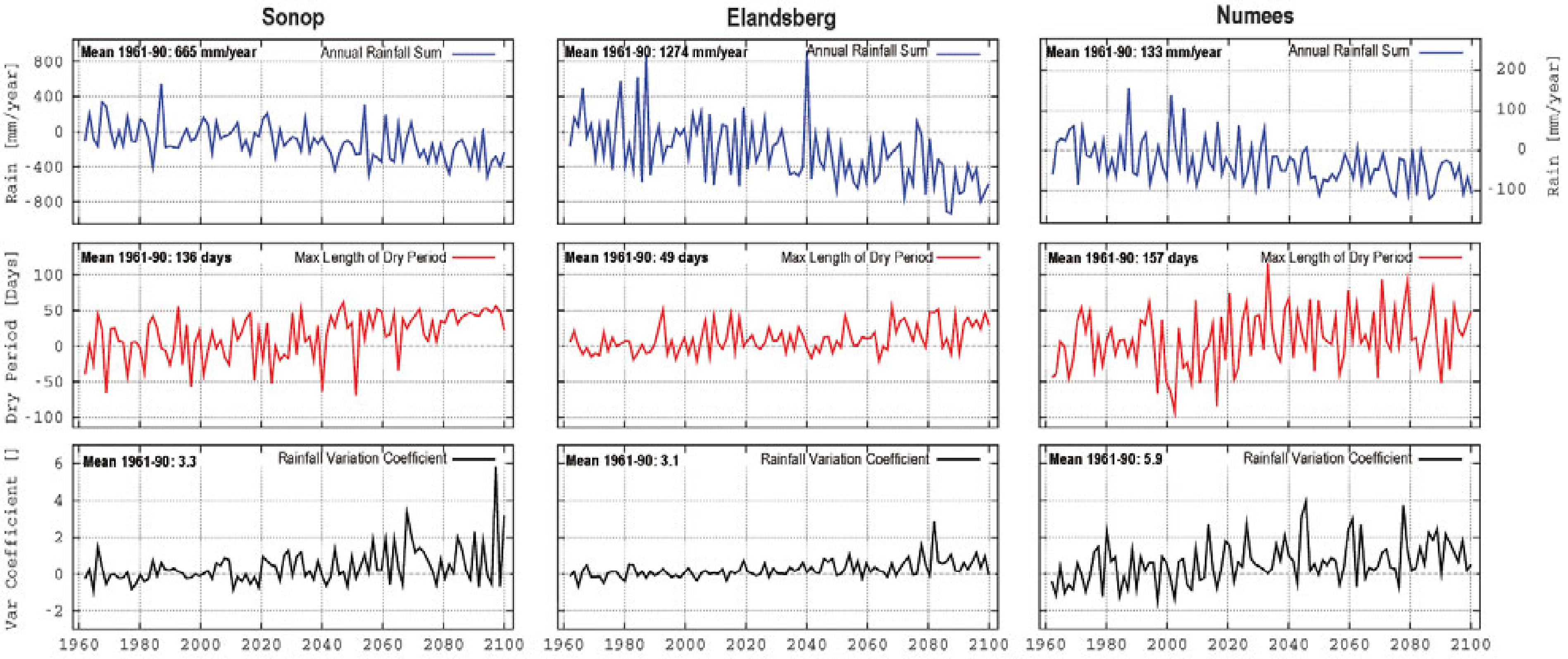

Fig. 3: Deviation of annual values from the 1961–1990 control period mean for annual rainfall (upper panels), maximum number of consecutive days without rainfall (middle panels) and rainfall variation coefficient (lower panels) for three different stations along the BIOTA transect: The geographical coordinates of the stations are as follows: Sonop - 19.07 S/18.90 E, Elandsberg - 33.43 S/19.03 E and Numees - 28.29 S/16.95 E. The respective simulated mean values for the control period are given in each plot. (Note that the scale for the Numees-Richterveld station for annual rainfall is different to the other stations).

stations show a substantial decrease in annual rainfall for the second half of the 21st century, as it was also projected to occur along the whole transect. The decrease in annual rainfall is accompanied by an increase in the maximum dry period length, especially at the two more humid stations. Additionally, increased rainfall variability is projected for these two stations in the future. In summary, the projected time series for the three stations indicates that future rainfall will be even less reliable than current conditions, especially as dry spells become more frequent.

Discussion

The REMO simulations project severe warming accompanied by a substantial change in future hydrological conditions along the BIOTA transect. Generally, there is a marked decrease in future water availability. This decrease is a result of extended dry periods and increased rainfall variability, both of which have the potential to increase water stress situations in the future. Furthermore, the projected changes are expected to have a substantial impact on the region's biodiversity, as a decrease in water supply strongly affects the state of ecosystems (Midgley & Thuiller 2007).

However, when interpreting the results of the REMO projection one has to keep in mind that the simulation involves a particular degree of uncertainty. The current projection is only one realisation of a long-term high-resolution climate change projection for the southern African region. To come up with a more robust assessment of future climate change, ensemble projections based on several simulations should be taken into consideration. Such ensembles of high resolution climate change projections can be achieved by using different RCMs and downscaling techniques and also by using different boundary fields. Furthermore, it would also be beneficial to consider different GHG emission scenarios to investigate the full range of potential climate changes over the region.

Additionally, it is important to note that the presented projections do not include any feedback from future landuse changes or soil degradation processes on the climate. As these processes have the potential to amplify projected changes, they should also be integrated in future simulations.

Nevertheless, due to the immense computational effort, only modern high performance computation systems allow for such long simulations at such a fine scale. The first step in the right direction is the COordinated Regional climate Downscaling EXperiment (CORDEX), which began in 2009 and in which the REMO model will also be used for transient climate change projections, including land cover change studies over the African continent. Although the presented REMO projection is affected by some uncertainty, it has been proven to have added value in its representation of regional scale processes and feedbacks compared to the available coarse resolution global climate model data. Consequently, impact studies on a regional or local scale will likely benefit from using data of high-resolution climate change projections.

Acknowledgements
The authors' general acknowledgements to the organisations and institutions, which supported this work are provided in Volume 1.

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Elevation profile along transects

Manfred Keil*, Ursula Gessner & Christian Hüttich

Summary: As a supplement to map products presenting spatial elevation information, altitudinal profiles along the north-south and west-east transects were derived from the digital elevation model (DEM), based on the Shuttle Radar Topographic Mission (SRTM). The elevation profiles expose both heterogeneous and homogeneous topographic units along the BIOTA Southern Africa transects and deliver information on slopes, peaks and depressions.

Source of data

Elevation profiles were derived from the digital elevation model based on the Shuttle Radar Topographic Mission (SRTM, for further information see Art. III.2.2). The digital elevation model (based on the C-band component of the SRTM mission) was available at a spatial resolution of about 90 m by 90 m (i.e. 3 arc-sec by 3 arc-sec, USGS 2007). The location of the north-south transect and of both west-east transects is shown in Fig. 1, including identification numbers of the Observatories.

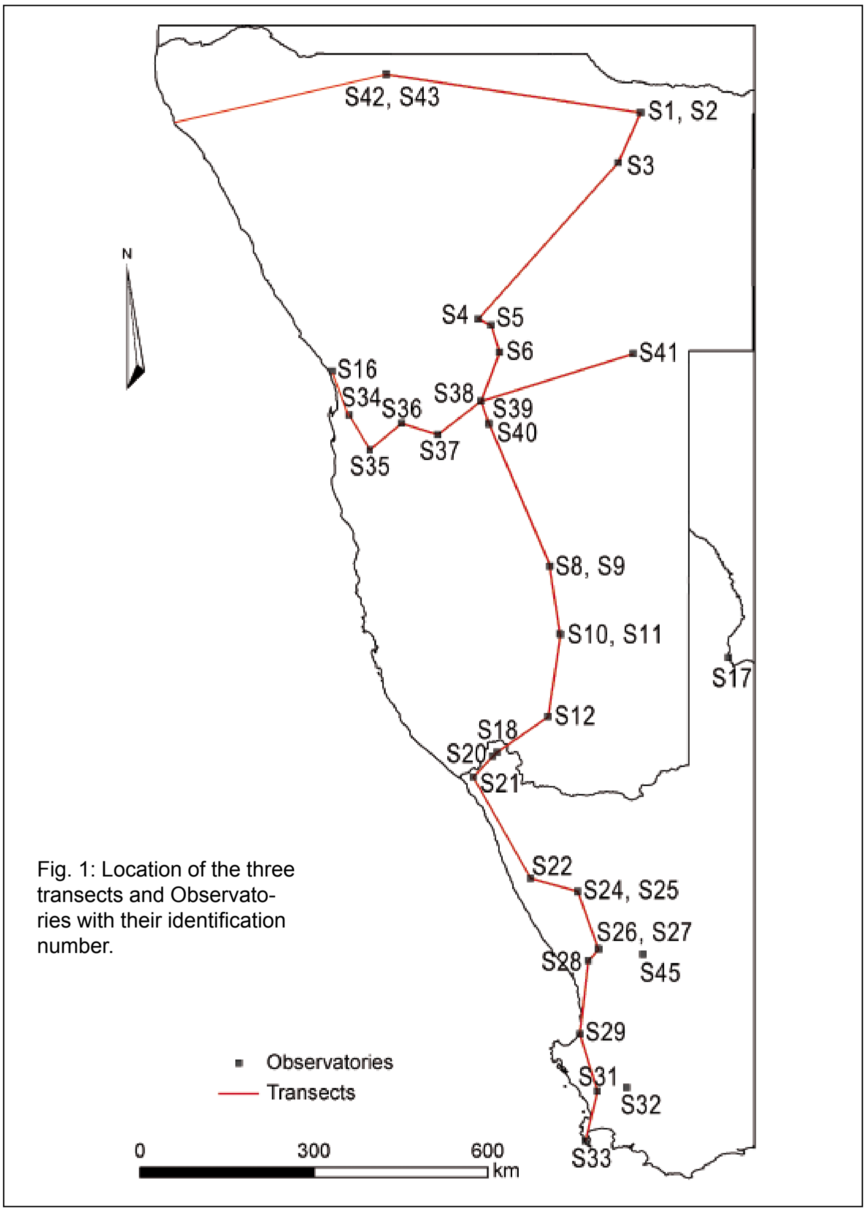

Fig. 1: Location of the three transects and Observatories with their identification number.

Table 1: List of numbers and names of Observatories

No.	Observatory
S01	Mile 46
S02	Mutompo
S03	Sonop
S04	Toggekry
S05	Otjiamongombe
S06	Okamboro
S08	Niko North
S09	Niko South
S10	Gellap Ost
S11	Nabaos
S12	Karios
S16	Wlotzkasbaken
S17	Alpha
S18	Koeroegap Vlakte
S20	Numees
S21	Groot Derm
S22	Soebatsfontein
S24	Paulshoek
S25	Remhoogte
S26	Goedehoop
S27	Ratelgat
S28	Moedverloren
S29	Rocherpan
S31	Riverlands
S32	Elandsberg
S33	Cape of Good Hope
S34	Kleinberg
S35	Gobabeb
S36	Ganab
S37	Rooisand
S38	Claratal
S39	Narais
S40	Duruchaus
S41	Sandveld
S42	Ogongo
S43	Omano go Ndjamba
S45	Nieuwoudtville

The north-south transect

The north-south transect starts in the Kavango in north-east Namibia at the Observatories Mile 46 (S01) and Mutompo (S02) at an elevation level of about 1200 m (see Fig. 2). Towards the centre of Namibia, the topography rises quite steadily. About 40 km south of Okamboro (S06), the abrupt altitude increase marks the Khomas Highland with the highest altitudes along the transect (almost 1900 m). The Observatory Claratal (S38, altitude 1800 m) is situated at the southern fringe of the Khomas Highland. Towards southern Namibia, elevation decreases more or less steadily, before the terrain becomes quite rough again between the Observatories Gellap Ost (S10)/Nabaos (S11), Karios (S12) and the Observatories in the Richtersveld (Koeroegap Vlakte S18 and Numees S20). Here the profile reflects the relief of the Fish River Canyon and its tributaries as well as the Gariep River valley.

In South Africa, South of the Richtersveld, the elevation along the transect is mainly below 300 m before the Kamiesberg Mountains rise to altitudes of more than 1000 m (with Paulshoek (S24) at an altitude of 1016 m). The transect then crosses the lowlands of the Western Cape, ending at the Observatory of Cape of Good Hope (S33), south of Table Mountain.

The west-east transect in northern Namibia

The northern west-east transect starts at Cape Frio in the west along the Skeleton Coast at the Atlantic Ocean, with steep slopes towards the mountains of the Kaokoveld, rising up to altitudes of 1300 m (see Fig. 3). The depression of the Cuvelai Drainage system is reflected between profile-km 300 and profile-km 500, with elevations between 1120 m and 1095 m. The Observatories Ogongo (S42) and Omano (S43) are situated in this region. Slowly, the elevation rises towards the east to the regions of open woodland in the Kavango, with the Observatories of Mile 46 (S01) and Mutompo (S02) at the eastern end of the transect (altitude: 1170 m). The flat relief east of profile-km 200 is explained by the soft, sandy geology of the dominating Kalahari sands.

The west-east transect in central Namibia

The southern west-east transect, crossing the central part of Namibia, starts at the Observatory of Kleinberg (S34) in the Namib Desert in the west (see Fig. 4). Kleinberg is about 40 km from the coast, and the altitude is about 187 m above sea level. A steady slope can be observed towards the Observatory Ganab (S36). From the Observatory Rooisand (S37) to the east, the terrain gets rougher towards and along the Khomas Highland with the Observatory Claratal (S38) at profile-km 286. The Auas Mountains represent the highest peaks along the transect at 2240 m and 2200 m (passing near the “Moltkeblick” [2479 m] at profile-km 330 and 357). Along the eastern part of the transect towards the Observatory Sandveld (S34), the relatively flat basin structure of the Kalahari at an altitude around 1500 m is visible again.

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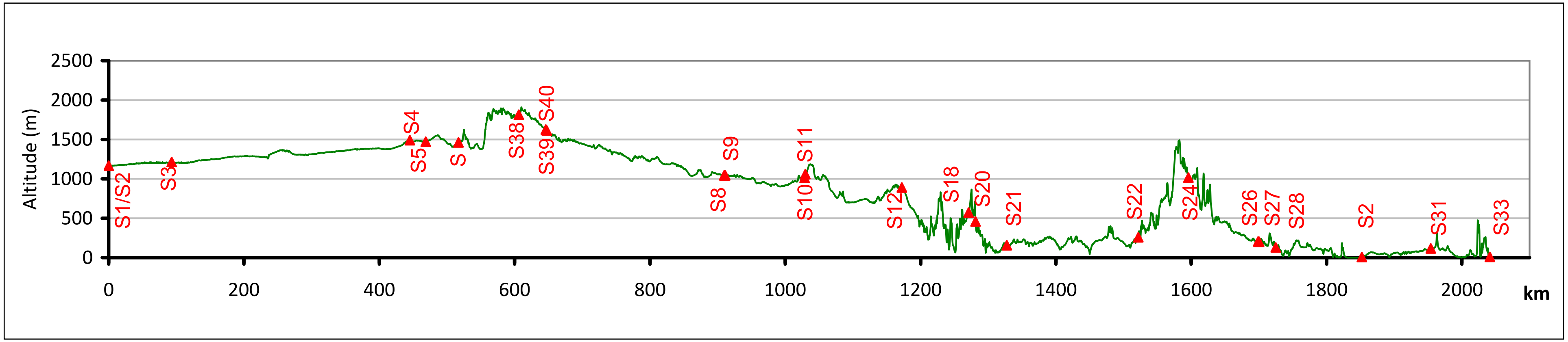

Fig. 2: North-south transect (length about 2040 km) showing the altitudes above sea level.

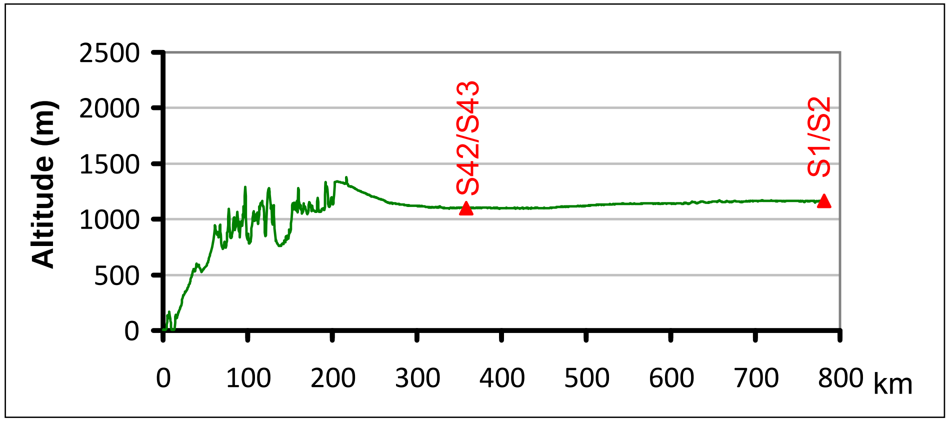

Fig. 3: The northern west-east transect showing the altitudes above sea level (length about 780 km).

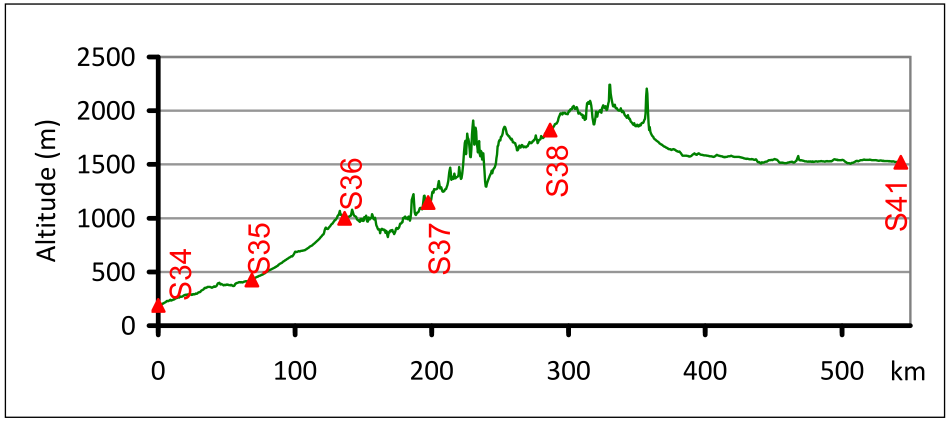

Fig. 4: The west-east transect in central Namibia, showing the altitudes above sea level (length about 540 km).

Soils along the BIOTA transects

Andreas Petersen, Alexander Gröngröft*, Anthony Mills & Günter Miehlich

Summary: Soil analytical and taxonomic data of 27 Observatories, being distributed along the BIOTA transects from Northern Namibia to the Cape Peninsula and produced with a standardised procedure for each site have been evaluated with respect to overarching factors for the soil genesis and pedodiversity. Of twelve soil reference groups found, Arenosols and Leptosols were dominant. Significant trends between topsoil median values (pH, electric conductivity, organic carbon content) and annual precipitation could be described; nevertheless for all distributions some Observatories exhibit special conditions. For both rainfall regimes (summer and winter rainfall) the total organic carbon stored within the soil profiles seems to have the same positive correlation to annual rainfall, however for identical rainfall amounts the carbon pools are varying by a factor of three, among other factors controlled by soil clay content. The pedodiversity of the studied sites varies strongly (2–20 types of 25 possible). In general, soilscapes predominantly build up by aeolian sands are mostly homogenous whereas soils in mountainous areas exhibit the highest richness. Plains and salt enriched areas are of medium pedodiversity.

Introduction

The description of the Observatories in Part II has offered a detailed insight into the individual areas including their soil communities and soil properties. Each of the observatories exhibits special features and thus by focusing on individual sites it is not evident whether there are overarching relationships between the areas or along the transects. With regard to the factors relevant for soil genesis (see concept of Jenny 1941), the differences between the studied areas may result i) from the climate gradient, ii) from the parent material or iii) from the type and intensity of landuse. With the exception of the southernmost observatories all sites can be classified as semiarid to arid, but with differing rainfall regimes, some sites have developed on aeolian sands and many on weathered acid rocks, and most sites are used as more or less intensively grazed rangelands.

This chapter summarises the results of the soil classification as well as the pedodiversity and the parametric behaviour of selected soil properties by focussing on the overall pattern of soil units and selected soil properties. This enables both an overview of the predominant soil units and a comparison of the variability of soil properties along the transects. The soil properties can be used to analyse patterns of plant species richness along the transects, as has already been done by Medinski et al. (2010) for selected soil features and Petersen et al. (2010) for pedodiversity in general.

Methods

As described in Part II, soils on the BIOTA Observatories were investigated with a standardised procedure. The general characteristics of the methodological approach were: site selection by a stratified random procedure, soil description and classification acc. to FAO (2006a, b), profiles at 4 m south of ha-centre points, sampling of all horizons, laboratory analyses of numerous soil variables (details are given in Jürgens et al., submitted, and Petersen 2008). Here, the data of 27 Observatories were included (Fig. 1), normally investigated with 25 profiles each. For the balancing of soil contents across the profile depth, the analysed concentrations of each horizon (weight %) were multiplied by the thickness, the bulk density and the volumetric share of the fine earth (100% minus percentage of rock fragments). The total soil content was the sum of all horizons. The taxonomic pedodiversity was determined according to Petersen et al. (2010).

Results and discussion

Soil distribution and properties

Fig. 2 exhibits the frequency distribution of the soil reference groups—the highest level of classification—summed up for the transects. The great variety is highlighted by the occurrence of 12 out of 32 reference groups possible in the worldwide valid system. With regard to their distribution, two groups can be distinguished: i) Arenosols, Leptosols, Regosols, Cambisols, Calcisols, and Solonshaks, recorded with 49–122 cases each and being widely distributed, at least on eight observatories each, and ii) the group of Solonetz, Durisols, Luvisols, Podzols, Fluvisol, and Gypsisols recorded with only 2–39 cases each on one to five observatories. Due to the subjective selection of observatories and resulting substrate dominances, this overview cannot provide a representative pattern of the occurrence of reference groups in the entire study area, but will summarise the results for the transects. Calcisols for instance show a relatively high abundance, which is most likely due to the regional setup of the observatories Narais (S39) and Duruchaus (S40) in a calcrete-dominated landscape, while on the remainder of the transects Calcisols occur only sparsely. Also, the relatively high number of sites with aeolian sand deposition (5) in the observatories favours the dominance of Arenosols. Leptosols are the most commonly distributed across the

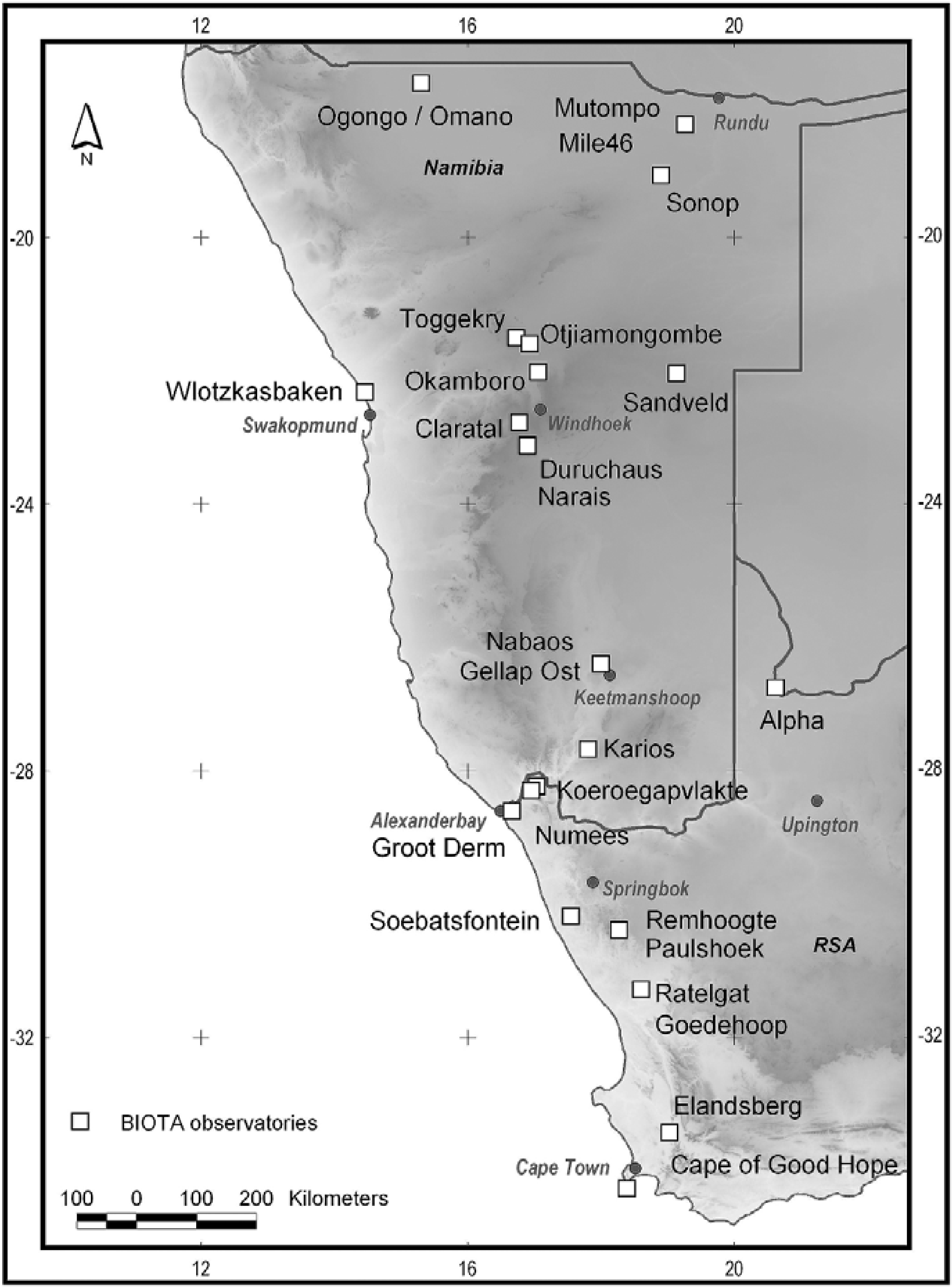

Fig. 1: Map of the Observatories included in the study.

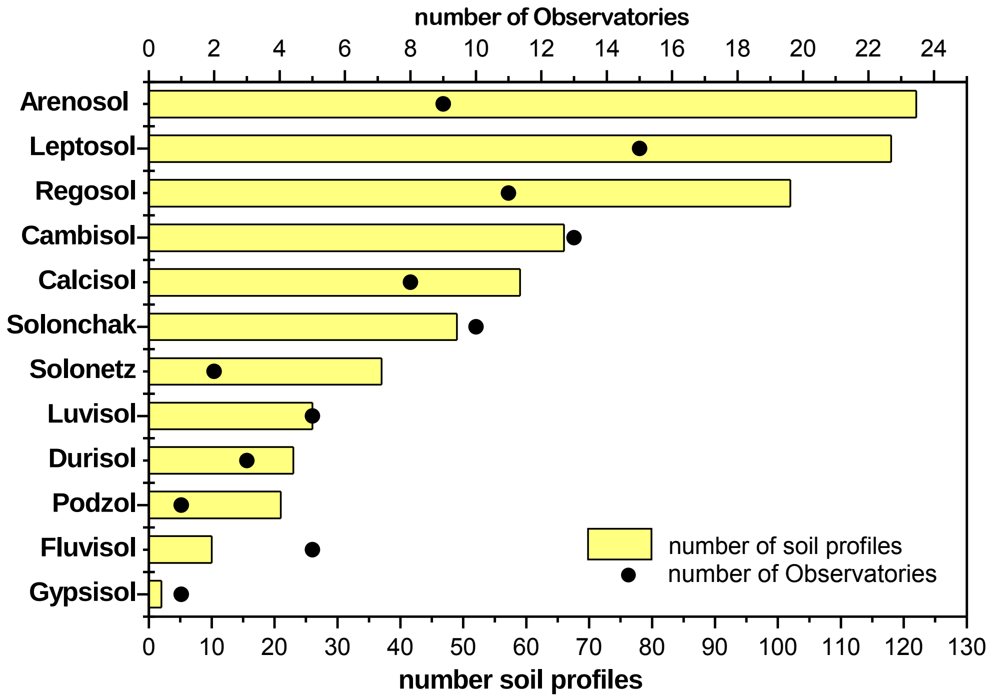

Fig. 2: Frequency distribution of soil types (WRB 2006) in all studied observatories.

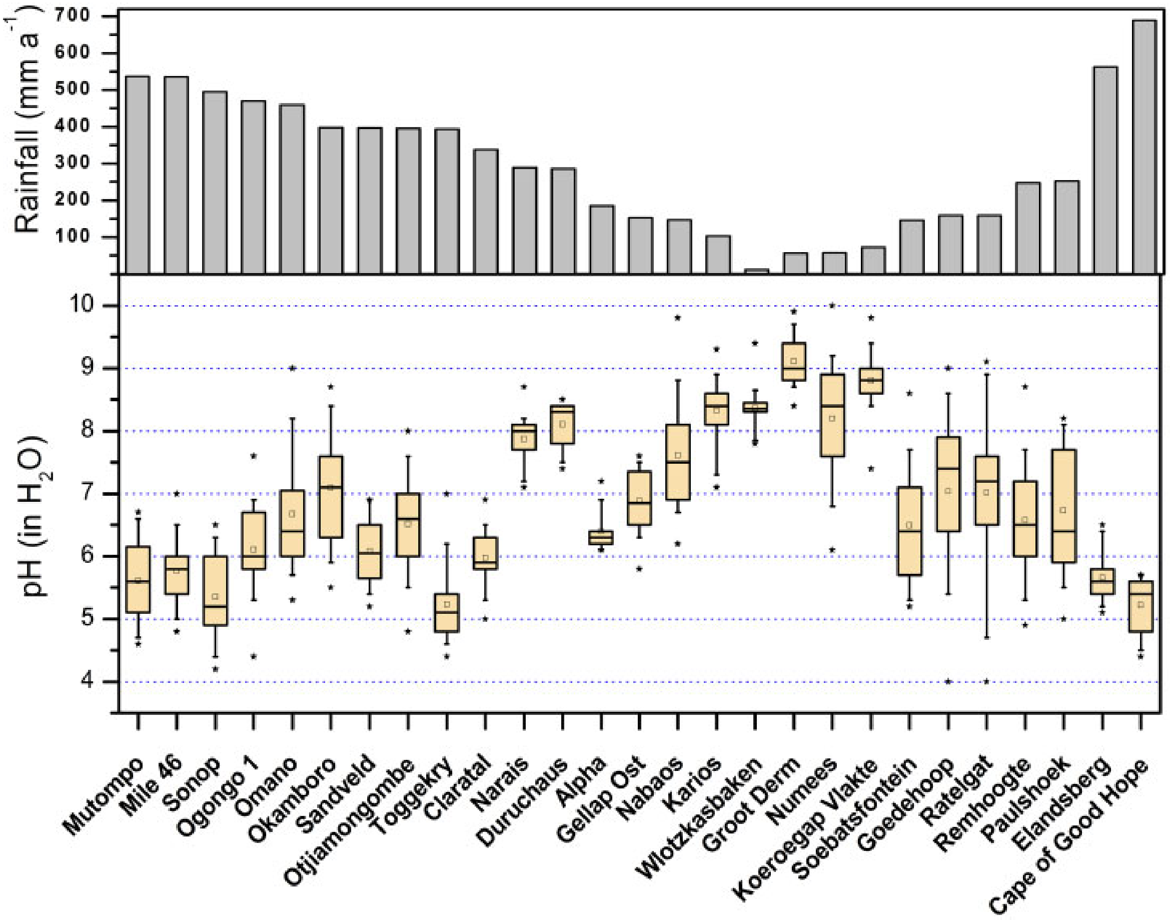

Fig. 3 : Distribution of topsoil pH along the rainfall gradient.

observatories, achieving a high frequency due to a large number (7) of observatories located in mountainous regions of the escarpment, especially in South Africa. A few reference groups occur exclusively in individual observatories such as Solonetz, typical for the Oshana region, Gypsisols, which are prominent in the coastal desert, and Podzols occurring on the Cape Peninsula. These examples illustrate that regional aspects strongly affect the depicted frequency distribution of soil groups.

Examples of range and variability of selected topsoil properties along the transects are shown in Fig. 3, 5, and 7. Within these graphs, all Observatories were arranged along the natural rainfall gradient—decreasing summer and increasing winter rainfall—with sites from the main transect being integrated climatically and not by latitudes. The most evident trend is shown with the pH-value (Fig. 3) and the amount of soluble salts (Electric conductivity value, see Fig. 5). The pH-values exhibit a reciprocal trend compared to the mean annual rainfall. The highest pH-values are found in the arid border zone between summer and winter rainfall and the costal desert on site S16 Wlotzkasbaken (Fig. 4). The within-site variability is largest in the central Namibian savanna and the winter rainfall dominated Namaqualand in South Africa. Here on the Observatories Soebatsfontein (S22) to Paulshoek (S24), significantly wide ranges of pH-values are related to small scale patterns of salt accumulation. Additionally sampled small-scale transects revealed that on these Observatories the higher pH-values are restricted to areas of former termite nests (“Heuweltjies”, see Chapter IV.4), which are characterised by higher concentrations of calcium carbonate than the adjacent soils.

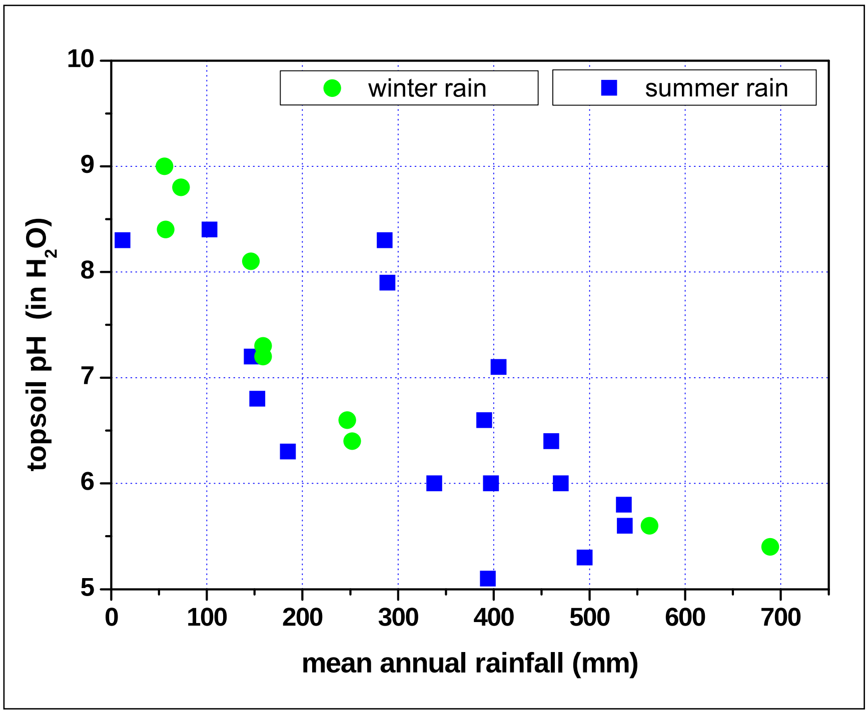

Fig. 4 : Median topsoil pH in relation to mean annual rainfall.

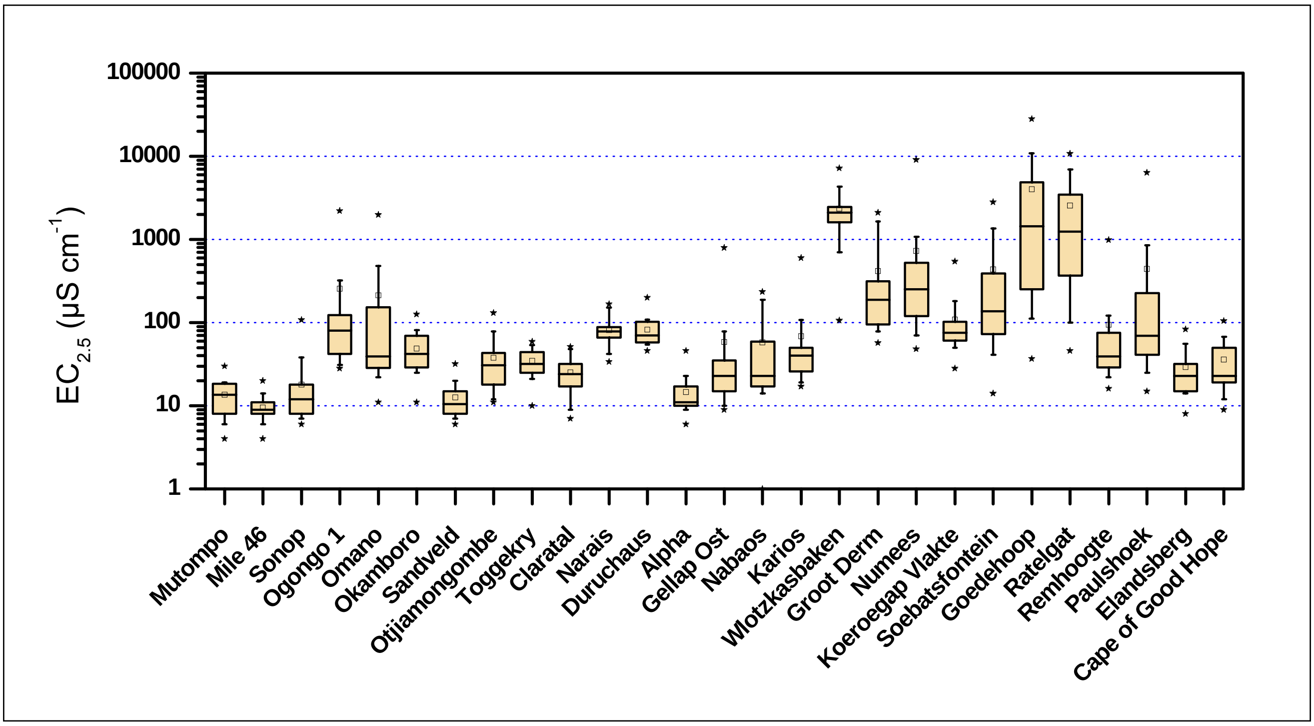

Fig. 5 : Distribution of topsoil electric conductivity (EC) along the rainfall gradient. Rainfall gradient see Fig. 3.

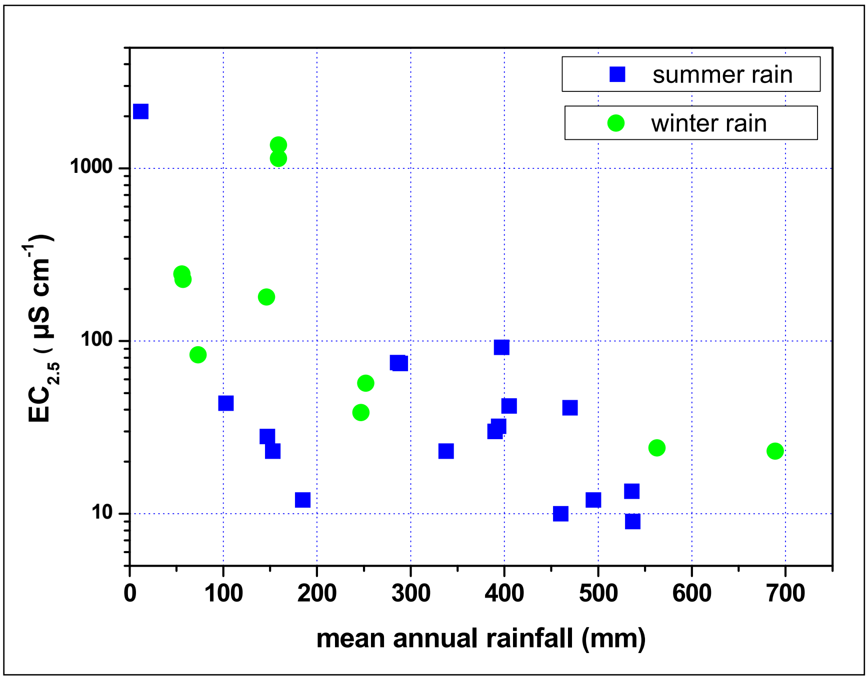

Fig. 6 : Median topsoil electric conductivity (EC) in relation to mean annual rainfall.

The alkalisation of soils is related to the accumulation of strong cations (i.e. sodium) in combination with the loss of strong anions (i.e. chloride and sulphate). The dominance of $NaHCO_3$ and Na_2CO_3 leads to pH-values of 8.3 to 11 (Thomas 1996). The potential to accumulate cations in the soils is correlated to the rainfall for example, the winter rain events in Namaqualand tend to be of low intensity and thus are unable to effectively leach ions.

The trend of electrical conductivity values along the transects is less closely related to the amount of rainfall as is the case for the pH-value (Fig. 6). The electric conductivity shows low values and small ranges in the summer rainfall affected sites and the widest range and highest values in the drier parts of the winter rainfall area. Besides other salt accumulation affecting parameters such as coastal distance, location in an evaporative landscape with water run-on (Oshana region: Observatories S42 Ogongo and S43 Omano), soil texture, clay dispersibility (Mills et al. 2006) etc., here the rainfall regime rather than the rainfall amount seems to have an impact on salt accumulation. Compared to sites with the same amount of rainfall but higher intensities of rainfall events, drainage of accumulated soluble substances is probably reduced by low intensity rainfalls and less drainage. This difference is especially obvious within the annual rainfall amount of 100–200 mm. Additionally, the accumulative effects of ancient termite activity led to patches with higher concentrations of in salts. The results of the electric conductivity values lead to the hypothesis that in the summer rainfall driven ecosystems drainage occurs regularly, although these might occur only every few decades within the drier regions. The fact that very low electrical conductivity values are evident in soils up to a depth of 1 m provides the basis for this hypothesis, which implies drainage over at least 1 m depth. Otherwise, the accumulation of salts, at least of chloride from atmospheric deposition, would exceed the analysed values. These findings are supported by the fact that in the sampled soils often marginal differences in texture go along with differences in electric conductivity values, i.e. higher electric conductivity values in loamier soils of Observatory Otjiamongombe. This also underlines the described drainage effect, which is stronger on sandier soils.

For most dryland areas, the amount of soil organic carbon (SOC) in the topmost soil layer is very low (0.1–0.4%). Fig. 7 shows an overarching decreasing trend running from the higher summer rainfall areas in the north to the arid areas in Southern Namibia. With the transition to the winter rainfall area, the SOC increases again and remains relatively stable with a median of 0.6–0.8% with ranges indicating a high variety of microhabitat conditions. Three exceptions exist in the overall trend: i) higher concentrations of SOC (median 1.08%) on site S38 Claratal, here associated with high altitude (about 2000 m), strong erosive processes and shallow profiles, ii) elevated SOC values on the sites S39 Narais and S40 Duruchaus (0.58, 0.80%), which are combined with very stable conditions of high pH-values in a calcium carbonate rich environment, a situation favouring the persistence and sequestration of organic carbon, and iii) an intensive accumulation of SOC median (2.63%) in a strongly acid nutrient poor and water logging environment on the Cape Peninsula, a situation, which hinders the decomposition of organic carbon. In contrast to the demonstration of SOC in the first horizon, Fig. 8 shows the total amount of SOC in the profiles. The results are substantially different to just the concentration of topsoil SOC, because the profile thickness and their contents of coarse fragments in these areas vary significantly.

The general correlation of SOC to mean annual precipitation is obvious (Fig. 9). Here, both rainfall regimes seem to overlap. The high topsoil SOC values reported for site Claratal above is unremarkable with regard to the total SOC storage, because the low soil depth and the high contents of coarse fragments reduce the storage potential. Irrespective of the overall regression, there are variances of SOC storage with the same rainfall amount of about a factor of three. The sites S06 Okamboro and S05 Otjiamongombe for instance, just 48 km apart and with the same rainfall of nearly 400 mm a^{-1} are quite different in total carbon storage with median values of 1.4 and 4.1 kg SOC m^{-2}, respectively. This example shows, that even a correlation with an aridity index (see Jenny 1941, Donkin & Fey 1993), which generally seems to be a more appropriate

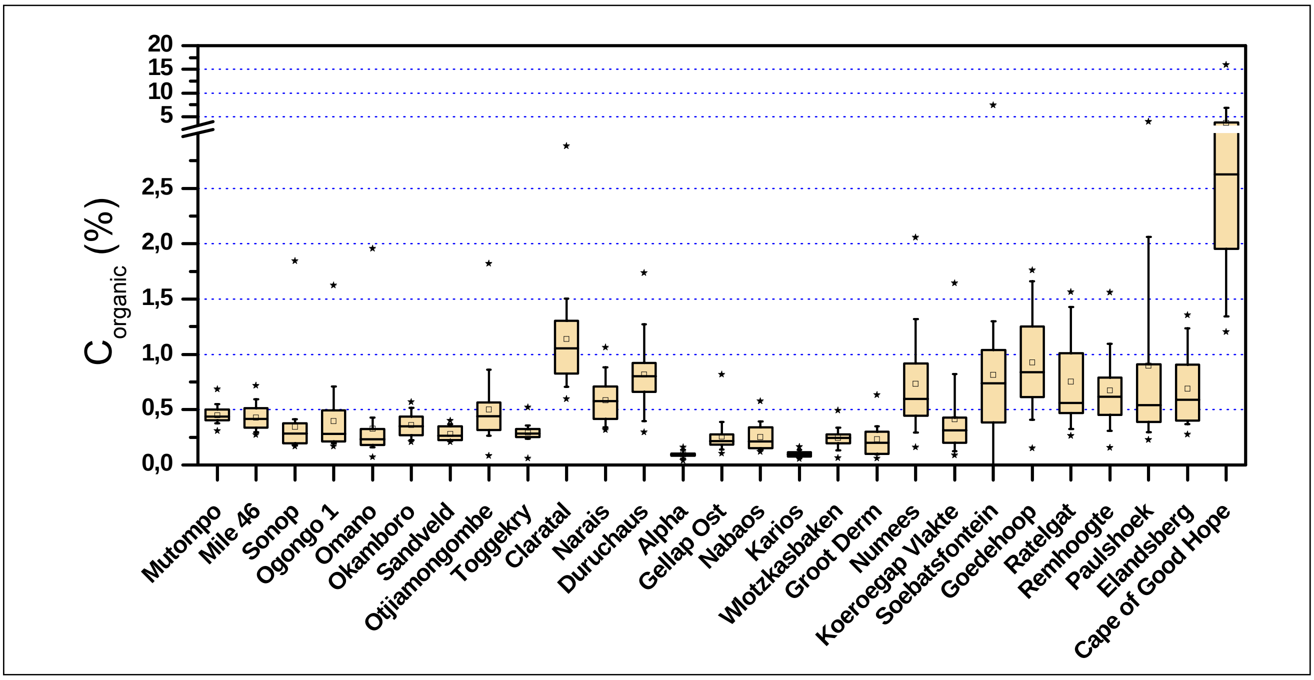

Fig. 7 : Distribution of topsoil soil organic carbon (SOC) along the rainfall gradient. Rainfall gradient see Fig. 3.

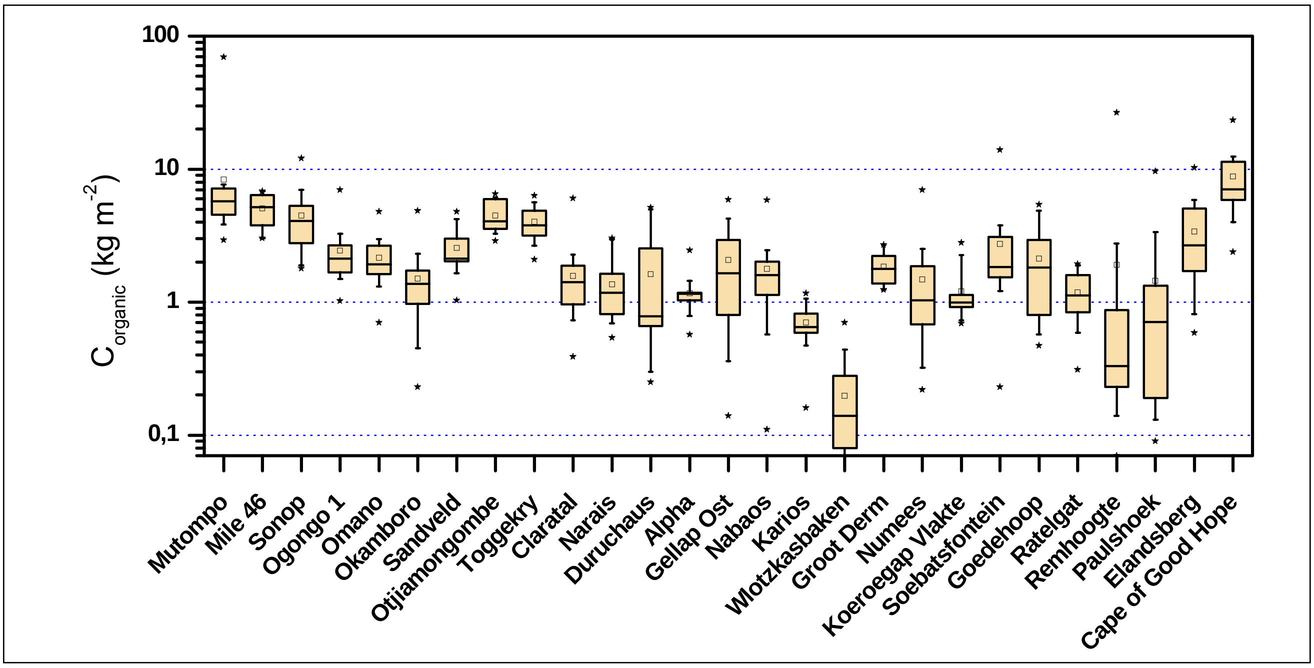

Fig. 8 : Distribution of total soil organic carbon (SOC) along the rainfall gradient. Rainfall gradient see Fig. 3.

variable to describe the complex climatic influence, will result in some variation of SOC storage with identical external impacts. One factor controlling the total SOC is the amount of clay in the soils, which is known to stabilise the organic fractions (Oades 1988) and is about four times larger on the Otjiamongombe site compared to Okamboro.

Pedodiversity

According to McBratney (1992) pedodiversity is “the variation of soil properties or soil classes within an area”. After the introduction of the term in the early 1990s, the concept of pedodiversity has been applied with varying meanings and aims. However, since the early approaches by Ibanez et al. (1990) until today (see literature overview in Petersen 2008) no consistent approach to compare the pedodiversity of small-sized areas on the basis of detailed and standardised soil profile descriptions and analyses has been published yet.

Fig. 10 depicts the taxonomic richness (R) and the Shannon evenness (E) based on the classification of soil profiles with

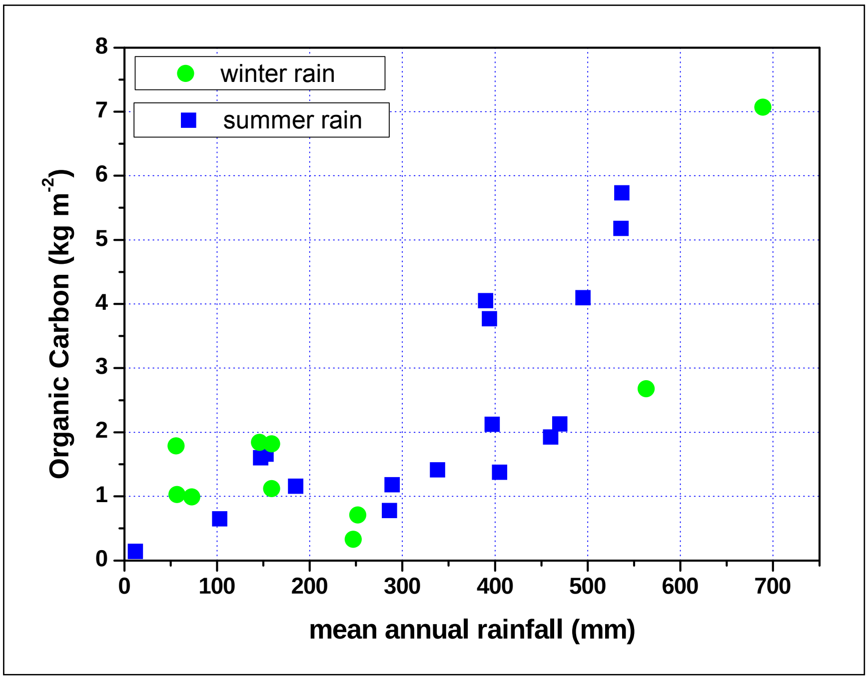

Fig. 9 : Median total soil organic carbon (SOC) in relation to mean annual rainfall.

the WRB (FAO 2006a) on the two-qualifier level. Considering a potential richness of *R* = 25, which means that all profiles belong to different soil units, the Observatories vary between *R* = 2 and *R* = 20, thus indicating a broad range of pedodiversity along the transects. The general trend along the precipitation gradient gives indications for a symmetrical relation with lowest values at the wet ends of the transects, a tendency for high pedodiversity in the intermediate range and a central minimum at smallest rainfall amounts. However, as the differences in pedodiversity with similar rainfall amount indicate, there have to be other controls of soil unit richness on the Observatories. Fig. 11 exhibits the pedodiversity richness with respect to rough landscape characteristics. Therefore the Observatories have been classified to four subunits: i) areas formed by aeolian sands (within the Kalahari basin: S02 Mutompo, S01 Mile 46, S03 Sonop, S41 Sandveld, S17 Alpha; coastal dune veld: S21 Groot Derm), ii) mountainous areas with steep slopes and rock outcrops (S06 Okamboro, S38 Claratal, S10 Gellap Ost, S11 Nabaos, S20 Numees, S22 Soebatsfontein, S25 Remhoogte, S24 Paulshoek), iii) areas with dominating salt enrichment (S43 Omano, S42 Ogongo, S16 Wlotzkasbaken, S26 Goedehoop, S27 Ratelgat), and iv) the remaining sites, mostly plains (S05 Otjiamongombe, S04 Toggekry, S39 Narais, S40 Duruchaus, S12 Karios, S18 Koeroegap Vlakte, S32 Elandsberg, S33 Cape of Good Hope).

With this clustering, some factors controlling pedodiversity become clearer: Soilscapes predominantly build up by aeolian sands as parent material, in general are mostly homogenous (*R* = 2–10). The comparatively high pedodiversity on the Observatory Sonop (*R* = 10) results from the inclusion of the patchy and extended interdune part of the area, where Cambisols of different pH and Calcisols are mixed with the predominant Arenosols of the region. The five salt enriched areas have a medium to high pedodiversity. Especially the two neighbouring sites in

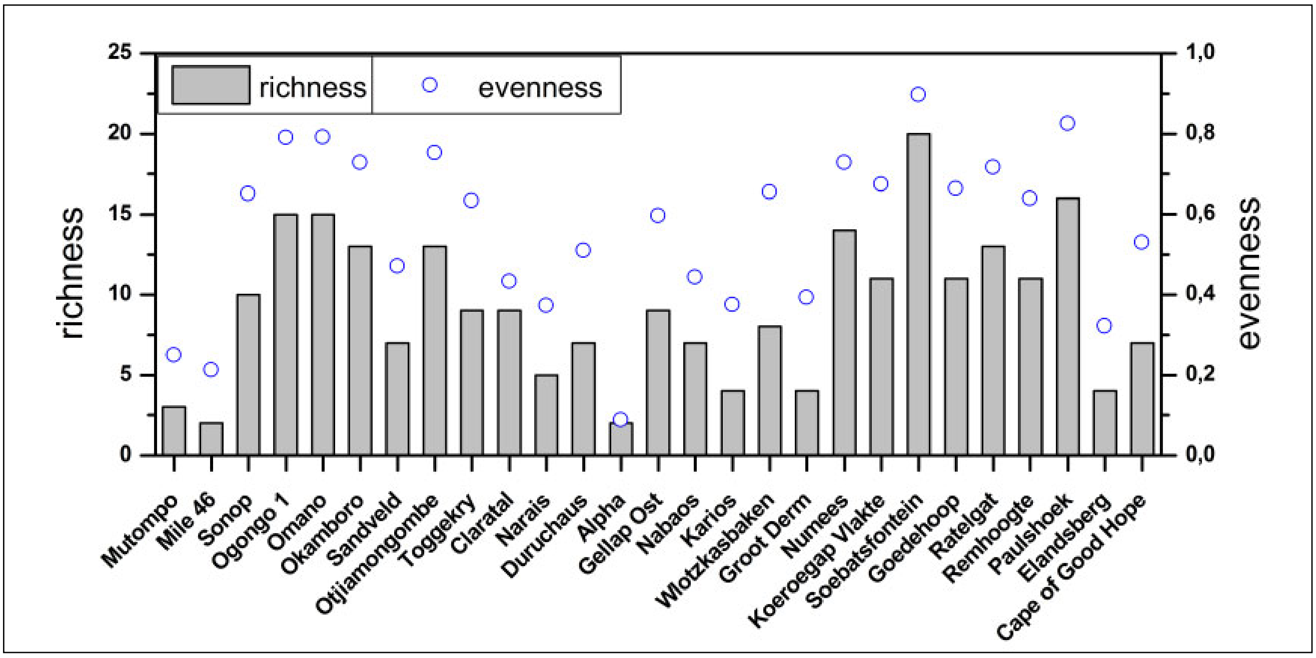

Fig. 10 : Distribution of taxonomic soil richness (R) and Shannon evenness (E) along the rainfall gradient. Rainfall gradient see Fig. 3.

the Oshana region (Ogongo, Omano) are rich in soil units (*R* = 15), based on the spatial variation of sodium dominance, total salt contents and carbonate enrichment, all three further varied by their vertical distribution within the soil. Here, the applied classification system is rather sensitive and even profiles with similar morphology may be differing on the upper level of soil reference group. On-site topographic variability may have a strong influence on the pedodiversity, but for the same annual rain amount, in some cases the richness is only 7 (Nabaos) whereas on other areas the highest pedodiversity for all sites was found (Soebatsfontein, *R* = 20). Plains exhibit a medium range of pedodiversity (*R* = 4–13). From the comparison it can be concluded, that even by introducing the rough landscape qualifier, the richness of comparable sites has a variation in pedodiversity of about a factor three. The topographic variability, which in case of missing other information is regarded as a dominant factor for geodiversity, thus explains part of the pedodiversity, but other factors are of same significance. A decrease in pedodiversity with annual rainfall > 500 mm, which could be explained by the intensification of soil genetic processes, seems to be unlikely. At the wettest region at the Northern end of the transects, the study sites are developed in degraded dunes and thus present low pedodiversity, while the southernmost sites on the Cape Peninsula are developed in weathered material of nutrient poor sandstones, and thus of low pedodiversity as well.

The Shannon evenness has a strong and nearly linear correlation to the richness (Fig. 12). This indicates an increasing similarity of the frequency distribution of soil units with increasing pedodiversity. Two areas are remarkable with E below the trend, which means a strong dominance of one soil unit (Alpha, Claratal) and one area (Wlotzkasbaken) with E above mean trend, meaning a rather similar distribution of found soil units.

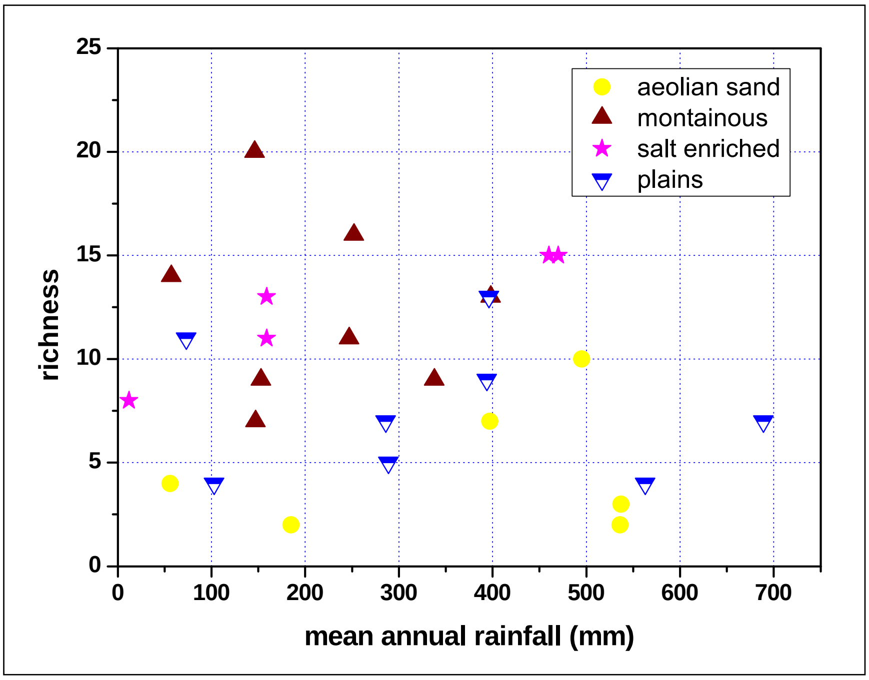

Fig. 11 : Soil richness (R) in relation to mean annual rainfall.

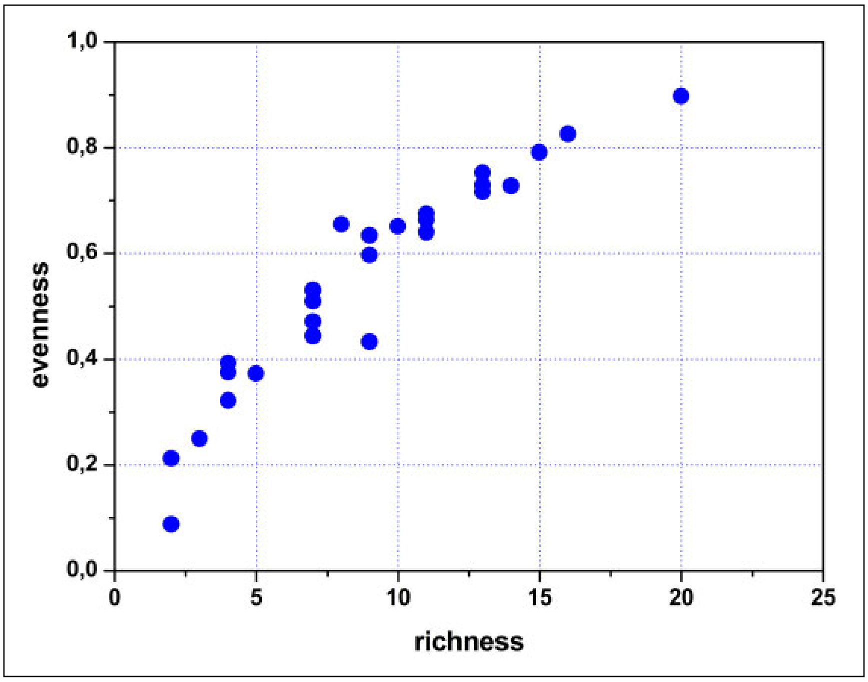

Fig. 12 : Relation between soil Shannon evenness (E) and richness.

Conclusions

In summary, it can be stated that the variability of soil properties in the studied drylands is high for both the overall transects and within the observatories. Looking at the different scales of soil patterns along the transects, distinct differences were evident. Whereas the main substrate-driven changes in the northern part of the transects occurred at a distance level of 100–300 m, the southern part of the transects was additionally small-scale structured (1–100 m). Examples are Observatory Soebatsfontein with a high impact of heuweltjie structures and the Observatories Ratelgat and Goedehoop with small-scale changes in pH-values and salt content. These changes occurred within few meters. Additionally, the small-scale changes and structures of bedrock in mountainous and shallow developed sites seem to be a major factor for ecological niches driven by soil physical factors. This 'flower pot' principle is very obvious on steep slopes in Numees but missing on the morphologically comparable site Claratal. Here, the weathering structure of the bedrock and the intensity of soil erosion control the occurrence of the small scale structuring of the soilscape.

The diversity of soil properties on the studied Observatories is a valuable proxy for the phytodiversity of areas (Petersen et al. 2010). This knowledge is especially relevant for the restoration and protection of degraded landscapes (e.g. mining or strongly overgrazed areas). Here, as proposed by Eviner & Hawkes (2008), in the re-construction of cover soils the diversity of site properties should be taken into account to substantially improve the future diversity of the vegetation.

Acknowledgements

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Biological soil crusts along the BIOTA Southern Africa transects

Burkhard Büdel*, Kirstin Deutschewitz, Stephanie Dojani, Thomas Friedl, Tatyana Darienko, Katrin I. Mohr & Bettina Weber

Summary: Biological soil crusts (BSCs) were reported from six out of seven biomes along the BIOTA Southern Africa transects. Seven morphological BSC types were distinguished: three cyanobacteria-dominated crusts (types 1and 2), one with additional cyanolichens (type 3), one type with chlorolichens (4), and one with bryophytes—either liverworts (type 5a) or mosses (type 5b). The hypolithic crust type (6) was restricted to quartz gravel pavements, and another one comprised the unique lichen fields of the Namib Desert (type 7). In total, at least 120 different species with 58 cyanobacteria, 29 green algae, one heterokont algae, 12 cyanolichens, 14 chlorolichens, two genera of liverworts, and three genera of mosses were found, placing these BSCs among the most diverse worldwide. They contribute considerably to the biodiversity of the arid and semi-arid regions of south-western Africa. The taxonomic diversity of cyanobacteria was higher in the winter rainfall zone than in the summer rainfall zone (54 versus 32 species). Soil photosynthetic biomass, carbon content and the number of BSCs revealed the same significant distribution patterns. Rainfall frequency and duration of dry periods rather than the precipitation amount seem to be the main factors influencing BSC growth and succession. This article is mostly based on the publication of Büdel et al. (2009).

Introduction

Biological soil crusts (BSCs) are an integral component of dry lands on all continents. They are an assemblage of microorganisms including cyanobacteria, algae, microfungi, lichens, liverworts and mosses in different proportions, which stabilise the upper few millimetres of the soil (Belnap et al. 2001) Their significant role within terrestrial ecosystems has only been recognised since the mid 20th century (Halperin et al. 1976, Komáromy 1976, Rogers et al. 1966, Shields et al. 1957, Skarpe & Henriksson 1987).

Within the sub-Saharan region, the southern and south-western parts of the African continent seem to be centres of BSC development (Ullmann & Büdel 2001). Vogel (1955) was one of the first to describe cyanobacterial and algal crusts underneath quartz gravels (= hypolithic) of the desert pavement, a community that was later named the “hypolithon” (Schlesinger et al. 2003). Cyanobacterial soil crusts have been reported from the Kalahari region in South Africa, where they cover 11 to 95% of the Kalahari ground surface (Thomas & Dougill 2006, 2007).

In this investigation, we tested the following hypotheses: (1) the presence of BSCs on the soils of arid and semi-arid biomes is the rule and not the exception; (2) BSCs contribute considerably to the biodiversity of these biomes and are the primary colonisers of bare soils after disturbances of either natural or artificial disturbances; (3) BSC biomass (as chlorophyll content) rises with increasing species diversity; (4) the duration of drought periods and the frequency of rainfall events are the driving factors for the presence and development of BSCs and their diversity rather than the total amount of annual rainfall; (5) the structural composition of soils influences the presence and diversity of BSCs.

Material and methods

For a detailed description of material and methods see Büdel et al. (2009).

Results

Classification of biological soil crusts

Seven main BSC types were distinguished in the 28 Observatories along the BIOTA transects (Figs. 1, 4–9). (1) Early successional crusts were brittle, less than three millimetres thick, and could be recognised with the naked eye by a slight and patchy discoloration of the soil surface (Fig. 4). They were composed of filamentous cyanobacteria, e.g. *Microcoleus* and *Leptolyngbya*. (2) The intermediate succession crust was a well established cyanobacterial crust, up to 3.9 mm thick, and included additional cyanobacterial species. The soil was not only stabilised by the presence of this crust type but also had a predominantly dark discoloration on its surface. When undisturbed, this type could develop into the late succession crust, which included (3) cyanobacterial lichens (Fig. 5), (4) chlorolichens or both (Fig. 6). Where precipitation events like rain or dewfall were frequent enough, (5a) liverworts (Fig. 7) or (5b) mosses developed. Later on, type 5a and 5b may have occurred without cyanobacteria and lichens. (6) Hypolithic crusts were restricted to the occurrence of translucent quartz gravel on the ground (Fig. 8). (7) Due to their structure and high green algal lichen diversity, the crusts of the Namib Desert were considered as a unique BSC type (Fig 9).

The effectiveness of the presented classification scheme was reflected by significant

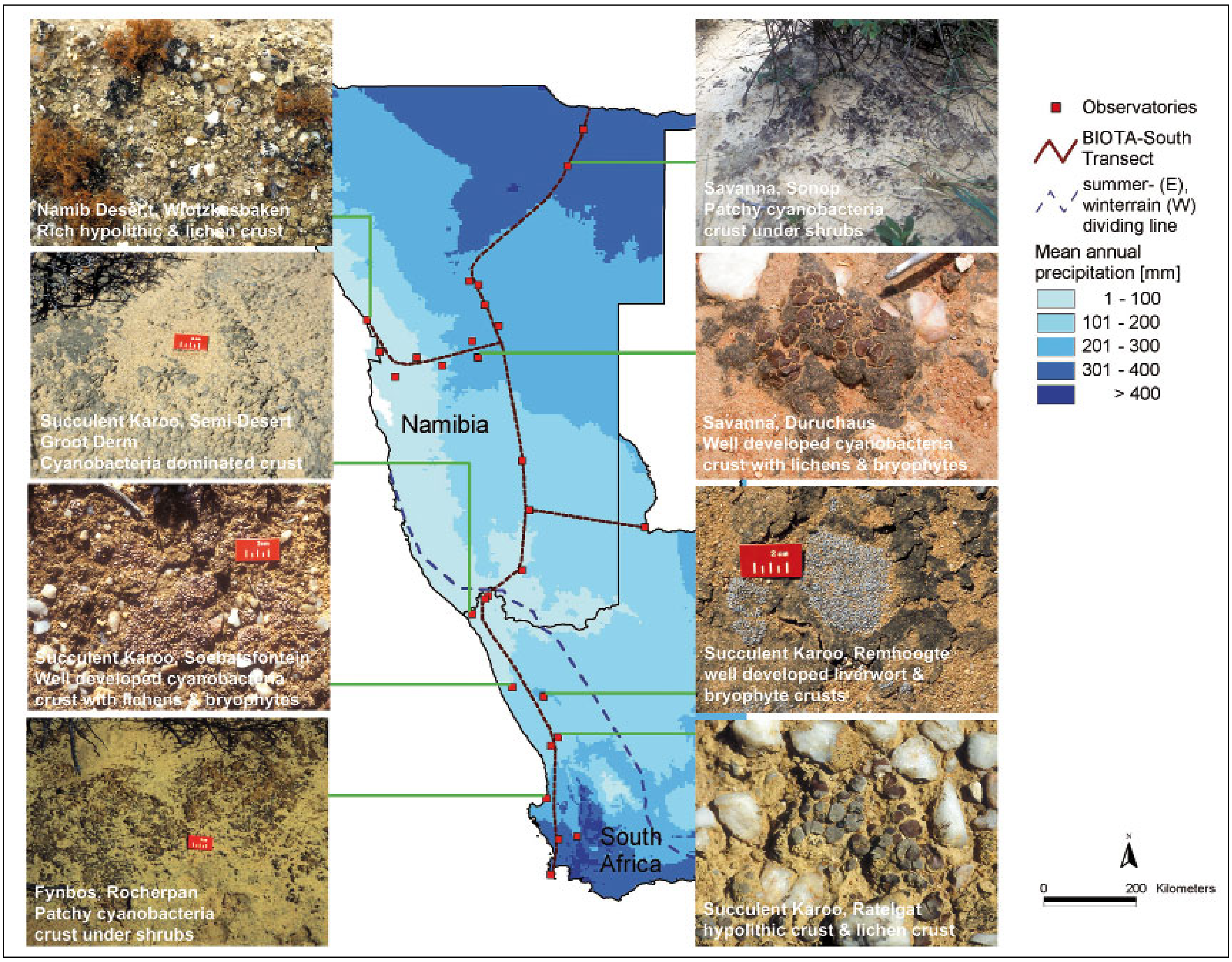

Fig. 1: Crust types occurring at the Observatories along the transects.

differences of several parameters between crust types. Crust thickness of the three BSC types increased with crust development from the early (type 1; 2.7 ± 0.224 mm, N = 4) to the intermediate (type 2; 3.4 ± 0.99 mm, N = 13) and the late (type 3; 4.4 ± 0.89 mm, N = 13) successional stages. In a one-way ANOVA, crust thickness was shown to be significantly different between the groups ($p = 0.002$, $N = 3$), and posterior F statistics revealed significant differences between both types 1 and 3 ($p = 0.002$) and types 2 and 3 ($p = 0.006$).

Similarly, the biomass values increased with higher successional stage. Chlorophyll$_a$ and chlorophyll$_{a+b}$ both revealed a considerable increase from an early succession crust stage (type 1; 31.8 ± 14.97 mg chl$_a$/m^2, 49.3 ± 28.25 mg chl$_{a+b}$/m^2) to the intermediate (type 2; 67.9 ± 46.33 mg chl$_a$/m^2, 112.5 ± 80.89 mg chl$_{a+b}$/m^2) and the late (type 3; 86.3 ± 31.62 mg chl$_a$/m^2, 135.8 ± 46.5 mg chl$_{a+b}$/m^2) successional stages. For both factors, significant differences between the groups were shown using a one-way ANOVA (chl$_a$, $p = 0.005$, chl$_{a+b}$, $p = 0.004$), and posterior F statistics revealed significant differences between crusts of types 1 and 2 (chl$_a$, $p = 0.026$, chl$_{a+b}$, $p = 0.014$) as well as types 1 and 3 (chl$_a$, $p = 0.001$, chl$_{a+b}$, $p = 0.001$). Besides that, we found that high chl$_a$ values were also associated with a high number of different BSC types (Pearson correlation coefficient 0.64). There was no correlation between BSC characteristics and carbon or nitrogen content of the soil.

Distribution patterns of BSC types and abiotic factors along the transects

BSCs of various types were found in all biomes except for the Fynbos biome. The highest degree of coverage (up to 70%) was observed in the Namib Desert with crust types 6 and 7, a value close to those found by other authors of up to 87% of the soil surface (Lalley et al. 2006, Schieferstein & Loris 1992). This was followed by the Savanna ecosystems (up to 60%) with mainly crust types 1–4 and rarely 5, and the Succulent Karoo (up to 35%), where all types of crusts were present, except the lichen field type 7. In the Nama Karoo, mostly the early successional stages of BSCs (type 1) were observed, with a low coverage of less than 6%. Hypolithic crusts (type 6) were also scattered over the area.

At the Zambesian dry forest Observatories, mainly type 1 and rarely type 2 BSCs with low-coverage values for both (< 1%) were encountered and their presence was restricted to recently burned areas. The Woodland Savanna Biome

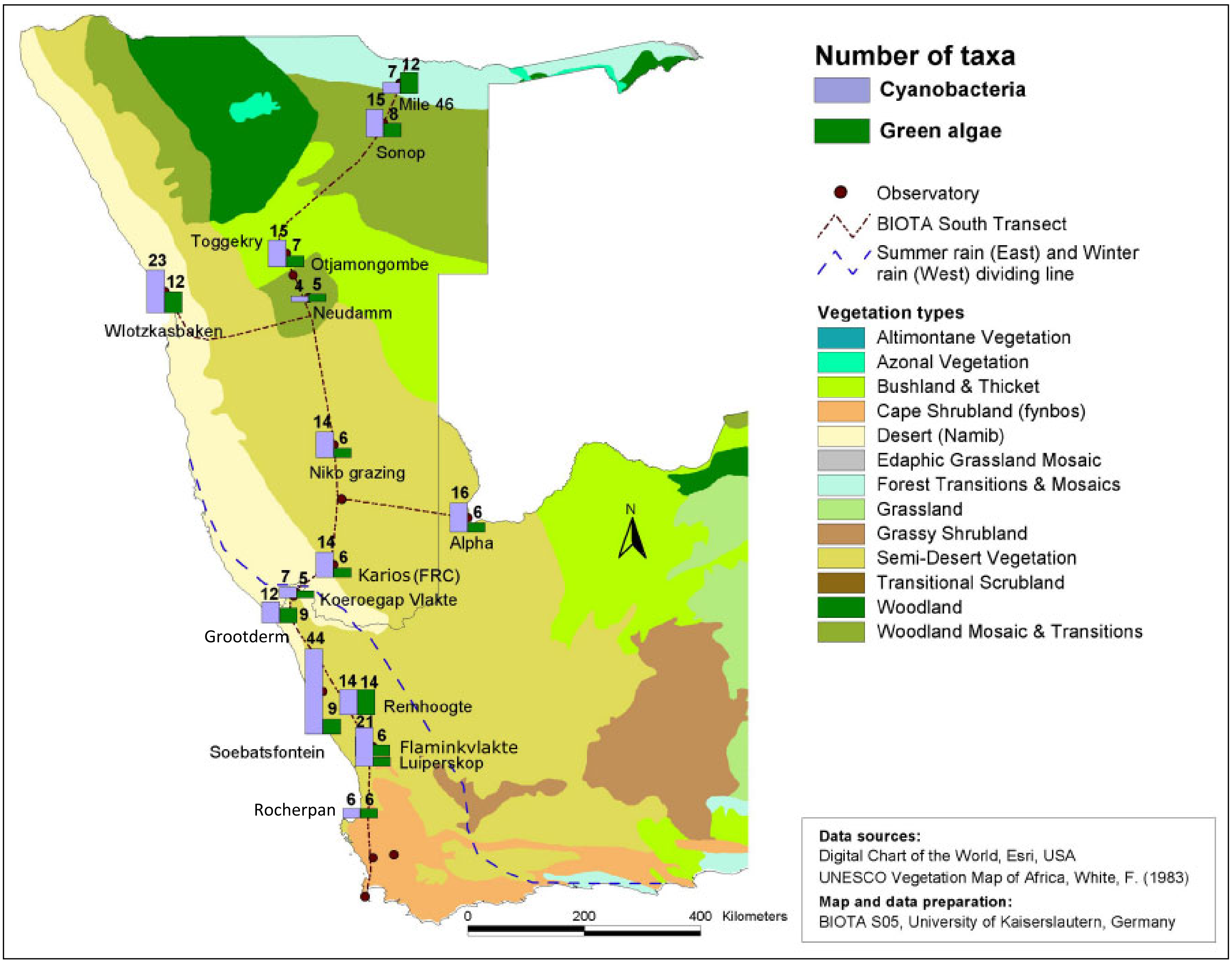

Fig. 2: Number of algal taxa at the different Observatories along the transects.

exhibited BSC types 1–4 and 6, which grew underneath exposed, scattered quartz rocks, with type 2 and 4 BSCs being the most common. BSC coverage was between 20–60%. Bryophyte crusts were extremely rare in this biome. BSCs of the types 1–2 (very rarely type 4 and 5) often occurred underneath the canopy of shrubs. In the Namib Desert, the especially diverse BSC type 7 occurred within the spectacular lichen fields, but type 6 BSCs were also common within the quartz gravel pavements. In the fog zone of the desert, type 7 crusts covered up to 70% of the total area investigated revealing chlorophyll values of 156.2 ± 64.68 mg chl_a/m^2 and 230.5 ± 98.33 mg chl_{a+b}/m^2 ($N = 9$). Although present in the Kalahari Highveld, type 1 BSC occurrence was very scattered, patchy and of extremely low biomass. BSCs in the Nama Karoo biome mainly belonged to type 1, but type 6 crusts were also common where a quartz gravel pavement was present. Here, BSCs were found only at one BIOTA Observatory (i.e. Niko North, Observatory S08, coverage up to 5%).

The Succulent Karoo Biome was commonly inhabited by six types of BSCs, with the large quartz fields of the Knersvlakte being characterised by a particularly high coverage and species diversity of type 6 BSCs (up to 25% of the soil surface). These hypolithic crusts of the Knersvlakte comprised mean chlorophyll values of 74.5 ± 37.11 mg chl_a/m^2 and 107.3 ± 47.13 mg chl_{a+b}/m^2 ($N = 8$). Biological soil crusts with cyanolichens and/or chlorolichens as well as liverworts and/or mosses (type 5a and b) were well developed within this Biome. The Observatory in the Fynbos biome showed some growth of pro- and eukaryotic algae in the soil, but despite intensive searching, no crust formations were detected on the soil surface. In the savanna and semi-desert biomes, early succession crust types were often observed developing in the dripping zone of shrubs.

The soils along the transects were generally nitrogen depleted and exhibited values between 0.1 g/kg (Zambesian dry forest) and 0.6 g/kg (dry Savanna, Succulent Karoo) total nitrogen per dry matter. This resulted in high C:N values (e.g. above 100 in the Nama Karoo), indicating the limiting role of N in the soil. A positive correlation between the number of BSC types and the proportion of silt and clay in the soil (Pearson correlation coefficient 0.52, $p = 0.04$) was found.

Diversity of species

BSCs were present in all biomes except the Fynbos and at most Observatories along the transects (Fig. 2). In total, we recorded 58 species of cyanobacteria, 29 green algae, one heterokontophyte, 12 cyanolichens and 14 chlorolichens. Many cyanobacteria taxa were only found at one or two Observatories. The majority of cyanobacteria occurred in Observatories of both major rainfall regimes. For a list of species see the detailed Observatory descriptions in Part II of this book. The number of cyanobacteria species was considerably higher in the winter rainfall zone (54 species) than in the summer rainfall zone (32 species). In the winter rainfall zone, the cyanobacteria reached their highest diversity in the Succulent Karoo (49 species), whereas in the summer rainfall zone the highest species diversity was recorded in the Thornbush Savanna (22 species).

The diversity of eukaryotic algae was similar in both rainfall regime types with 23 species in the winter rainfall zone and 22 in the summer rainfall zone (Fig. 2). The highest species numbers were found in the Succulent Karoo Observatories (19 species, winter rainfall) and the Observatories of the dry savanna (16 species, summer rainfall). Species numbers in the other biomes were all below ten. Generally, the species-rich biotopes were located in the northern parts of the transect and along the coast. Among the eukaryotic algae, 15 species were found at least three times. Most of them were observed in both winter and summer rainfall zones, with only four occurring exclusively in the summer rainfall zone and none exclusively in the winter rainfall zone.

The initial stages of soil crusts were always composed exclusively of cyanobacteria. Eukaryotic algae were common soil organisms and were also present in the BSCs reported here. However, they were not observed to form BSCs themselves in the biomes along the transect. While the cyanobacterial diversity correlated significantly with the mean chl_a and chl_{a+b} content (Pearson correlation coefficients of 0.58 and 0.51), this was not the case for green algae. Of the 26 recovered lichen species 12 were cyano- and 14 chlorolichens.

Relevance of rainfall frequency and regime

Total precipitation was significantly higher in the summer rainfall zone compared to the winter rainfall zone, while the duration of drought was significantly shorter in the winter rainfall zone. The mean chlorophyll content in the winter rainfall zone (67 mg chl_a/m^2, 102 mg chl_{a+b}/m^2; $N = 29$) was significantly higher than in the summer rainfall zone (39 mg chl_a/m^2 and 68 mg chl_{a+b}/m^2; $n = 27$). Maximum values in the winter rainfall zone were well above 100 mg chl_a/m^2, and 200 mg chl_{a+b}/m^2. Dry-matter-related biomass in terms of carbon content was also significantly higher in the winter rainfall zone (1.9 versus 1.1, $U_{21,\,21} = 135$, $p = 0.031$) and the number of BSC types per Observatory was also significantly higher (1.8 versus 1.1; $U_{27,\,29} = 261.5$, $p = 0.028$).

Diversity, rainfall regime/ frequency, and soil

Relating BSC characteristics to site characteristics along the transects (Fig. 3), we found a positive correlation between the number of BSC types as well as chl_a content with winter rainfall frequency (Pearson correlation coefficient: 0.51, $p = 0.036$, and 0.6, $p = 0.01$), and a negative correlation between the number of BSC types with summer rainfall frequency (Pearson correlation coefficient: −0.54, $p = 0.024$). The winter rainfall zone was characterised by a significantly shorter annual dry period (89 days versus 153 days in the summer rainfall zone, $U_{8,\,9} = 5.0$, $p = 0.003$) with a more even distribution of rainfall events over the year (64 days in summer versus 80 days with rain in the winter rain zone, not significant) and a higher winter rainfall frequency (number of rainy days during the winter period from April to September).

Discussion

Species richness

The cyanobacterial diversity recorded in this study is probably the highest reported so far for BSCs occurring in arid and semi-arid regions around the world, with a total of 58 species of which 49 occurred in the Succulent Karoo and 24 in the Namib Desert.

Many of the 31 eukaryotic algal species detected in soil crusts along the Namibia–South Africa transect have already been reported from BSCs of other continents. As already described for cyanobacteria, the green algal diversity was highest in the BSCs of the Savanna (20) and the Succulent Karoo (29) biomes. No other BSC reported so far has shown such a high species richness in eukaryotic algae. The pro- and eukaryotic algal α-diversity of different BSC types seems to be correlated with a higher fine-grain fraction in the soil. For lichens and bryophytes, we have not yet been able to show a clear distribution pattern with regard to macroclimatic factors. With regard to total species richness of lichens and mosses, our random sampling showed its weaknesses. Since most lichens (26 species in 14 genera) and also many bryophytes have patchy distributions, we in all likelihood failed to collect the complete diversity. For comparison, in BSCs of the Columbia Basin (USA) as many as 144 lichen species were reported (McCune & Rosentreter 2007). Nevertheless, it appears that their occurrence in BSCs depends on longer periods between disturbances and more frequent rainfall events with shorter drought periods in between (Belnap & Lange 2001).

Our results reveal a significantly higher cyanobacterial species richness of BSCs in winter rainfall areas (summer versus winter, 32:54 species). This finding partly confirms the third hypothesis in that BSCs contribute to the biodiversity of their biomes. An increasing diversity of cyanobacteria was found with an increasing diversity of BSC types, which partly confirms our third and fifth hypotheses. An increase in cyanobacterial species numbers was found to be correlated with a biomass increase, partly confirming our fourth hypothesis.

Biological soil crust presence, diversity

The successional progress starting from BSC type 1 containing only cyanobacteria and ending with types 3, 4, and/or 5 illustrates the importance of cyanobacterial sheaths for crust development and soil consolidation, whereas lichens and bryophytes contribute mainly to the high chlorophyll (biomass) values of BSCs. In the *Acacia mellifera* thorny shrubland of the Kalahari Desert, Botswana, an ex-

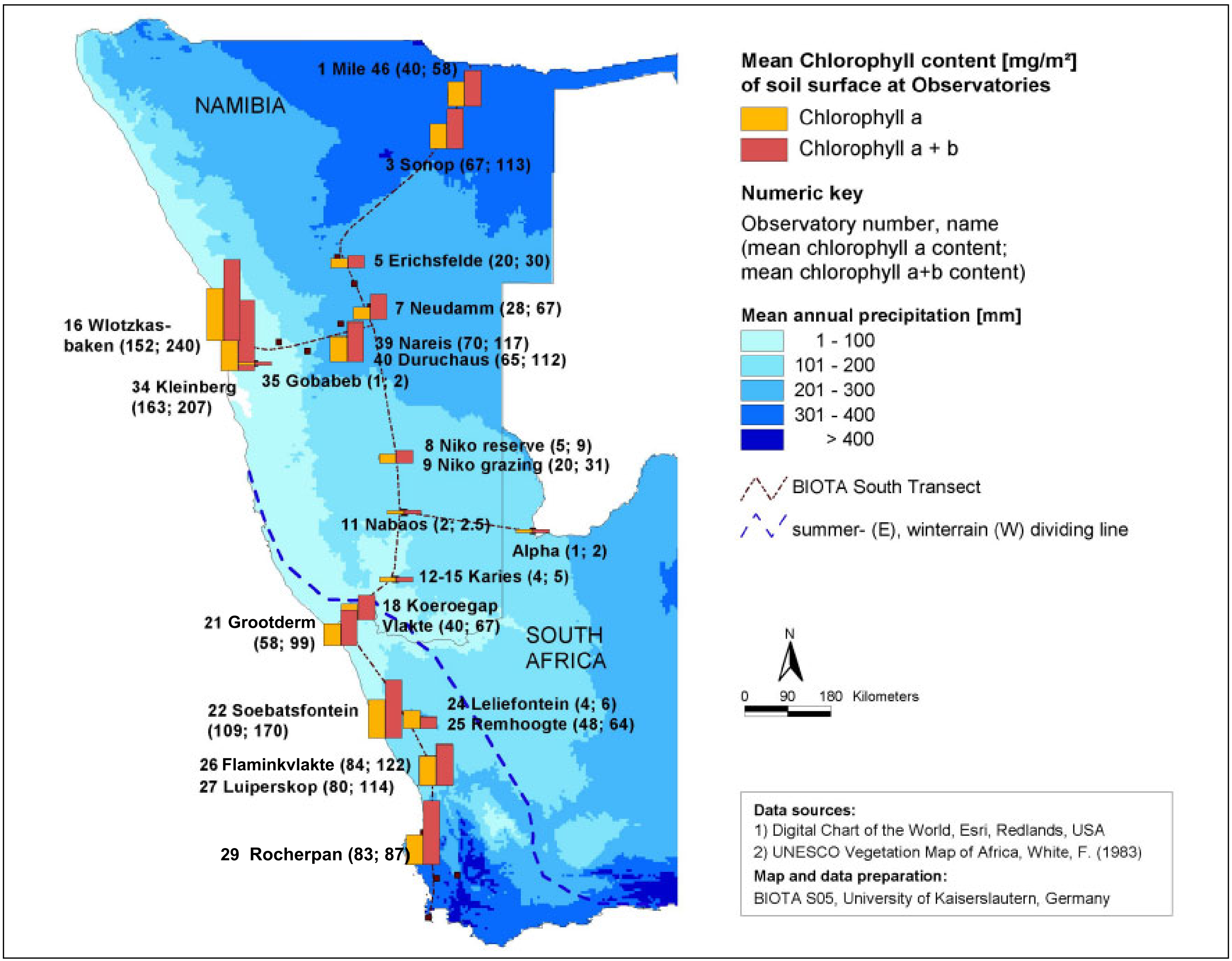

Fig. 3: Chlorophyll content of BSCs at the different Observatories along the transects.

tensive cyanobacterial crust was found, 3–4 mm thick and comparable to type 1 and 2 of our study, that covered between 11 and 95% of the bare soils (Dougill & Thomas 2004, Thomas et al. 2002, Thomas & Dougill 2006, 2007).

The very specialised hypolithon (type 6) is not only composed of a number of different cyanobacteria and green algae, but lichens and bryophytes are also reported from their protecting and moisture gathering habitat (Büdel & Schultz 2003, Vogel 1955, Werger & During 1989). While the hypolithic crust (type 6) also occurs in other arid and semi-arid parts of the world (Cockell & Stokes 2004, Schlesinger et al. 2003), the lichen fields (type 7) are unique to the Namib Desert with their unrivalled but not yet fully known lichen diversity and their wide extent (Loris et al. 2009, Articles III.3.6, III.3.7). They differ considerably from the other BSC types along the BIOTA Southern Africa transects. In addition to terricolous crustose lichens involved in crust formation, foliose and fruticose lichens occurred. Chlorophyll values of the Namib Desert crusts represent the highest ones measured along the transect, reaching mean values of 156.2 mg chl_a/m^2 and 230.5 mg chl_{a+b}/m^2. In a *Lecidella crystallina*-dominated crust system, Lange et al. (1994) determined as much as 508 mg chl_{a+b}/m^2, a chlorophyll content amongst the highest values known for BSCs worldwide (Lange 2001). They have two unique features: the absence of cyanolichens (O.L. Lange, personal communication), and the apparent limitation of cyanobacteria to hypolithic habitats.

From the above we can confirm hypothesis 1, that BSCs are a regular and common part of the vegetation in southwestern Africa, with the exception of the Fynbos Biome. The recording of seven different BSC types confirms our second hypothesis. The lack of BSCs in the Fynbos Biome is puzzling, especially since free-living soil algae are known to be present. Until now, we have been unable to explain this absence, but it is interesting to note that within the Fynbos Biome the soil pH is always well below pH 4 (Petersen 2008). While BSC type 1 is always an early succession type, crusts of type 2 can either be intermediate successional stages, eventually developing into types 3–4, or are the final stage (“climax”) reached under the given circumstances. Biological soil crusts of types 3 and 4 are late successional stages and may develop into type 5, but can also be climax stages. Biological soil crusts of types 6 and 7 always represent “climax” crusts.

Fig. 4: Early successional crust composed of cyanobacteria, type 1, Otjiamongombe, savanna.

Fig. 5: Intermediate to later successional crust with cyanobacteria and first cyanolichens (*Heppia* sp., *Collema* sp.), type 3, Duruchaus, savanna.

Fig. 6: Late successional/climax crust with additional chlorolichens (*Psora decipiens*), type 4, Soebatsfontein, dry savanna to semi-desert.

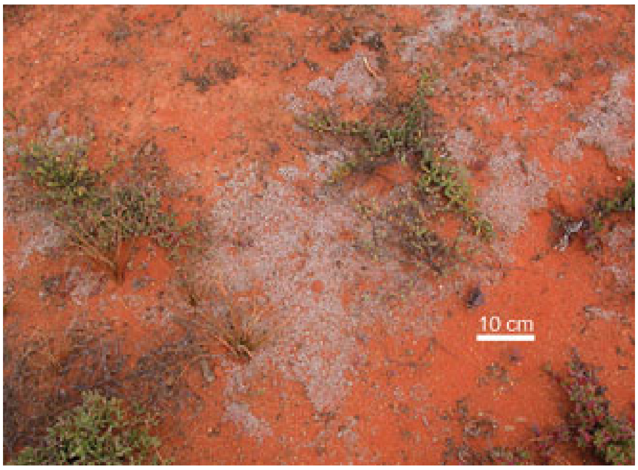

Fig. 7: Climax crust with the liverwort *Riccia* sp., type 5a, Soebatsfontein.

Fig. 8: Hypolithic crust with cyanobacteria, type 6, Karios near Fish River Canyon, Desert Biome.

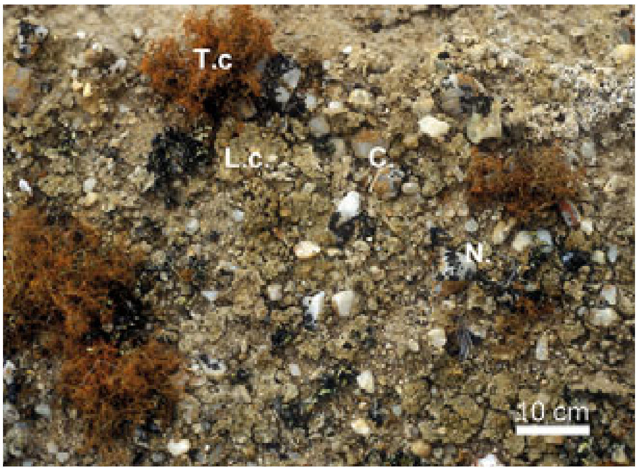

Fig. 9: Climax crust: the unique lichen fields of the Namib Desert (chlorolichens and a few cyanobacteria), type 7, Wlotzkasbaken, Desert Biome. L.c. = *Lecidella crystallina*, N. = *Neofuscelia* sp., T.c. = *Teloschistes capensis*, C. = *Caloplaca* sp.

Climatic and edaphic factors

Since BSC diversity and species richness, as well as biomass were correlated with a higher rainfall frequency and with shorter annual dry periods in the winter rainfall zone, it would appear that precipitation frequency rather than the total amount of annual precipitation is the discriminating factor for BSC growth and succession. However, it is necessary to point out, that a higher rainfall frequency will only enhance BSC development if rainfall events are substantial enough to allow the organisms to reach or exceed their photosynthetic net compensation points. If precipitation during rainfall events is too low or air temperatures are very high, this may lead to a carbon deficit, and frequent recurrence of such conditions may even cause the death of the organisms. These correlations corroborate our fourth hypothesis, suggesting that long drought periods slow down BSC succession, reduce biomass gain, and negatively affect organisms sensitive to drought periods, such as lichens and bryophytes. A positive correlation between the number of BSC types and the proportion of silt and clay in the soil (Pearson correlation coefficient 0.52, $p = 0.04$) might indicate that fine-grained soils are important for BSC development. It also appears that higher chl_a content is associated with fine-grained soils, thus confirming our fifth hypothesis.

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Patterns of soil lichen diversity along the BIOTA transects in relation to climate and soil features

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Summary*:* The present study was undertaken to assess species number and turnover of soil lichens occurring along the BIOTA Southern Africa transects, analyse their association with environmental parameters and to identify floristic affinities among the Observatories. In total, 73 soil surface lichen species were recorded. Species richness was highest in the Succulent Karoo, followed by the Savanna and Desert Biomes, while soil lichens were absent (or scarce) in the Nama Karoo Biome. The Observatories subject to winter rainfall were lichenologically clearly distinct from the ones in the summer rainfall area. In order to identify the environmental factors most related to lichen richness at the different Observatories, a multivariate analysis with selected climatic (temperature, air humidity and rainfall) and soil (acidity, electrical conductivity) parameters, and altitude was carried out. While humidity, soil salinity, air temperature and altitude proved to be significantly correlated with lichen richness in most sites, soil acidity and precipitation amount were relevant only in few cases.

Introduction

Soil-inhabiting lichens are an important component of the biodiversity in arid and semi-arid regions of the world. They colonise open space between individual higher plants and, through their anchoring structures—rhizomorphs and rhizohyphae—act as mechanical stabilisers of the soil surface, protecting it against wind and water erosion. Furthermore, lichens contribute to soil fertility, including the nitrogen fixing by photobionts of cyanolichens. They are functionally important as food source and camouflage for certain invertebrates and as nesting substrate for birds and insects (Cornelissen et al. 2007). Soil lichens also occur on less disturbed soils and in later colonisation stages of biological soil crust development (Belnap et al. 2001).

In comparison to vascular plants, lichens are known to be strongly influenced by certain environmental factors, such as atmospheric moisture and temperature, but less by soil moisture (Ellis et al. 2007). However, soil lichens are closely related to other features of the soil, particularly its texture and chemistry (Eldridge 2001, Rosentreter & Belnap 2001). It is apparent that macro- and microclimate are the primary determinants for the distribution patterns of soil lichens (Cornelissen et al. 2007) but it is largely unknown, which are the most important drivers of lichen diversity in southern Africa.

Hitherto, accounts of lichen diversity patterns across biomes or climatic gradients in southern Africa have been restricted to a few case studies, results of which cannot be extrapolated to other ecosystems. For instance, several authors have investigated lichen communities and species composition changes in the Namib Desert (Jürgens & Niebel–Lohmann 1995, Schieferstein & Loris 1992, Lalley & Viles 2005, Wirth et al. 2007, Wirth & Bungartz 2009), or studied the lichen mycota and communities of the Knersvlakte (Succulent Karoo) (Zedda & Rambold 2009). Extrapolations are indispensable for predicting ecosystem processes that promote and maintain biodiversity (Schmiedel & Jürgens 2005). Only the study by Zedda & Rambold (2004) compared the diversity of lichens along the BIOTA transects in southern Africa while species compositions of different Observatories and in different vegetation types were analysed in detail by Zedda et al. (submitted).

Global climate change may become a severe factor affecting lichen diversity, especially in arid and semi-arid regions like southern Africa. Understanding and predicting the response of species to climate change is essential for the development of long-term conservation strategies (Hannah et al. 2002), however, simulation models are generally restricted to a limited range of organisms, predominantly animals and vascular plants, and has only rarely considered lichens.

The following study hypothesises diversity shifts among soil lichens recorded across different biomes covered by the BIOTA transects, under different climatic and soil conditions, and aims to assess species richness typical of each biome. Finally, this work investigates, which ecological parameters are associated with diversity of lichen species and the degree of lichenological affinity among the Observatories.

Material and methods

Lichen diversity was investigated at 30 Observatories along the BIOTA Southern Africa transects covering all biomes of this region: Fynbos, Succulent Karoo, Nama Karoo, Savanna and Desert (Fig. 1, Table 1). General information on Observatories and biomes is provided in volume 1 of this book.

Representative material of all soil-growing lichen species at each Observatory was collected for subsequent

Table 1: List of recorded species at the investigated sites (SA = Savanna; DE = Desert; NK = Nama Karoo; SK = Succulent Karoo; FY = Fynbos), percentage and absolute frequency of species in the regions characterised by summer (SR) and winter rainfall (WR)

Code	01	02	03	04	05	06	41	38	39	40	36	37	16	34	35	09	08	11	10	12	20	22	24	25	26	27	28	32	31	33			
Seasonality of rainfall	SR																				WR											SR	WR
Locality	Mile 46	Mutompo	Sonop	Toggekry	Otjiamongombe	Okamboro	Sandveld	Claratal	Narais	Duruchaus	Ganab	Rooisand	Wlotzkasbaken	Kleinberg	Gobabeb	Niko (grazed)	Niko (reserve)	Nabaos 7	Gellap Ost	Karios Gondwana	Numees	Soebatsfontein	Paulshoek	Remhoogte	Goedehoop	Ratelgat	Moedverloren	Elandsberg	Riverlands	Cape of Good Hope	Frequency (%)	Presence	Presence
Biome type	SA	SA	SA	SA	SA	SA	SA	SA	SA	SA	SA	SA	DE	DE	DE	NK	NK	NK	NK	NK	SK	SK	SK	SK	SK	SK	SK	FY	FY	FY			
Lichen taxa																																	
Acarospora sp. 1*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	1	.	.	.	.	7	0	2
Acarospora sp. 2*	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	7	2	0
Anthracocarpon virescens	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	3	0	1
Buellia sipmanii	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	1	0
Buellia sp. 1*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	1	.	.	1	.	.	.	.	13	0	4
Buellia sp. 2*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	1	.	.	.	10	0	3
Buellia sp. 3*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	3	0	1
Buellia sp. 4*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	3	0	1
Caloplaca sp. 1*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1	1	1	.	.	.	13	0	4
Caloplaca sp. 2*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	.	.	.	7	0	2
Caloplaca volkii	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	1	0
Cladonia cervicornis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	3	0	1
Cladonia sp.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	3	0	1
Cladonia symphycarpa	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1	7	0	2
Collema coccophorum s.l.	1	.	1	.	1	1	.	.	1	1	.	1	.	.	.	.	.	.	.	.	1	1	1	1	1	1	1	1	.	.	50	7	8
Collema crispum	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	1	0
Collema tenax	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	7	1	1
Collema texanum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	3	0	1
Diploschistes aeneus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	3	0	1
Diploschistes cf. *thelenelloides*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	3	0	1
Diploschistes hensseniae	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	1	.	.	1	1	.	1	.	.	17	1	4
Endocarpon cf. *pallidulum*	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	1	0
Endocarpon cf. *simplicatum*	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	1	0
Endocarpon sp.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	3	0	1
Eremastrella crystallifera	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	1	1	.	.	13	0	4
Heppia adglutinata	.	.	.	.	1	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	13	3	1
Heppia arenacea	.	.	.	.	.	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	7	2	0
Heppia cf. *conchiloba*	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	1	0
Heppia despreauxii	.	.	1	1	1	1	.	.	1	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	23	7	0
Lecidella crystallina	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	7	2	0
Lichinaceae sp. 1*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	3	0	1
Lichinaceae sp. 2*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	.	.	.	7	0	2
Lichinaceae sp. 3*	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	1	0
Lichinella stipatula	.	.	.	.	1	.	.	.	1	1	.	1	.	.	.	.	.	.	.	.	.	1	.	.	1	.	.	.	.	.	20	4	2
Peccania arabica	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	1	1	1	.	1	.	.	.	20	0	6
Peccania cf. *subnigra*	.	.	.	1	.	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	1	1	.	.	.	.	.	.	.	.	17	3	2
Peccania font-queriana	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	1	1	.	1	.	.	.	17	0	5
Peltula coriacea	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	3	0	1
Peltula patellata	1	1	1	.	1	1	.	.	1	1	.	1	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	30	8	1
Peltula radicata	.	.	.	.	1	1	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	10	3	0
Phloeopeccania pulvinulina	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	1	0
Phloeopeccania sp. 1*	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	1	0
Placidium lacinulatum	.	.	1	.	1	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	10	3	0
Placidium semaforonense	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	.	.	.	.	.	.	.	7	0	2
Placidium squamulosum	.	.	.	.	1	1	.	.	1	1	.	.	.	.	.	.	.	.	.	.	1	1	1	1	1	1	1	1	1	.	43	4	9
Placidium tenellum	.	.	.	.	1	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	1	1	1	1	1	1	1	1	.	.	37	3	8
Protoparmelia sp. 1*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	3	0	1
Psora aff. *cerebriformis*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	3	0	1
Psora crenata	.	.	.	.	.	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	1	1	1	1	1	1	1	.	.	.	30	2	7
Psora sp. 1*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1	1	1	.	.	.	.	.	13	0	4
Ramalina sp.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	1	0
Sarcogyne sp. 1*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1	.	.	.	.	.	7	0	2
Siphula flavovirens	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	3	0	1
Teloschistes capensis	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	1	0
Toninia aff. *lutosa*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	1	1	.	.	10	0	3
Toninia australis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1	1	1	1	.	.	.	17	0	5
Toninia cerebriformis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	3	0	1
Toninia lutosa	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	.	1	1	1	.	.	.	17	0	5
Toninia ruginosa subsp. *pacifica*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1	.	.	.	.	.	7	0	2
Toninia ruginosa subsp. *ruginosa*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1	.	.	.	.	.	7	0	2
Toninia sp.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	7	1	1
Verrucaria compacta agg.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	3	0	1
Xanthoparmelia aff. *imitatrix*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1	.	.	.	7	0	2
Xanthoparmelia amphixanthoides	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	3	0	1
Xanthoparmelia crassilobata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	3	0	1
Xanthoparmelia epigea	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	3	0	1
Xanthoparmelia hyporhytida	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	3	0	1
Xanthoparmelia leonora	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	1	.	.	.	10	0	3
Xanthoparmelia prolata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	3	0	1
Xanthoparmelia simulans	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	1	.	.	.	10	0	3
Xanthoparmelia sp. 1*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	3	0	1
Xanthoparmelia sp. 2*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	3	0	1
Xanthoparmelia terricola	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	3	0	1
Total	2	1	4	2	13	5	0	0	14	11	0	4	9	2	0	0	0	0	0	0	19	24	7	8	30	16	17	9	4	1			

* undescribed species

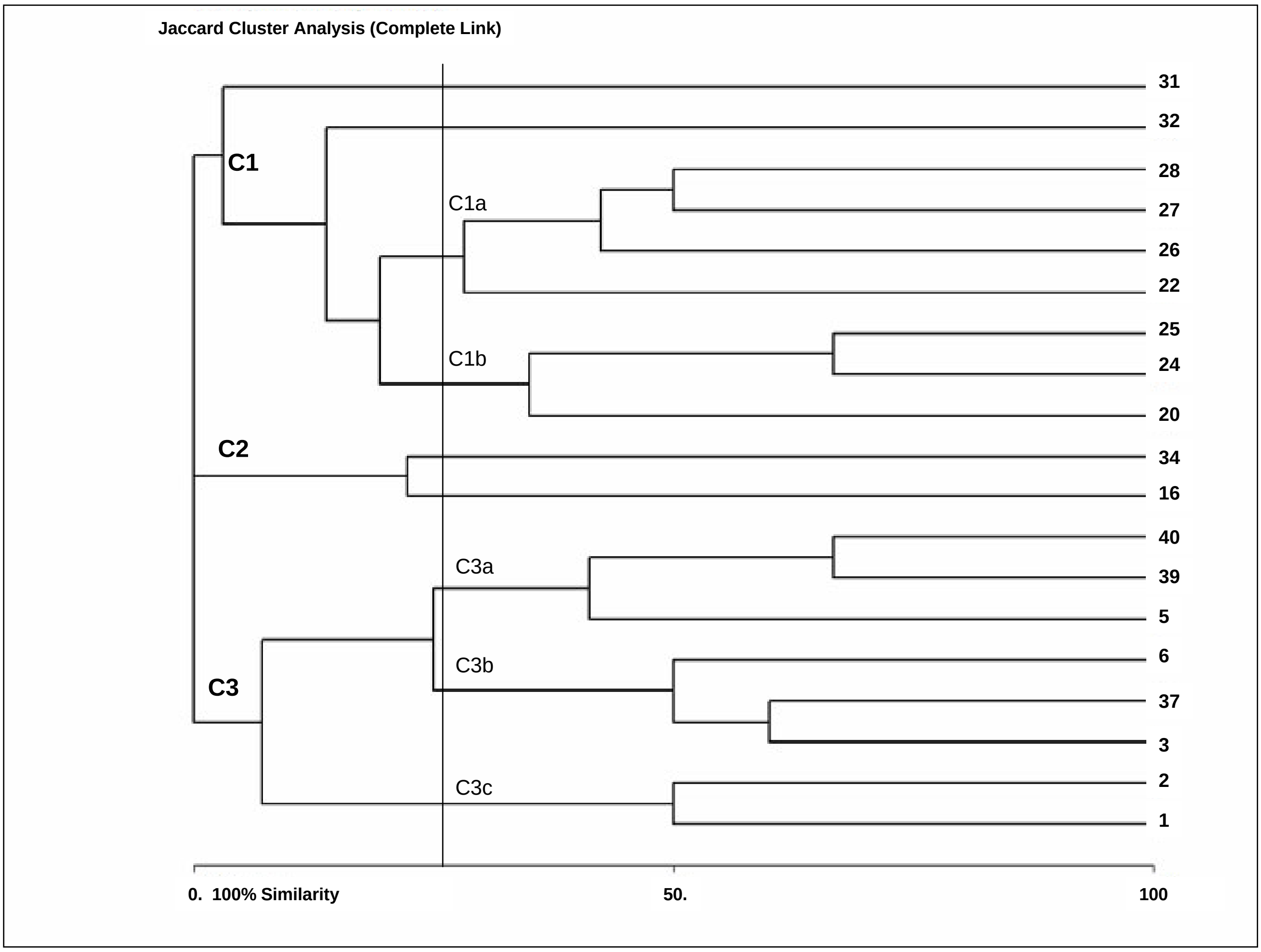

Fig. 1: Similarity between Observatories on the basis of their lichen composition.

identification. For soil analysis, 25 one hectare plots were chosen randomly on each Observatory in the different strata where one profile was surveyed, 4 m south of the centre point of each hectare plot.

Lichen material was morphologically and chemically analysed in the laboratory, and identified using keys listed in Zedda & Rambold (2004, 2009) as well as the interactive identification keys of the online project LIASlight (Rambold et al. 2001–2010). Soil samples were air-dried and sieved to < 2 mm. Soil pH was measured in 0.01 M $CaCl_2$ (10 g dry weight + 25 ml solution) with a pH-electrode after stirring for 1 hour. Analysis of electrical conductivity of the soil solution followed the same procedure using distilled water (Reeuwijk 2002).

Average values for soil pH and electrical conductivity were calculated for each Observatory. Average values of rainfall, temperature and air humidity were calculated for the period 2001–2009. For those sites lacking BIOTA climatic data, the climate datasets of South Africa (Schulze 1994) and Namibia (Mendelsohn et al. 2002) were consulted.

A Cluster Analysis (including the Jaccard coefficient and Complete Link for sites with at least two lichen taxa) and a Principal Component Analysis (PCA), with a significance level $p = 0.05$ was calculated using XLSTAT 2008.

Results

Seventy three soil-inhabiting lichen taxa were recorded along the transects (Table 1). In the Succulent Karoo, Goedehoop (30 spp.), Soebatsfontein (24 spp.), Numees (19 spp.) and Moedverloren (17 spp.) had the highest number of species.

Considering the frequency of species, the most common ones were *Collema coccophorum* and *Placidium squamulosum* (present in 50% and in 43% of sites, respectively), *P. tenellum* (37%), *Peltula patellata* (30%) and *Psora crenata* (30%). A large group of 54 species (74% of total) was present in less than 10% of the Observatories and are therefore considered here as rare. Eleven taxa, having in most cases higher frequency of occurrence, were present in the summer rainfall as well as in the winter rainfall regions (*Collema coccophorum*, *Heppia adglutinata*, *Lichinella stipatula*, *Peccania* cf. *subnigra*, *Peltula patellata*, *Placidium squamulosum*, *P. tenellum*, *Psora crenata* and *Toninia* sp.), whereas 17 species were restricted to the Observatories characterised by summer rainfall regime, and a larger group of 45 species only occurred in the winter rainfall region.

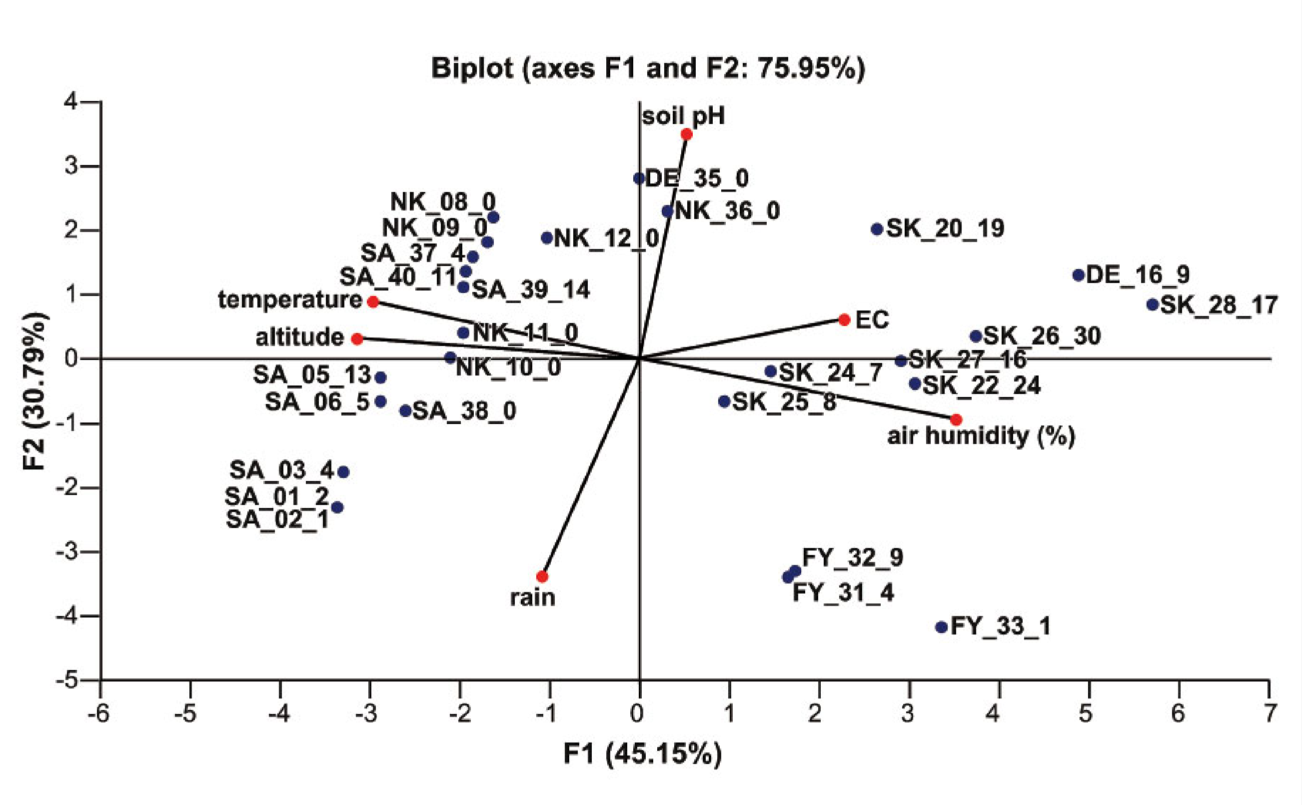

Fig. 2: PCA ordination plot of investigated sites according to main environmental parameters. Designation of sites include indication of biome type (DE = Desert, FY=Fynbos, NK= Nama Karoo, SA = Savanna, SK = Succulent Karoo), Observatory number (e.g. 27) and lichen species richness.

The number of lichen species richness was highest in the Succulent Karoo with a maximum of 30 species and a minimum of seven on these sites (Table 1). In this biome, lichens were found on all Observatories investigated. Lichen richness of all Observatories of the Succulent Karoo amounts to 48 taxa, corresponding to a 66% of the total number of species recorded along the BIOTA Southern Africa transects. More details on the soil-inhabiting lichens of the Knersvlakte (Succulent Karoo) are given in Zedda & Rambold (2009). In the Savanna Biome the highest richness observed was 14 species, but some Observatories lacked any lichens. Soil-inhabiting lichen were absent on all Observatories in the Nama Karoo, whereas in the Fynbos, lichens always occurred, however, with lower species numbers compared to other biomes (1–9 spp.). In the Namib Desert, 9 species occurred on Observatory S16, while on other sites, fewer than 2 species were present.

The cluster analysis in Fig. 1 shows that species composition of the Observatories in the winter rain region (group C1, South African Observatories) is clearly distinct from the ones characterised by summer rainfall (groups C2 and C3, Namibian Observatories). Nevertheless, coastal Observatories (C2) are also separated from the inland one (C3) in Namibia. Considering a similarity of at least 25%, the sites in the Fynbos Biome (S31, S32) appear distinct from those in the Succulent Karoo, and within the Succulent Karoo a further separation is present among cluster C1a, composed of Knersvlakte and Soebatsfontein sites (S22) and the cluster C1b, represented by the more inland sites S24 and S25, and by Numees (S20). Among the inland Namibian Observatories, the most northern sites (S01, S02) are clustered in C3c. Narais, Duruchaus and Otjiamongombe (S39, S40 and S05) (C3a) differs from C3, which includes Sonop, Okamboro and Rooisand (S3, S6 and S37).

The first component of the PCA explained 45.2% of the variance of the ecological factors from all 30 Observatories studied, while the second explained another 30.8% (Fig. 2). The axis ‘F2’ of the PCA is dominated by air humidity, soil salinity, air temperature and altitude, whereas axis ‘F1’ is ruled by soil acidity and annual rainfall. The biome affiliations of the sites are found in distinct areas of the PCA graphs. While, the Fynbos sites are clearly isolated from the others, the Succulent Karoo sites have some overlap with those of the Desert Biome which itself overlaps the Nama Karoo. The numerous Observatories from the Namibian savanna only exhibited some overlap with those of the Nama Karoo but not with other biomes. The sites with the highest lichen diversity belong to the Succulent Karoo and are characterised by higher air humidity and soil salinity and relatively lower mean annual temperature (Fig. 2). Lichen richness was also related to altitude. In this regard, annual rainfall as well as soil acidity is apparently also associated with lichen species richness. The Fynbos sites (S31, S32 and S33) with low lichen diversity, for instance, were associated with higher rainfall and lower pH. The Observatory Numees (S20),

Photo 1: Lichen fields of the Namib Desert.

having high lichen diversity, was associated with increased soil pH and low rainfall. Nevertheless, as shown by PCA, the two ecological factors are nearly oppositional and their individual effects cannot be clearly separated.

The association of climatic factors and altitude with lichen richness was also clear in the Savanna Biome, as demonstrated for the two lichen rich Observatories 39 and 40, located at high altitude (c. 1,650 m), characterised by relative lower annual rainfall (200–300 mm) compared to other savanna sites, and low soil acidity.

Comparisons of two pairs of neighbouring Observatories with strongly contrasting grazing intensity (39 and 40 in the Savanna, 24 and 25 in the Succulent Karoo) indicate that, with increased grazing a reduction in species number occurs (Savanna: 14 → 11 species; Succulent Karoo 8 → 7 species).

Discussion

Our results suggest that strong spatial differentiation of soil lichen diversity and composition along the BIOTA Southern Africa transects is mainly due to considerable latitudinal extension of the Observatories and to the corresponding macroclimatic and vegetation differences. Compared to other arid to semi-arid regions of the world, species richness of soil-growing lichens from the study area is relatively high. Previous reports for Africa by Büdel (2001) of 19 soil lichens and 59 species by Zedda & Rambold (2004) for southern Africa are extended considerably in the current study. Considering that the present study only investigated a total area of 29 km^2 actual numbers of soil lichen species can be assumed to be much higher. Eldridge (2001) has reported a total of 250 taxa of lichens and bryophytes in biological soil crusts in arid and semiarid regions at a global scale. About twenty taxa recorded along the BIOTA transects are common and widespread in southern Africa and have also been reported as common and ubiquitous in dry inland sites of other semi-arid regions of the world (Belnap et al. 2001, Rogers 2006). The occurrence of such rich lichen mycota in the Succulent Karoo needs to be further investigated. Despite of comparable air humidity and fog conditions, the Fynbos Biome houses much less soil-inhabiting lichens and have a partly different lichen mycota. This could be explained with the less favourable soils in the Fynbos Observatories (often sandy, acidic soils), by the higher plant cover and by the greater occurrence of fire events. In the Succulent Karoo, higher plants spatial distribution is more open while soils are compact and stable, with higher content of calcium carbonate, all favourable conditions for lichen growth.

In the present study, the climatic factors with a significantly stronger relationship with lichen species richness were air humidity and temperature. The association of species distribution with altitude most probably represents an indirect correlation with dewfall occurrences. Dewfall is a common phenomenon at higher altitude sites because of low nocturnal temperatures. However, to date, no dewfall measurements are available from the Observatories, but the occurrence of dew was frequently observed in the field in the early morning. Dewfall is an important source of moisture in savannas characterised by low air humidity and absence of fog in contrast to other biomes. The dependence of lichens on nightly dewfall in dry conditions has been demonstrated by Lange (2000) and by Lange et al. (1970) for other arid to semi-arid regions.

Results suggest that increased rainfall positively influence the presence of certain species (e.g. *Cladonia symphycarpa*) in southern Africa, but a decline in rainfall seems to have a negative impact on lichen occurrence as a whole, especially in areas where fog or dew events are also limited (i.e. in the Nama Karoo). The influence of fog could not be investigated in detail in this work due to the lack of data from many Observatories. But several works carried out by other authors have demonstrated the beneficial effects of fog for the lichen diversity in the Namib Desert (Lange et al. 1990, 1994, Lalley & Viles 2005, Wirth et al. 2007).

Unsuitable climatic conditions are significantly correlated with lichen absence, as it is the case in the Nama Karoo. Low air humidity, high temperatures and low rainfall amounts appear to be the most important climatic factors limiting lichen development there. Also in the Namib Desert, lichens are rarer or absent with a decreasing positive influence of fog and dew from the coast to inland. Other studies in dry regions of the world have also shown absence of lichens under comparable climatic conditions (Belnap et al. 2001, Rogers 2006). Lichen species richness in the central-northern savannas of Namibia and in the summer rainfall region appears most significantly correlated with altitude, and floristic composition appear to be also distinct at higher altitude, as shown in Fig. 1 (cluster C3a).

Although intensive grazing increases the proportion of open patches and thus the potential living space for soil lichens, it is most likely that a decrease in species numbers is caused by the enhanced trampling and the effects of soil surface disturbance.

The absence of lichens in potentially suitable sites (e.g. favourable climatic conditions), is possibly a consequence of unfavourable soil conditions. Except for a few cases (Numees, Fynbos Observatories), the relationship of lichens with soil acidity was weak, but the relationship with soil salinity appeared stronger. This correlation could simply be an indirect one due to particular climatic conditions at sites with saline soils, commonly found close to the coast. However, it could also be related to an elevated calcium carbonate content of saline soils and to a lower competition pressure between higher plants and lichens. A direct salt intake in aerosols for water capture can also be hypothesised, since salinity is known to positively affect the moisture regime of lichen thalli (Zedda et al., submitted). The weak relationship with soil acidity could be due to the fact that mean values from 25 samples per Observatory were calculated for characterising soil acidity of each site. Other correlations carried out at a smaller scale, however, show a much stronger positive relationship between lichen richness and abundance with this soil parameter (unpublished data). Soils are often very patchy within one site and a mean value may not be a suitable parameter representing soil acidity of a given site.

This study suggests that there is potential to use species number of lichens as a predictor of the effects of future climate change, however further studies are necessary for a better understanding of the bioindicative value of lichens in southern Africa. It is expected that a reduction of air humidity, fog, dew and rainfall, and increasing temperatures as a consequence of predicted global climate warming, would have a significant negative influence on lichen diversity within the study area.

Photo 2: Soil-inhabiting lichens in the Savanna Biome (Otjiamongombe).

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Changing patterns of lichen growth form distributions within the lichen fields of the Central Namib

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Summary: Lichen vegetation in the Central Namib Desert, which extends from the coast to over 45 km inland, was classified into six zones based on species composition and sensitivity to wind erosion and drought. The lichen vegetation zones, which occur with increasing distance from the coast, are the *Caloplaca* crustose coastal zone, *Xanthoparmelia walteri* coastal zone, *Teloschistes capensis* zone, Inner *Xanthoparmelia walteri* zone, *Xanthoparmelia hottentotta* zone, and *Xanthoparmelia serusiauxii* zone. The sensitivity of the different lichen growth forms in these zones to abrasion by wind borne sand particles and rainfall were assessed from their measured distributions and condition prior to and following significant storm events. Within the lichen field near Wlotzkasbaken, a storm event in 1989 eroded approximately 4 metric tons of lichen dry mass, which represented 0.2% of the approximately 2000 metric tons present in the *Teloschistes capensis* zone. A thunderstorm in 2003 eroded about ten to hundred times as much as the storm event in 1989. Taking differences in recovery processes into account, the response to wind-erosion can be considered as the most important functional parameter of the lichen species of this harsh habitat.

Introduction

The Namib Desert is a narrow "peneplain" extending between the Atlantic Ocean in the west and the escarpment in the east. Although smaller in extent than other deserts, its climate (Logan 1960, Ward & Corbett 1990) and vegetation (Besler 1972, Loris et al. 2004, 2009, Seely 1987, Walter 1986) are extremely variable. Along the coastal belt extending 60 km inland, climatic conditions are harsher than those in other subtropical deserts (Goudie 1972, Lancaster et al. 1984, Logan 1960, 1968). The average 15 mm of precipitation received per year makes the Namib one of the most arid global ecosystems, although this hyper-aridity is moderated by low temperatures, high atmospheric relative humidity, frequent cloud cover and intermittent fog and dew precipitation (Henschel & Seely 2008). These variable climatic conditions favour the growth of poikilohydric lichens and biological soil crusts (BSC) (Büdel et al. 2009, Lange et al. 1990, 1991, 1994, Ullmann & Büdel 2001, Wessels & van Vuuren 1986, Wirth et al. 2007).

Lichen species diversity and cover is not evenly distributed in the Namib. Areas with high lichen species richness and cover alternate with barren plains comprising only a few individuals of crustose lichens. Near Wlotzkasbaken (Observatory S16) and Cape Cross, dense stands of foliose and fruticose lichens occur. They are collectively referred to as "lichen fields" (Mattick 1970) and, together with other lichen fields of various sizes and composition, have subsequently been described by various authors (i.e. Wessels & van Vuuren 1986, Wessels 1989, Schieferstein & Loris 1992, Loris et al. 2004, Schultz 2006, Wirth et al. 2007, Loris et al. 2009). Initially, differences in fog precipitation were considered as crucial in determining the composition and structure of lichen fields. However, Loris et al. (2009), in their study of the dynamics of these lichen fields, identified a number of other geomorphological, edaphic and climatic factors, such as episodic bergwinds, sand- and thunderstorms as being important too.

Materials and Methods

Study area

The study area in the Central Namib Desert comprised the lichen field extending from the coast at Wlotzkasbaken, 35 km north of Swakopmund (22°21’ S, 14°26’ E) and 45 km inland in a northeasterly direction. Other lichen fields in the region of similar composition include those in the southern Namib described by Jürgens & Niebel-Lohmann (1995) and in the northern Namib described by Lalley & Viles (2005).

Lichen species and their growth forms

Since this report was focussed on lichen growth forms and their distribution rather than biodiversity, only dominant and common species were used for classifying different lichen vegetation zones. Four lichen growth forms were distinguished:

Crustose lichens have the highest species diversity and grow in the broadest spectrum of habitats. Apparently, they are most wind-resistant. Examples are: *Acarospora* sp., *Caloplaca elegantissima*, *Caloplaca namibensis*, *Caloplaca testudinea*, *Xanthoparmelia dregeana*, *Xanthoparmelia tentaculina*, and the crustose-like appressed foliose *Xanthoparmelia serusiauxii*. One specialised group are **gypsicolous crustose** lichens: *Caloplaca volkii*, *Lecidella crystallina*. **Foliose** lichens include some of the most abundant lichen species in terms of

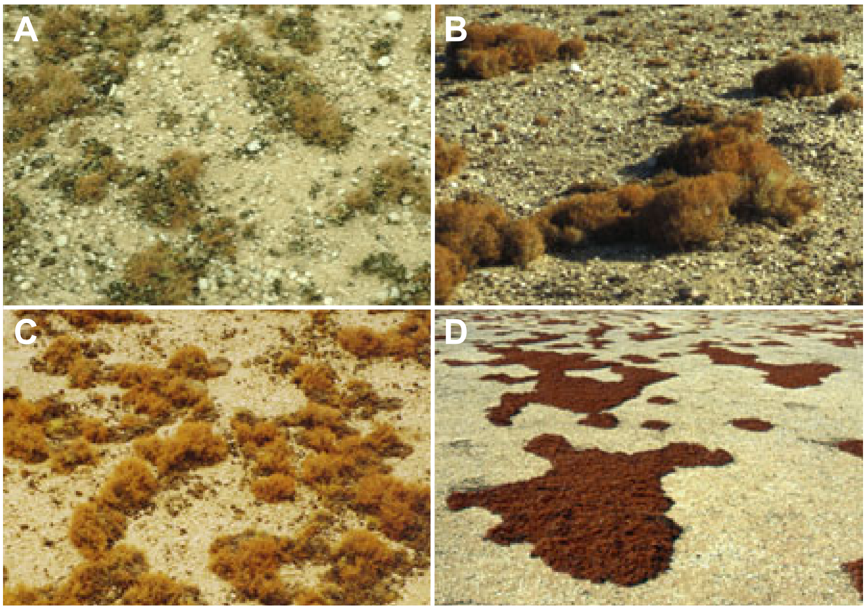

Photo 1: Different growth forms of *Teloschistes capensis*: Tufts (A), cushions (B), mats (C), aggregated mats (D). After Loris et al. 2009.

biomass and distribution: *Xanthoparmelia convoluta*, *Xanthoparmelia walteri*. **Fruticose** lichen species are well-adapted to fog precipitation: *Ramalina* sp., *Teloschistes capensis*.

Besides the different lichen growth forms, one species, *Teloschistes capensis*, shows an astonishing plasticity in growth patterns and shape (Loris et al. 2009). This fruticose species grows most abundantly in small individual tufts (Photo 1A) and dominates the central parts of the lichen fields as cushions (Photo 1B) or is adjoined to mats (Photo 1C). When such mats are pushed into each other during storm events, they may become piled into several layers, and the lower parts of these aggregated mats (Photo 1D) subsequently decay.

Lichen distribution patterns

Ground based observations supplemented by aerial photographs and satellite based imagery (Schultz 2006) was used to monitored changes in the size, shape, structure and composition of the lichen field between 1987 and 2006, and the changes were compared to published historical records (Schieferstein 1989, Schieferstein & Loris 1992, Müller 2003, Loris et al. 2004, Loris et al. 2009). These observations, combined with estimates of lichen ground cover and dry mass, enabled the quantitative estimation of erosion and translocation of lichen biomass during storm events.

Results and Discussion

Lichen distribution patterns

Six distinct lichen zones differing in growth form and species composition were distinguished and named according to Loris et al. (2009).

Crustose coastal zone, CRZ

This zone was populated mainly by the crustose species *Caloplaca elegantissima*, *C. namibensis*, *C. testudinea*, *Xanthoparmelia dregeana* and *X. tentaculina* of the floristically defined distribution type 1 (Wirth et al. 2007 and Article III.3.7). The zone commenced immediately behind the coastal dunes and extended approximately 50 m inland except at its northern and southern limits where it stretched several hundred meters further inland, forming a horseshoe shape. The crustose species occurred on gravel substrates in between furrows that were orientated in an inland direction. *Lecidella crystallina* and *Caloplaca volkii* developed stable biological soil crusts on fine, sandy and gypsic substrates. Autochthonous fruticose and foliose lichen species were absent, except for small fragments blown in by wind (Fig. 1).

Xanthoparmelia walteri coastal zone, XWCZ

This zone lays adjacent to the Crustose zone on its northern and southern flanks (Fig. 1) and comprised the foliose lichen *Xanthoparmelia walteri* attached directly to the gravel substrate on which the crustose lichens occurred (Fig. 1).

Teloschistes capensis zone, TCZ

This zone was dominated by the fruticose lichens *Teloschistes capensis* (Photo 1A–D) and *Ramalina* spp., and commenced 300 m from the coast and extended about 10 km inland. Its western boundary was not parallel to the coastline but followed the undulating relief (Fig. 1). Foliose and crustose lichens were still present in this zone but restricted to smaller gravels not suitable as stable substrates for the larger fruticose lichens. *T. capensis* was seldom found on gravel substrates, but was generally attached to *Xanthoparmelia walteri*, which in turn normally grew on top of *X. dregeana* s.l. and various crustose species.

Within this zone, lichen density and total dry matter per area (of which *T. capensis* provided the largest fraction) increased inland from the coast reaching maximum levels ca. 1.5 km inland and decreased asymptotically thereafter (Wirth et al. 2007). However, total lichen dry mass remained more or less constant further inland as the cover of foliose and crustose lichens fluctuated only slightly, which does not correspond with decreasing amounts of fog precipitation (Loris et al. 2009). The different growth forms displayed by *T. capensis was noteworthy*. Tufts attached to gravels and *Xanthoparmelia walteri* near the coast, which were not distributed homogeneously but clustered into shapes resembling polygons and circles ranging from 0.1 to more than 1 m in diameter, were most abundant. These formed matrices resembling reticulate grids at high densities. Mats and cushions accompanied the tufts up to 2 km inland after which their occurrence terminated abruptly. The tufts remained but their abundance and size decreased gradually with increasing distance inland, with crustose lichens and the foliose *X. walteri* again becoming more prominent.

Inner *Xanthoparmelia walteri* zone, IXWZ

Where *X. walteri* dominated the landscape again, large and steeper dolerite ridges emerged, so that the gravel plains were dissected and drastically reduced in size. The continuous lichen fields were consequently dissected into isolated patches. In this zone, crustose lichens of the floristically defined distribution type 3 (Wirth et al. 2007 and Article III.3.7) were associated with *X. walteri*, which became steadily more sparse. The same applied to *T. capensis,* which was restricted to the lee sides of large rocks and vanished beyond ca. 30 km from coast. This zone was distinct from the *Xanthoparmelia walteri* coastal zone due to these differences, although they are connected at the northern and southern edges of the lichen field and change gradually.

Xanthoparmelia hottentotta zone, XHZ

This zone, occurring between 15 and 35 km inland, comprised isolated lichen patches found on gravel plains dissected by steep dolerite ridges (up to 50 m height). It was dominated by *Xanthoparmelia hottentota,* which is resistant to the abrasive impact of sand storms (evident from the wind-polished rocks) when the broad and upright thalli are in a dry state. This lichen occurred together with crustose lichens such as *Caloplaca elegantissima* and *Teloschistes capensis,* which were restricted to the more moist habitats, on the south-western sides of rocks, caused by the prevailing fog from the south west.

Xanthoparmelia serusiauxii zone, XSZ

This zone was located at over 35 km distance from the coast and comprised *X. hottentotta* and *X. walteri* (which were restricted to rare wind-protected habitats), the wind-resistant *X. serusiauxii* and *X. Dregeana,* and a few crustose lichens such as *C. elegantissima* and *Acarospora* species (Wirth et al. 2007 and Article III.3.7). The zone is subject to the abrasive action of strong easterly and south westerly winds transporting abundant sand materials, and to more severe drought due to less frequent fog occurrence.

Lichen sensitivity to storm events

Lichen sensitivity to abrasion by wind born sand particles and rainfall were assessed from their measured distributions and condition prior to and following significant storm events in 1989, 2002 and 2003 (one example is illustrated in Fig. 2).

A powerful bergwind in 1989 severely affected the fruticose lichens *Teloschistes capensis* and two different *Ramalina* species (Article III.3.7). Their thalli were torn from the tufts and cushions and these were dispersed widely over the lichen field, with the strongest wind gusts even breaking the stones to which lichen tufts were attached and scattering them across the gravel plains. This process started on the eastern boundary of the fruticose *Teloschistes capensis*-zone at a distance of 10 km from the coast, where the detached lichen thalli were transported towards the coast. Considerable amounts of lichen material trapped by bushes growing on the beach rim indicated that large amounts of the eroded lichens were transported into the ocean. Wind dispersed lichen fragments were also trapped by more firmly attached lichen cushions, thus increasing their size with vast amounts of transported lichens, which were also deposited on the lee sides of slopes and ridges as well as in trenches and ephemeral rivers. Estimated quantities of lichen fragments trapped by shrubs from artificially constructed fences of similar dimensions was approximately 4 metric tons of lichen dry mass, which represented 0.2% of the approximately 2000 metric tons of lichen dry mass present in the *Teloschistes capensis* zone (Schieferstein & Loris 1992) of this lichen field.

The most disastrous impacts on lichens during the 1989 bergwind event were observed at a distance of 15 km from the coast where vast amounts of sandy materials were transported by the wind. Both crustose lichens such as *C. elegantissima* and *C. namibensis,* and those with a crust-like thallus such as *X. dregeana* s.l., as well as the wind-resistant *X. hottentotta* were severely damaged during the 1989 storm, with *T. capensis* tufts on the south-western side of rocks completely abraded

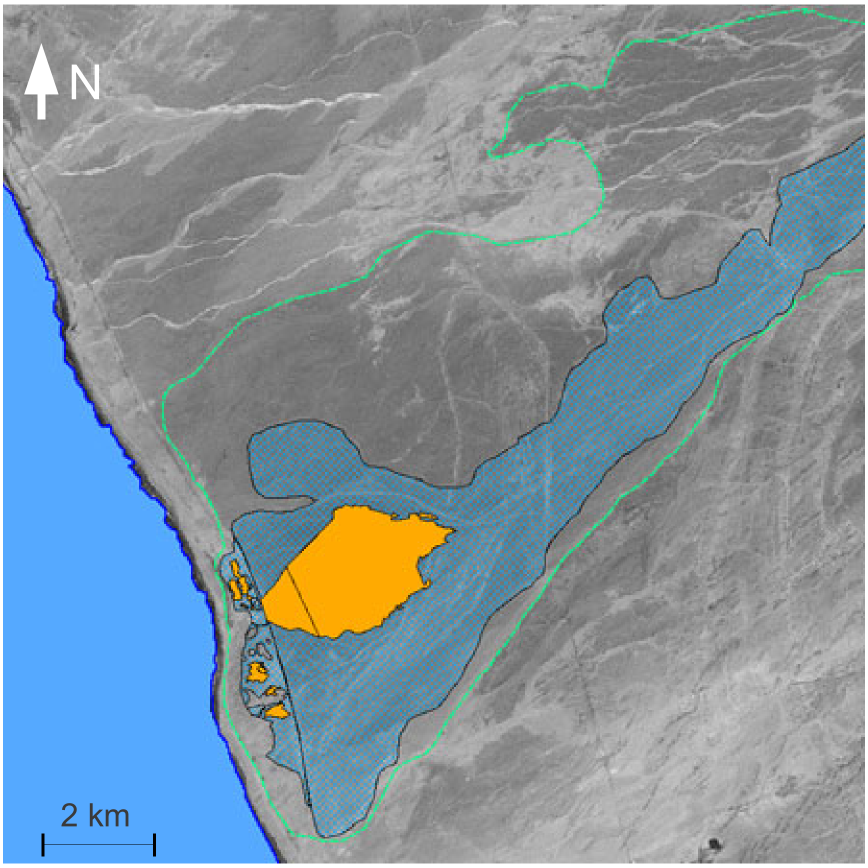

Fig. 1: Zonation of the coastal parts of the lichen field near Wlotzkas Baken as recorded in march and April 2006. *Teloschistes capensis* zone TCZ (solid), *Xanthoparmelia walteri* coastal zone CXWCZ (shaded), outline of the crustose zone CRZ (dashed line). Shading of the landscape is given by a Modis Terra Scene.

Fig. 2: Sand blasts in the Namib desert during a föhnstorm (bergwind). RGB composite (Terra Modis Sensor) from 9 July 2004, 9:35 UTC; provided by the NASA Goddard Space Flight Center.

to the point of attachment. Despite the massive damage, sufficient lichen fragments capable of regeneration survived, resulting in negligible effects on overall lichen diversity. However, regeneration rates were extremely slow with rates of ca. 2 mm per decade measured in fruticose and foliose lichens over a 10 year (1992 to 2001) observation period. Apart from the most storm resistant *C. elegantissima,* crustose lichens exhibiting even slower regeneration rates.

Thunderstorms in 2002 and 2003 had a somewhat different affect on the lichens. Tufts and cushions of *T. capensis* were aggregated into undulating mats in exposed areas and into compressed mats on the leeward side of hills and ridges (Photo 2A & B) indicating that rain water is also involved in the aggregation processes. This is supported by Meteosat-data, which showed expanding clouds of exceptional size and height over the Inner Namib during this period. The situation changed strikingly once again during a thunderstorm in 2003. From the coast to about 6 km inland, almost all cushions of *T. capensis* disappeared from the substrates further inland with their tufts detached entirely, and *X. walteri* lost most of its thalli. Eroded lichen tufts and cushions were compressed and accumulated into piles several square meters in area and up to 15 cm in height, with large shrubs such as *Arthraerua leubnitziae* and *Salsola* sp. completely covered by the eroded lichen material (Photo 2C). The total amount of wind eroded lichen material was estimated to be two orders of magnitude higher in 2002 and 2003 than after the storm event in 1989.

Conclusions

This study demonstrates that lichen zonation and distribution in the Central Namib is not only a function of decreasing fog amounts and frequency inland from the coast as previous studies have implied (Mattick 1970, Wessels & van Vuuren 1986, Walter 1986), but is also a function of increasing wind severity and abrasiveness. As shown here, different lichen growth forms exhibit different sensitivities to such events. Wind-sensitive fruticose species such as *Teloschistes capensis* and *Ramalina* spp. are distributed closer to the coast than wind and abrasive resistant lichens such as the crustose *Caloplaca elegantissima* or species with adnate thalli, such as *X. serusiauxii*, which occur under the harsher conditions further inland.

Storm events that transport large amounts of eroded lichen materials towards the coast are important for the distribution of lichen biomass, and this process also relies on the existence of higher plants to trap these materials. These higher plants in turn depend on higher amounts of available precipitation, and thus the influence of climate on lichens and higher plants has to be considered extremely complex and sensitive to changes in any direction. The rate of regeneration is also likely to plays a major role. Recovery can take place fairly rapidly, for example crustose lichens have a growth rate of 2 mm every 10 years (Loris et al. 2009), while *Teloschistes capensis* shows a higher growth rate and, as described above, a higher rate of dispersal.

Therefore, response to wind-erosion can be considered as a lichen adaptation, which is ecologically significant in these harsh habitats. Presumably, it is manifested in the different growth forms, which separates species into different functional types that populate different ecological niches. In all cases, interactions between lichens, higher plants and climate are complex. As described here, these interactions not only involve competition in single habitats but also processes arising from episodic dry matter translocation on a larger scale.

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Photo 2: Wind erosion of lichens near the coast at LF 4. Photos A and B were taken from the same position and perspective, A dating from 2000 and B after the thunderstorm in April 2003. C shows a nearby shrub of *Salsola* sp. completely covered by wind-accumulated lichen materials. After Loris et al. 2009.

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Lichen distribution along an ocean-inland transect in the fog zone of the Central Namib

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Summary: The lichen flora on gravel plains in the Namib-Desert fog zone north of Swakopmund in Namibia was investigated at 25 sites along a transect extending from the coast 40 km inland. In total, 42 lichen species were found, which were classified into four groups with different distribution patterns, namely: (1) *Caloplaca testudinea* group comprising *C. testudinea*, *C. namibensis*, *C. volkii*, *Buellia incrustans*, *Lecidella crystallina*, *Xanthoparmelia walteri,* and *X. namibiensis* (within the taxonomical group of *X. dregeana* s.l.) present both inland and along the coast, (2) *Teloschistes* group comprising *Teloschistes capensis*, *Ramalina* spp. and *Xanthoparmelia tentaculina* restricted to the coast, 3) *Caloplaca rubelliana* group consisting of *C. rubelliana*, *Buellia peregrina*, *B. stellulata*, *Lecidella placodina*, *Xanthoparmelia incomposita* and *Acarospora* species common inland but absent from the coast, and 4) *Xanthoparmelia serusiauxii* group comprising *X. serusiauxii*, *X. evernica*, *X. lapidula* occupying a zone even further inland. Both climatic and mechanical factors affect these lichen distribution patterns.

Introduction

An astonishing phenomenon of coastal subtropical deserts, especially the hyperarid Atacama and Namib, is their exceptionally high biodiversity. Frequent fog and dew precipitation facilitates the survival of flora and fauna in the coastal parts of these deserts despite the low rainfall. Fog precipitation is most easily utilised by lichens, which therefore play an important ecological role in these so-called "fog deserts".

In the Namib Desert, lichens occur so frequently that they dominate the landscape. Mattick (1970) defined such areas as "lichen fields", eight of which occur between the Kuiseb and Ugab rivers (Schieferstein & Loris 1992). Lichen fields dominated by the fruticose lichen *Teloschistes capensis* are well known for their orange coloured mats of high biomass, which seemingly cover the soil surface and they are consequently described as terricolous (Lalley & Vlies 2005) even though most of these and other co-occurring lichen species are indeed saxicolous, depending on gravel substrates for their establishment.

Previous studies of the coastal lichen fields in the Namib Desert between Swakopmund and Ugabmond have shown that the lichen species are not distributed homogeneously (Walter 1937, Giess 1981). The conspicuous *Teloschistes capensis*, which is dominant along the coast, declines in density inland with a somewhat similar pattern displayed by the greenish foliose lichen *Xanthoparmelia walteri*. In more inland areas, crustose lichens and those with adnate foliose thalli such as *Xanthoparmelia incomposita* and *serusiauxii* are more common. These diverse patterns of lichen species distribution have been attributed to a decline in the amount and frequency of fog precipitation, which is necessary for intermittent lichen thallus hydration with increasing distance from the coast (Walter & Breckle 1991: 282, Lange et al. 1991).

Photo 1: *Xanthoparmelia tentaculina* of distribution type 2. Photo: V. Wirth.

Materials and methods

The study area comprised a transect aligned almost perpendicular to the coastline (Fig. 1) extending from the coast at Wlotzkas Baken, which is 40 km north of Swakopmund (22°22'17" S 14°25'50" E), to a point approximately 40 km inland (22°08'35" S 14°42'16" E). Twenty-five evenly spaced sampling sites were established along this transect when suitable habitats allowed. Each selected site comprised a uniform gravel plain composed of more or less rounded, partly embedded, pebbles of similar size covering between 40% and 60% of the soil surface. At each site, lichen species composition and abundance were determined in 10 x 0.1 m^2 fully randomised plots, each subdivided into 10 x 0.01 m^2 subplots, applying the method described by Kirschbaum & Wirth (1995).

Results

Lichen diversity

A total of 42 lichen species was recorded along the 40 km transect (Table 1) with species diversity ranging between 12 and 22 species at the 25 sites. The average lichen species diversity for the sites closer to the coast (Sites 1–11) was 13.6 ± 0.4, which increased to an aver-

Table 1: List of observed and identified species. For the more common species relative frequency (%) as compared to the total frequency of all lichens (= 100%) at all sites are given in brackets

Taxon	%
Acarospora ochrophaea	
Acarospora sp.	
Acarospora luederitzensis	0.7
Acarospora gypsi-deserti ad int.	
Buellia follmannii	3.3
Buellia incrustans	6.1
Buellia peregrina	2.5
Buellia sipmanii	
Buellia stellulata	
Caloplaca elegantissima	2.2
Caloplaca lactea-group	
Caloplaca namibensis	7.0
Caloplaca rubelliana	
Caloplaca sp.	
Caloplaca testudinea	14.3
Caloplaca volkii	2.0
Diploschistes henssenii	
Lecidea sarcogynoides	
Lecidella crystallina	10.2
Lecidella placodina	
Ramalina cf. *angulosa* ("*irritans*")	3.3
Ramalina spec. II ("*namibica*")	
Staurothele dendritica	
Teloschistes capensis	5.1
Toninia lutosa/australis	0.9
Xanthoparmelia arrecta	
Xanthoparmelia hueana	
Xanthoparmelia dregeana s.l.	12.7
Xanthoparmelia equalis	
Xanthoparmelia evernica	
Xanthoparmelia follmanni	
Xanthoparmelia hottentotta	
Xanthoparmelia incomposita	
Xanthoparmelia lapidula	
Xanthoparmelia namibiensis	
Xanthoparmelia serusiauxii	
Xanthoparmelia tentaculina	2.1
Xanthoparmelia walteri	11.1

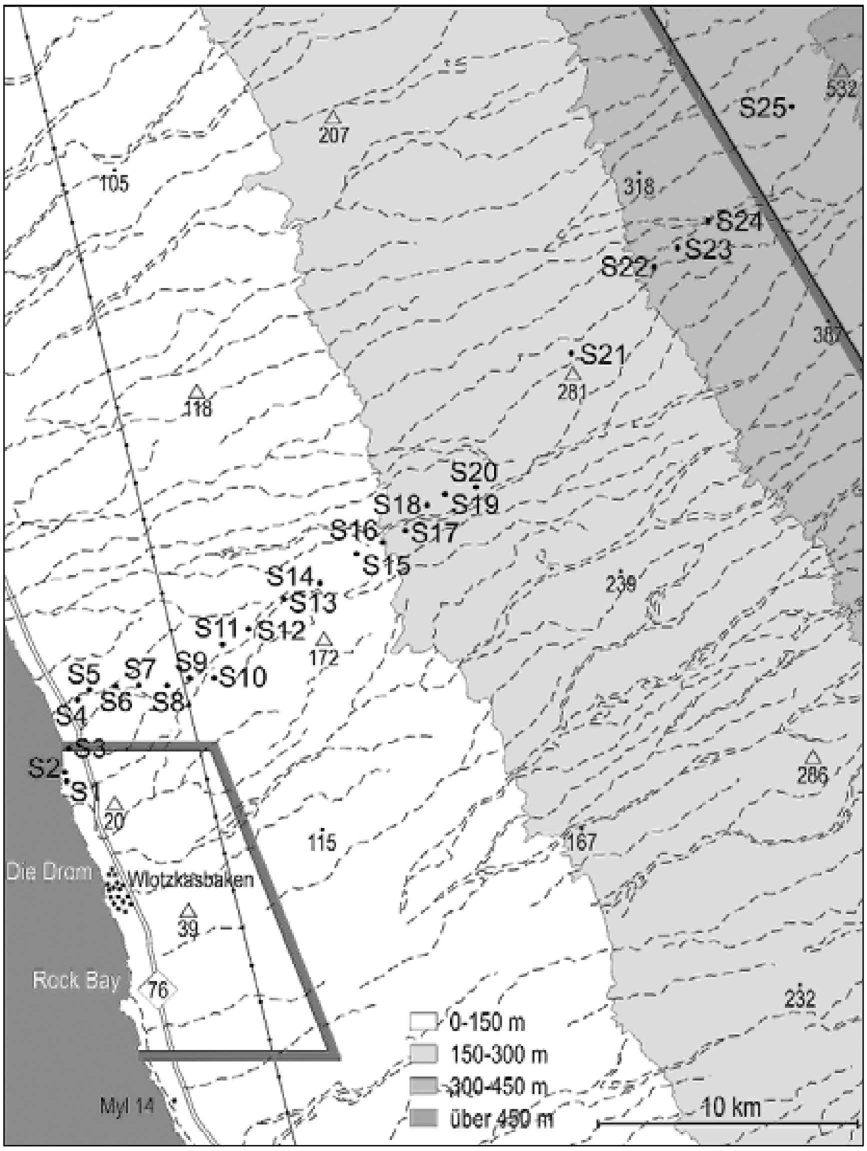

Fig. 1: Locations of the 25 investigated sites (Site 1 to Site 25) along the transect running from SW to NE. Broken lines = ephemeral creeks, thick lines = administrative units, unbroken thin line = power line, numbers triangles = altitude above sea level.

age of 17.5 ± 0.8 on inland sites (Sites 12– 25).

Lichen cover and frequency

Near the coast, total lichen cover averaged 6% at Sites 1–3 with a cover as low as 3% recorded at Site 1 where the sparse lichen population displayed reduced vigour. A steep increase in lichen cover inland of Site 3 was observed, with 42.5% lichen cover recorded at Site 5, which was the highest value recorded along the entire transect (Fig. 2). This was mainly due to the presence of *Teloschistes capensis* (see also Fig. 3). A continuous decline in lichen cover was observed even further inland, to values of 9% at Site 22, 7.5% at Site 23, 6% at Site 24 and 3% at Site 25, with one exception at site 17, which had 5% total lichen cover.

There was generally a poor correspondence between the cover of individual lichen species and their total frequency. A typical example was *Xanthoparmelia walteri* with a measured cover of less than 1%, but a recorded frequency of 100% at Site 14 (Figs. 2 & 3). Substantial heterogeneity in frequency of lichen species was observed between Site 1, where the average of the frequencies of all species was found at 6% and Site 8, where an average as high as 22% was recorded. However, total frequency of lichen species varied less between Site 14 and Site 24, where average frequencies ranged uniformly between 13.5% and 18.8%, Thus, frequency values do not reflect the decrease of lichen cover towards inland. The most common species in the study area was *Caloplaca testudinea* with a relative frequency of 15%, followed by species included in the *Xanthoparmelia dregeana* group (from the coast up to Site 10 almost exclusively *X. namibensis*, further inland mainly *X. dregeana* s.l. and *X. incomposita*), with relative frequencies ranging between 10.2% and 14.3%. Approximately one quarter of all observed lichen species displayed relative frequencies below 1%.

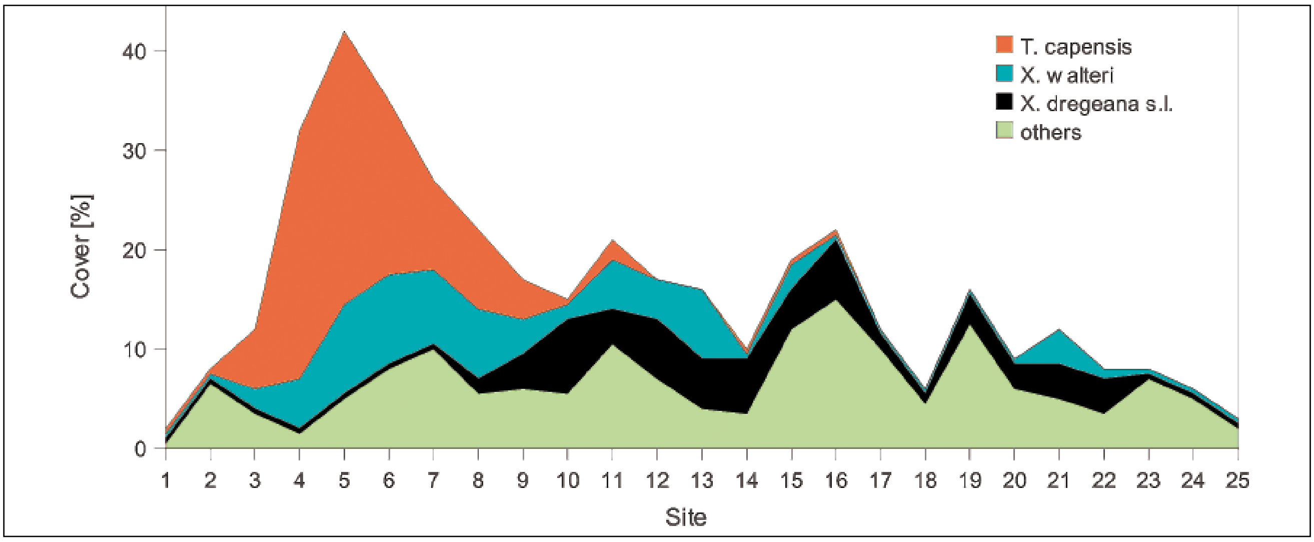

Fig. 2: Coverage (%) of *Teloschistes capensis, Xanthoparmelia walteri, Xanthoparmelia dregeana* s.l. and the coverage of all other observed species along the transect.

Lichen distribution types

Four groups of lichen species with different distributions were distinguished. These were as follows:

Distribution type 1 (*Caloplaca testudinea* group): This group comprised eight lichen species present both inland and close to the coast. Eight species were distributed from the coast to the inland sites, of which *Buellia incrustans*, *Caloplaca testudinea*, *Lecidella crystallina*, brown species of the *Xanthoparmelia dregeana* group (without *X. tentaculina*), and *X. walteri* occurred throughout (Fig. 3). *Caloplaca namibensis* and *C. volkii* were absent at two sites, and *Toninia lutosa/australis*, which generally occurred at very low frequencies, was absent from six sites.

Among the species belonging to the species complex of *Xanthoparmelia dregeana* s.l., *X. namibiensis* was distributed along almost the entire transect (recorded in Sites 1, 2, 4–10, 12, 16, 19, 21–24). Since this species could only be determined by thin layer chromatography of random samples next to plots, it is likely to have occurred at all sites along the transect.

Close to the coast, several species of this distribution type showed a relatively low frequency and often reduced vigour, such as *Caloplaca namibensis*, *Buellia incrustans*, *Xanthoparmelia walteri* and the *X. dregeana* s.l. (Fig. 3). Whereas *X. dregeana* s.l. and *X. walteri* attained high frequency values between Sites 4 and 8 (i.e. the zone of the *Teloschistes* group, see below), the frequency of *Caloplaca volkii* and especially *C. namibensis* remained low in this area, and that of *C. testudinea* dropped considerably. Further inland of the *Teloschistes* zone, the frequency of *C. testudinea*, *C. namibensis* and *Xanthoparmelia dregeana* s.l. increased to up to 100%. Beyond Site 15 the frequencies of *Caloplaca namibensis* and *Xanthoparmelia walteri* decreased continuously, but transitorily rose again at Site 21. Due to the discrepancy between the frequency of *Caloplaca namibensis* at the first ten sites and along the rest of the transect, this species showed a tendency to distribution type 3.

Xanthoparmelia walteri was present in nearly all quadrats from Sites 3 to 15, beyond which its frequency decreased and it occurred only occasionally at sites near the inland end of the transect. *X. dregeana* s.l., which reached a frequency of 100% at Site 8, maintained this frequency up to Site 22, despite a low cover value of only 1–4%.

Distribution type 2 (*Teloschistes* group): This group was composed of lichen species occurring from the coast up to Site 16, with their frequency or coverage decreasing from Site 12 at the latest. At least four species belonged to this group, i.e. *Xanthoparmelia tentaculina*, *Teloschistes capensis*, *Ramalina angulosa*, and *Xanthoparmelia hueana.* The first two species occurred up to Site 16, the *Ramalina angulosa* complex (representing two species, whose proportions could not be differentiated, although both species were certainly present at Sites 4, 5 and 6) was only recorded up to Site 11 (Fig. 3), but otherwise behaved similarly to *Teloschistes capensis*. The vagrant lichen *Xanthoparmelia hueana* was confined to sites very close to the coast and the beginning of the *Teloschistes* field (Sites 1, 3, 4 and 5).

Distribution type 3 (*Caloplaca rubelliana* group): Species of this group were absent from the coastal section of the transect but occurred more or less far into inland areas. Approximately seven species belonged to this group. *Buellia peregrina* was present fairly regularly (14 times) from Sites 9 to 24 and *B. stellulata* (14 times) from Sites 7 to 25. *Acarospora luederitzensis* did not appear until Site 14, but then it occurred regularly; it was only recorded occasionally but was distributed equally in its range (Fig. 3). *Caloplaca rubelliana* (recorded 8 times: Sites 12, 14, 16–21), *Lecidella placodina* (recorded 10 times) and *Buellia follmannii* s.l. (recorded 12 times) first appeared at Site 12. Among the species of *Xanthoparmelia dregeana* s.l., *X. incomposita* (recorded 11 times: Sites 10 to 25) belonged to this group. *Staurothele dendritica*, although only present at Sites 18 and 20, may also be considered as a member of this distribution type.

Distribution type 4 (*Xanthoparmelia serusiauxii* group): The most characteristic members of this group were the two extremely drought-resistant foliose species *Xanthoparmelia evernica* (Site 23) and *X. serusiauxii* (Sites 24 and 25) with adnate thalli, and their appearance caused a distinct change in lichen vegetation. Other notable species that occurred furthest inland and even in extension to the transect were *Acarospora ochrophaea* (from Sites 19 to 25, with an isolated occurrence at Site 14; Fig. 3) and *X. lapidula* (Sites 21 and 25).

X. dregeana s.s. (Site 21), *X. equalis* (Site 25), *Acarospora "gypsi-deserti"* (Site 21, Sites 23–25, but also in Site 2 as a small thallus of reduced vigour) and a sterile grey areolated crustose species (cf. *Acarospora* sp.) (Sites 19 and 20) probably also belonged to this distribution type.

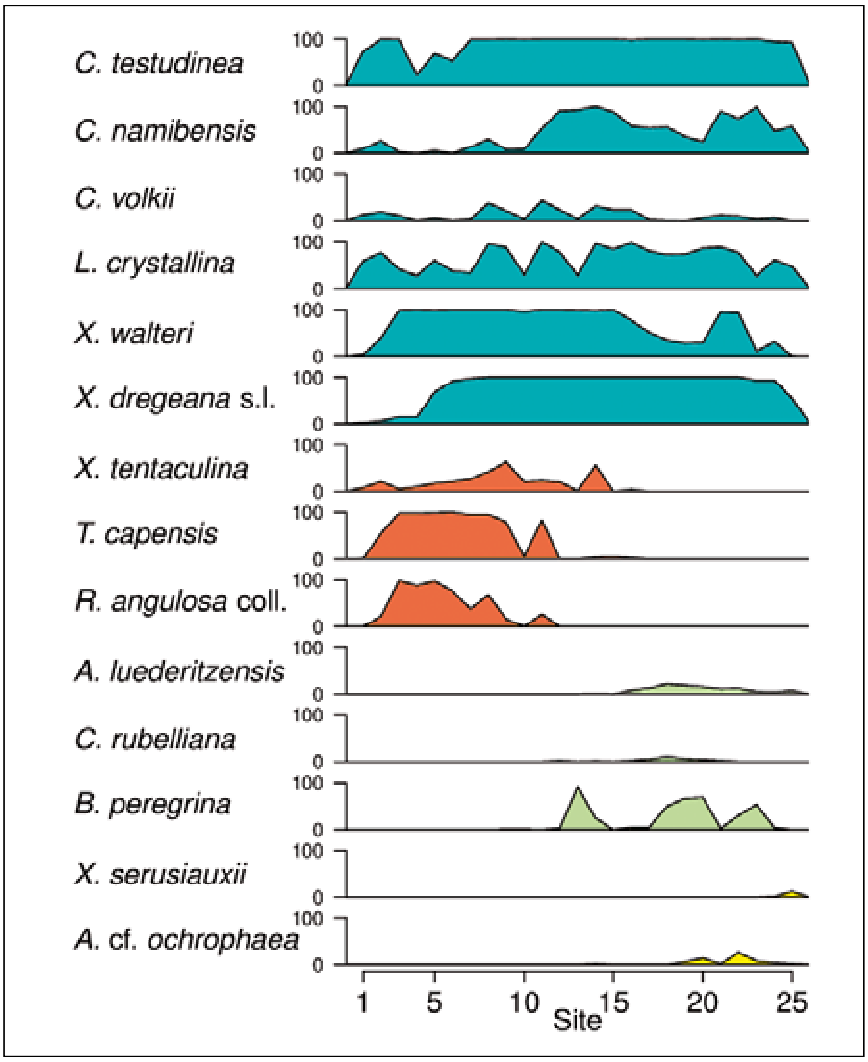

Fig. 3: Frequency (%) of selected lichen species along the transect. Distribution type 1: *Caloplaca testudinea, C. namibensis, C. volkii, Ledidella crystallina, Xanthoparmelia walteri, X. dregeana* s.l. Distribution type 2: *Xanthoparmelia tentaculina, Teloschistes capensis, Ramalina angulosa* coll. Distribution type 3: *Acarospora luederitzensis, Caloplaca rubelliana, Buellia peregrina*. Distribution type 4: *Xanthoparmelia serusiauxii, Acarospora ochrophaea*.

Discussion

Number of species

The number of more than 40 lichen species recorded along the transect is surprisingly high in view of the chosen sampling sites at very similar and uniform gravel plains. The increase in the number of species from coastal to inland sites was not expected considering the corresponding decrease in lichen cover and biomass (Schieferstein & Loris 1992). This change occurs rather abruptly from Site 11 inland, where fruticose lichens disappear. One reason for the relatively limited diversity in the *Teloschistes* zone is the rich development and high biomass of fruticose lichens, which outcompete crustaceous species growing close to the soil surface (see below). Further inland, in parallel with the disappearance of *Teloschistes*, biotic conditions are more favourable for crustose lichens. Another reason may be a greater diversity of suitable substrates, especially of dolerite pebbles, which are more conducive to the establishment of subneutrophytic species.

Lichen cover and frequency

Apart from the closely neighbouring sites (Sites 1 to 3), lichen cover is highest at the sites up to 4 km inland of the coast, a zone characterised by the dominance of *Teloschistes* and *Ramalina*. The high percentage cover of fruticose lichens is associated with poor cover of several crustaceous lichens, e.g. *Caloplaca testudinea* and *Buellia incrustans*. It can be assumed that the fruticose lichens intercept a high percentage of fog moisture, thus reducing the amount available for the crusts. Furthermore, *Teloschistes* cushions can be moved by wind, often with an attached crust of soil substrate. Where they accumulate they may cover pebbles and the crustaceous lichen species growing on them. Inland of Site 5, total lichen cover decreases significantly (Fig. 3), mainly due to the decline of *Teloschistes* itself (Fig. 2) and of *Ramalina* sp. The disappearance of *Teloschistes*, *Ramalina* and *Xanthoparmelia tentaculina* is compensated for in terms of species numbers, but not cover, by the "inland-species" such as *X. incomposita* and *Caloplaca rubelliana*. Even the increase in cover of the crustaceous species of distribution type 1 (e.g. *Caloplaca testudinea*, *C. namibensis*, *Buellia incrustans*), which might be due to the absence of fruticose lichens, does not compensate for the loss of cover due to the disappearance of *Teloschistes* and *Ramalina*.

Distribution of lichen species

Based on the distribution types 2, 3 and 4, it is possible to divide the Namib Desert into floristically defined sections (Wirth et al. 2007). In terms of distances, the first third to half of the transect up to Site 16 (about 15 km from the coastline) the lichen zone is characterised by the occurrence of *Teloschistes capensis*, *Ramalina* sp., *Xanthoparmelia tentaculina* and possibly *X. arrecta*. Inland from Site 16 the Namib is characterised by *Xanthoparmelia incomposita*, *X. lapidula*, *X. serusiauxii*, *X. evernica*, and the concentration of all *Acarospora* species. Functional types are unevenly distributed: fruticose species are confined to the coastal half of the transect and crustaceous lichens and *Xanthoparmelia* species with thalli reminiscent of placodioid crustose lichens dominate the inland half, and the only typical foliose lichen, *Xanthoparmelia walteri*, decreases considerably in cover and frequency here too.

Using a more detailed subdivision, four floristic-phytosociological sections can be distinguished. The first quarter (Site 1 to approximately Site 11) is delimited by a high percentage frequency of *Teloschistes*, the exclusive occurrence of *Ramalina angulosa* s.l. and *Xanthoparmelia hueana* and the constant presence of *X. tentaculina*; the second quarter (approximately Sites 11 to 16) is characterised by species, which are transient in nature with *Teloschistes* and *Xanthoparmelia tentaculina* quickly decreasing, *Caloplaca namibensis* (Fig. 3) and *Buellia peregrina* increasing, and *Xanthoparmelia incomposita*, *Caloplaca rubelliana*, *Lecidella placodina,* and *Buellia follmannii* s.l. appearing. In the third quarter (Sites 17 to 20) *Staurothele dendritica* is found, as well as species of *Acarospora*, namely *A. luederitzensis* (as from Site 14, Fig. 3) and *A. ochrophaea* (as from Site 19, Fig. 3). These species remain present in the last quarter (Site 21 to 25), which is characterised by the inland species *Xanthoparmelia serusiauxii*, *X. evernica*, *X. equalis*, *X. lapidula*, *Acarospora* "*gypsi-deserti*" and the optimal development of *A. ochrophaea.*

Ecological conclusions

Reasons for the described distribution patterns of the lichen species along the transect are complex. Edaphic-petrographic factors probably do not play a decisive role (possibly with the exception of the calcicolous crust *Buellia peregrina*); they certainly have no influence on the strikingly unequal distributions of species in the coastal areas (group 2, *Teloschistes capensis*, *Ramalina* sp., *Xanthoparmelia tentaculina*) or, for example, the decline of the important foliose lichen *Xanthoparmelia walteri*, since favoured substrates (quartz pebbles, gravel sand) are present throughout the length of the transect.

It is obvious, following the general assumption that fog precipitation decreases moving inland, that the high biomass and the luxurious development of lichens in the *Teloschistes* zone are clearly correlated with the particularly favourable moisture conditions close to the coast, and the decrease in cover and finally disappearance of the species of group 2 beyond Site 5 are related to successively more unfavourable conditions caused by diminishing moisture input.

Surprisingly, a significantly greater water input by fog precipitation close to the coast could not be confirmed by measurements in the lichen field of Wlotzkas Baken (close to Observatory S16). According to these measurements fog precipitation is a limiting factor further inland, but not along the coastal part of the transect and therefore does not significantly influence species distribution or biomass in the *Teloschistes* zone (Loris et al. 2004). Nevertheless, near the coast and in the first quarter of the transect, water relations for lichens are more favourable than further inland. The soaking of thalli after dew fall or fog moistening during the night lasts longer because the fog-bank disappears more slowly than further away from the coast—a well known phenomenon (Wirth, own observations). Furthermore, humidity often increases during the afternoon close to the coast with the consequence that fruticose lichens with their multibranched structure take up enough water vapour that the moisture compensation point may be reached (Lange et al. 1990). This probably occurs especially when stratus clouds migrate inland from the ocean, which happens quite often in the late afternoon. Investigations have shown that hydration remains above the compensation point for two hours longer in the zone of high biomass in comparison to inland sites (Loris & Pfiz, unpubl.). This indicates a considerable surplus in carbon balance and is responsible for the high biomass at sites Sites 4 and 5. At least these data suggest there is an ecophysiologically effective gradient in water supply from the coast to inland areas.

However, thunderstorms from the northeast and episodic warm winds, with or without transported sand, also play an important role (Loris et al. 2004, Loris et al. 2009) in lichen distribution. This is especially obvious with the vagrant lichen *Xanthoparmelia hueana.* This species, which does not shed attachment organs, is blown over the plots in the transect, but usually remains in sheltered depressions and between obstacles, as in the case of fruticose thalli in Sites 3 and 4. In a similar manner, wind or thunderstorms may have a considerable influence on the distribution of the easily transportable thalli of *Teloschistes capensis* and *Ramalina* sp. With strong winds these fruticose thalli together with interwoven *Xanthoparmelia walteri* are torn off, and whole tufts and cushions are lifted up with the adherent substrate, and blown away. The material is transported towards the coast, but gets partly trapped around obstacles such as plants (*Arthraerua leubnitziae*, *Lycium tetradum*, *Galenia africana*, Mesembryanthemoideae) or protruding pebbles and rocks.

The restriction of *Xanthoparmelia tentaculina* to the *Teloschistes* zone cannot be explained by storm or leeward effects. A selective accumulation of small pebbles supporting this species by means of wind was not observed and must be excluded as an explanation. It is highly likely that the distribution of this species depends on the moisture gradient.

Similar investigations on mountain slopes almost 100 km further north support the argument that moisture gradients influence floristic changes. Wirth & Heklau (2006) found that only fog precipitation could be responsible for the considerable differences in species composition along transects, which also included a *Teloschistes* zone (at the wettest sites) and zones with *Caloplaca rubelliana* and *Xanthoparmelia serusiauxii* (at distinctly drier sites), where other "inland" species (group 3 and 4) were also found, e.g. *Acarospora* *luederitzensis*, *A. ochrophaea*, *Lecidella placodina*, *Xanthoparmelia incomposita,* and *Staurothele dendritica.* These species are apparently more tolerant to desiccation and better adapted to the relatively dry conditions towards the inland end of the transect. The dark colour of the dolerite substrate may also intensify the dry conditions of the sites by quickly warming the pebbles during insolation.

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Patterns and dynamics of vascular plant diversity along the BIOTA transects in southern Africa

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Summary: Patterns of vascular plant diversity were studied at different spatial scales (100 m^2, 1000 m^2, 1 ha and 1 km^2) along the BIOTA Southern Africa transects from the Kavango in northern Namibia to the Cape of Good Hope in South Africa, covering six biomes in the western part of southern Africa and a steep rainfall gradient. We analysed family richness, species richness, as well as *z*-values (i.e. the slopes of power-law species-area relationships as measures of β-diversity) on all these spatial scales in order to provide baseline data for biodiversity assessment in the region and an understanding of the influence of potential drivers on various dimensions of biodiversity. For the last purpose, we related our biodiversity parameters via correlations, linear and polynomial regressions as well as analyses of variance (ANOVAs) to potential drivers such as geography, landuse, climate, and soil. Finally, we used the time-series data of the BIOTA Observatories to analyse whether a change in species richness occurred during the project period.

The mean species density along the transects was 23.9 species for 100 m^2, with an absolute minimum of 0 (Desert Biome) and an absolute maximum of 128 (Fynbos Biome). The mean value for 1000-m^2 plots was 40 species (maximum: 169; Fynbos Biome), and 159 species (maximum: 385; Elandsberg Observatory, S32, Fynbos Biome) at the 1-km^2 scale. Elandsberg Observatory in the Fynbos Biome showed exceptionally high species richness at all spatial scales.

The following environmental factors showed the strongest relationship with species richness at the 1000-m^2 scale: mean annual precipitation (positive), precipitation seasonality (winter rainfall >> summer rainfall), mean annual temperature, length of dry season, and median pH values (all negative). The complex-factor soil ecotype richness, as an expression of the variability of plant-relevant soil features per 1 km^2, was only related to species richness at the 1-km^2 scale. Spatial species turnover (expressed as *z*-values), was highest in the arid parts of the transect (Desert and Succulent Karoo) and lowest in the Fynbos Biome.

The time series of annual monitoring data of up to nine years revealed a slight but significant mean annual increase in woody plant species richness at the 1000-m^2 plot level for most of the Observatories along the transect. The maximum mean annual increase recorded was +2.2 woody plant species in the Koeroegap Vlakte Observatory (S18, Succulent Karoo). The positive increase corresponds well with the findings of our individual-based plant population monitoring in the Succulent Karoo, which also indicated a stable to increasing development of the plant populations, irrespective of inter-annual variability. The only Observatory with a significant decrease was Wlotzkasbaken (S16) with on average –1.0 woody plant species per year.

We discuss the role of the various drivers of plant diversity at different spatial scales along the transect and relate them to previous studies on regional and global plant diversity patterns. Finally, we highlight that the vascular plant data of BIOTA Southern Africa are a highly valuable, globally unique macroecological dataset in as far as they (i) combine large spatial extent with fine to medium grain, (ii) use a highly standardised sampling approach, including (iii) various spatial scales, (iv) time series, and (v) direct measures of many potential drivers of biodiversity.

Introduction

Southern Africa is renowned for its rich biodiversity (Barnard et al. 1998, Simmons et al. 1998, Goldblatt & Manning 2002, Burke 2003, Linder et al. 2010). The region accommodates two of the global biodiversity hotspots (i.e. Cape Floristic Region and Succulent Karoo, Jürgens 1986, Myers et al. 2000, Kier et al. 2005) and numerous local centres of plant-diversity and endemism (Nordenstam 1969, Davis et al. 1994), several of which are covered by the BIOTA Southern Africa transects: e.g. Cape Peninsula (Goldblatt & Manning 2002), Nieuwoudtville (Snijman & Perry 1987), Knersvlakte, Kamiesberg, Richtersveld (Nordenstam 1969, Hilton-Taylor 1994), and the Okavango Region (Maggs et al. 1998). Despite this species richness and numerous studies on local or regional plant diversity patterns and their drivers (e.g. Cowling 1990, Cowling et al. 1989,

Photo 1: Small-scale richness of succulent plants in the Succulent Karoo. Photo: U. Schmiedel.

Photo 2: Mosaic of different habitats at the Observatory Gellap Ost (S10) in the Nama Karoo. Photo: N. Dreber.

1992, 1994, 1996, 1997, 1998, Goldblatt 1997, Goldblatt & Manning 2002, Linder et al. 2010), studies that provide measures of species richness at different spatial scales in a standardised manner and which relate them to site-specific environmental drivers are scarce. A first comprehensive approach towards a regional comparison has been provided by Cowling et al. (1989).

The landscapes in the study region are prone to transformation and subsequent species loss due to unsustainable landuse (Hoffman & Todd 2000, Hoffman & Ashwell 2001) and projected climate change (Midgley et al. 2003, Thomas et al. 2004, Thuiller et al. 2006, Midgley & Thuiller 2007, Biggs et al. 2008). Vascular plants, the main primary producers, are likely the first to be affected by transformation, which has strong knock-on effects on other groups of organisms (e.g. Blaum et al. 2007, 2009, Siramin et al. 2009, see also Articles III.4.4, III.4.6, III.5.7, III.5.8) and the abiotic environment, such as the soil (Article III.5.4) and microclimate. The consequences might be irreversible losses of biodiversity, with negative effects on the resilience and productivity of the systems.

The extent of changes is hard to quantify, because benchmark data on current and historical states of the environment, which are required to reconstruct the changes over time at a given site, are scarce. Where such data have been available, it has provided valuable insight into environmental changes (Kraaij & Milton 2006, Rahlao et al. 2008). Historical landscape photographs are valuable substitutes for quantitative site-specific data on historical vegetation cover and species composition (Articles III.1.2, III.1.3). Several case studies have used space as a substitute for time by analysing landuse impacts along fence-line contrasts or gradients of landuse intensity around stock posts and water points. These studies, which have been conducted in different biomes of southern Africa, have shown that unsustainable land management may result in changes to the species- and life form composition of vascular plants (Todd & Hoffman 1999, 2009, Riginos & Hoffman 2003, Anderson & Hoffman 2007, Haarmeyer et al. 2010, Wesuls & Lang 2010, and Article III.5.5).

The analysis of fence-line contrasts or resampling of historical permanent plots enables quantification of changes over a given time period, but it does not provide information on the responsible processes and their drivers. Only continuous long-term monitoring of biodiversity and their potential drivers (i.e. climatic factors, landuse management) can provide process-oriented information. The objective of the BIOTA Observatories in southern Africa is to provide baseline data for analysis of biodiversity patterns in southern Africa and, based on annual monitoring, to provide the required evidence for changes in species composition, and the processes and drivers of such change.

In this article, we analyse current patterns of vascular plant species richness at different spatial scales (i.e. 100 m^2, 1000 m^2, 1 km^2) along the BIOTA Southern Africa transect and relate them to major environmental drivers (i.e. mean annual precipitation, rainfall season, soil heterogeneity). Based on nine years of monitoring data, we further provide a quantitative analysis of the changes in species richness of perennial plant species at the BIOTA Observatories.

Methods

Sampling was carried out on 36 of the 37 BIOTA Observatories (see Subchapter II.1.2; insufficient data for Nieuwoudtville, Observatory S45, for our analysis) along the BIOTA transects in southern Africa (see Subchapter II.1.1). From these Observatories, we used 29 environmental variables as predictors, and 12 parameters describing various “dimensions” of vascular plant diversity at different spatial scales as dependent variables. The data availability ranged from 22 to 36 Observatories, depending on the type of variable. The Electronic Appendix 1 gives an overview of the data used, while precise information on their measurement and calculation can be found in Subchapter II.1.3.

Two variables with strongly skewed distributions (electrical conductivity and organic carbon) were log-transformed for the analyses, while all other variables showed distributions sufficiently close to normal to allow the application of parametric statistical tests (see Quinn & Keough 2002). Box-whisker plots were used to display the biodiversity

Table 1: Variables used in the statistical analyses
The majority are metric variables, while ordinal or categorical variables are indicated in square brackets. Similarly, transformations applied to achieve approximate normality of the data are given in square brackets. Detailed information on each of the variables is available in Subchapter II.1.3

Type	**Variable group**	**Variable(s)**
Predictor	General data	Latitude; Longitude; Altitude; Rainfall season [2 categories]; Biome [6 categories]; Intensity of landuse [4-point ordinal, in correlations treated as quasi-metric]
	Climate (modelled data from Worldclim, Hijmans et al. 2005)	Mean annual temperature; Minimum annual temperature; Maximum annual temperature; Annual temperature range; Diurnal temperature range; Annual precipitation; Percentage winter precipitation; Length of dry season; Aridity index (De Martonne)
	Climate (data from BIOTA weather stations)	Inter-annual precipitation variability; Relative humidity; Wind speed; Solar radiation; Potential evapotranspiration; Aridity index (UNEP)
	Soil (chemistry)	pH; Electrical conductivity [log-transformed]; Organic carbon [log-transformed]
	Soil (pedodiversity, after Petersen 2008, see also Petersen et al. 2010)	Reference group richness; Soil unit richness; Soil unit evenness; Soil ecotype richness; Parametric space
Biodiversity (dependent variable)	α-diversity	Cumulative family richness (1 km^2); Cumulative species richness (1 km^2); Species richness (1 km^2, selected year); Mean species richness (1 ha); Mean species richness (1000 m^2); Maximum species richness (1000 m^2); Mean species richness (100 m^2); Maximum species richness (100 m^2)
	β-diversity	*z*-value (1000 m^2 to 1 km^2); *z*-value (1000 m^2 to 1 ha); *z*-value (100–1000 m^2, calculated for individual pairs of nested plots); *z*-value (100–1000 m^2; "mean-to-mean", i.e. calculated between the mean richness values per Observatory at that scales)

values of the individual hectare plots on the Observatories along the transects, arranged according to decreasing summer and increasing winter rainfall. Although analysis of variance (ANOVA) with post hoc tests had revealed that Observatories could be arranged in many distinct groups according to their diversity values, we did not include them as we do not consider them as particularly meaningful here.

For the inferential statistical tests, we used only one value for each Observatory, i.e. mean, median, minimum, or maximum, depending on the specific variable. The analyses were carried out in a two-step approach. First, we established Pearson correlation matrices among the predictors (Electronic Appendix 2), among the dependent variables (Electronic Appendix 3), and between predictors and dependent variables (Electronic Appendix 4). Then we applied linear regression analyses for combinations of predictors and dependent variables with significant and strong correlations and for which a causal relationship was plausible. We used both simple linear and second-order polynomial regressions when the data distribution suggested the latter as the more appropriate model. In this case, we used the Akaike information criterion (AIC), calculated in PAST (Hammer et al. 2001) as an additional measure of goodness-of-fit in comparison of models with different complexity (see Quinn & Keough 2002). In one case, we applied the regression analyses separately for the Observatories of the two rainfall regions (i.e. winter vs. summer rainfall), as the correlations had indicated a strong additional effect of rainfall season. In order to analyse the effects of categorical or ordinal variables on biodiversity measures, we applied ANOVAs.

Finally, we calculated the mean annual change (between consecutive years) in species richness of perennial woody plants (i.e. phanerophytes and chamaephytes) for the 1000-m^2 plots. We did this calculation for each of the 1000 m^2-plots sampled within an Observatory. This resulted in typically 20 values per Observatory (depending on the number of 1000 m^2-plots sampled; see Part II) of a linear increase/decrease rate per Observatory. These change rates per plot were then graphically displayed and subjected to a *t*-test in order to see whether the observed mean change was significantly different from zero.

Results

Relationships among the biodiversity parameters

The majority of the biodiversity parameters were strongly positively correlated to each other (see Electronic Appendix 1). The only exceptions were the *z*-values, which showed—apart from one case—negative and only partly significant correlations to the various richness parameters. Since *z*-values are a measure of β-diversity, this finding means that the relative increase in species richness with spatial scale was generally lower when the small-scale richness was already high. The richness values for the four different spatial scales (100 m^2, 1000 m^2, 1 ha, 1 km^2) within individual years showed the highest Pearson correlation coefficients among all parameter pairs (r = 0.783–0.985), with the values increasing with decreasing plot size differences. The correlation of species richness for 1 km^2 cumulated over all years with the single-year richness values was clearly lower (r = 0.535–0.887), indicating biases caused by the different numbers of years sampled as well as varying "identification rates". The latter might cause "inflated" richness values due to varying field names for the same taxon in different years (see Part II). (Cumulative) family richness was positively correlated with cumulative species richness (r = 0.713) as well as with all other richness values.

Biodiversity patterns along the transects

The number of observed vascular plant families ranged from 1 in the Namib Desert (S34 Kleinberg) to 62 for two of the Fynbos Observatories (S31 Riverlands, and S32 Elandsberg; see Electronic Appendix 1). Generally, the family richness was highest in the Woodland Savanna and the Fynbos, lowest in the Namib Desert, and intermediate in the three other biomes (Fig. 1). For species richness, the differences between the biomes were even more pronounced at the analysed spatial scales of 100 m^2, 1000 m^2, 1 ha, and 1 km^2 (Fig. 1 and Electronic Appendix 1). The Observatories in the Fynbos Biome were the richest at all spatial scales except 1 km^2, where the Observatories in the Succulent Karoo were equally species rich (Figs. 1 & 2). The mean species density along the transects on 100 m^2 was 23.9 species, with an absolute minimum of 0 (at various Observatories, mainly in the Namib Desert) and an absolute maximum of 128 (S32 Elandsberg) (Fig. 2). The mean species density for 1000-m^2 plots was 40 species (maximum: 169 in S32 Elandsberg), 53.6 species for 1-ha plots (maximum: 183 in S32 Elandsberg; note that this scale was probably undersampled at various Observatories), and 159 species at the 1-km^2 scale (minimum: 1 in S34 Kleinberg; maximum: 385 in S32 Elandsberg) (Fig. 2).

Drivers of biodiversity

The 30 abiotic parameters used to explain the biodiversity patterns showed a clear correlation pattern, with each of the parameters being significantly correlated with several other parameters (see Electronic Appendix 2). Apart from trivial relationships such as those between decreasing mean annual temperature and increasing winter precipitation with increasing latitude, differently transformed variants of the same variable, or different measures of similar parameters (e.g. annual precipitation, length of dry season, and De Martonne's aridity index, or among the various pedodiversity measures), the matrix also showed some more subtle connections between various aspects of the environment that need to be considered when interpreting correlations between biodiversity parameters and environmental predictors. The strong negative correlation (|r| > 0.75) of soil pH with mean annual precipitation and with the two aridity indices was one of the more interesting relationships. Furthermore, mean annual temperature was strongly positively correlated to diurnal temperature range and strongly negatively correlated to annual temperature range in the study region. Finally, relative humidity was strongly negatively correlated to diurnal temperature range. Many further, less strong, but still significant correlations can be found in the Electronic Appendix 2.

Regarding species richness (density) as the most important measure of plant diversity, we found clear and consistent relationships for the spatial scales 100 m^2 to 1 ha (see Electronic Appendix 3). The strongest predictors were the precipitation-related parameters, given here in decreasing order of importance: length of dry season (negative, Fig. 6c), De Martonne's aridity index (positive), mean annual precipitation (positive, Fig. 6b), and percentage winter precipitation (positive), while the UNEP aridity index was only correlated at the hectare scale. The second most important predictor group were the soil chemical parameters, organic content (positive) and pH (negative, Fig. 5d). At the 1000-m^2 scale, mean annual temperature was also a weak negative predictor (Fig. 5a). Species richness at the 1-km^2 scale showed similar patterns as at the three smaller scales, but with lower r-values in all cases. Additionally, species richness

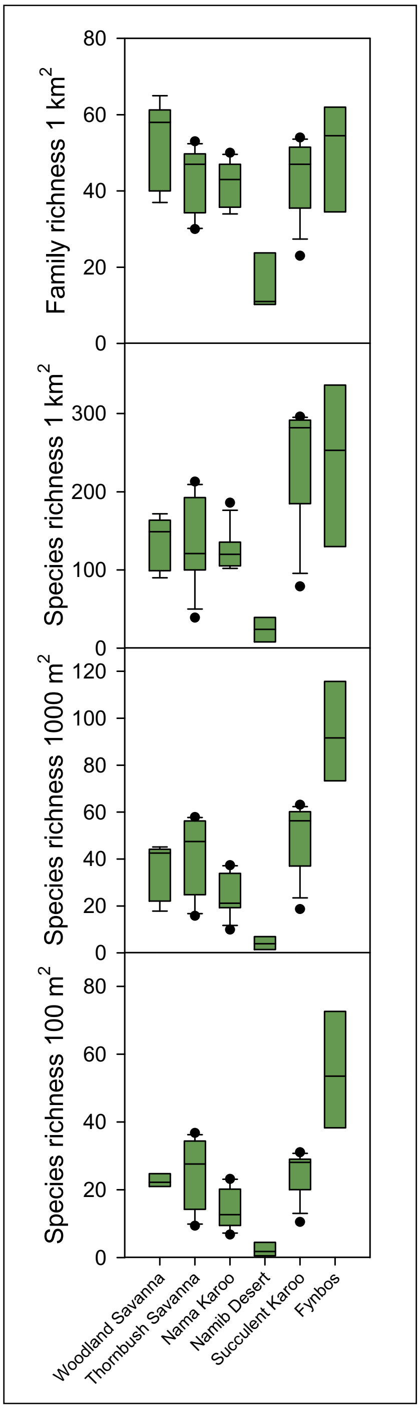

Fig. 1: Variability of the mean vascular plant taxon richness at different spatial scales compared between the Observatories of the six analysed biomes. Family richness is given as a cumulative value over all study years for the entire square kilometre. Species richness values at 1 km^2 are for a selected year with particularly high recorded species richness (mostly 2008; see Electronic Appendix 1), while the species richness data at the two smaller spatial scales are based on means over all years and all sampled hectare plots. The graphs depict medians (lines), inter-quartile ranges (boxes), inter-decile ranges (hinges), and extreme values (dots). The differences between the biomes were significant in all cases (tested with ANOVAs; p = 0.004 for family richness and p < 0.001 for all other parameters).

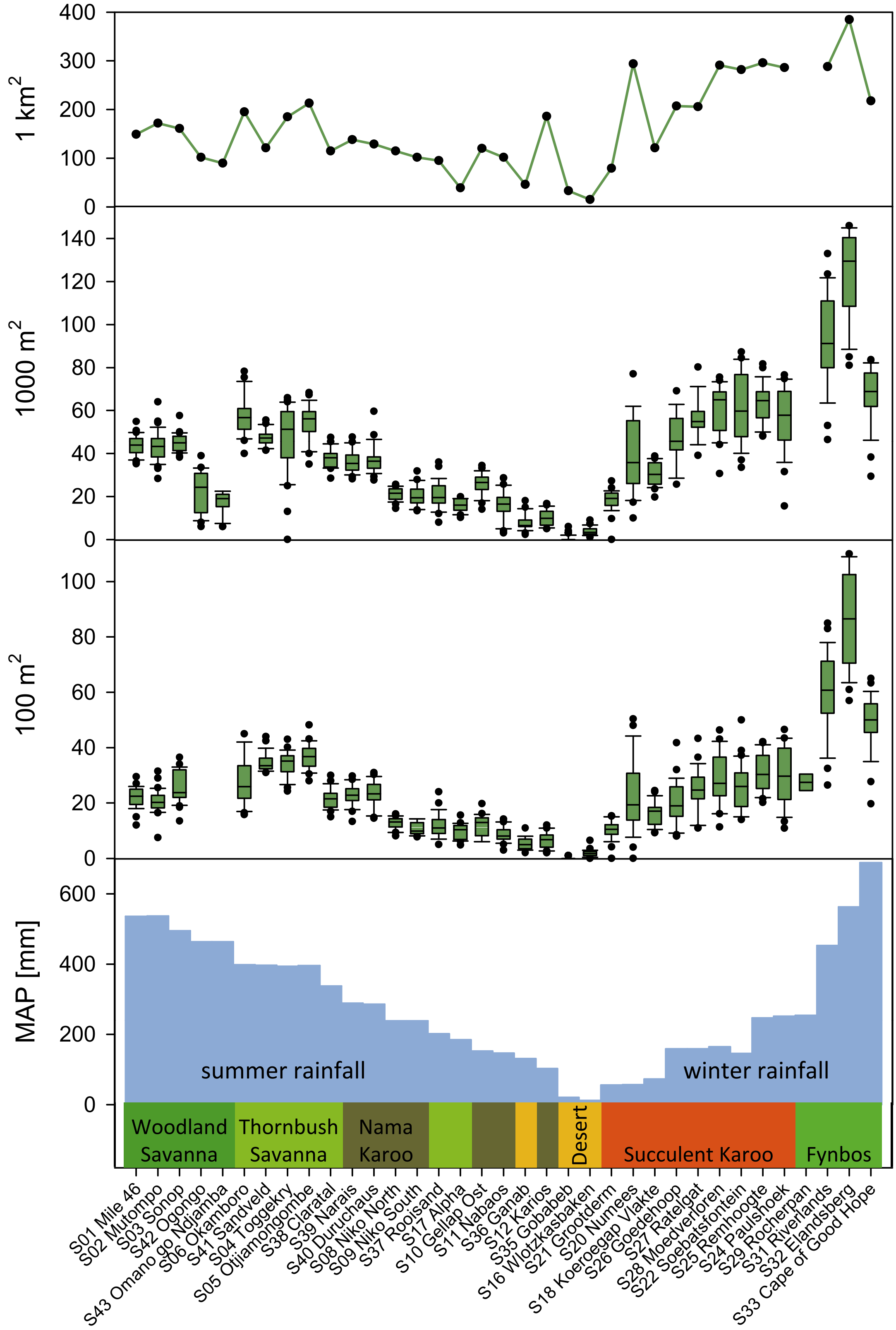

Fig. 2: Variability of vascular plant species richness along the BIOTA transects in southern Africa at three different spatial scales and compared to mean annual precipitation (MAP). The species richness values at the 1-km² scale are those for a selected year with particularly good recording quality (mostly 2008; see Electronic Appendix 1). For the graphs at the two smaller spatial scales, mean richness values of the individual hectare plots were used (i.e. averaged over all years). The graphs depict medians (lines), inter-quartile ranges (boxes), inter-decile ranges (hinges), and extreme values (dots).

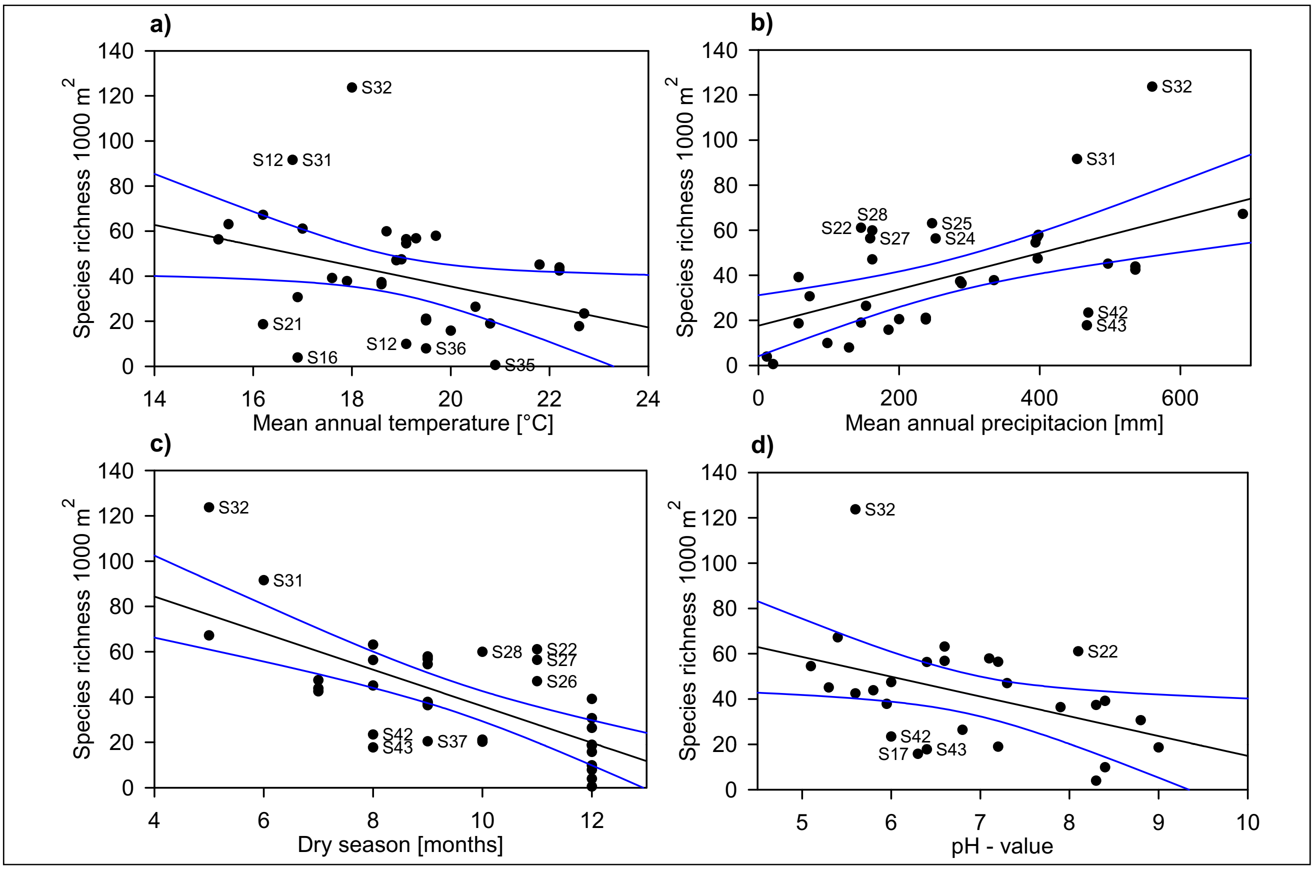

Fig. 5: Regressions of vascular plant species richness at 1000 m^2 vs. four strong environmental predictors. The graphs show the linear regression lines with their 95% confidence intervals. Dots for Observatories with unusually high or low richness values are labelled with their number (for meaning, see caption of Fig. 2). The regression functions for the predictors (x) are: (a) mean annual temperature [°C]: $S = 126.4 – 4.5\ x$, $r^2 = 0.1241$, $p = 0.041$; (b) mean annual precipitation [mm]: $S = 17.64 + 0.08\ x$, $r^2 = 0.5553$, $p < 0.001$; (c) Length of dry season [months]: $S = 116.6 – 8.1\ x$, $r^2 = 0.4622$, $p < 0.001$; (d) median soil pH: $S = 102.3 – 8.7\ x$, $r^2 = 0.1822$, $p = 0.026$.

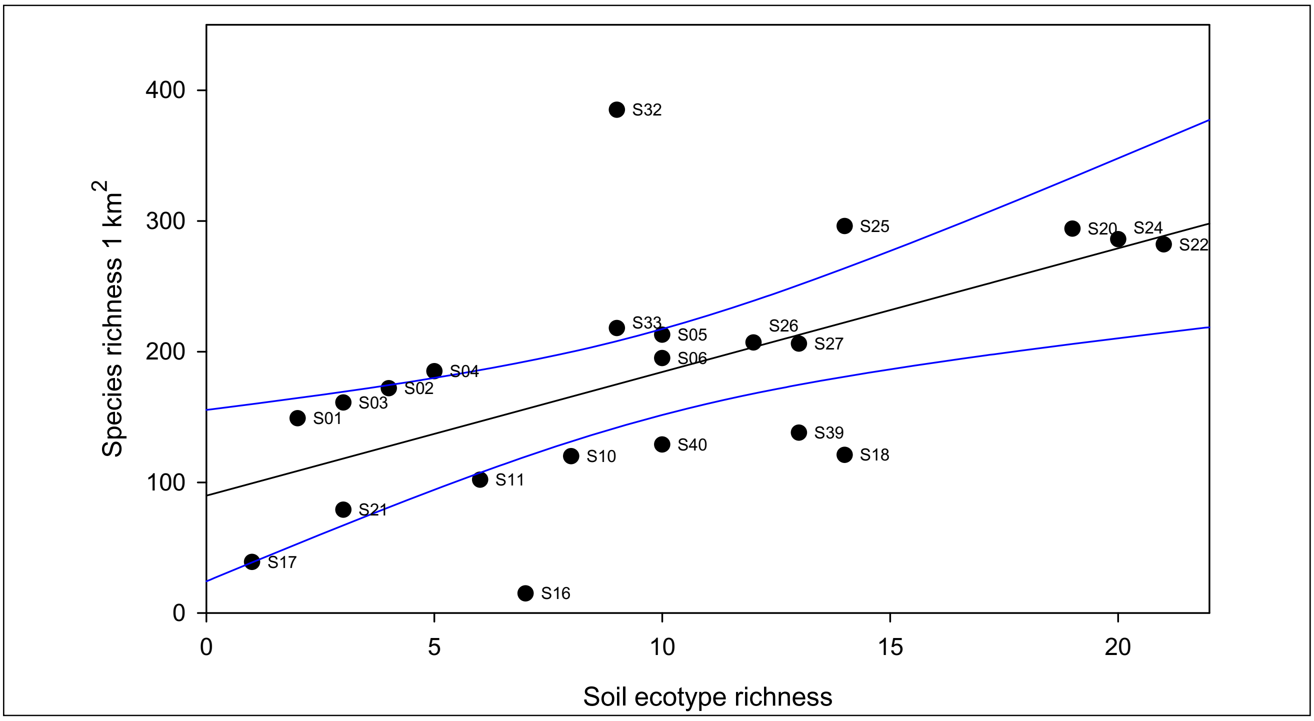

Fig. 6: Linear regression of vascular plant species richness (S) dependent on soil ecotype richness (a measure of pedodiversity) at the Observatory level (x). The graph shows the regression line with its 95% confidence interval. The points are labelled with the Observatory numbers (see caption of Fig. 2). The linear regression ($S = 89.9 + 9.5\ x$) was highly significant ($p = 0.003$; $r^2 = 0.3616$).

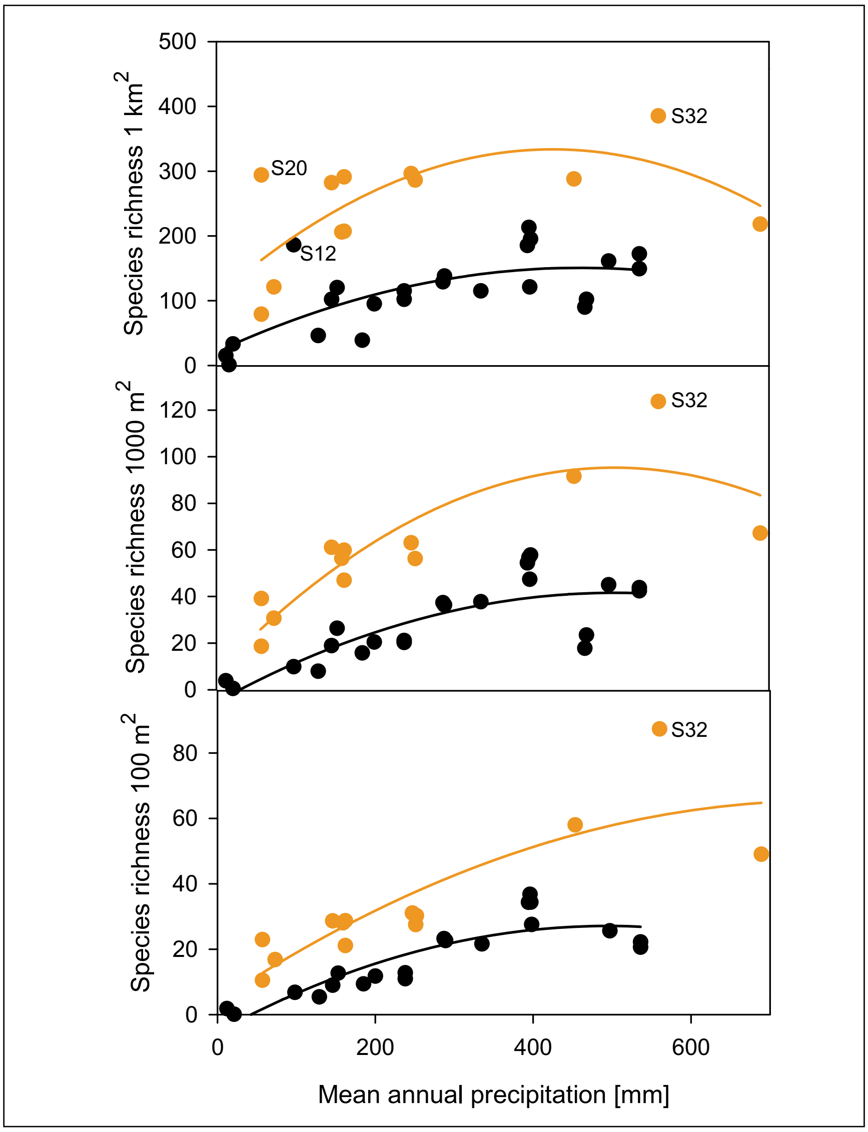

Fig. 7: Second-order polynomial regressions for species richness at three different spatial scales dependent on mean annual precipitation and distinguished between winter rainfall regions (orange; WR) and summer rainfall regions (black; SR). Observatories with unexpectedly high richness values are indicated with their number (for meaning, see caption of Fig. 2). The functions of the regressions of species richness (*S*) on mean annual precipitation/mm (*x*) are: 1 km^2/WR: $S = 105.64 + 1.07\,x – 0.0013\,x^2$, $R^2 = 0.4505$, $p = 0.068$; 1 km^2/SR: $S = 20.92 + 0.56\,x – 0.0006\,x^2$, $R^2 = 0.5003$. $p < 0.001$; 1000 m^2/WR: $S = 7.87 + 0.35\,x – 0.0003\,x^2$, $R^2 = 0.7673$, $p = 0.001$; 1000 m^2/SR: $S = –5.70 + 0.20\,x – 0.0002\,x^2$, $R^2 = 0.6526$, $p < 0.001$; 100 m^2/WR: $S = 3.98 + 0.16\,x – 0.0001\,x^2$, $R^2 = 0.7344$, $p = 0.001$; 100 m^2/SR: $–5.33 + 0.13\,x – 0.0001\,x^2$, $R^2 = 0.7699$, $p < 0.001$.

at this scale was strongly positively correlated to various measures of pedodiversity, in particular to soil ecotype richness (Fig. 6) and to soil parametric space. A closer look at the link between precipitation patterns and species richness at three different spatial scales, revealed that both the total amount of precipitation and the season in which it mainly falls, play a crucial role (Fig. 7). Winter rainfall regions have a consistently two to three times higher species richness than summer rainfall regions with the same total amount of precipitation. Furthermore, the addition of a second-order polynomial term in all six cases lead to a strong increase in explained variance, while the AIC decreased in four cases compared to a simple linear model (meaning that the quadratic model is more appropriate), remained identical in one case, and slightly decreased in the last case (100 m^2, winter rainfall). The always negative quadratic term in the polynomial regressions of Fig. 7 indicates that, beyond a certain threshold, additional precipitation did not further increase richness and could even be associated with lower species richness. Finally, it should be mentioned that some of the Observatories had unexpectedly high or low richness values that could not be explained by any of the analysed predictors. Most notable was the Observatory S32 Elandsberg, with richness values always occurring far above the regression lines (Figs. 5–7). The Observatories Soebatsfontein (S22), Remhoogte (S25), and Riverlands (S31) also showed unexplainably high richness values. Negative deviations from regression lines were much more idiosyncratic, with only the Observatories Ogongo (S42) and Omano go Ndjamba (S43) frequently showing negative deviations.

Family richness responded very similarly to the species richness values of the different scales to mean annual precipitation, aridity indices, soil organic carbon content, and pH (see Electronic Appendix 4). In addition, we found significant influences of landuse intensity (weakly positive), electrical conductivity of the soils (strongly negative), annual temperature range (weakly positive), and solar radiation (weakly negative), while the pedodiversity measures were completely irrelevant for this biodiversity parameter (Electronic Appendix 4).

Interestingly several environmental parameters were of secondary importance and showed no, or only very few, significant (linear) relationships with any of the biodiversity measures. These parameters were altitude, soil-taxonomic richness and evenness of soils, maximum temperature, diurnal temperature range, relative air humidity (only a weak relationship with $S_{100\ \mathrm{m}^2}$). Landuse intensity showed a weak positive correlation with family richness at the 1-km^2 scale and with the β-diversity at the transition from 100 m^2 to 1000 m^2.

Scale-dependence of biodiversity

One means of to describing scale-dependency of taxon richness, the fundamental measure of biodiversity, is through the so-called *z*-values. They represent the slope of the species-area relationship in the log-log representation, and thus describe the relative increase of richness with increasing grain size, but can also

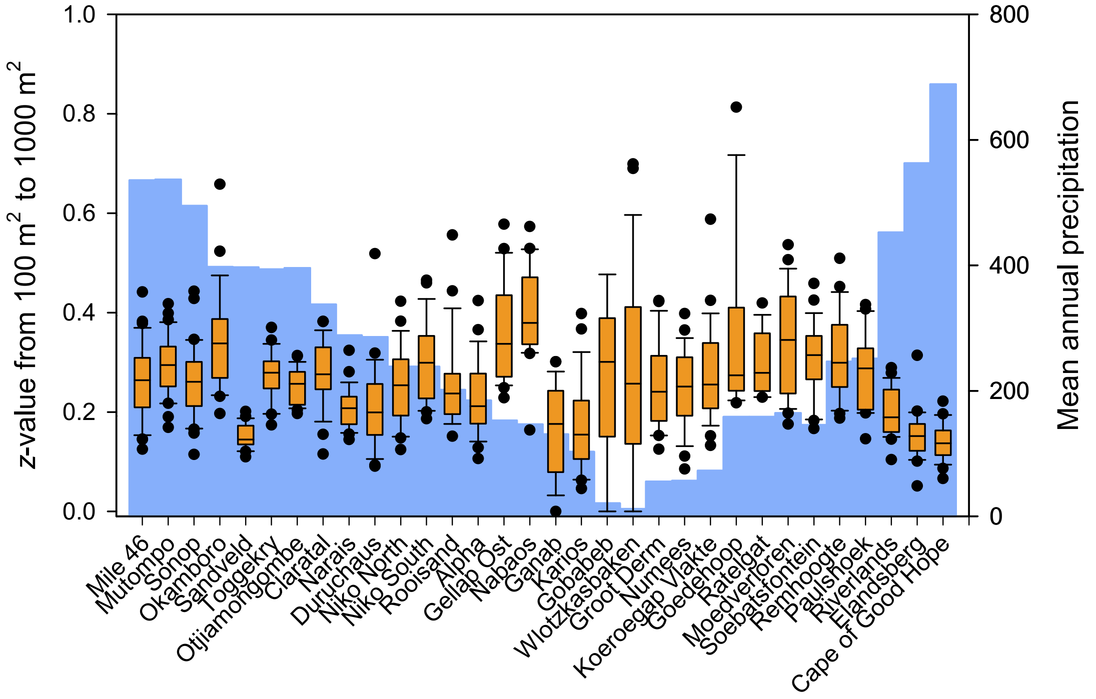

Fig. 3: Variability of the *z*-values within and between Observatories along the BIOTA transects in southern Africa. The *z*-values shown are for the transition from 100 m² to 1000 m² and based on means per hectare plot (i.e. averaged over all years). The graphs depict medians (lines), inter-quartile ranges (boxes), inter-decile ranges (hinges), and extreme values (dots).

be considered as a measure of β-diversity because high *z*-values represent a high spatial turnover in species composition. Furthermore, comparison of *z*-values between spatial scales allows for the investigation of the scale-dependence itself, i.e. how the degree of scale-dependence changes with grain size.

The *z*-values varied widely within most of the Observatories, and this variability was particularly high in the driest parts of the BIOTA transects (Fig. 3). The mean *z*-value of the transition from 100 m² to 1000 m² ("mean-to-mean") for all studied Observatories was 0.2679, with a minimum of 0.1369 at Cape of Good Hope (S33) and a maximum of 0.8373 at Gobabeb (S35) (see Electronic Appendix 1). The mean *z*-value of the transition from 1000 m² to 1 km² was only slightly lower (0.2207) with a minimum of 0.1313 at Alpha (S17) and a maximum of 0.5927 at Gobabeb (S35). In contrast, the mean *z*-value at an intermediate scale (1000 m² to 1 ha) was only 0.1171 (Electronic Appendix 1), indicating that the allocated time did not allow complete censuses of the hectare plots at many Observatories. The 1-ha scale is therefore not analysed further. The *z*-value for the transition from 1000 m² to 1 km² was higher than that for the transition from 100 m² to 1000 m² for only five out of 32 Observatories, with two out of three of these being Fynbos Observatories. The variation of the *z*-values between Observatories was much lower than the variation within Observatories (Fig. 3), with only slightly significant differences among the six biomes (Fig. 4). The lowest *z*-values at both of the two transitions studied were found in the Fynbos Biome, while above-average *z*-values occurred at the Observatories of the Suc-

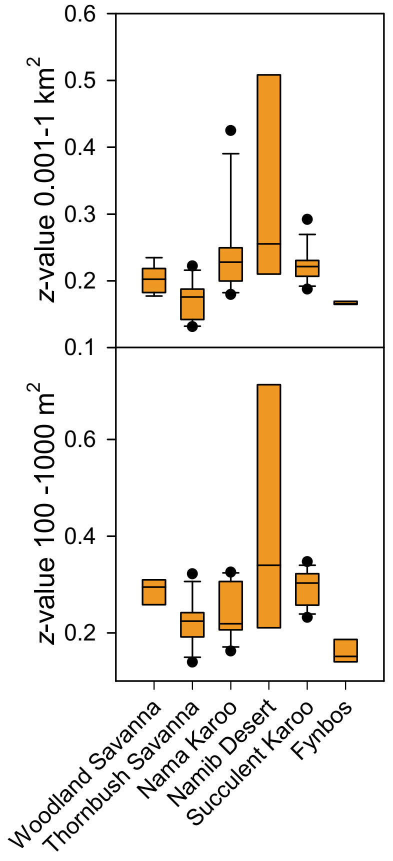

Fig. 4: Variability of the mean z-values between the Observatories of the different biomes. The *z*-values are the slopes of a power-law species-area relationship in log-log representation and here based on the comparison of mean richness values for the different spatial scales within the particular square kilometre of the respective Observatory ("mean-to-mean"). The graphs depict medians (lines), inter-quartile ranges (boxes), inter-decile ranges (hinges), and extreme values (dots) within the biomes. The differences between the biomes were significant in all cases (tested with ANOVAs; $p = 0.023$ for $z_{1000\,m^2-1\,km^2}$, $p = 0.044$ for $z_{100-1000\,m^2}$).

Photo 3: Vegetation at the Observatory Ogongo (S42) in the Oshana system of the Woodland Savanna. Photo: N. Classen.

Photo 4: Thornbush Savanna vegetation at the Observatory Okamboro (S06). Photo: J. Deckert.

Photo 5: Nama Karoo vegetation at the Observatory Gellap Ost (S10). Photo: A. Hoffmann.

Photos 6: *Arthraerua leubnitziae* along a dry river bed at the desert Observatory Kleinberg (S34). Photo: N. Jürgens.

Photos 7: Succulent Karoo vegetation at the Observatory Goedehoop (S26). Photo: U. Schmiedel.

Photo 8: Fynbos vegetation at the Observatory Elandsberg (S32). Photo: G. Miehlich.

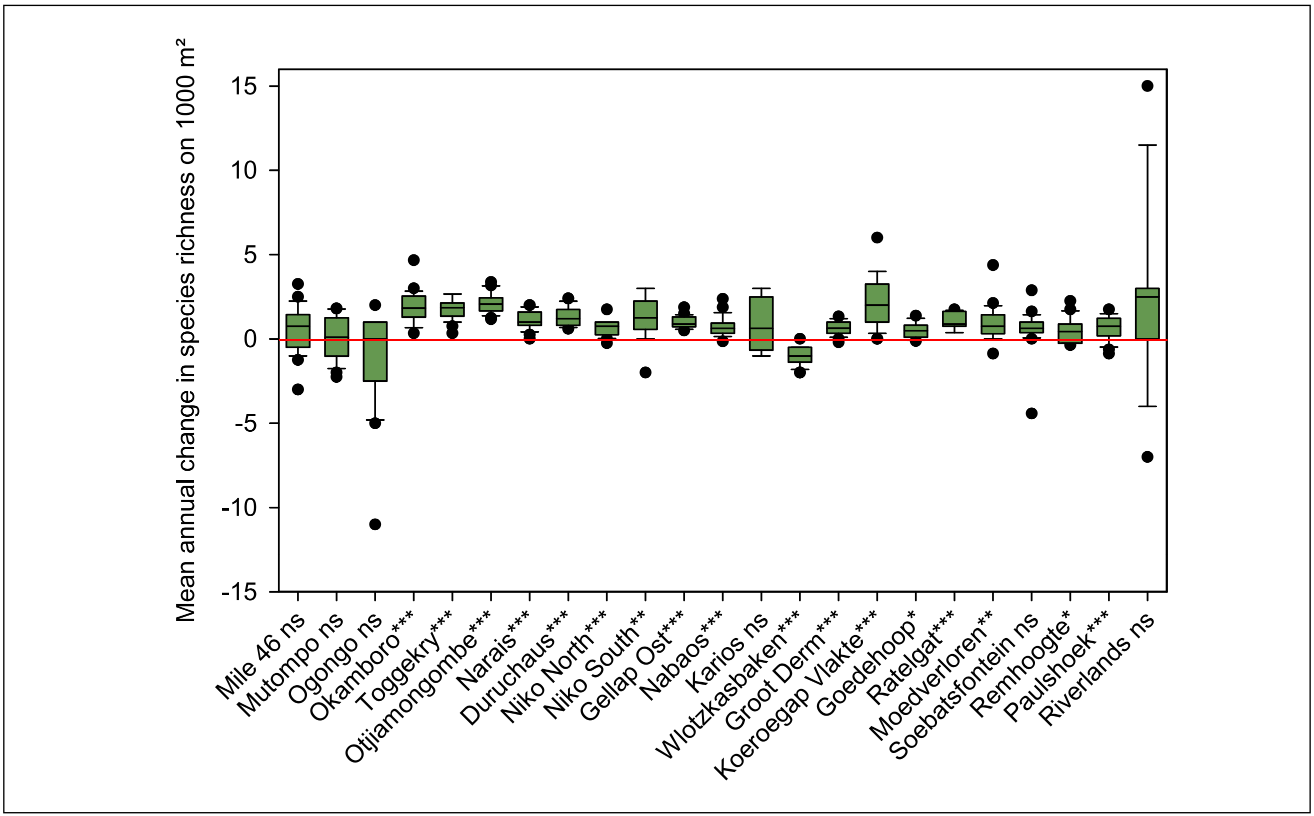

Fig. 8: Mean annual changes in species richness of the major perennial life forms phanerophytes and chamaephytes on 1000-m^2 plots over the observed period (2–9 years). The graphs depict medians (lines), inter-quartile ranges (boxes), inter-decile ranges (hinges), and extreme values (dots). The symbols after the Observatory names denote the significance of richness changes: ns: $p \geq 0.05$; *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$.

culent Karoo and the Namib Desert, and also in those of the Nama Karoo at the larger scale (Fig. 4).

The *z*-values for the transitions 100–1000 m^2 and 1000 m^2–1 km^2 (as measures of β-diversity) were related to quite different environmental variables than the α-diversity measures (see above results on biodiversity patterns along the transects). Most strikingly, the *z*-values at both scales showed inverse relationships to mean annual precipitation, length of dry season, and De Martonne's aridity index, i.e. they increased with increasing aridity (Electronic Appendix 4). Furthermore, the *z*-values at the larger scale also showed a positive relationship to soil pH (i.e. they increased with increasing pH). The *z*-values were positively correlated with minimum temperature and with pedodiversity measures, with significant relationships to soil reference group richness at both spatial scales and additional strong relationships to soil ecotype richness and parametric space at the larger scale.

A final aspect of scale-dependency is the question of whether the ranking of different habitats according to species richness or the relative importance of drivers varies at different spatial scales (i.e. grain sizes). While we found rather consistent patterns at all analysed spatial scales from 100 m^2 to 1 km^2 in the majority of cases (see Electronic Appendices 3 and 4), there were some striking exceptions. For example, the Fynbos Biome was by far the most species rich at the 100-m^2 and 1000-m^2 scales, but at the 1-km^2 scale the Succulent Karroo reached the same level of biodiversity (see Fig. 1, Table 2). For species richness, similar predictors played a role at the three spatial scales of 100 m^2, 1000 m^2, and 1 km^2, but their relative importance clearly changed (see Electronic Appendix 4). Soil ecotype richness was only a significant positive predictor at the 1-km^2 scale, and soil parametric space increased in importance with increasing grain size. The importance of pH-value, mean annual precipitation, De Martonne's aridity index, and the length of dry season for species richness decreased with increasing grain size, while the importance of mean annual temperature, percentage winter precipitation, and inter-annual precipitation variability increased.

Change of biodiversity in time

During the nine-year study period, most Observatories showed highly consistent diversity changes, i.e. there were only minor variations among the different 1000-m^2 plots within individual Observatories (Fig. 8). Only the Observatories S31 (Riverlands) and S42 (Ogongo) showed higher within-Observatory variation. Of the 23 Observatories analysed, 16 showed an increase in richness, six no significant change, and only one a decrease (Fig. 8). The highest significant mean annual increases in species richness at the 1000-m^2 plot level occurred on the Observatories Koeroegap Vlakte S18 (+2.2 species year^{-1}), Otjiamongombe, S05 (+2.1 species year^{-1}), and Okamboro S06 (+1.9 species year^{-1}), while the only significant decrease was at the Observatory Wlotzkasbaken S16 (–1.0 species year^{-1}).

Discussion

Biodiversity patterns along the transect

The species richness at different spatial scales along the BIOTA Southern Africa transects responded positively to the mean annual precipitation, but there were some exceptions. In northern Namibia in the Woodland Savanna, species richness was not higher than for the Thornbush Savanna, regardless of the higher mean annual precipitation there. Species richness in the north-west of Namibia at the two Observatories, Ogongo (S42) and Omano go Ndjamba (S43), was even lower than that of the Thornbush Savanna and had values similar to the much more arid Nama Karoo. These two Observatories fall within the northern Namibian vegetation type Mopaneveld (dominated by mopane, *Colophospermum mopane*), which forms part of the Woodland Savanna and is characterised by dense canopy cover and comparatively sparse understorey vegetation. The Mopaneveld in the more humid northern Namibian is known to be particularly species poor compared to less humid Mopaneveld in other southern African regions (Siebert et al. 2003). Species richness of Mopaneveld has often been found to be dependent on the cover of mopane. High cover of mopane results in low species richness, whereas a higher species richness is noted in areas with low mopane cover (O'Connor 1992, cited in Siebert et al. 2003). Landuse effects on Omano go Ndjamba have an additional negative effect on species richness outside the Agricultural Research Station Ogongo (see Part II, Observatory S43). The two Observatories also represent unusual habitat conditions due to ephemeral, additional water influx from Angola (i.e. Oshana system) as well as the high accumulation of salt in the subsoil layers (compare Part II, Observatory S42 and S43).

The species richness on the Fynbos Observatories was significantly higher than on any other Observatories along the transect. The Fynbos Biome with its Mediterranean climate is renowned for its high species richness, which is described to be particularly high even in terms of global standards (Mutke & Barthlott 2005), at larger spatial scales (> 10 km^2) but only moderately so on smaller spatial scales (< 0.1 ha) (Cowling et al. 1996, 1998). According to our data (low *z*-values), the species richness of the Fynbos Biome shows a lower relative increase with increasing plot sizes than it does in the other biomes. At our largest spatial scale of 1 km^2, the cumulative species richness of the Succulent Karoo and the Fynbos Biomes were comparable. Cowling et al. (1997) have shown that "local" (i.e. 1000 m^2 = 0.1 ha) species richness in the Fynbos Biome is similar to, or even lower than, that of the Succulent Karoo and the Savanna. The "regional" species richness (i.e. biome-scale) of the different Fynbos types, however, exceeds that of all other biomes. The differences in species richness between Fynbos and the other biomes as described in the literature (see above) may only become measurable at larger spatial scales that are not covered by the BIOTA Observatory design (i.e. > 10 km^2).

The plant diversity at Elandsberg Observatory (S32) was exceptional at all spatial scales and was an outlier in all regressions of species richness with potential soil-related and climatic drivers of plant diversity. With regard to soil features (see Article III.3.3), the Elandsberg Observatory did not show any unique characteristics compared to the less diverse Observatory at Cape of Good Hope (S33), for instance. Most of the vegetation at the Elandsberg Observatory forms part of the Swartland Alluvium Fynbos, but it also borders the Swartland Shale Renosterveld (Rebelo et al. 2006, see also Part II, Observatory S32). The exceptionally high species richness on Elandsberg Observatory may also be caused by its ecotone character between the two vegetation types, Fynbos and Renosterveld. The high species richness could additionally be related to the geomorphologic situation of the Observatory at an alluvial fan, which might have caused and still cause an input of diaspores of mountainous plants into this low-lying area. The species richness of the Elandsberg area has been known to science for some time and this is the reason for its conservation (Part II, Observatory S32) and the various research activities of BIOTA at that site (Chapter III.5).

Beta-diversity within the Observatories along the transect

The very high range in species turnover (β-diversity) on the desert Observatories reflects the huge relative difference between the extremely low species richness (i.e. even completely vegetation-less plots are frequent) at the small and medium plot scale (i.e. 100 m^2 and 1000 m^2) and reasonable totals of 28 (Wlotzkasbaken, S16) and 33 species (Gobabeb, S35) at the 1-km^2 scale. This high species turnover is driven by micro-topography that influences the run-on and -off of the surface water during scarce rainfall events and exposure to fog, i.e. climatic and soil-related drivers that are not reflected in the parameters included in our analyses.

The comparatively high beta-diversity values for the two Nama Karoo sites, Gellap Ost and Nabaos (S10 and S11), which exceeded that of all other Nama Karoo, Thornbush and Woodland Savanna Observatories, can also be related to small-scale differences in water supply (Petersen 2008). This author describes these differences as being related to soil physical properties such as texture and the available rooting space, i.e. content of coarse fragments and depth to bedrock.

The extraordinarily broad range of *z*-values at the Succulent Karoo site Goedehoop (S26) and the comparatively high mean values for the Moedverloren Observatory (S28) are to a large extent related to soil heterogeneity that is also reflected in the high diversity of soil ecotypes. These two Observatories are characterised by the dominance of a special habitat type, the quartz fields. High variance in soil chemical features like soil pH and electrical conductivity within a distance of a few meters, which is typical for the quartz fields (Schmiedel & Jürgens 1999, Schmiedel 2002, see also Chapter III.4), drives the extraordinarily high species turnover in this landscape (Schmiedel 2002). The quartz fields at the Ratelgat Observatory (S27) are less pronounced and more strongly mixed with zonal soils within the plots, thus, resulting in relatively higher species richness per 100 m^2 and 1000 m^2 plot but also in lower species turnover (lower *z*-values) between the different sized plots.

The low β-diversity of the Fynbos Observatories at a scale of up to 1 km^2 reflects the generally high species richness in this biome, which showed a comparatively low relative increase between the spatial scales covered by the Observatories (100 m^2 to 1 km^2). However, a significant increase in species richness can be expected at larger spatial scales (> 10 km^2), along topographic and soil-fertility gradients, as described by other studies (Cowling 1990, Cowling et al. 1996).

Drivers of biodiversity

Climatic drivers

Mean annual precipitation and length of dry season showed a significant relationship to species richness at the 1000 m^2 scale. Length of dry season was negatively correlated whereas mean annual precipitation was positively correlated with species richness. Both variables were strongly negatively correlated to each other as the length of dry season depends on the mean monthly precipitation, which is typically low in the arid regions. This correlation was not unexpected, taking into account the steep rainfall gradient along which the BIOTA Observatories had been arranged. The Fynbos Observatories with the highest species richness were associated with a short dry season, whereas the desert Observatories with the longest dry season had the lowest species richness. Mean annual precipitation was closely related to species richness for the 1000-m^2 plots, with the Observatories of the Namib Desert having lowest species richness. The Fynbos Observatories, which receive the highest annual precipitation along the transect, possess the highest species richness. However, we cannot exclude with our data that other factors that change collinearly with mean annual precipitation and rainfall season, also play a role in creating and maintaining the exceptional species richness in the Fynbos Biome.

The significant overall difference between species richness in the winter and the summer rainfall regions is not completely new to science. In their comparison of the two arid biomes of the Succulent Karoo and Nama Karoo, Cowling et al. (1994, 1998) identified the much higher diversity in the Succulent Karoo and related this mainly to climatic factors such as the higher predictability of winter rainfall (lower coefficient of variation) in the Succulent Karoo (see also Hoffman & Cowling 1987). In addition to this, our data show that the low winter rainfall regions are characterised by high richness in soil ecotypes (see also Article III.3.3), which has a strong positive relationship with species richness at 1 km^2 in the Succulent Karoo.

Soil-related drivers

Median soil pH per Observatory was negatively correlated with species richness. As soil pH is typically low in regions with high annual precipitation in the study area due to leaching of the soils, which reduces soil pH (see also Article III.3.3 and discussion on the findings in a global context), this does not necessarily mean a causal relationship, while on the other hand this collinearity does also not exclude that soil pH might affect plant diversity directly. The same negative relationship between single values of soil pH and species richness per plant life form per 100 mm^2 was found by Medinski et al. (2010) along the same transect. They further showed that the species richness of the five main life forms (i.e. chamaephytes, phanerophytes, hemicryptophytes, therophytes and geophytes) responded differently to the tested soil properties. They concluded that soil infiltration, clay and silt content, electrical conductivity, and soil pH are the most relevant properties to be tested in plant diversity research. However, our analyses using mean values of electrical conductivity per Observatory did not reveal any significant relationship between electrical conductivity and plant species richness. For future analyses we plan to use single values and ranges of electrical conductivity as well as other soil parameters such as clay and silt content.

In the Succulent Karoo, where the majority of the precipitation occurs as low-intensity rainfall from low pressure cells (Desmet & Cowling 1999), the leaching effect of precipitation is typically lower (Article III.3.3). This results in higher overall soil pH-values overall but also a broader range of pH-values due to small-scale patterns of surface water run-on and run-off. These differences in soil acidity drive species turnover and thus species richness at larger spatial scales (Schmiedel & Jürgens 1999).

This important influence of soil and habitat diversity on species richness in southern Africa is revealed by the highly significant regression between vascular plant species richness and soil ecotype richness at 1 km^2. The complex parameter "soil ecotype richness" reflects the diversity of the combinations of four plant-relevant soil properties recorded at each Observatory. These are soil pH (indicating acidity and alkalinity), electric conductivity as a measure of salt enrichment, amount of fine particles (i.e. clay and silt) as a proxy for water storage ability, and organic carbon content, which is thought to reflect nutrient supply. The spatial distribution of this complex-parameter along the transect revealed highest values for the Succulent Karoo (see Electronic Appendix 3). This high diversity in soils of the Succulent Karoo Biome has been described earlier (Francis et al. 2007, Herpel 2008, Petersen 2008, as well as Article III.3.3) and its role as general driver of the species richness in the Succulent Karoo has been illustrated by various studies (Jürgens 1986, Schmiedel & Jürgens 1999, Herpel 2008, see also Chapter III.4). However, other factors not included in the analysis, such as the predictability of winter rainfall (Hoffman & Cowling 1987), moderate temperature conditions, as well as regular occurrence of droughts, which result in high within-site species turnover (Jürgens et al. 1999) have also been described as potential drivers of the high species richness of the arid Succulent Karoo (Cowling et al. 1998).

Plant diversity in the Fynbos Biome

The Elandsberg Observatory (S32) always and the Riverlands Observatory (S31) frequently were outliers in our regression analyses, for both climatic and soil related predictors (Figs. 5–7). They even exceed the species richness of the Observatory Cape of Good Hope (S33) on the Cape Peninsula, which had been reported as one of the most species-rich phytogeographic centres of the Cape

Floristic Kingdom at larger spatial scales (Goldblatt & Manning 2002). The extraordinarily high species richness on these Observatories can only partly be explained by the analysed variables. Other biotic and abiotic drivers such as topographic diversity, nutrient-poor soils, fire, and floristic and climatic history have been identified as responsible factors driving this exceptional species richness (Cowling 1990, Goldblatt & Manning 2002). Finally, it should be highlighted that our mean species richness for 1000 m^2 on Elandsberg (123.7) already exceeds the highest single species richness count (i.e. 121 species) that has been published for Fynbos vegetation to our knowledge so far (Cowling et al. 1992), while our maximum single-count values for both Observatories Elandsberg (168) and Riverlands (143) are far above.

Landuse as a driver

The impact of landuse along the BIOTA transect, as an important driver of plant species richness at the local- to biome-scale was not the focus of this transect-wide analysis. The absence of significant effects of the simplified landuse intensity classes and species richness along the transect does not mean that landuse intensity does not have an impact on plant diversity. Various aspects of landuse impact on plant diversity are presented elsewhere in this book (e.g. Articles III.5.6, III5.5, III.5.7, and Part IV). Further analysis of landuse impact on plant diversity and species composition based on the botanical data from the BIOTA Observatories will be the focus of separate analyses at the local- to biome scale. However, some of the Observatory pairs with different landuse intensity (i.e. Ogongo – Omano go Ndjamba, Gellap Ost – Nabaos, Remhoogte – Paulshoek) seem to show a trend of lower species richness at both 100-m^2 and 1000-m^2 scales under intensive landuse. However, this trend is not consistent and the effect seems to be strong at a small scale at some sites and at larger scales at other sites. Decline in total species richness does not seem to be the main effect of landuse impact. Studies from different biomes of southern Africa rather showed that unsustainable land management may change the species and life form composition of vascular plants (Todd & Hoffman 1999, 2009, Riginos & Hoffman 2003, Anderson & Hoffman 2007, Haarmeyer et al. 2010, Wesuls & Lang 2010, and unpublished results of D. Wesuls & J. Dengler). The main change is often described as a shift in the ratio woody to non-woody plants. In the Succulent Karoo Biome, species composition changed from vegetation dominated by palatable shrubs to sparser perennial vegetation, with mainly non-palatable shrubs (e.g. *Galenia africana*, kraalbos) and more annuals and geophytes, which cover the open patches after good seasonal rains (Todd & Hoffman 1999, 2009). Vegetation changes in the Thornbush Savanna are characterised by an increase of medium-sized *Acacia* trees (e.g. *Acacia mellifera*) that replace the palatable grass biomass (de Klerk 2004).

Change of biodiversity in time

A clear majority of the Observatories (16 of 23) showed increases in species richness over the years of the BIOTA project. This increase was fairly evenly distributed along the transect, although it was slightly less in the southern parts of the Succulent Karoo and in the Cape region. By contrast, only one Observatory experienced a significant decrease in species density.

The observed increase in species richness could partly be an artefact of improved performance of the collectors of monitoring data and the project as a whole. Particularly in the larger plots, observers would more likely find species whose occurrence they knew from the previous year(s) than detect an unexpected “new” species. In this way, the number of species recorded per plot might have increased over the years more than the actual species number did. However, a similar increase of species richness was also found for the smaller plot sizes (100 m^2, data not shown), where the chance of missing a species were much lower, suggesting that this pattern likely reflects real increase in species richness on the Observatories over the study period. Furthermore, the observation data also indicated repeated phases of species richness decrease (e.g. in drought years) and recovery (e.g. following good rains). Furthermore, a positive trend (increase in species richness) has also been observed in many extremely meticulous local case studies such as those carried out in the Richtersveld at Numees (S20) (compare Part II, Observatory S20) and in the Knersvlakte of the Succulent Karoo. Despite an increase in inter-annual variability of precipitation and of annual maximum and mean temperatures during the last decades, populations of Knersvlakte endemic, quartz field-dwelling plants showed an increase in species richness over 13 years of monitoring (U. Schmiedel, unpublished data). Overall, we consider the measured increases in species diversity in this study during the last decade to be a robust result. However, this finding does not justify an overoptimistic projection of southern African’s biodiversity into the future, as passive warming experiments have shown that projected future climate change may have a detrimental impact on just these species (Musil et al. 2009).

The findings seen in a global context

It is not an easy task to compare our richness values from southern Africa at spatial scales between 100 m^2 and 1 km^2 with data from other regions of the World, because spatially representative, high-quality biodiversity data at that grain size are globally still very scarce. At the 1-km^2 scale, to our knowledge, only the Swiss Biodiversity Monitoring (BDM) has produced similar data representative for the whole of Switzerland, which is still a small area compared to the region covered by BIOTA Southern Africa (see Table 2). As the 1-km^2 data shown in this article, also the Swiss data are not really complete censuses of the square kilometre but are based on a 2.5-km transect systematically arranged within the one square kilometre, with the species at both sides of the transect being recorded (BUFA 2009). However, the degree of completeness might be similar to our case where the 1-km^2 values are usually based on 20 hectare plots that are placed in a stratified-random manner. The values of our Fynbos and Succulent Karoo Observatories exceed the average Swiss biodiversity level,

Table 2: Vascular plant species richness values at 1 km^2, 1000 m^{2,} and 100 m^{2,} reported from various studies worldwide that cover a larger region with a representative sampling

Study area	**Biome**	**Source**	**Extent [km^2]**	***N***	**Remarks**	**1 km^2**		**1000 m^2**		**100 m^2**	
						Median	**Range**	**Median**	**Range**	**Median**	**Range**
Southern Africa	All	This book	1,200,000	35*		138	1–385	38.4	0–169	22.6	0–128
Southern Africa	- Woodland Savanna	This book		5*		149	90–172	42.5	0–70	22.2	0–39
Southern Africa	- Thornbush Savanna	This book		7*		121	39–213	47.4	0–113	27.6	3–70
Southern Africa	- Nama Karoo	This book		7*		120	102–186	21.1	0–83	12.6	0–45
Southern Africa	- Namib Desert	This book		4*		24	1–46	3.9	0–20	1.8	0–12
Southern Africa	- Succulent Karoo	This book		9*		282	79–296	56.3	0–106	28.1	0–59
Southern Africa	- Fynbos	This book		3*		288	218–385	91.6	19–169	58.0	12–128
Tropical zones	Tropical forest	Plotkin et al. (2000)	5 plots	5	0.5 km^2 instead of 1 km^2 and only woody plants	305	68–1171	–	–	–	–
SE United States	Nemoral and laural zonobiome: mostly natural habitats	Fridley et al. (2005)	485,000	1472		–	–	55.0	6–179	30.3	5–91
United Kingdom: East Berkshire	Nemoral zonobiome: cultural habitats	Crawley & Harral (2001)	465	465 – 67 – 88		140	60–512	32.0	7–90	16.0	1–47
Switzerland	Nemoral zonobiome: natural, semi-natural, and cultural habitats	BAFU (2009)	41,000	390	line-transect of 2.5 km length within the 1 km^2	239	15–400	–	–	–	–
Russia: Curonian Spit	Transition nemoral-boreal zonobiome: natural and semi-natural habitats	Dolnik (2003)	100	130	900 m^2 instead of 1000 m^2; *including approx. 50% non-vascular plants*	–	–	*88.0*	*2–168*	*51.0*	*1–94*

* indicates that the number of smaller-sized plots (1000 m^2, 100 m^2) was approximately 20 times higher than the number of 1-km^2 plots, but the precise number varies slightly between Observatories and between years.

while the four other biomes lie below (Table 2). The reported values for a relatively small section of a cultural landscape in the United Kingdom (Crawley & Harral 2001) lie far below Switzerland and correspond well to the median value of our complete transects (Table 2). For tropical forests as the most species-rich habitat type at larger spatial scales, we are not aware of any complete censuses of all vascular plants for full square kilometres, but there are various detailed counts of woody plants (which are the absolutely dominating life form there) of 0.5-km^2 areas (Plotkin et al. 2000). While the maximum values there far exceed our data range, the median value is very similar to our two most species rich biomes (Table 2).

For the scales of 1000 m^2 and 100 m^2 slightly more data are available, mostly from the temperate zones. According to an extensive global compilation of published richness maxima at different spatial scales (J. Dengler, unpublished data), the documented maximum value for 1000 m^2 seems to be 179 vascular plant species in an open *Pistacia* shrubland in Israel (Mediterranean zonobiome; Naveh & Whittaker 1979) as well as in one plot in North Carolina, United States (laural zonobiome; vegetation type not reported; Fridley et al. 2005). On average, the values in the temperate zones are much lower and their medians are below the values of our Fynbos and Succulent Karoo Observatories, partly also below the values of the two savanna biomes (Table 2). The highest species densities at 100 m^2 are known from semi-natural dry grasslands in the temperate zone of Europe with a maximum of 133 (M. Chytrý, Brno, pers. comm.) and 127 (Dengler et al. 2009) vascular plants species in managed semi-dry grasslands of Czechia and Romania, respectively, and 140 species when including also non-vascular plants (cryptogam-rich dry grassland in Estonia; Dengler & Boch 2008). At the 100-m^2 and 1000-m^2 scales, tropical rain forests are typically less species-rich (see Williamson 2003). Thus, we can conclude our recorded maxima (169 vascular plant species on 1000 m^2 and 128 on 100 m^2, both on Observatory Elandsberg, S32) as well as our median values (see Table 2) place the Fynbos among the biomes and habitats with the highest species density at that scale worldwide.

The *z*-values are a widely used and readily interpretable way to measure scale dependency and spatial turnover of biodiversity (e.g. Drakare et al. 2006, Dengler 2009). The range of values recorded in our study, with a mean of 0.268 for the transition 100–1000 m^2 and 0.221 for the transition 1000 m^2–1 km^2, is similar to values reported worldwide (Crawley & Harral 2001, Dolnik 2003, Fridley et al. 2005, Drakare et al. 2006). Given the fact that for most Observatories the richness values at the 1-km^2 scale are probably underestimations (see above), we found on average hardly any scale-dependency of *z*-values. This contrasts to the findings of Drakare et al. (2006) who in their meta-analysis found a systematic increase of *z*-values between 1 m^2 and 1 km^2 for nested sampling designs, while Crawley & Harral (2001) in their single study found an increase up to approximately 1 ha followed by a decrease thereafter. The fact that we found much more variation in *z*-values within rather than between Observatories is similar to the higher variation within rather than between European dry grassland vegetation types (Jeschke et al. 2007), and indicates that *z*-values are obviously not a property specific to vegetation types but more determined by small-scale variation patterns in abiotic conditions or disturbance. Finally, we could not confirm in our dataset the pole-ward decrease of *z*-values found by Drakare et al. (2006) in their meta-analysis.

Regarding the drivers of biodiversity patterns, a recent comprehensive meta-analysis by Field et al. (2009) compared six non-exclusive types of hypotheses: (i) climate/productivity; (ii) environmental heterogeneity; (iii) edaphics/nutrients; (iv) area; (v) biotic interactions; and (vi) dispersal/history. They found that, for plants, generally climate/productivity and edaphics/nutrients are the most important diversity drivers and that edaphics/nutrients are particularly important at scales below 1 km^2, while measures of environmental heterogeneity (such as our pedodiversity parameters) do not play a particularly important role. Our results are in line with these general findings as we found the strongest relationship of species richness at 100 m^2–1 km^2 with factors related to climate-driven water availability, and the second strongest to soil chemical parameters, while soil heterogeneity only played a role at the 1-km^2 scale.

However, when considering the individual parameters, our findings show clear deviations from patterns found elsewhere or at a global scale. Generally, a positive relationship between energy, measured for example as mean annual temperature or potential evapotranspiration (PET), is assumed (Gaston & Spicer 2004), and has been proven at a global scale for many taxa, including vascular plants (Mutke & Barthlott 2005, Kreft & Jetz 2007). We found no effect of PET and even a negative correlation of species richness with mean annual temperature, which deviates from these widely accepted macroecological patterns. This variation could be attributed to peculiarities of our study region, e.g. the widely acknowledged, yet not fully understood unique position of the Cape Floristic Kingdom among the Floristic Kingdoms of the world (Kreft & Jetz 2007). However, we also assume that the very different grain sizes analysed contribute to the differences in the results from those global-scale studies. Mutke & Barthlott (2005) and Kreft & Jetz (2007) based their analyses on species richness counts standardised to 10,000 km^2, while we analysed grain sizes of 0.0001–1 km^2. It is generally accepted though rarely tested directly that different processes shape diversity patterns at different spatial scales (e.g. Willis & Whittaker 2002, Field et al. 2009).

While decreasing species richness with altitude or a mid-altitudinal peak in species richness are among the most frequently reported macroecological patterns for many taxa at practically any grain size (e.g. Gaston & Spicer 2004, Wohlgemuth et al. 2008), we did not find such a pattern in our data. One explanation could be that collinearity of altitude with other, stronger predictors masked the altitudinal pattern. For example, our summer-rainfall Observatories were located at a mean altitude of 1124 m a.s.l., while the mean altitude of the winter-rainfall Observatories was only 383 m a.s.l. (see Electronic Appendix 1) which together with the strong positive effects of winter rainfall (see Results) could explain our failure to detect an altitudinal pattern.

Soil reaction (pH or calcium content) is typically highly important for plant species richness at the plot scale (e.g. Schuster & Diekmann 2003, Pärtel 2002, Chytrý et al. 2007) but also at the 1-km^2 scale (e.g. Wohlgemuth et al. 2008). In temperate and boreal regions, usually positive or unimodal relationships are found, whereas in most tropical or subtropical regions the relationship is negative, which is explained historically by the predominating soil pH in the evolutionary centres of the floras (Pärtel 2002, Ewald 2003, but see Medinski et al. 2010 for a unimodal relationship for individual 100 m^2-plots along BIOTA transect). According to the global meta-analysis of Pärtel (2002), the correlation coefficient between richness and soil pH shows a strong latitudinal pattern, with the mean *r*-value ranging from –0.5 at the equator to approx. +0.8 in the boreal zone. The expected value for our study region should thus range from –0.20 in northern Namibia to +0.05 at the Cape, while our observed correlation values for the whole transects were between –0.15 (1 km^2) and –0.51 (100 m^2), depending on the spatial scale analysed. However, in the study region as in all arid regions, soil pH is strongly negatively correlated with mean annual precipitation (e.g. Chytrý et al. 2007 and discussion above) and due to this collinearity it is not possible to disentangle the effects of both environmental variables on species richness. Still it is remarkable that we found the very opposite pattern to what Chytrý et al. (2007) found in the forest-steppe transition zone of southern Siberia, despite both regions being considered to have evolutionary centres with high soil-pH values (Pärtel 2002).

Finally, it is worth comparing the biodiversity patterns we found at small grain sizes with those shown in coarse-grain maps of vascular plant diversity (Kier et al. 2005, Mutke & Barthlott 2005). The diversity gradients depicted in the map of Mutke & Barthlott (2005), with a grain size of 10,000 km^2, are very similar to our findings, with the Fynbos Biome being rated in density zone 9 (4,000–5,000 species per 10,000 km^2) and the Succulent Karoo in density zone 8 (3,000–4,000 species per 10,000 km^2). Such a coincidence of diversity patterns across such widely differing spatial scales is not a general finding (see Dengler 2009). Only the very species-poor Namib Desert is not depicted as such in the map of Mutke & Barthlott (2005), but this is likely a modelling artefact rather than a real pattern. Our finding that small-scale species densities in the Fynbos Biome are amongst the highest values worldwide correspond well with the strong positive deviation of the Cape Floristic Kingdom from the global vascular plant diversity model at the 10,000-km^2 scale with contemporary environmental variables as predictors (Kreft & Jetz 2007). However, our results contradict the literature on the diversity of the Fynbos (e.g. Cowling et al. 1996, Goldblatt 1997, Goldblatt & Manning 2002), according to which this biome is not unusually rich at small grain sizes (1000 m^2) but becomes exceptional on a global standard only at larger grain size (> 10 km^2).

Conclusions

The observed plant diversity measures show great variability within the geographical areas studied. Many parameters change gradually along the transects. Our analysis showed that there is not a single predictor for plant species richness along the transect. Mean annual precipitation was among the most important drivers for species richness at small grain sizes, however, other parameters which are strongly correlated with mean annual precipitation (aridity index, length of dry season, median soil pH) were also important. The importance of soil diversity (e.g. richness in soil ecotypes per Observatory) increased with increasing grain size. Future analyses of the same datasets will further reveal the relationships between plant species and life-form diversity in southern Africa and soil and climatic parameters at different spatial scales.

The discussion of the data in the global context revealed that the botanical diversity data along the major climatic gradient and across six biomes in southern Africa is unique not only in terms of regional but also global standards. Comparable data assessed at different spatial scales and with a standardised approach are scarce. Our data thus support, amend, and refine existing comparative analyses on the diversity patterns of biomes in southern Africa. They also provide the basis for further analyses of local to regional plant diversity patterns and their abiotic and biotic drivers. Particularly unique in our study is the combination of large spatial extent with small to medium spatial grain, as most ecological studies are either “small extent/small grain” or “large extent/large grain”. The study of small-scale phenomena over huge spatial extents likely will bring us closer to a real understanding of the processes that shape biodiversity patterns on Earth.

During the decade of monitored for the BIOTA project, no major declines of botanical diversity were observed except for a slight increase in perennial species (dwarf shrub, shrubs and trees). These data provides critical benchmark information on the current state of diversity of vascular plants along the transect. The annual monitoring of plant diversity on these plots have the potential to provide evidence for changes that may occur due to climate change and human landuse.

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Life forms along the BIOTA transects—new perspectives on biomes in southern Africa

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Summary: The concept of life form is one of the cornerstones in ecology. Insight into the relationship between life form and climate leads to the classification of biomes, which is largely based on the dominance of plant life forms. The BIOTA Observatories along the southern African transects covered six different biomes in southern Africa. After nine years of observation, data from these Observatories were analysed for patterns of relative cover and richness of the five basic life forms of Raunkiaer as well as extended life forms along the major climatic gradient. Our findings partly confirmed, and to some extent modified existing biome classifications for southern Africa. Furthermore, the relationship between life form composition and precipitation along the transects was analysed in a direct gradient analysis using fuzzy set ordination. The gradient analysis revealed species richness per life form as a suitable proxy to quantify life form occurrence in relation to annual rainfall. Finally, it was shown that not all proposed biomes can be separated clearly regarding richness or relative cover of life forms.

Introduction

Climate is known to be a major determinant of the distribution of plant life on Earth. Early approaches to classify macroecological units were mainly based on climate (Schimper 1898, Köppen 1936, Holdridge 1947) or on soil-climate interactions (Walter & Box 1976). The widely applied biome concept classifies major landscape units on the basis of dominant plant strategy types (Odum 1945, 1971), which are understood as a response of the vegetation to macroclimatic conditions. Thus, it is not surprising that large scale climate models use the distribution of biomes to project possible effects of climate change on the biota (Claussen 1994, Cramer et al. 1999).

The definition of biomes is based on the composition of dominating plant strategy types or life forms. However, due to a limited set of life form types employed, a limited number of their combinations make an objective classification a challenging task. In particular, the definition of the term ‘dominant’ remains vague. The classification of the seven biomes of southern Africa (Rutherford & Westfall 1994), for instance, is based on the ordination of life form combinations in their relation to rainfall and temperature. A similar approach was applied by Irish (1994) for Namibia, resulting in four biomes there. Both classifications rely on a database consisting of hundreds of vegetation relevés from various sources, which rely largely on unpublished data or semi-quantitative information such as personal communications and photographs. From these various sources, the dominating life form combinations were identified for areas where no other information was available. For example, a combination defined as “phanerophytes and hemicryptophytes” would result in the typical composition for the Savanna Biome (Irish 1994). Hence, the resulting borders of the biomes are still based rather on interpretation than on an objective classification, making decisions on boundaries hardly reproducible.

It is widely accepted that classifications based on quantitative data result in better representations of the real world than presence and absence data (Fielding 2007). Hence, a more quantitative definition of dominance, related to a standardised area, would contribute to a better and more objective biome classification. Furthermore, such quantification in terms of species richness or abundance of a particular life form could also serve as an indicator for potential changes in the environment. For example, climate change is more likely to drive gradual changes in the dominance of certain life forms than their mere presence or absence. Therefore, we apply our quantitative life form data, i.e. both cover and species richness on standardised Observatory plots, along the BIOTA transects to compare them with the description of the existing biome classifications. This will provide a quantitative verification of previous findings or might even lead to local adjustments. Our data may also help to detect possible intersections or gradual transitions of biome borders.

Identifying fuzzy boundaries has become an important task for dealing with uncertainty in ecology in order to describe gradual transitions between two or more states (Regan et al. 2002). Hence, the application of Fuzzy theory was assumed to have a large impact on vegetation science (Mucina 1997). Recent applications in a wide range of ecological studies confirm this statement. For example, Fuzzy theory helped to improve the classification of vegetation communities (Moraczewski 1993, Zhang & Meng 2007), identify ecotones in vegetation dataset (Arnot & Fisher 2007, Mahecha et al. 2009) and allowed better classification of remotely sensed images (Foody 1992, Lucieer 2006, Oldeland et al. 2010). Fuzzy set ordination (FSO), invented by Roberts (1986), allows testing a-priori hypotheses of climate-vegetation interactions with multivariate datasets. This approach inverts the exploratory character of common ordination techniques, such as PCA or CCA, where the observer is subjectively looking for patterns in ordination space. FSO has already been applied in several gradient analysis studies (Banyikwa et al. 1990, Boyce 1998, Boyce et al. 2005, Zhang & Meng 2007). However, all of them were focussed on species rather than on life form composition.

The major aim of this study was to analyze the distribution of life forms on the Observatories along the BIOTA transects covering both summer and winter rainfall regime. For this approach, we used the widely applied life form concept of Raunkiaer (1934), which was also employed by Rutherford & Westfall (1994) as well as Irish (1994) for their biome classifications in southern Africa. In addition we used an extended life form concept (sensu Ellenberg & Mueller-Dombois 1965) in this case proposals made by Jürgens (1986, 1990), which further subdivide the basic life forms of Raunkiaer into finer size classes. In addition to the classification by Rutherford & Westfall (1994) and Irish (1994), we employed four quantitative categories regarding life forms: i.e. 1) richness of basic life forms, 2) abundance of basic life forms, 3) richness of extended life forms, and 4) abundance of extended life forms. First, we analyze our quantitative categories for each Observatory along the transects and compare our findings with those of Rutherford & Westfall (1994) (for South Africa) and Irish (1994) (for Namibia). Secondly, we apply FSO in order to test which of the four quantitative descriptors best explains the life form distribution along the rainfall gradient. Finally, reproducibility of biomes according to FSO results is tested in a post-hoc analysis approach.

Material and Methods

Among the many proposed life form concepts, the system of Raunkiaer (1934) is still the most frequently applied. Raunkiaer classified plant species based on the height of their perennial buds relative to the ground surface and defined five categories: **phanerophytes**, **chamaephytes**, **hemicryptophytes**, **crypto-** or **geophytes,** and **therophytes**. Apart from these five basic life forms, a further subdivision of phanerophytes based on size classes exists. For this study, we used the vegetation data, comprising information on basic (Raunkiaer 1934) and extended life form types (Jürgens 1986, 1990, see Table 1), gathered on the 32 Observatories along the BIOTA transects, which extended across summer and winter rainfall regime. Cover relative to the total cover per plot (in the following "relative cover") and mean species richness per basic and extended life form category were calculated for the 20 m x 50 m permanent plots of all BIOTA Observatories. Cumulative species richness per life form category as well as average cover values were calculated for each Observatory over all years where data existed, using the software BIOTABase (Muche et al. 2009).

Table 1: Subdivision of extended life form categories according to height classes (ranges in cm); C = Chamaephytes and P = Phanerophytes; sub = submerged, nan = nano, mic = micro, mes = meso

	Csub	Cnan	Cmic	Cmes	Pnan	Pmic	Pmes	Pmac
Height [cm]	< 1	< 5	5–15	15–50	50–200	200–500	500–2000	> 2000

We followed Irish (1994) and Rutherford & Westfall (1994) in our definition of biomes, i.e. biomes are labelled "Desert" (D), "Fynbos" (F), "Nama Karoo" (NK), and "Succulent Karoo" (SK). To avoid having 12 of the Observatories fall into the broad category "Savanna Biome" and to reflect the difference between the dense woodlands in the north and the open savannas in central Namibia, we followed Mendelsohn et al. (2002) and further distinguished between "Thornbush Savanna" and "Woodland Savanna".

The information on annual precipitation was extracted from the Worldclim 30 arc-second raster dataset "BIO12" (Hijmans et al. 2005), representing the mean annual precipitation from 1950–2000. Values were extracted at the centre coordinate of each permanent plot, of which 20 existed per Observatory (compare Volume 1, Part II). In order to differentiate between summer and winter rainfall regime in the ordination space, values for winter rainfall areas were assigned a negative algebraic sign.

Fuzzy set ordination (FSO) is a direct gradient analysis, which allows the a-priori testing of relationships between one single gradient and a multivariate dataset. This is achieved by hypothesising a relationship between a certain factor and the vegetation. In our case, we hypothesised that 'annual rainfall' as a major gradient is responsible for the differences in life form richness and abundance, the latter expressed as relative percentage cover per 20 m x 50 m. In order to construct a FSO, five iterative calculations were carried out in which membership values, ranging from 0–1, were assigned to each plot. First, plots with high summer rainfall were assigned high membership values, expressed as fuzzy set $\mu_A(x)$. Then, plots with high winter rainfall were assigned high membership values, leading to the fuzzy set $\mu_B(x)$. This means that in set $\mu_B(x)$, the plot with the highest winter rainfall (i.e. most negative) precipitation was assigned a '1' and the plot with the highest summer rainfall precipitation is assigned a value of '0'. Then, the similarity of the life form composition between the plots in set $\mu_A(x)$, called $\mu_C(x)$, was calculated as:

$$\mu_C(x) = \frac{\sum_{y\neq x}[S_{xy}\left(\mu_A(y)\right)]}{\sum_{y\neq x}[\mu_A(y)]}$$

Where S_{xy} is the similarity between the plots x and y, $\mu_A(y)$ is the membership of plot y in the set of high precipitation plots, and $\mu_C(x)$ is the membership of plot x in the set of plots similar to high precipitation plots. For calculating the similarity between the plots we chose Euclidean Distance because of its good interpretability and the fact that we had less than 5% zeros in our life form dataset. In the next step, $\mu_D(x)$ was calculated in a similar manner, by just substituting μ_A with μ_B. Finally, a fuzzy set μ_E was calculated by addressing a "while-not" relationship, i.e. the set of plots similar to high precipitation plots "while not" similar to low precipitation plots. This relationship was called the anti-commutative difference (Roberts 1986) and was calculated as;

$$\mu_E(x) = \frac{\{1 + [1 - \mu_D(x)]^2 - [1 - \mu_C(x)]^2\}}{2}$$

For full mathematical details see Roberts (1986). The final fuzzy set μ_E can be described as 'apparent precipitation' indicating plots with a similar richness or abundance of specific life forms at high or low precipitation values. The 'apparent precipitation' μ_E can be plotted against the actual precipitation μ_A in order to determine how much variation in life form composition is explained by precipitation. Pearson *r* between μ_E and μ_A was used to quantify the correlation between μ_E, i.e. for relative cover and mean richness per basic and extended life form, and precipitation expressed as μ_A.

In order to test whether biomes differed significantly in their mean membership value distribution of μ_E, we used Tukey's post-hoc test of "honest" significant difference. Differences between groups below the 5% level were considered as significant. All calculations were carried out in the R-software environment (R Development Core Team 2010); fuzzy set ordination was applied using the additional package 'fso' (Roberts 2007).

Results & Discussion

Distribution of life form richness and relative cover along the transects

Mean relative cover and mean richness of life forms per Observatory were plotted for each biome by following the BIOTA transects, e.g. from areas of high summer to high winter rainfall (Fig. 1). In the following subsections we will compare the results presented in Fig. 1 with the classifications by Rutherford & Westfall (1994) and Irish (1994).

Our findings confirm the existing biome classifications only to a certain extent. We found that in nearly all cases the relevance of the therophytic component was underestimated compared to our data. This might be due to the nature of the data used by Rutherford & Westfall (1994) who used different kinds of information. Our data was gathered over several years based on a standardised permanent plot design. Although the permanent plots covered less total area, they allowed a more detailed description of the long-term vegetation composition. The repeated measurements also allowed capturing the variability in cover and richness of plant species and hence life forms over the years. It appears that applying permanent sampling of plots improves the identification of the role of life forms in the vegetation structure.

The reverse situation was found for the Desert Biome, where we found that therophytes were overestimated by Rutherford & Westfall (1994). Jürgens (1991) and Irish (1994) disagree with their statement and showed that chamaephytes may play an important role in the Desert Biome as well. This is especially true for those coastal and winter rainfall parts of the Desert Biome, which are showing a gradual transition to the neighbouring biome, i.e. the Succulent Karoo (Jürgens 1991, 2006). Vegetation data were collected for two Observatories in the Desert Biome, however, life form cover was only included for Wlotzkasbaken Observatory (S16). Here, chamaephytes dominated while nanophanerophytes also contributed to cover. These life forms dominate the aspect of the vegetation throughout the year. Only after rare rain events, the desert aspect changes completely due to the mass occurrences of therophytes, which only lasts for a couple of weeks. These rare events have to be differentiated from the general aspect of plant strategy types that are able to survive the regional environmental conditions all. Thus, our data support the statement that therophytes are not as important as chamaephytes for the Desert Biome in terms of relative cover.

The biome classifications according to Rutherford & Westfall (1994) and Irish (1994) did not subdivide the Savanna Biome into separate classes. The two dominant life forms for savannas in general are phanerophytes and hemicryptophytes, i.e. mainly perennial graminoids, while chamaephytes do also occur but are of minor importance (Irish 1994). Our data confirm the prevalence of phanerophytes and hemicryptophytes for both the Woodland and the Thornbush Savanna in terms of relative cover. However, therophytic species play an important role in the richness and cover of these two biome subtypes. Our findings thus show only subtle differences between the two Savanna types that might have been easily overlooked if a standardised design was not applied. However, beyond the basic and extended Raunkiaer life forms considered in this study, Woodland Savanna in northern Namibia is well distinguished from Thornbush Savanna based on leaf morphology (i.e. broad-leafed versus fine-leafed) and on the biogeography of phylogenetic units (Jürgens, unpublished data).

A rather unclear situation in terms of life form dominance arises in the Nama Karoo Biome. The Nama Karoo, a grassy dwarf shrubland (Edwards 1983) is dominated by chamaephytes and hemicryptophytes. Rutherford & Westfall (1994) noted that the high variability of the hemicryptophytic and chamaephytic components is heavily influenced by grazing pressure. Grazing related patterns were found on six of the seven Observatories. All but Observatory S12 in the Nama Karoo were installed as pairs in order to investigate the influence of landuse, mainly in terms of grazing pressure. The Observatory pairs in the Nama Karoo are S39/S40, S08/S09 and S10/S11. We identified differences between Observatory pairs mainly in the relative cover of phanero-, chamae-, and hemicryptophytes. For example, at the Observatory Gellap Ost (S10) with moderate grazing pressure, relative cover of hemicryptophytes was about 35%, whereas at the adjacent Observatory Nabaos (S11) with high grazing pressure, it dropped to almost 1%. This contrast shows the difficulty of obtaining an objective classification also of macroecological units when the human induced variability is not taken into consideration.

The winter rainfall biomes show characteristic differences when compared to the summer rainfall biomes. In particular, the increase of cover and species richness of geophytes has to be noted. While geophytes were not considered in the original classification due to a lack of data, the standardised permanent plot design allowed gathering precise information on richness and abundance of this life form. According to Rutherford & Westfall (1994), the dominant life forms are mainly leaf-succulent chamaephytes. Our data clearly confirms the high dominance of chamaephytes. Additionally, we observed an almost linear increase in richness and relative cover for chamaephytes with increasing winter rainfall. Rutherford & Westfall (1994) list phanerophytes, chamaephytes and hemicryptophytes as the main life forms for the Fynbos Biome. Again, our data confirm their classification. However, due to the extended life form system that we used, it becomes clear that only nanophanerophytes contribute to the phanerophytic component. This information might be important in comparisons with the other biomes as it characterises the uniqueness of the Fynbos Biome. Indeed, Rutherford & Westfall (1994) comment that the phanerophytes in the Fynbos Biome are typically less than 2–3 meters tall and larger phanerophytes are rare, even in areas with higher rainfall.

The extended life form system, as demonstrated here, offers some new insight into the biome classification but also shows some limitations. A better discrimination due to the additional differentiation in height, especially of phanerophytes, has proven to be meaningful for the Fynbos and the Woodland Savanna. However, when relative cover or species richness per life form is compared, subdivision of phanerophytes, for instance, into subclasses leads to a different ranking of the life form; mostly resulting in an underestimation of the phanerophytic layer.

Relationship between life form composition and precipitation

We tested whether relative cover or mean species richness as a quantifying value applied to either the Raunkiaer or the extended life form classification better reflected the biomes along the precipitation gradient (Fig. 2). The Pearson correlation between the actual precipitation μ_A and the membership values μ_E of the anti-commutative fuzzy set were highest for species richness as a quantifying value in general and for the extended life form system in particular. Relative cover for the extended life form system showed only slightly higher correlation than the basic Raunkiaer system.

In other words, for the analysed dataset, the actual precipitation seems to be able to explain variations in species richness per life form better than variations in mean relative cover. Furthermore, this implies that species richness per life form might be a better proxy for distinguishing biomes along the considered precipitation gradient than their relative cover.

Several possible explanations can be highlighted to explain the differences in the correlation values between species richness and relative cover as quantifying values. Species richness as a quantifying value for life forms is less prone to possible observer bias than estimation of cover, although the ability to identify or find rare species depends on the experience of the observer (Kercher et al. 2003). A more important source of bias is the variation in sampling time, i.e. the time span after 'biologically important' rain events (Ogle & Reynolds 2004). These rain events stimulate plant growth and reproduction. Depending on the time when sampling is conducted, the vegetation aspect and thus cover can dramatically change within a few weeks, leading to differences in cover estimates over time. However, the same holds for species richness per life form, although again less severely. Finally, within a given Observatory, the intra-annual variation in relative cover seems to be stronger than the variation in species richness, possibly due to habitat specific variations. This seems to be especially true for the Desert and Nama Karoo Biomes, where species richness shows very little variation but a large discrepancy is found in relative cover between single plots.

Differences in biomes according to life forms

The Tukey HSD post-hoc test was applied to the pooled membership values per biome for the two quantifying values (i.e. species richness and relative cover) and the two life form systems, in order to test whether biomes can be differentiated according to their mean 'apparent precipitation' (Fig. 3). For species richness per life form, five groups (Fig. 3a–e) were distinguished, while for relative cover only four groups were found (Fig. 3a–d). Interestingly, only the variant 'richness of basic life forms' was able to significantly distinguish between Woodlands and Thornbush Savanna. In contrast, this was the only variant in which Desert and Nama Karoo were not considered as significantly different.

In both life form systems, cover-based quantifying values did not separate Thornbush and Woodland Savanna nor Fynbos and Desert in terms of their membership values to a significant extent. While the low separation of the first pair is understandable due to the minor differences in spread, the statistical insignificance for the latter pair (Fynbos vs. Desert) is not that easy to comprehend. Firstly, the variation for Desert is very large, compared with Fynbos, and especially when compared with the very low variation for richness-based quantifying values for the Desert. The large variation in cover values for life forms in the Desert Biome (Fig. 3), leads to different membership values. However, it has to be noted that we applied relative cover (i.e. related to total area covered per plot) instead of absolute cover (related to total area of the plot) in order to stress differences in life form composition rather than general differences in vegetation density.

Conclusions

The aim of this study was to analyse patterns of species richness and relative cover per life form along the BIOTA transects. In particular, we compared mean values from nine years of observations from 32 Observatories with existing biome classifications. Interestingly, with a relatively small set of 32 samples from six different biomes, we were able to confirm and (partly) suggest some adjustments for these classifications. Furthermore, we quantified the

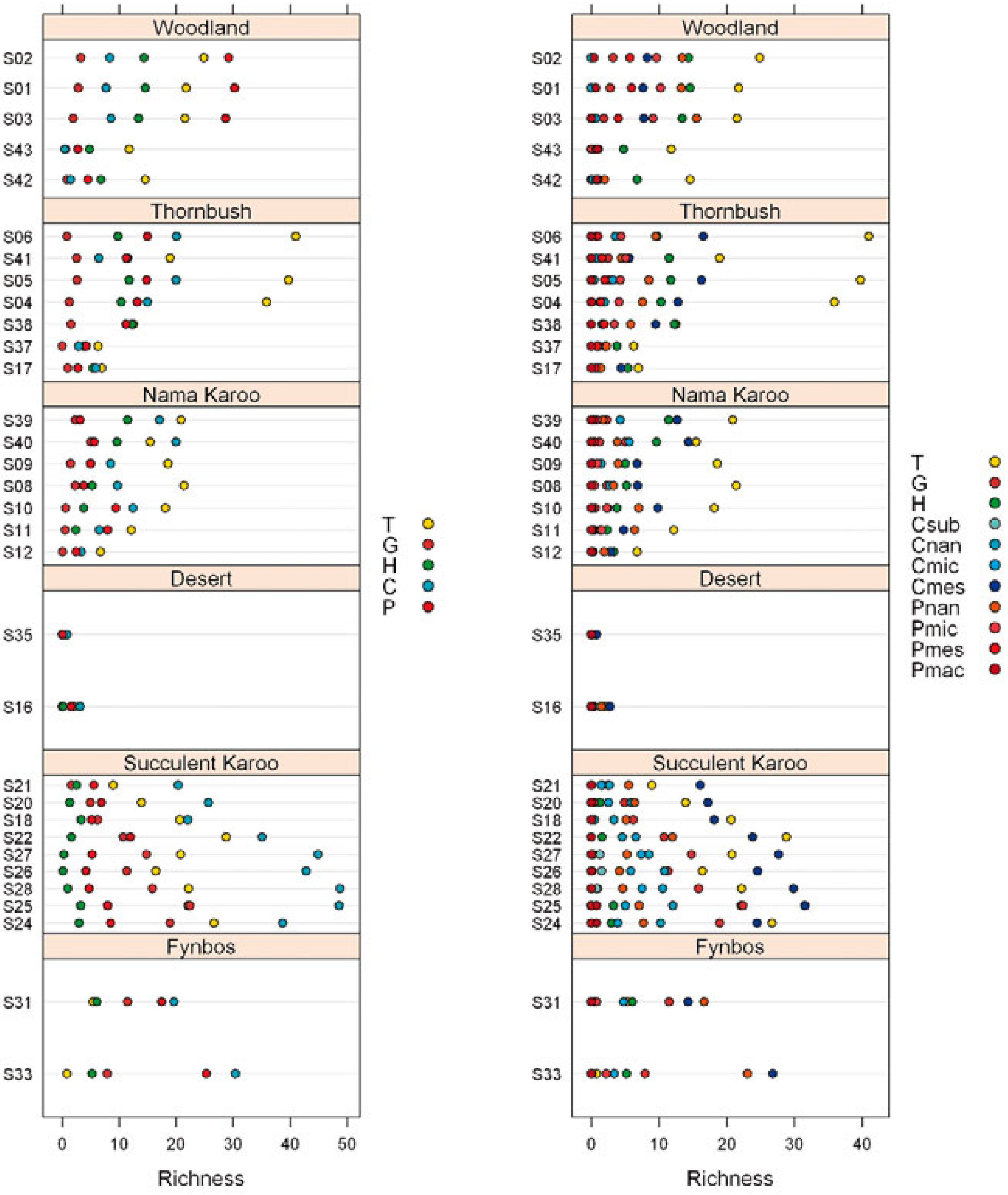
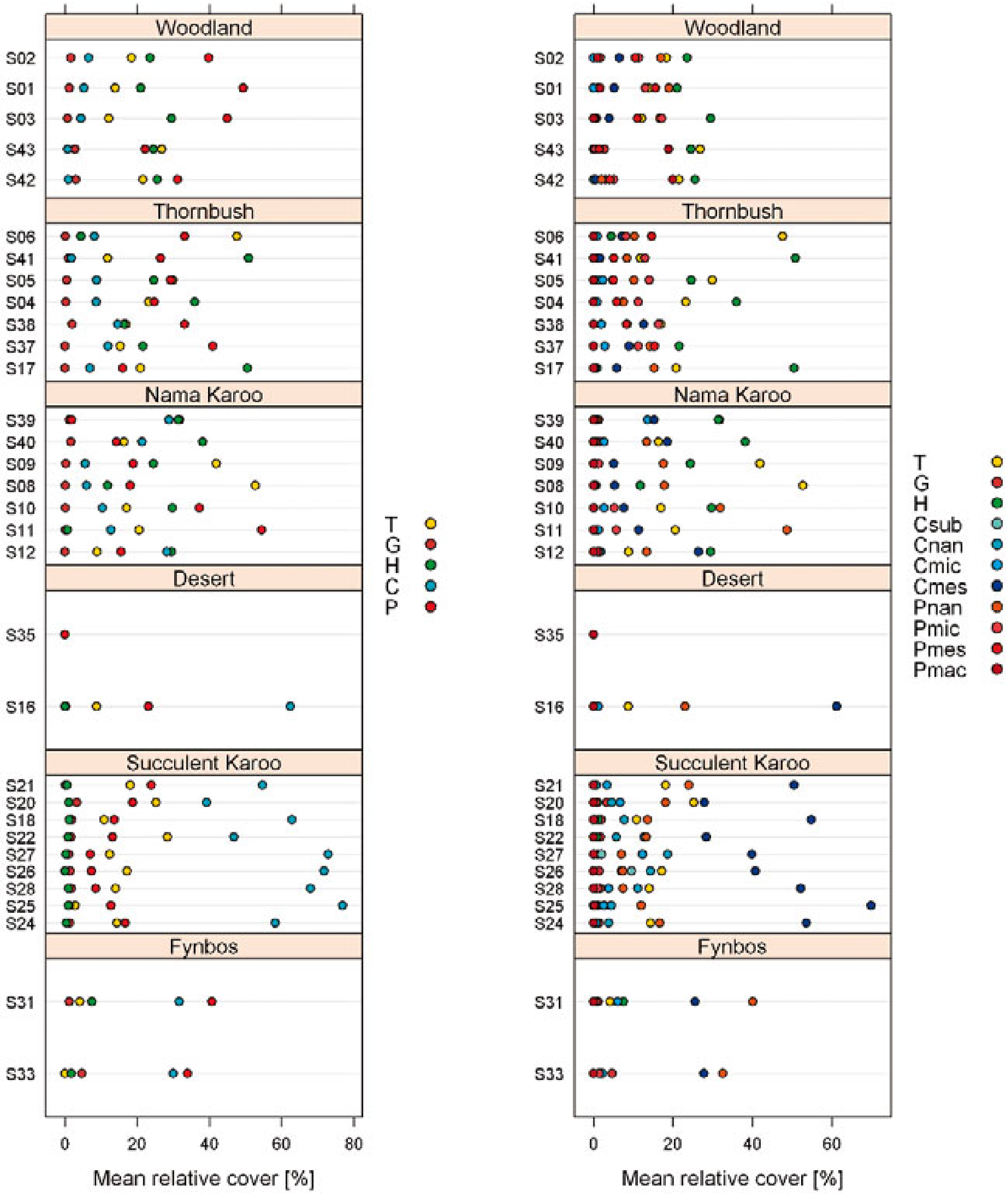


Fig. 1: Richness and relative cover of life forms along the precipitation gradient. For each biome, richness and relative cover of Raunkiaer's simple and extended life form system are presented in different colors. Each line represents one Observatory, which are ordered from highest precipitation of summer rainfall to highest precipitation of winter rainfall.


Woodland
S02
S01
S03
S43
S42
Thornbush
S06
S41
S05
S04
S38
S37
S17
Nama Karoo
S39
S40
S09
S08
S10
S11
S12
Desert
S35
S16
Succulent Karoo
S21
S20
S18
S22
S27
S26
S28
S25
S24
Fynbos
S31
S33
0
20
40
60
80
Mean relative cover [%]
T
G
H
C
P
Woodland
Thornbush
Nama Karoo
Desert
Succulent Karoo
Fynbos
0
20
40
60
Mean relative cover [%]
T
G
H
Csub
Cnan
Cmic
Cmes
Pnan
Pmic
Pmes
Pmac

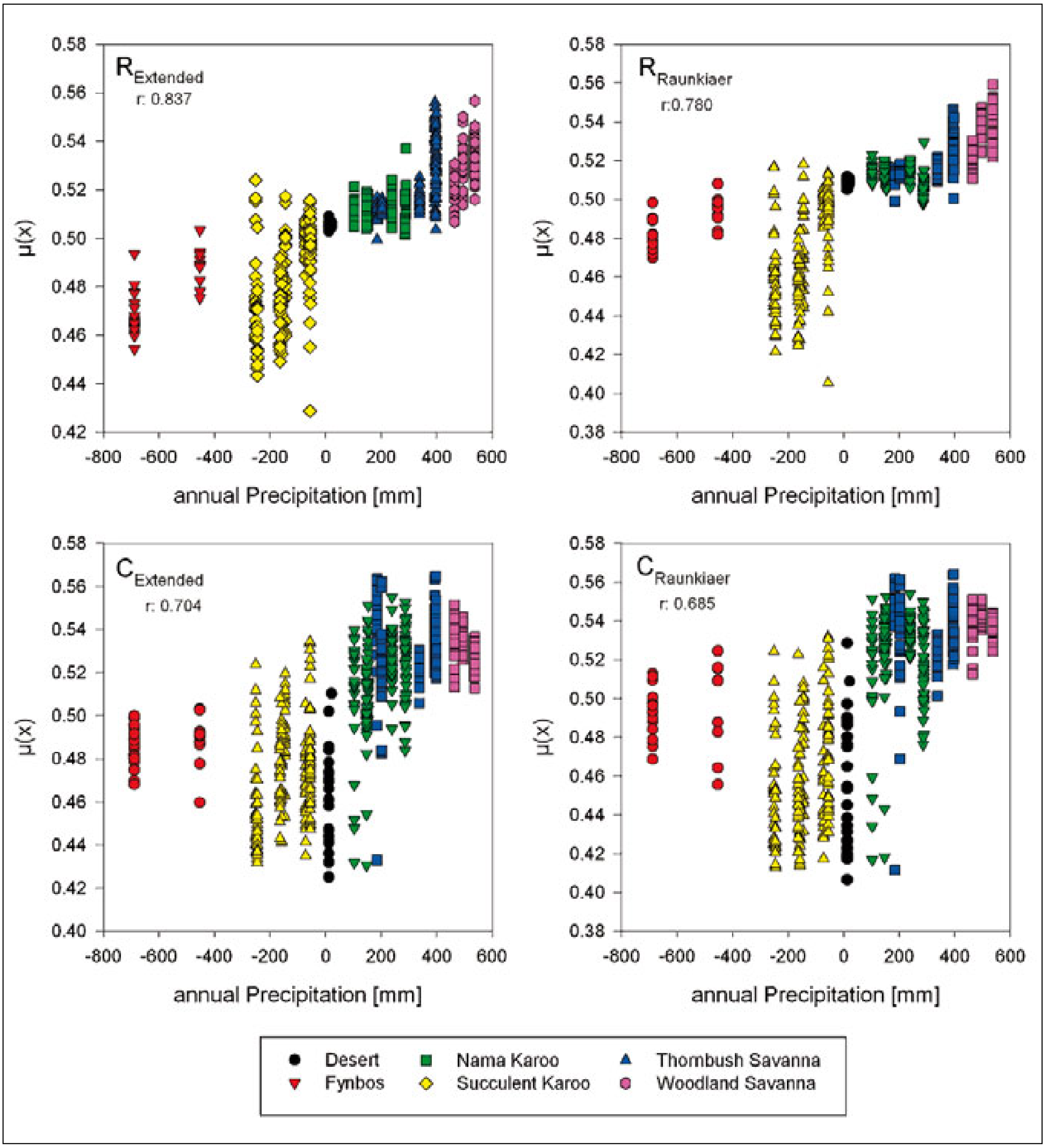


Fig. 2: Fuzzy set ordination of life form information per 20 m x 50 m plot along the precipitation gradient. Negative values on the x-axis reflect the winter rainfall, while positive values indicate a summer rainfall regime. The y-axis represents membership values for the fuzzy set μ_E. The r-value represents Pearson correlation between precipitation and membership value *μ(x)*. Upper left: richness of extended life forms, upper right: richness of Raunkiaer life forms, lower left: cover of extended life forms, lower right: cover of Raunkiaer life forms.

relationship between life form composition and precipitation along the gradient, showing that species richness per life form is a good proxy for the rainfall gradient stretching across summer and winter rainfall regimes. Finally, we analysed the distinctness of the biomes according to life form composition. We showed that, with the two life form systems employed in this study and the particular type of analysis, Woodland and Thornbush Savanna could not be separated except in one analysis. It might be useful to incorporate other traits of high adaptive value, like succulent organs, leaf morphology or growth form characteristics that better describe the plant architecture into an adjusted biome classification.

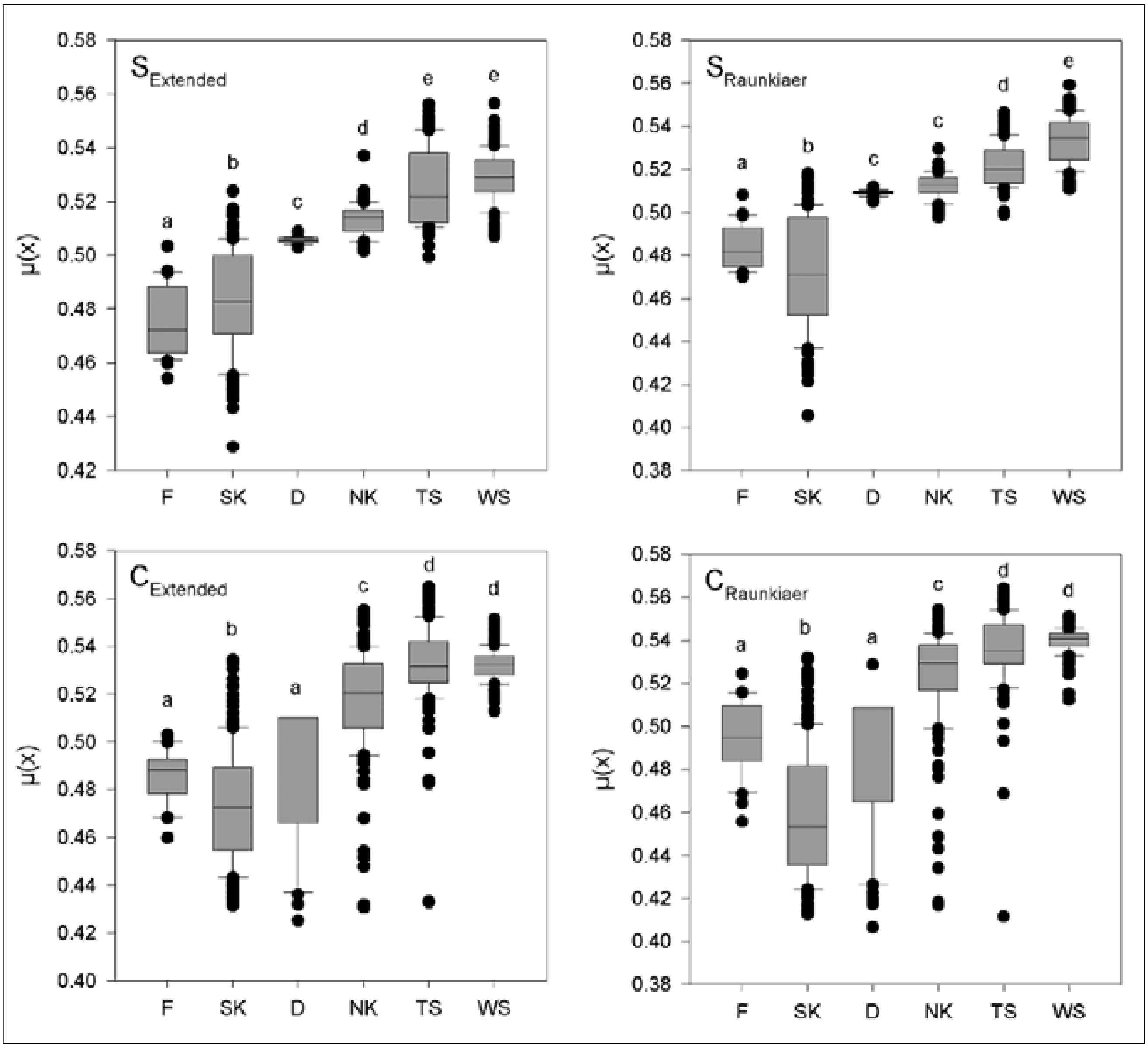


Fig. 3: Comparison of mean membership values (*μ(x)*) per biome. Significance of differences was calculated using TukeyHSD post-hoc test. Groups with the same letters are not significantly different at the 5% level.

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Using the MODIS Enhanced Vegetation Index (EVI) for BIOTA transect analyses

Manfred Keil*, Ursula Gessner & Christian Hüttich

Summary: Remotely sensed biophysical parameters such as the Enhanced Vegetation Index (EVI) based on MODIS time series aided in characterising gradients of vegetation productivity and density along the BIOTA Southern Africa transects. These parameters deliver valuable indicators of standing plant biomass and net primary production (NPP). Mean annual EVI values were plotted along the north-south and west-east orientated transects. The comparison of dry and wet vegetation periods provided additional information on the temporal variation of vegetative productivity along the transects.

Source of data

One of the key purposes of the BIOTA Observatory network was to capture the climatic gradients along the variety of biomes in southern Africa. The Enhanced Vegetation Index (EVI) derived from MODIS time series indicates the degree of standing plant biomass and net primary production (NPP). The mean annual EVI values were measured along the main north-south transect and the two west-east orientated transects covering the BIOTA Observatories, and plotted to visualise climatic and topographic gradients controlling vegetative productivity.

The north-south transect

The location of the BIOTA Observatories is indicated in the 2000 km north-south EVI transect (Figs. 1 & 2). It is apparent that the Observatories capture a range of different bioregions including the northern Woodland Savanna, characterised by the occurrence of a distinct tree layer (e.g. Mile 46 S01 and Sonop S03), the Thornbush Savanna (e.g. Otjiamongombe S05), the Dwarf shrub savanna in the Nama Karoo Biome (e.g. Gellap Ost S10 and Nabaos S11), the arid (e.g. Koeroegap Vlakte, S18) to the semi-arid vegetation types of the Succulent Karoo Biome (e.g. Soebatsfontein S22), and the productive Fynbos Biome (e.g. Rocherpan S29 and Cape of Good Hope S33). Incised drainage systems, indicated by the distinct peaks of the Fish River and its tributaries and the Orange River, between the arid Observatories Nabaos (S11) and Numees (S20), are important areas of water supply and grazing: the peak at profile-km 1100 is a result of irrigated fields near the Naute Dam, located at a tributary of the Fish River. Due to higher vegetation coverage and higher vegetation productivity throughout the year, the Fynbos Biome of the Cape region has slightly higher EVI values in comparison to the woodlands of the northern Kavango.

The west-east transect in northern Namibia

The northern and southern west-east transects (Figs. 3–6; compare also Fig. 1 in Article III.3.2) depict the increasing vegetation coverage as a result of an increasingly tropical and humid climate. The hyper-arid coastal deserts of the Skeleton Coast and Namib Desert show no remarkable vegetation activity. The transition from desert conditions via sparse grasslands towards dwarf shrub vegetation and very open shrublands are indicated by a steep increase of photosynthetic activity along the first 250 km of the transect. The transition to the Mopane forests and open woodlands of the Kavango are characterised by a second increase of EVI at profile-km 500. The region around the Observatories Omano go Ndjamba (S42) and Ogongo (S43) is characterised by a fine-scale mosaic of various vegetation types in the Cuvelai drainage system, indicated by higher local variations of EVI with partially distinct increases of the EVI amplitude. The Mile 46 (S01) and Mutompo Observatories (S02) mark the eastern border of the transect in the open Kavango woodlands.

The west-east transect in central Namibia

The central west-east transect (Figs. 5 & 6) shows a similar EVI gradient, driven climatically by the cold Benguela Current in the west (Namib Desert) and increasingly humid sub-tropical conditions towards the east. An increase in precipitation is reflected in increasing biomass and productivity towards the east. The Observatory Rooisand (S37) is situated near the western edge of the Khomas Hochland where climatic conditions allow increasing vegetation productivity in the Thornbush and Camelthorn Savanna vegetation types and the adjacent Kalahari (up to Sandveld S41).

Conclusions

The lower vegetation productivity during the below average rainy season of 2004/2005 and the higher vegetation productivity during the above average rainy season of 2005/2006 along the BIOTA transects indicates the dependency of vegetation on water supply in the rainfall

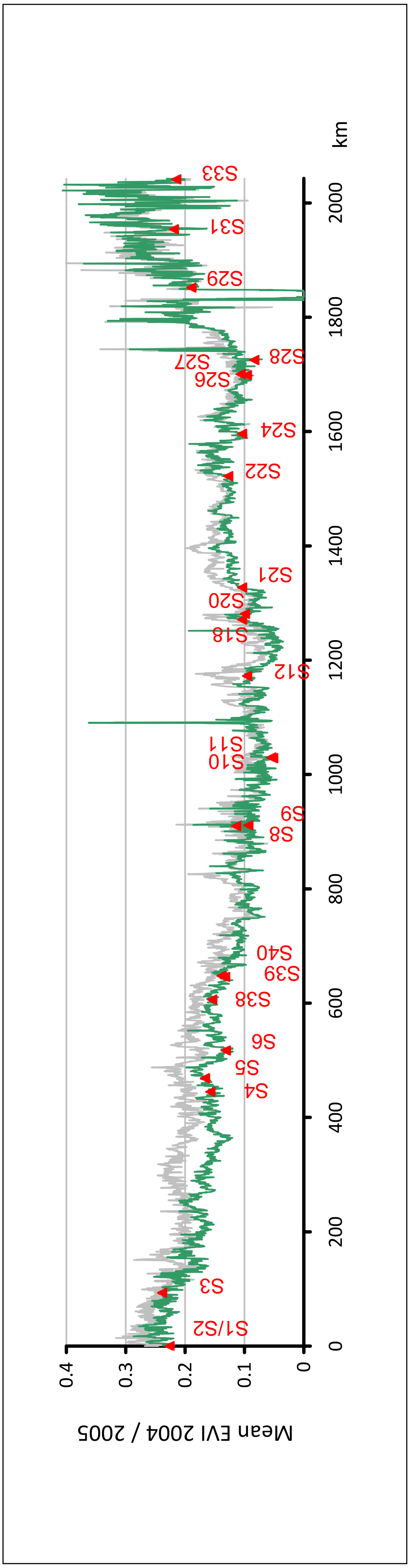

Fig. 1: Enhanced Vegetation Index (EVI) at the Observatories along the north-south transect for the dry rainy season 2004/2005. The grey line indicates the wet rainy season conditions of 2005/2006.

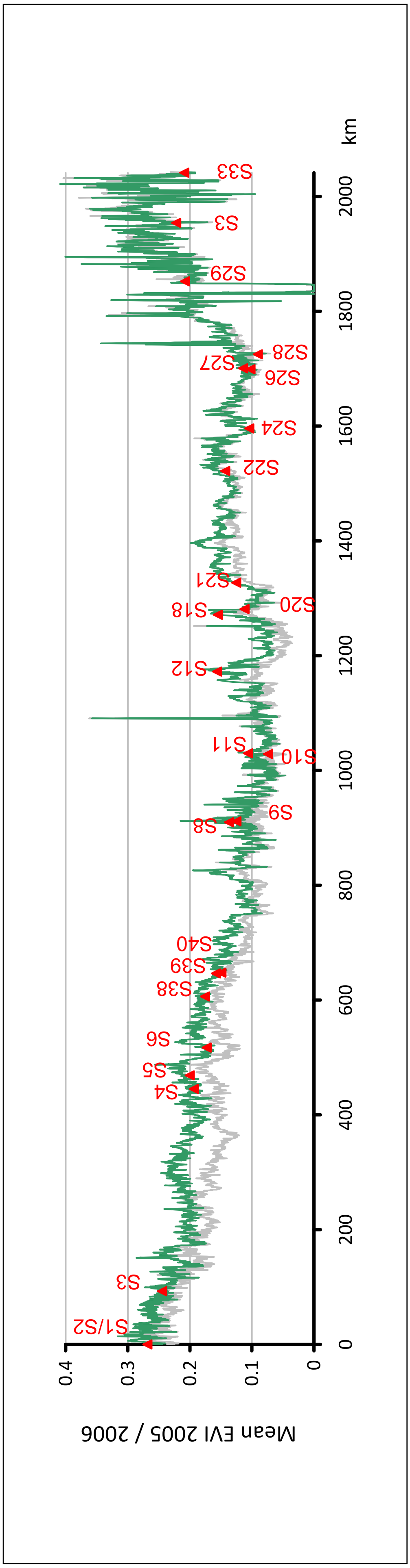

Fig. 2: Enhanced Vegetation Index (EVI) at the Observatories along the north-south transect for the wet rainy season 2005/2006. The grey line indicates the dry rainy season conditions of 2004/2005.

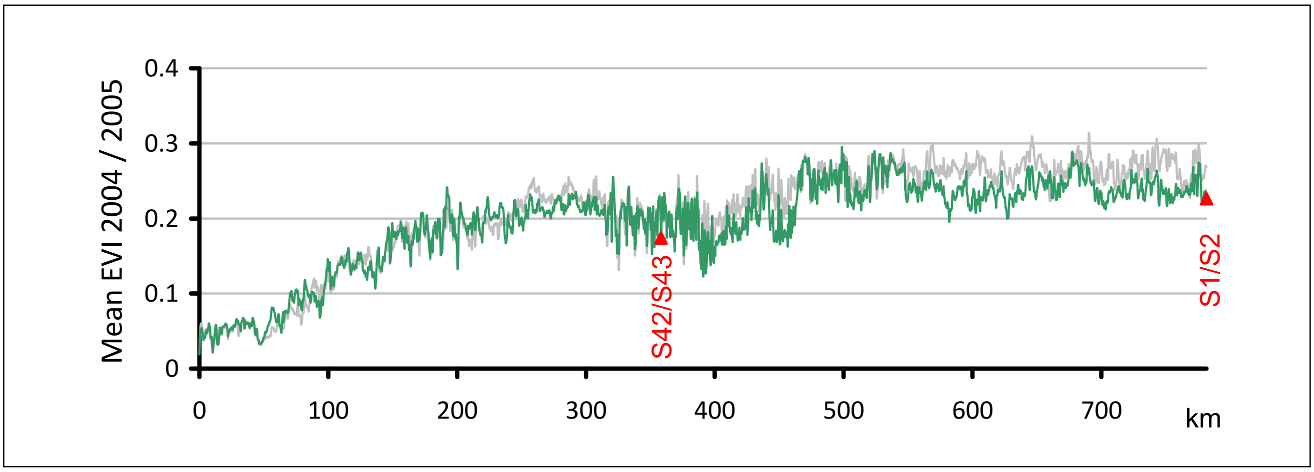

Fig. 3: Enhanced Vegetation Index (EVI) along the northern west-east transect for the dry rainy season 2004/2005 with BIOTA Observatories. The grey line indicates the wet rainy season conditions of 2005/2006.

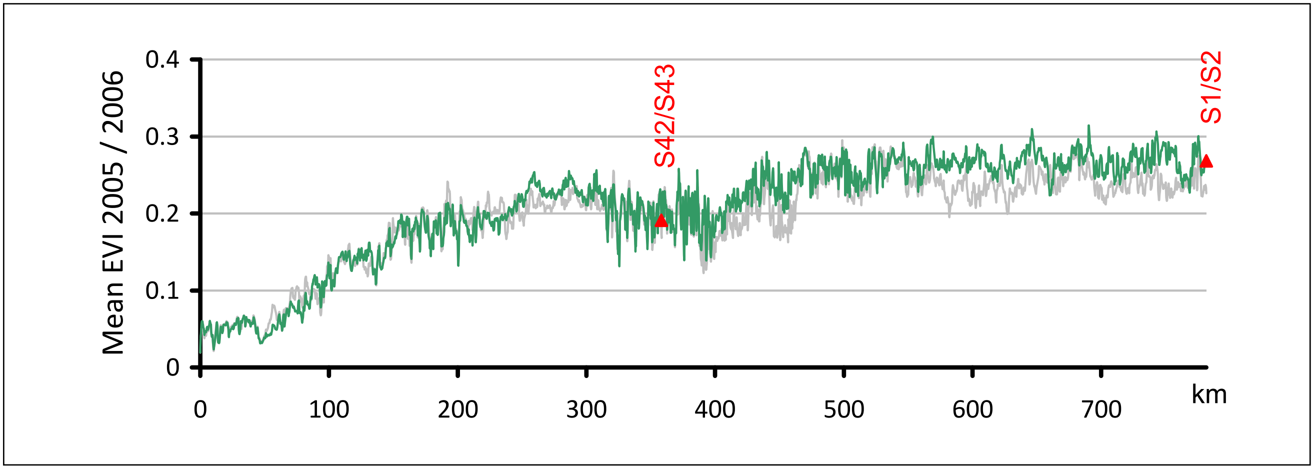

Fig. 4: Enhanced Vegetation Index (EVI) along the northern west-east transect for the wet rainy season 2005/2006 with BIOTA Observatories. The grey line indicates the dry rainy season conditions of 2004/2005.

driven ecosystems of the southern African savannas, deserts and semi-deserts.

As depicted in the north-south transect (Figs. 1 & 2), the impact of the lower rainfall in 2004/2005 is most visible in the open and very open shrublands of the Kalahari and Thornbush Savanna of central Namibia. Similar patterns were observed for the Kavango woodlands along the northern west-east transect. The central Namibian west-east transect indicates general decreased vegetation activity over all bioregions in central Namibia with below average rainfall although the arid grasslands and dwarf shrublands of the Namib and Namib-Kalahari transition were most affected by the drought during the growing season of 2004/2005.

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The authors' general acknowledgements to the organisations and institutions, which supported this work are provided in Volume 1.

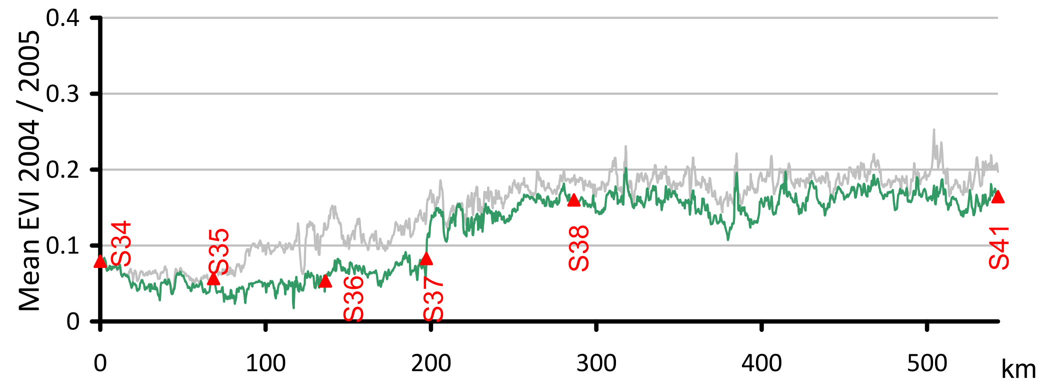

Fig. 5: Enhanced Vegetation Index (EVI) along the central west-east transect for the dry rainy season 2004/2005 with BIOTA Observatories. The grey line indicates the wet rainy season conditions of 2005/2006.

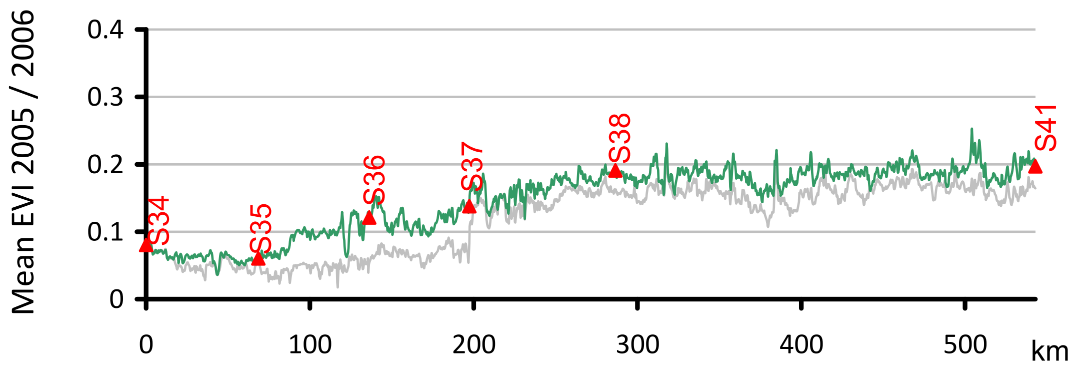

Fig. 6: Enhanced Vegetation Index (EVI) along the central west-east transect for the wet rainy season 2005/2006 with BIOTA Observatories. The grey line indicates the dry rainy season conditions of 2004/2005.

Basic patterns of Lepidoptera diversity in Namibia

Wolfram Mey

Summary: The Lepidoptera fauna of Namibia was investigated intensively during the last decade. Samples of butterflies and moths were collected from the BIOTA Observatories and additional sites all over Namibia. This material provided the basis for an analysis of the Lepidoptera at a regional scale. The Lepidoptera fauna is adapted to arid and semi-arid conditions and the associated drought periods of varying lengths. Lepidoptera species richness in Namibia is similar to that found in South Africa although there are some unique peculiarities in terms of distribution, diversity, faunal composition, seasonality and endemism. The article provides a brief outline of the major characteristics of the Namibian Lepidoptera fauna.

Photo 1: *Ornativalva kalahariensis* (Gelechiidae), Namibia, Brandberg. Photo: Wolfram Mey, 2010.

Introduction

The Lepidoptera fauna of Namibia is still inadequately studied (Barnard 1998, Mendelsohn et al. 2002). Although a checklist of the southern African species is available (Vári et al. 2002), the included species are listed without supplementary geographic data that precludes the extraction of Namibian records. Despite some progress in recent years (e.g. Braine 2002, Händel 1998, Kühne 2000, Mey 2004, 2007, 2010, Swart 2004), vast areas of the country, including a number of special habitats (e.g. salt-pans, wetlands, coastal dunes), have remained unexplored. Also, inventories for the BIOTA Observatories have not yet been compiled due to unresolved taxonomic problems in nearly all groups. Registration of the complete spectrum of autochthonous assemblages would necessitate year-round sampling and ongoing faunal observations with an intensity that could not be performed within the framework of the BIOTA project. So far, we have only sampled parts of the fauna using a standardised method of systematic sampling. These parts or fragments were used for comparisons among different Observatories or with other localities and provided insights into some general features of the Lepidoptera fauna in this part of Africa.

Features of the fauna

Distribution

The Lepidoptera fauna of Namibia is richest and most diverse in terms of species numbers and abundance in the north and north-eastern regions of the country. Towards the arid and semiarid regions in the south and along the Atlantic coast the fauna becomes less species-rich although abundance can still be very high. This pattern corresponds with the distribution of mean annual precipitation and the diversity patterns of vascular plants in Namibia. The Lepidoptera as a phytophageous insect group simply follow this rainfall gradient (Figs. 1–3). This decline towards the Atlantic coast, however, is not only a gradual impoverishment of a rich fauna that becomes more and more fragmented. At the same time it is characterised by a gradual change in species, species groups and genera. Some groups disappear or become rare whilst new species appear and alter the faunal composition. The changes in Lepidoptera fauna follow more or less the distribution of the Biomes in Namibia (Irish 1994), which are based on the vegetation (life form dominance) and abiotic factors.

Namib Desert: The Namib is not a compact, homogenous and isolated desert. It is largely influenced by the neighbouring areas. There are many river beds, almost dry for most of the year, which cut through the Namib and reach the Atlantic coast, especially in the northern and central parts. They are lined with remnants of river bank vegetation that is well developed in the interior of Namibia. Together with the host plants many Lepidoptera species follow the river banks, and thus occur in the middle of the Namib without being true desert species. An example is *Ornativalva kalahariensis* (Gelechiidae), a common species, which together with its host plant *Tamarix usneoides* reaches the coastal dunes (Photo 1). This distribution pattern is not restricted to Lepidoptera but occurs in many insect, including aquatic orders, e.g. Odonata (Suhling et al. 2009).

Another landscape structure that contributes to landscape heterogeneity are inselbergs. They receive more precipitation via coastal fog than the surrounding plains and thus possess a richer flora and

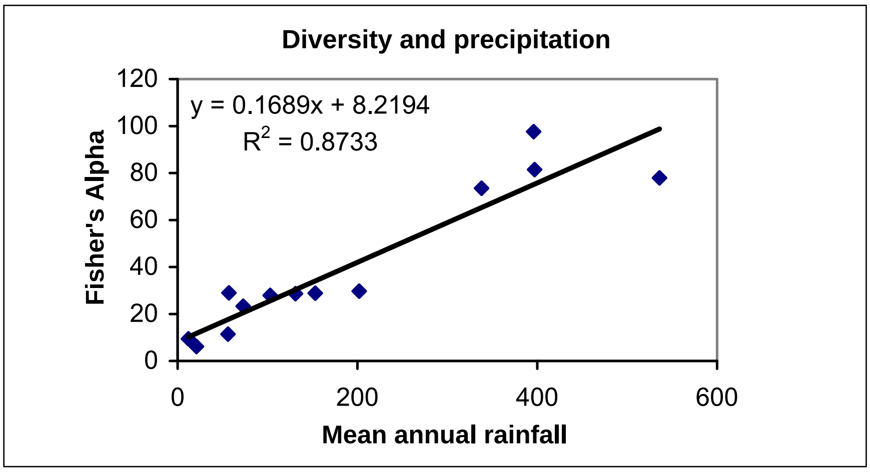

Fig. 1: Relationship between Lepidoptera (excl. Rhopalocera) diversity and annual precipitation (in mm) at BIOTA Observatories in Namibia and South Africa.

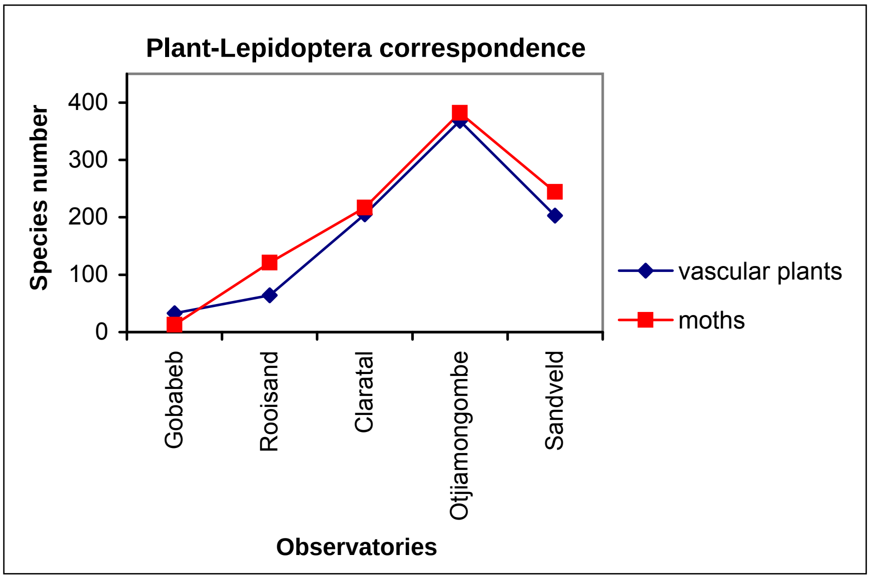

Fig. 2: Correspondence in the distribution of species numbers between Lepidoptera (excl. Rhopalocera) and vascular plants.

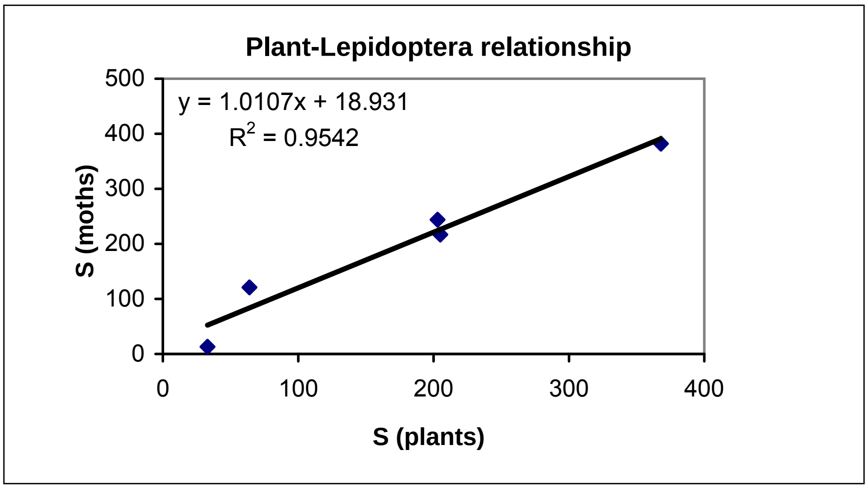

Fig. 3: Relationship between the number of vascular plants and the number of Lepidoptera species at Observatories of the west-east transect in January 2007.

fauna. Such localities can be considered as enclaves of the adjacent Nama Karoo Biome according to the plant species occurring there.

Lichen fields are another special biotope (habitat) in the Namib Desert. Within the Lepidoptera, species of the subfamily Lithosiinae (Arctiidae) are known to be specialised lichen feeders (Pinhey 1975). Several species of this group occur in the Namib Desert and on the offshore Guano islands (Mey 2010).

Nama Karoo: The Lepidoptera of the Nama Karoo Biome form very interesting assemblages. This biome is in general a transition between the Desert and the Savanna Biomes. Species numbers are usually lower, and widespread species dominate the communities (Photo 7). However, this biome is home to a large number of endemic species. This is due mainly to the mountainous nature of the biome. But the wide and undulating Nama Karoo plains in the south of Namibia also possess a heterogeneous Lepidopteran fauna including endemic species.

Succulent Karoo: In contrast to the other biomes, the Lepidopteran fauna of the Succulent Karoo is very peculiar. The large number of endemic, mostly succulent plants is mirrored by a high number of endemic species and genera of moths. Subterranean ground dwellers feeding on roots are abundant (e.g. Noctuidae). Leaf-miners are scarce but species with larvae, which bore into stems and twigs, or case-bearer are well represented. Detritophageous species are also common. This species composition closely resembles those of desert communities, but with much higher species numbers. The common southern African butterflies, abundant in the neighbouring Nama Karoo, are rarely seen whilst the abundance of the few endemic butterfly species is always low.

Thornbush Savanna: In terms of Lepidoptera species numbers, the Thornbush Savanna represents the richest biome in Namibia. Samples from light collecting usually yield more than 300 species per night (Mey 2010), whereas outside of this biome catches rarely exceed 150 species. Noctuidae, which have a wide distribution in Africa, are the dominant family with many species

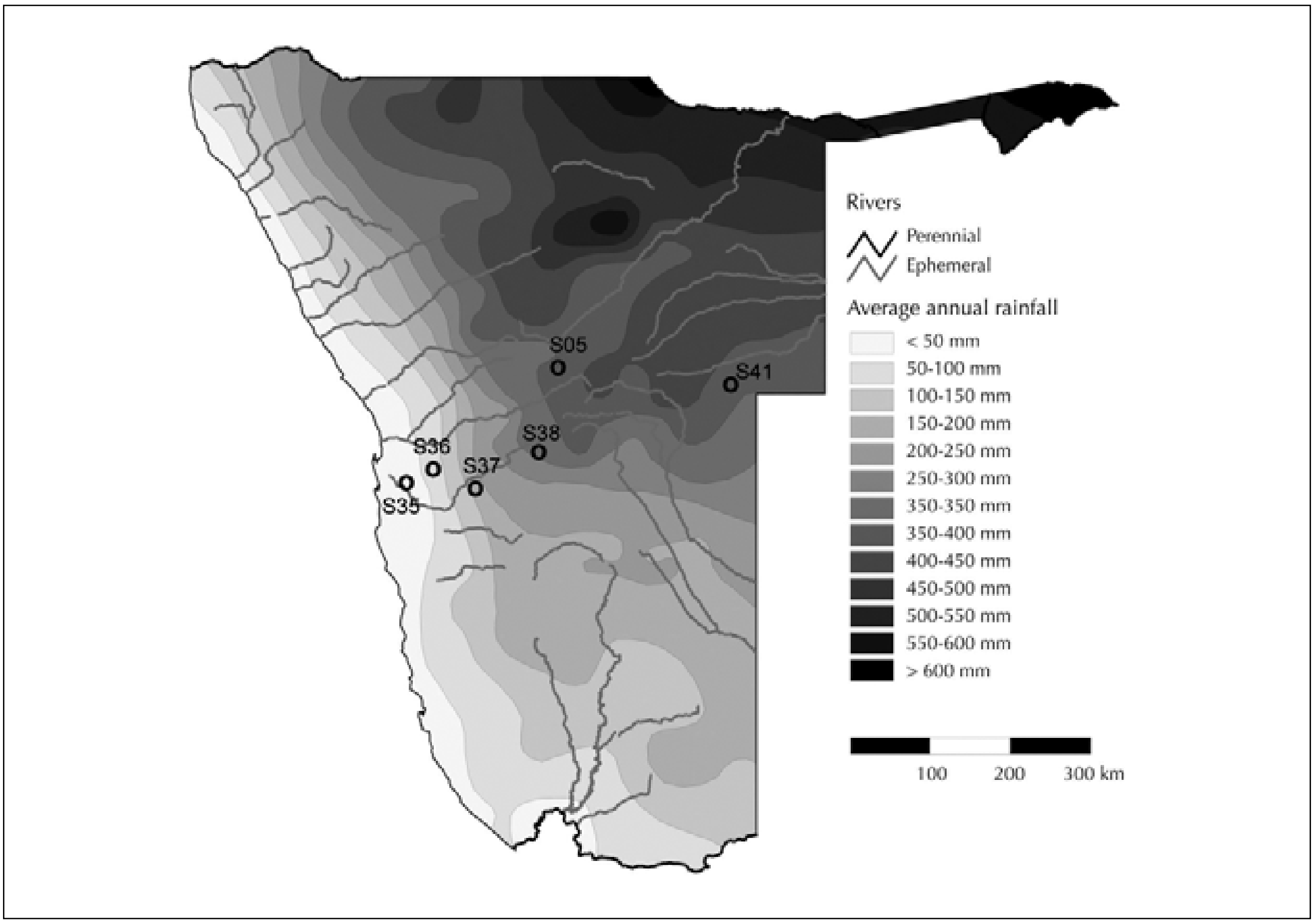

Fig. 4: Location of Observatories of the west-east transect in Central Namibia: Gobabeb (S35), Ganab (S36), Rooisand (S37), Claratal (S38), Otjiamongombe (S05), Sandveld (S41).

occurring only in this part of Namibia. Many species of the large and conspicuous Macrolepidoptera occur, which is in sharp contrast to other Biomes in Namibia where this group is poorly represented. Pyraloidea and Microlepidoptera are also well represented, with numerous species confined to the Savanna Biome and not found elsewhere in Namibia. As a rule, the Lepidoptera associations of the various vegetation units within this biome are not dominated by a small number of abundant species as is the case in the drier biomes. The abundance is more evenly distributed and the number of species represented by single individuals (= singletons) is usually high.

Diversity and faunal composition

The variation of faunal composition and species diversity among Lepidoptera was examined along the west-east transect in Central Namibia (Fig. 4). The transect corresponds with the precipitation gradient and cuts through the Desert, Nama Karoo and Savanna Biomes. It covered the six BIOTA Observatories Gobabeb, Ganab (S36), Rooisand (S37), Claratal (S38), Otjiamongombe (S05) and Sandveld (S41). The Observatories are situated roughly along the 23° S line of latitude (Tropic of Capricorn) and represent typical habitats and vegetation types in the three occurring biomes. Field work was carried out in January and April 2007. Moths were sampled with automatic light traps and butterflies using hand-nets. The material was analysed at the species level. Relative proportions were calculated from species and specimen numbers.

Proportions of the Lepidoptera groups changed distinctly along the transect (Fig. 5). Though Microlepidoptera was the dominant group in all samples, the micromoths contributed more strongly to ensembles in arid and semiarid areas with Gelechiidae as the most speciose family. Pyraloidea showed a similar pattern, with the Pyralidae as the dominant family. Macrolepidoptera (excl. Noctuidae) and butterflies were species-poor groups whose numbers decreased dramatically from East to West. They contributed little to the Lepidoptera diversity. Noctuidae was the family with the highest species number. It is the most species-rich family in southern Africa (Krüger 2007). Its species diversity ranked first in all Observatories and other sampling sites independent of biome type.

Local species diversity was highest in the Observatories of the Thornbush Savanna Biome and decreased gradually with increasing aridity. The diversity pattern of Lepidoptera corresponded with the precipitation- and vegetation gradient (Fig. 1). Changes in diversity corresponded to changes in the dominance structure of the local ensembles. High dominance values were observed in the arid and semi-arid Observatories Ganab, Rooisand, Gellap Ost (S10) and Karios (S12) whereas low values were typical for the Observatories in

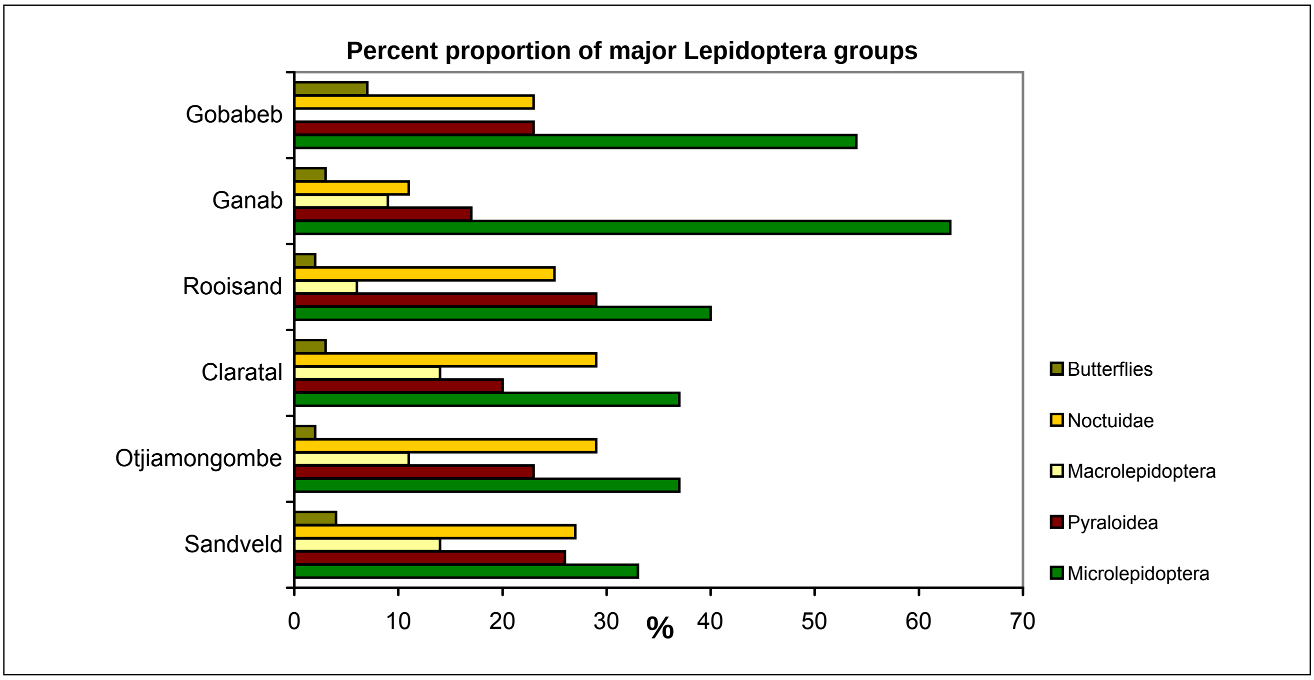

Fig. 5: Composition of Lepidoptera at the Observatories of the west-east transect in Namibia in January 2007.

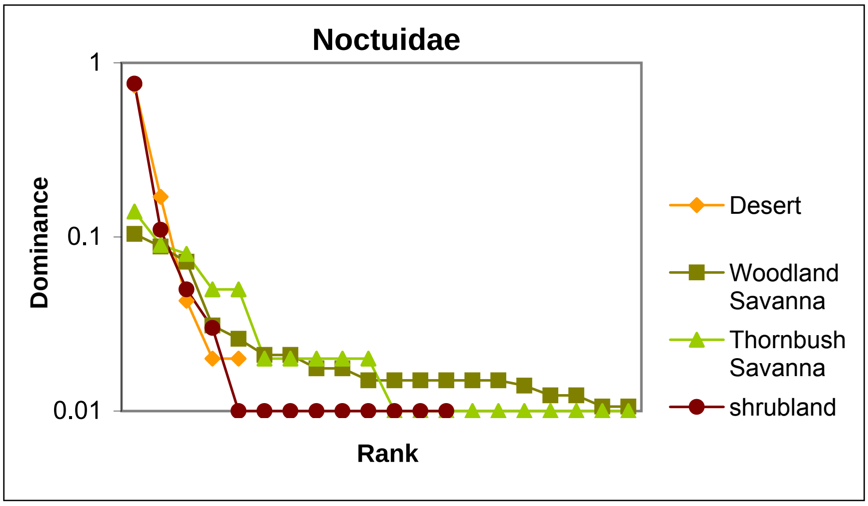

Fig. 6: Dominance structure (Berger-Parker Index) of Noctuidae in different vegetation types.

the Thornbush Savanna Biome (Fig. 6), where ensembles were not dominated by one or two species.

Seasonality

Namibia is a dry country during most of the year. Summer rainfall occurs from December to April and from May to September in the winter rainfall area in south-western Namibia. This pronounced change between dry and wet seasons determines the development and phenology of the vegetation and consequently governs the dynamics of the Lepidoptera fauna. In general, the beginning of the rainy season triggers the emergence of the majority of butterflies and moths. From this peak emergence, abundances decline towards the end of the rainy season. During dry months Lepidoptera are on the wing in low numbers. The flight periods of species are adjusted to this annual change in different ways. Although most species of moths come out with the rain, there are groups, which appear either before the rain, after the rain or at the end of the rainy season, or in the dry season only. Therefore, the taxonomic composition of the Lepidoptera ensembles at the study sites changes during the course of the year. The observed succession of species is not only a matter of dry versus wet season, but it represents an intra-seasonal change too. The faunal differences could be surprisingly wide at all Observatories. As an example, the faunal similarity of moths was calculated between samples from the beginning and samples from the end of the rainy season from six Observatories in Namibia (Fig. 7). The similarity expressed by the Jaccard Index was variable and ranged from 0 to 0.34, meaning a rather low level of shared species in all groups. In other words, both samples had a high complementarity. This result clearly shows that seasonality is an important factor influencing the Lepidopteran fauna and contributes towards increasing diversity. As a consequence, many consecutive samples had to be drawn within a single season in order to record species richness comprehensively.

In arid and semiarid biomes, rainfall does not have a strong influence in terms of driving Lepidoptera dynamics. In the Namib Desert, seasonal differences are small and aseasonality of the fauna is expected. Interestingly, this holds true only for species with detritophageous and coprophageous larvae, e.g. *Hypotia* species (Pyralidae) (Photo 2), *Trichophaga cuspidata* (Tineidae) (Photo 3), which were encountered year-round. Species feeding on desert plants have a restricted flight period and are on the wing during a short time of the year only, e.g. *Scythris vogelfederbergensis* (Scythrididae) (Photo 4). At the end of the rainy season ubiquitous species are frequently observed in the desert. They are migrants from the Nama Karoo and Savanna Biomes and appear together with different species in different localities, contributing to the often surprising dissimilarity and seasonality of local assemblages in the Namib Desert (Fig. 8).

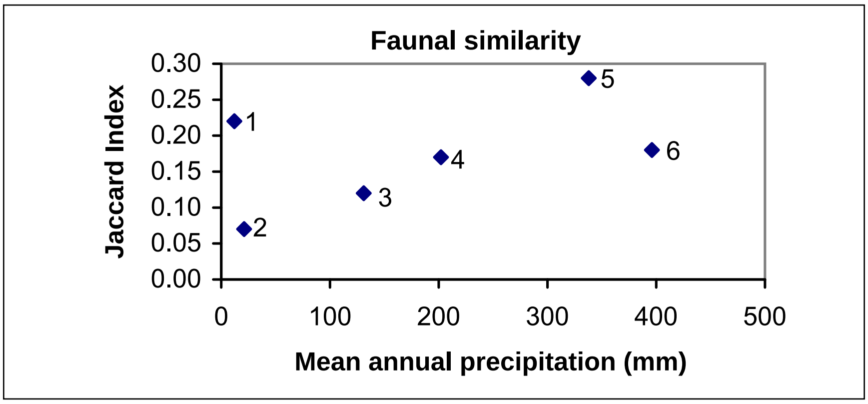

Fig. 7: Faunal similarity of Lepidoptera (excl. Rhopalocera) between January and April 2007 at six Observatories. 1 = Wlotzkasbaken (S16), 2 = Gobabeb (S35), 3 = Ganab (S36), 4 = Rooisand (S37), 5 = Claratal (S38), 6 = Otjiamongombe (S05).

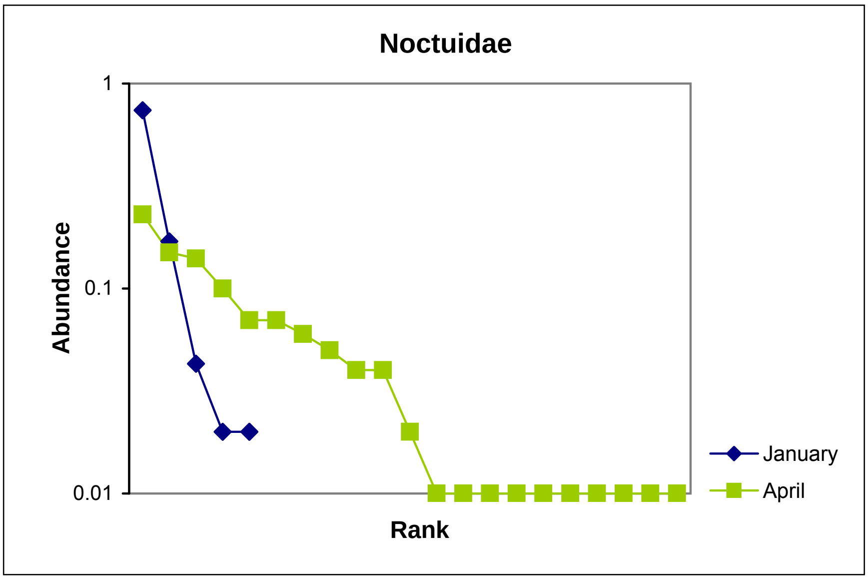

Fig. 8: Rank/abundance plot of Noctuidae on Wlotzkasbaken in 2007. The graphs are significantly different (Kolmogorov-Smirnov test).

Endemism

The arid and semiarid biomes are home to nearly all endemic Lepidopteran species of Namibia. These biomes are unique and confined to this part of Africa whilst the more humid areas covered by savanna and woodland have a much larger area of distribution extending from Namibia to Central and East Africa. The majority of endemics belong to the Microlepidoptera, Pyraloidea and the families Noctuidae and Geometridae whereas other Macrolepidoptera families have only a few endemic species. There are a few endemic subspecies of butterfly. However, knowledge of the distribution of all endemics is not comprehensive, and some of them might have ranges that include southern Angola and/or Namaqualand in South Africa.

There are only a small number of true desert species. They either have larvae, which feed on detritus or that feed monophageously on endemic desert plants, mainly of the families Zygophyllaceae and Mesembryanthemaceae. An example of this group is *Pecticossus gaerdesi* (Cossidae) (Photo 5) whose larvae bore into stems and roots of *Zygophyllum stapffi* in the Central Namib (Daniel 1956). Until now no Lepidoptera species is known to feed on *Welwitschia mirabilis*.

The Western Escarpment Mountain chain, from the Kaokoveld in the north to Cape Town in the south, encompasses numerous localities with a permanent water supply that usually supports richer vegetation. Some of these localities can be regarded as refugial areas for Lepidoptera (Mey 2010). In addition, numerous inselbergs contribute to habitat heterogeneity and offer environmental conditions for species to survive periods of climate and vegetation change. Such isolated places provided the geographic location for evolutionary processes that eventually resulted in the development of endemic species. Their ranges can either be very small or extend more widely. For example, most of the 124 species described as new from the Brandberg in Namibia (Mey 2004, 2007) have subsequently proved not to be endemics of that single mountain massif but to be more widely distributed along the escarpment with its various mountain ranges (pers. observations).

The Succulent Karoo Biome in the south-west of Namibia contributes a unique set of species to the overall diversity and endemism of the country. However, the species are biome-specific, often not confined to Namibia but also occurring in South Africa. A typical element of this biome is the genus *Centrarthra* of the family Noctuidae (Photo 6) with nearly 30 described species, 8–10 of which can be found at a single locality. The biology of the species is unknown (Janse 1937).

An often asked question is: “How many endemics occur in the country?” The question cannot be answered for Lepidoptera at the moment because a

Photo 2: *Hypotia bolinalis* (Pyralidae), Namibia, Wlotzkasbaken (S16). Photo: Wolfram Mey, 2008.

Photo 3: *Trichophaga cuspidata* (Tineidae), RSA, Richersveld, Koeroegap Vlakte (S18). Photo: Wolfram Mey, 2010.

Photo 4: *Scythris vogelfederbergensis* (Scythrididae), Namibia, Vogelfederberg. Photo: Wolfram Mey, 2010.

Photo 5: *Pecticossus gaerdesi* (Cossidae), Namibia, Wlotzkasbaken (S16). Photo: Wolfram Mey, 2010.

Photo 6: *Centrarthra* sp. (Noctuidae), Namibia, Aus.
Photo: Wolfram Mey, 2010.

Photo 7: Aggregation of females of *Catopsilia florella* imbibing mineralised water from paddles and damp sand.
Photo: Jürgen Deckert, 2010.

catalogue or a check-list of all recorded species does not exist for Namibia. As a substitute, we can use the species numbers of the Brandberg, the best explored local fauna in Namibia. Of a total of 611 species, 124 species (approximately 20%) were described as new. A relatively high number of species are not yet identified, and will probably increase the proportion of new taxa. All of them can be considered as candidates to be Namibian endemics (Mey 2007). Judging from this count, about 25–30% of the Brandberg fauna should belong to this group. By applying the numbers to the whole of Namibia, a rough estimate of Lepidoptera endemicity is approximately 25–30%. This level of endemicity is comparatively high, and confers a large responsibility on the country of Namibia for conserving this wealth.

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Part III

III.4 Case studies on biodiversity patterns

Mapping of biological soil crusts in the Succulent Karoo using hyperspectral remote sensing data

Bettina Weber*, Claas Olehowski, Kirstin Deutschewitz & Burkhard Büdel

Summary: Biological soil crusts (BSC), which occur worldwide in arid and semiarid regions, were successfully mapped on the basis of hyperspectral CASI 2 data and spectral field data for the Succulent Karoo, South Africa. Since there were no unambiguous spectral characteristics of BSC over a wide spectral range, small-scale spectral features, that unequivocally characterise BSC, were extracted utilising the methodology of continuum removal. Under application of this newly developed Continuum Removal Crust Identification Algorithm (CRCIA), 16.2% of the 24 km² study area were classified as BSC-covered. The classification revealed that BSC are abundant over large areas of the study area. However, increased grazing and disturbance intensity was reflected by local patches devoid of any BSC. The next step will be to use this classification method as a basis to create a methodology, which can be transferred to a variety of sensors, scales and in different environments.

Introduction

Biological soil crusts (BSC) are formed by a close association between soil particles and different proportions of cyanobacteria, green algae, lichens, bryophytes and microfungi, and occur within or immediately on top of the uppermost few millimeters of the soil (Belnap et al. 2001a). They occur worldwide in arid and semiarid regions, which cover more than 35% of the Earth's land surface, or locally wherever a semiarid to arid microclimate occurs. Within these habitats BSC are known to play a major role as primary producers and therefore represent the main elements not only in the local but also global C- and N-cycles (Evans & Lange 2001, Elbert et al. 2009). They also greatly improve soil stability, have an influence on soil hydrology and play a key role in succession (Belnap & Eldridge 2001; see also Chapter III.3). The impact of BSC on the seed germination of vascular plants (here termed "plants" or "vegetation" for simplicity) is complex and not yet fully understood. However, overall they appear to have a positive effect on the growth and nutrient status of the adjacent vegetation (Belnap et al. 2001b).

Due to their extremely patchy occurrence over vast landscapes and their disguised growth on often vividly colored soils, mapping of BSC using standard methodologies is not possible on larger geographical scales. The possibility of using remotely sensed imagery to aid with the mapping of BSC was first described by Wessels & van Vuuren (1986), using false color composites of Landsat 3 data to identify lichen-dominated BSC in the Namib Desert, Namibia. Since then, the spectral characteristics of different types of BSC were investigated in a number of studies (e.g. Graetz & Gentle 1982, O'Neill 1994, Pinker & Karnieli 1995, Karnieli & Sarafis 1996) with the absorption feature of chlorophyll a at 675 nm being observed as a universal feature in all of these investigations. Based on these studies, Karnieli (1997) designed a spectral crust index [CI] that was used to classify BSC on Landsat TM images (spatial resolution: 30 m). More recently, Chen et al. (2005) published the so-called biological soil crust index [BSCI] to classify lichen-dominated BSC using analysis of Landsat 7 ETM+ data. By applying this index to BSC in the Gurbantunggut Desert, Northern Xinjiang, China, they obtained fairly good classification results with a κ [Kappa] coefficient of 0.76 (Zhang et al. 2007). Within the BIOTA project, Schultz (2005) mapped the lichen fields of the Namib Desert and investigated spatiotemporal changes on the basis of Landsat TM and ETM+ data. Hill et al. (1999, 2008) utilised color aerial photographs (with high spatial, but limited spectral resolution) and hyperspectral imagery (approximately 10 m spatial resolution) in an attempt to classify BSC at the Israeli-Egypt border in the Nizzana. They stratified the true-color aerial photographs into vegetated and non-vegetated spatial domains, defined individual spectral endmember sets for both, and successfully used spectral mixture analysis to produce detailed BSC distribution patterns. However, based on the hyperspectral imagery, a reliable differentiation between BSC, vegetation and soil could not be obtained.

Until now, several attempts have been made to spectrally delineate BSC against other materials, but a transferable methodology to map BSC has not been developed yet (Karnieli et al. 2001). Therefore, a new method to reliably differentiate between BSC on the one hand and vegetation and soil on the other has been developed. The classification results, obtained for the Succulent Karroo, South Africa will be explained in detail in this study.

Data acquisition and analysis

On October 28 2004, between 11:20 a.m. and 12:00 a.m., hyperspectral CASI 2 (Compact Airborne Spectrographic Imager) data for a 4 x 6 km area south of Soebatsfontein (comprising the Observatory S22) were acquired by ITRES Research Limited (Calgary, Canada). To obtain imagery with a spatial resolution of 1 m, the flight height was 366 m above ground level. Spectrometric reference measurements were conducted on the ground with a UV-VIS-NIR-spectrometer S2000 (Ocean Optics Inc., EW Duiven, Netherlands) at the same time as the flight collected the Hyperspectral CASI 2 data, and was used for atmospheric correction and data analysis. Radiance calibration and atmospheric correction of the imagery was performed in a cooperative approach with Prof. J. Hill (University of Trier) applying the AtCPro radiative transfer code (Hill & Sturm 1991, Hill et al. 1995, Röder et al. 2005).

To test the existing indices, the CI (Karnieli 1997) and the BSCI (Chen et al. 2005) were applied to the acquired imagery. Unfortunately, with κ indices of 0.41 and 0.43 respectively, neither produced satisfying results. The methodology of Hill et al. (2008) to stratify between vegetated and non-vegetated spatial domains was not applicable to our imagery. Larger shrubs could be masked out successfully but there were also patches of grasses, seedlings and smaller plants, which could not be identified as vegetation using this method.

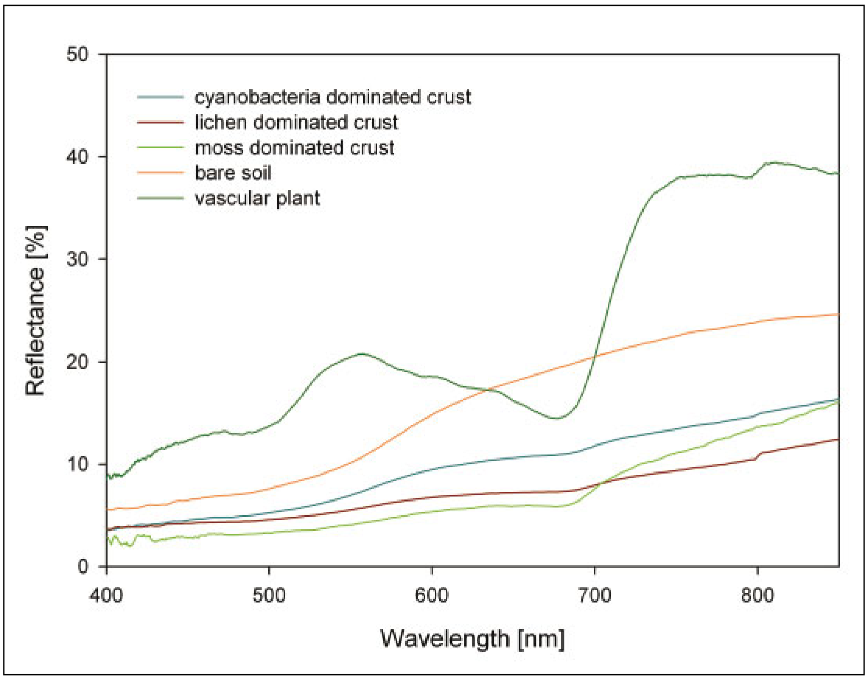

Fig. 1: Spectral characteristics of different BSC types compared to those of bare soil and a vascular plant (*Ruschia cyathiformis*, Aizoaceae). Curves represent mean values of five replicates each.

The first step towards the development of a new algorithm was to take field spectra of a variety of targets, and possible spectral endmembers were examined to elucidate the distinct characteristics of the different materials (Fig. 1). The spectra of bare soil, characterised by local mineral absorption and reflective properties, increased towards higher wavelengths without a local reflectance minimum around 680 nm. Vascular plants revealed a characteristic spectrum with a reflectance maximum at 550 nm, a pronounced absorption maximum around 680 nm (due to chlorophyll absorption) and a distinctive increase at 700 nm (red edge). The spectra of cyanobacteria-, lichen- and moss-dominated crusts resembled a mixture of the upper two spectral features to some extent with a latent "dip" of the signature within the absorption region of chlorophyll a. At higher wavelengths, the reflectance of cyanobacteria- and lichen-dominated BSC increased only gradually, whereas moss-dominated BSC registered a stronger increase.

To improve comparability, the field spectra were resampled to the CASI channels. Spectra were extracted from the CASI image at the same sites where field spectra were collected. Comparison of both signature sets revealed non significant differences between both data sets. However, analysis of the signatures showed that the different BSC classes could not be characterised by unique spectral characteristics over a wide spectral range because the transition between the different types was often gradual. In order to identify small-scale spectral features, which unequivocally characterised BSC, the continuum removal approach (Clark & Roush 1984) was applied. This method models the continuum within a reflectance spectrum as a mathematical function, which is used to isolate a particular absorption feature for analysis. Using ENVI 4.3, continuum removal was applied to both the resampled field spectra and spectra extracted from the imagery over the complete range of 36 CASI channels. Comparison of the spectra of the different types of material revealed that BSC have two absorption regions within the visible part of the spectrum: one around 516 nm and the second between 667 and 682 nm. The form and value of these features and of the areas in between were used to differentiate BSC from both bare soil and vegetation. For calculation details, see Weber et al. (2008). The newly developed "Continuum Removal Crust Identification Algorithm" (CRCIA) was applied to 49 BSC- and 46 non-BSC validation sites, resulting in a Kappa index of 0.831, which certified accurate classification results.

Distribution patterns of BSC

Analysis of the CASI images showed that 16.2% of the area can be classified as BSC. Analysis of the images for those parts of the study area, which possessed typical natural vegetation only (an area

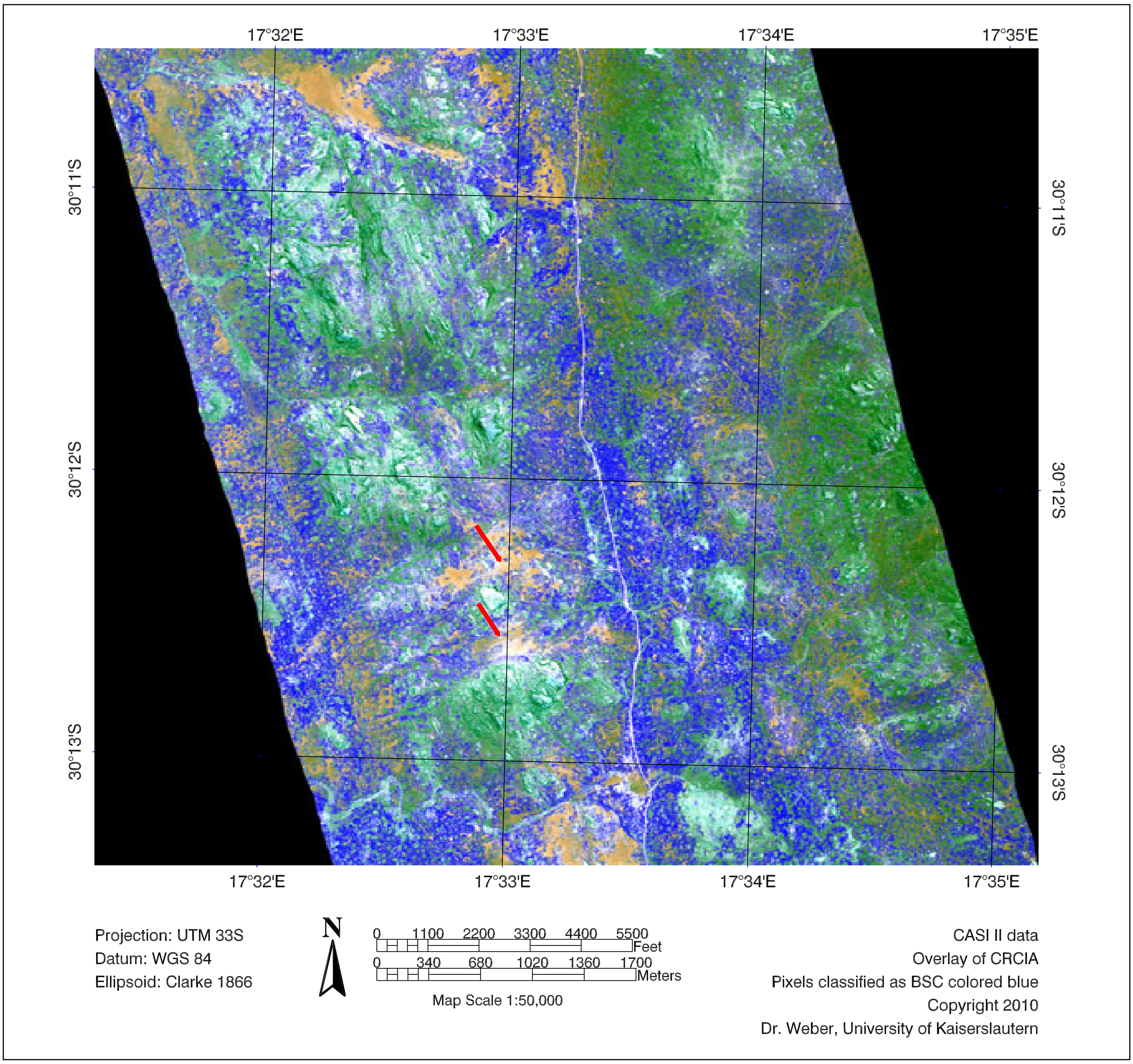

Fig. 2: True-color composite (channels 16-9-3) of CASI 2 imagery overlaid by classification results based on the newly developed Continuum Removal Crust Identification Algorithm (CRCIA). Blue: Classified pixels (containing BSC). Red arrows: areas without major BSC coverage as discussed in the text.

of 4.7 km²) and omitting inselbergs and roads resulted in a higher BSC coverage value of 26.8%. Since BSC are only detectable if they have a coverage of 30% or more within one pixel, and BSC below shrubs cannot be detected, actual coverage values are expected to be even higher.

The classification of all the CASI 2 imagery reflects that the main gravel road was completely devoid of BSC (Fig. 2), which corresponds to the actual on-site conditions. On the inselbergs west of the gravel road, there were only smaller areas classified as BSC where crusts were growing in small depressions on the inselbergs where soil had accumulated. Furthermore, the unclassified inselberg areas demonstrated that the delimitation between BSC and rock-inhabiting lichens, which cover major areas of the inselbergs, was successful.

Throughout all imagery for the study area there were circular structures with a diameter of approximately 20–25 m. These are fossil and/or presently active termite mounds, also known as “heuweltjies”, which are found in many parts of western South Africa (Lovegrove & Siegfried 1986, Picker et al. 2007).

There were two large patches between the inselbergs in the western part of the study area where almost no BSC coverage was classified (Fig. 2, red arrows). These areas were characterised by a coarse soil structure and more intense grazing and trampling impacts by sheep and goats, causing these areas to be almost completely devoid of BSC.

In a subset of Fig. 2 covering the Observatory and part of the neighbouring camps north of the Observatory

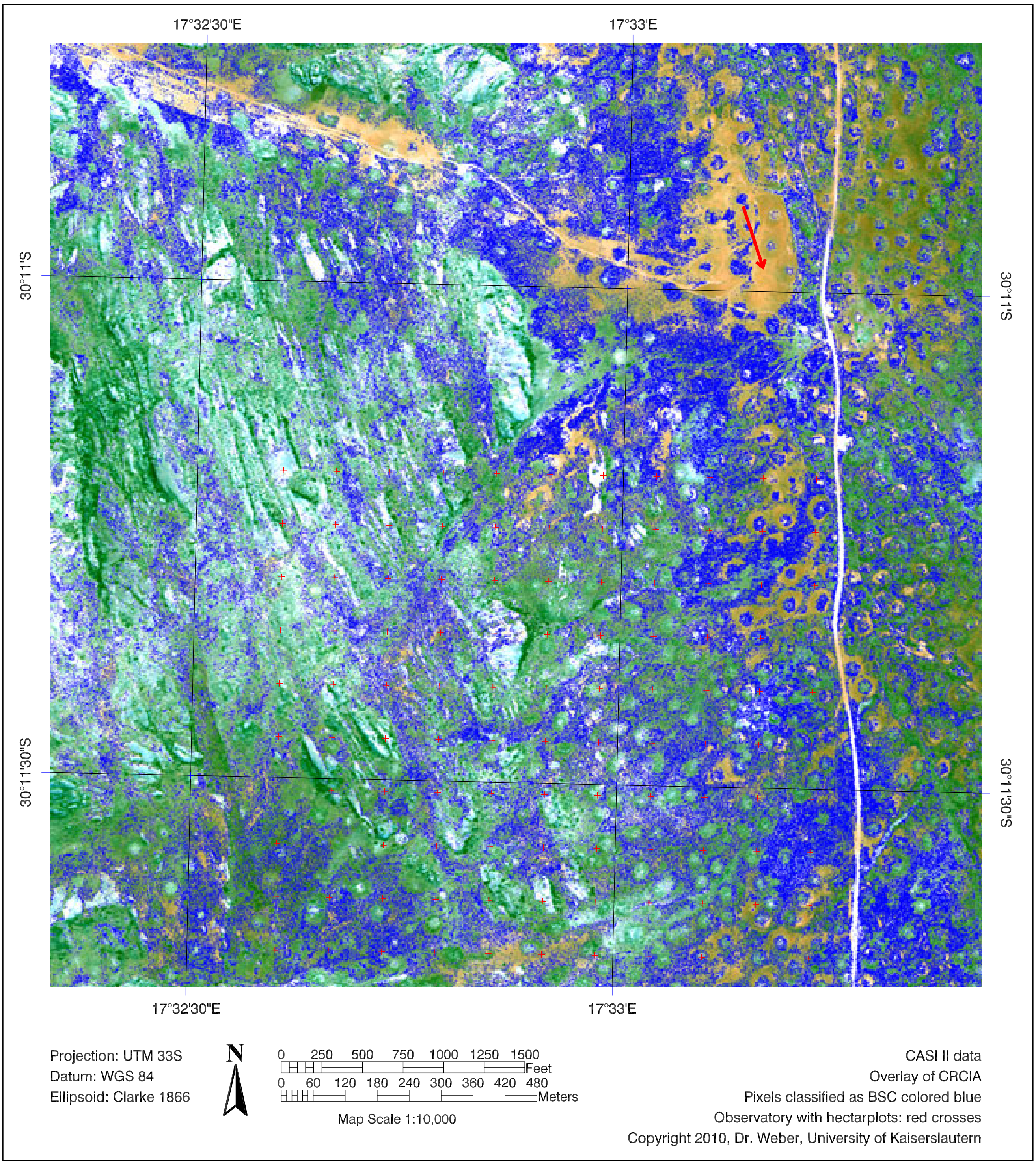

Fig. 3: Subset of figure 2, comprising Observatory S22 and parts of the neighbouring farms (Rooshogte and Langcamp). Red arrows: areas without BSC coverage discussed in the text.

(Rooshogte) and east of the main gravel road (Langcamp), large variations in BSC coverage were visible (Fig. 3). While well developed BSC occurred next to rocky outcrops and dense vegetation on the Observatory and surrounding camp (Kateklip), as expected, the road and major parts of Rooshoogte were devoid of BSC. The corner between the main gravel road and a secondary road running to the west into the Rooshoogte camp, in particular, possessed a very large patch without any crust coverage (Fig. 3, red arrow). This area is known to be heavily utilised by sheep and goats as a water point is situated there.

At this scale it is also clear that heuweltjies often support a particularly dense cover of BSC, while the surrounding areas are sometimes completely devoid of BSC. This pattern coincides with our observations made in the field.

Particularly high BSC densities were observed on 6–8 m wide strips along roadsides over large distances. This was a result of fencelines running parallel to the roads, which effectively created strips that were “grazing exclosures”, thus protecting the intact BSC.

These examples show that hyperspectral imagery combined with spectral endmember field data can be used to classify BSC in the Succulent Karroo with high precision. The next step is to use this classification method as the basis for creating a methodology, which can be transferred to a variety of sensors, scales and in different environments.

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Snail shells as shelters for arthropods in the sand dunes of the Namaqualand Sandveld (Northern Cape Province, South Africa)

Frank Koch

Summary: Empty large snail shells of *Trigonephrus* (Mollusca: Gastropoda: Dorcasiidae) were collected in the Groot Derm (around BIOTA Observatory S21) and around Port Nolloth, both falling within the so called Namaqualand Sandveld vegetation of the northern Succulent Karoo Biome in the Northern Cape Province, South Africa. These snail shells are considered as important microhabitats, used by various arthropod species as nesting cavities, temporary shelter or food source. A total of 39 arthropod species of 21 families or subfamilies emerged from these shells. The female of the chrysidid wasp *Chrysis grootdermensis* was discovered for the first time. The records of the genera *Nortonia* (Eumeninae), *Lepisiota* (Formicidae) and *Exoprosopa* (Bombiliidae) provided valuable knowledge regarding their distribution. A few other species, especially bees, seem to be new to science.

Introduction

The present work was inspired by an unexpected observation on supposedly empty snail shells collected from the BIOTA Observatory Groot Derm (Observatory S21) in the north western part of the Northern Cape Province of South Africa in 2001. Thirteen snail shells of *Trigonephrus* were collected as samples, and deposited in a box in the zoological collection of the Museum of Natural History, Berlin.

Surprisingly, approximately half a year later, eight mason bees (Megachilidae: Osmiini: *Hoplitis*), two potter wasps (Vespidae: Eumeninae: *Alastor*) and one parasitic wasp (Chrysididae) hatched out of the shells and were discovered dead in the box. The chrysidid wasp was identified as a new species and described by Koch (2006): *Chrysis grootdermensis*.

Based on these results, the BIOTA field trips in 2007 and 2008 were focused on collecting more empty snail shells with the aim of finding additional arthropod species using the shells as shelter in this desert habitat.

The snails of *Trigonephrus* are endemic to southern Africa and their empty, sun-bleached shells are found in large numbers in the sandy, sparsely vegetated areas of western Namaqualand and south-western Namibia. They typically accumulate in shallow hollows in these wind-shaped landscapes.

These snails have adapted to withstand extreme heat and seasonal shortages of water and food. They are mainly active in winter, when the humidity is high and the soil is moist. Under these conditions they emerge from the subsoil and move to the surface to feed on higher plants and lichens.

Gess & Gess (1999, 2008) collected empty snail shells in different places of the winter-rainfall zone of western South Africa and southern Namibia. Their study in the semi-desert areas north and south of the Gariep River mouth (Oranjemund, Rosh Pinah, Alexander Bay, Port Nolloth, and Brandkaros) was particularly valuable in order to compare the results of the recent investigations.

Study areas and methods

The first study area was the BIOTA Observatory Groot Derm, located about 20 km northeast of Alexander Bay and 10 km southwest of the Gariep River (28°37’ S, 16°40’ E). It is a locality in the Yellow Dunes, part of the Namaqualand, in the Richtersveld National Park, Northern Cape Province, South Africa (Photo 1).

The area is situated in the northern part of the Succulent Karoo biome and is characterised by the presence of extensive dune fields. Shallow hollows between the sand dunes are covered by a crust of organic soil. In these hollows thousands of sun-bleached shells of *Trigonephrus* sp. can be found. The very sparse vegetation is dominated by *Euphorbia* (Euphorbiaceae), *Indigofera*, *Lebeckia* (Fabaceae), *Sarcocaulon* (Geraniaceae), *Oncosiphon* (Asteraceae), and a few species of Aizoaceae (see Part II, Observatory S21).

The second study area was located near the main road from Steinkopf to Port Nolloth, about 5 km east of Port Nolloth close to the border of the Diamond Area (29°16’ S, 16°54’ E). This landscape is shaped by more or less continual strong winds from the Atlantic Ocean and the vegetation is similar to that occurring at the Groot Derm Observatory (Photo 2), although the deep blue flowers of *Heliophila* sp. (Brassicaceae) are conspicuous here. Both study sites were located on the sandy coastal plain in Sandveld vegetation, which can be further subdivided into Northern Richtersveld Yellow Duneveld SKs 2, and Richtersveld Coastal Duneveld SKs 1 (Mucina & Rutherford 2006).

The Groot Derm Observatory was visited during October and December 2007, and the Port Nolloth study area during September and December 2008. At each

Photo 1: Landscape with the yellow dunes on the farm Groot Derm. Photo: Frank Koch.

Photo 2: Landscape near Port Nolloth, with sun-bleached, empty snail shells of *Trigonephrus*. Photo: Frank Koch.

study site 60 preferably large shells of these snails were collected, both empty and filled with sand. The shells were transported to the Museum of Natural History in Berlin in large plastic bottles. They were then placed in large insect boxes where they were observed to see if any insects emerged.

The dimensions of the heliciform shells were measured according to Connolly (1938) and the following measurements were documented:

- Groot Derm: diameter 35–46 mm; height 37–49 mm.
- Port Nolloth: diameter 34–42 mm; height 37–46 mm.

Arthropods as users of snail shells

A total of 118 specimens of 39 species belonging to 21 families or subfamilies emerged from the shells between March and May in 2008 and 2009 (years after collecting), see Table 1. Most of the insects could be identified to the genus level but only four species were identified to species level. It is suspected that several forms are new to science.

A total of 53 species in 21 families or subfamilies were recorded from the empty snail shells. Table 1 shows the species of the following arthropod groups that were also reported by Gess (1996) and Gess & Gess (1999): Clubionidae, Salticidae, Chrysididae, Eumeninae, Nyssonidae, Megachilidae, and Bombyliidae.

Separation of the recorded arthropods into hypothetical ecological groups

Primary tenants: The first arthropods to colonise empty shells for breeding: Linyphiidae, Clubionidae, Thomisidae, Salticidae, Masarinae, Eumeninae, Sphecidae, Megachilidae, and Anthophoridae.

Secondary tenants: Arthropods that use the shells for breeding when the primary tenant has emerged and left the shelter: Lepismatidae, Linyphiidae, Clubionidae, Thomisidae, Salticidae, and Specidae.

Associated with tenants: Arthropods that are parasitoids, parasites, predators, commensals, phoretics (use the tenant as a carrier) or thief of food (as a cleptoparasite): Acarina, Cleridae, Meloidae, Chrysididae, Mutillidae, Eupelmidae, Formicidae, and Bombyliidae.

Utiliser of products: Arthropods that use the waste products (waste products of nutrition, pollen, excrement and other organic material) of tenants of the empty shells: Lepismatidae, Acarina, Oniscidea, Dermestidae, Curculionidae, and Formicidae.

Users of temporary shelter: Arthropods that use empty shells when the weather conditions and/or the time of the day or the time of the year is unfavourable for activity: Oniscidea, Curculionidae, and Specidae.

It is likely that Gess & Gess (1999) discovered additional species, and it is possible that some others are missing from their collections. Unfortunately, it was not possible for us to examine their available specimens. In particular, it has thus far not been possible to compare their results for spiders, pollen- and potter wasps, and leaf-cutting bees. It is designated as a self-contained project. In contrast to the Gess & Gess (1999) collection, the currently examined area was small and the samples were collected randomly, at different times and during different weather conditions. This is reflected in the relatively small, but nevertheless valuable, amount of arthropods recorded in this study.

Arthropds of special interest in terms of taxonomy, distribution and ecology

Chrysidid wasps

Chrysis grootdermensis

The species was described after a single male hatched from a snail shell collected in 2001 at Groot Derm (Koch 2006). In the present material the unknown female was found based upon two specimens from Groot Derm and one specimen from Port Nolloth.

Allocoelia mocsaryi

Three light brown cocoons, which were 3.17 mm in length and 2.08 mm in width were found. Two of them were empty and one was closed and contained a dead imago. The imago was very small (3.3 mm) and identified as *Allocoelia mocsaryi*. This species is currently only known to occur in the Cape Province (South Africa) and Zimbabwe [Southern Rhodesia] (Edney 1947) and Namibia (Kimsey & Bohart 1990). It has a light to dark brown abdomen, and according to Gess (1996) it is known to be a parasitoid of *Quartinia vagepunctata*. However, *Q. vagepunctata* is not known to occur in this area. Gess & Gess (1999) found and identified a blackish species of *Allocoelia* and six empty cocoons (3.67 mm length and 2.50 mm width). The dimensions of these cocoons are very different to those found at Groot Derm, and they thus seem likely to belong to another *Allocoelia* species.

Pollen wasps

Quartinia, *Quartinoides*

Gess (2007) provided a key for the genus *Quartinia*. Therefore, it was possible to identify *Quartinia refugicola* and *Q. conchicola*. One *Quartinia* specimen and two *Quartinoides* specimens were unidentifiable and may be unknown species.

Potter wasps

Alastor ricae, *Nortonia*

Besides *Alastor ricae* reported by Koch (2006), the *Nortonia* sp. was the second record of potter wasps for this area. The type locality of *A. ricae* is Namaqualand, Klip-Vlei, Garies (Giordani Soika 1934). It was not possible to identify the emerged *Nortonia* species using the key of Giordani Soika (1938) and it may therefore be a new species. Gess & Gess (1999) recorded a few potter wasps, which emerged from snail shells. They assumed that they were probably the Eumeninae referred to by Hesse (1944), but so far it is not clear what Hesse's wasp was (Gess & Gess 1999).

Ants

Lepisiota

This species is similar to *Lepisiota capensis*, but it seems to be a hitherto unknown species. *Lepisiota capensis* is known from a single locality in KwaZulu-Natal as well as from the Comoros Islands. This specimen is the first record for the western part of South Africa. A total of 5 species of the ant genus *Lepisiota* are known for the Afrotropical region (Fisher 2002). They have been reported from Kenya, Comoros, Madagascar, Reunion, and South Africa (KwaZulu-Natal). The record of a single worker of this species from Groot Derm is very unusual considering that this genus is unknown for the western part of South Africa.

Table 1: A survey of the arthropod material that emerged from empty snail shells collected at Groot Derm and Port Nolloth from 2007 to 2008 in comparison to Gess & Gess (1999)

Taxa		**Grootderm** 17.X.2007	**Grootderm** 12.XII.2007	**Port** 20.IX.2008	**Nolloth** 03.XII.2008	**Gess & Gess** (1999)
ZYGENTOMA (silver-fishes)						
Lepismatidae	sp. 1		●			
	sp. 2		●	●		
ARANEIDA (spiders)						
Linyphiidae	sp.			●		
Clubionidae	sp.			●		
	sp. Gess					●
Thomisidae	sp.		●			
Salticidae	sp. 1		●		●	
	sp. 2		●			
	sp. 3			●		
	sp. Gess					●
ACARINA (mites)						
	sp.			●		
ONISCIDEA (woodlice)						
	sp.			●		
COLEOPTERA (beetles)						
Dermestidae	sp.			●		
Cleridae	*Trichodes aulicus*					●
Meloidae	*Ceroctis* sp.		●			
Curculionidae	*Tychius* sp. 1			●		
	Tychius sp. 2				●	
	Brachycerus sp.		●			
HYMENOPTERA (wasps)						
Chrysididae	*Chrysis grootdermensis*		●	●		
	Allocoelia mocsaryi			●	●	
	Allocoelia sp.					●
Mutillidae	*Tricholabiodes* sp.					●
Masarinae	*Quartinia refugicola*		●			
	Quartinia conchicola		●			
	Quartinia sp.		●			
	Quartinia sp. Gess 1					●
	Quartinia sp. Gess 2					●
	Quartinoides sp. 1				●	
	Quartinoides sp. 2			●	●	
Eumeninae	*Alastor ricae*		●			
	Nortonia sp.	●				
	sp. Gess					●
Formicidae	*Crematogaster* sp.			●	●	
	Leptothorax sp.			●	●	
	Lepisiota sp.		●			
Nyssonidae	*Stizus* sp. 1		●			
	Stizus sp. 2	●		●		
	Bembecinus sp.					●
Megachilidae	*Othinosmia* sp. 1	●				
	Othinosmia sp. 2			●		
	Hoplitis sp. 1	●	●			
	Hoplitis sp. 2	●				
	Hoplitis sp. Gess					●
	Afranthidium sp. 1			●		
	Afranthidium sp. 2			●		
	A. cf. *odonturum*					●
	Wainia sp.					●
Anthophoridae	*Anthophora* sp.	●				
Eupelmidae	sp.					●
DIPTERA (flies)						
Bombyliidae	*Exoprosopa* sp. 1		●			
	Exoprosopa sp. 2		●			
	Exoprosopa sp. 3		●			
	Apolysis capicola					●

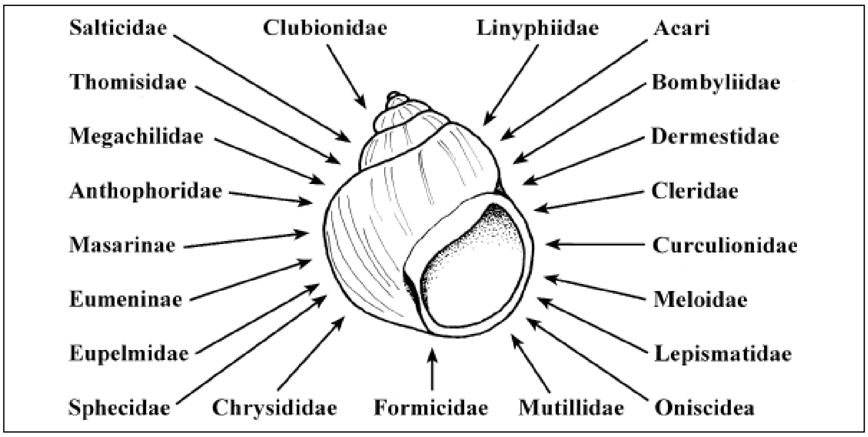

Fig. 1: Arthropod groups containing species that use empty snail shells as shelter.

Flies

Exoprosopa

In the material from Groot Derm three species of the bombyliid genus *Exoprosopa* ermerged from snail shells collected at Groot Derm were found, that at first glance seem to be an *Anthrax* species. *Anthrax anthrax* is known as a parasitoid of Megachilidae in Europe (Westrich 1990), and likewise in Australia, an *Anthrax* species is a parasitoid of Megachilidae (Naumann & Cardale 1987). One species with three large imagines (11.7–12.5 mm) is presented, another species with conspicuously different head morphology was stuck in the pupal case, and for a third species only an empty pupal case was found. All of these pupal cases are different. Until now, no species of *Exoprosopa* is reported in association with snail shells of the north western part of the Namaqualand.

Gess & Gess (1999) found a bombyliid species that is very likely to be *Apolysis capicola* (length: 1.84–2.84 mm) (Hesse 1975) emerging from *Quartinia* cocoons. So far, only this single species was known to be associated with tenants of snail shells. The length of the very small *Apolysis* species varied from 1.2 to 3.5 mm (Hesse 1975).

Weevils

Brachycerus, *Tychius*

The species of the weevil genus *Brachycerus* feed on decayed plant material and on roots. It is suspected that the recorded species utilises waste products for nutrition or uses the shells as temporary shelter. The imagines of the genus *Tychius* eat flower buds and are very likely to use the empty shells as temporary shelter, too.

Conclusions

The empty shells of snails are used predominantly by numerous species of insects: bees (Anthophoridae, Megachilidae), wasps (Chrysididae, Mutillidae, Masarinae, Eumeninae, Eupelmidae, Sphecidae), ants (Formicidae), beetles (Dermestidae, Cleridae, Meloidae, Curculionidae), flies (Bombyliidae), silverfish (Lepismatidae), and additionally by other groups of arthropods: spiders (Linyphiidae, Clubionidae, Thomisidae, Salticidae), mites (Acarina), and woodlice (Oniscidea).

The use of empty snail shells by solitary bees for nesting is a widespread habit in the Northern Hemisphere, and is very similar in all other biogeographic regions (O'Toole & Raw 1991). This behaviour also predominates among bees in semi-desert habitats of the winter-rainfall areas in southern Africa. These areas have limited availability of natural cavities, which can serve as nest-sites for these pollinators. Therefore, it seems that empty snail shells are an important component of these ecosystems.

After the hatching of the arthropod specimens the empty snail shells were investigated for other material. Many destroyed specimens of other arthropods that belong to the abovementioned ecological groups were found. Therefore, further studies are necessary.

Acknowledgements

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Dispersal strategies of desert inhabiting dragonflies—comparative population genetic study of five widely distributed species

Sandra Damm* & Heike Hadrys

Summary: Odonates—dragonflies and damselflies—with their complex but short life cycles, habitat specificity, and fast reaction times to changes in habitat quality are excellent bioindicator species for evaluating the quality of all types of freshwater ecosystems. Knowledge on biodiversity dynamics can be particularly helpful in detecting and foreseeing the consequences of anthropogenic development and/or natural changes in ecosystems. Especially in areas of limited water resources like in the arid country of Namibia, gene flow and genetic diversity within and between populations are important parameters, which influence the ability to react to and survive in a changing environment. Although dragonflies as freshwater organisms are not expected to be present in desert regions, there are species, which are able to adapt to this special environment and establish stable and large populations. In this study we used the mitochondrial ND1 sequence marker to compare the genetic diversity patterns in five desert-inhabiting species from different genera (*Anax imperator, Orthetrum chrysostigma, Paragomphus genei, Trithemis kirbyi* and *Pseudagrion massaicum*), which are all widespread in Namibia. Our results indicate that at the interspecific level the widely distributed species show significantly different genetic diversities and population substructures across genera. Some of the findings contradict organismic monitoring data on population size and abundance, which had suggested similar genetic diversities and population structures. This pattern cannot be seen on the phenotypic level, but is well reflected in the genetic data.


Photo 1: Imago of *Anax imperator*. Photo: Sandra Damm.

Introduction

Dragonflies, with their fast reaction times to environmental changes, serve as excellent indicators for evaluating biodiversity dynamics in freshwater ecosystems. Because of their complex lifecycle, with larval development in the water and specific terrestrial habitat selection of the imagos around the water, they mirror the status quo conditions of these ecosystems (e.g. Corbet 1999, Sahlen & Ekestubbe 2001). Furthermore, assessing biodiversity dynamics of dragonflies can be particularly helpful in detecting and foreseeing changes in the environment. In extreme and specialised climates, the ability to react to a changing environment becomes particularly important. For already endangered species, a good parameter to measure the degree of endangerment is the variation within a gene pool.

Namibia is one of the world's most arid regions, with ephemeral waters that depend on unpredictable rainfall (Barnard 1998). Odonates are freshwater-associated organisms and it would therefore be expected that they should be absent or poorly represented in desert environments. However, deserts do contain wetlands, which are colonised by a number of aquatic animal groups, including dragonflies and damselflies (Suhling et al. 2009). Springs in mountainous regions provide permanent water bodies and episodic rainfall may establish ephemeral (or temporary) rivers or ponds. Additional water resources occur along the course of the normally dry ephemeral rivers at rare places where groundwater surfaces, depending on geology or topography (Suhling et al. 2006). Many odonates are excellent flyers, which enables them to cover long distances and colonise even the most isolated habitats (Corbet 1999: 394–422). Although there are a few desert endemic odonates, the majority of species inhabiting deserts or dry savannah regions are widespread in Africa (Suhling et al. 2003). These temporary biotopes are inhabited by desert dwelling dragonflies, which are characterised by generalistic life history traits, such as high mobility and multivoltine life cycles with short larval development times (Corbet 1999: 409–414, Johansson & Suhling 2004).

The high mobility of dragonflies in general makes it difficult to study their distributional range and their migratory patterns. With the use of molecular methods it is now possible to analyse a great variety of additional aspects, from population genetics to speciation and phylogeography. In conservation biology population genetics helps to quantify

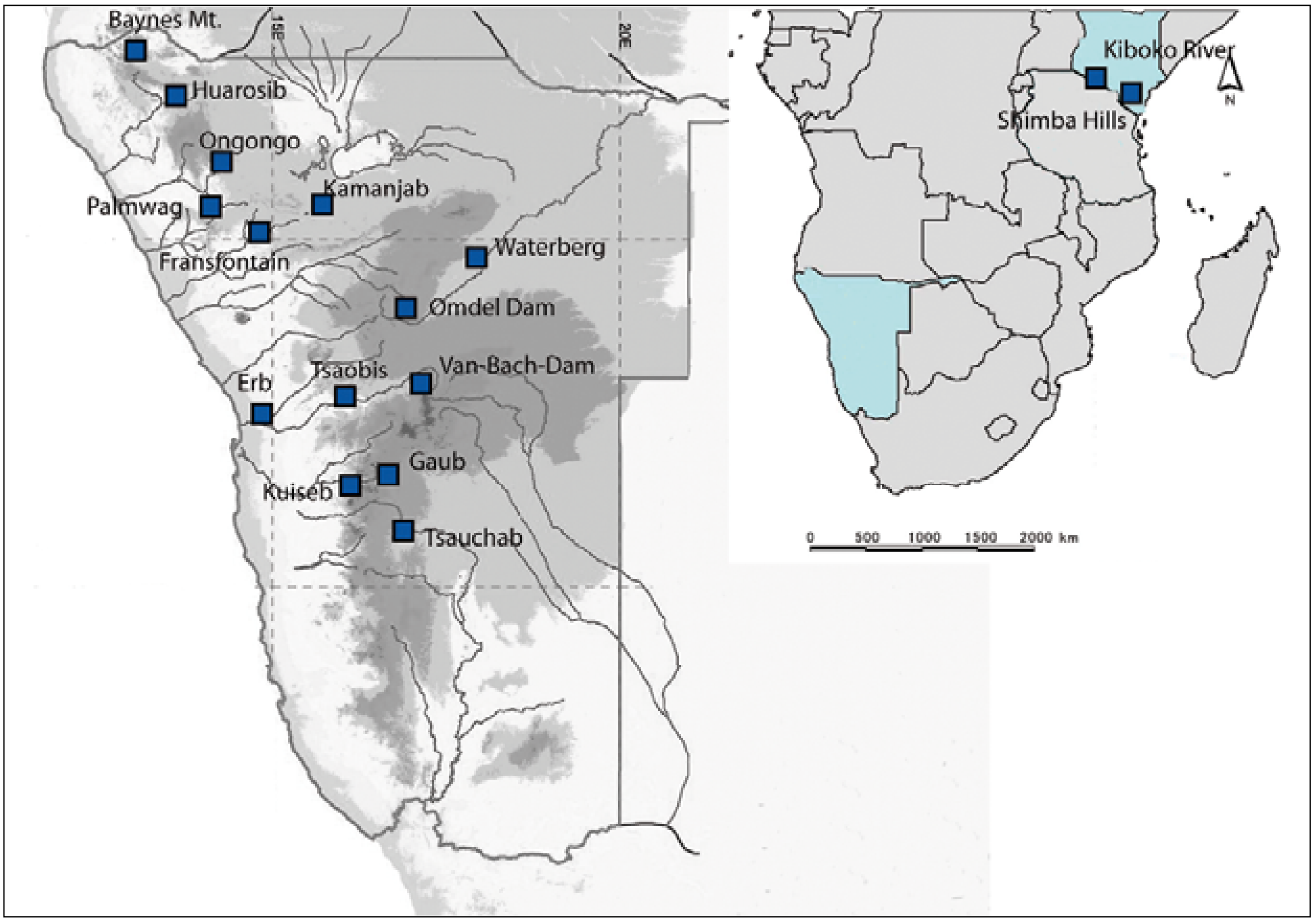

Fig. 1: Map of Namibia and southern Africa with collection sites of *A. imperator, T. kirbyi, O. chrysostigma, P. genei* and *P. massaicum* in Namibia and Kenya.

important factors such as effective population size, inbreeding, migration and gene flow (Hartl 2000, DeSalle & Amato 2004). This provides specific and comparable quantifications of processes that affect endangered populations and enables the analysis of genetic diversity (Avise et al. 2008). High genetic diversity gives a population the ability to adapt to changes in their environment and to avoid inbreeding depression (Hartl 2000, Frankham et al. 2002). Since "isolation by distance" and reduced gene flow can promote speciation, a basic step for understanding diversification is to analyse intraspecific dispersal abilities and population structures (Wright 1943). These population genetic parameters can be analysed with a variety of modern techniques like microsatellites or sequence markers. Despite the lead of odonate research within the insect orders, only a few studies of African dragonflies, which also integrate genetic data exist (Damm & Hadrys 2009, Damm et al. 2010a, b, Dijkstra et al. 2007, Groeneveld et al. 2007, Hadrys et al. 2006).

In this study we wanted to analyse the consequences of living in a desert environment as a freshwater associated organism. We therefore compared the genetic structures of five species, which are all widespread and common throughout Namibia. We chose two Libellulidae *Orthetrum chrysostigma* and *Trithemis kirbyi*, the Aeshnidae *Anax imperator,* the Gomphidae *Paragomphus genei*, and a damselfly species, the Coenagrionidae *Pseudagrion massaicum*. A study by Suhling et al. (2009) assigned Namibian dragonfly species, according to their ecological traits and distributional patterns, to six different categories with respect to their colonisation of deserts. The species in this study belong to the group of desert-biased species according to these categories. Although the five species belong to the same group, they show different abundances in real desert regions ranging from 56% (*T. kirbyi*) to 13% (*P. massaicum*). We address the question of how differences in dispersal strategies influence gene flow and genetic diversity by comparing genetic data with the habitat specificity and distribution patterns of the five species.

Material and Methods

Tissue samples were non-destructively collected (Fincke & Hadrys 2001) along a N/S transect in Namibia and at various sites in Kenya (Fig.1, in cooperation with E07). Odonate specific primers were used to amplify a 480 bp fragment of the mitochondrial ND1 gene according to Rach et al. (2008). Purified PCR products were directly sequenced using an automated ABI capillar sequencer. Uncorrected Hamming distances were calculated with the aid of PAUP* (Vers. 4.0, Swofford 2002). Gene flow and population substructuring were analysed by means of *F*-statistics and Mantel-test by

Table 1: Population genetic parameters of the five analysed species

Species (*N*)	Populations	Variable nucleotide sites	Haplotypes	F_{st}-values	Mean genetic distances between populations	
					Namibia	Namibia/Kenya
T. kirbyi (25)	5	16	12	–0.048	0.3%	0.2%
A. imperator (91)	12	19	22	0.040	0.3%	0.3% (to Europe)
O. chrysostigma (25)	5	6	6	0.242	0.3%	0.5%
P. genei (25)	5	21	17	0.225	0.8%	1.1%
P. massaicum (38)	6	6	5	0.869	0%	0.8%

Shown are the number of analysed individuals (*N*) and populations, variable nucleotide positions, haplotypes, mean F_{st}-values between populations and the mean genetic distances between populations of Namibia and Namibia vs. Kenya (or Europe).

using AMOVA (Analysis of Molecular Variance, Excoffier et al. 1992), which was implemented in the ARLEQUIN package (Vers. 3.0, Excoffier et al. 2005). A mutational network demonstrated genealogical relationships between haplotypes (TCS, Vers.1.13, Clement et al. 2000). A detailed description of methods used can be found in Damm et al. (2010b).

Table 2: Distribution of genetic variance via hierarchical AMOVA and F_{st}-values among the analysed populations

	Percentage of variance	F_{ST}-values
T. kirbyi		
among populations	–4,75%	F_{ST} = –0,048
within populations	104,75%	
A. imperator		
among populations	4%	F_{ST} = 0,04***
within populations	96%	
O. chrysostigma		
among populations	11.5%	F_{ST} = 0.114**
within populations	88.6%	
P. genei		
among populations	11.3%	F_{ST} = 0.113***
within populations	88.6%	
P. massaicum		
among populations	83.53%	F_{ST} = 0.835***
within populations	16.42%	

Significant *p*-values are displayed with * $p < 0.05$, ** $p < 0.001$ and *** $p < 0.0001$.

Results

Despite widely shared ecological characteristics, such as a wide distribution, high abundance and ecotolerance, the five species showed different genetic diversities and population substructuring. The main genetic parameters are summarised in Tables 1 and 2 and the mutational networks shown in Figs. 2–6 depict the differences in haplotype numbers, distribution, frequencies, and genealogies.

In the analysed population of *T. kirbyi*, a high number of variable nucleotide positions were found resulting in twelve different haplotypes. The *F*-statistics as well as AMOVA analyses demonstrate high levels of gene flow and no spatial substructuring between populations. Genetic distances within and between populations were low. With one main haplotype found in all populations, the star-like pattern of the other haplotypes was typical for species with high migration potential (Fig. 2).

Nearly the same pattern was found in *A. imperator* (Fig. 3). With 19 variable nucleotide positions resulting in 22 different haplotypes, the genetic diversity in this species was higher than in *T. kirbyi*, but *F*-statistics, AMOVA and genetic distances also showed no spatial structuring of the population. Because of the wide geographical range of *A. imperator*, populations from Germany were included in the study, but no indication for isolation by distance was found.

In contrast to the above described species, *O. chrysostigma* showed only six variable nucleotide positions resulting in six haplotypes (Fig. 4). Although the genetic diversity of *O. chrysostigma* was much lower than in *A. imperator* and *T. kirbyi*, a slight population structuring was found. The northern Namibian populations shared the same haplotypes while the southern Namibian populations and the Kenyan populations were more differentiated. Therefore the *F*-statistics and AMOVA indicated limited gene flow between the North Namibian and Kenyan populations (F_{st} = 0.242; $p > 0.05$).

In *P. genei*, 21 variable nucleotide positions were found resulting in 17 different haplotypes (Fig. 5). Together with *A. imperator, P. genei* showed the highest genetic diversity, but here most of the haplotypes were private in single populations. *F*-statistics and AMOVA indicated restricted gene flow between all populations in Namibia and Kenya (F_{st} = 0.225; $p = 0.05$). Genetic distances between populations ranged between

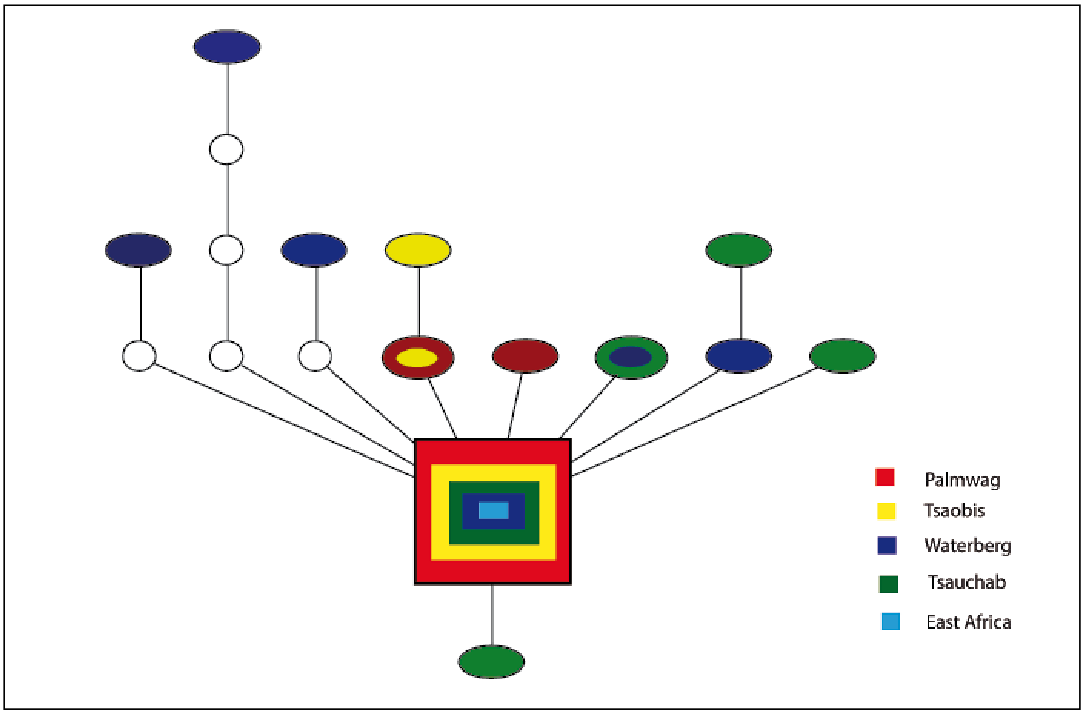

Fig. 2: Mutational haplotype network based on statistical parsimony representing the genealogical relationships between the haplotypes in the analysed populations of *Trithemis kirbyi*. Rectangles are haplotypes considered ancestral. The size of the ovals and rectangles reflects relative haplotype frequencies. Colour patterns represent different populations. Haplotypes separated by single lines represent a single mutation step and small, blank circles missing haplotypes.

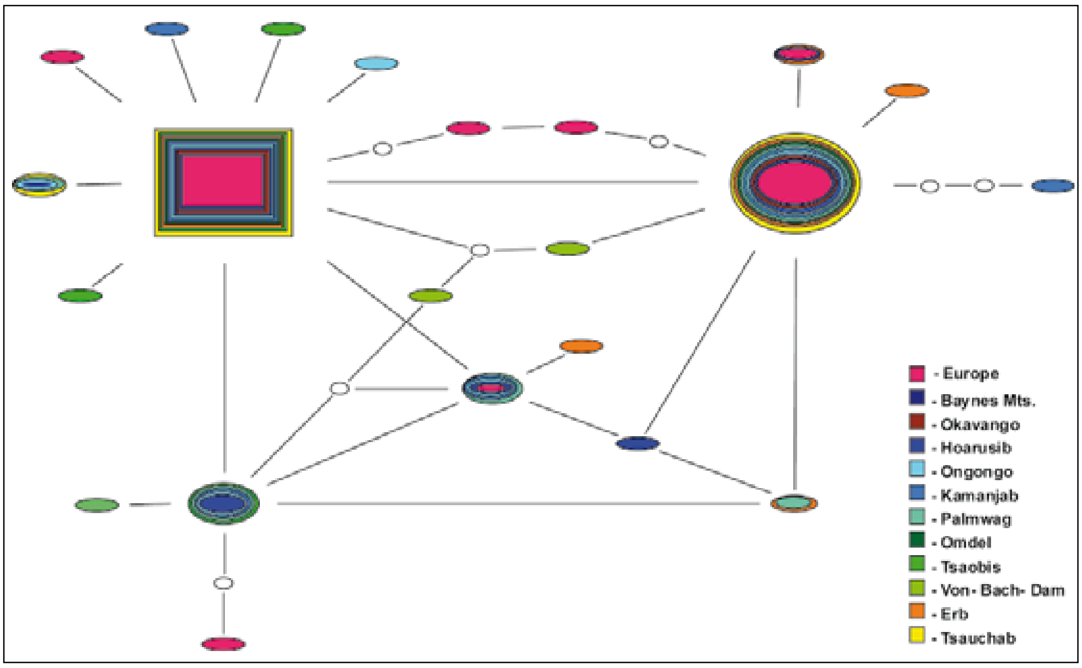

Fig. 3: Mutational haplotype network based on statistical parsimony representing the genealogical relationships between the haplotypes in the analysed populations of *Anax imperator*. Further explanations see Fig. 2.

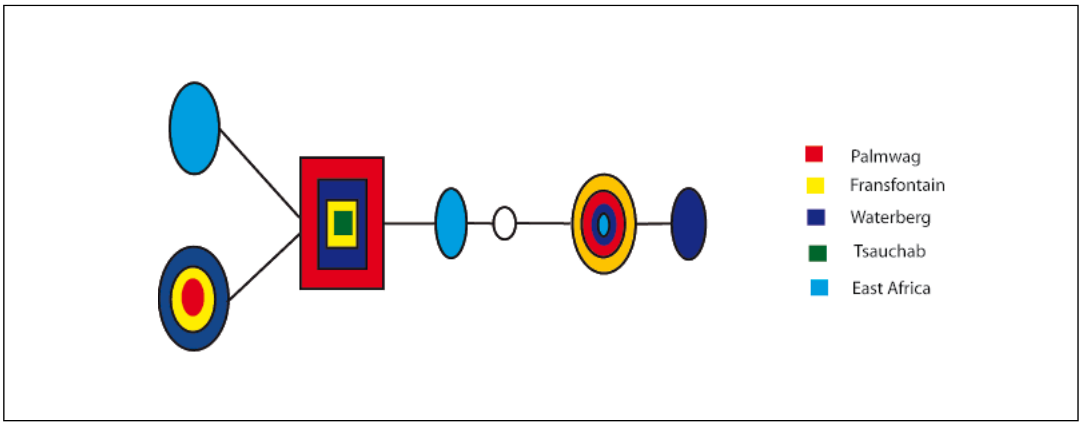

Fig. 4: Mutational haplotype network based on statistical parsimony representing the genealogical relationships between the haplotypes in the analysed populations of *Orthetrum chrysostigma*. Further explanations see Fig. 2.

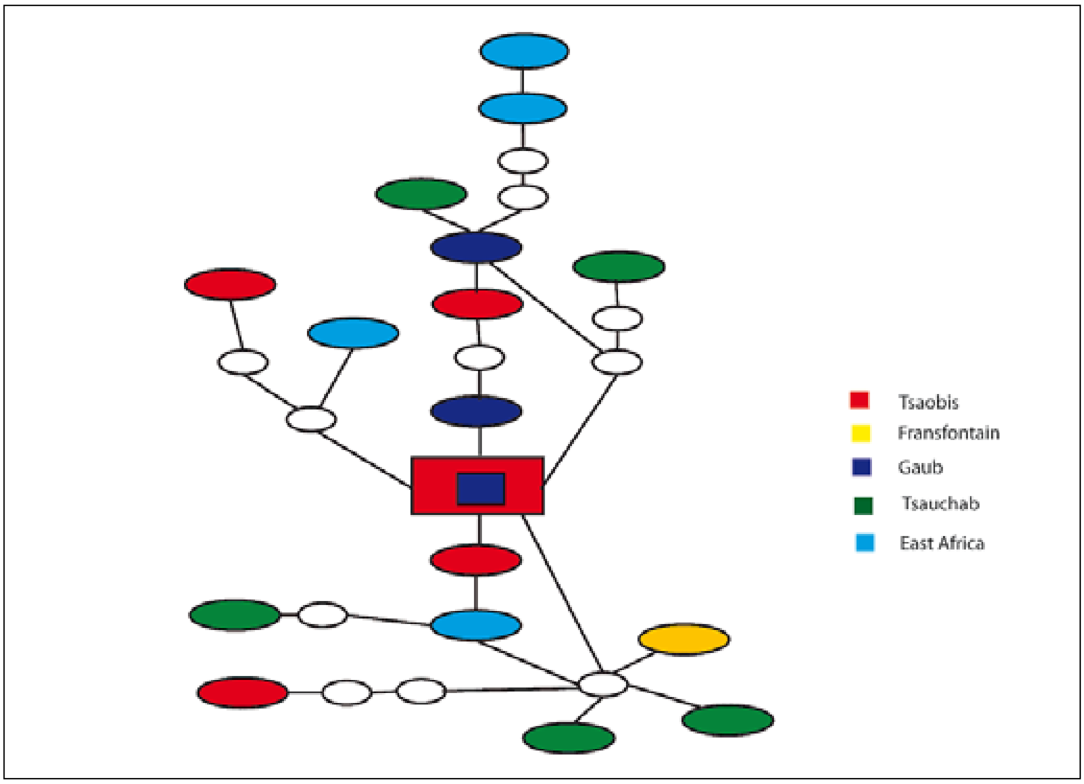

Fig. 5: Mutational haplotype network based on statistical parsimony representing the genealogical relationships between the haplotypes in the analysed populations of *Paragomphus genei*. Further explanations see Fig. 2.

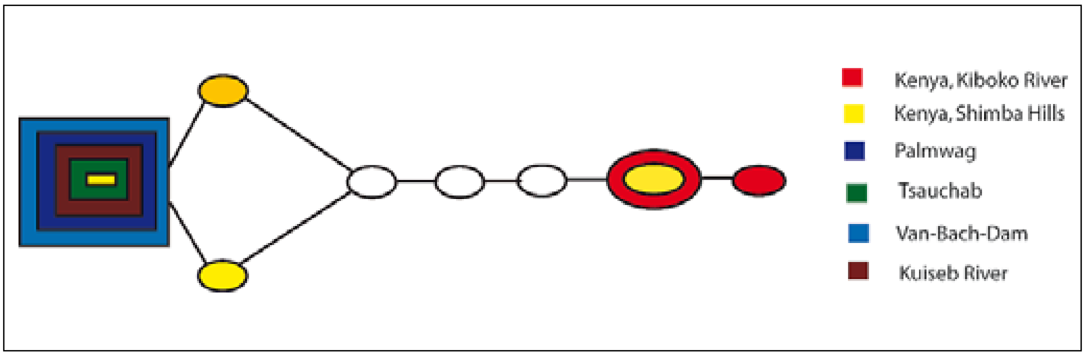

Fig. 6: Mutational haplotype network based on statistical parsimony representing the genealogical relationships between the haplotypes in the analysed populations of *Pseudagrion massaicum*. Further explanations see Fig. 2.

0.6% and 1.1% with the highest distances being between Namibian and Kenyan population.

A completely different pattern was found in *P. massaicum*. Here only six variable nucleotide positions were found defining five different haplotypes (Fig. 6). Genetic distances between populations were 0% between the Namibian populations, but up to 1% between Kenyan and Namibian populations. F-statistics indicated that there is no gene flow between Kenya and Namibia ($F_{st} = 0{,}869$; $p = 0$). Interestingly, the Kenyan populations harboured four of the five haplotypes while there was no genetic diversity within populations from Namibia, with only one haplotype.

Discussion

Genetic diversity and population structure

Although all analysed species are widely distributed across Namibia and are desert-biased species (Suhling et al. 2009), their genetic diversities and population structures indicate differences in dispersal patterns. In the following we discuss the different population genetic patterns of the odonate species in this study under the aspect of habitat specificity and their different abundances in desert environments.

The most similar genetic structure was found in *T. kirbyi* and *A. imperator*. Here high levels of gene flow, also between distant populations, indicate that both species are able to cover long geographical distances. The genetic diversity within populations is high, which suggest that both species are also able to establish stable populations in regions with more or less rare freshwater habitats. Therefore, *T. kirbyi* and *A. imperator* seem to be best adapted to the habitat conditions in Namibia, but for different reasons related to the ecological traits of the specific species. *A. imperator* is an authentic habitat generalist with a geographical distribution from southern Africa up to northern Europe and occurring in nearly every type of freshwater habitat (Suhling & Martens 2007). The high genetic variability as well as high levels of gene flow are also confirmed by microsatellite data of this species (Hadrys et al. 2007,

Photo 2: Imago of *Trithemis kirbyi*. Photo: Sandra Damm.

Timm 2003). However, *T. kirbyi*, which is also widely distributed on the African continent, preferred open habitats without much vegetation, such as rocky pools, and it was also observed at swimming pools or water tanks. It regularly uses temporary waters and has very fast larval development (Suhling et al. 2005). These special ecological features make *T. kirbyi* one of the most widely distributed species in Namibia and it was found at 56% of the surveyed desert localities (*N* = 351) in Namibia. Likely for the same reasons, *T. kirbyi* is much rarer in the more tropical regions like Kenya and Tanzania and only a few individuals were observed in the more humid northern parts of Namibia (Pinhey 1970, Suhling 2007).

A comparable genetic structure was expected in *O. chrysostigma*, which is also a widespread species in most parts of Africa. It occurs at all types of habitats from perennial springs to ephemeral rivers with a representation in desert environments of 40% and, like *T. kirbyi*, has a short larval development stage (Johansson & Suhling 2004, Suhling et al. 2009). Nevertheless, a different population genetic pattern was found in *O. chrysostigma*, with only low genetic diversity in Namibia and Kenya. The northern Namibian populations show the same haplotype frequencies indicating high levels of gene flow between them. But only low genetic diversity was found at the Tsauchab population (southern Namibia) although species abundance is high. Low genetic diversity at this specific population site was also found in other analysed species e.g. *P. massaicum, A. imperator, A. speratus,* and *T. arteriosa* (Giere 2002, Timm 2003). It seems likely that a recurring reduction in population sizes in the past due to environmental causes might be the reason for this. A recurrent decline of the population size could reduce the number of haplotypes and no new or private haplotypes could evolve. Drought periods every ten to twenty years in which the rainy season bears no rainfall at all are known to occur in Namibia (Mendelsohn et al. 2002) and these climatic fluctuations often resulted in the desiccation of water sources in the Naukluft Mountains. Interestingly, in *O. chrysostigma* and *T. arteriosa* (Giere 2002, Damm & Hadrys, unpublished data), the southern Namibian populations show more genetic similarities to the East African populations in Tanzania and Kenya than to the Northern Namibian populations. A reduction in gene flow from North to South Namibia might be caused by a gap of the escarpment and the lack of suitable habitats inbetween (Suhling et al. 2009).

The forth dragonfly species, *P. genei*, showed an additional genetic pattern. This species also occurs at a variety of fresh waters habitats (with a representation in desert environments of 25%), but it prefers rivers, where it is often the dominant dragonfly at ephemeral rivers during times of floods (Suhling et al. 2009). Compared with the other three species, which have already been discussed, *P. genei* shows higher genetic diversity in all analysed populations and a high degree of population substructure. Most of the haplotypes are private and the genetic distances are high, with up to 1% between population sites. The results indicate that *P. genei* is able to establish stable populations, but only disperse within a geographically restricted range. Comparison of the genetic data with monitoring data indicates that dispersal along the river catchments is the most probable explanation for this genetic pattern. The ephemeral river catchments are dry for most of the year and are orientated predominantly in a West-East direction. Although dry, these rivers have permanent green bands of riparian vegetation, which could serve as a pathway for many species. The population sites of *P. genei* belong to different river catchments and the population structuring might be a result of restricted gene flow between the catchments. To confirm these results more population sites within each catchment must be analysed.

The only damselfly species analysed in this study was *P. massaicum*. The lack of gene flow between Kenya and Namibia was more or less expected due to the low dispersal abilities of this species. *P. massaicum* is also the only species with a significant test for isolation by distance (Hadrys et al. 2006). Although the species was found at many sites in Namibia, there seems to be no gene flow between population sites. The preferred habitats of *P. massaicum* are well-vegetated perennial lotic and lentic waters. While the abundance of such habitats is much higher in Kenya, in Namibia these sites are mostly confined to natural sources in ephemeral rivers or in mountain regions like the Naukluft Mountains. The lack of optimal habitats between the analysed population sites might be a reason for the restriction in gene flow. A second interesting result is the total lack of genetic diversity in Namibia. This can be explained by a reduction in population size. The species could have gone through one or multiple bottlenecks (possible due to drought), which led to extinctions at many sites. In the surviving individuals the only haplotype found in Namibia got fixed. A similar picture was found in *Pseudagrion kersteni*, a sister species of *P. massaicum* (Groeneveld 2003, Hadrys et al. 2006). Here also, only one haplotype is found in Namibia while in Kenya the genetic diversity is high. In *P. kersteni* the only exception is the population in the Baynes Mountains. Differences in the genetic composition of this region to the other sites in Namibia were also found in other odonate species like *T. arteriosa* and *A. speratus*, probably due to more "genetic input" via gene flow from the bordering countries.

Importance for conservation

Comparison of the five odonate species, which are, at first view, all habitat generalists with high ecotolerance, reveals completely different dispersal strategies and genetic diversities. Genetic diversity is expected to be lower in arid Namibia than in the more tropical East Africa (Kenya and Tanzania) because of its demanding habitats. This is true for some odonate species but not for all. Species with lower dispersal ability show the same (*P. genei*) or higher (*P. massaicum* and *P. kersteni*) genetic diversity in East Africa than in Namibia. The other studied dragonflies with long-range dispersal abilities show lower genetic diversity in East Africa when comparing both regions (*O. chrysostigma*, *Anax ephippiger*, *T. arteriosa*) (Giere 2002, Habekost 2002, Timm 2003). Therefore knowledge about genetic diversity at a specific population site, as well as dispersal strategies of a species in general, is of great importance for conservation management. Preserving genetic diversity within populations is extremely important to allow evolution in response to environmental changes, which are ever-present.

The main mechanisms leading to loss of genetic diversity, genetic drift and inbreeding are dependent on population size. Here the effective population size (N_e), in contrast to the census size, is the deciding parameter. If the population size fluctuates over time, the loss of genetic diversity is most strongly influenced by the minimum population size. In *P. massaicum* and *O. chrysostigma*, genetic variability is low in Namibia, which suggests past or recent bottleneck situations at the analysed population sites. This could also be true for the other species but *A. imperator* and *T. kirbyi* might have recovered their genetic diversity through migration. Dispersal ability is of great importance in the desert where the risk of spatial contraction or complete desiccation of water resources is a recurrent threat. For conservation reasons it is therefore important to have a good knowledge of dispersal pathways to prevent isolation of populations. In Namibia, two different strategies seem to be most common for widespread species with higher tolerance in habitat choice. On the one hand, there are the good flyers, which can cover long distances (*T. kirbyi* and *A. imperator*) and on the other hand, species which have either lower dispersal ability (*P. genei*) or need vegetated surroundings (*O. chrysostigma* and *T. arteriosa*) and disperse along the riparian habitats of river catchments. For the latter species, the water resources in these catchments and the associated vegetation are of high relevance for conservation.

Photo 3: Mating dragonflies (*Orthetrum julia*). Photo: Sandra Damm.

The comparison of population genetic parameters of different environments, such as in this study between Namibia and East Africa, can provide additional information when analysing species and/or ecosystems of high conservation value. Different ecological conditions can lead to differences in dispersal behaviour and may result in changes to the population structure and therefore genetic diversity like in *O. chrysostigma*, *P. massaicum* and *P. kersteni*. An extreme example is *Trithemis arteriosa*, in which sex-biased dispersal as a special adaptation to the habitat conditions in Namibia was discovered in a population genetic study using the sequence marker ND1 and species-specific microsatellites (Giere & Hadrys 2006, Damm & Hadrys, unpubl. data).

Water is generally one of the most relevant and highly limited resources in Namibia (Barnard 1998) and is therefore highly affected by human impacts. Increased habitat fragmentation can be expected, which will increase the amount of small, genetically isolated populations with reduced reproduction potential and will therefore reduce the genetic diversity (Frankham et al. 2002). This is especially true for species with specific habitat requirements. Isolated population sites and/or the pressure to adapt to special habitat conditions could also lead to speciation processes. Often such processes can only be revealed with molecular methods, such as with the genus *Trithemis*. Here surprisingly, two new and cryptic species were discovered during a population genetic study on *T. stictica* (Damm & Hadrys 2009, Damm et al. 2010b). *T. morrisoni* and *T. palustris* co-occur at the Okavango and Zambezi floodplains, but within different habitats.

Conclusion

Our study firstly provides insights into the possible dispersal strategies of desert-inhabiting dragonfly species. We showed that the five odonate species, which are all widespread in Africa, evolved different dispersal strategies to survive in the arid environment of Namibia. Although the analysed species show high abundances at most population sites, their genetic diversity differed. Our results demonstrate the importance of applying molecular techniques to conservation biology and biodiversity research. In general, for freshwater habitats in Namibia, odonates serve as an excellent bioindicator species (e.g. Clausnitzer et al. 2009). At longer timescales, odonates can be used as model organisms for understanding the evolutionary processes of speciation and biogeography by combining genetic data with geography and ecology (e.g. Damm et al. 2010a, Groeneveld et al. 2007). The continuing development of new informative molecular markers (e.g. microsatellites) and high throughput detection methods allows analyses on different evolutionary timescales and a fast assessment of biodiversity and conservation patterns. But the integration of biogeography, morphology, genetics and ecology, in particular, could assist us to evaluate how changes in major environmental parameters like climate and hydrology influenced the evolution of species in the past and what consequences we can expect in the future.

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Reptile diversity in savanna rangelands at a regional scale

BERND WASIOLKA



Photos 1–3: A selection of photographs of some reptile species occurring in the southern Kalahari: Spotted Sand Lizard (*Pedioplanis l. lineoocellata*), Western Sandveld Lizard (*Nucras tessellata*) and Puff Adder (*Bitis caudalis*) (from left to right).

Summary: We investigated the impact of habitat degradation on regional reptile diversity, and the role perennial grasses play in maintaining reptile diversity, in the southern Kalahari, South Africa. Reptile diversity was assessed in five different vegetation states, ranging from high perennial grass cover and low shrub cover to low perennial grass and high shrub cover, which were distinguishable along a grazing gradient. Results showed that reptile diversity and abundance declined with habitat degradation characterised by increasing shrub cover and loss of perennial grasses. As a consequence of reduced perennial grass cover in degraded habitats, the availability of reptile prey and potential sites for thermoregulation (especially shady sites for cooling down) declined. In addition, predation risk increased as a result of the altered vegetation structure and diversity. These three factors appear to have caused lower reptile diversity and abundance in degraded habitats. Therefore, it appears that habitat degradation caused by overgrazing has a negative impact on reptile communities in semiarid rangelands. Conversely, perennial grasses, which are a characteristic structural element of non-degraded savannas, play an important role in preserving reptile diversity.

Introduction

The vegetation of savanna rangelands in the southern Kalahari is characterised by a continuous grass layer interspersed by woody vegetation (trees and shrubs). Land use practices such as intensive livestock farming and the resultant overgrazing have altered the vegetation structure and composition of these rangelands. Proportions of shrubby vegetation have increased significantly, which has resulted in a reduction of perennial grasses, herbaceous vegetation and plant diversity (Wiegand et al. 2005). Shrub encroachment leads to reduced structural diversity of the vegetation (Tews et al. 2004) and to a consequent loss of diversity across a range of animal taxa (e.g. birds: Thiele et al. 2008, mammals: Blaum et al. 2007, invertebrates: Blaum et al. 2009). While the effects of habitat degradation on mammal, bird and invertebrate diversity are well studied, knowledge of how reptile diversity is affected remains sparse.

The main components of structural diversity in savanna rangeland are trees, shrubs and perennial grasses. Trees provide roosting and nesting sites for birds, safe sites for lizards (Broadley 1967) and shade for large mammals (Dean et al. 1999, Eccard et al. 2004), and shrubs provide safe refuges for small carnivores (Blaum et al. 2007). The importance of trees and shrubs for faunal diversity are well documented, but the influence of perennial grass cover on faunal diversity is not well studied.

Key questions

(I) Does overgrazing and the resultant habitat degradation have a negative impact (decline in species diversity and abundance) on reptile communities at a regional scale?

(II) Does perennial grass play a role in maintaining reptile diversity?

Methods

The study area was situated directly south of the Kgalagadi Transfrontier Park in the Northern Cape Province of South Africa and covered approximately 10,000 km² (N-S: ~110 km, W-E: ~90 km). Five

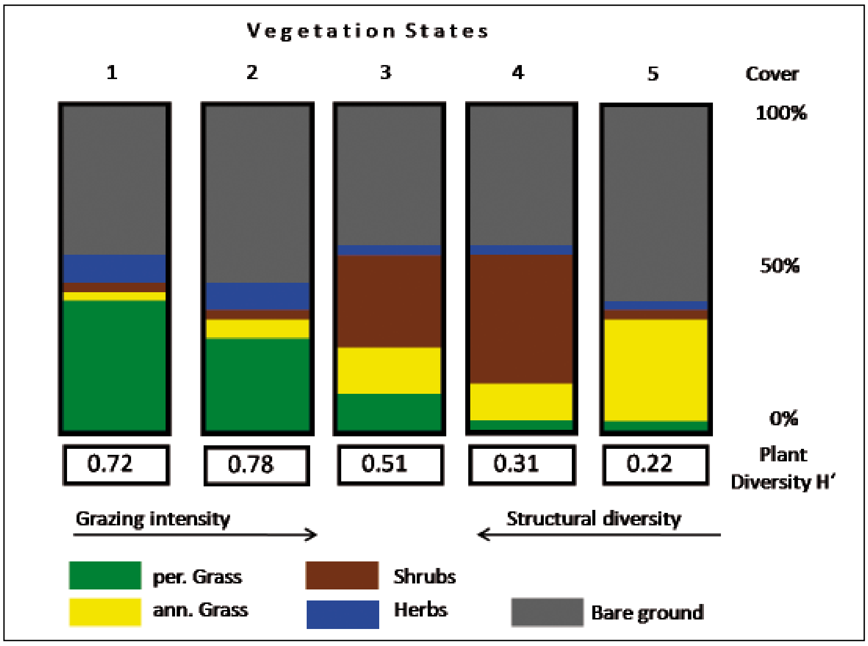

Fig. 1: Plant diversity (Shannon Index) and mean cover (%) of perennial grasses, annual grasses, shrubs, herbs and bare ground for the five vegetation states (states 1 & 2: non-degraded habitats; states 3–5: degraded habitats).

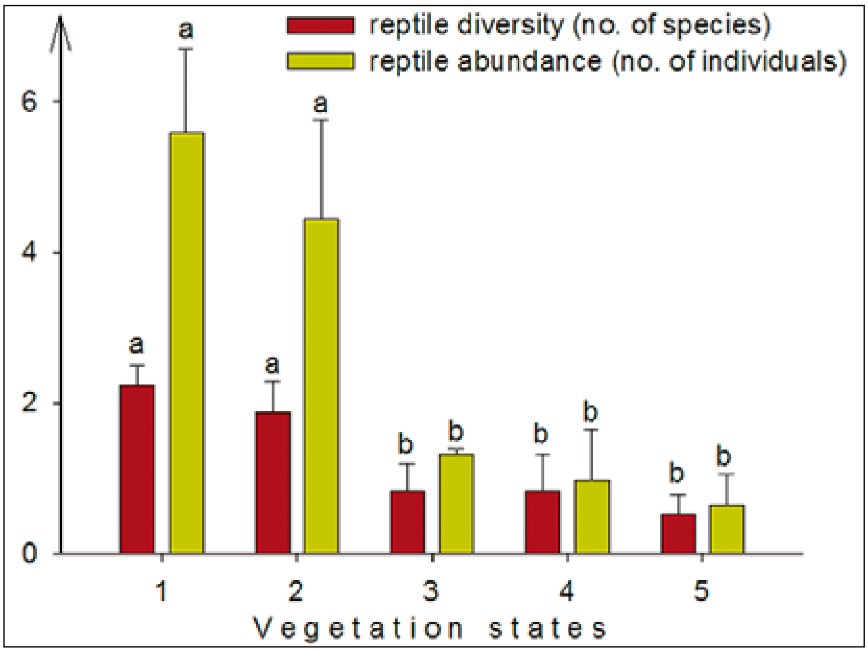

Fig. 2: Means ± SE reptile species richness (no. of species) and reptile abundance (no. of individuals) for the five vegetation states (states 1 & 2: non-degraded habitats; states 3–5: degraded habitats). Different letters (a, b) indicate significant differences between the different vegetation states (ANOVA, Tukey Post Hoc Test, $p < 0.05$).

different vegetation states were chosen to investigate the impact of overgrazing on reptile communities and to analyse the role of perennial grass in maintaining reptile diversity (Fig. 1). The five vegetation states represented typical vegetation states of Kalahari savanna rangelands and were characterised on the one hand by a decline in perennial grass cover and plant diversity, and on the other hand by an increase in shrub cover and/or annual grass cover. Reptile (lizards, snakes and tortoises) diversity and abundance was estimated by time and area constrained Visual Encounter Surveys (for a selection of photographs of encountered reptile species see Photos 1–3). We sampled 12 transects in each vegetation state. Each transect was surveyed four times (Oct. 2004, Jan. 2005, Oct. 2005 & Jan. 2006). Reptile diversity and abundance was analysed using a one-factor ANOVA (© SPSS Inc., Version 11.5). To test for significant differences between the vegetation states we used a Post-Hoc-Test (Tukey-Test). Multiple regression analysis was used to assess the influence of perennial grass cover on reptile diversity. Refer to Wasiolka (2007) for a detailed description of the study site and methods, as well as a list of the reptile species encountered.

Results and discussion

Reptile diversity and abundance

In vegetation states 1 and 2 (high perennial grass cover & plant diversity; low shrub & annual grass cover) reptile species richness ($F_{4,51} = 44.57, p < 0.001$) (Fig. 2) and abundance ($F_{4,51} = 58.36, p < 0.001$) (Fig. 2) was significantly higher than in vegetation state 3, 4 and 5 (low perennial grass cover & plant diversity; high shrub & annual grass cover). Furthermore, regression analysis showed a linear response of reptile species richness to perennial grass cover ($R^2 = 0.777, p < 0.01$), with reptile species richness increasing with perennial grass cover (Fig. 3). These results demonstrate the negative effects of overgrazing, and resultant shrub encroachment, on the reptile communities of the southern Kalahari. These negative effects were found across study sites at a regional scale ($\sim$10,000 km^2). Additionally, the results reveal that it is not only trees and shrubs that play an important role in maintaining faunal diversity, but that perennial grasses are important too.

Declining plant diversity and a loss of perennial grass cover results in a decrease in reptile prey abundance as shown by previous work on arthropod abundance in the Kalahari by Blaum et al. (2009) and Wasiolka et al. (2009a), and could be a major reason for reduced reptile diversity and abundance in vegetation states 3–5 (degraded habitats).

Photos 4–6: Plant structure of a perennial grass species (Tall Bushman Grass, *Stipagrostis ciliata*), a shrub species (Three Thorn, *Rhigozum trichotomum*) and an annual grass species (Kalahari Sour Grass, *Schmidtia kalihariensis*) (from left to right).

Not only is plant diversity and perennial grass cover reduced in the degraded habitats but *Schmidtia kalahariensis* and *Rhigozum trichotomum*, (the dominant annual grass and shrub species in degraded habitats, respectively) do not provide as much cover as the perennial grass tussocks (Photos 4–6). Therefore, opportunities for reptiles to thermoregulate (by resting in shaded areas) are reduced and the risk of predation increases. These factors coupled with the reduced availability of prey have the potential to contribute to the decline of reptile diversity and abundance in the region.

Prey availability

Grasshoppers (Order: Orthoptera), which feed on grassy vegetation (Hutchinson & King 1980), are one of the main prey sources of Kalahari Lizards (Pianka 1986), which are all insectivorous (Pianka 1986, Branch 1998). Orthoptera abundance is significantly lower in degraded habitats as a consequence of decreased perennial grass cover (Wasiolka et al. 2009a, Wasiolka 2007). Furthermore, lizards form an integral part of the diet of many snake species (Branch 1998, Marais 2004), and the loss of lizard prey may therefore indirectly affects snake communities negatively too. Non-degraded savannah habitats (e.g. vegetation states 1 & 2) are therefore important as they provide higher prey availability to lizards and snakes.

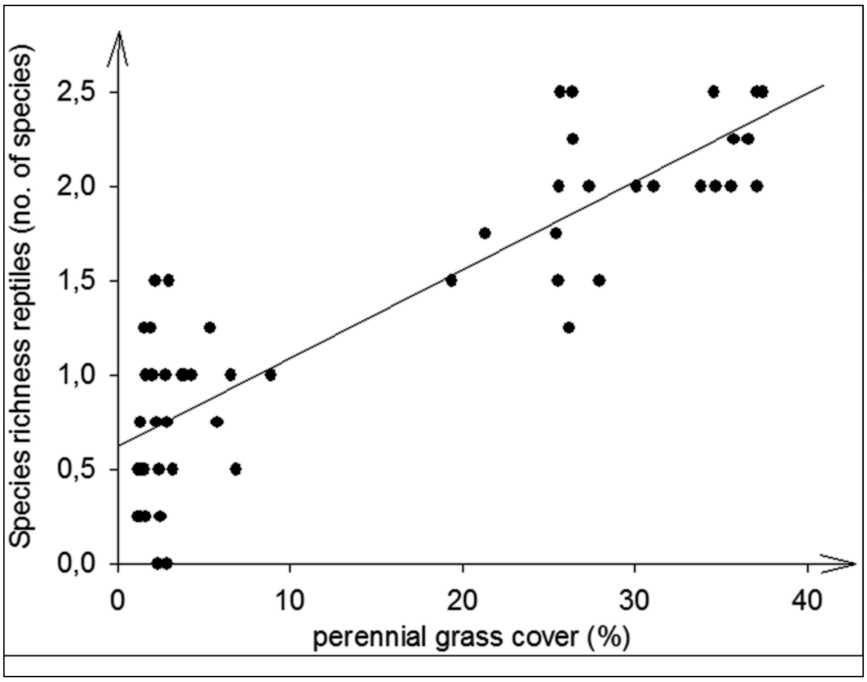

Fig. 3: Effects of perennial grass cover on reptile species richness (no. of species) across five vegetation states (states 1 & 2: non-degraded habitats; states 3–5: degraded habitats). Solid black line shows regression over all transects.

Thermoregulation

In Kalahari savannas, day time temperature maxima are lowest below perennial grasses (43.2°C), whereas the temperature under shrubs (48.4°C) and especially below annual grasses (56.4°C) are considerably higher (unpublished data). A loss of perennial grass cover results in a loss of suitable sites (shaded spots) that reptiles can visit to cool down. Therefore, the availability of microhabitats for reptiles to thermoregulate is reduced in degraded habitats, which are characterised by a loss of perennial grasses.

Predation risk

While perennial grasses provide reptiles with safety from predators (Bock et al. 1990), the loss of dense vegetation cover is associated with increased predation risk (e.g. Bentley et al. 2000). Reptile tail loss (caudal autotomy), which is known as an escape and defence strategy against predators (e.g. Fox & McCoy 2000), was significantly lower in non-degraded habitats (Wasiolka 2007) than in habitats with high perennial grass cover. Furthermore, due to the limited prey availability in degraded habitats, reptiles have to cover longer distances in search of prey (Wasiolka et al. 2009b) and are thus more conspicuous to predators (e.g. Downes & Shine 2001). Additionally, reptiles have to spend more time searching for prey (Wasiolka et al. 2009a) and consequently have less time for other daily activities such as thermoregulation.

Conclusion

The results of this study indicate that reptile diversity and abundance on the regional scale is vulnerable to overgrazing and resultant shrub encroachment. Reptile diversity and abundance is significantly reduced in degraded habitats, which are characterised by losses of plant diversity and perennial grasses that are replaced by sparser shrubs and annual grasses. This decline can be attributed to decreased prey availability, limited opportunities to cool down body temperature, and increased predation risk.

Perennial grasses are particularly important as they provide lizards with optimal habitat for thermoregulation and protection from predators, as well as providing a critical food resource to Orthoptera, which are a main prey source of Kalahari lizards. Perennial grasses are therefore an important structural component of Kalahari rangelands for supporting high reptile diversities and, in combination with trees and shrubs, they play a crucial role in maintaining biodiversity in these savannas.

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Coloniality of birds in the Kalahari—spatial distribution of trees and nests of the Sociable Weaver (*Philetairus socius*)

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Summary: The spatial distribution of suitable nest sites is a limiting resource for many colonial breeding animals. Therefore, we investigated and mapped the spatial distribution of nests of Sociable Weaver (*Philetairus socius*) to evaluate whether the size and distribution of suitable nesting trees influences the variability of colony size and spatial distribution of colonies in two study sites in the Kalahari, South Africa. We used spatial statistics to describe characteristics of point patterns. Nests of communal weavers were clustered at distances up to 300 m, whereas nests were distributed regularly at distances greater than 1,000 m. We therefore suggest that functional colonies of the social weaver consist of several nests on adjacent trees. From our analyses the question arises why sociable weavers establish sub-colonies instead of adding more chambers to the natal nest.

Introduction

Coloniality is a common phenomenon of many animal species. For instance, 13% of bird species breed in colonies (Lack 1968). Brown & Brown (2001) define bird species as colonial when nests are clustered close enough to show interactions between neighbouring conspecifics. Furthermore, individuals within such a colony often feed in flocks with cooperative responses to predator approach (Brown & Brown 1996, 2001, Wittenberger & Hunt 1985).

Many studies discuss the reasons for the evolution of coloniality (e.g. Brown et al. 1992, Brown & Brown 1996, Danchin & Wagner 1997, Rolland et al. 1998, Siegel-Causey & Kharitonov 1990). Three factors seem to be of importance: 1) sufficient food supply in the nesting area, 2) limited space for nesting sites and 3) cooperative defence against predators (Siegel-Causey & Kharitonov 1990). Colony sizes vary in orders of magnitude even within single species (e.g. Ambrosini et al. 2002, Brown et al. 1990, Forero et al. 2002, Gibbs & Kinkel 1997, Griffin & Thomas 2000, Møller 1987, Safran 2004). This variation seems to be triggered by environmental heterogeneity (Lack 1968, Brown et al. 1990, Brown & Brown 1996, 2001, Danchin & Wagner 1997). Thus, temporal and spatial differences in the availability of food or nesting sites, for example, might predispose colonial birds to aggregate and influence competition among neighbouring colonies (Forbes et al. 2000, Forero et al. 2002, Furness & Birkhead 1984, Griffin & Thomas 2000).

The Sociable Weaver (*Philetairus socius*) is such a colonial breeding bird species. It is a sparrow-sized passerine, endemic to southern Africa and associated with arid savannahs (e.g. the southern Kalahari; Mendelsohn & Anderson 1997). The species forms impressive communal nests that can reach 7.5 m in diameter and weigh several hundred kilograms with up to 350 nesting chambers (Covas 2002, Maclean 1973b, Marsden 1999). Weaver nests are used over many years by successive generations of birds and are constructed on the branches of large trees like *Acacia erioloba* or *Boscia albitrunca*. Occasionally, alien trees and artificial structures like telephone poles are used (Maclean 1973b). Most authors refer to a colony as the sum of all nests on a single tree whereas Maclean (1973a) supposes that a colony might consist of several nests on nearby trees rather than of a single nest on one tree.

Our survey focussed on colony characteristics of the sociable weaver. More

Table 1: Basic characteristics of the two study sites at Askham Kerk and Inversnaid, South Africa

	Askham Kerk	Inversnaid
Study area size [km^2]	63.0	31.0
Mean vegetation cover [%]	24.0 ± 5.6	28.0 ± 6.4
Range vegetation cover [%]	8–36	0–46
Precipitation	< 200 mm year^{-1}	< 200 mm year^{-1}
Number of suitable trees [trees per km^2]	3,093 (50)	1,597 (52)
Number of occupied trees [% of all suitable trees]	222 (7.2%)	91 (5.7%)
Number of nests per km^2	3.6	2.9
Total colony number	183	58
Colony density [colony km^{-2}]	2.91	1.81
Mean colony size [chambers]	54.6 ± 44.3	62 ± 39.3
Range colony size [chambers]	1–377	2–248

Photos 1 and 2: Weaver nests in *Acacia erioloba* and on a power pole, Askham Kerk Farm, South Africa. Photos: U.C. Gießelmann.

specifically, we investigate whether 1) the variation in colony size is related to tree size and 2) the spatial distribution of occupied trees is related to the overall spatial pattern of suitable nesting trees. We propose that weaver nest trees should be clumped at smaller scales (within the dispersal radius of weavers). However, due to competition among neighbouring colonies, we expect a regular distribution at larger spatial scales. These patterns ought to be independent of the underlying pattern of suitable nesting trees.

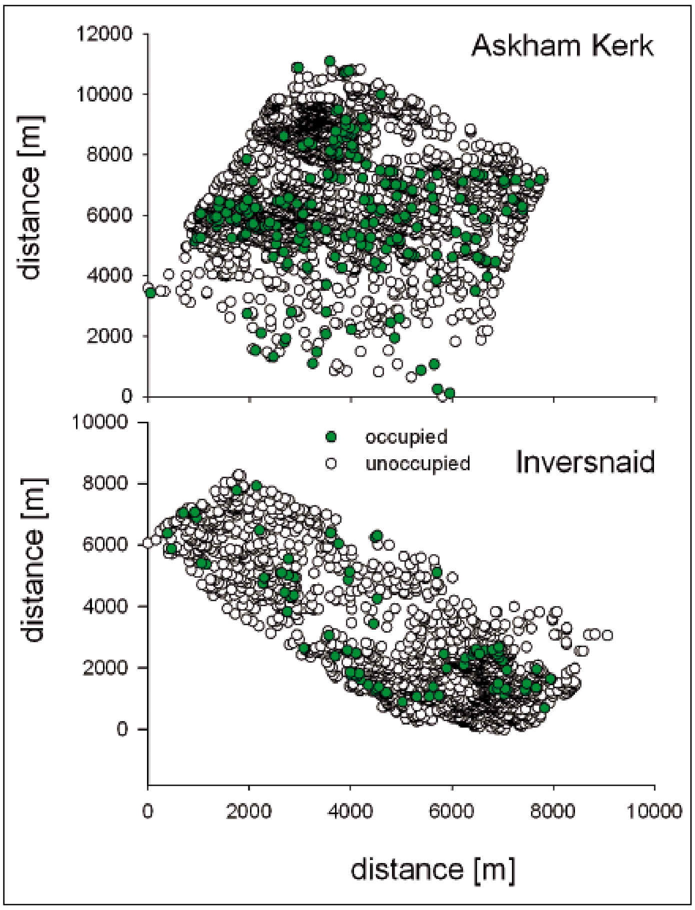

Fig. 1: Spatial distribution of occupied trees (filled circles) and unoccupied trees (empty circles) on Inversnaid and Askham Kerk, South Africa (modified after Gießelmann et al. 2008).

Material and Methods

The study was conducted in November 2004 and March 2005 on two farms, Askham Kerk (app. 27°00’ S, 20°46’ E) and Inversnaid (app. 26°55’ S, 20°45’ E) situated in close vicinity to the Kalahari Gemsbok Park in the Northern Cape Province, South Africa. The study sites were characterised by a semi-arid climate with low and unpredictable rainfall. The two farms were mainly used for sheep farming. The study areas were of different sizes (Table 1) and the vegetation on both farms consisted of open savannah with single *Acacia erioloba* trees and shrubs scattered in a grass matrix.

For our analysis we inspected all weaver colonies at the study sites. We established fixed transect lines at several hundred metres distance for inspections and counting. Colonies were recorded as active when either birds or fresh faeces were detected at sites. At all colonies we counted the number of intact nest chambers as a proxy for colony size. Furthermore, we recorded the stem diameter at breast height (DBH) and crown diameter of the trees as a measure of tree size. As controls, we collected data on randomly selected trees with no nests. We used digitised and rectified aerial photographs with a resolution of 4.0 m (Department for Land Affairs – South Africa) to identify potentially suitable trees for nesting. On the basis of pixel values, we performed a segmentation (eCognition software v3.0.6, Definiens 2006) and made a manual image object classification to extract the coordinates of the large trees in the study area. Due to the very sparse tree cover in the study region we were able to identify individual tree canopies on the aerial photographs. Field data were used to identify trees, which were occupied by our focal species as a reference to enable recognition of suitable unoccupied trees on the basis of canopy size. The classification accuracy was assessed by comparing the identification based on aerial photographs with field inventory data of a training area. We acquired an accuracy of 83%. The 17% error was caused mainly by trees that were standing close together and were therefore merged on the aerial photographs, resulting in two suitable trees being identified as one. Ripley`s K-function and pair correlation function were applied for analyses of spatial distribution patterns in relation to nest-trees and non-occupied trees (Ripley 1976, Stoyan & Stoyan 1994). All analyses were performed with the grid-based software Programita (Wiegand & Moloney 2004) using a cell size of 10 m × 10 m. For detailed information see Gießelmann et al. (2008).

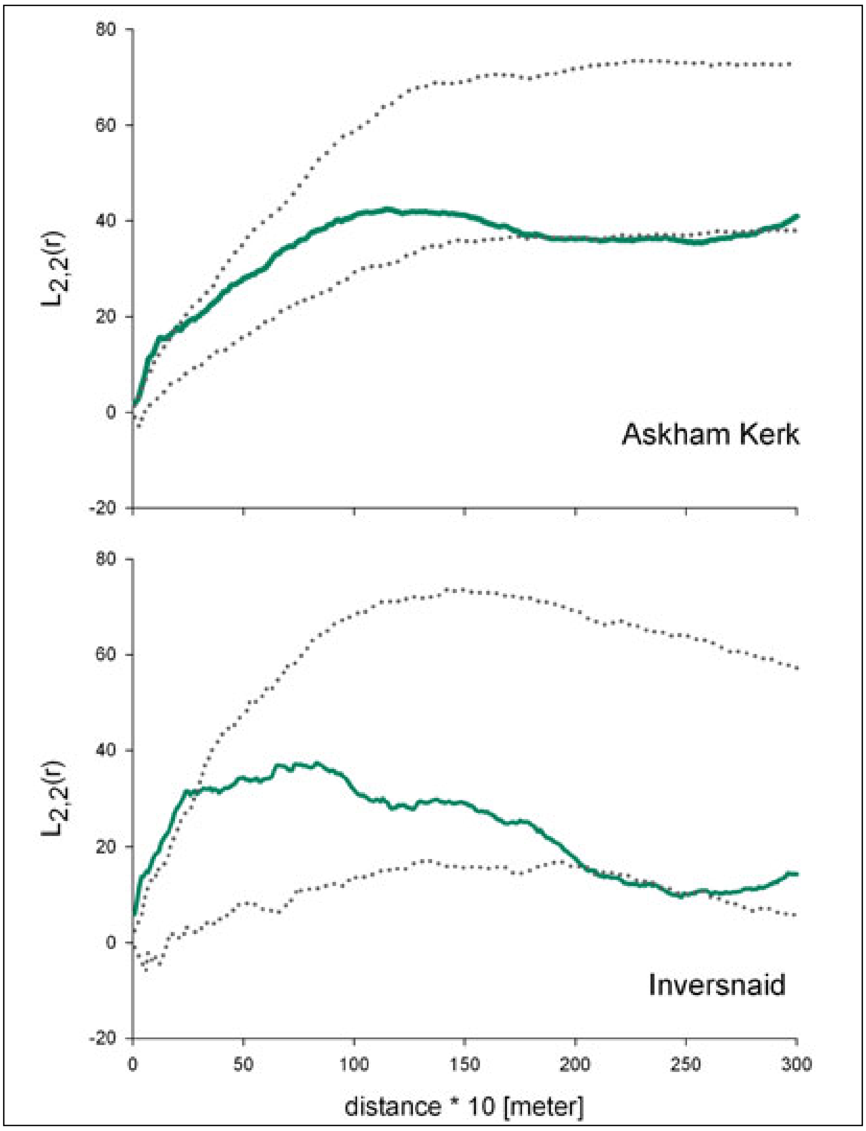

Fig. 2: Ripley's L-function for nests of the Sociable Weavers (*Philetairus socius*) on two farms (Askham Kerk and Inversnaid) in South Africa. The 99% confidence limits are shown as grey dotted lines. Maximum distances are limited to 3,000 metres to focus on the relevant sections of the functions. Graph modified after Gießelmann et al. (2008).

Results and discussion

We found similar characteristics for both study sites concerning the density of nesting trees and the spatial distribution of colonies (Table 1). The density of suitable trees per square kilometre was 50 on Askham Kerk and 52 on Inversnaid. Only 222 (7.2%) and 91 (5.7%) of the suitable nesting trees were occupied by social weavers, respectively (Table 1, Fig. 1). Even though nesting trees showed considerable variation in stem and crown diameter (range stem diameter: 0.16–1.03 m, crown diameter: 4.0–9.0 m) the size of nesting trees did not differ significantly between Askham Kerk and Inversnaid (Tukey HSD for unequal N; both $p = 0.08$). At both study sites weaver birds preferred large trees for nesting and the colony size, in terms of chamber numbers, increased with tree size. However, besides tree size, which only explained a small part of the variation in colony size, other factors such as rainfall or predation seem to affect colony size too. For instance, the weaver`s breeding success is strongly affected by rainfall and predation by, for example, the Cape Cobra *Naja nivea* and Pygmy Falcon *Polierax semitorquatus* (see Covas 2002, Maclean 1973c, d, Marsden 1999).

Our analyses revealed the following spatial distribution patterns of weaver nests. Sociable Weavers aggregated their nests stronger than expected by chance, with Ripley`s K showing a significant clustering of trees with nests up to of 200 m (Askham) and 280 m (Inversnaid; Fig. 2, Gießelmann et al. 2008). Furthermore, the results of Gießelmann et al. (2008) indicate that nesting trees are significantly more clustered than trees without nests. This suggests that *P. socius* might enlarge their colonies by adding new nests to adjacent and suitable tree instead of building new chambers on existing nests. This might be due to space limitations on the trees of the source colonies. The aggregation of nest trees on a small spatial scale points to a lack of intraspecific competition between nearby nests. Thus, we conclude that groups of weaver nests clustered on small spatial scales are single colonies.

Contrary to the findings on small spatial scales (colony level), we found a

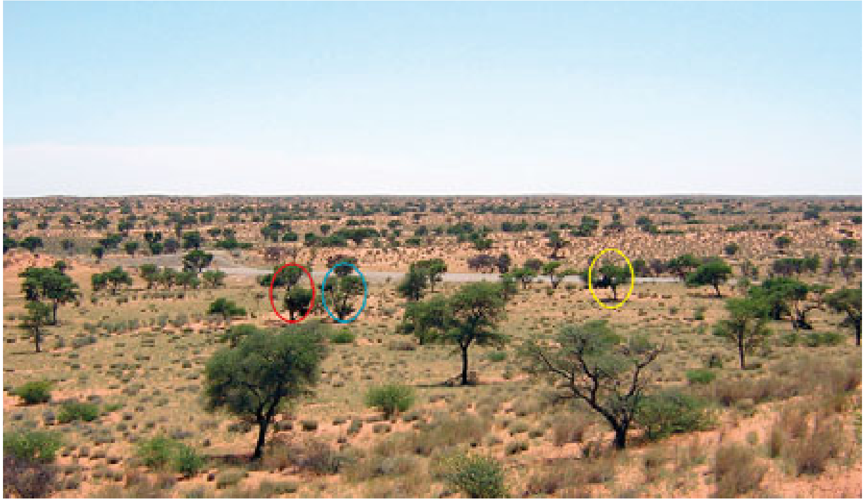

Photo 3: Savannah images (landscape) from the same area as illustrated in Photo 4. Photo: U.C. Gießelmann.

Photo 4: Savannah images from the same area as illustrated in Photo 3. Satellite image: Google Earth.

significant trend towards evenly distributed nesting trees at scales larger than 1,000 m (see Fig. 2). This trend towards regularity was consistently stronger for trees with nests than for trees without nests (Gießelmann et al. 2008). This suggests intercolonial territoriality and therefore competition between nests or groups of nests (Maclean 1973a). The scale at which this regular distribution occurred, corresponds approximately with the foraging range of this species (Maclean 1973e). However, our approach does not allow the inference of processes unambiguously from the observed pattern. For example, there might be other factors influencing the arrangement of nests in space and time, such as the size of foraging ranges, food availability (sufficient grass and bush cover) or other habitat requirements.

To conclude, while trees with weaver nests were evenly distributed at larger spatial scales, single colonies of *P. socius* seem to consist of several nests on clustered trees at smaller spatial scales. We therefore predict that individuals from such clustered nests are more closely related than individuals from more distant colonies.

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Photo 5: Weaver nests in *Acacia erioloba*, Askham Kerk Farm, South Africa.
Photo: U.C. Gießelmann.

Shrub pattern affects reproductive success in the Yellow Mongoose (*Cynictis penicillata*)

Niels Blaum* & Eva Rossmanith

Summary: Although shrub encroachment in savanna rangelands is assumed to affect species diversity negatively, shrubs may be important to animals by providing shelter and nesting sites. In this study the importance of shrubs as habitat structures for the Yellow Mongoose (*Cynictis penicillata*) were analysed at two spatial scales in southern Kalahari rangelands. To investigate this at the microhabitat scale, the locations of 24 reproductive burrows were recorded and group size and number of young were determined at each. At a larger scale (250 ha around reproductive burrows) relative abundance of Yellow Mongooses was determined. Yellow Mongooses preferred to build their reproduction burrows under shrubs greater than 0.8 m in height and with diameters exceeding 5 m. This indicates that shrubs are important at the microhabitat scale because they reduce predation risk for occupants of burrows, improve microclimatic conditions inside the burrows, and protect burrows from trampling by larger herbivores. However, shrub encroachment at larger scales affected group size and number of young negatively. Shrub cover ranging between 15% and 17.5% was a critical upper threshold limiting reproduction. The hump-shaped relationship between shrub cover and relative abundance indicates a trade-off between abundance of suitable shrubs for burrows (protection service) at smaller spatial scales and shrub cover at larger spatial scales (reduced prey availability) for Yellow Mongoose territory selection.

Photo 1: The Yellow Mongoose (*Cynictis penicillata*). The photo shows a subordinate male standing in front of the exit of a reproduction burrow in an alarm position and protecting the young inside the burrow.

Introduction

In structurally poor Kalahari savannah habitats, large *Acacia* trees are keystone structures, which significantly contribute to maintaining species diversity of plants and animals (Milton & Dean 1995). For example, large *Acacia erioloba* trees are used by birds, reptiles and mammals for perching, foraging, nesting, reproduction, and shelter (Huey & Pianka 1977, Dean et al. 1999, Eccard et al. 2004). While the importance of large trees to species diversity in savannas is widely recognised, the value of shrubs is poorly understood, and often considered to be negative.

From an ecological perspective, highly overstocked and shrub encroached savannah habitats are often species-poor (e.g. reptiles: Wasiolka 2007, rodents: Blaum et al. 2007b, carnivores: Blaum et al. 2007c, d, Blaum et al. 2009b, insects: Blaum et al. 2009a, birds: Sirami et al. 2009). Also, from a rangeland perspective, the role of shrubs is generally judged to be negative because shrub encroachment reduces grazing capacity and therefore farming profits (Tainton 1999). However, single shrubs or shrub patches have the potential to provide similar functions as large Acacia trees e.g. providing shelter and nesting sites for small mammals.

The relevance of shrubs for Yellow Mongooses differs across spatial scales

The Yellow Mongoose *Cynictis penicillata*, a predominantly diurnal ground dwelling small carnivore of southern Africa, is a species of open habitats living in family groups of four to 13 individuals, and uses communal below ground burrows as temporary shelter and for reproduction (Du Toit 1980, Rowe-Rowe 1978, Wenhold 1990, Lynch 1980, Wenhold & Rasa 1994). Although this small carnivore is a species of open habitats (Skinner & Chimimba 2005), the importance of shrubs to Yellow Mongooses differs across spatial scales.

Importance of shrubs at the microhabitat scale

A recent study by Blaum et al. (2007a) in the southern Kalahari showed that, at a microhabitat scale, the location of the below ground burrows used for reproduction or shelter are crucial for the reproductive success of Yellow Mongooses. Yellow Mongooses in the southern Kalahari favored burrow locations underneath

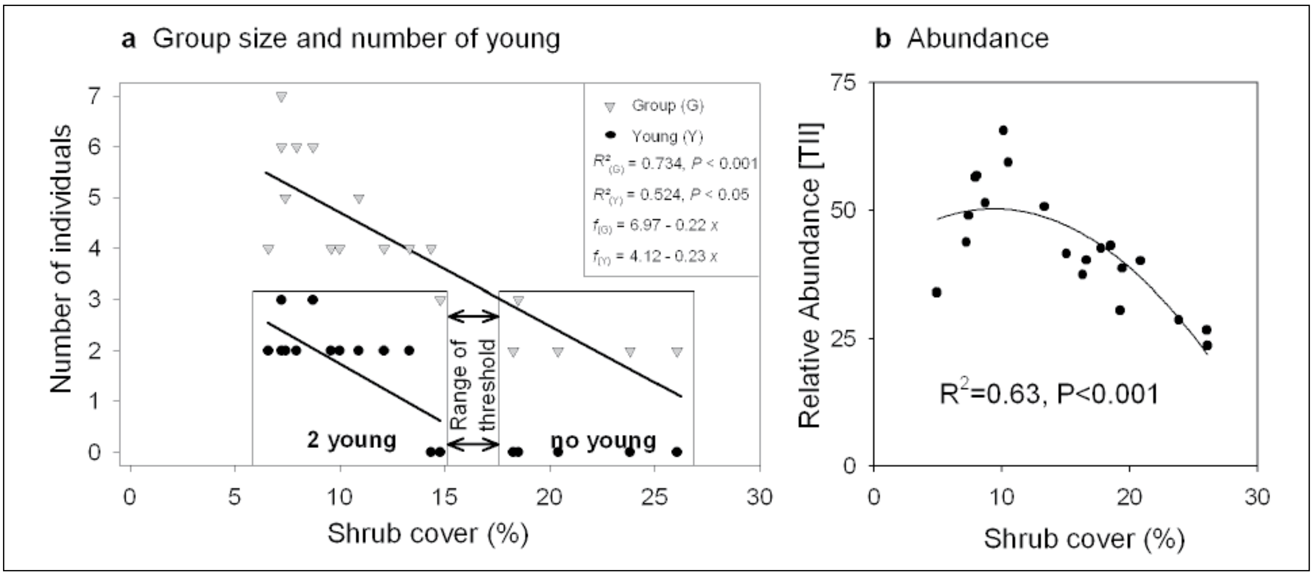

Fig. 1: Group size, number of young and relative abundance of the Yellow Mongoose along a gradient of shrub cover. a) Group size and number of young observed with 10 × 50 binoculars at a distance of 50–100 m from the reproduction burrow for 2 h (commencing 30 min before sunrise) from the crest of a neighbouring dune. b) Relative abundance of Yellow Mongooses determined by the track intrusion index TII (Blaum et al. 2008) at a larger spatial scale (250 ha around reproduction burrows). [Fig. 1a reprinted with permission from the American Society of Mammalogists and Allen Press, Inc. from Blaum et al. 2007a]

shrub canopies with 69% of the sheltering burrows and 75% of the reproductive burrows being located under *Acacia* shrubs (i.e. *A. hebeclada* and *A. mellifera* while *Grewia flava* and *Lycium* spp. were not used at all). Shrub size also influenced the location of reproductive burrows, with shrubs greater than 0.8 m in height and diameters exceeding 5 m being used.

Burrows located under tall and dense shrub thicket benefit from three protective functions of shrubs. Firstly, burrows under shrubs confer a significant thermoregulatory advantage in buffering extreme summer and winter ambient temperature for yellow mongooses (Earlé 1981, Wenhold 1990). In particular, the shade of shrubs reduces high summer temperatures at burrow exits, and also enables the young to be outside the burrow. This is clear when maximum summer temperatures of bare ground and shrub-covered patches are compared: on bare ground temperatures often exceed 50°C, while temperatures under shrubs only reach about 35°C. Similarly, temperatures inside burrows were significantly lower when burrows were located under a large shrub e.g. *Acacia mellifera* (burrows not covered with vegetation: 29.85°C ± 6.45 SD; burrows under large *Acacia mellifera* shrubs: 25.23°C ± 0.73 SD).

Secondly, the sharp thorns of *Acacia* shrubs act as a barrier to livestock movement and effectively protect Yellow Mongoose burrows from trampling. Even though the leaves and fruits of shrubs are foraged upon by wild- and domesticated ungulates, trampling effects in the southern Kalahari were mostly observed outside the cover of shrubs. In a study by Blaum et al. (2007a), six out of 24 reproductive burrows were not situated under shrubs, and over the course of a year, five of these six burrows had been destroyed by herbivore trampling, while none of the 18 burrows covered by shrubs had collapsed.

Thirdly, predation by raptors represents a considerable threat to small mammal reproductive success with young Dwarf Mongooses, for example, suffering heavy predation losses due to raptors (Rasa 1989). The young of Dwarf Mongooses (Rasa 1989), Banded Mongooses (Rood 1975) and Suricates (Clutton-Brock et al. 1999) are fed at the burrow for only a short period and must accompany adults foraging at three to four weeks of age. In contrast, Yellow Mongooses are fed at the burrow until approximately eight weeks of age (Rasa et al. 1992). After this intensive and lengthy nursing period, the size of the young exceeds the usual prey size of many medium-sized raptors and they also have improved agility, which helps them to avoid aerial attacks (Rasa et al. 1992). Therefore, burrows with shrub cover are important to the Yellow Mongoose as they provide added protection, especially to young mongooses, from raptor predation. The use of dense shrub vegetation for protection has also been shown for Degus (*Octodon degus*), which increased their use of open spaces when predators were experimentally excluded (Lagos et al. 1995).

Interestingly, Yellow Mongoose selection of shrubs for reproductive burrows showed a characteristic spatial pattern, with a minimum distance of 10 m between neighbouring shrubs. This open area allows for easier detection of terrestrial nest predators (e.g. Cape Cobra *Naja nivea*; Rasa et al. 1992) or mammalian carnivores (e.g. Cape Fox *Vulpes chama*, Black-backed Jackal *Canis mesomelas*, or Caracal *Caracal caracal*; Avenant & Nel 2002, Kok & Nel 2004, Melville et al. 2004).

Influence of shrubs at larger spatial scales

Home ranges of Yellow Mongooses vary between 6 to 30 ha in radius from a colony (Zumpt 1976) and territories in the southern Kalahari occupy areas ranging from 100 to 300 ha (Taylor & Meester 1993). Although Yellow Mongooses strongly depend on shrubs as habitat structures for safe reproductive- and sheltering burrows, increasing shrub cover at larger spatial scales affect this species negatively.

For example, in a one hectare area around reproductive burrows, Yellow Mongooses prefer areas with significantly lower vegetation cover, particularly of *Rhigozum* shrubs (Blaum et al. 2007a), which corresponds to their general preference for open habitats (Skinner & Chimimba 2005). Also, the availability of Yellow Mongooses prey is strongly reduced in shrub dominated Kalahari savannah habitats. The abundance of most insect species, which are the preferred prey during the dry season in winter decline with increasing shrub cover (Seymour & Dean 1999, Blaum et al. 2009b). Similarly, the abundance of rodents, which are the preferred prey used to feed the young of Yellow Mongooses at the burrow (Rasa et al. 1992) is low in shrub dominated habitats (Bowland & Perrin 1989, Blaum 2007b). Consequently, the reduction in prey availability affects Yellow Mongoose abundance negatively. Both group size and the number of young of yellow mongooses decrease with increasing shrub cover at larger scales (250 ha around reproduction burrows, Fig. 1a). It was also notable that high shrub cover resulted in a threshold response for the number of young. At shrub densities above the threshold (shrub cover above 15%), successful reproduction in Kalahari rangeland areas was not observed and group size was on average 2.2 individuals. Below the threshold, mean litter size was 1.85 and group size averaged 4.7 individuals (Blaum et al. 2007a).

Conclusions

Territory selection among yellow mongooses is a trade-off between the abundance of suitable shrubs for reproductive burrows (protection service) at small spatial scales and the extent of shrub cover at larger spatial scales (which reduces prey availability and probably detection of terrestrial predators). This trade-off is supported by the hump-shaped abundance pattern of Yellow Mongooses across a shrub cover gradient, with maximum abundance in areas where shrub cover was 10% (Fig. 1b).

It would therefore seem likely that long-term heavy grazing, which results in widespread shrub encroachment of savanna rangelands is a threat to this small mammalian predator. Conversely, moderate livestock grazing that leads to shrub cover below 15% is expected to have minor or no negative impacts on the reproductive success of the Yellow Mongoose since the number of young in rangeland areas where shrub cover is below 15% corresponds to the average value of 1.9 young observed in the neighbouring Kgalagadi Transfrontier Park (Rasa et al. 1992), where habitat conditions can be regarded as a natural baseline for the reproductive success of Yellow Mongooses.

Nevertheless, only a few studies have demonstrated that shrubs provide crucial functions for species and offer important services for sustaining species diversity in arid and semi-arid ecosystems (Parmenter & MacMahon 1983, Tews et al. 2004, Thompson 1982), and this needs to be considered before initiating shrub removal programmes aimed at increasing grazing capacity.

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Part III

III.5 Human impacts on biodiversity

Biodiversity conservation under Namibian environmental law

Manfred O. Hinz* & Oliver C. Ruppel

Summary: This article intends to give a synoptic overview of the structure of environmental law in Namibia with a special focus on biodiversity conservation. The article is substantially based on Hinz & Ruppel (2008)—a publication, which gives an account of the research done at the Faculty of Law of the University of Namibia within the ambit of the BIOTA project component administered by the Namibian Faculty of Law and which primarily focuses on the role of customary law in conserving biodiversity. Research completed after the quoted publication is considered for publication in a second volume. However, customary law does not work in isolation: it was, therefore, important to set out the broader framework of general environmental law.

Relevant provisions in the Constitution of Namibia are highlighted before turning to statutory law pertinent to the protection of biodiversity. As the customary law forms part of the law of the land, its relevance for environmental law is briefly discussed and selected provisions are outlined. The role of international environmental law in Namibia and specific international agreements applicable in Namibia connected to the current subject are introduced.

Introduction

The aim of environmental protection in general and biodiversity maintenance in particular can be achieved by different means (Barnard 1998: 283ff.). Traditional legal methods inter alia include establishing protected areas, to regulate harvesting and trade in certain species, to manage habitats and ecosystems, to prohibiting the introduction of new, alien or invasive species. Pollution control and the management of hazardous substances are other effective mechanisms to contribute to the preservation of biological diversity. Other innovative regulatory techniques or policies to preserve biological diversity include the access to genetic resources, biotechnology as well as access to and transfer of technology. All aforementioned methods are to a certain extent governed by legal mechanisms and the success of Namibia's effort to control, manage, and conserve the sustainable use of biodiversity depends to a large extent on the effectiveness of the different legal instruments in place.

Namibia has gained its independence on 21 March 1990. Much has been achieved regarding environmental legislation in Namibia in these 20 years of independence. The roots of environmental law in Namibia must, however, be traced far back in the legal history of the country as the laws that were in force in Namibia at Independence remain in force until repealed or amended by Act of Parliament or until declared unconstitutional by a competent court. Thus, today, Namibian environmental law is a complex and interlocking system of statutes, policies, treaties, common, customary, and case law with the Constitution as the supreme law of the land and therefore the ultimate source of law in Namibia. However, research done under the BIOTA project administered in the Faculty of Law of the University of Namibia has demonstrated that many obstacles prevent the societally expected degree of implementation. Statutory environmental law meets challenges from customary law (cf. Article III.5.2, but also Falk 2008, Pröpper 2009). Apart from this, environmental policies and their translation into law are, in general and this as in all parts of the world, faced with economic interests of the members of the society, which are not easy to harmonise with each other. How to balance environmental policies with economic interests, given the conditions of Namibia, is still an area where more research is needed. Groenewaldt (2008) submitted BIOTA-based legal research in which possibilities to provide incentives in support of individual measures to prevent land degradation were analysed.

National environmental law

The constitution

According to its Article 1 (6), the Constitution of the Republic of Namibia is the law above all laws. Therefore all legislations ought to be consistent with the provisions of the Constitution. Although the Constitution so far contains no enforceable environmental right as such (Ruppel 2010), the foundation is laid for all policies and legislation in Namibia. Two key "environmental clauses" relevant to sustainable use of natural resources are included in the Constitution: On the issue of biological diversity and its protection, the Namibian Constitution is very clear. It is one of the provisions enshrined under the chapter on principles of state policy. The relevant clause is Article 95 (l), which stipulates that the state shall actively promote and maintain the welfare of the people by adopting policies, which include the ". . . maintenance of ecosystems, essential ecological processes and biological diversity of Namibia and utilisation of living natural resources on a sustainable basis for the benefits of all Namibians both present and future . . .". With this particular Article Namibia is obliged to protect its biological diversity and to promote a sustainable use of its natural resources. Furthermore, Article 91 (c) includes in the functions of the Ombudsman "the duty to investigate complaints concerning the over utilisation of living natural resources, the irrational exploitation of non-renewable resources, the degradation and destruction of ecosystems and failure to protect the beauty and character of Namibia." In addition to these clauses it needs to be emphasised that Article 100 provides that, all natural resources, including water, vest in the State, unless otherwise legally owned.

The Constitution sets the framework and Independence created the opportunity to revise a wide range of national policies and laws. This, together with the emphasis placed on environmental concerns at the Rio Summit in 1992, and the increasing awareness, triggered widespread legislative reform particularly in terms of natural resource management. Thus, recent policy and legislative reforms have created a unique opportunity for Namibia to incorporate environmental sensitivity, and as a result Namibian legislation is supported by sound policy direction regarding sustainable development and sustainable use of natural resources (Ruppel 2008).

Statutory law

So far, no specific Act dealing with the conservation of biological diversity as a main topic has come into force. However, the Draft Bill on Access to Biological Resources and Associated Traditional Knowledge was formulated in 2000. This draft bill, which is aimed specifically at the protection of biodiversity and traditional knowledge has not yet been passed in Parliament.

The Namibian Government has, however, developed Namibia's National Biodiversity Strategy and Action Plan. The goal of this action plan is to protect ecosystems, biological diversity and ecological processes, through conservation and sustainable use, thereby supporting the livelihoods, self-reliance, and quality of life of Namibians in perpetuity (Barnard et al. 2000: 13). The action plan attempts to provide a national strategic framework for natural resource management activities involving biological resource management and the natural environment, including trade and economic incentives, and to prioritise, through detailed action plans, activities and measures needed to address this strategy effectively for the next decade, with cost estimates for each.

As shown by Hinz & Ruppel (2008) sectoral legislation covering the protection of biodiversity is wide ranging in Namibia. A myriad of legislative instruments provide for the equitable use of natural resources for the benefit of all. Only the most relevant legal instruments will be introduced briefly.

One of the major biodiversity related laws in Namibia is the legislation governing the conservation of wildlife, and protected areas, the Nature Conservation Ordinance 4 of 1975. The Ordinance was amended by the Nature Conservation Amendment Act 5 of 1996. One of its major highlights is the creation of conservancies in communal areas (Article III.6.5). In terms of the amendment, rural communities have to form a conservancy in order to be able to acquire the use-right over wildlife.

The Environmental Management Act No. 7 of 2007 requires adherence to the principle of optimal sustainable yield in the exploitation of all natural resources. The Act gives effect to Article 95 (l) of the Constitution by establishing general principles for the management of the environment and natural resources. It promotes the coordinated and integrated management of the environment and sets out responsibilities in this regard. Furthermore, it intends to give statutory effect to Namibia's Environmental Assessment Policy, and to enable the minister responsible for the environment to give effect to Namibia's obligations under international environmental conventions; and to provide for associated matters. The Act promotes intergenerational equity in the utilisation of all natural resources. Environmental impact assessments and consultations with communities and relevant regional and local authorities are provided for to monitor the development of projects that potentially impact on the environment.

The proposed Parks and Wildlife Management Act will protect all indigenous species and control the exploitation of all plants and wildlife. The preamble clearly states that the Bill is intended to give effect to paragraph (l) of Article 95 of the Constitution by establishing a legal framework to provide for and promote the maintenance of ecosystems, essential ecological processes and the biological diversity of Namibia and to promote the mutually beneficial co-existence of humans with wildlife, to give effect to Namibia's obligations under relevant international legal instruments including the Convention on Biological Diversity (CBD) and the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). In keeping with the Constitution the principles underlying the draft Act, are simply that biological diversity and essential ecological processes and life support systems be maintained. In case the proposed Act comes into force, it repeals the Nature Conservation Ordinance 4 of 1975.

Water related legislation is manifold in Namibia (Ruppel & Bethune 2007). Although the new Water Resources Management Act of was approved by Parliament in 2004 the rather out-dated Water Act No. 54 of 1956 remains in force until the new act comes into force upon signature by the Minister. The new act is currently being amended to take into account practical aspects of implementing it. The Water Act of 1956 does not directly refer to the protection of biological diversity; it however contains provisions relating to water quality and conservation,which are at least indirectly beneficial for the maintenance of biodiversity (Mapaure 2010, Falk et al. 2009).

The Marine Resources Act, No. 27 of 2000 provides for the conservation of the marine ecosystem and the responsible utilisation, conservation, protection and promotion of marine resources on a sustainable basis. For that purpose it provides for the exercise of control over marine resources and for matters connected therewith. It replaces the Sea Fisheries Act, No. 29 of 1992, which in turn replaced the Sea Fisheries Act, No. 58 of 1973.

The Aquaculture Act, No. 18 of 2002 regulates and controls aquaculture activities and the sustainable development of aquaculture resources (Bethune et al. 2004). All aquaculture ventures will be subject to strict licensing. Section 27 is of most relevance for the protection of biodiversity. A person may not, without written permission granted by the Minister, introduce or cause to be introduced into Namibia or any Namibian waters any species of aquatic organism or any genetically modified aquatic organism or transfer any species of aquatic organism from one aquaculture facility to another or from any location in Namibia to another.

The Inland Fisheries Resources Act, No. 1 of 2003 deals with the conservation and utilisation of inland fisheries resources and allows for the updating and development of new policies for the conservation and sustainable utilisation of Namibia's inland fisheries. It encourages cooperation with neighbouring countries regarding the management and conservation of shared waterways.

Legislation on forest is one further important mosaic in the legal system of biodiversity conservation in Namibia. In 2005 almost 7.7 million hectares of Namibia's land were covered by forests, which corresponds to 9.3% of the total land area (FAO 2005). Almost 2% of the forest area has disappeared since 1990. Major threats to forests in Namibia include the expansion of land for agriculture; the use of fuelwood and charcoal for domestic use; tobacco curing and brick kilning; land clearing for infrastructure development; uncontrolled wild fires; selective logging through timber concessions and unlicensed curio carving; and habitat destruction by elephants (Groenewaldt 2008).

The Forest Act, No. 12 of 2001 consolidates the laws relating to the use and management of forests and forest produce, provides for the control of forest fires and creates a Forestry Council. Protection of the environment is found in part IV of the Act. This part of the Act deals with protected areas, protection of natural vegetation and control over afforestation and deforestation. Purpose of the Act is to conserve soil and water resources, maintain biological diversity and to use forest produce in a way, which is compatible with the forest's primary role as the protector and enhancer of the natural environment.

In recognising the worldwide diversity situation, the Government of Namibia enacted the Biosafety Act, No. 7 of 2006 after having signed the Cartagena Protocol on Biosafety to the CBD, which was adopted in 2000. The Act provides for measures to regulate activities involving research, development, production, marketing, transport, application and other uses of genetically modified organisms and to establish a Biosafety Council. The objective of the Act is inter alia to introduce a system and procedures for the regulation of genetically modified organisms in Namibia in order to provide an adequate level of protection to the conservation and the sustainable use of biological diversity.

Biodiversity and customary law in Namibia

The majority of indigenous Namibians live in accordance with their Customary Laws. Thus, Namibia gave equal recognition to the Customary Laws as accorded to common law. This is contained in Article 66 of the Constitution, which states that both Customary Law and common law are to be recognised as far as they are not repugnant to the provisions of the Constitution. This hybrid system has led to the existence of a two legal systems in one, called legal pluralism (Griffiths 1986). The Namibian Traditional Authorities Act, No. 25 of 2000 in its Section 1 describes Customary Law as the ". . . norms, rules of procedure, traditions and usages of a traditional community."

As demonstrated by Hinz & Ruppel (2008) there is a broad recognition of the contribution that traditional knowledge can make to both, the conservation and the sustainable use of biological diversity and of the need to ensure the equitable sharing of benefits arising from the utilisation of traditional knowledge. Many indigenous communities live in areas where the vast majority of the world's genetic resources are found. Their cultures and knowledge are deeply rooted in the environment on which they depend and biological diversity is a substantial element of their lives (Hinz 2003).

Enshrined in Article 102 (5) of the Constitution is that there shall be a Council of Traditional Leaders to be established in accordance with an Act of Parliament, and such Traditional Leaders are to advice the President, inter alia, on the control and utilisation of communal land. Section 3 (3) (c) of the Traditional Authorities Act 25 of 2000 inter alia gives Traditional Authorities the power to make Customary Laws; to administer and execute the Customary Law of that traditional community; and to ensure that the members of his or her traditional community use the natural resources at their disposal on a sustainable basis and in a manner that conserves the environment and maintains the ecosystems for the benefit of all persons in Namibia. Many Customary Laws contain rules that directly or indirectly contribute to the conservation of biological diversity. The rules that occur most frequently are those on water, fish, wild animals, and plants (Hinz 1998).

The 1993 laws of Oukwanyama for example provide for the protection of trees, fruit trees in particular, plants, and water. It is an offence under the laws of Kwanyama to cut fruit trees und all water has to be kept clean. The laws of Ondonga provide for the protection of trees with specific reference to fruit trees, palm trees, and the marula tree (Section 8), and the use of fishing nets in the river is prohibited without permission of the traditional authority (Section 19). The Laws of Uukwambi provide for rules for the protection of water (Section 13), the protection of trees (Section 14A), wild animals (Section 14B), and grazing grass (Section 14C).

International environmental law

International law

As to the application of international law, the Namibian Constitution in its Article 144 provides that "[U]nless otherwise provided by this Constitution or Act of Parliament, the general rules of public international law and international agreements binding upon Namibia under this Constitution shall form part of the law of Namibia."

The Constitution explicitly incorporates international law and makes it part of the law of the land. Thus, public international law is ab initio part of the law of Namibia. It needs no transformation or subsequent legislative act to become so (Ruppel 2008: 108f.). However, as the Constitution is the supreme law of Namibia, international law has to be in conformity with the provisions of the Constitution in order to apply domestically. In case a treaty provision or other rule of international law is inconsistent with the Namibian Constitution, the latter will prevail.

The global level

On the global level, several Multilateral Environmental Agreements have been established that directly or indirectly contain provisions relating to the protection of biological diversity. Apart from the Convention on Biological Diversity (CBD), one of the most well known international biodiversity related agreements is the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES).

Due to the fact that the trade in wild animals and plants crosses borders between countries, the effort to regulate it requires international cooperation to safeguard certain species from over-exploitation. CITES was conceived in the spirit of such cooperation. Today, it accords varying degrees of protection to more than 30,000 species of animals and plants, whether they are traded as live specimens, fur coats or dried herbs. CITES was drafted as a result of a resolution adopted in 1963 at a meeting of members of IUCN (The World Conservation Union) and entered in force in 1975. Namibia has acceded to the Convention in 1990 and the Convention came into force for Namibia in March 1991.

The CBD was signed by Namibia on 12 June 1992 in Rio de Janeiro and ratified it on 18 March 1997. Accordingly Namibia is obliged to ensure that its domestic legislation is conform with the objectives and obligations of the CBD. Namibia gives effect to the CBD inter alia by implementing the National Biodiversity Strategy and Action Plan and has issued its third national report under the CBD (Government of Namibia 2005).

The regional level

Major Foundations of biodiversity protection on the regional level are the African Union's Convention on the Conservation of Nature and Natural Resources as well as specific SADC Protocols (e.g. on Fisheries, on Forestry, on Wildlife Conservation and Law Enforcement, on Shared Watercourse Systems).

The original African Convention on the Conservation of Nature and Natural Resources was adopted in Algiers, Algeria in September 1968 and entered into force in June 1969. Of the 53 member States 40, excluding Namibia, have signed the Convention of which 30 have ratified it. Recognising that soil, water, flora, and faunal resources constitute a capital of vital importance to mankind, the Convention's fundamental principle is that the contracting States shall undertake to adopt the measures necessary to ensure conservation, utilisation, and development of soil, water, flora, and faunal resources in accordance with scientific principles and with due regard to the best interests of the people. The Convention contains several provisions related to the conservation and perpetuation of species. Special provisions as to protected species and trade in specimens are formulated.

The Revised African Convention on the Conservation of Nature and Natural Resources was adopted by the second ordinary session of the Assembly of Heads of States and Government of the African Union in Maputo, Mozambique, in July 2003. It commits parties in particular to manage their natural resources more sustainable. The Convention has however not yet come into force, as the requirements for coming into force have so far not been fulfilled: According to Article 38 the Convention comes into force on the thirtieth day following the date of deposit of the fifteenth instrument of ratification, acceptance, approval or accession with the Depositary. While 34 of 53 member states have so far signed the convention, it has only been ratified by 7 States, namely Burundi, Comoros, Libya, Lesotho, Mali, Niger, and Rwanda. Provisions directly related to the protection of biodiversity are contained in Article IX on Species and Genetic Diversity; Article X on Protected Species; Article XI on Trade in Specimens and Products thereof; and Article XII on Conservation Areas.

The parties to the Convention shall maintain and enhance species and genetic diversity of plants and animals whether terrestrial, fresh-water or marine. They shall for that purpose, establish and implement policies for the conservation and sustainable use of such resources. Parties are obliged to undertake to identify the factors that are causing the depletion of animal and plant species, which are threatened or which may become so, with a view to their elimination, and accord a special protection to such species. Furthermore, domestic trade in as well as the transport and possession of specimens and products must be regulated by the parties appropriate penal sanctions, including confiscation measures must be provided. To ensure the long term conservation of biological diversity, the Parties shall establish, maintain and extend conservation areas.

Other regional agreements relevant for biodiversity protection are the various protocols under the umbrella of the Southern African Development Community (SADC), which has been in existence since 1980, when it was formed as a loose alliance of nine majority-ruled States in Southern Africa known as the Southern African Development Coordination Conference (SADCC), with the main aim of coordinating development projects in order to lessen economic dependence on the then apartheid South Africa. The SADCC was the transformed from a Coordinating Conference into a Development Community (SADC) in August 1992 in Windhoek, Namibia.

The Parties may conclude Protocols as may be necessary in each area of co-operation, which shall spell out the objectives and scope of, and institutional mechanisms for, co-operation and integration. So far, 23 of such protocols have been concluded. SADC Protocols of major concern with regard to biodiversity conservation are the Protocols on Fisheries; on Forestry; on Wildlife Conservation and Law Enforcement and on Shared Watercourse Systems.

Concluding remarks

Since Namibia's independence in 1990, one goal has been to achieve a new era of environmental management and development. The United Nations Conference on the Environment and Development (UNCED) in Rio de Janeiro in 1992 two years after Namibian's Constitution came into force formally marked this new era. From the beginning of Namibia's young democracy, the twining of environment and development issues has been pivotal. As Namibia is an arid country and strongly dependent on natural resources, this association is critical to the country's future. Therefore, the Constitution explicitly promotes development through sustainable resource use and the protection of biological diversity and ecosystems for present and future generations. Namibia has taken up the challenge to conserve species and ecosystems to limit the increasing rate of loss of biological diversity in various aspects. The challenge is not an easy one and it takes time to realise this ambitious aim in the best possible manner. While some of the laws contributing to the conservation of biological diversity might be outdated from the vantage point of the present, Government with its respective Ministries is endeavouring to improve, perfect and adjust existing and where necessary to enact new laws. Without any doubt, this process demands its time and is of continuous nature. With regard to the lessons learned from BIOTA research, it can be concluded that where environmental law finds its limits, the complementary nature of customary law comes into focus.

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Traditional and modern use of biodiversity—customary law and its potential to protect biodiversity

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Summary: This article presents an evaluation of legal anthropological research focusing on the interface between statutory and customary law. Customary law is the law owned by the people and therefore holds great potential for the protection and conservation of biodiversity. However, although relevant statutory enactments are necessary to complement customary law, they have failed in many instances to recognise customary law in a way that would allow it to perform to its full potential in protecting and conserving biodiversity. There is a challenge to consider amendments to existing statutory enactments as a component of legal reform. There is also a need for training programmes to build capacity amongst biodiversity policy-makers and legislators who often have a weak understanding of customary law.

Introduction

The environment and human beings are closely linked in traditional communities. While customary law generally reflects this holistic approach to the environment, the majority of the laws made by the state do not, resulting in conflict between customary law and the laws of the state (see Article III.5.1). Research conducted by BIOTA Southern Africa has shown that navigating the interface between traditional and statutory biodiversity conservation requires an understanding of the concept of legal pluralism. Hinz & Ruppel (2008) gave an account of the research done at the Faculty of Law at the University of Namibia within the ambit of the BIOTA project. This article takes note of the conclusions drawn by Hinz & Ruppel but concentrates on research conducted thereafter. The research has shown that African customary law has the potential to influence policies, which would improve conservation and the protection of biodiversity.

African tradition, law, and biodiversity conservation

The research on traditional communities in Namibia has shown that traditional societies have their own unique visions for the use of natural resources. These often differ from the generally held vision of biodiversity that developed under the auspices of European biological philosophy and which has found its way into the national legislation of many African states.

Before describing our recent findings from the BIOTA project, it is important to note that most African countries have established a legislative system governing the various branches of industry, including biodiversity conservation. Namibia has enacted several pieces of legislation concerning the conservation and utilisation of biodiversity, including the constitution itself. These state laws stipulate that the state is the owner of all natural resources in Namibia. However in reality, these laws remain merely a claim, as a real juridicial prerogative would not be accepted without great resistance from the users of natural resources under customary law.

Therefore, what effectively characterises Namibian natural resource laws, like elsewhere in Africa, is the existence, parallel to written laws, of a body of customary laws and ethical commands, which originated largely in pre-colonial times. In a country where the majority of the population is living under the guidance of customary laws, official written legislation tends to be overridden by customary laws with regards to the exploitation of the natural resources by the local inhabitants. Research in traditional communities of Namibia has shown that the laws of the state will not achieve the objectives of biodiversity conservation without the involvement of those who are in charge of the traditional laws. Namibian traditional authorities and members of the traditional communities act as the intermediaries between the largely rural population and the central state administration. Connected to this and in the light of the views of traditional authorities in Namibia, nobody with the ambition of creating acceptable juridicial norms can ignore the essential contribution of customary law to biodiversity conservation and utilisation. If law disregards them, then such law is bound to be rejected. Any government programme based on such state law is bound to encounter many setbacks in its implementation at the traditional community level.

Biodiversity conservation and traditional norms: the Namibian experience

Several dissertations and theses have been produced in the context of the BIOTA project in the Faculty of Law at the University of Namibia. This research has generally focused on the exploration of the interface between customary law

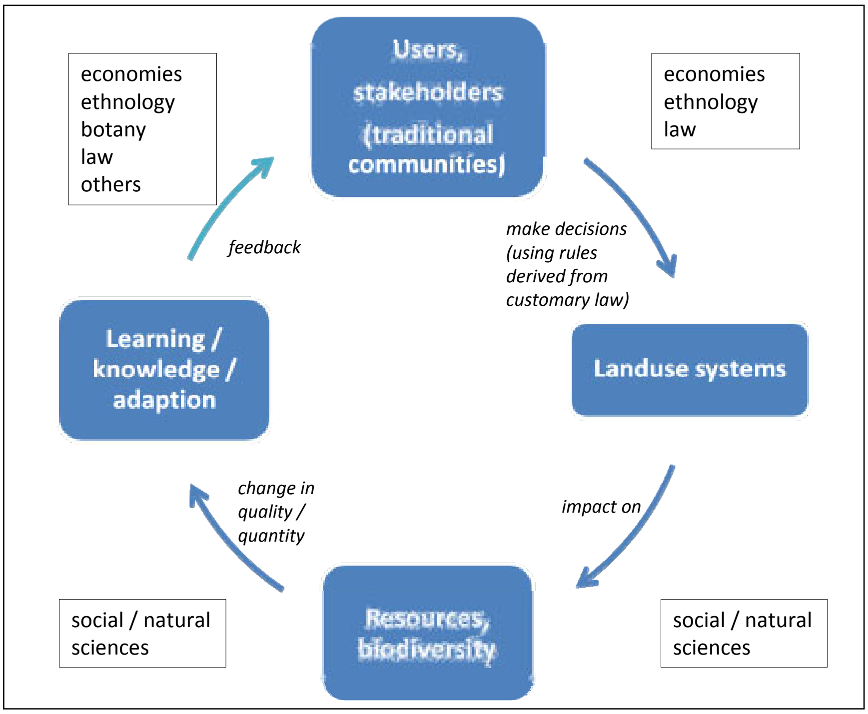

Fig. 1: Simplified model of traditional forestry. Source: Mapaure (2008) as adapted from Domptail & Hecht (presentation at the BIOTA congress, Würzburg, 2005).

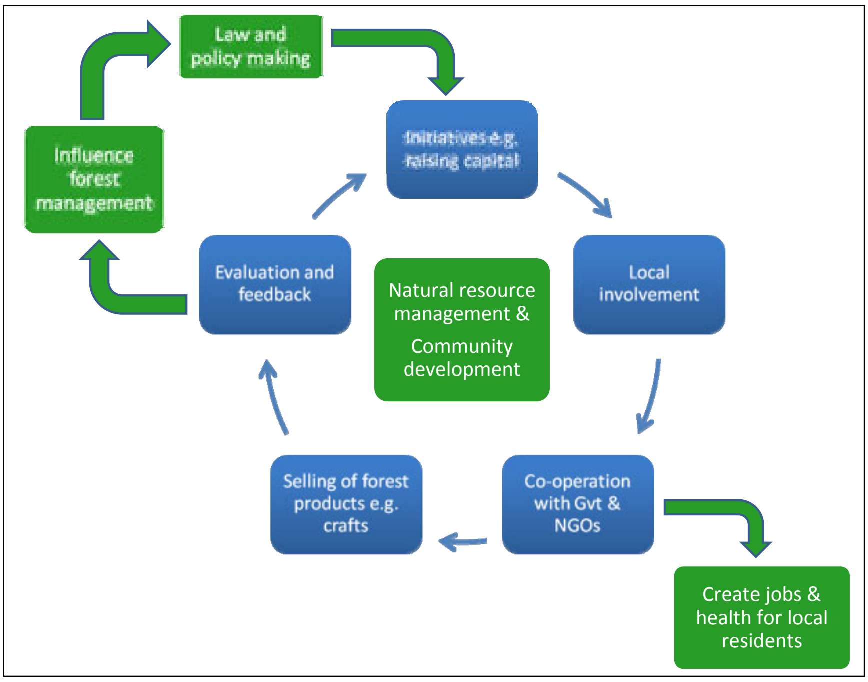

Fig. 2: Simplified model of forestry framework under legislation. Source: Mapaure (2008).

and state laws with regard to the conservation of biodiversity (for more detailed explanations of previous research, see Hinz 2008). In doing so, the research has paid special attention to the shortcomings and limitations of both customary and statutory law. The orientation and some of the results of the research are summarised below.

Research conducted by Clever Mapaure on community forests in the Kavango Region showed that there is a discrepancy between state laws and customary laws regarding the ownership of forest resources (Mapaure 2008). Whereas state laws stipulate that all natural resources belong to the state, local communities regard themselves as the owners of the natural resources surrounding them. The perception and position of the community that they own the trees on communal land emanates from the concept of aboriginal title to land, which is an ancient right held by the pre-colonial occupants of land. Because this title predates and supersedes any right granted under colonial or current state laws, it poses an obvious threat to the success of state conservation laws and policies being implemented in these communities. This is a clear case of the internal conflict of laws. This internal conflict of laws places biodiversity conservation at a crossroads particularly in terms of natural resource utilisation. For example, the state classifies the harvesting of trees by local communities as 'illegal logging' whereas communities believe they are acting 'legally' under their customary laws and traditional beliefs and that they are utilising their 'god given' resource (see also Hinz 1998). Fig. 1 shows a simplified model of traditional forestry.

Under customary forestry laws, the major stakeholders are the communities. Decisions regarding the utilisation of trees are made at the traditional level and customary law is the supreme law. These decisions affect landuse systems, which in turn has an impact on biodiversity in general, and in particular on the quantity and quality of the elements of biodiversity regulated by such laws. This is a learning process, which produces traditional knowledge necessary for further planning and hence feedback. This is a simplified summary of the concept of traditional forestry adapted from Domptail & Hecht's (2005) ideas.

The idea of traditional forestry is reflected in the Forest Act of 2001 but there are certain elements alien to traditional forest management introduced by the Forest Act. These include state enforcement institutions including the Directorate of Forestry and the national police force, which fall outside of the traditional forest management system (Ensminger 1996:194). The approach of the government is summarised in the simple diagram in Fig. 2. This diagram indicates that the concept of forestry under the Forest Act is centered around natural resource management and community development.

Subsequent research conducted by Mapaure (2010) in the Kavango, Otjozondjupa and Ohangwena Regions of Namibia demonstrated that communities also regard themselves as the owners of water, which is contrary to the position of government officials who say that water is owned and administered by the state for the benefit of the traditional communities who have user rights only. The position of government officials is based on the Constitution and the Water Act, No. 54 of 1956. This act provides for water to be owned privately or publicly and takes a monistic position that all water in the republic should be utilised in terms of the Act itself. Although this is the position of the statute, communities apply both customary laws and the Act in the conservation and utilisation of water.

Photo 1: A hand dug traditional well in Ohakane Village, Otjozondjupa Region. The community decided to dig for water because of the inconsistent supply of water by the government. Photo: Ndilimeke Amunyela.

This dualism, which has caused differences in perceptions has resulted in conflicting institutional relations regarding water management and utilisation and proves that the plurality, or at least the duality of legal systems, is a reality, which needs to be recognised and dealt with in regard to the management of natural resources.

Research conducted by Emilia Namwoonde in Kavango around the registration of communal land rights as required by the Communal Land Reform Act, No. 2 of 2002, (cf. Section 25 of the Act) has shown that traditional communities apply both state- and customary laws in the use and allocation of land (Namwoonde 2008). They navigate between the two types of law by limiting the application of either whenever they feel it is appropriate to do so. In this sense, the traditional communities in the Kavango Region have rejected the statutory requirement to register their land because such registration is said to be in conflict with their customary land laws. This is an interesting relationship between the application of customary law and statutory law in land management. It is interesting in the sense that, whereas Article 66 of the Constitution states that statutory law overrides customary law when the two are in conflict, according to the traditional communities, customary law takes precedence.

In subsequent research in the Caprivi and Kavango Regions, Namwoonde (2010) discovered that the land allocation procedures on communal land found in these regions are twofold. Firstly, there are allocations performed according to the Communal Land Reform Act, and secondly there are allocations performed according to customary law. Although there was an attempt to incorporate customary land law concepts into the Communal Land Reform Act, it became clear from her research that traditional communities preferred to manage communal land under customary land law as opposed to state laws. The contracts signed by traditional authorities when handing over large tracts of land to investors in the biofuel industry have clauses, which are at variance with community land laws.

Namwoonde's research concludes that the current rush to produce biofuel on a large commercial scale on communal land is ill-conceived and under-researched, and could contribute to unsustainable utilisation of natural resources, which will not solve the problems of climate change, poverty, and energy and food security (see similar comments in Hinz 1998). Therefore, questions arise regarding the nature of the land tenure created when chiefs use their customary law powers to give areas of communal land to investors who then manage the land outside the realm of customary law. Namwoonde concluded that if the community members in Kavango entered into farming contracts with private investment companies, the application of the customary laws of traditional communities would be limited by such contracts and they would not be able to implement or enforce such laws on these companies (Namwoonde 2010). This is because once the contract is signed the companies operate according to the terms of the contract and state laws, both of which do not incorporate customary law. This will have a serious impact on the effectiveness of customary law as a biodiversity protection mechanism.

Research conducted by Aubrey Ndlovu in the Kavango region analyses the relevance and contribution of indigenous knowledge systems to the conservation of wildlife (Ndlovu 2009). The research indicates that without indigenous knowledge systems there would not be effective conservation of wildlife, especially in the area of community based natural resource management. Ndlovu discovered that traditional communities used to retain a sufficiently high level of internal cohesion when it came to the application of traditional knowledge concerning the conservation and utilisation of wildlife. However, this cohesion and systematic use of traditional knowledge were undermined when state or corporate bodies established control over the natural resources (Ndlovu 2009) through law or administrative discretion. This 'interference' by the state or corporate bodies led to the gradual wasting away of traditional knowledge and beliefs as instruments of biodiversity conservation and has led to the degradation of natural resources and the disappearance of wildlife around the villages.

Nowadays, the people do not hunt anymore, not because their customary laws do not allow them to but because the state prohibits hunting without a license. Because the Nature Conservation Ordinance, No. 4 of 1975 requires anybody who wants to hunt to do so with a licence issued by governmental officials, some traditional knowledge systems, which guided how animal species should be conserved are being eroded. The erosion of traditional hunting knowledge systems has caused traditional communities to change their survival patterns (Hinz 2003). Such shifts in survival patterns highlight the social adaptive capacity of traditional communities (Mapaure 2009). Ndlovu (2009) observed that traditional knowledge systems remain in the memories of the older generation, although they are unable to apply this traditional hunting knowledge due to the conflicts that exist between their traditional knowledge systems and the Nature Conservation Ordinance.

In light of the above, many indigenous peoples are seeking new ways of adapting their traditional beliefs to modern realities, often using a combination of animism and formal religion as source of inspiration for their new way of natural resource management. This has been demonstrated by Mapaure (2010) who conducted research on the management and utilisation of water in the Kavango River. Some of the people who live along the Kavango River believe that the way they use the water is closely monitored by a mystical creature called 'ekongoro' (a mermaid), which can punish polluters and abusers of the water resource (Mapaure 2010). Because people claim to have seen 'ekongoro' and there is a belief that it has drowned people who defecated in the water some residents of Kapako and Sivara villages went to the extent of saying that 'ekongoro' owns the water in the Kavango River. Interestingly, they believe that while God (the Christian God) created water, Ekongoro holds more power in controlling its conservation and utilisation.

The findings of Ndlovu (2009) were also reflected in the research by Prisca Anyolo who investigated the relationship between customary law and state laws in the conservation of wildlife in the Uukwaluudhi Conservancy (Anyolo 2010). The Namibian government decided to create a platform through which traditional communities could be directly involved in management of their wildlife. This platform included in situ conservation of natural resources through the establishment of communal conservancies. The creation of conservancies was meant to conserve biodiversity as an output with community development as an incentive. With this in mind, the Namibian Parliament passed the Nature Conservation Amendment Act, No. 5 of 1996, which now stands as the main state law concerning the management of biodiversity in conservancies. Although this piece of state law is the main guideline for the management of conservancies, Anyolo (2010) showed that traditional norms of biodiversity conservation play a vital role in the conservation of wildlife in the Uukwaluudhi Conservancy.

Even though most of the legal instruments used by the communities are inclined towards the application of state laws only, traditional communities always turned to their customs for controlling the utilisation of natural resources such as game and trees. This reversion to their own customs by applying customary law took place either when there was a loophole in the state law, or when state law was silent, or when traditional authorities invoked their powers under section 3 (2) (c) of the Traditional Authorities Act, No. 25 of 2000. This act stipulates that the Traditional Authority must "ensure that the members of his or her traditional community use the natural resources at their disposal on a sustainable basis and in a manner that conserves the environment and maintains the ecosystems for the benefit of all persons in Namibia".

Conservancies are largely governed by the statute and other legal instruments required under the Act. In this light, because state law is regarded as superior to customary law and because of the top-down approach in the management of conservancies, some local people have lost their customary rights over the land and it's wildlife to the conservancy without being compensated. Therefore, Anyolo (2010) concludes that although some customary laws are applied in the management of natural resources in conservancies located on communal land, the Nature Conservation Amendment Act does not offer protection to those traditional community members affected by the change in the land tenure system from communal land to conservancy.

Conclusion: issues for consideration in law reform

The general message from the BIOTA research regarding biodiversity legislation in Namibia is that policy and legal approaches that do not involve the traditional community and their customary laws are very likely to fail. All laws that affect biodiversity conservation, especially at the community level, must take customary law and traditional structures into account in order to achieve a sustainable vision for the conservation of biodiversity. The mastery of local knowledge in natural resource management and an understanding of the sources of conflict are necessary for the implementation of sustainable projects, which favour partnerships between traditional and modern biodiversity management.

State laws and institutions, on the one hand, and customary law and traditional governance institutions, on the other, are both important for the management of biodiversity. Biodiversity management should not be administered exclusively by the authorities of the state, and neither should it be the sole responsibility of traditional institutions. Cooperation is necessary, but such cooperation is strongly influenced by the way in which biodiversity laws and policies are designed. Emphasis should be placed on the participation of local traditional communities and use should be made of traditional local knowledge. Such measures greatly increase the chances of real success in the implementation of conservation projects. It is important to note that the challenge is not to reproduce old customs, but rather to catch their spirit in order to renew and enhance them and create new collective memories in the field of biodiversity conservation.

Knowledge of how property rights regimes function in relation to humans and their use of the environment is critical to the design and implementation of effective environmental protection laws and policies. Government should therefore make balanced decisions, which benefit both the environment and rural communities with regard to poverty alleviation programmes.

As long as state laws favour top-down approaches, customary law will not be able to contribute to the conservation of biodiversity to its full potential. The findings of the research confirm that there is a lack of understanding about customary law amongst biodiversity policy-makers and legislators, a weakness, which calls for changes through legal reform, but also through training and a commitment to relevant capacity building.

Acknowledgements
The authors' general acknowledgements to the organisations and institutions, which supported this work are provided in Volume 1.

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Economic and ecological indicators of land reform projects in eastern Namibia

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Summary: Land reform is a controversial and dogmatic topic of discussion in southern Africa. One side views examples of failed reforms in the region as proof for the inevitable failure of land reform in general. The other side views land reform as an important means for leading scores of previously discriminated poor into a bright and wealthy future. After 18 years of land reform implementation in Namibia we evaluated the success of projects in the Omaheke region of Namibia. We compared economic and ecological indicators describing both management preconditions and outcomes of the two main instruments of the Namibian land reform process, the Resettlement Programme and the Affirmative Action Loan Scheme (AALS). The main objective of this paper was to document to what extent currently implemented land reform is instrumental in achieving government objectives. The analysis highlighted the main problems, which should be considered during the planning and implementation of ongoing and future projects. For this purpose, rangeland condition and business performance indicators were collected on the farms of 68 land reform beneficiaries. Results showed that rangeland condition on the redistributed farms was on average worse than measured by Zimmermann (2009) in 2005 who assessed 12 farms under leasehold agreement and 13 freehold farms in the same region. Furthermore, we found that the majority of land reform projects are not profitable and depend on non-agricultural income. Unless urgent measures are taken to improve the business and agricultural performance of land reform beneficiaries, the Namibian land reform programme will at best merely provide a platform for citizens who subsidise a life dream with alternative income and will place beneficiaries without alternative income at risk of indebtedness and even deeper impoverishment.

Introduction

Land reform, if well planned and implemented, as in Asia after World War II, not only reduces former significant inequalities in asset distribution and historical injustice, but also significantly improves the well being of rural households and can have a positive long-term impact on investment in education and training of the younger generation (Deininger 2003, de Janvry et al. 2002, Kirk 1999). However, land reform has too often been guided by short-term political objectives or an exclusively “agrarian” focus on full-time farming, with little emphasis placed on productivity aspects, farm management issues, and entrepreneurial skills, and they have thus had a limited impact on poverty alleviation.

Both the preconditions and outcomes of land reform projects must be viewed in the context of Namibian Land Reform’s multiple objectives. Firstly, it addresses historical imbalances in the distribution of land. It also aims to contribute to the economic and political stability of the nation. And finally, land reform and in particular the resettlement programme is supposed to reduce income inequality and alleviate poverty (Kaukungua et al. 2004, Werner 2004, Legal Assistance Centre 2005, Republic of Namibia 2007, Werner & Kruger 2007). Resettled farmers should therefore become economically self-reliant, participate in the wider economy and create job opportunities (Kaukungua et al. 2004).

The Resettlement Programme is administered by the Ministry of Lands and Resettlement. It targets poor and landless Namibians by redistributing land on state-acquired commercial farms. The Namibian state has a preferential right to purchase agricultural land whenever any owner of such land intends to dispose of it (Republic of Namibia 1995a). Any Namibian citizen who has been socially, economically or educationally disadvantaged by past discriminatory laws can apply for an allotment of land acquired by the government for resettlement (e.g. Republic of Namibia 2002). Successful applicants then sign a 99-year lease agreement with the government.

The Affirmative Action Loan Scheme (AALS) is implemented by the Agricultural Bank of Namibia on behalf of the Ministry of Agriculture, Water and Forestry in collaboration with the Ministry of Finance and the Ministry of Lands and Resettlement. It assists emerging commercial farmers to acquire commercial farms through subsidised interest rates and loan guarantees by the state. This has two purposes: On the one hand it aims to empower emerging commercial farmers, and on the other it aims to reduce pressure on communal land (Republic of Namibia 1995b, Harring & Odendaal 2007).

The progress of land reform is often measured by the amount of land redistributed. On September 3, 2009 the Ministry of Lands and Resettlement published figures indicating that 795 farms (564 AALS and 261 for resettlement) with a total area of 4,358,000 ha (3,000,000 ha for AALS and 1,358,000 ha for resettlement) had been procured since independence in 1990. This is still far from the government target of 15,000,000 ha of white-owned farmland to change hands by 2020. Regardless of whether these figures can be interpreted as a success or a failure, they tell little about the success or failure of land reform at the farm level. Therefore, we assessed:

a) Whether land reform beneficiaries are able to make a living on their newly assigned land?
b) Whether they are able to maintain their resource base?

Kaukungua et al. (2004) conducted an initial assessment of land reform projects in Namibia and came to disappointing conclusions. In this study we analysed economic and ecological indicators describing both management preconditions and outcomes for the Omaheke region in eastern Namibia.

Research site and methods

The research was carried out in the Omaheke region in eastern Namibia. Mean annual rainfall in the area is between 300 mm and 400 mm and decreases from north to south. The main agricultural activity in the region is large stock farming.

Our sample was selected from lists of resettlement and AALS farmers made available by the Emerging Commercial Farmers Support Program (ECFSP). 15 AALS and 53 resettlement farmers took part in the study. Respondents in our study had gained access to redistributed land 9.5 years ago on average, although this ranged from a minimum of one year to a maximum of 23 years.

In order to generate economic indicators, all respondents were interviewed on the basis of an existing ECFSP monitoring questionnaire, which focussed on farmer expenses in 2008 as well as sources of farm income. Only a few farmers answered the questions based on proper record keeping, and the majority had to answer them from memory alone. The approach allowed us to differentiate between running and investment expenses for the calculation of more meaningful profit figures. The interview approach may have allowed farmers to overestimate their burdens and problems in order to stress their need for external support. There was no simple solution for this bias and it was kept in mind when interpreting any data. The scope of the problem was reduced by asking farmers for a catalogue of detailed financial subfigures instead of requesting summarised numbers. In addition, comparison of the given income figures with livestock sales and actual market prices did not reveal obvious mismatches.

For measurement of indicators of rangeland condition on each land reform farm a sample site was selected by asking farmers to choose a site that best represented the rangeland condition of the whole farm. Measurements of rangeland characteristics were taken at 100 sample points located within the sample site, which was approximately 250 m x 130 m, as described by Zimmermann (2009). Sample points were located by roughly uniform pacing along transects combined with a dart thrown over the shoulder in order to provide some degree of randomness. There were 25 dart points per transect and four transects per sample site. Various measurements were made at sample points as described by Zimmermann (2009), from which the following were calculated for each sample site:

1) The rangeland condition index, based on a combination of the perennial grass species composition and density.
2) The percentage of ground covered by canopies of encroacher bush species.

In this paper we summarise the results derived from the collected data using descriptive statistics. T-tests or Wilcoxon Rank Sum tests were applied to compare values between AALS and resettlement farmers. Correlation coefficients were also calculated.

Summary of ecological indicators

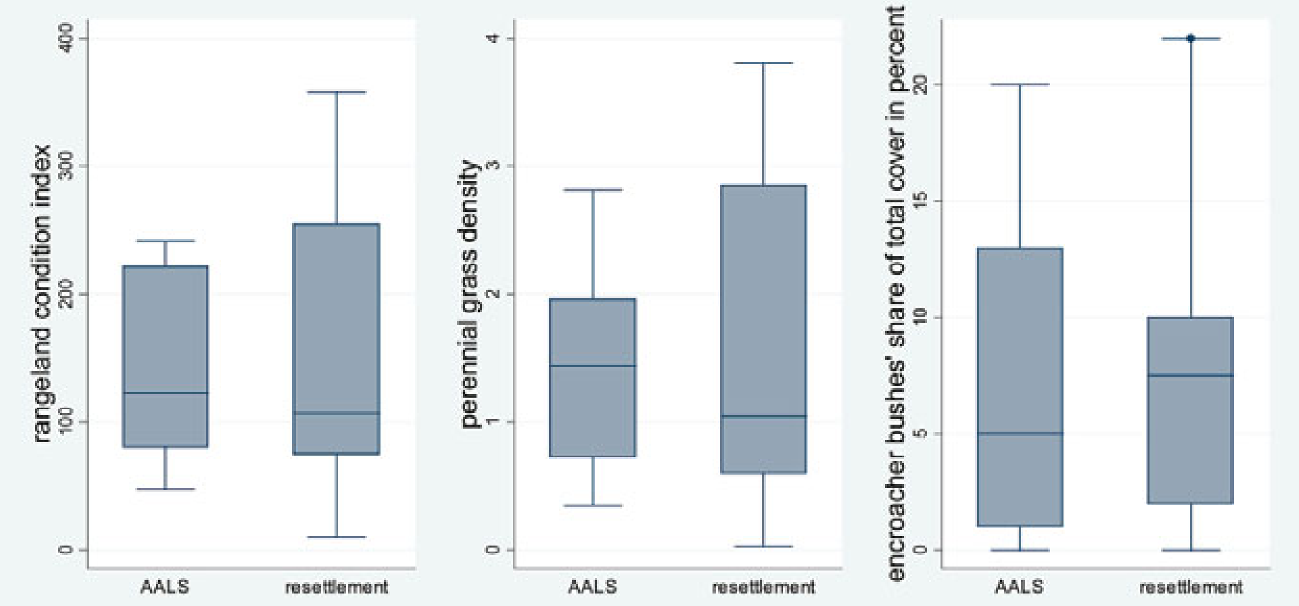
The assessment of rangeland quality showed that there were on average 1.52 individuals of perennial grasses of at least 5 cm basal diameter per square meter on the assessed farms, with no significant difference of the means between AALS and resettlement farms[1] (see Fig. 1). This mean of 1.52 grasses per m² is somewhat lower than that measured at 25 different sites in the Omaheke region during 2005 (Zimmermann 2009), comprising 12 sites on leasehold land with a mean of 1.92 grasses per m² and 13 sites on freehold land with 2.11 grasses per m².

The Rangeland Condition Index (Zimmermann 2009) is a more meaningful indicator and considers the economic and ecological value of different grass species, as well as grass density. The average score was 145.5 with a minimum of 10 and a maximum of 358 (see Fig. 1). There was no significant difference between the means of the two groups[2]. Fig. 2 depicts the distribution of the index. The mean score of 145.5 was considerably lower than the mean score of 253 (min 40; max 650) measured at 25 different leasehold and freehold sites in the Omaheke region during 2005 (Zimmermann 2009). Generally the AALS and resettlement farms had rangeland in poorer condition than that of other farms in the region.

Bush encroachment is one of the most common forms of rangeland degradation in the Savanna Biome of Namibia, but is not yet at an advanced stage in most of the research region. The mean percentage of ground covered by canopies of encroacher bush species was 7.4 percent, with a minimum of zero and a maximum of 22 percent, which was more than double the mean of 3.3 percent cover (min 0; max 14.2) measured at 25 different leasehold and freehold sites in the Omaheke region during 2005 (Zimmermann 2009). There were no significant differences between the means or variances of the two groups[3]. Bush encroachment appeared to be moderate in the study area, especially when compared with farms in the Otjozondjupa region where encroacher bush species cover exceeded 60 percent in places.

Summary of economic indicators

We added up all on-farm income during 2008 to obtain an estimate of farm profits. Very few investments are profitable in



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(The band in the box represents the median, the box represent 25th and 75th percentiles, and the wiskers the lowest datum still within 1.5 interquartile range of the lower quartile, and the highest datum still within 1.5 interquartile range of the upper quartile.)

Fig. 1: Boxplots of rangeland condition index, grass density, and cover of encroacher bushes—comparing AALS and resettlement farms.

the short run. We therefore only deducted running expenses from the gross income and did not consider any investment costs. The average annual gross margin of AALS farmers was €1.5 per ha and €7,549 per farm[4]. Resettlement farmers experienced average losses of €0.4 per ha and €230 per farm. One fifth of the AALS and half of the resettlement farmers were making losses. Our analysis shows far lower income estimates than the Resettlement Survey Report 2003/2004 of the Permanent Technical Team on Land Reform, which found that resettlement farmers generate an average farm income of approximately €880[5] per annum without indicating, however, the variance in their sample (Kaukungua et al. 2004). In order to interpret these numbers it is helpful to look at Conroy & Kwala's (2006) estimates of expected gross margins. They calculated that possible gross margins for a 1,000 ha mixed livestock farm in central Namibia were €2.5/ha for low capacity utilisation and poor management and €6.7/ha for high capacity utilisation and optimal management. The average farmer in our sample generated far less profit than even the worst case calculations of Conroy & Kwala (2006) predict.

We suspected that certain investment costs were hidden in our gross margin calculations. A commonly mentioned hypothesis is that many land reform beneficiaries are still investing in their herds. Not selling livestock can be viewed as a type of investment (Kaukungua et al. 2004). Therefore, we added the average annual herd growth since land redistribution to the gross margin (Fig. 2). The average annual gross margin of AALS farmers including the investment in livestock was €1.8 per ha and €9,660 per farm. Including livestock investments, resettlement farmers had an average profit of €0.8 per ha and €1,141 per farm in 2008. One quarter of the AALS and 45 percent of the resettlement farmers were still making losses even when livestock investments were included. This was the most optimistic profit calculation but still below the worst case scenario of Conroy & Kwala (2006).

We than turned to the assessment of the net farm income, which considered fixed costs and investments. This changed the figures in particular for AALS farmers who bought their land with subsidised loans. Many of them are in debt and have high annual instalment burdens. On average, AALS farmers had a debt of €127,709 with a maximum of €296,700. In comparison, resettlement farmers were on average only in debt by €899. In 2008, the average liability payment of AALS farmers was €10,072. Harring & Odendaal (2007) predict that the Agricultural Bank of Namibia will repossess most of the AALS farms since farmers will not be able to pay their instalments. Our 2008 net farm profit assessment, which includes fixed costs, 2008 investment costs, and 2008 liability payments provides evidence for this concern (see Fig. 2). Only one fifth of the AALS farmers made a profit, with a maximum of €7,675. The average loss was €6,762, with a maximum of €17,647. At least one third of the resettlement farmers were making a profit, with a maximum of €9,573. The average loss of this group was €1,726, with a maximum of €25,255. Therefore the average farmer in our sample performed much worse then Conroy & Kwala's (2006) net farm income prediction for a 1,000 ha mixed livestock farm in central Namibia under low capacity utilisation and poor management, which estimated a worst case loss of €419.

The high number of farmers making losses or very low profits can be carried by alternative income generating activities that most land reform beneficiaries are

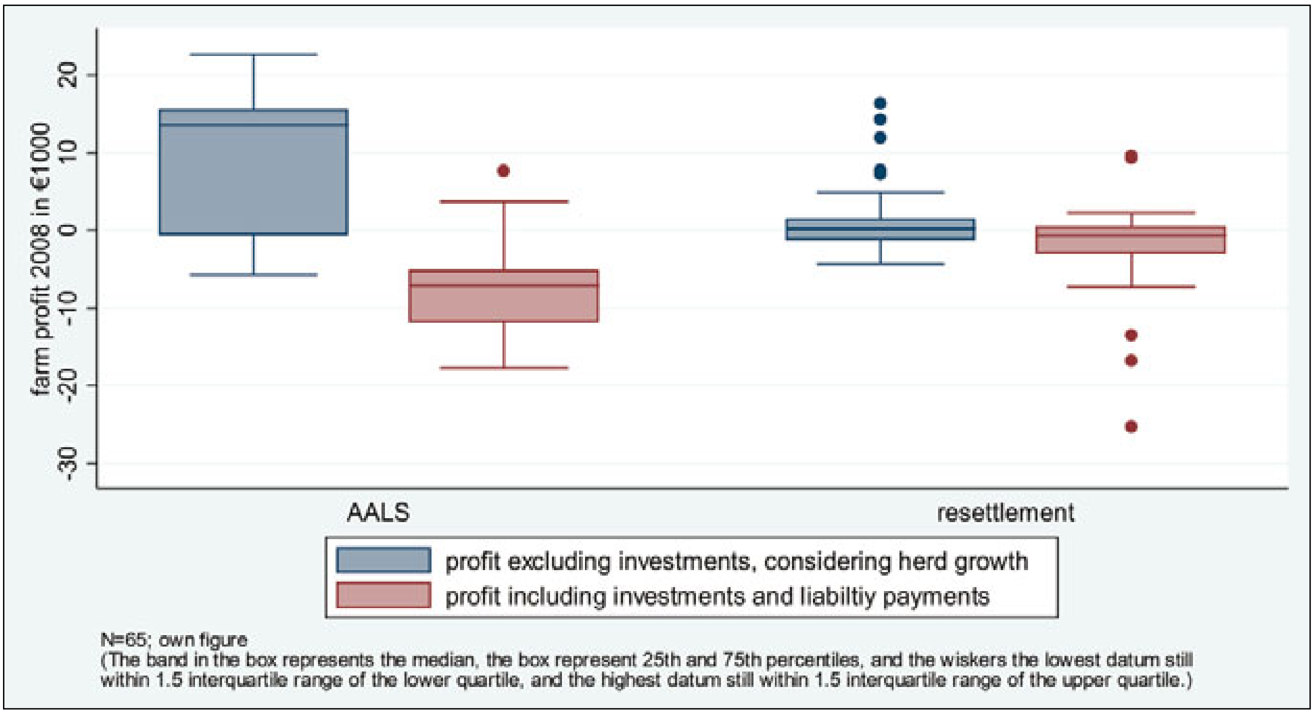

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Fig 2: Boxplots of farm profit in 2008 in €—comparing AALS and resettlement farms.

engaged in (Kaukungua et al. 2004). The majority of land reform beneficiaries in our sample had alternative sources of income (two thirds of the AALS farmers and three quarters of the resettlement farmers) with no significant difference between the two groups[6]. Two thirds of the farmers in our sample were employed—again with no variance between AALS and resettlement farmers[7]. The results are in line with the findings of the Resettlement Survey Report 2003/2004 of the Permanent Technical Team on Land Reform, which found that 71 percent of the beneficiaries viewed off-farm income as their main source of income (Kaukungua et al. 2004).

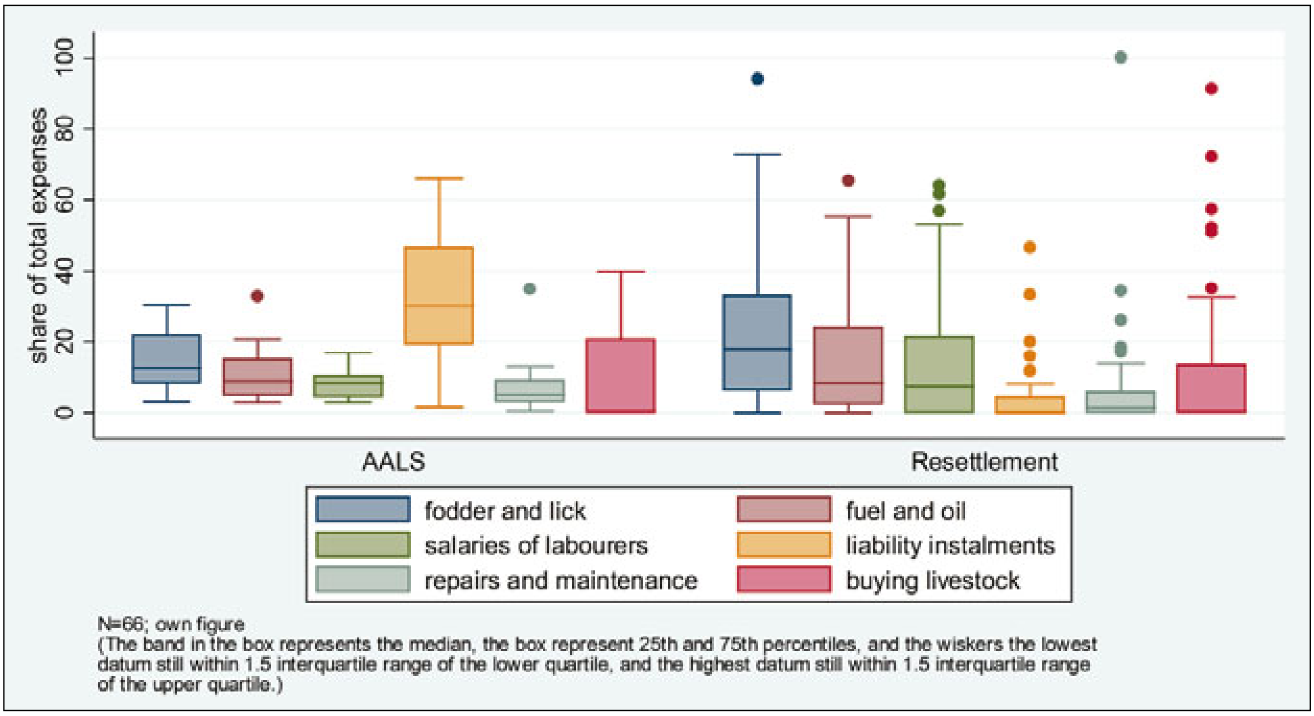
Discussion

Comparing the measured rangeland condition indicators with the ones Zimmermann (2009) assessed in the same region in 2005 on 25 farms reveals that the natural capital basis and therefore the production capacity of land reform farms is below the average of the farms assessed in his study. It is difficult to draw conclusions as to whether this is the result of the previous or new farmers' management as no historical rangeland condition data exist. However, it is likely that more farms in poor condition are made available to the resettlement programme since commercial farmers have greater incentive to hold on to farms with rangelands, which are in good condition.

Considering stocking rates as one key management parameter, our interviews reveal that two thirds of the respondents in 2008 had a stocking rate below the recommended carrying capacity of 12 ha/LSU. It should be borne in mind that rangeland condition is both a determinant and an effect of stocking rates. The low stocking rates could be a consequence of rangelands that can no longer support high stocking rates. It could also be a management decision aimed at improving the condition of the rangelands. In addition, there are factors other than stocking rate that influence rangeland condition, such as the timing of grazing and resting periods. More than one fifth of the resettlement farmers in our sample claimed not to practice rotational grazing. This may be one reason why rangeland condition is relatively poor even though stocking rates are low. The fact that AALS farmers use significantly more camps per herd for rotation[8] is influenced by the fact that they own larger farms with more camps available[9]. Despite this fact, no significant differences between the rangeland condition indicators on AALS and resettlement farms could be detected.

Our profit calculations clearly show that both AALS and resettlement farmers struggle to generate a significant or even positive gross margin and net farm profit (see also Kaukungua et al. 2004). Concerning income, Kaukungua et al. (2004) argue that not utilising the land to its full capacity is one main reason for the low profits of resettlement farmers. The relatively low stocking rates of most respondents could be interpreted as a sign that farmers are still in a herd building phase (see also Werner & Kruger 2007). However, some farmers are selling their herds in order to cover costs or to pay their credit instalments. One quarter of both the AALS and resettlement farmers in our sample had lower livestock numbers in 2008 than at the time of land redistribution. The design of land reform projects should therefore make provisions to support beneficiaries in making efficient and sustainable use of the natural resources' capacity.

We also closely examined costs. Fig. 3 depicts the most important specific expenses as a percentage of the total expenses. As



N=66; own figure
(The band in the box represents the median, the box represent 25th and 75th percentiles, and the wiskers the lowest datum still within 1.5 interquartile range of the lower quartile, and the highest datum still within 1.5 interquartile range of the upper quartile.)

Fig. 3: Boxplots of farm expenses in 2008 as a percentage of total expenses—comparing AALS and resettlement farmers.

mentioned before, AALS farmers spend a large proportion of their expenses on liability instalments. High land prices are the main reason for the high levels of debt despite the fact that large amounts of government subsidies are paid into the scheme. The most important expenses for resettlement farmers are fodder, licks, fuel, oil, and labourer salaries.

In terms of both economic and ecological indicators our results point out the strong need to develop the human capacity of land reform beneficiaries. Kruger (2004) highlights the extreme importance of farming knowledge and skills for successful land redistribution (see also Harring & Odendaal 2007). Our data show that AALS farmers that participate in agricultural training have a higher perennial grass density on their farms[10]. One quarter of the resettlement farmers in our sample and 7 percent of the AALS farmers claim to have had no farming experience when first gaining access to the land. Only 18 percent of the respondents had experience in a commercial farming environment with no significant difference between the groups. After land redistribution, four fifths of the resettlement farmers did not receive any agricultural training while 73 percent of AALS farmers did participate in such training[11]. One reason why it is difficult to provide land reform beneficiaries with agricultural training is the fact that the majority of them only farms part time and are busy with other livelihood activities the rest of the time.

Kruger (2004) conducted a study to determine the training demands based on a self-assessment by the farmers. Mentioned needs ranged from technical skills such as welding and mechanical maintenance to improved knowledge about livestock breeding and animal health as well as financial management. In view of these diverse demands and the fact that many beneficiaries are not permanently on their farms, training support needs to be flexible in terms of content, the manner in which it will be presented and the human resources to be mobilised for this purpose. Certain aspects lend themselves to mentoring by established farmers. These include improved resource management such as effective rotational grazing as well as breeding practices based on practical experience. In addition to this, farmers' days and exposure visits are very useful in sharing problems and knowledge as well as building relationships based on confidence between established farmers and land reform beneficiaries.

Our results indicate that short and long-term business planning has to be improved in order to enhance the economic performance of beneficiaries. Farming in a setting of individual land units has to be more strongly perceived as a business enterprise. Each expense has to be critically assessed according to cost-benefit considerations and marketing should be applied strategically as instruments for pasture and business management. A stronger focus on business planning is therefore important.

In the context of the Resettlement Programme, poor management can not be associated solely with insufficient training. The delay in issuing leasehold agreements, as criticised by Werner (2004), reduces tenure security. Exactly half of the interviewed resettlement farmers have not received any document proving their entitlement to farm on the land. The other half has received leasehold agreements from the ministry but the land has only been officially handed over to a minority of them. Also, Kruger (2004) highlighted that the majority of respondents in his study could not provide valid proof of their land rights. As a result, the lack of a sense of ownership has a negative impact on incentives for sustainable farm management.

Kaukungua et al. (2004) mention the government's financial and human capacity constraints as the main reasons for this problem. Before a farm is handed over to a farmer, the farm infrastructure has to be repaired by the government.

Another institutional aspect, which requires attention is the facilitation of cooperation amongst land reform beneficiaries and other farmers. For example, resettlement farmers who use relatively small farm units can accomplish economies of scale by jointly managing farm infrastructure. Two specific challenges exist in the context of resettlement farms. On the one hand, a group of farmers occupying parcels of a larger farm are forced to jointly manage farm infrastructure, which has been originally designed for central management (Werner & Kruger 2007). On the other hand, farmers with heterogeneous backgrounds are arbitrarily resettled on one farm (Kaukungua et al. 2004). Kruger (2004) stresses that well functioning community-based structures are crucial for the success of resettlement projects. Such structures need to be established from the beginning. Our results show that both resettlement and AALS farmers cooperate in maintaining infrastructure, exchanging knowledge or sharing physical capital[12]. However, we frequently heard complaints about fellow farmers not contributing to maintenance work.

Extending cooperation to joint livestock and rangeland management has more benefits than simply the potential to accomplish economies of scale. Such a management system would be better adapted to Namibian ecosystems, which have been used traditionally on much larger scales at overall higher production/ha (Fynn 2009). Cooperative rangeland management on a larger scale by groups of neighbouring farmers, who still own their livestock privately, could contribute to increased productivity of farms, reduced risks and the prevention of ecological degradation (McAllister et al. 2006).

Conclusion

The results from the rangeland condition assessment show that land reform beneficiaries have to farm with rather moderate pasture capacity. Whether this is the result of the management of current or previous users can not be determined as historical data are lacking. Our study shows, however, that the preconditions for land reform beneficiaries are worse compared to commercial farms in the region. At the same time our results indicate that special attention must be paid to proper rangeland management practices on these farms as many are in an ecologically vulnerable state.

The economic analyses clearly show that land reform beneficiaries struggle to generate income from farming on redistributed land. It can be assumed that there are more profitable investment opportunities available in Namibia. Kaukungua et al. (2004) conclude that the poverty reduction impact of land reform remains low if people with already well established income sources and income levels are resettled. Our profit calculations raise the question of whether resettling people without established incomes would have a more positive impact on achieving these goals. Unless urgent measures are taken to improve the business and agricultural performance of land reform beneficiaries, the land reform programme will merely provide a platform for citizens who subsidise their life dream with alternative income and put beneficiaries without alternative income at risk of debt and even deeper impoverishment. Only 43 percent of the AALS farmers in our sample have the perception that their economic situation improved after purchasing the land. Slightly more than half of the resettlement farmers mentioned an improvement after resettlement.

Our research confirms the conclusion of Werner & Kruger (2007) who argue that recreating sustainable livelihoods on redistributed land is a much more difficult challenge than simply the acquisition of land. Kaukungua et al. (2004) highlight the need to distinguish between farmers who are in need of land and those who are able to make efficient use of it for their own benefit as well as that of society. Everybody loses out if land reform beneficiaries are recording high financial losses, are becoming increasingly frustrated and contributing to high social opportunity costs. It is important to assess, which pre- and post-resettlement assistance in terms of training and investment support would be necessary to enable beneficiaries to farm successfully. For improved monitoring of land reform projects, standardised rangeland condition and farm business assessments of each farm prior to land redistribution are advisable.

Acknowledgements
The authors' general acknowledgements to the organisations, which supported this work are provided in Volume 1. The study was conducted in cooperation with the Emerging Commercial Farmer Support Programme (ECFSP), the GTZ Namibia, the Polytechnic of Namibia, and the Ministry of Agriculture, Water, and Forestry (MAWF).

Endnotes

[1] Two-sample (AALS vs. resettlement) t-test with unequal variances for variable "mean density of perennial grasses": $t = -0.3115$, $Pr(|T| > |t|) = 0.7571$, $N = 68$.

[2] Two-sample (AALS vs. resettlement) t-test with unequal variances for variable "rangeland condition index": $t = -0.5241$, $Pr(|T| > |t|) = 0.6032$, $N = 41$.

[3] Two-sample (AALS vs. resettlement) t-test with unequal variances for variable "relative encroacher bush cover": $t = -0.2744$, $Pr(|T| > |t|) = 0.7859$. Test on the equality of variances between two samples (AALS vs. resettlement) according to Brown and Forsythe (1974): $f = 1.3063$, $2{*}P(F < f) = 0.5422$, $N = 41$.

[4] All calculations for 2008 on the basis of the exchange rate € 1 = 0.086 N$.

[5] All calculations for 2003 on the basis of the exchange rate € 1 = 0.118 N$.

[6] Two-sample (AALS vs. resettlement) Wilcoxon rank-sum (Mann-Whitney) test for variable "having alternative sources of income": $z = -0.877$, Prob $> |z| = 0.3805$, $N = 69$.

[7] Two-sample (AALS vs. resettlement) Wilcoxon rank-sum (Mann-Whitney) test for variable "employment as sources of income": $z = -0.476$, Prob $> |z| = 0.634$, $N = 69$.

[8] Two-sample (AALS vs. resettlement) Wilcoxon rank-sum (Mann-Whitney) test for variable "camps per herd for rotation": $z = 2.921$, Prob $> |z| = 0.0035$, $N = 65$.

[9] Spearman's rank correlation coefficient for variables "camps per herd for rotation" and "size of farm": Spearman's rho = 0.3805, Prob $> |t| = 0.0019$, $N = 64$.

[10] Pairwise correlation between the variables "perennial grass density" and "farm trainings in weeks" for AALS farmers: coefficient = 0.5627, sig. level = 0.0362, $N = 14$.

[11] Two-sample (AALS vs. resettlement) Wilcoxon rank-sum (Mann-Whitney) test for variable "participated in farming training": $z = 3.866$, Prob $> |z| = 0.0001$, $N = 69$.

[12] Two-sample (AALS vs. resettlement) Wilcoxon rank-sum (Mann-Whitney) test for variable "diversity of fields of cooperation": $z = -0.027$, Prob $> |z| = 0.9781$, $N = 62$.

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Evaluation of the soil degradation state along fence-line contrasts

Alexander Gröngröft*, Denise Mager, Tanya Medinski, Anthony Mills, Andreas Petersen & Annette Eschenbach

Summary: Five pairs of Observatories with contrasting landuse types and/or landuse intensities, located in the Woodland Savanna, Thornbush Savanna, Nama Karoo, and Succulent Karoo biomes were investigated to examine the influence of landuse on soil properties. To eliminate local characteristics, the comparison was conducted using the predominant soil types in each pair of Observatories. For the Woodland Savanna in the Kavango Woodlands, topsoil properties were statistically different in relation to varying fire frequency (increased water soluble ions, C/N-ratio, exchangeable potassium with higher fire frequency). For all other pairs of Observatories, contrasting grazing intensities resulted in some significant differences in topsoil properties. In general, increased grazing led to higher pH-values and water soluble sodium concentrations in all regions. It is concluded that these differences are related to shifts in topsoil hydrology as a consequence of lower vegetation coverage. The use of soil pH and water soluble cation concentration is predicted to be important indicators for future rangeland monitoring.

Introduction

Based on the hypothesis that both sides of a fence-line initially had identical soil and ecological conditions, the study of systems adjacent to fence-lines can be approached by investigating the type and intensity of landuse in the study area. This can be done through two approaches: a) studying of systems with controlled landuse impacts in an experimental design on one or both sides of the fence; and b) an investigation of systems with obvious fence-line contrasts, where the difference in landuse practice is determined by local landusers. There are pros and cons to each approach. The advantage of the first approach is that the influence of landuse can be quantified empirically; however, the time needed to achieve ecological equilibrium may be in the dimension of decades. Where clear fence-line contrasts are observed (i.e. differing vegetation composition or structure), it is often difficult to obtain reliable information on the past and present landuse management for both sides of the fence. Nevertheless, this 'incidental approach' (Zimmermann 2009) is time-efficient and the ecological effects of different management strategies can often be elaborated with sufficient precision even when applied to different systems. This approach has been used to study plant diversity and communities in rangelands (Todd & Hoffman 1999, 2009), pollination of bees (Mayer 2005), soil nutrient status (Allsopp 1999), soil organic matter (Mills & Fey 2004a) and rangeland conditions (Zimmermann 2009).

Heavy grazing may result in changes in plant biodiversity, and in soil physical and chemical properties (Milchunas & Lauenroth 1993). For example, intensive grazing may lead to shifts from perennial plants to annuals, an increase of unpalatable or even poisonous plants (Todd & Hoffman 1999), or a shift in the population of small mammals (Hoffmann & Zeller 2005). Among the soil properties likely to be affected by varying grazing intensity are: total and available carbon, available nitrogen and phosphorus, macro (Ca, K, Mg, Na) and trace elements (Fe, B, Cu, etc.), pH, electrical conductivity, soil structure, bulk density and aggregate stability (e.g. Ayuba 2001).

Furthermore, grazing animals may affect soil infiltration by breaking soil


Fig. 1: Landscape with obvious fence-line contrast (BIOTA Observatories S39/S40, higher grazing intensity on right side).

Table 1: Landuse characteristics of pairs of Observatories on both sides of a fence

Landuse	Biome	Oshana Region	Woodland Savanna	Thornbush Savanna	Nama Karoo	Succulent Karoo
Comparably low (L)	No	S42 Ogongo 1	S01 Mile 46	S39 Narais	S10 Gellap Ost	S25 Remhoogte
	Type	Agricultural research station: rotational grazing system with cattle, goats and sheep	Agricultural research station: breeding of cattle	Commercial farming with rotational grazing	Agricultural research station: breeding of sheep (esp. Karakul), rotational grazing	Commercial farming with rotational grazing
	Intensity	Stocking rate not recorded, but low	Grazing not recorded, but low. Rare bush fires	Grazing of large stock, camp for 10 years unused, average stocking rate below farm mean (1 LSU/17–20 ha)	Stocked at lower rates (1 SSU/18 ha) than recommended by MAWF (1 SSU/6 ha)	Moderately grazed: stocking rate about 1 SSU/ 12 ha
Comparably high (H)	No	S43 Omano	S02 Mutompo	S40 Duruchaus	S11 Nabaos	S24 Paulshoek
	Type	Communal agro-silvi-pastoralism: proportions of acres (esp. pearl millet), protected and open access grazing areas (large & small stock)	Communal agro-silvi-pastoralism: first acres since 2004, predominantly open access grazing, illegal logging	Commercial farming with rotational grazing	Communal rangeland: open access grazing areas, grazing mainly by goats and donkeys	Communal rangeland: open access grazing with herder, mainly goats and sheep, also donkeys
	Intensity	Stocking rate not recorded, but high	Grazing not recorded, but low. Regular bush fires	Grazing of large & small stock, average stocking rate 1 LSU/10–12 ha	About 1 SSU/5 ha (mean acc. to veterinarian office, 1995–2002, on Observatory most likely higher)	Mean stocking rate (30 years): 1 SSU/~6 ha, in good years is higher

no = number and name of Observatory, SSU = small stock units, LSU = large stock units, MAWF = Namibian Ministry of Agriculture, Water and Forestry

crusts as well as compacting soils. Breaking of crusts may promote infiltration and aeration, while compaction may reduce soil pore size and infiltration (Toit 2009). In addition, soil infiltration is correlated to other soil properties, such as pH, electrical conductivity, soil nutrient content (e.g. Ca and Na), and aggregate stability. Changes in the above soil properties may change infiltration. For example, overgrazing could result in lower Ca and organic matter returns to soil. This would increase soil dispersion, and as a result reduce infiltration and ultimately reduce soil quality (Mills & Fey 2003).

Recent research has yielded new insights into the grazing effect on soil nutrients. For example, studies in a woodland savanna in Nigeria have shown considerable changes in soil properties in grazed areas (Ayuba 2001). Intensive grazing resulted in a significant decline in total nitrogen, cation exchange capacity, exchangeable Ca and Mg, and in a significant enrichment in organic C and available P. In another study in the Negev, Stavi et al. (2008) found no effect of grazing on mean soil properties but rather an increase in their spatial heterogeneity. Whether the effect of grazing on ecosystem functioning may be reversed, or whether it potentially drives the system beyond its resilience, is not clear yet. In each particular case it is likely to depend on veld conditions and grazing pressure.

It remains to be determined whether soil properties in landscapes with fence-line contrasts in south western Africa are sensitive to different landuse management. This knowledge is important because soil properties form the abiotic backbone of plant growth, e.g. nutrient reserves, water holding capacity or temperature buffering potential. The study of a broad range of soil properties in landscapes with fence-line contrasts may thus be used for monitoring of landuse impacts (Gröngröft et al. 2006) and the development of comprehensive restoration and management strategies for preventing land degradation.

Material and methods

Site characteristics

As discussed in Volume 1, Part I, existing fence-line contrasts was one criterion for the selection of the BIOTA Observatories. The study of fence-line contrasts was carried out in five biomes: Oshana region (special part of the Woodland Savanna), Woodland Savanna of the Ka-

Table 2: Comparison of landscape structure and soil communities according to the Renkonen similarity index

	Oshana-Region	Woodland Savanna	Thornbush Savanna	Nama Karoo	Succulent Karoo
similarity of habitat distribution	0.85	0.76	0.88	0.75	0.74
similarity of soil type distribution	0.32	0.96	0.80	0.50	0.64

vango, Thornbush Savanna, Nama Karoo (all Namibia), and Succulent Karoo (South Africa). The five pairs of Observatories are described in detail in (Volume 1, Part I). Table 1 lists the relevant site characteristics. For each pair, differences in landuse intensity at both sides of the fence could be addressed. For four pairs, the difference resulted from grazing pressure, and for the Woodland Savanna site, the fire frequency on both sides of the fence differs.

Sampling and analytical procedures

As described in Volume 1, Part I, soils on the BIOTA Observatories were investigated with a standardised procedure. The general characteristics of the methodological approach were: site selection by a stratified random procedure, soil description and classification acc. to FAO (1998, 2006a, b), profiles at 4 m south of ha-centre points, sampling of all horizons, laboratory analyses of numerous soil variables (details are given in Jürgens et al., submitted, and Petersen 2008).

Composite soil surface (2 cm depth) samples (comprising 12 subsamples) were also collected on the border of 10 x 10 m^2 plots situated within the centres of the 10,000 m^2 blocks using a grouting trowel. An infiltrability index (hereafter referred to as infiltrability) was determined on these samples using a rapid laboratory syringe method (Mills & Fey 2004b). This method involves leaching of an agitated 1:5 soil-water suspension through a packed soil column. The results correlate strongly with a rainfall simulation method, although infiltrability through a syringe is approximately 10 times greater than rainfall simulation and is therefore not directly comparable with infiltration in the field. It, however, can provide an index of the inherent crusting tendency of the soil, which is a function of a number of soil properties, such as soil particle size distribution, electrical conductivity, pH, and clay mineralogy (Mills et al. 2006).

Statistical tests

The pairs of fence-line Observatories were compared with respect to landscape structure. Sample means from both sites of a fence were compared using the t-test for independent variables. Statistical analyses were carried out using SPSS 16.0 and Statistica 9 for Windows. To avoid the influence of differing soil composition in both samples compared, only those soil profiles were included in the t-tests, which are dominant on both areas. These were Episalic Solonetz for the Oshana region, Ferralic Arenosol (Dystric) for the Woodland Savanna, Hypercalcic Calcisol for the Thornbush Savanna, Regosols for the Nama Karoo, and Leptosols for the Succulent Karoo.

In order to evaluate the similarity between these pairs of Observatories, the Renkonen "percentage similarity" index (1938, cited in Wolda 1981) for habitat and soil type was calculated as follows:

$$S = \sum_{i=1}^{n} \min(p_{i1}; p_{i2})$$

where S as the similarity index, p_{i1} as the proportion of unit i of area 1, p_{i2} proportion of unit i of area 2, and n as the total number of units. The application of the test to the similarity of soil type distribution was based on the soil units acc. to WRB (World Reference Base for Soil Resources; FAO 2006a) with two additional qualifiers, where the prefix qualifiers were regarded as dominant to the suffix qualifiers.

Results

Site comparison

The comparison between landscape structure and soil type for the different pairs of Observatories is shown in Table 2. According to the Renkonen similarity index, habitat distribution and soil type distribution of Thornbush Savanna are similar (88 and 80% respectively). Pairs from the Nama and Succulent Karoo have to be highlighted as their habitats have the lowest S values, with only 50 to 64% of the soil profiles having an overlap in classification. The low similarity of soil type distribution for the Oshana region is caused by the strong differentiation of saline soils in the WRB (FAO 2006a).

Differences in soil properties

In general, differences in soil properties are observed for all paired Observatories. Nevertheless, these differences are of varying magnitude (Table 3). These differences can be summarised as follows (L indicating lower, H for higher landuse intensity):

- **Oshana region** (analysed data incomplete): significant elevated topsoil pH values were observed on the fence side with higher landuse intensity ($p < 0.05$; median value in H_2O L 6.0 and H 6.6, see Fig. 2). Additionally, the topsoil organic carbon (Fig. 3) and total nitrogen were lower on that side.
- For the **Woodland Savanna**, the comparison resulted in some differences in the total elemental composition of the topsoils (Na and K lower on side H). Although the sandy substrate seems to be very homogenous, these differences indicate some minor trends in the mineralogical composition. On the communal area (H), the concentrations of soluble ions (e.g. Na, Cl, SO_4) and electrical conductivity were higher. Additionally, the exchangeable K content of the topsoil was significantly higher on the communal area (median values L 0.82; H 2.35 $mmol_c\ kg^{-1}$). Soil acidity and C/N-ratio were also higher in the communal area compared to the

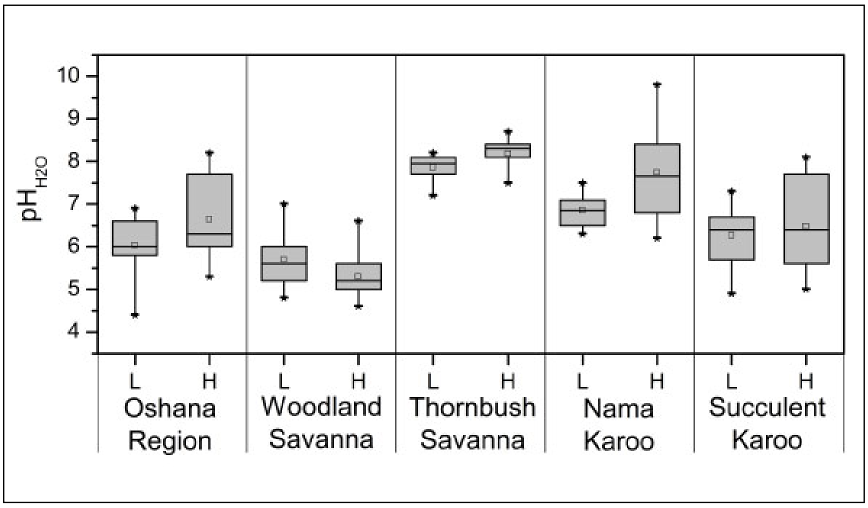

Fig. 2: Topsoil pH distribution for five pairs of Observatories (L: low, H: high landuse intensity).

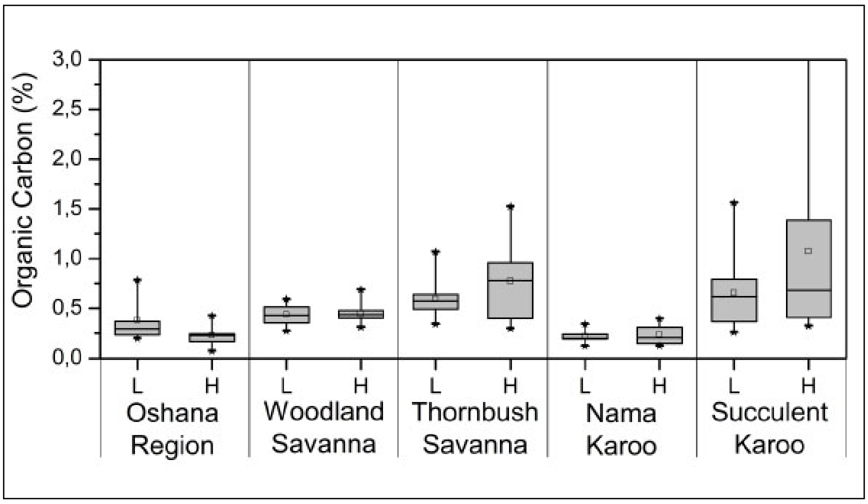

Fig. 3: Topsoil organic carbon distribution for five pairs of Observatories (L: low, H: high landuse intensity).

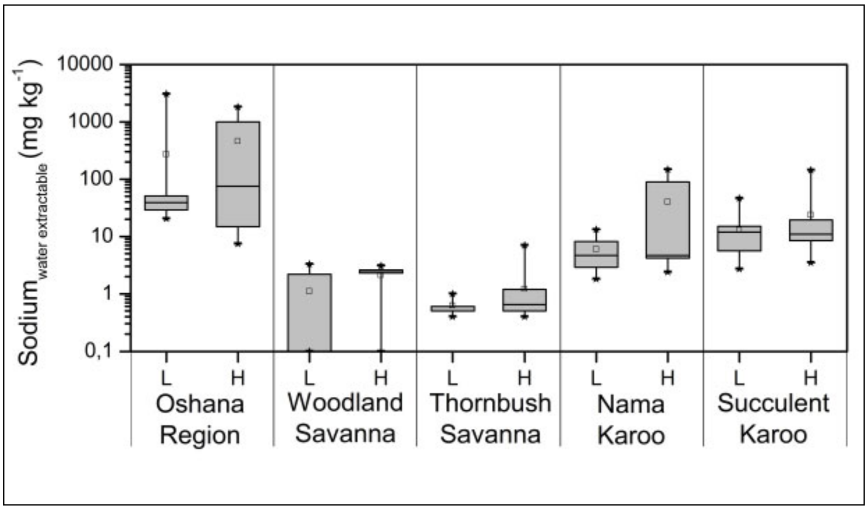

Fig. 4: Topsoil water extractable sodium distribution for five pairs of Observatories (L: low, H: high landuse intensity).

research farm. An interesting finding is that K availability increased with increasing landuse intensity, while the total K significantly decreased.

- For the pair of Observatories in the **Thornbush Savanna** a significant elevated level of topsoil alkalinity, inorganic carbon, total and exchangeable Ca, and CEC (cation exchange capacity) were observed with higher grazing pressure. This shift in topsoil conditions was accompanied by a difference in cations availability. While the content of total and exchangeable Ca and the CEC increased significantly, the exchangeable K, Mg and Na content decreased. In addition, P availability decreased and organic carbon content increased (median L 0.59; H 0.77%) however, these differences were not significant. The amount of soluble nitrate decreased, whereas total N as well as the C/N-ratio did not change significantly with increasing grazing intensity.
- **Nama Karoo**: due to the history of overgrazing in the communal area, a significant increase in topsoil pH (median values pH in H_2O L 6.9; H 7.6; Fig. 2), soluble and exchangeable Na (Fig. 4) and a reduction in Mg availability were found.
- The topsoils of the two Observatories in the **Succulent Karoo** are characterised by differences in the soluble salt concentration. Here, the stronger grazing resulted in significant increases of electrical conductivity (median L 57; H 109 $\mu S\ cm^{-1}$), corresponding to more water soluble Ca, Mg and sums of cations and anions. Also exchangeable Mg increased.

No significant differences between paired Observatories were found for infiltrability.

Discussion

Landuse impact on soil properties

Differences in landuse between paired Observatories were most prominent in the Kavango woodlands, probably being related to regular bush fires as opposed to grazing intensity. For example, the increase in C/N-ratio in the topsoil (Fig. 5)

Table 3: Results of the comparisons of sample means of site specific soil properties of biomes with a high and low landuse intensity (unpaired t-test, *p* given, profiles with identical typology)

Biom variable	Oshana Region	Woodland Savanna	Thornbush Savanna	Nama Karoo	Succulent Karoo
Number of profiles (L/H)	**13/11**	**13/15**	**14/14**	**10/10**	**19/15**
pH (in H_2O and in $CaCl_2$)	**< 0.05**	**< 0.1***	**< 0.05****	**< 0.1**	
Electric. Cond. (1:5 extract)					**< 0.05**
Water soluble anions		**Cl < 0.1** **SO_4 < 0.05**	**NO_3 < 0.1**		
Water soluble cations		**Na < 0.05**		**Mg < 0.05** **Na < 0.1**	**Ca < 0.05** **Mg < 0.1**
Inorganic Carbon			**< 0.05**		
Organic Carbon	**< 0.05**				
Total Nitrogen	**< 0.05**				
C/N-ratio	**< 0.05**	**< 0.05**			
Plant available K		**< 0.1**			
Plant available P					
Exchangeable K		**< 0.01**	**< 0.1**		
Exchangeable Na			**< 0.1**	**< 0.1**	
Exchangeable Mg			**< 0.05**	**< 0.01***	**< 0.1**
Exchangeable Ca			**< 0.01**		
Total exchangeable cations			**< 0.05**		
Total micronutrient concentration (B, Cu, Fe, Mo, Mn, Zn)			**Zn <0.05**	**Mn, Zn < 0.1**	**Mn < 0.1** **Zn < 0.05**
Total macroelement concentration		**Na < 0.1** **K < 0.05**	**Na < 0.01** **Ca < 0.05** **Mg < 0.01**	**Fe < 0.05**	
Infiltrability					

blue color indicates a significant decrease in soil properties content/values with increase in landuse intensity; **red color** indicates a significant increase with increase in landuse intensity; gray shade indicates that no data are available.

compared to background levels is a typical indicator of an increase in charcoal as a result of incomplete burning of the biomass. This effect is especially prominent in soils with low organic matter content in the topsoil (dystric Arenosols) where more samples were affected by this influence in the communal area. Additionally, the increase in pH as well as K availability on the communal area (Fig. 6) in relation to the better fire-protected area and caused by ash accumulation after accidental fires has also been observed in other regions (Snyman 2003).

Contradictory to the findings of some other studies (Bird et al. 2000, Mills & Fey 2004a), the regular bush-fires did not affect the amount of topsoil organic carbon, and although total nitrogen content was reduced, it was not statistically significant. The difference in the topsoil organic matter content may not be significant because the reference area was also affected by rare fires.

The general problem with studying grazing effects by the 'incidental approach' is the uncertainty regarding the similarity of preconditions on both sides of the fence. For instance, the location in the Nama Karoo is most likely the result of a first rough appraisal of the landscape by primary colonists, who decided to leave the lower productive area to the North—now the communal area—out of production. Currently, both areas differ not only in different grazing intensity and vegetation distribution, but also the communal area has substantially more soil erosion than the governmental research farm. Differences are not only due to the grazing impact but also relate to the geomorphology of the area (catchment of runoff and downward slope). Although the comparisons are based on profiles with identical soil types, there may be natural trends in the landscape. Herpel (2008), who did a detailed small-scale study of topsoil variability, attributed the grazing influence to a stronger pronunciation of shrub - open soil differentiation, detected for the topsoil organic carbon, total nitrogen and electrical conductivity values. Herpel's findings indicate, that irrespectively of observed differences,

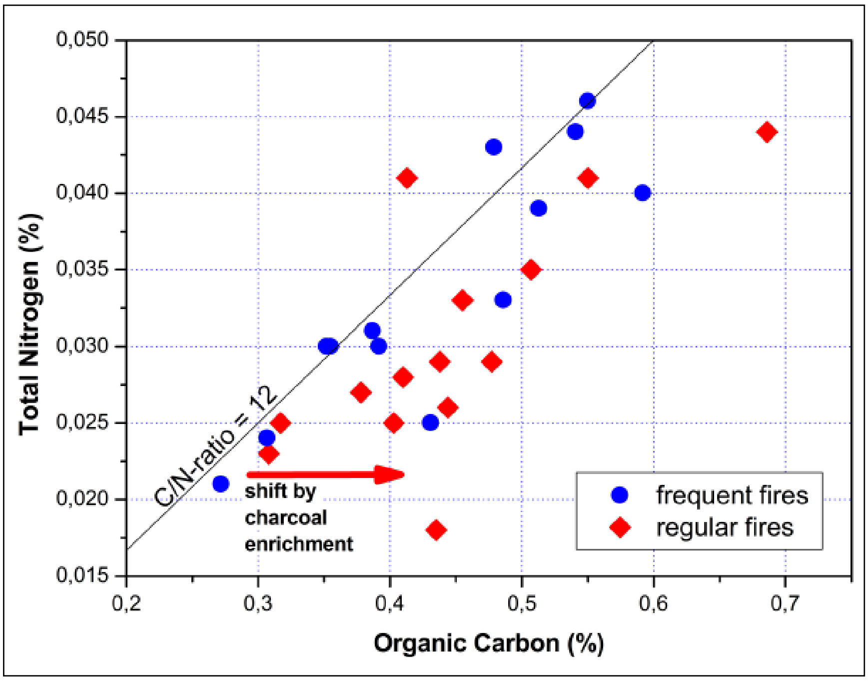

Fig. 5: Correlation between topsoil nitrogen and organic carbon contents at sites with different fire histories (Woodland Savanna).

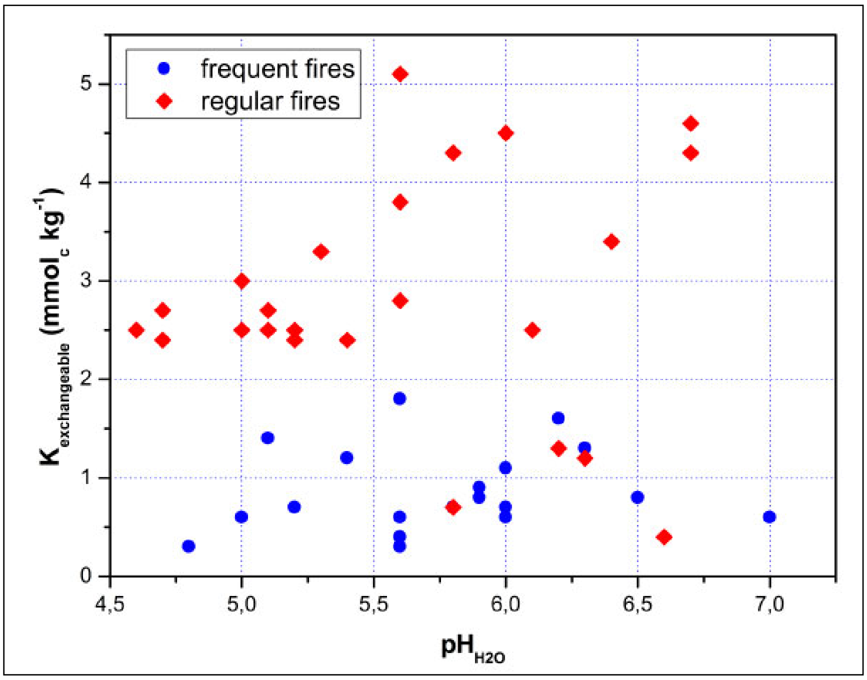

Fig. 6: Correlation between topsoil potassium and pH at sites with different fire histories (Woodland Savanna).

there may also be other significant contrasts related to the small-scale spatial heterogeneity of the area (see Stavi et al. 2008).

The medium-scale variability within the areas is another factor in producing significant differences with a manageable effort. The pedodiversity analysis resulted in highest diversity indices for the Succulent Karoo sites. For these sites, Petersen (2008) found 11 and 16 different soil units for the low and high grazing intensity area, respectively. This diversity is combined with a strong variability in topsoil properties such as pH, electrical conductivity and organic carbon. The detection of significant fence-line contrasts in landscapes with this extraordinary variability needs an adapted sampling design, in any case a larger sample size as presented here. Therefore, topsoil differences between both sides of the fence might exist, which could not been detected yet.

The results on the role of grazing on dryland soil properties seem to be related to the shift in topsoil hydrology. With the reduction of vegetation cover and the conversion to more annual plants, more evaporation is promoted, resulting in an increased accumulation of salts in the soil. Sodium is generally accumulated in overgrazed topsoil and has a strong influence on the pH-value. The accumulation of Na may lead to a reduction in Mg, but this shift may also be related to plant composition and nutrient demands.

It cannot be concluded from the presented data alone whether soil properties have exceeded their resilience. The reduction in vegetation cover through overgrazing may increase soil erosion, an effect, which could be observed at both the Nama Karoo and Succulent Karoo sites. Prevailing sheet erosion may influence topsoil chemical properties, however, whether rill or gully erosion is only restricted to a small surface area or spreads wider, is not evident from this study. For the Oshana and the Thornbush Savanna area, the on-site observations do not reveal a non-reversible change in soil conditions.

The use of soil properties as robust indicators of land degradation often lacks sufficient data (Klintenberg & Seely 2004). Nevertheless, soil properties are considered useful indicators of environmental degradation, e.g. the soil nutrient level and organic matter content (soil fertility surveys), the extent and severity of erosion, the accumulation of pesticides and residues (measured by microbial activity) and salinity (MET 2001). This study shows the importance of using pH and water soluble cation concentration as useful indicators for future rangeland monitoring. For topsoil, the effort of sampling and analyses is comparably low and thus the production of large datasets is possible. Keeping the strong soil heterogeneity in mind, inexpensive and standardised indicators with sufficiently high sensitivity to the tested degradation-related processes are needed. Both arguments favour the application of these indicators. By comparing different management strategies within one area, benchmarks sites can be used to obtain a background level as indicator values and thus classify the status of soils for large areas.

In summary, whether landuse intensity has caused increased soil erosion and land degradation is still under debate. A decrease in vegetation cover, however, could ultimately lead to an increase in soil erosion (Lal 2001). Ultimately, increased soil erosion would also be related to a decrease in soil stability and fertility. Different studies have aimed at better understanding of ecosystem changes at different grazing disturbances (Ayuba 2001, Stavi et al. 2008), however, drylands have been notable for their resilience, often recovering rapidly from disturbances. This implies that ecological changes have occurred independent of soil water and nutrient availability. Further studies are still needed to better understand dryland surface processes that could lead to the development of management plans to improve the sustainability of pastoralism in Southern Africa.

Acknowledgements

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Impact of landuse at landscape scale, using fenceline contrasts and a best-practice case study

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Summary: Spatial heterogeneity is an important part of biodiversity that used to support high animal numbers at a regional scale before fencing subdivided the land for sedentary farming and led to reduced carrying capacity. Farmers either have to make do with the limited spatial heterogeneity occurring within their farm boundaries, or gain temporary access to other land.

This study made use of the opportunity provided by fenceline contrasts in Namibia to learn from farmers who achieved different levels of success. The 34 investigated contrasts were mostly clustered within the vegetation types Camelthorn Savanna and Thornbush Savanna, with one in the Highland and two in the Dwarf Shrub Savannas of Namibia.

Rangeland measurements focussed on well established perennial vegetation to avoid the fluctuating effect of ephemerals. Eight characteristics were measured and significant ($p < 0.05$) differences occurred in at least one of these at each contrast. Five examples of fenceline contrasts are presented; one illustrating each of the most likely single causative factors of bush clearing; bush thinning; stocking rate; stocking density; and period of rest.

At most of the contrasts it was not possible to determine whether past management had a greater influence on rangeland condition than current management. However, this was clearly the case at one site where there was still a strong fenceline contrast, despite both sides having been subjected to the same management for the past 14 years since the farmer acquired the neighbouring degraded land.

Particularly useful lessons were learnt from the case study of an innovative farmer who adapted his management based upon his keen observations of rangeland dynamics. The observations relate to aspects such as animal behaviour and performance, animal trampling, and applications of grazing and fire. Some of these observations are presented together with their possible explanations and their management applications. Of critical importance is the strategic timing of management interventions on different parts of the farm in relation to rainfall events, texture and organic content of the soil as well as maturity of the vegetation.

Introduction

Spatial heterogeneity contributes to healthy ecological functioning that supports high productivity thanks to provision of critical resources from different parts of the landscape at different times (Scoones 1995). Seasonal migrations of large herbivores and pastoralists often occurred along rainfall and landscape gradients, while opportunistic movements over long distances used to occur in response to localised rainfall and fires (Fynn 2009). These seasonal migrations and irregular movements allowed animals to optimise their nutrition through more and longer availability of green leaves, while subsequently providing sufficient rest for recovery of the grazed grasses (Fynn 2009). The provision of borehole water and subdivision of land by fencing has greatly restricted the scale at which systems can now operate, thus reducing the carrying capacity and productivity of rangelands, while often leading to land degradation (Sinclair & Fryxell 1985). Farmers either have to make do with the limited spatial heterogeneity occurring within their farm boundaries, or gain temporary access to other land.

Although fences have wrought havoc to ecological functioning, they also provide research opportunities. Numerous fenceline contrasts are clearly evident when flying over Namibian rangeland or zooming into Google Earth. Different management practices that have brought about the contrasting and persistent rangeland conditions are a valuable source of information. Fenceline contrasts have been used to study differences in soil quality (Mills & Fey 2004), landscape function (Palmer et al. 2001), plant diversity (Rutherford & Powrie 2010), birds and small mammals (Joubert & Ryan 1999) and arthropods (Rivers-Moore & Samways 1996).

This study made use of the opportunity provided by fenceline contrasts to measure differences in rangeland and learn from farmers about the inputs and outputs of management on both sides of the fence. An important objective was to capture some of the existing knowledge, process it and make it available to land-users to help them make wiser decisions on how to manage the land.

The 34 measured fenceline contrasts were mostly clustered within the vegetation types (Giess 1971) Camelthorn Savanna and Thornbush Savanna of Namibia, with only one in the Highland Savanna, and two in the Dwarf Shrub Savanna (within the Nama Karoo Biome). The contrasts occurred in areas receiving long-term mean annual rainfall ranging from 235 mm at the most southerly contrasts, to 475 mm at the most northerly contrasts.

Methodology

Site selection

Identification of fenceline contrasts in the Thornbush and Dwarf Shrub Savannas was done by the remote sensing team of BIOTA, who kindly provided Landsat images of Namibia, taken on 17 May 2000. Each image had been superimposed with farm boundaries and names, and had clear fenceline contrasts marked on them in red by an automated function in GIS software. The images did not cover most of the Camelthorn Savanna, as they had been purchased to cover only the BIOTA Observatories. Therefore the identification of fenceline contrasts in the Camelthorn Savanna was based on consultation with farmers met previously and knowledge of the area acquired during previous practical exercises done in the area with students of the Polytechnic of Namibia.

In the Thornbush and Dwarf Shrub Savannas, fenceline contrasts suitable for the purpose of the study were identified from the images. Thereafter the names of farmers on both sides were obtained from the data base of the Namibian Agricultural Resources Information System (NARIS) of the Ministry of Agriculture, Water and Forestry (MAWF 2003). The farmers were contacted and asked whether they were willing to participate. Thereafter the final selection of fenceline contrasts to be measured was made, also taking into account factors such as accessibility and proximity to a camping site, to ensure a manageable number that would cover a spectrum of management differences.

The most striking contrasts were those where the symptoms of bush encroachment had recently been controlled. Management aimed at controlling the causes of rangeland degradation, such as herbivore and fire management, is likely to provide more useful information, although their fenceline contrasts may not be so striking. Therefore in the final selection of fenceline contrasts to measure, an attempt was made to strike a balance between different types of contrast, within the limits of the logistical constraints.

Rangeland measurements

Rangeland measurements, on each side of the fenceline contrasts, were conducted towards the end of the growing season. They focussed on well established perennial vegetation to avoid the fluctuating effect of ephemerals. Perennial grasses were only measured if they had a basal diameter of at least 5 cm. One hundred sample points were generated by throwing a dart over the shoulder along four transects within the sample area of 250 m x 130 m. Ten variables were measured, representing eight characteristics. Two of the variables were measured at the points: (i) ground level cover of the soil (whether rock, bare soil, mulch or base of live perennial grass) (ii) woody canopy cover over the sample point (by species or “no cover”). Seven of the variables were measured within a radius of 75 cm from the points: (iii) density of perennial grasses; (iv) density of woody plants shorter than 0.5 m; those measured within a radius of 5 m from the points were: (v) distance from sample point to nearest perennial grass; (vi) species of nearest perennial grass; (vii) distance to nearest bush; (viii) height class of nearest bush; (ix) species of nearest bush. One variable was measured at every fourth point only: (x) woody canopy cover by species, using a Bitterlich gauge (Friedel & Chewings 1988). A rangeland condition index was calculated based on the data from the distance to nearest perennial grass and the species, as described by Zimmermann (2009).

Learning from farmers

The farmers responsible for management on each side of fenceline contrasts were interviewed with the help of a formal questionnaire. Some questions were those aimed at gaining insight into the previous and current management applied to the farms, while others aimed at quantifying the production levels achieved. Certain answers that raised points of interest were followed up with further questions as necessary during and after the interviews. On one of the farms, where the adaptive management was selected as a case study, visits were made with the respective farmer to various sites on the farm, where he showed the effects of different management and described his observations that had led to him trying out various strategies.

Sharing results

Results from the research were summarised and presented to farmers at workshops for discussion between commercial farmers, affirmative action farmers, communal farmers, resettled farmers and extension workers.

Findings

Results from interviews

The results of interviews with 36 farmers indicated that the most common farming enterprise was the sale of cattle, practiced by 92% of the interviewed farmers, followed by goats at 44%, sheep at 31% and trophy hunting at 19%. Median values were a stocking rate of 44 kg liveweight ha^{-1} a^{-1} (10 ha AU^{-1} a^{-1}), animal production of 8 kg liveweight $ha^{-1}a^{-1}$, paddock size of 214 ha, 488 ha per water point and 1.0 workers employed per 1,000 ha. Most of the farmers (89%) relied on visual judgement to determine the carrying capacity of their rangeland. A minority (28%) applied continuous grazing and 31% set aside a portion of their farm to receive a full growing season’s rest. Of the 29 farmers who undertook rotational grazing, 31% applied fixed rotations because it was easy for their workers to follow a regular routine. No bush control had been undertaken by 42% of the farmers, while the main bush control strategy

Table 1: Some characteristics of management and rangeland found at five fenceline contrasts

Major input difference →	**Stocking rate**		**Period of rest**		**Stocking density**		**Bush thinning**		**Bush clearing**	
Photo of fenceline contrast	**Photo 1**		**Photo 2**		**Photo 3**		**Photo 4**		**Photo 5**	
Mean rainfall (mm a^{-1})	**320**		**380**		**250**		**400**		**380**	
Stocking rate (kg ha^{-1} a^{-1})	105	42	45	38	33	67	36	51	40	Hay
Stocking density (kg ha^{-1})	315	588	45	228	132	402–4000	144	204	360	Hay
Animal Production (kg ha^{-1} a^{-1})	8	8	11	10	7	12	7	6	9	Hay
Type of animals (G = game; C = cattle; S = small stock; E = equines)	C, S, E	C	G	C	C	C, S	C	C	C	Hay field
Growing season rest (weeks)	4	14	0	6	26	5	6	8	8	All
Paddocks per herd of animals	3	14	1	6	4	6	4	4	9	n/a
Rangeland condition index	202	650	306	434	40	225	85	335	205	275
Perennial grass density (plants m^{-2})	2.1	5.0	1.7	2.9	0.4	1.8	0.9	3.0	1.8	2.3
% Mesophytes among grass spp.	8	90	79	99	2	5	25	3	72	82
Cover of mulch & grass bases over the soil (%)	31	16	15	22	8	9	7	26	24	17
Median distance to nearest bush (cm)	271	142	131	140	82	148	119	244	122	> 5 m
% Canopy cover of bushes	29	32	8	23	33	20	36	8	27	0
% Encroacher spp. among bushes	3	23	54	31	70	66	53	19	60	n/a

Shaded pairs of cells indicate rangeland characteristics that differed significantly ($p < 0.05$) across the fenceline. In all five cases the poorer side appears first, on the left, and the better side on the right of the paired results.

applied was arboricides by 25% of the farmers, chopping bushes by 11%, stem burning by 11%, and controlled veld fires by 6%. *Stipagrostis uniplumis* was mentioned by most farmers as a useful plant while *Acacia mellifera* was reported by most farmers to be harmful, although some considered it to be useful. Vultures were considered by most farmers as useful birds and the dung beetle as a useful insect. Most farmers (89%) recognised different soil or landscape types on their farms and out of those, 53% applied different management to them, such as stocking them at different rates or preferentially grazing them at different seasons. The majority (54%) of farmers moved livestock between other distant farms that they owned, usually on rare occasions when severe drought hit one of their farms, while the others occasionally accessed other land through renting or the goodwill of relatives with land.

Results from fenceline contrasts

Significant ($p < 0.05$) differences occurred in at least one variable measured at each of the 34 contrasts. At 22 of the contrasts the rangeland condition index was significantly ($p < 0.05$) higher on one side of the fence compared to the other side. There was no clear way to distinguish between the influence of different types and timings of management inputs that may have caused the fenceline contrasts. Therefore, subjective judgment was relied upon to identify bush thinning as the most likely single causative factor at six contrasts, bush clearing at four contrasts, stocking rate and period of rest at five contrasts each, and stocking density at two contrasts. An example of a fenceline contrast falling under each of these five most likely causative factors was selected to illustrate the main differences in both management and condition of the rangeland (Table 1).

Example of fenceline contrast likely caused by difference in stocking rate

The side in poor condition was stocked with cattle, sheep, goats, horses and donkeys at an extremely high rate, estimated to be 105 kg liveweight ha^{-1} a^{-1}, whereas the side in good condition was stocked with cattle at 42 kg liveweight ha^{-1} a^{-1}. This contrast appears in Photo 1. The good side supported 5.0 grasses m^{-2}, 90% of which were broad leaved (mesophytic) species, compared to a density of 2.1 grasses m^{-2}, of which only 8% were mesophytic. In the case of the unpalatable woody geophyte, *Elephantorrhiza elephantina*, a significantly ($p < 0.05$) higher number of stems were found on the poor side, giving a mean density estimate of 3,230 plants ha^{-1} compared to 170 plants ha^{-1} on the good side.

Example of fenceline contrast likely caused by difference in period of rest

The poorer side was on a game farm stocked continuously at 45 kg liveweight ha^{-1} a^{-1} with a wide diversity of game species, dominated by gregarious selective grazers such as blue and black wildebeest. The better side was stocked with cattle at about 38 kg liveweight ha^{-1} a^{-1} and received rest in the growing season of about six weeks, compared to no rest on the game farm. This contrast appears in Photo 2. The perennial grass density was higher on the side of this fence that received rest, estimated at 2.9 grasses m^{-2} compared to 1.7 grasses m^{-2} on the continuously grazed side.

Example of fenceline contrast likely caused by difference in stocking density

The poor side received a slow fixed rotation through four paddocks per herd of cattle stocked at 33 kg liveweight ha^{-1} a^{-1}, providing six months of rest after two months of grazing at a stocking density of about 130 kg liveweight ha^{-1}. The better side supported cattle, sheep and goats stocked at 67 kg liveweight ha^{-1} a^{-1} rotated quickly in the growing season. The farmer had made keen observations, which he applied successfully to adaptive management on his farm, which is why his management was selected for the case study. The rate of rotation and paddocks per herd varied, with short trampling by all animals on the farm combined into one herd applied strategically, such as soon after good rain to increase grass establishment and conserve soil water by breaking the capillary connections to the soil surface. The more common stocking density was approximately 400 kg liveweight ha^{-1}, but was increased more than tenfold to above 4,000 kg liveweight ha^{-1} for only a day or two when strategic trampling was applied. This contrast appears in Photo 3.

The perennial grass density was very low at the poor side, with only 0.4 grasses m^{-2}, compared to 1.8 grasses m^{-2} at the better side. There was also more of the palatable leguminous perennial forb, *Otoptera burchellii*, of which the density was estimated at 450 plants ha^{-1}

Photo 1: Both sides of fenceline contrast between leasehold land stocked at 105 kg liveweight ha^{-1} a^{-1} (top) and commercial land stocked at 42 kg liveweight ha^{-1} a^{-1} (bottom); March 2005. Photos: Ibo Zimmermann.

Photo 2: Both sides of fenceline contrast between continuously grazed game farm (top) and rotationally grazed cattle farm (bottom); April 2004.
Photos: Ibo Zimmermann.

Photo 3: Both sides of fenceline contrast between land under slow fixed rotation (top) and strategic trampling (bottom); March 2005.
Photos: Ibo Zimmermann.

Photo 4: Both sides of fenceline contrast between untreated land (top) and bush thinned land (bottom); April 2005.
Photos: Ibo Zimmermann.

on the poor side and 2,150 plants ha^{-1} on the better side. However, the bush density was higher on the poor side, with a median distance to nearest bush of only 92 cm and a canopy cover of 33%. This compared to a median distance to nearest bush of 148 cm and a canopy cover of 20% on the better side.

Example of fenceline contrast likely caused by bush thinning on one side

The poor side had not undergone any bush control whereas the good side had received arboricide application selectively by hand a few years previously. As a result it could be stocked more heavily, at approximately 51 kg liveweight ha^{-1} a^{-1}, compared to the 36 kg liveweight ha^{-1} a^{-1} on the other side of the fence. The poor side is also a guest farm where trophy hunting takes place. Both farms provided four paddocks per herd of cattle, although the growing season rest period was a little longer on the good side, at eight weeks compared to six weeks on the poor side. In addition, the good side was provided with a complete growing season rest once every five years. This contrast appears in Photo 4.

The mulch cover was three times higher, at 24%, on the good side. The perennial grass density was also higher, estimated at 3.0 plants m^{-2}, compared to 0.9 plants m^{-2} on the poor side. However, the proportion of mesophytes amongst the grasses was greater on the poor side, comprised mainly of *Eragrostis rigidior*, although both sites were dominated by *Stipagrostis uniplumis*. As expected the bush density and canopy cover were higher on the untreated side of the fence. Despite domination by *Grewia flava* on both sides of the fence, the species composition differed, with a greater proportion of *Acacia mellifera* and *Dichrostachys cinerea* on the untreated side, and a correspondingly greater proportion of *Acacia luederitzii* on the bush thinned side, even though all these three species had been targeted for arboricide application on the good side.

Example of fenceline contrast likely caused by bush clearing on one side

The better side was a hayfield that had been cleared of bushes approximately eight years previously, by chopping and digging out the bushes. Hay was mown every year, except in an extreme drought. The poorer side was an adjacent paddock where bushes had been thinned by selective hand application of arboricide more than ten years previously. The farm was stocked with cattle at roughly 40 kg liveweight ha^{-1} a^{-1} that were rotated through nine paddocks per herd, with weekly shifts in the growing season providing eight weeks of rest. This contrast appears in Photo 5.

This contrast did not indicate significant ($p > 0.05$) differences in soil cover and perennial grass species composition. However, the perennial grass density on the hayfield was estimated at 2.3 grasses m^{-2}, compared to 1.8 grasses m^{-2} on the previously thinned site. The canopy cover of bushes and trees had been reduced to zero on the hayfield, but had increased to 27% on the previously thinned site, which was dominated by *Acacia mellifera*, the main target of the previous arboricide application, followed by *Grewia flava* and *Acacia hebeclada*.

Example of fenceline contrast that persisted despite similar management for 14 years

On one farm there was still a strong fenceline contrast, despite both sides having been subjected to the same management for the past 14 years since the farmer acquired the neighbouring degraded land to extend his own farm. Cattle were stocked at 24 kg liveweight ha^{-1} a^{-1} and moved through seven paddocks per herd. This contrast appears in Photo 6. The poorer side had a perennial grass density of 3.1 grasses m^{-2}, compared to 5.3 grasses m^{-2} on the better side. The organic cover of the soil was estimated at 4% on the poor side, compared to 14% on the better side.

Lessons learnt from the fenceline contrast study

Management contributed to both causes and consequences of fenceline contrasts. The negative correlation between

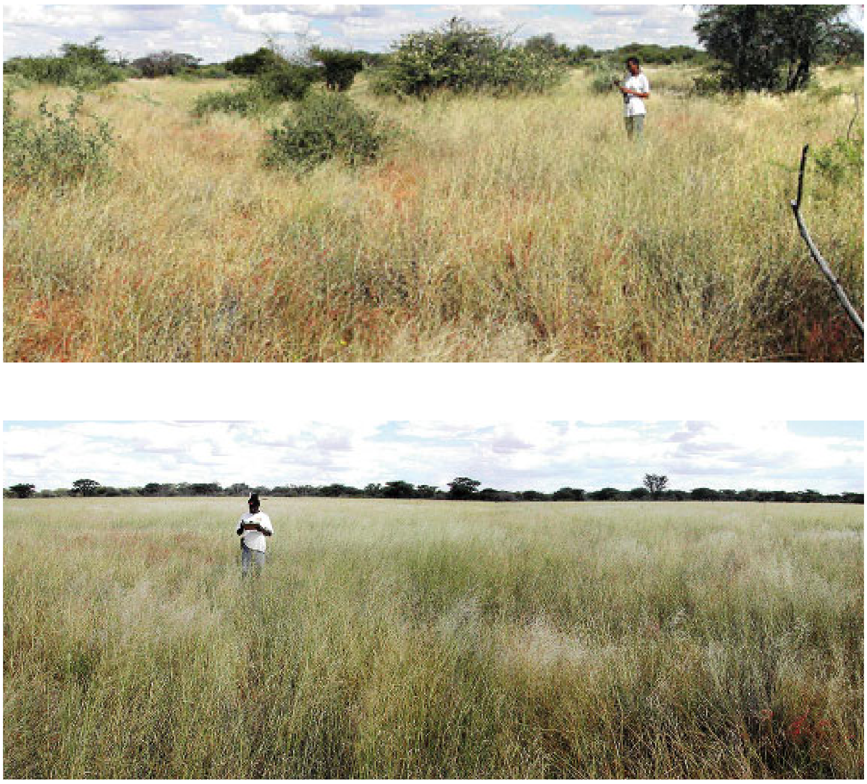

Photo 5: Both sides of fenceline contrast between previously bush thinned paddock (top) and hayfield (bottom); April 2004.
Photos: Ibo Zimmermann.

Photo 6: Both sides of fenceline contrast between a paddock that was previously heavily stocked before being lightly stocked with cattle for 14 years (top) and a paddock on the same farm stocked lightly with cattle for several decades (bottom); March 2005.
Photos: Ibo Zimmermann.

Table 2: Observations by case-study farmer related to animal trampling, and their conversion to management applications

Observation of farmer	Possible explanation given by farmer	Management application
1. Trampling on soil low in organic matter results in abundance of the weed *Tribulus terrestris* and encourages establishment of bush seedlings, while trampling on soil with sufficient organic matter results in abundance of grass, after rain.	Soil low in organic matter gets hotter than soil with sufficient organic matter. Grass seed cannot survive or germinate successfully in hot soil, while *Tribulus terrestris* and bush species can.	Only apply a lot of trampling where the soil organic matter content is high or there is a lot of standing dry grass to trample down into the mulch layer.
2. Trampling on sandy soil in the dry season does not increase subsequent perennial grass density, while trampling it in the growing season does, if followed by rest.	Trampling in the dry season loosens the soil around grass roots, so that they become desiccated or uprooted. If soil is moist it is not loosened so easily and hoof marks remain fairly firm.	Only apply trampling to sandy soil in the growing season (if soil organic content is sufficient).
3. Trampling on loamy soil with low organic matter when it is moist causes hardening of the soil.	Moist loamy soil cannot resist trampling pressure and gets compacted. If hard and dry it resists compaction.	Reduce the stocking rate on loamy soil in the growing season.
4. Trampling before rain on loamy soil improves water infiltration and establishment of grass seedlings.	Trampling causes hoof marks that encourage seeds and mulch to settle into them before rain and hold water during rain.	Apply brief trampling before rain to capture more rain water, seeds and mulch.
5. Trampling after rain on soil with sufficient organic matter conserves the moisture already in the soil. If low in organic matter, the loosened soil dries out fast.	Trampling breaks the capillary connections to the soil surface, so reducing capillary rise of water after evaporation of surface moisture.	To reduce evaporation loss from the soil, apply brief trampling after good rain, provided there is sufficient organic matter in the soil.
6. Trampling after good rain on soil where there are few perennial grasses tends to favour bush growth.	The soil moisture conserved by the trampling gets used by bushes, since there are insufficient grasses to use it.	Rather trample such poor paddocks after first rain of season, to encourage perennial grass emergence.
7. Damara and Van Rooi sheep provide a better trampling service on hard ground than Dorper sheep.	Damara and Van Rooi sheep have sharper hooves than Dorper sheep and have retained their herding and mothering instincts better.	Farm mainly with Damara and Van Rooi sheep, mixed with limited Dorper genes to provide a larger animal demanded by the market.
8. The presence of a few jackals causes sheep to remain bunched together and provide a better trampling service.	Sheep feel more secure when bunched together, in the presence of jackals. Therefore they create a higher density of hoof marks.	Control jackals to a limited extent and sacrifice the loss of a few sheep, so that the herd bunches well and mothering instincts continue to be selected for.

stocking rate and rangeland condition index was weak ($r = -0.2575$, $p = 0.04$, $N = 64$), suggesting that there may have been more farms where a higher stocking rate was the cause of poorer rangeland than farms where the higher stocking rate was the consequence of better rangeland raising the carrying capacity. Although auto-correlation would be expected in both, the stronger correlation between profit and income ($r = 0.9288$, $p < 0.001$, $N = 25$) than between profit and expenditure ($r = 0.0267$, $p = 0.899$, $N = 25$), suggests that farmers should focus on reducing non-essential expenditure to increase profitability.

Some farmers are aware that their management harms the rangeland but feel they are forced to do so, to meet their living standards from the limited resources available to them. Limited size of farm forces some farmers to overstock. The seasonal availability of water over parts of some farms limits the opportunity to rest certain areas at critical times.

Game farming can earn high income, but continuous selective grazing by gregarious game animals may lead to poor rangeland condition.

It was not possible to determine whether past management had a greater influence on rangeland condition than current management, except at the contrast of the last example where both sides experienced similar management for the previous 14 years. Degradation caused by the pursuit of short term gain may take several decades to heal.

Case study

The case study recorded 31 observations of the innovative farmer, relating to aspects such as animal behaviour and performance, animal trampling, applications of grazing and fire. Based on his observations, he stated that the strategic timing of management interventions on different parts of the farm in relation to rainfall events, texture and organic content of the soil and maturity of the vegetation is of critical importance. The farmer stopped using chemicals to treat his livestock for internal parasites, after observing the death of dung beetles that fed on dung from treated animals. The fenceline contrast of the case-study farm with one of the neighbouring farms is shown in Photo 3. Eight of the observations related to trampling have been selected for presentation in Table 2. Further details of the study have been published by Zimmermann & Smit (2008).

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Plant functional traits and types as a tool to analyse landuse impacts on vegetation

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Summary: Landuse, such as livestock grazing, has a major impact on the vegetation of semi-arid and arid ecosystems in southern Africa. Plant functional types and traits have proven to be useful tools in helping to understand the complexity of vegetation responses to landuse change, and to predict the impacts of landuse on the vegetation. Plant functional approaches were applied and tested in various studies of vegetation change along landuse intensity- and environmental gradients within the BIOTA project.

In the Thornbush Savanna of Namibia, a monitoring tool based on plant functional types and Landscape Function Analysis (LFA) was developed in order to characterise the state of the rangelands. In a trait based study in central Namibia, the influence of different major habitat types was found to be important for patterns of plant trait responses along grazing gradients. In studies of trait composition under different landuse intensities in the southern Kalahari, fleshy-fruited species were found to have decreased while poisonous and spiny species increased with increasing landuse intensity. Furthermore, it was observed that range condition influences plant life form composition. In the same study region, it was found that intensive sheep farming leads to an increase of animal dispersed plant species. A study of the seed bank composition in Nama Karoo rangelands of southern Namibia revealed varying patterns of seed distribution depending on seed size and microtopographical soil surface parameters. In the Succulent Karoo of South Africa, it was found that the recovery of vegetation on abandoned agricultural fields depends on landuse management practise, as indicated by the composition of plant growth forms and life history traits.

The results of all these studies contribute towards improved monitoring and management of semi-arid and arid rangelands. Further studies of plant functional types and traits could provide valuable information with regards to the restoration of degraded rangelands.

Introduction

Landuse by humans has a major impact on the biodiversity and functioning of ecosystems worldwide. In southern Africa the main landuse is grazing by either domestic livestock or wildlife. Grazing by large wild herbivores was common before humans became sedentary, but since then grazing has been dominated by domestic livestock with grazing intensity and behaviour being completely different to that of wildlife. Today, overgrazing is one of the greatest threats to the semi-arid and arid ecosystems of southern Africa, i.e. the Karoo and Savanna ecosystems. Vegetation patterns caused by grazing have been described in many papers, summarised for the Karoo by Haarmeyer et al. (2010) and the Savanna by Skarpe (1991) and Scholes & Archer (1997). Consequences of these impacts have now focused attention on the need to understand, model, and predict the interactions between the changed environment and plant species not only due to landuse change but also climate change. Plant functional types (PFT) and/or specific functional traits (FT) are recognised as practical constructs to simplify community complexity to understand the mechanisms behind vegetation dynamics and to improve interpretation and modelling (PFT: Shugart 1997, Diaz et al. 1998, McIntyre & Lavorel 2001, Moog et al. 2005; FT: Kahmen 2004, Poschlod et al. 2005, Diaz et al. 2007, Kahmen & Poschlod 2008).

Therefore, this approach was the basis of different studies conducted by BIOTA on changes in vegetation and biodiversity along landuse intensity- and environmental gradients. Vegetation changes were analysed in both directions i.e. degradation and recovery. For the degradation processes the effects of landuse (emphasis on grazing practices and cropping) and climate change were investigated. For the recovery processes the pathways, states and possible endpoints in the natural recovery process after human-induced disturbances were investigated. The focus in both cases was on quantifying trait responses and their effects on ecosystem function and population dynamics. Traits were selected according to their relation to landuse/grazing intensity (see Table 1).

In the following paragraphs, BIOTA results regarding plant functional approaches as a tool to analyse different landuse impacts will be presented and briefly discussed.

User-friendly rangeland monitoring with plant functional types in central Namibia

The most prominent indicators of desertification in Namibia are considered to be (a) soil erosion, (b) loss of the tree layer,

Table 1: Association of plant functional traits with plant responses to natural and anthropogenic disturbance processes (according to Cornelissen et al. 2003)

	Natural disturbance processes		Anthropogenous disturbance processes (land use types or practices)			
	Drought	Fire	Grazing/ browsing	Arable field use	Fertilization/ nutrient deposition	Wood cutting
Whole plant traits						
Growth form	●	●	●	●	●	●
Life form	●	●	●	●	●	●
Plant height	●	●	●	●	●	●
Clonality	●	●	●	●	●	●
Spinescence			●			●
Palatability			●		●	
Flammability		●				●
Leaf traits						
Specific leaf area	●		●	●	●	
Leaf size	●		●		●	
Leaf dry matter content	●	●	●		●	
Leaf N and P concentration			●		●	
Physical strength of leaves	●	●	●		●	
Leaf lifespan	●	●	●		●	
Leaf phenology	●		●		●	
Photosynthetic pathway	●					
Stem and belowground traits						
Stem specific density		●			●	●
Specific root length	●				●	
Distribution of rooting depth	●				●	
95% rooting depth	●				●	
Nutrient uptake strategy					●	
Regenerative traits						
Dispersal mode			●	●		
Dispersule shape and size			●	●		
Seed mass	●	●	●	●	●	
Resprouting capacity		●	●	●		

(c) a decrease or loss of preferred grass species and shrubs, (d) bush encroachment, and (e) decreased soil fertility (de Klerk 2004). Changes of these indicators happen slowly and are thus not easily recognised over short periods of time (under 5 years). Such changes can be detected with regular monitoring practices. However, monitoring takes up time and resources and is itself not an income-generating activity, but it is an essential early-warning tool that can be used by land managers to improve their rangeland management practices. Effective monitoring tools thus need to be cost-effective or simple enough to be applied by landusers themselves, they need to address the major components and driving factors within an ecosystem, and they need to be scientifically reliable. In Namibia, where livestock production on rangelands forms a major part of the country's economy, there is a great need for such a monitoring methodology to ensure the long-term sustainable use of rangelands.

Patterns within a landscape are the result of a variety of processes that redistribute and cycle vital resources over space and time. Even at a small scale, patterns have a functional role. Highly functional landscapes are able to retain most resources within the landscape. Increased leaking of resources indicates the increasing dysfunction of a landscape.

The Landscape Function Analysis (LFA) technique (Tongway & Hindley 2000) is a rapid monitoring procedure, using field-assessed indicators to determine the functionality of landscapes at the hill slope or patch-inter-patch scale. LFA concentrates on the nature of patch- and inter-patch zones, characterising these according to various soil variables and soil-vegetation relationships that influence small-scale surface hydrology. The "traditional" LFA concentrates on soil surface properties and vegetation cover. The method was expanded to record the vegetation according to easily recognisable plant functional types to enable the landuser to monitor a change in vegetation composition as well, concentrating especially on the different types of perennial grasses. LFA surveys are conducted towards the end of the dormant

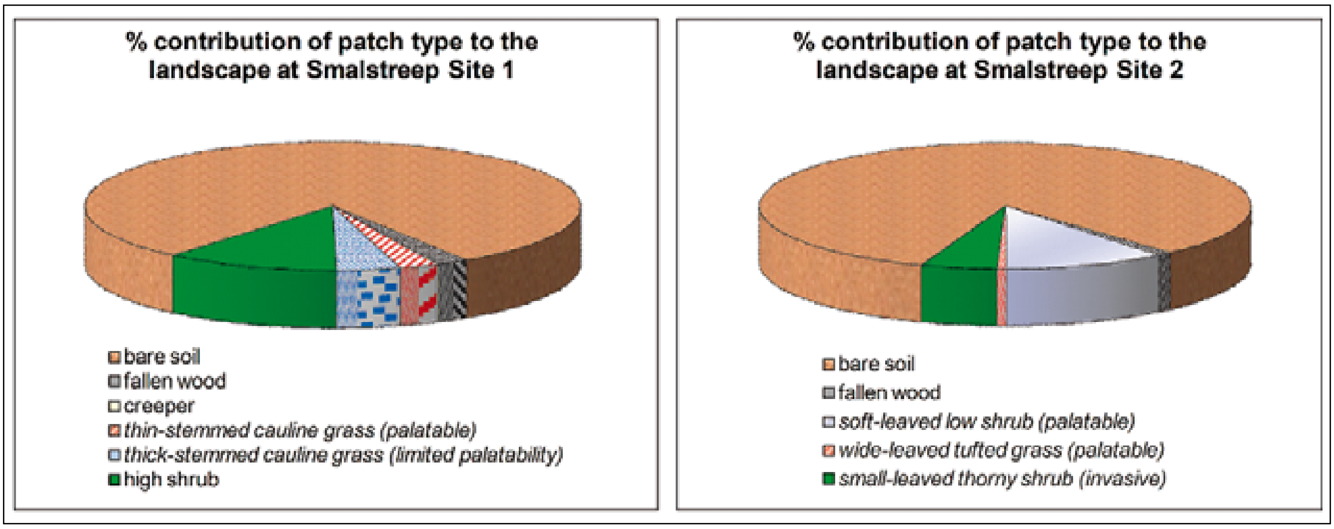


Fig. 1: Schematic representation of landscape composition in terms of the proportions of different patches—in this case, either bare soil or type of vegetation cover at Smalstreep. The high amount of bare ground and low cover of perennial palatable grasses should be of concern to rangeland managers. The corresponding indices for Site 1 and Site 2 are: Stability: 47.4 and 45.7 (78), Infiltration 24.2 and 21.3 (45), Nutrient Value 15.9 and 15.6 (33) respectively. The values in parentheses indicate what is regarded as optimal values for grasslands. Optimal values for Namibian savannas still need to be determined, but are assumed to be higher than the index values that were obtained.

season (July/August), when perennial herb cover is at its most vulnerable to overgrazing, and soils most vulnerable to erosion after rainfall impact of the first thunderstorms of the rainy season. Only when done at the time of peak landscape vulnerability, will LFA results truly show the stability of a landscape.

Collected data are entered into a spreadsheet to calculate indices for stability, infiltration and nutrient state, derived from the nature and state of the various patches encountered. Repeat measures at the same site over time show trends of either rangeland degradation or improvement. This technique was tested on the farm Smalstreep in the Etjo Erosion plains, Namibia, where the field condition was perceived to be moderate, and the results (Fig. 1) showed just how vulnerable the field actually was to erosion, judging by the low cover of stable perennial vegetation during the dormant season.

LFA is designed to derive relatively standardised indices, regardless of climate or specific vegetation type. Indices vary naturally across broad types of vegetation, e.g. savannas vs. grasslands. From the indices obtained for Smalstreep, the importance of soil surface cover for improving soil stability, water infiltration rates and nutrient accumulation became clear. However, compared to optimal grassland, the overall index values for the sample sites appeared relatively low. The values obtained thus need to be put into context. Data need to be collected from reference or benchmark sites to be able to determine the following:

- What do the index values mean?
- What, in a specific Namibian vegetation type, is a good index value, what is “good enough” (or not degraded)?

Such data are not available for all rangelands in Namibia, thus most data will have to be collected, compiled and analysed over time. However, even without an index-reference system, the expanded LFA technique described above can, if done annually, provide a good indication of the effects of rangeland management practices. As many farmers are not always familiar with exact species names and species cannot always be identified properly during the dormant season (when the LFA is supposed to be conducted), the use of easily recognisable PFT’s proves to be a suitable way of describing the vegetation, and provides the land manager with an instant overview of the composition of the veld.

Plant trait responses to livestock grazing in central Namibia

The area around the district town of Rehoboth in central Namibia is characterised by commercial livestock farming with cattle, sheep and goats on privately owned farmland. Most of the farms are relatively small in size (i.e. less than 3,000 ha, Lang 2005) compared to the average size of private Namibian farms (about 4,000–5,000 ha). Overstocking of these semi-arid rangelands, which have a very low carrying capacity is a widespread problem and has often led to degradation. In order to establish indicators of overgrazing based on plant functional types, quantitative and categorical whole plant, leaf and regenerative traits were recorded along grazing gradients (so called “piosphere transects”) on several farms in the Rehoboth area. The farms or farm camps differed in size, grazing management and dominant habitat parameters. With the aim of finding consistent grazing response traits, a partial direct analytical approach was used in order to remove the effect of differences in habitats, farm management and sampling in different years.

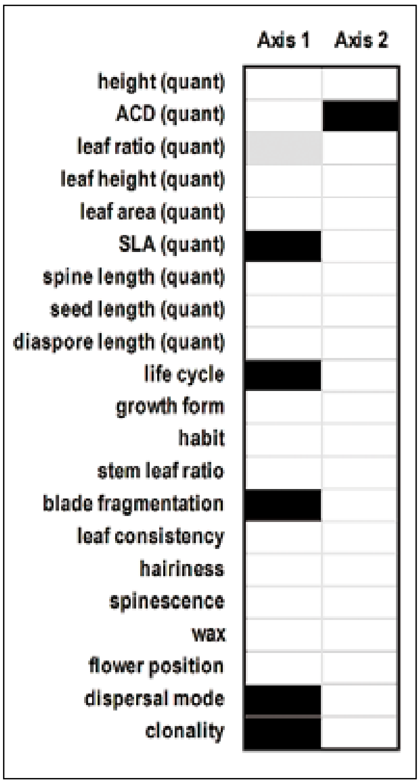
The effect of sampling in different years (2007 low rainfall and 2008 high rainfall) and in different major habitat types on plant trait composition was stronger than the effect of grazing. With the help of the partial analysis, confounding environmental effects besides grazing could be removed. The most important environmental parameters in the partial analysis were distance from water point, cover of dung, soil pH and electrical conductivity, which are all indicators of grazing pressure (Rietkerk et al. 2000, Smet & Ward 2006). Traits with a negative grazing response, i.e. traits that decrease with increasing grazing pressure, were perennial life cycle, leaf ratio (leaf length/width), rhizomatous habit, leafy stem, entire leaf blade, anemochorous dispersal, and belowground clonality. Traits with a positive grazing response, i.e. traits that increase with increasing grazing pressure, were specific leaf area (SLA), annual life cycle, herbaceous forb growth form, prostrate-creeping habit, compound leaves, no clonality, and endo- or exozoochorous dispersal (see also Fig. 2).

One important outcome of this analysis was that some traits, which are described in the literature as responsive to grazing may also vary with environmental factors that are related to different habitat conditions. Some examples of these environmental factors are soil depth, the percentage of coarse material in the soil (skeleton content), slope, and the surface cover of gravel and stones. Some examples of important traits that are related to changes in habitat conditions are above cover density (ACD, i.e. the percentage cover of the plant canopy above a vertically projected contour of the plant), plant height and growth form. It is therefore important to consider the habitat diversity of the rangeland when using plant functional traits as indicators. Leaf ratio, SLA, life cycle, leaf blade fragmentation, dispersal mode and clonality (Fig. 2) were traits found to be responsive to grazing across habitats and different sampling years on a regional level. These results are consistent with the findings of other trait based approaches (Cingolani et al. 2005, Diaz et al. 2007, Golodets et al. 2009) and these traits can thus serve as potential indicators of rangeland condition.

Response of vegetation patterns and plant traits to livestock grazing in the Kalahari

Vegetation pattern in the Kalahari is strongly affected by the mosaic of single trees and the matrix in-between. Subcanopy species composition differs markedly from the matrix species composition. Mechanisms causing this pattern, as well as how this pattern is affected by different landuse intensities were studied in the Nossob river valley north of Upington. Three sites were selected: a reference site (site one) with no management since at least 1974 in South Africa; a farm (site two) with a low-intensity grazing regime by wildlife (ostriches and antelope, mostly springbok) in South Africa; and communal land (site three) heavily grazed by goats, sheep and cattle in Botswana. Studies on the vegetation patterns were performed from 2001 to 2003, and a comparative study on the effect of different landuse intensities was conducted in 2001.

Subcanopy habitats strongly supported the occurrence of many fleshy-fruited shrubs or herbs, grasses and specific annual species. The matrix was characterised by herbs, grasses and other annual species. Contrary to existing hypotheses, shading, narrower temperature fluctuations and dispersal, but not higher nutrient contents in the soil, were correlated with the specific subcanopy flora (Hoffmann 2001, Kos 2007). Plant trait responses in the subcanopy were a slower germination and root growth rate in annuals (Fig. 3; Kos & Poschlod 2010), a higher germination rate with narrower temperature fluctuations (Kos & Poschlod 2007), and a high endozoochorous dispersal potential revealed by faeces caught in seed traps (Kos 2007).



	Axis 1	Axis 2
height (quant)		
ACD (quant)		■
leaf ratio (quant)	▨	
leaf height (quant)		
leaf area (quant)		
SLA (quant)	■	
spine length (quant)		
seed length (quant)		
diaspore length (quant)		
life cycle	■	
growth form		
habit		
stem leaf ratio		
blade fragmentation	■	
leaf consistency		
hairiness		
spinescence		
wax		
flower position		
dispersal mode	■	
clonality	■	

Fig. 2: Results of the fourth corner statistic with regard to quantitative (quant) and whole categorical traits (all other traits) and the first two axes of the partial RLQ analysis. The first axis represents a grazing gradient where high values indicate high grazing pressure and low values indicate low grazing pressure. The second axis represents differences in habitat conditions and farm management. Black boxes indicate a positive, and grey boxes a negative significant relationship between traits and axes. ACD = above cover density, SLA = specific leaf area.

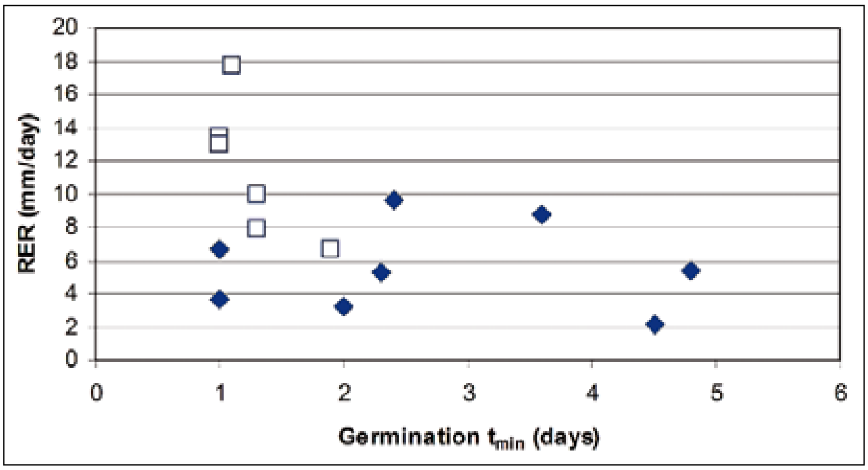


Fig. 3: Germination speed (tmin = time of germination commencement) and root elongation rate (RER) in annuals of the subcanopy (closed rhombs) and the matrix (open quadrats) in the Kalahari duneveld (according to Kos & Poschlod 2010).

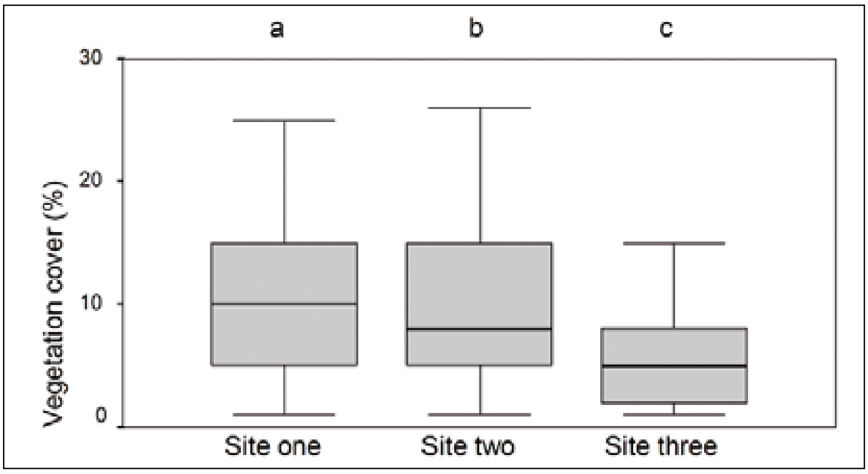


Fig. 4: Vegetation cover on a site with no management (site one), a site with low-intensity grazing (site two), and a site with high intensity grazing (site three). Sites were sampled using 280 plots in each. Significant differences between sites are indicated by letters (a, b, c).

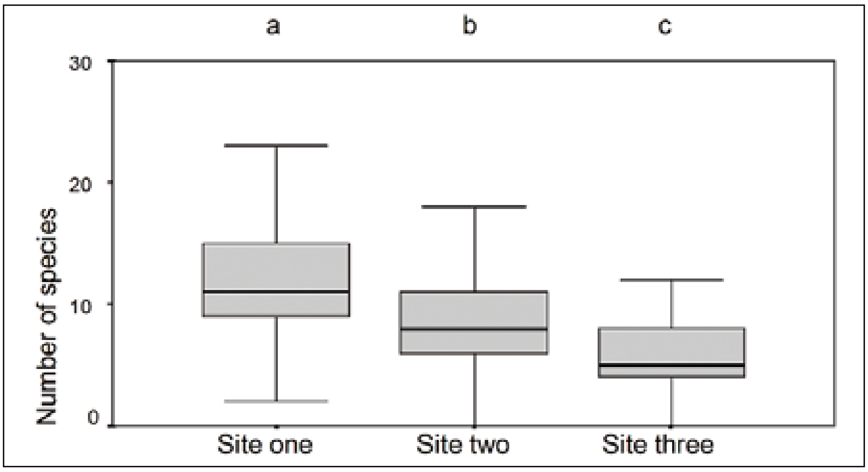


Fig. 5: Number of species on a site with no management (site one), a site with low-intensity grazing (site two), and a site with high intensity grazing (site three). Sites were sampled using 280 plots in each. Significant differences between sites are indicated by letters (a, b, c).

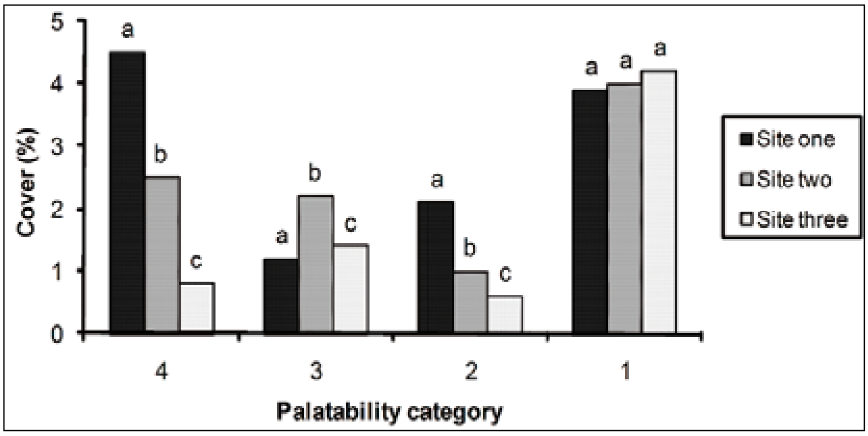


Fig. 6: The median cover values of vegetation palatability classes (4 = very good to good; 3 = medium; 2 = poor; 1 = poisonous or not grazed) on a site with no management (site one), a site with low-intensity grazing (site two), and a site with high intensity grazing (site three) (*N* = 280, per palatability class and per site). The letters (a, b, c) indicate significant differences in the cover for a particular palatability class between the three sites ($p \leq 0{,}01$; *N* = 560; for all significant differences).

Whereas vegetation cover and species richness was high in the subcanopy habitats of the reference site and the low-intensity grazing site, the opposite was found at the high-intensity grazing site. Vegetation cover and species richness strongly decreased along the landuse intensity gradient (see Figs. 4 & 5) as well as the cover and number of fleshy-fruited and highly palatable species (see Fig. 6). In contrast, poisonous and spiny species increased with increasing land-use intensity. The proportion of alien species was significantly higher on the communal land where grazing pressure was highest.

This shift in the proportions of functional traits is clearly related to a grazing intensity gradient. Since landusers may not possess detailed species knowledge or may not be able to measure their functional traits, easily recognisable traits may allow a clear assessment of the impacts of a certain landuse type or intensity. Cover and occurrence of fleshy-fruited species, and the presence or absence of aliens have been shown to be strongly correlated to landuse type and intensity. These species are easy to recognise and may therefore serve as suitable indicators to define suitable management interventions.

Effect of grazing intensity on the dispersal potential of plant species in the Kalahari

Heavy grazing is known to affect the functional composition of savanna vegetation, leading to an increase of annual and small woody species, and leaving only bare ground in extreme cases (e.g. Walker et al. 1981, Skarpe 1990, Jeltsch et al. 1997). Whereas these effects are well known, the impacts on functional trait spectra have received little scientific attention. To determine the impact of landuse on plant dispersal, seeds of 57 of the most common species in the Southern Kalahari Duneveld were collected and subjected to standardised dispersal potential measuring experiments (Horn 2008, modified after Knevel et al. 2005). In the next step, dispersal potential was combined with plant cover values in 10 m

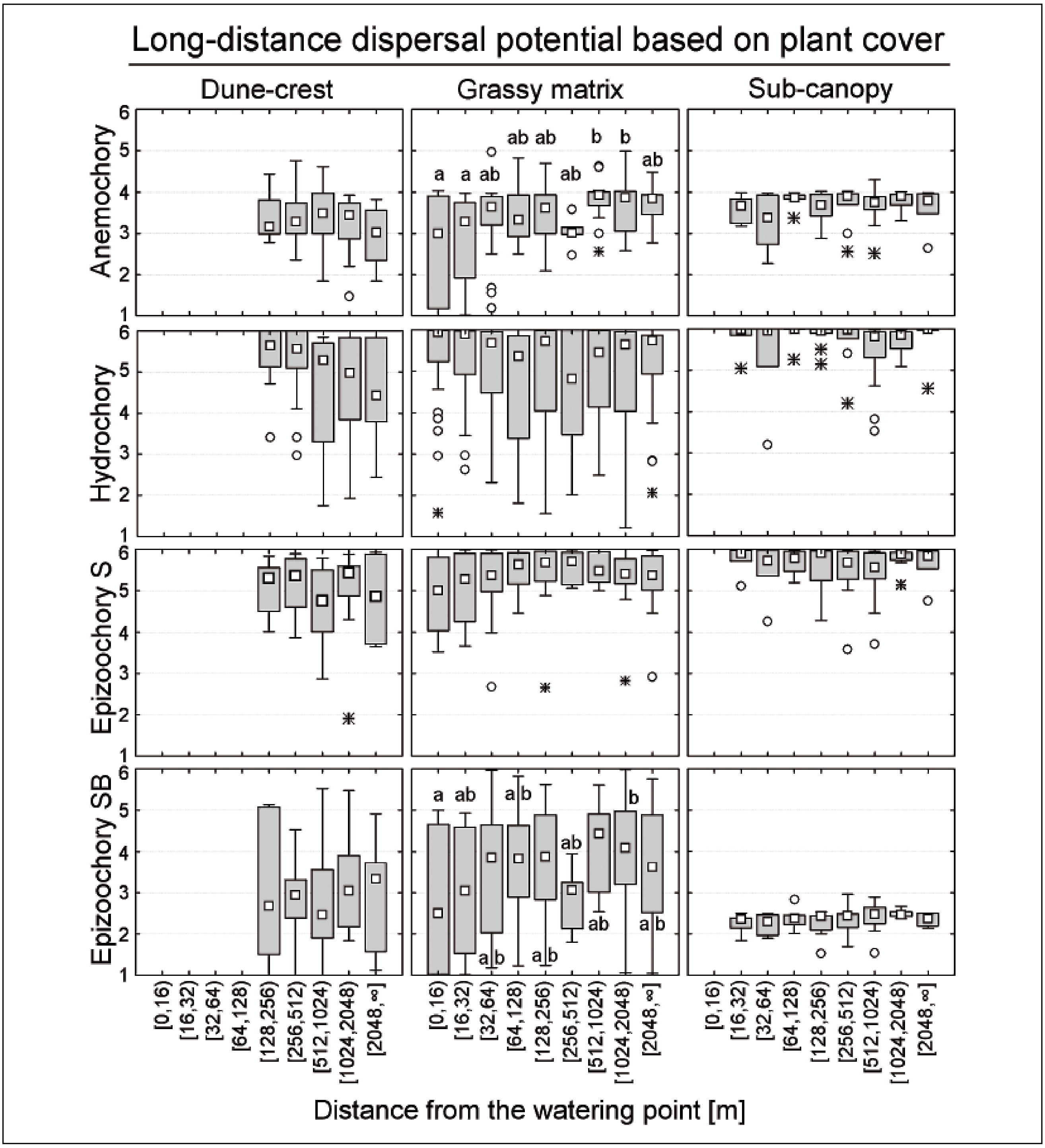


Fig. 7: Long distance dispersal potential (1 = very low to 6 = very high) of duneveld vegetation based on plant cover values in different habitats. Epizoochory S: Dispersal in sheep fur; Epizoochory SB: Dispersal in springbok fur. Significant differences are indicated by letters (Kruskal-Wallis test) (box = 25–75 % with median, brackets = non outlier max and min, o = outliers, * = extreme values).

x10 m plots placed at increasing distances from a watering point, up to a distance of over 2 km in ca. 350 ha sheep camps, to search for trends in dispersal strategies. Three habitat types were analyzed, namely the grassy matrix, the subcanopy habitat and the dune crests.

The three habitats exhibited different sensitivity to grazing and only the grassy matrix vegetation showed significant trends (Horn et al. 2008, Fig. 7). In agreement with other studies described in this article, the results showed that plant species with high wind dispersal potentials had higher cover values in areas with lower landuse intensity, i.e. greater distances from the watering point in this case. Furthermore, wind dispersal potentials were generally low as many species possessed large seeds. Plants with high dispersal potential in either sheep wool or springbok fur showed a similar pattern, which is believed to be due to a putative correlation of traits enabling either wind dispersal or external zoochory (i.e. dispersal by the seed attaching to an animal). In contrast, hydrochory potential did not respond to landuse pressures and is likely to be of little relevance, since flowing surface water only occurs a few times every century. Seventeen of the 57 species exhibited germination percentages of over 10% after artificial chewing and digestion and most of these species could be successfully dispersed endozoochorously (Horn 2008). These species showed a slight decrease in cover with increasing distance from the watering point, but since only up to 40% of the total cover values were represented by those 17 species, this trend might be an artefact of the small dataset and is therefore not included in Fig. 7.

It is concluded that sheep farming does have an effect on the distribution of dispersal traits in the landscape and could lead to an increase of animal-dispersed species in heavily used areas. As seedbanks of perennial grasses are often depleted in degraded areas (O'Connor & Pickett 1992) and most grasses showed only low to moderate wind dispersal potential, re-seeding or introduction of soil from intact areas need to be considered as options for restoration in these environments. Although dispersal potential in sheep wool was generally high, the proportion of seeds transported in sheep wool that would actually fall off and are thus able to germinate and establish needs to be studied in further detail before sheep can be considered as effective dispersal vectors for externally dispersed seeds.

The facilitation of spread of animal-dispersed species could be a serious problem in heavily grazed areas, such as in the case of the internally dispersed shrub *Grewia flava* (Tews et al. 2004), but a more important issue is probably the long-term sensitivity of the palatable perennial grasses to heavy grazing, because of depleted seedbanks and low abiotic dispersal potentials. Because of this, successful restoration is likely to be a laborious and costly process that needs to be studied further to identify the most effective strategies. It is important to remind landusers that an abundance of forage can be deceptive, and forage is virtually irreplaceable if used unsustainably.

Functional analysis of vegetation response to landuse intensity in the Kalahari

Environmental factors act as filters that select for those plant traits that promote species establishment, persistence and reproduction (Woodward & Diament 1991, Diaz et al. 1998). Landuse is an important filter that determines plant species assemblages and their associated plant traits in an area. The southwestern Kalahari is characterised by duneveld with relatively homogenous soils of aeolian origin, and is ideally suited for comparative analyses of the influence of landuse practices on vegetation structure and plant functional attributes. The influence of historic grazing intensity was investigated by comparing plant life forms, species richness and the Shannon-Wiener index of diversity and selected plant trait attribute scores across a range condition gradient. Range condition was determined for ten commercial livestock farms and one communal farm using line transect surveys in the dune street, dune slope and dune crest habitats of each farm. A selection of 112 dominant plant species was investigated for 46 vegetative and reproductive plant traits.

Principal coordinate analyses of plants species revealed that prominent growth forms constituting trees, shrubs, perennial, and annual grasses, as well as perennial and annual herbs could be further subdivided into various plant trait group permutations. Major life forms were linked with range condition over the study gradient. In the dune street habitat, perennial grass cover decreased and annual grass cover and shrub cover increased with decreasing range condition (Fig. 8a). In the dune crest habitat, perennial grass cover decreased and bare surface area increased with decreasing range condition (Fig. 8b). Plant species richness was positively correlated with increasing range condition in the dune street and dune crest habitats, and the Shannon-Wiener index was positively correlated with increasing range condition in the dune street and dune slope habitats.

Bush encroachment as an indicator of range condition deterioration due to sustained intensive grazing (Kalikawe 1990, Skarpe 1990, Skarpe et al. 2007) was supported by this study. In addition to increases in shrub cover by species such as black thorn (*Acacia mellifera*) and driedoring (*Rhigozum trichotomum*), other indicators of range condition can also be employed. Bare surface area in the dune crest habitat and annual grass cover (predominantly Kalahari sour grass *Schmidtia kalahariensis*) in the dune street habitat are also good indicators. Improved management of land should lead to greater species diversity and species richness, although higher species numbers may be encountered during the transition phase from good to poor range condition due to the simultaneous presence of late successional and pioneer species.

Interaction between diaspore size, microsites and livestock pressure in the Nama Karoo

It is well known that seed traits interact with microsite characteristics, which determine where a ground-drifting seed comes to rest (Chambers 2000). This interaction contributes to the spatial variation in seed abundance and specific seed distribution patterns at both community- and population levels. In a rangeland context, the degree of disturbance by grazing (i.e. the condition of the biophysical environment) selects for diaspore attributes that are linked to successful incorporation into the soil seed bank (Navie & Rogers 1997). This issue was investigated at the adjacent BIOTA Observatories Gellap Ost (S10) and Nabaos (S11) using data on seed densities in different microsites and diaspore mass as a proxy of seed size (N. Dreber, University of Hamburg, submitted).

In arid south-central Namibia, rangeland productivity is low due to a mean annual rainfall of 150 mm, high spatio-temporal variability of this rainfall, and frequent droughts. The vegetation is therefore sensitive to overgrazing and rangelands deteriorate easily. At the communal rangelands of Nabaos, situated near the town of Keetmanshoop in Namibia, long-term overstocking has con-

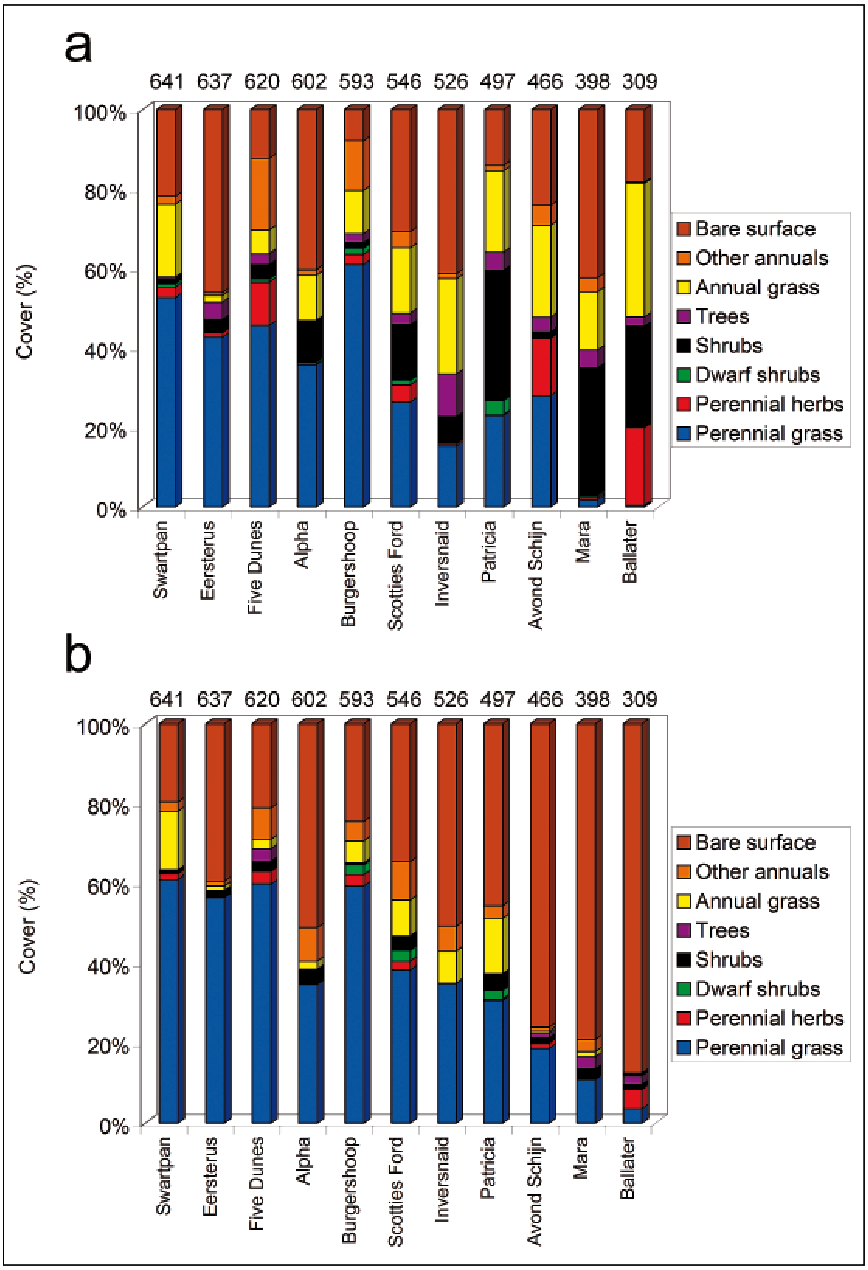


Fig. 8: The contributions of different life forms to vegetation cover (as percentage of total cumulative cover) across a previously identified range condition gradient in (a) the dune street habitat and (b) the dune slope habitat of the southwestern Kalahari. The farms are arranged from those representing good range condition on the left to those representing poor range condition on the right, with range condition scores (indicated as a score out of 1,000) on top of the bars.

tributed to a transformation of formerly grassy shrublands into open shrublands with perennial grasses replaced by annual, grazing resistant species. This degradation is expected to have altered the seed bank composition, and thus species related traits. In this regard, the response of mean diaspore size of seed bank species to the grazing regime, and the role of the grazing regime in the spatial patterning of the soil seed bank was analysed.

Seed densities were assessed at Nabaos (hereafter referred to as DEG for ‘degraded’) using the seedling emergence method, and compared with seed densities from the adjacent non-degraded Gellap Ost as a reference (REF). Sampling took place in January 2007 and 2008 just before summer rains and the onset of germination events. In order to account for small-scale spatial heterogeneity, seed banks were sampled in distinct microsites: (1) under shrubs (termed ‘CAN’ for canopy), (2) small physical barriers in the inter-shrub matrix (termed ‘OBS’ for obstacle), and (3) bare ground (‘BG’). OBS included grass tussocks, surface rocks, deadwood and soil depressions, which were all regarded to be able to trap ground-drifting seeds. In 2009, mature diaspores of the most common species previously found in the seed bank (N = 35) were collected in the standing vegetation, and the mean dry-mass (including appendages and enclosing structures, N = 90–100 diaspores species^{-1}) used as a measure of diaspore size. Diaspores were classified into four size categories: tiny = < 0.3 mg, small = 0.3–0.9 mg, medium = 1–5 mg, and large = > 5 mg.

The mean diaspore size of seed bank species for both years combined did not differ significantly between REF (mean 2.0 mg) and DEG (mean 2.7 mg). However, abundances of diaspores according to size varied with grazing intensity (Fig. 9). Overall seed densities were significantly higher in the degraded rangeland, which was particularly pronounced in 2008. While small diaspores constituted a dominant fraction of the seed bank at both REF and DEG, high grazing pressure clearly favoured the abundance of species with tiny diaspores (the most dominant being *Trianthema parvifolia*), which were considerably less abundant in the seed bank of REF. In contrast, medium-sized diaspores were more common under low grazing pressure (the most dominant being *Dicoma capensis* and *Stipagrostis hochstetteriana*). Most large-sized diaspores were detected in samples collected on DEG (Fig. 9).

Diaspore size also interacted with microsite, but patterns varied with sampling year due to the availability of readily germinable seeds in the seed bank (Fig. 9). There was an overall trend of decreasing seed densities in the order of CAN, OBS, BG, particularly in 2008. However, this pattern was less pronounced for tiny-sized and small-sized diaspores in the seed bank of DEG, where obstacles in the inter-shrub matrix trapped a similar amount of diaspores as shrubs. Large diaspores were clearly associated with CAN, which was obvious in 2008 when more readily germinable diaspores of this size were present in the seed bank. Most

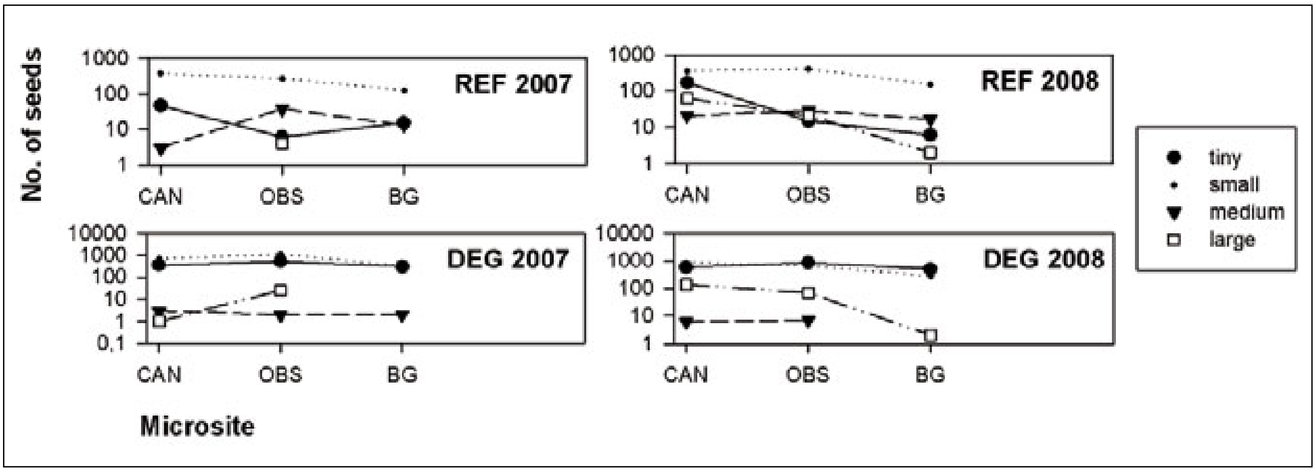


Fig. 9: Spatial distribution of diaspores by size among the sampled microsites according to their abundance in the germinable seed bank. REF = Gellap Ost (reference), DEG = Nabaos (degraded), CAN = canopy, OBS = obstacle, BG = bare ground.

diaspores of this size category belonged to the shrubs *Calicorema capitata*, *Phaeoptilum spinosum*, and *Rhigozum trichotomum*. Their high abundance under shrub canopies indicates either short distance dispersal and/or the harvesting activity of rodents, which have their burrows underneath shrubs. The seed bank in 2007 comprised less large diaspores, and those found belonged to the open-matrix forbs *Tephrosia dregeana* and *Tribulus terrestris*, with the former being very common in the standing vegetation of both REF and DEG. This is a possible reason why this size category was only abundant in OBS-microsites of the open-matrix. At REF, tiny diaspores (the most dominant being *Mollugo cerviana* and *Setaria verticillata*) were more common than expected by chance in CAN, as were medium-sized diaspores in OBS. Overall, bare ground was only able to retain mainly tiny or small diaspores, which might be due to its smooth and crusted soil surface. The high abundance of this seed size category on DEG and the fact that bare ground is more prominent at DEG (Petersen 2008) indicates a selection for species adapted to bare environments, under high grazing pressure.

The results show shifting patterns of diaspore distribution in response to spatial heterogeneity and grazing. Besides differences in the ability to trap and accumulate diaspores (e.g. large physical barriers such as shrubs are most effective in doing so), the type of microsite acts as a filter to some degree for certain diaspores. Most obvious was a tradeoff between the number of diaspores and their size, which was characteristic for DEG. Smaller seeds are more likely to get incorporated into the soil seed bank, even when the soil surface is smooth. This interaction is important as it shows, for example, that for bare land restoration in arid Nama Karoo ecosystems, loosening crusted soil surfaces has to be considered in order to promote accumulation of a variety of different sized diaspores. However, detailed investigation is needed to provide clarification on the interactions between soil surface structures and morphological diaspore traits at the patch-scale.

Plant functional types as indicators of landuse impacts in the Succulent Karoo

The Kamiesberg region has been the home of colonising farmers and indigenous herders for many centuries (Adamson 1938, Archer et al. 1989, Hoffman et al. 2007). However, unpalatable forage, a paucity of grasses and the lack of water limit livestock grazing and related agricultural practices not only on commercial farms, but also on the communal lands in this area. Most of the region is currently still utilised for extensive grazing by domestic livestock such as goats and sheep, resulting in overgrazing being a major environmental problem, which influences people's daily livelihoods (Baker & Hoffman 2006, Anderson & Hoffman 2007). While stocking rates on privately owned or commercial farmland have generally adhered to those recommended by the government, adjacent communal areas in the region have been stocked at approximately twice this rate over a period of decades (Hahn et al. 2005). Destructive agricultural practices, specifically large-scale cultivation and small-scale crop farming, have resulted in severe disturbance of the natural vegetation leaving patches of degraded land struggling to recover via natural successional processes. Many fallow or abandoned agricultural fields in the region, which were ploughed for cropping in previous years, are now only grazed by livestock (Kellerman & van Rooyen 2009).

Plant functional types were used as a tool to analyse and/or describe the effect of overgrazing and rotational crop farming in order to assess landuse impacts on the vegetation of abandoned agricultural fields (old fields) on communal and commercial farmland. Plant functional traits, which were recorded, measured, and analysed for selected plant species dominating old fields of different ages included the following: (a) growth form, (b) plant height, (c) canopy diameter, (d) percentage plant cover, (e) leaf surface area, (f) fresh and dry leaf mass, (g) leaf length and width, (h) specific leaf area, (i) percentage leaf water content, (j) dispersal mode, (k) diaspore morphology, and (l) seed mass (Cornelissen et al. 2003).

In 2005 and 2006, 44 plots of 50 x 20 m were surveyed on selected old fields throughout the Kamiesberg region (Shmida 1984, Stohlgren et al. 1995). Fifteen of these plots were representative of communal farmland and 29 of privately owned land, all at varying altitudes. Within each plot, all plant species were recorded and the cover of each species was visually estimated. Each species was assigned to one of ten plant functional types based on growth form and life history, and included the following categories: (a) annuals/ephemerals, (b) annual grasses, (c) geophytes, (d) perennial forbs, (e) perennial grasses, (f) dwarf succulents, (g) dwarf succulent shrubs, (h) succulent shrubs, (i) dwarf woody shrub, and (j) woody shrub.

Preliminary findings indicated that the practice of sustained heavy grazing on communal farmland in the Kamiesberg region leads to a decrease in palatable perennial woody and succulent shrubs and a shift towards annuals and geophytes. The sustained heavy grazing retarded vegetation recovery on the old fields. Rotational grazing on commercial farms promoted the recovery of the disturbed vegetation and led to an increased occurrence of palatable woody and succulent shrubs on old fields of commercial farms, with a general reduction in cover of ephemeral plants and geophytes.

Conclusions and identified research needs

A variety of plant functional approaches regarding the impact of different landuse regimes or landuse changes were applied in various regions and on different spatial scales within the BIOTA Southern Africa framework. Common features of all the different study areas were the semi-arid to arid climate and the pastoral landuse, either on communal or privately owned rangeland. Differences in plant functional trait patterns and plant functional type composition were studied along grazing gradients under different land tenure systems taking habitat and microsite variability into account.

One common goal of the trait based approaches within BIOTA was to identify indicators of rangeland states in response to grazing history and present grazing intensity. In this context, the use of plant traits instead of species enables the identification of general patterns in vegetation response to livestock disturbance across taxonomic levels. Another reason for using traits as surrogates for species is that not all landusers are familiar with species names and proper species identification. The use of traits could thus facilitate regular monitoring activities for land managers—a crucial requirement in these variable semi-arid/arid environments, which are expected to face additional future problems caused by climate change. A simple, yet effective monitoring tool is the adapted Landscape Function Analysis (LFA, Tongway & Hindley 2000). This tool, coupled with the use of plant traits to indicate a pioneer or a late successional state of the vegetation, could be a promising way to support landusers in their management decisions. Detailed growth form features, which have been proven to decrease or increase with increasing grazing pressure (e.g. in the Namaqualand region of South Africa) can easily be incorporated into rangeland monitoring tools such as LFA. However, the task still remains to adapt monitoring tools based on plant functional types to the different biomes or to broad vegetation types. Furthermore, even at the landscape scale, major changes in habitats require indicator traits that respond consistently to grazing across different soil types or other environmental parameters related to these habitats. Traits that fulfilled this criterion in a study in central Namibia were specific leaf area (SLA), life cycle, leaf blade fragmentation, clonality and dispersal mode. Seed traits, such as the dispersal ability, are highly indicative of landuse changes and were found to be influenced by grazing in the southern Kalahari. Here, animal dispersed species were more likely to occur in areas that were heavily utilised by livestock. Furthermore, it was shown that the cover and occurrence of fleshy-fruited plant species was strongly correlated to landuse type and intensity. These species are easy to recognise and may therefore serve as suitable indicators to define suitable management strategies and grazing intensities. Other seed traits, such as diaspore size and morphology, interact with the physical environment during dispersal which, in combination with a certain grazing intensity, significantly influences the spatial distribution and composition of seed banks as shown in the Nama Karoo. The seed bank in turn is a crucial factor with respect to the restoration of degraded rangelands. Further studies of the distribution of dispersal traits and factors influencing the seed bank composition under different landuse intensities will help to make future restoration efforts more cost effective and successful.

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The impact of grazing on pollinators and pollination

Carolin Mayer

Summary: The effects of livestock grazing on plant-animal interactions such as pollination processes have rarely been studied. Since plant diversity and flower occurrence can be substantially reduced by grazing, presumably associated insect assemblages are also affected. In our study, along with flower availability insect abundance as well as species diversity was diminished under heavy grazing. However, trapping methods can be biased. Colour traps for example compete with flowers for the attraction of pollinators. The observed reduction of fruit set in the investigated plant species apparently did not result from pollination limitation since seed production was fairly similar for all species. For two closely investigated species, even more flowers remained un-pollinated under low grazing pressure. Obviously, the site with a long grazing history still supports a vivid pollinator community.

Photo1: Monkey beetles (Hopliini) meeting to mate in flowers of *Ruschia goodiae*. Photo: Carolin Mayer.

Introduction

Many studies on the impact of grazing in the Succulent Karoo Biome have centred on vegetation (Milton & Dean 1990, Milton 1995, Steinschen et al. 1996, Riginos & Hoffman 2003, Hendricks et al. 2005), and abiotic conditions relating to vegetation e.g. soil properties (see Chapter IV.4). So far, not many publications exist on biotic interactions of the vegetation with other organisms such as pollinators, seed dispersers or herbivores other than livestock. For example, among the publications reporting on the grazing impacts to arthropod diversity in South Africa (Seymour & Dean 1999, Gebeyehu & Samways 2002, 2003, Fabricius et al. 2003), only one specifically focused on an insect group that is important for pollination (Colville et al. 2002). However, since about 90% of all flowering plants in the world rely on animals as pollen vectors (Kearns & Inouye 1997, Ingram et al. 1998) it is also necessary to look at the impact of grazing on a crucial step in plant reproduction, i.e. pollination success.

In general, grazing is considered to have negative impacts on pollination systems (Kevan 1999, Devoto & Medan 2004). Very often only the reproductive deficits suffered by plants are investigated but there is a lack of concrete data regarding the impact of grazing on pollinator communities (but see Gess & Gess 1993, Thomson 2001, Devoto & Medan 2004).

Grazing can affect pollinating insects through altering the availability of nesting sites, water resources and vegetation. Decreasing plant diversity and decline of floral resources often reduces pollinator abundance and diversity (Memmott et al. 2004, Kremen et al. 2007). Trampling by livestock can directly destroy the habitat of ground nesting bees and wasps while compacted soil aggravates nest construction. Many ground nesting insects that depend on shallow water pools for nest construction can suffer from altered water regimes on rangeland (Gess & Gess 1993, Mayer 2004). Within BIOTA we investigated whether livestock grazing negatively affects the habitat quality for pollinating insects in terms of flower availability and whether pollinator assemblages are reduced in abundance and diversity on heavily grazed land. We further looked at possible consequences on the reproductive success of certain plant species, all belonging to the Aizoaceae, one of the major the families occurring in the Succulent Karoo.

Impact on flower occurrence

The findings of other studies that heavy livestock grazing reduces the number of flowers per individual plant (Milton 1992, Ehrlen 1997, Todd & Hoffman 1999) could be confirmed for most of the examined plant species of the Aizoaceae family (*Cheiridopsis denticulata*, *Cheiridopsis imitans*, *Ruschia viridifolia*, *Ruschia goodiae*, *Ihlenfeldtia excavata*, *Leipoldtia schultzei*), however not in every year of study (Table 1).

It is supposed that the late and scanty rainfall in 2003 (compare Observatories II.6.5, II.6.6) was responsible for the insignificant differences found in flower numbers for plants growing under high and low grazing pressures. Grazing pressure was significantly reduced in this year since herd sizes were enormously diminished.

Total flower occurrence for perennial plants was reduced in heavily grazed areas, while for annual plants and geophytes flower display area increased (Fig. 1).

Table 1: Flower numbers per plant volume—differences between heavily and lightly grazed site

		Mean ± SD							
Plant species	**Year**	**Lightly grazed (*N* = 30)**			**Heavily grazed (*N* = 30)**			***Z*/*t* (*df*)**	***p*-level**
Cheiridopsis denticulata	2002	0.00049	(±0.00047)	A	$3.32\ e^{-10}$	($\pm 7.42\ e^{-10}$)	A	2.626	**0.009**
	2003	0.00049	(±0.00044)	A	0.00027	(±0.00052)	A	2.642	**0.008**
	2004	0.00243	(±0.00124)	B	0.00333	(±0.00218)	B	–1.769	0.077
Cheiridopsis imitans	2002	0.0251	(±0.0164)	A	0.0475	(±0.0393)	A	–2.447	**0.014**
	2003	0.000027	(±0.000013)	B	0.000027	(±0.000027)	B	–0.057 (58)	0.955
	2004	0.0083	(±0.0072)	C	0.0198	(±0.0411)	C	–0.016	0.987
Ruschia goodiae	2002	0.0024	(±0.0017)	A	0.0022	(±0.0022)	A	0.902	0.367
	2003	0.00073	(±0.0022)	B	0.00055	(±0.0011)	B	–0.843	0.399
	2004	0.0094	(±0.0043)	C	0.0092	(±0.0069)	C	–1.109	0.268
Ruschia viridifolia	2002	0.0104	(±0.0073)	A	0.0059	(±0.0036)	A	2.794	**0.005**
	2004	0.0171	(±0.0160)	A	0.008	(±0.006)	B	–1.994	**0.046**
Ihlenfeldtia excavata	2003	0.0804	(±0.0624)	A	0.0943	(±0.0644)	A	–1.050	0.294
	2004	0.0457	(±0.0190)	B	0.0363	(±0.0159)	B	–2.088 (58)	**0.041**
Leipoldtia schultzei	2004	0.041	(±0.0270)	A	0.0068	(±0.0061)	A	–6.047	**0.000**

Rows that share the same letter do not differ significantly between the years (Mann-Whitney-U or Students' t test). *R. viridifolia* and *L. schultzei* flowered too late in 2003, *I. excavata* and *L. schultzei* were not investigated in 2002.

Impact on pollinators

Insect abundance was reduced by grazing, as results from transect walks and Malaise traps confirmed (Fig. 2, Mayer 2004). However, the number of individuals counted during transect walks differed significantly within one site from year to year. One must be cautious not to make spurious conclusions regarding pollinator decline. Probably only longer term studies will provide meaningful insights in pollinator population changes.

Whether pollinator richness and diversity are negatively impacted by grazing, is more difficult to confirm and depends on the sampling method that is employed. A reduction of pollinator diversity could be demonstrated with Malaise traps, while colour trapping gave a different picture (Figs. 3 & 4). But these results have to be interpreted with care since they could represent an artefact of sampling procedure. The results from colour traps are influenced by several factors that lead to this reversal of results. These factors include

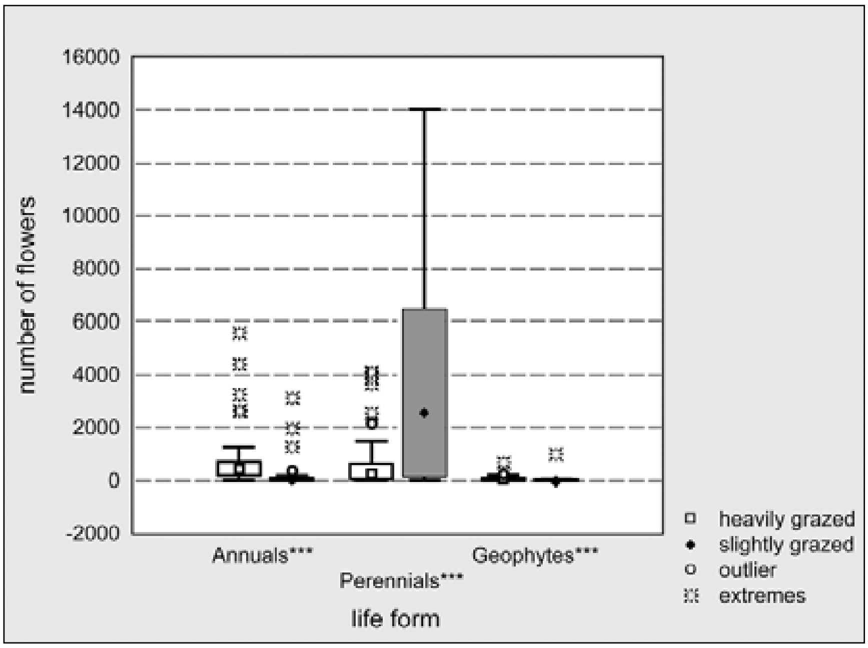

Fig. 1: Flower counts from plants with different life forms on heavily and slightly grazed sites as recorded during transect walks in 2003 and 2004. (Annuals: $Z = 5.21$, $N = 57$ & 41, $p < 0.0001$, perennials: $Z = –4.59$, $N = 59$ & 67, $p < 0.0001$, geophytes: $Z = 3.89$, $N = 50$ & 26, $p < 0.0001$).

plant cover, plant height and, most importantly, flower numbers and flower display area. Colour traps compete with flowers for the attraction of bees (Mayer 2005). In general, insect abundance and diversity was also greatly affected by climatic conditions. The species composition was more similar between grazed and ungrazed sites than within one site among different years. However, looking at single pollinator groups, e.g. monkey beetles (Hopliini, Scarabeidae, Fig. 4), a change in the community composition can be observed under heavy grazing pressure (Mayer et al. 2006).

Impact on fruitset

The fruit set of plants, i.e. several Aizoaceae species, was diminished by grazing. All examined plant species showed lower fruiting success under high grazing pressure (Fig. 5), yet not in the drought year. Again, most probably the late rainfall in 2003 and the resulting diminished grazing pressure increased similarities between grazed and ungrazed populations (Pufal et al. 2008).

However, the reduction of fruit set mainly did not result from pollination limitation. Closer inspections on flowers of *C. imitans* and *L. schultzei* showed significantly higher fruit loss due to pollination deficits on the slightly grazed site. In addition, all flowers of individuals of *C. imitans* protected against grazing on the heavily grazed site were pollinated (Pufal et al. 2008). For the majority of investigated plant species seed production was not reduced (Fig. 6). Apparently, the site with a long grazing history also still supports an adequate flower visiting insect society to guarantee pollination of the considered plant species. Since their pollination system is a generalised one, any insect carrying outcross pollen is capable of leading to pollination of a flower (Mayer & Pufal 2007). The decreased fruit set is a consequence of direct grazing of flowers and fruits. In general, fruit or flower loss may not only depend upon livestock grazing, but also on other, more subtle herbivores such as caterpillars or rodents. Livestock, however, accounted

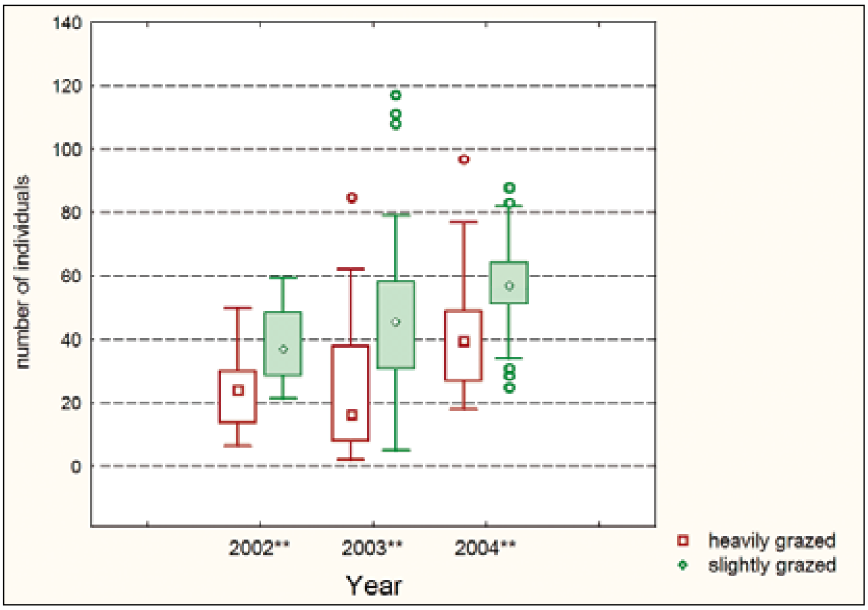

Fig. 2: Mean number of insects as observed during transect walks in different study years. Highly significant differences are marked with **. (2002: $t = -6.03$, $df = 86$, $p < 0.0001$, 2003: $t = -4.26$, $df = 68$, $p < 0.0001$, 2004: $Z = -6.51$, $p < 0.0001$, $N = 40$).

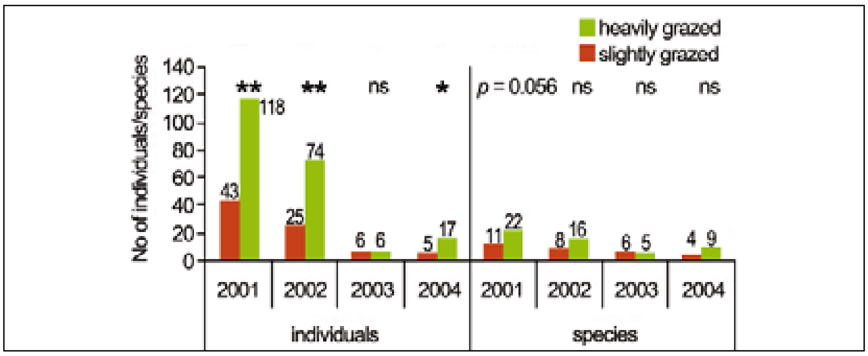

Fig. 3: Malaise traps—number of individuals (left) and species (right) of bees caught in subsequent years.

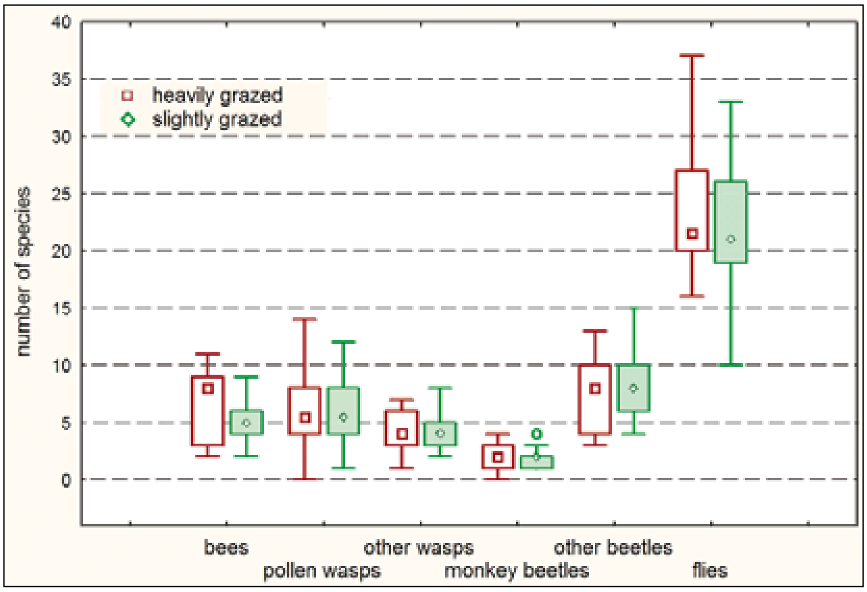

Fig. 4: Mean number of species of different pollinator groups as caught in 2004 with colour traps.

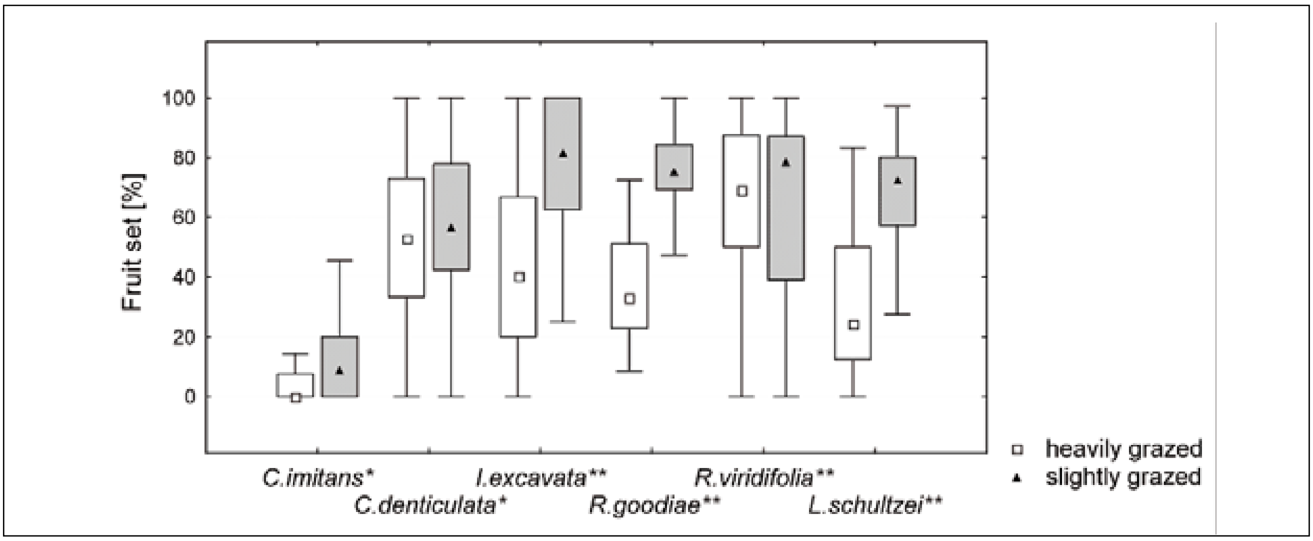

Fig. 5: Fruit set of the examined species in 2004. Significant differences between heavily and slightly grazed sites are marked with * ($p < 0.05$) and ** ($p < 0.01$).

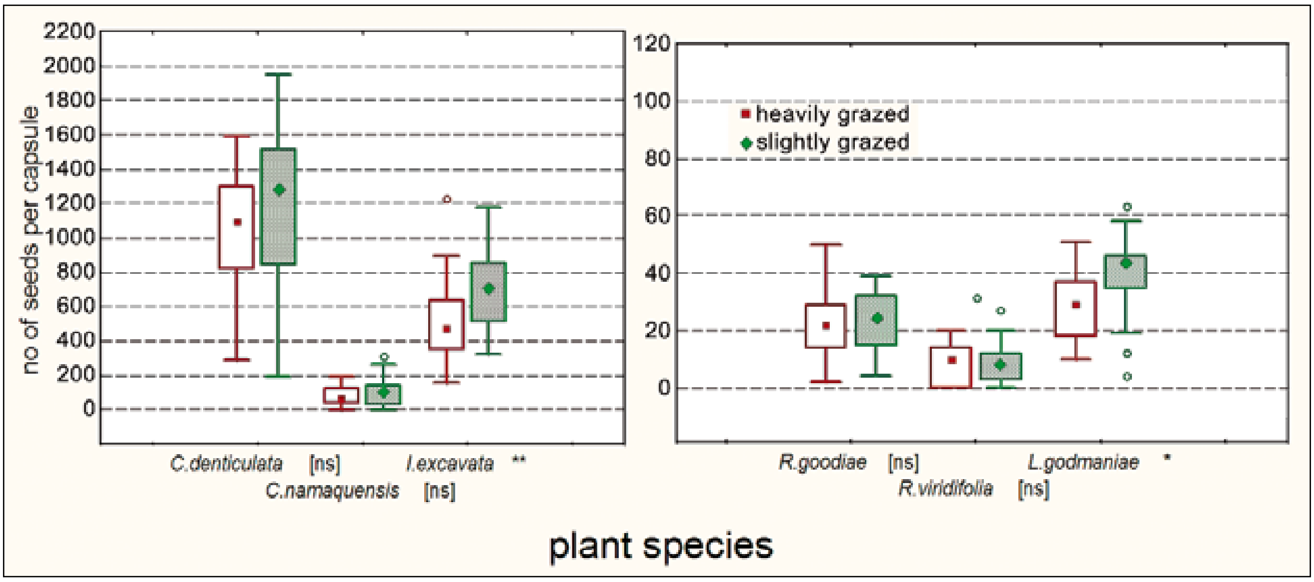

Fig. 6: Average number of seeds per fruit capsule for seven plant species. Significant differences are marked with *.

for the extra loss of fruits on the heavily grazed site (Pufal et al. 2008).

Conclusions

The present study clearly confirmed previous work conducted in the Succulent Karoo in that plant recruitment is seed-limited due to lower flower and fruiting success in overgrazed areas. The indirect impact of domesticated herbivores on plant reproduction via deterioration of pollination systems could not be demonstrated unequivocally. Aspects of decline of insect abundance and diversity could be shown, although it remains unclear how strongly diversity is affected. Since generalised pollination systems are proposed for Namaqualand, pollinators may be able to switch from perennial to annual plants and might thus not be affected in normal years. In drought years, however, pollinators could likely experience food shortages and suffer from reproductive failure (Mayer & Kuhlmann 2004). Therefore, with the risk of climate change and aridification in the Succulent Karoo (compare Article III.1.1) there is a threat that pollination systems may break down. This study focused on generalistic plant species, more specialised systems are probably more vulnerable (Mayer & Kuhlmann 2004) and remain to be investigated.

Implications for conservation management

It seems that the major impact of high grazing pressure acts directly on the vegetation by reducing the reproductive capability of plants. For some species (e.g. *Cheiridopsis denticulata*) it might

Photo 2: Geoffrey Soka catching monkey beetles with colour traps.
Photo: Carolin Mayer.

Photo 3: *Cheiridopis imitans* heavily grazed by livestock.
Photo: Carolin Mayer.

be sufficient to release grazing pressure to improve reproductive output. The traditional method of livestock husbandry practised in Namaqualand would allow bypassing plant populations during the time of flowering and fruiting. The herds of goats and sheep are kept at 'stockposts' over night from where they are released in the morning and follow daily grazing routes (Riginos & Hoffman 2003). These animals are often accompanied by a herder who searches for the best areas for grazing. Normally, flowering Mesembryanthema are targeted as fodder supply since livestock especially head for the nutritious flowers when foraging. Nevertheless, by increasing the awareness among local people for the necessity to improve shrub recruitment herders could guide their stock to avoid at least some of the flowering patches. Since seedling establishment is not supposed to be reduced by grazing or trampling (Milton 1994, Riginos & Hoffman 2003) this could help to improve recruitment of young plants. Other measures, such as grazing exclosures, would support regeneration and could also serve as source populations for both plants and insects for rehabilitation of surrounding areas. Restrictions of fire wood collection would enhance the availability of suitable nesting sites for many arthropods and safe sites for seedling recruitment. These are, however, more expensive measures and it is arguable whether communities can and are willing to afford them (Mayer 2006).

Acknowledgements
The authors' general acknowledgements to the organisations and institutions, which supported this work are provided in Volume 1.

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Overgrazing favours desert species—differences in arthropod and small mammal communities of the twin sites Gellap Ost and Nabaos

Anke Hoffmann*, Katrin Vohland & Ulrich Zeller

Summary: The impact of two different grazing systems on arthropod and small mammal communities was investigated by comparing species diversity and abundance between Gellap Ost (S10) and Nabaos (S11) on two-hectare plots seasonally during the period 2001–2003. Assessing and monitoring of the small mammal populations was achieved using capture-mark-recapture methods. Arthropods were collected in pitfall traps. For both groups, species richness, total abundance and species diversity were lower in the overgrazed area. The most abundant small mammals were two gerbil species. The Bushveld Gerbil (*Gerbilliscus leucogaster*) occurred frequently at Gellap Ost but did not occur at the overgrazed Nabaos site, while *Gerbillurus vallinus*, a species adapted to xeric conditions, favoured the degraded land. It is also obvious that uncontrolled grazing in the communal lands has led to land degradation, which has affected the biodiversity as indicated by the shift from "savannah communities" to "desert communities" of beetles and small mammals.

Photo 1: Weighing of a captured Bushveld Gerbil. Photo: Anke Hoffmann.

Introduction

The study was conducted on two neighbouring areas with different landuse practises in the Nama Karoo in Namibia. The Nabaos (S11) communal area is highly overgrazed mainly by goats, whereas the adjacent Karakul sheep breeding farm at Gellap Ost (S10) is only moderately grazed. In contrast to the uncontrolled grazing in Nabaos, Gellap Ost is under a rotational grazing system with a lower stocking rate (for more details see Chapter II.4, Observatories S09, S10, S11).

The different grazing systems of these areas not only determine vegetation patterns but also impact animal communities such as small mammals and arthropods. Both groups fulfil important functions in ecosystems. Arthropods play an important role in pollination and contribute to nutrient turnover and soil engineering. Furthermore, they serve as a food source for other animals such as small mammals and birds. Small mammals are important consumers (Kerley 1992a), predators and dispersers of seeds (Price & Jenkins 1986), burrowers, and prey for carnivores and raptors (Kotler 1984, Hughes et al. 1994). Changes in habitat structure and complexity are known to be associated with changes in small mammal community structure and species richness (Rosenzweig & Winakur 1969, Grant et al. 1982, Rowe-Rowe & Meester 1982, Abramsky 1988, Kerley 1992b, Els & Kerley 1996, Avenant 2000). Large herbivores (e.g. livestock) can modify the vegetation layer in terms of structure and species composition to a state where small mammals are affected (Bowland & Perrin 1989, Keesing 1998, Hoffmann 1999, Blaum et al. 2009).

The aim of this study was to assess the influence of the different landuse intensities at Gellap Ost and Nabaos on the diversity and ecology of arthropods and small mammals.

Methods

A two-hectare plot was selected at each Observatory. Small mammal population ecology data (diversity, abundance, reproduction, survival) were assessed during a 2-years capture-mark-recapture study, which was conducted over four consecutive trapping nights per season (= one trapping session) on each plot. 90 Sherman® folding live traps spaced at 15 m intervals were used per plot. Captured animals were individually marked, weighed and sexed (Photo 1). Between October 2001 and August 2003, eight trapping sessions per plot were conducted.

At the same time, 10 pitfall traps were set along a line over a period of eight days in each season to analyse arthropod activity. The arthropods were identified taxonomically at least to family level, and for beetles, specimens were allocated to different size classes

Table 1: Size classes in beetles (Coleoptera) allocated according to their dry weight

Size class	Dry weight [mg]
1	0–0.99
2	1–9.99
3	10–99.99
4	100–199.99
5	200–299.00
6	> 300

Table 2: Ant species at Gellap Ost and Nabaos (Koch & Vohland 2004)

	Gellap Ost	Nabaos
Formicinae		
Camponotus exsanguis Forel, 1990	+	
Camponotus fulvopilosus (De Geer, 1788)	+	+
Camponotus mystaceaus Emery, 1886		+
Myrmicinae		
Messor capensis (Mayr, 1862)	+	
Ocymyrmex dekerus Bolton & Marsh, 1989	+	+
Tetramorium rufescens Stitz, 1923	+	+
Tetramorium sericeiventre Emery, 1877	+	+
Ponerinae		
Pachycondyla cf. *caffraria* (F. Smith, 1858)	+	
Dolichoderinae		
Tapinoma sp.		+
Sum of species number	**7**	**6**

(Table 1). More details can be found in Hoffmann & Zeller (2005) and Vohland et al. (2005).

Results and discussion

Arthropod communities

A total of 16,713 epigaeic arthropods (without considering mites and collembola) from 19 orders were collected over 1,280 trap-nights. Ants (9,466 specimens), beetles (1,673 specimens), and termites (747 specimens) were the dominant arthropod taxa collected. Most animals were trapped during February in both years, during the rainy season (Fig. 1). There was less arthropod activity at Nabaos than at Gellap Ost, with only 38% of the ground active arthropods being trapped at Nabaos.

Ants dominate

Typically, ants were trapped in high abundances and with high biomass. These successful insects mainly act as decomposers, soil engineers and seed dispersers in ecosystems (Hölldobler & Wilson 1990). At Gellap Ost and Nabaos, nine species were identified, with only slight differences in species composition and diversity between the sites (Table 2).

Termites—the omnipresent workers

Three termite species were found at both Observatories: *Baucaliotermes hainesi*, *Hodotermes mossambicus*, and *Psammotermes allocerus* (Vohland & Deckert 2005).

B. hainesi was mainly recorded as alates after the rain in May 2002. This species is endemic to the Northern Cape Province of South Africa, and to southern

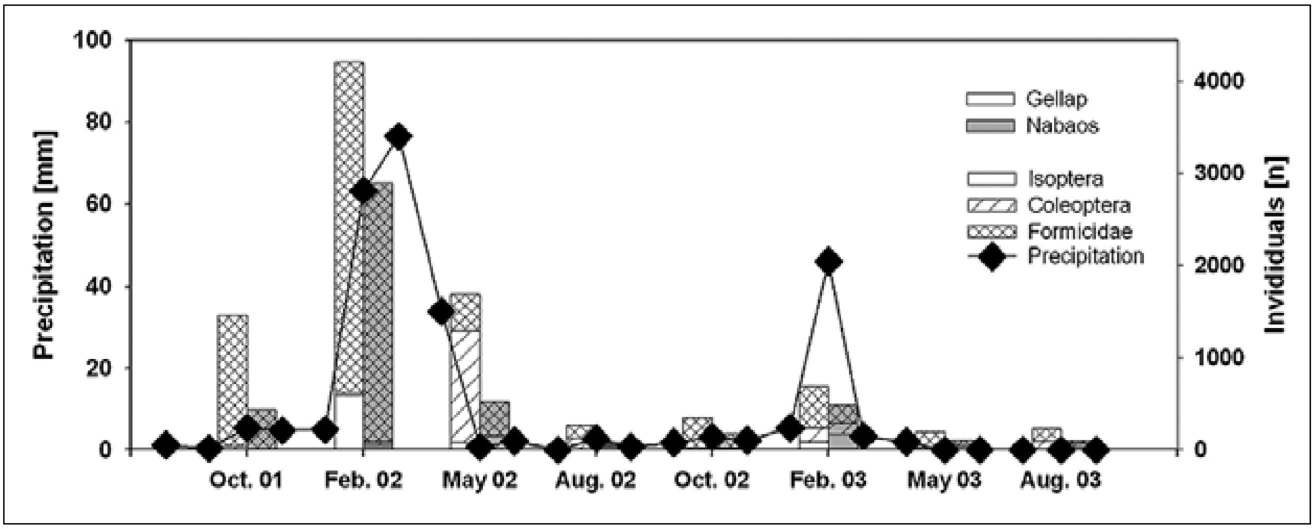

Fig. 1: Monthly precipitation and abundance of the dominant arthropod groups: termites (Isoptera), beetles (Coleoptera) and ants (Formicidae). During the rainy season in February of both years arthropod activity was higher than during the rest of the year. Actual precipitation from 2001–2003 as measured by the BIOTA weather station (K. Berger, pers. comm.).

Namibia. It is distributed in the Nama and Succulent Karoo biomes, where it occurs in the succulent steppe, semi-desert savanna transition, and dwarf shrub savanna (Coaton & Sheasby 1973, Uys 2002). *B. hainesi* build subterranean nests, which can be recognised as small heaps on the ground. This nocturnal species feeds on coarse and fine litter as well as on herbivore dung.

The harvester termite *H. mossambicus* is one of the most widely distributed species in southern Africa (Coaton & Sheasby 1972). It can process large amounts of soil (Grube 2001) and therefore contributes to bioperturbation, and increases water infiltration and nutrient turnover in the soil (Holt & Lepage 2000). On the other hand, *H. mossambicus* can become a pest (Coaton 1958, Mitchell 2002). Even in years with average rainfall, this species is estimated to consume about 25% of the standing grass crop (Coaton & Sheasby 1972). Especially in habitats with sparse vegetation cover, it can locally become a serious pest, as they prefer to settle on bare soil (Coaton 1958). However, despite competition between this species and livestock/game for grass, it probably has an overall positive effect on ecosystem functioning (Logan 1992). As shown in Fig. 2, abundances at Nabaos were lower than at Gellap Ost. This could be a result of the almost complete absence of grassy vegetation cover at Nabaos. The soil at Gellap Ost had a higher organic content and a higher water infiltration rate, which promotes vegetation growth.

P. allocerus is known to consume wood, and has been known to attack man-made wooden structures such as houses, but they also feed on grass detritus (Coaton & Sheasby 1973, Crawford & Seely 1994).

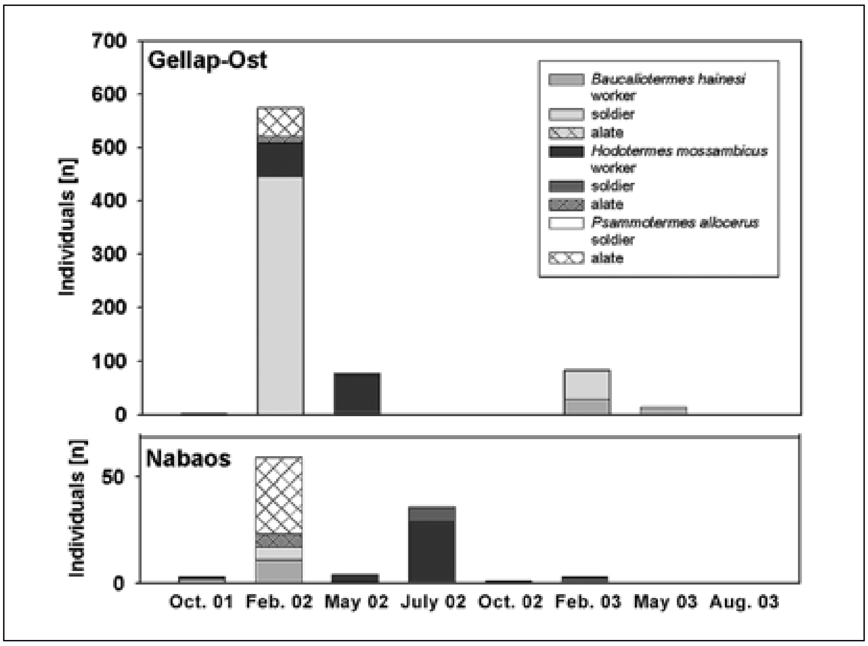

Fig. 2: Termite species at Gellap Ost and Nabaos. Species identity, developmental stage and abundance.

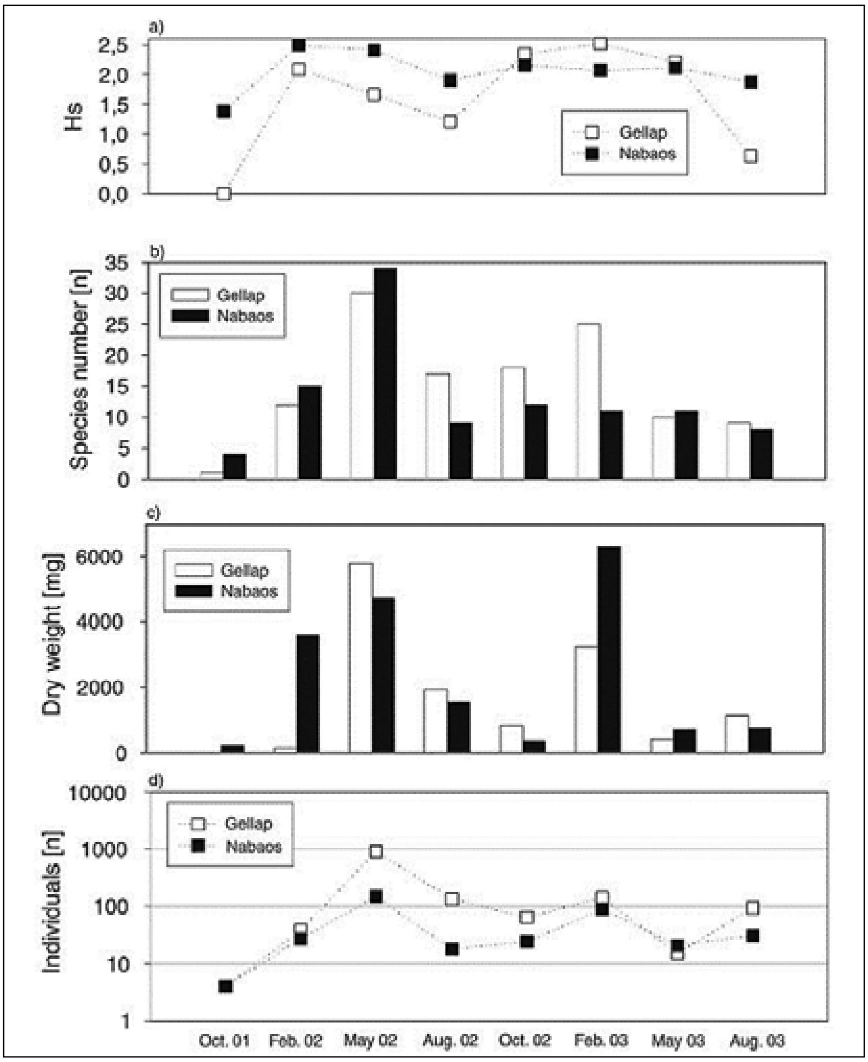

Fig. 3: Coleoptera diversity, abundance and biomass. a) Shannon Wiener index of diversity (HS); b) species number; c) biomass distribution; d) number of individuals (from Vohland et al. 2005 [Copyright Wiley-VCH Verlag GmbH & Co. KGaA. Reproduced with permission]).

Coleoptera—degradation favours desert beetles

Beetles represented the most species rich taxa (Fig. 3), and many species remain undescribed. Beetles had a variety of forms and functions. As was the case for all groups, the actual results were biased due to the trapping method used. Pitfall traps reflect activity density rather than abundance. However, the results do re-

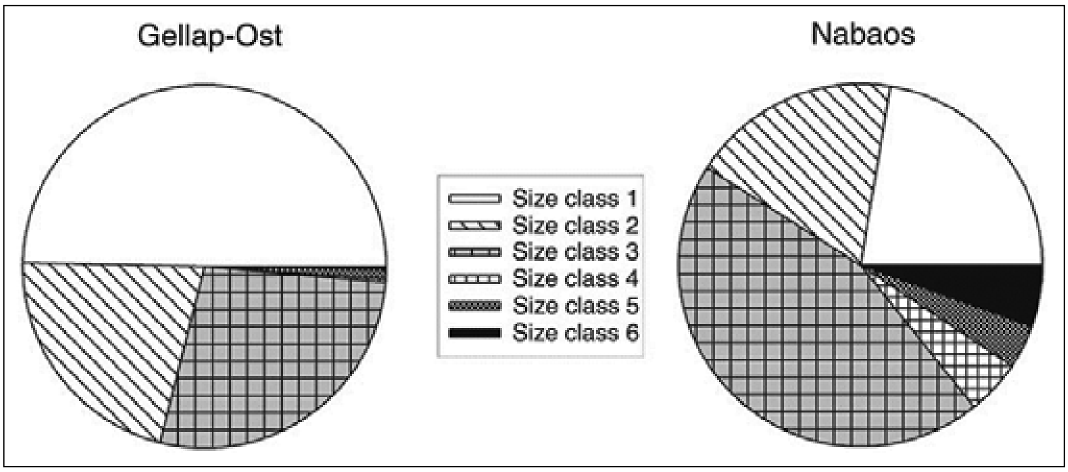

Fig. 4: Coleoptera size class distribution from 1 (light) to 6 (heavy), cf. Table 1 at Gellap Ost and Nabaos, data pooled (from Vohland et al. 2005 [Copyright Wiley-VCH Verlag GmbH & Co. KGaA. Reproduced with permission]).

Table 3: Species diversity and abundance of small mammals at Gellap Ost and Nabaos

		Nabaos		**Gellap Ost**	
	per plot 2880 trap nights	**ind.**	%	**ind.**	%
Macroscelididae					
	Elephantulus intufi	**1**	0.92	**9**	4.45
Muridae	**Gerbillinae**				
	Desmodillus auricularis	**10**	9.17	**3**	1.49
	Gerbilliscus leucogaster			**118**	58.42
	Gerbillurus paeba	**1**	0.92		
	Gerbillurus vallinus	**80**	73.39	**44**	21.78
	Murinae				
	Micaelamys namaquensis	**1**	0.92	**13**	6.44
	Mus indutus			**2**	0.99
	Rhabdomys pumilio	**12**	11.01	**4**	1.98
Nesomyidae	**Cricetomyinae**				
	Saccostomus campestris	**4**	3.67	**9**	4.45
	total individuals	109		202	
	Σ captures	282		629	

veal fundamental ecological differences between the sites.

The largest proportion of beetles trapped were non-alate tenebrionid beetles (Tenebrionidae). The adjacent plots at Gellap Ost and Nabaos shared more or less the same species, i.e. 19 taxa (Vohland et al. 2005). This is in accordance with general knowledge on the Tenebrionidae (darkling beetles), for which the soil substrate is the most important variable in terms of habitat quality (Louw 1983). Tenebrionidae are also known to be affected by habitat modification and diminished habitat diversity, which was clearly visible in this study. Seven species were recorded only at Gellap Ost, whereas only three Adesmiini species were recorded at Nabaos. The higher abundance of Adesmiini in Nabaos was the main contributor to the difference in species composition between plots. These medium to large sized darkling beetles are desert adapted insects that show morphological and behavioural adaptations to cope with arid conditions (Rasa 1994, Naidu 2001, Parker & Lawrence 2001).

The species composition of scarab beetles (Scarabaeidae) is mainly affected by soil characteristics, vegetation and dung quality (Davis 1996, 2002). Therefore, it is possible that the higher dung resource availability at Nabaos is the reason for the higher diversity of dung beetles at this Observatory compared to Gellap Ost.

High diversity of ground beetles (Carabidae) is interpreted as an indicator of complexity in agro-ecosystems and natural habitats (Rainio & Niemala 2003). The diversity and abundance of Carabidae was clearly higher at Gellap Ost than at Nabaos. Carabidae are predators, and they are therefore higher up on the food chain. Therefore, they act as indicators of complex dietary networks. Denser and more diverse vegetation offers more potential prey and shelter, which is reflected in the higher abundance of Carabidae at Gellap Ost.

The higher abundance of large beetle species at Nabaos (Fig. 4) might be due to the lower vegetation cover here, which does not restrict the movements of these predatory beetles, which hunt by sight.

Small mammal communities

A total of 311 individuals (911 captures) representing nine species were caught over 5,760 trap-nights (Table 3). The overall species richness and abundance was lower at Nabaos than at Gellap Ost. This is also expressed by the Shannon Wiener diversity index (Hs): Nabaos (Hs 0.95; 7 species, 108 individuals), Gellap Ost (Hs 1.29; 8 species, 202 individuals). Although fewer species were recorded per trapping session at Nabaos (Fig. 5) compared to Gellap Ost, there was an overlap in the species occurring at the two plots (Table 3).

The most frequently trapped species at the Gellap Ost Observatory, the Bushveld Gerbil (*Gerbilliscus leucogaster*), prefers

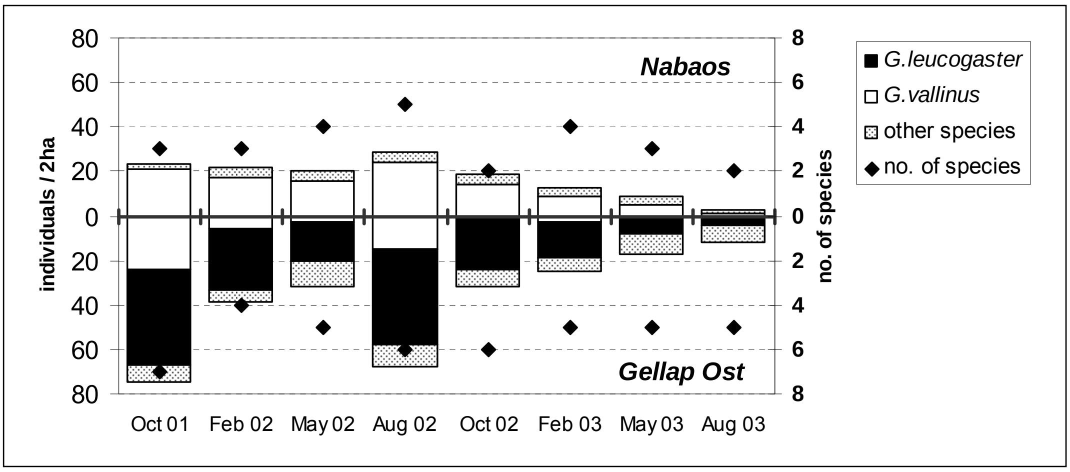

Fig. 5: Species richness of small mammals at Gellap Ost and Nabaos. All captured species and the total recorded individuals ($N = 311$) over all trapping sessions (5,760 trap-nights). One 'trap-night' refers to one trap being set for 24 hours.

Photos 2 and 3: The most abundant rodent species at Gellap Ost and Nabaos: Bushveld Gerbil (*Gerbilliscus leucogaster*) and the Bushy-tailed Hairy-footed Gerbil (*Gerbillurus vallinus*). Photos: S. Bengsch and S. Lüdecke.

savannah environments (DeGraaff 1981), and did not occur at the degraded Nabaos site (Fig. 5, Photo 2). At Nabaos, the Bushy-tailed Hairy-footed Gerbil *Gerbillurus vallinus*, which is a desert inhabitant, was the dominant species. This species was subdominant in Gellap Ost where extreme fluctuations within the population were documented (Fig. 5, Photo 3).

At both sites, the highest recruitment of small mammals was observed in August 2002, due to high reproduction activity during the rainy season.

Intensive and uncontrolled grazing by livestock in the communal area of Nabaos not only had a clearly negative impact on small mammal diversity and abundance, but it also had an impact on their settlement and survival. Considering all individuals, which had been trapped over at least two successive sessions (≥ 11 weeks), we found a lower overall recapture rate at Nabaos (19.3%, $N = 109$) than at Gellap Ost (31.8%, $N = 202$). Five species were recaptured at Gellap Ost: *G. leucogaster*, *G. vallinus*, *M. namaquensis*, *E. intufi*, *S. campestris*. At Nabaos only *G. vallinus* and *D. auricularis* were recaptured. *G. vallinus* showed a distinctly higher recapture rate and a longer 'survival' period at Nabaos than at Gellap Ost (Hoffmann & Zeller 2005). The higher 'survival' rate of *G. vallinus* at Nabaos indicates that this xeric adapted species, which is confined to the western sector of the South West Arid Zone and is known to prefer sandy substrates (DeGraaff 1981, Dempster et al. 1999), has found a more suitable habitat in the degraded lands than in the grassy areas of Gellap Ost. This is in line with the results of a biodiversity study in the rangelands of South Africa (Fabricius et al. 2003), where a communal grazing area was characterised by xeric adapted reptiles and predatory arthropods, whereas a nature reserve and commercial farmland supported more mesic-adapted species.

Conclusion

Although a high resilience is ascribed to the study area (Kuiper & Meadows 2002), we conclude that the land degradation caused by uncontrolled grazing accounts for the impoverished flora and fauna of Nabaos in comparison to Gellap

Ost. The degraded vegetation provides few resources. In comparison with Gellap Ost availability of food is lower, there is less shelter and moisture from dew for arthropods and small mammals. This might lead to a reduction of ecosystem functions provided by arthropods and small mammals, such as soil turnover and soil engineering, and can subsequently reduce water infiltration and cause higher erosion rates. On the other hand "pasture pests" such as *Hodotermes* might benefit. Therefore, reduced abundance and species diversity of arthropods are a clear indicator of vegetation in a degraded state.

In addition, the disruption of habitat structure, cover and shelter leads to a higher predation risk for small mammals. The low species diversity and abundance of small mammals, and especially the dominance and high survival rate of the desert species, *G. vallinus,* in the communal land at Nabaos clearly indicates that landuse at this site has caused deterioration of the ecological conditions there. According to Avenant (2000), biodiversity of small mammals can be used as an indicator of disturbance in an ecosystem, and the dominance of an indicator species, low species richness and low diversity are useful tools for indicating disturbance on the primary producer level. In this study, the gerbil *G. vallinus*, a species adapted to xeric conditions, indicates that the Nabaos communal land is experiencing desertification.

This study also indicates that carabid beetles and some better known darkling beetle groups are suitable indicators for long term monitoring in the Nama Karoo, as they can be identified easily, and results can be compared with future assessments, especially after the application of restoration measures.

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Part III

III.6 Expanding knowledge through experiments

Responses of dwarf succulent plants, lichens, and soils to experimental climate warming in an arid South African ecosystem

Charles Musil*, Justine Nyaga, Khumbudzo Maphangwa & Lincoln Raitt

Summary: The effects of daytime passive heating averaging 3.8°C above ambient, achieved with clear acrylic hexagonal open-top chambers, on the vegetation and soils in an acknowledged centre of floral diversity and endemism in the arid southern bioregion of the South African Succulent Karoo Biome was examined. After 12–months warming, populations of all eight dwarf succulent species examined displayed diminished numbers of live leaves (increased leaf mortalities), the effects more prominent in small, sparsely branched species with single leaf pairs than larger, shrubby or creeping species with multiple leaves. Similarly, the four lichen species examined displayed diminished photosynthetic quantum yields in response to experimental warming, which were of much greater magnitude than the reductions in numbers of live leaves measured in the dwarf succulents indicating that lichens may provide more sensitive indicators of climate change. Substantially higher soil CO_2 effluxes were measured in soils with moderate than sparse vegetation cover, but the experimental warming had only small statistically insignificant effects on soil CO_2 effluxes. It is concluded that even mild anthropogenic warming is likely to exceed the thermal thresholds of many southern African lichens and quartz field succulent plants leading to metabolic impairment and increased likelihood of localised extinction. Also, arid ecosystem soils are likely to have a minor impact on atmospheric CO_2 with global warming as they are relatively small sources of CO_2 emissions.

Introduction

The unprecedented accumulation of carbon dioxide and other greenhouse gases in the atmosphere since pre-industrial times has already had a discernible influence on global temperature and is forecast to cause further warming this century (IPCC 2007). Diminished plant productivities in response to increased temperatures in experimental warming trials have been reported in Forest, Grassland, high and low latitude/altitude Tundra biomes (Rustad et al. 2001) implying that plant productivity could be expected to decrease further in subtropical and tropical ecosystems. However, there are few data on plant and lichen responses to climate warming in arid subtropical ecosystems, especially in the southern African Succulent Karoo Biome listed among 34 global biodiversity hot spots (Myers et al. 2000). Here, current thermal regimes for many of the almost 1,600 endemic succulent species of the subfamily Ruschioideae, which rapidly diversified in the region during the cooler Pleistocene period (Klak et al. 2004), are likely closely proximate to their tolerable extremes.

Apart from the flora, soils are the major reservoir of carbon in terrestrial ecosystems, containing more than two-thirds of the total carbon in the terrestrial part of the biosphere (Lin et al. 1999). The flux of carbon from soils to the atmosphere in form of carbon dioxide accounts for about 25% of the global CO_2 exchange (Jia & Zhou 2008). Almost 10% of the atmosphere's CO_2 passing through soils each year, which is more than 10 times the CO_2 released from fossil fuel combustion (Schlesinger & Andrews 2000, Raich & Tufekcioglu 2000). A variety of temperature-manipulation experiments around the world have shown that soil respiration generally increases with warmer temperatures in relatively wet soils (Zhou et al. 2006) with small climatic-induced changes in soil respiration (20% for a 6.0°C increase) expected to have large effects on atmospheric CO_2 concentrations with potential feedbacks to climate change (Reichstein et al. 2003, Sánchez et al. 2003). The focus on soil carbon fluxes has mainly been in tropical ecosystems due to their dominant contribution to global carbon emission budget (Adachia et al. 2006) but there are few data on gaseous carbon emissions in arid ecosystems, which though low at a global scale do exhibit huge pulses during intermittent wet phases (Amy et al. 2004). In view of these deficiencies in knowledge, the potential impacts of climate warming approximating a future climate scenario on the flora and soil carbon exchange were tested experimentally in an arid South African ecosystem. The study forms a component of a BIOTA Phase III overarching theme, which seeks to assess the current state and monitor the intensity and direction of change of biodiversity.

Methodology

The study area was the arid southern bioregion of the South African Succulent Karoo Biome, known locally as the Knersvlakte, which is an acknowledged centre of floral diversity and endemism

(Hilton-Taylor 1996). Daytime passive heating of the natural vegetation and soils was achieved with clear acrylic hexagonal open-top chambers 120 cm in diameter and 50 cm high (Fig. 1A). Demarcated plots of equivalent open-top chamber dimensions enclosed by 40 cm high steel fencing with a 5 cm diameter mesh comprised the controls, which represented ambient conditions. At the centers of the open top warming chambers and control plots, polyvinyl chloride (PVC) soil collars with an internal diameter of 10 cm and a length of 5 cm were buried to a depth of 4 cm for soil carbon flux measurements. Also installed in the open top chambers and control plots were atmospheric, soil temperature and moisture sensors interfaced with miniature loggers, set to record hourly, mounted in radiation shields (Watch Dog 450, Spectrum Technologies Inc., Plainfield, Illinois, USA). The average 3.8°C temperature increase above ambient measured in the open top warming chambers closely approximated the mean annual temperature increase of 4.5°C (means of 7 GCM models) predicted by the SRES A2-high climate sensitivity scenario for the Succulent Karoo Biome towards the end of the century (Hulme et al. 2001). Sixty experimental warming chambers and control plots were randomised on substrates overlaid with quartz-gravel and shale, phyllite and limestone with different vegetation cover and composition at the beginning of winter to allow gradual acclimation of the flora and soil microorganisms to the artificially elevated temperatures. The floral species included in six or more of the experimental warming chambers and control plots included the lichens *Xanthoparmelia austroafricana, Xanthoparmelia hyporhytida, Xanthoparmelia* spp. (un-described) and *Xanthomaculina hottentotta*, and the common dwarf succulent plants *Oophytum oviforme, Conophytum minutum* var. *minutum, Agyroderma pearsonii, Cephalophyllum spissum, Dactylopsis digitata, Cephalophyllum framesii, Drosanthemum diversifolium* and *Ruschia burtoniae*.

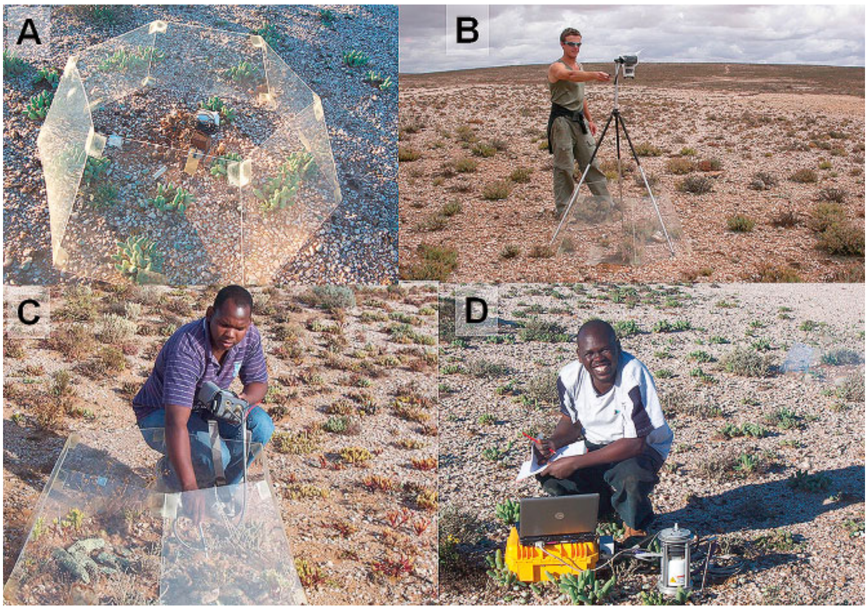

Fig. 1: Measuring climate warming impacts on the vegetation and soils in the arid South African Succulent Karoo Biome. A: Clear acrylic hexagonal open-top warming chamber with miniature data loggers connected to soil moisture and temperature sensors. B: Photographing succulent plant populations with high resolution digital camera. C: Khumbudzo Maphangwa measuring photosynthetic quantum yields of lichens with modulated fluorescence meter. D: Justine Nyaga measuring soil respiration with an infrared gas analyzer.

Responses of the dwarf succulent plant species to the experimentally elevated temperatures were determined at 3-monthly intervals. Photographs of the succulent plant populations present in each chamber and control plot were obtained with a high resolution, three-band Foveon X3 sensor, Sigma SD10 digital camera suspended above the chambers and control plots (Fig. 1B). The numbers of visibly live leaves present on each dwarf succulent plant species in each chamber and control plot were precisely determined with the aid of image analysis software (Image-J ver.1.34I, National Institute of Health, USA: http://rsb.info.nih.gov/ij/). These were summed for the entire species population in each chamber and control plot and expressed on a uniform m² basis.

Responses of the lichen species to the experimentally elevated temperatures were determined between 08h00 and 10h00 at monthly intervals. The lichens in each chamber were hydrated with 50 ml of water applied as a fine mist spray and their photosynthetic quantum yields at a steady-state determined with a modulated fluorescence meter (OSI-F1, Opti-Sciences Inc., Hudson, USA) following a 0.8 s light pulse of 15,000 µE (Fig. 1C). Responses of soil carbon flux to the experimentally elevated temperatures were determined at monthly intervals. Four measurements of soil CO_2 efflux spaced two hours apart were taken inside the polyvinyl chloride (PVC) soil collars within each top warming chamber and control plot (Fig. 1D) with a portable Li-Cor 8100 infrared gas analyzer (Li-Cor BioSciences, Lincoln, Nebraska, USA). Measured soil respiration rates as µmol CO_2 m^{-2} s^{-1} were averaged for the day and converted to g CO_2 m^{-2} d^{-1}.

Statistical analyses

All measurements were $\log_e$ transformed before statistical analysis to reduce the inequality of variance in the raw data. As the experimental designs were not fully balanced, a REML (residual maximum likelihood) variance component analysis (repeated measures mixed model) was applied to test for significant effects of warming using the Wald X² statistic generated by REML. Warming treatment and either succulent plant species, lichen species or soil vegetation type were fitted in the fixed model and season and measured plant, lichen or soil variables in the random model. Differences exceeding twice the mean standard errors of differences were used to separate

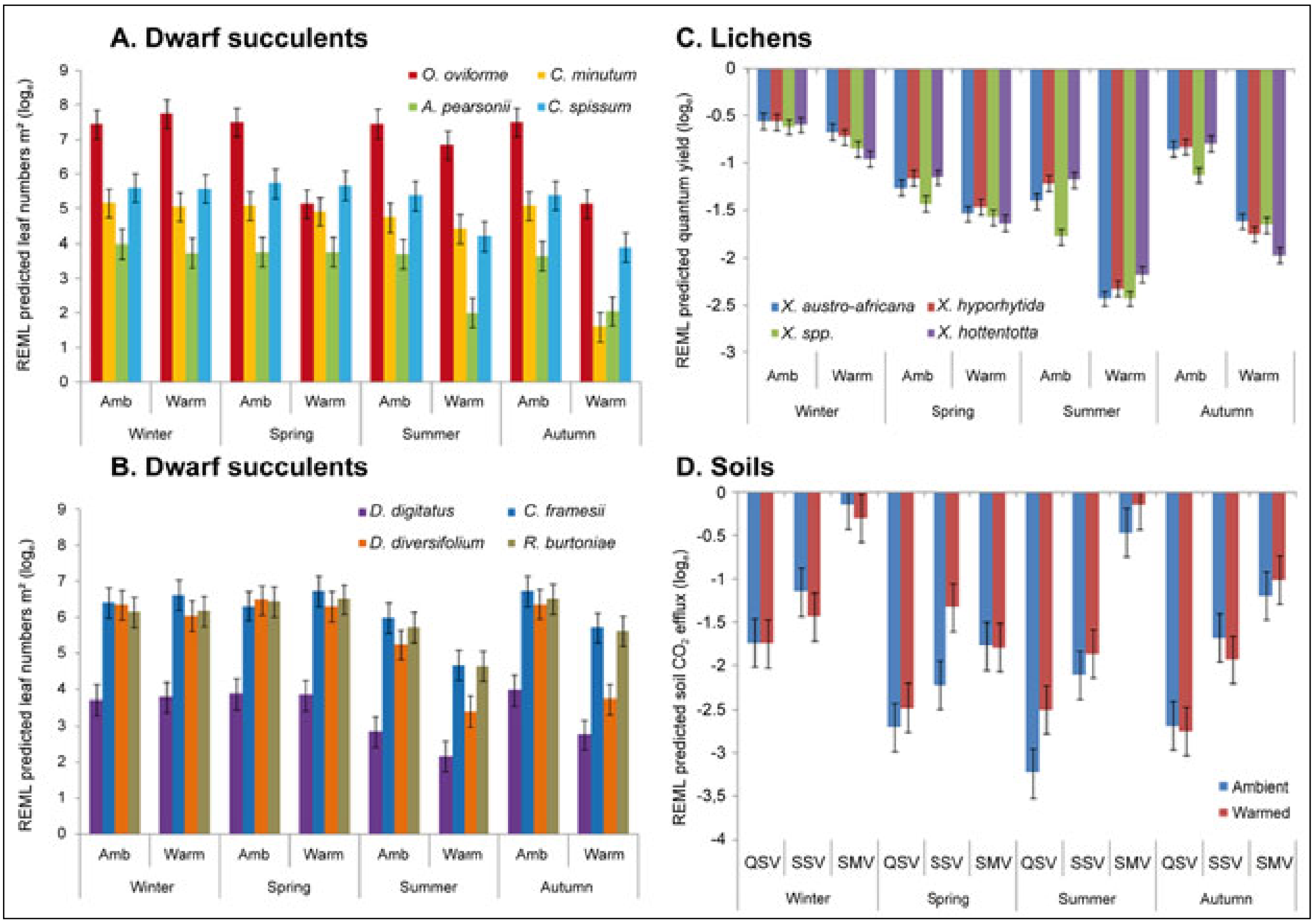

Fig. 2: Seasonal responses to experimental warming of eight dwarf succulent plant species, four lichen species and soils from three different soil vegetation units, viz: quartz-gravel substrates with sparse vegetation cover (QSV), and shale, phyllite and limestone derived substrates with sparse vegetation cover (SSV) and moderate vegetation cover (SMV). Predicted means with non overlapping standard error bars significantly different at $p \leq 0.05$.

significantly different treatment means at $p \leq 0.05$. This based on the fact that for a normal distribution from REML estimates, the 5% two-sided critical value is two.

Results and discussion

Populations of all eight dwarf succulent species displayed significantly ($p \leq 0.05$) diminished numbers of live leaves (increased leaf mortalities) in response to experimental warming, which were of greatest magnitude in late autumn 12-months after open top warming chamber placement (Fig. 2). Small, sparsely branched succulent plant species comprising single, highly connate, spheroid leaf pairs per axis, such as *O. oviforme, C. minutum,* and *A. pearsonii*, exhibited much greater decreases in numbers of live leaves (range: 33.8% to 68.4%) than populations of larger, shrubby or creeping species with multiple leaves, such as *C. framesii* and *R. burtoniae* (range: 9.1% to 13.7%). These differences explained by the much higher air temperatures leaves of small unbranched species located at or close to the soil surface were exposed to than larger branched shrubby species with multiple leaves elevated above the soil surface. In fact recorded soil surface temperature extremes in the open-top chambers of 54.8°C were close to the temperature threshold of 55°C considered tolerable by most vascular plants (Kappen 1981). Higher thermal thresholds (range: 66.4°C to 70.0°C) have been reported in a diverse array of succulents (Nobel 1989). However, thermal thresholds of southern African specialised dwarf succulent forms are allegedly lower due to the milder thermal regimes (up to 3°C lower) they experience on the highly reflective quartz substrates (Schmiedel & Jürgens 2004). This suggestion supported by the abrupt decline in the activation state of the photosynthetic enzyme Rubisco measured in one dwarf succulent *C. spissum* from around 90% to 92% at temperatures between 40°C and 52°C to about 72% at 54°C (Musil et al. 2009). This decline in Rubisco activity preceded by a decrease in PSII electron transport commencing at temperatures much lower than the threshold for Rubisco de-activation, as well as to an increased depletion of succulent leaf water reserves during the dry season through intermittent transpiration to prevent excessive heat accumulation in leaves (Musil et al. 2009). The latter exemplified by the observed restriction of all surviving dwarf succulent populations to the edges of the open-top chambers where greater amounts of fog and dew fall intercepted by the chamber walls provided localised areas of higher soil moisture conducive for transpiration to cool leaf surfaces (Musil et al. 2009).

All four lichen species displayed significantly ($p \leq 0.05$) diminished photosynthetic quantum yields, a sensitive indicator of photosystem II efficiency and stress (Golding & Johnson 2003), in response to experimental warming with the greatest reductions (range: 46.8% to 149.2%) also apparent in late autumn 12-months after open top warming chamber placement (Fig. 2). These measured declines in photosynthetic quantum yield in response to experimental warming were generally of much greater magnitude than the reductions in numbers of live leaves measured in the dwarf succulents implying that lichens may provide sensitive indicators of climate change. In fact, a recent study in the Netherlands has identified recent major changes in lichen distribution independent of pollution since 1979. Warm-temperate lichen species have significantly increased, and species characteristic of cold environments have either decreased or disappeared (van Herk et al. 2002). One example is that of *Flavoparmelia soredians* a drought resistant, warm-temperate lichen species presently common in the Netherlands but rare before 1900 with its northern most limit until recently in southern England (Seaward & Coppins 2004).

Substantially higher soil CO_2 effluxes were measured in soils with moderate than sparse vegetation cover (Fig. 2), a consequence of the added contribution of root respiration and leaf fall detritus decomposition to total soil respiration (Huxman et al. 2004). In the moderately vegetated soils, approximately 62% of the total soil CO_2 efflux was contributed by root respiration, this percentage only slightly higher than the reported 53% contribution by root respiration to total soil CO_2 efflux in the Duke forest in USA (Hui & Luo 2004). The experimentally elevated temperatures in the open top warming chambers generally had only small statistically insignificant ($p \geq 0.05$) effects on soil CO_2 effluxes in the moderately vegetated soils with only two incidences of significantly ($p \leq 0.05$) elevated soil CO_2 efflux in the sparsely vegetated soils (Fig. 2). The 22.4% increase in soil CO_2 efflux in response to an average 3.8°C increase in the open top warming chambers measured on the quartz gravel substrates during summer at the study site concurred with a reported 25.8% increase in soil CO_2 efflux in response to a similar temperature increase of 4°C in an Alaskan boreal forest (Bergner et al. 2004). However, on the shale, phyllite and limestone derived substrates at the study site a much higher 40.3% increase in soil CO_2 efflux was recorded during spring. These increases in soil CO_2 effluxes coinciding with intermittent precipitation events, which are known to provide an enormous stimulus to microbial activity resulting from an accumulation of nutrients in the soils during the extensive dry periods. This unique feature of arid regions designates them as sinks for carbon-based compounds during dry periods and sources of atmospheric CO_2 during wet periods (Huxman et al. 2004). Nevertheless, the measured soil CO^2 effluxes in this study (range: 0.11 to 6.15 g C m^{-2} d^{-1}) were over 3 times less than those reported for temperate and tropical forest ecosystems (up to 34.3 g C m^{-2} d^{-1}), though during intermittent wet phases soil respiration rates pulses were up to 15 orders of magnitude greater than those during dry phases but still only comparable in magnitude with those reported for temperate semi-arid grasslands (up to 7.3 g C m^{-2} d^{-1}).

Conclusions

This study's findings confirm that even mild anthropogenic warming is likely to exceed the thermal thresholds of many southern African lichens and quartz field succulent plants leading to metabolic impairment and increased likelihood of localised extinction. They also concur that arid ecosystem soils are relatively minor sources of CO_2 emissions and likely to have a minor impact on atmospheric CO_2 with global warming.

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Exclosures and experimental grazing plots at the BIOTA Observatories Narais and Duruchaus

Ibo Zimmermann* & Dirk Wesuls

Summary: Unreplicated plots of 1.4 ha were established alongside BIOTA Observatories on the farms Narais (S39) and Duruchaus (S40). One plot on each farm was fenced to exclude livestock. Another fenced plot, the rest treatment, was grazed twice a year by livestock until grass in this plot was at the same level as that in the surrounding paddock. A control plot remained unfenced in the surrounding paddock, subjected to rotational light grazing on Narais and continuous heavy grazing on Duruchaus. After three years perennial grass became moribund in the exclosure and was invigorated in the rested plot. Annual species fluctuated in response to rainfall.

Introduction

The construction of exclosures usually leads to remarkable growth of grass inside, compared to the grazed surroundings. However, farmers are rarely impressed by this abundant grass, since the exclosures contribute no direct benefit to farm production. In addition, in semi-arid areas that receive seasonal rainfall, the grass becomes moribund and rangeland condition deteriorates after a few years of excluding animal impact, which would otherwise stimulate the grass (Holecheck et al. 2006). Therefore, when exclosures were being planned for some observatories, it was decided to include seasonal exclosures that would be grazed at the same overall stocking rate as the surrounding paddock in terms of kg liveweight grazing days ha^{-1}, but with the grazing provided intensively only twice per year, once in the growing season and once in the dry season. These seasonal exclosures could eventually serve as benchmarks, indicating the potential of the land under the climatic conditions being experienced and helping to differentiate between influences of climate and management.

Site description

The study site straddled the fenceline contrast between two Observatories on a 400 ha paddock on farm Narais (Observatory S39) and a 200 ha paddock on farm Duruchaus (Observatory S40). Although officially classified as falling within the Highland Savanna (Giess 1971), the appearance of these two farms was more similar to the nearby Dwarf Shrub Savanna of the Nama Karoo Biome (see Chapter II.4). The mean annual rainfall on the farms is approximately 250 mm (Fig. 1). The paddock on Duruchaus was stocked with cattle, sheep, goats, and horses at approximately 70 kg liveweight ha^{-1} a^{-1}. Grazing here was continuous and only the small stock were herded, primarily for protection against predation and theft. Narais was a rotationally grazed farm with seven paddocks per herd and a period of absence of approximately 12 weeks. The paddock with the experimental plots was farthest from the homestead and was stocked more lightly (4 kg liveweight ha^{-1} a^{-1} and rest period of approximately 12 weeks) than the remainder of the farm (24 kg liveweight ha^{-1} a^{-1} and rest period of approximately 3 weeks). This was due to the fact that its water had to be pumped at great expense up a considerable height, resulting in the farmer making less use of that paddock compared to other paddocks on the farm. The water points on both paddocks were a little over 1 km from the experimental plots.

Methods

Unreplicated experimental plots of 1.4 ha were established on the two neighbouring farms to demonstrate and compare the effect of (1) the normal grazing applied by the farmer in the surrounding paddock (Normal); (2) zero stocking

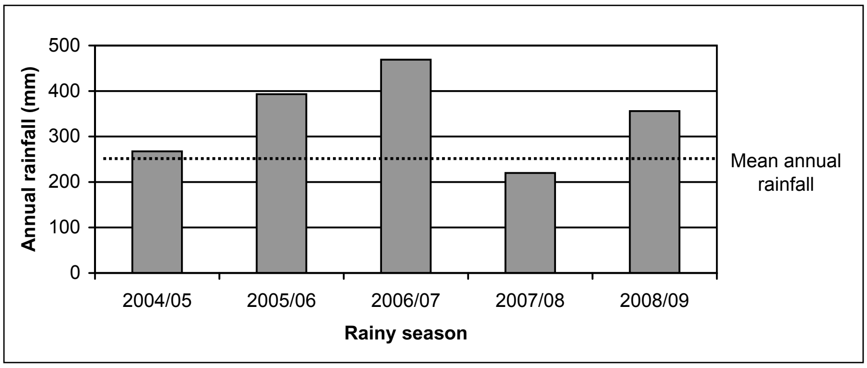

Fig.1: Annual rainfall recorded by Duruchaus farmer nearby experimental grazing plots, in relation to the long-term mean annual rainfall of 250 mm.

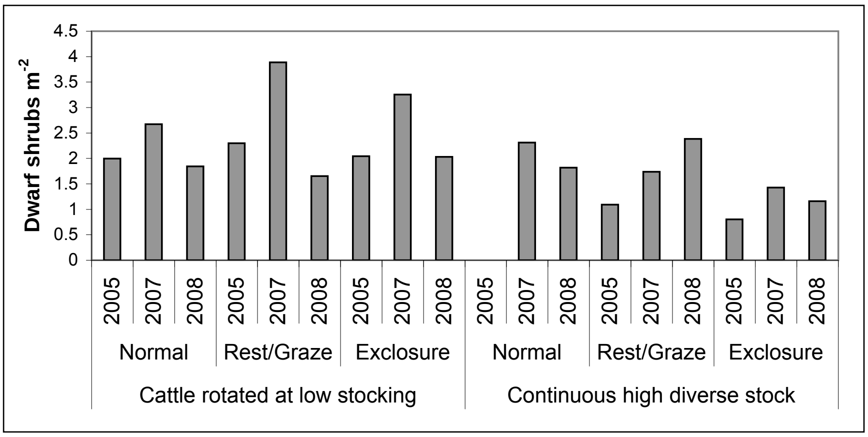

Fig. 2: Density of dwarf shrubs on each of the experimental plots on Narais (left) and Duruchaus (right) over three years. There were no data in 2005 for the normal plot on Duruchaus.

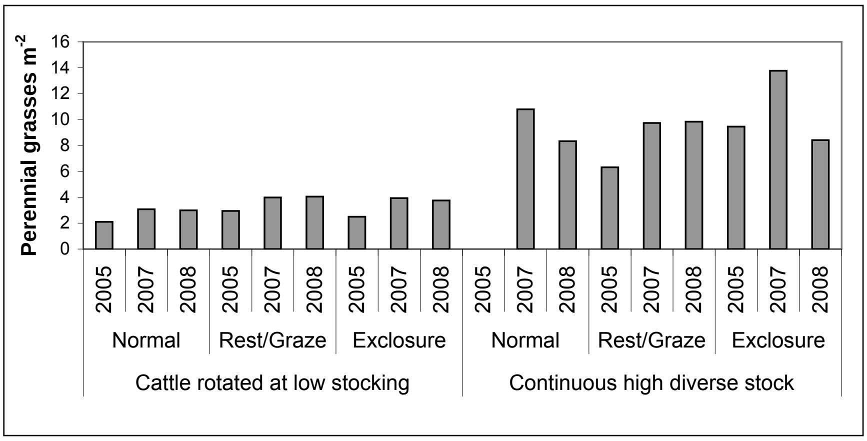

Fig. 3: Density of perennial grasses on each of the experimental plots on Narais (left) and Duruchaus (right) over three years. There were no data in 2005 for the normal plot on Duruchaus.

Photo 1: Duruchaus fenceline between the grazed and rested plot on left and exclosure on right. Photo: Ibo Zimmermann.

(Exclosure); and (3) long rest interrupted twice a year by brief grazing at the same overall stocking rate as the surrounding paddock (Rest/Graze; Photo 1). The rest/graze plot was supposed to be grazed by the same animals that graze in the surrounding paddock and at the same overall stocking rate, but with much longer rest. However, since the plot on Duruchaus (next to BIOTA Observatory S40) is about 0.5% of the size of the surrounding paddock, and on Narais (next to BIOTA Observatory S39) about 0.25% of the surrounding paddock, this would mean the plots would be stocked for only a few hours each season, by the animals in the surrounding paddock. The livestock herded into the plot for such a short time, did not settle down and graze to the extent that represented their grazing in the surrounding paddock. Therefore instead of basing the stocking on a fixed time period, the para-ecologist was asked to keep the animals grazing in the plot until the grass had been grazed down to roughly the same height as that in the surrounding paddock, as subjectively assessed by the para-ecologist.

Densities of dwarf shrubs and perennial grasses of at least 5 cm basal diameter were counted within a radius of 75 cm from 100 points per plot. The points were generated by throwing a dart over the shoulder from uniformly spaced GPS coordinates, to provide a degree of randomness.

The baseline measurements were taken when the plots were established in 2005. However, data from 2005 from the normally grazed plot on Duruchaus were rejected because they were wrongly taken in an area that did not compare well to the experimental plots. Follow-up measurements were made two and three years later, in 2007 and 2008. Due to the large variation in annual rainfall, the change over time within a plot was more likely the consequence of changing rainfall than of grazing treatment. Therefore, the effects of treatments were analysed by assessing differences in the patterns of change each plot experienced over time.

In addition, the species composition and cover was recorded annually on five permanent 10 m x 10 m quadrats per treatment since 2005 and on five reference plots per paddock since 2006.

Photo 2: Responses of the grass *Stipagrostis obtusa* to the treatments in the experimental plots on continuously grazed farm Duruchaus, (a) with weak regrowth in the normally grazed plot, (b) vigorous regrowth in the rested and grazed plot and (c) moribund in the exclosure. The photos were taken in March 2008, before the rested and gazed plot was to be stocked and when the exclosure had received rest for over three years. Photos: Ibo Zimmermann.

Results

On Narais the pattern of change was similar for all three plots, therefore no difference could be attributed to treatment. This is not surprising given the very low stocking rates and long periods of absence of grazing. The dwarf shrub density increased between 2005 and 2007, but then decreased again by 2008 (Fig. 2) probably a reflection of the previous season's rainfall (Fig. 1). The perennial grass density followed a similar pattern (Fig. 3).

On Duruchaus the patterns of change differed among treatments. In the exclosure the pattern for dwarf shrub density was similar to those in all three plots on the other farm, with a peak in the 2007 records. In the normally grazed plot the pattern of decline from 2007 to 2008 was similar, while the pattern before 2007 could not be discerned due to lack of 2005 data. However, for the grazed and rested plot the pattern differed (Fig. 2), indicating a steady increase in dwarf shrub density between 2005 and 2008. A similar difference in pattern was evident for perennial grass density (Fig. 3).

The difference in patterns suggests that both dwarf shrubs and perennial grasses were increasing in the rested and grazed plot on Duruchaus. This can be attributed to the long rest periods, interspersed with stimulatory grazing, received since 2005. Visually the tussocks of *Stipagrostis obtusa* appeared to be more vigorous (Photos 2a & b), although no formal measure of vigour was attempted. On the other hand the sharp decline in the perennial grasses on the Duruchaus exclosure from 2007 to 2008 suggests that they were starting to suffer from over resting. Visually the tussocks of *Stipagrostis obtusa* appeared to be more moribund in the southern half of the exclosure (Photo 2c), while on the northern half the activity of harvester termites appeared to have removed many of the dead leaves from the grasses, possibly preventing them from becoming moribund.

Within the time period 2005–2008 there was no apparent change in species composition in the exclosures and in the graze/rest treatments. In the ordination of species composition and cover for each treatment the distinct species composition of both farms too remained constant, which is to be recognised by the separation of the two farms along the first axis

Photos 3 and 4: Permanent quadrat in the Duruchaus exclosure plot in March 2005 (left) and March 2008 (right). The most apparent change is the cover of annual species recognisable by the reduced proportion of bare soil in 2008 due to higher rainfall compared to 2005. Photos: Dirk Wesuls.

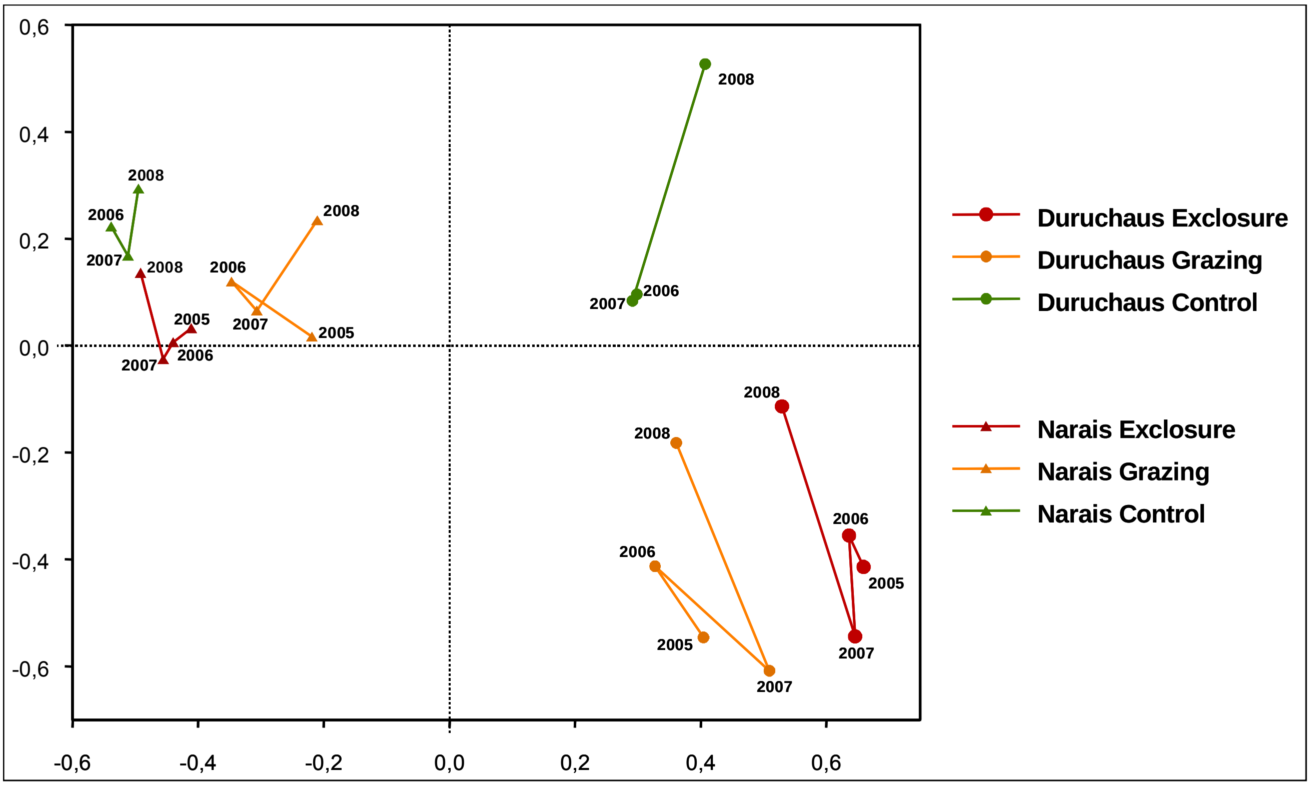

Fig. 4: Change of species composition on exclosure, graze/rest and control plots. Each point is the average sample score of the first two axes of a correspondence analysis from five samples per treatment.

of Fig. 4. The fluctuations of the species composition along the second axis of Fig. 4 is mainly due to a change in annual species (Photo 3 & 4) driven by differences in rainfall in the respective years.

Changes made to treatment

After learning of the successful implementation of a simple grazing strategy in the North West Province of South Africa (Dames 2009), the farmers agreed to try this on their rest/graze plots. This would be by alternate resting for a full year and keeping the gate open for a full year to achieve the recommended 80% utilisation of grass. Since the Duruchaus farmer in any case intended to provide rest in the surrounding paddock for the whole of the 2010 growing season, the rest cycle in the rest/graze plots would coincide with this cycle. This long rest would not require increasing the stocking rate on the remainder of the farm, since the Duruchaus farmer has rented land elsewhere for cattle and greatly reduced the size of his sheep and goat herd. It is hoped that monitoring can continue, but if not the plots will at least provide a visual indication of the effects.

Acknowledgements
The authors' general acknowledgements to the organisations and institutions, which supported this work are provided in Volume 1.

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Restoration of a gully system in the Highland Savanna of Namibia

Justus Kauatjirue, Kuniberth Shamathe, Hugh Pringle & Ibo Zimmermann*

Summary: The Ecosystem Management Understanding (EMU) Process was developed in Australia with the participation of numerous pastoralists. EMU is about understanding and adapting to, rather than fighting against natural processes. Its roots are in southern Africa with the novel participatory ecology of Dr Ken Tinley.

In 2003, EMU was introduced to Namibia in a workshop with members of the Auas-Oanob Conservancy. Farmers recorded a baseline of ecological and production information on clear overlays over maps or images of their properties. Through the mapping, followed by a group field tour of affected areas, it became apparent that the valleys of this upland Conservancy were becoming severely degraded by erosion processes, destroying the highly productive seasonally inundated grasslands.

A trial restoration project was initiated in one of these valleys during 2007, using anchored scrub filters of *Acacia mellifera* placed at strategic points. Initial results indicate an improvement in landscape functioning and it is hoped that the perennial grasses establishing in and upslope of scrub filters will permanently replace the latter as they decay. The strength of this approach from a geomorphic perspective is that flows are filtered, rather than checked, which would cause further problems. However, an integrated, cross-property strategy of innovative interventions is also needed, differing according to geomorphic nature of local landscapes and the availability of resources for restoration work. No single style of intervention will suffice in harnessing the intrinsic restoration capacity of complex catchment ecosystems.

Introduction

The Auas-Oanob Conservancy is situated in the Highland Savanna of central Namibia. A priority concern of the farmers is that the landscape is becoming more “leaky”, as gullies proceed to cut their way up valleys over large parts of the rangelands. This became apparent during an Ecosystem Management Understanding (EMU) Process workshop facilitated by an expert team from Australia.

The EMU Process was developed in Australia with the participation of numerous pastoralists (Pringle & Tinley 2001). It is underpinned by a philosophy of living within ecosystems, rather than as master of them. It suggests that the best way to maintain profit and bring about other successes are through working out what the land is doing, and how pastoral activity can best fit into it without causing damage.

The ecological model used by EMU is novel in many ways; it approaches issues from a hierarchical perspective (Wu & David 2002), in which the area of interest is examined first on a large scale, then focusing on smaller landscape patterns in what is termed ‘a hierarchy of salience’ (Tinley 1987). Fundamental to this approach is a better understanding of the influence of geomorphology on landscape processes, and how biotic relationships are influenced by changes in soil moisture balance regimes.

Traditional ecological assessments of land degradation focus on explaining dynamics in situ (Pringle & Tinley 2003), whilst the EMU approach places any area of concern into its wider process context and focuses as much on process patterns as on components of a dysfunctional system (McHarg 1992). While this approach is more complex it is usually better understood by landusers who continually have to deal with the complexity of their environment as part of their land management.

The importance of landscape incision and the lowering of depositional (“soft”) base levels is largely overlooked by rangeland ecologists (Pringle & Tinley 2003), despite the fact that it effectively sucks rainfall out of landscapes and so leads to progressively smaller areas that remain moist and productive—and for shorter periods (Fig. 1).

EMU workshop with conservancy farmers

The two-day EMU workshop consisted of mapping sessions (see below) alternated with trips to explore relevant landscape features. Two days later, and after the participants had had time to reflect on the knowledge they had mapped, a tour was convened through the conservancy; each farm guided by its participating farmer.

For the mapping exercise, farmers used their farm maps and aerial photographs. Various colour-coded features and processes were mapped onto overlays to identify key areas for priority management on the rangelands. Upland fertile valley systems were identified as key features requiring improved management. Although the total area occupied by these valleys is a small proportion of the conservancy area, they are extraordinarily important when intact

Photo 1: An intact grassy upland fertile valley acts as a benchmark, providing a vision for restoration of eroded valleys. Photo: Ibo Zimmermann.

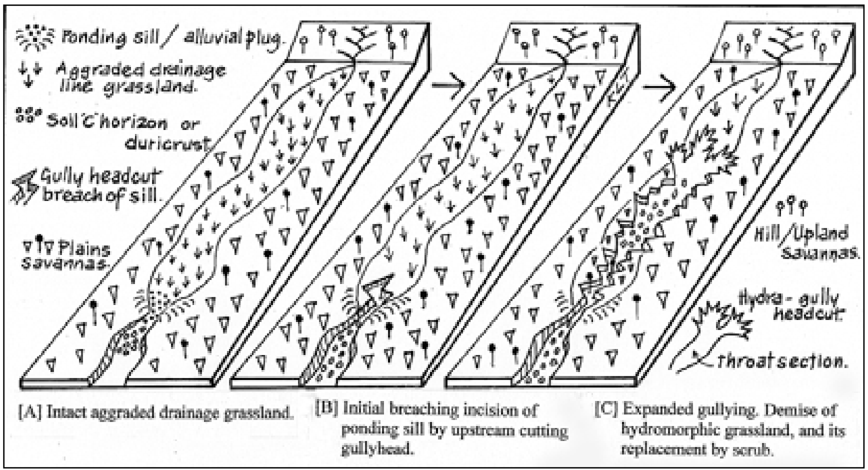

Fig. 1: Landscape segments to illustrate progression of gully erosion up a grassy valley. Diagrams kindly drawn and supplied by Ken Tinley.

due to their high productivity that plays a critical role in buffering the impact of droughts. Periodic waterlogging used to ensure that these valleys were dominated by palatable perennial grasses (Photo 1, Fig. 1A), but many of the valleys have been subject to varying degrees of gully erosion that also favoured encroaching bushes (Fig. 1B, C). The root cause was identified as overgrazing during the early establishment of these farms (ca. 1900–1940). The positive effect of the introduction of a more suitable rotational grazing management of livestock, introduced after 1940, was gradually counteracted by high game numbers. These high game densities originated as game learned to follow the cattle grazing rotations, benefiting from the exposure of shorter, softer grass, as well as greatly improved year-round water availability created for livestock production. In response, a regular off-take of game for local trade was initiated in 2006. Despite these improvements in grazing management, the deep gullies hindered spontaneous recovery of the rangelands, necessitating restorative interventions by landusers.

The fundamental source of this ecologically and commercially debilitating, cascading landscape incision is always a "nick point" in the land, where the head can form and then migrate upslope. Nick points may be natural (e.g. a major change in slope), but are more commonly associated with human activity (most commonly tracks dug below landscape level). Water flows downslope, gullies migrate and spread upslope.

Pilot restoration project

A farmer couple of the conservancy volunteered to host a "putting the plug back in the bath" project in an area that had been a continuous stock route across their farm and where severe gully erosion had degraded two connected valleys. Past efforts to stop the erosion with solid waste put into the gullies only increased the gully depth, as the energy of flows increased below these new obstructions.

The mean annual rainfall of the restoration site is approximately 300 mm and the soil texture is predominated by sandy loam. The gully system, with a slope of about 1:70 (angle of about 0.8°), was treated in March 2007 with filters made of branches cut selectively from *Acacia mellifera* growing in dense stands nearby. The branches were packed at strategic locations to slow down flowing water and trap sediment, while allowing excess water to pass through. The locations included gully heads (Fig. 1), junctions (where gullies meet), "pinch points" (where valleys become narrow and concentrate the water flow) and along key-lines (where slopes change from steep above to gentle below) (Fig. 2). Intervals between filters were short enough to ensure that the water would not regain much of its destructive speed before being slowed down again by the next filter. In gullies, the branches were packed together and on top of each other, while outside of gullies the branches were placed individually. Sometimes the packed branches in gullies were woven with wire and tied to trees, or onto a steel post (Photo 2). The restoration work along roughly 2 km of rills and gullies took about 100 person days and materials used included 30 steel posts (90 cm long) and about 900 m of fencing wire.

Determining restoration progress

Ten of the treated features were selected for comparison with ten similar features in untreated gully systems. Half of the monitored erosion features on both treated and untreated systems were fenced to exclude cattle. The sampled features were assessed annually using the Landscape Function Analysis (LFA) method (Tongway & Hindley 2004), with transects running across rills or gullies. In addition to the LFA soil surface assessment and vegetation measurements, depth of rills and gullies was determined by measuring the height from the floor of the rill or gully to the tape measure pulled tightly between the pegs that marked the start and end of each permanent LFA transect.

The first rainfall event that was suitable to evaluate the effectiveness of the filters occurred in March 2008, when a thunderstorm yielded about 50 mm rain within 30 minutes. It resulted in some sediment being trapped (Photo 3), while big tufts of perennial grass later established close to many of the filters (Photo 4). Several of the filters became partially dislodged and required repair. Cross section monitoring over rills and gullies showed variable results over the first two years. At the biggest gully confluence in the treated system, soil was deposited above the filter, improving soil surface condition. However, below the filter the gully eroded further over the first year. Despite this, after just two years since the interventions, grasses established on the floor of the gully here, below this confluence (Photos 5 & 6).

The LFA measurements of nearest perennial grass of at least 5 cm basal diameter failed to detect significant change, because most change occurred within the rills and gullies, whereas the LFA transects stretched at least 15 m each side. Therefore, In March 2009 the density of perennial grasses of at least 5 cm basal diameter was measured at various locations. This was done by throwing a dart over the shoulder from a predetermined location and twirling a 75 cm rod 360° around the dart point while counting all the perennial grasses of sufficient size crossed by the rod. In the treated valley the dart was thrown into filters, 45 of them in rills and

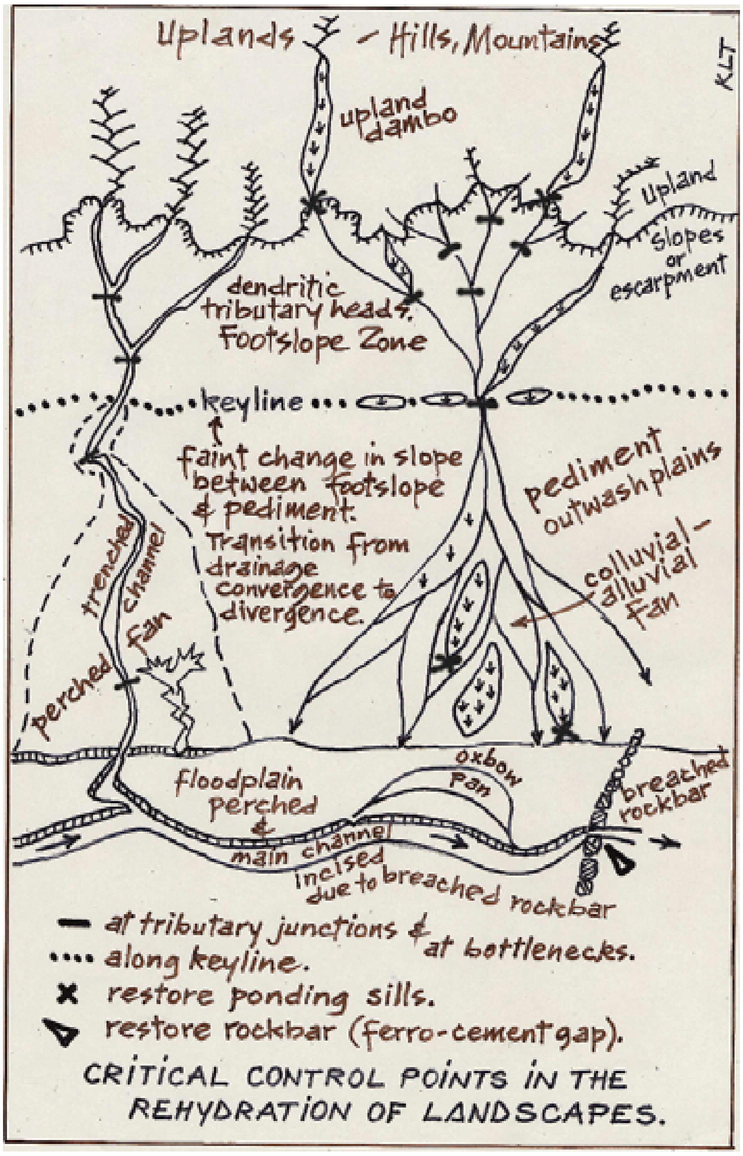

Fig. 2: Landscape view to illustrate location of critical control points for restoration efforts. Diagram kindly drawn and supplied by Ken Tinley.

Photo 2: Where there is no tree nearby to tie the wire to, a steel post is hammered in. Photo: Ibo Zimmermann.

Photo 3: Soil and mulch are trapped on the upslope side of a filter. Photo: Ibo Zimmermann.

Photo 4: Lush grass establishes on the downslope side of a filter at a gully head. Photo: Ibo Zimmermann.

Photos 5 and 6: Below the main confluence, filters placed on all sides (left) allowed grasses to establish on the gully floor two years later (right). Photos: Ibo Zimmermann.

gullies, and 54 outside rills and gullies. After counting the grasses under the filter, the dart was removed from the filter and thrown over the shoulder upslope and then downslope, to count grasses within 75 cm. In the untreated valleys the dart was thrown from similar types of locations in and out of rills and gullies, for comparison with the treated valley.

The density of newly established perennial grass was lower underneath the filters (Fig. 3), probably due to too much shading from packed branches. Perennial grasses established relatively well above and below the filters within rills and gullies, compared to outside eroded water washes. This can be attributed to the effect of the filters, as verified by the perennial grass density at the untreated gully systems. The most common perennial grass species were *Schmidtia pappophoroides* (Sand Quick), *Heteropogon contortus* (Spear Grass), *Eragrostis echinochloidea* (Tick Grass), and *Cenchrus ciliaris* (Buffalo Grass).

Conclusions

Soil surface traits monitored with the LFA technique did not show many significant changes over the first two years, yet from the amount of newly established grasses, the branch-filters appear to be effective in gradually reversing erosion processes. In fact, the density of these grasses is expected to keep the grass layer stable enough to replace the branch-filters as they decay over the following seasons. It is envisaged that this will return the system to capturing resources rather than losing them and thereby facilitate further spontaneous regeneration.

There was no evidence that fencing assisted the restoration process, suggesting that the grazing management applied by the farmer is sufficient to allow perennial grasses to establish. However, this may not always be the case and formal rest of restored areas is recommended.

On the local scale, the pilot restoration project in the Auas-Oanob Conservancy has proven effective in increasing rainfall infiltration and so regenerating the

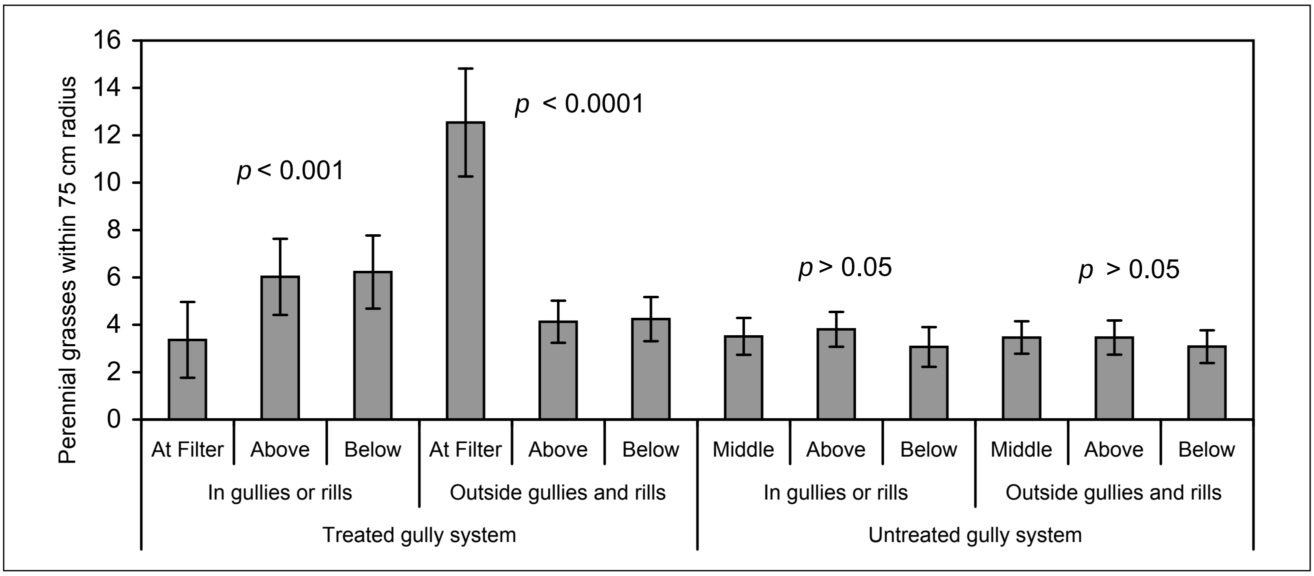

Fig. 3: Densities of perennial grasses of at least 5 cm basal diameter recorded under filters and in the open, almost two years after placement of the filters. Error bars indicate 95% confidence intervals. They are not strictly valid for the first and fifth columns, for which the data are not normally distributed. P-values indicate significance of differences among the three positions within each of the four zones, as determined by Kruskal-Wallis ANOVA test. When the combined second and third columns were compared to the combined fifth and sixth columns, the difference was significant ($p < 0.05$), as determined by Mann-Whitney U test. When the combined second and third columns were compared to the combined eighth and ninth columns, the difference was highly significant ($p < 0.0001$), as determined by t-test.

productivity of the land (Shamathe et al. 2008). Equally important, however, is a wider, increasingly inquisitive approach of landusers to bush encroachment and erosion, who are now able to recognise the greatly variable factors that can drive an undesirable ecological succession (Pringle et al. 2009).

The EMU process, together with a new appreciation and more effective use of local knowledge, is a powerful tool that empowers landusers to broaden and enhance their land management options. To use the EMU process and all its techniques more effectively and on a larger scale in the country, however, requires a major shift in policy relations and a new focus on ecological processes as key values or assets (McHarg 1992).

Acknowledgements
The authors' general acknowledgements to the organisations and institutions, which supported this work are provided in Volume 1.

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The effectiveness of sucrose applications as a restoration aid in transformed lowland fynbos ecosystems

Sheunesu Ruwanza*, Charles Musil & Karen Esler

Summary: The effectiveness of applying rapidly available sources of carbon, such as sucrose, to reduce high soil N levels in transformed lowland fynbos ecosystems in order to enhance the competitiveness of native species was tested in field and greenhouse trials. Carbon as sucrose was added to normal and heat sterilised soils and its effects on soil nitrogen concentrations and on the photosynthesis and growth of ten introduced native species examined. Sucrose additions reduced leaf chlorophyll contents, photosynthetic efficiencies and biomass accumulation in the great majority of the introduced native species. These sucrose-induced growth and photosynthetic inhibitions were more pronounced in normal than sterilised soils, but no corresponding reductions in soil nitrogen levels were observed. The elevated microbial concentrations found in sterilised soils and the absence of any effects of sucrose applications on soil microbial concentrations in both normal and sterilised soils indicated an abiotic rather than a biotic mechanism of sucrose induced plant photosynthetic and growth inhibition. It is concluded that slower releasing sources of carbon such as sawdust, reeds and chopped wood may provide a more efficient and economical means of reducing soil fertility over the long term.

Introduction

The proliferation of invasive alien grasses in abandoned agricultural fields due to past fertilisation have raised concerns about their potential displacement of wildflowers, which form the basis of a growing, lucrative nature-based tourist industry in southern African Cape Floristic Region (Milton 2004). Techniques examined for restoring transformed ecosystems in the Cape Floristic Region include alien grass removal by indigenous herbivores (Midoko-Iponga et al. 2005), by mowing, hand-clearing, light and intense burning and pre-emergent herbicide application (Musil et al. 2005). It was concluded that successful restoration initiatives over the long-term control would require an integrated management approach, which would seek to limit factors that promoted success of non native species, such as soil nutrient enrichment (Musil et al. 2005).

Abandoned agricultural fields in the Cape Floristic Region do have high residual soil nitrogen levels, which promote alien species (Milton 2004). A commonly applied technique in restoration initiatives for reducing soil N levels to promote the competiveness of native species adapted to nutrient impoverished soils is the addition of organically rich compounds such as sucrose, sawdust, straw, grain hulls and chopped wood. These compounds, which are high in carbon and low in nitrogen content stimulate soil microbial activity leading to a depletion of available soil N (Blumenthal et al. 2003, Eschen et al. 2006). Their application lead to increased rates of microbial N mineralisation (Johnson & Edwards 1979, Gilliam et al. 2005) and nitrification (Gilliam et al. 2005) with consequent reduced ammonium (Hopkins 1998) and nitrate (Blumenthal et al. 2003) concentrations in soils. Such organic matter additions have been applied successfully in restoration initiatives that have sought to stimulate the growth of native and late seral species in alien invaded ex-arable lands enriched from past fertilisation (Corbin & D'Antonio 2004, Blumenthal et al. 2003). However, effects on plant growth and soil N depletion differ according to carbon source with rapidly available forms of carbon, such as sucrose, stimulating microbial activity within hours (Mack et al. 2000, Corbin et al. 2004) while other structurally more complex carbon sources, such as sawdust or wood chippings, having a delayed effect on microbial activity as they take longer to degrade (Mack et al. 2000, Corbin et al. 2004, Perkins 2006). Also, plant growth reductions not corresponding with any observable changes in soil N content in response to sucrose additions have been reported, these implying an abiotic mechanism of plant growth inhibition induced by exogenous sucrose addition. In view of these ambiguities, this study examined the effects and mechanism of action of a rapidly available source of carbon such as sucrose on soil N levels and growth of introduced native species in a transformed lowland fynbos ecosystem. The study forms a component of a Biota Phase III overarching theme that seeks to develop tools and schemes for various interventions (restoration, conservation, sustainable management) of biodiversity.

Methods and materials

Field trial

The field trial was conducted in the Elandsberg Private Nature Reserve in an area of degraded natural vegetation (old field) situated in a transition zone between Swartland Shale renosterveld and Swartland Alluvium fynbos. The split plot experimental design comprised twenty-four 1.5 m square plots, each subdivided into six 0.375 m^2 sub-plots, randomised in an old field (Fig. 1A). Four soil nutrient amendment treatments were randomly assigned to the 24 plots, each treatment replicated six times. The treatments comprised 1) a control in which no chemicals were added to the soil and 2) a soil nitrogen amendment treatment in which carbon as industrial sucrose was added to the soil at a concentration of 200 g m^{-2} per application. Sucrose applications were performed monthly over the rainy season extending from late autumn (May) to early spring (September). Six indigenous shrub species of similar age and height (range: 25 cm to 30 cm) were randomised among the 6 subplots in each plot at the beginning of the winter season (June). They included the typical renosterveld shrubs *Olea europaea* subsp. *africana*, *Salvia africana-lutea*, *Rhus lucida* f. *lucida,* and *Pelargonium cordifolium*, and the alluvium fynbos shrubs *Leucadendron xanthoconus* and *Leucospermum praecox* .

Greenhouse trials

The greenhouse trials were conducted in a passively ventilated green house in the Kirstenbosch National Botanic Gardens. There were two trials both comprising split-plot designs. In the first trial, ninety six soil cores (28 cm wide x 30 cm long x 10 cm deep) were excavated from the peripheries of the field plots. The soil cores were individually placed into plastic containers of the same dimensions and these arranged into six blocks located at different positions in the greenhouse. Each block comprised 16 soil bearing containers arranged into four columns and four rows. The four soil nutrient amendment treatments were randomly assigned to the four columns in each block and applied at the same frequencies and concentrations on an area basis as in the field trial. Four indigenous species, introduced as seeds, were randomly assigned to four rows in each block. They comprised the annuals *Arctotis acaulis*, *Dimorphotheca pluvialis* and *Ursinia anthemoides* subsp. *anthemoides,* and the shrub *Rhus laevigata* var. *villosa*. Three weeks after germination the seedlings of each species were thinned to four individuals per container. A fifth species comprised the naturally occurring geophyte *Oxalis purpurea* whose bulbs were a common component of the soil in all the containers. Individuals of this species were also reduced to four per container. Amounts of precipitation supplied daily to the soil-bearing containers by an automated irrigation sprinkler system (ca 4 mm d^{-1}) approximated the daily average amount of rainfall (ca 5 mm d^{-1}) received by field plots during the winter rainy season.

In the second trial, an additional 48 soil cores were excavated from the peripheries of the field plots and eight added to each of the existing six blocks where they were arranged into four columns and two rows. There were four treatments comprising two soil nutrient amendment treatments combined with two soil sterilisation treatments. The two soil nutrient amendment treatments comprised a control and a sucrose treatment applied at the same frequency and concentration on an area basis as in the field trial. These were randomly assigned to the four columns in each block. The two soil sterilisation treatments comprised a control in which the soil was sieved though a 2 mm mesh to remove plant detritus and larger plant propagules such as *O. purpurea* bulbs, and a heating treatment in which the soil was exposed to 220°C for 72 hours in a forced draft oven to destroy all soil micro fauna and flora. These were randomly assigned to the two rows in each block. Two indigenous annuals, namely *D. pluvialis* and *U. anthemoides,* introduced as seed, were each randomly assigned to four of the eight soil bearing containers in each block and thinned to four individuals per container three weeks after germination.

Plant photosynthetic efficiency

A chlorophyll content meter (Model CCM-200, Opti-Sciences Inc., Hudson, NH, USA) measured foliar chlorophyll indices and a modulated chlorophyll fluorometer (Model OSI-FI, Opti-Sciences Inc., Hudson, NH, USA) measured photosynthetic quantum yields at a steady state (Y_s) in all the introduced species. Measurements were conducted on fully expanded apical leaves during the active growing period in early spring and confined to clear sky conditions between 11:00 and 13:00 SAST.

Plant growth and nutrient uptake

Below and above-ground parts of all introduced annual species were harvested at reproductive maturity in late spring and those of all introduced shrub species at the end of the dry summer season. Plant parts were dried in a forced draft oven at 65°C to a constant mass and weighed. Nitrogen concentrations in dry plant tissue sub-samples were determined with an elemental analyser (FP-528, LECO Corporation, USA) at a combustion temperature of 900°C (Horneck & Miller 1998). The total amounts of taken up by plants in each container were computed from the products of their total dry mass (roots plus shoots) and their measured tissue N concentration (% dry mass/100).

Soil elemental and microbial concentrations

200 cm^3 samples of soil were collected from the field plots and from the soil-bearing containers in the greenhouse after the introduced species had been harvested. Total numbers of bacterial cells present in 10 g sub samples of fresh soil diluted 10-fold were assayed applying the membrane plate streak method and the numbers of coliforms present in the diluted soil sub samples assayed applying the membrane filter method (Finney et al. 2003). For N and C analysis, the soil samples were dried at 30°C in a forced draft oven, sieved to $\leq$ 2 mm particle size. Total N and C content of the soils were measured by complete combustion using a Eurovector Euro EA Elemental Analyser.

Statistical analyses

All measurements were $\log_e$ transformed before statistical analysis to reduce the inequality of variance in the raw data. The experimental designs were not fully balanced, due to missing measurements resulting from unforeseen plant mortalities and equipment malfunction. A REML (residual maximum likelihood) variance component analysis (linear mixed model) was

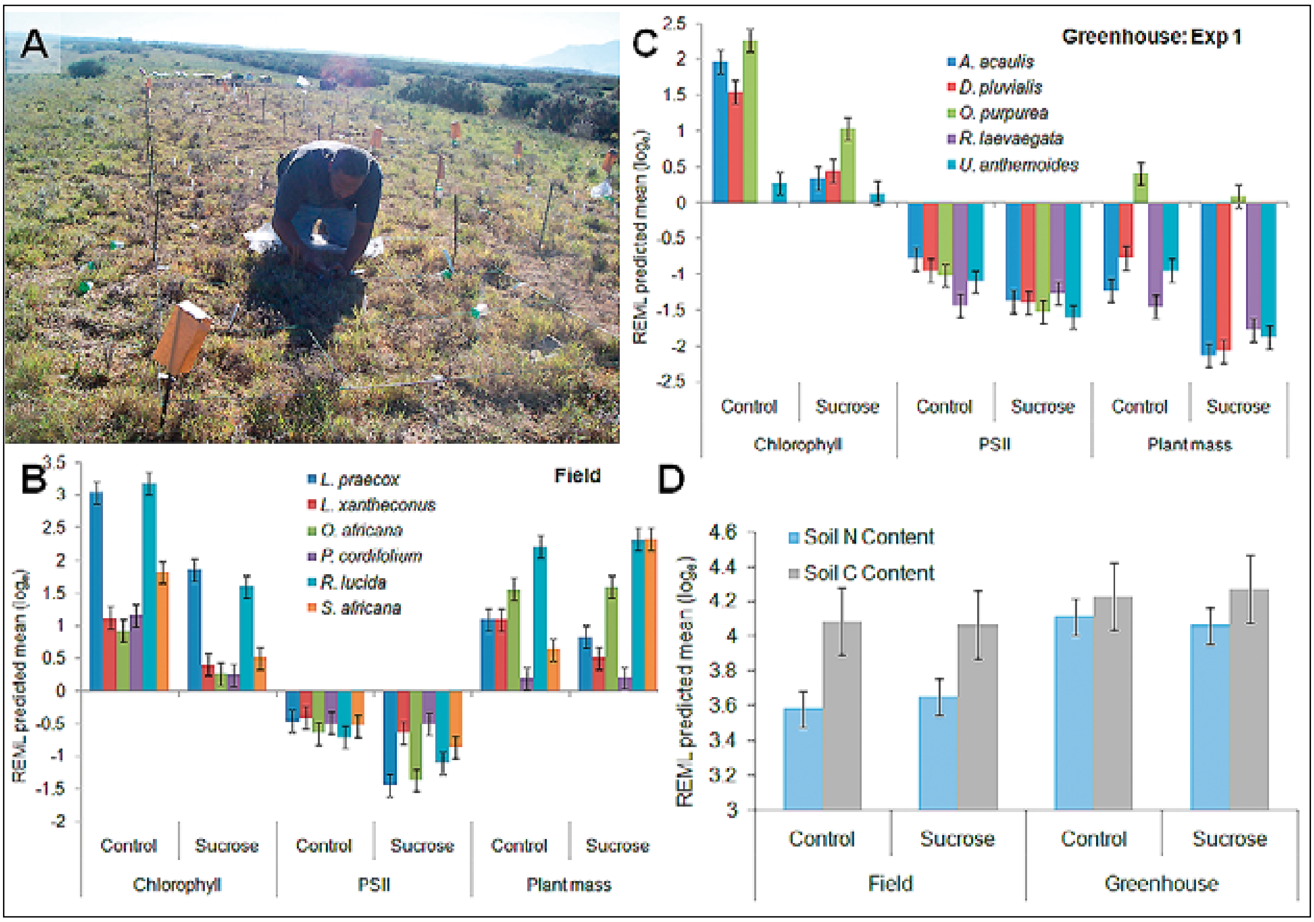

Fig. 1: Field and greenhouse trials. A) Typical field based restoration plot subdivided into subplots into which native species introduced. Effects of sucrose addition on leaf chlorophyll contents, quantum yields of photosynthetic system II (PSII) and masses of introduced species in B) field trial, C) greenhouse trial and D) soil N and C contents in field and greenhouse trials.

applied to test for differences between treatment effects using the Wald X^2 statistic generated by the REML. Sucrose and soil sterilisation treatments and introduced species were fitted in the fixed model and the plots and sub-plots in the random model. Differences exceeding twice the mean standard errors of differences were used to separate significantly different REML predicted treatment means at $p \leq 0.05$.

Results and discussion

Most of the introduced annuals in the first greenhouse trial (Fig. 1C) displayed diminished leaf chlorophyll contents, photosynthetic quantum yields and biomass accumulation in response to the increased levels of sucrose as reported in other early seral species (Redente et al. 1992). However, these reductions, especially that of leaf chlorophyll content and photosynthetic quantum yield, were also commonly observed among the introduced shrub species in the field trial (Fig. 1B), though less evident in their biomass accumulation due to their high mortalities (> 90%) over the dry summer season. Taken together, these findings did not conform with previous reports that sucrose applications inhibit growth of faster growing early seral species (annuals) with high nutrient demands to a greater extent than that of slower growing late seral species (perennials) adapted to low nutrient environments (Averett et al. 2004, Eschen et al. 2006). Also, the sucrose additions did not result in depleted soil N levels or elevated C levels (Fig. 1D). This possibly due to the highly acid soils (pH range: 4.7–5.6), which may have restricted bacterial soil N immobilisation processes as these are most efficient in slightly acidic to neutral soils in the pH range 5.5 to 7.0 (Busman et al. 2002).

The enhanced photosynthesis and growth of introduced plants observed in the sterilised soils (Fig. 2A & C) conformed with reports that soil sterilisation by application of chemicals, steam, or dry heat improves plant growth and soil nutrient availability and reduces seedling mortality (Will & Bassett 1962, Ingestad & Nilsson 1964). This explained by the release of plants from their natural pathogens in compliance with the enemy release hypothesis (Mitchell & Power 2003). Noteworthy was that sucrose applications resulted in much greater reductions in biomass accumulation and nitrogen uptake in normal than sterilised soils (Fig. 2A & C), which implied a bacterial component immobilising soil nitrogen essential for plant photosynthesis and growth. Indeed, interactions between soil microbial communities may be altered by sucrose addition leading to a proliferation of sucrose utilising microbial species (Shaban 1996) and

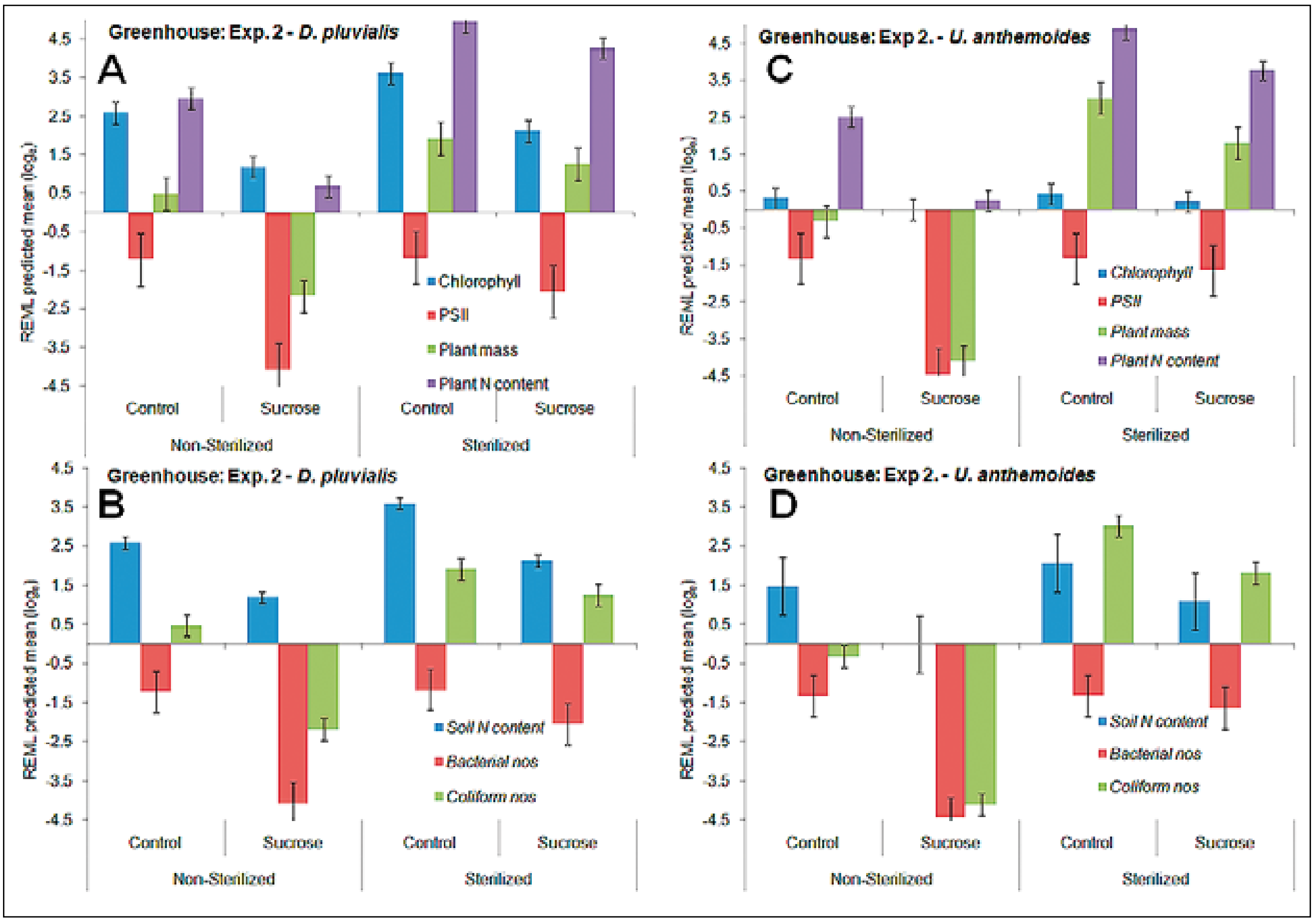

Fig. 2: Effects of sucrose additions to sterilised and non sterilised soils on leaf chlorophyll content, quantum yield of photosynthetic system II (PSII), masses and total N contents of A) *D. sinuata* and C) *U. anthemoides* and corresponding changes in soil N content and microbial (bacteria and coliform) numbers in soils in which B) *D. sinuata* and D) *U. anthemoides* cultivated.

an increased production of metabolites of fermentation, such as acetate, typical of sucrose-amended soil (Paul et al. 1989), that may retard root elongation and inhibit plant growth (Blank & Young 2009). However, there were contradictions to these suggestions. These included the substantially smaller numbers of total bacteria and coliforms measured in normal than sterilised soils (Fig. 2B & D). This is a possible consequence of reduced competition and predation from other soil micro-flora and fauna exterminated during soil sterilisation, and the absence of any increase in total bacterial and coliform numbers, with one exception, following sucrose applications as reported in other studies (Blumenthal et al. 2003, Averett et al. 2004, Eschen et al. 2006).

These contradictions pointed rather to an abiotic mechanism of sucrose induced inhibition of plant photosynthesis and growth. Several studies have reported that exogenous sucrose additions reduce foliar concentrations of both chlorophyll *a* and *b* and net photosynthetic rates (Mosaleeyanon et al. 2004). This attributed to the accumulation of hexose (Hdider & Desjardins 1994) and starch in chloroplasts (Capellades et al. 1991, Mosaleeyanon et al. 2004) causing feedback inhibition of photosynthesis and consequent decreased plant growth (Langford & Wainwright 1987). Addition of exogenous sucrose at high concentrations has also been shown to inhibit both root and shoot growth in rice (Thapa et al. 2007), hypocotyl elongation (Jang et al. 1997) and light-induced cotyledon opening (Dijkwel et al. 1997, Jang et al. 1997) of *Arabidopsis thaliana* seedlings (Ohto et al. 2001) and also causes flowering delays in *A. thaliana* (Zhou et al. 1998, Ohto et al. 2001), the latter attributed to a metabolic rather than an osmotic effect (Ohto et al. 2001).

Conclusions

The inhibitory effects of sucrose applications on plant photosynthesis and growth and its greater cost relative to other carbon sources render it as an impractical means of amending soil fertility in restoration initiatives. Other slower releasing sources of carbon, such as sawdust, reeds, chopped wood or a mixture of these may provide a more efficient and economical means of reducing soil fertility over the long term.

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Understanding norms and propensities for cooperation and collective action: economic experiments within BIOTA

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Summary: This article acquaints the reader with a few major results obtained from economic field experiments conducted in the communal areas of Namaland, Kavango and Namaqualand. Experiments were applied by BIOTA researchers mainly to investigate social norms and to analyse the performance of different institutions. Experimental results show that social norms of trust and cooperation are well established in our study areas and that external intervention, if not backed by the majority of resource users, may crowd-out intrinsic motivation to cooperate.

Introduction

Experiments are a well established empirical method applied not only in economics but also in other behavioural sciences, such as anthropology and psychology. Experiments can be described as data generating processes under controlled conditions, generally used to investigate causal relationships among variables and to test hypotheses. Most economic experiments are similarly structured. They usually confront participants with a set of choices, which determine their scope of action. Likewise, they contain the information conditions and a monetary incentive structure, which translates decisions into payoffs (Croson & Gächter 2010).

In the BIOTA context, researchers carried out experiments in the communal areas (see Table 1) mainly to investigate the efficiency of different institutions and proposed policies, as well as to gain a better understanding of the preferences and social norms of resource users, which affect economic development in general, and resource use in particular.

In the communal areas, natural resource use constitutes a major livelihood strategy for the majority of inhabitants. Grazing, forest, and other natural resources are common-pool resources (CPR), characterised by rivalry in consumption and costly exclusion of outside users. It has been argued that strong formal institutions are necessary to prevent degradation of common-pool resources in communal areas. However, external interventions run the risk of undermining existing informal arrangements, thus destabilising the community (Ostrom 1990), and of crowding-out intrinsic motivation to cooperate (Gneezy & Rustichini 2000, Fehr & Rockenbach 2003).

Experiments enable researchers to test various institutions and their impact on individuals' propensities to cooperate, as well as their efficiency and acceptance, and thus aid in recommending certain institutional designs to policy makers. One of the advantages of experiments is control. Control refers to the ability to hold most factors, which influence behaviour (e.g. economic returns from grazing) constant and varying only the factor of interest (in this case, the implementation of an institution). The controlled variation of factors enables the experimenter to draw causal inferences. For example, if we observe a strong increase in cooperation after the implementation of an institution while holding all other factors constant, we could conclude that the institution helped resource users to gain more efficient outcomes. In naturally occurring decision situations, on the other hand, the circumstances under which decisions occur are often unknown or unobservable to the researcher and "cannot be influenced or occur simultaneously with other conditions, such that it is not possible to say anything about causality" (Gächter 2009: 4).

External institutions interact with behavioural norms, which evolve within a certain cultural and social context (Ostrom 2000), implying that some institutions can work well in one society but may not yield the desired outcomes in another where social norms and the historical or ecological contexts are different. Norms of fairness, cooperation, trust, and reciprocity are crucial for successful common-pool resource management. To gain a better understanding of these norms, and to complement the controlled interactions of experiments with real-life decision-making, BIOTA researchers carried out socio-demographic and ethnographic surveys. In contrast to other complementary empirical methods, experiments use real monetary incentives by paying participants according to their decisions. This is a unique feature of experiments and makes them less prone to surveyor effects, the idealised persona bias and hypothetical bias, which are potential shortcomings of surveys (Cardenas & Carpenter 2005). To understand the benefit of providing material incentives, consider the following example of a common interview question. If farmers were asked "Would you reduce your herd size if everybody else did so", the majority of respondents would probably answer this question with "yes" to signal cooperativeness. However, the question is hypothetical and there is no incentive for farmers who would not reduce their herd size to reveal their true character. On the contrary, in experiments designed to investigate individuals' propensity to

Table 1: Overview of experiments conducted in the communal areas of Namibia and South Africa by BIOTA researchers

Researcher(s)	Year	Region	Experiment	Purpose
Pröpper	2007	Rural Kavango	Trust game	Inter and intra community trust levels
Vollan	2007	Namaland (NAM) and Namaqualand (RSA)	CPR game	Efficiency of communication, external punishment and rewards
Vollan	2006	Namaland & Namaqualand	Trust game	Cross-cultural comparison of trust and reciprocity
Vollan	2007	Namaland & Namaqualand	Prisoner's Dilemma game	Third party punishment and kinship
Vollan & Prediger	2007	Namaland & Namaqualand	Grazing game (CPR)	Efficiency of real-life institutions (rotation, lottery and herd size regulation)
Pröpper & Vollan	2008	Rural Kavango	Public goods game on forest resource management	Testing of cooperativeness, internal and external sanctioning mechanisms
Prediger	2008	Namaland	Risk and Time preferences	Risk attitudes and patience
Prediger & Vollan	2008	Namaland & Namaqualand	Grazing game (CPR)	Efficiency of property rights allocation mechanisms and communication
Prediger	2009	Dreihuk communal area	Public Good game on water management	Peer punishment, impact of informal sanctions on cooperative behaviour
Prediger & Vollan	2009	Namaland	Joy of destruction game	Relation between antisocial preferences (spite) and resource scarcity
Falk	2009	Omaheke (Resettlement farms)	Computerized bio-economic experiment	Responses of resettled farmers to ecological and economic signals

cooperate in common-pool resource dilemmas, subjects must forego immediate personal earnings to engage in cooperative behaviour. That is, cooperative behaviour is costly to participants (in the short-term) and they therefore have an incentive to truthfully reveal their character. In other words, experiments using material payoffs are incentive compatible.

However, experiments also have their pitfalls. Experiments can lack internal and external validity and may not always yield results that are easily generalised (see for example Levine & List 2007 for a detailed discussion of methodological problems). It is therefore desirable to combine experiments with other methods, such as surveys, expert interviews, or ethnography, to test and improve the validity of experimental results.

Some major results from experiments carried out by BIOTA researchers

In this section we provide a review of some experimental results obtained from trust games, grazing games and standard CPR experiments. Due to space constraints, we do not discuss all the results obtained by BIOTA researchers.

As outlined above, BIOTA researchers paid special attention to the investigation of social norms that promote collective action amongst resource users. Collective action (i.e. the pursuit of a common goal by a group) is crucial for sustainable resource management, especially when formal institutions, which govern resource management are weak and imperfectly enforced, as in the communal areas of Namibia and South Africa.

Important preconditions for collective action are trust among resource users and reciprocity. An elegant way to measure trust and reciprocity is the so called trust game developed by Berg et al. (1995). BIOTA researchers (Pröpper 2008, Vollan 2008) adapted the trust game methodology and tuned the experimental design to guarantee comparability of results. The trust game is played by pairs of individuals, who are randomly matched. Both players are given N$10 and the game consists of two stages. In stage 1 the first player decides how much of his endowment to transfer to an anonymous second player. All money transferred is tripled (e.g. if the first player transfers N$4, then the second player receives N$12). In stage 2, the second player then has to decide how much of his money (the initial endowment of N$10 plus the amount received from the first player) to return to the first player. In this game, only the first players who trust their anonymous partners will send a positive amount of money. Because the trust game is played once only and anonymously, only social history about the use of trust within a group is common information.

Vollan (2008) found levels of trust to differ remarkably between residents from communal areas in Berseba (Namibia) and Namaqualand (South Africa), which are both predominantly populated by Nama people. In Namibia, subjects sent on average 41% of their initial endowment compared to only 21% in South Africa. Modes also differed between the countries: In South Africa the mode was zero, while in Namibia people transferred 25% of the endowment. The results show that trust among community members is substantially lower in South Africa than in Namibia. This was explained by differences in historical developments in general between the two countries, and negative experiences with maladministration, corruption and contested land privatisation attempts in South Africa, in particular, which have created divided factions and bitterness within the communal areas of Namaqualand (Vollan 2008). Both trust and reciprocity differed significantly between the two countries. Reciprocity is measured as the ratio between the amount sent/received and the amount returned. While the majority of South Africans exhibited a norm of "balanced" reciprocity (that is, the second players returned the same amount that they received), Namibians often returned nothing, which indicates a strong norm of "generalised" reciprocity. Generalised reciprocity is the dominant exchange system of the Nama (Klocke-Daffa 1999) and refers to generosity and sharing between community members without the expectation of a return. This form of reciprocity among the Nama serves as a security mechanism and creates and maintains social relations.

It has been argued that experimental decisions are influenced by common cultural background (social norms, beliefs, established mechanisms of interaction), which strongly influences the framing of experiments (Cronk 2007, Henrich et al. 2004, Lesorogol 2005). Ethnography is a useful tool for assessing these framing factors, adapting the experimental design, and interpreting experimental results in the light of background knowledge (e.g. systematically assessed by census). In a study carried out in the Kavango region of North-East Namibia in 2007, Pröpper combined results from economic trust game-experiments conducted in three communities with data from ethnographic research that had been carried out since 2004 (Pröpper 2008, 2009).

Ethnographic research found that Kavango villages consist of cooperative networks with known social histories. Repeated interactions are a basis for trust-based relationships and reciprocity among people who are regularly struggling with resource shortages and do not have a lot to give away for free. However, sharing and gentle behaviour are observable norms.

Compared to levels of trust observed in trust games conducted in other sub-Saharan African countries (Cardenas & Carpenter 2005), Pröpper found that levels of trust and reciprocity in rural Kavango villages were relatively low. It appears that trust in circumstances of single anonymous interactions is risky. Data analysis revealed that subjects transferred on average 41% of their initial endowment, but that calculating overall mean values could blur intra-village differences. Examination of the return ratios (returned amount : sent amount) revealed that the dominant strategy was for people to keep a major part of the endowment for themselves while using the remainder for small scale reciprocity. However, contrary to game-theory predictions, 'zero offer/return' was never the dominant strategy. Most players decided to play with small contributions, indicating a low level of trust and an existing norm of small scale reciprocity that was especially visible in the strategies of two women reciprocating with a zero offer. The norm of small scale reciprocity matched ethnographic predictions of preferred self-reliance where cooperation was not needed. Reciprocity was the same in situations of general poverty where a norm of "anything given is already generous" seemed to exist, although there were several mechanisms for helping the weakest. Amongst farmers, an absolute fairness norm of a return ratio of 2 (meaning that the investment gain would be shared equally between both players) did not turn out to be the dominant strategy, as was non-reciprocity, which was extremely rare as well. This interpretation matches ethnographic findings, which clearly indicate that small-scale giving is widespread whereas larger scale sharing is restricted to well known kin.

Besides such general findings, interesting differences between villages were observed, which may represent ethnological differences between villages. Under game conditions, particularly young and educated males who were roadside farmers took the liberty to act free of cultural constraints and rules, while in the inland villages, with higher average ages of community members, trust and reciprocity levels were higher. Against the theory that market integration promotes fairness (Ensminger 2004) it was found that older, more remotely living villagers with a lower education level were more willing to trust and reciprocate than younger roadside farmers who had better access to markets. It can be hypothesised that amongst these inland villagers, traditional norms of reciprocating are more internalised and a cash free subsistence is practised more often, while younger, mobile roadside villagers have more contact with the goods of modern consumerism and thus a stronger incentive to acquire cash. Combined results have shown that external incentives can have strong effects but that well established cultural norms and especially social institutions play an important role in guiding cooperation between resource users.

Ethnographic interviews revealed that the trust game can be seen as offering participants the freedom of anonymity. Anonymity facilitated a decision free of social history, reputation, and the constraints of being a member of tight social exchange networks. Such a free situation is probably not unknown to actors but rare, and it could be argued that at least the more self-oriented players would have interacted less "freely" in a real-life exchange situation with intact norms. Another important aspect to note was the fact that the financial incentive was provided by the researcher, who was not perceived as culturally equal. Against this background, a fairness norm of cultural equality might have been suspended for the time of the game, resulting in a more self-oriented strategy of "each one on his/her own" that might have affected the players that could return money, in particular.

As mentioned above, most resources in the communal areas are common-pool resources. CPRs are at risk of degradation in cases of overuse, which often has disastrous consequences for the resource users themselves. BIOTA researchers paid special attention to individuals' inclination to cooperate in common-pool resource experiments and the impact of different institutions on their behaviour.

An example of this kind of experiment is a "grazing game" (Vollan et al. 2009, Prediger et al., unpublished). Grazing

Photo 1: Para-ecologist Richard Isaacks explaining the grazing game experiment.

games were conducted with 5 rural farmers per session and lasted for 20 rounds. The design of the experiment reflected the typical problems CPR users face in the real world. It provided individual incentives to apply the highest possible stocking rates, i.e. to extract as much as possible from the grazing resource, because higher stocking rates yielded higher monetary earnings. However, if all participants did so, the grazing resource degraded and individual earnings diminished substantially as a direct consequence. Thus, short-term individual payoff maximisation negatively affected the entire group in the long run. Such a situation is referred to as the "tragedy of the commons". Only if subjects cooperated, i.e. applied moderate stocking rates, could resource degradation be avoided, with a consequence that higher earnings could be realised in the long-run.

We conducted the grazing game experiments with rural farmers in Namibia and South Africa and found a highly significant difference between countries. Farmers from Namibia cooperated better, sustained more pastures in good condition, and achieved resource recovery faster and more frequently than South African farmers, and consequently yielded higher earnings. It became apparent from statistical analysis that Namibian farmers are willing to forego higher earnings for the sake of resource protection. Prediger et al. (2010) attributed the differences between countries to higher payoffs for cooperation (preventing irreversible degradation) in everyday life in Namibia, stemming from ecological context factors, which are different in South Africa.

An important question for policy makers is whether external interventions can steer resource users towards more sustainable resource management. We therefore tested the impact of various institutions on the behaviour of individuals in CPR experiments, which included a rotation rule, external regulations, rewards, property rights allocation mechanisms, lotteries and communication forums (Vollan 2009, Vollan et al. 2009). In most cases the subjects themselves could vote to choose which institutions would be implemented. Our major findings can be summarised as follows: Firstly, the promotion of deliberative community meetings helped subjects to manage the resource more successfully and increased equity amongst community members (Vollan 2009). Secondly, efficiency further increased if mutual agreements were enforced, albeit imperfectly, by an external agency. Thirdly, rule choice was often driven by individual perceptions of whether the rule was efficient and advanced self-interest (Vollan et al., unpublished). Therefore, if politicians want to promote any rule changes, they need to convince community members of the personal benefits associated with the new rules. Fourthly, in South Africa, all rules that were tested improved performance in comparison to an open-access situation. The regulation of individual grazing intensities (i.e. restricting herd sizes) was particularly successful in South Africa. In Namibia, on the contrary, the impact of institutions was ambiguous. Most institutions that were tested neither increased nor decreased efficiency. However, we did find that experimental external herd size regulation had negative impacts on individual behaviour, as subjects were less willing to cooperate, at least when group support for that rule was low (Vollan 2009). This phenomenon is called the crowding-out effect and refers to situations where intrinsic motivation to cooperate is "crowed-out" by an external intervention, which is often perceived to be paternalistic and to reduce self-determination. Such a crowding-out effect of cooperative behaviour can only occur when people have already reached a high degree of cooperation before the implementation of an external intervention. These results show that policy makers should only implement institutions, which have strong support from the community.

Finally, the analysis of rule following behaviour revealed that regular monitoring and penalties for rule infringement were crucial for sustaining rule efficiency. Subjects who were monitored frequently were significantly less likely to deviate from the agreed-upon rule and thus more willing to cooperate.

Conclusions

Experiments have become an important methodological tool in anthropology and economics in the last two decades. Unique features of experiments are control and the use of monetary incentives to avoid several biases that may arise in complementary empirical methods.

BIOTA researchers used experiments to investigate social norms in the communal areas of Namibia and western

South Africa. It was found that norms of cooperation, trust and generalised reciprocity are still strong in the communal areas of southern Namibia. In grazing game experiments as well as in simple common-pool resource experiments, Namibians exhibited a high propensity to cooperate and to manage a grazing resource sustainable, even though cooperation required them to forego immediate benefits. The experiments further revealed that institutional arrangements, which facilitate communication and/or regulate individual resource extraction would help South Africans to manage resources more sustainably. However, the same institutions may crowd out intrinsic motivation to cooperate in Namibia.

The work of Pröpper demonstrates the complementary application of experiments and ethnography. The small contributions of villagers from Kavango indicated relatively low levels of trust and an existing norm of small scale reciprocity, which confirms ethnographic findings that small-scale sharing occurs in everyday life but that large-scale giving is restricted to well-known kin. His experimental results further match ethnographic predictions of preferred self-reliance when cooperation is not needed. Pröpper also highlights the importance of influences such as market access and consumerism incentives on traditional norms of trust and reciprocity, as was found with young educated male farmers with better access to infrastructure, who were less inclined to follow cultural rules and norms.

The huge behavioural differences observed within and between the two countries demonstrated that socio-cultural, historical and ecological contexts are important. Therefore, policy-makers need to broaden their understanding of social norms and interactions amongst target groups before implementing new policies. Experiments offer an appropriate and low-cost tool to investigate the efficiency and impact of projects before they are implemented in the real world.

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Part III

III.7 Expanding knowledge through models

The role of models in biodiversity observation schemes

Florian Jeltsch* & Niels Blaum

Summary: This introductory chapter briefly discusses the relevance of ecological models in the framework of biodiversity observation and monitoring initiatives. It highlights the important contributions of modelling in (i) integrating empirical information and data, (ii) detecting mechanisms and key processes, and (iii) forecasting and scenario development. Emphasising the role of mechanistic, process-based models this chapter also gives a brief outlook to the following modelling articles.

The role of models in biodiversity observation schemes

Integrating the large amount and broad range of inter- and transdisciplinary information and bringing it into application, e.g. through management and decision making support, is a key challenge for any interdisciplinary monitoring or observation scheme. While well-organised databases are a helpful and important tool to structure available information they do not per se allow to identify interacting mechanisms, feedbacks and multi-dimensional correlations. Here, models can be an additional instrument to integrate and filter complex information, guided by a clear research question, and thus also identifying knowledge gaps and future research needs. However, data integration and analyses are not the only potential benefits of models in observation schemes.

Clearly, management support and decision making in biodiversity conservation must not only be based on a thorough understanding of past and ongoing mechanisms and processes. Considering the current situation of rapid regional and global environmental change, there is also a strong need to develop and forecast ecological scenarios. According to Clark et al. (2001), "ecological forecasting is defined ... as the process of predicting the state of ecosystems, ecosystem services, and natural capital, with fully specified uncertainties, and is contingent on explicit scenarios for climate, landuse, human population, technologies, and economic activity." Currently, most ecological forecasts analyse existing datasets solely with statistical, phenomenological models, which are then extrapolated into the future (top-down approach) (e.g. Araújo et al. 2005). Such statistical models, particularly those focusing on spatial processes, are considered suitable tools for detecting and describing patterns, and for forecasting long-term effects of environmental change on species, species groups and species diversity. Nevertheless, they lack the implementation of processes and possible synergistic effects, e.g. between interacting species, and they ignore transient dynamics under changing environmental conditions (e.g. Thuiller et al. 2008). Purely statistical approaches are thus increasingly questioned as appropriate tools for forecasting biodiversity responses to environmental change (Botkin et al. 2007). So-called mechanistic or process-based models provide an alternative or at least supplementing approach that can also be combined with statistical correlations. Such process-based models integrate information on key mechanisms, such as demographic processes, dispersal or competition for scarce resources to develop a bottom-up mechanistic understanding of pattern and dynamics observed in nature (Jeltsch et al. 2008). As shown in the following chapters, process-based ecological, eco-hydrological or bio-economic models thus provide suitable platforms to integrate a given variety of incoming information (e.g. from climate to socio-economy to biodiversity) and form a suitable basis for process understanding and ecological forecasting. In close linkage to climate modelling and empirical research they provide powerful tools to analyse complex interacting mechanisms and feedbacks, test alternative management and decision making options and identify sustainable strategies, e.g. of future landuse under scenarios of climate change. A further advantage of mechanistic, process-based models is their transferability into user-friendly tools for education, management and decision support that explicitly includes temporal dynamics and non-linear interactions of driving factors (see Article III.7.6). For example, integrated information on mechanisms and processes are logically interlinked to provide users with implications of wide ranges of possible landuse options under different climatic scenarios. This relates to single farms or whole regions and can be used for training (future) decision-makers and stakeholders as well as giving guideline and support for concrete decision making processes.

The current expertise in linking observation with modelling was tested and further developed in an African context within the framework of the BIOTA project. Here, in addition to advanced statistical modelling approaches, special emphasis was put on mechanistic, process-based models covering research in different fields of biodiversity research under climate change and landuse (see the following Articles). Research on ecohydrological processes and maintenance of biodiversity (see Article III.7.2; Reineking et al. 2006, Popp et al. 2009a, b, Tietjen et al. 2010), landuse impact (see Article III.7.2; Weber et al. 2000a, b, Tews et al. 2006), population dynamics and gene flow in fragmented landscapes (see Articles III.7.3 and III.7.4; Blaum & Wichmann 2007), and ecological-economic implications (see Article III.7.5; Popp et al. 2009c) will be presented. This bottom-up modelling approach proved to be crucial to analyse and understand ecological and other processes in situations of changing, transient conditions and complex interactions. Moreover, the bottom-up approach was integrated into a normative model of rangeland management, which anticipated range quality changes under different use intensities and which was used to find sustainable strategies (Article III.7.5; Domptail et al. 2008).

While these and other examples already show the usefulness of process-based modelling in the larger framework of observation schemes, they also highlight key challenges in further improving the integration of incoming data into process-based models, identifying reliable future ecological scenarios and developing tools for management and decision making. One key challenge in process-based model development and model driven analysis of climate-landuse-ecosystem interactions is the need to integrate different spatial scales ranging from interacting individuals to landscapes, farms or even beyond. Here, special emphasis is needed in the development of scaling-up approaches of process-based models (e.g. Popp et al. 2009b). Depending on the research focus and the spatial scale of interest, scaling up also allows to further link spatially-explicit models with remote sensing information (see Volume 3, Subchapter IV.2.2).

While in principle observation and monitoring schemes can be implemented without an integrated mechanistic modelling component, the BIOTA example showed that this would substantially reduce the benefit of the overall effort. A close linkage of empirical and modelling methods does not only improve information integration, process understanding and scenario development, but will significantly contribute to decision support and management.

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Modelling vegetation change in arid and semi-arid savannas

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Summary: Within the BIOTA project a range of ecological savanna models were developed and successfully applied. The dynamic vegetation models allowed to systematically analyse the mechanisms that drive the specific savanna systems under different scenarios of future climate and landuse. Integrating and linking to the interdisciplinary empirical research within BIOTA these models simulated key population-level processes such as reproduction, mortality and dispersal in relation to environmental conditions.

In this chapter we briefly present the general approach and key findings for selected sites along the BIOTA Southern Africa transect, compare degradation risks along the transect, and present results from studies regarding selected plant species in these systems. Further modelling studies that are based on, or extrapolate and generalise findings shown here to larger scales within the Thornbush Savanna Biome are presented in Volume 3 of this book.

Introduction

Predicted climate change and increasing landuse pressure pose major threats to productivity and biodiversity in drylands worldwide (Reynolds et al. 2007). Many dry savanna rangelands, where livestock production is the dominant type of landuse, are negatively impacted due to unsustainable practices such as overgrazing by livestock (Tietjen & Jeltsch 2007). Overgrazing, especially in combination with unfavourable rainfall conditions, can lead to a loss of vegetation cover, which increases the risks of erosion, or can cause bush encroachment where woody vegetation increases at the cost of palatable herbaceous vegetation (e.g. Weber & Jeltsch 2000, Weber et al. 2000).

Current models of climate change typically predict an increase in the probability of unfavourable climatic periods such as altered precipitation patterns, with increased temperatures and decreased mean annual precipitation (Solomon et al. 2007), which are likely to strongly affect vegetation dynamics in these water-limited savanna systems.

Climate change and unsustainable landuse may not only reduce rangeland productivity, but are also likely to change the structural diversity of these dry savanna landscapes. Animal diversity may therefore also be at risk due to altered precipitation-driven food availability and climate- or landuse driven changes in habitat structure, including the availability of key structural resources such as solitary nesting trees, foraging grounds, hiding places and safe migration routes (e.g. Dean et al. 1999, Tews et al. 2004a, Blaum & Wichmann 2007, Blaum et al. 2007).

A major aim of the modelling component in the BIOTA project was to improve our understanding of the mechanisms through which climate and livestock production drive the interlinked dynamics of woody and herbaceous vegetation in the dry savanna sites of the BIOTA transect. This understanding is a crucial prerequisite for sustainable savanna management and biodiversity conservation.

Shrub-grass dynamics in Thornbush Savanna and Nama Karoo: impacts of livestock production and climate change

General modelling approach

Within the three BIOTA phases, three generations of vegetation model were developed and applied, and successively improved and refined with regard to the leading research questions of each phase (see below, basic model versions are given in Weber & Jeltsch 2000, Weber et al. 2000, Tews et al. 2006, Popp et al. 2009a, Tietjen et al. 2010). In general, all model generations consisted of two submodels (vegetation model and soil-water model), which included the main aspects of soil-water balance and vegetation dynamics. The vegetation models included woody (shrubs and trees) and non-woody vegetation components (annuals and perennial grasses) as the most important life forms. Vegetation models explicitly simulated key population and demographic processes of these life forms including establishment, growth, mortality and competition for space and water. Grazing was also incorporated into the models. The vegetation submodel was linked to a soil-water submodel, which allowed us to systematically explore alternative climatic conditions. Soil moisture was typically represented in two layers in the models. Relevant data from the BIOTA Observatories were integrated into the models either for parameterisation or for model testing (e.g. elevation data, soil data, vegetation data, climate data). Further details on the models can either be found in the cited references, in this chapter, or in Volume 3 of this book.

BIOTA Observatory area: Alpha, Southern Kalahari (S17, mean annual precipitation approx. 185 mm, sandy soil)

A well-established savanna model of the southern Kalahari (Jeltsch et al. 1996, 1997a, b, 1998, 1999) was modified for the research at the South African BIOTA site located in the southern Kalahari. On the basis of annual time steps this spatially-explicit, stochastic model simulated the spatial dynamics of the major life forms (i.e. trees, shrubs, perennial grasses and herbs, and annuals) according to the impacts of variable precipitation, herbivory, tree harvesting and fire events. The explicit dynamics of vegetation structure could therefore be simulated under selected scenarios of climatic change and landuse impact. Realistic scenarios of future developments and changes were identified based on BIOTA field surveys and literature studies for both landuse and climate.

For climatic change scenarios, most current climate change models predict a decrease of mean annual precipitation and/or an increase in extreme events in this region (Weltzin et al. 2003, Solomon et al. 2007). Changes in precipitation influence soil moisture, modifying plant competition and establishment, and plant biomass production, which has a further impact on fire occurrence. Thus, changes in precipitation lead to a cascade of consequences at different organisational levels of the ecological system. Simulations showed that predicted climate change trends in this region generally led to a decrease in tree density and thus to changes in structural diversity (Tews et al. 2004a, 2006, Tews & Jeltsch 2004). The reduction in tree numbers was more pronounced for an assumed reduction in mean annual rainfall as compared to an assumed increase in extreme rainfall years. In general, the increase of extreme rainfall years further led to a change in tree spatial pattern towards more clumping.

Two major forms of landuse, which have an impact on structural diversity in this system need to be considered. They are overgrazing and wood harvesting for fire wood or charcoal production. Overgrazing has two major effects on the coexistence of woody and herbaceous vegetation. Firstly, overgrazing leads to a reduction of grass biomass, which, in combination with trampling, gives local competitive advantages to the woody vegetation (Weber & Jeltsch 2000, Weber et al. 2000). Secondly, reduced grass biomass may lead to a decrease in fire occurrence. Fire can cause mortality of trees and shrubs and reduced fire occurrence therefore also reduces the mortality of these life forms. This twofold advantage led to an increase in tree and shrub density under high simulated grazing intensities in years with sufficient rainfall. An increase in tree density was often accompanied by a trend towards increase in tree clumping and patch size caused by the higher seed availability in these areas (Tews et al. 2006). Seed dispersal by cattle was also found to further increase the rate of shrub encroachment under heavy grazing pressure (Tews et al. 2004b, c).

A simulated increasing intensity of wood harvesting significantly reduced the availability of subcanopy habitat (provided by large trees) for plants and animals. Based on the results of a field survey it was calculated that the mean rate of wood removal can be up to 0.5% of the trees per year for non-commercial harvesting and up to 5% of the existing trees per year for commercial wood harvesting. Simulation results showed that significant negative effects on vegetation structure over relevant timescales only occurred under the commercial wood cutting scenario. Under high rates of tree harvesting, tree density decreased significantly within a few decades and there were changes in tree age structure caused by selective logging of large trees. Effects of tree harvesting were further intensified by a reduction in overall tree seed production (caused by a lower number of large adult trees) and thus reduced recruitment. For consequences of changes in structural diversity see Subchapter IV.2.4.

BIOTA Observatory area: Sandveld (S41, mean annual precipitation approx. 400 mm, sand and loam with concretions of carbonates, silicon and iron)

The vegetation in this study region is a semi-arid Thornbush Savanna with *Acacia erioloba* and *A. mellifera* being the most dominant woody species. *Grewia flava*, *Tarchonanthus camphorathus* and *Terminalia sericea* occur at higher densities locally. The region is prone to shrub encroachment, which causes severe problems since it is one of the most important cattle production regions of Namibia. The focal point of the research for this region was to better understand the dynamics of shrub encroachment at different time scales and under different grazing intensities.

Earlier modelling studies in the southern Kalahari have shown that shrub encroachment may show non-linear dynamics with a threshold response to increasing stocking density (Jeltsch et al. 1997a, b, Weber et al. 1998, 2000, Weber & Jeltsch 2000). Here, we systematically tested these earlier findings with a new eco-hydrological model based on the ECOHYD model also applied to Otjiamongombe (see below, Tietjen et al. 2009). The model version applied to the Sandveld region was a combination of a dryland vegetation model that calculated the biweekly growth of three plant life forms (shrubs, perennial grasses and annual grasses) with a grid-based model (HydroVeg) of daily moisture dynamics (Tietjen et al. 2009). The spatial resolution of the two submodels was 5 m x 5 m making up a grid of 30 x 30 cells, thus simulating an area of 2.25 ha. Vegetation growth depended on the water availability in two soil layers, and competition for water and space of the three life forms. Grazing was incorporated into the model to analyse the impacts of different landuse intensities.

Simulation results showed that there was also a clear threshold pattern in the vegetation response to livestock production for the Sandveld region (Fig. 1). This pattern became more pronounced with longer periods of grazing impact. Both mean vegetation cover and herbaceous biomass production remained stable under low grazing pressure (i.e. high values of ha/LSU; LSU = livestock units) but became more sensitive around the threshold range of 20–15 ha/LSU. Higher grazing pressures (less than 15 ha/LSU) on average led to a noticeable increase in shrub cover within one decade and to significant shrub encroachment after 30

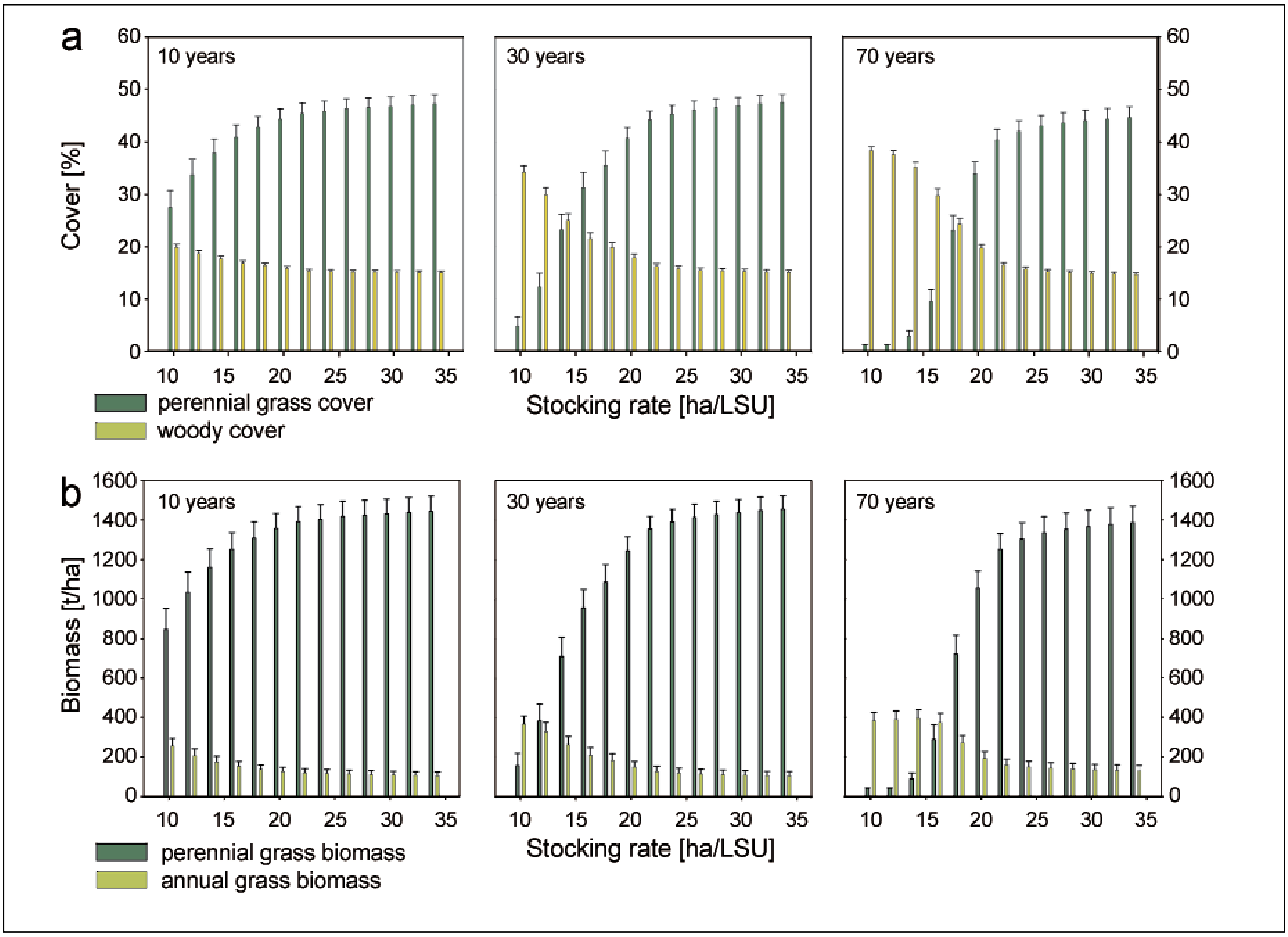

Fig. 1: Vegetation response: (a) mean cover of shrubs and perennial grasses, (b) mean biomass of perennial grasses and annuals to different grazing intensities applied for 10, 30 and 70 years. Grazing was simulated for different stocking densities in 30 replicates per stocking scenario with a set of 30 different rainfall time series (produced with a rainfall simulator for Namibia, NamRain v.101, M. Köchy, unpubl.). Initial vegetation cover was set to 20% shrub cover and 40% perennial grass cover on average (drawn from uniformly distributed cover values between 0 and 2 x mean cover per grid cell). Analyses only started after 30 initial years of very low grazing pressure (40 ha/LSU) to avoid artefacts of initial distributions.

to 70 years. These results only give general trends since there was no variability or adaptation of stocking density included, however they do assist in understanding basic dynamics. For a more detailed analysis of the interplay between ecology and the economy see the chapters on bio-economic modelling (Article III.7.5) and ecological-economic modelling in Volume 3 (Subchapter IV.2.3).

BIOTA Observatory area: Otjiamongombe (S05, mean annual precipitation approx. 400 mm, sandy loamy soil)

Understanding and predicting the combined impacts of livestock production and climate change on savanna vegetation requires a comprehensive understanding of the complex interaction of climatic drivers, soil moisture and vegetation dynamics (Tietjen & Jeltsch 2007). The coupled water-vegetation system is characterised by multiple feedbacks. For example, if climate change modifies water availability, vegetation cover changes and results in altered infiltration, evapotranspiration, and runoff. Similarly, heavy grazing can shift the vegetation to a state with lower grass : shrub ratios or higher proportions of bare ground, which results in reduced forage availability.

This complex interplay of herbivory, climate change and vegetation dynamics was explored in detail at the Observatory area of Otjiamongombe (Tietjen et al. 2010) by applying a novel ecohydrological model, ECOHYD (Tietjen et al. 2009). The model consisted of two submodels (vegetation model and soil-water model) and included the main aspects of the soil-water balance and vegetation dynamics. Data from the BIOTA Observatory Otjiamongombe (elevation, soil, vegetation and climate) were gathered and prepared for modelling, and were used to test and parameterise the model. We tested alternative climate change scenarios including altered precipitation patterns with a decrease in mean annual precipitation and an increase in intra-annual variability, increased temperature, and elevated atmospheric CO_2 (Solomon et al. 2007). CO_2 was an important factor to include in such a study since the water use efficiency of plants increases with CO_2 concentration. Additionally, increased atmospheric CO_2 levels result in higher growth rates, mainly for C_3 plant species but also for C_4 species (Tietjen et al. 2010). An increase in rainfall variability, including more extreme rainfall events, can lead to higher water losses caused by

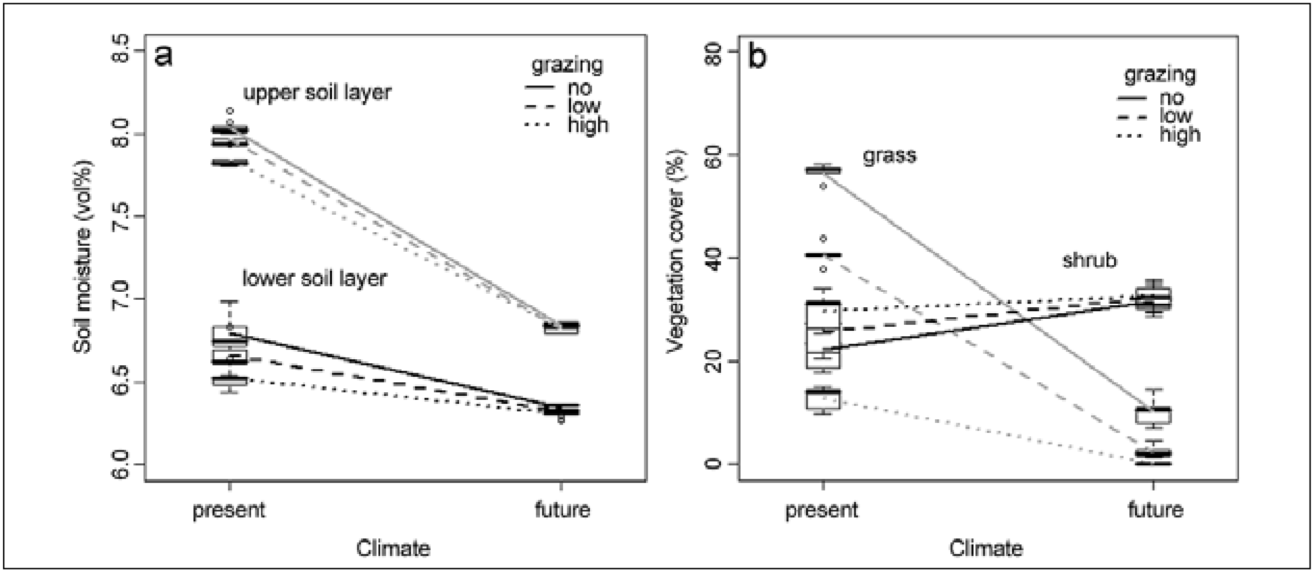

Fig. 2: Simulated impacts of climate change on (a) soil moisture in two layers and (b) vegetation cover of perennial grasses and shrubs under three levels of herbivory. Resulting mean vegetation cover and soil moisture were evaluated for current conditions and for a climate change scenario with strong simultaneous changes in precipitation patterns, temperature, and atmospheric CO_2. For each scenario, mean results and quartiles of five model runs are shown.

an increase in runoff depending on soil type, topography and vegetation cover.

For the Otjiamongombe area, all climate change scenarios led to a clear decrease in soil moisture, especially in the upper soil layer (Fig. 2a). Grass cover declined as a result of reduced water availability, while shrubs were able to increase due to their higher water use efficiency and reduced competition from grasses (Fig. 2b).

These results indicate that climate change will increase the amount of bare soil, and thus the risk of soil erosion, and will further promote shrub encroachment in the Otjiamongombe region. Further simulation experiments for this region showed that heavy livestock grazing could lead to a decrease in soil moisture caused by a decline of grass cover and an increase in shrub cover even under unchanged climatic conditions. Therefore, future climate conditions combined with high grazing pressure, could result in soil moisture falling below a critical threshold for vegetation growth. Interestingly, active veld management in the form of bush-thinning could lead to an improvement in soil moisture in the lower layer because of reduced water losses through transpiration. Bush-thinning can also lead to an increase in rangeland productivity, with grasses being released from the high competitive pressure of shrubs (Tietjen et al. 2010).

Further details and information on the ecohydrological modelling approach are given in Subchapter IV.2.3.

BIOTA Observatory pair: Gellap Ost and Nabaos (S10 and S11, mean annual precipitation approx. 150 mm, loamy sandy soil)

The BIOTA Observatory pair at Gellap Ost and Nabaos in the Keetmanshoop region were situated in the Nama Karoo Biome. Although not part of the Thornbush Savanna Biome, we briefly present the modelling studies for this dwarf shrub-dominated biome, since similar modelling approaches were applied and similar questions were tackled.

The first step was to develop a high resolution (3 m x 3 m) grid-based computer model to simulate the population dynamics of the four most abundant life forms (i.e. perennial grass, annuals, dwarf shrubs and shrubs) interlinked to hydrological processes. Ecohydrological interactions gain importance particularly in rangelands with sloped terrain where vegetation cover serves to obstruct run-off and decreases evaporation from the soil. Disturbances like overgrazing influence these positive feedback mechanisms by affecting vegetation cover and composition. Simulation results showed that in this region, the sensitivity of ecosystem functioning to grazing is strongly influenced by topography (Popp et al. 2009a). Low stocking densities maintained the vegetation in an undisturbed state on gentle slopes where run-off and evaporation were low. However, on steeper slopes, water retention potential decreased leading to lower productivity and higher levels of run-off and evaporation. Overgrazing reduced vegetation cover, biomass production and altered life form composition, and the landscape therefore became less efficient at trapping run-off, leading to high losses of water even in landscapes with gentle slopes. The abundance of perennial grasses and dwarf shrubs decreased with increasing slope angle as well as grazing pressure, and dominance was shifted towards larger shrubs and annuals (Popp et al. 2009a). This shows that different life forms differ not only in their capacity to provide forage but also to regulate ecosystem functioning. Particularly on hilly rangelands, good cover of perennial vegetation minimised water loss from the system, which reduced the decreases in forage production caused by “artificial droughts”.

These results were confirmed in an up-scaled version of the model that allowed linkages to GIS and remote sensing

(Popp et al. 2009c). Model results could successfully be compared with historical, remotely sensed estimates of total biomass production (I-NDVI) from 1981 until 2001 on the sustainably utilised research farm Gellap Ost and the degraded communal farming land at Nabaos. Our simulation experiments showed that spatial interaction by exchanging water among vegetation patches also increases biomass production at light grazing intensities at larger spatial scales. In contrast, overgrazing destabilised positive feedbacks through vegetation and hydrology and decreased the number of hydrological sinks. The buffer capacity of these hydrological sinks disappeared and runoff increased. Spatial interactions caused downstream of the simulated system and "artificial droughts" occurred even in years with good precipitation.

We further developed an integrated ecological-economic modelling approach for the Gellap Ost-Nabaos region that consisted of an ecological and an economic module and combined relevant processes on each level (Popp et al. 2009b). The economic module was used to analyse decision making of different virtual 'farmer types' regarding annual stocking rates depending on their knowledge of how the ecosystem works and on current climatic conditions. A dynamic linear optimisation model (GAMS mathematical programming software) was used to simulate farm economics and livestock dynamics (see also below, and Article III.7.5). The ecological module was used to simulate the impacts of farmer landuse decisions, derived from the economic module, on ecosystem dynamics and the resultant carrying capacity of the system for livestock. Vegetation dynamics, based on the concept of 'state-and-transition' models, and forage productivity for both modules was derived from the small-scale vegetation model described above. Simulation results showed that sustainable management of semi-arid and arid rangelands relies strongly on farmer experience and knowledge of how the ecosystem works. Furthermore, our simulation results indicated that the projected lower annual rainfall due to climate change adds an additional layer of risk to decision making in these ecosystems that are already prone to land degradation (Popp et al. 2009b).

Comparison of sites

The different BIOTA Observatories in Namibia are characterised by different climatic conditions (mean precipitation and mean temperatures) and different soil characteristics. Given these differences it was our aim to develop a generic ecohydrological model that allowed comparisons of the different sites, using site specific climatic and soil conditions to parameterise and specify regional model versions. In order to compare the model outputs for different sites and conditions we developed a simple index *deg* to describe vegetation changes and possible degradation trends under the impact of livestock production. The absolute value of this index denoted the loss of perennial grass cover under different levels of grazing intensity as compared to a situation without grazing ($|deg| = |\Delta \text{ cover perennial grasses}|$). To give an indication of the increase of shrub cover the index was multiplied by (+1) (i.e. gave positive values) if the absolute value of shrub cover and the mean increase of shrub cover within the given timeframe was larger than 5%, otherwise it was multiplied by (–1). Thus positive values of the index indicated that there was a significant increase in shrub cover, with a possible risk of shrub encroachment if the value of the index was high. Negative index values indicated that the risk of soil erosion was more prominent than shrub encroachment, at least if index values were high. Low index values indicated a small loss of perennial grass cover and thus a low risk of degradation. For example, Fig. 3 shows the indices for the climatic conditions of the BIOTA Observatory Sonop (S03) in the Grootfontein region, which was tested for different hypothetical soil conditions, four different grazing intensities and at two timescales. This example shows that the different soil conditions have a profound impact on the degradation dynamics, with sandy soils leading to the highest risk of shrub encroachment under heavy grazing pressure. The positive index values indicate that under these relatively mesic conditions (approximately 495 mm/year mean annual rainfall) an increase in shrub cover is rapid.

Comparison of the indices for different sites along the BIOTA Southern Africa transect on the basis of site specific climatic and soil conditions revealed interesting differences (Fig. 4). After 10 years, only the most mesic site at Grootfontein (Sonop) showed a noticeable increase in shrub cover for all grazing intensities (indicated by positive index values), whereas the drier sites at Sandveld and Otjiamongombe only experienced a problem with increasing shrub cover under higher grazing pressure. However, after 30 years, shrub cover had also increased significantly under moderate grazing pressure for all but the most xeric site, Gellap Ost/Nabaos (indicated by negative index values). For the latter site, loss of vegetation cover was more relevant than shrub encroachment. Index values showed that for all sites along the rainfall gradient, the two highest levels of grazing intensity led to comparable degradation risks within a few decades, either in the form of soil erosion or shrub encroachment.

Further results using this generic model and the vegetation change indices for a broader range of Thornbush Savanna sites in Namibia are given in Volume 3 of this series.

Sample responses of selected species to landuse and environmental changes

Motivation

Based on field studies within the BIOTA project and on the literature, a number of spatially-explicit, stochastic population models of selected animal and plant species were developed (see also Article III.7.3). Home ranges of selected species cover a variety of spatial scales and they differently depend on habitat structures ('structural diversity'). The systematic evaluation of the impact of changes in structural diversity on the population dynamics and survival of these indicator species led to an improved understanding of the linkage between structural and species diversity. Furthermore, an integrated view was gained by combining the more

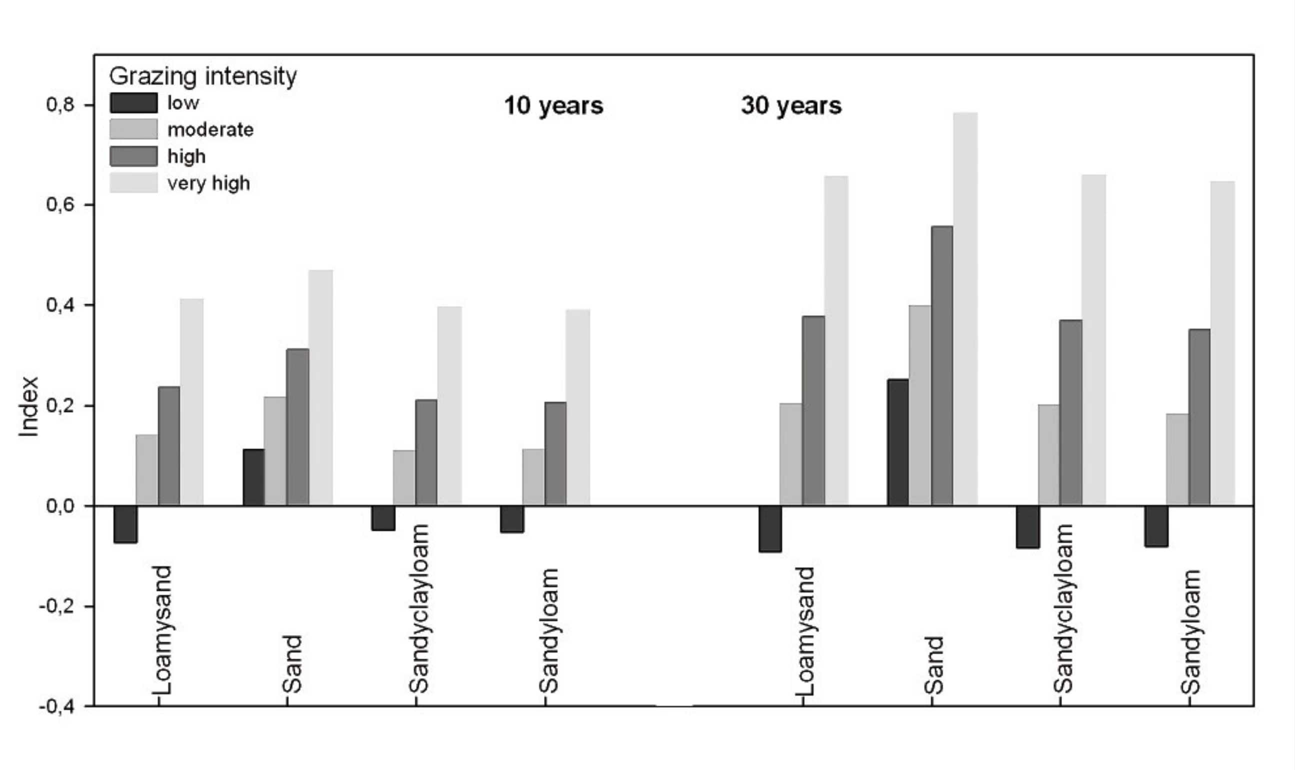

Fig. 3: Index *deg* of vegetation change and degradation dynamics after 10 and 30 years under four levels of grazing intensity tested for different soil types. Grazing intensity is represented here as an annual loss of perennial grass cover caused by grazing. This loss can be compensated for by growth and new establishment of grasses if moisture conditions are sufficient and competition from shrubs is not too high (from 'low' = annual loss of 2%, to 'very high' = annual loss of 20%). Results are based on climatic conditions at Grootfontein. The index value describes the loss of perennial grass cover under grazing as compared to ungrazed vegetation.

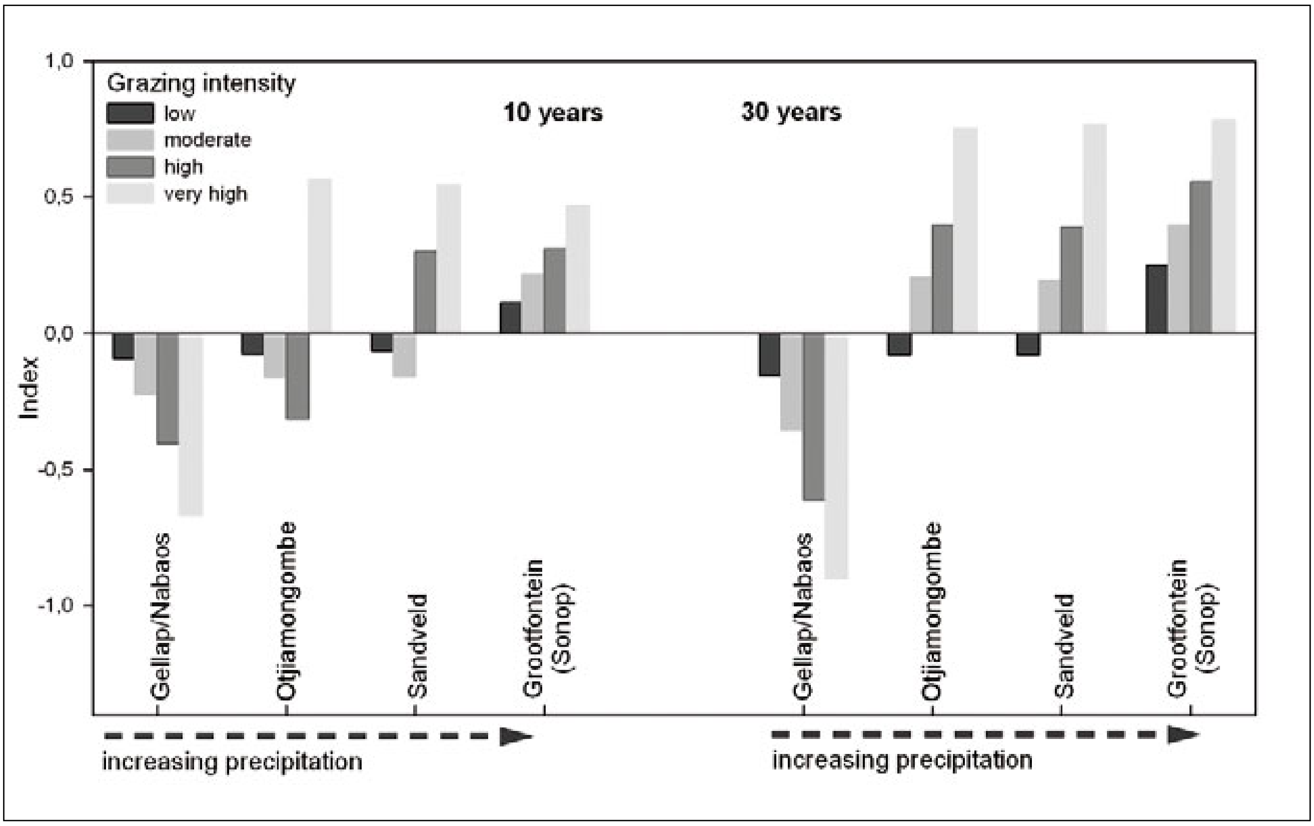

Fig. 4: Index *deg* of vegetation change and degradation dynamics after 10 and 30 years under four levels of grazing intensity at four different sites along the BIOTA transect. For definition of grazing intensities see Fig. 3.

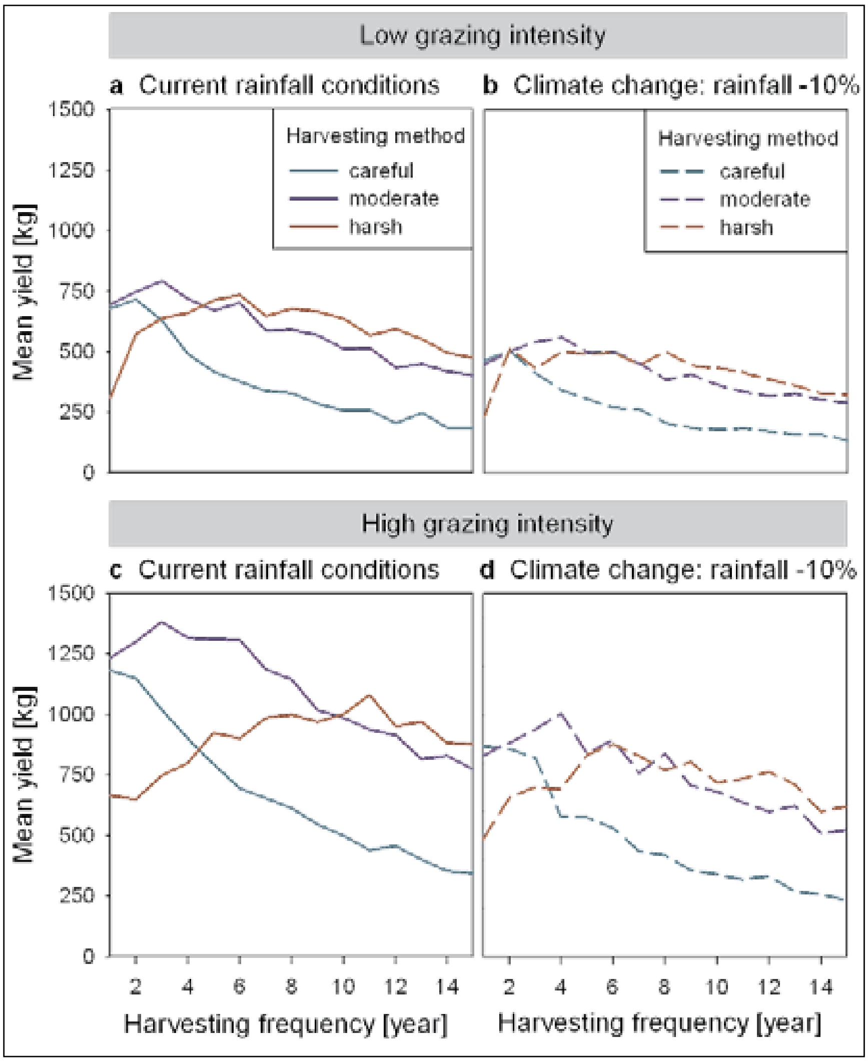

Fig. 5: The impacts of different harvesting strategies on the harvesting yield of Devil's Claw (*Harpagophytum procumbens*). (a) Yield under low grazing impact with current rainfall conditions and (b) under climate change, (c) reduction of the mean annual rainfall by 10%, yield under high grazing impact with current rainfall conditions and (d) under climate change.

general vegetation studies described above and the more specific population models (e.g. Tews et al. 2006). Here, we briefly summarise key results regarding the selected plant species.

Acacia erioloba

The importance of trees as a key structure in the dry savannas of the southern Kalahari has already been mentioned above (Observatory area farm 'Alpha'). In particular, the Camelthorn (*Acacia erioloba*) has been identified as a keystone tree species in the Kalahari Desert and in African savannas (Dean et al. 1999, Eccard et al. 2006, Moustakas et al. 2006). Larger trees affect soil quality, and produce large patches of shade, pods, gum, and fuel wood. Large trees reduce nutrient leaching, increase nutrient levels beneath their canopies (as a result of nutrient cycling and concentration of livestock dung), mitigate soil degradation, prevent soil erosion on steep slopes, sequester carbon and replenish organic matter (Barnes 2001). An empirical BIOTA study on the use of Camelthorn wood addressed the concerns of the South African Department of Water Affairs and Forestry and of the Northern Cape Department of Tourism, Environment and Conservation (Raliselo 2002). These empirical and modelling studies on sustainable wood harvesting contributed to resolving disputes between wood harvesters and tree protection agencies, and aided in the formulation of policy on the sustainable use of trees and woodlands in the Northern Cape Province of South Africa. A model integrating the long-term effects of climate change and landuse on *Acacia erioloba* was also integrated into the KBioSim tool described below (Article III.7.6).

Grewia flava

Grewia flava (Velvet Raisinbush) is a fleshy-fruited, woody plant species occurring in the southern Kalahari savannas. Due to bird-mediated seed dispersal, *G. flava* often recruits under the canopy of large, solitary Camelthorn trees (*Acacia erioloba*), which are usually widely scattered throughout the grassy vegetation matrix. However, under high cattle grazing *G. flava* increasingly establishes in the open grassland matrix (Tews et al. 2004c). The simulation results of a spatially explicit computer model of *G. flava* population dynamics showed that cattle may facilitate this process of shrub encroachment (Tews et al. 2004c). For high stocking densities and without grass fires, the model predicts up to 56% shrub cover after 100 years. Shrub encroachment of *G. flava* could be countered by frequent fires and controlling cattle movement to areas with a high proportion of fruiting *G. flava* shrubs. While cattle grazing increased population densities of *G. flava*, the commercial harvest of *A. erioloba* trees had a significantly negative impact. The loss of *A. erioloba* strongly decreased *G. flava* population density because *G. flava* depends on tree microsites as potential recruitment sites. This process may also be relevant for other plant species because of the ecological keystone function of these trees (Tews et al. 2004a). The spatially explicit, stochastic computer model of *G. flava* was also used to investigate the impact of climate change on population performance (Tews & Jeltsch 2004). Four contrasting climate change scenarios were considered for the southern Kalahari: (1) an increase in annual precipitation by 30–40%, (2) a decrease by 5–15%, (3) an increase in variation of extreme rainfall years by 10–20%, and (4) an increase in temporal auto-correlation, i.e. increasing length and variation of periodic rainfall oscillations related to El Niño/La Niña phenomena. Based on the simulation experiments we generally observed positive population trends for scenario (1) and negative trends for scenarios (2), (3) and (4). However, in terms of projected rates of precipitation change, population dynamics were stable for scenarios (3) and (4). Furthermore, the negative effects (i.e. increasing local extinction rates for *G. flava* populations) found under positive auto-correlated rainfall support current ecological theory, which states that periodically fluctuating environments can reduce population viability because species spend too much time in an unfavourable environment.

Harpagophytum procumbens

The Devil's Claw (*Harpagophytum procumbens*), an endemic plant species of semi-arid rangelands in southern Africa, is an important medicinal plant and source of cash income for many rural communities (Hachfeld 2003, Strohbach & Cole 2007). A fast growing export market and the absence of long-term resource management strategies have resulted in a decline of this species, especially of dense populations (Strohbach & Cole 2007). The aim of this modelling study was to analyse the long-term impacts of different harvesting strategies (harvesting method and intervals) on population structure, dynamics and crop yield of the Devil's Claw to provide decision support for developing a sustainable harvesting strategy. The model simulated the growth and biomass status of the secondary tuber which is the plant part harvested for medicinal purposes.

Model results showed that harvesting yields were highest under moderate harvesting (removing 70% of the secondary tubers) and a harvesting cycle of three years, regardless of grazing impact (Fig. 5a, b). This harvesting strategy was the best trade-off between crop yield and population stability, whereas more conservative or intensive harvesting methods and frequencies either diminished the crop yield or the population size. Under the predicted decrease in mean annual rainfall by 10%, harvesting yield decreased significantly (Fig. 5c, d). The model suggests that a better harvesting strategy under predicted climate change would be to increase the harvesting cycle length from three to four years while using a moderate harvesting method. This model is the first process-based approach that aims to identify sustainable harvesting strategies for the Devil's Claw. This approach can be improved with additional field data for different savanna regions (Schütze 2009). On the basis of this simulation model, an educational and management simulation tool was developed enabling the systematic exploration of the impacts of different harvesting strategies on population size and harvesting yield under different landuse and climate scenarios (Article III.7.6).

Acknowledgements
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Modelling animal responses to changes in climate and landuse

Niels Blaum*, Eva Rossmanith, Alexander Popp, Monika Schwager, Jutta Steinhäuser, Matthias Wichmann & Florian Jeltsch

Summary: In this chapter we will show how landuse and climate induced changes in vegetation cover and structural diversity of savannas affects animals across taxa and spatial scale. Key findings will be presented in four subchapters: (i) impacts of wood harvesting on animal population dynamics, (ii) impacts of grazing induced shrub encroachment on the occurrence of a small mammalian carnivore, (iii) challenges in predicting the impacts of climate change on animal population dynamics, and (iv) impacts of coupled landuse and climate change effects on gene flow of a savanna rodent.

Photo 1: The Tawny Eagle (*Aquila rapax*). Photo: Bernd Wasiolka.

Introduction

In the previous article, model based analyses of generic savanna vegetation models showed that landuse and climate change can lead to significant changes in vegetation cover and structural diversity of savanna landscapes. In this article we will focus on the effects of these landscape changes on selected animal species at the population and genetic level.

Landuse in semiarid savannas of southern Africa includes livestock production, game ranching and firewood harvesting (e.g. Skarpe 1991, Scholes & Walker 1993, Jeltsch et al. 1996, Dean et al. 1999). Over the last century, heavy livestock grazing combined with unfavourable rainfall has often resulted in widespread shrub encroachment at the cost of palatable herbaceous vegetation (e.g. Sankaran et al. 2005; see Subchapter IV.2.3). At present, savanna landscapes increasingly consist of habitats dominated by shorter grasses with sparse tree and shrub cover (pristine savanna habitats), separated by large shrub dominated areas. This trend towards an increasing proportion of shrub dominated areas has major implications for the demographic and genetic structure of savanna animals, since populations in small and isolated habitat remnants are at higher risk of genetic drift, and local extinction (Andren 1994, Vellend et al. 2006). Indeed, animal diversity in shrub dominated savanna habitats across taxonomic groups is often low (e.g. reptiles: Wasiolka 2007, rodents: Blaum et al. 2007b, carnivores: Blaum et al. 2007c, d, Blaum et al. 2009a, insects: Blaum et al. 2009b, birds: Sirami et al. 2009). Furthermore, firewood harvesting for charcoal production has increased dramatically over the last decades, which is particularly problematic since large trees are key vegetation structures used by birds, reptiles and mammals for perching, foraging, nesting, reproduction and sheltering (e.g. Dean et al. 1999, Wichmann et al. 2003, Steinhäuser 2004, Schwager et al. 2008) and thus contribute to maintaining animal diversity (e.g. Huey & Pianka 1977, Milton & Dean 1995, Dean et al. 1999, Eccard et al. 2004).

The effects of both heavy grazing and firewood harvesting on animal populations are predicted to intensify with climate change. In particular, the amount and variability of rainfall (see Subchapter IV.2.3) affects animal populations directly by changing basic life conditions such as the availability of water and food, and also indirectly by changing the structural diversity of the landscape (e.g. Popp et al. 2007, Blaum & Wichmann 2007, Schwager et al. 2008). Landuse and climate change are likely to affect habitat quality in space and time, and create highly dynamic savanna landscapes, where the coupled effects of landuse and climate change on animal population dynamics and genetic structure may enhance or mitigate each other.

In the following examples we present key findings of animal responses to landuse and climate change. In particular, we will show (i) the impacts of different wood harvesting scenarios on animal population sizes; (ii) the effects of grazing induced shrub encroachment on the occurrence of a small mammalian carnivore; (iii) challenges in predicting the impacts of climate change on animal population dynamics; and (iv) the impacts of coupled landuse and climate change effects on gene flow of a savanna rodent. Further modelling studies from the Thornbush Savanna are presented in Chapter IV.2.

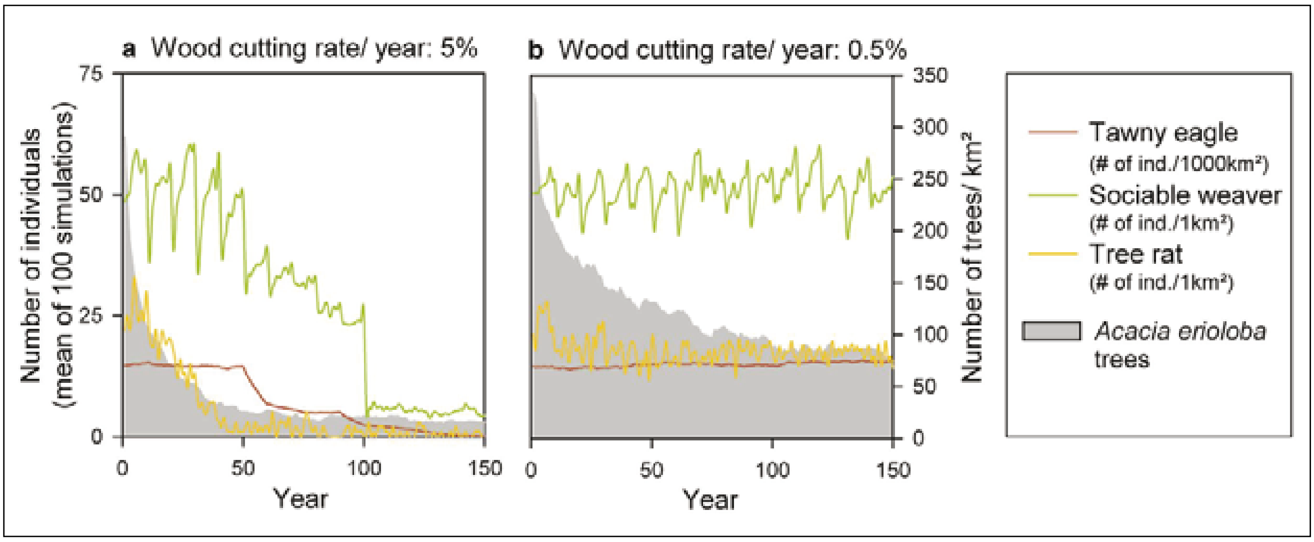

Fig. 1: Impacts of wood harvesting practises (a: high annual wood harvesting rate of 5%, b: low annual wood harvesting rate of 0.5%) on the population dynamics of the Tawny Eagle, the Sociable Weaver and the Tree Rat.

Impacts of wood harvesting on animal population dynamics

Focal species and modelling approach

Understanding the consequences of tree felling is essential for the development of policy for the conservation of arid savannas. Camelthorn trees (*Acacia erioloba*) are keystone vegetation structures, which provide animals across taxonomic groups with sites for foraging, perching, nesting and sheltering (see also Subchapter IV.2.3). Felling of trees changes the structure of the habitat, with assumed negative consequences for indigenous birds, reptiles and mammals (Milton & Dean 1995, Dean et al. 1999). A survey by the Nature Conservation group of the University of Stellenbosch has shown that average rates of wood removal can vary between 0.5% and 5% of the total trees per year depending on the tree density and whether wood harvesting is for commercial reasons or not (Tews et al. 2006).

Here we compare the impacts of two scenarios of wood harvesting—a low (0.5%) and a high (5.0%) annual removal rate on the population dynamics of three savanna animal species, namely the Tawny Eagle (*Aquila rapax*), the Sociable Weaver (*Philetairus socius*), and the Black-tailed Tree Rat (*Thallomys nigricauda*). All three species depend on large *Acacia* trees for reproduction and nesting, and sufficient suitable nesting trees are therefore crucial for the survival of these species. While Tree Rats depend on old trees with hollows for nest sites, sociable weavers and Tawny Eagles rely on trees that are large enough to carry their nests. For example, the nests of sociable weavers can measure a few meters in diameter, with up to 400 birds living in a single nest. For each species, individual and process-based simulation models were developed (see model structure, rules and parameters in Wichmann et al. 2003 [Tawny Eagle], Schwager et al. 2008 [Sociable Weaver], Steinhäuser 2004 [Black-tailed Tree Rat]) and linked to a savanna model that simulated vegetation dynamics of the five major life forms, namely perennial grasses, annual grasses, herbs, shrubs and trees (Jeltsch et al. 1997, 1999, see also Subchapter IV.2.3).

Tree density threshold explains changes in population size

The decline in *Acacia* tree density under the high annual wood cutting rate of 5% led to a significant decrease in the population sizes of all three animal species, with a collapse of Tree Rat and Sociable Weaver populations after 150 years (Fig. 1a). In contrast, the model predicted no or only minor negative effects on the population sizes of the three species for the low wood cutting scenario (0.5%) (Fig. 1b). Model results indicated a species specific tree density threshold that sustained viable populations of all species. In particular, when tree densities fell below 50 trees/km², the probability of finding a suitable nesting tree for reproduction was limited and the population size of tree rats decreased significantly. The critical threshold for finding a suitable nesting tree for the Sociable Weaver was 25 trees/km² and 15 trees/km² for the Tawny Eagle. Despite the significant decrease in *Acacia* tree density under the low wood cutting scenario (0.5%), tree density did not fall below the critical threshold of less than 50 trees/km², which explains why the population sizes of the selected species were not affected (Fig. 1b).

These species specific differences in threshold values can be explained by home range size and social system. The threshold for minimum tree density increased with home range size (i.e. species with larger home ranges need fewer trees/km²), with home range sizes of the three focal species in this study increasing from Tree Rat to Tawny Eagle. A colonial social system reduced the minimum tree density threshold since living in colonies (e.g. Sociable Weavers) enabled the species to live in high numbers on single trees, and therefore build up large and persistent populations using fewer trees. Therefore, Sociable Weavers are expected to be able to persist at lower tree densities compared

Photo 2: The Sociable Weaver (*Philetairus socius*). Photo: Bernd Wasiolka.

Photo 3: The Black-tailed Tree Rat (*Thallomys nigricauda*). Photo: Bernd Wasiolka.

to many other sparrow sized birds, which do not live in colonies.

To conclude, sustainable wood harvesting strategies are in line with biodiversity conservation, while high wood harvesting rates threaten the occurrence of keystone structures that many animal species indirectly rely on for survival.

Impacts of grazing induced shrub encroachment on the occurrence of a small mammalian carnivore

While the importance of large trees to species diversity in savannas is widely recognised, the value of shrubs is poorly understood, and often considered to be negative since shrub dominated savanna habitats are often species-poor (e.g. reptiles: Wasiolka 2007, rodents: Blaum et al. 2007b, carnivores: Blaum et al. 2007c, d, Blaum et al. 2009a, insects: Blaum et al. 2009b, birds: Sirami et al. 2009). However, single shrubs or shrub patches can provide similar functions as large *Acacia* trees in providing shelter and nesting sites for animals (Blaum et al. 2007a). Knowing how the density and spatial pattern of shrubs affect species diversity is an important issue in conservation biology because shrub encroachment due to heavy livestock grazing is widespread in African savannas (Sankaran et al. 2005). However, little is known about the importance of shrub structures for species diversity.

Here we present key results of a BIOTA modelling study investigating the impacts of shrub cover and spatial pattern on the population dynamics and abundance of the Yellow Mongoose in the southern Kalahari. Results from the individual-based model showed a unimodal relationship between species abundance and shrub cover, with very low and very high shrub cover values affecting the population dynamics and occurrence of the Yellow Mongoose negatively (Popp et al. 2007). However, the negative effect of high shrub cover values was more relevant than for low shrub cover values. The model could explain this relationship by highlighting the relevance of protective shrubs as sheltering and reproduction sites, and by the need for areas dominated by grasses with low shrub cover for Yellow Mongoose foraging where prey availability was high (Blaum et al. 2007d).

The strength of this effect was related to the spatial distribution of shrubs: a clumped pattern increased the negative effect in savanna habitats with low shrub cover, while it mitigated the effect in habitats with high shrub cover. This is an important finding indicating that the density of vegetation structures, which is often used as a measure of structural diversity (e.g. Thiollay 1990, Milton & Dean 1995, Halaj et al. 2002, Poulsen 2002, Brose 2003), may not be sufficient and should be supplemented with the spatial pattern of the vegetation structure in the landscape.

Using real-world shrub clumping data (derived from remote sensing), the model predicted a hump-shaped relationship between shrub cover and abundance of Yellow Mongooses with maximum abundance in savanna habitats occurring at approximately 12% shrub cover. This is in line with the results obtained from a BIOTA field study (Blaum et al. 2007a). This suggests that shrub encroachment is a threat to the Yellow Mongoose, as well as other small carnivores like the Bat-eared Fox (*Otocyon megalotis*) and Small-spotted Genet (*Genetta genetta*), which also rely on shrubs for shelter and on the herbaceous matrix for their food supply (compare also Subchapter IV.2.4).

Challenges in predicting the impacts of climate change on animal population dynamics

Predicting how climate change will affect the abundance, distribution and composition of species is a major challenge in current ecological research. However, predictions on future consequences of climate change are difficult to make, because biological systems are complex, long-term data sets are rare, and the validation of models is difficult (Ives 1995, Rastetter 1996, Hughes 2000). Still, such predictions are crucial for identifying vulnerable species or systems, and for planning conservation measures.

Currently, two major modelling approaches for predicting the effects of climate change on animal populations and range dynamics are applied. Firstly, there are climate envelope models, which model predictions of future species ranges based on correlation analysis between the current geographic distribution of a species and a set of climatic and other environmental variables (e.g. Iverson & Prasad 1998, Erasmus et al. 2002, Thomas et al. 2004). Although these static models provide a good and rapid assessment of potential future range shifts, they have been criticised for not considering the underlying processes such as dispersal, interactions between species, and local adaptations that influence the predicted changes of future species occurrences (e.g. Pearson & Dawson 2003, Hampe 2004).

Secondly, there are process-based dynamic population models, which model predictions based on the relation-ship between population processes and environmental conditions, which are mostly triggered by climate. Several process-based population models simulating animal responses to changes in climate were developed within the BIOTA research framework. (e.g. Wichmann et al. 2003, Blaum & Wichmann 2007, Popp et al. 2007, Schwager et al. 2008). Based on known effects of climatic conditions on specific processes of population growth, physiology, or behavior, dynamic population models project the details of population dynamics into the future under different scenarios of climate change. In comparison to static approaches, dynamic population models have an inherent advantage in that species response to climate is not static but as result of certain mechanisms and processes. However, most of these models only consider short-term processes, as they occur under current climate in a restricted area, and therefore disregard mechanisms of slow adaptation or other long-term mechanisms that may buffer negative effects of climate change. The relevance of such mechanisms was shown in three BIOTA modelling studies. For example, Schwager et al. (2008) showed that short-term responses of the reproductive output of the Sociable Weaver (*Philetairus socius*) to changes in annual rainfall were buffered by long-term processes. Long-term processes that may buffer the effects of future climate change are adaptation or plasticity in life history, physiology or behavior (e.g. Rossmanith et al. 2006), shifts in interactions with other species on the same or on different trophic levels (e.g. Ives 1995), or differences in the environment, e.g. vegetation structure (e.g. Blaum & Wichmann 2007). Similarly, the predicted increase in extinction risk of the Tawny Eagle (*Aquila rapax*) due to climate change was much lower when behavioral adaptations to the new climatic conditions were considered (increase in territory size in relation to rainfall) (Wichmann et al. 2005).

These examples highlight the need, and also the challenge, to consider slowly adapting processes, such as changing interactions between species, changes in habitat structure or evolutionary adaptations, since long-term processes concerning physiology and population dynamics are hardly known.

Impacts of coupled landuse and climate change effects on gene flow of a savanna rodent

Introduction

In Kalahari savanna rangelands, areas of high shrub encroachment, which have completely lost perennial grasses are typically found close to watering points as a result of heavy grazing. These shrub dominated areas are often 2–3 km^2 in size and act as a barrier to rodents that usually live in grass dominated savanna habitats (Blaum et al. 2007b). The rainfall in this area is highly variable and has a long-term annual mean of 174 mm. Exceptionally high rainfall may occur every 16 to 20 years (Tyson et al. 2002). These rare events lead to mass germination and growth of the dominant dormant annual grass *Schmidtia kalahariensis*, and subsequently, the degraded shrub areas can transform into hospitable habitat for a short period of time. Blaum & Wichmann (2007) found that such rainfall events trigger short-term habitat transformation and thus allow gene flow between otherwise separated populations of a dominant Kalahari rodent species (*Gerbillurus paeba*).

The key question of this BIOTA study was how changes in landuse intensity affect gene flow under current climate and predicted climate change (i.e. decrease in mean annual rainfall and increase in rainfall variability) (Solomon et al. 2007).

Simulating gene flow in a virtual experimental system

We used an agent-based model simulating the population dynamics and the genetic structure of Hairy-footed Gerbils (*Gerbillurus paeba*) in two neighbouring savanna habitats and in the separating shrub areas to understand how changes in landuse (and associated effects on shrub encroachment) and climate (i.e. amount and variability of rainfall) may affect gene flow among subpopulations. For a detailed model description see Blaum & Wichmann (2007). The genetic difference between the allele composition of the two neighbouring subpopulations was calculated using *F*-statistics (F_{ST}) according to Wright (1965). F_{ST} values ranged from zero, i.e. no difference in allele composition between the two subpopulations (connectivity), to one, i.e. complete difference in allele composition between the two subpopulations (fragmentation, $F_{ST} = 1$ at model initialisation). F_{ST} calculations based on large sample sizes are a strong indicator of the connectivity of subpopulations at a certain point in time (Slatkin 1993).

Implications of landuse and climate change for gene flow

Although shrub dominated areas of approximately 2.5 km² (used as a default value in the model) were expected to separate rodent subpopulations, rare events of exceptionally high rainfall resulted in short term hospitability of the shrub area with mass occurrences of Gerbils. Such population outbreaks in shrub dominated areas have been found during high rainfall

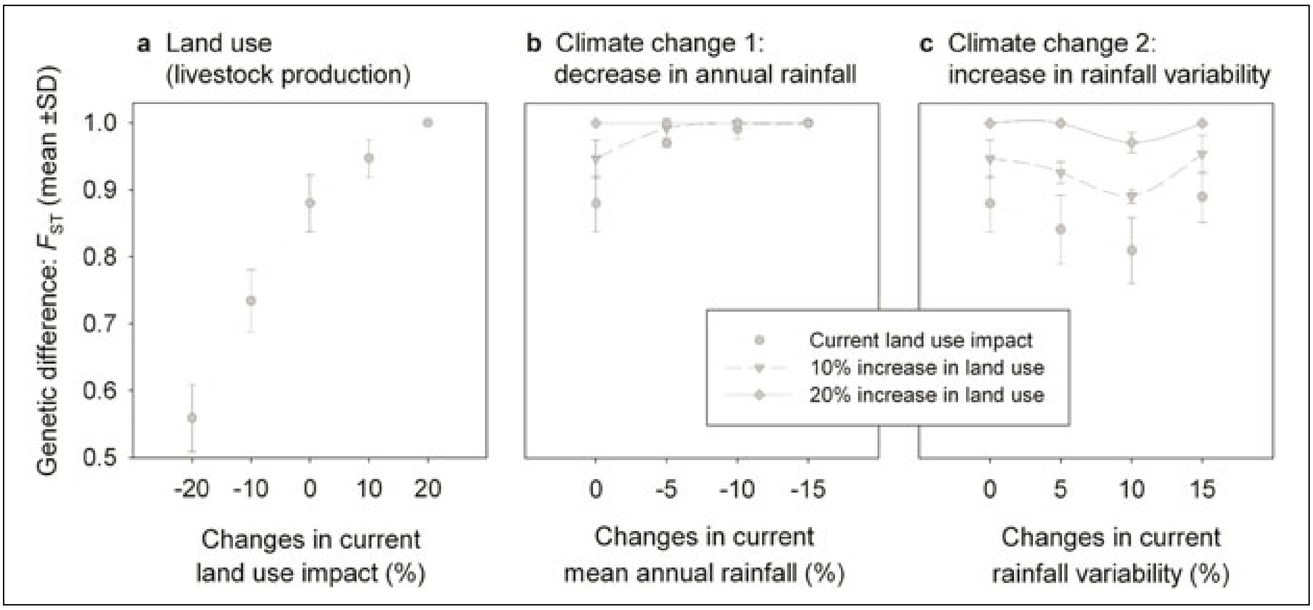

Fig. 2: Impacts of landuse and climate change on gene flow between two neighbouring Gerbil populations. A: landuse scenario, the default value indicates the typical size of shrub dominated areas (2.5 km²) around water points in Southern Kalahari rangelands. B: climate change scenario 1: decrease in mean annual rainfall, the default value indicates the long-term average rainfall of 174 mm. C: climate change scenario 2: increase in rainfall variability (coefficient of variation [CV] of mean annual rainfall), the default value indicates the CV of the long-term average annual rainfall in the study area (CV = 0.41).

years in field studies (Blaum & Wichmann 2007). Rainfall triggered population outbreaks and enabled gene flow across the shrub dominated area, despite the relatively low dispersal abilities of *Gerbillurus paeba* (home ranges are only about 0.1 ha in size, Ascaray & McLachlan 1990). The expected negative effects of fragmentation were therefore mitigated (Fig. 1). A similar genetic pattern was found in a BIOTA field study where samples from Gerbil individuals across 21 Kalahari farms were analysed (Meyer et al. 2009). However, model results indicated that a 10% increase in the typical extent of shrub dominated areas was likely to separate rodent populations while a decrease of 10% would significantly improve their connectivity (Fig. 2a).

Similarly, the model predicted that the decrease in mean annual rainfall (climate change scenario 1) reduces connectivity. Assuming no changes in landuse impact (i.e. no change in the spatial configuration of shrub dominated and grass dominated areas) the model predicted a low connectivity under the predicted decrease of mean annual rainfall by 5%. However, an increase in landuse impacts by 10% coupled with climate change led to a separation of rodent populations (Fig. 2b).

The second IPCC scenario for climate change, which predicts an increase in rainfall variability (climate changes scenario 2, Solomon et al. 2007) promoted gene flow between the neighbouring Gerbil populations and decreased genetic differences (Fig. 2c) under current landuse impact. However, when landuse intensity increased by 10%, gene flow was hindered despite the positive effects of increased rainfall variability (Fig. 2c). This example highlights the importance of incorporating the coupled effects of landuse impacts and climate change on animal dynamics in highly variable environments for landscape and conservation planning.

Conclusions

Climate change and landuse (in the form of livestock grazing and wood harvesting) modify the amount of vegetation cover, the proportions of woody and herbaceous vegetation cover, and change the structural diversity of savannas. The examples in this chapter show that changes to the structural diversity of woody vegetation, in particular, can have major impacts on animal diversity across taxonomic groups. Nevertheless, the detection of changes in animal diversity as a result of landuse practices remains challenging since there is often a time lag in the response of animal populations to habitat changes. Furthermore, the major challenge under predicted climate change is the explicit consideration of coupled effects of landuse impacts and climate change on vegetation dynamics, habitat structure, and the consequences of this for animal population dynamics. An understanding of these coupled effects will be necessary to adapt landuse management to predicted climate change in order to sustain both human livelihoods and biodiversity conservation. The presented simulation models help to understand coupled effects of environmental change and detect changes in animal diversity.

Acknowledgements

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A spatially explicit model for interacting populations of dragonflies in arid Namibia

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Summary: In order to understand the spatial and seasonal distribution of dragonflies in western Namibia we developed a model framework based on habitat suitability models, a local population dynamic model of interacting species and a dynamic landscape model combined with a spatially explicit model. Local population dynamics as well as the spatial patterns of the aggregated model showed good accordance with field data. Therefore, the model approach may be useful for the identification and understanding of dragonfly spatial patterns as well as for predicting future spatial patterns, which are influenced by changes in the water balance due to climate change.

Introduction

Models can contribute to obtaining information about the regional distribution of coexisting predator species under varying environmental conditions by helping us to understand existing patterns and by analysing the impact of external changes on future distribution patterns (Segurado & Araujo 2004). While many models simulate single species and their responses to environmental variables (see review in Elith et al. 2006), community interactions often remain unconsidered (Araujo & Luoto 2007). Communities are usually defined by spatial, functional, or taxonomic relationships or by interactions within the food web (Schluter & Ricklefs 1993). It is well documented that dragonfly community structure is affected by various biotic interactions, including fish predation and intraguild predation (Johnson 1991, Stoks & McPeek 2003). This is particularly true in the arid Namibian landscape where freshwater bodies are rarely perennial, so that larger predators like fish are uncommon (see Article III.2.7). Moreover, in temporary habitats the frequency of disturbance is known to exert influence on the community structure (Williams 2006).

The aim of this contribution was to present a simulation model approach that allowed the study of how the population dynamics of locally interacting dragonfly metapopulations may be altered by a change of the seasonal distribution and quality of their reproduction habitats. We developed a spatially explicit model for the distribution of Odonata in the landscape with several components (Braune 2005). The components were: (1) habitat suitability models; (2) local population models with cannibalisms and intraguild predation; and (3) a dynamic landscape model with rules for dragonfly dispersal. The model was used to simulate the occurrence of dragonfly species with different ecological characteristics to different scenarios of dynamic landscape change. For example, we simulated population trends according to seasonal changes in water balance in a landscape in central Namibia. Two common species of dragonfly belonging to different ecological categories with different habitat requirements, flight and dispersal behaviours and life-history parameters served as model organisms: *Pantala flavescens* and *Crocothemis erythraea* (Table 1). Both species are widespread desert Odonata, but whereas *C. erythraea* is present most of the year, *P. flavescens* is a seasonal invader (Suhling et al. 2009, Article III.2.7). The larvae of the species differ particularly in growth rates (Johansson & Suhling 2004). For a detailed version of this study see Braune (2005).

The model components

Habitat suitability models

Besides the permanence of aquatic habitats (cf. Johansson & Suhling 2004) several other variables may determine the habitat selection of dragonflies (for an overview see Corbet 1999). Habitat suitability models were created using logistic regression, a special case of a Generalised Linear Model (GLM), capable of dealing with presence/absence data. The database for the models was built from a survey of 279 sites throughout the ephemeral river

Table 1: Characteristics of two categories of dragonfly species, which are widespread in the Namibian deserts according to Suhling et al. (2009)

Characteristic	*Crocothemis erythraea*	*Pantala flavescens*
Category	widespread desert species (resident)	seasonal invader (migrant)
Major habitat type	from temporary to perennial waters	mainly temporary waters
Habitat specificity	pronounced	none
Dispersal mode	good disperser	obligate migrant, long-distance disperser
Phenology	little seasonality	highly seasonal (rainy season)

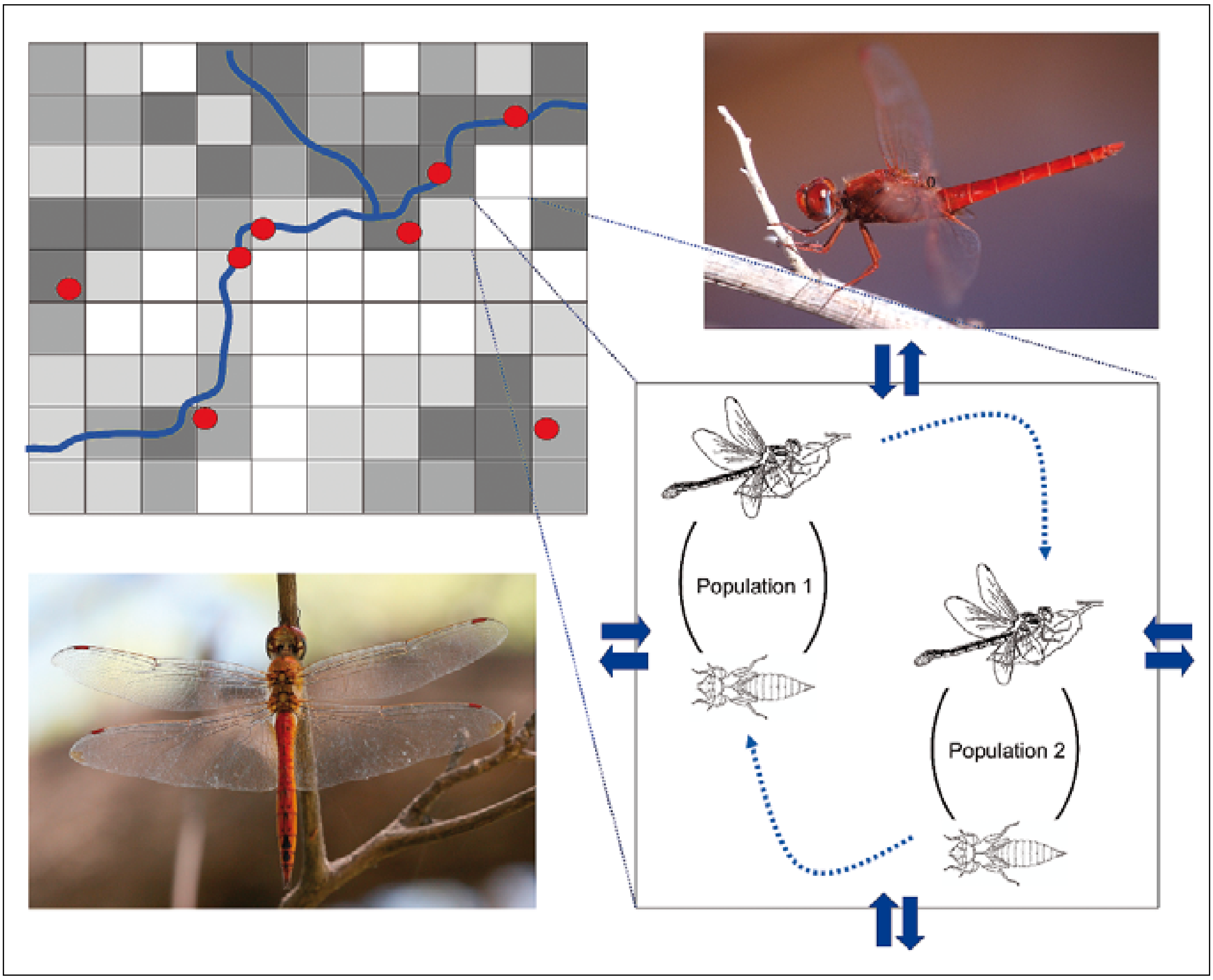

Fig. 1: Model structure. The landscape was divided into cells with different habitat characteristics, for example, permanency of water and structural diversity, which were represented by the different colours. At each cell the local population dynamics of the two species, which was dependent on the appropriate habitat quality, was evaluated. Both species prey upon each other and are also cannibalistic. Based upon dispersal rules the adult dragonflies dispersed into surrounding habitats. The habitat quality of each cell was dynamic and changed, for example, with annual variations in hydrology. The two model species are also depicted: *Pantala flavescens* (below left) and *Crocothemis erythraea* (top right).

catchments of western Namibia (for sample sites see Suhling et al. 2006). Habitat suitability models provided the probability of dragonfly occurrence dependent on habitat characteristics. We evaluated univariate models (only one factor involved) as well as multivariate ones (many factors involved). Several habitat variables were tested as summarised in Table 2. Variables were selected according to their relevance for the survival of the aquatic stages (eggs, larvae, e.g. water quality parameters) or of their importance for habitat selection by adults (e.g. presence of edge vegetation).

Vegetation structural diversity was a composite variable that was used to distinguish between different habitats. This variable combined the presence of all other vegetation structures listed in Table 2, which were recorded during dragonfly sampling. Vegetation structural diversity was regarded to be high where most or all of these structures were present, and if none or only few were present then the diversity was regarded as low. The two dragonfly species reacted differently to this variable: the probability of occurrence of *Crocothemis erythraea* increased with increasing vegetation structural diversity, while for *Pantala flavescens* no significant correlation was found. We therefore classified *C. erythraea* as having pronounced habitat specificity, while *P. flavescens* was considered to be nonspecific (Table 1).

The dynamic model for interacting dragonfly populations

The population dynamics were modelled using an extended Leslie Matrix approach (Söndgerath & Richter 1990), assuming an age-structured Leslie model for each of the life-cycle stages. For modelling purposes the life-cycle of Odonata species was distinguished as an egg stage, three larval size classes (small, medium, and large sized larvae), and two adult stages (immature and mature adults) with different durations and survival probabilities (Table 3). Survival probabilities described the transition within one stage, i.e. the ageing process. For the larvae these probabilities were formulated as a linear combination of

Table 2: Results of univariate habitat suitability models for *Crocothemis erythraea* and *Pantala flavescens* with different environmental variables

Habitat variable		*Crocothemis erythraea*			*Pantala flavesens*	
	p	R^2_N	trend	*p*	R^2_N	trend
Altitude	***	0.066	negative	*	0.014	positive
Width of habitat	NS	-	-	**	0.016	positive
Length of habitat	*	0.017	positive	NS	-	-
Water depth	***	0.044	negative	NS	-	-
% submerged plants	***	0.033	positive	NS	-	-
% algae & floating leaf plants	***	**0.115**	**positive**	NS	-	-
% rushes & sedges	***	**0.109**	**positive**	NS	-	-
% higher reeds	***	0.072	positive	NS	-	-
% bushes & trees	**	0.019	negative	*	0.010	positive
% floating grasses	***	0.099	positive	NS	-	-
% herbaceous plants	***	0.040	positive	**	0.018	positive
% no plants	***	**0.151**	**negative**	NS	-	-
Vegetation diversity	***	**0.302**	**positive**	NS	-	-
% detritus	***	0.030	positive	NS	-	-
% sand	NS	-	-	NS	-	-
% gravel	NS	-	-	NS	-	-
Current velocity	**	0.020	positive	NS	-	-
Conductivity	*	0.020	positive	**	0.025	positive
pH	*	0.019	positive	*	0.022	positive
Temperature	***	0.062	positive	NS	-	-
% riparian vegetation	***	0.033	positive	NS	-	-
% riparian rocks	**	0.033	positive	NS	-	-
% shadow	***	0.060	positive	**	0.034	positive

Significant models are indicated by asterisks: * $p \le 0.05$, ** $p \le 0.01$, *** $p \le 0.001$; NS = not significant. Bold values indicate high correlation (R^2_N values > 0.1). The correlation trend is also indicated. For *C. erythraea* several variables were significant but only a few, all associated with aquatic vegetation structure, had high correlations. In *P. flavescens* only a few variables were significant models and none had high correlation.

basic survival rate and food- and density dependent mortality. Transition probabilities described the transitions from one stage to the next, i.e. the development process. These probabilities were mainly dependent on the amount of ingested food, leading to density dependent development (at low larval densities there is enough food resulting in an optimal development rate whereas at high larval densities the development rate decreases due to the limitation of food). In this manner development units for each stage were calculated. In order to take natural variability into account, these development units were superimposed on a Weibull type distribution function (Söndgerath & Müller-Pietralla 1996), which gave the final transition probabilities for our model.

Intraspecific competition and cannibalism are factors, which significantly change the size-distribution of Odonata populations (van Buskirk 1992; cf. Article III.2.7). Additionally, the order of arrival and oviposition of species are fundamental factors for the establishment of a population in a habitat (Padeffke & Suhling 2003). Therefore, the one-species model was extended to a two-species model sharing the habitat and exploiting the same food resources. From field observations in artificial ponds (Suhling et al. 2004) we concluded that when temporary water bodies are initially filled with water there is enough nonspecific food (e.g. chironomid larvae) resulting in very low cannibalism and intraguild predation. With decreasing availability of nonspecific prey, medium-sized larvae prey upon smaller larvae and larger larvae prey upon medium-sized larvae, both within the same species and between species. Intraguild predation and cannibalism was density dependent, i.e. onset was when the dragonfly density became higher than that of the available food per time unit. The function describing the response of the development rate to available food was fitted to data from Hassan (1976). The time-step of the model was one day because the development time of the species is 30–60 days and longer time-steps would therefore hide relevant processes.

Table 3: Parameters for the population dynamic model

Parameter	*Crocothemis erythraea*	*Pantala flavescens*
Duration of egg stage [d]	9	5
Duration of 1st larval stage [d]	15	10
Duration of 2nd larval stage [d]	20	11
Duration of 3rd larval stage [d]	25	13
Duration of immature stage [d]	13	13
Duration of mature stage [d]	50	50
DSR of egg stage	0.92	0.97
DSR of 1st larval stage	0.97	0.90
DSR of 2nd larval stage	0.97	0.96
DSR of 3rd larval stage	0.97	0.96
DSR of immature adults	0.94	0.94
DSR of mature adults	0.94	0.94

All parameters were derived from our own laboratory experiments and field studies in artificial ponds in Namibia (Johansson & Suhling 2004, Suhling et al. 2004, Suhling et al. 2005, and Suhling unpublished data). DSR: daily survival rate.

Generally the model reproduced the typical pattern of multivoltinism (i.e. completing more than two generations per year) for the two modelled species. It produced comprehensive results for different levels of prey density as well as for the efficiency by which prey could be used as a food resource. In the model, the migrant species was able to complete up to two generations more than the resident species during the three years of simulation. Furthermore, the model showed good accordance with experiments describing priority effects (Padeffke & Suhling 2003).

The dynamic landscape model

A landscape in the Swakop River catchment was chosen for the spatially explicit dispersal model. It encompassed the region around the S.-von-Bach Dam near Okahandja and the Swakoppoort Dam, both reservoirs used for the water supply of Windhoek. The landscape was 50 x 50 km and was described by a lattice with identical cell sizes of 1 km^2. The properties of a cell considered in the model were the presence of open water as a minimum habitat requirement and the aquatic vegetation diversity (cf. above for habitat suitability models). The presence of open water was derived from Landsat 7 ETM+ satellite images taken in spring 2000. These were analysed for the presence of open water using ERDAS Imagine 8.5. We distinguished between permanent and ephemeral habitats with the help of expert knowledge. The basis for aquatic vegetation diversity was the NDVI (Normalised Difference Vegetation Index) obtained using the Image Analyst extension of ArcView, accompanied by knowledge gained during the dragonfly surveys (cf. Suhling et al. 2009).

The dynamic nature of this landscape is characterised by the fragmentation of freshwater habitats during dry periods and the reconsolidation of these habitats at the onset of the rainy season. Due to their aquatic development dragonflies rely on freshwater, and they either rely on perennial or temporary water bodies depending on the larval development time. In our model the presence of open water was dynamic, changing daily as a function of precipitation and evaporation. To create a pattern describing temporary water body dynamics, the coefficient of variation of rainfall from Mendelsohn et al. (2002) was used. A high coefficient of variation in the rainfall led to a more random drying and wetting of these temporary habitats. In the model the larvae inhabiting a cell with temporary water died when the cell dried out. An increasing number of ephemeral habitats therefore led to gaps in habitat continuity and to a reduction of optimal conditions for completing the life-cycle.

Dragonfly populations were able to freely disperse between the cells. As there is little empirical data available regarding the dispersal modes of the two model species, we decided to use exponential functions (cf. Conrad et al. 1999). For each time step this function gave the probability for the dispersal-distance. It yielded high probabilities for short distances but it was still possible to have high probabilities for long dispersal distances. The differences between migrant and resident species could be described by the different slopes.

How do the populations behave in the seasonally changing landscape? A simulation

We performed a simulation, in which *Crocothemis erythraea* and *Pantala flavescens* co-existed in the chosen landscape section and interacted as described in 2.2 above. The resident *C. erythraea* developed peaks with high adult population densities in the permanent habitats with high aquatic vegetation diversity during the dry season (Fig. 3A) and the rainy season (Fig. 3B). This confirms the assumption that the permanent wetlands serve as a refuge during the dry season. Even during the rainy season, when additional temporary freshwater habitats were available along the river course, the main areas of distribution were permanent habitats, although the temporary habitats were in reach. *C. erythraea* was excluded from the temporary habitats due to intraguild predation by the migrant *P. flavescens*. In contrast, the migrant *P. flavescens* was able to make use of the temporary waters existing along the Swakop River during the rainy season and retracted to the perennial habitat during the dry season.

The results of this model simulation corroborate the processes described in Article III.2.7: resident species can only survive the invasion of migrants due to more or less permanent (non-seasonal) reproduction and they thus require

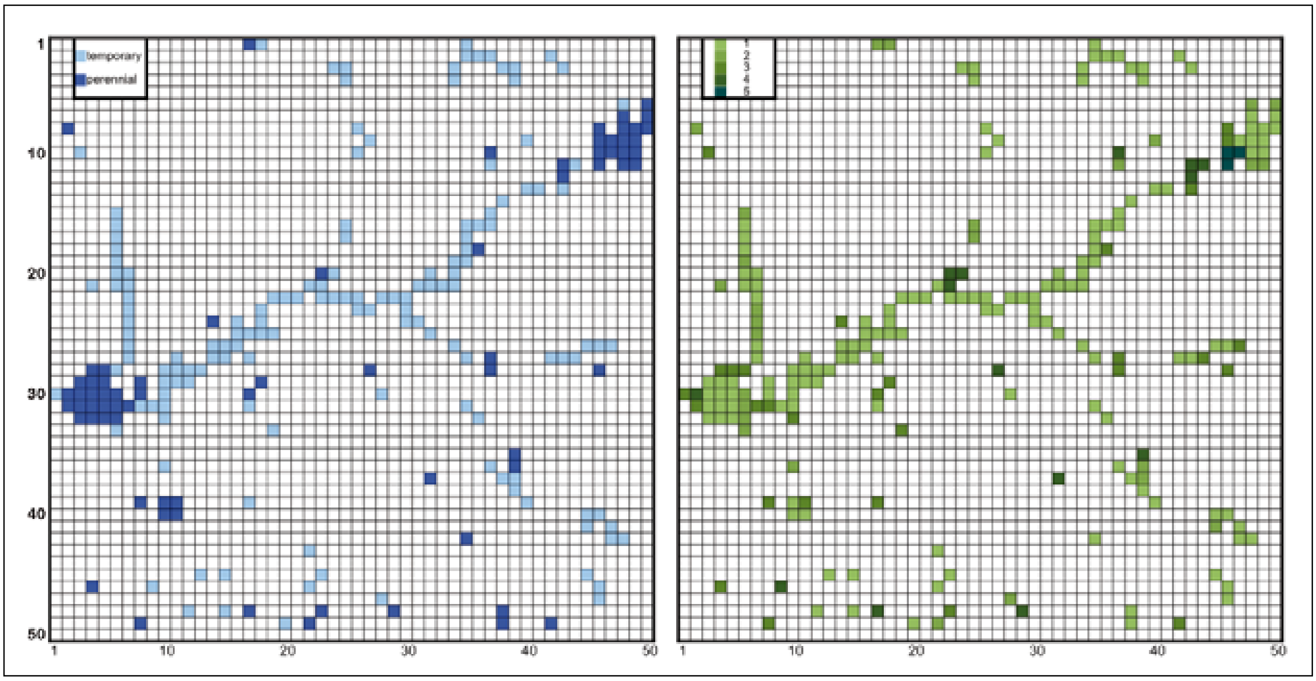

Fig. 2: Landscape layers used to describe the properties of each 1 x 1 km cell in the dynamic landscape model. Left: presence of open waters during the climax of the rainy season under current climatic conditions. Dark blue cells: permanent waters, light blue cells: temporary waters. Right: aquatic vegetation structural diversity index as defined above in subsection "Habitat suitability models". Dark green cells: permanent waters, light green cells: temporary waters.

perennial water bodies. Resident species can be largely excluded from temporary water bodies due to intraguild predation. We conclude that the modelling approach presented in this work enables the prediction of the spatial patterns of dragonfly communities in the arid regions of Namibia. Other species or communities can be modelled by changing the appropriate life-history parameters. Furthermore, the inclusion of other ecologically relevant properties of the landscape is possible if the information for the construction of the landscape layer exists. Other dragonfly communities can therefore potentially be modelled with little effort. This model system can be used as a tool for the assessment of Odonata biodiversity and can help to identify and emphasise valuable regions for freshwater conservation management.

Acknowledgements

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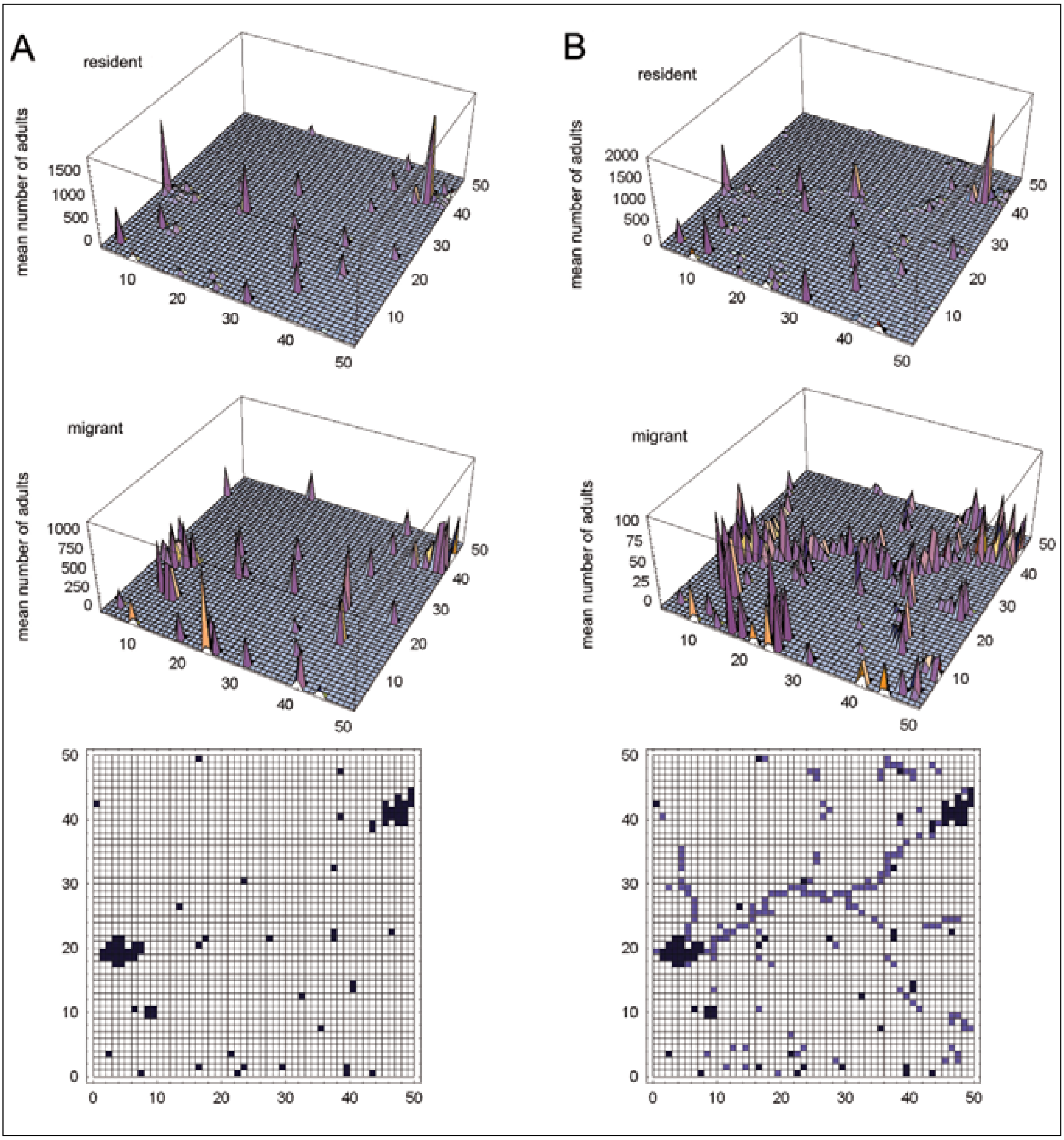

Fig. 3: Simulation results for patterns of co-existence between the resident species *Crocothemis erythraea* and the migrant species *Pantala flavescens* on a 50 x 50 km landscape near Okahandja. (A) shows the adult densities of the resident- and migrant species per cell at the climax of the dry season when only permanent water bodies (black squares) remain in the landscape. (B) shows the situation at the climax of the rainy season with several temporary water bodies present (blue squares).

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Bio-economic modelling in BIOTA Southern Africa: approaches developed, empirical foundation, results, and lessons learnt

Ernst-August Nuppenau*, Stephanie E. Domptail & Tarig Gibreel

Summary: This chapter deals with a bio-economic modelling concept that was applied by BIOTA Southern Africa. Bio-economic modelling facilitates a better understand of interactions between landusers and ecosystems. In particular, we are able to identify economic factors, which are driving forces of landuse change and degradation. In cases where degradation is a significant feature of ecosystems under human use (such as savannas in Namibia) bio-economic modelling can help researchers to understand feedback loops between ecosystems and economic systems. Bio-economic modelling can be used to highlight incorrect landuser management practices and be used as a tool for formulating alternative management strategies. For example, through bio-economic modelling we can demonstrate to farmers, stakeholders, and governments how by adapting behaviour and policy instruments land degradation caused by livestock ranching can be reduced. Bio-economic modelling is a mathematical and statistical tool, which enables simulations of the future depending on different management strategies (e.g. short term income optimisation vs. long-term conservation). It helps to detect interdependence between ecosystem dynamics and the dynamics of landuser strategies relating to the management of natural resources (landuser strategies are necessary to cope with drought and price fluctuations), and to depict the impacts of herd dynamics (timing and intensity of grazing) and resource extraction. Therefore we could show, for instance, how farmers contribute to bush encroachment and veld degradation through resource use, which is based on inappropriate management practices.

Objectives and outline

The primary objective of the bio-economic modelling conducted by BIOTA was to illustrate the potential for performing quantitative analysis on landuse strategies in semi-arid savanna rangelands, which show signs of degradation. Rangelands are a natural resource, which provide income to farmers. However, rangeland degradation (changes in species composition, bush encroachment, etc.) and lowered productivity caused by overutilisation by farmers (in an attempt to maximise income) are prevalent features of rangelands in the savanna biome of southern Africa. Human impacts were analysed by examining the effects of different management practices on the biodiversity of savanna rangelands. Various farmer strategies were identified and we studied their impact on the range quality and biomass provision of specific ecosystems. The secondary objective was to find appropriate management practices, which would be more suitable for long-term income aspirations of farmers while at the same time being more conducive to the conservation of natural resources. To conduct the research a conceptual framework of a bio-economic model was developed and a model for the optimisation of management decisions was programmed. Fig. 1 outlines the general conceptual ideas regarding objectives, feedback loops between the environment and dynamic decision making, and natural conditions in the study area. In the design of the model and regional priorities in the model outlines, we included different farming types, which were representative of the area.

Modelling approach

Fig. 1 illustrates some elements, which are necessary in a bio-economic model for range management. The first step was to develop a prototype of a dynamic programming model for commercial farmer decision making in central Namibia (Buß 2006). The focus of the model was on the mathematical representation of decisions and constraints, which were linked by equations such as biomass availability, herd growth and financial balances. In order to represent interlinked decision making for a farm operation over a period of thirty years, a decision support tool on the basis of a specific dynamic programming model was designed and programmed. This model had discrete time steps and contained feedback loops. Fig. 2 depicts the model structure, which we adopted in our research work. In principle, the landuser (farmer) maximises an objective function given the dynamics of the system.

Such a modelling concept requires a rather technical description to understand the background. Only key aspects can be highlighted here (for details see Buß 2006). It is crucial in bio-economic modelling to integrate feedbacks between the environment, agronomy and decision making. These feedbacks are normally dynamic. For instance, a high grazing pressure (today) will impact negatively on the species composition and biomass

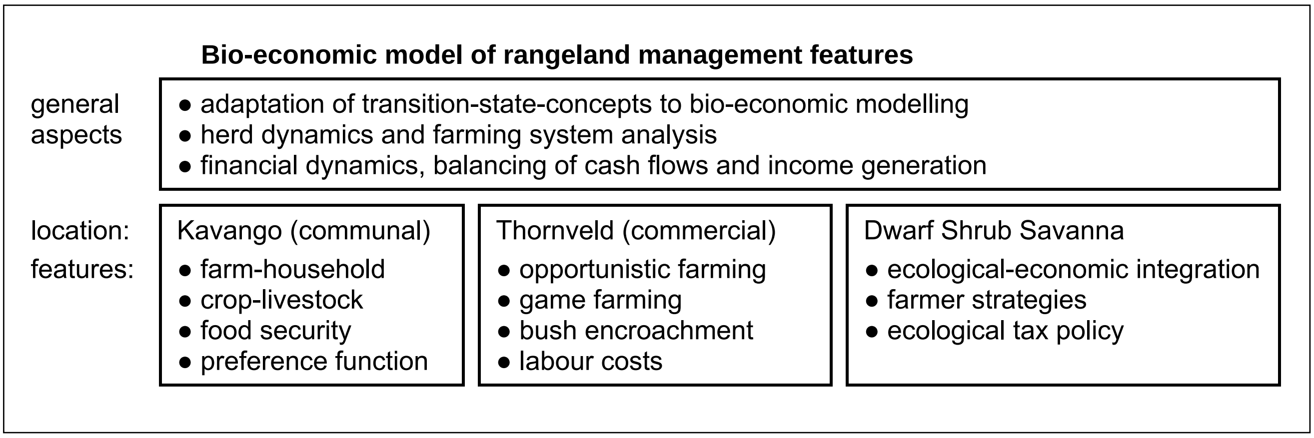

Fig. 1: An overview on model features and objectives in model design. Source: own design.

production (e.g. less perennial grasses, and eventual bush encroachment in future). The farmer can anticipate this via a feedback loop, which provides him with alternative grazing intensities. The dynamics of our bio-economic model followed the concept of a closed-loop-control (as a feedback), which is depicted in Fig. 2. A “control” meant that a farmer could control the condition of his range in the future. For example, in order to avoid future degradation a farmer could limit the number of animals on his land. This would mean that the farmer would incur costs in terms of reduced short-term income. However, there are normally several management options available to a farmer and an optimal strategy can be chosen. Decisions and feedbacks ran through cycles of 30 years in our model making the analysis complex. Decisions were interdependent throughout the evolution of the ecological system and we needed a mathematical algorithm to optimise decisions. The algorithm had to operate in a mathematical structure. For instance, technically, as can be seen in Fig. 2, a change of the state variables of the system (in our case: resource productivity) from “*t*–1” to “*t*” renews the decision needs. Again, technically, it meant that the vector $X'(t)$ (which gave the change in range condition, herd size, etc.) was determined by a function of the same state variables in the previous timestep t–1 [i.e. $X(t–1)$]. As has been mentioned, the model followed a mathematical concept of using variables, which represent decisions (control variables) and changes of the agronomic environment (state variables).

The farmer, at different periods in time, links the variables by his decision making. For instance, the farmer controls the range quality indirectly through stocking rates, which determine forage availability and quality. In addition, he may control other input variables in time *t* such as purchased fodder and the addition or reduction of animals through buying and selling. It is possible to distinguish control and state variables. $U_c(t)$ in Fig. 2 are control variables, which are endogenous. $X(t)$ is a vector of state variables. For example, we can use 100 variables (in a vector) comprising elements of farm management such as herd composition, discrete grazing classes (animals per ha), animal composition (sheep, goat, cattle, etc.), and cash flow, which are all linked through resource constraints. Furthermore, all these variables have cost and revenue implications in terms of farm management, which need to be integrated and represented in the objectives of farmers. The objective function can be specified as income maximisation, but also recognise range quality. Furthermore, the model is stochastic, and there are uncontrolled exogenous variables $U_e(t)$, which are factors that fluctuate such as rainfall and farm gate prices. Finally the model works with given parameters or coefficients for the system, shown as α_S in the Fig. 2 (see Lenz 1993).

Ecological aspects of the model incorporated problems like degradation, herd mismanagement, and financial factors, which force farmers to overstock their land. In addition, we used an ecological conceptual framework of states-and-transitions for rangeland dynamics (Westoby et al. 1989). Using a special type of the model for central Namibia we investigated the economics of bush encroachment and of bush clearing measures. Various types of bush clearing and their costs, as well as preventative measures such as veld resting and low grazing pressure, were investigated. Special attention was also paid to the management of fire, as well as stocking and destocking in years of good and bad rainfall. In addition, we extended the model to a first approach of a stochastic model. We thought stochastic modelling was more suitable for the management of arid rangelands than a fixed coefficient model. Since biomass growth is not constant (as rainfall is highly erratic in reality in the study area) management and modelling has to address the problem. We attempted to accommodate stochastic events as much as possible as this is a prerequisite for modelling the stochastic nature of savanna environments. Consequently we applied flexible responses of farmers to vegetation change. The aim, in the case of commercial farming, was to keep the range in a healthy condition for the future and to optimise income.

Extension of the model to communal farmers

In a second bio-economic model for northern Namibia (Hecht 2009), the time frame of thirty years for the simulation and the conceptual framework of transition states were maintained. In this instance the model was adapted to the investigation of a communal farming system in a specific cropping area of northern Namibia (Observatory Mile 46). A communal, mixed farming system is much more complex to model than a single commercial farming system. This is because communal farmers derive income from a range of sources including arable land, rangeland, and bush commodities, for example. In addition, the scale of analysis is the household and the community, not just a single farm (for comparisons see Kruseman 2000). Using our bio-economic modelling tool, we investigated the consequences of the labour economy of a subsistence farming system on resource extraction (based on biomass). Firstly, we wanted to show how undesirable landuse practices contribute to putting pressure on natural resources (e.g. soil fertility, thatching grass, trees, and animal fodder). Secondly, the model was sensitive to aspects of food security, poverty, and the remoteness of populations in northern Namibia. It was found that these problems fuel land expansion and do not necessarily contribute to sustainable biomass extraction; rather the opposite tends to occur. Driving forces such as population growth, higher income aspirations, non-recognition of degradation, preferences for livestock etc. (all as quantitative relationships) could be identified by examining the dynamics of the model. The bio-economic model was also orientated around food security, and our objective was to show how weak local food security conditions relate quantitatively to degradation. Finally, a specific model variant for small-scale pastoralist farmers in communal areas was transferred to southern Namibia with the aim of investigating the impacts of pastoralist practices and preferences (for livestock) on the range quality and productivity, and ecology of the area. In order to apply weights to the preferences of farmers, a preference ordering experiment was conducted. This enabled us to identify the impact of food insecurity on rangeland resources in these arid areas.

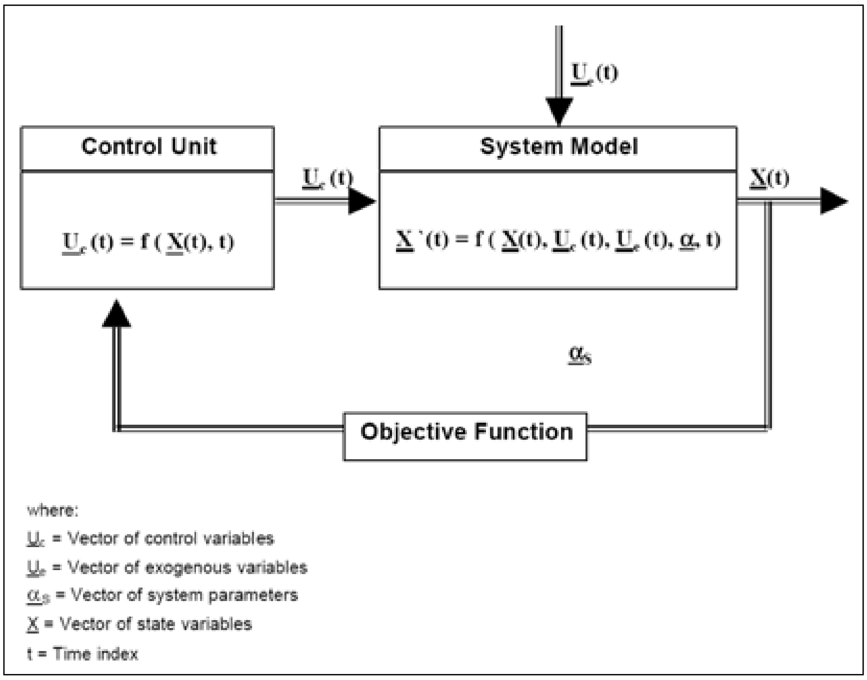

Fig. 2: Close loop control of a dynamic system and decision making. Source: Buß (2006, adapted from Lentz 1989).

Extension of the model to commercial farmers

A third bio-economic model was developed for the commercial farmers of southern Namibia (Domptail et al. 2009a). Here, the main focus was on designing a bio-economic approach, which integrated two models: an economic decision making model and an ecologically-based spatial vegetation model. In this context, the impact of farmers' knowledge (including rangeland dynamics and climate change) on their landuse choice and the subsequent states of the rangeland were investigated. We used a double exchange of data between the ecological and the economic model (Popp et al. 2009b) to connect the models. A new feature of this bio-economic modelling approach was the recognition of farmer strategies.

The preparatory and explorative phases of the project revealed that farmers do not appear to be homogenous in their farming objectives. Therefore, whereas most bio-economic models simply assume that farmers are maximising their discounted income, our bio-economic model attempted to investigate strategic aspects of farmer behaviour. For example, the extremely stochastic rainfall in Namibia forces farmers in these arid rangelands to be cautious about increasing herd sizes: They may under-stock during wet years in order to ensure that there is sufficient fodder during years of drought and over-stock in drought years because of herd maintenance. We attempted to gain insights by employing the appropriate modelling of these aspects through the use of complex objectives (Domptail et al. 2009). These aspects were complemented by the findings from corresponding field studies, which found that most farmers do not only consider income but also range health in their decision-making. This complexity creates challenges for bio-economic modelling, such as dealing with decisions under uncertainty, which we addressed in our approach.

Another aim was to find and test policy instruments, which aid in obtaining and promoting sustainable landuse. In particular, the impact of a land tax scheme on farmer strategies was evaluated. An alternative design for a land tax scheme, in the form of a "Payment for Ecosystem Service", was proposed. We found that such taxes can influence farmer strategies in a manner that increased rangeland conservation.

Approaches developed for integrating ecological and economic models

Our modelling approach specifically aimed to integrate ecological and economic aspects of rangeland utilisation. The approach was built on the concept of a time-discrete, linear programming model (McCarl & Spreen 1997). In the synthesised model we depicted farmers' options for range management in detail, and showed how current decisions impact on future decisions. We were seeking to achieve a newly developed bio-economic modelling design, which explicitly integrates ecological dynamics with the detailed decision making of farmers. Comparable studies were not available when we started. As an innovative component, we coupled an ecological and an economic model by giving them the feature of modules, which resulted in our synthesised model (Domptail et al., in press). The internal complexity of both models was therefore maintained and the depiction of most relevant elements in each model was not compromised. However, this type of approach required the explicit specification of an interface between the two types of models and also that they mutually fed data into each other.

For the BIOTA project, much research efforts on bio-economic modelling were based on the coupling of a farm-based economic decision model (Giessen University) and a structural simulation model (Potsdam University). Interactions between the two models provided us with new insight on the best techniques for establishing and practically running such a synthesised "model" (including distinct model philosophies, and in particular, on event driven ecological models and normative economic decision models). This is the first time that an interface has been developed between an economic decision model and a structural simulation model. On the conceptual and programming side, a transition matrix (Buß 2006) was developed, which provided probabilities of the transitions between the discrete ecological states of rangelands (Popp et al. 2009). These probabilities were calculated to represent landuse dependent changes in rangelands. Rangelands can switch from one ecological state to another from one year to the next, and the ecological states were assimilated to vegetation classes. The ecological module used tested management practices (from the economic module), which were translated into causal factors (events), which impacted on the vegetation dynamics. Categories such as stocking rates of grazers and browsers as well as the option of 'veld resting' became inputs for the ecological model. Then, as an output, the contingent dynamics of the proportions of land in the different identified states (from the state-and-transition model) could be calculated.

An emphasis of the approach was the influence of the ecological model on farming practices. Based on economic optimisation, and vice versa, the influence of the economic model on ecological events could provide insights into predicting management strategies. It was therefore possible to obtain a data set, which followed the important recommendation of Stern (2003), which is to work with non-stationery ecosystems. In particular, ecological thresholds and non-linear effects could be empirically accommodated. Another emphasis was on the inclusion of degradation threats in the economic module of the bio-economic model. After the integration of the ecological module, farmer decision-making was strongly exposed to the danger that resource extraction had long-term impacts on the rangeland condition and hence on the profitability of farming. Threats could be explored by creating different scenarios (see examples). Moreover, as an important aspect of the model, the land value at the end of the simulation period had to enter into the decision making, because the value depended on the range quality after the envisaged time horizon. It is important to note that farmers, to varying degrees, consider land value, apart from income, as a crucial criterion for successful farming. The model is therefore attractive because it shows the consequences of farmer decisions on future land values.

Furthermore, our bio-economic model enables the specification of ecological and economic objectives jointly. Since rangeland condition output is given as states (categories), the model can explicitly handle these states as an ecological indicator. States arise as a consequence of farming practices and they are ecologically identifiable (Westoby et al. 1989). We worked with six states in central Namibia, for example (Fig. 3). These different states are present on farms in different proportions. This has an impact on the forage production on each farm, which in turn is reflected in how the land is used based on the ecological states.

Farm land switches from one state to the other based on certain probabilities. Recovery of desirable states can occur depending on farm practices such as resting.

We also dealt with sustainability in our model. From a normative point of view, we can say that a "good" ecological state is a societal aim. However, since humans still need income (the wealth objective, which is implicitly the driving force in all bio-economic models of resource use), the desire to pursue ecological objectives is constrained by income aspirations. We can simulate income aspirations of farmers as constraints to ecologically oriented farming, as we did in a trade-off analysis (see results in Chapter IV.3). The model was able to provide a pathway for range development by predicting range quality based on the interaction of the ecological and economic models.

The model is therefore able to help decisions makers to understand the interaction between ecology and economy and provide them with guidelines for optimising policy instruments. For example, we showed the impacts of introducing land taxes using specific simulations.

Empirical foundation

The quality of models, in particular decision and management models, depends strongly on their empirical foundation. The empirical foundations of the BIOTA ecological and economic modules of the model were done separately. During the first phase, the ecological data needed for the model was not available yet and we started with an internal "ecological" module, which had its empirical foundation in "expert knowledge" on rangeland development based on management principles (Rothauge 2002). For instance, probabilities of changing rangeland states were derived from the experience gained by collaborating with and interviewing farmers. To a certain extent we maintained this approach when it came to the modelling of restoration interventions such as bush clearing to combat bush encroachment. Bush encroachment is a problem in central Namibian savannas and therefore gained our interest. It was assumed that farmers experiment and gain knowledge on stocking intensities and the corresponding consequences in terms of bush encroachment. For this we retrieved costs. Much effort was devoted to finding specific relationships between typical farm practices, such as combining different types of animals (sheep, goats, cattle) and resting (for restoration, fodder storage, etc.) and the consequences of these practices on rangeland quality in a dynamic context.

In the second funding phase of BIOTA Southern Africa (2004–2006) the empirical foundation for the models was gained from BIOTA's own ecological investigations in southern Namibia. This is a different ecological zone (i.e. dwarf shrublands of the Nama Karoo compared to Thornbush Savanna of central Namibia); states for the state-transition-model were jointly identified with ecological scientists. Some farm management practices were also transferable from central to south Namibia. In particular, farm practices such as opportunistic range management vs. fixed herd management and the corresponding grazing dynamics were investigated.

During phases two and three particularly, the empirical foundation of the bio-economic model for south Namibia was based on our own investigations of vegetation types, vegetation cover, biomass availability, etc. (conducted by a joint interdisciplinary team of economists and ecologists). The team agreed on distinguishable ecological states (Popp et al. 2000a) and used them as interfaces. The empirical foundation of the ecological model (Popp et al. 2009b) took place at the level of plants. We included plant growth and competition, vegetation cover, biomass growth, etc. as dependent on environmental conditions (such as rainfall, soils, aspect, slope, etc.) as well as management practices (such as grazing intensities, and whether browsers or grazers were farmed). Management practices could therefore be empirically distinguished and specified, which enabled the integration of the results from the ecological module into the joint bio-economic model. This resulted in high quality simulations enabling the prediction of the effect of different management strategies on rangeland condition.

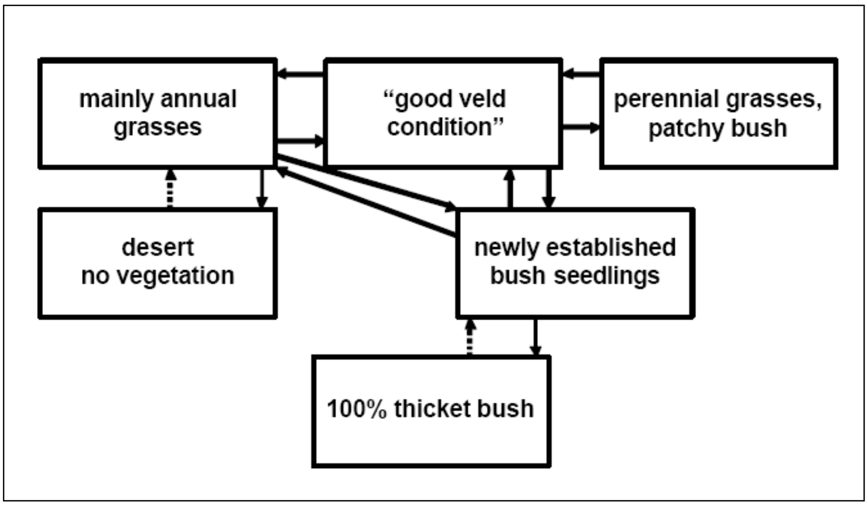

Fig. 3: A simplified state transition model for central Namibia. Source: Buß (2006).

In particular, the ecological module gained from the explicit depiction of farmer strategies with respect to the inclusion of sales and purchasing options. For farmers these aspects are of great relevance, i.e. price fluctuations, costs, and investment requests (e.g. for boreholes and fences) are driving forces. Prices of animals and fodder influence the calculation of optimal practices and it is possible to depict changes in price levels as categories, which are driving forces for landuse change and in particular degradation. We gained insights into how optimal landuse practices become relevant for rangeland ecological dynamics. Also, in particular, price instability, rainfall uncertainty, and other typical problems facing farmers, were quantified. Scenarios included the search for new opportunities to improve farming practices and achieve sustainable practices. This could be partly tested, such as for farming with Karakul, Dorper and Damara breeds, for example. These scenarios delivered relevant information for conservation. They can be used for ecological forecasts based on driving economic forces, and stakeholders and policy makers can look for alternatives, including new strategies such as game ranching etc. (see Chapter IV.3).

Examples of empirical results

In this sub-chapter we briefly demonstrate the potential of our bio-economic model to address management and policy problems for the conservation of rangeland. Fig. 4 shows that herd composition should be flexible at a central Namibian farm. Flexibility is an opportunistic farming strategy as opposed to farming in which strict rules for grazing patterns are followed. In particular, our model indicates that adjusting the numbers of male cattle is a viable opportunistic management strategy. Opportunistic farming in this context would involve buying and selling animals according to vegetation biomass availability, which would alleviate stress on the range in years of bad rainfall.

However, the results have to be seen in the context of simultaneous price fluctuation and discounting. Fig. 5 depicts different model runs (scenarios) under different discount rates. In resource economics, discount rates can be interpreted as a way a farmer values the future or as

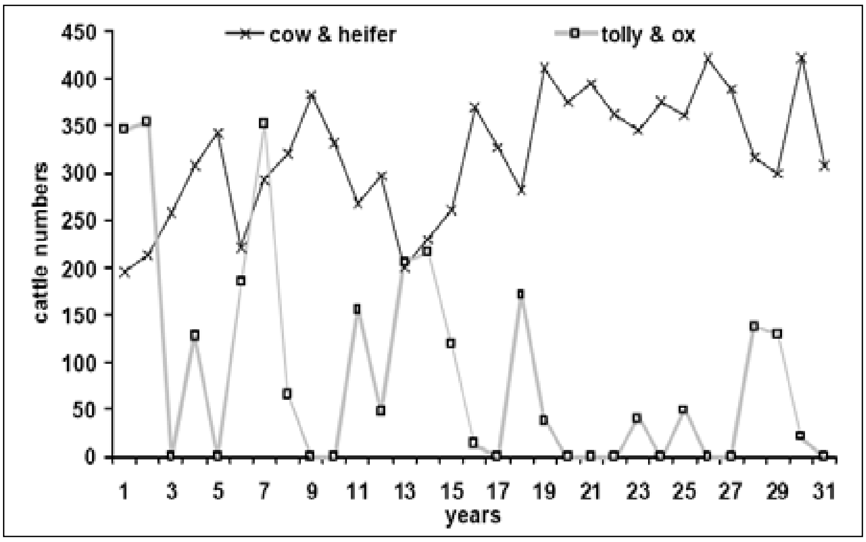

Fig. 4: Simulated optimal herd size at a central Namibian farm. Source: Buß (2006).

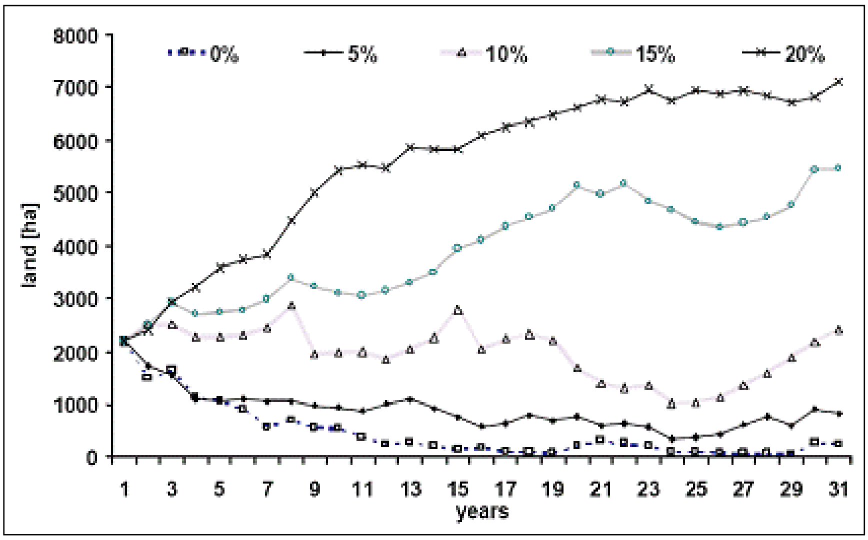

Fig. 5: Optimal farm development dependent on discount rates. Land in degrade states. Source: Buß (2006).

interest rates a farmer has to pay on credit. In our baseline scenarios we worked with a discounted income stream. Our model shows that this farming objective poses a danger of declining future income as a consequence of heavy resource extraction, especially, if discounting is high. An increase in the discount rate strongly increased the amount of land in degraded states. For instance, high discount rates are suggested in cases where farmers fear losing their land and therefore resort to resource overutilisation.

Lessons learnt and preparations for policy dialogue

From our investigations into the opportunities for establishing a bio-economic approach for rangeland management, lessons can be learnt in three areas: (1) opportunities to link ecological and economic models, (2) integration of farmers' knowledge, and (3) relevance for policy making and communication with policy makers:

1. In terms of opportunities to link models, an important lesson is that the different conceptual frameworks of a "causal model" in ecology and a "normative model" in economics can create misunderstandings. Causal modellers tend to derive average behavioural recommendations from their simulations (e.g. average stocking rates and thresholds). Economic modellers think more flexibly about farmer behaviour based on foresight. Both groups of modellers need to envisage the advantages of linking the models by inputs and outputs. Seeing the advantages is not trivial and requires the calculation of joint variables. However, since variables in ecology and economy by definition are not the same we need a compromise. This compromise involved agreeing on the natural "states" of the rangelands and that these "states" were temporally adjustable to management.
2. Regarding the integration of farmers' knowledge we learnt that, in principle, both ecological and economic modellers rely on communication with landusers. However, we also supplemented this information through literature review and information from soil science partners in BIOTA was also obtained. We used communication with farmers to identify the ecological states of rangelands and gain information on farming strategies. It has been shown that the proper investigation of farming strategies is important in creating accurate bio-economic models (Popp et al. 2009). The accuracy of bio-economic modelling is still a problem because researchers can either put emphasis on conservation or extraction. Our experience is that the issue of simulating "more extractive vs. conservation" strategies has an impact on the way models work and results can be obtained. Models still comprise a subjective element and team work between opposing interests can promote objectivity.
3. Communication with policy makers led to mixed results. Although the modelling of rangeland management has shown the potential to be integrated with policy instruments, such as a modified land tax scheme, policy makers were sceptical and asked for more evidence on the reliability of the tools. There emerges a new role for model-

lers as evidence providers, responsible for verifying the practicability of their propositions. Policy makers ask for justifiable results, which are liable for trial in a court, and the task of proof is shifted to researchers. This is difficult for researchers because relevant coefficients may not be sufficiently tested to stand in public discussion. Another problem is that policy makers and researchers may have different issues in mind without making them explicit.

As a final remark on lessons learnt we would like to briefly touch on the challenges of integrating economics and ecology at the practical level of team work. An observation is that interfaces of communication need a well-defined working structure and team building. In our case a joint definition of states for a state-transition-analysis and a mathematical tool (a matrix as a formal description of the eco-system dynamics imbedded in farmer knowledge on rangeland dynamics) enabled a coordinated effort. Ecological and economic investigators worked together to develop a joint tool. Problems were the sequencing of input and output, and mutual understanding of ecological and economic concepts. On the one hand the ecologist needs to understand the economics, and on the other hand the economist needs to understand range ecology. The rangeland health orientated concepts of interventions must become rooted in the minds of both. This aspect needs to be well planed.

Acknowledgements
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Model-based simulation tools

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Summary: This chapter will give a short introduction on how process-based simulation models can be further developed into management and educational tools and will present three BIOTA modelling tools, which address different key problems of landuse management and climate change impacts in African savannas: (1) the Devil's Claw Simulation tool (DCSim), which simulates the population dynamics of a medicinal plant endemic to southern Africa, (2) the Ecological-Economic Savannah Rangeland Management tool (EESRaM), which simulates a livestock farm in a thornbush savanna in Namibia, and (3) the BIOTA Kalahari Biodiversity Simulator (KBioSim), which simulates population dynamics of four species indicative of a particular spatial scale and depend on large trees as vegetation structures for e.g. nesting and sheltering. The three modelling tools address different key problems of landuse management and climate change impacts in African savannas to communicate and visualise problem oriented research on ecosystem and population dynamics under e.g. different landuse and climate change scenarios.

Introduction

Process-based simulation models are ideal tools to communicate and visualise problem oriented research on ecosystem and population dynamics under e.g. different landuse and climate change scenarios. A further didactic development of such simulation models would offer an excellent opportunity to develop educational and management tools that are equipped with a user-friendly interface.

The current progress of technical opportunities enables the implementation of interactive computer tools that simulate complex ecosystem and population dynamics "on-demand". The user will quickly understand animations or graphs showing the impacts of e.g. different management options on savanna vegetation dynamics. The advantages of such tools are that the user can systematically explore and change management parameters (e.g. stocking rates, harvesting cycles, etc.) at different time scales and evaluate the impacts of his or her own decisions immediately. This playful exploration allows for a quick understanding of ecosystem dynamics under different landuse and climate change scenarios. Hence, such tools can aid communication of findings, ecosystem understanding, have the potential to support a decision making process, and enhance transdisciplinary communication.

In particular, rule- and individual-based models (IBMs) developed within the BIOTA research framework, have also been developed as educational and management tools (e.g. the Kalahari Biodiversity simulator). Compared to other modelling approaches (algebraic or statistical models), the basic rules, model structure and output of rule-based IBMs are easy to understand and also comprehensible for non-expert target groups and stakeholders such as rangeland managers, farmers or politicians. Thus, this modelling approach allows direct communication with stakeholders and more importantly the inclusion of feedback from stakeholders for model tool improvement.

In this chapter we will present three BIOTA modelling tools to address different key problems of landuse management and climate change impacts in African savannas.

First we will present the **D**evil's **C**law (*Harpagophytum procumbens*) **Sim**ulation tool (DCSim), which simulates the population dynamics of a medicinal plant endemic to southern Africa. This model allows impact testing of different harvesting strategies (under different grazing impacts) on population dynamics and yield of storage tubers, which are used for medicinal purposes (see Article III.7.2).

The second tool, the **E**cological-**E**conomic **S**avannah **Ra**ngeland **M**anagement tool (EESRaM), simulates a livestock farm in a thornbush savanna in Namibia and it is based on an agent-based, ecological-economic simulation model (see Chapter IV.2). Here, different management strategies can be tested while the user can virtually buy and sell animals exploring the economic impacts as well as the ecological state of the savanna vegetation.

Third we will show the BIOTA **K**alahari **Bio**diversity **Sim**ulator (KBioSim) (Blaum et al. 2008). This educational and management tool simulates population dynamics of four species indicative of a particular spatial scale and depend on large trees as vegetation structures for e.g. nesting and sheltering. Spatial-temporal changes in population size can be tested under various combinations of landuse (livestock production and wood cutting) and climate change scenarios.

The Devil's Claw simulation tool (DCSim)

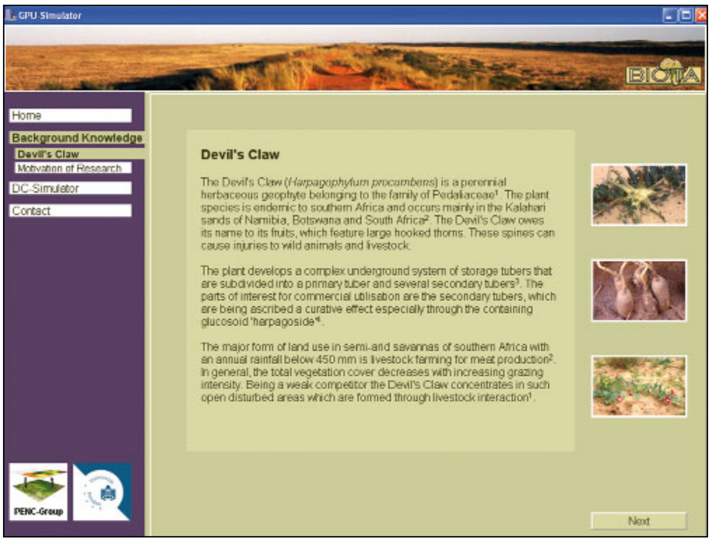
The aim of DCSim is to identify sustainable harvesting strategies for the storage tubers of this medicinal plant, which are often an important additional income for the poorest people in communal areas (Strohbach & Cole 2007). DCSim is based on an individual- and rule-based simulation model developed within the BIOTA framework (Schütze 2009). DCSim is the first simulation tool, where the impact of different harvesting strategies and grazing intensities on population structure, dynamics and crop yield of this endemic plant can be systematically explored. The structure of the user-friendly computer program surface is similar to well designed webpages. The navigation bar includes background information on the Devil's Claw, harvesting methods and strategies, while the user can choose between different harvesting methods and harvesting cycles in the simulation section (Fig. 1).

In the simulation section, the user can develop his or her own harvesting strategy by choosing between three methods (from careful removal of some secondary tubers to harsh removal of all secondary tubers) and harvesting frequency (e.g. each year, every 5 years, etc.). After selecting a simulation time, the user can explore the impact of the chosen harvesting strategy on crop yield and population dynamics. Initial results will show changes of the spatial dynamics of juveniles, reproductive and non-reproductive individuals for a rangeland area of 20 ha. Further, time series of population size and storage tuber yield for one exemplary annual rainfall time series will be displayed. Averaged trends from repeated simulations for a specific harvesting strategy can also be explored.

The navigation bar also provides a direct link to compare the impacts of all harvesting options (Figs. 2 & 3). This option allows the identification of the most sustainable harvesting strategy (i.e. a strategy with the highest yield and the least impact on the Devil's Claw population size for a selected time horizon).

The Ecological-Economic Savannah Rangeland management tool (EESRaM)

EESRaM enables users (such as rangeland managers, farmers, etc.) to systematically explore the impacts of different rangeland management strategies (regarding temporal dynamics of number and type of cattle—i.e. in what situation to buy or sell a certain number of



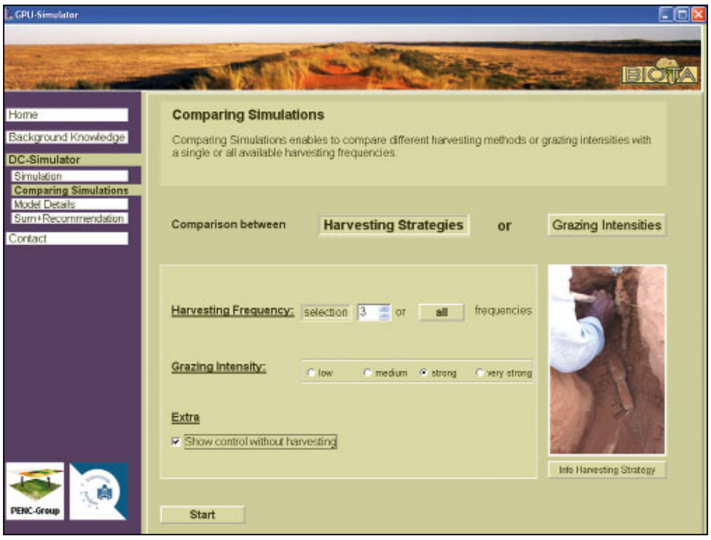
Devil's Claw

The Devil's Claw (*Harpagophytum procumbens*) is a perennial herbaceous geophyte belonging to the family of Pedaliaceae¹. The plant species is endemic to southern Africa and occurs mainly in the Kalahari sands of Namibia, Botswana and South Africa². The Devil's Claw owes its name to its fruits, which feature large hooked thorns. These spines can cause injuries to wild animals and livestock.

The plant develops a complex underground system of storage tubers that are subdivided into a primary tuber and several secondary tubers³. The parts of interest for commercial utilisation are the secondary tubers, which are being ascribed a curative effect especially through the containing glucosoid 'harpagoside'⁴.

The major form of land use in semi-arid savannas of southern Africa with an annual rainfall below 450 mm is livestock farming for meat production². In general, the total vegetation cover decreases with increasing grazing intensity. Being a weak competitor the Devil's Claw concentrates in such open disturbed areas which are formed through livestock interaction¹.

Fig. 1: User surface and structure of the Devil's Claw Simulator tool (DCSim).



Comparing Simulations

Comparing Simulations enables to compare different harvesting methods or grazing intensities with a single or all available harvesting frequencies.

Comparison between Harvesting Strategies or Grazing Intensities

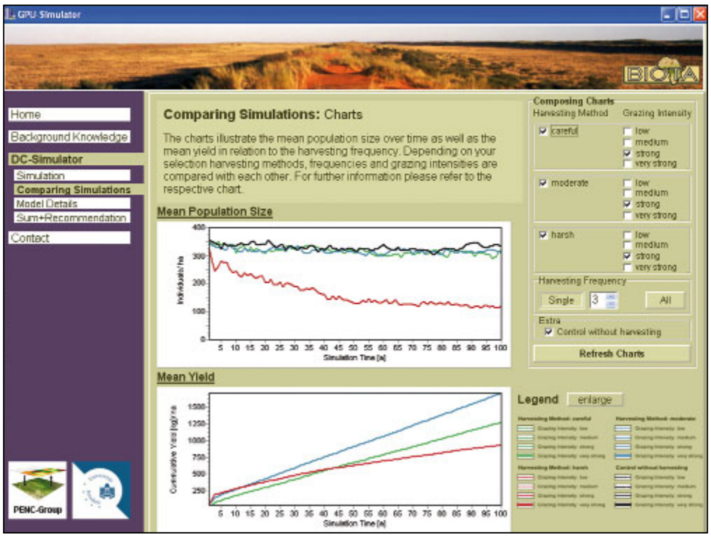
Harvesting Frequency: selection 3 or all frequencies

Grazing Intensity: ○ low ○ medium ● strong ○ very strong

Extra

☑ Show control without harvesting

Fig. 2: Screen shot of DCSim showing the options for harvesting strategies.



Comparing Simulations: Charts

The charts illustrate the mean population size over time as well as the mean yield in relation to the harvesting frequency. Depending on your selection harvesting methods, frequencies and grazing intensities are compared with each other. For further information please refer to the respective chart.

Composing Charts

Harvesting Method / Grazing Intensity

☑ careful: ☐ low ☐ medium ☑ strong ☐ very strong

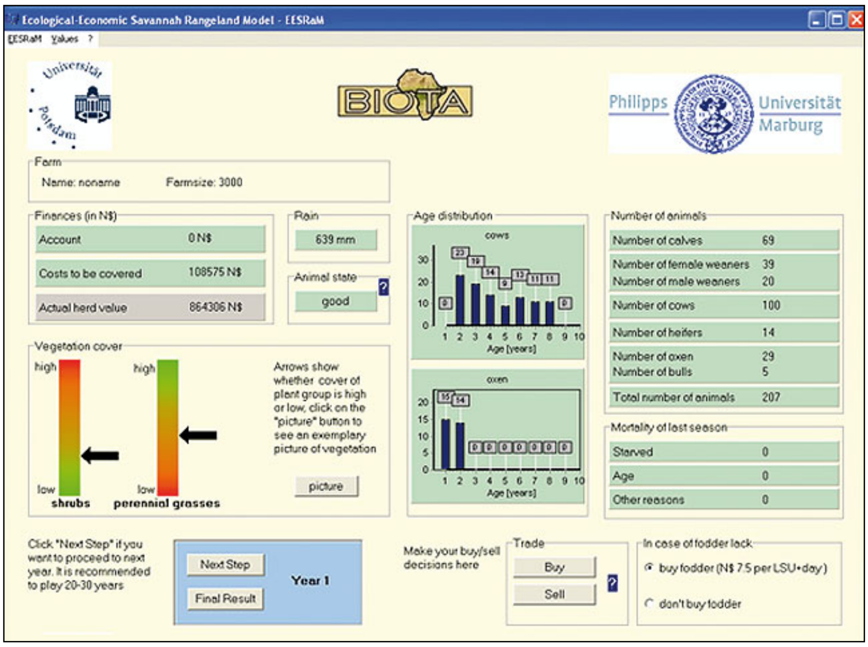
☑ moderate: ☐ low ☐ medium ☑ strong ☐ very strong

☑ harsh: ☐ low ☐ medium ☑ strong ☐ very strong

Harvesting Frequency: Single 3 All

Extra: ☑ Control without harvesting

Fig. 3: Screen shot of the impacts of different harvesting methods with a harvesting frequency of three years on population size and yield.



Farm
Name: noname Farmsize: 3000

Finances (in N$)

Account	0 N$
Costs to be covered	108575 N$
Actual herd value	864306 N$

Rain: 639 mm

Animal state: good

Number of animals

Number of calves	69
Number of female weaners	39
Number of male weaners	20
Number of cows	100
Number of heifers	14
Number of oxen	29
Number of bulls	5
Total number of animals	207

Mortality of last season

Starved	0
Age	0
Other reasons	0

Vegetation cover

Arrows show whether cover of plant group is high or low, click on the "picture" button to see an exemplary picture of vegetation

Click "Next Step" if you want to proceed to next year. It is recommended to play 20-30 years

Year 1

Make your buy/sell decisions here

Trade

In case of fodder lack
● buy fodder (N$ 7.5 per LSU•day)
○ don't buy fodder

Fig. 4: Screen shot of EESRaM, showing the ecological state, herd information, account balance and other farm data including buy/ sell decisions options.

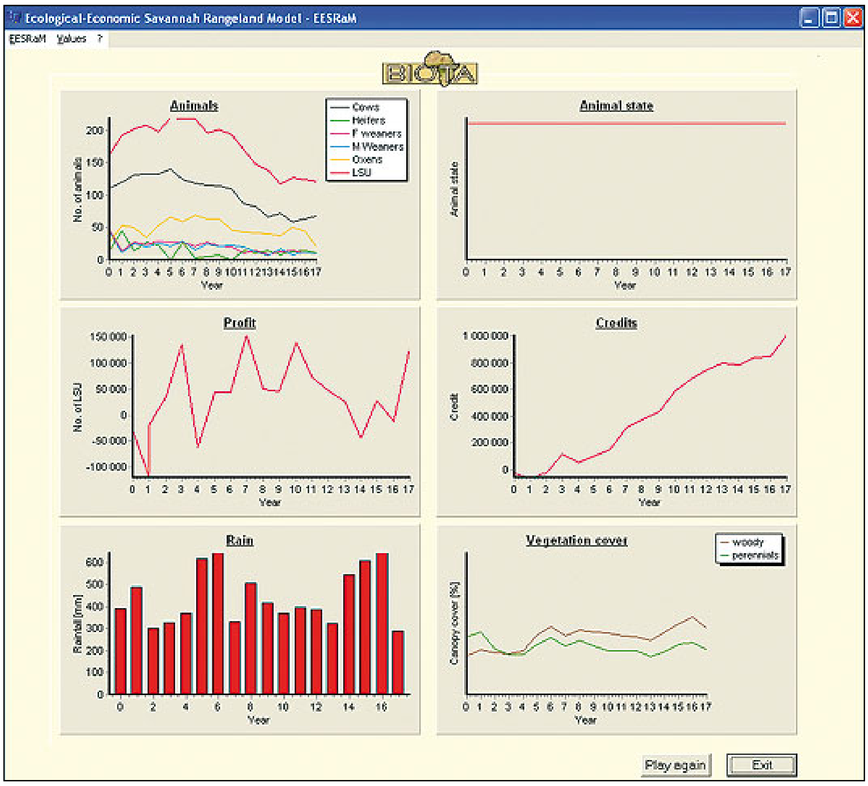


Fig. 5: Screen shot of EESRaMs, showing the simulated time series of rainfall, account balance, animal numbers, profit, animal conditions and vegetation cover.

livestock) on vegetation dynamics and economic costs and benefits for a single livestock farm in a semi-arid savanna. The tool is based on two dynamically linked simulation models, parameterised for the Omaheke region in eastern Namibia with a mean annual precipitation of ~400 mm and a high inter-annual variation, including:

1) an ecological model, which simulates the dynamics of perennial and annual grasses, woody vegetation, and the corresponding biomass production (based on Tietjen et al. 2009), and
2) an economic farm model that simulates cattle production including herd dynamics, productivity, costs and income of a cattle farm (see Subchapter IV.2.6).

At the start screen, the user can decide relevant farm management information such as the size of the farm, number of workers, number of animals to start the business, water infrastructure (number and type of water pumps) and number of simulation years. After entering database information, users can access the main tool interface (Fig. 4), including information on: (1) finances, (running costs, bank account balance), (2) livestock (number, type, age and condition of the animals), (3) mortality in the last season, (4) vegetation condition (shrub and perennial grass cover), and (5) current season rainfall totals .

Based on this information, the user can decide upon the number and type of livestock (cow, oxen, male/female weaners, heifers) bought and sold season by season. In order to visualise current veld condition, pictures representing the given vegetation state will appear (note: representative pictures of the current veld and animal condition can be displayed on demand at any time).

At the end of the simulation, a summary containing time series of animal numbers, account balance, animal condition, cover of perennial grasses and shrubs, and seasonal rainfall will appear (Fig. 5). This enables the user to evaluate the impacts of different management decisions on veld and animal conditions, economic performance, and to identify possible relationships between the given factors. For example, one can test for correlation between stocking rate, rainfall and vegetation state or costs, by simulating either stable herd sizes over time or adapt them to the precipitation. Note: Simulation results can only be interpreted as trends, and not as quantitative measures of landuse outcomes. Nevertheless, the real-time simulations reflect state of the art knowledge in the area and are useful for communicating systems' dynamics, trade-offs and correlations.

Recently, a similar version of the tool was used to conduct surveys with resettlement farmers in the Omaheke region. Hereby, discussion was stimulated and understanding was improved for both sides—researchers and farmers. This also enabled the inclusion of feedback from stakeholders for current tools' improvement. In this sense, simulation tools have proven to encourage transdisciplinary communication for a better development between research and application.

The Kalahari Biodiversity Simulator (KBioSim)

KBioSim is a non-profit educational and management tool that demonstrates and explores the complex responses of four indicative species on possible climate and landuse changes in the southern Kalahari rangelands. The four representative species (Tree Rat *Thallomys nigricauda*, Sociable Weaver *Philetairus socius*, Raisin Bush *Grewia flawa* and Tawny Eagle *Aquila rapax*) were selected based on their specific dependence on woody vegetation structures, influence of landuse activities—i.e. trees (wood harvesting) and shrubs (overgrazing)—and differences in their spatial scale of dispersal, home range and migration (Fig. 6).

The main objective of KBioSim is to improve the understanding of ecological mechanisms and processes on different spatial scales that have to be considered when trying to predict the consequences of management decisions or environmental changes on the sensitivity of species. The tool dynamically links a savanna vegetation model (Jeltsch et al. 1997) to five dynamic single species population models Camelthorn *Acacia erioloba* (Jeltsch et al. 1999), Tree Rat *Thallomys nigricauda* (Steinhäuser 2004), Sociable Weaver *Philetairus socius* (Schwager et al. 2008), Raisin Bush *Grewia flawa* (Tews et al. 2004) and Tawny Eagle *Aquila rapax* (Wichmann 2002).

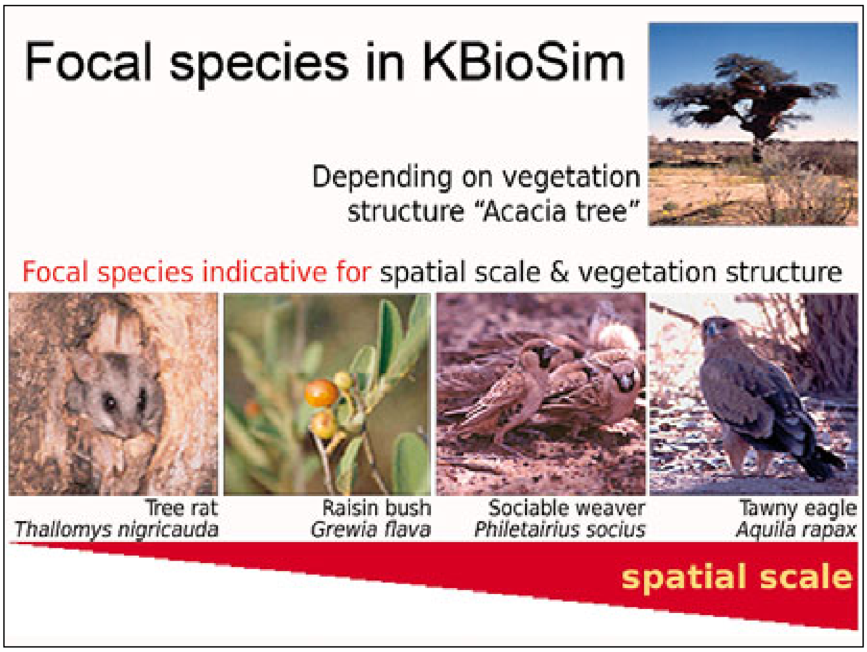
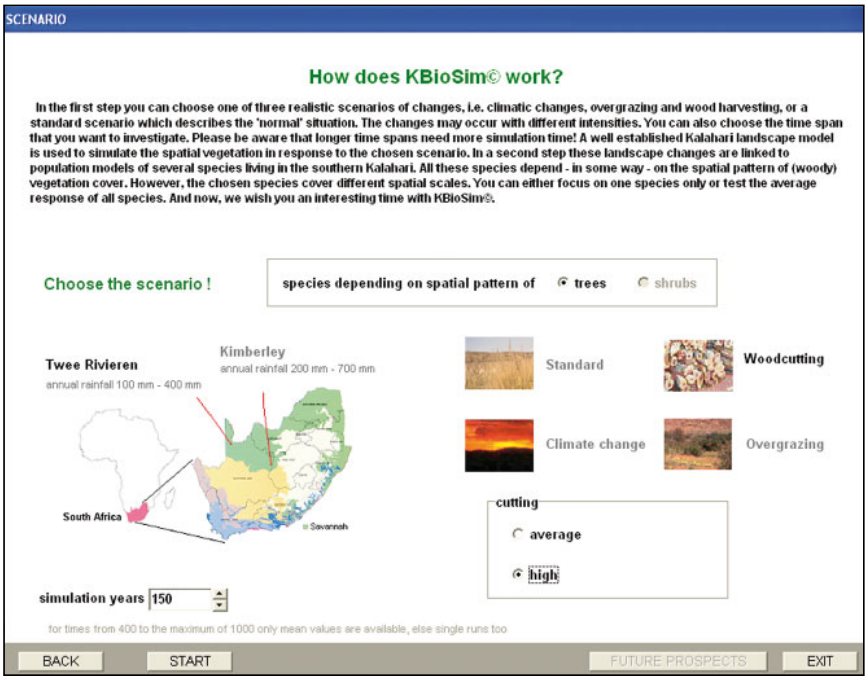


Fig. 6: Focal species of KbioSim depending on large Acacia-trees as vegetation structure: Tree Rat (*Thallomys nigricauda*), Sociable Weaver (*Philetairus socius*), Raisin Bush (*Grewia flawa*) and Tawny Eagle (*Aquila rapax*).



How does KBioSim© work?

In the first step you can choose one of three realistic scenarios of changes, i.e. climatic changes, overgrazing and wood harvesting, or a standard scenario which describes the 'normal' situation. The changes may occur with different intensities. You can also choose the time span that you want to investigate. Please be aware that longer time spans need more simulation time! A well established Kalahari landscape model is used to simulate the spatial vegetation in response to the chosen scenario. In a second step these landscape changes are linked to population models of several species living in the southern Kalahari. All these species depend - in some way - on the spatial pattern of (woody) vegetation cover. However, the chosen species cover different spatial scales. You can either focus on one species only or test the average response of all species. And now, we wish you an interesting time with KBioSim©.

Choose the scenario !

species depending on spatial pattern of ● trees ○ shrubs

cutting
○ average
● high

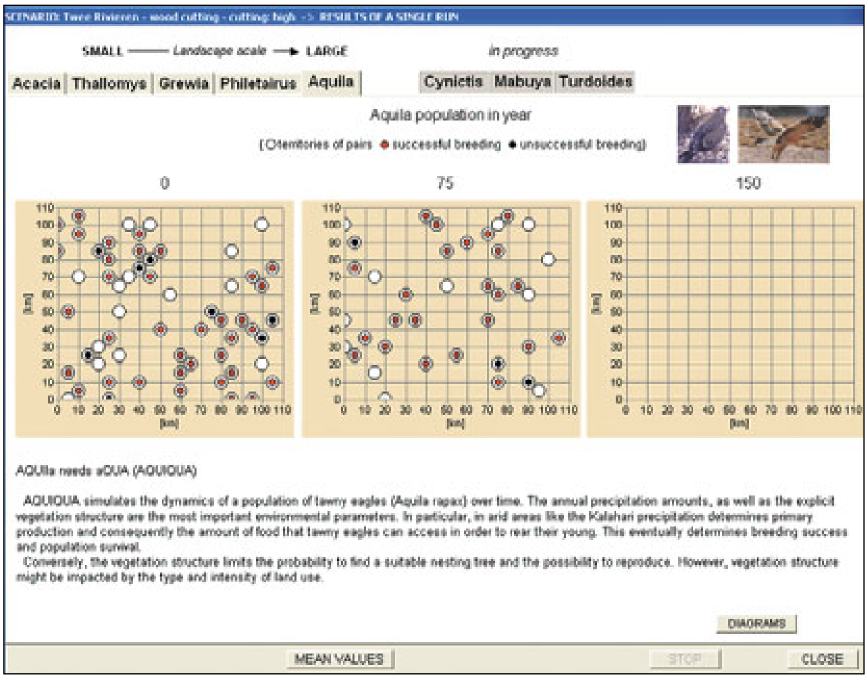
simulation years 150

for times from 400 to the maximum of 1000 only mean values are available, else single runs too

Fig. 7: User surface of Kalahari Biodiversity Simulator (KBioSim) showing user's manual and landuse and climate scenarios options for two rainfall areas (Twee Rivieren and Kimberley, SA).

At the start screen of KBioSim the user will receive brief guidelines (Fig. 7). First, the user can choose between exploring the impacts of landuse (high versus low wood cutting rate, and high versus moderade livestock grazing) and climate change scenarios (decrease in mean annual rainfall or increase in annual rainfall variability) on population dynamics of the focal species. Second, the impacts of the selected scenario can be explored for two rainfall regimes (high 350 mm versus low 175 mm annual rainfall). A simulation time can then be selected.

After the real time simulation, basic information of the two focal regions is displayed and the user can explore the impacts of the selected scenario on the spatial (animated) and temporal dynamics of the focal species for one time series (Fig. 8). In the final screen, a comparison across the focal species enables the user to evaluate the impacts of the selected scenarios (Fig. 9).



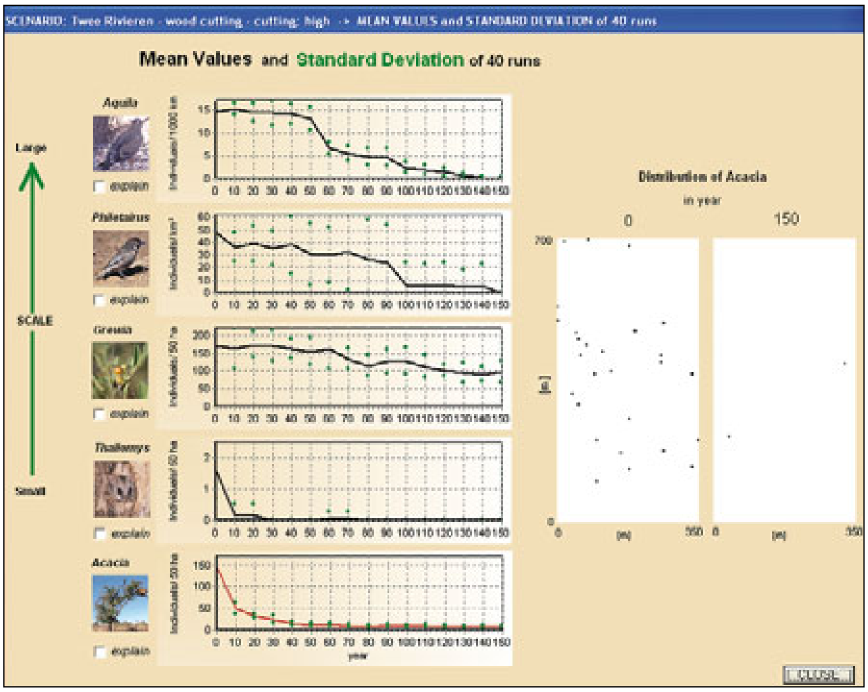
SCENARIO: Twee Rivieren - wood cutting - cutting: high -> RESULTS OF A SINGLE RUN

AQUila needs aQUA (AQUIQUA)

AQUIQUA simulates the dynamics of a population of tawny eagles (Aquila rapax) over time. The annual precipitation amounts, as well as the explicit vegetation structure are the most important environmental parameters. In particular, in arid areas like the Kalahari precipitation determines primary production and consequently the amount of food that tawny eagles can access in order to rear their young. This eventually determines breeding success and population survival.

Conversely, the vegetation structure limits the probability to find a suitable nesting tree and the possibility to reproduce. However, vegetation structure might be impacted by the type and intensity of land use.

Fig. 8: Screen shot of the spatial dynamics of tawny eagle breeding pairs for a landuse scenario of 'annual wood cutting rate 5% in Twee Rivireren'.



SCENARIO: Twee Rivieren - wood cutting - cutting: high -> MEAN VALUES and STANDARD DEVIATION of 40 runs

Fig. 9: Screen shot of the temporal dynamics of all indicative species for a landuse scenario of 'annual wood cutting rate 5% in Twee Rivireren'.

Acknowledgements

The authors' general acknowledgements to the organisations and institutions, which supported this work are provided in Volume 1.

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Part III

III.8 Stakeholder interactions and capacity development

BIOTA's strategies for stakeholder interaction and capacity development

Thomas Falk*, Ute Schmiedel, Ibo Zimmermann, Dave F. Joubert, Michael Pröpper, Martin Gruber, Bettina Koelle, Stephanie E. Domptail, Bertchen Kohrs & Noel Oettle

Summary: Applied biodiversity research that aims to improve the livelihood conditions of people and to promote sustainable biodiversity management must integrate the local landusers and decision makers into various stages of the project. This chapter gives an overview of the various approaches followed by BIOTA in its interaction with stakeholders at different phases of the project. The subsequent chapters describe the approaches in more detail.

Introduction

The involvement of stakeholders into the **various stages** of a research project like BIOTA requires a commitment to constantly rethink and adjust the subject and goal of the research, and in this way eventually contribute to an improvement of the situation under study. Combining the knowledge, perspectives, and resources of scientific and non-scientific stakeholders is precondition for research that addresses relevant issues and provides the basis for the implementation of innovations (Neef & Heidhues 2005). Moll & Zander (2006) highlight the need for more emphasis on an implementation-orientation of science as the precondition for science-based decision-making. An important goal of BIOTA Southern Africa was to facilitate the generation of knowledge for decision makers towards sustainable management of natural resources, by taking into account natural as well as socio-economic conditions and constraints. Over nine years of research a broad range of results relevant for sustainable biodiversity and resource management emerged, covering a variety of themes as summarised within this book. Based on scientific knowledge and methodologies, BIOTA contributed to the process of improving the understanding of the current status and management of the environment. This was accomplished through the identification and evaluation of social and environmental changes, searching for solutions for identified challenges, analysing the findings and feeding these back to the stakeholders (Neubert 2005). BIOTA contributed to the process of understanding the current condition and management of the social and natural environment, the identification, analysis, and evaluation of changes, and the search for solutions for identified challenges. The process supported resource users, statutory and customary policy makers, extension officers and development agents so as to improve decision making. This chapter summarises the approaches applied by the team to involve stakeholders and to disseminate results.

Approaches applied

Whereas in the first phase of the project the research goals were mainly defined by the academic researchers, stakeholders played an increasingly important role throughout the subsequent phases of the cyclic BIOTA research process as visualised in Fig. 1. Even though each researcher was responsible for involving stakeholders and disseminating results, several workpackages (e.g. F1–F4 during the third phase of BIOTA Southern Africa, see Subchapter I.3) had the specific task of promoting trans-disciplinary research and thus to encouraging the integration of the findings.

The research process started with the joint identification of relevant research questions in individual or group meetings with policy makers, resource users or representatives of civil society (Fig. 1, step 1). Over the years of cooperation, the BIOTA team established deeply rooted relations of trust with a wide range of stakeholders. Trust is a precondition for open and constructive discussions, and was manifest at formal and informal meetings and workshops during which priorities for research were formulated. Beyond this, team members were regular participants of national and regional conferences and workshops on environmental management, enabling them to build strong relations with other members of the research and landuser communities. From the beginning, many BIOTA colleagues strongly supported and participated in the annual meetings of the Arid Zone Ecology Forum (AZEF), a forum for southern African dryland ecologists from science and practice. BIOTA also organised and financed the Namibian Rangeland Forum 2009, an annual workshop for farmers, extension workers, and scientists, with a common interest in the ecologically and economically successful management of Namibia's rangelands. These various opportunities for direct communication allowed focus on the special fields of interest of the communication partners and facilitated the adjustment of the "language" to suit the needs of the target groups (e.g. government, NGO, farmer, donors).

In step 2 stakeholders were integrated into the empirical research. In a participatory approach BIOTA researchers and farmers developed, applied, monitored, and evaluated, for example, farm management trials (e.g. environmental parasite control and restoration trials) (see Article III.8.2). One of BIOTA's primary methods of involving resource users in the research process has been the training and employment of para-ecologists (Article III.8.3). The support of qualified para-ecologists in our interaction with communities and their assistance in empirical field-work were a great asset for the BIOTA project. Another key instrument was the participatory production of films, which provided a platform for local resource-users, government officials, traditional authorities, and NGOs to discuss, negotiate, and communicate critical biodiversity-related management challenges (see Article III.8.4). This dialogue facilitated the empowerment in particular of weaker players in the natural resource management arena. The film production also constituted an important tool for training and capacity development. More generally, the involvement of stakeholders in the research process enabled them to take greater ownership of the process and the emerging findings. Increasing feelings of ownership of research results enhances the probability of the implementation of science-based innovations.

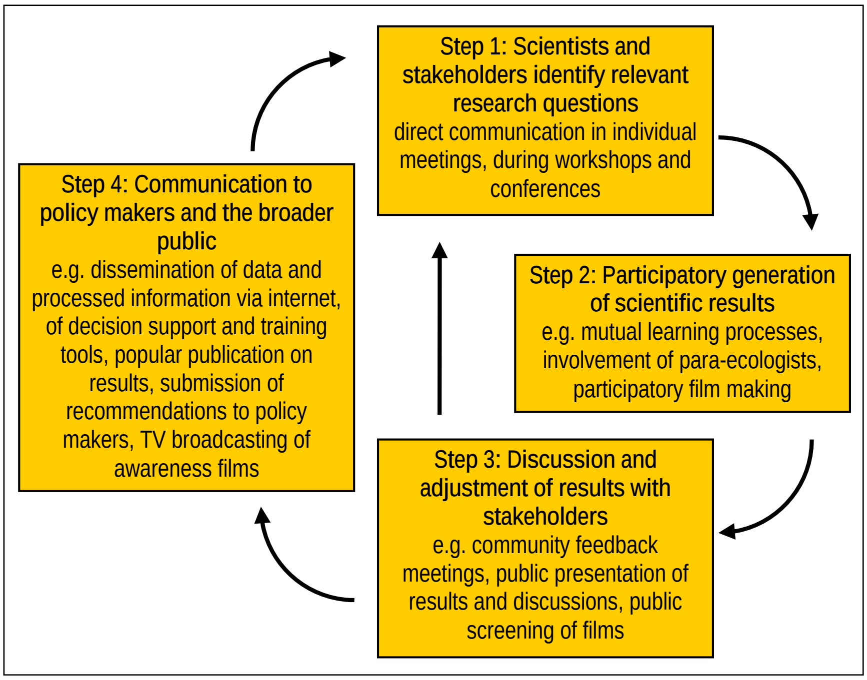

Fig. 1: Steps of stakeholder involvement in the BIOTA research process.

In step 3, the results of academic as well as participatory research were repeatedly fed back and discussed with different stakeholders in order to stimulate mutual learning processes between scientists and stakeholders. Special attention was paid to community workshops during which resource users expressed their perceptions of key problems and how those are linked to rangeland degradation and biodiversity loss. During the workshops, scientific findings and the need to adjust management measures were discussed. As a result of interaction in the course of BIOTA-organised farmers' days, bilingual botanical field guide for farmers were developed (Wesuls et al. 2009, Wasiolka & Blaum 2010). The different forms of community workshops often resulted in the formulation and refinement of hypotheses and were the starting point for a new research cycle.

In order to interact with a broader range of stakeholders, public talks and discussions were carried out. Landusers, government officials, scientists, students and consultants, representatives of development agencies, and journalists participated in debates on topics ranging from restoration of degraded ecosystems to the impact of ongoing decentralisation policies on resource management and livelihoods. This dialogue was a crucial platform of knowledge generation for decision makers as well as for the project. It revealed and resolved resource managers' misconceptions. Misleading interpretations of key ecological processes are often the reason for suboptimal decisions and a root cause of environmental degradation.

In a fourth step, after before-mentioned consultations and verifications, research results were communicated to the wider public. An important tool for this was the BIOTA Data Facility that collated the data from various sites and disciplines and made user-relevant information available at the BIOTA website free of charge (Article III.8.6). To reach the broader stakeholder community, including those without internet access, documentary and awareness films produced by BIOTA were broadcast on TV and screened at public events organised by a para-ecologist and other project members. The intention was, on the one hand, to inform immediate resource users about crucial findings, make them aware of the close interdependence between biodiversity and human behaviour and to empower them to integrate this information into their land management. On the other hand, public discussions were facilitated, initiating communication and negotiation processes amongst decision makers at different levels regarding possible changes to resource management.

In 2009, Namibian policy makers requested BIOTA to give input into the process of drafting the Namibian Rangeland Policy and Strategy. For this purpose BIOTA invited farmers, scientists, students, and government officials to present and discuss challenges and perspectives of future range-management during the Namibian Rangeland Forum 2009. The results of these discussions were summarised and submitted to the Ministry of Agriculture, Water and Forestry. Consultations and reports concerning the work regarding the application of a land tax system, which provides economic incentives for sustainable rangeland management were requested by, and given to the Ministry of Lands and Resettlement. These are just two examples of how BIOTA directly contributed to the adaptation of the regulatory framework of natural resource management. The strong interest of the Ministry of Agriculture, Water and Forestry in the results of the BIOTA project was also manifested when it published project results in its leaflet "Spotlight on Agriculture" (Blaum et al. 2008, Falk & Bock 2008b, Shamathe & Zimmermann 2008, Tjilumbu & Zimmermann 2008). This popular publication was widely distributed in Namibia amongst farmers and technical government staff. Farmers' unions also showed a great interest in the work of BIOTA and published two articles on results of research conducted in the commercial farming systems of the central and southern Savanna in the magazines "Farmers' Weekly", "Agriforum" (Buss & Bezuidenhout 2003, Lamprecht 2008) and Agricola (Zimmermann et al., submitted). Farmers and technical government staff were further reached by the participatory development and distribution of different decision support and training tools (Articles III.7.6, III.8.5). The tools help decision makers to rethink their management strategies and to deepen their insight into the complex interactions between their actions and the ecosystem. Last but not least, BIOTA contributed to the public debate on urgent policy issues in daily newspapers (e.g. Falk & Bock 2008a). Feedback received from recipients of this information through these diverse media was again channelled into the formulation of new research questions starting a new research cycle.

Finally, BIOTA undertook a research process to document the learning processes from the BIOTA project cycle, focusing especially on the implementation of trans-disciplinary research and recommendations for future research projects (Article III.8.7).

Acknowledgements

The authors' general acknowledgements to the organisations and institutions, which supported this work are provided in Volume 1.

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Learning from each other: participatory research with landusers on management applications

Ibo Zimmermann*, Ute Schmiedel & Clement Cupido

Summary: BIOTA undertook several approaches towards learning partnerships between academic researchers and farmers in order to develop and evaluate management measures. This chapter describes several examples of how researchers and landusers identified the challenges, discussed the possible measures, decided what and how to test them and conducted and evaluated experiments together. The examples show that farmers are innovative, experimental and eager to learn about new ways of how to improve their land management. The partnership approach revealed new perspectives for farmers, farm workers and researchers: The joint research resulted in more biodiversity-friendly land management, tested strategies for restoration of degraded rangeland based on better insight into ecological processes for farmers and researchers.

Introduction

The ultimate aim of applied research is to improve people's lives. In the case of biodiversity research, the expected improvement should come about through enhanced ecosystem services that biodiversity provides, through improved management by landusers. To reach this goal, decisions on land management need to be based on better understanding of biodiversity's functions and how these are influenced by different management strategies. In order to empower landusers to apply effective management, the focus of agricultural extension has shifted from prescriptive to participatory. Before solutions can be found it is necessary to understand why farmers use the land unsustainably (Düvel & Lategan 1997). Participatory methodologies, such as those of Participatory Learning and Action (Pretty et al. 1995), provide useful learning tools for both farmers and researchers, if adapted to local conditions and capable of overcoming accustomed expectations (Treurnicht et al. 2001). Participatory action research can be usefully applied to landuse management (Shah 1997) and lead to participatory trials (Mapfumo et al. 2008) that enable farmers to find ways to improve their farming practices.

Despite the mainstreaming of unsustainable farming practices over the past decades, some farmers have maintained or developed biodiversity-friendly approaches to farming. The effectiveness of these approaches can be scientifically tested in partnerships between farmers and scientists and publicised among farmers through farmer organisations and extension services, to encourage others to experiment with them. Some of the participatory projects applied in BIOTA research are presented below, divided into those that: (i) introduced innovative practices that were new to farmers, (ii) learnt from practices already being applied by innovative farmers, and (iii) jointly developed and applied practices that addressed the farmers' needs.

Projects that suggested new practices

Biodiversity-friendly control of internal parasites

The increasing use of toxic chemicals by farmers poses a threat not only through worms developing resistance to the chemicals (van Wyk et al. 1998) but also to essential ecological services provided by dung beetles, such as cycling mineral nutrients through the soil and burying dung that would otherwise breed flies and spread diseases (Walters 2008).

During a workshop held with farmers in Rehoboth in 2007, the analytical tool of a problem tree (Fussel 1995) was used to analyse the sequence of events that eventually lead to roundworm infestations. Diagnosis through drawing a problem tree is useful in allowing the consequences of different interventions to be better visualised and understood, thereby guiding decisions on management of the problem. Management that addresses causes higher up a problem tree, closer to the root causes, is likely to be more effective in the long run than management that addresses the proximate causes or symptoms at the bottom of a tree. The root causes as perceived by farmers included the increased human population, easier access to loans and the El Niño weather phenomenon. Root causes from a more ecological point of view included the provision of permanent water from boreholes, the control of large predators, the use of poisons to control parasites, premature weaning, aggressiveness in the handling of livestock and the kraaling of livestock (Zimmermann et al. 2009). This allowed farmers to view roundworm infestations as a symptom caused by imbalances in regulatory processes. Treating the imbalances will be far more effective for long-term sustainability than will treating the symptoms with quick fix toxic chemicals. Although the overall problem tree appears complicated at first glance (e.g. Fig. 1), it becomes clearer when interpreted one step at a time, as in the presentation inserted as Electronic Appendix or available at www.biota-africa.org/PublPDF/Abstracts/Problem_tree_step_by_step.ppt

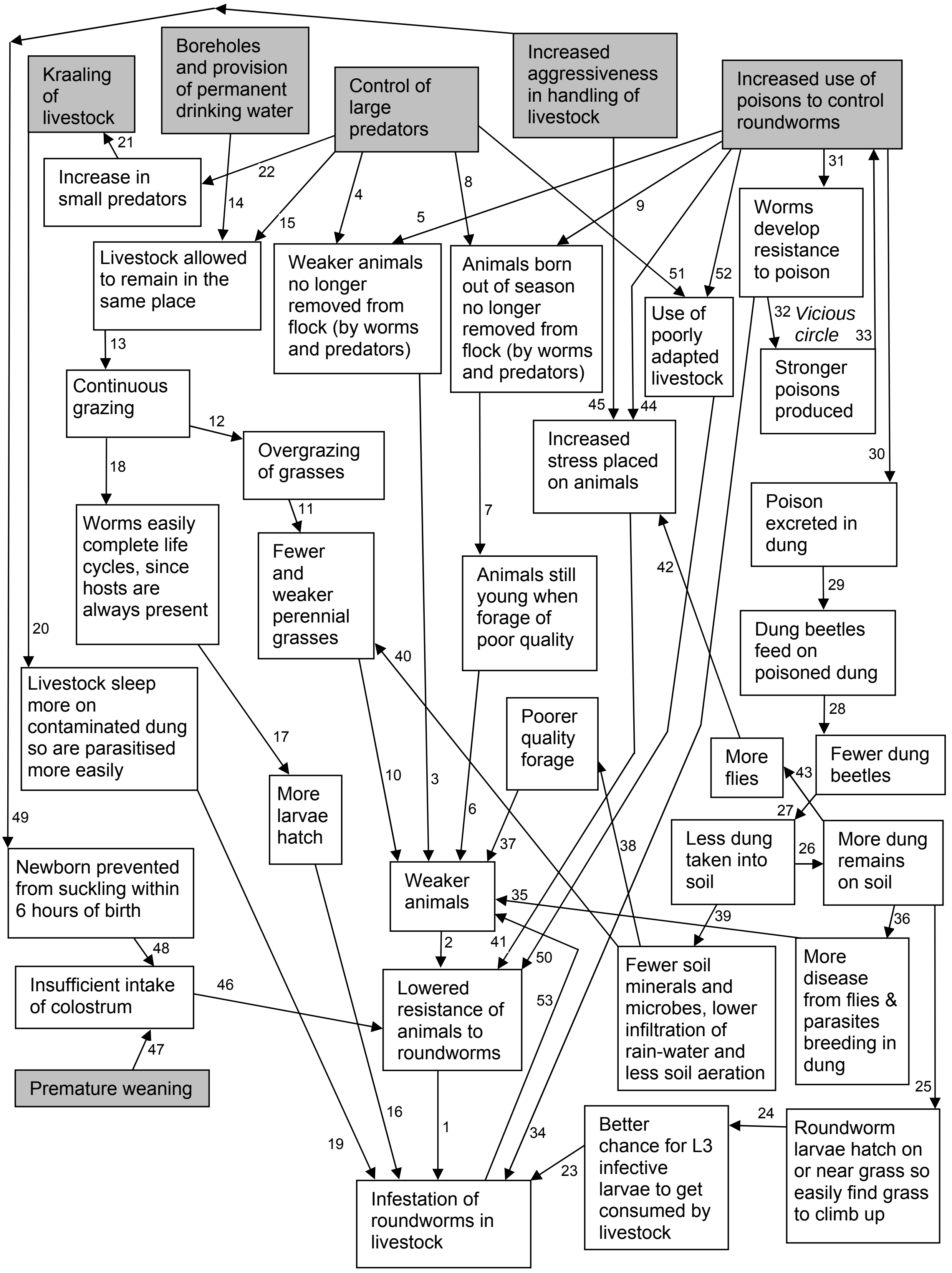

Fig. 1: Diagnostic problem tree for the infestation of intestinal roundworms in livestock, with root causes shaded.

Photo 1: A farm worker receives his certificate from the Polytechnic of Namibia for participating in a research trial. Photo: Justus Kauatjirue.

The project also learnt from farmers who successfully raise sheep and goats without the need for any remedies, whether toxic chemicals or environmentally friendly ones. Treating the symptoms with environmentally friendly remedies could be viewed as a temporary measure until the wider imbalances have been corrected. While constructing the problem tree, the farmers learnt about another Namibian farmer who stopped his use of toxic chemicals to treat sheep and goats against intestinal worms, after observing the death of dung beetles that fed on the dung of recently treated animals (Zimmermann & Smit 2008). He was able to avoid treating his animals because the rotational grazing disrupted the worm life cycles and provided nutritious forage that maintained animal resistance to parasites, while the overnighting of animals on the rangeland avoided close contact with worm larvae in kraals. However, many other farmers are not yet able to apply management closer to the root causes, as they lack the means to rest rangeland sufficiently and to control predators, so are forced to kraal their livestock. Therefore, as a temporary measure the use of biodiversity-friendly treatments against parasites was investigated. This would at least allow dung beetles to continue to perform ecological services, while farmers jointly plan how to manage their animals in a way that raises their resistance to parasites.

A participatory trial was initiated with five farmers in the Rehoboth District of Namibia and jointly analysed by farmers and researchers to evaluate alternatives. Groups of sheep received the following different treatments: conventional treatments with chemicals, two different environmentally-friendly treatments based upon Effective Microorganisms (EM, i.e., a consortium of naturally-occurring lactic acid bacteria, yeasts and phototrophic bacteria) and no treatment as the control. The sheep were weighed every two months, when dung samples were also collected for determination of parasite loads. No significant differences in weight gains and parasite loads were found among groups (Muheua & Zimmermann 2009). Nevertheless, the farmers noticed other improvements in the groups receiving the EM treatments, such as better meat quality and cleaner carcasses, while a herder observed that the EM sheep grazed more voraciously early in the morning and subsequently stopped grazing before the other sheep did.

The experiments and workshops inspired several farmers to initiate further activities in this field: The farmers also experimented on their own with other uses for the EM, such as successfully treating sheep that had consumed poisonous plants and applying it on external wounds to speed up the healing process. One of the farmers even bought EM to provide to his other sheep and goats that were not included in the trial. He continued to do so after cessation of the trials. Another farmer offered financial support for a former student to establish a business of producing a herbal vermicompost (i.e. compost made from earth worms that ate herbs) that boosts immunity. Following the suggestion from one of the farmers involved, farm workers who had learnt how to produce and administer the EM derivatives used in the trials, received certificates at the final workshop (Photo 1).

Biodiversity-friendly tick control

In another project, farmers became aware that it sometimes takes the extermination of a species to gain appreciation of its value. This was the case with oxpeckers (*Buphagus erythrorhynchus* and *B. africanus*), which are now valued for their role in helping to control ticks in parts of South Africa where the previous use of acaricides resulted in their local extermination. Bird capture teams have come to Caprivi Region of Namibia to translocate oxpeckers to South Africa (Stutterheim & Panagis 1987). However, the increasing use chemical acaricides in Caprivi Region now threatens its oxpeckers.

During workshops, the construction of problem trees by farmers (Photo 2) revealed their perceptions of the root causes of tick infestations as the suspension of free dipping services by government and the prohibition on burning grass. Root causes from a more ecological point of view were similar to those mentioned above for the problem tree of roundworm infestations, as indeed dung beetles are also threatened by acaricides (Chihiya et al. 2006), especially the systemic products that get poured onto animals' backs.

The project learnt from farmers in areas prone to tick infestations who manage to raise cattle without the use of chemical acaricides. They tend to treat the root causes, by resting rangeland and applying breeding seasons to ensure that calves are born with maximum immunity, thus

Photo 2: A problem tree shows the causes of tick infestation as perceived by farmers in Kwandu Conservancy. Photo: Ibo Zimmermann.

preventing the conditions that favour ticks. They also welcome low levels of ticks to maintain immunity against ticks amongst their cattle (Rechav et al. 1991). Communal farmers are not yet in a position to apply such management. This project therefore tried EM derivatives for treating the symptoms of tick control on cattle in partnership with farmers in the Kwandu and Salambala Conservancies of Caprivi Region. The process of the project experienced some challenges as treatments that were to be applied weekly were often neglected, such as when the farmers were too busy working in their crop fields. The effectiveness of the EM treatments only became apparent on the cattle of some of the farmers during some of the months of tick counting (Liyemo & Zimmermann 2009). When tick numbers became very high, most of the farmers applied chemicals to all their cattle, including those that were supposed to receive only the EM treatments. Most farmers were unaware that small numbers of ticks are helpful to maintain immunity amongst their cattle. They rather viewed ticks as enemies that must be exterminated. The majority also viewed oxpeckers as pests that cause wounds on their cattle and donkeys. The threat of toxicity from chemicals seemed to be of little concern to most farmers. It was rather the high cost of the chemicals which prevented their more frequent use, while even the students assigned to this project seemed to perceive chemical treatment as the superior method of tick control. Thus, the process helped to gain insight into the perceptions of farmers towards tick infestations but basically failed to dissuade the farmers from wanting to use toxic chemicals.

Research projects on management strategies of innovative farmers

Patch burning in Namibia's Thornbush Savanna

More Namibian farmers are coming to realise that their success at controlling lightning induced fires over the past decades has been a major contributor to bush encroachment and a less diverse rangeland. A few farmers have addressed this by applying prescribed fire to patches on their farms and this project made use of this opportunity by taking measurements on three such farms.

At two of the farms, the reason for burning patches of approximately 130 ha each was to control bushes. The fires reduced the height of established bushes, but they virtually all re-grew. The mortality of the encroaching *Acacia mellifera* saplings was higher on the burnt patches than on unburnt control plots on only one of the farms, while seedlings virtually all died, both in the burnt and control plots (Tjilumbu & Zimmermann 2009). At the other farm, the burning of patches of approximately 10 ha was for the purpose of improving biodiversity. Here the soil was more fertile where a patch had been burnt two years earlier, compared to the unburnt control (Zimmermann et al. 2008b).

This project indicated that fires increased the mortality rates of smaller plants, many of which seem to have died from the exceptionally long dry period before the burning in 2007. The main lessons learnt from this project are that the use of fire after such a premature end to the rainy season may be inappropriate for most rangeland management objectives. The application of fire should rather await appropriate conditions, such as those appearing after season of exceptionally high rainfall. The farmers provided not only the opportunity for the measurements to be taken, but also assistance with transporting of students. One of the farmers requested that markers of transects and measured plants be left in place after completion of the project, so that further monitoring may continue.

The farmers appreciated having quantified results in the form of charts that showed the consequences of their patch burning, while other farmers may use the information to decide whether they too should apply patch burning.

Trampling in Namibia's Thornbush Savanna

An innovative farmer gained useful experience with trampling, through his adaptive management (Zimmermann & Smit 2008). His observations suggested that brief trampling after good rain, on soil with the right texture and organic matter content, conserved soil moisture, possibly by breaking the capillary connections that suck moisture from lower layers in untrampled soil. This project therefore undertook to investigate the influence of trampling on soil moisture and vegetation, in partnership with three farmers.

The three farms in eastern Namibia were selected due to their grazing management comprising fast rotation of large herds through many paddocks. The high stocking density provided short trampling followed by a long period of absence during which the grazed and trampled plants could recover whenever moisture was available. Gypsum blocks were buried at four depths, both in and outside exclosures replicated five times per farm (Zimmermann et al. 2008a). An electronic meter for reading the blocks was left with each of the three farmers, for them to take measurements whenever they had an opportunity to do so. The farmers submitted the collected data and were later provided with charts that provided a visual impression of the changes in soil moisture profile. The farmers were able to observe the fenceline contrasts at the exclosures, while data from vegetation measurements

Photo 3: Participants of the Namibian Rangeland Forum view a gully treated with branches of *Acacia mellifera*. Photo: Ibo Zimmermann.

Photo 4: Members of the Griqua Community install the developed restoration treatments on the farm Ratelgat in the Succulent Karoo in September 2004. Photo: Ute Schmiedel.

were converted to charts that the farmers were provided with.

Initial results from the gypsum blocks were inconsistent among replicates. However, a few examples with greater consistency hinted that trampled sites experienced greater infiltration and less evaporation. The density index of plants, mostly annual grasses, was significantly higher outside most of the exclosures. This increase of annual grasses on trampled sites may be responsible for subsequently transpiring more water out of the soil, resulting in higher grass productivity from trampling (if followed by sufficient rest), but not in moister soil by the end of the growing season.

As a consequence of the mutual learning experience, one of the farmers added a fenced plot alongside three of the exclosures on his farm at his own expense, to investigate the effect of applying a large flock of sheep for a short time. Another farmer constructed five additional exclosures along a landscape gradient, to learn more after completion of this project.

The farmers appreciated having quantified results in the form of charts that showed the consequences of their short-duration grazing, while other farmers may use the information to decide whether they too should apply occasional trampling on any part of their farm.

Projects that jointly addressed farmers' needs

Restoration of a gully system in Namibia's Highland Savanna

In 2003, the participatory process of Ecosystem Management Understanding (EMU) (Pringle & Tinley 2001) was introduced to Namibia by three EMU facilitators during a workshop with members of the Auas-Oanob Conservancy. EMU approach aims to help landusers to understand and adapt to natural processes rather than fighting against them. This approach and the pilot restoration project of eroded gully systems that emanated from it are described in detail in Article III.6.3. The conservancy members often visit the site and are impressed with the results. The treated and untreated gully systems also serve as a demonstration site for visits by interested groups (Photo 3).

Participatory experiments in the Succulent Karoo

Locally degraded rangelands which are caused by farming management measures (stock posts, water points, gathering places for livestock near gates but also installations of infrastructure etc.), typically show poor recovery even many years or decades after the land management changed (Walker 1993). Due to poor vegetation cover, they provide poorer grazing resources (Milton & Hoffman 1994, Todd & Hoffman 1999) and are often the starting point of soil erosion. Many farmers have a negative perception of these degraded areas and feel compelled to improve them by changing management measures or actively restoring degraded sites. BIOTA researchers have often been approached about options for restoration of such sites. In the Succulent Karoo, concrete questions and discussions resulted in participatory projects where BIOTA researchers together with the landusers developed and tested restoration measures for particular situations (near Observatory S22; see also Chapter IV.4). On the newly established communal land of Soebatsfontein (Chapter IV.4) farmers felt very proud of their sustainable management practices and thus would like to restore the bad patches in the landscape inherited from the previous landowner. In the Knersvlakte on the farm Ratelgat (near Observatory S27), owned by the Griqua Ratelgat Development Trust since the year 2000, more than 10 km of trenches that had been dug for the installation of water pipes left poorly recovering scars in the landscape. In the newly implemented Richtersveld Community Conservancy, a new World Heritage Site, the wish had been expressed to restore the vegetation around the settlement Eksteenfontein that had been degraded due to many years of overgrazing. In all cases, BIOTA researchers and landusers held workshops and discussed the ecological processes that might be

Photo 5: Members of the Tweerivier Community identifying indicators for assessing and monitoring of rangelands. Photo: Melvin Swarts.

Photo 6: Livestock keepers from the Leliefontein community rank the most common perennial plant species according to palatability to livestock. Photo: Melvin Swarts.

the reason for the degradation and poor recovery. During these workshops, farmers and researchers together developed restoration treatments, taking into account the local availability of material and resources. The restoration treatments were applied as trials at selected sites, employing scientifically suitable design of replications and controls. The farmers supported the work by providing material, transport and manpower (Photo 4).

The subsequent regular monitoring of the trials was conducted by the BIOTA botanical researchers and the BIOTA para-ecologists (see Article III.8.3). The vegetation and soil data from the trials were finally analysed (Meyer 2009, Hanke et al., submitted), the results shared with the farmer communities during feedback workshops and visits. Based on the findings the environmental impact of overutilisation and mechanical disturbance as well as ideas for adjusted trials and future implementation on larger scale were discussed. Beyond the sharing of the results with the farmers, the results were also presented at a local conference (Meyer et al., oral presentation at the at the Arid Zone Ecology Forum, Graff Reinet, South Africa, 2009) as well as prepared for scientific publication.

Indicators for assessing and monitoring rangeland condition in the Succulent Karoo

For centuries before colonisation the Nama people have freely utilised the semi-arid Namaqualand rangeland as grazing land. Under the Apartheid government the transhumance movements of the Kamiesberg herders were limited with the establishment of the 192,000 ha "Coloured Reserve" of Leliefontein. Today, livestock mobility is still very much part of these livestock keepers as they continue to seasonally move with their flocks of goats up and down the Kamiesberg in search of grazing opportunities and water. The ephemeral wetlands of the Kamiesberg Upland, which provide water in the dry season, are unique features in this semi-arid ecosystem. Many rangeland scientist and agricultural extension officers have deemed the grazing land as being degraded. Despite these claims the Leliefontein Communal Area continues to be productive without significant subsidies or additional fodder being fed to livestock during the dry season. The Agricultural Research Council (ARC), which has worked in this area for more than more than 15 years, uses a participatory research approach to collect social and environmental data. In studies by the ARC, which formed part of the BIOTA project, two questions were raised at these workshops:

(1) what indicators do livestock owners perceive to be most important in monitoring rangeland condition?, and
(2) what plant species should be considered for rehabilitation of rangeland in order to improve the grazing capacity?

Two workshops were held respectively in the Upland village of Leliefontein and in the Midland village of Tweerivier. The objective was to obtain some insight on the perception of livestock keepers in terms of what they regard as the most important indicators in qualifying rangeland condition. Firstly, possible environmental and livestock indicators were brainstormed within smaller groups (Photos 5 & 6) and each group came up with its own set of indicators. These keywords were, through consensus of the larger group, formalised into what was termed key indicators for rangeland condition assessment and monitoring. These indicators were as follows: soil erosion, palatable plants, livestock deaths / health, presence of *Galenia africana* (unpalatable plant harmful to small stock), plant moisture, soil, moisture, animals and insects and ephemeral plants. Indicators were then ranked by the participants as a group exercise, using a pair wise ranking system. The result is summarised in Table 1.

This result shows that livestock owners consider the condition of their livestock as the most important indicator to assess and monitor rangeland condition. Unnatural livestock deaths cause great economic losses and are mainly caused by livestock accidentally, or under stressful conditions, consuming poisonous plants. Livestock keepers generally perceive rangeland condition as poor when poisonous plants tend to increase. Poor animal health is an indication of the absence of nutritious plants on the rangelands. Livestock condition has also been identified as an indicator for local level rangeland monitoring the semi-arid areas of Botswana (Reed et al. 2006a, b) and Namibia (Desert Margins Programme 2005). The presence of palatable species was ranked second, followed by plant moisture. Surprisingly vegetation cover, also identified by Esler et al. (2006) as one of the key indicators for assessing semi-arid and arid rangeland condition, was not identified by participants. This would suggest that livestock keepers do not perceive that bare areas are a major concern in the Kamiesberg. Samuels (I. Samuels, pers. comm.) has indicated piospheres are relatively small and that the sacrifice zones radii are seldom longer then 50 m. Allsopp (1999) recorded that a diverse shrubland community can easily be replaced by a single unpalatable species, such as *Galenia africana*, when overgrazed. The acknowledgement of unpalatable plants, such as *Galenia africana*, indicates that livestock owners are aware of the fact that the ratio between palatable and unpalatable should continuously be monitored.

During the course of the workshop participants realised that even though they do not formally assess and monitor rangeland condition, they actually do take a lot of variables into consideration. They also realised what indicators they tend to consider as more important when assessing or monitoring rangeland condition. This workshop opened the door for further discussion on the need and development of a local level monitoring (LLM) system best suited for their conditions. ARC researchers learned in the process that it would be fruitless to introduce a LLM system, developed in a different biome with different livestock management practices, to the communities of Namaqualand. This is underlined by the fact that the indicator 'vegetation cover', which is considered important in various LLM systems in semi-arid southern Africa, was not considered by the Namaqualand livestock owners.

Table 1: Important indicators in qualifying rangeland condition, identified and ranked by farmers during workshops at Leliefontein and Tweerivier in the Kamiesberg area of the Succulent Karoo

Key Indicators	Ranked
Livestock deaths/health	1
Palatable plants	2
Plant moisture	3
Unpalatable plants harmful to livestock	4
Ephemeral plants	5
Soil erosion	6
Wild animals and insects	7
Soil moisture	8

Conclusions

The different steps used in each of the seven participatory projects are summarised in Table 2, indicating the division into projects that: (i) introduced innovative practices that were new to farmers, (ii) learnt from practices already being applied by innovative farmers, and (iii) jointly developed and applied practices that addressed the farmers' needs.

The joint learning approaches were most successful where farmers felt the urgency for taking action, as was the case for restoration of obviously degraded environment (see also Article III.6.3).

Table 2: Summary of different approaches used in each of the seven participatory projects

Type of project →	Projects that suggested new management practices		Research projects on management strategies of innovative farmers		Projects that jointly addressed farmers' needs		
Project →	Internal parasite control	Tick control	Patch burning	Trampling	Restoring gully system	Restoring pipe trench scars	Rangeland condition indicators
Project steps applied ↓							
Scientists suggested the project	✓	✓					
Farmers already applied innovative approaches			✓	✓			
Farmers identified priority problem					✓	✓	✓
Workshops with farmers	✓	✓			✓	✓	✓
Problem tree used	✓	✓					
Farmers were exposed to management practices of innovative farmers elsewhere	✓	✓			✓		
Experiments conducted	✓	✓	✓	✓	✓	✓	
Results fed back to farmers	✓	✓	✓	✓	✓	✓	✓

When farmers are unaware that their actions are leading to degradation, they tend to respond less favourably to actions that emerged from the participatory process. The tick control project, for instance, failed to achieve its objective of encouraging biodiversity friendly methods of tick control. The farmers were preoccupied with chasing symptoms of different problems they faced, some of which had resulted from the inadvertent harm caused to biodiversity's services. Such farmers are in need of assistance to transform to proactive management. The use of the analytical tool of a problem tree helped farmers of the roundworm control project to differentiate between symptoms and different levels of causes. Although the treatment of causes is better for long-term sustainability, sometimes it is necessary to treat symptoms too, in order to speed up recovery or as a stepping stone to proactive management. Innovative farmers who already apply preventative, biodiversity-friendly management are useful research partners for joint learning, as they are eager to learn and to improve their management as well as being in better control of their situations. This was the case for the farming communities in the Succulent Karoo that had perceived the disturbed areas on their farm as being problematic and searched for means to reverse the situation. Participatory action research depends on innovative farmers who are curious to learn and prepared to continuously adjust their management. As lead farmers they may later convince the larger community by showing that agricultural production can be both economically and ecologically viable.

The main lessons learnt from these participatory projects are: Farmers are more motivated to participate if their priority need is addressed, than when scientists suggest a project for them.

Innovative sustainable farmers are important research partners for other farmers and researchers to learn from and set as their benchmark.

Problem trees are useful in situations where farmers tend to treat the symptoms of a problem rather than the causes.

When provided with the opportunity, farmers experiment and find solutions beyond those recommended by scientists.

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The BIOTA para-ecologist programme—towards capacity development and knowledge exchange

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Summary: Within the framework of the para-ecologist programme, BIOTA employed and trained eight members of local landuser communities as para-ecologists over a period of five and a half years. The aim of this programme was to empower members of local communities to understand and support current research activities and to facilitate the communication of research results to the landuser communities to improve landuse management. Beyond that, para-ecologists developed the capacity to conduct important tasks in long-term biodiversity monitoring, and supported the regular work at the BIOTA Observatories and other research activities of the BIOTA scientists. The employment and capacity development of community members aided in the sharing of scientific findings and experiences of local landusers, and raised interest in the results of the research activities within the communities. This article provides an overview of the concept and implementation of the programme, describes the capacity development component of the programme, and shares some of the experience from both the scientists' and the para-ecologists' perspectives.

Introduction

Contemporary understanding of applied biodiversity research acknowledges the need to integrate the perspective of landusers as key custodians of biodiversity into the research process (Akhtar-Schuster et al. 2005, see also Article 8 of Convention on Biological Diversity 1992, Millennium Ecosystem Assessment 2005). Through this integration, emerging management recommendations take the experiences, availability of resources and perceptions of the environment of landusers into account and are thus more likely to be implemented successfully (Drechsel et al. 2005, Shindler et al. 2004). Furthermore, indigenous knowledge is considered to be crucial for scientific quality (Mauro & Hardison 2000, Thomas & Twyman 2004). To achieve this goal, a participatory research approach is required in which relevant stakeholder groups are involved in designing the research approach itself, and contributing to the evaluation of findings and the development of management recommendations.

During the course of the project, BIOTA Southern Africa focussed increasingly on stakeholder involvement and knowledge exchange (see other contributions in this Chapter). One major undertaking was the para-ecologist programme of BIOTA Southern Africa that was launched in 2004, during the second phase of the project. Within this programme, BIOTA employed and trained eight members of rural landuser communities that were situated in the close vicinity of BIOTA Observatories on a fulltime basis. These para-ecologists were individuals without prior formal training and they benefited from an intensive capacity development programme in the fields of ecology and biodiversity monitoring during the course of their employment.

This article describes the concept of the programme, the main training components, and the work conducted by the para-ecologists. It also discusses the experiences from both researchers' and para-ecologists' perspectives.

Concept

The para-ecologist programme was initially developed following the example of the parataxonomist programme of the Parataxonomist Training Centre in Madang in New Guinea (now New Guinea Binatang Research Centre, www.entu.cas.cz/png/parataxoweb.htm). The latter was initiated in 1997 with the aim of training local people in biodiversity research, facilitating their collaboration with scientists, and fostering their involvement in conservation education efforts targeted at broader audiences.

The para-ecologist programme followed the same principles and vision but placed emphasis on ecological research, thus the adjustment of the name to para-ecologists. In the beginning, the programme was mainly aimed at training local staff to eventually take over large parts of the monitoring activities. The support of the para-ecologists with the monitoring work should not be underestimated. However, it turned out that they would not be able to take over all monitoring tasks completely. For instance, the flora was too complex for some para-ecologists to know well enough to conduct vegetation monitoring independently; there were often more than 300 species per Observatory, which is a challenging task even for professional ecologists. However, already during the implementation phase of the programme, other aspects, which were related more to the para-ecologists

Photo 1: Para-ecologists during the sixth training course in Nieuwoudtville, South Africa.
Photo: Ute Schmiedel.

as local contacts and resource persons for the BIOTA project, became increasingly important—an asset that only emerged as the project progressed and the para-ecologists took on more project responsibilities that were not directly related to monitoring activities.

Implementation

Para-ecologists were selected from the communities in the vicinity of eight BIOTA Observatories between the Cape and Kavango. In most cases, the posts were advertised locally and interviews were conducted with selected applicants. In other cases, the selection of candidates was left to the leadership of the local community; or candidates were selected based on their performance as BIOTA field assistants or interpreters prior to the commencement of the para-ecologist programme. The main selection criteria were that the candidates had no tertiary education, were self-motivated, interested in nature, and willing to work in the field. An additional criterion was that the candidates had engaged in voluntary community work prior to their employment. A completed high school education (matriculation) was excluded from the list of criteria in order to offer work and capacity development opportunities to young people who would otherwise have little alternative opportunities.

The formal employers of the para-ecologists were the chairs of the South African and Namibian BIOTA steering committees. The para-ecologists were employed fulltime for the second funding phase of the project, with the option of extending their employment into the third funding phase. Four (two Namibians, two South Africans) of the eight para-ecologists employed in October 2004 remained in this post for the entire duration of the programme (i.e. five years and six months). Three others resigned and were replaced; in only one case did BIOTA not extend the contract into the third phase of the project.

The languages spoken by the para-ecologists were Afrikaans, Nama, and Rukwangali, as their mother tongues, and English, as the only language in common. English was therefore chosen as the language for mutual communication and training.

The working time of the para-ecologists was 40 hours per week. They received a monthly salary and were beneficiaries of a medical aid plan. Their main place of work was at the Observatory/ Observatories closest to their village but they also travelled around with various scientists according to project needs. Each para-ecologist was supervised by a BIOTA scientist working in the respective areas and to whom the para-ecologist reported to on a monthly basis.

Beyond the regular fieldwork with their supervisors, the para-ecologists also worked with many other scientists who also supported their capacity development. Each para-ecologist was equipped with a laptop, digital camera, GPS, work boots, sleeping bag, back-pack and, where required, a bicycle, tent and mattress.

The training courses

A three weeks training course was held once a year at different locations along the BIOTA Southern Africa transects, close to where one of the para-ecologist was situated (i.e. Gobabeb and Keetmanshoop in Namibia, and Kamieskroon, Vanrhynsdorp, Nieuwoudtville in South Africa). The sites were selected according to logistical considerations such as the availability of suitable, cost effective venues.

The training courses comprised practical and theoretical components and covered various aspects of the para-ecologists' work:

- theoretical background: classification of organism groups; biodiversity; drivers of biodiversity; calculation of areas, volumes, distances; various other topics as requested by participants;
- technical skills: management and use of computers, digital cameras, GPS, maps, weather stations etc.;
- methodological skills: collecting, processing and identifying plants and animals; plant photography; conducting vegetation surveys; interviews with landusers; video filming;
- communication skill: preparation and presentation of talks; providing and receiving feedback; sharing local knowledge;
- organisational skills: project planning; reporting on activities; planning of own work;
- soft skills: conflict management.

A variety of different processes were applied in the classes. The theoretical background was often presented by the trainer, whereas for the methodological, technical, and communication skills there was a strong focus on interaction and hands-on training, role playing, peer teaching and practical exercises that were similar to the real-life tasks. Training classes were always combined with creative- and relaxation exercises to ensure that trainees remained energised and alert. For each course, a booklet with the resource- and training material was compiled and handed out to the participants. At the end of each course, the participants wrote a test on the course topics (see Electronic Appendix) and feedback was collated in preparation for the following training course. Beyond these regular training courses, the para-ecologists participated in several additional training workshops.

One highlight of the para-ecologist training courses was the participatory video workshop held by Martin Gruber in April and May 2009. During this workshop the para-ecologists conceptualised, planned, and produced a documentary video on the para-ecologist programme (Schmiedel et al. 2009, Electronic Appendix). The concept and process of this project is described in detail by Gruber (see Article III.8.4).

Photo 2: Para-ecologists during computer training during the training course in 2006. Photo: Ute Schmiedel.

Further exposure and learning experiences

Skills and methods are only thoroughly mastered if they are applied repeatedly in practice, and on-the-job training was therefore even more important than the training courses for the capacity development of the para-ecologists. The para-ecologists were involved in the monitoring of biodiversity on the BIOTA Observatories and, amongst other activities, they conducted monthly phenological monitoring of plants, engaged in their own research or awareness raising projects, organised and co-facilitated workshops, took notes during meetings, documented events photographically, wrote monthly reports about their work, and planned their own work processes.

Beyond this, para-ecologists were also exposed to various special events. Every year, all para-ecologists participated in the annual conference of the Arid Zone Ecology Forum in South Africa where they presented posters and talks. Testament to the success of the para-ecologist programme is that individual para-ecologists were repeatedly acknowledged for best poster or oral presentations. The para-ecologists also participated in various other national and international conferences, e.g. the Namibian Rangeland Forum, and the international BIOTA conference "Biodiversity of Africa" 2008 at Spier, South Africa. They repeatedly had the opportunity to represent the BIOTA para-ecologist programme at international events, e.g. the INSITE - Science Fair in Pretoria, South Africa, the BIOTA side-event of the COP 9 in Bonn, Germany, as well as at various national meetings and events.

Due to their regular fieldwork and attendance of events, the para-ecologists travelled much more often and much further than they would have done outside of the project context. Their exposure to different places and to people with different cultural and social backgrounds broadened their horizons regarding their own and their communities' future opportunities. In rural areas of southern Africa, intercultural exchange is comparatively low, irrespective of the richness in cultures and ethnic groups of the region. The para-ecologists perceived the travelling as a rich inter-cultural learning experience.

Work conducted by the para-ecologists

The para-ecologists supported the regular fieldwork of natural (e.g. botanists, zoologists, soil scientists) and social scientists (e.g. anthropologists and economists) at and around the BIOTA Observatories. The para-ecologists provided invaluable support during the extremely time-consuming annual botanical monitoring on the Observatories. They conducted the monitoring of the 100 m² plots, and took the standardised plot photos and other plant photos where needed. For the social scientists, the local knowledge and language-skills of the para-ecologists were key for allocating, contacting and making appointments with local informants. Para-ecologists translated or even conducted the interviews for the social scientists. They organised meetings and workshops, and co-facilitated as well as translated during these events.

During the long phases of absence of scientists, the para-ecologists continued with the regular monitoring activities (e.g. rainfall, soil properties, plant phenology, arthropods, livestock numbers)

Photo 3: Para-ecologists Marianna Lot and Theodor Cloete during fieldwork at the training course in 2005. Photo: Ute Schmiedel.

and coordinated aspects of participatory projects (restoration experiments, activities with schoolchildren) that were initiated together with the scientists. One para-ecologist was responsible for the screening of the BIOTA awareness-raising film on illegal logging in the small communities of the Kavango (see Article III.8.4). The para-ecologists also maintained the research equipment, facilitated communication between the landuser communities and researchers, and kept the scientists informed about their work progress and developments in the natural environment or within the communities.

The para-ecologists also worked with researchers from other projects or NGOs that were not part of the BIOTA project but working in related fields. This was strongly supported and even motivated for by the coordinator of the programme, as any kind of professional work experiences beyond the BIOTA context was expected to contribute to the capacity development of the para-ecologists.

The para-ecologists were also encouraged to develop their own projects within the context of BIOTA. Some of them initiated concrete project ideas, which they then managed to implement. Among these were awareness-raising projects with schoolchildren, a scorpion project, and booklets on the use of local medicinal plants.

Dealing with potential challenges

Despite the overwhelming advantages and positive impacts, the para-ecologist programme also posed challenges for the scientists and para-ecologists. These challenges and the lessons learnt by the team are shared below and may be helpful for future projects.

Long-term perspective: The employment and training of personnel is likely to create expectations among the para-ecologists with regard to employment beyond the funding phase of the project. The BIOTA project was an initiative to create Observatories and a baseline for time-series that might form the basis for long-term biodiversity monitoring activities as part of an international monitoring network (see Volume 1, Part I). Therefore, the future of the para-ecologists is closely linked to the future of the Observatories. The presence of local para-ecologists at the monitoring sites with the capacity to conduct standard biodiversity monitoring to a large extent, will be of advantage for future host institutions or projects. As long as the future of the BIOTA Observatories is unclear, employment of the para-ecologists in this context also remains uncertain. Nevertheless, the employment prospects for the para-ecologists in related fields (nature conservation, environmental education, landuser–researcher cooperation, research assistance in future related projects) are seen as much improved compared to other community members who have not received comparable training and work experience. This has already been proven as one of the para-ecologists has been permanently employed by CapeNature, the conservation authority of the Western Cape Province of South Africa. Other para-ecologists are employed by local NGOs and research institutions and have the opportunity to gain further employment in future projects.

Cultural differences and language barriers: All parties in the project experienced strong cultural differences within the team. These were differences between members of different social and ethnic groups (among para-ecologists and scientists of different ethnic groups, landusers and scientific communities). If cultural differences are not brought to light or communicated, and remain below the surface, they may cause severe misunderstandings within the team. Para-ecologists often found themselves in the awkward position of having to defend themselves for incidents that occurred due to lingual or cultural misunderstandings or miscommunications between them and their supervisor or other scientists. For many of the scientists and all the para-ecologists, English was not their mother tongue. Due to the limited English skills, misunderstandings in communication occurred frequently and were often misinterpreted as content-related disagreements. Furthermore, most of the para-ecologists had very little exposure to other African ethnic groups before they joined the para-ecologist programme. There was thus a strong emphasis placed on soft skills, such as avoiding and solving misunderstandings through effective communication, during the para-ecologist training. Over the years, consciously dealing with cultural differences resulted in new experiences, social learning, and individual capacity development.

Discrepancies between new perspectives and old rules and constraints: The training courses and the work of the para-ecologists, which was accompanied by travelling, visiting new places and communities, and meeting and working with members of foreign cultures brought new and unusual experiences to the para-ecologists. These experiences obviously broadened their horizons and changed their perspectives on their natural and social environments. Consequently, the para-ecologists sometimes became involved in conflicts within their home communities due to clashes between their newly gained perspectives and the established rules and constraints in the community. These new perceptions of the social and natural environment can potentially lead to conflict if they clash with existing superstitions. This may even lead to the community preventing further research on a topic, such as spiders, which is perceived as culturally inappropriate.

Envy within the community: The most serious challenge, which the para-ecologists had to face was social envy from within their own communities. Most members of the communities perceived the para-ecologist programme as a great opportunity and advantageous for the community. For others however, the obviously unusual type of work (which comprised being employed by a comparatively wealthy project, receiving training, attending conferences, travelling to other research sites, conducting odd work that was often misinterpreted by community members, etc.) raised questions and envy among younger community members. This was particularly true at the beginning of the programme, when the concept was still new to the para-ecologists and their social environment. Para-ecologists sometimes experienced difficulties with these social tensions within their own communities. Particularly for the younger and less experienced para-ecologists, problems like these seemed almost impossible to cope with and to solve due to the very close and interwoven personal relationships within the communities. Therefore, the para-ecologist training attempted to illustrate ways of coping with these difficulties by unpacking and analysing particular situations through role playing. During the course of the project, appreciation for the para-ecologists and their skills grew and they were increasingly viewed as a valuable resource by their communities.

Photo 4: Para-ecologists learning identification of plants at the Compton Herbarium in Cape Town, South Africa. Photo: Ute Schmiedel.

Supervision: Some para-ecologists were affiliated with local institutions or organisations, where they worked on the daily basis. These organisations also took over their supervision. However, where such hosting organisations were not available, para-ecologists worked from home and were largely left on their own for most of the time. They were supervised via telephone, fax or email and only met their supervisors in person once a month or even once a year. The frequency of telephone contact was partly hampered by technical problems. Also, this distant supervision of para-ecologists had to compete with the many other urgent commitments of scientists and therefore tended to fall short if it was not also demanded from the para-ecologist's side. Therefore, the lack of day-to-day supervision for solving emerging problems, immediate response to questions, and monitoring of professional performance was one of the biggest challenges for both the scientists and para-ecologists. Future para-ecologist programmes should learn from this experience and arrange for the affiliation of each para-ecologist with an on-site supervising organisation. Alternatively, for more remote places where there is no supervising organisation nearby, regular face-to-face meetings with a supervisor, who should be based within a manageable distance, is advisable.

Feedback from para-ecologists on the programme

The description of the experiences with the para-ecologist programme provided in this article is based on numerous formal and informal feedback sessions between scientists and para-ecologists. However, the overwhelmingly positive impact that this programme had on the personal and professional development of the para-ecologists can best be expressed in their own words. Some of their summarised feedback is therefore quoted below.

- "The reason why I became a para-ecologist is obvious: I don't have a tertiary education like a degree or a diploma that would have allowed me to learn things that I know now. I got the opportunity to learn this while working and during training courses. I am ready to share information that I have gained through my training that I have received through BIOTA." (Richard Isaacks from Keetmanshoop, Namibia)
- "I love being an outreach para-ecologist [i.e. a para-ecologist that interacts

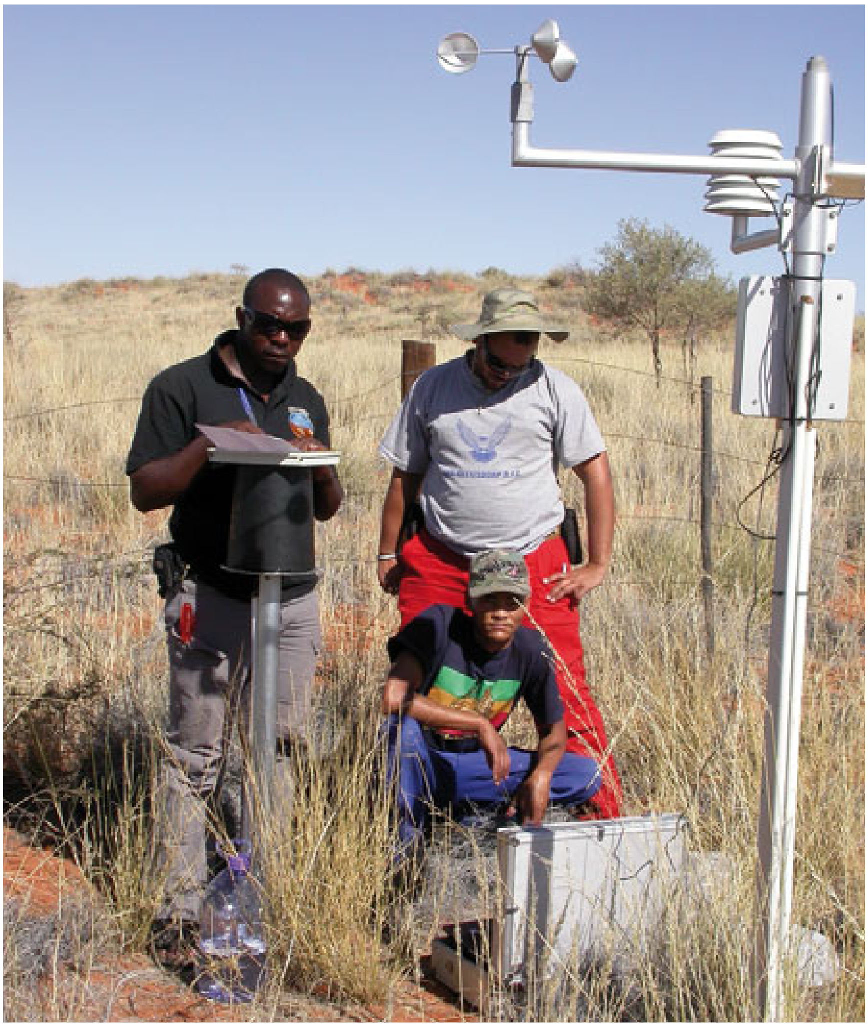

Photo 5: Para-ecologists downloading data from a weather station. Photo: Ute Schmiedel.

with community members] because I have gained skills and experiences through BIOTA and I hope that I will use it well one day after the BIOTA project ended. BIOTA has made my future bright." (Jeannete Swartbooi from Gobabeb, Namibia)

- "I have learned a lot about biodiversity; now I see conservation of plants and animals in a new perspective and understand how important each of them is in life." (Donna Kotze from Nieuwoudtville, South Africa)
- "I am able to do the work of a researcher due to the training that I received during the last seven years of work and the experiences I gathered in BIOTA. I also learnt a lot about how to work on my own and to conduct projects self-reliantly. If it has not been for BIOTA Southern Africa that gave me the opportunity, I would not have developed so much knowledge." (Reginald Christiaan from Soebatsfontein, South Africa)
- "The message that I learnt is to protect and to let live. Now I can also distribute this message among other people in the community." (Marianna Lot from Paulshoek, South Africa)
- "Getting involved with a project like BIOTA opened my mind to learn about nature. This job also gave me the opportunity to give presentations at conferences and international congresses like COP 9 [Conference of the Parties of the Convention on Biological Diversity] in Bonn and to meet different people from different cultures." (Robert Mukuya from Rundu, Namibia)
- "I have learnt how to do proper field work, like monitoring of plants and how to download weather stations. I have also learnt how to give presentations like at the international BIOTA congress. As a local member of a rural community it gave me hope for the future to see that I can be part of the scientific community in a special way." (Wynand Pieters from the Knersvlakte, South Africa)
- „I want to use the training and experiences I gained through this BIOTA project to become a local tour guide within my community in order to put my community on the tourism map and to claim our fair share of the tourism cake, for the benefit of the community and Namibia as whole". (Sebedeus Swartbooi from Gobabeb, Namibia)

Conclusions

The experiences show that the involvement of para-ecologists in the project helped to better understand the landusers' perspective of the natural and social environment as well as the constraints, challenges and incentives for their land management decisions. Also, the para-ecologists became instrumental in knowledge exchange between scientists and landusers as well as in awareness-raising and environmental education among local communities. Thus, the para-ecologist programme contributed towards the empowerment of the local landuser communities, and to expanding their knowledge base by referring to observational data, which aided their management decisions. In this way, the programme contributed strongly to the overall success and positive perception of the BIOTA project among landuser communities.

The employment and training of para-ecologists required strong personal commitment from scientists and para-ecologists. Problems, which arise, might differ depending on the social, economic, and political environment of such a programme. Due to differences in culture and codes between scientists and para-ecologists, difficulties that are caused by miscommunication and differences in perception will almost certainly arise. These structural, intellectual or social challenges might even cause personal crises among the trainees, and they need to be overcome with efforts from all parties, i.e. para-ecologists, supervisors, and scientists. However, if the group is willing and able to face the challenges, and if the para-ecologists are empowered to grow with their tasks and responsibilities, this close collaboration between landusers and scientists in applied, biodiversity or landuse-focussed research can be very fruitful, productive, and highly rewarding for both sides.

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Film making as an instrument of research communication and capacity development

Martin Gruber

Summary: BIOTA produced three films to communicate its research activities to different audiences between 2007 and 2009. The first film "Wiza Wetu! – Our Forest!" depicts the illegal logging of trees in the Kavango Region of Northern Namibia. It aims to raise awareness about the problem and introduce alternative modes of income to local communities. The second film "Biodiversity is our Life" documents landuser perspectives on biodiversity issues such as the use of natural resources, biodiversity perceptions and biodiversity change, as well as sustainable resource management. It was screened to researchers and policy-makers during the "Convention on Biological Diversity" COP 9 conference in Bonn in May 2008. The film "Bridging the Gap" was made by BIOTA para-ecologists as part of a training workshop and presents the para-ecologist programme from the para-ecologists' perspective.

All films were made with different degrees of collaboration and participation. The films therefore not only contributed to the communication of research results to various audiences and to raising awareness about existing ecological and social problems. They also constituted an important aspect of capacity development and stakeholder involvement in the project.

Introduction

Film as a medium has played an important role in the communication of BIOTA's project activities and research results. Between 2007 and 2009 the project commissioned three films, which were intended for different purposes and audiences. What these films have in common is an anthropological as well as participatory approach, which implies that local stakeholders were included in the process of filmmaking in some way or another. This chapter will provide a brief overview of BIOTA's filming activities and their contribution to the project's internal and external communication as well as their role in capacity development.

Ethnographic and participatory film

Ethnographic filmmaking is a method of research: the conceiving of a film, as well as the shooting and editing are parallel analytical processes that generate insight into the subject matter, which is represented in the resulting film (Ruby 2002). The inclusion of members of the groups being studied into the filmmaking process has a long tradition and is one of the hallmarks of ethnographic filmmaking (Rouch 2003, MacDougall 1998). Some anthropologists make the technology available and teach their informants how to make films themselves. Their aim is to either analyse the films and draw conclusions about their subjects' perspectives on reality and their culture (Worth & Adair 1975) or to offer their collaborators a way of expressing themselves to a wider public in their struggle against oppression (Turner 1992). Some of these ideas have been integrated into the method of "participatory video" (PV) by development experts. The beneficiaries are enabled to communicate their different views, initially within their peer groups, and then to outside audiences such as representatives of donor organisations or the government (Braden 1998).

Following these ideas, development as well as research projects such as BIOTA can benefit from the use of film in various ways. Firstly, film constitutes a powerful means of communicating research results and project activities to different groups of recipients. It is possible to reach large numbers of people—both broad and specific audiences alike—through different channels such as screenings as part of awareness campaigns, conferences, TV broadcasts, or the distribution of DVDs to journalists and policy-makers. Film is particularly suitable for reaching non-academic audiences since the medium is capable of presenting the complex findings of scientific research in a concrete and tangible way. Secondly, ethnographic filmmaking serves as a method of research, as described above. This aspect is especially promising if representatives from local stakeholder groups participate in the process of filmmaking because the resulting films can be seen as the participants' own representations. This additional perspective contributes to the understanding of their daily lives, worldviews, norms, problems, etc. Thirdly, participatory filmmaking is an important tool for capacity development. The participants of such film projects not only take advantage of a thorough training in camera use and editing, but conceiving and executing films is a complex and demanding procedure that prepares the participants for other difficult tasks and thus increases employment opportunities. Lastly, there is potential for participatory films to include local stakeholders in research projects. Enabling stakeholders to participate and contribute actively is likely to strengthen their ownership of the project and identification with its goals. This positive effect can be passed on to the audience of the film. Through certain components such as common language, known places, personally known protagonists and so on, the recipients of the film are involved and identify with its subject matter. We experimented with many of these aspects in the different films produced for the BIOTA project. Here we describe these projects and our experiences in more detail.

Wiza Wetu! – Our Forest!

The first film produced within BIOTA Southern Africa, was made in cooperation with BIOTA anthropologist Michael Pröpper in 2007. Pröpper had been doing anthropological research in the Kavango Region of Northern Namibia for several years. During his fieldwork on the cultural dimensions of biodiversity, he realised that the illegal logging and trade of trees is one of the main threats to the environment in the area (see also Chapter IV.1). In order to raise awareness about the ecological consequences and inform the local population about alternative modes of income, he had the idea of using film as a means of communication. Pröpper approached me and together we developed and produced the 53-minute film in the Rundu area (Electronic Appendix). In order to make the film as meaningful and authentic to local audiences as possible, we included two local stakeholders in the film crew. The region's BIOTA para-ecologist Robert Mukuya (Photo 2) was not only our main informant and link to the local communities but was also involved in the conception of the film and played the main character. In the film, Mukuya visits different places, which are significant for the production and trade of illegally harvested wood and talks to relevant people. As a local expert on biodiversity he investigates the different aspects of the problem, explains them to the audience and guides through the film. Raphael Sikumba, who had been working for Pröpper as an interpreter and field assistant before, was employed as a production assistant (Photo 1). He was trained as a camera assistant, made many suggestions regarding the content and style of the film and was especially important as a translator and during filming and editing. Apart from these two collaborators in the production team, we included various local stakeholders and resource-users as protagonists. Some of them were interviewed as experts to explain their view of the situation; others, like the traditional authorities, were given a platform to make a political statement at the end of the film.

Photo 1: Raphael Sikumba and Martin Gruber shooting the felling of a tree for "Wiza Wetu!". Photo: Michael Pröpper.

Photo 2: Robert Mukuya watching the broadcast of "Wiza Wetu!" on national television. Photo: Michael Pröpper.

A re-enacted sequence at the beginning of "Wiza Wetu!" in which three villagers perform the illegal felling of a tree is of special interest. The approach of improvising significant situations from the protagonists' lives goes back to ethnographic filmmaker Jean Rouch's work of the 1950s and 1960s and was termed "ethnofiction" by film critics (Stoller 1992). The underlying idea is that the fictional framework provokes the protagonists to act out and discuss important issues in ways that would not be probable

Photo 3: Jeannete Swartbooi and Reginald Christiaan interviewing Snake Vilho Mtuleni for "Bridging the Gap". Photo: Ute Schmiedel.

through conventional documentary approaches (Sjöberg 2008). This method can therefore disclose hidden aspects of the protagonists' realities. In our case it would not even have been possible to document and discuss the process of felling a tree without potentially harming the protagonists, since the action is illegal and might have caused their prosecution. Consequently the film crew decided to work with "ethnofiction". We obtained a permit from the Namibian Authorities to fell a tree in the forest near Rundu and hired a few young villagers who would usually log illegally to carry out their work for the film. Our protagonists not only demonstrated the logging, which gave an impressive illustration of their hard and strenuous work, but also improvised some discussions about the problems connected to their clandestine activities. The conversations contained important information that might otherwise not have been revealed. This example demonstrates compellingly how fictional elements can be used as an alternative method of enquiry. It was of no surprise to me that local audiences especially appreciated this particular sequence. The enthusiasm and conviction with which the protagonists acted out the situation, makes the film a fascinating and authentic document. I assume that re-enactments and other fictional approaches are especially popular amongst local audiences since they draw on local story-telling traditions and media preferences and thereby playfully combine information with entertainment (Gruber 2008).

An important aspect of the project was the distribution of the film amongst rural communities throughout the Kavango Region. The forests in the Kavango are mostly communal land, which implies that its resources belong to the public. Nevertheless, only a few individuals usually benefit from the illegal activities by generating a private income, while the majority of the population loses out – through decline of natural resources and ecological destruction. The aim of our film was to initiate a critical discussion amongst the landuser communities that would ideally contribute to more sustainable management of the forest and a fairer distribution of the forest-related income. The para-ecologist Robert Mukuya was equipped with a generator and video projector and travelled to numerous villages all over the Kavango Region. He screened the film, answered emerging questions and moderated the discussion amongst the viewers. Unfortunately the reception of the film was not analysed in any structured way, but according to Mukuya, the film raised many questions and initiated intensive discussions amongst the local viewers. It therefore contributed to raising awareness in the intended way. Apart from these screenings, the film was also adopted by the Namibian Directorate of Forestry and the German Development Service (DED) in order to inform rural communities interested in establishing Community Forests about the concept of community based natural resource management. Furthermore it was broadcast twice by the Namibian Broadcasting Corporation's (NBC) national TV programme and contributed to the discussion at a national level. Additionally, BIOTA distributed hundreds of DVD copies of the film to other researchers, journalists and policy-makers. "Wiza Wetu!" was presented to academic audiences at the Universities of Basel, Göttingen and Hamburg and it was screened for several weeks as part of an exhibition about BIOTA para-ecologists at the Biocenter Klein Flottbek at the University of Hamburg in 2009. It is evident that the film reached a large and diverse audience and therefore contributed significantly to the communication of BIOTA's research.

Biodiversity is Our Life

The second BIOTA film was produced to inform an audience of researchers and policy-makers about landuser perspectives on biodiversity during the "Convention on Biological Diversity" COP 9 conference in Bonn in May 2008. The 10-minute film was screened as a loop at the stand of the German Federal Ministry of Education and Research as well as during the BIOTA-Side Event at COP 9. "Biodiversity is our Life" introduces the BIOTA AFRICA research project by dealing with issues such as the use of natural resources, biodiversity perceptions and biodiversity change, as well as different strategies of sustainable resource management.

The idea behind the film was to convey authentic local perspectives by editing amateur footage shot by researchers as well as para-ecologists and other non-academic African project members. While six representatives from the different parts of BIOTA in West, East and southern Africa initiated the project, I was hired to draw a concept and do the actual editing. During an initial meeting we decided to apply a participatory approach, which gave the six BIOTA members a high degree of decision-making power and responsibility. They made suggestions regarding the content and style of the film and contributed by selecting, classifying and translating the footage to be edited. Since all decisions were made collectively and the participants in the project were spread all over Germany, communication had to be facilitated by phone-calls and email-correspondence. During the later editing stages, the participants could access the different versions of the rough-cut via the internet. This collective approach proved to be efficient since all participants were satisfied with the process and its outcome.

The challenge was to edit roughly 20 hours of video footage into a 10-minute film, but from an early stage it became clear that there was not sufficient material. On the one hand the quality was often not good enough due to low camera quality and unskilled camera handling. On the other hand, the footage consisted mostly of interviews and some observational material, while the necessary contextualising images of landscapes, plants etc. were missing. In order to compensate for missing images, we decided to include still photographs taken by BIOTA researchers during their fieldwork. Additionally we had to rely on a voiceover commentary to convey the missing information and as a binding element. The film was screened and distributed during the COP 9 conference and on other occasions. The original idea, to tell the story through images taken by local stakeholders and project members, was only partially realised. This experience highlighted the necessity to train project members in filmmaking in order to use their footage for future projects and it therefore inspired the BIOTA film project discussed below.

Photo 4: Jeannete Swartbooi filming Robert Mukuya and Wynand Pieters. Photo: Ute Schmiedel.

Bridging the Gap—para-ecologists in action

The 20-minute film “Bridging the Gap” is the outcome of a para-ecologist training workshop held in South Africa during April 2009 (see also Article III.8.3). The documentary introduces the para-ecologist programme to a broad audience and presents the para-ecologists’ expertise to other research projects, and conservation- and development agencies. The film was conceived and shot entirely by the para-ecologists (Electronic Appendix). The idea behind this approach was not only to teach local project members practical filmmaking skills that they could use for the project, and that would qualify them for future employment. More importantly, the participatory process of conceiving and making the film also afforded the participants the opportunity to (re)define their role within the project and within broader contexts. The filmmaking was thus meant to strengthen the ties between BIOTA and the para-ecologists, to open up new perspectives on the project, increase their work-related motivation and strengthen their self-awareness.

Ute Schmiedel, the coordinator of the para-ecologist programme, initiated the film workshop as part of their annual training. We jointly conceptualised, organised and moderated the three week-long workshop, which took place in the small village of Niewoudtville in the Northern Cape Province of South Africa. None of the para-ecologists had any significant filmmaking-experience and we began the workshop with a theoretical introduction to documentary filmmaking, followed by practical training in camera and sound recording as well as different interview techniques (Photo 3). At the same time, the para-ecologists discussed the aim as well as the content and style of the film. It was decided that the main intention of the film was to inform other researchers and NGOs about the BIOTA para-ecologist programme. Additionally the participants also wanted to create a film that they could use to present themselves and the work they do to colleagues, friends, family, and also to potential future employers. Another important goal was to motivate the youth from the underprivileged communities where the para-ecologists come from, to get involved and seek further capacity development that might help them to find a job.

When discussing the content and structure of the film, the para-ecologists decided to start the piece with a personal introduction by each member to provide an idea of the cultural and personal diversity of the group. They also wanted

Photo 5: Martin Gruber, Wynand Pieters and Richard Isaacks discussing during the editing process. Photo: Ute Schmiedel.

their daily work to play a central role in the film and they therefore filmed three typical work situations, namely their job at the BIOTA Observatories (Photo 4), a livestock census, and community outreach work. During the shoots, the participants switched their responsibility for each scene so that everyone had worked as director, camera-operator and actor at least once. The end of the film is comprised of a sequence on the participants' training and of an outlook on the participants' future. All sequences were specially arranged for the film but still convey an authentic image of the routines of the para-ecologists. While the shooting of the film was accomplished entirely by the participants, I operated the editing machine with the para-ecologists repeatedly giving feedback and making suggestions (Photo 5). In terms of the methodology, it would have been preferable to have the participants do the editing on their own but it was impossible to teach the rather complex editing software within the limited time of the workshop. Nevertheless the participants had a high degree of decision-making power and were responsible for the implementation of this complex project.

"Bridging the Gap" was screened at several international conferences and, like "Wiza Wetu!", at the para-ecologist exhibition at the Biocenter Klein Flottbek of the University of Hamburg. Numerous DVDs of the film were distributed amongst interested researchers and policy-makers in the field of biodiversity research. Unlike "Wiza Wetu!" this film was not based on a "research with the camera" approach as postulated by visual anthropology. Rather, it is a self-representation of the para-ecologists and an introduction to the para-ecologist programme of BIOTA. The film's greatest potential lies in the area of capacity development, empowerment and stakeholder inclusion.

Conclusions

All of the films described above were based on an ethnographic and participatory approach—but to varying degrees and with different intentions. At the same time, each of the productions experienced particular challenges. "Wiza Wetu!" constituted a genuine platform for discussion and negotiations between a diverse group of stakeholders. The film represented the different perspectives and communicated them to a wide audience, and it thereby contributed to setting the agenda and raising awareness about illegal logging in the Kavango Region. The use of "ethnofiction" proved to be highly effective since it allowed documenting and discussing issues that would have been difficult to record using other approaches. One of the film's limitations regarding participation was that the members of our German-Namibian production team made most of the important decisions on the content and structure of this film on their own. It would certainly have changed the outcome of the project if we included other stakeholders in these decisions. Another limiting factor was our decision not to focus on politically sensitive issues, such as mismanagement and corruption, in order to avoid political tensions and the impression of a post-colonialist research agenda that implicitly blames the Namibians exclusively for the situation. When some of these issues arose during our research, we had long discussions on how to deal with the situation. We finally decided not to highlight them in the film but to concentrate on a completely different aspect, namely alternative modes of income through forest resources.

"Biodiversity is our Life" was participatory in the sense that a large group of people was involved as the authors of the film. It was a very positive experience to bring all the different parties together and find collective solutions. The film is also interesting regarding its use of amateur footage, which evokes a feeling of presence and directness that is difficult to achieve with professional recordings. African resource-users are presented as local experts with a strong and compelling voice that might not reach Western audiences otherwise. Difficulties that occurred in this project were mostly of technical nature, which highlights the need for training. In this regard, it is important to compromise between the authenticity of footage taken by non-professionals and the requirements of a film produced for a broad audience.

"Bridging the Gap" is founded on a high degree of participation as the authorship and most of the technical production was handed over to the protagonists. This makes it a self-representation more than a film "about" para-ecologists. Even though we wanted to control as little as possible, it must be acknowledged that the organisers of the workshop influenced the content and style of the film to a certain degree. At the same time, there are always many other factors that influence such films, which makes the notion of capturing an "unspoilt" or "non-Western" perspective through this method impossible. Nevertheless it is a very specific point of view that is presented in this film, namely the perspective of young women and men who were struggling to make a living before they received training and work in the BIOTA project. It is therefore not a neutral film about the para-ecologist programme but a positive, and even partly idealised, image of the protagonists' role within BIOTA and society at large. The fact that the protagonists chose to convey such a positive impression is likely to be motivated by their optimistic perceptions of BIOTA's activities—for their personal situation as well as for the wider community. The energy and involvement with which the participants took part in the project made it an exceptional experiment.

In summary, the filming activities within BIOTA played an important role in the overall project. On the one hand, they contributed to the communication of research results to various audiences and to raising awareness about existing ecological and social problems. On the other hand, they constituted an important aspect of capacity development and stakeholder involvement in the project. Film as a method of research was however not comprehensively applied within the project. In order to take full advantage of the potential that the medium of film offers to development and research projects, the practices described in this chapter should be developed further.

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The films "Wiza Wetu!" and "Bridging the Gap" are provided as avi files on the CD (back of Volume 3). They can also be ordered free of charge as long as stock lasts from Ute Schmiedel (Uschmiedel@botanik.uni-hamburg.de).

Recommendations and decision support for local to national level decision makers

Dave F. Joubert*, Ibo Zimmermann, Jens Fendler & Heike Winschiers-Theophilus

Summary: A Decision Support System (DSS) was developed for management of semiarid rangelands in Namibia. During five workshops with farmers, the knowledge base, software and usability were tested. The DSS (http://chameleon.polytechnic.edu.na/wiki/) comprises 21 questions and 22 decisions divided into three parts, according to the type of decisions suggested. (1) Adaptive or opportunistic management decisions; (2) "Treating the symptoms" management decisions and (3) ongoing good preventative management decisions. A booklet is also available. The DSS is interactive, and adhered to a number of critical success factors (CSF) during its development, which is ongoing. Challenges to its development and use are discussed.

Introduction

BIOTA has produced prodigious amounts of research results in the form of academic publications. Like all similar finite projects, there is a risk of these results and publications remaining academic, with little input into policy or translation into improved management. One might argue that this is the nature of research. However, in today's crisis situation regarding biodiversity loss, degradation and climate change, an emphasis is required to "fast track" applied research results into improved management. This is no easy task, and there is a risk of overemphasising the applicability of research which is not conclusive in its findings. BIOTA Southern Africa has developed a number of decision support initiatives in an attempt to meet this challenge. The modelling approaches (tools) have been more comprehensively described in Article III.7.6.

One such tool developed during BIOTA Phase 3 is a decision support system (DSS) for savanna rangeland management, with particular emphasis on the prevention of transitions from an open grassy productive savanna to a shrub encroached savanna (Joubert et al. 2008a). The system is based largely on a conceptual model (Joubert et al. 2008a) and a problem tree (Zimmermann et al. 2008) that address the dynamics of shrub encroachment, particularly by *Acacia mellifera*, in Namibia. Based on our experience, we felt strongly that the use of simple decision support systems (what others may refer to as expert systems) held great promise for improving rangeland management, and thus pursued this approach, as described.

Development and structure

The knowledge base (decisions, questions and rules) was largely constructed from the authors' accumulated expert knowledge, literature and from the knowledge of rangeland managers and advisers.

The knowledge base was summarised in the form of a decision tree (Fig. 1) that captures the sequence of questions and answers ultimately arriving at a decision. This provides a useful visual representation of the sequence of steps taken in making the decisions. Farmers at workshops also found it useful to take a page with the decision tree into the field to facilitate in situ decision making.

Five workshops with farmers were used to: 1) compare the knowledge base and decisions with the decisions taken by farmers (Photo 1), and 2) to test the software and usability issues of the interface (Photo 2).

The involvement of the farmers and land managers provided a forum to compare the farmers' decisions with those recommended through the DSS. Through this we gained insights into decision making by farmers. It gave us a sense of how varied farmers' decisions were for various scenarios (Joubert et al. 2008b). Their involvement also encouraged farmers to take ownership of the DSS and helped to gauge their expectations.

At an early stage of development, we decided to simulate the software DSS in a hard copy format (Joubert et al. 2009) with one page per question or decision. This is unusual, but, in instances where computers are not available, or are an unfamiliar tool to farmers, it is likely to prove useful, especially if translated into local languages.

During the evaluation of the software we identified the need for an online feedback tool. Many of these features are readily available through Wiki technology which allows users to interactively create, edit and link web pages. We installed the "DokuWiki" software and pasted a set of pages from the booklet version of our DSS (Joubert et al. 2009). Software and usability issues were tested, by filming the participants using the DSS, analysing their responses to the interface, and by asking direct questions through questionnaires. We used this to modify the interface. In this way, end user concerns and ideas were accounted for in the development of the DSS.

Participants were asked to test the DSS and provide feedback, both on the knowledge base and the interface. The DSS was also introduced to the Extension Services of the Ministry of Agriculture, Water and Forestry in 2007 and to the rangeland research and management community as presentations at many fora

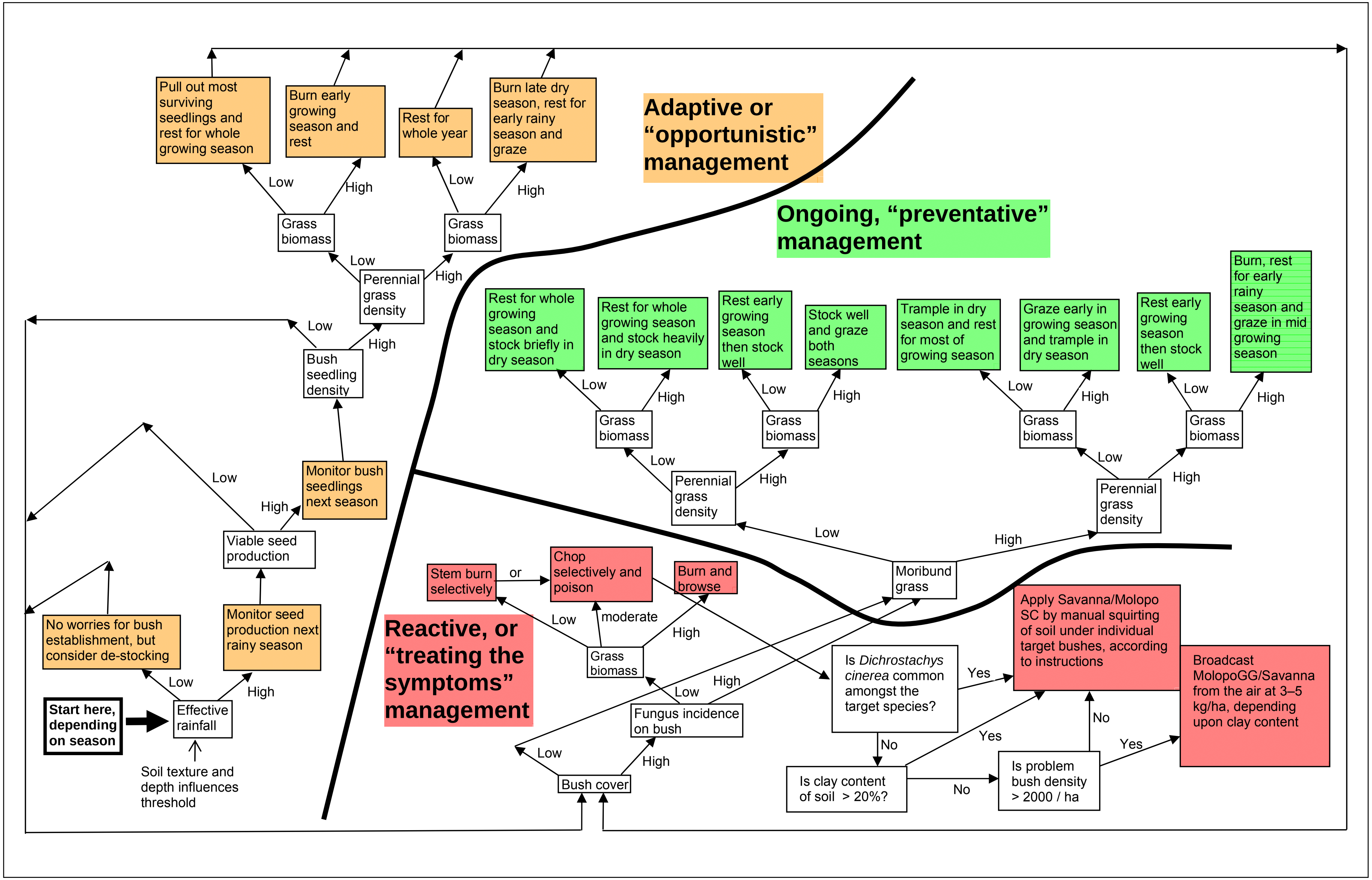

Fig. 1: Decision flow diagram for rangeland management. Decisions are in shaded rectangles.

Photo 1: Reinholdt Kambuli (a workshop facilitator) asks a farmer (right) to explain his management decision for a given scenario during a workshop. Photo: Ibo Zimmermann.

Photo 2: Polytechnic facilitators and farmers evaluate the usability of the DSS during a workshop. Photo: Ibo Zimmermann.

in Namibia, South Africa and even China (Joubert et al. 2008b). A BIOTA Day in November 2009 was also used to promote the DSS to invited key stakeholders, as well as the general public.

The current version of the DSS has a series of 21 questions and 22 decisions. The answers to questions are mostly qualitative, and the vast majority require simple "yes/no" responses. The decision pathway represented with either "no" or "low" answers moving left from the question, whereas "yes" or "high" answers branch to the right. The DSS can be divided into three parts according to the type of management decisions suggested. These are (1) **Adaptive or opportunistic** management decisions, including monitoring prompts that are related to decisions to be taken as a consequence of extreme rainfall events (depending upon *A. mellifera* seed production, and potential seedling survival in the seasons following). (2) "**Treating the symptoms**" management decisions (restoring an existing bush thicket to an open savanna), and (3) **Ongoing good preventative** management decisions that are not particularly related to extreme climatic events but refer to situations in which bush thickening is not yet a problem. The online wiki DSS (http://chameleon.polytechnic.edu.na/wiki/) has a series of embedded information that can be accessed through links. This provides background information, articles, photos and links to other sites of relevance to the user, without being distracting. Through this, managers are exposed to information that may lead them to consider leaving patches of thickets in a more open savanna matrix, to maximise diversity.

Any version of a page can be referred to at any time while the risk of users accidentally removing important information through editing is virtually non existent. The Wiki format is therefore safe but also flexible. Ideally the DSS should be used in conjunction with suggested monitoring procedures (Zimmermann et al. 2003) but this is not essential.

The DSS in its wiki format is essentially "low key" currently, with limited logical flexibility. However, the information required to solve rangeland challenges is more heuristic than mathematical, thus negating the need for a complex DSS. Also, precise values of parameters at which thresholds occur are not known and vary with changes in many other parameter values. Rangeland managers have different perceptions of what constitutes bush thickets, and would differ in opinion regarding a threshold for action. The wiki DSS allows a constantly changing knowledge base and can be adapted by farming communities to suit local circumstances, thus serving as a vehicle for adaptive management (Starfield & Bleloch 1991).

Currently the DSS operates at the paddock scale, with occasional reference to what could be going on in other paddocks within the same farm. To be more realistic, decisions at the paddock and farm scale should account for processes at the landscape scale (Pringle & Tinley 2003). Another challenge will be to incorporate economic details into the DSS, both in terms of cost implications and expected benefits over the short, medium and long terms.

How successful is our DSS or how successful will it be?

Ideally, the improvement of rangeland management after the application of a DSS would be the best indicator of DSS success, but this is obviously not possible to prove in most cases. We have incorporated many of the "critical success factors" (CSFs) (for example Guimaeres et al. 1992, Averweg & Erwin 1999, Newman et al. 2000) to evaluate the success of our DSS (Table 1).

Our greatest challenge remains the fact that the DSS is meant for a farming community that is at best connected through study groups and Farmer's associations. Decision making in the farming environment is independent of corporate goals and rules, and is consequently very individualistic. This is borne out by the diverse array of responses for each scenario provided by farmers during workshops (Joubert et al. 2008b). DSS development has almost exclusively been around corporate situations. In a corporate situation, DSSs are introduced, employees are trained and there is thus responsibility and ownership instilled. We hope

Table 1: Critical Success Factors (CSF) in the literature (see text) and an evaluation of our incorporation of them

Critical Success Factor	Evaluation
Users involved in a participatory development process	The DSS was modified after: ● Five workshops with farmers. ● Discussions with rangeland experts (including farmers, researchers and extension officers) As the DSS grows, farmers associations will hopefully be facilitated to: ● Develop DSSs for different species and different situations.
Users trained	● Farmers and extension workers received some training during the workshops mentioned above. ● It is envisaged that the DSS (and similar ones developed later) will be used as a training tool for extension workers, who will in turn use it as a training and discussion tool with farmers.
Easy to use	● Workshops allowed us to improve the interface. ● We believe in many cases training will still be necessary though. The farming community in Namibia has diverse experiences in education ranging from those with tertiary education to those with no formal training who are illiterate.
Manageable and small in scope	● The DSS is highly manageable and is currently small in scope. There is a demand for it to become more complex, from: ● Rangeland scientists, who believe there should be more quantified thresholds. ● Software experts, who suggest more complex powerful shells are useful (particularly to deal with complex data). ● The farming community, who insist that an economic component is necessary. The future challenge will particularly be to address this perceived need of farmers, since they are the end users.
A high level of top management support and managerial activity exist	● MAWF have expressed much interest in using this. ● We envisage that NGOs will also buy into the concept, although much more promotional activity is required in this regard still. ● Its use by extension officers could be seen as the managerial activity.
Information is easily available	● The DSS booklet is potentially available to all users. ● The wikiDSS will become more easily available as farmers’ access to internet improves. ● The use of cell phone technology is an attractive option to be investigated. ● The wikiDSS allows access to many other sources of information, and this will grow as the DSS is maintained and added to.

that Extension Services may act to unite farming groups into a “quasi” corporate unit, at least with regard to DSS use.

Another major challenge is to maintain, promote and sustain the DSS. Currently, the DSS is at an early stage of acceptance. There is always a looming danger that a potentially useful intervention, developed during a funded project, can become lost, through lack of continuity of staffing, a lack of commitment and a lack of funding. BushExpert (Barac et al. 2004), a DSS which focuses on case studies and symptom treatment, was developed at great cost and effort, but fell into complete disrepair due to a lack of funds, and an inability to maintain software. With software development and change occurring at an ever increasing pace, it will be necessary for the DSS to be housed, maintained and developed by dedicated staff. Currently the housing at Polytechnic of Namibia seems appropriate, since the developers of this DSS are all permanently employed there. Currently the DSS is still not being used by farmers. Once the Ministry of Agriculture, Water and Forestry starts to use the DSS for training, and extension officers in turn train farmers and use it as a discussion tool with farmers, we can then begin to determine its value to the Namibian rangeland community.

The acceptability of the DSS still needs to be tested over longer periods of time on farms. The validity of the decisions also requires more testing in the field. Ongoing research and experience by farmers as well as researchers will be used to update the knowledge base. Research is currently underway to test rules that are in dispute, or not yet well established by previous research (particularly the role of fire). The authors have found that, not only is the DSS a vehicle for fast tracking research results and concepts into management practice, it has also allowed us to revisit hypotheses, and refocus research priorities.

Acknowledgements

The authors’ general acknowledgements to the organisations and institutions, which supported this work are provided in Volume 1.

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Data access and availability: BIOTA Data Facility

Gerhard Muche *; Thomas Hillmann, Andrzej Suwald & Norbert Jürgens

Summary: The BioMonitoring Data Facility is an infrastructure that serves all the regional projects within BIOTA AFRICA, i.e. BIOTA Maroc, BIOTA East Africa, BIOTA West Africa, and BIOTA Southern Africa. BIOTA AFRICA aims to provide robust scientific information about the current status, recent change and future development of biodiversity in the major African biomes. The present activities of the BioMonitoring Data Facility focusses on a continuous effort to enable inventorying and archiving of all Observatory-relevant BIOTA data, the presentation of data and information via the internet, and the facilitation of web communication between all BIOTA partners.

Since the start of the BIOTA AFRICA project in the year 2000, a wide array of digital data has been gathered relating to over 50 subprojects, work-packages and core topics of BIOTA and its associated projects. Due to the different subjects and key questions within the various disciplines, this data is of relatively heterogeneous structure. For establishing a BIOTA AFRICA data archive, the data files in their different formats were collected and archived in a central data pool at the Biocentre Klein Flottbek, University of Hamburg.

The internet offers an easy way to identify and access the data that BIOTA AFRICA supplies. Direct download from the website www.biota-africa.org is offered for a wide spectrum of open access data. More complex data requests have to be processed upon request. The conditions of data access are fixed in the Data Sharing Protocol of BIOTA AFRICA.

Introduction

Modern global change science provides various types of outputs such as scientific publications, recommendations for practitioners, and tools for stakeholders. In the third phase of BIOTA Southern Africa, the following work layers were distinguished: A Drivers of Change, B Monitoring of Change, C Land Use, Impact & Value, D Process Analysis, E Interventions & Restoration, F Transformation & Capacity Development (see www.biota-africa.org, Part I). All these work layers produce quite different types of data and they should all be made available to a broad range of users (from land managers to policy makers). Amongst the different elements, a very strong focus of BIOTA AFRICA has been on long-term observation. The observations result in data that robustly document environmental changes and they are also the basis for empirical testing of hypotheses. Such data are often collected to answer a particular research question. At the same time they are a reference of the state of biodiversity at a specific point in time. Therefore, these data need to be continuously archived, technically maintained, understandable, utilisable and made available for unpredictable future research needs. Safeguarding the long-term availability of the BIOTA AFRICA data is one of the main objectives of the BIOTA Data Facility or BioMonitoring Data Facility.

The Data Facility attends to data management of the regional projects BIOTA Southern Africa, BIOTA West Africa, BIOTA East Africa, and BIOTA Maroc. This data management includes the online presentation of working groups and their achievements, the processing of the data according to professional standards, the supply of datasets for interested persons or institutions, and archiving of data for future use. The BIOTA Data Facility, together with the African host countries, presently also aims to facilitate the hosting, maintenance and provision of data beyond the funding period of BIOTA AFRICA.

One of the main tasks of the Data Facility is the design and maintenance of the BIOTA AFRICA website. There are several arguments for the importance of this task. The internet is an important platform for disseminating information regarding projects and their achievements, so that potential users can learn about the available databases. Websites also facilitate a) communication between the data provider and data user; and b) availability of data packages at anytime from anywhere and for everyone. The availability of data via websites has much more impact than delivery on request via e-mail, for instance (for similar experiences with another research project see Göttlicher & Bendix 2004).

The BIOTA AFRICA website provides information on the goals, approaches and structure of the project. Furthermore, each of the many working groups and subprojects supplied information on their specific expertise, their research and research findings. The BIOTA website is accessible at www.biota-africa.org.

Data availability and access

Users of the BIOTA AFRICA website can gain access to data in various ways:

Open access via the website: a fundamental organisational aspect within

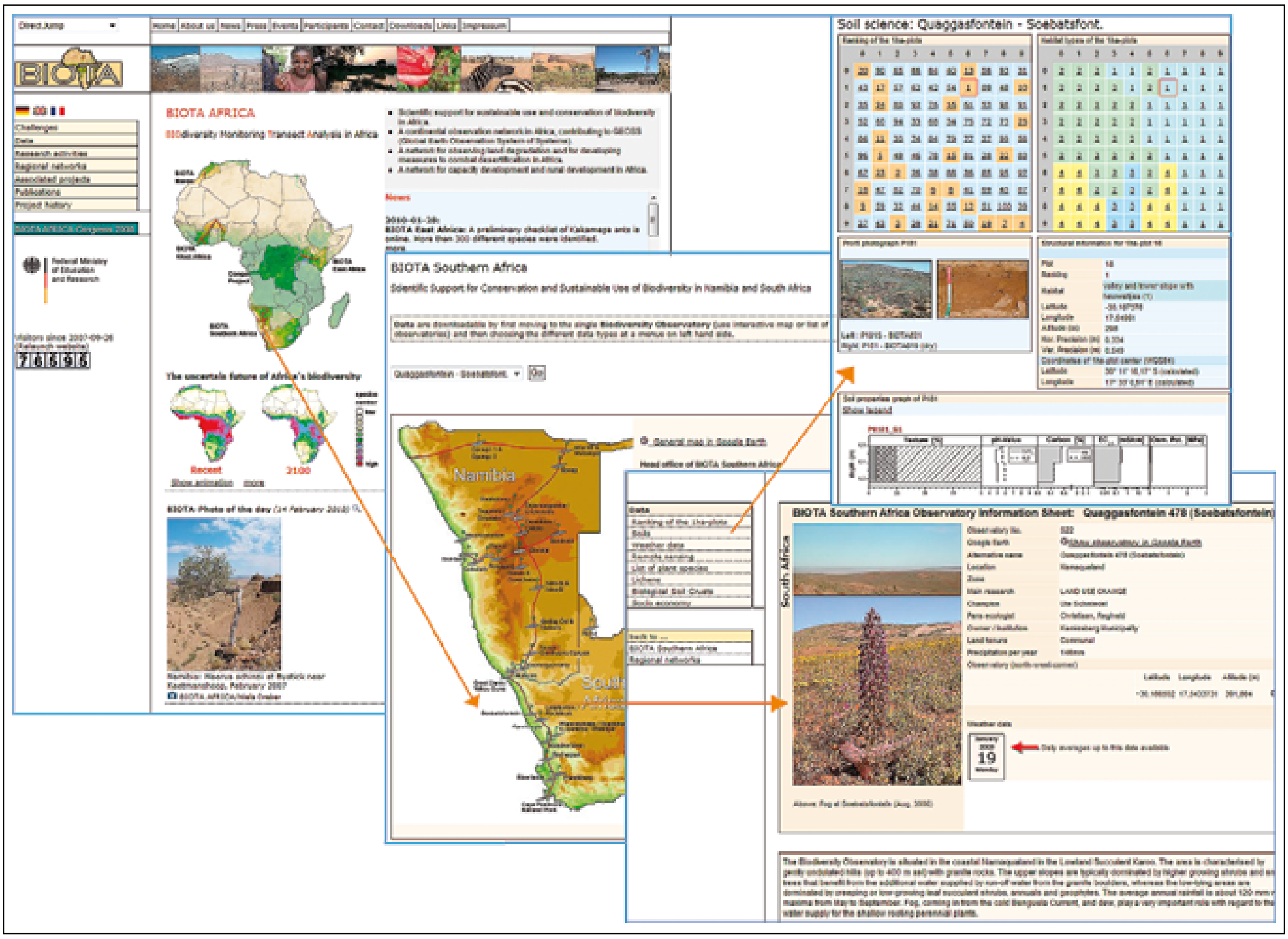


Fig. 1: Website of BIOTA AFRICA—three clicks from homepage to data access.

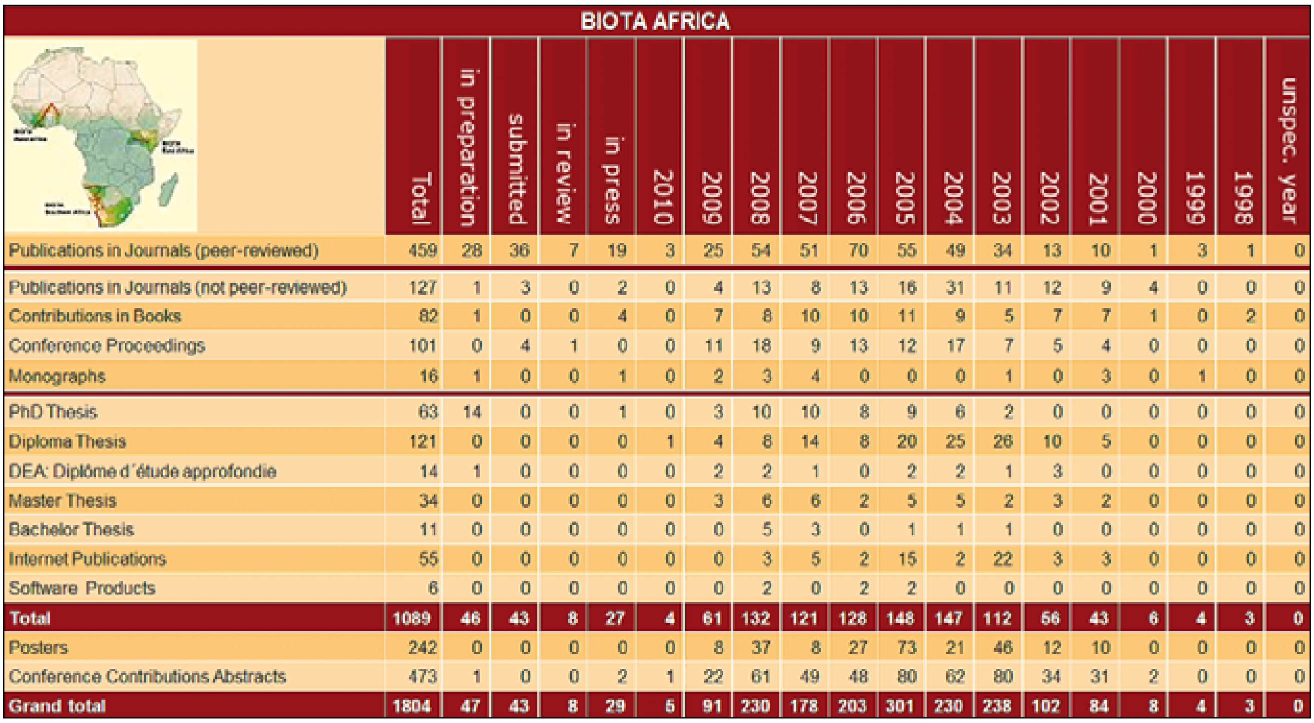
BIOTA Southern Africa is the arrangement of research sites along transects. Transects and BIOTA Biodiversity Observatories (hereafter called BIOTA Observatories) are shown on the homepage of the website on an interactive map and by clicking on the symbol of a BIOTA Observatory, the user reaches the page of that specific Observatory. Some texts and figures are shown on a compact information sheet. A menu on the left hand side offers more complex datasets. Each BIOTA Observatory may show a slightly different menu because data availability may differ between the Observatories. The data relates to topics such as weather, vegetation, soil, lichens, crusts, insects and socio-economy. In this way the user can easily find what type of data (i.e. topic or discipline) is available for a particular site. Alternatively, a user may be interested in a particular topic or discipline and want to find all data relating to it along the BIOTA transect. If the user is interested in soil data for instance, he or she will find general information about soil science research and from there go to all BIOTA Observatories where the available data are displayed. A user can conveniently move to the information on any of the Observatory sheets with a few mouse clicks (Fig. 1).

Another means of accessing data is via the **metadatabase**. Metadata describes the contents (types of data, e.g. vegetation data), format (e.g. BIOTABase), and availability (e.g. open access) of data. The open access datasets, as well as datasets which are only available on request in order to protect PhD and other projects in progress, are listed within the metadatabase.

Besides metadata and open access information, published articles and books are also data which is generated by the BIOTA AFRICA initiative. The **List of Publications** is an online database of all publications that have emerged from BIOTA AFRICA. The details of the publications are searchable with flexible search functions. Abstracts are provided for downloading, and often the entire publication is available in pdf-format (see Fig. 2).

The BIOTA AFRICA staff and team members are listed in an online database named **List of Participants**. This makes it easy for users to contact a data provider or any expert on the BIOTA AFRICA network.

The BIOTA AFRICA website was initially only hosted in Hamburg/Germany, but a mirror has been established in Windhoek, Namibia (http://www.nbri.org.na/BIOTA/). This **Namibian data mirror** has been installed for two reasons. Firstly, the German-hosted website responded relatively slowly when accessed from Namibia because of the limited infrastructure there. The website response has improved significantly since the National Botanical Research Institute of Namibia (NBRI) in Windhoek



BIOTA AFRICA

	Total	in preparation	submitted	in review	in press	2010	2009	2008	2007	2006	2005	2004	2003	2002	2001	2000	1999	1998	unspec. year
Publications in Journals (peer-reviewed)	459	28	36	7	19	3	25	54	51	70	55	49	34	13	10	1	3	1	0
Publications in Journals (not peer-reviewed)	127	1	3	0	2	0	4	13	8	13	16	31	11	12	9	4	0	0	0
Contributions in Books	82	1	0	0	4	0	7	8	10	10	11	9	5	7	7	1	0	2	0
Conference Proceedings	101	0	4	1	0	0	11	18	9	13	12	17	7	5	4	0	0	0	0
Monographs	16	1	0	0	1	0	2	3	4	0	0	0	1	0	3	0	1	0	0
PhD Thesis	63	14	0	0	1	0	3	10	10	8	9	6	2	0	0	0	0	0	0
Diploma Thesis	121	0	0	0	0	1	4	8	14	8	20	25	26	10	5	0	0	0	0
DEA: Diplôme d´étude approfondie	14	1	0	0	0	0	2	2	1	0	2	2	1	3	0	0	0	0	0
Master Thesis	34	0	0	0	0	0	3	6	6	2	5	5	2	3	2	0	0	0	0
Bachelor Thesis	11	0	0	0	0	0	0	5	3	0	1	1	1	0	0	0	0	0	0
Internet Publications	55	0	0	0	0	0	0	3	5	2	15	2	22	3	3	0	0	0	0
Software Products	6	0	0	0	0	0	0	2	0	2	2	0	0	0	0	0	0	0	0
Total	**1089**	**46**	**43**	**8**	**27**	**4**	**61**	**132**	**121**	**128**	**148**	**147**	**112**	**56**	**43**	**6**	**4**	**3**	**0**
Posters	242	0	0	0	0	0	8	37	8	27	73	21	46	12	10	0	0	0	0
Conference Contributions Abstracts	473	1	0	0	2	1	22	61	49	48	80	62	80	34	31	2	0	0	0
Grand total	**1804**	**47**	**43**	**8**	**29**	**5**	**91**	**230**	**178**	**203**	**301**	**230**	**238**	**102**	**84**	**8**	**4**	**3**	**0**

Fig. 2: List of Publications—statistics as of February 2010.

began hosting the Namibian data mirror. Secondly, the Namibian data mirror supports the notion of ownership of African data by Africans.

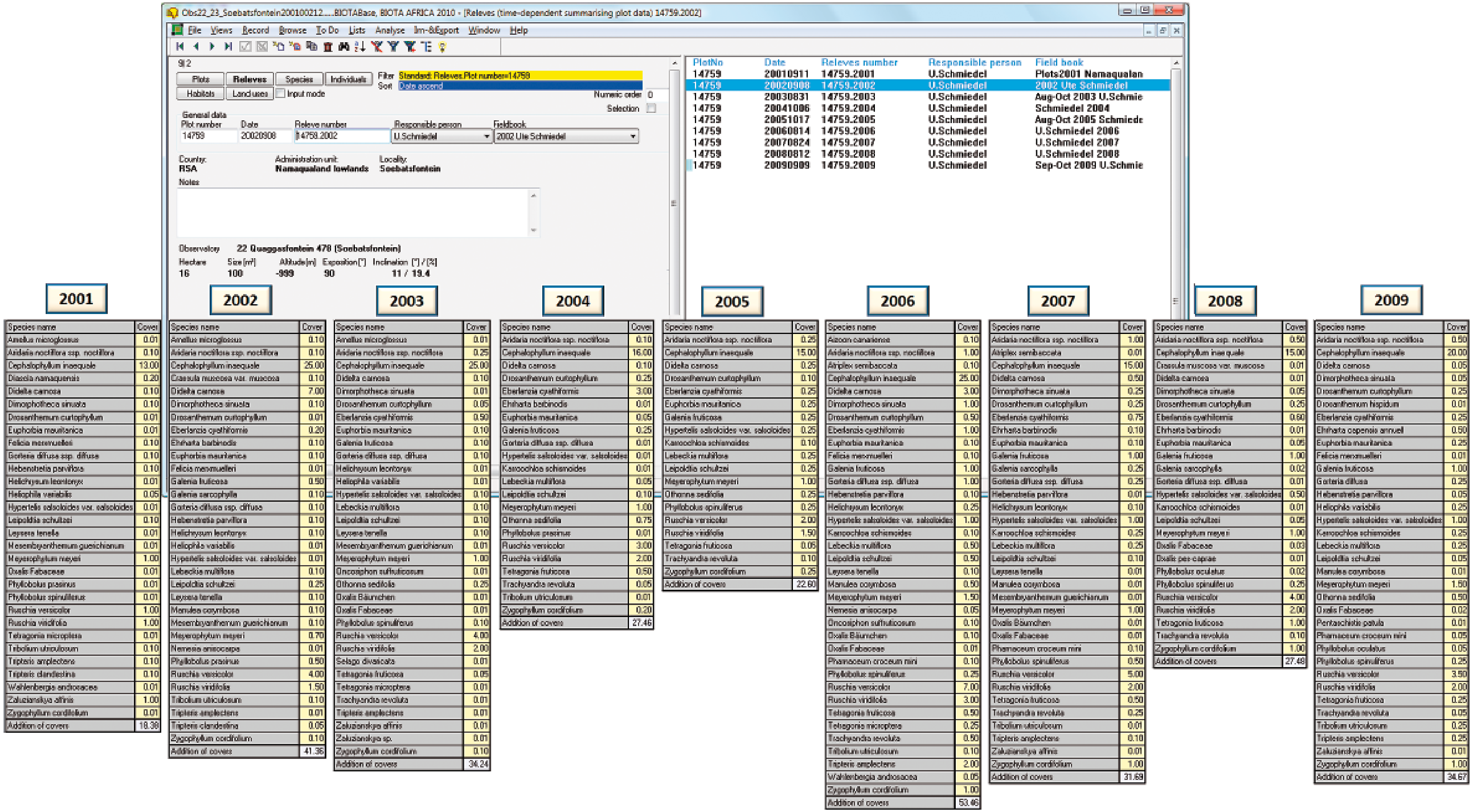
To facilitate the exchange, presentation and analysis of data, the datasets are stored as digital files. Special software has been designed to read and process these files. In addition, descriptions of the data are provided so that the user can understand the components of the data. Simple datasets often consist of a single file which can be managed with commonly available software packages, and are filled with content which can be interpreted by any user. With complex datasets, special software is necessary and detailed documentation of the content of tables and single fields is indispensable. This important information regarding datasets, their formats and documentations is provided in the metadatabase (see: www.biota-africa.org > Data > Metadata). There is also information provided on data availability and limitations on accessibility. The fact sheets in Part II provide an overview of the data collected at each BIOTA Observatory.

The rules for data access were formulated jointly by scientists of the participating countries within a Data Sharing Protocol which defines the conditions for providers and users of data produced by the BIOTA AFRICA initiative (Electronic Appendix). The spirit of the BIOTA AFRICA **Data Sharing Protocol** is based on the Open Access paradigm that is documented, for example, in the Berliner Declaration (Gruss 2003). However there are several obvious reasons limiting immediate delivery of data to everybody. For example, based on national law, geographical distribution data of endangered and protected species may not be published, and these datasets are supplied exclusively for scientific use. Another reason for limitations is that some datasets are restricted to those people who have collected the data and who have the right to publish their findings and scientific results first. After a few years, such data become openly accessible.

Products of the BIOTA Data Facility

Within the framework of the BIOTA AFRICA project, the need for software that enabled data storage and processing emerged. Field work observations are typically recorded on standardised data sheets and these records then have to be digitised so that they can be analysed with the help of computer software. At the beginning of the project it was impossible to find an adequate software package which met the requirements for the ambitious scientific approach. Such software should be able to handle (a) time series, (b) data from nested plots of the standardised BIOTA Observatories, (c) undescribed or unidentified species, and (d) data on the abiotic environment (e.g. topography, geology, soil). To fulfil all these requirements the IT team of BIOTA AFRICA undertook the development of a software package named BIOTABase which met the needs for the storage, administration and analysis of the BIOTA Southern Africa vegetation and ecological data (see Muche & Finckh 2009). BIOTABase can be downloaded free of charge from the BIOTA AFRICA Website (www.biota-africa.org > Downloads > BIOTABase), so that everybody can share and store BIOTA data in the original BIOTABase format. The software may also be used for building up new databases, independent of BIOTA AFRICA.

BIOTABase enables a user to store time series data from the same plot, which emerges from the annual surveys



Filter Standard: Releves.Plot number=14759
Sort Date ascend
Numeric order 0

Plot number	Date	Releve number	Responsible person	Fieldbook
14759	20020908	14759.2002	U.Schmiedel	2002 Ute Schmiedel

Country: RSA
Administration unit: Namaqualand lowlands
Locality: Soebatsfontein

Observatory 22 Quaggasfontein 478 (Soebatsfontein)

Hectare	Size [m²]	Altitude[m]	Exposition[°]	Inclination [°] / [%]
16	100	-999	90	11 / 19.4

PlotNo	Date	Releves number	Responsible person	Field book
14759	20010911	14759.2001	U.Schmiedel	Plots2001 Namaqualan
14759	20020908	14759.2002	U.Schmiedel	2002 Ute Schmiedel
14759	20030831	14759.2003	U.Schmiedel	Aug-Oct 2003 U.Schmie
14759	20041006	14759.2004	U.Schmiedel	Schmiedel 2004
14759	20051017	14759.2005	U.Schmiedel	Aug-Oct 2005 Schmiede
14759	20060814	14759.2006	U.Schmiedel	U.Schmiedel 2006
14759	20070824	14759.2007	U.Schmiedel	U.Schmiedel 2007
14759	20080812	14759.2008	U.Schmiedel	U.Schmiedel 2008
14759	20090909	14759.2009	U.Schmiedel	Sep-Oct 2009 U.Schmie

2001

Species name	Cover
Amellus microglossus	0.01
Aridaria noctiflora ssp. noctiflora	0.10
Cephalophyllum inaequale	13.00
Diascia namaquensis	0.20
Didelta carnosa	0.10
Dimorphotheca sinuata	0.10
Drosanthemum curtophyllum	0.01
Euphorbia mauritanica	0.01
Felicia merxmuelleri	0.10
Gorteria diffusa ssp. diffusa	0.10
Hebenstretia parviflora	0.10
Helichysum leontonyx	0.01
Heliophila variabilis	0.05
Hypertelis salsoloides var. salsoloides	0.01
Leipoldtia schultzei	0.10
Leysera tenella	0.01
Mesembryanthemum guerichianum	0.01
Meyerophytum meyeri	1.00
Oxalis Fabaceae	0.01
Phyllobolus prasinus	0.01
Phyllobolus spinuliferus	0.01
Ruschia versicolor	1.00
Ruschia viridifolia	1.00
Tetragonia microptera	0.01
Tribolium utriculosum	0.10
Tripteris amplectens	0.10
Tripteris clandestina	0.10
Wahlenbergia androsacea	0.01
Zaluzianskya affinis	1.00
Zygophyllum cordifolium	0.01
Addition of covers	18.38

2002

Species name	Cover
Amellus microglossus	0.10
Aridaria noctiflora ssp. noctiflora	0.10
Cephalophyllum inaequale	25.00
Crassula muscosa var. muscosa	0.10
Didelta carnosa	7.00
Dimorphotheca sinuata	0.10
Drosanthemum curtophyllum	0.01
Eberlanzia cyathiformis	0.20
Ehrharta barbinodis	0.10
Euphorbia mauritanica	0.10
Felicia merxmuelleri	0.01
Galenia fruticosa	0.50
Galenia sarcophylla	0.10
Gorteria diffusa ssp. diffusa	0.10
Hebenstretia parviflora	0.10
Helichrysum leontonyx	0.10
Heliophila variabilis	0.01
Hypertelis salsoloides var. salsoloides	0.01
Lebeckia multiflora	0.10
Leipoldtia schultzei	0.25
Leysera tenella	0.10
Manulea corymbosa	0.10
Mesembryanthemum guerichianum	0.10
Meyerophytum meyeri	0.70
Nemesia anisocarpa	0.01
Phyllobolus prasinus	0.50
Ruschia versicolor	4.00
Ruschia viridifolia	1.50
Tribolium utriculosum	0.10
Tripteris amplectens	0.01
Tripteris clandestina	0.05
Zygophyllum cordifolium	0.10
Addition of covers	41.36

2003

Species name	Cover
Amellus microglossus	0.01
Aridaria noctiflora ssp. noctiflora	0.25
Cephalophyllum inaequale	25.00
Didelta carnosa	0.10
Dimorphotheca sinuata	0.01
Drosanthemum curtophyllum	0.05
Eberlanzia cyathiformis	0.50
Euphorbia mauritanica	0.10
Galenia fruticosa	0.10
Gorteria diffusa ssp. diffusa	0.10
Helichrysum leontonyx	0.01
Heliophila variabilis	0.01
Hypertelis salsoloides var. salsoloides	0.10
Lebeckia multiflora	0.10
Leipoldtia schultzei	0.10
Leysera tenella	0.10
Mesembryanthemum guerichianum	0.01
Meyerophytum meyeri	1.00
Oncosiphon suffruticosum	0.01
Othonna sedifolia	0.25
Oxalis Bäumchen	0.01
Oxalis Fabaceae	0.01
Phyllobolus spinuliferus	0.10
Ruschia versicolor	4.00
Ruschia viridifolia	2.00
Selago divaricata	0.01
Tetragonia fruticosa	0.05
Tetragonia microptera	0.01
Trachyandra revoluta	0.01
Tripteris amplectens	0.01
Zaluzianskya affinis	0.01
Zaluzianskya sp.	0.01
Zygophyllum cordifolium	0.10
Addition of covers	34.24

2004

Species name	Cover
Aridaria noctiflora ssp. noctiflora	0.10
Cephalophyllum inaequale	16.00
Didelta carnosa	0.10
Drosanthemum curtophyllum	0.25
Eberlanzia cyathiformis	3.00
Ehrharta barbinodis	0.01
Euphorbia mauritanica	0.05
Galenia fruticosa	0.25
Gorteria diffusa ssp. diffusa	0.01
Hypertelis salsoloides var. salsoloides	0.01
Karoochloa schismoides	0.01
Lebeckia multiflora	0.05
Leipoldtia schultzei	0.10
Meyerophytum meyeri	1.00
Othonna sedifolia	0.75
Phyllobolus prasinus	0.01
Ruschia versicolor	3.00
Ruschia viridifolia	2.00
Tetragonia fruticosa	0.50
Trachyandra revoluta	0.05
Tribolium utriculosum	0.01
Zygophyllum cordifolium	0.20
Addition of covers	27.46

2005

Species name	Cover
Aridaria noctiflora ssp. noctiflora	0.25
Cephalophyllum inaequale	15.00
Didelta carnosa	0.25
Drosanthemum curtophyllum	0.10
Eberlanzia cyathiformis	0.25
Euphorbia mauritanica	0.25
Galenia fruticosa	0.25
Hypertelis salsoloides var. salsoloides	0.25
Karoochloa schismoides	0.10
Lebeckia multiflora	0.25
Leipoldtia schultzei	0.25
Meyerophytum meyeri	1.00
Othonna sedifolia	0.25
Phyllobolus spinuliferus	0.25
Ruschia versicolor	2.00
Ruschia viridifolia	1.50
Tetragonia fruticosa	0.05
Trachyandra revoluta	0.10
Zygophyllum cordifolium	0.25
Addition of covers	22.60

2006

Species name	Cover
Aizoon canariense	0.10
Aridaria noctiflora ssp. noctiflora	1.00
Atriplex semibaccata	0.10
Cephalophyllum inaequale	25.00
Didelta carnosa	3.00
Dimorphotheca sinuata	1.00
Drosanthemum curtophyllum	0.50
Eberlanzia cyathiformis	1.00
Euphorbia mauritanica	0.10
Felicia merxmuelleri	0.10
Galenia fruticosa	1.00
Gorteria diffusa ssp. diffusa	1.00
Hebenstretia parviflora	0.10
Helichysum leontonyx	0.25
Hypertelis salsoloides var. salsoloides	1.00
Karoochloa schismoides	0.10
Lebeckia multiflora	0.50
Leipoldtia schultzei	0.50
Leysera tenella	0.10
Manulea corymbosa	0.50
Meyerophytum meyeri	1.50
Nemesia anisocarpa	0.05
Oncosiphon suffruticosum	0.10
Oxalis Bäumchen	0.10
Oxalis Fabaceae	0.01
Pharnaceum croceum mini	0.10
Phyllobolus spinuliferus	0.25
Ruschia versicolor	7.00
Ruschia viridifolia	3.00
Tetragonia fruticosa	0.50
Tetragonia microptera	0.25
Trachyandra revoluta	0.50
Tribolium utriculosum	0.10
Tripteris amplectens	2.00
Wahlenbergia androsacea	0.05
Zygophyllum cordifolium	1.00
Addition of covers	53.46

2007

Species name	Cover
Aridaria noctiflora ssp. noctiflora	1.00
Atriplex semibaccata	0.01
Cephalophyllum inaequale	15.00
Didelta carnosa	0.50
Dimorphotheca sinuata	0.25
Drosanthemum curtophyllum	0.25
Eberlanzia cyathiformis	0.75
Ehrharta barbinodis	0.10
Euphorbia mauritanica	0.10
Galenia fruticosa	1.00
Galenia sarcophylla	0.25
Gorteria diffusa ssp. diffusa	0.25
Hebenstretia parviflora	0.01
Helichysum leontonyx	0.10
Hypertelis salsoloides var. salsoloides	1.00
Karoochloa schismoides	0.25
Lebeckia multiflora	0.25
Leipoldtia schultzei	0.10
Leysera tenella	0.01
Manulea corymbosa	0.01
Mesembryanthemum guerichianum	0.01
Meyerophytum meyeri	1.00
Oxalis Bäumchen	0.01
Oxalis Fabaceae	0.01
Pharnaceum croceum mini	0.10
Phyllobolus spinuliferus	0.50
Ruschia versicolor	5.00
Ruschia viridifolia	2.00
Tetragonia fruticosa	0.50
Trachyandra revoluta	0.25
Tribolium utriculosum	0.01
Tripteris amplectens	0.10
Zaluzianskya affinis	0.01
Zygophyllum cordifolium	1.00
Addition of covers	31.69

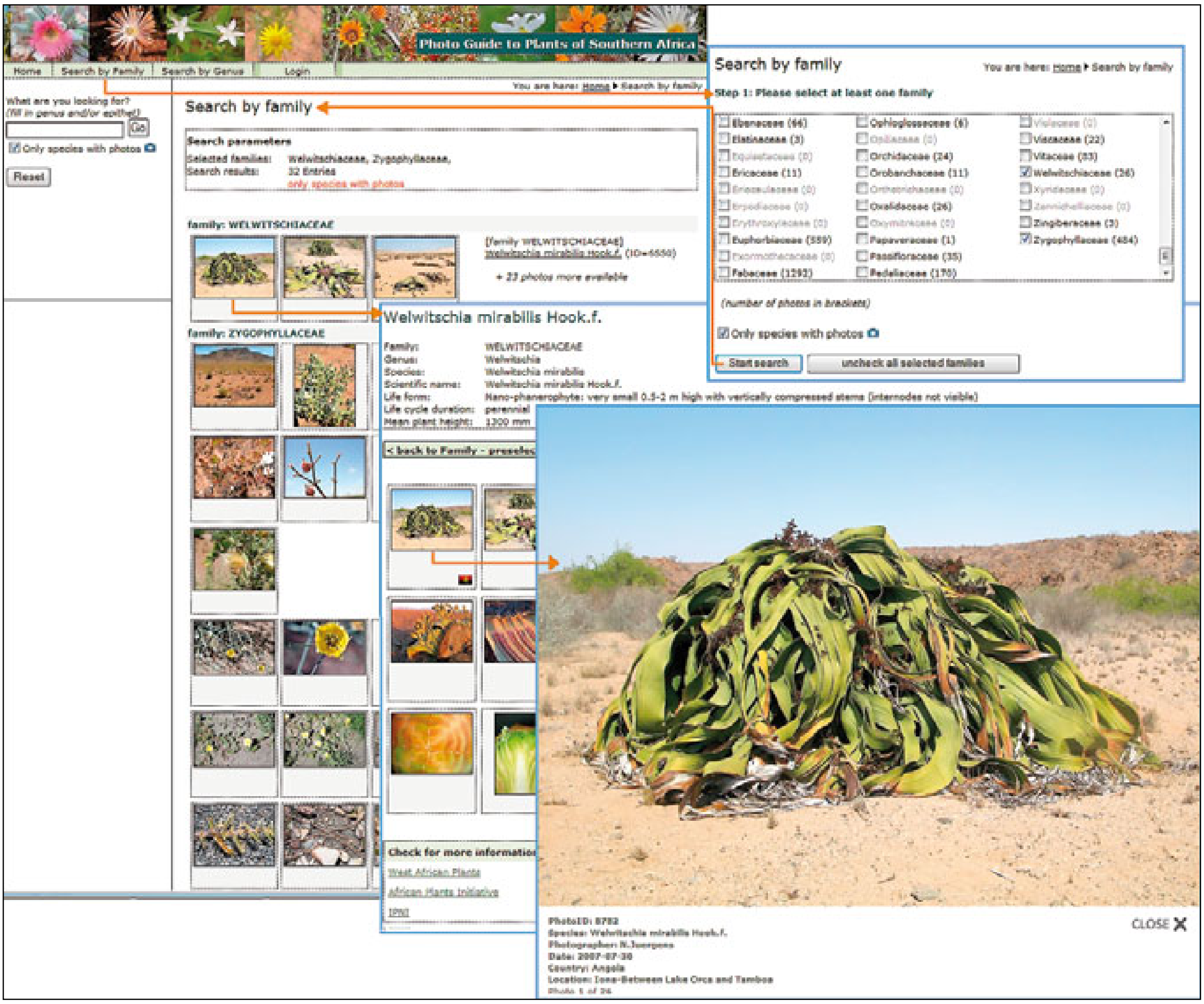
2008

Species name	Cover
Aridaria noctiflora ssp. noctiflora	0.50
Cephalophyllum inaequale	15.00
Crassula muscosa var. muscosa	0.01
Didelta carnosa	0.01
Dimorphotheca sinuata	0.05
Drosanthemum curtophyllum	0.25
Eberlanzia cyathiformis	0.60
Ehrharta barbinodis	0.01
Euphorbia mauritanica	0.05
Galenia fruticosa	1.00
Galenia sarcophylla	0.02
Gorteria diffusa ssp. diffusa	0.01
Hypertelis salsoloides var. salsoloides	0.50
Karoochloa schismoides	0.01
Leipoldtia schultzei	0.05
Meyerophytum meyeri	1.00
Oxalis Fabaceae	0.03
Oxalis pes-caprae	0.01
Phyllobolus oculatus	0.02
Phyllobolus spinuliferus	0.25
Ruschia versicolor	4.00
Ruschia viridifolia	2.00
Tetragonia fruticosa	1.00
Trachyandra revoluta	0.10
Zygophyllum cordifolium	1.00
Addition of covers	27.48

2009

Species name	Cover
Aridaria noctiflora ssp. noctiflora	0.50
Cephalophyllum inaequale	20.00
Didelta carnosa	0.05
Dimorphotheca sinuata	0.05
Drosanthemum curtophyllum	0.25
Drosanthemum hispidum	0.01
Eberlanzia cyathiformis	0.25
Ehrharta capensis annuell	0.50
Euphorbia mauritanica	0.25
Felicia merxmuelleri	0.01
Galenia fruticosa	1.00
Gorteria diffusa	0.25
Hebenstretia parviflora	0.05
Heliophila variabilis	0.25
Hypertelis salsoloides var. salsoloides	1.00
Karoochloa schismoides	0.25
Lebeckia multiflora	0.25
Leipoldtia schultzei	0.05
Manulea corymbosa	0.01
Meyerophytum meyeri	1.50
Othonna sedifolia	0.50
Oxalis Fabaceae	0.02
Pentaschistis patula	0.01
Pharnaceum croceum mini	0.05
Phyllobolus oculatus	0.05
Phyllobolus spinuliferus	0.25
Ruschia versicolor	3.50
Ruschia viridifolia	2.00
Tetragonia fruticosa	0.25
Trachyandra revoluta	0.05
Tribolium utriculosum	0.25
Tripteris amplectens	0.25
Zaluzianskya affinis	0.01
Zygophyllum cordifolium	1.00
Addition of covers	34.67

Fig. 3: BIOTABase: relevés of BIOTA Observatory S22 Soebatsfontein, hectare 16, rank 1, size 100 m², time series of species occurrence.



Search parameters
Selected families: Welwitschiaceae, Zygophyllaceae,
Search results: 32 Entries
only species with photos

family: WELWITSCHIACEAE
(family WELWITSCHIACEAE)
Welwitschia mirabilis Hook.f. (ID=5550)
+ 23 photos more available

family: ZYGOPHYLLACEAE

☐ Ebenaceae (44)	☐ Ophioglossaceae (6)	☐ Violaceae (0)
☐ Elatinaceae (3)	☐ Opiliaceae (0)	☐ Viscaceae (22)
☐ Equisetaceae (0)	☐ Orchidaceae (24)	☐ Vitaceae (53)
☐ Ericaceae (11)	☐ Orobanchaceae (11)	☑ Welwitschiaceae (26)
☐ Eriocaulaceae (0)	☐ Orthotrichaceae (0)	☐ Xyridaceae (0)
☐ Erpodiaceae (0)	☐ Oxalidaceae (26)	☐ Zannichelliaceae (0)
☐ Erythroxylaceae (0)	☐ Oxymitraceae (0)	☐ Zingiberaceae (3)
☐ Euphorbiaceae (559)	☐ Papaveraceae (1)	☑ Zygophyllaceae (404)
☐ Exormothecaceae (0)	☐ Passifloraceae (35)	
☐ Fabaceae (1292)	☐ Pedaliaceae (170)	

(number of photos in brackets)

☑ Only species with photos

Welwitschia mirabilis Hook.f.

Family:	WELWITSCHIACEAE
Genus:	Welwitschia
Species:	Welwitschia mirabilis
Scientific name:	Welwitschia mirabilis Hook.f.
Life form:	Nano-phanerophyte: very small 0.5-2 m high with vertically compressed stems (internodes not visible)
Life cycle duration:	perennial
Mean plant height:	1200 mm

PhotoID: 8782
Species: Welwitschia mirabilis Hook.f.
Photographer: N.Juergens
Date: 2007-07-30
Country: Angola
Location: Iona-Between Lake Orca and Tambos
Photo 1 of 26

Fig. 4: Photo Guide to Plants of Southern Africa.

according to the standards of the BIOTA Observatories (Part I). Occurrence (presence-absence), species quantity measures (abundance, cover) as well as locality and date of occurrence are recorded. Thus, spatial and temporal patterns of species occurrence from all BIOTA Observatories along the 2,000 kilometres of the southern Africa transect can be analysed.

Independent of the observational and collection data, valuable reference data covering the nine year period of the BIOTA AFRICA project has been compiled. Reference data includes a) taxa (**Taxa Reference List**), b) geomorphology (**Reference List of Geomorphological Terms**) and c) landscape characteristics (> 25 km x 25 km, SOTER = Global and National Soils and Terrain Digital Databases, FAO; van Engelen & Wen 1995, Tempel 2002).

Another product—named BIOTACollections—has been designed at the requests of several users. BIOTACollections, the compact version of BIOTABase, has the advantage of storing simple collection data and observational data in a practical flat structure. It can also be downloaded from the BIOTA AFRICA website free of charge.

BIOTABase and BIOTACollections are offline tools for the flexible creation and use of datasets. Databases are subject to constant changes during the compilation of new datasets, as new records have to be added or changed in the process of data cleaning. Such activities should be carried out offline, even if the data are intended for public use. The taxa reference list of the research area has been made available for the public and linked to another nice feature: **The Photo Guide to Plants of Southern Africa** (see: www.southernafricanplants.net, see Fig. 4).

African plants have evolved an overwhelming diversity of forms and functions in many different habitats. Due to the limited number of published plant field guides, species identification is still a large problem, especially when large numbers of specimens need to be identified within a limited time. Besides using published identification keys and identification based on herbarium records, the screening of a sufficient number of good photographs can be an efficient method of plant identification for many taxonomic groups. The development of a regional online photo guide for southern Africa is aimed at enhancing the identification of African plant species. The guide presents plant photographs in phylogenetic order, thus allowing rapid visual comparisons. A number of tools allow the users to scan taxonomic groups such as genera and families. Online accessibility enables non-scientific users with limited access to taxonomic literature to gain knowledge on the regional flora and to identify plant taxa. The website also allows users to identify unknown species by entering plant characteristics such as dominant flower colour, life form, and growth form into a multi-access key.

The Guide to southern African Plants includes a comprehensive and rapidly growing representation of all known plant species of the southern African region. At present, Namibia and the western parts of South Africa are best represented, while a growing number of photos from Angola, Botswana and Zambia are also included. The Guide to southern African Plants has received contributions (photographs, identification data, quality control checks) from the National Botanical Research Institute of Namibia (NBRI), the Biocentre Klein Flottbek, the Botanical Garden and Herbarium of the University of Hamburg, and independent botanists from Namibia and South Africa. Contributions from the South African National Biodiversity Institute (SANBI), the Harry Oppenheimer Okavango Research Centre (HOORC), and from Angolan colleagues at Luanda and Lubango, as well as the Research Institute Senckenberg in Frankfurt are also to be included.

A second photo guide has been developed in a similar manner: **The Photo Guide to Plants of Southern Morocco** (see: http://plantsofsouthernmorocco.biota-africa.net) aims at presenting the diversity of vascular plant species which occur in the transition zone between the High Atlas Mountains and the Sahara Desert. Morocco is a hotspot of plant diversity in the western Mediterranean region, and the High Atlas Mountains constitute an important centre of endemism in Morocco. The Photo Guide to Plants of Southern Morocco received images from the Institut Agronomique et Vétérinaire Hassan II in Morocco, the BioCentre Klein Flottbek, and the Botanical Garden and Herbarium of the University of Hamburg.

The **West African Photo Guide**, published in 2008 by the colleagues of BIOTA West Africa, inspired these initiatives (www.westafricanplants.senckenberg.de; Brunken et al. 2008). The three online photo guides provide free access to a large number of African plant species.

Acknowledgements
The authors' general acknowledgements to the organisations and institutions, which supported this work are provided in Volume 1.

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Lessons learnt from interdisciplinary participatory research in the BIOTA project

Bettina Koelle*, Noel Oettle & Ute Schmiedel

Summary: BIOTA has been supported and carried by a range of research organisations, scientists and students as well as a range of local stakeholders. This article draws on research undertaken by Indigo development & change in collaboration with other BIOTA researchers about the interdisciplinary and participatory aspects of BIOTA, and reflects experiences of researchers as part of BIOTA and other larger interdisciplinary research processes. On the basis of these experiences and findings, recommendations are made regarding the planning and implementation of large research projects.

The BIOTA experience

Looking back at nine years of research in BIOTA Southern Africa

BIOTA Southern Africa engaged scientists from a number of research institutions in South Africa, Namibia, and Germany. BIOTA sought to deepen understanding of complex environmental dynamics related to diversity loss and climate change, and thus mobilised scientists from many disciplines to fill gaps in knowledge not only about the affected biophysical systems, but also about the behaviour and management of associated social-ecological systems. Management of these systems requires a fully integrated, interdisciplinary approach (Miller et al. 2008). The diversity of the research reflects the challenge inherent in integrating the various research disciplines and engaging meaningfully with affected stakeholders to ensure that the research findings do indeed contribute to improved land management practice by supporting improved decision making by land managers. The participating researchers in BIOTA applied a variety of methods to enhance the integration of disciplines and promote the effective dissemination of results (see also Article III.8.1). It was thus decided to document the rich and diverse learning processes from this project to allow future research initiatives to improve interdisciplinary research design and practice. A questionnaire survey was undertaken of participating researchers, and the results are summarised in this article.

Stakeholder involvement and scientist interaction

One key objective of the BIOTA research was to bring the results to the attention of landusers so as to improve land management practice. BIOTA therefore engaged in participatory research and planning processes where appropriate. To contribute effectively to the improvement of landuse practice it was imperative that the researchers should synthesise their findings and include the knowledge of landusers so as to ensure that practical and workable recommendations were made. In this light the integration of disciplines has been crucial. This aspect of the research was dependent upon the willingness of participating BIOTA scientists to share their insights and learning from the BIOTA processes they participated in.

Training to develop researchers capacity

In the course of the BIOTA Southern Africa process a strong focus was placed on the science–local stakeholders interaction. In this context some BIOTA scientists especially focussed on the effective communication with landusers and local municipalities. However, facilitation of interactive and participatory processes is often not part of the academic curriculum of BIOTA scientists and students, and after the first phase of the project, the need was expressed to develop capacities of research teams in this area. As a result a series of training courses was offered to BIOTA researchers to develop capacities in related areas. Training courses were convened in Hamburg in June 2005 and December 2007, Cape Town in February 2006 and March 2008, and Nieuwoudtville in October 2006. Each training workshop was documented and evaluated. Feedback in the evaluations following the training workshops was overwhelmingly positive. A respondent to the questionnaire survey noted that it was of great value to be able to attend the BIOTA capacity building events, particularly the workshop on interdisciplinarity. Back stopping was offered to researchers who wanted to include interactive processes with local stakeholders to enhance the learning processes. This resulted in an increased implementation of landuser–scientists interaction in the BIOTA Southern Africa project. It was also clear from the experiences in BIOTA that an ongoing support in facilitation of community interactions is important to ensure that the methods of the training workshops could be adjusted to suit local conditions and finally be applied in the field.

Methodology to document learning

In the course of implementing BIOTA Southern Africa, the interactive process was documented and analysed. This included BIOTA workshops, planning meetings and conferences, research publications, and ongoing processes. As it was not possible to document all interactions and collaborative efforts that took

Photo 1: Training workshop on facilitation and participatory GIS in South Africa. Photo: Bettina Koelle.

place within the lifespan of BIOTA, particular processes of relevance were selected, including some smaller and more informal processes and all of the larger co-ordination events. Experiences of some other interactions have been captured in the questionnaires submitted by individual participating researchers.

Many of the BIOTA research components focussed on highly specialised aspects of the ecosystems where the BIOTA Biodiversity Observatories were based (see Volume 1, Part II). However, in this article we focus on the inter- and transdisciplinary participatory aspects of BIOTA research that aimed at integrating various disciplines and, as far as possible, incorporating local knowledge.

Questionnaires were sent out to all BIOTA researchers who had participated in BIOTA in the course of the nine years of the project, including students, junior and senior researchers attached to academic and other research institutions. Respondents were invited to share their experiences, insights, and learnings. The responses were collated and analysed to provide an overview and to inform recommendations. A rich literature base exists regarding interdisciplinary and transdisciplinary research, and was drawn on in the process of formulating the recommendations. Acknowledging the fact that many researchers involved in other large interdisciplinary projects would also have valuable learning to contribute, participating researchers were encouraged to also share insights from other large research projects. Our reflection of the experiences within BIOTA is based on a broad range of literature on transdisciplinarity (e.g. Wohl 1955, Tuckman 1965, Max-Neef 1991, Mittelstrass 2001, Jacobs & Frickel 2009).

Learning from our practice— some findings

Planning the project and processes

Initiating the project

BIOTA Southern Africa drew upon a range of relevant disciplines so as to ensure that integrated solutions could be offered to landusers and other stakeholders—thus ensuring that the scientific knowledge was translated into improved livelihoods and resource management. BIOTA Southern Africa thus integrated a host of disciplines in a single joint approach. In order to draw on experiences in the first phase of the project, discussions were initiated with BIOTA partners from South Africa and Namibia in preparation for the second and third phases. Local steering committees in South Africa and Namibia and the co-ordination structure in Germany contributed to the active integration of disciplines. The Observatories also proved to be an important point of contact—and often resulted in spontaneous collaboration efforts of, in particular, junior scientists. As one respondent noted “communication (was enhanced when) students invest(ed) time in participating, as guests, in the data collection of other students. That increased understanding and respect of each other’s work tremendously. This was possible because we were all working at the same Observatories and had in common a problematique and a location for its analysis”.

In the light of the different paradigms and methodologies that the different project components were operating in, effective integration of research reflecting the complexity of the natural and social environments was a major challenge. Many respondents to the questionnaires expressed the view that a more formal approach of maintaining integrated research platforms would have helped the integration of disciplines and promoted a transdisciplinary approach. In the view of one respondent, BIOTA researchers encountered problems of perception and understanding in relation to trans- and interdisciplinary work, and inadequate integration took place between working groups. This observation can be associated with another respondent’s reflection that selection of the members of the BIOTA team was based on disciplinary excellence, but not necessarily on interest in inter- or transdisciplinary research. Another respondent called for “a work package ... that focuses purely on synthesising the science and the practical lessons learned”.

The degree of complexity of the problem being researched, and the range of methods that might be needed to understand it adequately, will indicate whether monodisciplinary or multidisciplinary research is appropriate. Even greater complexity might indicate a need for interdisciplinary or even transdisciplinary research (see Fig. 1). If the problem is situated at the interface between the natural world and human decision making, it is probably necessary to engage a range of disciplines from the natural and social sciences to adequately analyse the complex causal relationships, and to support the decision makers in making the necessary shifts in understanding and motivation to enable them to intervene effectively to improve the situation (Daily & Ehrlich 1999). BIOTA engaged scientists from the natural and social sciences to address the daunting problems of rural livelihoods, species loss and climate change in Africa. In this context BIOTA achieved inter- and sometimes even transdisciplinary integration.

Within any research team, there is a potential tension between the richness of the divergent knowledge bases, opinions and perspectives that individuals bring. Selection of team members who individually and collectively have the necessary ability to undertake the work and have the respect of their peers across disciplines is crucial to the success of interdisciplinarity or even transdisciplinarity. Daily & Ehrlich (1999) argue that a prerequisite of doing successful transdisciplinary and interdisciplinary work is to choose collaborators from among those who are respected in their home disciplines, whose contributions to joint work one can trust. BIOTA succeeded in assembling researchers with internationally renowned research expertise in the relevant fields, and their mutual respect was a characteristic of the entire process. However, respondents regarded the absence of a "master plan" for inter- and transdisciplinary work, or a research co-ordinator with specific responsibility for promoting disciplinary integration and synergies as a shortcoming.

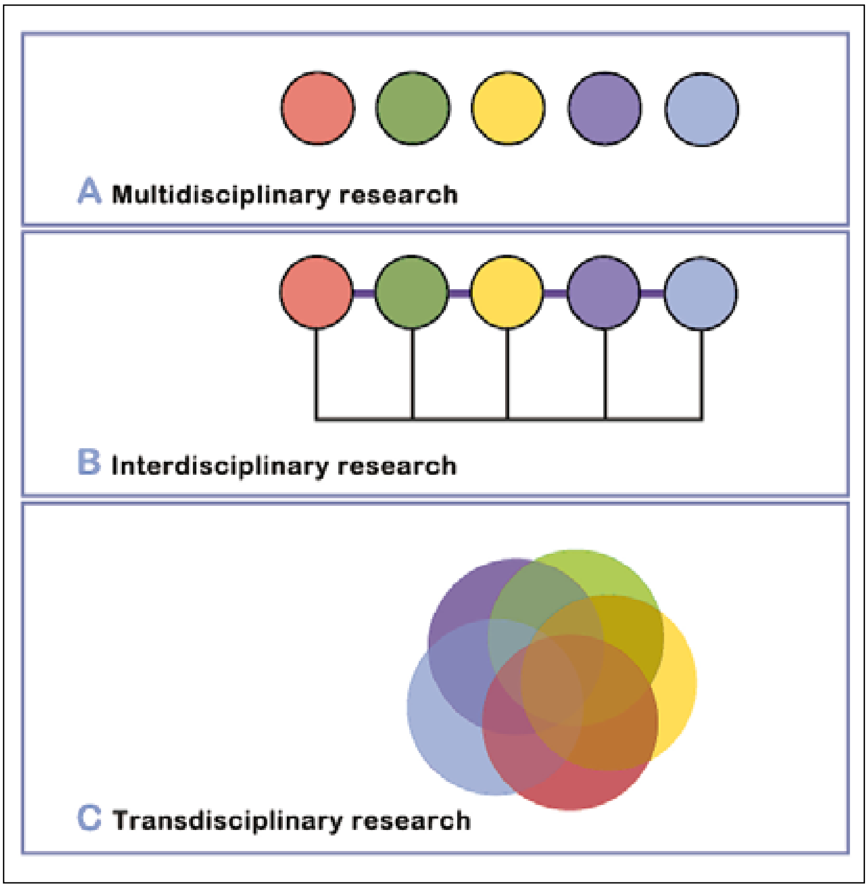

Fig. 1: Multi-, inter- and transdisciplinary research describe different levels of integration of various disciplines: interdisciplinary research means that the different disciplines collaborate, share knowledge and thus produce some integrated results. Transdisciplinary research includes the formulation of joint research questions, regular joint research processes of integrated research teams and thus profoundly integrated results (Max-Neef 2005).

On the other hand, within teams that conform too closely to a dominant paradigm or approach the phenomenon known as "group think" (Janis 1972: 9) can limit the ability of team members to think "outside the box". It is thus vital to ensure that members and potential members of the research team feel able to contribute ideas and concepts that may not conform to the dominant orthodoxy of the group, and to establish a group culture that welcomes critical thinking. If not, critical thinking may at best be regarded as an unnecessary nuisance, and at worst as subversive to the intent of the research process. In the view of respondents, the size of BIOTA, as well as the divergence of approaches and disciplines mitigated against this phenomenon, although within discipline-specific teams it may well have been a limiting factor.

BIOTA was structured with many semi-autonomous, disciplinary working groups, which generally functioned well. However, in the view of respondents little integration took place between working groups. Problems were exacerbated by a perceived "top down approach in communication patterns", associated with occasional insufficient transparency of communication.

Formulating the research questions

In the formative phase of shaping a project or initiative, it is important to engage a wider circle of stakeholders as early as possible. This engagement need not be a formal process to start with, and could be a series of conversations or informal meetings. However, if it is possible to create a true openness in terms of the research agenda that invites non-academic stakeholders to participate, it is likely that the planning phase will be well informed in terms of their interests, needs and requirements. This will also create a sound foundation for broad ownership of the research process and its findings later on.

In the formative phase, it is of great help to have resources committed to the development of the project concept and proposal. Some enlightened funders recognise this, and provide "project development funds". Funding of this nature allows people to travel and meet face to face, which greatly deepens and broadens their common understanding and enables them to develop the research undertaking on the basis of mutual respect and appreciation, coupled with more profound insight into the research question/s that will be addressed collaboratively. Questionnaire respondents noted a lack of funds to participate in joint learning

Photo 2: Communication and transparency are key. Photo: Bettina Koelle.

with other members of the team as a factor limiting interdisciplinary collaboration within BIOTA. However the joint annual team meetings and the steering committees were perceived to be positive to promote integration. The participatory process of designing the second and third phase was perceived as having enhanced integration and enabling joint research questions to be addressed.

Forming the research team

Team building is a process that should receive attention from the earliest stages. Even if the research idea is not yet clearly formed and funding is not yet committed, a facilitated process will help the co-researchers to form sound foundations for future collaboration. It is valuable at this stage to establish a set of common principles that the future partnership will be founded on. Charles McNeill of the UNDP (United Nations Development Programme) defined a useful set of principles for effective partnerships (McNeill, pers. comm. to N. Oettlé, 2002):

- Partnerships are built on trust and partnerships enhance trust.
- Effective partnerships require transparency and access to information.
- Partnerships must provide members with equal voice and shared decision-making responsibility, while recognising comparative advantage.
- Partnerships must be goal-oriented, results-driven and progress towards these results must be measurable.
- Partnerships must reflect local priorities and help create an enabling environment for effective action.

The values and hierarchical approaches of academic and scientific institutions are not necessarily consistent with these principles. However, jointly establishing the principles of collaboration that will guide the research undertaking can bolster it against divisive pressures.

In order to effectively integrate the necessary stakeholders into the research process the team should agree upon the boundaries of the research process. It is also important to define the area of research, and the wider arena that the research process seeks to inform and/or influence.

Allocating resources in a way that all partners will perceive as equitable is an important aspect of forming a functional interdisciplinary team. This requires a deeper level participation and transparency than is usual in other projects, where the lead agency allocates resources in consultation with partners, but frequently without full disclosure of the total budget available or the details of the trade-offs that must inevitably be made between competing claims on resources. If competing claims can be discussed in an open manner, creative resource allocation that serves the needs of all can be achieved, and reasonable compromises can be made.

Within BIOTA there was a strong recognition that effective team work is vital to the success of projects of this nature, and 50% of respondents had very positive experiences of partnership and collaboration. Good relationships, open mindedness and sound communication were also perceived by the respondents as contributing greatly to the success of the project. This does not imply that there was no room for improvement: 42% of the respondents to the questionnaire called for improved dialogue and communication within the research team.

Formulating the project proposal

Choice of research methodologies influences how the team functions internally and interacts with stakeholder communities. The choice of methodology will determine the sort of data obtained and influence the way respondents regard the research endeavour, the reliability of its results and the validity of the conclusions that are drawn from them. Extractive data gathering that does not engage the respondents as partners or co-researchers is likely to alienate them from the process, and they are unlikely to embrace its conclusions. In the natural sciences, data gathering in pursuit of research objectives that are not understood by local stakeholders might be perceived as intrusive, threatening or frivolous. For these reasons multiple methodologies will be necessary, and the team will need to explore how they can potentially be integrated or aligned, and need to be able to avoid deployment of methodologies that are fundamentally at odds with one another.

Drafting proposals for research funding that respond effectively to the donor call and/or other funding criteria, yet at the same time remain true to the requirements of interdisciplinary research can be a daunting task. Nevertheless, team work can mobilise the necessary experience, knowledge and insight to formulate an appropriate proposal that meets the donor's requirements whilst retaining the necessary integrity and allocating enough funding for interactive research processes.

BIOTA benefitted from being able to build upon the experiences of the first phase of the project in formulating the second, and finally the third phase. As one respondent noted, "learning has taken place within the structure of BIOTA, which was illustrated by the ... establishment of a different (less disciplinary) structure of work packages for the third phase of BIOTA".

Implementation

Establish and managing the working team

Following proposal approval, the lead agency is under pressure to sign all the necessary contracts so that the funds can be transferred and the research team can get down to work. However, at this stage it is vital clarify how the respective contributions of the team members will need to mesh together and how these commitments can be translated into contracts that reflect clear and achievable commitments. As noted by one respondent, BIOTA benefitted from strong and visionary leadership that was focused on the overall success of the project, and this translated into clear contractual obligations.

A common preliminary understanding of how their responsibilities should complement one another will provide a sound point of departure from which a healthy collective and individual responsibility for the research process and its outcomes can develop over time. One respondent referred to common misunderstandings within multidisciplinary projects concerning the roles of specific disciplines, leading to the perception that it is responsibility of some, and not others, to "do the talking with the farmers", or indeed "to turn a classic scientific approach into a transdisciplinary one".

Interdisciplinary research requires more time to be spent on interactive processes that monodisciplinary research. A respondent noted that "one challenge for the interdisciplinary exchange was certainly also that this process was not structured or organised a way that it automatically or inevitably became part of the process. This way it remained (dependent on) bilateral cooperation based on personal relationships or at least (individual) initiative". If this time is not adequately catered for in terms of budgetary allocations, and if team members do not have clear obligations to contribute their time to meetings and working groups, the process might founder from lack of engagement in team workshops, seminars and other processes that have been agreed to. An appropriate approach will enable partners to move away from rigid ideas about structure, relations or practical aspects of what the necessary tasks are, and how they should be undertaken. Flexibility is essential for the processes of negotiating the methodological and disciplinary aspect of the collaborative research undertaking.

Managing processes and resolving conflicts

The importance of formal contracting of partners to undertake their research in an interdisciplinary manner should not be allowed to diminish the equal prominence that should be given to formulating team contracts that describe not only what will be done by whom, but also the manner in which it will be done and the principles that will be upheld by team members. Such "team contracts" should be living documents that draw on the norms and values of the team members, reflect their knowledge and insights and also respond to emerging experiences and learning within the research process. Team contracts are best drawn up interactively in a facilitated process that ensures that all points are consensually agreed upon and supported. If not, the contract will have little value. The team contract should provide a valuable platform for reflection and adjustment at all future meetings of the research team.

In the course of all human endeavours and undertakings, conflict of some sort is inevitable. In research teams it occurs not only in the "storming" phase, but to a lesser extent in all phases of implementation. Conflict can cripple collaborative work, and indeed undermine the very basis of the research undertaking if it is not managed effectively. On the other hand a certain amount of creative tension between team members may also provide opportunities for learning and change.

Ensure that all team members embrace the concept that all feedback provides rich opportunities for learning and improvement, even if this is not immediately obvious and the criticism is felt to be negative or even destructive. A culture of valuing feedback can be developed if both giver and receiver keep in mind the notion that "feedback is a gift".

Creating exchange platforms

Communication between disciplines and in fact individual researchers and local stakeholder is key to allow synergies to emerge and to formulate integrated solutions. In the BIOTA context, sharing information with stakeholders was seen by one respondent as "important but ... not essential to the success of the project". The respondent was concerned that researchers undertook planned research in good faith, and subsequently "fed it back to the stakeholders, hoping it would help them". This statement reflects the importance of ensuring that research questions address the felt needs of stakeholders, of communicating findings in ways that address these needs.

It is sometimes assumed that feedback to stakeholders is process that can take place successfully without structure or facilitation. Whereas this is sometimes the case, the constraints of research practice frequently oblige the researcher to engage in key activities of the research before considering processes. As such it is crucial that the project design includes research platforms and that the process in these is carefully facilitated throughout the project cycle. The format of these platforms may vary and should be supported by all team members including the local stakeholders if and when appropriate. If interdisciplinary engagement is part of the core activities of each researcher it will get the attention and focus that is needed to formulate integrated synthesised research outcomes that can inform land management practice.

Bridging the gaps between disciplinary perspectives demands more active engagement with the norms and processes of science in the development of interdisciplinary research (Miller et al. 2008). The BIOTA experience was that more attention should be given to supporting and advancing interdisciplinary work. In a vastly ambitious research undertaking such as BIOTA, it is vital to identify the steps that are necessary to synthesise the findings. A critical mass of researchers in any research project must pay adequate attention to following these steps and achieving a meaningful intellectual synthesis of all of the findings (MacMynowski 2007). This will enable those who subsequently use the research findings to more easily avoid applying simplistic solutions that merely provide temporary relief and leave new and more daunting sets of challenges in their wake.

BIOTA brought together participating scientists from the natural and social sciences on a number of occasions throughout the life of the project to share knowledge and experiences, and to jointly plan the future of the project. In the course of these meetings research questions were formulated or re-formulated, and difficulties and possible solutions to these were discussed. Research findings were presented and critically reflected on by other members of the projects team. Access to a broad range of disciplines within the project team was identified by 25% of respondents to the questionnaire survey as an important strength of the project. These strengths no doubt also contributed to the experience of 25% of respondents of good collaboration in generating publications based upon BIOTA.

Including local knowledge

Local knowledge has been widely recognised as important knowledge that can make a significant contribution towards our research results (Pretty 1995). Even more importantly is the exchange of scientists and local knowledge holders to ensure that all possible aspects are included in developing integrated solutions to complex problems. The participation of local stakeholders in a true partnership approach can also support the later implementation of jointly formulated solutions as they do not require an extension phase.

33% of respondents to the questionnaire saw a need for enhancing stakeholder communication, recognising that this is essential to improving participation and uptake of research findings. BIOTA trained members of the local stakeholder communities as para-ecologists (see Article III.8.3). The para-ecologists served as research assistants, and they played an important role in linking the project more closely with the land users. 17% of the respondents in the questionnaire survey stated that the role of para-ecologists should be strengthened in future projects.

Conclusions

In conclusion, the planning and preparation phase of a project is crucial to ensure a structure, team constellation and underlying processes that will ensure integrated and synthesised research results that will ultimately result in practical solutions to complex problems. The planning process should lay the groundwork for teamwork that enables the members to interact effectively, to take responsibility for addressing the inevitable conflicts, frustrations and inadequacies, and to learn effectively from one another within and beyond the bounds of their disciplinary expertise. Furthermore, the planning process should include the wider group of stakeholders, and establish the basis for developing robust relationships with the members of this group. In this way the foundations can be established for a set of processes that will carry the research process forward for years to come.

The social factors of trust, cooperation, patience, and openness are as important to interdisciplinary success as the ideas themselves (Daily & Ehrlich 1999). The importance of trust within the research team cannot be overemphasised if the team is to function well and produce integrated results. Trust is crucial in the realms of sharing data with fellow scientists and other stakeholders, in the discourse and exchange of ideas and ultimately in joint publications.

Discipline-specific terminology and jargon poses a challenge to effective communication within the team. Appropriate and creative communication within the team can address some of these challenges and broaden understanding of the methods employed and the findings themselves. Creating formal discussion platforms to discuss complex issues including several disciplines, and creative team processes using “softer” technologies and methods of interaction and exploration of knowledge can enable team members to establish different sorts of rapport amongst one another, and can validate and make accessible other forms of knowledge.

Interdisciplinary research is not sufficiently rewarded in academic systems to encourage many scientists to venture into this complex field. Within the BIOTA project interdisciplinary work tended to be regarded as an additional commitment that scientists were expected to contribute to, over and above the excellent scientific work that they were expected to produce within their primary discipline. Fortunately the academic landscape is slowly changing, and ever more peer reviewed journals are focussing on integrated science. This is promising as the global climate change debate demands more integrated research results to address the complex and enormous challenges facing humankind.

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BIOTA transect and the Biodiversity Observatories in southern Africa.

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Number, name and respective biome of the BIOTA Biodiversity Observatories. Page number refers to the description of the Observatory in Volume I.

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Biodiversity is important for sustaining life on Earth yet it is threatened globally. The BIOTA Southern Africa project analysed the causes, trends, and processes of change in biodiversity in Namibia and western South Africa over nearly a full decade, from 2001 until 2010. This book, which is comprised of three volumes, offers a summary of the results from the many and diverse subprojects during this first period of long-term observation and related research, at both local and regional scales, and with a focus on sustainable land management options for the region.

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