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

Luciana Zedda*, Alexander Gröngröft, Matthias Schultz, Andreas Petersen, Anthony Mills & Gerhard Rambold

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

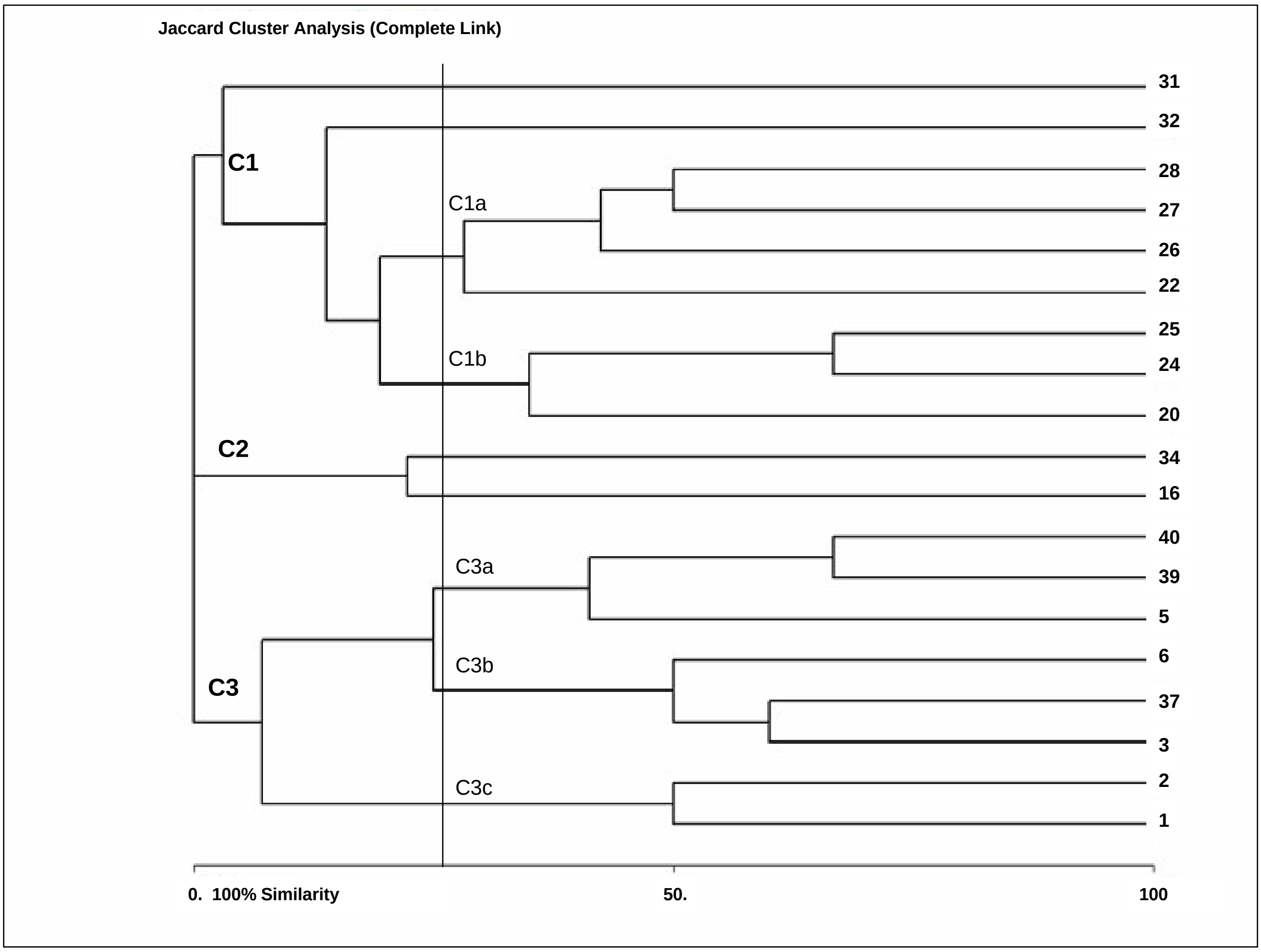

Fig. 1: Similarity between Observatories on the basis of their lichen composition.

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.

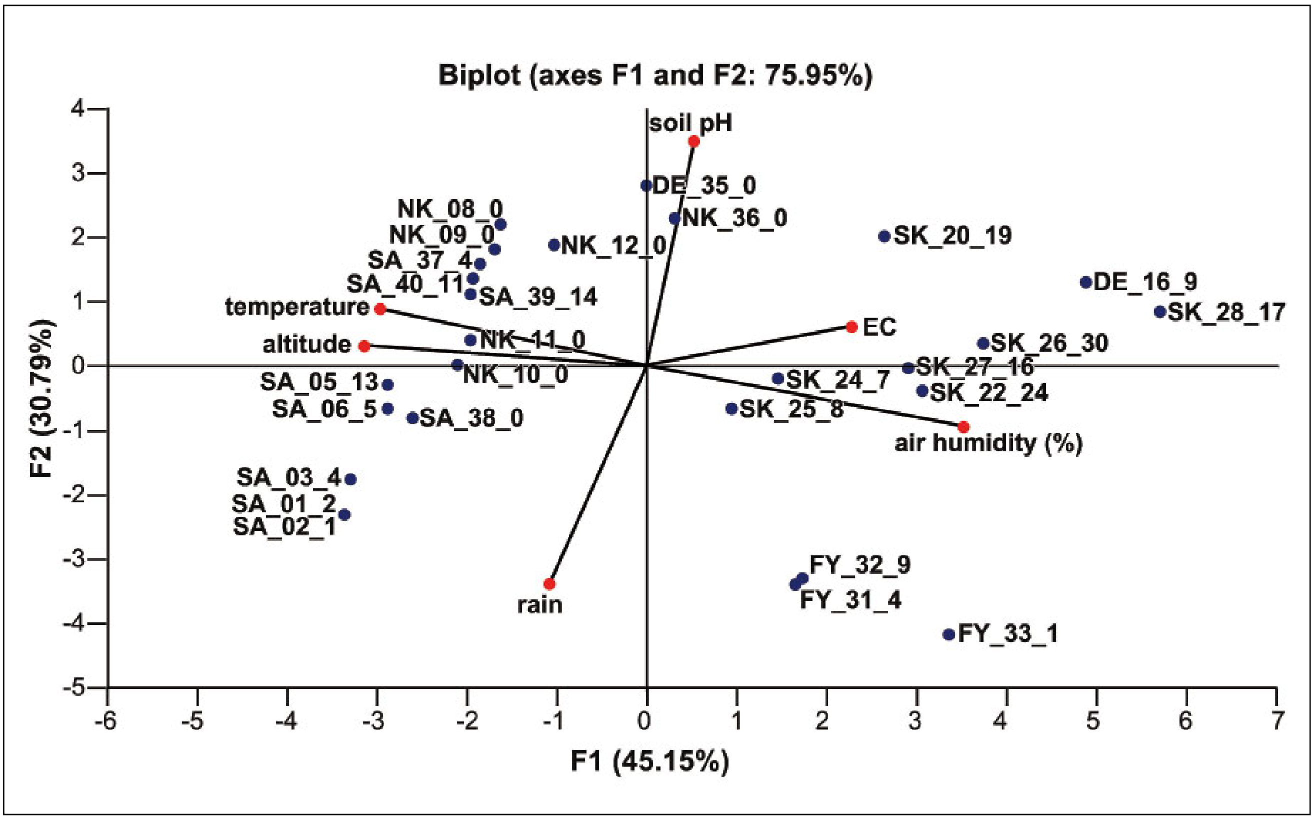

Fig. 2: PCA ordination plot of investigated sites according to main environmental parameters. Designation of sites include indication of biome type (DE = Desert, FY=Fynbos, NK= Nama Karoo, SA = Savanna, SK = Succulent Karoo), Observatory number (e.g. 27) and lichen species richness.

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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