



# Morphological groups as a surrogate for soil lichen biodiversity in Southern Africa

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**Abstract:** To establish a routine procedure for surveying lichen diversity in biological soil crusts across different biomes in Southern Africa (Namibia and the western part of South Africa), the use and analysis of digital plot images proved to be most effective. Soil lichen taxa were classified into ‘morphological groups’ (MGs) which could be easily recognized by imaging systems. MGs were defined by the presence and variance of two macro-morphological traits (growth form and colour of the thallus surface) and the type of the primary lichen photobiont. A classification is presented. The distribution of the various lichen MGs and their cover were assessed by analyzing soil surface digital images. Richness of lichen species and MG cover were compared on the basis of these image data. Results show that lichen richness at hectare plot and at 1 km<sup>2</sup> level strongly correlates with lichen morphogroup richness, while the total lichen cover on the same plot has a weaker relationship with species and MG richness. Lichen richness at the hectare plot level is strongly associated with morphogroup richness, and is correlated with increasing air humidity and winter rainfall but negatively linked with higher temperatures. The use of morphogroups corresponds to the temporal and spatial cover of soil lichen biodiversity in Southern Africa, with no significant loss of relevant information.

**Keywords:** biodiversity, monitoring, morphological groups, soil lichens, Southern Africa

## Introduction

Lichens are among the most frequently used bioindicators for monitoring environmental changes. In arid and semi-arid regions of the world, they have only re-

cently been used for detecting the intensity of human disturbance and the effects of global climate change on terrestrial ecosystems (BELNAP et al. 2001a, 2001b; ROSENRETER & ELDRIDGE 2002).

There are more than 100 soil lichen taxa listed from Southern Africa (SCHIEFERSTEIN & LORIS 1992, JÜRGENS & NIEBEL-LOHMANN 1995, RAMBOLD et al. 2001–2009, ZEDDA & RAMBOLD 2004, 2009, WIRTH et al. 2007, SCHULTZ et al. 2009). A large number of these (73) were recorded from different sites located in Namibia and western South Africa and correlations of distribution patterns with climate (rainfall seasonality, air humidity, fog, dewfall and temperature) and with given soil features (pH, electroconductivity) were pointed out by ZEDDA et al. (2011). Many of the soil-inhabiting lichen species of Southern Africa, however, are still poorly known or not described and in general are difficult to identify in the field without optical aid. Problems with identification, especially of small or sterile thalli, can make monitoring of soil lichens most challenging. To overcome these problems in a survey, lichens may be classified into morphologically distinguishable groups, based on a selection of traits easily recognized in the field by a human operator as well as by imaging applications. This approach is supported by the strong morphological relations and congruent morphology also in phylogenetically unrelated taxa due to their parallel morphological response to specific environmental conditions (BELNAP et al. 2001a). The identification of morphological groups by non-phylogenetic classifications has been primarily applied to higher plants. Interest in applying the functional group concept has grown over the past few years, particularly as an approach for predicting species, community and ecosystem responses, e.g., biodiversity decline due to human impact (CORNELISSEN et al. 2007, FRANKS et al. 2009).

Hitherto, lichen morphological groups have been little used for investigating the effects of land use on lichen diversity and very little is known about their functional traits. This means that the patterns or trends in the relative importance of given lichen traits along different kinds of gradients (i.e., land use or climatic ones) have been poorly investigated (STOFER et al. 2006). Nevertheless, STOFER et al. (2006) did use this approach to identify patterns of epiphytic lichen functional groups along a land use gradient across Europe, as a way to avoid the problems linked to the variability of species composition found within the different European biogeographic regions. A classification of soil lichens into morphological groups from arid to semi-arid regions in Australia and North America was firstly proposed and applied by ELDRIDGE & KOEN (1998) and by ROSENRETER & ELDRIDGE (2002), who defined them as “superficially similar species that are difficult to differentiate in the field, but which possess similar morphologies and function”.

The present study aims to obtain a robust classification of groups with similar morphology among Southern African soil-inhabiting lichens. The working hypothesis is that there is a relationship between species richness, measured at different scales, and morphogroup richness. The study also tests whether lichen cover is related to lichen richness or to the richness of morphogroups. Furthermore, the work intends to analyse the distribution of lichen richness at different sites, located along a climatic gradient from northern Namibia to the Cape Peninsula in South Africa, and to compare this with the richness of lichen morphogroups at the same sites. Finally, the relationship with selected

environmental factors and the richness and cover of lichens and of their morphogroups are investigated. It is hypothesized that lichen morphogroups can be effectively used for soil lichen monitoring, based on the assumption that strong correlations do in fact exist between selected lichen traits and environmental conditions as well as between lichen morphological traits and ecological preferences.

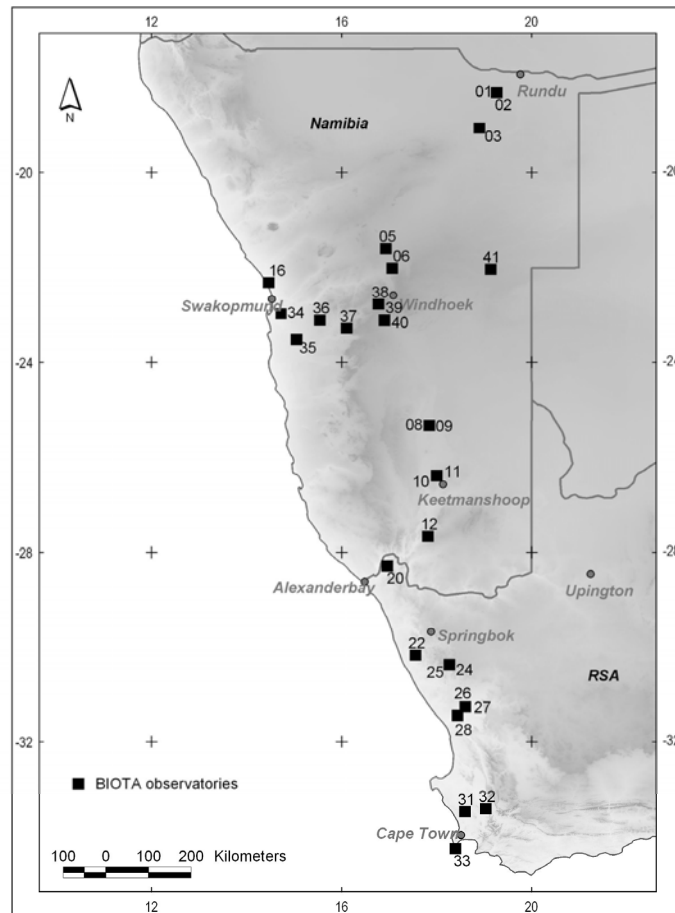
### Material and methods

**Study area:** Investigation sites are located along a climatic and vegetation gradient (= transect) in Namibia and the western part of South Africa (Fig. 1). They represent all main five biomes of the study area, whose ecological conditions are summarized in Table 1. Precipitation has a clear gradient from north to south and from west to east over the entire area. Isotherms predominantly run parallel to the coast. The highest temperatures are recorded in areas with the highest degree of continentality (WERGER 1986). More detailed information on each investigated site is available online ([www.biota-africa.org](http://www.biota-africa.org)).

**Field work:** Lichen collecting and measurements of lichen cover by morphogroups were carried out at 25 investigation sites corresponding to the observatories of the BIOTA project (Biodiversity Monitoring Transect Analysis in Africa) which are used for standardized, interdisciplinary biodiversity research. These are 1 km × 1 km (= 1 km<sup>2</sup>) in size and are subdivided into 100 one-hectare plots for biodiversity monitoring at different scales (SCHMIEDEL & JÜRGENS 2005). Initially, a general floristic survey of each site was carried out to assess lichen diversity at 1 km<sup>2</sup>-scale. All different lichen species found on the soil were collected and identified.

For analysis of lichen richness and cover at ha-plot level, 10 1-ha plots were chosen randomly in each site, following the BIOTA ranking conventions. Selected ha-plots covered the different habitat strata of the site, and were surveyed by taking ground digital images of plots with a size of 2000 to 3600 cm<sup>2</sup>. These plots were located immediately north of the 1-ha plot centre point. In total, 271 1-ha plots were investigated along the large-scale climatic transect. Species occurring in the photographed plots were identified in the field. Where ad-hoc identification was not possible, representative samples of the unknown taxa were collected in close proximity to the photographed plot for subsequent identification in the laboratory. This only concerned taxa actually present in the photographed plot and occurring on a range of maximum 1 m. The lichens occurring within the sampling plot were not collected, to permit a future long-term monitoring of lichen MGs. Sampling was carried out in the years 2001–2007.

Most climate data (rainfall, temperature and relative air humidity) were recorded in the field at each site during the period 2001–2009 by the BIOTA project. Images were taken with a SLR digital camera fixed on an aluminium square-shaped frame support, which made it possible to take image sequences of the ground. The image stitching method was preferred over a general picture of the ground, as it provided higher resolution of necessary detailed structures. Methods are described in more detail on the BIOTA Southern Africa website ([http://biota-africa.uni-bayreuth.de/wiki/Main\\_Page](http://biota-africa.uni-bayreuth.de/wiki/Main_Page)).



**Fig. 1.** Map of the study area with location of the investigated sites.

**Lichen identification and trait selection:** Lichen identification was carried out in the laboratory by means of morpho-anatomical and chemical analyses. Lists of all taxa recorded on soil were published by SCHULTZ et al. (2009), ZEDDA & RAMBOLD (2004, 2009), and ZEDDA et al. (2010), and also include several saxicolous species on small pebbles. Table 2 contains a list of species and their frequency at the sampling plots. Specimens were deposited in the lichen collections of the herbaria PRE (Pretoria National Herbarium, RSA), WIND (National Botanical Research Institute, Windhoek, Namibia) and M (Botanische Staatssammlung München, Germany).

Primary lichen photobiont and two major macro-morphological traits (growth form, colour of the thallus surface) were selected according to ROSENTERER & ELDRIDGE (2002) as traits indicating most ecologically distinct habitats and most closely linked to climate changes. On the basis of molecular analyses of the photobiont of terricolous lichens occurring along the same climatic gradient, this trait is also considered important and closely related to climatic factors (in prep.). The three selected traits, being broken down into 19 character states (RAMBOLD et al. 2001–2010), are all easily recognized in the field and by digital analysis systems (Tab. 3).

**Table 1.** Investigated sites across the different biomes of Southern Africa and ecological conditions characterizing the biomes. Site codes correspond to BIOTA observatory numbers.

<b>Biome</b>	<b>Sites</b>	<b>Rainfall Seasonality</b>	<b>Rainfall [mm, yr<sup>-1</sup>]</b>	<b>Temperature [°C, yr<sup>-1</sup>]</b>	<b>Air Humidity [%]</b>	<b>Altitude [m a.s.l.]</b>
Savanna	01, 02, 03, 04, 05, 06, 38, 39	summer	200–600	20–21	<40	1100–1800
Namib Desert	16	summer	<50	16	>85	70
Nama Karoo	08, 09, 10, 11, 12, 37	summer	100–350	20–21	<40	900–1100
Succulent Karoo	20, 22, 24, 25, 26, 27, 28	winter	100–250	16–24	60–75	130–1050
Fynbos	31, 32, 33	winter	250–600	16–18	60–85	80–150

**Table 2.** List of taxa recorded from the sampling sites, name abbreviation and absolute frequency at the investigated plots.

<b>Taxon</b>	<b>Abbreviation</b>	<b>Frequency</b>
<i>Collema coccophorum</i>	COLCO	65
<i>Placidium squamulosum</i>	PLASQU	37
<i>Psora crenata</i>	PSOCR	34
<i>Placidium tenellum</i>	PLATEN	32
<i>Toninia australis</i>	TONAU	19
<i>Toninia lutosa</i> s. lat.	TONLU	15
<i>Heppia despreauxii</i>	HEPDE	14
<i>Teloschistes capensis</i>	TELCA	10
<i>Xanthoparmelia walteri</i> s. lat.	XANWA	10
<i>Caloplaca elegantissima</i>	CALEL	9
<i>Lecidella crystallina</i>	LEDCRY	9
<i>Neofuscelia dregeana</i> s. lat.	NEODR	9
<i>Caloplaca testudinea</i>	CALTE	8
<i>Caloplaca volkii</i>	CALVO	8
<i>Xanthoparmelia simulans</i>	XANSI	8
<i>Peccania subnigra</i>	PECSU	7
<i>Peltula patellata</i>	PELPA	7
<i>Ramalina</i> sp.	RAM01	7
<i>Caloplaca</i> sp. 1	CAL01	6
<i>Xanthoparmelia</i> aff. <i>imitatrix</i>	NEOIM	6
<i>Peccania</i> cf. <i>arabica</i>	PECAR	6
<i>Acarospora</i> sp. 1	ACA01	4
<i>Cladonia symphyicarpea</i>	CLASY	4
<i>Eremastrella crystallifera</i>	ERECR	4
<i>Lichinella stipatula</i>	LICST	4
<i>Peccania fonte-queriana</i>	PECFO	4

**Table 2.** List of taxa (continued).

<b>Taxon</b>	<b>Abbreviation</b>	<b>Frequency</b>
<i>Peltula radicata</i>	PELRA	4
<i>Xanthoparmelia leonora</i>	XANLE	4
<i>Xanthoparmelia</i> sp. 1	XAN01	4
<i>Buellia</i> sp. 1	BUE01	3
<i>Buellia</i> sp. 2	BUE02	3
<i>Buellia</i> sp. 5	BUE05	3
<i>Heppia arenacea</i>	HEAR	3
<i>Lichinaceae</i> sp. 1	LIC01	3
<i>Psora decipiens</i>	PSODE	3
<i>Collema tenax</i>	COLTE	2
<i>Diploschistes hensseniae</i>	DIPHE	2
<i>Paraparmelia prolata</i>	PARPRO	2
<i>Toninia ruginosa</i>	TONRU	2
<i>Toninia</i> sp. 1	TON01	2
<i>Xanthoparmelia terricola</i>	XANTE	2
<i>Anthracoarpon virescens</i>	ANTVI	1
<i>Bacidia</i> sp. 1	BAC01	1
<i>Cladonia cervicornis</i>	CLACE	1
<i>Diploschistes</i> cf. <i>thelenelloides</i>	DIPTE	1
<i>Endocarpon</i> sp. 1	END01	1
<i>Phloeopeccania pulvinulina</i>	PHLPU	1
<i>Placidium semaforensis</i>	PLASE	1
<i>Toninia cerebriformis</i>	TONCE	1
<i>Xanthoparmelia amphinxanthoides</i>	XANAM	1
<i>Xanthoparmelia crassilobata</i>	XANCR	1
<i>Xanthoparmelia epigea</i>	XANEP	1
<i>Xanthoparmelia hyporhytida</i>	XANHY	1

**Table 3.** Description of classified lichen morphogroups and trait states used for the classification.

	<b>Growth Form</b>	<b>Colour of Thallus</b>	<b>Photobiont</b>	<b>Most Representative Genera</b>
<b>MG01</b>	squamulose	pink	algae	<i>Psora</i>
<b>MG02</b>	squamulose	brown	algae	<i>Placidium, Eremastrella, Endocarpon, Verrucaria, Anthracocarpon</i>
<b>MG03</b>	squamulose, foliose to subfruticose	black	cyanobacteria	<i>Collema, Peccania, Lichinella, Phloeopeccania</i>
<b>MG04</b>	squamulose	whitish grey	algae	<i>Buellia, Toninia</i>
<b>MG05</b>	crustose	pale brown (beige)	algae	<i>Diploschistes, Lecidella, Caloplaca</i>
<b>MG06</b>	foliose	yellowish green	algae	<i>Paraparmelia, Xanthoparmelia</i>
<b>MG07</b>	crustose	orange to orange-red	algae	<i>Caloplaca</i>
<b>MG08</b>	squamulose	brownish grey	algae	<i>Toninia</i>
<b>MG09</b>	crustose	yellow	algae	<i>Acarospora</i>
<b>MG10</b>	foliose	black	algae	<i>Neofuscelia</i>
<b>MG11</b>	peltate, squamulose	brownish green (olive)	cyanobacteria	<i>Peltula, Heppia</i>
<b>MG12</b>	fruticose	greenish grey	algae	<i>Ramalina</i>
<b>MG13</b>	fruticose	orange to orange-red	algae	<i>Teloschistes</i>
<b>MG14</b>	primary squamulose thallus	greenish grey	algae	<i>Cladonia</i>
<b>MG15</b>	placoid	orange to orange-red	algae	<i>Caloplaca</i>



**Data analysis:** A hierarchical, agglomerative clustering method was applied to a matrix of taxa by trait states in order to extract emergent groupings of taxa (i.e. morphogroups), using the XLSTAT 2008 software (Bray-Curtis Cluster analysis, Complete Link). A Mantel Test (Two-tailed test) based on two dissimilarity matrices calculated by Euclidean distance (matrix A = lichen taxa occurring at the different hectare plots; matrix B = occurrence of trait states in the same lichen taxa) was performed with the same application. The p-value was calculated using the distribution of  $r(AB)$  estimated from 10,000 permutations. Scatter plots and related correlation significance tests were performed with the Statistica 7.0 software, in order to analyse the relationships between lichen taxa, morphogroups (here as ‘MGs’) and cover (%). Box plots were performed with the same software to show variance in mean richness of lichen taxa and of morphogroups at the different sites placed along the climatic gradient. Significance was tested in all cases at a minimal level  $p = 0.05$ . PCA analysis was carried out with XLSTAT 2008 to test the relationships between selected environmental factors (precipitation, temperature and rainfall seasonality, percentage of higher plant cover, lithic cover and altitude) and total lichen cover (%), richness of lichen species and richness of MGs per sampling plot.

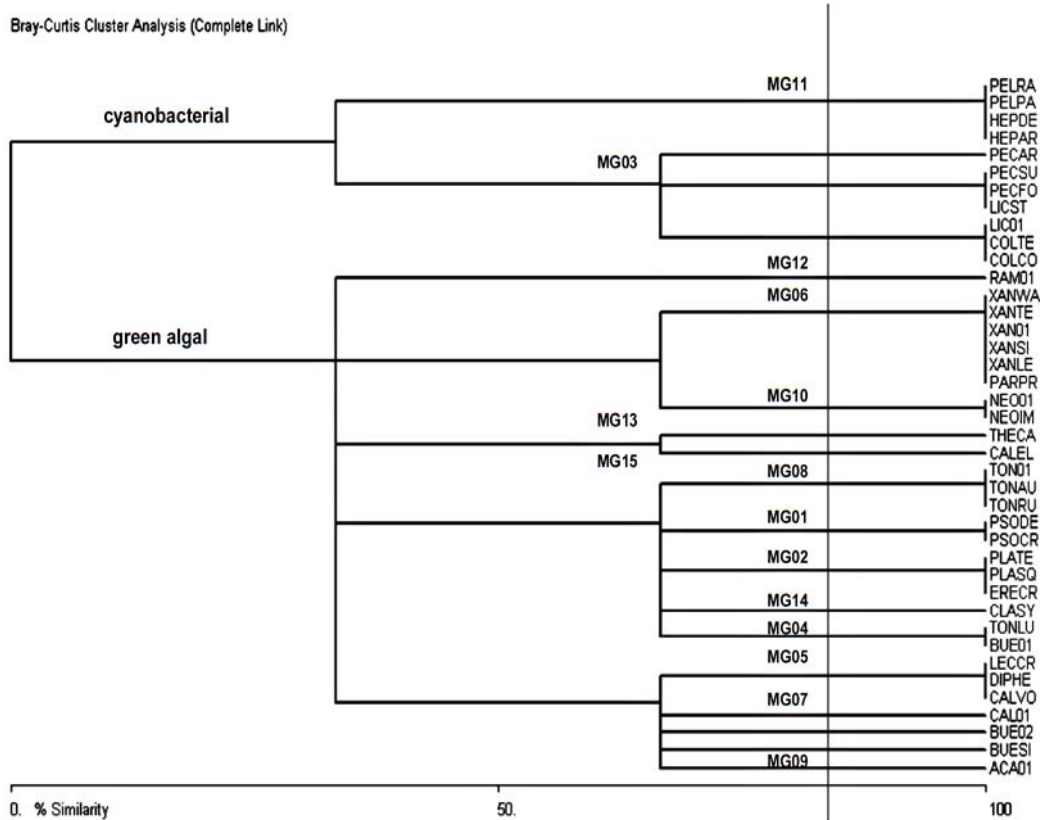
**Image processing:** Within the photographed plot, a cut-out of 20 cm × 50 cm (1000 cm<sup>2</sup>) was selected for image processing (= sampling plot). This size was found to be representative of the whole plot, and has been frequently used in other studies on biological soil crusts (BELNAP et al. 2001a, 2001b). Two image processing steps were applied to quantify the percentage cover of the lichen morphogroups and other biotic and abiotic objects. Firstly, images were colour-calibrated using Adobe Photoshop, an essential adjusting step for images taken under different light conditions. In the second step, images were classified by using the object-oriented application eCognition v. 4.1, which can recognize the different elements of one picture on the basis of both their pixel values and their form. For further details on these methods see the BIOTA Southern Africa website ([http://biota-africa.uni-bayreuth.de/wiki/Main\\_Page](http://biota-africa.uni-bayreuth.de/wiki/Main_Page)).

## Results

Lichens are present at 111 (41%) of the 271 examined 1-ha plots. Of the 73 recorded taxa for the BIOTA observatories (ZEDDA et al. 2010b), only 53 are found in the photographed sampling plots within each 1-ha plot. The most common species are *Collema coccophorum* Tuck. (at 24% of the plots), *Placidium squamulosum* (Ach.) Breuss (14%), *Psora crenata* (Taylor) Reinke (13%) and *Placidium tenellum* (Breuss) Breuss (12%). All other species have a rate of occurrence of less than 7% and 41 species occur at least at two different 1-ha plots (Tab. 2).

Different morphogroups emerge from the classification of species recorded in at least two different 1-ha plots (Fig. 2). The basal furcation in the dendrogram corresponds to the photobiont type, cyanobacterial versus green algal species. Among the cyanobacterial lichens, one group separates based on the peltate growth form and the olive-brown thallus colour. These are species belonging to the genera *Heppia* and *Peltula*. They form a well-delimited morphogroup

(similarity 100%) named MG11. The second group of cyanobacterial lichens, on the contrary, is phylogenetically heterogeneous and diverse in growth form, with *Collema* being foliose, *Lichinella* small fruticose and *Peccania* squamulose and fruticulose. Despite their diverse growth forms, species of this group are not easily distinguishable from one another in the field or in a digital image, as they are usually very small. Therefore, they have been included in one morphogroup (**MG03**), which corresponds to the cluster formed at a similarity level of 65%.



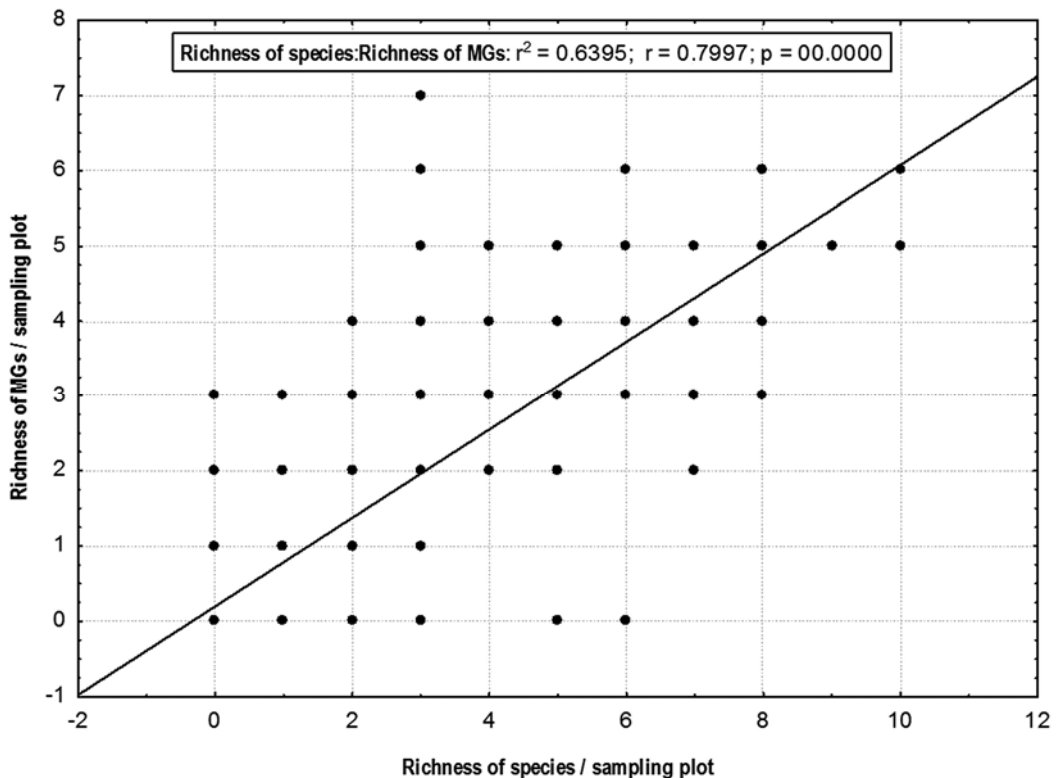
**Fig. 2.** Classification of most common lichen taxa (41) according to the selected morphological trait states (see Tab. 2 for taxa abbreviations).

Within the main cluster of the green algal lichens, MG12 is separated from the remaining groups by including only species of *Ramalina* with fruticose growth form and a greenish-grey pigmentation. MG06 and MG10 share a foliose growth habit, but differ in the pigmentation of the thallus upper surface, the members of MG06 being yellowish-green and those of MG10 being blackish-brown. All should belong to the genus *Xanthoparmelia* according to Blanco et al. (2004), and include the former genus *Neofuscelia* (MG10). MG13 and MG15 have in common the orange-red pigmentation of the thallus, but differ substantially in their growth form, MG13 being fruticose (*Teloschistes*) and MG15 placodioid crustose (*Caloplaca*).

Morphogroups MG01, MG02, MG04, MG08 and MG14 share the squamulose growth form. They differ, however, in the colour of the thallus, as members of MG01 (*Psora*) have a pink-brownish thallus, those of MG02 are pigmented brown [*Placidium* and *Eremastrella crystallifera* (Taylor) Gotth. Schneid.], of MG04

have a pruinose, whitish-grey thallus surface, and include *Buellia* with a subsquamulose thallus and *Toninia*, species of both genera being difficult to distinguish without considering ascomal and ascospore characters. MG08 also includes *Toninia* species, but only those with a darker, brownish-grey, thallus surface. *Cladonia* spp. with a squamulose to small foliose, greenish-grey pigmented primary thalli are representative of MG14. Crustose MG05 and MG07 are represented by species of *Diploschistes*, *Lecidella* and *Caloplaca* with pale brown (beige) thallus surface (MG05) and *Caloplaca* species with orange thallus surface (MG07). Species of genus *Acarospora*, with yellowish crustose thallus form MG09. The features of the different morphogroups and the selected trait states are summarized in Tab. 3.

The richness of MGs in the sampling plots is significantly and linearly related to the richness in lichen taxa in the same plots (significance values are reported in the graphs) (Fig. 3). The total amount of lichen cover in the sampling plots is also positively correlated with the richness of lichen taxa (Fig. 4) and of MGs (Fig. 5), but this relationship is weaker ( $R^2 = 0.11$  and  $R^2 = 0.19$ , respectively). The relationship between mean richness in lichen taxa at the sampling plots and total number of species found within the entire 1-km<sup>2</sup> site is also positive and significant (Figs 6 & 7). Similar results are obtained if the mean richness of MGs at the investigated hectare plots is correlated with the total species richness of the 1-km<sup>2</sup> site.



**Fig. 3.** Scatter plot of richness of lichen morphogroups in the sampling plots vs. species richness in the same plots.

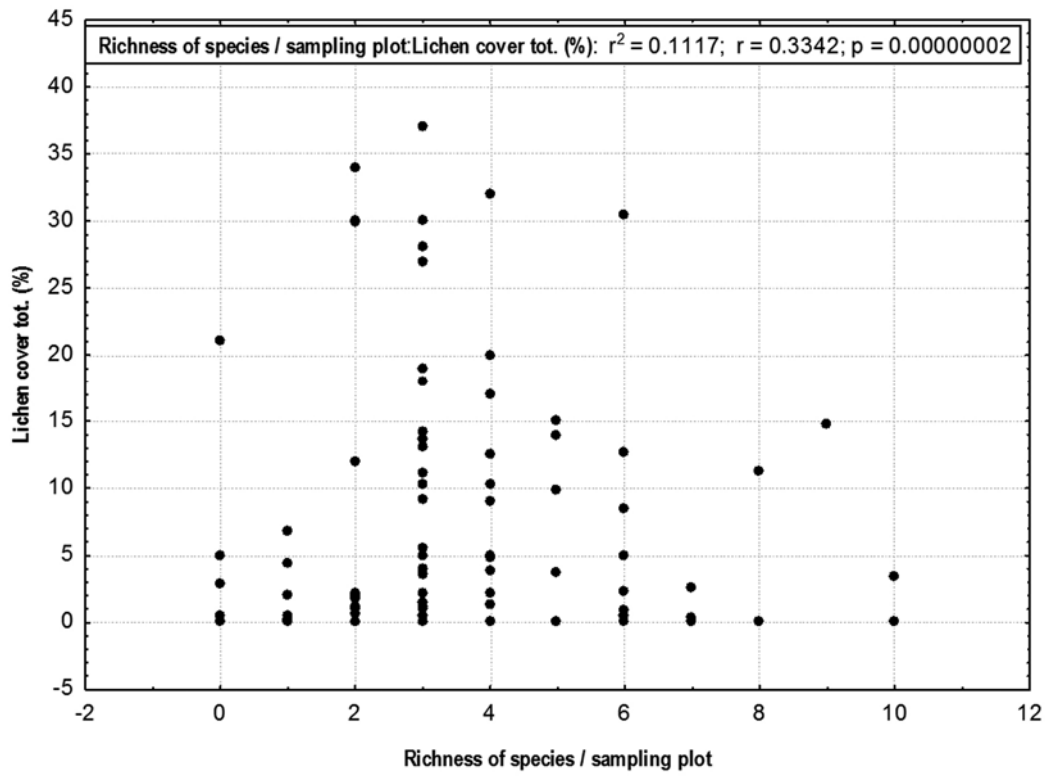


Fig. 4. Scatter plot of total lichen cover vs. species richness/sampling plot.

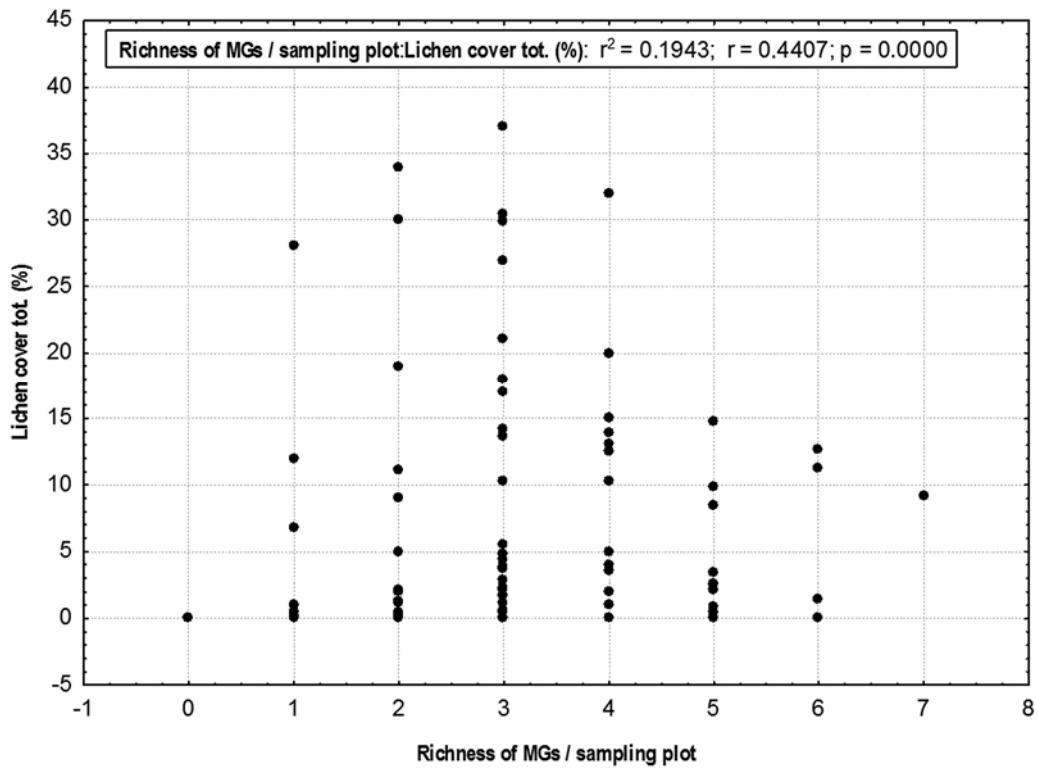
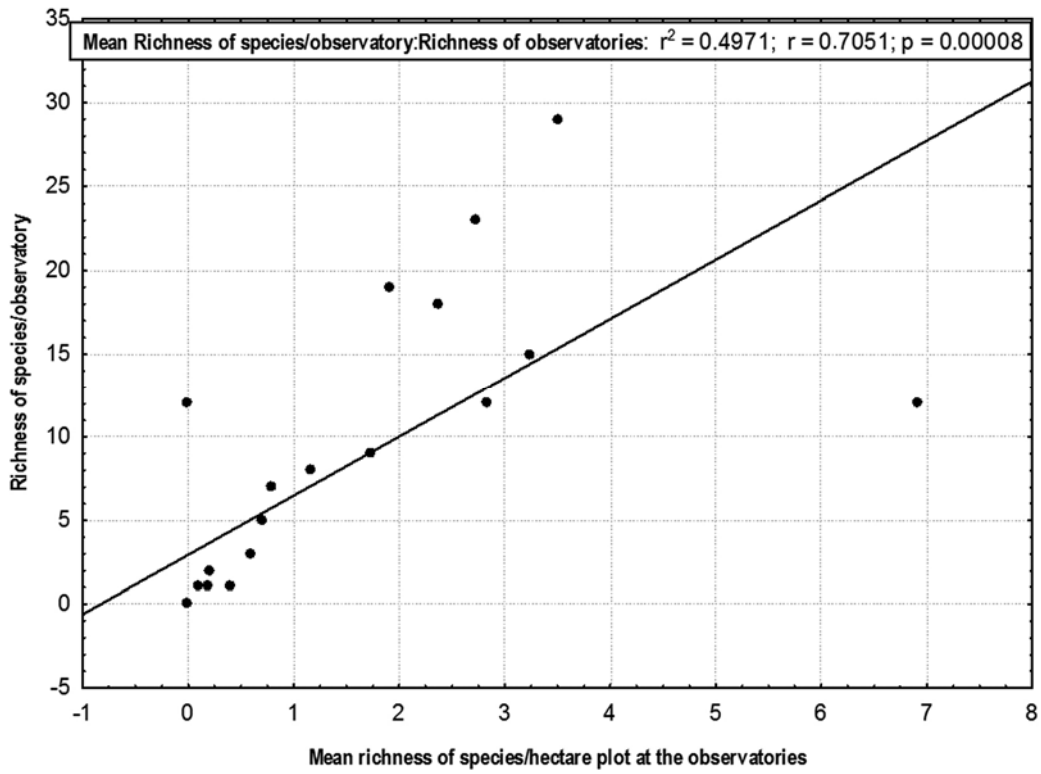
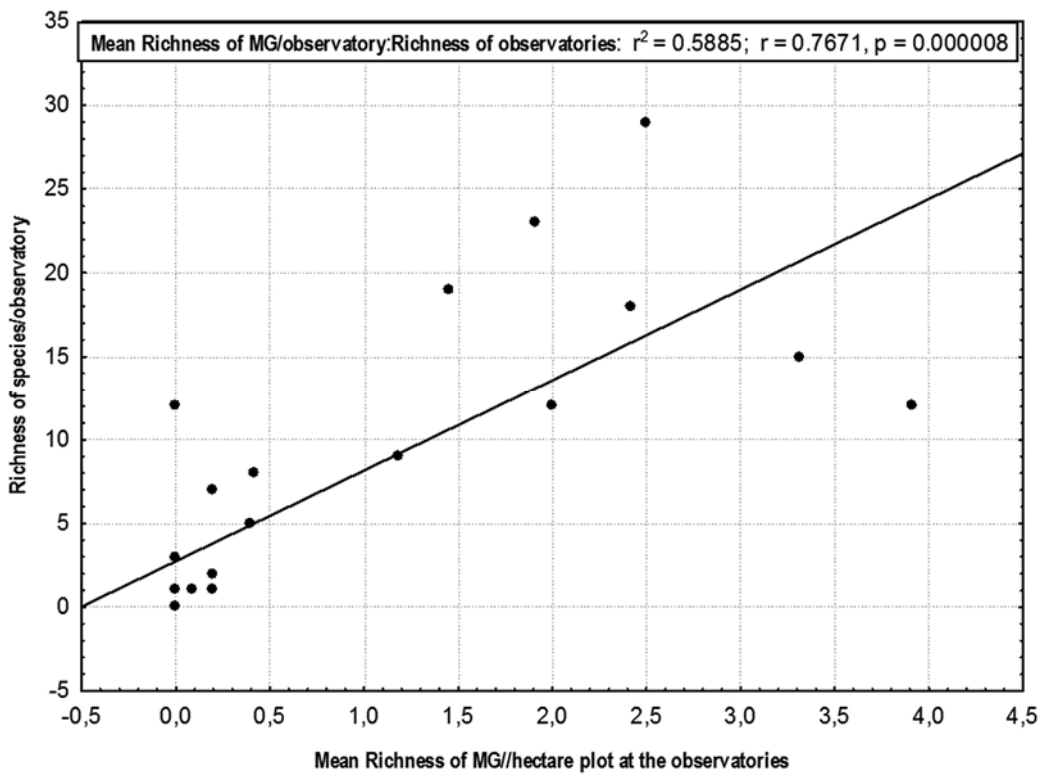


Fig. 5. Scatter plot of total lichen cover vs. richness of MGs/sampling plot.



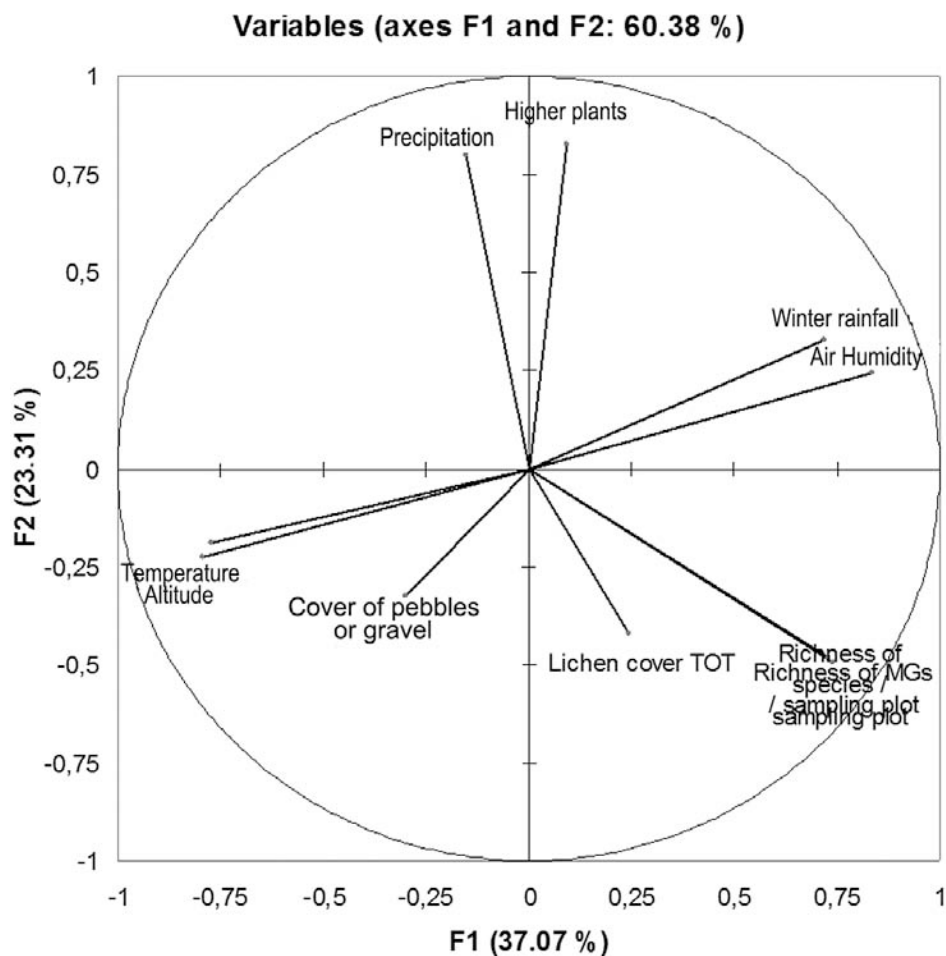
**Fig. 6.** Scatter plot of total lichen richness at the 1 km<sup>2</sup>-sites (“observatory”) vs. mean richness of lichen species occurring at the investigated sampling plots of the same observatories.



**Fig. 7.** Scatter plot of total lichen richness at the 1 km<sup>2</sup>-sites (“observatory”) vs. mean richness of morphogroups occurring at the investigated sampling plots of the same observatories.

A Mantel Test on dissimilarity matrix A, represented by lichen taxa occurring at the different sampling plots of one observatory, and on matrix B (occurrence of trait states in the same lichen taxa), shows that both matrices are significantly related ( $r(AB) = 0.069$ ;  $p\text{-value} = 0.000$ ;  $\alpha = 0.05$ ). As the computed  $p$ -value is lower than the significance level  $\alpha = 0.05$ , one should reject the null hypothesis  $H_0$ , and accept the alternative hypothesis  $H_a$ . This strongly supports the relationship of morphological traits with environmental conditions.

The first principal component of the PCA (Fig. 8) explains 37% of the variance of the parameters examined at all study sites, while the second component explains another 23%. The first axis is best explained by environmental factors such as precipitation (mean annual rainfall), the second by air humidity (mean annual percentage) and the winter rainfall regime. Both species richness (number of species/sampling plot) and MG richness (number of MGs/sampling plot) are strongly correlated to one another and are positively linked to air humidity and winter rainfall conditions. However, they are negatively related to increased precipitation and temperature, which is higher in inland areas. Lichen cover is also related to the same environmental factors, but correlates more weakly to lichen species and MG richness.



**Fig. 8.** PCA of selected environmental factors, lichen total cover (%), lichen species richness/sampling plot and the richness of lichen MGs/sampling plot.

## Discussion

Macro-morphological traits such as growth form, thallus colour and photobiont type can easily be observed without a microscope. They are often used to classify morphological groups, as various authors have highlighted their relatively high adaptive value to climatic conditions (INSAROV & SCHROETER 2002, ROSENRETER & ELDRIDGE 2002). As shown in the dendrogram (Fig. 2) and as reported by different authors (BARKMANN 1958, WOLSELEY 1997), the photobiont type is an important trait, known to be highly significant with regard to dependence on environmental factors, mainly climatic ones. Cyanobacterial lichens, for instance, are represented in much higher proportion in the drier areas of subtropical Australia (ROGERS 2006) and are known to have different water requirements and greater tolerance to aridity than green algal lichens (Lange 2000). This is also well reflected in their distribution within the study area, as cyanobacterial taxa appear to be most common in dry inland areas, especially in the Savannah biome. On the contrary, green-algal lichens are most abundant at coastal sites with high levels of air humidity and fog (ZEDDA et al. 2011).

Growth form is another important character for distinguishing the soil lichen MGs as resulting from the cluster analysis. ELDRIDGE & KOEN (1998) and ELDRIDGE & ROSENRETER (1999) already recognized the importance of this trait for the classification of soil lichen morphological groups. As reported by ZEDDA & RAMBOLD (2004) and by ZEDDA et al. (2011), foliose and fruticose lichens, which are members of MG06, MG10 and MG13, are restricted to the sites closer to the Atlantic coast of Southern Africa. These are known to be strongly dependent on fog and dew (LANGE et al. 1990, 2006). These coastal communities also include crustose and placodioid lichens (i.e., corresponding to MG04, MG05, MG07, MG08, MG09). According to ZEDDA et al. 2011, squamulose and peltate lichens, which constitute MG01, MG02, partly MG03 and MG11, appear with greater frequency in the inland sites. This might be explained by the special form of their thallus, formed by often concave squamules which facilitate water capture during rainfall and dewfall. Due to their reduced surface area, they are also well adapted to withstand drought (VOGEL 1955).

The pigmentation of the upper thallus surface also appears to be related to climatic factors as pointed out in other studies carried out along the BIOTA transect (ZEDDA et al. 2011). Lichens with dark (brown to black) thallus most frequently occur in areas with summer rain regime and low relative air humidity, while lichens with lighter pigmentation are most common in areas with higher air humidity and frequent fog and dew (i.e., MG02, MG03, MG11). This agrees with the findings of SHOWMAN (1972), who explained the densely pigmented cortex of phycobiontal lichens with a high light sensitivity of the green algal bionts.

Scatter plots and regression analyses demonstrate that the richness of MGs per sampling plot is a very good indicator for indirectly assessing lichen diversity in the same plot as well as at square kilometre level, and could well substitute time-consuming taxa inventories in biodiversity monitoring surveys. In contrast, results suggest that total lichen cover is less reliably predicted by MGs. According to ROSENRETER & ELDRIDGE (2002), cover on its own is generally a poor predictor of rangeland health in eastern Australia, and the degree of cover of a single taxon or morphological group is not always a reliable indicator of disturbance.

However the change over time of both the cover and composition of MGs is informative.

Results suggest that both species and MG-richness are linked to increased air humidity and winter rainfall seasonality, while increased temperature is negatively associated with lichen diversity. This may explain the complete absence of soil lichens in the Nama Karoo biome, which is characterized by drier conditions. Increasing rainfall also appears to negatively impact the richness and cover of both species and MGs, probably due to the resulting higher angiosperm cover and consequent greater grazing impact, as shown in the PCA.

It can be concluded that morphogroups can be representative of lichen richness at species level, and can be applied for monitoring soil lichen diversity and its potential shifts in Southern Africa due to climate changes. In view of the high number of plots examined along a transect crossing many different biomes, results can be considered representative for the entire study area. The use of lichens for monitoring biodiversity and potential shifts due to environmental changes is important since these organisms are abundant in the investigated biomes in Southern Africa and are a significant component of arid to semiarid ecosystems. A rapid and easy monitoring method is essential for the assessment of lichen biodiversity and trait occurrence shifts in the study area, which can be related to changing climatic factors, such as air humidity, precipitation and temperature. The main advantages of replacing species with morphogroups are the following:

- A) MGs are easier to identify in the field
- B) Non-invasive surveys (MGs may be characterized from photographs, limiting destructive sampling)
- C) Surveys are based on digital imaging applications
- D) This method minimises subjectivity and enables fairly accurate measurement of the lichen cover

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