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The influence of multi-scale environmental variables on the distribution of terricolous lichens in a fog desert

Lalley, Jennifer S.[1*]; Viles, Heather A.[1,2]; Copeman, Neil[1,3] & Cowley, Catherine[1,4]

[1]*Oxford University Centre for the Environment, Dyson Perrins Building, South Parks Road, Oxford, OX1 3QY, UK;*
[2]*heather.viles@ouce.ox.ac.uk;* [3]*neil.copeman@st-edmundhall.oxon.org;* [4]*catherine.cowley@wales.gsi.gov.uk;*
[*]*Corresponding author; Fax +44 1865271929; E-mail j.s.lalley@worc.oxon.org*

Abstract

Question: How do environmental variables in a hyper-arid fog desert influence the distribution patterns of terricolous lichens on both macro- and micro-scales?

Location: Namib Desert, Namibia.

Methods: Sites with varying lichen species cover were sampled for environmental variables on a macro-scale (elevation, slope degree, aspect, proximity to river channels, and fog deposition) and on a micro-scale (soil structure and chemistry). Macro-scale and micro-scale variables were analysed separately for associations with lichen species cover using constrained ordination (DCCA) and unconstrained ordination (DCA). Explanatory variables that dominated the first two axes of the constrained ordinations were tested against a lichen cover gradient.

Results: Elevation and proximity to river channels were the most significant drivers of lichen species cover in the macro-scale DCCA, but results of the DCA suggest that a considerable percentage of variation in lichen species cover is unexplained by these variables. On a micro-scale, sediment particle size explained a majority of lichen community variations, followed by soil pH. When both macro and micro-scale variables were tested along a lichen cover gradient, soil pH was the only variable to show a significant relationship to lichen cover.

Conclusion: The findings suggest that landscape variables contribute to variations in lichen species cover, but that stronger links occur between lichen growth and small-scale variations in soil characteristics, supporting the need for multi-scale approaches in the management of threatened biological soil crust communities and related ecosystem functions.

Keywords: Biological soil crust; DCA; DCCA; Namib Desert; Namibia.

Introduction

The unique climate of fog deserts, combining hyper-aridity with regular fog exposure, has led to an unusual biodiversity that includes diverse and widely distributed lichen communities. In the fog deserts of southwest Africa, the west coast of South America, and Baja California, terricolous (ground-dwelling) lichens can be the dominant vegetation in vast areas where aridity precludes the establishment of higher plants (Hachfeld 2000; Belnap et al. 2001). The domination of lichen growth is particularly conspicuous in the Namib Desert of Namibia where lichens flourish from the regular uptake of fog, growing contiguously in areas up to 400 km^2 (Schieferstein & Loris 1992). The ecological and geomorphic importance of these lichen communities are related to the biological soil crusts that they form, which has encouraged research on these communities in many deserts of the world. Lichen-dominated soil crusts are known to be primary sources of nitrogen and carbon fixation in arid environments (Beymer & Klopatek 1992; Evans & Belnap 1999), vital soil stabilizers (Belnap & Gillette 1998; Eldridge 1998; Eldridge & Leys 2003), and providers of habitat and food sources for other organisms (Zaady & Bouskila 2002; Lalley et al. 2006). Lichens have also been found to be highly vulnerable to human disturbance in this terricolous niche (Beymer & Klopatek 1992; Belnap & Gillette 1998; Eldridge 1998). Nevertheless, little work has focused on the unusual and highly vulnerable terricolous lichen communities occurring in fog deserts. In order to fully understand the many ecological functions of these important lichen communities and give them the appropriate protection, it is important to understand the variables that encourage or inhibit their growth.

The growth patterns of lichens have been assessed in many environments, and their patchy distribution and varying morphological structures have been attributed to environmental factors such as elevation (Pirintsos et al. 1995), substrate aspect (John & Dale 1990), exposure to radiation (Bjelland 2003), and rainfall patterns

(Eldridge & Tozer 1997), in addition to smaller scale factors such as substrate stability and chemistry (Ponzetti & McCune 2001; Belnap & Gillette 1998). At present, the variation in lichen communities occurring across fog desert regions, and the mosaic growth patterns seen within lichen-rich zones on a micro-scale, are poorly understood. Nash et al. (1979) suggest that lichen communities in the fog desert of Baja California are linked to fog deposition along an elevation gradient. Schieferstein & Loris (1992) and Zedda & Rambold (2004) have qualitatively linked lichen distribution patterns to fog exposure in the Namib Desert, affected by slope, aspect, and inland (elevation) position. On a smaller scale, Lalley & Viles (2005) showed the influence of soil crust thickness and gravel clast sizes on lichen cover in the northern Namib Desert.

To our knowledge, the current study is the first exploration into the influence of both macro-scale and micro-scale environmental variables on lichen growth patterns in a fog desert. Focusing on the northern Namib Desert of Namibia, this study measures macro-scale variables, namely elevation, proximity to river channels, slope degree, aspect, and quantity of fog deposition. Measured micro-scale variables include soil particle size, soil chemistry, and soil surface strength. Through this multi-scale approach, the research asks the question: how do environmental variables within the hyper-arid, fog-driven Namib Desert influence soil crust lichen distribution patterns at regional and local scales?

Study area

The entire coastline of Namibia falls within the Namib Desert, and lichen-dominated soil crusts are found on gravel plains occurring from less than 1 km from the coast to 70 km inland (Schieferstein & Loris 1992). Other geomorphic features of the Namib Desert are large sand dune systems, ephemeral riverbeds, inselbergs, and mountain outcrops (Goudie 2002). Annual rainfall along the coast is less than 20 mm, increasing on an inland gradient (Lancaster et al. 1984). Precipitation in the Namib is mainly in the form of fog, and is estimated at 37 mm/year in the central region of the Namib (Southgate et al. 1996) and as much as 130 mm on the coast (Olivier 1992). The heaviest fog events occur in the winter months of May to September (Olivier 1992).

The study sites were all located in the northern Namib Desert, falling inside the Skeleton Coast National Park in the remote northwest region of Namibia (Fig. 1). During this study, human activity in the area was restricted to low volume tourism and small-scale mining, so there was little chance of sample sites being disturbed. Sampling occurred in four areas with terricolous lichen cover that were previously identified by Lalley & Viles (2005). Soil sediments ranged from thick gypsum crusts to loose sand sediments with thin crusts (Table 1). Lichen cover ranged from crustose species that adhere directly to soil sediments, to fruticose and foliose species that adhere to both soil and gravel, contributing to the surface layer of the biological soil crust.

Field Methods

Macro-scale – landscape variables

Five landscape variables were measured (elevation, distance to river channels, slope degree, aspect, and fog deposition), following the suggested links to fog movement and exposure by Schieferstein & Loris (1992), Olivier (1992, 1995), and Hachfeld (2000). A nested sampling design was used that included three plots spaced 500 m apart in each of the four sites. One of the three plots was located in the local variable sampling area of each site (see below). Each plot was assessed for fog deposition with one fog trap. Within 10 m of the fog trap, five subplots were placed in which elevation, distance to riverbed, slope degree, aspect, and lichen communities were measured (N = 15 for each of the four sites).

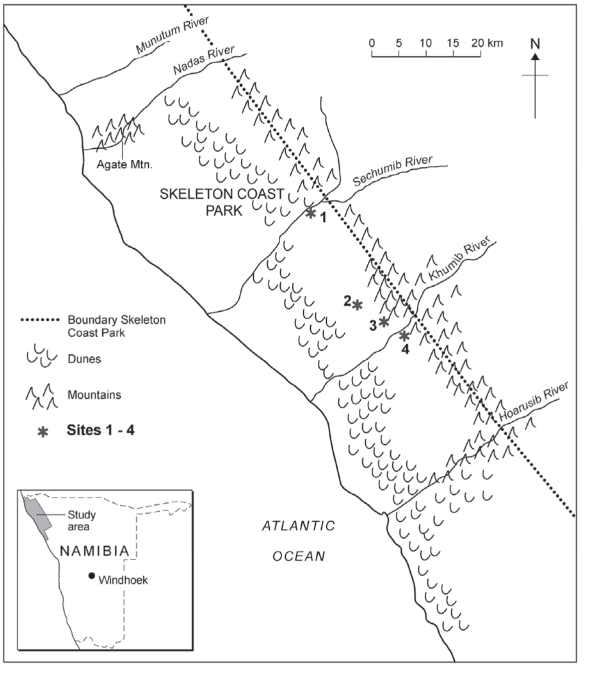

Fig. 1. Map of the northern Namib Desert in Namibia and the location of the four sampling areas.

Table 1. Mean values of environmental and lichen community variables in sites 1–4.

Sites:	1	2	3	4
Environmental variables				
Elevation (m)	385	386	350	325
Proximity to riverbed (km)	0.5	5.9	3.4	1.2
Slope degree	3.0	0.7	5.0	1.0
Aspect	W, NW	SE	W, SW	NW, W, SW
Fog deposition (ml)	9.70	35.23	15.23	10.92
Conductivity (μS/cm)	699.89	312.20	1948.39	148.06
pH	8.01	8.66	8.23	9.31
Soil surface strength (kgf /cm^2 0-5)	2.02	1.61	1.36	1.6
Chloride (ppm)	37.23	84.40	74.69	4.77
Sulphate (ppm)	109.31	2.53	339.49	7.71
Nitrate (μm)	2.42	1.25	0.69	1.71
% gravel (> 2.0 mm)	31.96	21.11	27.57	11.66
% coarse sand (0.5 – 2.0 mm)	16.32	14.69	17.58	10.70
% fine sand (0.25 - 0.0625 mm)	35.94	48.22	40.36	54.06
% silt (< 0.0625 mm)	4.77	7.90	6.32	7.79
Lichen variables (% cover in 1 m^2)				
Total lichen cover	89.00	12.00	54.17	31.00
Caloplaca elegantissima	2.25	0	0.5	0.88
Crustose spec., i.e. *Lecidella* and *Buellia* spp.	21.5	0	0	0
Neofuscelia namibensis	3.88	2.25	6	0
Teloschistes capensis	3.00	0.37	2.47	0
Xanthomaculina hottentotta	2.63	0	0	0
Xanthoparmelia walteri	53.88	11.75	41.38	28.13

Fog deposition measurements were made with a simple fog trap design based on that used by Hachfeld (2000), which consisted of a standard rain gauge in which plastic-coated wires were fanned along the top to optimize fog collection with a greater surface to area ratio. Fog was collected in the winter month of July, because fog events in the winter season are some of the heaviest in the year, which ensured maximum collection in a short sampling period (Olivier 1992). Furthermore, this measurement period ensured that no rainfall would interfere with fog trap sampling, and the cooler winter temperatures also reduced chances of evaporative loss of samples. To further prevent evaporative loss, 2 ml of vegetable oil was added to each trap. We were able to measure fog deposition on a total of 15 days in the period of one month.

Elevation was measured with a GPS. The distance from ephemeral river channels was measured to the metre, after sites were plotted on a topographical map using ArcView GIS (version 3.2). Slope degree was measured using a handheld clinometer, and aspect was measured with a compass and recorded as one of 8 categories (N, NE, E, SE, S, SW, W, NW). These categories were given values from 1–5. SW was the maximum value (5), based on the capturing of south-westerly, fog-carrying winds, as described by Schieferstein & Loris (1992). Subsequent values were given as follows: S and W = 4; SE and NW = 3; E and N = 2; NE = 1.

Micro-scale – local variables

Within each of the four sampling sites, sampling of local variables occurred along a line transect that ran 40 m into the lichen soil crust area from a randomly chosen location on its edge. Twenty soil samples, each one measuring 7 cm in diameter, were taken from the top 2 cm of soil at four locations placed 10 m apart along the line transect. Each of the collected samples was evaluated for soil particle size distribution, soil chemistry, and soil surface strength. Soil particle size distributions were established through standard dry-sieving techniques and then divided into five groups: gravels (> 2 mm), sand (coarse) (0.5 - 2 mm); sand (0.25 - 0.5 mm); sand (fine) (0.0625 - 0.25 mm); silt (< 0.0625 mm). The soil chemistry of each soil sample was evaluated in the laboratory. Sub-samples consisting of 2 g of soil were removed from each sample and prepared in 20 ml of deionized water. Chloride, nitrate, phosphate, and sulphate were measured simultaneously using a Dionex ion chromatograph. Measurements of pH and soil conductivity (as a measure of total dissolved salts) were made separately using 10-g samples mixed with 20 ml of deionized water. In each of the soil sample locations, soil surface strength measurements were made using a handheld penetrometer measuring kgf /cm^2 on a scale of 0 to 5.

Lichen sampling

Two sets of lichen data were used in this study to correspond with fog trap locations and soil sampling plots. The first set of lichen community data was collected in five sampling plots placed within 10 m of each of the fog traps for the macro-scale analysis. The second set of lichen data consisted of lichen community evaluations at each soil sampling location (micro-scale). In all of these sampling sites, lichen cover was assessed in 50 cm × 50 cm grid plots, comprised of 100 subdivisions measuring 5 cm × 5 cm. Total lichen cover was assessed by counting the number of subdivisions containing lichen growth, following Lalley & Viles (2005). The same method was carried out for individual lichen species. The species assessed here included five common species that represent five different morphological types, and one general category for lobeless, mostly adnate, crustose species that are either unclassified or difficult to distinguish in the field without colour testing, such as unclassified *Buellia* spp. This allowed for consistent measurements by field researchers whose expertise in lichen taxonomy varied.

Data analysis

To analyse the variation in lichen cover as a function of the environmental variables, Detrended Canonical Correspondence Analysis (DCCA) was used in conjunction with Detrended Correspondence Analysis (DCA), using CANOCO 4.5 (ter Braak 1988). DCCA is a useful analytical tool for deriving patterns and hypotheses from species-environmental data sets. It is a direct gradient analysis using weighted averaging on the associated environmental variables to guide an ordination of sampling sites and species, with a final step that removes much of the arch effect found in correspondence analyses. Moreover, it can handle data sets containing both continuous and categorical data (ter Braak 1988; Palmer 1993).

While constrained ordination techniques (CCA and DCCA) are merited for their ability to extract the significance of explanatory variables from varying strengths of data, it is entirely dependent on the given set of variables and gives little room to interpret the existence of additional, unmeasured explanatory variables. To address this issue, Økland (1996) recommended the combined use of constrained ordination (CCA or DCCA) with a form of unconstrained ordination such as detrended correspondence analysis (DCA). The latter of these techniques will ordinate the species data along axes that are dictated by unknown variables, leaving the analysis more open to interpretation. Here we use DCCA in combination with DCA to strengthen the interpretation of explanatory variables. DCCA and DCA results were compared by assessing eigenvalues and testing for correlations between the two sets of sample scores along the first axis, using Pearson's correlation coefficient.

Macro-scale analysis

The landscape data used in the macro-scale ordination analysis consisted of 60 samples (15 per site), all of which were entered into the DCCA. Mean fog deposition from each fog trap was entered as a repetitive variable for the set of five samples that was associated with that trap. The overall DCCA and the first DCCA axis were tested for significance using Monte Carlo permutation tests. The same species data set ($N = 60$) was used for the DCA.

Micro-scale analysis

Of the 80 samples (20 per site) in the micro-scale data set, 56 were entered into a second DCCA. This subset of data excluded all samples in which there was no lichen cover, in which measurement errors occurred, or where soil chemical analyses were incomplete. Given the reduced size of the data set, we reduced the number of environmental variables by eliminating highly inter-correlated variables, in order to lower the risk of overfitting the data in the ordination (Palmer 1993). Variable reduction was based on two subsets of intercorrelated variables. The first was related to soil particle sizes, where the size groups > 2 mm and 0.25-0.0625 mm were chosen to represent the distribution of soil particle sizes, as these showed the lowest correlation with one another. The second set of intercorrelated variables was soil chemistry. Nitrate, sulphate, and chloride were measured simultaneously in a chromatograph and their values are thus interrelated. Nitrate was the least correlated with all other variables and was chosen to represent the group. The reduced number of environmental variables was entered in the DCCA with all lichen species data. Monte Carlo permutation tests were used to test the significance of the first axis and the overall ordination. The micro-scale DCA was run using the same lichen species data ($N = 56$).

Lichen gradient analysis

We tested both macro- and micro-scale environmental variables against an overall lichen cover gradient using the non-parametric Kruskal Wallis test in SPSS software version 11.5 (Kinnear & Gray 2000). This analysis was used as a means of comparing the significance of both macro and micro-scale environmental variables from a common data set that included 12 overlapping samples. Only variables that were key drivers in the DCCA analyses were tested here. The lichen cover gradient of 0 - 4 was defined as follows: 0 = 0% cover; 1 = 1 < 20 % cover ; 2 = 20 < 50% cover; 3 = 50 < 75% cover; 4 = 75 < 100% cover.

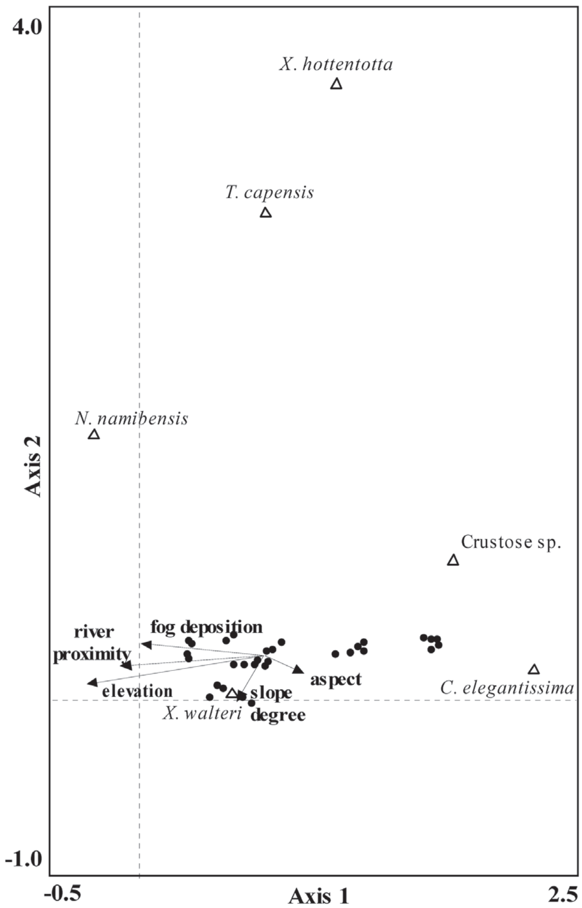

Fig. 2. Detrended Canonical Correspondence analysis biplot of macroscale landscape variables, lichen species, and sampled sites. △ = species; ● = sample site.

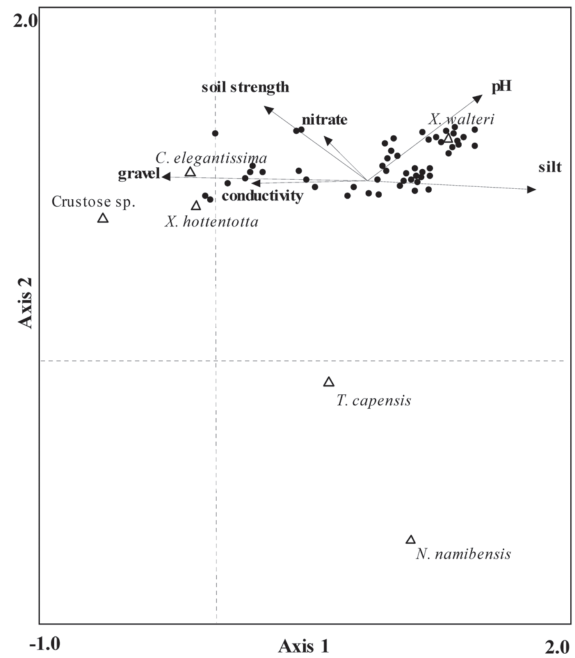

Fig. 3. Detrended Canonical Correspondence analysis biplot of micro-scale environmental variables, lichen species and sampled sites. △ = species; ● = sample site.

Results

Macro-scale analysis

The first axis of the macro-scale DCCA (eigenvalue = 0.254) explained 32.8% of the variation in lichen species cover and 81.6 % of the species-environment relation, and was found to be significant ($F = 20.45$; $P = 0.002$). Elevation featured as the most significant variable on the first axis (canonical coefficient = –0.682), followed by proximity to rivers (canonical coefficient = –0.554) (Fig. 2). Axis 2 explained only a minor percentage (1.2%) of the variation in species cover and only an additional 5.6% of the species - environment relation. The overall ordination was significant ($F = 5.39$; $P = 0.002$), explaining 35.2% of the variation in species cover and 99.5% of the species-environment relation (total inertia = 0.776; sum of eigenvalues = 0.303).

The DCA explained 89.6% of the variation in lichen species cover (eigenvalues for axes 1, 2: 0.469, 0.187; sum of eigenvalues = 0.695; total inertia = 0.776). When sample scores were compared between the DCCA and DCA, there was a highly significant correlation ($r = 0.840$; $P < 0.0001$). This suggests that the environmental variables in the DCCA encompass significant spatial patterns in the lichen species data and can be confidently interpreted. However, there is a considerable difference between the percentages of explained species variation between the DCCA and DCA, which needs to be considered. This percentage is expected to be somewhat lower in the DCCA, as species and sites are constrained along linear gradients, so there would be a loss of non-linear relationships to the environment (ter Braak 1986; Oliveira-Filho et al. 1998). Nevertheless, the extremely high percentage of species variations explained by the DCA axes suggests that unmeasured environmental variables contribute to additional compositional gradients (Økland 1996).

Micro-scale analysis

The DCCA of local variables (Fig. 3) explained 56.8% of the variation in species cover and 90.1% of the species-environment relation (sum of eigenvalues = 0.383; total inertia = 0.614). Axis 1 (eigenvalue = 0.309) was significant ($F = 32.40$; $P = 0.002$), explaining 50.3% of the variation in species cover and 82.5% of the species-environment relation. Soil particle size distribution was the most significant environmental variable on Axis 1, represented by gravel (> 2 mm) content (canonical coefficient = –0.839), and silt content (canonical coefficient = 0.657). The second most influential variable on both Axis 1 (canonical coefficient = 0.523) and Axis 2 (canonical coefficient = 0.532) is soil pH. Axis 2 (eigenvalue = 0.020), explained an additional 3.3 % of species variation and 7.6% of the species-environment relation. The Monte Carlo permutation test of the overall DCCA resulted in a significance of $P = 0.002$ (F = 8.86).

Results of the DCA showed that 67.6% of the variation in lichen species cover was explained by the axes (eigenvalues for axes 1, 2: 0.364, 0.042; total inertia = 0.614; sum of eigenvalues = 0.415). DCA eigenvalues were only slightly higher than those found in the DCCA, suggesting that lichen species - environment gradients have been well accounted for by the measured environmental variables. The comparison of DCCA and DCA sample scores resulted in a highly significant correlation ($r = 0.849$; $P < 0.0001$).

Lichen cover gradient

All environmental variables that were highlighted as significant drivers of lichen species cover in the DCCA analyses, were tested against a lichen cover gradient. Soil pH was the only variable to show a significant ($H = 7.7$; $P < 0.05$) relationship to the lichen cover gradient, using the Kruskal Wallis test.

Discussion

Macro-scale environmental variables

The findings of this research suggest that elevation and proximity to river channels affect lichen species cover in terricolous lichen communities in the Namib Desert.

The foliose species *X. walteri* and *N. namibensis* were positively correlated with elevation, while the crustose species *C. elegantissima* and the crustose group were negatively associated with elevation, indicating that they occur at lower elevation (Fig. 2). Similar divisions of lichen morphotypes occurred in relation to river proximity. Foliose species were positively linked to increasing distances from rivers, while crustose species were linked to areas close to rivers. Such relationships may be associated to the soil profiles occurring along elevational gradients or to variations in fluvial deposits radiating from major ephemeral rivers. The overall moisture regime of each sampled area (not measured here) would also be affected by the measured landscape variables. The poikilohydric nature of lichens causes most species to be highly correlated with environmental variables controlling substrate moisture retention or ambient humidity.

Olivier (1992) related topography to the significant differences found between commencement and cessation times for fog events in three different sampling sites in the central and southern Namib Desert. Ephemeral riverbeds are well known to facilitate fog movement by channelling intruding coastal winds (Olivier 1992, 1995), and elevated slopes can intercept fog-carrying winds (Schieferstein & Loris 1992; Hachfeld 2000). These landscape features may also dictate fog cessation times due to variations in air movement along differing topographies, surface temperatures related to elevation and sloping, aspect-related sun exposure leading to evapotranspiration, or soil depressions with greater moisture retaining capabilities.

While no significant relationship was found between fog and lichen cover in this study, fog data collection focused only on the quantity of deposition and did not include the duration of fog events or post-fog moisture availability. The duration of moisture availability, as opposed to quantity, may be a key driver of lichen occurrence and cover. Many lichen species in fog deserts have morphological adaptations that optimize moisture absorption, whereby thalli become optimally saturated in a light fog event or even in high humidity (Rundel 1982; Lange et al. 1990). Many desert lichen species are also slow in uptaking moisture (Lange et al. 1994). Therefore, a sequence of brief but heavy fog events may not be as effective in stimulating lichen productivity as would a lingering light fog event. Hence, the duration of lichen productivity may be dependent on landscape characteristics related to: elevation which effects fog exposure and the moisture regimes of soil profiles along elevational gradients; distance from wind-channelling riverbeds, which can prolong fog exposure; or several unmeasured macro-scale variables that may reduce evapotranspiration and surface air movement. Such unmeasured landscape variables may be driving the species variation that was illustrated by the DCA but was left unexplained by the variables of the DCCA.

Micro-scale environmental variables

On a micro-scale, the environmental variables most strongly affecting lichen species cover, as highlighted in the DCCA, were the percentage of soil particle sizes (gravel and silt) and soil pH. In the Namib Desert, gravel is an integral part of the soil profile. The classification of soil particle sizes will have an effect on soil stability and soil surface complexity, both of which have been linked to lichen cover in recolonizing communities in the Namib

Desert (Lalley & Viles in press), and in other less arid deserts (Eldridge & Tozer 1997; Eldridge & Koen 1998; Garcia-Pichel & Belnap 2001). Soil surface features would also be directly related to soil surface strength, although this variable had less explanatory power in the DCCA. Lichen growth is well known to stabilize soil surfaces and form soil-hardening crusts, and conversely, many lichens (e.g. crustose species) are known to grow only on previously stabilized surfaces (Belnap et al. 2001). In the DCCA, the crustose group and the common crustose species *C. elegantissima*, fell on the first axis, in close association to gravel cover, and directly opposite silt (Fig. 3). Many of these species are found growing on both soil and gravel, aggregating both substrates to form a soil crust. The foliose species *X. walteri* was the most closely associated with silt, which may be linked to gypsum crusts that are formed in silt soils. The occurrence of foliose species has been related to gypsum soils in previous studies in the Namib (Schieferstein & Loris 1992; Lalley & Viles 2005). No species showed relationships to soil surface strength, related to soil surface stability, which contradicts findings from other studies in the Namib and less arid deserts (Belnap & Gillette 1998; Eldridge & Koen 1998; Lalley & Viles in press). Links to soil infiltration rates and moisture retention capabilities of the soil were not measured here. As in the macro-scale analysis, such unaccounted variables could explain some of the relationships and lack of relationships found here. Moisture variations in the top layer of soil are most certainly a function of the structural characteristics of the soil surface, which deserves much more in depth investigation.

Soil pH was also significantly correlated with lichen species cover in the DCCA and in the Kruskal Wallis test, which is consistent with findings from other arid environments (Eldridge & Tozer 1997; Eldridge & Koen 1998; Ponzetti & McCune 2001). Low soil pH values have been positively linked with the occurrence of chlorolichens (Belnap et al. 2001), lichens containing green algal components and found extensively in fog deserts. In the DCCA diagram, *X. walteri* is dominating the link found between lichen cover and pH, but is not indicating an association with higher rather than lower values. Mean pH values in all sites were more alkaline (8.0-9.3) than acidic (Table 1), indicating that fog-adapted lichens in hyper-arid deserts may operate at different levels of pH than those found in less arid, rain-driven deserts.

Intercorrelations between macro-scale and micro-scale environmental variables were not assessed here, but may explain some of the relationships to lichen species cover and overall lichen cover gradients. For example, the micro-scale soil characteristics identified as explanatory variables, particularly soil particle classifications, would most likely follow landscape gradients such as elevation and river to plateau gradients. While this study did not sample soil along landscape gradients, the common relationships of soil characteristics and landscape variables to lichen growth, may be indicative of inherent multi-scale intercorrelations that require further investigation to fully interpret the findings of this study.

Conclusion

The findings of this research have further supported previous suggestions that lichen growth of fog deserts can be partially explained by macro-scale, landscape features. More importantly, the significant relationships of local variables to lichen species cover and overall cover gradients, indicate that complex networks of micro-scale variables may be influencing the mosaic growth patterns of lichens. This study introduces some potential explanations for heterogenous growth patterns at the understudied micro-scale, such as variations in soil surface structure and soil pH.

The relationships found here are uniquely isolated from the external denominators found in less arid deserts, such as the presence of vascular plants and human impacts. Hence, confident extrapolations can be made for management purposes, i.e. recognizing the need for multiscaled ecological analyses and conservation management practices in relation to terricolous lichens in fog deserts. As land managers of deserts increase their focus on the reduction of human impacts and the rehabilitation of disturbed areas, knowledge of biological soil crusts becomes increasingly important. Awareness of the key drivers of lichen-dominated soil crusts can improve conservation strategies in highly vulnerable fog deserts, and can be instrumental in the protection of lichen-associated habitats and organisms.

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