

Correlates of biological soil crust abundance across a continuum of spatial scales: support for a hierarchical conceptual model

MATTHEW A. BOWKER*, JAYNE BELNAP*, DIANE W. DAVIDSON† and HARLAND GOLDSTEIN‡

*US Geological Survey, South-West BSC, 2290 SW Resource Boulevard, Moab, UT 84532, USA; †Department of Biology, University of Utah, 257 South, 1400 East, Salt Lake City, UT 84112–0840, USA; and ‡US Geological Survey, PO Box 25046, Denver, CO 80225, USA

Summary

1. Desertification negatively impacts a large proportion of the global human population and > 30% of the terrestrial land surface. Better methods are needed to detect areas that are at risk of desertification and to ameliorate desertified areas. Biological soil crusts are an important soil lichen-moss-microbial community that can be used toward these goals, as (i) bioindicators of desertification damage and (ii) promoters of soil stability and fertility.

2. We identified environmental factors that correlate with soil crust occurrence on the landscape and might be manipulated to assist recovery of soil crusts in degraded areas. We conducted three studies on the Colorado Plateau, USA, to investigate the hypotheses that soil fertility [particularly phosphorus (P), manganese (Mn) and zinc (Zn)] and/or moisture limit soil crust lichens and mosses at four spatial scales.

3. In support of the soil fertility hypothesis, we found that lichen–moss crusts were positively correlated with several nutrients [Mn, Zn, potassium (K) and magnesium (Mg) were most consistent] at three of four spatial scales ranging from 3.5 cm² in area to c. 800 km². In contrast, P was negatively correlated with lichen–moss crusts at three scales.

4. Community composition varied with micro-aspect on ridges in the soil crust. Three micro-aspects [north-north-west (NNW), east-north-east (ENE) and TOP] supported greater lichen and moss cover than the warmer, windward and more xeric micro-aspects [west-south-west (WSW) and south-south-east (SSE)]. This pattern was poorly related to soil fertility; rather, it was consistent with the moisture limitation hypothesis.

5. *Synthesis and application.* Use of crusts as desertification bioindicators requires knowledge of a site's potential for crust cover in the absence of desertification. We present a multi-scale model of crust potential as a function of site properties. Future quantitative studies can use this model to guide sampling efforts. Also, our results suggest new directions in restoration research: enhancement of moisture residence time and fertilization with key nutrients (Mn, Zn, K and Mg). Re-establishment of soil crusts in desertified lands will help regain lost soil stability and fertility, and facilitate plant re-establishment.

Key-words: cryptobiotic soil crusts, cryptogams, hierarchical distribution model, microbiotic soil crusts, multi-scale distributions, semi-arid regions, soil chemistry

Journal of Applied Ecology (2006) **43**, 152–163
doi: 10.1111/j.1365-2664.2006.01122.x

Introduction

Biological soil crusts are a soil-surface community of cyanobacteria, mosses, lichens and other organisms, and are found in numerous habitats world-wide,

Correspondence: Matthew A. Bowker, Department of Biological Sciences, Northern Arizona University, Box 5640, Flagstaff, AZ 86011, USA (fax +1 928 523 7423; e-mail mab86@dana.ucc.nau.edu).

especially aridlands (Belnap & Lange 2003). By aggregating soil (Mazor *et al.* 1996), biological soil crusts reduce or prevent soil surface erosion in otherwise poorly vegetated ecosystems, and therefore have been considered ecosystem engineers (Jones, Lawton & Shachak 1997). Collectively, these organisms are major contributors to whole-system nitrogen (N) fixation (Belnap 2002) and carbon (C) fixation (Beymer & Klopatek 1991) and they enhance mineral nutrient content of soils and associated vascular plants (Harper & Belnap 2001). Because of these important traits, disturbance of biological soil crusts is both an accelerator and component of desertification (Belnap 1995), a costly global problem (Dregne & Chou 1992). Despite their potential as bioindicators of disturbance, predictive modelling of their potential distribution is quite rare (but see Rogers 1972; Eldridge 2003). Economical and universal restoration techniques are also lacking for these communities, in spite of their numerous important ecosystem functions (reviewed in Belnap & Lange 2003).

The distribution of biological soil crusts appears to be patterned, contingent upon the spatial scale of study (Eldridge 2003; Ullmann & Büdel 2003). On the Colorado Plateau, USA, patterns in the distribution of the lichen and moss crust components based upon habitat characteristics can be discerned at several different spatial scales. We hypothesized that patterns in lichen and moss distribution reflect resource (e.g. moisture and nutrients) limitation. Large-scale studies support the importance of moisture availability and soil properties (Ponzetti & McCune 2001; Ullmann & Büdel 2003; Bowker *et al.* 2005). At a small scale, within a given site, distinctive crust communities occur in shrub-shaded microsites compared with those in the interspaces (Maestre & Cortina 2002; Bowker *et al.* 2005). Lichens and mosses are also patchily distributed in the interspaces among vascular plants in otherwise homogeneous-appearing sites. It is common to observe very well developed lichen and moss crusts (+LMC microsites) directly adjacent to areas with very poorly developed or absent lichen and moss crusts (-LMC microsites), often with very abrupt transitions (Fig. 1b). These stark contrasts do not correspond to different hydrological regimes (e.g. run-on and run-off zones; Eldridge 1999) or disturbance histories. Patches may be as small as *c.* 0.25 m² but may be larger. At a still smaller scale, frost-heaved crusts exhibit a structure of numerous ridges and valleys (*c.* 5–10 cm vertical relief). Because of poorly understood mechanisms, the ridges (or pedicels) tend to have a long axis non-randomly orientated *c.* north-north-west (NNW) to south-south-east (SSE) (Fig. 1c), giving rise to distinct micro-aspects (George *et al.* 2000; Davidson *et al.* 2002) and microclimates (Bowker *et al.* 2002) on the various pedicel faces. Some crust organisms favour certain micro-aspects over others (George *et al.* 2000).

Ecological communities are always patterned to some degree, and it can be useful to visualize patterns in biological soil crust distribution as hierarchical levels of

organization (Allen & Starr 1982). Different levels of organization have characteristic spatiotemporal scales of study, and properties observed at one scale may or may not hold at another scale. Collective properties can be scaled up to the next highest level without a loss of information. Emergent properties occur when lower level properties cannot fully predict properties at a higher level. Emergent properties may often be better explained in a top-down fashion by properties of still higher levels of organization (Bissonette 1997). Emergent or scale-sensitive properties pose challenges to our ability to extrapolate our findings; however, multi-scale studies allow us to infer which patterns and properties may occur across scales.

To allow us to understand both the properties of crust distribution and their degree of collectivity, we adopted a novel four-scale approach (Fig. 1). For the purposes of our studies, we used the following hierarchy of terms to distinguish among scales: (i) macro scale, pertaining to a collection of sites within a relatively large area (in this study *c.* 800 km²) wherein soils are variable but climate is relatively homogeneous; (ii) microsite scale, pertaining to subdivisions of sites (ranging from 0.25 m² to *c.* 100 m² in our studies) and defined by crust patch structure; (iii) micro-aspect scale, pertaining to the comparison of different directional aspects on the faces of soil crust pedicels (described above); and (iv) organismal scale, pertaining to the comparison between habitats occupied by a lichen and directly adjacent uncolonized habitat.

Because manipulation of resource availability holds promise as a restoration method for lichen–moss crusts, we sought to determine to what degree lichens and mosses were moisture and nutrient limited, and which nutrients were the most consistent correlates with them. We focused on lichens and mosses because of their disproportionate contributions to C and N fixation and surface stabilization compared with other soil crust components. We tested three major hypotheses. (i) The high phosphorus (P) demands of N-fixers and the immobility of this nutrient make it a probable limiting nutrient, while previous evidence suggests Mn and/or zinc (Zn) may also limit N-fixing lichens (Bowker *et al.* 2005). We predicted that soil fertility, particularly P, Mn and Zn availability, limits lichen and moss abundance at macro, microsite, micro-aspect, and organismal scales. (ii) Correlations between soil fertility and lichen–moss crusts exhibit high collectivity, i.e. are similar across scales. (iii) Lichen and moss community composition is strongly influenced by cooler, wetter conditions at regional and microsite scale comparisons of shrub canopies to interspaces (Bowker *et al.* 2005), thus we proposed that this was a collective property that would be observable at smaller scales. We predicted that the more mesic east-north-east (ENE) and north-north-west (NNW) micro-aspects will support different lichen–moss community composition compared with dryer, warmer micro-aspects. Understanding the limiting factors of lichens and mosses, especially of widespread and N-

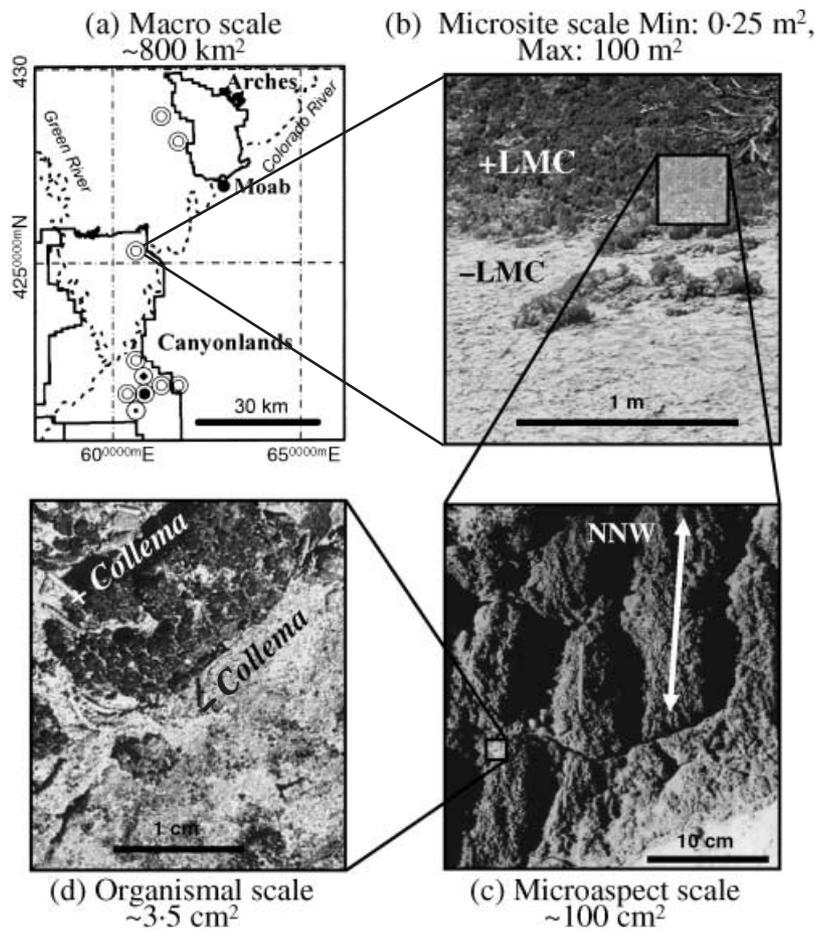


Fig. 1. Diagram of the four spatial scales of study in this paper. Clockwise from upper left: (a) map of the south-east Utah, USA, macrosite in study 1 plotting all sites used throughout the paper, ⊙ = site sampled in study 1, ⊗ = site sampled in studies 1 and 2, ⊕ = site sampled in studies 2 and 3; (b) a photograph of +LMC and -LMC microsites and their abrupt transition; (c) a photograph of NNW-SSE orientated linear ridges in a biological soil crust, with shadows demonstrating a differing light environment on the various micro-aspects; (d) a photograph at the organismal scale showing the lichen *Collema* (+*Collema*) and directly adjacent unoccupied habitat (-*Collema*).

fixing *Collema* F.H. Wigg. lichens, should contribute to two goals: (i) predictive models enabling range managers to compare actual lichen-moss crust distributions with their potential distributions (i.e. reference conditions) and using crusts as negative bioindicators of desertification, and (ii) the development of economical restoration methods for amelioration of desertification impacts via crust re-establishment.

Methods

In south-eastern Utah, USA, we conducted three multi-part studies. (i) The first study examined macro-scale heterogeneity in lichen and moss cover and composition among several nearby sites, and tested for microsite-scale heterogeneity in habitat characters between adjacent +LMC and -LMC patches within these sites. (ii) The second study investigated the heterogeneity in lichen-moss community composition among five micro-aspects of soil crust pedicels. (iii) The third study quantified characteristics of *Collema*-occupied habitat at microsite, micro-aspect and organismal scales. We then synthesized all the results.

STUDY 1: MACROSITE- AND MICROSITE-SCALE SAMPLING

Eight study sites were selected within a single macrosite, to represent considerable variation in south-eastern Utah's soil texture and chemistry. Soils ranged widely in CaCO₃ content (0.3–12.9%) and texture (60.8–89.7% sand). Calcium carbonate is important because it immobilizes nutrients (P, Mn and others) via adsorption onto its surface. Vascular plant communities were variable among sites in this and the following studies, the most common communities being dominated by *Achnatherum hymenoides* (Roemer & J.A. Schultes) Barkworth and *Hesperostipa comata* (Trn. & Rupr.) Barkworth, *Pinus edulis* Engelm. and *Juniperus osteosperma* (Torr.) Little, *Artemisia tridentata* Nutt. and *Coleogyne ramosissima* Torr. We selected sites from 1352 to 1831 m altitude and within 70 km of Moab, Utah, to restrain climatic variability. Historical precipitation records for the macrosite logged in Moab, two sites in Canyonlands National Park and Arches National Park were 22.9 cm, 22.9 cm, 21.6 cm and 22.1 cm, respectively (Western Regional Climate Center 2005). Six sites had been undisturbed

for at least 35 years while the other two showed little evidence of recent disturbance, possibly because of low amounts and poor quality of cattle forage or lack of water resources.

At each of these eight sites, we sampled five pairs of 25 × 25-cm quadrats (just three pairs at a site with low variability in crust cover within quadrat type) for a total of 75 quadrats. We believe this sample size was adequate to capture much of the spatial heterogeneity in lichen–moss crust cover at the macro- and microsite scales, because we intentionally built important edaphic gradients into the site-selection scheme and intentionally selected maximal +LMC/–LMC contrasts in the quadrat placement. Quadrat size was selected to accommodate the size of the smallest +LMC microsites. Each pair represented one +LMC and one –LMC microsite. Paired quadrats, separated by < 1 m in their respective microsites, were positioned non-randomly to capture the greatest possible within-microsite contrast. Biological soil crust cover in the vicinity of each quadrat pair averaged approximately the mean of that in the immediate vicinity. Categorization as +LMC or –LMC was relative to typical conditions within a site; as a result –LMC often contained some lichens and mosses (average cover 13% compared with 55% for +LMC). To keep microclimatic regimes approximately constant, we placed quadrats only in interspaces between shrubs. Within each quadrat, percentage cover was estimated visually to the nearest 5% for each moss and lichen species and for mineral crusts (whitish crust of unknown chemical composition), with additional observations of < 5% recorded as 2.5%. We used the field-based lichen key by McCune & Rosentreter (1995) and Flowers (1973) to identify lichens and mosses, respectively. For specimens not well covered in the keys, we consulted with Drs John Spence, Lloyd Stark (mosses) and Roger Rosentreter (lichens). Lichen nomenclature follows Esslinger (2004), except *Aspicilia aspera* which follows Hafellner, Nimis & Tretiach (2004), and moss nomenclature follows Zander (2004). Mean percentage cover values were estimated separately for +LMC and –LMC microsites at each site. Cover was computed as the percentage of available habitat, excluding litter and rock (by definition unavailable to soil crust organisms). This transformation did not strongly alter analysis results, as cover of unavailable habitat averaged only c. 8%. Voucher specimens from this and following studies (numbers BOWKER2005 :1–21) were deposited at the Boise State University (Idaho) Department of Biology herbarium.

After percentage cover was recorded, samples from the top 1 cm of soil were collected from at least 10 haphazardly positioned surface soil cores (2.5 cm diameter) in each quadrat, and compiled into a composite sample for that quadrat. Soils were sifted through a 2-mm sieve to remove rocks and litter. Lichens and mosses were also carefully removed at this time to allow us to distinguish between nutrients attributable to high lichen and/or moss cover, and those incorporated in or adherent to lichens and mosses. Within each site, composite

soil samples were created by combining soils within microsite type (+LMC vs. –LMC).

Samples were homogenized and split into duplicate sets of equal mass. One set of samples was sent to the Brigham Young University Soils laboratory (Provo, UT, USA) and analysed for sodium bicarbonate extractable P and K (K_a), exchangeable cations [K, sodium (Na), calcium (Ca), magnesium (Mg)], micronutrients [Zn, copper (Cu), iron (Fe), Mn], electrical conductivity (EC; a measure of salts more soluble than gypsum) and acid-neutralizing potential (ANP). ANP is a measure of $CaCO_3$ and other agents that buffer soil acids. Two forms of K were measured: K_a (the amount of K in solution), and K_c (the amount of K held electrostatically on colloids). Because some lichens are N-fixing organisms that strongly influence soil levels, we chose not to measure N. We analysed the second soil split at the USGS Earth Surface Processes laboratory (Denver, CO, USA) for percentage $CaCO_3$, particle size distribution and magnetic properties. We used a laser-light scattering method (capable of measuring particles from 0.49 to 2000 μm) to determine particle size as a percentage of total volume. We employed a combination of magnetic and reflected light petrographic methods to measure and confirm the following magnetic properties: (i) magnetic susceptibility (MS), a measure of all magnetic material but predominantly magnetite, and (ii) hard isothermal remnant magnetization (HIRM), an approximate measure of haematite (King & Channel 1991). Our study area included sedimentary parent materials only; therefore, the presence of these igneous-derived magnetic minerals indicated input of non-local eolian dust (Reynolds *et al.* 2001).

STUDY 2: MICRO-ASPECT-SCALE SAMPLING

To test for affinity between lichen–moss crust species assemblages and five micro-aspects, we selected three sites in Canyonlands National Park (c. 50 km from Moab). All sites were relatively flat, having similar climate and soils derived primarily from the Cedar Mesa Formation. Soils ranged from sandy loams to loamy sands and differed in depth and vegetative cover.

Within each site, three haphazardly selected microsites consisted of 10 soil crust pedicels that were sampled on five micro-aspects. Only pedicels with well-developed micro-aspects were sampled. Using a measuring tape, we sampled five miniature line intercept transects on each pedicel representing each micro-aspect [NNW, SSE, ENE, west-south-west (WSW), TOP; $n = 450$ total line intercept transects]. All transects paralleled the major axis of the pedicels (c. NNW–SSE) and were placed as follows: (i) NNW and SSE, centred on the major axis, running from base to top in the vertical plane; (ii) ENE and WSW, parallel to the major aspect, halfway between base and top in the horizontal plane; (iii) TOP, centred on the major axis, running from NNW to SSE. Transect length varied with the size and shape of the pedicel but generally ranged from 3 to 10 cm. Distance

intercepted by each moss and lichen species was recorded and converted to percentage cover for that given line intercept. Data from the 10 replicate pedicels within each possible site \times microsite \times micro-aspect combination were averaged prior to analysis (to reduce the large number of zero values encountered on individual pedicels). This procedure resulted in 45 sets of mean cover values (3 sites \times 3 microsites \times 5 micro-aspects).

STUDY 3: MICROSITE-, MICRO-ASPECT-, AND ORGANISMAL-SCALE *COLLEMA* STUDY

To determine which environmental variables were correlated with *Collema* cover at multiple small spatial scales (microsite, micro-aspect and organismal scales), we collected a series of 60 c. 200-g composite soil samples. Composite samples consisted of six subsamples from different pedicels wherein the top 3–5 mm of soil was shaved off with a knife and collected. Each composite collection was made from two adjacent microsites at haphazardly selected locations at a single site in Canyonlands. One of the microsites contained no *Collema* (10 composite samples) while *Collema* was found in the paired sample (50 composite samples, allocation of replicates detailed below). In the microsite with *Collema*, soils were collected independently from pedicels with no *Collema* (10 composite samples), low *Collema* (5–10% cover; 20 composite samples) and high *Collema* (> 10% cover; 20 composite samples) cover. For all sampled pedicels, replication was evenly split between ENE and WSW micro-aspects. On pedicels with *Collema*, paired samples were taken from *Collema* patches (*Collema* and the soil under it) and immediately adjacent areas lacking *Collema* (within 1–2 mm) on both micro-aspects. For each collection, the top 3–5 mm of soil was sampled. Samples were thoroughly homogenized, and then sent to Brigham Young University (BYU) for analysis of N, P and K_{ex} , exchangeable cations and micronutrients.

STATISTICAL ANALYSIS

Hypotheses about macro-scale lichen and moss distribution (in study 1) were tested using methods reviewed in McCune & Grace (2002). Non-metric multidimensional scaling (NMDS) was used in conjunction with the Bray–Curtis distance measure to ordinate species and plot vectors of environmental variables. To test for a significant correlation between community data and environmental variables, and to obtain a measure of ‘effect size’, we used the Mantel test first as a whole model test, then as a post-hoc test to determine which individual variables probably accounted for significance. Here and in all the following multivariate tests, all variables were relativized to their maxima to equalize their influence upon the analysis, and species with only one occurrence were omitted (McCune & Grace 2002).

Hypotheses regarding soil properties on microsite scales (study 1) were tested using perMANOVA (Anderson 2001). To focus the analysis on between-microsite rather

than among-site differences, we aligned median values of each response variable within each block to zero. Because whole model significance was detected, post-hoc ‘design matrix’ Mantel tests (McCune & Grace 2002) were used to characterize further differences in the individual soil parameters between the two types of microsite (+LMC and –LMC).

We analysed lichen–moss crust communities across micro-aspects (study 2) using a combination of perMANOVA and indicator species analysis. Indicator species analysis generates a percentage of perfect indication value (IV; ranging from 0 to 1) for each variable–group combination and employs a Monte Carlo test to determine the probability of obtaining an IV that equals or exceeds the calculated value. Kruskal–Wallis tests in conjunction with post-hoc Tukey HSD tests were used to test for significant differences in abundance of functional groups and species richness (based upon the finest taxonomic level we could attain) across micro-aspects.

Soil nutrient data from study 3 were analysed using two MANOVA models. The first compared nutrient abundances across microsites with and without *Collema*, and among micro-aspects, and the interaction of the two factors. The second compared nutrients on pedicels with high and low *Collema* cover, different micro-aspects and in adjacent habitat with and without *Collema* individuals, and all interactions. Post-hoc univariate ANOVAs were used to determine which variables probably accounted for significance. Statistics were conducted in PC-ORD version 4 (1999 MJM Software Design), JMP IN 4.0 (2002 SAS Institute) and PERMANOVA version 6 (2005 M. J. Anderson). In study 2, the sequential Bonferroni correction was applied so that table-wise $\alpha = 0.05$. We did not apply a correction for multiple comparisons in studies 1 and 3 because there was a high degree of intercorrelation of response variables. When response variables are highly correlated, Bonferroni-type corrections tend to be too conservative (Manley 2001).

Results

LICHEN–MOSS COMMUNITY ANALYSES WITHIN A MACROSITE

In a stable NMDS ordination (final stress = 10.4, final instability = 0.0004) of species’ distributions in the macrosite surrounding Moab (study 1), three axes accounted for a total r^2 of 0.76. Two species clouds were apparent (Fig. 2a), one composed of all of the common mosses (but also including *Collema tenax* and some rare lichens) and the other composed primarily of a different set of lichens (including several commonly observed on calcareous substrates; McCune & Rosentreter 1995; Ponzetti & McCune 2001). A Mantel test indicated an overall multivariate correlation ($P = 0.01$) between the species matrix and a matrix of 24 environmental variables. Post-hoc Mantel tests indicated that litter, Mn, P:CaCO₃, ANP and CaCO₃ probably accounted for this correlation (Table 1). The two species clouds were

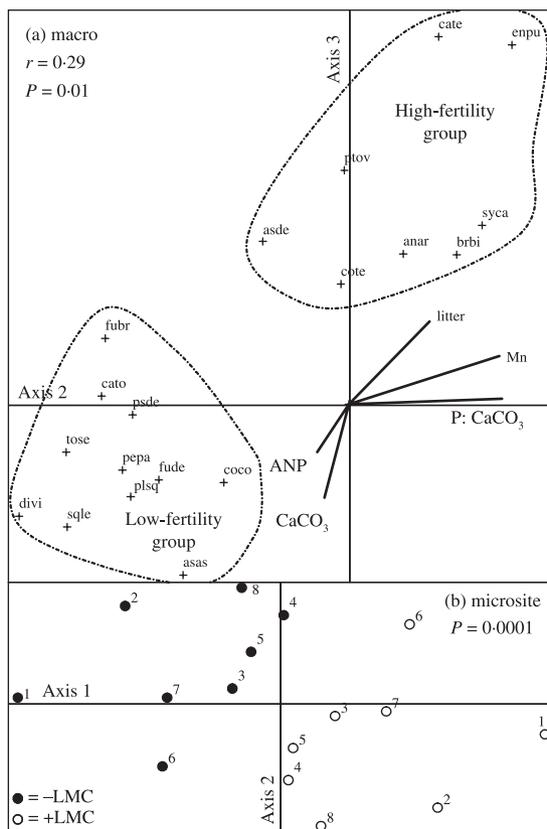


Fig. 2. NMDS ordinations of macro- and microsite-scale results (study 1). (a) Macro scale: the two most explanatory axes in a three-dimensional ordination of lichen and moss species (study 1). Significant environmental variables are represented as vectors (tests summarized in Table 1). r , Mantel statistic, a multivariate correlation coefficient. Species codes (mosses): anar, *Anomobryum* spp.; brbi, *Bryum* sp. (similar to *B. bicolor*); divi, *Didymodon vinealis*; ptov, *Pterygoneurum ovatum*; syca, *Syntrichia caninervis*. Species codes (lichens): asde, *Aspicilia desertorum*; asas, *A. aspera*; cato, *Caloplaca tominii*; cate, *Candellariella terrigena*; plsq, *Placidium* spp. (consisting of *P. squamulosum* and *lachneum*); coco, *Collema coccophorum*; cote, *C. tenax*; enpu, *Endocarpon pusillum*; fubr, *Fulgensia bracteata*; fude, *F. desertorum*; pepa, *Pelula patellata*; psde, *Psora decipiens*; sqle, *Squamarina lentigera*; tose, *Toninia sedifolia*. The lichens *Psora cerebriiformis* and *P. tuckermanii* were excluded because of rarity. (b) Microsite-scale ordination of +LMC and -LMC plots. Numbers designate site identity. Plot types were significantly different overall; test results for individual variables are given in Table 2.

split along a complex gradient, with the high fertility group positively correlated with litter, Mn and P:CaCO₃. The low fertility group was positively correlated with measures of calcareousness (CaCO₃ and ANP; Table 1).

SOIL ANALYSES ACROSS MICROSITES

perMANOVA detected significant differences ($P = 0.0001$) in physicochemical characteristics between +LMC and -LMC microsites (study 1; Fig. 2b). Fourteen specific environmental variables were positively correlated with one microsite type or the other (Table 1). Correlates of -LMC samples included higher rock cover, P and measurements of calcareousness. Correlates of +LMC

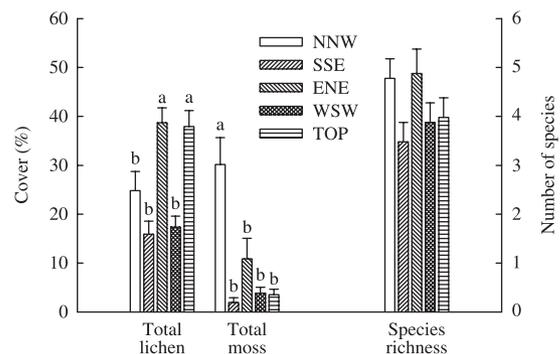


Fig. 3. Total moss and lichen cover and richness of five micro-aspects.

samples were higher mineral crust cover, EC, micro-nutrients and assimilated eolian dust.

COMMUNITY ANALYSES ACROSS MICRO-ASPECTS

Using perMANOVA, we detected a significant effect of the variables microsite nested within site [abbreviated as site (microsite)] and micro-aspect ($P = 0.0002$ in both cases) in study 2. The variable site and interaction terms were insignificant. Micro-aspect effects were consistent across all of the microsites. Post-hoc perMANOVA testing indicated that there were several differences between individual micro-aspects: (i) NNW was different in species composition from SSE, WSW and TOP ($P = 0.001$, 0.0004, 0.0006, respectively) and marginally different from ENE ($P = 0.02$; note $\alpha = 0.01$ because of a sequential Bonferroni correction); (ii) ENE and TOP were not significantly different ($P = 0.62$) and were significantly different from other aspects, except for a marginal difference between ENE vs. NNW (above) and TOP vs. WSW ($P = 0.02$; $\alpha = 0.01$); (iii) SSE and WSW did not differ from one another ($P = 0.80$), and were significantly different from the other aspects, except TOP vs. WSW (above). *Collema* spp. were significant indicators of ENE habitats (IV = 30, $P = 0.006$) and the moss *Syntrichia caninervis* was a significant indicator of NNW habitats (IV = 58, $P = 0.001$). Total lichen cover differed across micro-aspects (Fig. 3; $P < 0.0001$), with 1.5–2.5-fold greater cover on ENE and TOP vs. other micro-aspects. Total moss cover was at least 2.5-fold greater on NNW micro-aspects than on other micro-aspects (Fig. 3; $P = 0.0003$). Species richness per line intercept did not differ by aspect (Fig. 3; $P = 0.22$).

COLLEMA HABITAT ACROSS MICROSITE, MICRO-ASPECT AND ORGANISMAL SCALES

In study 3, a MANOVA of soil samples without lichen tissue found no significant differences in nutrient concentrations between microsites with and without *Collema* spp. ($P = 0.09$), ENE and WSW micro-aspects ($P = 0.07$) or in the interaction of these factors ($P = 0.11$). The marginal significance of the microsite effect was most

Table 1. Environmental variables and correlations with lichen–moss crusts measured in study 1. Significant variables (bold) have a positive Mantel statistic (r) and $P < 0.05$

Soil property	Local			Microsite		
	r	$P =$	Correlate	r	$P =$	Correlate
Litter	0.22	0.04	Moss, <i>C. tenax</i>	-0.01	0.55	
Surface rock	0.09	0.23		0.15	0.02	-LMC
Mineral crust	0.08	0.23		0.22	0.002	+LMC
Sand	-0.09	0.21		-0.07	0.16	
Silt	-0.14	0.08		-0.08	0.02	
Clay	0.06	0.26		-0.01	0.45	
P	0.12	0.20		0.41	0.001	-LMC
K _a	-0.04	0.43		-0.07	0.17	
pH	-0.04	0.37		0.88	0.001	-LMC
EC	-0.12	0.19		0.40	0.001	+LMC
Zn	0.19	0.07		0.39	0.001	+LMC
Fe	0.03	0.40		0.42	0.002	+LMC
Mn	0.30	0.002	Moss, <i>C. tenax</i>	-0.05	0.02	
Cu	0.07	0.28		0.20	0.04	+LMC
Ca	0.21	0.07		-0.04	0.41	
Mg	0.03	0.37		-0.04	0.41	
K _e	-0.01	0.49		0.08	0.11	
Na	0.10	0.22		0.01	0.39	
ANP	0.24	0.03	Lichen	0.07	0.043	-LMC
CaCO ₃	0.28	0.04	Lichen	0.22	0.02	-LMC
P:CaCO ₃	0.20	0.03	Moss, <i>C. tenax</i>	0.09	0.001	-LMC
Other buffers	0.15	0.06		0.02	0.28	
MS	-0.07	0.29		0.55	0.002	+LMC
HIRM	-0.02	0.49		0.02	0.26	

K_a is the amount of K in solution.

K_e is the amount of K held electrostatically on colloids.

strongly influenced by greater K_e, and that of the micro-
aspect effect was most probably accounted for by greater
K_a on ENE micro-aspects.

A second MANOVA analysis of data from the +*Collema*
microsite found a highly significant difference in nutri-
ent concentrations between pedicels with high vs. low
Collema cover ($P = 0.001$), no significant difference
between ENE and WSW micro-aspects ($P = 0.15$), and
a highly significant organismal-scale difference between
Collema tissue + underlying soil and adjacent soil ($P =$
 0.0001 ; main effects summarized in Fig. 4). Also sig-
nificant was the interaction of all three factors ($P = 0.02$)
and the interaction of pedicel \times micro-aspect ($P = 0.04$).
Concentrations of Cu and Ca were lower, and K_a higher,
on pedicels with high *Collema* cover. In habitat occupied
by *Collema* thalli, concentrations of several nutrients
(K_a, Zn, Fe, Cu, Mn, Mg and N) were higher than in
adjacent soils lacking *Collema* cover, while P was lower.

Discussion

Soil crust mosses and lichens were found to correlate
with similar moisture and nutrient gradients at several
spatial scales. We synthesized a model of these patterns
and present it as a starting point for quantitative
modelling of crust reference conditions for use in
range management. Using our findings as a springboard,
we propose new directions in soil crust restoration
involving enhancement of resource availability.

SUPPORT FOR THE MOISTURE AND NUTRIENT LIMITATION HYPOTHESES

Consistent with our hypotheses, nutrient and/or mois-
ture limitation is the simplest and most consistent
explanation of the patterns described in this study, and
is generalizable across scales. Our findings have much
in common with McCune (1993), who advanced the
similar gradients hypothesis that a similar moisture
availability gradient determined forest epiphytic lichen
community composition as a regional moisture regime,
stand age (older = wetter) and as a vertical gradient within
a forest.

The hypothesis that lichen–moss crusts are limited
by moisture availability is supported at the micro-
aspect scale (study 2; George *et al.* 2000). The ENE, TOP and
NNW micro-aspects offered favourable habitats for
lichen and moss communities, while the hot, xeric and
windward WSW and SSE micro-aspects were relatively
depauperate in moss and lichen cover. A previous study
addressed the distribution of the dominant cyanobac-
terium and selected lichen species on some of the aspects
treated here (George *et al.* 2000). In contrast to the pre-
vious study, this study identified TOP aspects as having
high lichen (especially *Collema*) cover and relatively
mesic NNW aspects as being moss-dominated. Both
studies recognized ENE micro-aspects as having the
greatest *Collema* abundance. In a field experiment,
Collema transplants on ENE and TOP micro-aspects

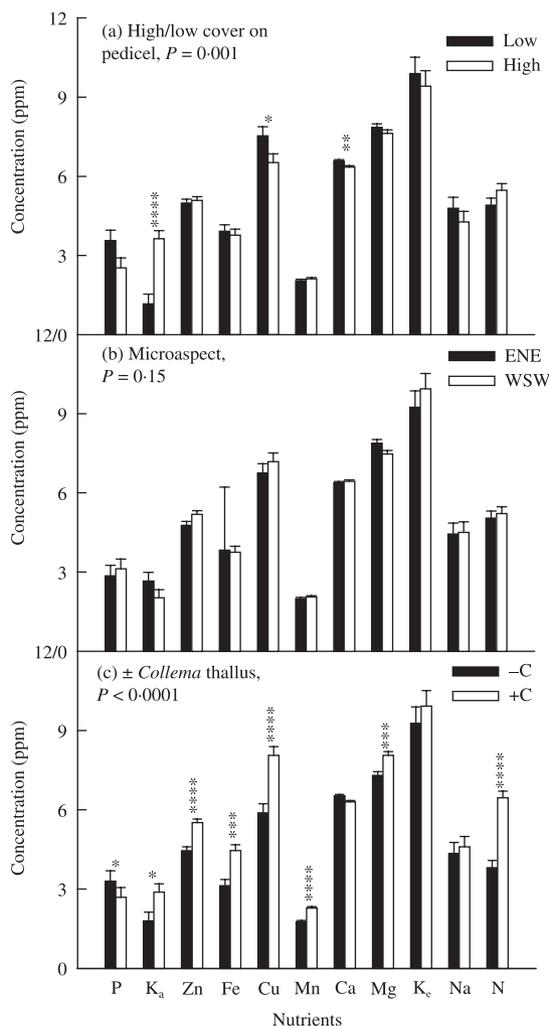


Fig. 4. Effects of high or low *Collema* cover on pedicel (a; microsite scale), micro-aspect (b) and presence/absence of *Collema* thalli (c; organismal scale) on concentration of several soil nutrients. For ease of viewing, P, Fe, Mn and are reported as p.p.m., Zn and Cu as p.p.m. $\times 10$, K_a , Mg, K_e and Na as p.p.m. $\times 10^{-1}$, N as p.p.m. $\times 10^{-2}$ and Ca as p.p.m. $\times 10^{-3}$. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, **** $P < 0.0001$.

generally fared better than those on other aspects (Davidson *et al.* 2002). In Bowker *et al.* (2005), several lichen and moss taxa correlated with wetter portions of a regional precipitation gradient and/or relatively mesic plant-shaded habitats. The finding of no difference in soil fertility between ENE and WSW habitats (study 3) probably indicates that the micro-aspect effect on lichen-moss crust is independent of nutrient availability but may involve microclimate effects or differential erosion (Davidson *et al.* 2002).

However, the nutrient limitation hypothesis is supported by positive correlations between lichen and mosses and several soil nutrients (frequently including two of our focal nutrients, Mn and Zn, and also Mg and K) at macrosite, microsite and organismal scales and for a portion of the lichen-moss crust community at the macro scale (studies 1 and 2). Similar gradients yielded similar patterns at regional and microsite scales

in previous work (Bowker *et al.* 2005). However, an emergent property occurs at the macro scale: most lichens are negatively associated with soil fertility and positively associated with calcareous soils. A calcicole-calcifuge dichotomy in lichen community composition has also been noted by other researchers (McCune & Rosentreter 1995; Ponzetti & McCune 2001). As it is unlikely that any of these species actually require low nutrient availability, we might hypothesize that members of this group are superior competitors under low nutrient availability but are subject to competition from the high-fertility group when released from limitation.

Contrary to our hypothesis and results from Bowker *et al.* (2005), P and the lichen-moss crust community (all or part) are negatively correlated at the macrosite (low-fertility group, study 1), microsite (study 1) and organismal (study 3) scales. The instances of negative correlation could conceivably be explained by uptake of P by lichens or mosses and conversion to unavailable organic forms, although further study is needed.

We cannot rule out alternative mechanisms that may explain some positive correlations between soil physico-chemical properties and lichen-moss crusts, including crust-mediated dust trapping. Reynolds *et al.* (2001) demonstrated that Mn, P and numerous other nutrients can be greatly enriched by dust input, and biological soil crusts can function as dust traps. There is some evidence for this hypothesis in study 1, where we found that +LMC microsites contained more dust-derived magnetic minerals than adjacent -LMC microsites.

SYNTHESIS: A MULTI-SCALE, HIERARCHICAL CONCEPTUAL MODEL OF LICHEN-MOSS CRUST COVER AND COMPOSITION

We applied a top-down hierarchical approach (O'Neill 1988) in a synthesis of the present study and complementary data from Bowker *et al.* (2005), adding a regional scale (a large area, generally 1000s of square kilometres, in which soils, vegetation and climate may vary greatly). A hierarchical conceptual model (O'Neill 1988) could predict lichen-moss crust occurrence as a function of climate and soil variables at five spatial scales on the Colorado Plateau and may be useful in other arid regions as well (Fig. 5). Regional and microsite scale patterns were derived from Bowker *et al.* (2005), while macrosite- additional microsite-, micro-aspect- and organismal-scale patterns were derived from this study. The strongest regional pattern was the virtual absence of lichens and mosses on bentonitic shale-derived soils compared with sandier substrates. Nested within the sandier substrates, a moisture-nutrient availability gradient was positively correlated with lichen and moss cover and diversity.

Macrosite- and microsite-scale patterns are combined at this point, because shrub canopy and interspace habitats are compared at the microsite scale, while the macro-scale data only reflect patterns in the interspaces because of our sampling scheme (study 2). This

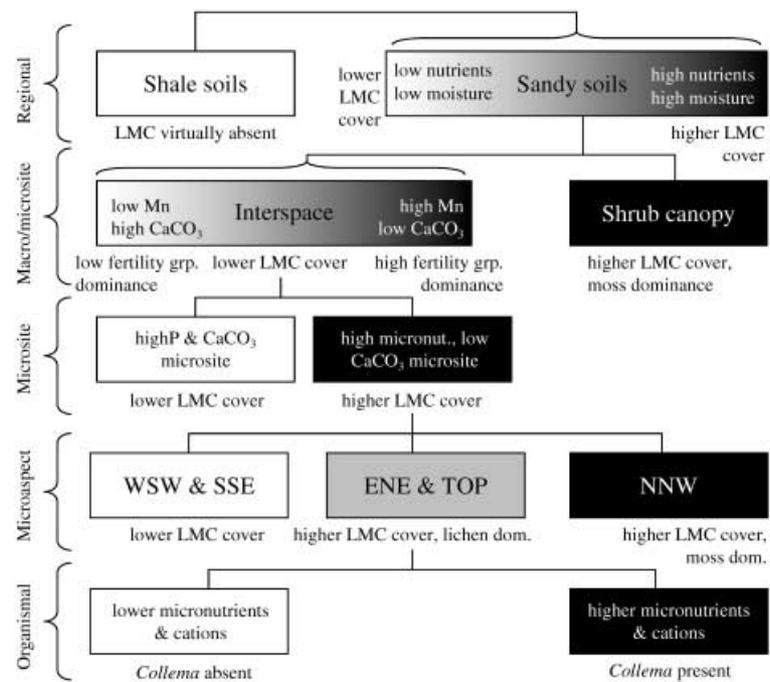


Fig. 5. Nested hierarchical conceptual model for lichen–moss crust (LMC in figure) cover and composition at multiple scales (organismal to regional scale) on the Colorado Plateau. Shading within boxes represents a continuous gradient while darker colours symbolize greater lichen and moss cover.

simplification is useful because shrub canopy-associated crust communities are less variable than those in interspaces (M. A. Bowker, personal observation; Bowker *et al.* 2005), possibly because shrub canopies present a buffered microclimate and enhanced fertility. Available substrates beneath shrub canopies tend to support greater lichen and moss cover, with mosses dominating. Litter may present somewhat of a trade-off for mosses and lichens, simultaneously competing for space but enhancing resource availability in crust-available habitat. Interspaces tended to have lower lichen–moss crust cover (when viewed as a percentage of available habitat) but species composition was contingent upon whether soils had high nutrient availability and low CaCO₃, or the opposite condition.

Nutrient concentrations are heterogeneous within interspaces, and this patchiness is, in turn, strongly related to lichen–moss crust cover. The higher fertility microsites support +LMC patches, while the more calcareous and less fertile (with the exception of P availability) microsites support –LMC patches. Within +LMC patches, we are likely to observe soil crust pedicels with well-developed micro-aspects. Soil fertility is not strongly related to micro-aspect (study 3) but it is likely that microclimate or wind erosion rates are (Davidson *et al.* 2002). The most mesic micro-aspect, NNW, had the greatest total lichen–moss crust cover and was dominated by mosses. TOP and ENE aspects supported moderately high lichen–moss crust cover and were dominated by lichens. The relatively xeric, hot and windward WSW and SSE aspects supported low lichen and moss cover.

At the organismal scale, *Collema* may colonize minus-

cule patches of higher soil fertility (study 3). In Fig. 5, this pattern is illustrated as occurring within ENE and TOP aspects, simply because that is where *Collema* is most abundant and where the pattern is likely to be most easily observed. However, in study 3 this pattern held on ENE and very different WSW micro-aspects, suggesting that this pattern is not constrained within micro-aspect but rather could potentially apply to any *Collema* occurrence.

MANAGEMENT APPLICATIONS

The data gathered here are useful primarily in the development of two distinct management applications: quantitative predictive modelling of lichen–moss crusts for range management, and cost-effective lichen–moss crust restoration methods applicable at multiple scales.

Developing predictive models

Predictive modelling of potential lichen and moss cover could provide the reference conditions needed to enable range managers and restoration practitioners to compare the current condition of these bioindicators with their potential condition. Given the great ecological importance of lichen–moss crusts in the world’s aridlands, a large departure from a potential lichen–moss crust condition may indicate desertification in progress and that a different management strategy is advisable. For example, the US Bureau of Land Management has used semi-quantitative reference conditions to evaluate crust condition in Idaho using an

internally developed system (R. Rosentreter, M. Pellant & J. H. Hilty, unpublished data).

In a multi-scale context, a nested hierarchy appears to be a useful way to visualize large- and small-scale lichen and moss distribution patterns and explore explanations. Predictive modelling ideally begins with such foundational research that is used to formulate a conceptual model (Guisan & Zimmerman 2000). The hierarchical model presented here can serve as a sampling design template for more quantitative lichen–moss crust (or biological soil crusts as a whole) predictive modelling efforts. Such a sampling scheme ensures that patterns we know to exist will be represented adequately while allowing for modelling with an appropriate statistical technique to discern additional, more subtle, patterns.

Development of restoration tools

Restoration of lichen–moss crusts (or biological soil crusts in general) has potential as a powerful tool to reverse existing desertification impacts in many regions of the world (Belnap 1995; Elmarsdottir, Aradottir, & Trlica 2003; Grettarsdottir *et al.* 2004; Li *et al.* 2004; Bowker *et al.* 2005). Field studies such as this one can be very valuable in narrowing the focus of subsequent applied experimental research. The large majority of crust restoration research is focused on inoculation of soil crust organisms (Buttars *et al.* 1998) and has seldom delved into manipulation of resource availability, which our work suggests may be quite important. Our research suggests that if moisture and particular nutrients are made more available, biological soil crust recovery time could be hastened. Research focused on resource manipulation may yield several novel techniques, and this paper is an early step toward this goal.

Moisture limitation of biological soil crusts is exploitable in two main ways: (i) timing of restoration activities and (ii) establishment of mesic microsites. The correlation of lichen–moss crusts and more mesic habitats at three scales (this study; Bowker *et al.* 2005) suggests that restoration activities will be more successful if they are applied in relatively moist weather. Relatively mesic microsites can be created by the establishment of a source of shade, or by promoting on-site run-off capture. Soil imprinting, fast growing plant establishment and brush pile application are techniques that could contribute to increasing the residence time of moisture on-site.

Our studies are perhaps most useful in designing experiments that alter the availability of nutrients. Fertilization-based treatments hold promise as lichen and moss restoration tools because they could be applied on large scales (such as a pasture) at a fairly low cost. Mn, Zn, Mg and K are the most consistent positive correlates with lichen–moss crust cover, thus these correlations are relatively collective properties (Table 2). Currently, controlled nutrient exclusion experiments are being conducted on *Collema* lichens [investigating

Table 2. Variables with potential for development as restoration applications (Bowker *et al.* 2005; this study). Only parameters that could feasibly be altered under field conditions are listed. Total numbers of positive and negative correlations provide an index of 'collectivity' or consistency across levels of organization. When numerous variables apply, only the most important are listed. N is not listed because its probable source is *Collema*. +, positive correlate; −, negative correlate

Scale	Organism(s) studied	EC	pH	CaCO ₃ /ANP	Cu	Ca	Fe	K _a	K _c	Mg	Mn	Na	P	Zn
Regional	Moss and lichen community					+			+	+	+		+	+
Regional	<i>Collema tenax</i>													+
Regional	<i>Collema coccophorum</i>					+						+		+
Local	Moss group (includes <i>C. tenax</i>)			−							+			
Local	Lichen group			+							−			
Microsite (<i>Collema</i> present vs. <i>Collema</i> absent)	<i>Collema</i> spp.							+	+	+				+
Microsite (interspace vs. shrub canopy habitats)	Moss and lichen community				−		+							
Microsite (+LMC vs. −LMC)	Moss and lichen community	+	+		+									
Microsite (low vs. high cover pedicels)	<i>Collema</i> spp.			−				+						
Micro-aspect	<i>Collema</i> spp.							+						
Thallus	<i>Collema</i> spp.				+		+	+	+	+	+		−	+
Total number of positive correlations		1	1	1	2	2	2	4	2	4	5	1	2	5
Total number of negative correlations		0	0	2	2	1	0	0	0	0	1	0	3	0

N, P, K, Ca, sulphur (S) and Mg] in a greenhouse setting. Interestingly, preliminary data suggest nearly complete P uptake when K is not also added; however, there is no evidence that greater P uptake results in better physiological status of *Collema* (S. L. Phillips *et al.*, unpublished data). A field P and K addition experiment was also conducted on transplanted *Collema*, but this had inconsistent and sometimes negative effects on *Collema* performance, perhaps because of disturbance during application (Davidson *et al.* 2002). Future experimentation should include Mn and Zn, and experimentation involving K and Mg should be expanded. It is imperative that any proposed restoration treatment involving resource manipulation also be investigated for its effects upon other community components, such as exotic vascular plants (e.g. *Bromus tectorum* on the Colorado Plateau). Expansion of exotics may greatly alter the soil environment (Belnap & Phillips 2001), potentially shifting the invaded system past a threshold beyond which it cannot be restored. Our results suggest that nutrient responses may sometimes be species-specific and interactions among community members could alter results (as suggested in study 1, macro scale). Because of these factors, experimentation should be conducted upon whole soil crust communities rather than isolated organisms, when possible.

Often, very different mechanisms may affect recovery of ecological communities at different spatial scales (Holl & Crone 2004). Fortunately, lichens and mosses appear to respond to similar gradients at both large and small scales, suggesting that small-scale fertilization experiments can be relevant to larger scale restoration. With further research focused upon resource manipulation, we may develop fertilization methods that speed recovery time of biological soil crusts and ameliorate some impacts of desertification.

Acknowledgements

Drs Marti Anderson, Mike Kearsely, Bruce McCune and Phil Service provided statistical advice. Leanne Henry, Sasha Reed, Sunny Holland, Tonya Troxler and Brandon Stevens provided laboratory or field assistance. We thank Drs Bruce Webb and Rich Reynolds and Isla Castaneda for soil analyses. Drs Mark Miller, George Koch, Nancy Johnson, Sue Phillips, Ed Grote and four anonymous referees enabled improvement of this manuscript. Difficult identifications were assisted by Drs Roger Rosentreter, Lloyd Stark and John Spence. Funding was provided by two USDA NRIGCP Awards and a Merriam-Powell Center for Environmental Research fellowship award (M. A. Bowker).

References

Allen, T.F.H. & Starr, T.B. (1982) *Hierarchy: Perspectives for Ecological Complexity*. University of Chicago Press, Chicago, IL.

Anderson, M.J. (2001) A new method for non-parametric multivariate analysis of variance. *Austral Ecology*, **26**, 32–46.

Belnap, J. (1995) Surface disturbances: their role in accelerating desertification. *Environmental Monitoring and Assessment*, **37**, 39–57.

Belnap, J. (2002) Nitrogen fixation in biological soil crusts from southeast Utah, USA. *Biology and Fertility of Soils*, **35**, 128–135.

Belnap, J. & Lange, O.L. (2003) *Biological Soil Crusts: Structure, Function, and Management*. Springer-Verlag, Berlin, Germany.

Belnap, J. & Phillips, S.L. (2001) Soil biota in an ungrazed grassland: response to annual grass (*Bromus tectorum*) invasion. *Ecological Applications*, **11**, 1261–1275.

Beymer, R.J. & Klopatek, J.M. (1991) Potential contribution of carbon by microphytic crusts in pinyon–juniper woodlands. *Arid Soil Research and Rehabilitation*, **5**, 187–198.

Bissonette, J.A. (1997) Scale-sensitive ecological properties: historical context, current meaning. *Wildlife and Landscape Ecology: Effects of Pattern and Scale* (ed. J.A. Bissonette), pp. 3–31. Springer-Verlag, New York, NY.

Bowker, M.A., Belnap, J., Davidson, D.W. & Phillips, S.L. (2005) Evidence for micronutrient limitation of biological soil crusts: potential to impact aridlands restoration. *Ecological Applications*, **15**, in press.

Bowker, M.A., Reed, S.C., Belnap, J. & Phillips, S.L. (2002) Temporal variation in community composition, pigmentation, and F_v/F_m of desert cyanobacterial soil crusts. *Microbial Ecology*, **43**, 13–25.

Buttars, S.A., St Clair, L.L., Johansen, J.R., Spray, J.C., Payne, M.C., Webb, B.L., Terry, R.E., Pendleton, B. & Warren, S.D. (1998) Pelletized cyanobacterial soil amendments: laboratory testing for survival, escapability, and nitrogen fixation. *Arid Soil Research and Rehabilitation*, **12**, 165–178.

Davidson, D.W., Bowker, M., George, D., Phillips, S.L. & Belnap, J. (2002) Treatment effects on performance of N-fixing lichens in disturbed soil crusts on the Colorado Plateau. *Ecological Applications*, **12**, 1391–1405.

Dregne, H.E. & Chou, N.-T. (1992) Global desertification dimensions and costs. *Degradation and Restoration of Arid Lands* (ed. H.E. Dregne), pp. 249–281. Texas Tech University, Lubbock, TX.

Eldridge, D.J. (1999) Dynamics of moss- and lichen-dominated soil crusts in patterned *Callitris glaucophylla* woodlands in eastern Australia. *Acta Oecologia*, **20**, 159–170.

Eldridge, D.J. (2003) Biological soil crusts of Australia. *Biological Soil Crusts: Structure, Function, and Management* (eds J. Belnap & O.L. Lange), pp. 119–132. Springer-Verlag, Berlin, Germany.

Elmarsdottir, A., Aradottir, A.L. & Trlica, M.J. (2003) Microsite availability and establishment of native species on degraded and reclaimed sites in Iceland. *Journal of Applied Ecology*, **40**, 815–823.

Esslinger, T.L. (2004) *A Cumulative Checklist of the Lichen-Forming, Lichenicolous and Allied Fungi of the Continental United States and Canada*. <http://www/ndsu.nodak.edu/instruct/esslinge/chklst/chklst7.htm>. North Dakota State University, Fargo, ND.

Flowers, S. (1973) *Mosses: Utah and the West*. Brigham Young University Press, Provo.

George, D.B., Davidson, D.W., Schleip, K.C. & Patrell-Kim, L.J. (2000) Microtopography of microbiotic crusts on the Colorado Plateau, and the distribution of component organisms. *Western North American Naturalist*, **60**, 343–354.

Gretarsdottir, J., Aradottir, A.L., Vandvik, V., Heegaard, E. & Birks, H.J.B. (2004) Long term effects of reclamation treatments on plant succession in Iceland. *Restoration Ecology*, **12**, 268–278.

Guisan, A. & Zimmerman, N.E. (2000) Predictive habitat models in ecology. *Ecological Modeling*, **135**, 147–186.

Hafellner, J., Nimis, P.L. & Tretiach, M. (2004) New records of *Aspicilia hispida* from Italy and Greece. *Herzogia*, **17**, 95–102.

- Harper, K.T. & Belnap, J. (2001) The influence of biological soil crusts on mineral uptake by associated vascular plants. *Journal of Arid Environments*, **47**, 347–357.
- Holl, K.D. & Crone, E.E. (2004) Applicability of landscape and island biogeography theory to restoration of riparian understory plants. *Journal of Applied Ecology*, **41**, 922–933.
- Jones, C.G., Lawton, J.H. & Shachak, M. (1997) Positive and negative effects of organisms as physical ecosystem engineers. *Ecology*, **78**, 1946–1957.
- King, J.W. & Channell, J.E.T. (1991) Sedimentary magnetism, environmental magnetism, and magnetostratigraphy. *US National Report to International Union of Geodesy and Geophysics* (ed. R. Pielke, Sr), pp. 358–370. American Geophysical Union, Washington, DC.
- Li, X.L., Xiao, H.-L., Zhang, J.-G. & Wang, X.P. (2004) Long-term ecosystem effects of sand-binding vegetation in the Tengger Desert, northern China. *Restoration Ecology*, **12**, 376–390.
- McCune, B. (1993) Gradients in epiphyte biomass in three *Pseudotsuga–Tsuga* forests of different ages in western Oregon and Washington. *Bryologist*, **96**, 405–411.
- McCune, B. & Grace, J.B. (2002) *Analysis of Ecological Communities*. MJM Software Design, Gleneden Beach, OR.
- McCune, B. & Rosentreter, R. (1995) *Field key to soil lichens of central and eastern Oregon*. Unpublished report. Oregon State University and USDI BLM.
- Maestre, F.T. & Cortina, J. (2002) Spatial patterns of surface soil properties and vegetation in a Mediterranean semi-arid steppe. *Plant and Soil*, **241**, 279–291.
- Manley, B.F.J. (2001) *Randomization, Bootstrap and Monte Carlo Methods in Biology*, 2nd edn. Chapman & Hall/CRC, Washington, DC.
- Mazor, G., Kidron, G.J., Vanshak, A. & Abeliovich, A. (1996) The role of cyanobacterial exopolysaccharides in structuring desert microbial crusts. *FEMS Microbiology Ecology*, **21**, 121–130.
- O'Neill, R.V. (1988) Hierarchy theory and global change. *Scales and Global Change* (eds T. Rosswall, R.G. Woodmansee & P.G. Risser), pp. 29–45. John Wiley & Sons Ltd, New York, NY.
- Ponzetti, J.M. & McCune, B.P. (2001) Biotic soil crusts of Oregon's shrub steppe: community composition in relation to soil chemistry, climate, and livestock activity. *Bryologist*, **104**, 212–225.
- Reynolds, R.L., Belnap, J., Reheis, M., Lamothe, P. & Luiszer, F. (2001) Aeolian dust in Colorado Plateau soils: nutrient inputs and recent change in source. *Proceedings of the National Academy of Sciences*, **98**, 7123–7127.
- Rogers, R.W. (1972) Soil surface lichens in arid and subarid south-eastern Australia. III. The relationship between distribution and environment. *Australian Journal of Botany*, **20**, 301–316.
- Ullmann, I. & Büdel, B. (2003) Biological soil crusts on a landscape scale. *Biological Soil Crusts: Structure, Function, and Management* (eds J. Belnap & O.L. Lange), pp. 203–213. Springer-Verlag, Berlin, Germany.
- Western Regional Climate Center (2005) *Historical Climate Information*. <http://www.wrcc.dri.edu>. Desert Research Institute, Reno.
- Zander, R.H. (2004) *Bryophyte Flora of North America*. <http://www.ridgwaydb.mobot.org/bfna>. Missouri Botanical Garden, St Louis, MO.

Received 4 July 2005; final copy received 31 August 2005

Editor: Rob Freckleton