

Small-scale patterns of abundance of mosses and lichens forming biological soil crusts in two semi-arid gypsum environments

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Abstract. Despite important advances in the understanding of biological soil crusts and their key role in ecosystem processes in arid and semi-arid environments, little is known about those factors driving the small-scale patterns of abundance and distribution of crust-forming lichens and mosses. We used constrained ordination techniques (RDAs) to test the hypothesis that the spatial patterning of lichens and mosses is related to surface and subsurface soil variables in two semi-arid gypsum environments of Spain. Our results show that the abundance of mosses and lichens forming biological soil crusts was related to a limited set of variables (cover of bare soil and litter, soil respiration, potassium content and aggregate stability). Moreover, they provide some insights into the importance of these variables as drivers of biological soil-crust composition and abundance in semi-arid gypsum environments.

Introduction

Biological soil crusts (hereafter termed ‘biological crusts’), composed of bacteria, cyanobacteria, algae, mosses, liverworts, fungi and lichens, are a major biotic component of arid and semi-arid ecosystems worldwide (West 1990; Eldridge and Greene 1994; Belnap and Lange 2001). These crusts frequently cover soil surfaces and exert a strong influence on critical ecosystem processes such as infiltration, carbon sequestration and nutrient cycling (Beymer and Klopatek 1991; Evans and Ehleringer 1993; Eldridge *et al.* 2000). They also influence the distribution and abundance of plants and animals (Prasse and Bornkamm 2000; De Falco *et al.* 2001; Shepherd *et al.* 2002). Lichens and mosses are important constituents of biological crusts, and usually appear during late stages of crust development (Lange *et al.* 1997). Over the last several decades there have been important advances in the knowledge of the physiology, dynamics, taxonomy, biogeography and ecology of biological crusts (reviewed in Belnap and Lange 2001).

Despite the large body of literature on biological crusts, little is known concerning those factors driving the patterns of distribution and abundance of crust-forming lichens and mosses at small spatial scales. Eldridge (1999) examined the distribution of terricolous mosses and lichens at relatively

small scales along a sequence of runoff, interception and run-on zones in a *Callitris glaucophylla* woodland in eastern Australia, and evaluated how these organisms were distributed in relation to different environmental variables. He found that soil-surface attributes such as cover, and variables related to soil erosion and stability were the most important factors associated with moss and lichen distribution. Recent studies conducted in *Stipa tenacissima* steppes of south-eastern Spain have quantified the spatial patterns of crust-forming lichens and mosses at plot (Maestre and Cortina 2002) and micro-site scales (Maestre *et al.* 2002; Maestre 2003a, 2003b). In these steppes, changes in microclimate and soil conditions induced by *S. tenacissima* tussocks modify the patterns of abundance at small spatial scales, as well as inter-specific interactions between these organisms.

Gypsiferous soils, characterised by high concentrations of sulfate and calcium, commonly occur in arid and semi-arid areas (Verheyne and Boyadgiev 1997). These soils support an interesting biological crust, which is characterised by a high degree of lichen diversity and rarity (Llimona 1974; Crespo and Barreno 1975; Anderson and Rushforth 1976; Tarazona *et al.* 1980; St Clair *et al.* 1993; Martínez-Sánchez *et al.* 1994; Guerra *et al.* 1995; Nimis *et al.* 1996;

Belnap *et al.* 2001). Owing to human-related activities, gypsum habitats are ranked among the most threatened ecosystems worldwide, and are considered a priority conservation concern (Gómez Campo 1987; Belnap *et al.* 2001; Mota *et al.* 2003). Despite their importance, little is known of the ecology and dynamics of biological crusts in these areas, nor the factors driving their distribution and abundance at different spatial scales (Evans and Johansen 1999). Conservation and restoration efforts in these environments can be greatly enhanced if we can determine which environmental factors are best correlated with the abundance of the different biological-crust components (Belnap and Eldridge 2001).

In this study we measured small-scale patterns of abundance of lichens and mosses forming biological crusts in two semi-arid gypsum areas of Spain, and related these patterns to different soil surface (cover of litter, bare soil, rocks and vascular plants) and subsurface (total nitrogen and carbon, soil respiration, potassium, aggregate stability and bulk density) attributes. To our knowledge, no previous study has evaluated such relationships in semi-arid gypsum areas. As observed in other semi-arid areas (Eldridge 1996, 1999; Eldridge and Tozer 1996, 1997), we hypothesised that subsurface soil attributes would exert a significant influence on biological-crust abundance at small spatial scales, and that this fraction of variation would not be coincident with that explained by the soil surface variables. Specifically, we aimed to address the following questions: (i) which soil attributes affect the small-scale patterns of abundance of crust-forming lichens and mosses in semi-arid gypsum areas; and (ii) what is the relative importance of surface *v.* subsurface soil attributes as drivers of such patterns?

Material and methods

Study sites

Two sites with similar overall soil characteristics, but differing in their disturbance history, vascular plant cover and climatic characteristics, were selected for this study. The first site (El Plano), is located close to Sax (38°32'N, 0°49'W, 500 m a.s.l.), in the province of Alicante (south-eastern Spain). The second site (Belinchón) is located near Tarancón (40°30'N, 3°1'W, 710 m a.s.l.), in the province of Cuenca (central Spain). The climate is Mediterranean semi-arid and dry at the El Plano and Belinchón sites, respectively. Mean annual temperature and rainfall are 16.5°C and 315 mm, and 13.7°C and 525 mm at the El Plano and Belinchón sites, respectively. Both sites experience an extremely intense summer drought, and have a bimodal rainfall distribution (with major rainfall periods in early spring and late autumn). The soil is in both cases a Typic Gypsiorthid (Soil Survey Staff 1990), with gypsum soil content (hydrous calcium sulfate) above 50%. Perennial plant cover is below 30% at both sites, and is dominated by specialised gypsophytes such as *Helianthemum squamatum* (L.) Dum.-Cours. and *Herniaria fruticosa* L. The El Plano site has a very open tree layer formed by *Pinus halepensis* Miller (Aleppo pine) from a 60-year-old plantation. Since it was planted, the plantation has not been disturbed and there is now a well-developed biological-crust cover between the trees. The Belinchón site has been affected by recent trampling by sheep; a flock

of approximately 500 sheep has occasionally crossed it during the last few years (I. Martínez, pers. obs.).

Field survey

At both study sites, 100 squares, 30 cm × 30 cm each, were non-randomly placed on areas with a flat and homogeneous microtopography, devoid of vascular plants (cover below 5% was visually estimated) and with well-developed biological crusts. We followed this approach to minimise the variability associated with small-scale differences in microtopographical features of the soil surface, and to capture the variability in biological-crust cover and species composition registered at each site. However, a minimum separation distance of 1.5 m between quadrats was established to minimise the risk of sampling non-independent areas (Maestre *et al.* 2005).

The cover of each species of moss and lichen was estimated at the two sites between August and September 2003 by the point sampling method. The sampling quadrat was divided into 169 sampling points, corresponding to the nodes of a 2.5 cm × 2.5 cm grid, and the identity of the species present at each node was registered. The cover of each species in each quadrat was estimated as the proportion of the 169 points occupied by it. Before sampling, the soil surface was sprayed with water to make biological-crust components more readily visible. Lichen and moss specimens were identified *in situ*, but small pieces of thalli were collected and examined later in the laboratory to confirm species identification. This survey was also used to obtain the cover of morphological groups in each quadrat. The classification of Eldridge and Rosentreter (1999), which establishes functional groups based on morphological attributes of the species, was used. This classification system allows for relatively easy interpretation of biological-crust constituents in relation to key ecosystem processes like sediment retention, rainfall infiltration, runoff generation and nutrient cycling (Eldridge and Rosentreter 1999).

In each sampling quadrat the following soil-surface attributes were measured by the point sampling method described above: litter cover, bare soil cover, rock fragment cover and vascular-plant cover. Vascular-plant cover was negligible at El Plano (see below), and this variable was not considered in the analyses of the data from this site. The following subsurface soil variables were also measured: respiration, total organic carbon, total nitrogen, bulk density, potassium and aggregate stability. These variables were selected because they may act as potential surrogates to explain the abundance patterns of crust-forming mosses and lichens at our study sites. Surface variables such as bare soil cover and rock fragment cover may act as good surrogates of the amount of space available for crust organisms, whereas others such as litter cover may be used as a proxy for organic matter enrichment and tree proximity (Anderson *et al.* 1982a). Subsurface variables such as organic carbon and respiration are related to soil microbial activity and to the overall fertility of the plots (Bulluck *et al.* 2002), whereas nitrogen strongly influences the distribution and abundance of those biological-crust components that do not fix atmospheric nitrogen (Mickiewicz 1976; Virtanen *et al.* 2000; Li *et al.* 2003). Last, microelements such as potassium and physical properties such as soil stability, which can be measured with the percentage of stable aggregates, may also influence the distribution of crust organisms (Ullmann and Büdel 2001; Li *et al.* 2003).

The sampling of subsurface variables was performed at the end of August (El Plano site) and September (Belinchón site) 2003, when the soil was dry after a pronounced summer drought. Twelve randomly placed 19.63-cm² circular soil cores (5 cm diameter × 1 cm depth) were sampled within each sampling quadrat. Samples collected from each quadrat were bulked and homogenised in the field, labelled and taken to the laboratory, where they were air-dried for 2 months and subsequently weighed. After weighing, samples were carefully hand-sieved at 2 mm, and the resulting fractions were also weighed

too. Weight corrections were made by using moisture contents of air-dried samples. Moisture content was determined by gravimetric analysis by drying below 50°C (to avoid loss of water molecules from gypsum, which is a hydrous calcium sulfate) until a constant weight was obtained (Porta 1996). Soil respiration rates were determined by NaOH absorption followed by titration with HCl (Zibilske 1994). Total organic carbon and nitrogen were determined by using finely powdered aliquots of the original samples by dry combustion followed by gas chromatography with a CN elemental analyser (EuroEA3000, Eurovector, Milan, Italy). Previously, carbonates of all aliquots were removed with diluted HCl. Aggregate stability was assessed on 0.25–2-mm-sized aggregates, following a slightly modified version of the method of Lax *et al.* (1994). Potassium content was evaluated by flame photometry after dilution of samples with 1 M ammonium acetate (Burt 2004).

Numerical analyses

We used constrained ordinations to examine the multivariate relationships between species cover and the measured soil variables (Legendre and Anderson 1999; Rubio and Escudero 2000). Our hypothesis is that soil variables influence the patterns of presence and abundance of the lichens and mosses forming biological crusts. With this in mind, a detrended correspondence analysis (DCA; Hill and Gauch 1980) with the cover dataset was conducted by detrending by segments and non-linear rescaling of the axes, which has the property that the extracted axes are scaled in units of average standard deviation (Gauch 1982). As the extracted gradients of the cover database were short (standard deviation units <2), we conducted a redundancy analysis (hereafter RDA) which is a constraining ordination technique that assumes linear responses of species with the extracted axes. The total variation explained was calculated as the sum of all extracted canonical axes (Borcard *et al.* 1992). A Monte Carlo permutation test (1000 randomisations) was performed to determine the accuracy of the relationship between the species cover and soil variables datasets, using the sum of all canonical Eigenvalues or trace to build the F -ratio statistic (ter Braak 1990; Verdonschot and ter Braak 1994; Legendre and Anderson 1999). If the RDA model was significant, a forward stepwise procedure was carried out to select a reduced model including only significant variables. We incorporated explanatory variables one at a time and step by step in the order of their decreasing Eigenvalues after partialling out the variation accounted for the already included variables. The process ended when the new variable entered was not significant ($P > 0.01$ after a multiple comparison correction). Improvement of the reduced model with each new selected variable was determined by a Monte Carlo permutation test with 1000 randomisations. A variance partitioning with RDA was performed to evaluate the relative importance of an environmental matrix after adjusting for the variability of other datasets, considered here as a covariable dataset (Borcard *et al.* 1992). This procedure has been called partial RDA because it determined the variation accounted for the environmental matrix after removing the variation explained by the covariable dataset. The treatment matrix was formed by the soil subsurface variables (the reduced model), whereas selected surface variables were considered as covariables. Specifically, we wanted to know whether the remaining information after adjusting species-cover dataset to the soil surface variables can be significantly explained by the subsurface variables. If not, both explanatory datasets are concomitant. Models were independently built for each site. All multivariate analyses were conducted with CANOCO for Windows v. 4.5 (ter Braak and Smilauer 1997).

Differences between study sites in the cover for different species, cover for morphological groups and soil variables were evaluated with randomisation tests (Manly 1997). These were conducted with 5000 randomisations, using the software Resampling 1.3

(David C. Howell, University of Vermont; downloaded from <http://www.uvm.edu/dhowell/StatPages/Resampling/Resampling.html>). The overall significance level ($\alpha = 0.05$) of these tests was adjusted for multiple testing by the false discovery rate method of Benjamini and Hochberg (1995).

Results

Species richness and cover

Total cover of soil lichens and mosses was significantly higher at the Belinchón site (79.54 ± 1.14 v. 65.32 ± 1.78 , mean \pm s.d., $n = 100$, randomisation test, $P < 0.05$). The number of species per quadrat was also higher at this site (6.71 ± 0.15 v. 5.39 ± 0.13 , mean \pm s.d., $n = 100$, randomisation test, $P < 0.05$). The cover of different lichen and moss species differed substantially between sites (Table 1). Some species were recorded at only one of the sites, such as *Acarospora nodulosa* var. *reagens*, *Barbula* sp., *Placidium squamulosum*, *Squamarina lentigera* and *Toninia albilabra* in Belinchón, and *Toninia diffracta* and *Tortula revolvens* in El Plano. *Diploschistes diacapsis*, *Fulgensia subbracteata*, *Psora decipiens* and *Toninia sedifolia* had higher cover in Belinchón, whereas *Collema crispum*, *Lepraria crassissima* and *Placidium rufescens* had higher cover in El Plano. We identified four morphological groups at our study sites (Fig. 1). The Belinchón site had a higher cover of crustose and squamulose lichens, whereas El Plano had a higher cover of gelatinous lichens and mosses.

Species–environment relationships

Important differences were found in the different soil surface and subsurface variables measured (Table 2). RDAs performed with both the subsurface and surface soil variables as constraining matrices were significant ($P < 0.001$), suggesting that both datasets were able to explain the cover of the different lichens and mosses at our study sites (Table 3). The total variation explained was, however, rather low, and remained below 18% in all cases. At Belinchón, only two variables from the subsurface matrix were selected by the forward stepwise procedure: potassium content ($F = 3.33$, $P = 0.004$) and soil respiration ($F = 2.69$, $P = 0.006$). In the case of the soil surface matrix, only bare soil cover was selected ($F = 9.16$, $P = 0.001$). Aggregate stability was the unique variable selected at El Plano from the subsurface matrix ($F = 3.66$, $P = 0.001$). At this site, two variables from the surface matrix were selected: bare soil cover ($F = 11.34$, $P = 0.001$) and litter cover ($F = 5.82$, $P = 0.001$).

As expected, selected variables were highly correlated with extracted axes. When the number of selected variables was two, the first one was correlated with the first extracted axis and the second variable with the orthogonal Axis 2 (see Fig. 2 for Belinchón, and Fig. 3 for El Plano). Although species did not cluster into well defined groups, some species were associated in similar ways with

Table 1. Cover of lichens and mosses at the two study sites

Data represent means \pm s.d. ($n = 100$). Different lower-case letters indicate significant differences ($P = 0.05$) after a permutation test (see text for details). Morphological groups were established according to Eldridge and Rosentreter (1999): GL = gelatinous lichens, CL = crustose lichens, SL = squamulose lichens, MO = mosses. Successional stages were established according to Belnap *et al.* (2001): EC = early successional species, MS = mid-successional species, LT = late-successional species

Species	Morphological group	Successional stage	Species abbreviation	Cover (%)	
				El Plano	Belinchón
<i>Acarospora nodulosa</i> (Dufour) Hue	SL	EC	Ar	–	1.13 \pm 1.76
<i>Collema crispum</i> (Huds.) F.H.Wigg.r	GL	EC	Ccr	14.42 \pm 9.07a	0.20 \pm 0.65b
<i>Diploschistes diacapsis</i> (Ach.) Lumbsch	CL	MS	Dd	8.28 \pm 16.2a	17 \pm 13.19b
<i>Diplotomma epipolium</i> (Ach.) Arnold.	SL	EC	De	–	2.73 \pm 3.50
<i>Fulgensia subbracteata</i> (Nyl.) Poelt	CL	MS	Fs	13.63 \pm 9.89a	28 \pm 11.07b
<i>Lepraria crassissima</i> (Hue) Lettau	CL	MS	Lc	6.53 \pm 7.63a	1.05 \pm 3.45b
<i>Placidium rufescens</i> (Ach.) A.Massal.	SL	EC	Pr	0.25 \pm 1.15a	0.10 \pm 0.46b
<i>Placidium squamulosum</i> (Ach.) Breuss	SL	EC	Ps	–	0.13 \pm 0.50
<i>Psora decipiens</i> (Hedw.) Hoffm.	SL	EC	Pd	1.13 \pm 3.52a	12.4 \pm 10.58b
<i>Psora saviczii</i> (Tomlin) Follmann & A.Crespo	SL	EC	Psv	–	1.66 \pm 3.27
<i>Squamarina cartilaginea</i> (With.) P.James	SL	EC	Sc	1.02 \pm 3.68a	0.34 \pm 0.96a
<i>Squamarina lentigera</i> (Weber) Poelt	SL	EC	Sl	–	0.24 \pm 0.62
<i>Toninia albilabra</i> (Dufour) H.Olivier	SL	EC	Ta	–	0.35 \pm 1.34
<i>Toninia diffracta</i> (A. Massal.) Zahlbr.	SL	EC	Td	0.22 \pm 1.12	–
<i>Toninia sedifolia</i> (Scop.) Tindal	SL	EC	Ts	5.02 \pm 7.13a	14.07 \pm 10.09b
<i>Barbula</i> sp.	MO	LT	Bb	–	0.04 \pm 0.16
<i>Tortula revolvens</i> (Schimp.) G.Roth	MO	LT	Tr	14.79 \pm 16.74	–

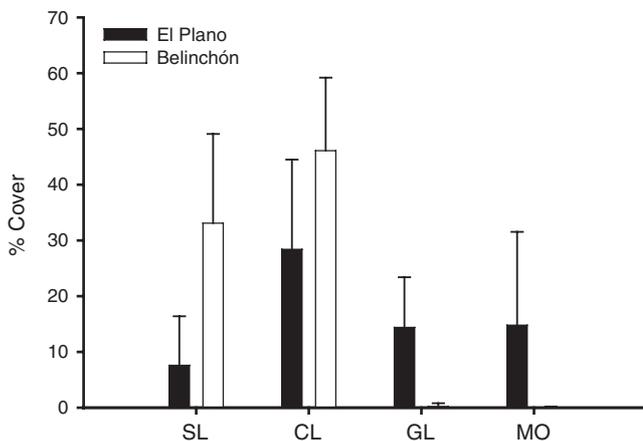


Fig. 1. Cover of the different morphological groups identified at the two study sites. Data represent means \pm s.d. ($n = 100$). The mean cover of each group differed significantly between sites (randomisation test with 10 000 permutations; $P < 0.05$). Morphological groups were established according to Eldridge and Rosentreter (1999): GL = gelatinous lichens, CL = crustose lichens, SL = squamulose lichens, MO = mosses.

the soil variables measured. For example, species such as *Diploschistes diacapsis* and *Psora decipiens* were associated at Belinchón with the highest respiration and potassium values, respectively. On the other hand, *Collema crispum* and *Lepraria crassissima* associated negatively with the latter variable (Fig. 2A). *L. crassissima* and *C. crispum* were positively correlated with bare soil, whereas *Toninia sedifolia*

Table 2. Surface and subsurface soil variables measured at the two study sites

Data represent means \pm s.d. ($n = 100$). Means followed by different letters are significantly different (at $P = 0.05$) after correction for multiple testing (see text for details)

Variable	Study site	
	El Plano	Belinchón
Litter cover (%)	10.97 \pm 11.05a	1.22 \pm 1.73b
Bare soil cover (%)	19.52 \pm 13.47a	18.43 \pm 12.17a
Rock fragment cover (%)	0.08 \pm 0.08a	0.43 \pm 0.68b
Vascular plant cover (%)	– ^B	0.43 \pm 0.68
Potassium content (mg K kg ⁻¹ soil)	81.99 \pm 28.96a	52.31 \pm 13.80b
Bulk density (g cm ⁻³) ^A	1.01 \pm 0.09a	0.91 \pm 0.06b
Respiration (mg C-CO ₂ kg ⁻¹ h ⁻¹) ^A	5.51 \pm 2.42a	3.46 \pm 1.09b
Total organic carbon (%) ^A	1.83 \pm 0.70a	1.38 \pm 0.28b
Total nitrogen (%) ^A	0.14 \pm 0.05a	0.15 \pm 0.04a
Aggregate stability (%) ^A	72.28 \pm 6.30a	55.92 \pm 11.53b

^AData come from Maestre *et al.* (2005).

^BVascular-plant cover was negligible at this site.

and *P. decipiens* were negatively correlated with this variable (Fig. 2B). It was not possible to identify well defined groups by using subsurface variables in El Plano, albeit *D. diacapsis* showed a weak negative correlation with aggregate stability (Fig. 3A). *C. crispum* and *L. crassissima* were positively associated with bare soil at this site. On the other hand, *T. sedifolia*, *Fulgensia subbracteata* and the bryophyte *Tortula revolvens* tended to be associated with plots with low bare-soil cover at this site (Fig. 3B).

Table 3. Redundancy analysis (RDA) models obtained at the two study sites, using the species cover matrix and two environmental datasets as constraining matrices (soil surface and subsurface variables)

Constraining matrix indicates dataset used to build models. λ_1 , λ_2 , λ_3 are the Eigenvalues of the corresponding extracted axes. Σ cons is the sum of all constrained axes. In partial RDAs, TVE = total variation explained (in %). F -ratio statistic was computed by using the trace or sum of all Eigenvalues. The level of significance of the model (P ; 1000 randomisations) is shown

Site and constraining matrix	λ_1	λ_2	λ_3	Σ cons	TVE	Monte Carlo test F -ratio	P
Belinchón site							
Subsurface attributes	0.057	0.036	0.021	0.135	13.5	2.314	0.001
Surface attributes	0.096	0.012	0.009	0.121	12.1	3.13	0.001
El Plano site							
Subsurface attributes	0.063	0.027	0.006	0.104	10.4	1.695	0.009
Surface attributes	0.121	0.031	0.018	0.17	17.0	6.198	0.001

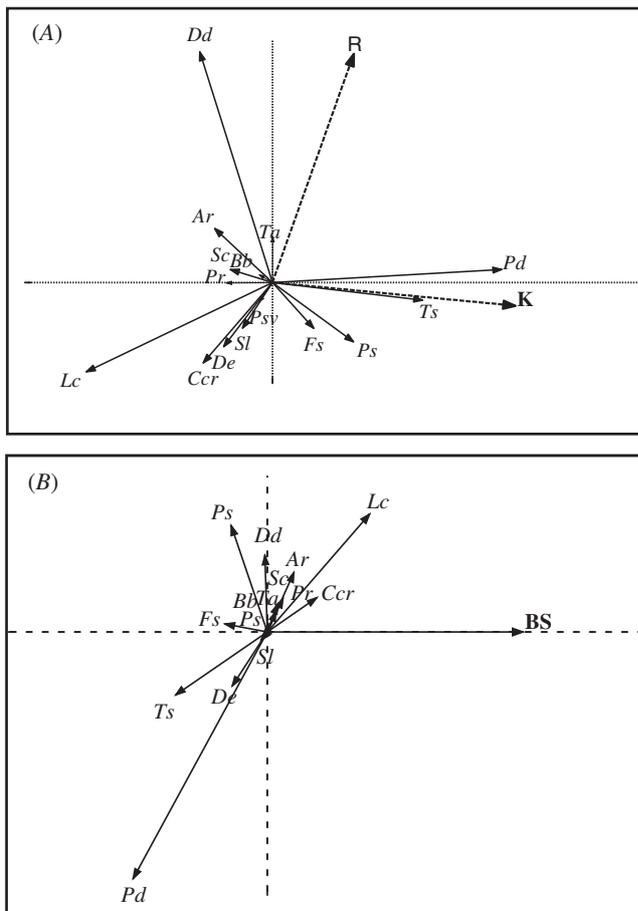


Fig. 2. First two axes of the redundancy analysis ordinations carried out at the Belinchón site on the basis of (A) soil subsurface and (B) surface variables. Only variables selected by the forward stepwise procedure are shown. R = soil respiration; K = potassium content; BS = bare soil cover. Species abbreviations are shown in Table 1.

Partial RDA models were significant in all cases, suggesting that surface and subsurface variables explained significant non-overlapping fractions of variation in the

matrix of species cover at both study sites (Fig. 4). The amount of variation of the species cover matrix explained by the surface matrix was higher than that explained by the subsurface matrix at both study sites. At the Belinchón site, the subsurface and surface matrices accounted for a total of 14.4% of the variation in the species cover matrix, and overlapped 2.9%. At the El Plano site, they accounted for 18.1% of the variation in the species cover matrix, and overlapped 0.1% (Table 4).

Discussion

The number of specialised lichens is very high at our study sites. Of the 17 species reported, *Acarospora nodulosa* var. *reagens*, *Diploschistes diacapsis*, *Fulgensia subbracteata* and *Psora saviczii* grow exclusively on gypsum soils, representing almost 24% of the species present at these sites. This high proportion of specialised species is one of the most outstanding features of the moss and lichen flora of semi-arid gypsum environments worldwide (Llimona 1974; Crespo and Barreno 1975; Martínez-Sánchez *et al.* 1994; Belnap and Lange 2001). Gypsum environments support one of the most important sets of specialised cryptogams, and are areas of global conservation priority (Gómez-Campo 1987; Mota *et al.* 2003).

Differences in species composition between the two evaluated sites were obvious. Despite the fact that El Plano receives substantially less rainfall than Belinchón, the composition of the biological crusts at the former site was characterised by a relatively high cover of mosses, which are generally considered dominant constituents of well conserved and late-successional crusts in arid and semi-arid areas (Cameron 1972; Danin and Barbour 1982; Belnap and Eldridge 2001). Studies conducted on Utah deserts have found contrasting effects of disturbances on moss cover. While Evans and Belnap (1999) reported that this cover was significantly higher in grazed than in non-grazed areas, Anderson *et al.* (1982a, 1982b) found that disturbance by grazing significantly decreased moss cover. Similarly,

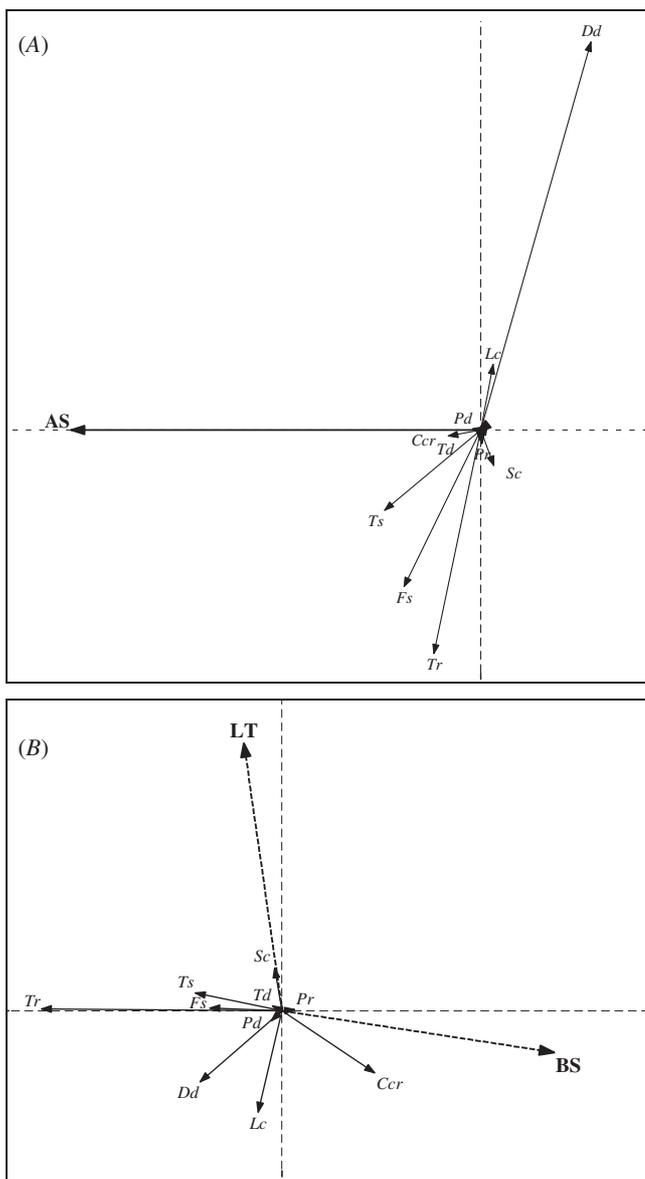


Fig. 3. First two axes of the redundancy analysis ordination carried out at the El Plano site on the basis of soil (A) subsurface and (B) surface variables. Only variables selected by the forward stepwise procedure are shown. AS = aggregate stability; LT = litter cover; BS = bare soil cover. Species abbreviations are shown in Table 1.

Meyer and García Moya (1989) found that disturbance by grazing reduced the cover of biological soil crust in semi-arid gypsum environments of Mexico. It is interesting to note that the early successional lichen *Collema* (Belnap *et al.* 2001) was more abundant in El Plano than in Belinchón. This suggests that the abundance of mosses may be due to factors other than the local successional status of the biological crusts. In fact, the existence of a tree canopy at El Plano may substantially increase the number of areas that are partially or permanently shaded, and this may

substantially alter soil moisture in favour of the mosses. It has been shown that shade reduces evapotranspiration and may thus increase soil moisture in semi-arid areas (Maestre *et al.* 2003), and that the development of mosses is strongly limited by low soil-moisture levels in these environments (Martínez-Sánchez *et al.* 1994). Increased cover of mosses in semi-arid areas has been reported for shaded microsites adjacent to perennial grasses and shrubs in contrast with open areas (Martínez-Sánchez *et al.* 1994; Maestre *et al.* 2002; Maestre 2003b). Differences in disturbance history could also help to explain the observed differences in moss cover between our study sites. In addition to the disturbance created by trampling, Meyer and García-Moya (1989) showed that grazing promotes a decrease in soil water availability in semi-arid gypsum environments of Mexico. If this pattern is occurring at the Belinchón site, such a decrease in soil moisture could also contribute to the low moss cover observed there. The presence of both late- and early successional biological-crust components in most of the quadrats at El Plano (mosses and *Collema* were present in 85 and 98% of the sampling quadrats, respectively), illustrates that small-scale heterogeneity in the composition of the biological crusts can be very high in semi-arid areas, even in places that have not been disturbed in decades.

Despite the growing interest in biological crusts, most of the studies evaluating how environmental variables influence the composition and abundance of crust constituents in arid and semi-arid areas have been conducted in the US (Kleiner and Harper 1977; Nash *et al.* 1977; Anderson *et al.* 1982a; Johansen 1993; Rosentreter and Belnap 2001) and Australia (Rogers and Lange 1971; Rogers 1972b; Downing and Selkirk 1993; Eldridge and Tozer 1997; Eldridge and Koen 1998). Very few studies have been carried out in other geographical areas (Eldridge *et al.* 2000, 2002; Ullmann and Büdel 2001). In most cases, these studies were carried out at relatively large spatial scales, where factors such as water availability or soil properties (e.g. calcium carbonate content, organic matter, pH and general soil-surface characteristics) were the major determinants of biological-crust cover and composition (Rogers 1972a; Nash *et al.* 1977; Anderson *et al.* 1982a; Eldridge and Tozer 1997; Eldridge and Koen 1998). However, the evaluation of the role of soil properties as drivers of the presence and abundance of biological-crust organisms at local scales has received much less attention (Rogers and Lange 1971; Ullmann and Büdel 2001).

At the Belinchón site, which has been affected by recent trampling by sheep, *Diploschistes diacapsis* and *Toninia albilabra* were positively related to areas of high soil respiration, whereas *Psora decipiens* and *Toninia sedifolia* were positively related to soil potassium. These soil variables are likely to be surrogates of healthy soils with high biological activity, stability and productivity, and therefore may sustain a diverse community of non-vascular plants (Li *et al.* 2003). *Collema crispum*, *Placidium rufescens* and

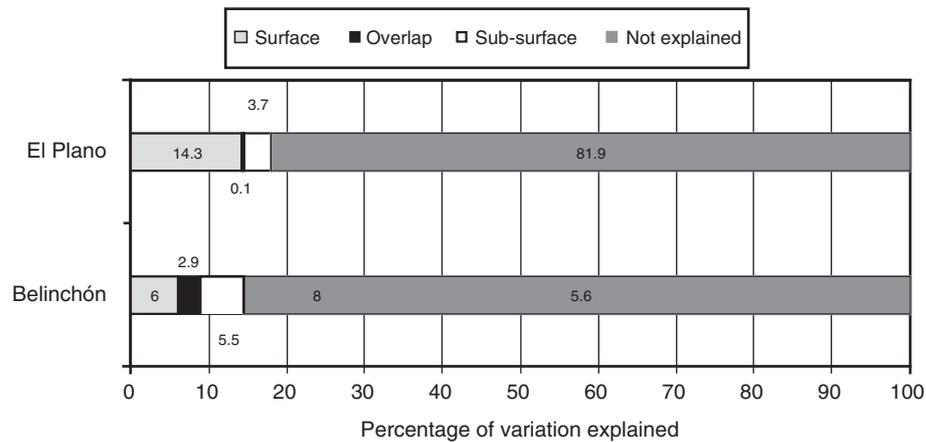


Fig. 4. Graphic summary of partial redundancy analyses performed to quantify the amount of variation in the species cover matrix explained by the fractions defined by the constraining matrices (represented by the bars). The numbers located in each bar represent the amount of variation in the species cover matrix explained by each fraction. All individual fractions of variation were significant ($P = 0.001$). Not drawn to scale.

Table 4. Partial redundancy analysis (RDA) models using the soil surface variables as the constraining matrix and the subsurface variables as a covariable matrix

Only the selected variables have been included. Constraining matrix indicates the dataset used to build models. Covariables indicate the covariable datasets for partial RDA models. λ_1 , λ_2 , λ_3 are the Eigenvalues of the corresponding extracted axes. Σ cons is the sum of all constrained axes. In partial RDAs, TVE = the proportion between the sum of all constrained Eigenvalues after fitting covariables and the sum of all unconstrained Eigenvalues after fitting covariables. The F -ratio statistic was computed from the trace of sum of all Eigenvalues as reference. The level of significance of the model (P ; 1000 randomisations) is shown

Site	Constraining matrix	Covariable	λ_1	λ_2	λ_3	Σ cons	TVE	Monte Carlo test F -ratio	P
El Plano	Surface	Subsurface	0.113	0.03	0.281	0.565	18.1	7.939	0.001
Belinchón	Surface	Subsurface	0.06	0.197	0.133	0.513	14.4	6.406	0.001

Lepraria crassisima were negatively associated with soil respiration and positively associated with bare soil cover, suggesting that these lichen species act as pioneers following disturbance (Eldridge 1999; Belnap *et al.* 2001). Furthermore, at the El Plano site these three lichens (*Collema crispum*, *Placidium rufescens* and *Lepraria crassisima*) were associated with areas of high bare-soil cover and low litter cover. None of the species showed a strong relationship to litter cover at this site, albeit *Squamarina cartilaginea* was positively, but weakly, related to this variable. This may be related to a preference by this species for those sites closer to the trees (which include the sites with greater litter accumulation; F. Maestre, pers. obs.).

Redundancy analyses carried out with morphological groups instead of species (results not shown) produced similar results to those presented here (the same set of subsurface and surface soil variables was selected at each site). The abundance of squamulose lichens observed in Belinchón agrees with the results of studies showing that this morphological group dominates during the early stages of biological-crust recovery after disturbance (Belnap *et al.* 2001). It has been reported that gelatinous species such

as *Collema* and crustose lichens such as *Diploschistes* are sensitive to disturbances by trampling (Rogers and Lange 1971). Our results partially agree with these observations, as we found higher cover of gelatinous (but not of crustose) lichens in El Plano, which has not been affected by recent disturbances. However, it must be noted that the differences observed in the cover of these groups between our study sites may be due to factors other than disturbance (e.g. distance to propagule sources, microclimate). The use of morphological groups in this study did not provide additional information to explain the patterns observed. However, the fact that the results of the ordinations obtained with the morphological groups were very similar to those obtained with the species suggests that they can be used in studies aimed to evaluate the factors that affect the distribution of biological-crust components. While the suitability of using morphological groups will depend on the objectives of the study (see Eldridge and Rosentreter 1999 for a discussion on the topic), our results indicate that they provide an efficient and cost-effective approach to monitoring soil-crust organisms in Mediterranean gypsum environments.

Our results have shown that the small-scale patterns of abundance of crust-forming mosses and lichens are related to a limited suite of soil surface and subsurface variables. However, our results must be interpreted with caution because of limitations of the observational approach followed. It must be noted that the correlations between species and environmental variables indicated by the RDAs do not imply that the soil variables selected by these analyses are driving the small-scale patterns of abundance of crust-forming mosses and lichens at our study sites. Moreover, the small proportion of the variation in species cover explained by our analyses (below 25%) clearly indicates that other variables are important drivers of such patterns. Previous studies conducted in semi-arid areas have found that variables such as pH and phosphorus are important determinants of the patterns of abundance of biological-crust components (Anderson *et al.* 1982a).

Despite its limitations, our study provided some insights on the potential importance of variables such as soil-aggregate stability, soil respiration and potassium content as relevant environmental variables determining the composition of biological-crust communities in semi-arid gypsum areas. Additional studies are needed to improve our understanding of the mechanisms underlying the relationships reported here, and to expand our knowledge concerning the composition, abundance and distribution patterns of biological crusts in semi-arid gypsum habitats in other geographical areas.

Acknowledgments

We thank Pilar Bernal and Rafael Clemente (CEBAS–CSIC) for help with C and N analysis. The work of FTM was supported by a MEC/Fulbright fellowship (FU2003–0398), funded by the Dirección General de Universidades and the Fondo Social Europeo. This research was supported by the Spanish Ministry of Science and Technology (project number REN 2003-03366) to AE and by the Community of Madrid (project number GR/AMB/0932/2004) to AE, FM and IM.

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Manuscript received 8 April 2005, accepted 27 October 2005