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Original article

Multiscale effects on biological soil crusts cover and spatial distribution in the Monte Desert

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ABSTRACT

Biological soil crusts (BSC) play diverse roles in arid and semi-arid ecosystems such as increasing soil fertility and reducing soil loss due to aeolian and hydric erosion, but they are very sensitive to disturbances. These attributes point to the relevance of BSC for soil conservation and restoration. In order to use BSC for restoration of degraded soils, we need to understand the ecological drivers of BSC. In this study, we analyzed the effect of environmental factors on BSC cover at different spatial scales in the central Monte Desert (Argentina), including landform, slope, aspect, vascular plants, and disturbance intensity. We evaluated the effects of different factors with linear mixed effect models, comparing the adjustment of models of different complexity, which included different number of factors. First, at the landscape scale, we analyzed BSC cover in two geomorphological units with different soils, topography, and vegetation. BSC cover was higher in the old riverbed, which has a higher proportion of fine clay soil particles, than in the aeolian plain. Disturbance effects were apparent in the old riverbed, showing increasing BSC cover at higher distances from settlements, and BSC located both, under and outside plant canopies. At the mesoscale, we found no differences of BSC cover in dune flanks and inter-dune valleys of the aeolian plain. Finally, at the microscale, BSC patches of higher surface cover were found in association with vascular plants (*Larrea divaricata*, *Bulnesia retama*, *Lycium sp.*), on mounds, and in microsites of southern exposure and high slopes. Our findings suggest that BSC develop preferentially associated with vascular plants, which generate mounds and sloped microsites with southern exposure, where lower irradiances reduce desiccation in these extremely dry environments.

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1. Introduction

Biological soil crusts are associations among mosses, lichens, cyanobacteria, eukaryotic algae, and soil particles. They are found in the surface soil of most arid and semiarid areas of the world (Bowker, 2007). They play important roles in the ecosystems where they live. For example, the atmospheric nitrogen fixed by cryptogamic covers, including cryptogamic species covering rocks, soils (BSC), and plant stems, as well as moss and lichen carpets, contributes half of the terrestrial nitrogen fixation worldwide (Elbert et al., 2012). Cyanobacteria secrete exopolysaccharides, which fix soil particles, preventing soil loss by erosion and runoff, and

facilitating colonization by other microorganisms (Belnap and Gardner, 1993). Yet, BSC are sensitive to disturbances, such as trampling by humans and domestic animals (Cole, 1990; Eldridge, 1998; Williams et al., 2008; Gómez et al., 2012), off road vehicles, and fires (Kröpfl et al., 2007; Hilty et al., 2004). Disturbances may reduce BSC cover and diversity, and change their species composition, transforming complex BSC communities into associations of a few species of cyanobacteria (Belnap and Lange, 2003; Eldridge et al., 2006). Estimated recovery rates of BSC after disturbances can be slow (Belnap and Eldridge, 2001), but there are studies that show rapid recovery, from months, after experimental disturbance in the Karoo, South Africa (Dojani et al., 2011), 14–18 years in Utah (Anderson et al., 1982), to 20 years in Australia (Read et al., 2011), with recovery times decreasing with inoculation (Belnap, 1993). The biomass and functional loss created by destruction of BSC may affect site productivity, due to the loss of nutrients and soil particles

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through erosion (Williams et al., 2012).

Soil degradation and desertification in arid and semi-arid areas, including the Monte Desert is a worldwide problem, due to increasing land use pressures and population growth (Van de Koppel et al., 1997; Asner et al., 2003; Villagra et al., 2009). However, studies relating degradation to the ecology of BSC are scarce in South America, and particularly in Argentina (Castillo-Monroy and Maestre, 2011). In the Austral and Central Monte Desert, three studies have reported negative effects of livestock activity on BSC, reducing their cover and altering their spatial distribution (Bertiller and Ares, 2011; Gómez et al., 2012; Tabeni et al., 2014). In contrast, BSC recovering in degraded arid areas may contribute to soil restoration and reduce the risks of further degradation (Eldridge and Greene, 1994; Bowker et al., 2005). Additionally, BSC contribute greatly to biodiversity, representing a high number of species of cyanobacteria, eukaryotic algae, lichens, mosses, and liverworts (Belnap and Lange, 2003; Bowker et al., 2008, 2010; Flechtner et al., 2013). Still, soil crust biodiversity studies in South American drylands are scarce and floristic surveys are needed (Castillo-Monroy and Maestre, 2011). Functional approaches to classify BSC are also relevant, because different types of BSC may modify different soil properties and can be indicators of successional stages (Eldridge and Rosentreter, 1999; Koch et al., 2013). Squamulose lichens may be more efficient for fine soil particle retention, increase of soil roughness, and protection against wind erosion, while crustose BSC may be more effective for moisture retention (Eldridge and Rosentreter, 1999; Ghorbani et al., 2012; Leys and Eldridge, 1998). Gelatinous BSC may retain soil moisture and are effective at protecting the surface against water erosion (Eldridge, 1996). Lichens with cyanobacteria symbionts may fix atmospheric N, increasing N availability in the soil (Evans and Ehleringer, 1993), while lichens with green algae may be less susceptible to light stress (Demmig-Adams et al., 1990).

BSC have interesting relationships with vascular plants, depending on plant functional groups (Berkeley et al., 2005; Eldridge, 1993; Thompson et al., 2006), the presence of livestock (Gómez et al., 2012) and microclimate (Belnap, 2006; Mager and Thomas, 2011). Livestock activity may directly or indirectly affect biological soil crusts, and their relationship with vascular plants. Domestic animals destroy aggregated crusts, or bury them by trampling, representing a negative effect (Eldridge, 1998; Concostrina-Zubiri et al., 2013). However, these animals also consume litter, grasses, or shrubs, which may relieve competitive interactions between vascular plants and soil crusts. A well-developed shrub layer may increase litter burial and decrease light intensity, limiting BSC development (Berkeley et al., 2005). Grasses may compete with BSC for resources in the Monte desert (Tabeni et al., 2014), while fine leaf, thorny shrubs may protect them from trampling, and allow enough light to reach soil spaces for crust development (Thomas and Dougill, 2006, 2007). BSC effects on seedling emergence varied in different deserts. Moss, cyanobacteria and algal dominated BSC facilitated survival and growth of two annual plant species (*Eragrostis poaeoides* and *Bassia dasyphylla*) in the Tengger desert (Li et al., 2005), while cyanobacteria dominated BSC inhibited seedling emergence of several perennial plants in the Negev desert (Prasse and Bornkamm, 2000). Topography and substrates, which can be modified by vascular plants, may affect BSC, interacting with microclimatic conditions such as radiation, temperature, humidity, and soil moisture (Eldridge and Tozer, 1997; Jiao et al., 2008; Li et al., 2010; Zhang et al., 2007). Consequently, these complex relationships among vascular plants, BSC, disturbances, and substrates, including BSC species composition, need to be analyzed in each region, in order to plan BSC conservation and soil restoration strategies.

In this study, we analyzed the abundance (% cover) and distribution (occurrence at three spatial scales) of BSC in an area of the Monte Desert used for extensive livestock production. The region is at risk of degradation because of population growth and changes in land use rights, but is located in a Natural and Cultural Reserve, having the potential to become a refuge for BSC. The balance between land use and conservation is especially delicate in this area because aboriginal land rights and conservation laws apply to the same area, without a knowledge of the effects of traditional land use on different organisms, or ecosystems.

The first objective of this study is to find areas where BSC reach maximum development at the landscape scale, in the old riverbed and aeolian plain. The second objective is to identify different factors that control BSC community abundance and distributions at the meso (dune landform) and micro (shrub versus shrub interspace) scale, including vascular plants, slope, and aspect. The analysis at each of the three scales includes the effect of livestock activity on BSC cover. The third objective is to start the taxonomic identification of BSC organisms in the region.

Because of the capacity of BSC to adhere to fine particles (Rozenstein et al., 2014), and the negative effect of crust burial by sand grains where soils are moved by winds, we expected to find a higher cover of BSC in the old riverbed, where soil particles are finer. We also expected higher BSC cover in inter-dune valleys than in dune flanks, because of higher soil movement, burial of BSC, and soil particle size in dune flanks. We expected to find a pattern of increasing BSC cover with lower grazing intensities, as in previous studies, because of the destruction of BSC by trampling (Concostrina-Zubiri et al., 2013; Williams et al., 2008). Finally, we expected significant effects of microenvironmental conditions, such as the presence of fine-leaved woody vascular plants, because they protect BSC from trampling and desiccation. Shrub mounds, aspect and slope were also expected to modify BSC cover, because they affect soil radiative and water balances.

2. Materials and methods

2.1. Study area

The study sites are located in the Telteca Reserve, approximately 120 km northeast of Mendoza city, Argentina (Fig. 1). The study area is within the Central Monte Desert, which is comprised of vast sandy aeolian plains with dune-interdune systems and old riverbeds. The sediments of dune-interdune systems are fine and very fine sands, with 90% of these sand classes, and 4–7% of silt and clay (Gomez et al., 2014). The old riverbed has higher proportions of fine particles, with 23–69% of fine and very fine sands, and 15–71% of silt and clay (Table S1, Supplementary online material). The climate is arid with hot summers (48 °C absolute maximum) and cold (−10 °C absolute minimum), dry winters (Meglioli, 2015). The mean annual temperature is 18.2 °C and mean annual precipitation is 156 mm, with precipitation occurring almost exclusively during the spring and summer (from October to March). This climate data were determined during a discontinuous period of 43 years (1971–2014), using the meteorological stations located as close as possible (<25 km) to the study sites. The meteorological stations were: "El Retamo" (32° 35′ S, 67° 28′ W), "Encón" (32° 15′ S, 67° 47′ W), "El Mateo" (32° 14′ S, 67° 41′ W) and "El Pichón" (32° 22′ S, 68° 03′ W) (Meglioli, 2015).

Characteristic plant communities of the Central Monte include the shrubby steppe dominated by Zygophyllaceae and the open woodland dominated by *Prosopis flexuosa* (Rundel et al., 2007). *P. flexuosa*, growing as either a tree capable of reaching 10 m in height, or a large shrub, is a facultative phreatophyte. It has an extended root system which acquires water from deep groundwater resources (Alvarez and Villagra et al., 2009), and dominates the tree
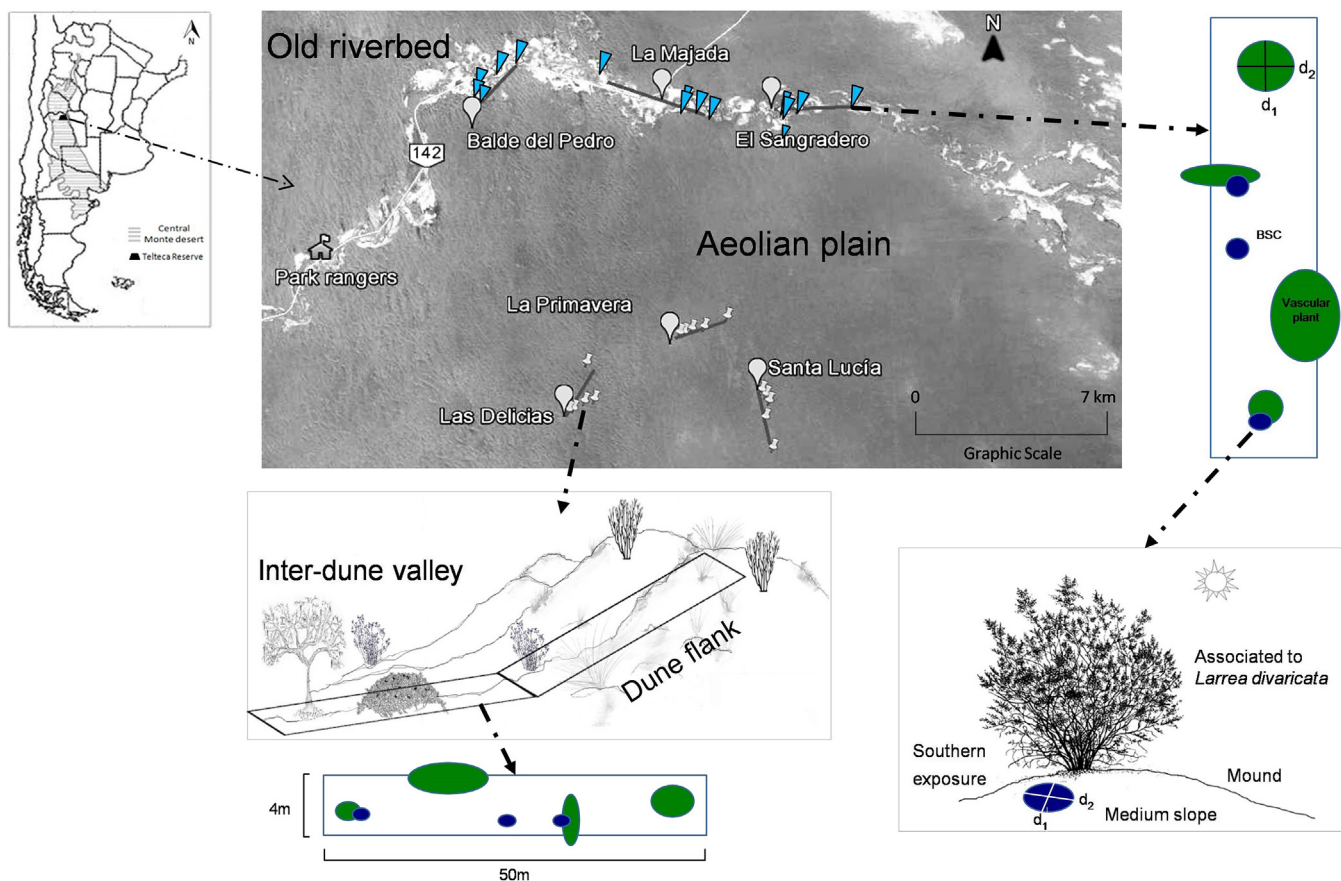
Fig. 1. Study site and sampling design. The landscape scale includes the old riverbed (El Sangradero, Balde del Pedro and La Majada) and aeolian plain (La Primavera, Las Delicias, Santa Lucía). Sampling sites at different distance classes from each settlement are indicated by triangles (in the aeolian plain) and pins (in the old riverbed). Two grids were laid in each sampling site, according to the drawing, where diameters of vascular plants (green ovals) and BSC (blue ovals) patches were registered. For the mesoscale, analyzed in the aeolian plain, a grid was laid in each, a dune flank and an interdune valley at each site. For the microscale, analyzed in the old riverbed, additional factors were estimated in each grid: slope, slope orientation, mound, and plant species associated to each BSC patch. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

layer in inter-dune valleys of the Telteca reserve. Plant species and life forms differ in dune flanks, interdunes, and old riverbeds, with a higher vegetation cover in inter-dune valleys than in the other landforms (Aranibar et al., 2014). Generally, as in other deserts, vascular plants form patches of several species, in a matrix of bare soil or annual grasses and herbs. Similarly, BSC are found in small patches, located mostly under plant canopies (Tabeni et al., 2014), probably because of disturbances and harsh conditions for BSC development.

Groundwater is found at depths of 6—15 m in inter-dune valleys and old riverbeds, allowing the establishment of livestock settlements. These settlements impact native vegetation, soil, nutrient, and water dynamics, causing patterns of increasing vegetation cover with increasing distances from settlements, up to 2 km from livestock accumulation areas (Goirán et al., 2012). Soils around settlements have higher nitrate and moisture contents, due to the accumulation of dung and urine (Meglioli et al., 2013), but lower organic matter and total N contents due to the partial removal of vegetation, litter consumption, and root decay.

2.2. Experimental design and sampling

The study was conducted in winter, from April to August 2013, in order to reduce variability given by summer precipitation. We considered three spatial scales of study, and designed sampling strategies accordingly (Fig. 1).

At the landscape scale, we analyzed the differences of BSC cover and distribution in two geomorphological units: aeolian plain and old riverbed. These units differ in topography, sediment size, and vascular plant communities. For these reasons we selected three livestock settlements in each geomorphological unit. Remote sensing in the aeolian plain (SATVI, Soil Adjusted Total Vegetation index) indicates that the maximum distance of significant livestock impact is about 2 km (Goirán et al., 2012), where vegetation reaches background values. Then, we selected settlements in the aeolian plain that presented rings of increasing vegetation with increasing distances from settlements, as indicators of decreasing disturbance intensities, using the following distance classes from the corrals: 100, 300, 600, 1000 and at least 2000 m. The most distant class represents control, relatively undisturbed areas. Because SATVI was not calibrated in the old riverbed, we selected settlements located at least 4 km from another settlement, assuming that distance from the settlements represented land use intensity gradients, similarly to the aeolian plain. Sites at different distances from the corrals were determined a priori based on the vegetation rings observed with SATVI for the aeolian plain, and using aerial images (Google Earth, 2013), to make sure that each site was not located at a lower distance from other existing settlements, or in unusual geomorphic features (i.e., clayey soil depressions in the aeolian plain). The settlements Balde del Pedro, La Majada and El Sangradero were located in the old riverbed unit, and Las Delicias, La Primavera, and Santa Lucía in the aeolian plain unit (Fig. 1). Selected sites (at different distance classes)

were located in the field with a GPS. At each of the resulting 30 sites, we laid two grids (4 m × 50 m) next to each other with tape measures, one directed to the top of a sand dune, and the other to the interdune valley (Fig. 1), with a total of 60 grids. In the aeolian plain we located the grids in different positions of the dune-interdune system (dune flank and interdune valley), while in the old riverbed, we laid the two grids in no particular direction. In each grid we recorded the following variables for each BSC patch found: highest and lowest diameter, location with respect to vascular plant (under, between, at the border of vascular plants), fragmentation (with categories from 1, continuous cover of colored, evident, photosynthetic organisms, to 4, discontinuous, very fragmented cover, similar to Tonway and Hindley, 2004), presence of physical crusts (abiotic soil particle adhesion), and type of BSC (M = moss dominated crust; CL = cyanobacteria and/or lichen dominated crusts). We identified patches of trees, shrubs, and dead wood trunks, and estimated the following patch characteristics: highest and lowest diameter, % cover of grasses and litter, presence of BSC, and name of plant species present in each patch (Fig. 1). Total BSC and vascular plant cover for each grid were considered response variables. Using the average of the two diameters measured in the field, we calculated the area of each vascular and BSC patch in cm^2, and then converted them to percentages on the entire grid. For BSC patches, the area of each patch was multiplied by a conversion factor given by fragmentation, according to the following values: non-fragmented crusts = 1; little fragmentation = 0.7; fragmentation = 0.4; high fragmentation = 0.1.

In order to analyze mesoscale effects given by different topographic positions of dunes in the aeolian plain, the two grids of each site were laid in different positions of the dune-interdune system. One grid was located in a dune flank (from footslope to top of the dune) and the other in the inter-dune valley (Fig. 1). This grid layout allows us to include all the variability of the dune-interdune system, and compare dune flanks with inter-dune valleys. We used the BSC cover value of each grid from the aeolian plain estimated in the landscape scale analysis, and compared differences between dune positions.

We analyzed microscale variations only in the old riverbed, where BSC were more abundant. In addition to the variables recorded for the landscape analysis (i.e., % cover of vascular plant and BSC patches), for each BSC patch we recorded ecological conditions, such as location with respect to vascular plants (under, at the border, between plant canopies), associated vascular plant species (defined as the name of the species found immediately above or next to the BSC patch, with an additional class corresponding to "outside plant canopy"), presence of shrub mounds, slope (low: $0°-15°$; intermediate: $16°-45°$; high: greater than $45°$), and slope orientation. The later, also named aspect, took the following categories: East, North (which aggregated N, NW and NE), South (which aggregated S, SW and SE), and West. Slope and aspect were visually estimated with the help of a compass.

2.3. Statistical analyses

We tested data for normality with the Shapiro—Wilk normality test, and transformed the data with logarithmic or root square functions when necessary. We then used linear mixed effect models to analyze drivers of BSC and vascular plant cover at the three spatial scales considered in the study. Using multi-model inference, we compared models with different levels of complexity (i.e., different number of explanatory variables and interactions), with the second order Akaike Information Criteria (AICc) using the MuMIn package (Barton, 2014), in the R statistical environment (R CoreTeam, 2014). AICc indicates the adjustment of different models, which include different number of independent

variables, or interactions among them, to a data set, yielding lower values for the model with better adjustment. AIC penalizes for increasing the number of parameters, discouraging over-fitting. Models were scored according to AIC weights (AICw). Candidate models that differed from the AICc of the best-fitting model by less than 4 (dAIC < 4) were retained for the mean parameter estimation, z (standard score) and p value statistics, using weighted model-averaging (Burnham and Anderson, 2002). We considered that the factors or their interaction were important to explain the data when the best model included them, with a significance of the factor indicated by the z and p value (if p < 0.05) estimated with the average parameters of better models (dAICc < 4 between best model and other models). At the landscape scale, we considered geomorphological units, with 2 levels (old riverbed and aeolian plain), and distance from settlements, with 5 levels (100, 300, 600, 1000 and 2000 m) as fixed factors, and settlements, with 6 levels (3 settlements in each geomorphological unit) as a random factor. Random effects represent the non-controlled variability given by the different land use managements (number and type of domestic animals, age of each settlement, patterns of settlement, abandonment and resettlement), topography (size and height of dune-interdune systems), and vegetation. In the landscape analysis, we compared models with and without the interaction between the fix factors (geomorphological unit and distance), for the following response variables: BSC, litter, grass, vegetation, and bare soil cover.

At the mesoscale, only analyzed in the aeolian plain, we considered landform unit (2 levels: dune flank and inter-dune valley), and distance (5 levels) as fixed factors, and settlements (6 levels) as a random factor. BSC cover values from each grid, calculated as explained above, were used as response variables.

Microscale effects were only analyzed in the old riverbed, because the aeolian plain had a very low cover of BSC. Each estimated value of soil crust cover (in m^2) for each BSC patch, was considered a separate datum. Fixed effects included distance (5 levels), slope (3 levels: low, intermediate, high), presence of mounds (2 levels), and aspect (5 levels: N, S, E, W, and no aspect), while random effects included the different settlements (six levels). Associated vascular plant species were analyzed by counting the number of BSC patches found under the canopy of each species, in the border of their canopies, or between plant canopies (outside canopies).

2.4. Taxonomic identification

Samples of BSC were collected from the best conserved transect of the old riverbed, Balde del Pedro, and were stored in paper bags. Identification to the genus level was done with light microscopy, using taxonomic keys from other drylands (Aragón, 2010; Rosentreter et al., 2007; Wirth et al., 2004). When genera could not be identified, we analyzed the type of symbiont of the lichens: green algae or cyanobacteria.

3. Results

3.1. Landscape scale

The cover of vascular plants (corresponding to tree/shrub patches), grass (% cover inside each vascular plant patch), litter, and BSC generally increased with increasing distance from settlements (Figs. 2 and 3). However, models that included distance as a fix factor did not improve adjustments if compared to the null model for vascular plant, grasses and litter cover (Table 1). Distance and geomorphological unit were clearly significant factors only for BSC cover, with higher values in the old river bed and at higher distances from settlements. The model selected for BSC cover
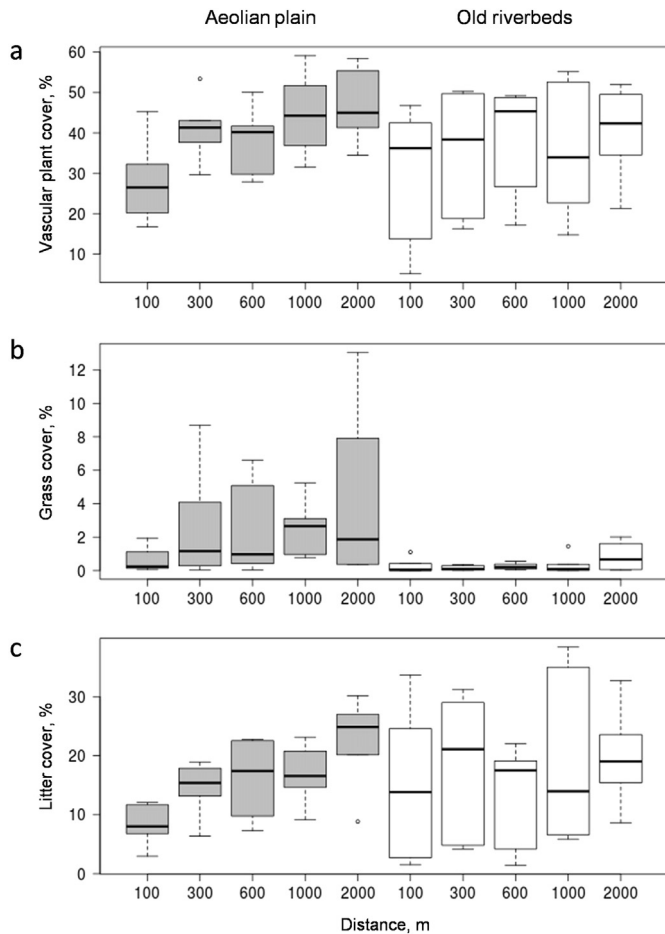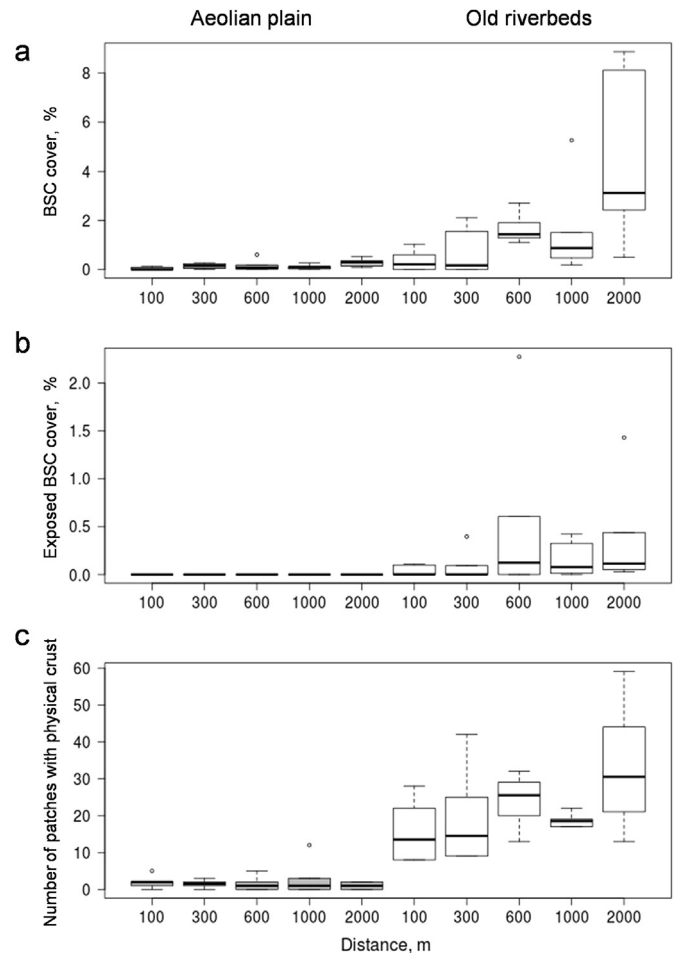
Fig. 2. Vascular plant (a), grass (b), and litter (c) cover at different distances from settlements in both geomorphological units.

Fig. 3. Total BSC (a), exposed BSC (located in interspaces between vascular plants) (b) cover, and number of physical crusts (c) found at different distances from settlements in both geomorphological units.

explained up to 48% of the variability, indicated by $R^2 = 0.48$. For the other response variables, the models proposed showed a poor adjustment, with $R^2 = 0.29$ for grasses, and $R^2 < 0.03$ for vascular plant and litter cover. Geomorphological unit marginally improved model adjustments over the null model for vascular plant, litter and grass cover (dAIC < 4 between the null model and the model that included geomorphological unit). The models that included the interaction between distance and geomorphological unit showed the highest AICc (worst model) and lower ranking for all variables, indicating similar effects in both geomorphological units (Table 1, Fig. 3). The number of patches with physical crusts was higher in the old river bed than in the aeolian plain (Fig. 3).

Of a total of 1576 vegetation patches recorded, 49% presented BSC. Of these, 90% were dominated by lichens and 10% by mosses. In the aeolian plain, all the crusts were associated with vascular plant patches. In the old river bed, although most BSC (86.5%) were associated with vascular plants, the rest of the crusts were located in exposed areas, between plant canopies, particularly at higher distances from the settlements (Fig. 3).

3.2. Mesoscale

The null model was the best model (AICw = 0.93), and the dAIC of models including other fixed factors were higher than 4 (with AICw = 0.05 or lower), indicating a lack of effect of landscape unit and distance on BSC at the mesoscale in the aeolian plain (see Fig. 4).

3.3. Microscale

We compared additive models that included distance, mounds, aspect, and slope as a fixed factors. The best model included distance and aspect, although the R^2 of the model was low (0.074) (Table 2). The null model was not selected among candidate models, because the dAIC was higher than 20, and the weight (AICw) equal to 0, indicating that all factors improved model adjustment. Among the 4 models that yielded dAIC < 4, distance was included in 3 models, mounds and slope in two models, and aspect in 4. Statistics calculated using average estimated parameters of the selected models indicated significant effects for aspect, particularly South and West, and distance. BSC with higher cover were found in microsites with mounds, south facing slopes, and medium and high slopes (Fig. 5, Table 2). Higher BSC covers were found in plants associated to *Larrea divaricata*, *Bulnesia retama* and *Lycium* sp (*Lycium chilense* and *Lycium tenuispinosum*). Other species that were associated with abundant soil crusts are *Capparis atamisquea*, *Geoffroea decorticans*, *Bougainvillea spinosa*, *Suaeda divaricata*, *P. flexuosa*, *Prosopis alpataco*, and dead wood trunks. Most BSC were located under these species, but at higher distances from settlements, BSC also occupied the canopy borders and the interspaces between plants (Table 3).

Lichens identified to the genera or species level include *Collema* spp., *Peltula* spp., *Endocarpon* spp., *Placidium squamulosum*, *Psora decipiens*, and *Clavascidium lacinulatum*. We also observed

Table 1
Landscape analyses. Model selection statistics of the landscape analysis to evaluate the effect of geomorphological unit and distance to settlements on vascular plant, BSC, litter, and grass, using multimodel inference. Models are ranked according to the second order AIC (AICc). Plus signs indicate factors included in each model. Models with dAIC < 4 with respect to best model are marked in bold, and were used to compute average model parameter and statistics. For the variables included in the selected models, z and p values are included, and marked in bold if p < 0.05. Signif. Codes: 0 '****' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1.

Fixed factor	Distance	Geomorphological unit	Interaction	R^2	dAIC	Weight of model
Response variables						
1-Vascular Plants cover		+		0.03	0	0.8
				0.02	3.28	0.155
	+	+		0.13	6.14	0.037
	+			0.12	9.34	0.007
	+	+	+	0.14	16.97	16.97
z value		0.526				
(Pr(>|z|))		(0.599)				
Signif. codes						
2-BSC cover	+	+		**0.48**	**0**	**0.505**
	+			**0.40**	**1.72**	**0.214**
		+		**0.24**	**1.85**	**0.2**
				0.14	**3.65**	**0.081**
	+	+	+	0.52	13.76	0.001
z value	**5.045**	**2.323**				
(Pr(>|z|))	**(4.54e-07)**	**(0.0202)**				
Signif. codes	***	*				
3-Litter cover		+		**0.00**	**0**	**0.69**
				0.00	**1.84**	**0.28**
	+	+		0.1	7.01	0.021
	+			0.1	8.76	0.009
	+	+	+	0.13	17.5	0
z value		0.312				
(Pr(>|z|))		(0.755)				
Signif. codes						
4-Grass cover		+		**0.29**	**0**	**0.818**
				0.18	**3**	**0.181**
	+	+		0.39	11.22	0.003
	+			0.29	14.14	0.001
	+	+	+	0.39	29.79	0
z value		0.376				
(Pr(>|z|))		(0.707)				
Signif. codes						

filaments of cyanobacteria with heterocytes (cf *Hassallia*, *Nostoc* sp.) and without heterocytes (*Leptolyngbyaceae* sp.). Identified mosses include *Tortula inermis* and *Crossidium* spp. The number of lichen genera increased along the grazing gradient, ranging from 3 to 8 genera found at 100—2000 m from the settlement (Table 4). In all

sites, cyanobacteria were the dominant lichen symbionts. BSC dominated by free living cyanobacteria were present at all sites, and were the most abundant at the most disturbed site. From 300 to 2000 m from the settlement, lichen dominated BSC were more abundant than cyanobacteria BSC. Moss dominated BSC were
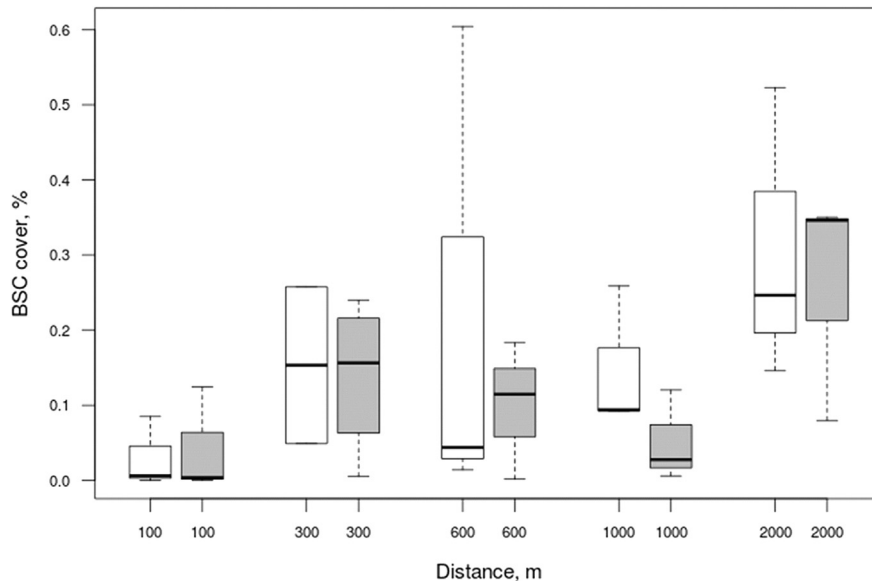
Fig. 4. BSC cover in different landscape positions in the aeolian plain. White bars indicate BSC cover in interdune valleys, while gray bars indicate BSC cover in dune flanks.

Table 2
Microscale analyses. Model selection statistics of the microscale analysis to evaluate the effect of distance, aspect, slope, and mound on BSC cover, using multimodel inference. Models are ranked according to the second order AIC (AICc). Plus signs indicate factors included in each model. Models with dAIC < 4 are marked in bold, and were used to compute average model parameter and statistics. For the variables included in the selected models, z value and probability values for each category, compared against the intercept, are included, and marked in bold if p < 0.05. Signif. Codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1.

Fixed factors included in each model				Statistics for each model		
Distance	Mound	Aspect	Slope	R^2	dAIC	Weight of model
+		+		**0.0740**	**0.00**	**0.531**
		+		**0.0598**	**2.20**	**0.177**
+	+	+		**0.0747**	**3.10**	**0.113**
+		+	+	**0.0752**	**3.55**	**0.090**
		+	+	0.0613	5.23	0.039
	+	+		0.0601	5.96	0.027
+	+	+	+	0.0759	6.72	0.018
	+	+	+	0.0617	9.03	0.006
			+	0.0438	20.98	0.000

Statistics for each fixed factor, estimated with models with dAICc < 4.
z value
(Pr(>|z|))
Significance codes

4.695	1.103	**South:**	High:
(2.7e-06)	(0.2700)	**6.332**	0.342
***		**(<2e-16)**	(0.7327)
		***	
		East:	Medium:
		0.501	1.009
		(0.6162)	(0.3129)
		West:	
		2.323	
		(0.0202)	
		*	
		North:	
		0.122	
		(0.9032)	

absent at the most disturbed site, and scarce in the others, with a lower number than those dominated by lichens and cyanobacteria.

4. Discussion

BSC cover and spatial distribution changed along disturbance gradients and in different geomorphological units, supporting our first hypothesis. Old riverbeds, which have fine soil particle sizes (dominance of silt, clay and very fine sands), often aggregated in physical crusts (Fig. 3), hosted the highest BSC covers, reaching up to 8% cover at the relatively undisturbed sites (located at 2 km from settlements). The abundance of clays and calcium compounds in the old riverbed may facilitate the formation of physical crusts, as indicated by the higher number of BSC patches with these features, where BSC may initially develop. Cyanobacteria produce EPS (exopolysaccharides), which have a chemical affinity for clays and calcium compounds, such as calcium carbonate and gypsum, and form soil micro-aggregates (Belnap and Gardner, 1993). Filaments of fungi and cyanobacteria create macro-aggregates, which physically stabilize soils (Bowker et al., 2008; Zhang et al., 2010). However, the lower BSC cover near livestock settlements indicates a disruption of this ecological function, with increasing risks of soil losses. BSC were mainly associated with patches of vascular plants along the grazing gradients, but in distant sites, they were also located outside plant canopies in the plant interspaces, pointing to the well-documented protective effect of vascular plants against trampling (Thomas and Dougill, 2006; Williams et al., 2008; Aguilar et al., 2009; Gómez et al., 2012), and the potential for BSC development and recovery when domestic animals are removed.

Cyanobacteria inoculation in Negev desert soils with different particle sizes resulted in more rapid development of BSC in soils with very fine sands, compared to soils with fine, medium, coarse and very coarse sands (Rozenstein et al., 2014). Larger sediment sizes in the aeolian plain, where fine sands dominate, may decrease abiotic soil particle adhesion (physical crusts) and adhesion by exopolysaccharides and microorganism filaments, preventing BSC development. BSC burial by sand dune movements, or by litter fall in the highly productive Prosopis forests of the aeolian plain may also reduce BSC cover (Belnap, 2002; Thomas and Dougill, 2007; Alvarez et al., 2009). Topography, vegetation, and texture differences in landform position in dune areas did not affect BSC cover, probably because of the overall low abundance of crusts found in the entire aeolian plain. Furthermore, when only BSC of the aeolian plain are considered, the effects of distance are not apparent, which agrees with the study of Tabeni et al. (2014), who did not find higher BSC covers at the most distant sites in this geomorphological unit.

These findings suggest that old riverbeds are priority areas for BSC conservation and restoration purposes, and should be protected against off road and livestock disturbances. Old riverbeds, because of their smooth slopes, are often used for traveling between areas (Villagra et al., 2004), and host a higher density of settlements than the aeolian plain (Goirán et al., 2012). Furthermore, the only paved road of the area (road 142) is located along a riverbed for most of its length, concentrating the impacts caused by horses, trucks, and other motorized vehicles. The old riverbed hosts two elementary schools, two churches, a community center, a park ranger station, and a sanitary post, in addition to several settlements. Due to this abundance of infrastructure surrounding the old riverbed, vehicle transit is higher here than in the aeolian plain. At present, there are no transit regulations in most of these areas, and vehicles circulate through different pathways, impacting a greater area than they would do if off roads were clearly marked. The presence of community centers offers an opportunity for outreach and education activities, aimed to value and conserve BSC. Contrary to the old riverbed, the aeolian plain, although less impacted by vehicles and with a lower density of settlements (Goirán et al., 2012), probably has a low potential for BSC development, or soil restoration.

The negative effect of livestock on BSC is clear, particularly in the old river bed, because the higher BSC covers are found in the most distant sites of the grazing gradients. This agrees with previous studies in the Monte Desert region and other deserts (Anderson et al., 1982; Gómez et al., 2012; Zhang et al., 2013). Tabeni et al. (2014) found the highest BSC covers at intermediate distances (500 m, in transects of 2500 m from settlements) in the aeolian plain, attributing this effect to competitive interactions with grasses, which are relieved under low levels of disturbance. At our study area during the year of sampling, grass cover was low because of severe droughts, and we did not find a clear effect of distance to settlements on BSC in the aeolian plain (Fig. 4).

Microscale factors have a high influence on BSC development, as shown by the better adjustment of models that incorporate factors other than distance from settlements, particularly aspect. Southern exposed slopes favored BSC. Vascular plants may be associated with the presence of shrub mounds, which may generate higher slopes and microsites of different aspects. BSC were predominantly associated with Larrea, Lycium and Bulnesia. These vascular plants may allow light to diffuse to the soil surface, and produce lower amounts of litter than other species such as P. flexuosa (Alvarez et al., 2009), leaving free spaces on the soils that can be colonized by cyanobacteria and lichens. Vascular plant mounds may generate surface roughness, sloped terrain, and different aspects, which affect microclimatic conditions. Higher slopes may produce different solar exposures with consequent variability in radiative and water
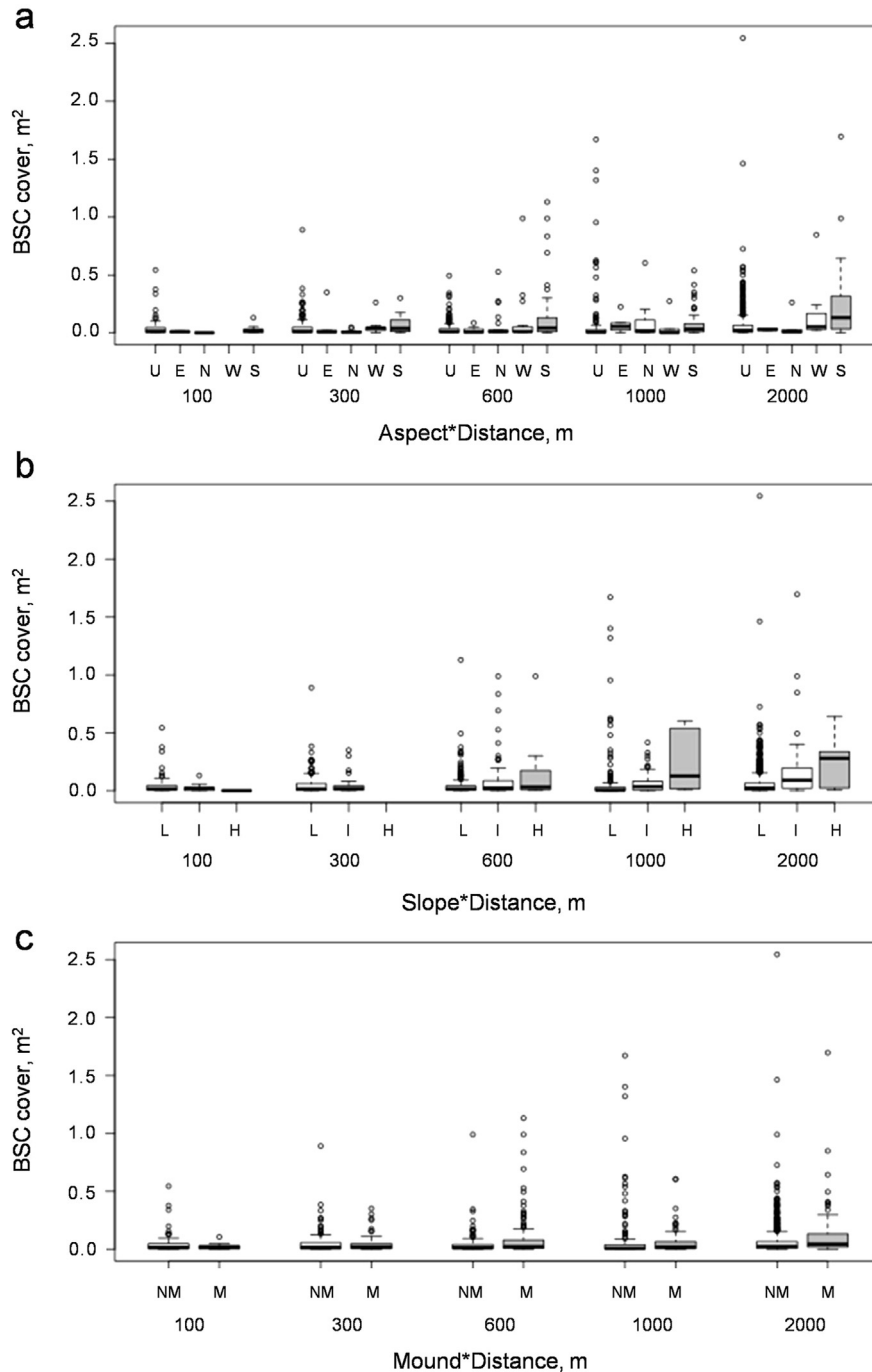
Fig. 5. BSC cover of each BSC patch, in m², for the old river bed, located at different microsites, along the grazing gradients. (a) BSC cover in microsites with different exposures. U = undefined, E = East, W = West, N = North, S = South. (b) BSC cover in microsites with different slopes. L = low (0°−15°), I = intermediate (16°−45), H = high (>45°). (c) BSC cover on microsites characterized as mounds (M) and not mounds (NM).

balances (Maestre and Cortina, 2002; Li et al., 2008, 2010). It is not surprising that more BSC patches with higher cover were found in microsites with southern exposure, where incoming radiation, temperatures, and desiccation are lower. However, in relatively undisturbed sites, which had insignificant livestock activity for several decades, large BSC patches were found in plant interspace areas, without marked slopes, aspect, or mounds, suggesting a development of BSC communities from protected sites to more harsh microenvironments.

Different restoration experiments have been done in deserts around the world. In the Moab (Utah) and inner Mongolia deserts,

soil were inoculated with cyanobacteria under field conditions (Belnap, 1993; Wang et al., 2009). These studies suggest that cyanobacterial inoculation would be a suitable and effective technique to recover biological soil crusts. After inoculation with cyanobacteria, and *Collema* lichen transplants in the Moab desert, lichens developed better on northern slopes of mounds (Davidson et al., 2002), suggesting that microsites characteristics are important for restoration success. Based on our results, we propose that restoration with BSC seeding should be started in enclosed areas with finer soil particles, protected from trampling and desiccation. This could be achieved by generating mounds with southern exposure slopes, associated to

Table 3
Spatial distribution of BSC in the old river bed. The numbers represent number of BSC patches found in different positions with respect to different species of vascular plants, and exposed areas. M crust = moss dominated crust; CL crust = cyanobacteria and/or lichen dominated crusts and CL/M = crust were comprised of cyanobacteria/lichen and mosses in nearly equal proportions. Under/border = this category includes large BSC patches located in both categories, under canopies but extended to the border, slightly exceeding plant canopies. Border/outside = this category includes large BSC patches located in both categories, border slightly exceeding plant canopies but extended outside to the plant canopies.

BSC composition	Location with respect to vascular plants	Associated vascular plant species				
		Larrea divaricata	*Bulnesia retama*	*Lycium* sp.	Others	Exposed areas
CL crust	Under	242	200	155	210	300
	Border	113	84	26		
	Under/border	19	7	8		
	Border/outside	20	7	8		
M crust	Under	–	2	2	0	0
	Border	–	1	–		
	Under/border	–	–	–		
	Border/outside	–	–	–		
CL/M crust	Under	7	29	7	9	4
	Border	2	1	–		
	Under/border	–	–	–		
	Border/outside	–	–	–		

Table 4
Floristic composition of BSC along the Balde del Pedro grazing gradient. The number of BSC patches dominated by each identified and unidentified lichen genera is indicated, as well as the type of photobiont and tallus. The number of moss and cyanobacteria dominated BSC is also indicated.

Type	Site 100	Site 300	Site 600	Site1000	Site 2000	Tallus	Photobiont
Lichen							
Clavascidium			1			Squamulose	Green algae
Collema	6	22	33	122	23	Gelatinous and minutely foliose or lobate	Cyanobacteria
Endocarpon			5	3	1	Squamulose	Green algae
Peltula		23	63	108	43	Squamulose	Cyanobacteria
Placidium	5	4	8	10	11	Squamulose	Green algae
Psora		1				Squamulose	Green algae
Unidentified 1	1			2	1	Squamulose	Cyanobacteria
Unidentified 2		9	7	77	10	Squamulose	Cyanobacteria
Unidentified 3				2	2	Squamulose	Cyanobacteria
Unidentified 4					2	Squamulose	Green algae
Cyanobacteria	26	23	7	26	14	–	
Mosses		4	3	5	3	–	

fine-leaved shrubs that provide shade, but allow free soil spaces for BSC development. In areas where livestock animals cannot be removed, the presence of dead wood and branches in the soil would offer some protection for BSC development.

With respect to the diversity of BSC, we only analyzed one grazing gradient, and found an increasing number of lichen genera with increasing distances from the settlement (Table 4). Cyanobacteria dominated BSC were the most abundant BSC type at the most disturbed site, while up to 8 genera of lichens were found at the sites most distant from the settlement. In all cases, lichens with cyanobacteria symbionts were the most abundant, and large functional changes were not evident. Because one grazing gradient is not enough to detect patterns of taxonomic or functional diversity, further studies that include species or functional classifications of lichens, mosses and cyanobacteria, are needed.

5. Conclusions

BSC cover was higher in the old riverbed than in the aeolian plain unit. Livestock activity reduced BSC cover, as reported in previous studies, particularly in the old riverbed unit. BSC were exclusively located under plant canopies in the aeolian plain unit, while in the old riverbed BSC were also found outside plant canopies. Dune landform positions in the aeolian plain did not affect BSC cover, with similarly low covers (<1%) in dune flanks and interdune valleys. At the microscale, BSC seem to be favored in slopes with southern exposures, and under the canopies of *B. retama, L.*

divaricata and *Lycium* sp. Our findings suggest that microsites generated by vascular plants or mounds in the old riverbed would facilitate BSC development.

Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.actao.2015.08.005.

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