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Biological soil crusts greatly contribute to small-scale soil heterogeneity along a grazing gradient

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ABSTRACT

Morphological and physiological characteristics of biological soil crusts (BSCs) enhance soil stability and fertility, and influence soil chemistry. However, the effect of BSCs on soil physico-chemical properties may vary depending on taxa (cyanobacteria, lichen, bryophytes) and species, and be susceptible to soil surface disturbance. We examined a wide variety of soil physico-chemical properties associated with five BSC components (cyanobacteria crust, one moss species, three lichen species) naturally occurring in the study area, and bare soil along a disturbance gradient in a semiarid grassland ecosystem in Central Mexico. We addressed the following questions: 1) Do different BSC components create distinct soil microsites characterized by a particular combination of physico-chemical properties? 2) Do distinct soil properties change beneath different BSC components? 3) Does grazing disturbance modify or override species-specific BSC effects? We found that BSC components and bare soil generated distinct soil microsites, however, this effect diminished with increasing grazing pressure. Also, most of the soil variables examined differed between BSC components and bare soil along the gradient. While soil properties associated with cyanobacteria were relatively similar compared to bare soil along the gradient, *Diploschistes diacapsis* and *Lecidella* sp. showed decreases in pH and marked differences in mineral nutrient concentration (i.e. variations in Na, Fe and Zn concentration respect to other BSC components and bare soil). Grazing intensity and frequency changed species-specific effects of *D. diacapsis*, specially modifying its effect on soil texture, diminishing its effect on pH, K and Na concentration, and increasing its effect on Ca and Zn concentration. We conclude that BSC components contribute to natural small-scale soil heterogeneity, and that soil disturbance substantially modifies the nature and magnitude of this effect with potentially important implications on ecosystem processes. Because of the potential influence of other factors (i.e. climate, vascular plants, microbial activity) on BSCs' relation to soil properties, this assertion should be tested including these factors and in multiple ecosystems.

1. Introduction

Dryland ecosystems are highly heterogeneous in space and time, due to biotic and abiotic factors related to the existence of a biphasic structure with vegetated patterns and bare areas and with profound implications in mineral nutrient distribution, soil resource availability and hydrological processes (Schlesinger et al., 1996; Burke et al., 1999; Garcia-Palacios et al., 2011).

BSCs are key structural and functional components of these ecosystems mainly consisting of soil cyanobacteria, microfungi, lichens and mosses (Collins et al., 2008; Eldridge et al., 2010; Bowker et al., 2011). BSCs contribute importantly to soil fertility and soil water retention, thus favouring plant productivity and the overall spatial patterns of ecosystem processes (Belnap and Harper, 1995; Maestre et al., 2005; Belnap, 2006). They influence soil chemistry and soil structure in complex ways: 1) they exude polysaccharides and other organic compounds, leach inorganic nutrients, and chelate elements into the soil surface (Harper and Pendleton, 1993; Johnson et al., 2007); 2) they discriminate among mineral nutrients

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during nutrient uptake (Bowker et al., 2006; Paul et al., 2009); 3) with their cushion-forming thalli and filaments they increase soil surface roughness and trap fine dust particles including bio-essential nutrients (e.g. N, P, K, Mg, Cu, Fe, Mn) (Reynolds et al., 2001; Delgado-Baquerizo et al., 2010); and 4) with their dense networks of rhizines, rhizoids, hyphae, and gelatinous filaments penetrating surface soil, they increase the concentration of soil organic carbon, the formation of soil aggregates and the stabilization of a cohesive crust (Bowker et al., 2008; Jiménez Aguilar et al., 2009; Chaudhary et al., 2009). Thus, BSC participate actively in soil surface heterogeneity dynamics, not only in terms of biological diversity but in relation to changes in soil function and physico-chemical properties associated with their spatial structure (Ettema and Wardle, 2002).

In the past, BSCs have been examined collectively as single ecosystem components (Maestre et al., 2005), or as relatively simple community assemblages grouped in conspicuous biological components (light and dark coloured cyanobacteria, lichen, bryophytes, liverworts). Any potential small-scale heterogeneity in surface soils caused by the presence, abundance, and differential functional trait compositions of BSC species has rarely been addressed. However, recent evidences suggest this small-scale heterogeneity may be essential for understanding how BSCs affect ecosystem processes such as their bidirectional relation with soil microbial communities and regulating function in plant interspaces (Castillo-Monroy et al., 2011b) and their filtering effects on species-specific seedling emergence and early establishment of vascular plants (Escudero et al., 2007). While soil spatio-temporal heterogeneity associated with perennial plants and its relevance in many ecosystem processes are well described for semiarid ecosystems (Jackson and Caldwell, 1993; Ryel and Caldwell, 1998) little is known of how different BSC organisms/species may generate or contribute to small-scale soil heterogeneity. This level of detail, however, may elucidate new important BSC species level effects on fine-scale soil physico-chemical characteristics and their potential functional role in arid and semiarid ecosystems. In contrast, "whole" BSC effects are expected to reflect a weighted average of a global functional crust effect on soil surface characteristics, whereby the resolution of small-scale spatial heterogeneity gets lost and/or remains unaccounted for. Some preliminary evidence suggests that BSC effects at the species level may be functionally more important than previously thought; some soil properties seem taxon-specific or at least related to a rough classification of BSC components, i.e. lichens, mosses and cyanobacteria (Bowker et al., 2006; Guo et al., 2008). If soil surface heterogeneity caused by BSC is functional and species-specific, we expect each individual of a given BSC species to contribute to a species-specific "emergent" soil microsite. We consider these microsites should be characterized by a set of specific soil physico-chemical properties including texture, organic matter, pH, electrical conductivity and soil nutrient concentration and differ for different BSC species and obviously from bare soil. Therefore, we define soil heterogeneity as the potential horizontal variation of topsoil properties associated to different BSC species and their particular functional traits.

The integrity, composition and function of BSCs are highly vulnerable to disturbance (Belnap and Eldridge, 2003; Jimenez Aguilar et al., 2009) and in particular to overstocking of livestock. In drylands, this is one of the main drivers of land degradation causing a decline in soil organic matter content, inorganic nitrogen and phosphate availability, erosion of fine soil particles, and soil compaction (Manzano et al., 2000; Neff et al., 2005). Intense livestock trampling has detrimental consequences on the functioning of BSC by reducing nitrogenase activity (Belnap et al., 1994) and thus the potential of N-fixation and N input (Liu et al., 2009), and by reducing soil stability provided by BSC (Chaudhary et al., 2009) and thus enhancing the loss of soil organic C and N through water erosion (Barger et al., 2006). As a response to disturbance a dominance ranking of biological components has been described with mosses < crustose lichens < cyanobacteria increasing their resistance to mechanical disturbance by trampling (Belnap and Eldridge, 2003; Muscha and Hild, 2006).

We propose the existence of a pronounced small scale heterogeneity related to the presence of different BSC species and groups (in the case of cyanobacteria), and bare soil (hereafter, both BSCs and bare soil will be referred to as Soil Surface Components, SSCs), which may be altered by the combined effect of livestock grazing and trampling. In particular, soil heterogeneity has traditionally been assessed at the plant-interplant scale. However, interplant spaces constitute a potential habitat for BSCs, which may contribute to the fundamental inherent natural heterogeneity of dryland ecosystems at a smaller yet unexplored spatial scale.

More specifically, we hypothesise that along a grazing gradient, where livestock impact increases, soil surface heterogeneity associated with different SSCs would be modified. This implies that livestock will alter this sharp small-scale soil heterogeneity by differentially affecting each biological SSC (species-specific vulnerability to trampling impact). To our knowledge potential species-specific effects of BSC organisms and the effect of grazing on a wide variety of soil physico-chemical properties linked to BSCs at such small scale have not been assessed yet, however are fundamental to increase our understanding on dryland ecosystem structure and functioning. Hence, the main goal of this study was to test our hypothesis by responding to the following questions: 1) Do different SSCs with high abundance and relative high soil cover create distinct soil microsites characterized by a particular combination of physical and chemical properties? 2) Do single soil properties change under different SSCs? 3) Does *Diploschistes diacapsis* (Ach.) Lumbsch (a soil lichen species present in all sites along the grazing gradient) exert specific effects on soil properties or does grazing intensity override these? To address these questions, we examined a wide variety of soil physico-chemical properties associated with three soil lichen species, one moss species, a cyanobacteria dominated crust and bare soil along a disturbance gradient in drylands of central Mexico.

2. Materials and methods

2.1. Study site

The study area is located in the physiographic subprovince Llanos de Ojuelos (21° 49′ N, 101° 37′ W, 2200 m a.s.l.), Jalisco (Mexico) at the southernmost tip of the North American *gramineetum* (Aguado-Santacruz and García-Moya, 1998). The climate is semiarid with mean annual precipitation of 450 mm, and annual mean temperature of 17–18 °C. The main rainfall season occurs between June and September. Topography is characterized by valleys and gentle rolling hills formed by rhyolitic rocks. Haplic xerosols characterized by sandy-loam texture is the dominant soil type (Aguado, 1993). Soils are shallow (0.3–0.5 m) with a calcareous caliche layer at 0.5 m depth. The vegetation is a native shortgrass steppe with *Bouteloua gracilis* H.B.K. Lag ex Steud as the keystone species and with *Bouteloua scorpioides* Lag, *Bouteloua hirsuta* Lag, *Aristida divaricata* Humb. y Bompl. ex Willd. and *Muhlenbergia rigida* (Kunth) Trin. as additional grass species (Aguado, 1993).

Historically the main land use type of the region has been extensive livestock production. Four habitat types linked to different intensities of livestock grazing are easily identifiable in the study area (Table 1): 1) long-term (27 years) grazing exclosure (1 ha) within a heavily grazed pasture (see 4), 2) moderate

Table 1
Vegetation characteristics of study sites along the grazing gradient and soil surface components (SSCs) sampled at each site.

Site	Soil surface components sampled	Dominant vascular species	Plant cover (%)	Above ground productivity (kg dry matter/ha)
Long-term grazing exclosure (Exclusion site, EX)	Cyanobacteria crust, *Bryum argenteum*, *Diploschistes diacapsis*, bare soil	*Bouteloua gracilis*	35–40	800–1200
Moderate continuous grazing (Low impact site, LI)	Cyanobacteria crust, *Diploschistes diacapsis*, *Lecidella* sp., bare soil	*Bouteloua gracilis*, *Muhlenbergia rigida*	25–30	1200
Heavy seasonal grazing (Medium impact site, MI)	Cyanobacteria crust, *Acarospora socialis*, *Diploschistes diacapsis*, *Lecidella* sp., bare soil	*Bouteloua gracilis*	15–20	350
Heavy continuous grazing (High impact site, HI)	Cyanobacteria crust, *Acarospora socialis*, *Diploschistes diacapsis*, bare soil	*Bouteloua gracilis*, *Isocoma veneta*, *Asphodelus fistulosus*	5–10	240–440

continuous grazing (observed stocking rate 8–10 ha/animal unit (AU) per year) for over 200 years on private land; 3) heavy seasonal grazing during and after the main rainy season (observed stocking rate 2–4 ha/AU·y) for more than 80 years on communal land (*ejido*); and 4) heavy continuous grazing all year around (observed stocking rate <1 ha/AU·y) for more than 80 years on communal land (*ejido*) (Aguado-Santacruz and García-Moya, 1998). Of the three sites, only the moderately grazed site had the recommended stocking rate for the region (COTECOCA, 1979). In terms of grazing impact (level of disturbance) and considering grazing intensity and frequency, we will refer to these sites hereafter, as exclusion site with no grazing (EX), low impact site (LI) with moderate continuous grazing; medium impact site (MI) with heavy seasonal grazing; and high impact site (HI) with heavy continuous grazing. The three grazing land use types are widely distributed in the region and accommodate a wide variety of BSC communities. The four sites were located no more than 2000 m apart with similar physiographic (altitude, slope, orientation), climate and topographic characteristics in order to minimize bias due to impossibility for site replication.

2.2. Soil sampling design

We examined soil physico-chemical properties under five different biological SSCs naturally found in the study area: one moss species, *Bryum argenteum* Hedw., three lichen species: two species with continuous crustose thalli (*D. diacapsis* and *Lecidella* sp.) and one with squamulose semicontinuous thalli (*Acarospora socialis* H. Magn.), and a conspicuous dark cyanobacteria-dominated crust where species were not identifiable in the field (the only aggregate SSC) (Table 1). Since the main objective of this study was to examine small-scale soil heterogeneity associated with BSCs (biological SSCs), we selected only species with high abundance and with a minimum surface area of 3.3 cm × 3.3 cm to assure that soil properties were well developed and related to each biological SSC. Cyanobacteria crust and *D. diacapsis* occurred abundantly in all sites, *B. argenteum* was abundant only in EX, *A. socialis* only in MI and HI, and *Lecidella* sp. in LI and MI (Table 1). In each site, we collected five composite samples within a 1 ha area to account for inherent site variability. Each composite sample consisted of 10 subsamples extracted from beneath 10 sites covered by each biological SSC. To collect each subsample, we first marked a 3.3 × 3.3 cm area by inserting a spatula 1–2 mm into the soil and then by carefully removing the immediate surface of the biological SSC. Then we excavated a 3.3 × 3.3 × 1 cm deep soil cube after having carefully removed the soil surrounding the cube. Each subsample was randomly collected in well-developed BSCs within each site. Also, we randomly collected samples (3.3 cm × 3.3 cm × 1 cm) of soil visually devoid of BSC as controls, without removing any surface crust. We are aware of potential presence of BSC in these areas; however, for practical reasons we will refer to them as "bare soil". At each site, we kept a constant minimum distance between SSC samples and grass tussocks to avoid potential interfering effects from neighbouring grass roots. All samples were stored in coolers for transportation. In the laboratory of Environmental Sciences of the Instituto Potosino de Investigación Científica y Tecnológica, San Luis Potosi, Mexico, samples were air-dried prior to analysis.

Soil sampling was done after the rainy season in November 2009. We chose this sampling time to assure BSC components had been active for several weeks and to find a potentially strong crust-type-specific "signal" in soil properties associated with different SSCs. We sampled only once, as our studied soil properties are mostly slowly changing variables considering ecosystem dynamics, in that they have long turnover times (Carpenter and Turner, 2000; Reynolds et al., 2007).

2.3. Soil analyses

Composite soil samples were passed through a 2-mm mesh sieve to remove roots and rocks. For soil texture analysis (sand, silt and clay), aliquots of 20 g of each soil sample were sent to the Soil Analysis Laboratory of the Colegio de Postgraduados en Texcoco, Mexico. Soil chemical analyses were conducted in the Laboratory of Ecology and Global Environmental Change and Laboratorio Nacional de Biotecnología Agrícola, Médica y Ambiental (LANBAMA) of the Instituto Potosino de Investigación Científica y Tecnológica, San Luis Potosi, Mexico. Concentration of soil organic matter (OM) was determined with the calcination method (600 °C, 2 h) (Storer, 1984). Soil pH and electrical conductivity (EC) were determined by dissolving 10 g of soil in 10 ml of distilled water. Soil samples were analysed for organic C after incubating soils with HCl for 12 h to remove soil carbonates (Midwood and Boutton, 1998) and total N using the ECS 4010 CHNSO elemental analyzer (COSTECH). Extractable P was analysed with the Bray and Kurtz method using 0.03 N NH_4F and 0.025 N HCl as extractable solution (Olsen and Sommers, 1982). Extractable calcium, potassium, magnesium, and sodium (Ca^{2+}, K^{+}, Mg^{2+} and Na^{+}) were determined by using 1 N CH_3COONH_4 solution, and extractable copper, iron, manganese, and zinc (Cu^{2+}, Fe^{2+}, Mn^{2+}, and Zn^{2+}) were determined by using 0.005 M DTPA solution with ICP-Mass Spectrometry (modified from Chapman, 1965; Liu and Evett, 1990).

2.4. Statistical analyses

To evaluate the effect of grazing regime on soil physico-chemical heterogeneity related to different SSCs, we considered grazing impact as a fixed factor consisting of a multinomial of four levels (Exclusion, Low, Medium, and High Impact sites), in which SSCs were nested as a second fixed factor. Soil texture <2 mm (sand, silt and clay fraction), soil OM, pH, and EC, organic C, total N, P, four macronutrients (Ca, K, Mg, Na), and four micronutrients (Cu, Fe, Mn and Zn) were the response variables.

To examine if SSCs form distinct "emerging" soil microsites characterized by a particular combination of soil physico-chemical properties and thus contributed to soil heterogeneity, we conducted a non-metric multidimensional scaling (NMDS) ordination with SSC specific soil property values. To test SSC effects on soil property combinations, we conducted a two-factor permutational multivariate analysis of variance (PERMANOVA) with the factor SSC nested within the factor grazing impact (four levels) as fixed factors ($N = 85$). To detect differences between levels of grazing impact for SSC specific soil property combinations, we conducted pairwise PERMANOVA tests. PERMANOVA was run using Euclidean distance calculated from standardised (by total) soil property data, due to the very large relative scale of values, and based on unrestricted permutation of raw data (9999 permutations), because of a small sample size ($n = 5$ per species cover and site). All multivariate analyses were performed with PRIMER v.6 (Clarke and Gorley, 2006).

To examine site/grazing-specific soil physico-chemical properties associated with specific SSCs, we conducted four separate analyses of variance (ANOVAs) for the EX, LI, MI and HI sites, with SSC as fixed factor (four or five levels, Table 2) and five replicates ($N = 20$ or 25). To compare individual soil chemical and physical properties associated with different SSC within these sites, we used Bonferroni's multiple comparison test. To examine, whether SSC effects/responses are fixed ("emerging") for a particular SSC (*D. diacapsis,* occurring in all four sites along the gradient) independently of grazing impact, or whether grazing modifies SSC effect/response pattern, we calculated the Relative Interaction Intensity (RII) index (Armas et al., 2004) for *D. diacapsis* and conducted 14 separate analyses of variance (ANOVAs) for each soil property with site as fixed factor (four levels) ($N = 20$). RII was computed as (Sdd − Sbs)/(Sdd + Sbs); where Sdd and Sbs are the values of a given soil variable under *D. diacapsis* and in bare soil, respectively. The RII values range from −1 to +1: a value of zero indicates no effects/response of *D. diacapsis* on the variable being measured. Positive values indicate positive effects/response of *D. diacapsis* on such variable, and negative values the opposite. To compare potential differences of RII among sites, we applied Bonferroni's multiple comparisons test. The ANOVAs and multiple comparison tests were performed with SAS v9 (SAS Institute Inc., 2009).

3. Results

3.1. Soil properties associated with different SSCs

NMDS ordination (Stress = 0.03, Fig. 1) of soil microsites associated with SSCs discriminated among sites along the grazing gradient (Fig. 1). Soil samples of different SSC separated clearly in EX and LI, while they appeared much more similar in MI and HI, since they partially overlapped (Fig. 1). *D. diacapsis* microsites grouped together independently of grazing impact level.

PERMANOVA results showed that grazing impact (factor site) and SSCs had a significant effect on soil properties (Table 2). In EX and LI, soil properties were different among all SSCs (Table 3). In MI, soil properties were similar for all SSCs (Table 3). In HI, they were different between bare soil and *A. socialis*, and also for *D. diacapsis* compared with all SSCs (Table 3).

Table 2
Results of PERMANOVA on Euclidean distances for soil property combinations of different soil surface components (SSCs) considering four different sites (Exclusion, Low, Medium, and High impact) along the grazing gradient.

Source	df	Mean square	Pseudo-*F*	*P*-value	CV (%)
Site	3	3119.80	132.82	**0.0001**	12.09
SSC (Site)	13	782.01	33.29	**0.0001**	12.32
Residual	68	23.49			4.85
Total	84				

Significant *P*-values (<0.05) are in bold.

3.2. Changes in soil properties associated with SSCs

We found that SSCs had a significant effect on most soil variables (13 of 16) in all sites of the study area (Table 4a,b,c,d). However, bare soil, cyanobacteria and *A. socialis* showed higher similarities for most soil properties along the perturbation gradient (Table 4a,b,c,d). *B. argenteum* had lower pH, EC, Na and K concentration than bare soil and cyanobacteria crusts in the EX site (Table 4a). *D. diacapsis* had lower pH, lower Ca concentration and higher Fe concentration than all other SSCs along the gradient (Table 4a,b,c,d). Also, *D. diacapsis* had lower silt and higher clay content than other SSCs in LI and HI (Table 4b,d). Furthermore, *D. diacapsis* cointained higher concentrations of N, P and Cu, and lower concentrations of K, Mg and Na than other SSCs along the gradient (Table 4a,b,c,d). *Lecidella* sp. had lower pH than bare soil in both LI and MI (Table 4b, c, respectively). Also, *Lecidella* sp. presented lower pH, lower silt and higher clay content than bare soil and cyanobacteria, higher P concentration than bare soil and cyanobacteria, lower K and Na concentration than bare soil, and higher concentration of the latter nutrients than *D. diacapsis* in LI (Table 4b).

3.3. D. diacapsis and bare soil along the grazing gradient

ANOVAs detected large and significant differences in the *D. diacapsis* effect (RII index) on all soil properties along the gradient, except for C and Mn (Table 5). The RII showed a negative sign for silt and a positive sign for clay in continuously grazed sites, and the opposite pattern was found in the seasonally grazed site (Fig. 2a). Also, the RII showed a negative sign all along the gradient for pH (Fig. 2b) and Ca concentration (Fig. 2d), decreasing and increasing in magnitude with grazing impact, respectively. The RII for P changed from negative in EX to positive in grazed sites for P (Fig. 2c), and the contrary for Mg concentration (Fig. 2d). Also, the RII changed from negative to positive with heavy grazing regime for EC (Fig. 2b) and Na (Fig. 2d). *D. diacapsis* had a large and positive effect on Fe concentration all along the gradient (Fig. 2e). Finally, it is worth to note that the RII for Zn showed a negative sign in all sites of the gradient except in HI (Fig. 2e), suggesting a change in *D. diacapsis* effect (i.e. from Zn uptake to Zn retention) on this soil property under heavy and continuous grazing.

4. Discussion

Our study shows that soil heterogeneity in drylands reaches far beyond the well studied patch-bare soil dichotomy and the important role of BSCs to contribute to such soil heterogeneity in semiarid grassland ecosystems in Central Mexico. In general, biological SSCs increased small-scale soil heterogeneity by modifying numerous soil properties, mostly related to macro and micronutrients and thereby creating distinct soil microsites. Depending on BSC identity and disturbance regime, these changes differed in nature and magnitude. The heterogeneity associated with BSCs was apparent in all sites along the grazing gradient; although our results also showed a notorious decrease in BSC − induced soil heterogeneity with increasing grazing impact. These findings confirm first the value of BSCs in soil functional aspects in dryland ecosystems (Harper and Belnap, 2001; Maestre et al., 2011) and, on the other hand, the importance of species-specific BSC effects on soil fertility and soil nutrient availability. They also confirm our working idea that the species level diversity of BSCs have been

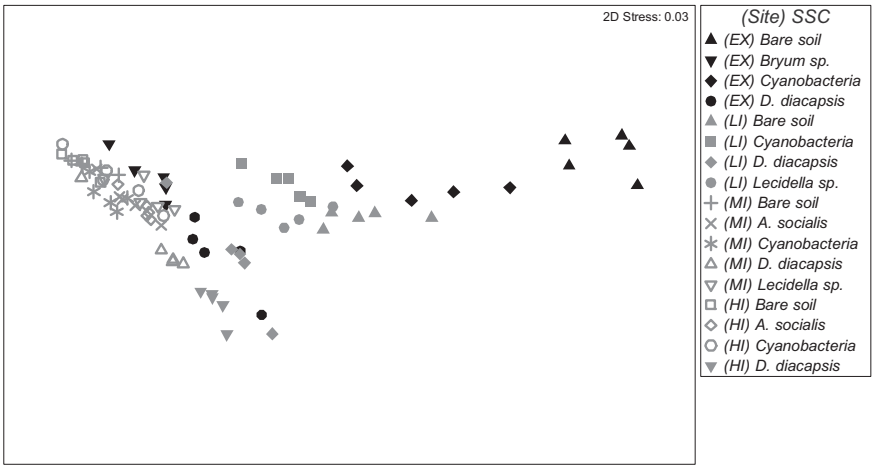

Fig. 1. Two factor non-metric MDS plot (2D configuration) of SSCs along the disturbance gradient. EX, exclusion site; LI, low impact site; MI, medium impact site; HI, high impact site. Each point represents a composite sample ($N = 85$).

underestimated, especially their effects on dryland ecosystem function. Also, they reveal that overgrazing threatens ecosystem integrity by reducing soil heterogeneity associated to BSCs in drylands. These interactive relations are currently discussed also for vascular plants (Suding and Hobbs, 2009) in a functional group context.

4.1. BSCs formed "emerging" microsites

As expected, soil covered by different biological SSCs was characterized by a combination of particular properties such as soil texture, acidity, and mineral nutrient concentrations. Vascular plants have been considered soil microsites in dryland ecosystems, since they modify soil moisture and mineral nutrient distribution and availability in their vicinity (Schlesinger et al., 1996; Puigdefabregas, 2005), and thus contribute to soil heterogeneity in these ecosystems. However, we found that biological SSCs also acted as distinct soil microsites for soil texture, chemical properties and mineral nutrient concentration. In previous studies, soil heterogeneity associated to BSC components included a wide variety of soil properties in terms of favourable physico-chemical microsites relevant for vascular plants (Garcia-Palacios et al., 2011; Escudero et al., 2007) and other communities of soil organisms (Ettema and Wardle, 2002). In turn, microbes and microfauna communities associated to BSCs (Garcia-Pichel et al., 2003; Bamforth, 2004) may also have a potential influence on soil physico-chemical properties, since they participate in several soil ecological processes such as soil nutrient cycling or soil respiration (Belnap, 2003). However, recent studies suggest that most BSC effects on ecosystem functioning are more pronounced than those associated to microbial organisms (Castillo-Monroy et al., 2011a).

Table 3
Results of pairwise PERMANOVA tests for soil property combinations comparing pairs of soil surface components (SSCs) for each site (Exclusion, Low, Medium, and High impact) along the grazing gradient. Significant *P*-values (<0.05) are in bold.

SSCs	Exclusion	Low impact	Medium impact	High impact
Bare soil vs. *Bryum argenteum*	**0.0077**	–	–	–
Bare soil vs. cyanobacteria	**0.0085**	**0.0098**	**0.0145**	0.0935
Bare soil vs. *D. diacapsis*	**0.0079**	**0.0081**	**0.0254**	**0.0082**
Bare soil vs. *A. socialis*	–	–	**0.0241**	**0.0102**
Bare soil vs. *Lecidella* sp.	–	**0.0238**	**0.0162**	–
Cyanobacteria vs. *D. diacapsis*	**0.0095**	**0.0099**	**0.0487**	**0.0074**
Cyanobacteria vs. *Lecidella* sp.	–	**0.0161**	**0.0423**	–
Cyanobacteria vs. *A. socialis*	–	–	0.1085	0.0950
D. diacapsis vs. *Lecidella* sp.	–	**0.0094**	0.1170	–
D. diacapsis vs. *A. socialis*	–	–	0.0776	**0.0064**
Lecidella sp. vs. *A. socialis*	–	–	0.2577	–
Bryum argenteum vs. cyanobacteria	**0.0080**	–	–	–
Bryum argenteum vs. *D. diacapsis*	**0.0101**	–	–	–

4.2. Soil property variation beneath different SSCs

When examining each soil property associated to specific SSCs, we found that cyanobacteria, one moss species and three lichen species contributed greatly but in a different fashion to soil heterogeneity, especially in terms of micronutrient fertility. Differences in various or single soil properties between different BSCs probably resulted from specific morphological and/or physiological characteristics of each BSC component. *B. argenteum* caused more acidic conditions when compared to bare soil. This did not concur in a previous study showing similar soil pH values under a moss crust compared to physical crust in a sand dune ecosystem (Guo et al., 2008), which suggests this effect may be context dependent or simply a variation related to the involved mosses. Other authors have found an increase of pH values up to 2–3 units under cyanobacterial crusts when compared to bare soil in a desert ecosystem (García-Pichel and Belnap, 1996), most likely related to photosynthetic activity of the crust components. Cyanobacteria crust increased Ca concentration in the exclusion site and the low grazing impact site. Polysaccharides produced by cyanobacteria increase cation exchange capacity, thus retaining and maintaining available macronutrients such as Ca, K and Mg (Harper and Belnap, 2001). *A. socialis* microsites had lower P and higher Fe concentration than bare soil. The lower P concentration may be related to phosphorus uptake by *A. socialis* (Bowker et al., 2006), while the increase in Fe concentration may be explained by the segregation of exopolymers that retain inorganic compounds near the lichen area of influence (Harper and Belnap, 2001). *D. diacapsis* retained more clay particles, acidified the soil and overall increased microsite fertility with higher concentrations of P and micronutrients, especially Fe. The thick and continuous thallus of *D. diacapsis* protects soil surface and seems to buffer soil erosion as demonstrated in previous studies (Lázaro et al., 2008; Chamizo et al., 2012), thereby maintaining a higher percentage of clay fraction and thus fertility even under continuous grazing, and also enhance soil stability

Table 4
Results of ANOVA with soil surface components (SSCs) as fixed effect for different soil response variables (mean ± 1 SE) and multiple comparisons (Bonferroni's test) between different SSCs in (a) the exclusion site (EX), (b) the low impact site (LI), (c) the medium impact site (MI) and (d) the high impact site (HI). Significant differences at the $P < 0.01$ level are presented in bold. Different letters within a row indicate significant differences at the $P < 0.01$ level between different SSCs (columns). Analyses for pH, P, Na, Cu, and Zn in LI were performed on log-transformed data. Analyses for EC, C, N, Na, Fe, and Zn in MI were performed on log-transformed data. Analyses for Na and Cu in HI were performed on log-transformed data.

(a)

EX				SSC			
Response variables	df	*F*	*P*-value	Bare soil	Cyanobacteria	*D. diacapsis*	*Bryum argenteum*
Sand (%)	3	5.97	**0.0062**	40.0 ± 1.6 a	38.6 ± 1.4 ab	32.3 ± 1.5 b	38.3 ± 1.0 ab
Silt (%)	3	1.69	0.2095	35.4 ± 2.6 a	35.4 ± 1.3 a	41.9 ± 3.3 a	36.4 ± 1.9 a
Clay (%)	3	0.15	0.9262	24.6 ± 1.3 a	26.1 ± 1.4 a	25.8 ± 2.2 a	25.3 ± 1.6 a
OM (%)	3	10.04	**0.0006**	6.3 ± 0.1 a	5.5 ± 0.2 b	6.0 ± 0.2 ab	6.6 ± 0.1 a
pH	3	39.70	**<0.0001**	7.7 ± 0.4 a	8.2 ± 0.2 a	5.3 ± 0.1 b	5.7 ± 0.2 b
EC (dS/m)	3	225.90	**<0.0001**	1.131 ± 0.009 a	0.321 ± 0.054 b	0.132 ± 0.030 c	0.121 ± 0.010 c
C (%)	3	5.09	0.0115	0.907 ± 0.081 a	0.673 ± 0.027 a	0.974 ± 0.029 a	1.027 ± 0.105 a
N (%)	3	5.05	0.0119	0.102 ± 0.006 a	0.082 ± 0.003 a	0.108 ± 0.002 a	0.112 ± 0.009 a
P (mg/Kg)	3	20.06	**<0.0001**	7.8 ± 0.5 a	3.2 ± 0.2 b	6.0 ± 0.6 a	6.0 ± 0.3 a
Ca (ppm)	3	12.89	**0.0002**	347.8 ± 33.7 bc	562.5 ± 38.0 a	325.8 ± 37.8 c	524.4 ± 22.6 ab
K (ppm)	3	74.15	**<0.0001**	850.1 ± 24.5 a	918.2 ± 55.8 a	367.2 ± 21.5 b	406.3 ± 18.2 b
Mg (ppm)	3	5.17	0.0109	31.6 ± 5.7 a	66.1 ± 9.6 a	54.2 ± 6.8 a	70.2 ± 7.9 a
Na (ppm)	3	107.95	**<0.0001**	1104.1 ± 62.6 a	631.0 ± 72.8 b	69.8 ± 8.1 c	60.7 ± 7.0 c
Cu (ppm)	3	23.31	**<0.0001**	0.253 ± 0.006 bc	0.215 ± 0.008 c	0.328 ± 0.009 a	0.296 ± 0.015 ab
Fe (ppm)	3	24.40	**<0.0001**	35.6 ± 6.3 bc	13.4 ± 1.6 c	66.7 ± 1.9 a	39.8 ± 5.7 b
Mn (ppm)	3	14.27	**<0.0001**	38.2 ± 3.9 a	22.9 ± 2.3 b	44.1 ± 1.2 a	40.5 ± 1.5 a
Zn (ppm)	3	0.64	0.6031	1.861 ± 0.071 a	1.456 ± 0.388 a	1.756 ± 0.159 a	1.770 ± 0.119 a

(b)

LI				SSC			
Response variables	df	*F*	*P*-value	Bare soil	Cyanobacteria	*D. diacapsis*	*Lecidella* sp.
Sand (%)	3	3.70	0.0339	20.4 ± 2.4 a	25.3 ± 0.9 a	23.9 ± 1.8 a	28.8 ± 1.8 a
Silt (%)	3	20.52	**<0.0001**	58.7 ± 2.1 a	52.8 ± 0.9 ab	45.0 ± 2.1 bc	39.3 ± 2.0 c
Clay (%)	3	38.23	**<0.0001**	20.9 ± 0.6 b	21.9 ± 0.3 b	31.1 ± 1.3 a	31.9 ± 1.2 a
OM (%)	3	9.04	**0.0010**	6.9 ± 0.1 b	7.4 ± 0.1 ab	7.7 ± 0.1 a	7.0 ± 0.1 b
pH	3	84.42	**<0.0001**	6.6 ± 0.2 b	7.6 ± 0.2 a	5.1 ± 0.1 c	5.4 ± 0.0 c
EC (dS/m)	3	6.91	**0.0034**	0.605 ± 0.101 a	0.338 ± 0.036 ab	0.189 ± 0.030 b	0.474 ± 0.079 ab
C (%)	3	4.54	0.0174	0.905 ± 0.032 a	1.032 ± 0.081 a	1.154 ± 0.029 a	0.984 ± 0.034 a
N (%)	3	10.80	**0.0004**	0.105 ± 0.002 b	0.112 ± 0.007 b	0.137 ± 0.003 a	0.115 ± 0.002 ab
P (mg/Kg)	3	11.43	**0.0003**	3.1 ± 0.1 c	3.2 ± 0.2 bc	4.7 ± 0.3 ab	4.9 ± 0.5 a
Ca (ppm)	3	27.82	**<0.0001**	639.1 ± 39.8 b	911.3 ± 27.4 a	412.7 ± 62.4 c	541.9 ± 14.2 bc
K (ppm)	3	52.19	**<0.0001**	1061.2 ± 70.3 a	1179.3 ± 32.0 a	503.0 ± 13.7 b	701.6 ± 37.1 b
Mg (ppm)	3	8.54	**0.0013**	140.1 ± 18.6 ab	171.3 ± 8.2 a	93.5 ± 8.5 b	113.9 ± 6.6 ab
Na (ppm)	3	33.43	**<0.0001**	491.0 ± 75.5 a	339.6 ± 44.4 ab	86.2 ± 10.1 c	238.2 ± 35.5 b
Cu (ppm)	3	34.89	**<0.0001**	0.176 ± 0.006 b	0.198 ± 0.012 b	0.308 ± 0.013 a	0.213 ± 0.005 b
Fe (ppm)	3	87.22	**<0.0001**	23.9 ± 2.0 bc	16.7 ± 2.9 c	78.0 ± 4.5 a	34.9 ± 1.2 b
Mn (ppm)	3	15.68	**<0.0001**	36.4 ± 4.2 ab	22.2 ± 3.1 b	49.7 ± 1.5 a	45.7 ± 2.9 a
Zn (ppm)	3	1.23	0.3315	1.284 ± 0.183 a	0.856 ± 0.155 a	1.202 ± 0.105 a	1.175 ± 0.305 a

(c)

MI				SSC				
Response variables	df	*F*	*P*-value	Bare soil	Cyanobacteria	*D. diacapsis*	*Lecidella* sp.	*A. socialis*
Sand (%)	4	2.02	0.1302	29.5 ± 1.9 a	25.3 ± 1.5 a	24.3 ± 1.3 a	25.5 ± 1.8 a	29.7 ± 2.4 a
Silt (%)	4	14.09	**<0.0001**	44.2 ± 2.0 bc	45.5 ± 0.9 abc	52.6 ± 1.5 a	52.3 ± 0.5 ab	39.2 ± 2.0 c
Clay (%)	4	7.85	**0.0006**	26.2 ± 0.9 ab	29.3 ± 1.6 ab	23.1 ± 1.4 b	22.2 ± 1.7 b	31.1 ± 1.1 a
OM (%)	4	3.81	0.0184	6.8 ± 0.2 a	7.0 ± 0.1 a	7.5 ± 0.1 a	7.0 ± 0.1 a	7.1 ± 0.1 a
pH	4	23.09	**<0.0001**	5.5 ± 0.1 a	5.3 ± 0.1 ab	4.8 ± 0.1 c	4.9 ± 0.1 bc	5.4 ± 0.0 a
EC (dS/m)	4	8.47	**0.0004**	0.070 ± 0.009 b	0.054 ± 0.005 b	0.138 ± 0.020 ab	0.217 ± 0.087 a	0.061 ± 0.016 b
C (%)	4	0.55	0.7026	1.008 ± 0.075 a	0.976 ± 0.048 a	1.076 ± 0.060 a	1.040 ± 0.022 a	1.002 ± 0.028 a
N (%)	4	1.21	0.3374	0.120 ± 0.006 a	0.120 ± 0.007 a	0.111 ± 0.008 a	0.106 ± 0.001 a	0.117 ± 0.002 a
P (mg/Kg)	4	10.44	**<0.0001**	9.6 ± 0.9 a	9.3 ± 0.3 ab	11.0 ± 0.5 a	11.2 ± 0.8 a	6.3 ± 0.3 b
Ca (ppm)	4	9.38	**0.0002**	589.9 ± 22.6 a	418.5 ± 27.3 bc	355.4 ± 36.8 c	516.0 ± 23.4 ab	459.8 ± 33.9 abc
K (ppm)	4	4.65	**0.0081**	362.7 ± 27.9 ab	284.3 ± 20.6 b	314.4 ± 16.0 ab	398.3 ± 23.1 a	345.9 ± 8.8 ab
Mg (ppm)	4	9.52	**0.0002**	104.1 ± 6.6 a	66.3 ± 5.9 b	63.6 ± 3.9 b	100.5 ± 8.4 a	94.4 ± 5.6 ab
Na (ppm)	4	8.23	**0.0004**	25.8 ± 5.5 ab	18.3 ± 1.8 b	28.9 ± 1.8 ab	55.8 ± 13.1 a	24.3 ± 2.5 b
Cu (ppm)	4	1.91	0.1482	0.255 ± 0.026 a	0.288 ± 0.014 a	0.295 ± 0.014 a	0.318 ± 0.018 a	0.270 ± 0.014 a
Fe (ppm)	4	14.07	**<0.0001**	33.7 ± 2.4 b	37.8 ± 2.0 b	55.2 ± 3.6 a	41.9 ± 2.7 ab	32.5 ± 0.9 b
Mn (ppm)	4	3.74	0.0197	56.9 ± 5.5 a	47.0 ± 1.9 a	60.0 ± 3.4 a	65.7 ± 3.8 a	53.9 ± 2.2 a
Zn (ppm)	4	4.43	**0.0100**	1.056 ± 0.160 ab	1.667 ± 0.321 a	0.893 ± 0.056 b	1.139 ± 0.051 ab	1.057 ± 0.081 ab

(d)

HI				SSC			
Response variables	df	*F*	*P*-value	Bare soil	Cyanobacteria	*D. diacapsis*	*A. socialis*
Sand (%)	3	0.41	0.7467	32.3 ± 2.2 a	31.3 ± 1.9 a	33.7 ± 1.4 a	30.6 ± 2.6 a
Silt (%)	3	17.9	**<0.0001**	45.7 ± 2.3 a	33.5 ± 1.7 b	31.4 ± 0.5 b	42.6 ± 1.6 a

(*continued on next page*)

Table 4 (*continued*)

(d)							
HI				SSC			
Response variables	df	*F*	*P*-value	Bare soil	Cyanobacteria	*D. diacapsis*	*A. socialis*
Clay (%)	3	17.2	**<0.0001**	22 ± 1.2 c	35.2 ± 1 a	34.9 ± 1.3 ab	26.8 ± 2.3 bc
OM (%)	3	3.81	0.0309	7 ± 0.2 a	6.3 ± 0.2 a	6.4 ± 0.1 a	6.7 ± 0.2 a
pH	3	33.38	**<0.0001**	5.5 ± 0 a	5.5 ± 0.1 a	4.6 ± 0.1 b	5.6 ± 0.1 a
EC (dS/m)	3	5.63	**0.0079**	0.046 ± 0.002 a	0.087 ± 0.02 a	0.092 ± 0.013 a	0.052 ± 0.003 a
C (%)	3	8.64	**0.0012**	0.645 ± 0.019 b	0.689 ± 0.028 b	0.865 ± 0.051 a	0.764 ± 0.025 ab
N (%)	3	10.22	**0.0005**	0.07 ± 0.002 b	0.078 ± 0.003 ab	0.093 ± 0.005 a	0.081 ± 0.002 ab
P (mg/Kg)	3	18.28	**<0.0001**	10.4 ± 0.5 ab	8.2 ± 1 bc	13.6 ± 0.8 a	5.8 ± 0.7 c
Ca (ppm)	3	20.33	**<0.0001**	480.9 ± 18.1 a	502.5 ± 45.4 a	219.1 ± 12.1 b	422.5 ± 27.5 a
K (ppm)	3	12.31	**0.0002**	275 ± 8.3 b	343.9 ± 12.8 a	302 ± 9 ab	351 ± 10.2 a
Mg (ppm)	3	11.54	**0.0003**	79.8 ± 3.4 a	87.7 ± 9.5 a	42.3 ± 2.8 b	83.4 ± 6.4 a
Na (ppm)	3	2.24	0.1233	1.3 ± 1.8 a	1.5 ± 4.2 a	1.3 ± 2.6 a	1.4 ± 1.9 a
Cu (ppm)	3	27.78	**<0.0001**	0.155 ± 0.003 b	0.195 ± 0.013 b	0.279 ± 0.015 a	0.187 ± 0.007 b
Fe (ppm)	3	106	**<0.0001**	23.3 ± 1.1 b	28.7 ± 1.6 b	54.6 ± 1.6 a	27.5 ± 1 b
Mn (ppm)	3	3.71	0.0336	42.6 ± 2.1 a	47.9 ± 1.1 a	40.6 ± 1.9 a	45.2 ± 1.3 a
Zn (ppm)	3	7.9	**0.0019**	0.27 ± 0.037 b	0.544 ± 0.062 a	0.574 ± 0.056 a	0.403 ± 0.04 ab

(Jimenez Aguilar et al., 2009). The retention of fine, nutrient rich particles and the secretion of organic acids by *D. diacapsis* may explain the lower pH values and an overall higher nutrient availability (Harper and Belnap, 2001; Beraldi-Campesi et al., 2009). Also, *D. diacapsis* seems to reduce phosphatase activity (Bowker et al., 2011), which may lead to a higher soil P concentration associated with this species. The concentration of macronutrients was relatively low in *D. diacapsis* microsites, particularly Ca, suggesting a high uptake rate of these nutrients. This may be related to the fact that this species is covered by a thick layer of pruina (calcium oxalate) previously identified as a protective mechanism against the high solar radiation (Magnusson, 1929) characteristic of open interspaces in drylands. Hence, the Ca uptake by *D. diacapsis* for pruina production may exceed Ca retention, leading to a decline in cation concentration and consequently reduced pH and CEC under *D. diacapsis* compared to bare soil and cyanobacteria microsites. Furthermore, soil of *D. diacapsis* presented higher concentration of Cu in continuously grazed sites (LI, HI), and a consistent increase in Fe concentration along the disturbance gradient compared with bare soil. *Lecidella* sp. showed similar effects on soil properties as *D. diacapsis* (higher percentage of fine fraction, lower pH, higher P concentration and lower macronutrient concentration) in the low impact site. Our results showed no effect of *D. diacapsis* on Mn concentration and a negative effect on Zn concentration. On the contrary, a previous study developed in a dryland ecosystem where grazing never occurred or occurred prior to a long resting period, found a positive correlation between two lichen species (*Collema tenax* and *Collema coccophorum*) and greater availability of both Mn and Zn (Bowker et al., 2005). The authors suggest that the greater availability of these nutrients may be due to the lichen effects on topsoil properties (Bowker et al., 2005), and this may enhance nutrient uptake in vascular plants (Harper and Belnap, 2001).

Table 5
Summary of ANOVA for *Diploschistes diacapsis* effect (RII index) with site (Exclusion, Low, Medium, and High impact) as fixed factor for different response variables (soil properties). Significant differences at the $P < 0.01$ level are presented in bold.

Response variables	df	Mean square	*F*	*P*-value
Sand (%)	3	0.13	9.63	**0.0005**
Silt (%)	3	0.30	25.47	**<0.0001**
Clay (%)	3	0.29	26.00	**0.0005**
OM (%)	3	0.04	24.86	**<0.0001**
pH	3	0.04	52.12	**0.0004**
EC (dS/m)	3	4.77	30.75	**<0.0001**
C (%)	3	0.05	6.61	0.0187
N (%)	3	0.11	14.95	**<0.0001**
P (mg/Kg)	3	0.32	15.40	**0.0013**
Ca (ppm)	3	0.29	6.29	**0.0008**
K (ppm)	3	0.70	107.73	**<0.0001**
Mg (ppm)	3	1.02	23.55	**0.0002**
Na (ppm)	3	3.45	78.51	**<0.0001**
Cu (ppm)	3	0.21	12.22	**0.0003**
Fe (ppm)	3	0.23	38.54	**0.0039**
Mn (ppm)	3	0.09	15.01	0.1505
Zn (ppm)	3	0.66	25.09	**<0.0001**

4.3. Grazing impact on BSC effects

Our results also indicate that with increasing grazing impact, SSC effects on microsite differentiation dilutes. This suggests that increasing grazing pressure reduces BSC specific effects on soil heterogeneity. The majority of changes in soil properties associated with cyanobacteria crust (organic matter, nutrient concentration) and *Lecidella* sp. (soil texture, nutrient concentration) disappear when grazing impact increased. Also, we observed a change in the nature and magnitude of RII associated with *D. diacapsis* along the perturbation gradient. The negative value of RII for pH decreased with grazing intensity, which may be due to a reduction in acid production by *D. diacapsis*. These changes in SSCs soil properties may be due to the potential damage exerted by mechanical impact on biological SSC structure and function, diminishing their species-specific effects. For instance, it has been observed that mechanical impact other than grazing decreases photosynthetic activity and nitrogen inputs in crusts (Belnap et al., 1994). Similarly, heavy and continuous grazing may exert a potential damage in Zn uptake mechanism of *D. diacapsis*, leading to a change in RII index nature (from negative to positive). In contrast, the positive value of RII for Ca concentration increased with grazing intensity. This may be due to an increase in solar radiation (reduced plant cover) which requires a higher pruina production by *D. diacapsis*. Overall, *D. diacapsis* maintained a relatively similar effect on soil properties throughout the disturbance gradient. The positive effect of *D. diacapsis* exerted on physico-chemical properties related to soil fertility is particularly noteworthy under the continuous grazing regime, suggesting that this species may have stronger effects on soil properties and may be more resistant to trampling than other BSCs. These results highlight the important ecological role of this species in semiarid grasslands where overgrazing threatens soil stability and fertility.

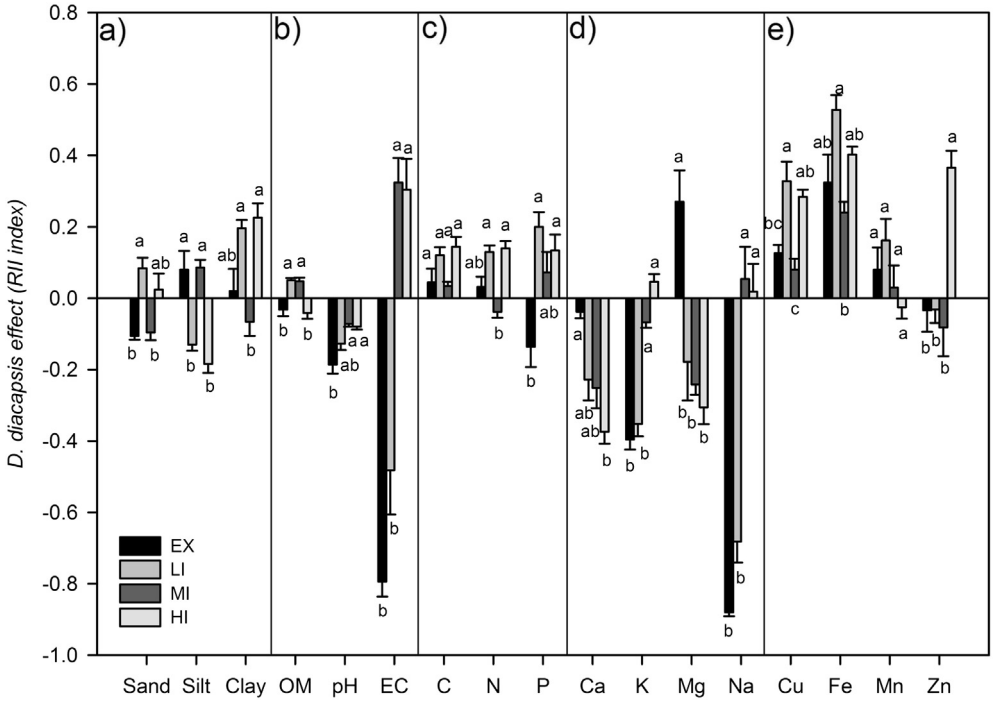

Fig. 2. Mean (±1 SE) of RII index for (a) soil texture (sand, silt and clay content), (b) OM, pH and EC, (c) C, N and P, (d) macronutrients (Ca, K, Mg, Na) and micronutrients (Cu, Fe, Mn, Zn). Different letters above/below bars indicate significant differences for RII index across sites at the $P < 0.01$ level.

5. Conclusions

Our study is one of the first to demonstrate quantitatively that BSC components contribute to soil heterogeneity at the species level in the vegetation free interspaces in the semiarid grassland ecosystem of Central Mexico. It provides new insights into species-specific effects on soil physico-chemical characteristics and their potential functional role on ecosystem processes. In particular, our study confirms the differential ecological/functional role of cyanobacteria, soil lichen and mosses in contributing to small-scale soil heterogeneity. By comparing physical and chemical properties in soil associated with different BSC species and the most conspicuous group and those found in bare soil, we could demonstrate that BSC presence is responding to and/or influencing local soil physical and chemical characteristics at a small spatial scale and at the species level. Also, by setting up the study along a grazing gradient including a long-term grazing exclosure, and seasonal and continuous, moderate and heavy grazing regimes, we could assess and separate different BSC patterns related to soil texture, chemical properties and soil nutrient concentrations.

In summary, BSCs contributed greatly to soil heterogeneity in this grassland ecosystem, both from a microsite perspective and in relation to particular soil properties; and heavy grazing pressure may alter this natural pattern. The contribution of BSCs to soil heterogeneity may be comparable to that provided by vascular vegetation in drylands ecosystems, yet at a smaller scale. This soil heterogeneity associated to BSC components includes a wide variety of soil properties in terms of physico-chemical microsites, not only relevant for vascular plants (Garcia-Palacios et al., 2011) but also for other communities of soil organisms (Ettema and Wardle, 2002). A multi-scale approach is needed for understanding both the spatiotemporal dynamics of soil heterogeneity and the complex relations and interactions between biotic and abiotic factors explaining this heterogeneity and its role in dryland ecosystem functioning (Maestre et al., 2005).

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