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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

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chelate elements into the soil surface (Harper and Pendleton, 1993; Johnson et al., 2007); 2) they discriminate among mineral nutrients 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 bioessential 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 *graminetum* (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