Original article

Biological soil crust recovery after long-term grazing exclusion in the Monte Desert (Argentina). Changes in coverage, spatial distribution, and soil nitrogen

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ABSTRACT

Disturbance by domestic grazing is recognized as the most widespread stressor of biological soil crust (BSC) communities. To assess the recovery of the BSC after grazing exclusion, we estimated the composition, cover, and spatial distribution of biological soil crusts, and their influence on soil nitrogen in a protected area after 40 years of grazing exclusion (Reserve MaB of Ñacuñán), and in its surrounding grazed matrix in the central Monte Desert. We considered two spatial scales: at the landscape scale we estimated vegetation and BSC cover in paired grazed and ungrazed sites of *Larrea* shrublands; at the microsite scale we assessed the influence of the dominant vascular plant, *Larrea cuneifolia*, on crust cover, and the influence of crust cover on soil nitrogen concentration. Grazing has a negative impact on soil crusts, which only develop under the protection of vascular plants in grazing areas. Grazing exclusion favors crust recovery, allowing black, lichen dominated crusts to develop in exposed areas between shrub canopies. The cover of the moss-dominated crusts was not significantly different at any of the two spatial scales analyzed. Soil nitrogen was higher in areas under *L. cuneifolia* and without BSC cover, suggesting that litterfall inputs currently exceed those from soil crust N_2 fixation, perhaps because crust function has not yet recovered.

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1. Introduction

Loss of landscape functional integrity in semiarid rangelands has been increasingly recognized all over the world, being partially the result of land degradation due to unsustainable livestock production (Jones, 2000; Okin et al., 2009). The integrity and patterns of ecosystem processes can be modified at different scales, affecting all components of biodiversity such as plants, animals and soil organisms, including biological soil crust communities (BSCs) (Ludwig et al., 2004). Recognized indicators of land degradation include the loss of vegetation cover, soil and organic matter, and reduced water-use efficiencies (Lechmere-Oertel et al., 2005). In drylands, properties of BSCs (e.g. diversity and coverage) are strong indicators of ecosystem health (Jones, 2000; Pellant et al., 2000; Maestre et al., 2005, 2010; Bowker et al., 2006). Disturbance by domestic grazers is recognized as a major stressor of crust communities (Bowker et al., 2006). Trampling by domestic herbivores reduces BSC cover, accelerating soil erosion and altering soil temperature, humidity, and aeration (Belnap et al., 2006). In addition, a reduction of biological soil crusts affects biogeochemical cycles, because soil crusts fix atmospheric carbon and nitrogen (N) that enter the local nutrient cycle and are used by higher plants (Thomas and Dougill, 2006). It has been demonstrated that a reduction of crust cover affects plant establishment and growth, by reducing their seed germination, seedling development, plant productivity, and survival (Harper and Belnap, 2001). Full recovery of BSC following disturbance may extend from a few years to several centuries, depending on the severity of the disturbance processes, the local conditions, and

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availability of inoculating material (Belnap, 1993; Belnap and Eldridge, 2001; Muscha and Hild, 2006; Lázaro et al., 2008).

Cyanobacterial soil crusts may develop differentially within subcanopy habitats, affecting the spatial heterogeneity of resources, ecosystem resilience, and long-term stability of rangelands (Berkeley et al., 2005). Of particular relevance for BSCs development is the composition and cover of higher plants in the area (Maestre, 2003). The spatial patterns of BSCs and vascular plants are usually closely related, with a higher occurrence of crusts in the interspaces between vascular plants because of crust burial by litter under plant canopies (Belnap et al., 2006; Berkeley et al., 2005). This determines an inverse relationship between total cover of crusts and vascular plants, because less plant cover leaves more soil surfaces available for crust colonization (Muscha and Hild, 2006). However, shrubby vascular plants can provide beneficial microclimatic conditions for crust recovery as they reduce insolation and desiccation, and increase soil fertility (Belnap et al., 2001; Jimenez Aguilar et al., 2009). The effect of vascular plants on biological soil crusts and their potential facilitative role on crust recovery greatly depends on the species being considered, the local environmental conditions, disturbance dynamics, and the balance between the amelioration of environmental conditions and crust burial by litter (Belnap et al., 2001; Maestre, 2003; Read et al., 2008).

The use of BSCs as bioindicators of desertification or land degradation and their potential use by managers for conservation and recovery of ecosystems require a knowledge of the properties and patterns of crust recovery after disturbance. In this context, relatively undisturbed communities are invaluable sources of ecological information to monitor the recovery of soil crusts (Jones, 2000). In many ecosystems, undisturbed reference areas are non-existent, but long-term protected areas can be used to monitor crust recovery (Bowker et al., 2006). In semiarid landscapes, reference sites for studying BSC structure and function comprise livestock enclosures and protected areas unaffected by direct anthropogenic uses (Shinneman et al., 2008). In South America, however, there only a few studies on the presence, composition, and ecology of soil crusts (Büdel, 2001), which do not include the central Monte Desert.

The main purpose of this study is to perform the first assessment of BSCs abundance, characteristics, and function in the central Monte Desert (Argentina), where soil crusts have not been widely studied (Castillo-Monroy and Maestre, 2011). This desert, as many other arid and semiarid regions around the world, is used by humans for livestock production or intensive agriculture, depending on the amount of water available for irrigation. Livestock production may be compatible with biodiversity conservation if management practices (i.e., livestock numbers, temporal and spatial distribution of grazing areas) allow the recovery of the vegetation and ecosystem function (Steinfeld et al., 2010). Because soil crusts are sensitive to livestock trampling, they may be useful indicators of land degradation or recovery. In this study we analyzed the abundance and spatial distribution of soil crusts and their influence on soil nitrogen after 40-years of grazing exclusion in a protected area (Reserve MaB of Ñacuñán) and its surrounding grazed matrix. We hypothesize that the reduced trampling by grazing animals in the reserve has facilitated soil crust recovery, modifying soil crust spatial distribution, and allowing them to grow in exposed areas where they would be destroyed by trampling in the presence of grazers. We also hypothesize that soil crust recovery would increase soil nitrogen inputs to the soil because of increasing biological N_2 fixation rates performed by free-living and lichen associated cyanobacteria, commonly present in BSCs. In order to test these hypotheses, we estimated soil crust cover and soil available and total nitrogen content in the Ñacuñán Reserve and its surrounding grazing areas, in patches located under Larrea

cuneifolia shrubs and in exposed areas, covered and not covered by BSCs. We made the following predictions: 1-The reserve will hold a higher cover of soil crusts than surrounding sites; 2-Crust cover will differ in spaces located under L. cuneifolia and its interspaces; 3-Soils covered by crusts will have higher nitrogen contents than soils not covered by crusts.

2. Materials and methods

2.1. Study site

The study area is located in the central Monte Desert, Argentina (Fig. 1), which constitutes the most arid rangeland of Argentina (Abraham et al., 2009). This region occupies the lowlands and plateau area between 32° and 37° S (Morello, 1958). The climate is semiarid and markedly seasonal, with cold dry winters (mean temperature $<10\,°C$) and warm rainy summers (mean temperature $>20\,°C$). Average annual rainfall is 324 mm (Estrella et al., 2001). The dominant landscape in the region is a gently undulating plain, with an overall average slope of 0.4% in West–East direction. Marked contrast of soils, slope, and vegetation physiognomy exist among the main habitat units (Roig and Rossi, 2001). Deep, sandy-silt soils, mainly of eolian origin and poor in organic matter, support open multistratified woodlands formed by an upper stratum dominated by Prosopis flexuosa and Geoffroea decorticans, a shrub layer of Larrea divaricata and Condalia microphylla, and a grass and herb layer. Loamy-clay soils of relatively low permeability are found in depressed areas, and are called Larrea shrublands due to the dominance of L. cuneifolia and grasses (Trichloris crinita and Pappophorum caespitosum). The central parts of these depressions are characterized by highly impermeable soils due to high amounts of clay, and sustain a sparse plant cover mostly of stunted L. cuneifolia.

Since the initiation of the European colonization of the region, at the beginning of the 19th century, several areas of the Monte Desert have suffered desertification due to severe exploitation of the Prosopis woodlands, followed by extensive cattle production (Abraham and Prieto, 1981; Roig, 1991; Villagra et al., 2009). The Natural Reserve of Ñacuñán (34° 02′ S, 67° 58′ W) was created in 1961 to protect the woodlands of P. flexuosa, one of the most conspicuous habitat types in the area. In 1986 the Reserve was
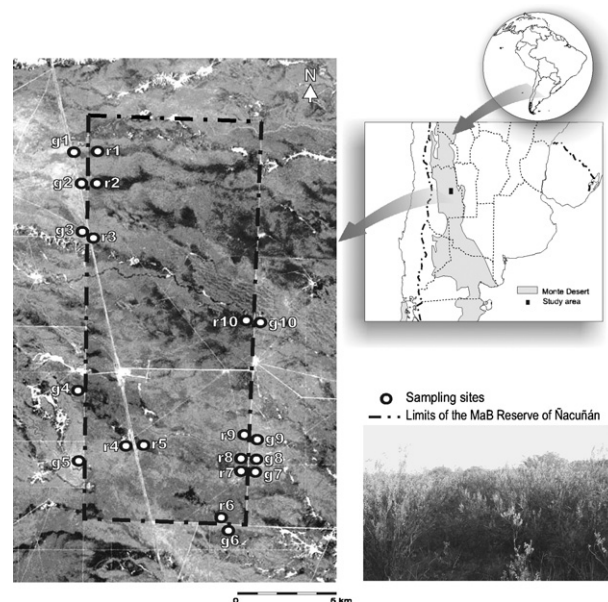

Fig. 1. Location of the Ñacuñán Reserve and its surroundings, indicating the ten paired sites inside and outside of the reserve.

incorporated into the UNESCO Man and Biosphere Reserve Network and for over 40 years cattle has been excluded from the area. This reserve is nowadays the most important reference site in Argentina for monitoring the ecological health of the Monte Desert (Ojeda et al., 1998). This long-term grazing exclusion exhibits a remarkable natural recovery of the autochthonous vascular vegetation (Rossi, 2004). The recovery of the biological soil crust communities and the potential ecological role of BSCs on this arid environment have not been assessed.

In the surrounding unprotected areas, grazing by domestic animals, predominantly cattle, has an average stocking density of 27 ha per animal unit (Guevara et al., 1976, 1996).

2.2. Experimental design

The study was carried out during April and May 2009 within the Ñacuñán Reserve and surrounding unprotected areas. A paired-site sampling design was used (Young et al., 2002), selecting each site in the reserve and a corresponding nearby site in the grazing areas. We selected ten paired sites that differed in cover and overall size of shrub individuals, comprising most of the *L. cuneifolia* shrublands of the reserve. The variability in *L. cuneifolia* communities is related to differences in soil texture and water availability due to the local topography, the pattern of water surface runoff (Tanquilevich, 1971; Rossi, 2004), and perhaps to land use history before the reserve was established. However, the species composition, climatic characteristics, soil classification, and time since domestic animals exclusion were similar in all sites, which form a continuous shrubland without isolating barriers that would cause genetic differentiation of plant communities. The similarities among biologic and environmental conditions of the 10 paired sites allowed a factorial design, with crossed fixed and random factors, and with all levels of each factor occurring in combination with every level of the other factors (Quinn and Keough, 2002).

Landscape and microsite scales were considered in this study. At the landscape scale, we analyzed the effect of the exclusion of domestic animals on the recovery of soil crusts by estimating vegetation and soil crust cover in 50 m transects in each of the ten reserve and grazed paired sites. We used the Point Quadrat method (Kent and Coker, 1992), with interceptions every 5 m along transects.

At the microsite scale, we evaluated two factors in addition to land use. First, we analyzed the effect of *L. cuneifolia* canopies on soil crust cover, estimating moss and black crust cover in quadrats located in different patches (covered by *L. cuneifolia* and in exposed areas between plant canopies). Every 5 m along each 50 m transect, we demarcated two 50 × 50 cm quadrats (one under a nearby *L. cuneifolia* canopies and the other in the adjacent exposed area), with 20 quadrats sampled in each transect, 10 in each microsite, totaling 400 quadrats. In each quadrat, we visually estimated the percent cover of black and moss-dominated crusts. The broad morphological differentiation of the biological soil crust in black and moss types follows Eldridge and Rosentreter (1999), based on the visual identification of moss dominance. Samples of the black and moss-dominated crusts were collected for later taxonomical determination in the laboratory. Finally, we evaluated the effect of land use, microsite, and crust cover on soil nitrogen content, determining soil N in soil samples collected in each of the quadrats, in sections covered and not covered by crusts.

2.3. Taxonomic identification

Identification of the black and moss-dominated crusts was based on morphological, anatomical and chemical spot tests of the specimens. The presence of cyanobacteria was checked using a compound light microscope. Morphological observations of lichens and mosses were made under a dissecting microscope, and anatomical features were examined by sections on water-mounted slides under a compound light microscope. Nomenclature for lichens and bryophytes follows Brummitt and Powell (1992). Voucher specimens are deposited at the Argentinean Institute of Snow, Ice and Environmental Sciences (IANIGLA).

2.4. Nutrient analyses

In each of the 20 transects, four composite soil samples were made from the samples collected at each quadrat, with the following combination of microsites: covered by crusts under *L. cuneifolia*; not covered by crusts under *L. cuneifolia*; covered by crusts in exposed areas; and not covered by crusts in exposed areas. The total of 80 resulting composite samples were sieved through a 2 mm mesh and divided into three subsamples. One set of subsamples was extracted with a 2 N solution of KCl (20 g of soils in 60 ml of 2 M KCl), and frozen until nitrate and ammonium determinations could be made. The second set of subsamples were dried at 100 °C for gravimetric soil moisture determination, and the third set of subsamples was air dried and analyzed for total soil N by Kjeldahl digestion. Available N was determined by spectrophotometry in the soil KCl extracts, with the spongy cadmium (Jones, 1984) and the phenol–hypochlorite method (Weatherburn, 1967) for nitrate and ammonium, respectively.

2.5. Statistical analyses

We used generalized linear mixed models (GLMM) to evaluate the effect of different factors on the response variables, at different spatial scales. At the landscape scale, we analyzed the effect of the grazing exclosure on vascular plants, soil crust, bare soil, and litter cover, considering "land use" as a fixed factor with two levels (reserve and grazing areas) and "site" as a random factor with ten levels (sites 1–10).

At the microsite scale, we analyzed the visual estimations of crust cover in 400 quadrats, considering "land use" and "microsite" (under *L. cuneifolia* and exposed areas) as fixed factors and "site" as a random factor with ten levels (sites 1–10). Soil nitrogen concentration was analyzed with a similar model as for crust cover, with the additional fixed factor "crust cover" with two levels (presence–absence). We checked whether the interaction between "land use" (reserve and grazing areas) and "microsite" (under *L. cuneifolia* and exposed areas) significantly improved the models of soil crust cover and soil N. For this purpose we used the Akaike Information Criterion (AIC) and analysis of variance (ANOVA) to compare the goodness of fit for models with and without the interaction (Bolker et al., 2008). With the best model for each variable resulted from the previous analysis, we determined the significance of each fixed factor. We conducted the GLMM analyses using the lmer function of the lme4 package (Bates and Maechler, 2009) with the R statistical software (R Development Core Team, 2009). The significance of each fixed factor was determined with estimated Markov Chain Monte Carlo *p* values (*MCMCp*) for the mixed model parameters using the "pvals.fnc" function of the languageR package for R (Baayen, 2008), with 100,000 iterations. The models used transformed data (log transformed for soil properties and arcsine for crust and vegetation cover) and assumed a normal error distribution.

3. Results

3.1. Biological soil crust composition

Biological soil crusts were composed of free cyanobacteria, coccoid green algae, lichens and mosses. All soil crusts analyzed

had cyanobacteria. Gelatinous lichen species were dominant in the black crusts, including *Collema coccophorum*, *C. crispum* and *Placynthiella uliginosa*. The moss crusts were mostly composed of the species *Dydimon vinelas*. The complete list of species identified in the crusts is shown in Table 1.

3.2. Landscape scale

Heterogeneity in vascular plant and biological soil crust cover within the study areas was relatively high, with more than 50% of variability in the cover of *L. cuneifolia*, grasses, and moss-dominated crusts being explained by differences among sampling sites (Table 2). Land use had a significant effect on bare soil, grasses and black soil crust cover, with higher values of grass and black soil crust cover, and lower values of bare soil in the reserve than in grazed sites (Fig. 2, Table 2).

3.3. Microsite scale

At the microsite scale, the effect of land use on crust cover was similar as in the landscape scale, showing a significant recovery of black crusts, and a non significant recovery of moss crusts (Table 3, Fig. 3). Soil crust cover was different in the two microsites considered, with black crusts presenting a higher cover in exposed areas, and moss crust under *L. cuneifolia* canopies (Fig. 3). The spatial distribution of black crusts differed with land use, with a higher cover of black crusts occurring in exposed microsites within the reserve, and underneath *L. cuneifolia* within grazing areas (Fig. 3, Table 3). In fact, the significantly better fit of the model that includes the interaction among land use and microsite type reflects the differential distribution of black crusts at microsite spatial scales within the landscape spatial scale (Table 3). Soils located underneath *L. cuneifolia* canopies had higher nitrate and total N concentrations than soils located in exposed microsites, and total soil N concentrations were higher in soils not associated to soil crusts than in soils covered by crusts (Table 3).

4. Discussion

The three times higher crust cover found in the reserve than in surrounding sites used for cattle grazing suggests that the exclusion

Table 1
Floristic composition of biological soil crusts in the Monte Desert, Argentina.

Cyanobacteria
  Microcoleus sp. Desmazieres ex Gomont
  Nostoc sp. Vaucher ex Bornet et Flahault
  Scytonema sp. C. Agardh ex Bornet et Flahault
  Osillatoria sp. Vaucher
Green algae
  Unidentified coccoid green algae
Lichens
  Aspicilia aff. *mastrucata* (Wahlenb.) Th. Fr.
  Collema coccophorum Tuck.
  Collema crispum (Huds.) Wigg.
  Collema tenax (Sw.) Ach.
  Endocarpon pusillum Hedw.
  Lichinella nigritella (Lettau) Moreno & Egea
  Peltula psammophila (Nyl.) Egea
  Placidium squamulosum (Ach.) Breuss
  Placynthiella sp. Elenk.
  Placynthiella uliginosa (Schrad.) Coppins & James
  Porina sp. Müll. Arg.
  Psora sp. Hoffm.
  Toninia ruginosa (Tuck.) Herre
  Unidentified species 1
  Unidentified species 2
Mosses
  Dydimodon vinealis (Bridel.) R. H. Zander

Table 2
Summary of the results of the Generalized Linear Mixed Model analyzing differences in vascular plant cover, and biological soil crust cover at the landscape scale. The random effect is evaluated with the percentage of the total variability explained by "site". The fixed factor "land use" is evaluated with the MCMCp-values (n = 100,000 simulations) of the mixed model parameters, with p < 0.05 (highlighted in bold) indicating significance.

Response variable	%-variability explained by sampling sites	MCMCp-value for Land use
L. cuneifolia	70.1	0.9268
Grasses	64	**0.0191**
Litter	46.4	0.166
Bare soil	8.9	**0.0013**
Black crusts	38.3	**0.001**
Moss crusts	70.5	0.2756

of domestic animals for 40 years has allowed the natural recovery of biological soil crusts, in agreement with our first prediction. These findings agree with those from other arid and semiarid ecosystems that showed a reduction of vegetation cover and a degradation of biological soil crusts with livestock grazing, and the recovery of the vegetation within a few decades of grazing exclusion (McKenna Neuman et al., 2005; Belnap et al., 2006; Jimenez Aguilar et al., 2009; Kettenring, 2001; Muscha and Hild, 2006; Thomas and Dougill, 2006). The significant increment of crust cover (about 300%) that occurred in the reserve is mainly attributed to black crusts composed of cyanobacteria and lichens (Fig. 2, Table 2), suggesting a differential recovery of the different soil crust types. Cyanobacteria are usually the first organisms to colonize disturbed areas, followed by lichens and mosses (Belnap and Eldridge, 2001). Usually lichens and mosses develop in close association (e.g. Belnap and Eldridge, 2001; Belnap, 2006; Langhans et al., 2010), a pattern that was not found in our study area where the recovery of lichens in open microsites was not accompanied by the recovery of mosses (Table 2). According to Belnap (1993) and Kidron et al. (2008) moss recovery is much slower than lichen recovery, suggesting that in our study area full recovery of the BSC communities has still not been attained and succession is still in progress. However, both in the reserve and in grazed areas mosses were mostly found growing in the shade of *L. cuneifolia* canopies. Although, as with lichens, mosses can survive large periods of drought, it has been shown that they are susceptible to high light irradiance during desiccation periods
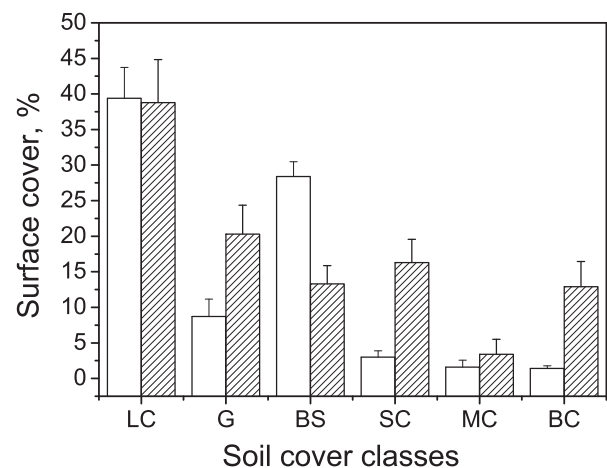

Fig. 2. Cover of Larrea cuneifolia shrubs (LC), grasses (G), bare soil (BS), total (SC), black (BC) and moss (MC) soil crusts outside (white bars) and inside (stripped bars) the Ñacuñán Reserve. Bars and error bars indicate means and standard errors of each class calculated with values from the ten paired sites.

Table 3
Summary of the results of the Generalized Linear Mixed Model at the microsite scale. The interaction between the fixed factors "land use" and "microsite" are evaluated comparing models with (m1) and without (m2) the interaction, with the Akaike Information Criterion (AIC). A dAIC (AICm2-AICm1)>2 and $p < 0.05$ (highlighted in bold) indicates a better fit of the model that considers the interaction. The best model for each variable was used to estimate the effects of "land use" and "microsite" on biological soil crust cover, and the effect of "land use", "microsite", and "crust cover" on soil N content. The effect of the fixed factors was evaluated with Markov Chain Monte Carlo p (MCMCp) values (n=100,000 simulations) of the mixed model paramenters, with $p < 0.05$ (highlighted in bold) indicating significance.

Response Variable	Interaction between land use and microsite: *dAIC*	Interaction between land use and microsite: ANOVA *p*- and *Chi square* values		MCMCp for land use	MCMCp for microsite	MCMCp for crust cover
Moss crust cover	−1.68	0.5718	0.32	0.146	**0.030**	NA
Black crust cover	**44.58**	**8.8e-12**	**46.58**	**0.0000**	**0.0189**	NA
Soil ammonium concentration	1.959	0.84	0.04	0.1613	0.3506	0.6002
Soil nitrate concentration	1.73	0.05355	3.73	0.0975	**0.0110**	0.0804
Total N concentration	−1105	1	0	0.2819	**0.0033**	**0.0034**

(Barker et al., 2005; Cole et al., 2008). Therefore, the non significant recovery of mosses in the study area could be also the result of physiological constraints in mosses for colonizing open microsites in warm desert environments.
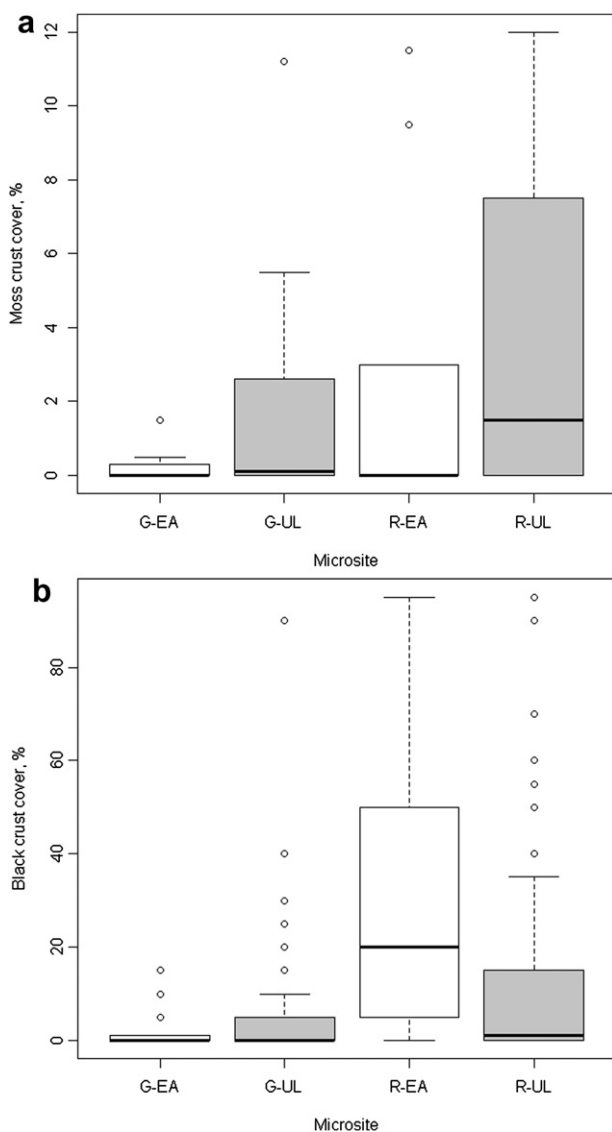

Fig. 3. Soil cover of moss (a) and black (b) crusts located in exposed areas (EA, white boxes) and under L. cuneifolia canopies (UL, filled boxes), inside (R) and outside (G) the Ñacuñán Reserve. Horizontal lines dividing each box in two indicate the median; box limits are the first and third quartiles of the distribution; whiskers extend to the most extreme data point, which is no more than 1.5 times the interquartile range from the box; circles indicate outlying data points falling beyond whisker limits.

Vascular plants have evidenced a significant recovery in the reserve (Rossi, 2004), with a concomitant reduction in the percentage of bare soil (Fig. 2, Table 2) The presence of *L. cuneifolia* influenced black and moss crust cover, in agreement with our second prediction. The spatial distribution of black soil crusts in relation to vascular plants was different in the reserve and in grazing sites (Fig. 3 and Table 3, interaction between microsite and land use), pointing to the interaction among different factors, such as animal trampling, the recovery of vascular plants, crust burial by litter accumulation, and the physiological characteristics of soil crust components. A similar differential distribution pattern of lichen- and moss-dominated biological soil crusts has been found in semiarid Mediterranean regions, where it has been proposed that the development of mosses is facilitated underneath vascular plant canopies by the amelioration of otherwise harsh environmental conditions (Maestre et al., 2002, 2009).

The preferential distribution of black crusts in open, exposed microsites within the reserve area (Table 3) is probably the result of the availability of bare terrain for colonization. However, it may also be the result of the ability of lichens to cope with conditions of high irradiance, by having a variety of physiological and anatomical photoprotective strategies (Demming-Adams et al., 1990; Nash, 1996). Rapid recolonization by the lichen species *C. coccophorum* and *P. uliginosa* could have been the result of their ability to be effectively dispersed by globular isidia, which were very abundant on the thalli surfaces. Vegetative reproduction by thallus fragmentation or by the production of vegetative propagules is considered of outmost importance for the rapid dispersion of pioneer species (Lalley and Viles, 2008). In addition, the success of lichen recovery is attributed to their poikilohydric character that allows them to survive during drought and to rapidly and efficiently use moisture when available (Nash, 1996). The restriction of soil crusts to sites under *L. cuneifolia* in grazing areas indicates that the destruction of soil crusts by domestic animals limits their distribution to protected microsites, where animal transit is lower. This finding agrees with studies in the Kalahari Desert, where soil crusts were evenly distributed in different microsites (under *Acacia mellifera*, interspace, and under *Grewia flava*) under low disturbances, but restricted to the thorny and wood encroaching *A. mellifera* in highly disturbed sites (Berkeley et al., 2005).

Formation of a BSC cover on the interspaces between vascular plants could have an ecological relevant function stabilizing the soil surface, creating a rough surface, regulating water runoff, and ameliorating local environmental conditions such as humidity and temperature (Maestre et al., 2005; Bowker et al., 2008; Belnap et al., 2009). These conditions probably facilitate vascular plant establishment by trapping seeds and favoring seedling establishment and survival (St. Clair et al., 1984; Langhans et al., 2010). Another relevant ecological role of the biological soil crusts is their contribution to soil fertility (Kettenring, 2001; Cornelissen et al., 2007), with cyanobacteria (free living and symbiont in lichens) having the capacity to
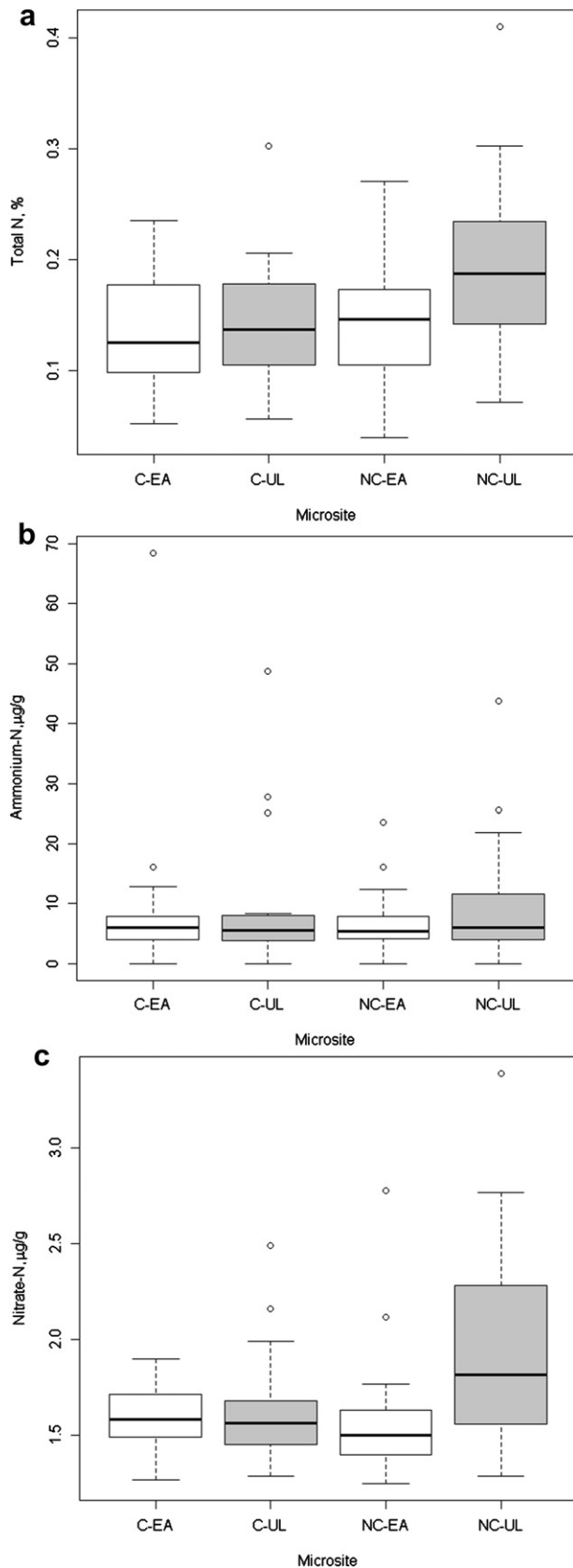
Fig. 4. Nitrogen concentration of soils covered (C) and not covered (NC) by soil crusts, located in exposed areas (EA, white boxes) and under *L. cuneifolia* canopies (UL, filled boxes). a — total soil nitrogen; b — ammonium; c — nitrate. Horizontal lines dividing each box in two indicate the median; box limits are the first and third quartiles of the distribution; whiskers extend to the most extreme data point, which is no more than 1.5 times the interquartile range from the box; circles indicate outlying data points falling beyond whisker limits.

fix atmospheric nitrogen (Aranibar et al., 2003), and other soil crust microorganisms to secrete phosphatases to the soil (Johansen, 1993; Eldridge and Greene, 1994). In our study, although cyanobacteria are a common component of the BSC (Table 1), we did not find higher nitrogen contents in soils associated to crusts (Table 3 and Fig. 4), contradicting our third prediction. These results partially agree with those of Castillo-Monroy et al. (2010), who did not find differences of ammonium between microsites, but found lower nitrate contents in soils under medium or well developed crusts. Grazing may have a long-term effect on nitrogen dynamics in restored areas, given that even when the biological soil crust has recovered, fixation of nitrogen remains low due to the loss of the specific lichen species with nitrogen fixing bacteria symbionts (Evans and Belnap, 1999; Lalley and Viles, 2008). The higher N content of soils not covered by crusts and under *L. cuneifolia* canopies (Fig. 4) suggests that the contribution of N to the soil caused by litterfall (Asner et al., 2003; Abril et al., 2009; Alvarez et al., 2009) exceeds that caused by the recovering soil crust N_2 fixation. However, the nutrient inputs to the soil during litterfall represent a recycling of nutrients that were already present in the ecosystem and were relocalized under *Larrea* canopies (Martínez Carretero and Dalmasso, 1992). Moreover, the effect of soil crusts on soil available nitrogen may not have been evident during the sampling period, at the end of the growing season. The nitrogen fixed by soil crusts may also be absorbed by neighboring plants during moisture peaks, without leaving a signature in the soil below the crusts. Additional studies would be needed in order to assess the existence and importance of N fixation by cyanobacteria in the Monte Desert, and the fate of the fixed N to other ecosystem components.

Soil crust cover and their spatial distribution may be used as an indicator of ecosystem recovery and health, but there are few examples of the use of soil crust abundance as an indicator of ecological condition in aridlands (Bowker et al., 2006). Other areas of the Monte Desert are subjected to different land use managements, including traditional pastoralism in state reserves (i.e., Telteca Natural and Cultural reserve), presumed to have a low impact on the ecosystem. Soil crusts in these areas are restricted to sites under shrubs that offer protection from animal trampling (i.e. the thorny shrub *Lycium tennuispinosum* and *Larrea* sp.) (Aranibar personal observation), suggesting that the current land use practices do not allow soil crust development and recovery. However, the effect of different land use practices (i.e., traditional or more intensive livestock grazing) on these ecosystems function and health has not been assessed. Our results suggest that biological soil crust cover and distribution may be useful indicators of ecosystem recovery and health in the central Monte Desert. However, further studies analyzing the relation between soil crusts characteristics and ecosystem thresholds and functions are needed in order to use soil crusts as indicators of ecosystem states, degradation, and recovery.

5. Conclusions

Our results clearly show the positive effect of domestic animal exclusion on the development of biological soil crusts in the central Monte Desert. Grazing exclusion modified the spatial distribution of black soil crusts, allowing them to grow in exposed areas instead of in protected sites under shrub canopies, as found in grazing areas. The recovery of soil crust communities in the reserve was not accompanied by increasing soil nitrogen content, suggesting that the ecosystem functions of soil crusts have not been recovered.

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