



Grazing effects on biological soil crusts and their interaction with shrubs and grasses in an arid rangeland

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Keywords

Cryptogams; Degradation; Livestock; Monte Desert; Spatial distribution; Species response curves; Thresholds; Watering points

Abbreviation

BSC = Biological soil crust

Nomenclature

Brummitt & Powell (1992)

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Introduction

Arid and semi-arid ecosystems are experiencing land degradation at different scales. This has led to increasing research aiming to detect early signs of degradation and predict potential undesirable transitions (Kefi et al. 2007). Non-irrigated arid ecosystems used for intensive or extensive grazing are some of the areas most at risk of desertification (Dawelbait & Morari 2012). Grazing disrupts vegetation organization patterns that unbalance the flow

Abstract

Question: Biological soil crust (BSC) communities can be used in the identification and monitoring of degradation. A key question is how landscape-scale live-stock disturbance and other local-scale factors influence BSC communities. We hypothesize that at the landscape scale, increased grazing pressure would lead to decreasing cover of BSC, but at the local scale biotic interactions between BSC and vascular plants would modulate the influence of grazing on BSC.

Methods: Spatially explicit sampling of vegetation composition and cover was conducted using point-sampling methods in digital images along two disturbance gradients in the central Monte Desert in Argentina.

Results: The grazing gradient is the major determinant of changes in the structure of plant communities at the landscape scale. Approximately 1500 to 2000 m from a watering point, there is a threshold in vegetation structure associated with a nonlinear trend of the BSC, herb, grass and shrub cover. Bivariate spatial patterns show attraction between BSC and shrubs in the vicinity of settlements, and repulsion between BSC and both grasses and litter in less disturbed sites.

Conclusion: Grazing affects BSC directly through trampling and indirectly by altering vascular plant communities that interact with the BSC communities. Both these effects vary according to the spatial scale being considered. The results evidence that understanding of livestock impact in structuring arid ecosystems requires an integrated analysis of BSC and vascular plant communities at different spatial scales.

of materials and organisms across the landscape (Alados et al. 2011). Much of the research has focused on the study of vascular plant patches, and less is known about the impact of grazing on microbiotic organisms growing on the ground surface (Bowker et al. 2006). It seems that microbiotic communities are more vulnerable to degradation than their associated vascular plant communities (Bowker et al. 2008).

Biological soil crusts (BSC) are specialized microbiotic communities composed of mosses, lichens, liverworts,

cyanobacteria and algae. They reach up to 70% of the living ground cover in some arid lands (Belnap et al. 2004), helping to stabilize the soil, regulate infiltration and run-off patterns, fix atmospheric N and C, retain moisture and in some cases facilitate vascular plant establishment (Bowker et al. 2011). Because of their importance in the functioning of desert ecosystems, it is highly relevant to understand the impact that grazing has on BSC communities and how this affects the process of desertification (Bowker et al. 2006; Eldridge et al. 2010).

Disturbance by livestock reduces lichen and moss cover and affects the functional role of BSC (Bowker et al. 2006). However, the interaction between vascular plants and microbiotic communities is complex, modulating the overall effect of disturbance on their diversity and cover. At low to intermediate levels of disturbance, bare patches provide suitable habitat for microbiotic communities that can compete with vascular plants for resources (Eldridge et al. 2010). In these cases, BSC and vascular plant cover are inversely related (Muscha & Hild 2006). In other cases, vascular plants have positive effects on BSC by ameliorating extreme environmental microclimate conditions and modifying locally available resources (Maestre et al. 2002; Zhang et al. 2013). For example, grasses appear to provide microsites that facilitate BSC establishment and development along water-centred grazing gradients (Williams et al. 2008; Jimenez Aguilar et al. 2009).

The composition and ecology of BSC has largely been overlooked in the context of degradation and desertification in South America (Büdel 2001; Toledo & Florentino 2009). In the southern Monte of Argentina it has been observed that grazing reduces BSC richness and cover, and that BSC are functionally relevant at retaining vascular plant seeds (Scutari et al. 2004; Bertiller & Ares 2011). In the central Monte of Argentina cattle have a negative impact on BSC communities that mainly develop under the protection of vascular plants in disturbed areas. Recovery of BSC communities is successful on sites where cattle have been removed for over 40 yrs (Gómez et al. 2012).

The process of desertification is increasing along the South American Arid Diagonal for anthropogenic and climate change reasons (Abraham et al. 2009). In this study, we examine the effect of grazing on the cover and spatial pattern of BSC at landscape and local spatial scales in the central Monte Desert in Argentina. Specifically, the following hypotheses were evaluated. (i) At the landscape scale, increased grazing pressure would lead to a decreasing cover of BSC because livestock disrupt BSC cover through trampling. (ii) At the local scale, grazing has an indirect effect on BSC cover and distribution through affecting vascular plant communities, and consequently biotic interactions.

Methods

Study area

The Argentinean central Monte Desert covers a wide northwest–southeast strip that is part of the South American Arid Diagonal. The study sites are located in the Telteca Natural Reserve (32°20'S, 68°00'W, 20 700 ha), central part of the Monte Desert. The climate is arid (total annual precipitation about 160 mm), with cold dry winters (mean temperature <10 °C) and warm rainy summers (mean temperature >20 °C). The dominant landscape is a gently undulating floodplain that presents sandy–silt soils mainly of aeolian origin (González Loyarte et al. 2000). Vegetation is relatively homogeneous in physiognomy and floristic composition (Abraham et al. 2009). Native woodlands of *Prosopis flexuosa* are confined to inter-dune valleys (González Loyarte et al. 2000). The lower stratum is a shrub layer composed mainly by *Larrea divaricata*, *Suaeda divaricata*, *Tricomaria usillo*, *Atriplex lampa*, *Capparis atamisquea* and *Lycium tenuispinosum*.

In these non-irrigated areas, people live in scattered livestock settlements supplied by hand-drilled water wells (Abraham et al. 2009). The water table lies between 6 and 15 m, and there are no surface water sources (Torres 2008). The economy is subsistence, without any livestock management strategy, neither in time (continuous grazing) or space (no fencing) (Torres 2008). The impact of livestock activity on vegetation is evident, with changes up to 15% in cover in a 2-km area around the settlements (Goirán et al. 2012). Unfortunately, there is a paucity of grazing intensity data for the area (Meglioli et al. 2013). Other human impacts are minor as there is no other economic activity in the area (Torres 2008).

Sampling of BSC and vascular plant cover and distribution

Vegetation surveys were performed in early summer along two transects extending from highly impacted settlements (La Primavera and Las Delicias settlements) to less disturbed sites. Sampling distances were ca. 10, 500, 900, 1500 and 2500 m from watering points. Landscape homogeneity and the minimal possible influence of confounding factors in the area (i.e. absence of surface water sources or other disturbance impacts), makes water-centred grazing gradients a suitable indirect approach to studying the effect of different grazing intensities on biological communities (Landsberg et al. 2003; Sasaki et al. 2008). We limited sampling sites to inter-dune spaces with a slight slope in order to minimize the influence of topography. Conditions are similar at both studied gradients since they are relatively close in the area. Our study

focused on two individual sites that we considered as representative of the study area since the area is relatively homogeneous in its climatic, physical and biological characteristics. This sampling strategy was chosen in order to achieve a high spatial resolution of BSC distribution at the local scale, according to the methods described below, although it confers a lower resolution at the landscape scale.

At each sampling site we mapped BSC and vascular plant cover in grids of 10×5 m divided into 200 square quadrats of 0.25 m^2 . We used high-resolution, image-based methods (Booth et al. 2008). Vertical images of each sampling quadrat were obtained using a digital camera (6.1 MP, focal length = 18–55 mm, equivalent to 27–82.5 mm format) positioned ca. 1 m above ground level, with the focal plane oriented parallel to the ground. Planar scale was provided through a rigid square frame that delimited the sampling quadrat. Digital images were processed in order to remove linear distortion along the measurement plane defined by the rigid frame. The resulting dimension of each image was 1500 pixels, in which each pixel corresponds to 0.3 mm in the field. This method has been shown to be successful in detecting vegetative cover changes due to grazing (Booth et al. 2008). Photographic methods have also been used for monitoring lichens, mosses and the BSC, indicating a close fit with other standard field monitoring methods (e.g. Vanha-Majamaa et al. 2000; Benavides & Sastre-De Jesús 2009; Jespersen 2013).

The spatial distribution of BSC and vascular plant cover was mapped through point-sampling of digital images using SamplePoint software, based on a 225-point systematic grid within each photograph (Booth et al. 2006). Sample points were classified into 17 different categories, including species of shrub (*Prosopis flexuosa*, *Geoffroea decorticans*, *Bulnesia retama*, *Lycium chilense*, *L. tenuispinosum*, *Condalia microphylla*, *Atriplex lampa*, *Suaeda divaricata*, *Ximenea americana*, *Capparis atamisquea*, *Grahamia bracteata* and an unidentified shrub), perennial grass, herb, BSC, litter and bare soil. This resulted in a database with 405 000 data points for presence/absence of the different species or vegetation group at each point. To estimate ground cover as a percentage of the total surface area, each sample quadrat was divided into nine sub-quadrats, and data within each sub-quadrat (25 data points) were averaged, resulting in a database with 16,200 data points that were used in the following statistical analyses.

We used hand lenses to perform floristic surveys of the crusts present within each sampling grid. Voucher specimens of the different lichen and moss species were collected for later taxonomic identification in the laboratory. The presence of cyanobacteria was checked using a compound light microscope, but they were not identified to

species level. Nomenclature follows Brummitt & Powell (1992).

Statistical analyses

We applied a detrended correspondence analysis (DCA) to identify general systematic changes in the composition and cover of the vegetation community. This method is adequate since we expected species composition to be mainly determined by the grazing gradient, and because the ordination axes can be interpreted in terms of the average SD of species turnover among sites and can be used to predict species distributions (Økland 1986; Jongman et al. 1995; Ejrnaes 2000; Rydgren et al. 2003). The matrix data consisted of the entire data set of percentage ground vegetation covers. Five vegetation variables were included in the analysis, i.e. BSC, herbs, grasses, *Lycium* spp. and all other species of shrub combined into a unique variable ('other shrubs'). Cover of *Lycium* spp. was considered an independent variable since it is the dominant shrub genus in the area. Detrending was performed by segment, and down-weighting of rare species was applied. The length of the first DCA axis was > 3 SD units, indicating that use of a unimodal model of species distributions is adequate (Jongman et al. 1995).

We also analysed the response of single vegetation groups to the disturbance gradient and to the ecological gradient defined by DCA axes. Ordination axes are surrogates of complex gradients of factors that vary more or less in relation to each other (Økland 1986). For this purpose, we applied a smoothing-fitting method based on locally weighted polynomial regressions (LOESS), using cover of vegetation groups as dependent variable and distance from watering point or DCA axis 1 as independent variable. These analyses allowed us to explore the major trends of variability in the cover of the different vegetation groups (whether linear, uni- or multimodal, or no trend). We selected the best smoothing parameters examining plots of the fit residuals vs the predictor variable, and we chose the model yielding no clearly discernible information on the fit residuals (Jacoby 2000).

Spatial pattern of vegetation groups

To test the influence of disturbance gradient on the spatial distribution of BSC and the changes in biotic interactions we conducted univariate and bivariate point pattern analyses (Wiegand & Moloney 2004). Second-order statistics such as the O-ring function characterize the number of points encountered in the neighbourhood of a ring of radius r centred on an arbitrary point of the pattern, allowing interpretation of spatial structure in terms of interactions (Wiegand & Moloney 2004).

First, we performed univariate analyses on each of the nine grids to examine whether spatial distributions of BSC along grazing gradients were random, clumped or regular. We chose a heterogeneous Poisson null model because we observed a heterogeneous density distribution of BSC points, corresponding to non-constant, first-order effects. We used a circular moving window estimator and selected a radius $r = 5$ and 10 cells, corresponding to 17 and 35 cm, respectively.

Bivariate O-ring statistics were performed to test the hypothesis that the distribution of BSC is independent of the distribution of vascular plants. We tested the relationship of BSC cover against the cover of grasses, shrubs and vascular plant litter cover. In addition, we tested the existence of the interaction between shrubs and grasses. To detect departure from independence, we applied a toroidal shift null model that indicates the existence of attraction or repulsion between the two patterns. The significant departure from univariate and bivariate null models was tested by constructing confidence envelopes with 999 Monte Carlo simulations (Wiegand & Moloney 2004).

Results

Biological soil crust composition

Biological soil crusts are composed of free cyanobacteria, coccoid green algae, lichens and mosses. All soil crusts analysed contain cyanobacteria, and the proportion of mosses in the crusts is minor. Dominant lichen species are *Collema coccophorum*, *C. tenax*, *Fuscopannaria* sp., *Heppia lutoso*, *Leptogium* sp., *Placidium squamulosum* and *Placynthium nigrum*. Mosses corresponded mainly to the species *Crossidium* sp. and *Tortula inermis*. A close inspection of the crusts made in the field with hand lenses did not indicate evident taxonomic differences along the studied gradients.

Vegetation variations along grazing gradients

The DCA ordination of sampling plots according to their vegetation composition indicates that the first and second axes represent the main compositional gradients in the data set, accounting for 27.2% and 19.7% of species variability, respectively (Fig. 1). Higher order axes explain less than 3% of species variability each, so they are considered unimportant. The first ordination axis is closely associated with the disturbance gradient, consecutively separating the centroids of sampling sites from sites close to watering points to less disturbed sites. The second ordination axis is mostly related to variability within the studied sites. High local-scale variability was expected, given the very small quadrat size used for vegetation sampling and the typical patch spatial pattern of vegetation in arid environments.

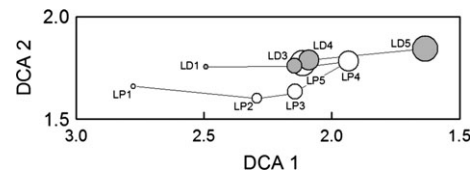


Fig. 1. Ordination diagram of the DCA of vegetation composition and cover for sampling plots. Vegetation trends are displayed as lines connecting the centroids of the successive sites, with increasing size of symbols corresponding to increasing distance from watering points. White and grey symbols correspond to the two grazing gradients analysed from the human settlements (La Primavera, LP and Las Delicias, LD) in the Telteca Reserve (Mendoza, Argentina).

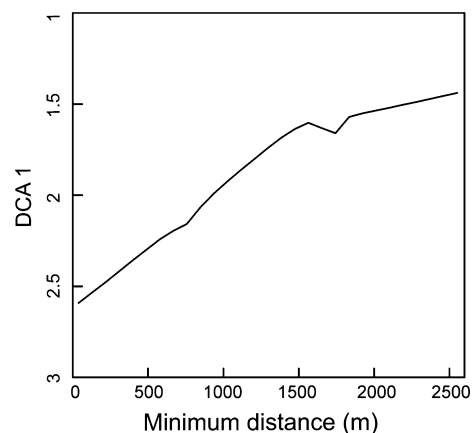


Fig. 2. Nonparametric smoothing showing the relationship between distance from watering points and sample plot scores of DCA1. The geographic gradient represents the changes in disturbance intensity as distance from settlements increases, and the scores of DCA axis represent an ecological gradient of floristic composition changes.

The nonparametric smoothing of the geographic distance from watering points against the ecological distance estimated by DCA1 shows that the relationship approaches a piece-wise model comprising two lines (Fig. 2), indicating a change in the rate of species turnover between 1500 to 2000 m from watering points. The relationship depicts that vegetation changes are faster at sites closer to watering points than at more distant and less disturbed sites.

Figure 3 shows the response pattern of vegetation groups along grazing and ecological gradients. BSC, herbs and 'other shrubs' (those not pertaining to the genus *Lycium*) show a similar pattern along the geographic gradient, with a peak in cover at ca. 500 m from watering points and lower cover further away. The cover of *Lycium* shrubs shows an indefinite response along the disturbance gradient. Grasses show relatively low cover near the watering points (approximately the closest 500 m), and a rapid cover increase further along the gradient, resembling a truncated unimodal curve (Fig. 3a).

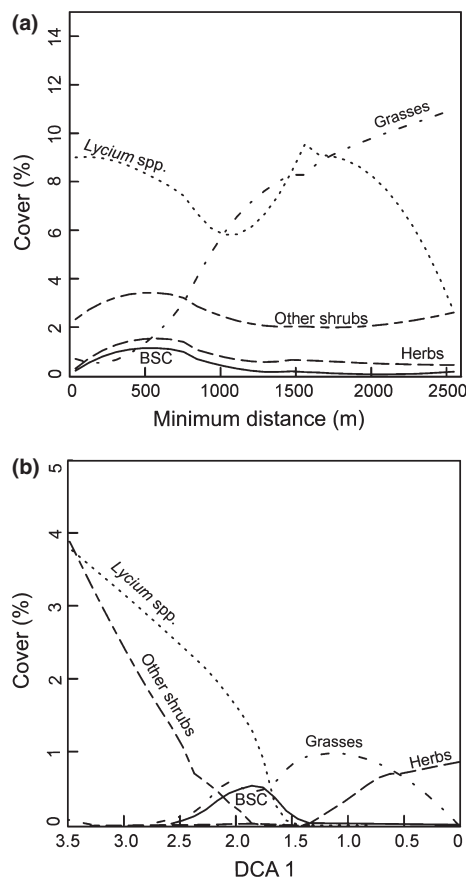


Fig. 3. Nonparametric smoothing showing the response pattern of cover of the different vegetation groups to: (a) disturbance gradient (distance from watering point) and (b) ecological gradient (sample plot scores of DCA1).

The patterns of response of vegetation groups to the ecological gradient depict their relative occurrence along the community gradient (Fig. 3b). *Lycium* and all other shrubs have the same location on the gradient, with a response pattern approaching a truncated distribution model, with their optima at the initial part of the community composition gradient. The behaviour of BSC suggests a unimodal shape of response change along the community composition gradient, with an optimum associated with a relatively high cover of *Lycium* spp. and an intermediate cover of grasses. Grasses exhibit a bimodal structure in the response curve, with one maximum at sites with high shrub cover and the other at sites with relatively low shrub cover. Herbs show increased cover at the end of the community gradient, coinciding with a high cover of grasses.

Spatial patterns

Univariate tests indicate an aggregated spatial arrangement of BSC at all six sampling sites where it was found with

relatively high cover (Fig. 4). The BSC occurred in clumps ranging from 7 cm (two cells) to 21 cm (six cells) along the gradient. The differences in aggregation scales seem not to be related to the grazing intensity gradient.

The bivariate O-ring statistic suggests interaction between shrubs and grasses at most of the studied sites (Table 1). The sites located at distances <1500 m from the watering point show, on average, more points of grasses closer to shrubs than would be expected under independence, thus indicating attraction. However, the distribution patterns of shrubs and grasses show repulsion with increasing distance from the watering point.

The relationships between distribution patterns of BSC and vascular components show a variety of responses (Table 1). At ca. 500 m from settlements, BSC shows a significant attraction to shrub cover, with an aggregation scale ≤ 70 cm. This is the site with highest cover of BSC (Fig. 3a). At distances > 1500 m from the watering point, the distribution of BSC was independent from shrubs. In contrast, the interaction between BSC and grasses and between BSC and vascular plant litter was determined through a random pattern near the settlements and a repulsion response on most of the sites further away from the watering point (distance >900 m).

Discussion

In arid areas, livestock rely on water from waterholes, generating gradients of decreasing grazing activity with increasing distances from animal concentration areas, such as corrals and watering points. Earlier studies describe decreasing linear responses of vascular plant diversity and cover along the grazing gradients, but more recent studies show thresholds in the patterns of vegetation changes and non-linear responses of species (Landsberg et al. 2003; Briske et al. 2005; Sasaki et al. 2008). However, few studies have included the responses of BSC communities, in spite of their importance as an integral component of desert environments (Belnap & Weber 2013).

As expected, our results show that the gradient from watering points is the major determinant of community structure at the landscape scale, determining changes in the relative cover of both BSC and vascular plants (Figs 1, 3a). Our survey design minimized the influence of confounding factors other than grazing impact along the water-centred gradients, thus the grazing gradient appears as the prevailing disturbance regime. In addition, our results show that the main ecological gradient is not linearly related to the geographic gradient, showing a break-point between 1500 and 2000 m from settlements (Fig. 2). According to Briske et al. (2005), an abrupt change in floristic composition along disturbance or natural gradients suggests the existence of an ecological threshold.

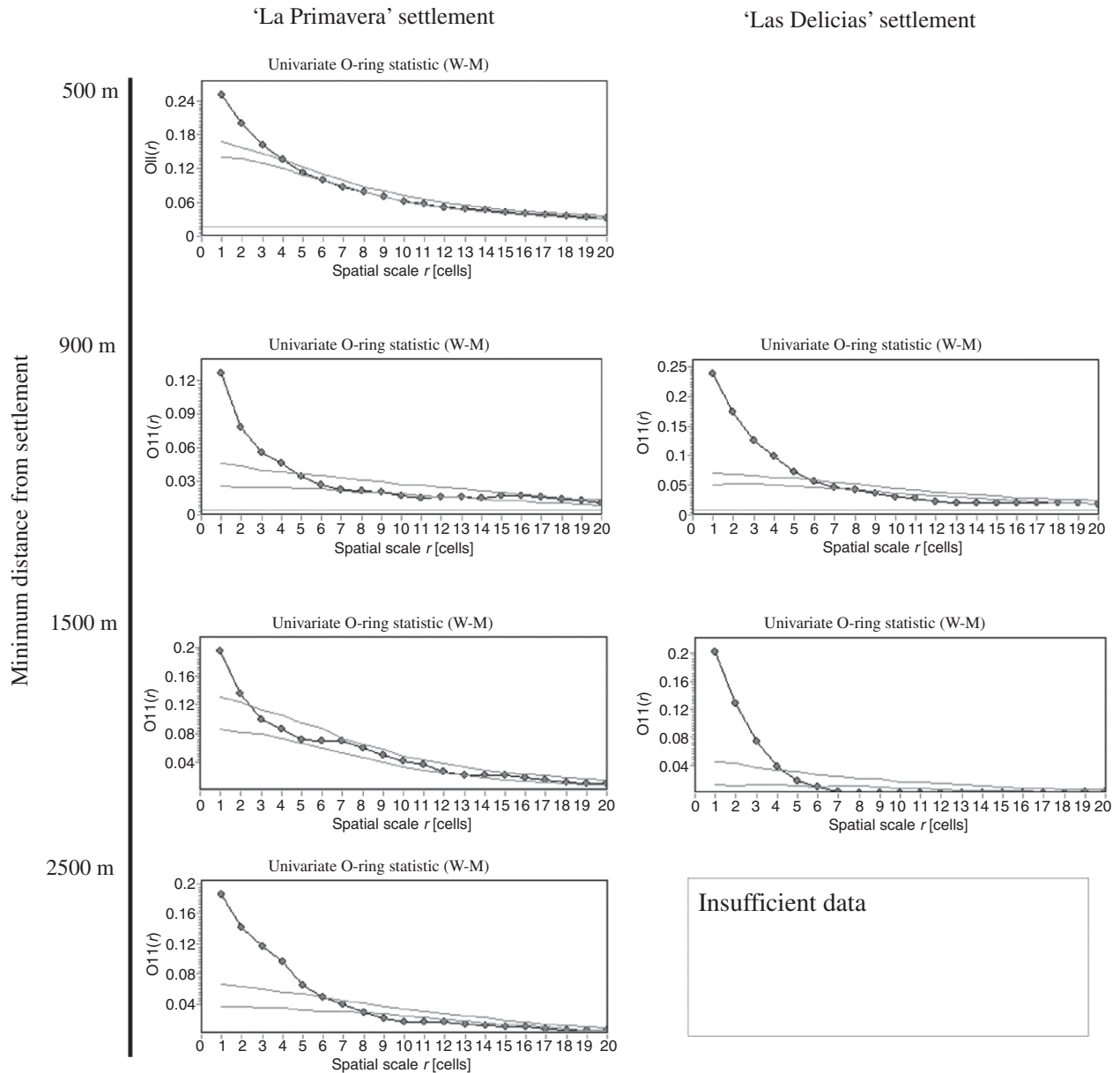


Fig. 4. Univariate point pattern analysis using the O-ring statistic (bold lines) in the sampling grids. Dashed lines indicate 95% confidence envelopes for the null model. Insufficient data indicate that the analysis could not be performed due to low cover of BSC in the study site.

Significant changes in vegetation cover within 2000 m of the watering points have been found from satellite imagery within the same area of our study (Goirán et al. 2012). Our study reinforces these results, indicating that changes in vegetation cover are associated with major community structural changes. Probably the threshold indicates differences between the vegetation communities developing within and outside the area of major influence of the grazers. A concentrated effect of grazing on the vegetation in small areas in the close proximity to watering points is typical of rangelands not subjected to animal management

strategies (Andrew & Lange 1986; Meglioli et al. 2013). The structural threshold we found between 1500 and 2000 m from watering points is mainly associated with an increasing dominance of grasses in the community (Fig. 3a,b). It is well known that selective grazing of livestock on grasses determines positive response curves for reduced grazing intensity (Williams et al. 2008; Wesuls et al. 2013). However, we found a bimodal pattern of grass response to the ecological gradient (Fig. 3b), suggesting that other factors might also be important for explaining the observed vegetation changes. Bimodal curves along

Table 1. Results of the bivariate point pattern analysis along a grazing disturbance gradient showing the scales of attraction and repulsion between the cover of different vegetation groups and the biological soil crust (BSC). Not available (na), indicates that the analysis could not be performed due to low cover or absence of BSC in the sites. Names of the sites as in Fig. 1.

	Distance from watering point (m)									
	10		500		900		1500		2500	
	LP1	LD1	LP2	LP3	LD2	LP4	LD3	LP5	LD4	
Shrubs × Grasses	Attraction (≤70 cm)	Attraction (≤70 cm)	Attraction (14–31 cm)	Random	Attraction (≤63 cm)	Repulsion (≤17 cm)	Random	Repulsion (≥56–70 cm)	Repulsion (≤63 cm)	
Shrubs × BSC	na	na	Attraction (10–70 cm)	Random	Random	Random	na	na	Random	
Grasses × BSC	na	na	Random	Repulsion (63–70 cm)	Random	Repulsion (17–56 cm)	na	na	Random	
Litter × BSC	na	na	Random	Repulsion (≤10 cm)	Random	Repulsion (42–70 cm)	na	na	Repulsion (≤17 cm)	

ecological gradients are usually related to mechanisms of species competitive interaction (Austin & Smith 1989). Our results of the bivariate analysis of the distribution of grass and shrub covers within grids (local scale) concur with this interpretation, showing a pattern of attraction on heavily grazed sites and of repulsion on moderate to less grazed sites (Table 1). Attraction is interpreted as a positive relationship between shrubs and grasses, probably related to the protection of grasses from being grazed beneath shrub canopies, and repulsion might be associated with the colonization of shrub interspaces by grasses as disturbance through grazing is relaxed.

The BSC are sensitive to trampling by livestock, thus reducing their cover as intensity of disturbance increases (Berkeley et al. 2005; Thomas & Dougill 2006, 2007). Williams et al. (2008) found exponential increases in the cover of cyanobacteria-dominated BSC as density of cattle decreased along a 500-m long, water-centred grazing gradient. To the best of our knowledge, our results are the first to provide insight into the responses of BSC cover along larger grazing gradients (2500 m), showing a non-linear response pattern with a peak at an intermediate level of grazing (Fig. 3a). This pattern has been commonly reported for several groups of vascular plants, and is interpreted to result from the ability of the species to tolerate intermediate grazing pressures, while plant decline at less disturbed sites is due to competitive interactions (Sasaki et al. 2008; Wesuls et al. 2013).

The distribution of increased BSC cover found at intermediate levels of disturbance (500 m from watering points) is closely related to the distribution of shrub cover, while at less disturbed sites further away from watering points, the distributions of BSC and shrubs are independent (Table 1). This suggests facilitation of BSC development beneath shrub canopies at relatively disturbed sites, while this interaction is not apparent at less disturbed sites. These results agree with those found in Kalahari

rangelands in showing that BSC development is restricted to sites beneath shrub canopies at high levels of disturbance, while interspaces and shrub subcanopies provide equally suitable habitat for BSC development under limited disturbance (Berkeley et al. 2005). They are also in agreement with the results of a previous study in the Argentinean central Monte Desert, which found that BSC communities are restricted to *Larrea* subcanopies at disturbed sites, but successfully recover in open spaces at sites where cattle have been removed for more than 40 yrs (Gómez et al. 2012).

The distribution of BSC cover shows patterns of repulsion towards grass and litter cover at sites with relatively low disturbance further than 900 m from watering points (Table 1). This result is in contrast to those studies that found a significant association between grasses and BSC due to modification of soil properties and buffering of abiotic stressors beneath tussocks (Bowker 2007; Read et al. 2008), but agrees with others that report the spatial segregation of BSC and grasses due to competition for natural resources or living space (Bowker et al. 2010; Peterson 2013). According to Bowker et al. (2010), occupation of more living space is the most important competitive factor structuring BSC communities, given that more space secures access to more resources. In addition, the observed negative spatial relationship between BSC and plant leaf litter can be related to BSC burial reducing the availability of light for photosynthesis (Berkeley et al. 2005; Thomas & Dougill 2007). Therefore, the diminished availability of bare soil due to both the increased cover of grasses and litter fall has a detrimental effect on the development of BSC at relatively undisturbed sites in our study area.

Conclusions

Our study analysed the changes in vascular plant and BSC in an arid ecosystem of central Argentina as a function of

major disturbance by livestock. The results suggest nonlinear responses of the different vegetation groups and the BSC to the disturbance intensity gradient. Development of grasses is possible in relatively highly impacted sites due to their being protected under shrub canopies. At these sites, development of BSC is also facilitated beneath shrubs. However, as livestock disturbance relaxes, it seems that increase in grass cover and plant leaf litter in interspaces between shrubs limits development of the BSC. Further studies should analyse the generality of our results for multiple ecological sites, and how the changes in vegetation patterns relate to processes that regulate the functioning of this desert ecosystem.

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Graphical Abstract

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Evidence suggests that the main biotic factors structuring biological soil crust communities in areas disturbed by grazing are the presence of shrubs and grasses, with opposite patterns across the gradient. There is a relationship of attraction between BSC and shrubs in the vicinity of the settlements, and of repulsion between BSC and both grasses and litter in less disturbed sites.