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Grazing pressure interacts with aridity to determine the development and diversity of biological soil crusts in Patagonian rangelands

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Author contributions

SVA, GRO, FTM and LY conceived the work and design the field experiment. SVA, GRO and LY performed the field experiment and collected data. SVA carried out the laboratory work, analyzed data and wrote the first version of the manuscript. SVA, GRO, FTM and LY equally contributed to the definitive version of the paper.

Conflict of interest

The authors declare no conflict of interest.

Abstract

Grazing is directly related to land degradation and desertification in global drylands. Grazing impacts on vascular plants, reasonably well known, depend on its intensity and are modulated by local aridity conditions. However, we do not know how the interplay of grazing intensity and aridity affect biocrusts, topsoil assemblages dominated by cyanobacteria, lichens and mosses that provide key ecosystem services in drylands. Here we determined how grazing affects biomass, total cover and richness of biocrust structural types across a regional aridity gradient in the Patagonian steppe. On average, grazing by sheep reduced biocrust biomass, total cover and richness of structural types by 55%, 90% and 59%, respectively. In general, high grazing pressures had a larger impact on biocrusts than moderate or light grazing pressures. For example, biocrust cover was reduced by 85%, 89% and 98% by light, moderate and high grazing pressures, respectively. Although a slightly different response to grazing was observed under low aridity conditions, these more benign climatic conditions did not compensate for the negative effects of trampling by domestic animals on biocrusts. Nonetheless, estimated biocrust recovery rates under medium aridity conditions were faster than previously thought: it took 24, 18 and 58 years to double biocrust biomass, total cover and richness of structural types. Sheep cannot be just removed in Patagonian rangelands because the production of meat and wool represents the main local economic activity. But landowners must consider our results to protect the ecosystem functions and services provided by biocrusts for future generations to come.

Introduction

Human activities are causing unprecedented changes in the structure and functioning of terrestrial ecosystems worldwide (Steffen *et al.*, 2015). Grazing by domestic animals is the most extensive land use on Earth (Eldridge *et al.*, 2017b). Along history, the production of meat, milk, eggs, leather, wool or honey has played a pivotal economical role in numerous societies (Sala *et al.*, 2017). However, high grazing intensities by domestic animals are directly related to land degradation processes (Asner *et al.*, 2004), which reduce the ecological health and promote the loss of essential services provided by ecosystems (Eldridge & Delgado-Baquerizo, 2017). Grazing by domestic animals modifies the abundance, richness and diversity of plants (Bisigato & Bertiller, 1997; Eldridge *et al.*, 2018; Hanke *et al.*, 2014; Oñatibia *et al.*, 2018), wild animals (Wallis de Vries *et al.*, 2007) and soil microorganisms (Eldridge *et al.*, 2017b; Olivera *et al.*, 2016), and alters multiple soil physicochemical properties that determine soil health (Eldridge *et al.*, 2017a). Overgrazing is also considered to be a major driver of desertification in terrestrial ecosystems (Cherlet *et al.*, 2018). Finding an optimal balance between animal production and the maintenance of the capacity of ecosystems to provide valuable services and habitat for wildlife is therefore a primary goal to manage rangelands.

Grazing is the main land use, and a key economic activity, in global drylands (Asner *et al.*, 2004), which occupy 45% of the Earth´s terrestrial surface (Prăvălie, 2016) and are home to more than 38% of the human population (Reynolds *et al.*, 2007). Grazing has severe impacts on biological communities in drylands, where recovery rates after disturbances are slower compared to more mesic ecosystems (D'Odorico *et al.*, 2013). These impacts depend on grazing intensity, but their consequences are modulated by local aridity conditions (Mallen-Cooper *et al.*, 2018). However, thus far, the interactive effects of grazing pressure and aridity conditions remain poorly studied in drylands (Oñatibia *et al.*, 2018). Moreover, while grazing effects on plants and soil processes have been extensively addressed, impacts on soil communities such as biocrusts, topsoil assemblages formed by cyanobacteria, other bacteria, archaea, algae, fungi, lichens and mosses that grow intimately associated with soil particles (Belnap *et al.*, 2016), have received comparatively less attention (Zaady *et al.*, 2016). To the best of our knowledge, only one study explores the effects of both grazing and aridity on biocrusts (Mallen-Cooper *et al.*, 2018). This is surprising because biocrusts cover approximately 12% of Earth´s terrestrial surface (Rodriguez-Caballero *et al.*, 2018) and occur in all biomes, although they are particularly abundant in sparsely vegetated ecosystems such as drylands (Bowker *et al.*, 2016). Considered to be the "living skin" of soils in drylands (Bowker *et al.*, 2018), biocrusts play key ecological roles: they stabilize soils, thus reducing rates of wind erosion and dust particle production (Belnap *et al.*, 2007), regulate soil surface temperature (Couradeau *et al.*, 2016), drive soil C (Grote *et al.*, 2010), N (Torres-Cruz *et al.*, 2018) and P (Baumann *et al.*, 2018) cycles, control runoff-infiltration dynamics (Chamizo *et al.*, 2016), and modulate the establishment of plants (Ferrenberg *et al.*, 2018). Although well adapted to harsh environmental conditions (extreme temperatures or UV radiation), biocrusts are highly susceptible to compressional forces, such as those generated from vehicle traffic associated with production or recreation activities. In recent years, various studies have demonstrated that biocrusts are negatively affected by several land uses such as agriculture (Zaady *et al.*, 2013), recreation (Ferrenberg *et al.*, 2015) and, especially, grazing (Zaady *et al.*, 2016).

The production of sheep in arid and semiarid steppes of the Argentinian Patagoni is carried out all year round. The introduction of sheep more than 100 years ago has led to profound changes in plant communities (Cheli *et al*., 2016; Oliva *et al*., 1998) and soil processes (Chartier *et al*., 2011). However, the effect of sheep grazing on biocrusts in these rangelands has not received much attention yet. In fact, only a few studies have assessed the effects of grazing on biocrusts in other Argentinian rangelands (García *et al*., 2015; Gómez *et al*., 2012; Tabeni *et al*., 2014). In South America, besides Argentina, only a few studies focused on biocrusts have been carried out in Chile (Baumann *et al.*, 2018), Bolivia (Flakus & Kukwa, 2014), Venezuela (Núñez Ravelo, 2014) and Ecuador (Castillo-Monroy *et al.*, 2016). Indeed, South America represents the largest geographical gap in the study of biocrusts (Bowker *et al*., 2016).

The goals of this study were to (a) assess the interactive effects of local aridity conditions and grazing intensity on biocrust development and diversity in Patagonian rangelands, and (b) evaluate recovery rates of biocrusts after grazing abandonment. In this field study, we estimated the effects of sheep grazing intensity on biocrusts in three sites located across a regional aridity gradient in the Patagonian steppe, whereas recovery rates after grazing abandonment were assessed in one site. We hypothesized that (1) grazing intensity will gradually reduce biocrust biomass and total cover, also modifying the richness and relative abundances of biocrust structural types, through direct (trampling) and/or indirect (shifts in vegetation and litter) effects mediated by the presence of sheep, (2) the effects of grazing on biocrusts will be larger under more arid conditions, and (3) recovery rates of biocrusts after grazing abandonment will range from decades to centuries (Belnap, 2003).

Materials & Methods

Study site

In summer 2017, we conducted a field survey in three sites located across a regional aridity gradient in the Chubut Province (Argentina) (Figure S1). The sites are located at a similar latitude (~45° S) but at different distances from the Andean Mountains, which generates a strong longitudinal precipitation gradient (Austin & Sala, 2002) (Table S1). Although there is a difference in altitude of 150 m among sites, all of them show similar radiation values and temperatures; radiation or temperature differences among sites are negligible relative to differences in precipitation. All sites belong to the Patagonian Phytogeographic Province (Oyarzabal *et al.*, 2018). The low aridity site (Low) is a grass steppe representative of the

Subandean District and dominated by *Festuca pallescens*. The medium aridity site (Medium) is a typical grass-shrub steppe of the Occidental District with *Pappostipa speciosa*, *Pappostipa humilis*, *Poa ligularis*, *Poa lanuginosa*, *Azorella prolifera* and *Adesmia volckmannii* as main plant species. The high aridity site (High) is a semi-desert area of the Central District dominated by *Nassauvia glomerulosa*, *Nassauvia ulicina* and *Chuquiraga aurea*. Rangelands in the study area are mostly used for wool and meat production, and have been grazed by sheep for more than 100 years (Oñatibia *et al.*, 2018). At all sites, grazing management is extensive, in large continuously grazed (all year round) paddocks (Oñatibia *et al.*, 2018).

Experimental set up: aridity × grazing experiment

Within each site, we set up four 50 × 50 m plots across a grazing gradient, from grazing exclosures (EX, established on average 26 years ago) to high-grazed areas (HG, 0.21 – 1.00 sheep ha^{-1}), including light (LG, 0.11– 0.40 sheep ha^{-1}) and moderate (MG, 0.14 – 0.75 sheep ha^{-1}) grazing conditions (Table S1). Plots were selected from the grazing pressure estimated as the quotient between the average forage consumption, obtained from the stocking rate (average of last 20 years), and the average aboveground net primary productivity (estimated from remote sensing MODIS imagery), weighed with a local index that considered the fecal pellets density. In this way, grazing pressure estimation captures the effect of the historical stocking rate of each paddock and the local and more recent grazing intensity in the measured area (Oñatibia *et al.*, 2018). We thus surveyed a total of 12 different conditions to assess the interactive effects of aridity (three levels) and grazing (four levels) on biocrusts. Because of the particular factorial design, with no combination of treatments truly replicated at the scale of plots, the generalization and extrapolation of our results have to be taken with caution.

Experimental set up: recovery rates experiment

In the medium aridity site, we monitored 50 × 50 m plots located in grazing exclosures established 47 and 66 years ago (in 1972, EX72, and 1954, EX54) (Table S1). These exclosures, along with another established 23 years ago (in 1996, EX96; EX plot in the aridity × grazing experiment), enabled us to have a temporal sequence of grazing abandonment. Because most part of the medium aridity site has a light-to-moderate grazing intensity management (Oñatibia & Aguiar, 2016), we used data from LG and MG conditions of the aridity × grazing experiment to obtain mean values of local grazing pressure effects ("grazing condition", GR). We then compared these data to those obtained in exclosure areas (EX96, EX72 and EX54) to assess recovery rates of biocrusts after grazing abandonment.

Data collection and preparation

In each plot we established four 50 m long transects, 10 m apart from each other, with the same orientation and slope. In each transect, we placed 25 successive 1.5 × 1.5 m quadrats that were used to visually determine the cover of four biocrust structural types: light cyanobacteria-, dark cyanobacteria-, lichen- and moss-dominated biocrusts (LC, DC, LI and MS, respectively). We added up cover data of biocrust structural types to obtain total biocrust cover (BC). In the same quadrats, we also estimated the cover of every perennial plant species, and the cover of bare soil (BS) and litter (LT). By merging cover data of perennial plant species, we obtained total plant cover (PC). We then estimated the area of covered soil (CS) as the sum of LT and PC (Table S1).

Sampling and laboratory procedures

In each plot, we took representative samples of biocrusts in 5 locations separated from each other at least by 20 m. After a general visual inspection, samples were randomly taken in open, biocrust-dominated areas of the plot, avoiding areas just below perennial plants. Samples were carefully taken down to ~1 cm deep by means of a dough steel scraper, and kept at dark and dry conditions in sterile, plastic 10-cm-Petri dishes. In the laboratory, we used a Zeiss Stemi 2000-C stereo-microscope to identify bryophytes and lichens. Lichen specimens were classified using the book by Pérez de la Torre (2008) and mosses were identified following Rosentreter *et al.* (2007) (Table S2). Cyanobacteria were not identified. Aerial content of chlorophyll *a* (chl *a*) was determined as a proxy of biocrust biomass (Fernandes *et al.*, 2018). Briefly, seven 0.4-cm-diameter cores were randomly taken in each Petri dish, mixed, and extracted in 95% ethanol at 4 ºC in the dark for 24 h. Extracts were then centrifuged (5000 rpm, 5 min, 4 ºC) and chl *a* concentrations determined according to Ritchie (2008) in a Shimadzu UV-1700 spectrophotometer.

Data analyses

We calculated the richness of biocrust structural types (BR) using the cover data of the four different biocrust types visually estimated. To estimate BR, as well as plant richness, Shannon evenness and Shannon diversity (Table S1), we used the “vegan” package (Oksanen *et al.*, 2018) written for R (R Development Core Team, 2017).

We analyzed the interactive effects of aridity and grazing (aridity × grazing experiment), or the effect of time since grazing abandonment (recovery rates experiment), on chl *a* using analysis of variance (ANOVA) models. Diagnostic plots did not reveal apparent deviations from homoscedasticity and normality in these models. ANOVA models were fitted using R, while Tukey´s HSD postdoc tests were computed using the “emmeans” R package (Lenth, 2018).

To analyze the interactive effects of aridity and grazing on BC and BR, as well as on LC, DC, LI and MS cover (aridity × grazing experiment), we used generalized additive models for location, scale and shape (GAMLSS models). GAMLSS models are recommended for highly skewed and/or kurtotic dependent variables, because they extend basic statistical models allowing flexible modelling of over-dispersion, excess of zeros, skewness and kurtosis in the dataset (Rigby & Stasinopoulos, 2005). GAMLSS models were computed using the “gamlss” R package (Rigby & Stasinopoulos, 2005). We fitted GAMLSS models for each dependent variable using aridity and grazing conditions as independent categorial variables (except in the case of DC and LI cover because we only found DC or LI biocrusts in the low aridity site) and PC and LT as independent continuous variables. In these models, aridity and grazing were treated as fixed categorical factors, PC and LT as fixed continuous factors, and quadrats (25) nested within transects (4) were treated as random effects. The model optimization process was as follows. First, we rescaled our dependent variables to 0 – 1 dividing each value by 100 (except BR). Second, we chose the best type of distribution (family) for each dependent variable using the fitDist() function. Then, we fitted the best model for each dependent variable using the stepGAICAll.A() function. We used the generalized Akaike information criterium (AIC) to compare and select among several models (Rigby & Stasinopoulos, 2005). We considered that ΔAIC values higher than 2 indicated significant differences between models. Likelihood ratio tests (LRT) were used to test for differences between chosen and null models. We tested for the significance of single and interaction terms (independent variables) in best-fitted GAMLSS models using LRT results. Finally, differences in the effects of fixed categorical variables on dependent variables after fitting GAMLSS models were assessed by comparing t-values to a random normal distribution. Diagnostic plots were used to visually assess potential deviations from homoscedasticity and normality of residuals after fitting GAMLSS models.

Temporal differences in BC and BR, as well as in LC and MS cover after grazing abandonment (recovery rates experiment), were also tested using GAMLSS models. We tested the effects of PC and LT as independent continuous variables, and the time after grazing abandonment as the only independent categorical variable. In these models, time after grazing abandonment was treated as a fixed categorical factor, PC and LT were treated as fixed continuous factors, and quadrats (25) nested within transects (4) were treated as random effects.

To determine recovery rates after grazing abandonment in the medium aridity site, we calculated average slopes across the four time points studied (0, 23, 47 and 66 years).

To ecologically interpret the impact of different grazing intensities at each site (aridity × grazing experiment), or the ecological importance of time on recovery rates of biocrusts after grazing abandonment in the medium aridity site (recovery rates experiment), we calculated effect sizes (as Cohen´s d values) and confidence intervals (Nakagawa & Cuthill, 2007). We present ecological effects of different grazing intensities in the three sites relative to EX conditions (aridity × grazing experiment), whereas we show the ecological effect of time after grazing abandonment in the different temporal exclosures relative to the GR condition (recovery rates experiment). Effect size calculations were computed using the "effsize" R package (Torchiano, 2017).

All plots were built in R using the package "ggplot2" (Wickham, 2009).

Results

Aridity × grazing experiment

Overall, grazing by sheep in Patagonian rangelands reduces biocrust biomass and total cover, but also decreases the richness of biocrust structural types and modifies their relative abundances (Figure 1 & 2). In the medium and high aridity sites, the higher the density of domestic animals, the deeper the changes are, although a different pattern emerges in the low aridity site, which generally shows the greatest grazing impacts.

The aridity × grazing interaction had a significant effect on chlorophyll *a* (chl *a*) ($p < 0.05$) (Table S3), indicating a different response of biocrust biomass to grazing intensity at each site (Figure 1A). Exclosure (EX) treatments always showed significantly higher chl *a* values than any other grazing level at all sites ($p < 0.05$) (Figure 1A). In the high aridity site, we observed a decrease of chl *a* across the grazing gradient, with the high-grazed (HG) treatment showing significantly lower chl *a* values than any other grazing condition (p <

0.05) (Figure 1A). A similar decrease in chl *a* was evident across the grazing gradient in the medium aridity site, but differences were not significant among light-grazed (LG), moderate-grazed (MG) and HG treatments (Figure 1A). In the low aridity site, the reduction in chl *a* was significantly higher in the MG than in LG or HG treatments ($p < 0.05$) (Figure 1A). The effect of grazing on biocrust biomass increased with grazing intensity in the medium and high aridity sites, and HG conditions showed the largest effects on chl *a* (Figure 1B). However, in the low aridity site MG conditions caused the largest effects on biocrust biomass (Figure 1B). Generally, the low aridity site showed the greatest grazing effects on chl *a* regardless of the grazing intensity (Figure 1B).

The aridity × grazing interaction did not have a significant effect on the total biocrust cover (BC). But we found a significant grazing effect on BC at all sites ($p < 0.05$) (Tables S4 & S5). BC was significantly higher in EX treatments than in any other grazing level at all sites ($p < 0.05$) (Figure 1C), LG and MG conditions showed similar effects on BC, and HG conditions showed significantly lower BC values than any other grazing treatment ($p < 0.05$) (Figure 1C). Compared to EX conditions, we found a mean reduction in BC of 85%, 89% and 98% for LG, MG and HG, respectively. BC negatively responded to litter cover (LT) in exclosures ($p < 0.05$) (Table S6). Irrespective of grazing conditions, total plant cover (PC) negatively determined BC in the low aridity site, whereas positively in the high aridity site ($p < 0.05$) (Table S6). The effect of grazing on BC clearly increased across the grazing gradient at all sites, with HG conditions causing the largest effects, especially in the high aridity site (Figure 1D). Irrespective of grazing intensities, the low aridity site showed the greatest grazing effects on BC, the high aridity site showed intermediate effects, and the medium aridity site showed the lowest effects (Figure 1D).

We did not observe a significant interaction of aridity and grazing on the richness of biocrust structural types (BR). But grazing had a significant effect on BR at all sites ($p < 0.05$) (Tables S4 & S5). We found significant differences in BR values among the four grazing conditions ($p < 0.05$) (Figure 2A). Grazing reduced BR by 43%, 54% and 80% for LG, MG and HG treatments, respectively. The effect of grazing on BR intensified across the grazing gradient in the medium and, particularly, in the high aridity site (Figure 2B). By contrast, in the low aridity site MG conditions caused the most profound effects on BR. Again, the low aridity site showed the greatest grazing effects on BR at LG and MG conditions (Figure 2B).

We did not detect a significant aridity × grazing interaction on light cyanobacteria-dominated biocrusts (LC). But we observed a significant grazing effect on LC at all sites ($p < 0.05$) (Tables S4 & S5). Exclosures showed significantly higher LC cover than any other grazing treatment, and LG treatments showed significantly higher values than MG or HG conditions ($p < 0.05$) (Figure S2A). LC negatively responded to LT in EX treatments at all sites ($p < 0.05$) (Table S6). Irrespective of grazing conditions, PC negatively and positively determined LC in the low and high aridity sites, respectively ($p < 0.05$) (Table S6). Generally, the effect of grazing on LC intensified across the grazing gradient, especially at high aridity conditions (Figure S2B). The high aridity site showed the largest grazing effects on LC, the low aridity site showed intermediate impacts, and the medium aridity site showed the lowest effects (Figure S2B).

We observed dark cyanobacteria-dominated biocrusts (DC) in the low aridity site only (Figure S2C). Grazing had a significant effect on DC cover in this site ($p < 0.05$) (Tables S4 & S5). DC cover was significantly higher in the exclosure relative to MG or HG conditions ($p < 0.05$) (Figure S2C), and the MG treatment showed significantly higher DC cover values than the HG condition ($p < 0.05$) (Figure S2C). Irrespective of grazing intensities, we found a significant, negative effect of PC on DC ($p < 0.05$) (Table S6). The grazing effect on DC was large at MG and HG conditions (Figure S2D).

Lichen-dominated biocrusts (LI) were found in the low aridity site only (Figure S3A). We did not detect any significant factor associated with LI cover (Tables S4 & S5), but we found higher LI at HG conditions relative to MG or EX conditions. The effect of HG on LI, although low, was positive (Figure S3B).

We did not find a significant aridity × grazing interaction on moss-dominated biocrusts (MS). But grazing had a significant effect on MS at all sites ($p < 0.05$) (Tables S4 & S5). We found a significantly lower cover of MS in HG conditions than under any other grazing treatment ($p < 0.05$) (Figure S3C). However, we did not find differences in MS cover among EX, LG and MG conditions. In general, the effect of grazing on MS intensified across the grazing gradient at all sites, with the HG treatment causing the greatest effects, especially under low and high aridity conditions, although the effect of MG conditions on MS cover was positive but low at high aridity conditions (Figure S3D).

We found differences in the relative abundance of biocrust structural types among grazing treatments within sites (Figure 2C). In the medium and high aridity sites, where only LC and MS were observed, we observed increasing high relative abundances of MS across the grazing gradient, although LC clearly dominated, especially at HG conditions. Under low aridity conditions, we also found DC and LI. In this site, the highest relative abundance of LI was found in the HG treatment, whereas the highest relative abundance of DC was found in the exclosure, MS were especially important in the LG treatment, and LC showed lower relative abundances in EX and LG compared to MG and HG treatments.

Recovery rates experiment

Biocrusts positively responded to the abandonment of grazing in the medium aridity site, with an evident increase in total cover and a palpable growth estimated through chl *a* content. A clear increase in the richness of biocrust structural types along time was also observed (Figure 3 & 4). Recovery rates of biocrusts were relatively fast: it took only 24, 18 and 58 years after grazing abandonment to double chl *a* content, biocrust cover and richness of biocrust structural types, respectively.

Time after grazing abandonment significantly determined chl *a* at the medium aridity site ($p < 0.05$) (Table S3). All temporal exclosures showed significantly higher chl *a* contents than the grazed area ($p < 0.05$) (Figure 3A). However, we did not observe significant differences between the 1972 (EX72) and 1954 exclosures (EX54) (Figure 3A). The effect of time on biocrust biomass after grazing abandonment increased along the chrono-sequence (Figure 3B).

Time after grazing abandonment significantly determined BC and BR at this site ($p < 0.05$) (Tables S7 & S8). All exclosures showed significantly higher BC (Figure 3C) and BR (Figure 4A) values that the grazed condition ($p < 0.05$), although we did not see significant differences between the 1996 exclosure (EX96) and the EX72 treatment, or between EX72 and EX54 treatments, for BC and BR, respectively. The effect of time since grazing abandonment increased along the chrono-sequence for both BC (Figure 3D) and BR (Figure 4B).

We observed that time after grazing abandonment had a significant effect on LC cover values at the medium aridity site ($p < 0.05$) (Tables S7 & S8). LC cover values were lower in the grazed treatment than in any exclosure (Figure S4A). However, we did not find significant differences between the grazed area and EX72 treatments. The EX96 treatment showed higher LC values than the EX54, and significantly higher than the EX72 ($p < 0.05$) (Figure S4A). The effect of time on LC after grazing abandonment was large at all exclosures except at EX72 (Figure S4B).

We found that time after grazing abandonment had a significant effect on MS cover values at this site ($p < 0.05$) (Tables S7 & S8). The highest and lowest MS cover values were found in the EX54 and grazed treatments, respectively (Figure S4C). The effect of time on MS cover values since grazing abandonment clearly increased along the chrono-sequence (Figure S4D).

A change in the relative abundance of biocrust structural types along time after grazing abandonment was evident in the medium aridity site (Figure 4C). In grazed and EX96 treatments, LC clearly showed high relative abundances, but MS were more abundant in EX72 and EX54 treatments.

Discussion

This study provides strong evidences that grazing reduces the biomass, total cover and richness of structural types of biocrusts across a regional aridity gradient in Patagonian rangelands (Figures 1 & 2). Heavily grazed fields experience larger reductions in biocrusts than light- or moderate-grazed paddocks. Consequently, there is a direct relationship between grazing intensity and biocrust degradation in these rangelands. Although a slightly different response to grazing intensity is detected in the low aridity site, where the impacts of highly-grazed conditions on biocrust biomass seem to be partially buffered compared to lightly-grazed fields, we observe that the greatest effects of grazing on biocrust assemblages, irrespective of its intensity, occur under the lowest aridity condition evaluated. Overall, our results indicate that (1) high grazing intensities have dramatic consequences for biocrusts in Patagonian rangelands under different aridity conditions, and (2) low aridity conditions are not enough to fully compensate for the pernicious effects of grazing on biocrusts. Nonetheless, grazing abandonment in the medium aridity site leads to palpable increases in biocrust biomass, total cover and richness of structural types in ~20 years, which means that natural recovery rates after grazing abandonment are faster than previously thought (Figures 3 & 4). In short, our results demonstrate that grazing intensity interacts with local aridity conditions to determine the development and diversity of biocrusts in Patagonian rangelands of Argentina.

Grazing interacts with aridity to determine biocrust biomass, cover and richness of structural types

During last decades, multiple studies conducted in USA, Australia, Israel, Mexico and China have reported negative impacts of grazing on biocrusts (Zaady *et al.*, 2016). In line with these studies, we observed a clear negative response of biocrusts to sheep grazing in our three Patagonian sites. Direct trampling unquestionably damages biocrusts by pulverizing them, especially when they are dry (Ferrenberg *et al.*, 2015). When the soil is disturbed in drylands, there is a production of fugitive particles (Belnap *et al.*, 2009). These soil particles can move at even low wind speeds (Belnap *et al.*, 2007), thus burying whole pieces of biocrusts, particularly if they are lichen- or moss-dominated. Once far from the soil surface, photosynthetic components of biocrusts able to colonize physically unstable sedimentary surfaces, especially cyanobacteria (Garcia-Pichel & Wojciechowski, 2009) and mosses (Antoninka *et al.*, 2016), cannot continue fixing carbon and die.

Our work extends previous results of field experiments that focused on the effects of domestic animals comparing grazed *vs.* ungrazed areas in specific sites of Argentina (Bertiller & Ares, 2011; García *et al.*, 2015; Gómez *et al.*, 2012; Tabeni *et al.*, 2014). Our work also widens the knowledge of the biology and ecology of biocrusts in South America, thus fulfilling an existing geographical gap (Bowker *et al.*, 2016). Our observations of a gradual decrease in the total biocrust cover (BC) and richness of biocrust structural types (BR) across the grazing gradient regardless of aridity conditions are similar to those reported by Concostrina-Zubiri *et al.* (2014) and Eldridge *et al.* (2015), who found a reduction in BC across grazing gradients in drylands of Mexico and Australia, respectively. However, and contrary to our expectations, biocrust biomass responses to grazing intensity were similar under light-grazed (LG) and high-grazed (HG) conditions in the low aridity site. At HG conditions we observed a high relative abundance of lichen-dominated biocrusts, and even a positive effect of HG conditions on lichens in this site. Under LG conditions we observed a high relative abundance of moss-dominated biocrusts in the low aridity site. Crustose and squamulose morphologies, such as those found in this site, can provide lichens with partial resistance to mechanical impact (Concostrina-Zubiri *et al.*, 2014; Jiménez Aguilar *et al.*, 2009). And mosses can recover from trampling by sheep relatively fast if damage is only partial because, as poikilohydric organisms, they have developed specialized leaf structures to collect water from many available sources (Pan *et al.*, 2016). Lichen- and moss-dominated biocrusts present higher chl *a* contents by surface unit than cyanobacteria-dominated biocrusts (Lan *et al.*, 2012). Therefore, biocrust biomass increases under low aridity conditions at LG, and even HG, conditions relative to moderate-grazed (MG) conditions.

The grazing effect on BC and BR increased across the grazing gradient at medium and high aridity sites. In other words, a continuous moderate-to-high grazing pressure in these rangelands generates a larger impact on biocrust assemblages than a light grazing intensity, especially under high aridity conditions. Mallen-Cooper *et al*. (2018) found evidences that the combination of increasing aridity and intensified livestock grazing reduces biocrust total cover and functional diversity in Australian drylands, with direct effects on ecosystem functioning. Our findings have direct implications for the management of the area, where ecosystem provisioning services to enhance meat and wool production needs to be maximized while the impacts on ecosystem regulating services reduced (Oñatibia *et al.*, 2015). Biocrusts with a good ecological health can fix up to 100 kg N ha^{-1} y^{-1} (Barger *et al.*, 2016). Undamaged biocrusts also accumulate soil P (Baumann *et al.*, 2018). These regulating services, which provide good habitat conditions for plant seeds to germinate (Ferrenberg *et al.*, 2018), can be reduced at moderate-to-high grazing intensities, as recently reported elsewhere (Eldridge & Delgado-Baquerizo, 2017). This decline will inevitably impact on provisioning ecosystem services, such as the supply of forage, thus decreasing meat and wool production (Oñatibia *et al.*, 2015) and jeopardizing the economic development of the region.

Contrary to our expectations, the effect of grazing on biocrust biomass and, especially, on BR was greater at MG conditions relative to LG and HG conditions at the low aridity site. LG and HG plots showed a higher plant cover compared to the MG treatment in this site. A study carried out in Spanish drylands shows that plant cover partly facilitates the presence of mosses, and this of some lichens, due to a “shade effect” (Castillo-Monroy *et al.*, 2010). Our results partially agree with this study because we observed higher cover values of lichens under LG conditions, and of mosses under HG conditions, relative to MG conditions in the low aridity site. BR can be stimulated under the plant canopy in rangelands because lichens and mosses can find both aeolian erosion and trampling protection. Mallen-Cooper *et al.* (2018) found an increase in biocrust richness mediated by livestock grazing through indirect effects on vascular plant richness. In line with our results, Tabeni *et al.* (2014) also showed that mosses are facilitated beneath plants in rangelands of Central-North Argentina. Moreover, soils are more stable under the canopy of plants in drylands, especially if sandy particles, such as those found in the low aridity site, are present (Li *et al.*, 2010). Local conditions of this site (total plant cover, plant richness and diversity, and soil texture) seem therefore to counterbalance the pernicious effects of grazing on biocrusts by partially protecting their biomass and richness of structural types at LG and HG conditions compared to MG conditions. Additionally, open spaces in drylands are directly related to the cover of cyanobacteria-dominated biocrusts (Zaady *et al.*, 2013). The proportion of covered soil is the lowest in the low aridity site at MG conditions. Hence, biocrusts have theoretically more “available soil surface” to establish, first as cyanobacteria-dominated biocrusts, then, if conditions are adequate, as more complex and diverse assemblages (Belnap *et al.*, 2016). In fact, under MG conditions at the low aridity site we observed high cover values and high relative abundances of light cyanobacteria- and dark cyanobacteria-dominated biocrusts compared to LG and HG conditions. Thus, our results suggest that moderate grazing conditions in this site partially promote the presence of early successional states of biocrusts through indirect effects on the proportion of cover soil mediated by sheep.

Surprisingly, the low aridity site was subjected to the strongest change in BC, irrespective of the grazing intensity. At LG and MG conditions, this site also showed the highest impacts of sheep on biocrust biomass and BR. Consequently, it stands to reason that more benign conditions in the low aridity site do not compensate for the negative effects of grazing on biocrusts. Recently, Oñatibia *et al.* (2018) showed that plant cover decreased with increasing sheep densities in the same rangelands, and the effects of grazing were the greatest at low aridity conditions. Our results show that light cyanobacteria- and dark cyanobacteria-dominated biocrusts negatively responded to plant cover under low aridity conditions, which indicates that early successional states of biocrusts will not benefit from plants at any grazing intensity in the low aridity site, contrary to what we observed in the high aridity site. However, biocrust assemblages need to counterbalance the effects of grazing in these rangelands. Cyanobacteria-dominated biocrusts can easily colonize bare soil areas in rangelands, rapidly responding to wetting events in their environments to grow, and then vertically migrating far from the surface (Rajeev *et al.*, 2013) to partially avoid the pernicious effects of grazing. Despite so, our results suggest that the frequency of wetting/desiccation cycles in our low aridity site is not enough to fully counterbalance grazing effects. The response of light cyanobacteria- and dark cyanobacteria-dominated biocrusts to grazing that we observed in the low aridity site contradicts the results found by Concostrina-Zubiri *et al.* (2014), who described a positive response of cyanobacteria-dominated biocrusts to grazing in Mexico.

Biocrusts recover in a few years after grazing abandonment

Biocrust recovery rates are difficult to compare because they depend on a variety of local conditions such as type of disturbance, soil type, plant cover or climatic conditions (Weber *et al.*, 2016). Recovery rates of biocrust biomass observed in our study were similar to those estimated by Kidron *et al.* (2008) in Israel, but faster than those reported by Belnap (1993) in USA, or slower than those observed by Dojani *et al.* (2011) in South Africa. Likewise, recovery rates of BC are in the same range as those estimated by Read *et al.* (2011) in Australia, although Xiao *et al.* (2014) observed lower recovery rates in China. In any case, we observed that only a few years are necessary to recover biocrusts in Patagonian rangelands, as previously reported in Australia (Read *et al.*, 2011, 2016). Temporal changes in the relative abundance of light cyanobacteria- and moss-dominated biocrusts in the medium aridity site agree with the general model of ecological succession of biocrusts. Bare soils, which are never sterile in nature (Colesie *et al.*, 2016), normally present cyanobacteria (Maier *et al.*, 2018), some of which are considered to be pioneers capable of initiating biocrusts formation (Garcia-Pichel & Wojciechowski, 2009). Once cyanobacteria create adequate conditions in dryland soils for biocrusts, local climatic or soil characteristics of the site dictate their composition, which may include lichens and mosses (Bowker *et al.*, 2016), and drive successional temporal shifts after grazing abandonment (Zhang *et al.*, 2016), as we observed. However, the absence of dark cyanobacteria- and lichen-dominated biocrusts in our sequence of temporal exclosures was surprising. The presence of medium sands and gravels in the soils of the medium aridity site can partially prevent the establishment of dark cyanobacteria, as Rozenstein *et al.* (2014) reported. Read *et al.* (2011, 2016) did not observe either dark cyanobacteria or lichens during the first stages of soil colonization after grazing abandonment in Australia, but a high relative abundance of mosses. Although we will never know how the biocrust community was before the introduction of sheep, *e.g.*, if lichens were an important component, our results undoubtedly show that sheep exclusion has led to, at least, a partial recovery of biocrusts in the Patagonian steppe.

Concluding remarks and management implications

We have observed that grazing pressure regulates biocrust biomass, total cover and richness of structural types across a regional aridity gradient in Patagonian rangelands. For example, and regardless of aridity conditions, light, moderate and high grazing pressures reduced the total cover of biocrusts by 85%, 89% and 98%, respectively. Because biocrusts with a good ecological health provide essential regulating ecosystem services in drylands worldwide, large-scale management efforts are necessary to preserve them. The production of meat and wool in Patagonian rangelands represents the most important local economic income. Consequently, it is not viable to simply remove sheep. And temporal rests of sheep grazing are almost impossible to apply. However, our results allow us to propose three general rules that would guide landowners in the battle to reduce biocrust degradation processes driven by sheep: (1) light-grazed fields are preferable over high-grazed fields, (2) high-grazing intensities must be definitively avoided under high aridity conditions, and (3) low aridity sites must not be considered as areas that can support any grazing intensity. The management of rangelands is undoubtedly a difficult task, but we need to definitively consider that grazing activities are negatively affecting biocrusts. To minimize grazing impacts on biocrusts while maintaining the capacity of these rangelands to provide essential ecosystem services, and thus the needs of future generations to come, it is necessary a common action implying scientists, landowners and politicians. And this study paves the road toward the implementation of an adaptive management plan to achieve these goals in rangelands of South America, where only a few studies have focused on biocrusts so far.

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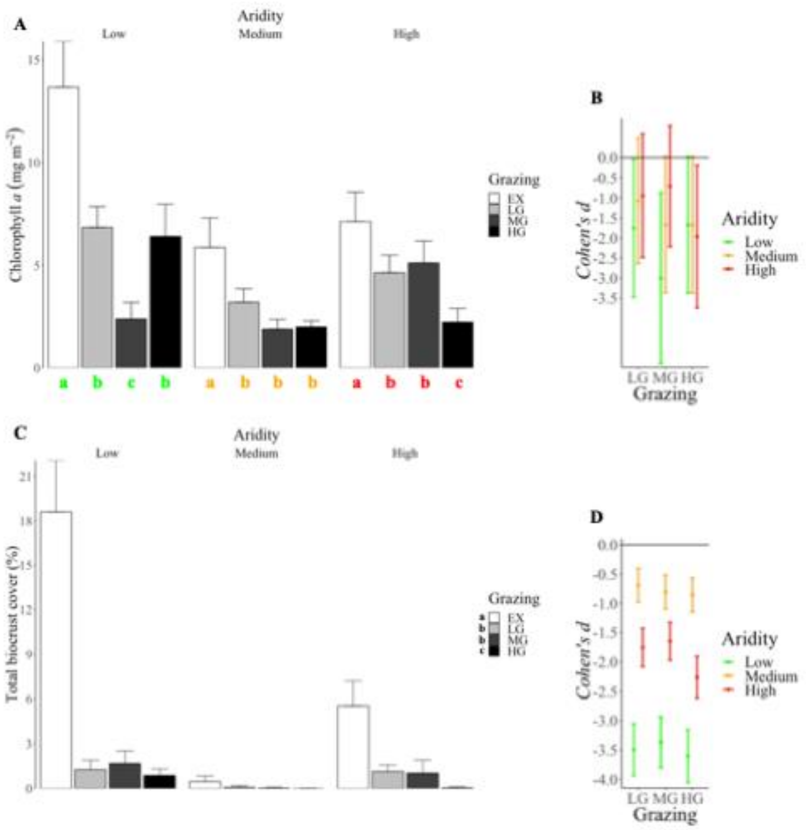

Figure 1. Biocrust biomass (as aerial chlorophyll *a* content) **(A)** and total biocrust cover **(C)** estimated at different grazing intensities under each aridity condition. Bars and errors show mean values ± 1 standard error (n = 5 and 4 for A and C, respectively). Effect size estimations (as Cohen´s d values and their confident intervals, ± 95%) for different grazing intensities on biocrust biomass **(B)** and total biocrust cover **(D)** under each aridity condition (EX, exclosures; LG, light-grazed areas; MG, moderate-grazed areas; HG, high-grazed areas) (lower-case color letters denote significant differences among grazing treatments within sites; lower-case black letters denote significant differences among grazing treatments considering all sites).

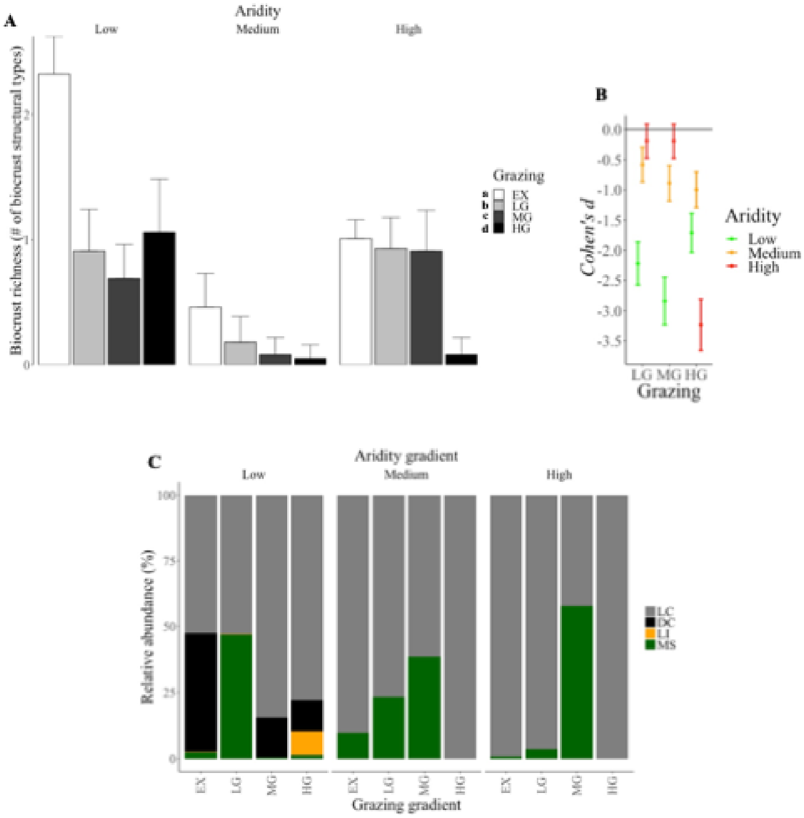

Figure 2. Biocrust richness (as # of biocrust structural types) **(A)** estimated at different grazing intensities under each aridity condition. Bars and errors show mean values ± 1 standard error (n = 4). Effect size estimations (as Cohen´s d values and their confident intervals, ± 95%) for different grazing intensities on biocrust richness **(B)** under each aridity condition. Biocrust composition (as relative abundances of light cyanobacteria-, dark cyanobacteria-, lichen- and moss-dominated biocrusts, LC, DC, LI and MS, respectively) for different grazing intensities **(C)** under each aridity condition (EX, exclosures; LG, light-grazed areas; MG, moderate-grazed areas; HG, high-grazed areas) (lower-case black letters denote significant differences among grazing treatments considering all sites).

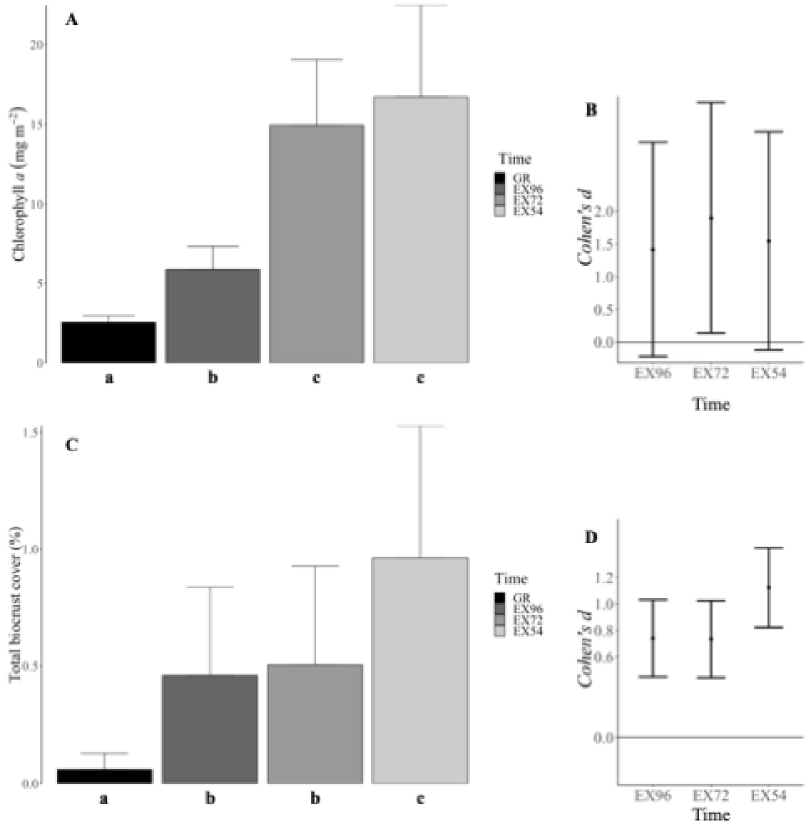

Figure 3. Biocrust biomass (as aerial chlorophyll *a* content) **(A)** and total biocrust cover **(C)** estimated at different exclosures, also including the grazing condition (GR), in the medium aridity site. Bars and errors show mean values ± 1 standard error (n = 5 and 4 for A and C, respectively). Effect size estimations (as Cohen´s d values and their confident intervals, ± 95%) for different time periods after grazing abandonment on biocrust biomass **(B)** and total biocrust cover **(D)**, also including the grazing condition (EX54, 1954 exclosure; EX72, 1972 exclosure; EX96, 1996 exclosure) (lower-case black letters denote significant differences among temporal exclosures).

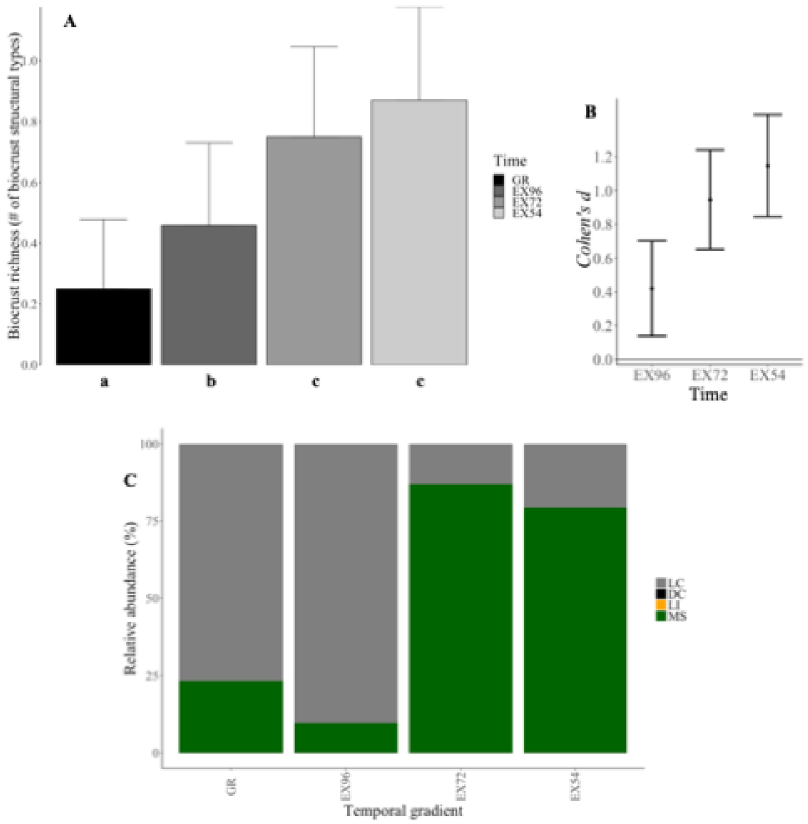

Figure 4. Biocrust richness (as # of biocrust structural types) **(A)** estimated at different exclosures, also including the grazing condition (GR), in the medium aridity site. Bars and errors show mean values ± 1 standard error (n = 4). Effect size estimations (as Cohen´s d values and their confident intervals, ± 95%) for different time periods after grazing abandonment on biocrust richness **(B)**, also including the grazing condition. Biocrust composition (as relative abundances of light cyanobacteria-, dark cyanobacteria-, lichen- and moss-dominated biocrusts, LC, DC, LI and MS, respectively) for different time periods after grazing abandonment on biocrust richness **(C)**, also including the grazing condition (EX54, 1954 exclosure; EX72, 1972 exclosure; EX96, 1996 exclosure) (lower-case black letters denote significant differences among temporal exclosures).