ARIDITY AND OVERGRAZING HAVE CONVERGENT EFFECTS ON ECOSYSTEM STRUCTURE AND FUNCTIONING IN PATAGONIAN RANGELANDS

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ABSTRACT

Over 65% of drylands are used for grazing of managed livestock. Understanding what drives grazing effects on the structure and functioning of rangelands is critical for achieving their sustainability. We studied a network of 239 sites across Patagonian rangelands (Argentina), which constitute one of the world's largest rangeland area. We aimed to (i) evaluate how aridity and grazing affect ecosystem structure and functioning and (ii) test the usefulness of the landscape function analysis (LFA) indices (stability, infiltration and nutrient cycling) as surrogates of soil functioning. Aridity decreased species richness and the cover of palatable grasses but increased the cover of palatable shrubs. Grazing pressure negatively impacted the cover of palatable grasses and species richness but did not affect the cover of shrubs. Aridity had direct and indirect negative relationships with the LFA indices. Grazing pressure had no direct effects on the LFA indices but had an indirect negative effect on them by affecting vegetation structure. The LFA indices were positively and negatively correlated with soil organic carbon and sand contents, respectively, suggesting that these indices are useful proxies of soil functional processes in Patagonian rangelands. Our findings indicate that aridity and overgrazing have convergent effects on the structure and functioning of ecosystems, as both promoted reductions in species richness, the cover of palatable grasses and soil functioning. Rangeland management activities should aim to enhance species richness and the cover of palatable grasses, as these actions could contribute to offset adverse effects of ongoing increases in aridity on drylands. Copyright © 2017 John Wiley & Sons, Ltd.

KEY WORDS: desertification; drylands; grass-shrub balance; species richness; landscape function analysis

INTRODUCTION

Grazing by managed livestock is a key driver of the structure and functioning of global rangelands (Asner *et al.,* 2004). The effects of grazing are, however, variable among ecosystems and depend on factors such as the identity and density of grazers, the grazing regime and the ecosystem attribute/process considered (Milchunas & Lauenroth, 1993; Eldridge *et al.,* 2016). For example, the effects of grazing on species richness range from positive (Waters *et al.,* 2016) to negative (Angassa, 2014). Depending on herbivore preferences, grazing generally reduces the abundance of palatable species and increases that of unpalatable species (Hendricks *et al.,* 2005). However, several studies have also demonstrated that grazing can increase the abundance of

highly palatable species (e.g. McNaughton, 1983). Divergent results have also been found in relation to the effects of grazing on the balance between grasses and shrubs (e.g. Scholes & Archer, 1997; Nano & Clarke, 2010).

Many rangelands are located in arid, semi-arid and dry-subhumid ecosystems (drylands), which cover about 41% of the Earth's land area (MEA, 2005). In these areas, vegetation structure exerts a strong control on processes such as nutrient cycling and infiltration and drives pathways of energy flow (Aguiar & Sala, 1999). Therefore, changes in vegetation structure induced by grazing can promote strong changes in ecosystem functioning in drylands (Adler *et al.,* 2001; Eldridge *et al.,* 2016). In addition to these indirect effects, grazing can have direct effects on ecosystem functioning. For example, herbivores affect physical soil properties through trampling (Steffens *et al.,* 2008) and modify the rates of organic matter decomposition and nutrient cycling by urine and dung deposition (Frank & Evans, 1997). Therefore, understanding what drives the

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effects of grazing on vegetation structure and on ecosystem processes sustaining the production of forage, such as nutrient cycling and infiltration (Milton *et al.,* 1994), is critical to promote a more sustainable use of rangelands (Augustine & McNaughton, 1998; Eldridge *et al.,* 2016).

The assessment and adjustment of grazing management practices require routine monitoring of ecosystem functionality (Pyke *et al.,* 2002). Measuring surrogates of ecosystem functioning *in situ*, such as the on-site retention of water and nutrients (Valentin *et al.,* 1999) or plant productivity (Cox *et al.,* 2006), is time-consuming and costly and may require laboratory equipment that is not available in all areas, particularly in developing countries. To overcome this, different monitoring methodologies based on readily measured soil and vegetation indicators have been developed over the last two decades (e.g. NRC, 1994; Tongway & Hindley, 2004; Herrick *et al.,* 2005). One of the most widely adopted methodologies is the landscape function analysis (LFA) developed in Australian rangelands (Tongway & Hindley, 2004). This method uses readily observable soil surface indicators, which are combined in three soil indices (stability, infiltration and nutrient cycling) that assess the degree to which resources tend to be retained, used and cycled within the ecosystem (Tongway & Hindley, 2004). Several studies have shown significant relationships between the LFA indices and quantitative measurements of these functions in dryland ecosystems from around the world (Ata Rezaei *et al.,* 2006; Maestre & Puche, 2009; Mayor & Bautista, 2012; but see Seaborn, 2005), and these indices are also being used to evaluate grazing impacts on ecosystem functioning (Soliveres & Eldridge, 2014; Eldridge *et al.,* 2016).

The Argentinian Patagonia (southern South America) is one of the world's largest rangelands. In this region, guanacos (*Lama guanicoe*) are the largest native herbivore and were present in large numbers over the past ~10,000 years before grazing by sheep were introduced about 130 years ago (Lauenroth, 1998). It has been hypothesized, therefore, that Patagonian rangelands have had a long evolutionary history of herbivory (Lauenroth, 1998). This strong selection pressure would have been complementary to that exerted by the arid climate of this region, resulting in plant species that are well adapted to both grazing and aridity (Milchunas *et al.,* 1988). While Patagonian drylands would, to some extent, be resistant to grazing, there is evidence that overgrazing by domestic livestock is a major anthropogenic force leading to their desertification (del Valle *et al.,* 1998). Several local-scale studies have shown that the commercial intensification of grazing has dramatically altered the structure of Patagonian rangelands (e.g. Aguiar *et al.,* 1996; Bisigato & Bertiller, 1997; Perelman *et al.,* 1997). However, there is a lack of studies evaluating the effects of grazing on ecosystem functioning at the regional scale and the factors controlling them. We aimed to do so using data available from the MARAS (Spanish acronym for 'Environmental Monitoring for Arid and Semi-Arid Regions') network, which consists of 350 monitoring sites located across a broad

environmental gradient in Patagonia (Oliva *et al.,* 2011). This monitoring network is based conceptually on the LFA methodology, but the functional LFA soil indices have not been validated in this region. This is a crucial step to test whether these indices adequately reflect the processes and functions that they aim to represent in Patagonian rangelands. Therefore, in this study, we have two objectives: (i) to evaluate how climate (aridity) interacts with grazing pressure to affect vegetation structure and soil functioning across Patagonia and (ii) to assess the relationships between the LFA indices and soil variables acting as surrogates of water availability and biogeochemical processes in drylands [soil organic carbon (SOC), total N and texture]. Our hypotheses are as follows: (i) aridity and grazing affect the structure and functioning of ecosystems in a similar way and (ii) the LFA indices are useful as surrogates of ecosystem functioning across Patagonian rangelands.

MATERIALS AND METHODS

Study Area

The study area is an 800,000-km^2 territory of Patagonian drylands, in southern Argentina. Mean annual precipitation and temperature range from 100 to 750 mm, and from 4·5° C to 16°C, respectively. The vegetation is dominated by grasslands, shrub-grass steppes and shrublands. The soils are sandy and loam-sandy textured, with little development of pedogenic horizons, and belong mainly to Aridisols and Entisols orders (del Valle, 1998).

Vegetation and Climatic Data

We were able to obtain data on stocking rate for 239 sites from the MARAS network (Figure 1). These sites were located in flat areas (slope < 10%) within ranches and display the typical diversity of livestock and rangeland management conditions found in Patagonia. Within each site, we placed two 50-m-long transects spaced 6·5 m apart on which we conducted vegetation surveys using the point-intercept method (Müller-Dombois & Ellenberg, 1974). Along each transect, we recorded the type of ground surface (plant species, bare soil or litter) every 20 cm (500 records per site). The cover of annual species in our sites was generally below 1%; thus, we recorded only perennial species. The number of perennial plant species recorded was used as our surrogate of species richness. The cover of a given species was calculated as the total number of records for that species in relation to the 500 records registered at each site. Each species was classified from 0 to 5 according to their preference by livestock (0: very low preference, species that are never or seldom eaten by livestock; 5: very high preference, species that are always eaten by livestock when present) following Somlo *et al.* (1985) and Nakamatsu *et al.* (1998). This classification is based on the floristic composition of herbivore diets determined through micro-histological analysis of faeces. Similar methodologies are commonly used to classify the palatability of plant species
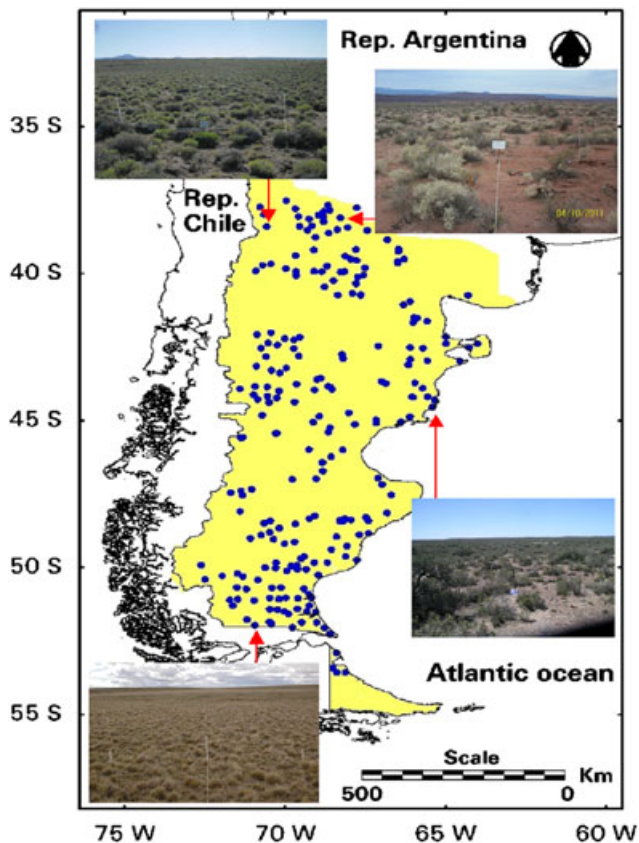
Figure 1. Location of sampling sites (blue dots), with some examples of the vegetation types studied. [Colour figure can be viewed at wileyonlinelibrary.com]

in rangelands worldwide (e.g. Bakare & Chimonyo, 2011). Species-specific cover values were grouped into unpalatable (classes 0 + 1) and palatable (classes 4 + 5) grasses and shrubs (see Table S1 for a full species list). We did not consider forbs and legume herbaceous vegetation in our analyses because their cover was very low across all the study sites: $5 \cdot 6 \pm 7 \cdot 6\%$ (mean ± standard deviation). The aridity [1 − aridity index (AI), where AI is precipitation/potential evapotranspiration] of each site was obtained from the Global Potential Evapotranspiration database (Zomer et al., 2008), which is based on interpolations provided by WorldClim (Hijmans et al., 2005).

Estimating Aboveground Net Primary Productivity

We used the annual integral of normalized difference vegetation index (I-NDVI), which has been shown as a good estimator of aboveground net primary productivity (ANPP; Prince, 1991). We acquired NDVI data from the MOD13Q1 product from MODIS, which provides 23 data per year with an approximated pixel size of 250 m × 250 m (Justice et al., 2002). We calculated I-NDVI for 11 growing seasons (from 2000 to 2001 to 2010–2011) as the sum of 23 data from July until June of the following year. The mean I-NDVI of the 11 growing seasons was used as our surrogate of ANPP for each site. Data were extracted for the pixel containing the field site; this results in a mismatch scale between stocking

rate (which are for the whole ranch; refer to subsequent text) and I-NDVI data. However, we believe that this spatial mismatch is reduced because the field sites were located in the most representative plant community of each ranch. To test that this is the case, we compared the I-NDVI of the site surveyed with the I-NDVI extracted from a square of 5,000 hectares centred in this site and repeated this for 85 randomly selected sites. We used 5,000 hectares because is about the average size of Patagonian ranches (MECON, 2002). We found a very close relationship between the field-sampled pixel and the 5,000-hectare I-NDVI values (Figure S2), suggesting that our ANPP estimates in the sampled area are representative of the whole ranch area.

Stocking Rate Data

We gathered stocking rate data directly from the land managers of the ranches where each site was located. For every surveyed site, we gathered information on the area of the ranch and the average number of sheep, cows, goats and horses feeding in the area during the last 5 years. We calculated stocking rate as livestock biomass per hectare. Livestock biomass was estimated as the product between the number of animals of each species and the individual average mass for each of them (according to national statistics; MECON, 2002): 37 kg for sheep, 400 kg for cows, 17 kg for goats and 200 kg for horses. In the region, grazing management is generally continuous, that is, the animals stay in the same paddock throughout the year (Golluscio et al., 1998; Oliva et al., 2012).

Oesterheld et al. (1998) found a positive relationship between stocking rate and I-NDVI in Argentinian rangelands. According to these authors, this relationship could be used to (i) infer the 'average' stocking rate that would be expected for a given site and (ii) indicate potential cases of overgrazing or underutilization. Following their approach, we analysed the relationship between I-NDVI and stocking rate and used the residuals of this relationship as our *proxy* of grazing pressure (Oesterheld et al., 1998). Positive values of these residuals would indicate overgrazing in a given site (i.e. observed stocking rate greater than predicted 'average' stocking rate that would be expected according to the empirical regional pattern), while negative values would indicate resource underutilization.

Measuring Soil Functional Attributes

Within each site, we placed a third 50-m-long transect, in which we collected a continuous record of vegetation and bare patches. From these records, we obtained the vegetation basal cover. In the first ten bare soil patches located along this transect, we evaluated 11 soil surface indicators (Supporting Information S3) following a semi-quantitative scale according to the guidelines of Oliva et al. (2011) and Tongway & Hindley (2004). These indicators were further combined to obtain the three LFA indices (stability, infiltration and nutrient cycling) as described in Tongway & Hindley (2004).

In each site, we obtained five subsamples (depth 0–10 cm) from the centre of randomly selected bare soil patches, which were pooled to obtain one composite soil sample. After field collection, the soil samples were taken to the laboratory, where they were air dried, sieved (2-mm mesh) and stored for laboratory analyses. The following soil variables were measured as surrogates of soil functioning in a subset of sites: SOC (Walkley-Black method; 255 sites), total N (Kjeldahl method; 215 sites) and texture (pipette method; 167 sites). SOC and total N were positively correlated (Pearson $r = 0.93$, $p < 0.0001$), while the texture fractions are interdependent. Thus, we selected for further analyses only SOC and sand content, which have been found to play a key role in controlling water availability, plant community structure and biogeochemical processes in drylands (Mills *et al.*, 2009).

Data Analysis

We conducted Pearson correlation analyses between LFA indices and soil variables. We used the structural equation modelling (SEM) to evaluate the relative importance and direct/indirect effects of aridity and grazing pressure as drivers of variations in structural and functional ecosystem attributes. We used as our response variable a latent variable: soil functioning. Latent variables are typically used to represent concepts, and they are not, in themselves, measured directly. Instead, they are informed by one or more variables that are indicators or proxies (Grace, 2006). In our study, we used the three LFA indices as indicators of our latent variable. SEM involves the testing of *a priori* model developed to understand how multiple factors affect our variable of interest (Grace, 2006). Following current ecological knowledge, we hypothesized a unique *a priori* model that shows hypothesized relationships between variables (Supporting Information S4) and tested their fit to our data. We used χ^2, normed fit index and root mean square error of approximation index as measures of model fit (Grace, 2006). Path coefficients estimates were obtained using the maximum likelihood estimation technique; they are equivalent to standardized partial regression coefficients and are interpreted as relative effects of one variable upon another (Grace, 2006). Statistical analyses were performed with SPSS 17·0 (SPSS Inc, Chicago, IL, USA) and AMOS 18·0 (SPSS Inc, Chicago, IL, USA).

RESULTS

Effects of Aridity and Grazing Pressure on Structural and Functional Ecosystem Attributes

The stocking rate was positively related to our surrogate of ANPP (I-NDVI, Figure 2). Our *a priori* SEM (Supporting Information S4) was consistent with our data, as indicated by the results from the different goodness-of-fit tests employed ($\chi^2 = 24.96$, $p = 0.16$, d.f. = 19; normed fit index = 0·97 and root mean square error of approximation
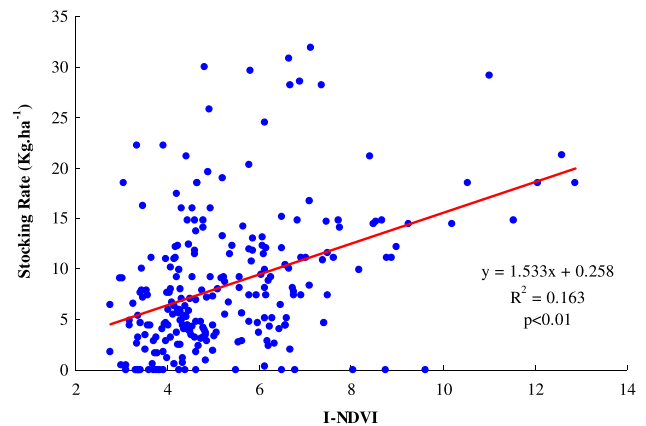

Figure 2. Relationship between the annual integral of NDVI (normalized difference vegetation index, I-NDVI) and stocking rate for the 239 sites studied across Patagonia. [Colour figure can be viewed at wileyonlinelibrary.com]

index = 0·03; Figure 3). This model explained 65% of the variation found in soil functioning. Additionally, our SEMs explained 20% and 50% of the variation found in the cover of palatable grasses and species richness, respectively. However, these values dropped to <5% for the cover of unpalatable grasses and both palatable and unpalatable shrubs.

Aridity had a direct negative effect on species richness and palatable grasses, and a direct positive effect on palatable shrubs (Figure 3). Aridity showed a significant direct negative relationship with soil functioning. Grazing pressure had direct negative effects on palatable grasses and species richness. Grazing pressure was not directly related to soil functioning but had an indirect negative effect on it mediated by the positive direct effect of palatable grasses and species richness on this variable.

Aridity was the variable with the largest total effects on the structural vegetation attributes except for unpalatable grasses, where grazing pressure had greater total effect (Table I). Aridity was also the variable with the higher total effects (negative) on soil functioning. About 60% of the total effect of aridity was direct, and the remainder was mediated by vegetation structure (Figure 4). Palatable grasses and species richness had positive total effects on soil functioning, which were about 70% and 40% of the total effects of aridity. Grazing pressure had only indirect negative effects on soil functioning, which was about 25% of the total effects of aridity (Figure 4).

LFA Indices as Surrogates of Soil Functioning

The three LFA indices (stability, infiltration and nutrient cycling) were significantly related to the surrogates of soil functioning evaluated. SOC was the variable that showed the highest positive correlations with these indices (Pearson $r = 0.38$, 0·50 and 0·64 for stability, infiltration and nutrient cycling indices, respectively; $n = 255$, $p < 0.001$ in all cases). The stability and nutrient cycling indices were negatively correlated with sand content (Pearson $r = -0.36$ and -0.28, respectively; $n = 167$, $p < 0.001$ in both cases).
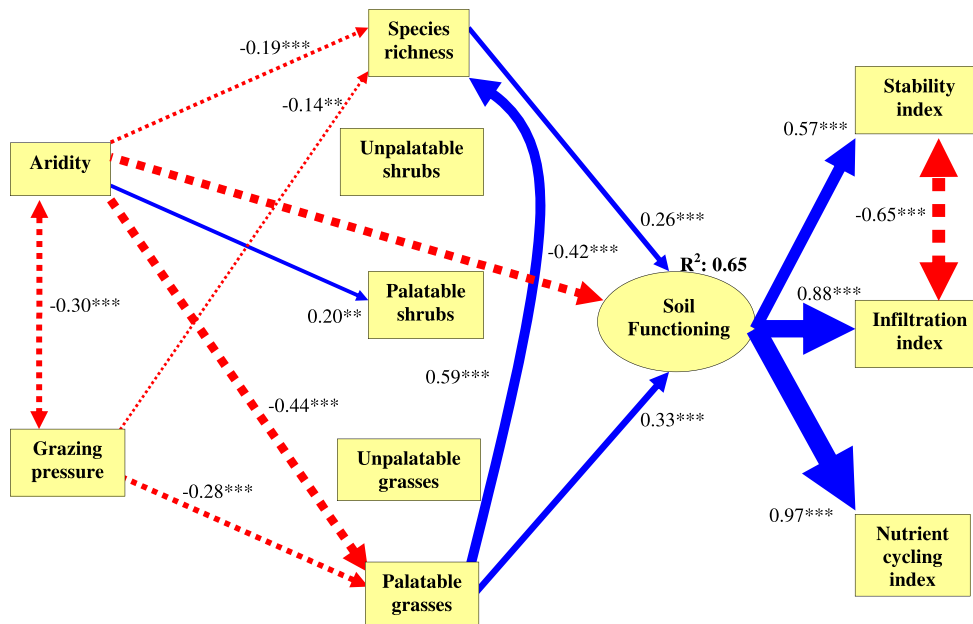
Figure 3. Structural equation model for the latent variable 'soil functioning'. Single-headed arrows indicate a hypothesized causal influence of one variable upon another. Double-headed arrows indicate correlation without causal relationship. The numbers adjacent to arrows are path coefficients; they show the strengths of the effect. The widths of the arrows are proportional to the path coefficients. Full blue and dotted red arrows indicate positive and negative relationships, respectively. Non-significant ($p > 0.05$) paths were eliminated. The R^2 next to response variables indicates the proportion of variance explained. Goodness-of-fit statistics: $\chi^2 = 24.96$, $p = 0.16$, d.f. = 19; normed fit index = 0.97 and root mean square error of approximation index = 0.03. Significance levels are as follows: **$p < 0.01$; ***$p < 0.001$. [Colour figure can be viewed at wileyonlinelibrary.com]

Table I. Standardized direct (SDE), indirect (SIE) and total (STE) effects of aridity and grazing pressure on species richness and the cover of palatable and unpalatable shrubs and grasses

		Aridity	Grazing pressure
Species richness	SDE	−0·19	−0·14
	SIE	−0·27	−0·16
	STE	−0·46	−0·30
Palatable shrubs	SDE	0·20	−0·03
	SIE	—	—
	STE	0·20	−0·03
Unpalatable shrubs	SDE	0·09	−0·05
	SIE	—	—
	STE	0·09	−0·05
Palatable grasses	SDE	−0·45	−0·28
	SIE	—	—
	STE	−0·45	−0·28
Unpalatable grasses	SDE	0·01	0·10
	SIE	—	—
	STE	0·01	0·10

Figure 4. Standardized direct (blue), indirect (yellow) and total (red) effects of predictor variables on the latent variable 'soil functioning'. [Colour figure can be viewed at wileyonlinelibrary.com]

DISCUSSION

Unlike previous case studies assessing grazing effects (e.g. Aguiar *et al.,* 1996; Cipriotti & Aguiar, 2012), or meta-analyses (Eldridge & Delgado-Baquerizo, 2016), our study includes a large number of field sites scattered over a large area comprising a wide variation in environmental conditions and surveyed using a standardized protocol. Thus, it provides important and novel insights into the effects of grazing on ecosystem structure and functioning, and how climate co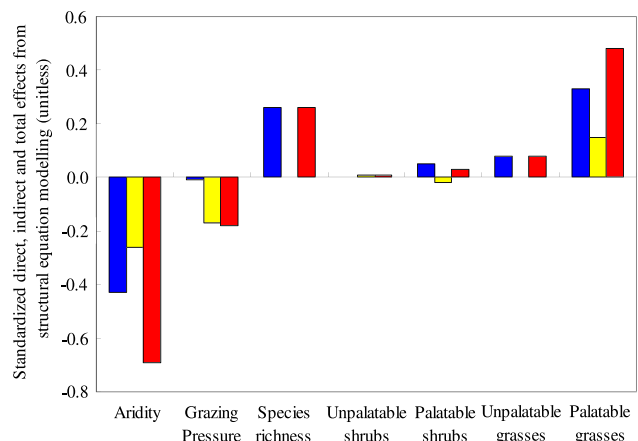ntrols them, at the regional scale. According to our first hypothesis, our findings suggest that aridity and overgrazing have convergent effects on structure and functioning of Patagonian rangelands, as both promoted reductions in species richness, the cover of palatable grasses and surrogates of soil functioning. Moreover, we found that readily-to-measure indicators, such as the LFA indices, are good surrogates of soil variables linked to key ecosystem functional attributes, which agrees with our second hypothesis.

Relationship Between I-NDVI and Stocking Rate

Oesterheld *et al.* (1998) found a very strong ($r^2 = 0.90$) positive relationship between I-NDVI and stocking rate. In

our study, we also found a positive relationship between these variables, although it was substantially weaker (r^2 = 0·16). This may be due to the differences in scale between the two studies; Oesterheld *et al.* (1998) worked with aggregate data at the county level, while we used data at the single ranch level. At the ranch level, factors other than primary productivity can affect stocking rate (e.g. land manager decisions, climatic events and predation). Despite this potential noise, we obtained a significant empirical model at the regional scale that allowed us to estimate the overutilization or underutilization of each site in relation to its productive potential.

Effects of Aridity and Grazing Pressure on Structural and Functional Ecosystem Attributes

Aridity had a major effect on vegetation structural attributes. We found a trend towards the increase and reduction in the cover of shrubs and grasses in the drier sites, respectively. Drought stress increases with aridity in water-limited ecosystems, which could explain the dominance of deep-rooted species, such as shrubs, at the drier sites. In addition, we found a decline in the cover of palatable grasses, while the cover of unpalatable grasses was not affected as aridity increases. Our findings are consistent with the hypothesis that aridity and grazing impose convergent selective pressures on grasses, such that traits selected for aridity would help plants to avoid or tolerate herbivory, and vice versa (Coughenour, 1985; Milchunas *et al.,* 1988).

Increases in grazing pressure reduced the cover of palatable grasses but had no effects on that of unpalatable grasses. These results suggest that as grazing pressure increases, the major shift occurring within this functional group is a relative increase in the cover of unpalatable grasses. However, we do not rule out that the size of the effect of grazing pressure on the cover of palatable and unpalatable grasses could be higher if we accounted for historical grazing. We acknowledge that this is a limitation in our approach, as most Patagonian ranches do not have historical records of stocking rate. Our study area has been grazed for over 100 years, during which global stock was variable: the maximum stock of sheep was 18 million of heads in 1958, while in 2014 it was about nine million (MINAGRI, 2015). Therefore, our field-measured structural and functional ecosystem attributes may be affected not only by recent grazing pressure but also by historic grazing pressure over the past century.

The conversion of grasslands to shrublands is a global phenomenon (Eldridge *et al.,* 2011) that is often associated with increases in grazing pressure (Buffington & Herbel, 1965; Scholes & Archer, 1997; Peng *et al.,* 2013). Some studies have found evidence that grazing tends to reduce the cover of palatable grasses, and to increase that of shrubs, in subhumid Patagonian grasslands (Bertiller *et al.,* 1995; Aguiar *et al.,* 1996). However, in our study, the cover of palatable and unpalatable shrubs was not affected by grazing pressure. This suggests that shrub encroachment driven by grazing is not a general phenomenon

in Patagonian rangelands. Our findings agree with those of previous case studies conducted in arid ecosystems of Patagonia, which have also found that grazing does not trigger shrub encroachment (Adler *et al.,* 2005; Cipriotti & Aguiar, 2012).

We found a decrease in species richness as grazing pressure increased. This is consistent with predictions by Milchunas & Lauenroth (1993). According to these authors, in dry environments with nutrient-poor soils and a long evolutionary history of grazing (such as Patagonian rangelands; Adler *et al.,* 2005), grazing pressure is expected to negatively impact species richness. This can be caused by increasing rates of local extinction due to grazing-induced modifications of soil and vegetation attributes, which affect plant recruitment by altering the microclimate and/or topsoil properties, and by promoting greater mortality after germination (Milton *et al.,* 1994).

While grazing did not directly impact soil functioning, as we hypothesized in the *a priori* model, it had an indirect negative effect on this ecosystem attribute, mediated by its negative effect on both species richness and the cover of palatable grasses. The positive effects of species richness on soil functioning observed are consistent with previous findings from the same region showing a positive effect of species richness on ANPP (Gaitán *et al.,* 2014a) and on the resistance of ANPP to drought (Gaitán *et al.,* 2014b). Our findings also agree with the growing literature showing positive effects of plant species richness and cover on ecosystem functioning at multiple spatial scales in drylands (e.g. Maestre *et al.,* 2012; Gherardi & Sala, 2015). Similarly, the cover of palatable (but not unpalatable) grasses had a positive effect on soil functioning. These results could be driven by the links existing between palatability, growth rate and litter decomposition (Augustine & McNaughton, 1998). Unpalatable species usually have higher contents of secondary compounds such as lignin and phenolics, which reduce herbivory and the decomposition of their litter compared with more palatable species (Wardle *et al.,* 2002). Therefore, ecosystems dominated by palatable grasses may have enhanced nutrient and carbon cycling (Moretto *et al.,* 2001). Furthermore, we hypothesize that the proportion of biomass of palatable grasses consumed by herbivores increases with grazing pressure, thereby reducing the input of organic matter to the soil. This may reduce the stocks of SOC, and thus those functions associated to it (such as stability and infiltration capacity). The lack of a direct effect of grazing pressure on soil functioning was unexpected because in many rangelands, trampling by herbivores disrupts physical and biological crusts, altering the redistribution of nutrients and water in the soil and increasing erosion (Allington & Valone, 2010). Our results can likely be explained by the coarse texture that is prevalent in the soils studied (the mean sand content across all sites was 70·5%, SD = 16·6%), as these soils do not develop a physical and biological crust (Belnap, 2006). Therefore, the direct effect of grazing pressure on soil functioning through trampling can be reduced in these rangelands.

LFA Indices as Surrogates of Soil Functioning

The relationships among the LFA indices and the soil variables measured are in accord with other studies in drylands showing that these indices are strongly related to quantitative measures of ecosystem processes such as soil aggregate stability, infiltration capacity, soil nutrient contents, respiration and ANPP (e.g. Ata Rezaei *et al.*, 2006; Maestre & Puche, 2009; Mayor & Bautista, 2012). In our study, SOC was strongly and positively correlated with the three LFA indices. These results are not surprising because many physical, chemical and biological soil properties are directly related to SOC, including the biogeochemical cycling of nutrients such as carbon and nitrogen (McGill & Cole, 1981) and the formation and stabilization of soil aggregates (Tisdall & Oades, 1982). Furthermore, the stability index was negatively related to sand content. Soils comprising more clay and silt-rich materials can have greater inter-particle bonding, leading to greater soil aggregate stability (Walker, 2012). Our results thus suggest that the LFA indices are useful proxies of key soil functional processes and indicators of ecosystem health in rangelands worldwide (Pyke *et al.,* 2002; Akiyama & Kawamura, 2007).

Conclusions and Implications for Rangeland Management

Our results indicate that overgrazing could shift vegetation composition towards a relative dominance of species avoided by grazers, which could reduce forage productivity. In addition, our results have important implications in the context of ongoing climate change, as climatic models predict an increase in aridity for drylands worldwide (Huang *et al.*, 2016). Forecasted increases in aridity could accentuate the negative effects of overgrazing on ecosystem functioning by inducing a reduction in the richness and cover of palatable grasses, which exert positive effects on soil functioning. These changes could reduce the capability of Patagonian rangelands to provide essential ecosystem services on which humans depend, such as forage production and carbon sequestration. Our results also suggest that maintaining and enhancing the cover of palatable grasses and species richness with appropriate livestock management could mitigate the negative effects of climate change on ecosystem functioning. The adjustment of grazing management practices requires routine monitoring of ecosystem health, for which land managers should regularly assess the composition of vegetation (cover of shrubs, palatable and unpalatable grasses) and the status of the soil surface using ready-to-measure indicators such as the LFA indices, which have been proven to be good surrogates of ecosystem functioning.

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REFERENCES

Adler PB, Milchunas DG, Sala OE, Burke IC, Lauenroth WK. 2005. Plant traits and ecosystem grazing effects: comparison of US sagebrush steppe and Patagonian steppe. *Ecological Applications* **15**: 774–792. https://doi.org/10.1890/04-0231.

Adler P, Raff D, Lauenroth W. 2001. The effect of grazing on the spatial heterogeneity of vegetation. *Oecologia* **128**: 465–479. https://doi.org/10.1007/s004420100737.

Aguiar MR, Sala OE. 1999. Patch structure, dynamics, and implications for the functioning of arid ecosystems. *Trends in Ecology & Evolution* **14**: 273–277. https://doi.org/10.1016/S0169-5347(99)01612-2.

Aguiar MR, Paruelo JM, Sala OE, Lauenroth WK. 1996. Ecosystem responses to changes in plant functional type composition: an example from the Patagonian steppe. *Journal of Vegetation Science* **7**: 381–390. https://doi.org/10.2307/3236281.

Akiyama T, Kawamura K. 2007. Grassland degradation in China: methods of monitoring, management and restoration. *Grassland Science* **53**: 1–17. https://doi.org/10.1111/j.1744-697X.2007.00073.x.

Allington GR, Valone TJ. 2010. Reversal of desertification: the role of physical and chemical soil properties. *Journal of Arid Environments* **74**: 973–977. https://doi.org/10.1016/j.jaridenv.2009.12.005.

Angassa A. 2014. Effects of grazing intensity and bush encroachment on herbaceous species and rangeland condition in southern Ethiopia. *Land Degradation & Development* **25**: 438–451. https://doi.org/10.1002/ldr.2160.

Asner GP, Elmore AJ, Olander LP, Martin RE, Harris AT. 2004. Grazing systems, ecosystem responses, and global change. *Annual Review of Environment and Resources* **29**: 261–299. https://doi.org/10.1146/annurev.energy.29.062403.102142.

Ata Rezaei S, Arzani H, Tongway D. 2006. Assessing rangeland capability in Iran using landscape function indices based on soil surface attributes. *Journal of Arid Environments* **65**: 460–473. https://doi.org/10.1016/j.jaridenv.2005.08.003.

Augustine DJ, McNaughton SJ. 1998. Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. *The Journal of Wildlife Management* **62**: 1165–1183. https://doi.org/10.2307/3801981.

Bakare AG, Chimonyo M. 2011. Variation in plant preferences of indigenous goats in a False Thornveld rangeland in South Africa. *Livestock Science* **139**: 206–212. https://doi.org/10.1016/j.livsci.2011.01.009.

Belnap J. 2006. The potential roles of biological soil crusts in dryland hydrologic cycles. *Hydrological Processes* **20**: 3159–3178. https://doi.org/10.1002/hyp.6325.

Bertiller MB, Elissalde NO, Rostagno CM, DeFossé GE. 1995. Environmental patterns and plant distribution along a precipitation gradient in western Patagonia. *Journal of Arid Environments* **29**: 85–97. https://doi.org/10.1016/S0140-1963(95)80066-2.

Bisigato AJ, Bertiller MB. 1997. Grazing effects on patchy dryland vegetation in northern Patagonia. *Journal of Arid Environments* **36**: 639–653. https://doi.org/10.1006/jare.1996.0247.

Buffington LC, Herbel CH. 1965. Vegetational changes on a semidesert grassland range from 1858 to 1963. *Ecological Monographs* **35**: 139–164. DOI:10.2307/1948415.

Cipriotti PA, Aguiar MR. 2012. Direct and indirect effects of grazing constrain shrub encroachment in semiarid Patagonian steppes. *Applied Vegetation Science* **15**: 35–47. https://doi.org/10.1111/j.1654-109X.2011.01138.x.

Coughenour MB. 1985. Graminoid responses to grazing by large herbivores: adaptations, exaptations, and interacting processes. *Annals of the Missouri Botanical Garden* **72**: 852–863. https://doi.org/10.2307/2399227.

Cox SB, Bloch CP, Stevens RD, Huenneke LF. 2006. Productivity and species richness in an arid ecosystem: a long-term perspective. *Plant Ecology* **186**: 1–12. https://doi.org/10.1007/s11258-006-9107-6.

del Valle HF. 1998. Patagonian soils: a regional synthesis. *Ecología Austral* **8**: 103–124.

del Valle HF, Elissalde NO, Gagliardini DA, Milovich J. 1998. Status of desertification in the Patagonian region: assessment and mapping from satellite imagery. *Arid Land Research and Management* **12**: 95–121. https://doi.org/10.1080/15324989809381502.

Eldridge DJ, Delgado-Baquerizo M. 2016. Continental-scale impacts of livestock grazing on ecosystem supporting and regulating services. *Land Degradation & Development.*. https://doi.org/10.1002/ldr.2668.

Eldridge DJ, Bowker MA, Maestre FT, Roger E, Reynolds JF, Whitford WG. 2011. Impacts of shrub encroachment on ecosystem structure and functioning: towards a global synthesis. *Ecology Letters* **14**: 709–722. https://doi.org/10.1111/j.1461-0248.2011.01630.x.

Eldridge DJ, Poore AG, Ruiz-Colmenero M, Letnic M, Soliveres S. 2016. Ecosystem structure, function and composition in rangelands are negatively affected by livestock grazing. *Ecological Applications* **26**: 1273–1283. https://doi.org/10.1890/15-1234.

Frank D, Evans R. 1997. Effects of native grazers on grassland N cycling in Yellowstone National Park. *Ecology* **78**: 2238–2248. https://doi.org/10.1890/0012-9658(1997)078[2238:EONGOG]2.0.CO;2.

Gaitán J, Bran D, Oliva G, Maestre F, Aguiar MR, Jobbágy EG, Buono G, Ferrante D, Nakamatsu V, Ciari G, Salomone J, Massara V. 2014a. Vegetation structure is as important as climate for explaining ecosystem function across Patagonian rangelands. *Journal of Ecology* **102**: 1419–1428. https://doi.org/10.1111/1365-2745.12273.

Gaitán J, Bran D, Oliva G, Maestre F, Aguiar MR, Jobbágy EG, Buono G, Ferrante D, Nakamatsu V, Ciari G, Salomone J, Massara V. 2014b. Plant species richness and shrub cover attenuate drought effects on ecosystem functioning across Patagonian rangelands. *Biology Letters* **10**. https://doi.org/10.1098/rsbl.2014.0673.20140673

Gherardi L, Sala O. 2015. Enhanced precipitation variability decreases grass- and increases shrub-productivity. *Proceedings of the National Academy of Sciences* **112**: 12735–12740. https://doi.org/10.1073/pnas.1506433112.

Golluscio RA, Deregibus VA, Paruelo JM. 1998. Sustainability and range management in the Patagonian steppes. *Ecología Austral* **8**: 265–284.

Grace JB. 2006. *Structural equation modeling and natural systems.* Cambridge University Press: Cambridge.

Hendricks H, Bond W, Midgley J, Novellie P. 2005. Plant species richness and composition a long livestock grazing intensity gradients in a Namaqualand (South Africa) protected area. *Plant Ecology* **176**: 19–33. https://doi.org/10.1007/s11258-003-0009-6.

Herrick JE, Van Zee JW, Havstad KM, Whitford WG. 2005. Monitoring manual for grassland, shrubland, and savanna ecosystems. In Design supplementary methods and interpretation, Vol. **II**. USDA-ARS: Las Cruces.

Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A. 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* **25**: 1965–1978. https://doi.org/10.1002/joc.1276.

Huang J, Yu H, Guan X, Wang G, Guo R. 2016. Accelerated dryland expansion under climate change. *Nature Climate Change* **6**: 166–171. 10.1038/nclimate2837.

Justice C, Townshend J, Vermote E, Masuoka E, Wolfe RE, Saleous N, Roy DP, Morisette JT. 2002. An overview of MODIS Land data processing and product status. *Remote Sensing of Environment* **83**: 3–15. https://doi.org/10.1016/S0034-4257(02)00084-6.

Lauenroth WK. 1998. Guanacos, spiny shrubs and the evolutionary history of grazing in the Patagonian steppe. *Ecología Austral* **8**: 211–215.

Maestre FT, Puche MD. 2009. Indices based on surface indicators predict soil functioning in Mediterranean semiarid steppes. *Applied Soil Ecology* **41**: 342–350. https://doi.org/10.1016/j.apsoil.2008.12.007.

Maestre FT, Quero JL, Gotelli NJ, Escudero A, Ochoa V, Delgado-Baquerizo M, García-Gómez M, Bowker MA, Soliveres S, Escolar C, García-Palacios P, Berdugo M, Valencia E, Gozalo B, Gallardo A, Aguilera L, Arredondo T, Blones J, Boeken B, Bran D, Conceição AA, Cabrera O, Chaieb M, Derak M, Eldridge DJ, Espinosa CI, Florentino A, Gaitán J, Gatica MG, Ghiloufi W, Gómez-González S, Gutiérrez JR, Hernández RM, Huang X, Huber-Sannwald E, Jankju M, Miriti M, Monerris J, Mau RL, Morici E, Naseri K, Ospina A, Polo V, Prina A, Pucheta E,

Ramírez-Collantes DA, Romão R, Tighe M, Torres-Díaz C, Val J, Veiga JP, Wang D, Zaady E. 2012. Plant species richness and ecosystem multifunctionality in global drylands. *Science* **335**: 214–218. https://doi.org/10.1126/science.1215442.

Mayor ÁG, Bautista S. 2012. Multi-scale evaluation of soil functional indicators for the assessment of water and soil retention in Mediterranean semiarid landscapes. *Ecological Indicators* **20**: 332–336. https://doi.org/10.1016/j.ecolind.2012.03.003.

McGill WB, Cole CV. 1981. Comparative aspects of cycling of organic C, N, S and P through soil organic matter. *Geoderma* **26**: 267–286. https://doi.org/10.1016/0016-7061(81)90024-0.

McNaughton SJ. 1983. Serengeti grassland ecology: the role of composite environmental factors and contingency in community organization. *Ecological Monographs* **53**: 291–320. https://doi.org/10.2307/1942533.

MEA. Millennium Ecosystem Assessment. 2005. Ecosystems and human well-being: desertification synthesis. World Resources Institute: Washington, DC.

MECON. Ministerio de Economía. 2002. Empadronamiento Nacional Agropecuario y Censo Ganadero. Ministerio de Economía: Buenos Aires, Argentina.

Milchunas DG, Lauenroth WK. 1993. Quantitative effects of grazing on vegetation and soils over a global range of environments. *Ecological Monographs* **63**: 327–366. https://doi.org/10.2307/2937150.

Milchunas DG, Sala OE, Lauenroth W. 1988. A generalized model of the effects of grazing by large herbivores on grassland community structure. *American Naturalist* **132**: 87–106. https://doi.org/10.1086/284839.

Mills A, Fey M, Donaldson J, Todd S, Theron L. 2009. Soil infiltrability as a driver of plant cover and species richness in the semi-arid Karoo, South Africa. *Plant and Soil* **320**: 321–332. https://doi.org/10.1007/s11104-009-9904-5.

Milton SJ, Dean WRJ, du Plessis MA, Siegfried WR. 1994. A conceptual model of arid rangeland degradation. *Bioscience* **44**: 70–76. https://doi.org/10.2307/1312204.

MINAGRI. 2015. Existencias ganaderas ovinas. http://www.minagri.gob.ar/site/ganaderia/ovinos/02=Estadisticas/02=Existencias/index.php

Moretto AS, Distel RA, Didoné NG. 2001. Decomposition and nutrient dynamic of leaf litter and roots from palatable and unpalatable grasses in a semi-arid grassland. *Applied Soil Ecology* **18**: 31–37. https://doi.org/10.1016/S0929-1393(01)00151-2.

Müller-Dombois DD, Ellenberg H. 1974. Aims and methods of vegetation ecology. Wiley: New York; 547.

Nakamatsu V, Lagarrigue M, Locattelli M, Sendin M, Elissalde N, Escobar J. 1998. Disponibilidad de forraje estimada a través del valor pastoral en zonas áridas del Chubut (Patagonia). *Revista Argentina de Producción Animal* **8**: 188.

Nano CE, Clarke PJ. 2010. Woody-grass ratios in a grassy arid system are limited by multi-causal interactions of abiotic constraint, competition and fire. *Oecologia* **162**: 719–732. https://doi.org/10.1007/s00442-009-1477-8.

NRC. National Research Council. 1994. Rangeland health: new methods to classify, inventory, and monitor rangelands. National Academy Press: Washington, DC.

Oesterheld M, DiBella CM, Kerdiles H. 1998. Relation between NOAA-AVHRR satellite data and stocking rate of rangelands. *Ecological Applications* **8**: 207–212. https://doi.org/10.1890/1051-0761(1998)008[0207:RBNASD]2.0.CO;2.

Oliva G, Ferrante D, Puig S, Williams M. 2012. Sustainable sheep management using continuous grazing and variable stocking rates in Patagonia: a case study. *The Rangeland Journal* **34**: 285–295. https://doi.org/10.1071/RJ12016.

Oliva G, Gaitán J, Bran D, Nakamatsu V, Salomone J, Buono G, Escobar J, Ferrante D, Humano G, Ciari G, Suarez D, Opazo W, Adema E, Celdrán D. 2011. Manual para la Instalación y Lectura de Monitores MARAS. PNUD: Buenos Aires, Argentina.

Peng HY, Li XY, Li GY, Zhang ZH, Zhang SY, Li L, Zhao GQ, Jiang ZY, Ma JY. 2013. Shrub encroachment with increasing anthropogenic disturbance in the semiarid Inner Mongolian grasslands of China. *Catena* **109**: 39–48. https://doi.org/10.1016/j.catena.2013.05.008.

Perelman SB, León RJC, Bussacca JP. 1997. Floristic changes related to grazing intensity in a Pantagonian shrub steppe. *Ecography* **20**: 400–406. https://doi.org/10.1111/j.1600-0587.1997.tb00385.x.

Prince SD. 1991. Satellite remote sensing of primary production: comparison of results for Sahelian grasslands 1981–1988. *International Journal of Remote Sensing* **12**: 1301–1311. https://doi.org/10.1080/01431169108929727.

Pyke DA, Herrick JE, Shaver PL, Pellant M. 2002. Rangeland health attributes and indicators for qualitative assessment. *Journal of Range Management* **55**: 584–597. https://doi.org/10.2307/4004002.

Scholes RJ, Archer SR. 1997. Tree–grass interactions in Savannas. *Annual Review of Ecology and Systematics* **28**: 517–544. https://doi.org/10.1146/annurev.ecolsys.28.1.517.

Seaborn VC. 2005. An assessment of landscape function analysis as a tool for monitoring rehabilitation success in the mining industry. M. Phil Thesis, University of Queensland, Brisbane, Australia, 205 p.

Soliveres S, Eldridge DJ. 2014. Do changes in grazing pressure and the degree of shrub encroachment alter the effects of individual shrubs on understorey plant communities and soil function? *Functional Ecology* **28**: 530–537. https://doi.org/10.1111/1365-2435.12196.

Somlo R, Durañona C, Ortíz R. 1985. Valor nutritivo de especies forrajeras patagónicas. *Revista Argentina de Producción Animal* **5**: 589–605.

Steffens M, Kölbl A, Totsche KU, Kögel-Knabner I. 2008. Grazing effects on soil chemical and physical properties in semiarid steppe of Inner Mongolia (P.R. China). *Geoderma* **143**: 63–72. https://doi.org/10.1016/j.geoderma.2007.09.004.

Tisdall JM, Oades JM. 1982. Organic matter and water-stable aggregates in soils. *Journal of Soil Science* **33**: 141–163. https://doi.org/10.1111/j.1365-2389.1982.tb01755.x.

Tongway DJ, Hindley N. 2004. Landscape function analysis: procedures for monitoring and assessing landscapes with special reference to minesites and rangelands. CSIRO Sustainable Ecosystems: Canberra, Australia; 82.

Valentin C, d'Herbes JM, Poesen J. 1999. Soil and water components of banded vegetation patterns. *Catena* **37**: 1–24. https://doi.org/10.1016/S0341-8162(99)00053-3.

Walker BH (ed). 2012. Management of semi-arid ecosystems. Elsevier: Amsterdam, The Netherlands.

Wardle DA, Bonner KI, Barker GM. 2002. Linkages between plant litter decomposition, litter quality, and vegetation responses to herbivores. *Functional Ecology* **16**: 585–595. https://doi.org/10.1046/j.1365-2435.2002.00659.x.

Waters CM, Orgill SE, Melville GJ, Toole ID, Smith WJ. 2016. Management of grazing intensity in the semi-arid rangelands of Southern Australia: effects on soil and biodiversity. *Land Degradation & Development* . https://doi.org/10.1002/ldr.2602.

Zomer RJ, Trabucco A, Bossio DA, van Straaten O, Verchot LV. 2008. Climate change mitigation: a spatial analysis of global land suitability for clean development mechanism afforestation and reforestation. *Agriculture, Ecosystems & Environment* **126**: 67–80. https://doi.org/10.1016/j.agee.2008.01.014.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web site:

Table S1. List of palatable and unpalatable shrubs and grasses. The identification of species was carried out according to Correa (1969, 1971, 1978, 1984, 1985, 1988, 1999).

Figure S2. Relationship between the annual integral of Normalized Difference Vegetation Index (I-NDVI) in the pixel where the field sampling site was located and the mean I-NDVI calculated from a square of 5,000 hectares centered on each site location. $N = 85$ sites randomly chosen.

Appendix S3. Obtaining Landscape Functional Analysis indices from Tongway & Hindley's methodology (Tongway & Hindley 2004) modified by Oliva *et al.* (2011)

Figure S4. *A priori* conceptual model depicting pathways by which aridity and grazing pressure may influence directly or indirectly (through its influence on vegetation structure) upon soil functioning latent variable. Arrows indicate a hypothesized causal influence of one variable upon another. The numbers in the arrows denote example references used to support our predictions, which can be found below. SR: species richness. US: unpalatable shrubs cover. PS: palatable shrubs cover. UG: unpalatable grasses cover. PG: palatable grasses cover. STA: stability index. INF: infiltration index. NUT: nutrient cycling index.