

Research

Regional productivity mediates the effects of grazing disturbance on plant cover and patch-size distribution in arid and semi-arid communities

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Patch-size distribution and plant cover are strongly associated to arid ecosystem functioning and may be a warning signal for the onset of desertification under changes in disturbance regimes. However, the interaction between regional productivity level and human-induced disturbance regime as drivers for vegetation structure and dynamics remain poorly studied. We studied grazing disturbance effects on plant cover and patchiness in three plant communities located along a regional productivity gradient in Patagonia (Argentina): a semi-desert (low-productivity community), a shrub-grass steppe (intermediate-productivity community) and a grass steppe (high-productivity community). We sampled paddocks with different sheep grazing pressure (continuous disturbance gradients) in all three communities. In each paddock, the presence or absence of perennial vegetation was recorded every 10 cm along a 50 m transect. Grazing effects on vegetation structure depended on the community and its association to the regional productivity. Grazing decreased total plant cover while increasing both the frequency of small patches and the inter-patch distance in all communities. However, the size of these effects was the greatest in the high-productivity community. Dominant species responses to grazing explained vegetation patch- and inter-patch-size distribution patterns. As productivity decreases, dominant species showed a higher degree of grazing resistance, probably because traits of species adapted to high aridity allow them to resist herbivore disturbance. In conclusion, our findings suggest that regional productivity mediates grazing disturbance impacts on vegetation mosaic. The changes within the same range of grazing pressure have higher effects on communities found in environments with higher productivity, markedly promoting their desertification. Understanding the complex interactions between environmental aridity and human-induced disturbances is a key aspect for maintaining patchiness structure and dynamics, which has important implications for drylands management.

Keywords: desertification, disturbance regime, grazing pressure, Patagonia, patchiness, sheep grazing, vegetation structure



Introduction

In recent years, it has been proposed that vegetation patchiness may be a warning signal for the onset of desertification and its relevance to monitor degradation processes in comparison with perennial plant cover has been discussed (Rietkerk et al. 2004, Kéfi et al. 2007, Maestre and Escudero 2009, Berdugo et al. 2017). In arid ecosystems, patchiness structure (i.e. patch-size distribution) controls ecosystem functioning (Aguiar and Sala 1999), including productivity, decomposition, water dynamics, nutrient cycling and demographic processes (Ludwig and Tongway 1995). The maintenance of this functioning is highly dependent on the conservation of patch attributes such as density and size distribution, which are associated with total plant cover (Ludwig and Tongway 1995, Maestre and Cortina 2004). Patch structure and dynamics may change according to the ecosystem. This is particularly true about ecosystem aridity, which determines primary production, an integrative attribute of ecosystem structure and functioning (McNaughton et al. 1989). Aridity usually strongly interacts with human-induced disturbances (commonly domestic grazing herbivory) (Kéfi et al. 2007). However, this interaction remains poorly studied.

Grazing by domestic livestock is a major disturbance factor in rangelands (Soriano et al. 1983, Ares et al. 1990, Milchunas and Lauenroth 1993, Oesterheld et al. 1999, Asner et al. 2004, Lal 2004) and it has been identified as one of the main causes of desertification (Brown et al. 1997). However, estimating grazing impacts is a controversial topic in rangeland ecology (Belsky 1992, Milchunas and Lauenroth 1993, Semmartin and Oesterheld 1996, Oesterheld et al. 1999, Taddese et al. 2002, Briske et al. 2008) and its effects on patchiness have been inconsistent in South American arid ecosystems (Bisigato and Bertiller 1997, Cipriotti and Aguiar 2005). It has been proposed that grazing effects on vegetation depend on the interaction between regional productivity (aridity) and plant traits associated to stress resistance, determining the community composition and vegetation responses to grazing (Milchunas et al. 1988, Stuth 1991, Agrawal 2000, Louthan et al. 2013). The simultaneous effects of stress by lack of resources and stress by grazing have been mainly studied through hypotheses developed and tested at individual plant level (Maschinski and Whitham 1989) or community level (Milchunas et al. 1988). Nonetheless, there is little evidence of how grazing disturbance interacts with regional productivity gradients and differently affects patchiness in rangeland communities.

Most of our knowledge about grazing effects on vegetation comes from studies that compare enclosure areas with grazed areas in one environmental location (Milchunas and Lauenroth 1993, Pizzio et al. 2016, Herrero-Jáuregui and Oesterheld 2018), generally without an accurate characterization of grazing pressure. Nevertheless, general models indicate that experimental evidence of different grazing pressures along productivity gradients is needed to test hypotheses about grazing effects (Milchunas et al. 1988, Westoby et al. 1989, Cingolani et al. 2005, Oesterheld and Semmartin

2011). Grazing pressure (herbivore consumption in relation to plant productivity) is an important driver which controls the impact of herbivores and vegetation responses (Hart et al. 1993, Oesterheld and Semmartin 2011). However, grazing pressure may covariate with primary production along regional productivity gradients, confounding effects and responses of vegetation when grazed and ungrazed situations are compared (Cyr and Face 1993, Bråthen et al. 2007, Oesterheld and Semmartin 2011, Louthan et al. 2013). Here, we estimated grazing pressure by the same herbivore species (sheep) and we used it as a predictive variable, obtaining the same range (from permanent enclosures to intensively grazed paddocks) in three rangeland communities with different productivity located in the same region. In this way, biogeographical history was also standardized.

The objective of our work was to study domestic grazing disturbance effects on patchiness in three rangeland communities located along a regional productivity gradient. Particularly, we estimated sheep grazing pressure impacts on patch density, patch-size distribution, inter-patch distance, vegetation cover and the abundance of dominant species composing vegetation patches. Our hypothesis states that grazing effects (degree of change in vegetation variables) depend on the plant community productivity. Changes produced by increasing grazing pressure are lower in communities found in environments with lower productivity because traits of dominant plant species adapted to high aridity allow them to resist or avoid herbivory (Coley et al. 1985, Coughenour 1985, Milchunas et al. 1988). This occurs because those traits enabling plants to withstand drought and grazing stress are similar, due to the fact that these selection pressures converge in more stressful ecosystems (Milchunas et al. 1988, Quiroga et al. 2010). Thus, the higher resistance of species covering patches in more arid communities reduces grazing effects, maintaining patch structure and vegetation cover. In contrast, in communities found in environments with higher productivity, herbivory resistance capacity is lower because those traits enabling dominant species to adapt to grazing, diverge from other environmental adaptations that enhance survival (e.g. higher aboveground growth to compete for light) (Milchunas et al. 1988).

Material and methods

Study site description

The study was conducted on different dominant plant communities in arid and semi-arid Patagonian rangelands, Argentina (Table 1), distributed along over a 150 km regional-transect. Communities are: (a) semi-deserts of Central District (45°20'S, 69°53'W), hereafter low-productivity community, (b) grass-shrub steppes of Occidental District (45°24'S, 70°17'W), hereafter intermediate-productivity community and (c) grass steppes of Subandean District (45°35'S, 71°25'W), hereafter high-productivity community (León et al. 1998; Fig. 1, Table 1). These rangelands are

Table 1. Characterization of the three studied communities located along a regional productivity gradient: low-productivity community (semi-deserts of Central District), intermediate-productivity community (grass-shrub steppes of Occidental District) and high-productivity community (grass steppes of Subandean District) (data from Defossé and Bertiller 1991, Fernández et al. 1991, Bustos et al. 1994, Bertiller et al. 1995, Schulze et al. 1996, Bertiller and Bisigato 1998, León et al. 1998, Paruelo et al. 1998, Jobbágy and Sala 2000, Austin and Sala 2002, Bertolami et al. 2002, Oñatibia et al. 2015, Oñatibia and Aguiar 2016).

Characteristics	Low-productivity community	Intermediate-productivity community	High-productivity community
Annual mean precipitation (mm)	125	170	360
Mean temperature (Jul/Jan)	4°C/18°C	2°C/14°C	3°C/12°C
Aridity index (precipitation/ potential evapotranspiration)	0.15	0.35	0.5
Soil type	Paleoargid	Calciorthid	Aridisol/Inceptisol
Soil depth (cm)	30	40	>200
Soil layers (cm)	0–30 clay with stones	0–40 fine sand and gravel	0–100 alluvial sandy loam and gravel
texture	30–50 caliche layer	40–70 caliche layer	
Total richness	20	27	35
Plant cover (%)	30	50	60
ANPP (g m ⁻² year ⁻¹)	22	56	101
Dominant species (life form)	<i>Nassauvia glomerulosa</i> (D)	<i>Pappostipa speciosa</i> (G) <i>Pappostipa</i>	<i>Festuca pallescens</i> (G)
D: dwarf shrub	<i>Chuquiraga aurea</i> (D)	<i>humilis</i> (G)	<i>Poa ligularis</i> (G)
G: grass	<i>Poa ligularis</i> (G)	<i>Poa ligularis</i> (G)	<i>Rytidosperma virescens</i> (G)
S: shrub	<i>Pappostipa humilis</i> (G)	<i>Mulinum spinosum</i> (S) ¹	<i>Bromus</i> spp. (G)
	<i>Pappostipa ibarii</i> (G)	<i>Senecio filaginoides</i> (S)	
		<i>Adesmia volckmannii</i> (S)	

¹*Mulinum spinosum* has been recently renamed as *Azorella prolifera*

mostly used for wool production and have been grazed by sheep for more than one hundred years. In general, along the three communities, grazing management is extensive, in large continuously grazed paddocks (Golluscio et al. 1998).

Data collection

Comparative studies were performed to evaluate grazing pressure effect on patchiness by recording density, size and composition (individual species cover) of vegetation patches in three communities located along sites with different regional productivity. Samplings were conducted in grazing exclosures and grazed commercial paddocks with ample differences in stocking rates during the last 20 years. We selected and evaluated 19 paddocks located in the low-productivity community, 14 in the intermediate-productivity community and 20 in the high-productivity community.

With this sampling effort, we assumed that the heterogeneity of grazing situations was represented in each community. In this sense, in all communities we measured in ungrazed paddocks (without domestic herbivores for more than 20 years), moderately grazed paddocks (0.12–0.15 sheep ha⁻¹ year⁻¹ in the low-productivity community, 0.2 sheep ha⁻¹ year⁻¹ in the intermediate-productivity community and 0.42–0.75 sheep ha⁻¹ year⁻¹ in the high-productivity community) and intensively grazed paddocks (0.21–0.22 sheep ha⁻¹ year⁻¹ in the low-productivity community, 0.5–0.6 sheep ha⁻¹ year⁻¹ in the intermediate-productivity community and 1–1.25 sheep ha⁻¹ year⁻¹ in the high-productivity community). In each paddock, we selected a representative area of the dominant plant community (topographic, physiognomic and floristically homogeneous). Inside this area, we randomly outlined a 50 m transect. Taking into account plant cover differences (i.e. patch grain) in the three communities, we recorded

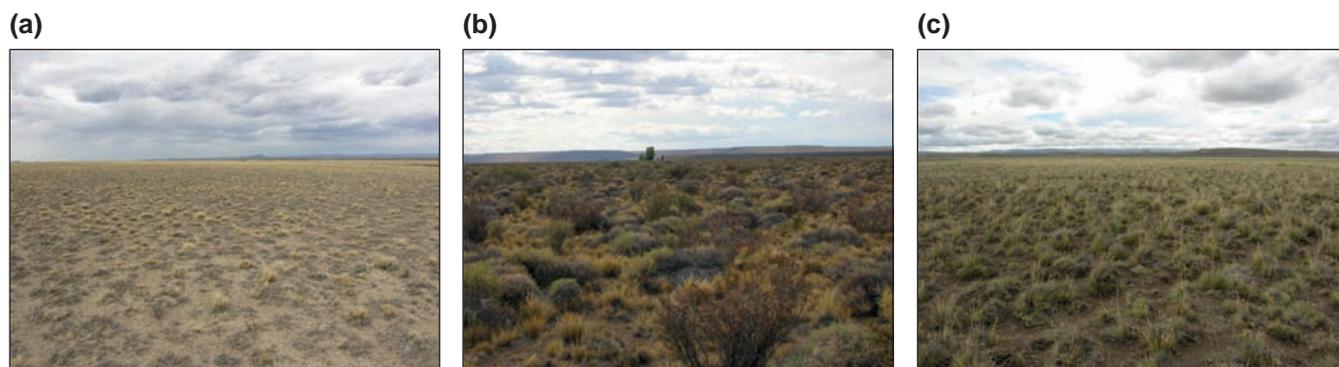


Figure 1. Patagonian steppe communities located along a regional productivity gradient: (a) low-productivity community (Central District, 45°20'S, 69°53'W), (b) intermediate-productivity community (Occidental District, 45°24'S, 70°17'W) and (c) high-productivity community (Subandean District, 45°35'S, 71°25'W). Photo credit: G. Oñatibia.

perennial plant cover (the identity of the species or standing dead biomass) or bare soil, every 0.1 m along that transect (in 500 consecutive segments). For the purpose of this study, a vegetation patch was defined as every discrete section of at least 0.1 m along each transect covered with perennial vegetation and/or standing dead biomass, separated by at least 0.1 m of bare soil. Thus, total cover, size and number of patches, distance between patches and specific cover of dominant species were estimated. Furthermore, sheep dung density was estimated as an independent index of local and more recent grazing pressure than the average stocking rate of the paddock during the last 20 years (Lange and Willcocks 1978, von Müller et al. 2012). Paddock heterogeneity determines local differences in grazing intensity, which can be indirectly estimated through dung density (Bisigato and Bertiller 1997, von Müller et al. 2012, Oñatibia 2017). We counted all faecal pellets into a 50 m-long 0.2 m-wide plot set along the same transect.

Grazing pressure estimation

Grazing pressure in each transect (Eq. 1) was estimated through the quotient between the average forage consumption of the paddock and the average aboveground net primary productivity (ANPP), weighed with a local index that considered the faecal pellets density in each transect (plot), related with the average density of all transects in each community. Thus, we capture the effect of the historical stocking rate of each paddock and the local grazing intensity in the measured area. In arid and semi-arid ecosystems such as the study sites, sheep faeces have a residence time of several years (Bahamonde et al. 2017) and are useful for estimating local medium-term grazing pressure. Therefore, grazing pressure for each transect (GP_{ti}) is:

$$\text{grazing pressure}_{ti} (GP_{ti}) = (C_{pi}/ANPP_{ti}) \times FI_{ti} \quad (1)$$

where C_{pi} is the average sheep forage consumption of the paddock i ($\text{kg dry matter ha}^{-1} \text{ year}^{-1}$), where transect i was outlined. This consumption was estimated multiplying the stocking rate of the paddock ($\text{sheep ha}^{-1} \text{ year}^{-1}$) (average of last 20 years, supplied by ranch owners or managers) by the forage consumption per sheep. We assumed that forage intake of a 40-kg sheep is $1 \text{ kg dry matter day}^{-1}$ (Agricultural Research Council 1980); $ANPP_{ti}$ is the average aboveground net primary productivity ($\text{kg dry matter ha}^{-1} \text{ year}^{-1}$) in transect i , estimated from remote sensing MODIS imagery (Supplementary material Appendix 1 Eq. A1); and FI_{ti} is the faecal index for transect i (Eq. 2).

$$\text{faecal index}_{ti} (FI_{ti}) = 1 + (\text{no. FP}_{ti} - \text{no. FP}_{xci})/\text{no. FP}_{xci} \quad (2)$$

where no. FP_{ti} is the faecal pellet density in transect i ; no. FP_{xci} is the average of faecal pellets density of all transects

outlined in grazed paddocks in community i (low-, intermediate- and high-productivity); and 1 is a corrector factor to make values positive. The term $(\text{no. FP}_{ti} - \text{no. FP}_{xci})/\text{no. FP}_{xci}$ had values from -1 to positive (with maximum around 1 for the faecal pellet density range of this study). Thus, the faecal index (FI) was zero when there were no faecal pellets in the transect (plot), had positive values when faecal density was > 0 and the maximum value of the index was around 2 with data from this study. In this latter case, the number of faeces in the transect approximately doubled the community average.

Data analysis

To evaluate grazing effects on vegetation cover and patchiness, regression analyses were performed between grazing pressure (Eq. 1) and different measured variables: total plant cover, patch average size, inter-patch distance and patch density. For these analyses, we used each transect average value of all variables ($n=19$ paddocks in the low-productivity community, $n=14$ in the intermediate-productivity community and $n=20$ in the high-productivity community). We compared two types of effect sizes to assess the influence of communities (related to the regional productivity) as control of grazing impacts: regression slope and Pearson's correlation coefficient (r) (Nakagawa and Cuthill 2007). Regression slopes (and y-axis intercepts) were compared among communities through F-test. Besides, in order to compare Pearson coefficients among communities, confidence intervals were generated using Fisher r to z transformation, which converts r distribution into the variable z that is normally distributed: $z = 1/2 \ln [(1+r)/(1-r)]$ (Nakagawa and Cuthill 2007). Specific cover was also assessed as a function of grazing pressure with regression analysis for each species. In the high-productivity community, we detected a non-linear response of the dominant species *Festuca pallescens*, and its cover was evaluated as a function of grazing pressure through non-linear regression.

To evaluate the effect of grazing on patch-size distribution in each community, curves of cumulative frequency of vegetation and bare soil patch-size were constructed. For this purpose, we used all measured patches and inter-patches areas in all paddocks, integrating paddocks in three grazing intensity levels, based on the stocking rate: ungrazed, moderately grazed and intensively grazed (see stocking rate values of each community and description in data collection section). Cumulative frequency distributions of each grazing intensity level were compared in pairs within each community using Kolmogorov–Smirnov tests for nonparametric distributions. Statistics D resulting from this test represents the distance between each pair of curves and reflects the effect size on patch-size and inter-patch-size distributions. Bonferroni corrections were applied in this analysis. Thus, significant differences were considered when p -value was < 0.016 .

Data deposition

Data available from the Dryad Digital Repository: < <http://dx.doi.org/10.5061/dryad.d9727v4> > (Oñativia et al. 2018).

Results

Increasing grazing pressure reduced total perennial plant cover along the three studied communities (Fig. 2a). However, grazing effect size was higher in the high-productivity community, where plant cover decreased by about 30% along the grazing gradient, from values close to 70% in enclosure areas to 40% in those intensively grazed. The regression slope between cover and grazing pressure was more pronounced (more than twice as high) and significantly differed from the other two communities ($F=6.08$, $p=0.02$ versus low-productivity community and $F=11.81$, $p < 0.01$ versus intermediate-productivity community). Pearson's correlation coefficient showed the same pattern (Supplementary material Appendix 2 Fig. A1a). In the low- and intermediate-productivity communities, plant cover similarly decreased between 10 and 15% along the grazing gradient, although average cover was lower in the low-productivity community

(equal slopes, $F=0.334$, $p=0.57$; unequal y-axis intercepts, $F=34.62$, $p < 0.01$ versus intermediate-productivity community) (Fig. 2a).

Average patch size decreased more than 10 cm along the grazing pressure gradient in the high-productivity community, decreasing to a lower extent in the low-productivity community and remaining unchanged in the intermediate-productivity one (Fig. 2b). Size effect estimated through Pearson's coefficients (Supplementary material Appendix 2 Fig. A1b) and regression slopes were marginally different between the low- and high-productivity communities (slopes, $F=3.2$, $p=0.08$), and similar between the low- and intermediate-productivity communities (equal slopes, $F=0.052$, $p=0.82$; unequal y-axis intercepts, $F=63.8$, $p < 0.01$) as between the intermediate- and high-productivity communities (equal slopes, $F=2.33$, $p=0.14$; equal y-axis intercepts, $F=0.483$, $p=0.49$). Grazing pressure effects on inter-patch distance were also higher in the high-productivity community (unequal slopes, $F=13.89$, $p < 0.01$ versus low-productivity community and $F=15.78$, $p < 0.01$ versus intermediate-productivity community), where average inter-patch distance increased from 17 cm to 40 cm along the grazing gradient (the slope was more than three times higher than in the other communities, Fig. 2c). In the low and

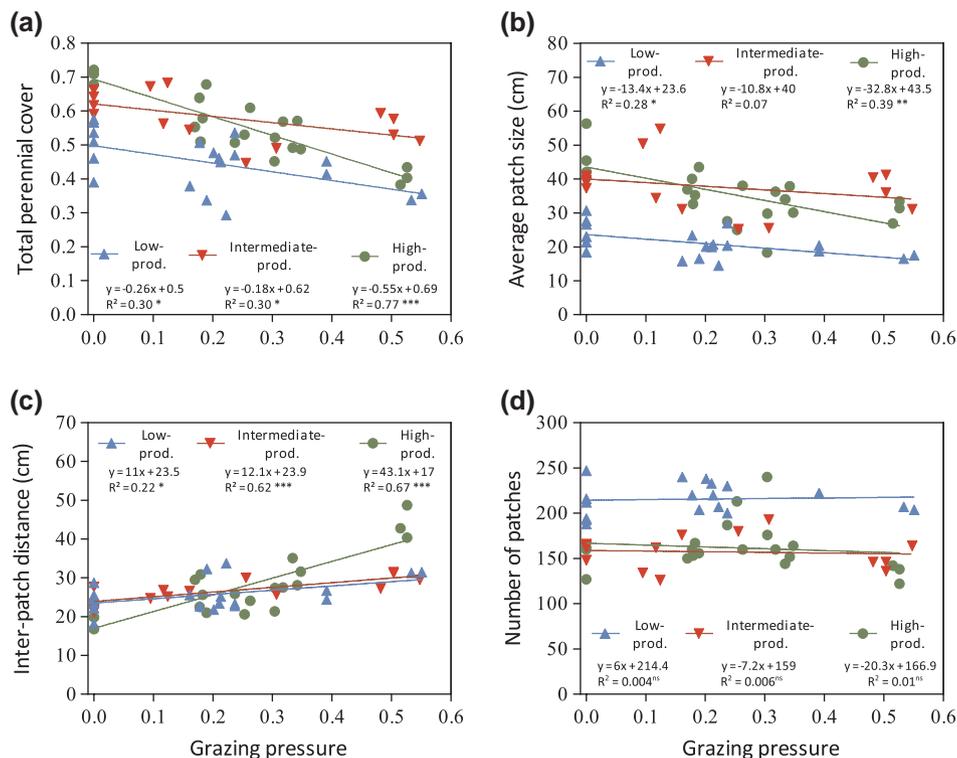


Figure 2. Linear regressions between grazing pressure and (a) total perennial cover, (b) average patch size, (c) average inter-patch distance and (d) the number of patches along 100 m. Blue triangles represent the low-productivity community, red triangles represent the intermediate-productivity community and green circles represent the high-productivity community. Asterisks next to the coefficient of determination (R^2) indicate p-values of each regression: (*) between 0.05 and 0.01; (**) between 0.01 and 0.001; (***) < 0.001; (ns) > 0.05.

intermediate-productivity communities, average inter-patch distance increased around 6 cm along the grazing gradient, and there were no differences between both communities (equal slopes, $F=0.034$, $p=0.85$ and equal y-axis intercepts, $F=0.33$, $p=0.57$) (Fig. 2c). Pearson's correlation coefficient for this variable only showed significant differences between the high- and low-productivity communities (Supplementary material Appendix 2 Fig. A1c). The number of patches was not affected by grazing in any of the three communities (Fig. 2d, 3d). Slopes and Pearson's correlation coefficients of regressions between the number of patches and grazing pressure did not differ from zero ($p > 0.05$ in all cases). Average patch number was higher in the low-productivity community

and significantly differed from the other two communities, independently of the grazing pressure (unequal y-axis intercepts; $F=83.41$, $p < 0.01$ versus intermediate-productivity community and $F=50.79$, $p < 0.01$ versus high-productivity community).

Patch-size and inter-patch-size distributions of each community were differently affected by grazing (Fig. 3). In the low-productivity community, grazing (both moderate and intensive) increased the frequency of small patches in comparison to those ungrazed (ungrazed versus moderately grazed: $D=0.1495$, $p < 0.001$ and ungrazed versus intensively grazed: $D=0.1322$, $p=0.002$) (Fig. 3a) and did not affect inter-patch-size distributions (Fig. 3d). In this

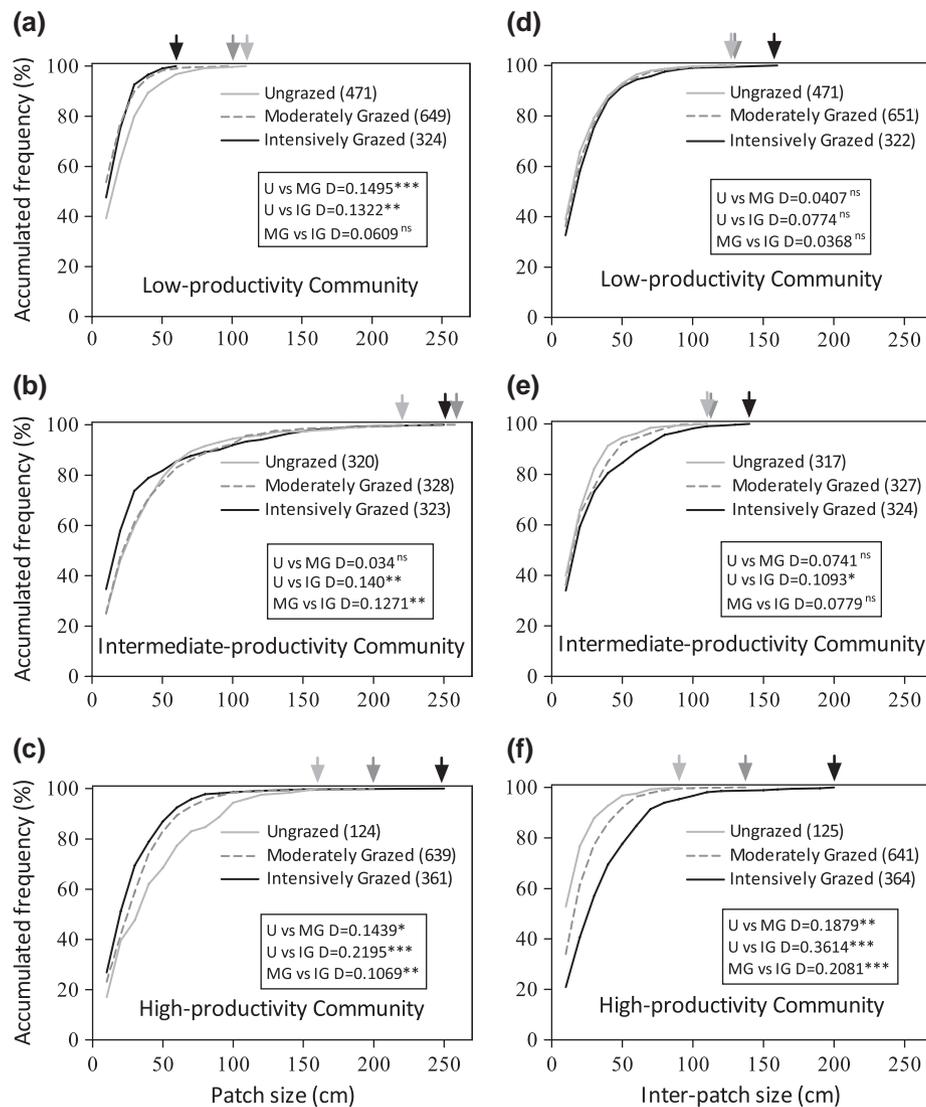


Figure 3. Accumulated frequency (%) of patch-size (patch-size distribution) and inter-patch-size (inter-patch-size distribution) in three communities located along a regional productivity gradient (low-productivity community, intermediate-productivity community and high-productivity community), under three grazing intensities (ungrazed, moderately grazed and intensively grazed). Arrows indicate the maximum size reached by each distribution. Numbers between brackets show the number of patches or inter-patches sections in each curve. Tables indicate the D statistics and p -values resulting from Kolmogorov-Smirnov test between each pair of distribution curves: (*) between 0.05 and 0.01; (**) between 0.01 and 0.001; (***) < 0.001 ; (ns) > 0.05 .

community, the effect of grazing on patchiness (comparing between ungrazed and intensively grazed) was lower than in the other communities. Besides, the range of patch sizes was also smaller (from 10 to 110 cm) and no patches larger than 60 cm in size were found under intensively grazed conditions (Fig. 3a). In the intermediate-productivity community, the frequency of small patches increased in intensively grazed sites ($D=0.140$, $p=0.003$ versus ungrazed and $D=0.122$, $p=0.009$ versus moderately grazed) (Fig. 3b) and the inter-patch-size distributions only marginally differed between ungrazed and intensively grazed sites ($D=0.109$, $p=0.04$) (Fig. 3e). This latter change was greater than in the low-productivity community (Fig. 3). Finally, the strongest effects of grazing were found in the high-productivity community. On the one hand, grazing greatly increased the frequency of small patches (ungrazed versus intensively grazed: $D=0.219$, $p < 0.001$; moderately versus intensively grazed: $D=0.107$, $p=0.009$ and ungrazed versus moderately grazed: $D=0.144$, $p=0.024$, being this latter difference marginal after Bonferroni correction). Nevertheless, the biggest patches were also found in grazed sites (200 cm in moderate grazing and 250 cm in intensive grazing). In other words, grazing increased the heterogeneity of patch-size distribution in this community (Fig. 3c). On the other hand, the highest frequency of small inter-patch areas was found in ungrazed sites (ungrazed versus moderately grazed: $D=0.188$, $p=0.001$ and ungrazed versus intensively grazed: $D=0.361$, $p < 0.001$) while the lowest frequency was found in intensively grazed sites (intensively versus moderately grazed: $D=0.208$, $p < 0.001$). The biggest inter-patch areas (200 cm) were found in intensively grazed sites (Fig. 3f).

Specific plant cover of perennial dominant species composing patches showed diverse responses to increasing grazing pressure, from neutral to positive and negative (Table 2). In the low-productivity community, plant cover of most of the few species composing patches presented low responses to grazing (Table 2). In the intermediate-productivity community, some grass species, *Poa ligularis*, *P. speciosa* and *Bromus pictus* markedly decreased, while *Pappostipa major* and *P. humilis* increased their cover along the grazing pressure gradient. Besides, grazing did not significantly change shrub species cover in this community (Table 2). In the high-productivity community, plant cover of *P. ligularis*, *B. pictus* decreased, while there were no significant positive linear responses to grazing. However, the dominant species (*F. palleescens*) showed a non-linear response, increasing its cover as grazing pressure changed from low (ungrazed) to moderate, and decreasing as pressure increased from intermediate to intensive ($F. palleescens$ cover (%) = -207.9 grazing pressure² + 128.4 grazing pressure + 11.34 , $R^2=0.34$). Finally, increasing grazing pressure markedly decreased standing dead biomass cover in this community (Table 2).

Discussion

In this Patagonian regional gradient, domestic grazing impacts on vegetation cover and patchiness depended on the local productivity context. Grazing disturbance decreased plant cover while increasing the frequency of small patches and the distance between patches in the three studied communities. However, these effects were, in general, more than

Table 2. Grazing pressure effects on plant cover (%) of perennial dominant species in three discrete communities located along a regional productivity gradient (low-productivity community, intermediate-productivity community and high-productivity community). Values in the table are slope, y-axis intercept, coefficient of determination (R^2) and p-value of the linear regressions between grazing pressure and plant cover of each dominant species. The species marked with an asterisk (*) presented a non-linear response, which was developed in Results section. Characterization of these dominant species can be found in Supplementary material Appendix 3 Table A1.

Community	Dominant species	Slope	y-axis intercept	R^2	p-value
Low-productivity	<i>Nassauvia glomerulosa</i>	4.17	32.63	0.01	= 0.7
	<i>Poa ligularis</i>	-4.75	2.17	0.14	= 0.11
	<i>Pappostipa speciosa</i>	1.17	0.12	0.08	= 0.25
	<i>Pappostipa ibarii</i>	-10.38	4.89	0.40	< 0.01
	Standing dead biomass	-9.65	5.94	0.29	= 0.02
Intermediate-productivity	<i>Poa ligularis</i>	-25.19	17.72	0.62	< 0.01
	<i>Pappostipa speciosa</i>	-11.45	9.71	0.47	< 0.01
	<i>Pappostipa major</i>	17.68	0.64	0.42	= 0.01
	<i>Pappostipa humilis</i>	9.39	2.80	0.55	< 0.01
	<i>Bromus pictus</i>	-1.86	0.83	0.56	< 0.01
	<i>Mulinum spinosum</i>	4.87	3.64	0.13	= 0.20
	<i>Senecio filaginoides</i>	1.14	1.04	0.04	= 0.49
	<i>Adesmia volckmannii</i>	-0.28	2.32	0.001	= 0.90
Standing dead biomass	-10.94	20.35	0.14	= 0.18	
High-productivity	<i>Festuca palleescens</i> *	19.55	20.71	0.07	= 0.28
	<i>Poa ligularis</i>	-13.28	6.97	0.17	= 0.07
	<i>Bromus pictus</i>	-19.13	7.39	0.29	= 0.01
	<i>Mulinum spinosum</i>	6.34	0.01	0.05	= 0.36
	Standing dead biomass	-36.42	23.28	0.52	< 0.01

twofold higher in the high-productivity community, in comparison with communities found in less productive environments. The results support our hypothesis because grazing effects depended on the degree of grazing resistance among dominant species in each community. In the low-productivity community, there were no substantial decreasing responses from dominant species (e.g. *Nassauvia glomerulosa*), indicating high grazing resistance of those species covering patches. In the intermediate-productivity community, there were species that decreased as a result of grazing (low-resistant species), although there were also neutral (shrubs) and positive responses from other grass species (resistant species), which increased their abundance, partially compensating the decrease of low-resistant species. Finally, in the high-productivity community, there were only significant linear negative responses to increasing grazing pressure from dominant species, indicating lower total resistance in these environments. In summary, patterns found in these South American rangelands with a similar biogeographical origin support the notion that patchiness response to grazing pressure may depend on the evolutionary context associated with the regional aridity, which determines dominant species idiosyncrasy (Milchunas et al. 1988). There is a broad theoretical discussion on the role that species identity and biodiversity play on community responses to stress. It has been demonstrated that higher biodiversity reduces ecosystem functioning variability and increases resistance to climatic stress (Tilman and Downing 1994, Loreau et al. 2001, Isbell et al. 2015). However, in communities with high dominance (most of plant cover explained by one or few dominant species) and submitted to different levels of biotic stress (grazing disturbance), the role of biodiversity is unclear. Indeed, the most diverse community of this study (higher richness) was the most affected by grazing, highlighting the role of dominant species identity as driver of community response to biotic stress.

One of the main results of our study was that plant cover decreased in the three studied communities, mainly associated to the miniaturization of patches as a consequence of grazing. Herbivores can degrade patches by persistent defoliation and trampling (Ludwig and Tongway 1995). The loss of large plant patches may trigger larger scale degradation and desertification processes (Maestre and Escudero 2009). This occurs because vegetation patches enhance functions such as productivity and nutrient cycling at spatial scales larger than their own canopies, being critical for the structure and functioning of arid and semi-arid ecosystems (Maestre and Cortina 2004). Patch-size distribution modifies the spatial patterns of soil moisture and transport of sediments and nutrients, being critical for the structure, functioning and the control of water and wind erosion rates (D'Odorico et al. 2007, Ravi et al. 2007, 2010). It has been proposed that in order to prevent arid-lands from degrading, a full range of large to small-scale patches should be maintained (Ludwig and Tongway 1995). Besides, our findings showed that grazing decreased the vegetation connectivity (i.e. increased inter-patch distance), which has been recently considered a key component of arid

land ecosystems function (Ravi et al. 2010, Okin et al. 2015). The greater inter-patch distance diminishes the propagules retention capacity and can increase the erosion risk, both of which, in rangelands, depend on bare soil extent and configuration (Aguiar and Sala 1994, 1997, Pueyo et al. 2008, Augustine et al. 2012). In contrast, where bare soil areas are small and interspersed with vegetated patches, erosion risk is minimal and retention capacity is enhanced (Aguiar and Sala 1997, Ludwig et al. 2007, Augustine et al. 2012).

Grazing disturbance promotes desertification in the high-productivity community since after degradation structural characteristics converge with those found in the low-productivity community. For example, plant cover of intensively grazed sites was as low as in environments originally presenting five times lower production, indicating an extremely severe change induced by grazing in the high-productivity community (Bertiller and Bisigato 1998). In our study, no significant pattern of species increase was detected in this community. Nevertheless, degraded sites usually present higher abundance of shrubs and more xeric grass species, which are generally dominant in environments with higher aridity degree (León and Aguiar 1985, Bertiller et al. 1995, Paruelo et al. 2008). This shrub invasion explains the emergence of some very large patches in intensively grazed sites, which are mainly composed by *Mulinum spinosum* plants (León and Aguiar 1985, Bertiller and Bisigato 1998). Besides, the dominant species of the high-productivity community (*Festuca pallelescens*) increased its cover under moderate grazing pressure in comparison with ungrazed situations, but decreased under intensively grazed conditions. This pattern indicates that this species has an intermediate sheep preference degree, though it is heavily consumed by sheep when other more highly preferred forage species decrease or disappear (Oñatibia et al. 2015, Oñatibia and Aguiar 2016).

Recently, it has been proposed that the structure and functioning of vegetation patches are linked to arid ecosystem resistance and resilience (López et al. 2013). Resistance is the ability of an ecosystem to tolerate a disturbance without suffering significant changes in its structure and functioning. Resilience is the capacity to return to the condition previous to a disturbance, once this is suppressed (Westman 1978, Stringham et al. 2003, López et al. 2013). Here, we showed that communities dominated by resistant species (low-productivity level) presented lower grazing effects on patchiness, thus reducing grazing impacts on ecosystem functioning (López et al. 2013). However, these more 'resistant' communities would present low resilience due to the fact that plant species growing under high aridity conditions present reduced potential to regrow after disturbances (Louthan et al. 2013, Oñatibia 2017). This represents a potential threat for ecosystems with high aridity degree, because once plant resistance critical threshold is crossed, damage could be irreversible (López et al. 2013). In this sense, it should be mentioned that here we evaluated the effects of grazing pressure during the last two decades. Previously, domestic grazing may have differentially affected the three evaluated communities,

leading to different degradation states (del Valle et al. 1998, Aagensen 2000, Mazzonia and Vazquez 2009). This could also be partly determining the responses magnitude found in the studied communities. Since there is no record of ecosystem structure before settlements solving this 'initial effect' in the Patagonian steppes, this issue is uncertain and remains contended (Verón et al. 2006).

Our approach to evaluate grazing impacts solved some current research limitations related to the complexity of rangeland plant communities. Generally, responses to grazing depend on local production potential, but studying influences of aridity (communities with different productivity level) and grazing pressure independently of each other becomes difficult because they often correlate across natural environmental gradients (Anderson et al. 2007, Bråthen et al. 2007, Louthan et al. 2013). Thus, the greater grazing effect on vegetation in communities with high productivity can be attributed to the fact that these rangelands have higher grazing pressure (Cyr and Face 1993). In our study, we deliberately controlled grazing pressure (measuring and using it as a predictive variable) in the three communities located along the regional productivity gradient. Thereby, we could separate the effects of grazing and the environmental gradient, concluding that grazing impact was higher in the high-productivity community, independently of the herbivore abundance and diversity. Besides, as the grazing pressure was estimated (i.e. contemplating the sheep consumption per unit area in relation to the ANPP while achieving continuous grazing pressure gradients), the approach is applicable to other ecosystems and the obtained results about grazing impacts are comparable among them.

The results of this study were obtained from three communities located along a regional productivity gradient, in which precipitation, soil properties and predominant life-form abundance co-vary in the same way determining the aridity level and primary productivity (Table 1). Vegetation patterns (and responses to grazing) in arid ecosystems can be controlled by water and nutrient scarcity, soil properties and woody species abundance (Aguiar and Sala 1999, von Hardenberg et al. 2001, Goslee et al. 2003, Soliveres et al. 2014). Here, the relative importance of these drivers on vegetation responses was not separately evaluated, which should be taken into account when interpreting results.

In conclusion, our study moves forward from describing changes in patchiness and plant cover over geographical gradients (Kéfi et al. 2007) in an attempt to infer putative controls of the degradation process induced by human land use intensification. Our findings suggest that plant cover and patchiness structure are more affected by domestic herbivores in communities found in environments presenting higher productivity. In these ecosystems, high grazing pressure degrades vegetation patches, promoting a desertification process (Schlesinger et al. 1990, Kéfi et al. 2007). On the contrary, communities found in environments with lower productivity showed high level of grazing resistance, as was measured in other arid rangeland ecosystems

(Augustine et al. 2012). Understanding the complex interactions between environmental aridity and human-induced disturbances is a key aspect for maintaining patchiness structure and dynamics and has very important implications for drylands management.

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Author contributions – GRO, LB and MRA conceived the ideas and designed the research; GRO and LB collected the data and conducted the analysis. GRO led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Supplementary material (available online as Appendix oik-05104 at <www.oikosjournal.org/appendix/oik-05104>). Appendix 1. Estimation of aboveground net primary productivity (Eq. A1). Appendix 2. Effect size of grazing, estimated through Pearson's correlation coefficients, in communities located along a regional productivity gradient (Fig. A1). Appendix 3. Dominant species ecological traits (Table A1).