Changes in vegetation structure induced by domestic grazing in Patagonia (Southern Argentina)

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ABSTRACT

We analyzed the structural differences associated with grazing exclusion on vegetation by studying 24 grazed—ungrazed paired sites in Patagonia (Argentina). Our objectives were to evaluate the effect of grazing on plant species composition, plant diversity, the relative abundance of plant functional types, and the vertical and horizontal structure of the plant community. This study across the shrub-grass steppes of Patagonia highlights some important characteristics of the vegetation response to a major disturbance factor we show that shrub encroachment is not a generalized response of the steppe to grazing. Grazed areas presented lower richness and diversity than exclosures. Physiognomic changes (as describe by relative abundance of plant functional types) were less important than those observed at the species level. These results shown that the status of the shrub-grass steppes of the Occidental district of Patagonia can not be characterized in terms of contrasting physiognomic states as in the case of the grass steppes of the Subandean district. Forbs and a few mesophytic and xerophytic grasses are the key elements to identify the condition of the steppe. Monitoring programs should focus on the relative abundance of these components.

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1. Introduction

Grazing affects the structure and functioning of grasslands, shrublands and savannas in a complex manner. The actual impact of herbivory on community structure or ecosystem processes has been controversial (McNaughton, 1979; Milchunas and Lauenroth, 1993; Oesterheld et al., 1999). Ecosystem changes associated with grazing varied according to the environmental conditions (water availability, nutrient pools, thermal environment), the type and body mass of the herbivore (Hoffman and Cowling, 1990), the temporal and spatial scale of the grazing event (Olff and Ritchie, 1998) and the relationship with other disturbances (fire or drought) (Díaz et al., 2007; Oesterheld et al., 1999).

Change in species composition is one of the most studied effects of grazing on the structure of rangeland areas. Milchunas and Lauenroth (1993) states that while in arid and nutrient-poor systems grazing would have neutral or negative effects on species

diversity, in humid and fertile sites grazing would increase diversity. These changes in diversity will influence community structure and dynamics (Chambers and MacMahon, 1994) and ecosystem functioning, particularly C and water dynamics (Aguiar et al., 1996; Paruelo and Sala, 1995).

Grazing may have a large impact on plant functional types (PFTs) abundance (Altesor et al., 2006; Ares et al., 1990; Hadar et al., 1999; León and Aguiar, 1985). Shrub encroachment of grasslands has been identified as a major grazing-induced change in many areas of the world (Archer, 1989). However, shrubs can decrease with grazing in both arid (Cipriotti and Aguiar, 2005) and sub-humid environments (Altesor et al., 2006). Given the tight connection between PFT abundance and ecosystem functioning, changes at this level may have larger consequences than in species composition (Aguiar et al., 1996; Díaz et al., 2007; Hadar et al., 1999).

In this article we analyzed the effect of grazing by domestic herbivores on different community structure attributes: floristic and PFT composition, diversity and vertical and horizontal distribution of plant biomass in the shrub-grass steppes of Patagonia (Southern Argentina) (Appendix1, "electronic version only"). The available evidence suggests important changes both in floristic and PFT composition associated with grazing. Most of this evidence is derived from the analysis of grazing gradients defined indirectly

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(León and Aguiar, 1985; Perelman et al., 1997), from fence contrasts (Borelli et al., 1988) or from the distance to water points (Bisigato and Bertiller, 1997).

Several studies have been based on the results of paired treatments using: grazed areas and herbivore exclosures (Allen et al., 1995; Angassa and Oba, 2007). However most of these studies did not cover enough sites or, if so, they were based on meta-analysis (but see Altesor et al., 2006).

In this study we analyzed the structural differences associated with grazing exclusion on vegetation by studying 24 grazed−ungrazed paired sites located in the arid and semiarid portion of Patagonia. Our objectives were to evaluate the effect of grazing on plant species composition, plant diversity, the relative abundance of PFTs, and the vertical and horizontal structure of the plant community. The effects of grazing on the structure grasslands and shrublands have generated controversy and debate in the literature (McNaughton, 1979; Milchunas and Lauenroth, 1993; Oesterheld et al., 1999). Aside from describing the effects of grazing on the above mentioned attributes we evaluated predictions of two general hypotheses (previously proposed) on the effect herbivory on community structure:

- Grazing by domestic herbivores promotes species coexistence by reducing competitive exclusion, by increasing colonization of bare soil patches formation and by reducing litter cover (Altesor et al., 2006). We predict that grazed areas would have a higher diversity.
- Selective grazing would reduce grass and forbs cover thereby increasing resources (mainly water) for shrubs (Sala et al., 1989). We predict that grazed areas would have a higher relative abundance of shrubs.

2. Materials and methods

2.1. Study sites and data collection

We selected two areas dominated by grass steppes and shrub-grass steppes in the Occidental and Subandean Districts of Patagonian Province (León et al., 1998) (Appendix1 "electronic version only"). The first area is located 30 km east of S.C. de Bariloche (North area, 71°10′ − 70°20′ W, 41°00′ − 41°15′ S, 600−1200 masl), in Rio Negro Province. The second one is located near Rio Mayo in Chubut Province (South area, 71°00′ − 71°35′ W, 45°40′ − 45°20′ S, 500−600 masl) The climate of the study sites is cold- temperate with precipitation concentrated in winter, between April to September (Paruelo et al., 1998). Total annual precipitation decrease from the Andes eastward (Ares et al., 1990; Jobbágy et al., 1995), varying from 200 to 770 mm in the northern site and from 190 to 350 mm in the southern one. Soils in the northern area corresponded to a complex of Ustic Paleargids, Udic Argiustolls y Typic Haplargides on the plain areas and Typic Haplargids y Lithic Haplargids on the hill. Near Rio Mayo soils had a xeric regimen with full saturation in winter. Taxonomically they corresponded to Typic Cryoborols toward the west side of the area and Calciorthids on the east.

Vegetation corresponds to a coenocline; in the eastern portion of both study areas vegetation presents an opened structure with cover <60% and height <180 cm (León et al., 1998). The main community is defined by *Jarava speciosa* (*Stipa speciosa*), *Jarava humilis* (*Stipa humilis*), *Adesmia campestris*, *Berberis heterophylla* y *Poa lanuginosa* (Golluscio et al., 1982). Others important species are *Senecio filaginoides*, *Mulinum spinosum*, *Poa ligularis*, *Bromus pictus*, and *Hordeum comosum*. In the west portion of the both areas vegetation cover is >50% of soil and the dominant species is *Festuca pallescens*. The dominat community of this area is defined by *F. pallescens*, *Rytidosperma pictum*, *Lathyrus magellanicus* and *Festuca pyrogea* (Golluscio et al., 1982).

We collected data from 24 paired sites. Twenty pairs of ungrazed and grazed sites were located in northern area, between 71°10′ W −− 41°00′ S and 70°20′ W − 41°15′ S. In this case, ungrazed areas correspond to exclusions generated by the fences of railroad. The plots sampled within the fences were located in areas not disturbed by the railroad construction or operation. Both, the grazed and ungrazed plots corresponded to the same landscape unit. The exclosures did not correspond to the original vegetation of the steppe because the fences were built after domestic herbivores introduction (at the end of the XIX century). Fences were set after 1939 and since then grazing was occasional and accidental. In the southern area, three paired sites were located at the Rio Mayo INTA Experimental Ranch (45°41′ S − 70°16′ W) using exclosures where large herbivores have been prevented access for 48, 28 and 15 years (Sala et al., 1989; Yahdjian et al., 2006). The last site corresponds to an exclosure located at the Media Luna Ranch (71°26′ W − 45°36′ S) constructed in the 80 decade (Bertiller, 1996). The primary criterion to select the sites was to avoid differences in any other factor other than grazing; avoiding any site with sings of old fires or with abrupt changes in its slope. In all cases we evaluated the presence of old sheep dung into the exclosure, and only native herbivores dungs was found. Historic stoking rates varying from 0.3 to 0.6 sheep/ha across the paired sites (Cipriotti and Aguiar, 2005; Soriano and Sala, 1983). Actual recommended stocking rates varied from 0.13 to 0.6 (Elissalde et al., 2008). We acknowledge that it may be some additional factors aside from the absence of grazing on the observed response. In fact our design (paired comparison across
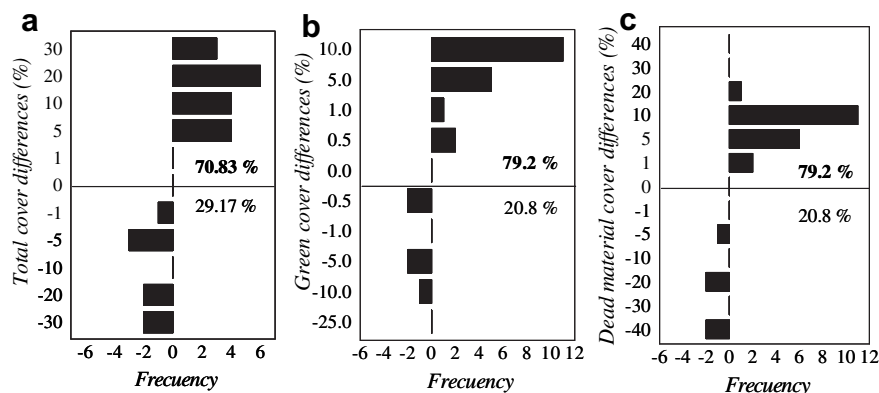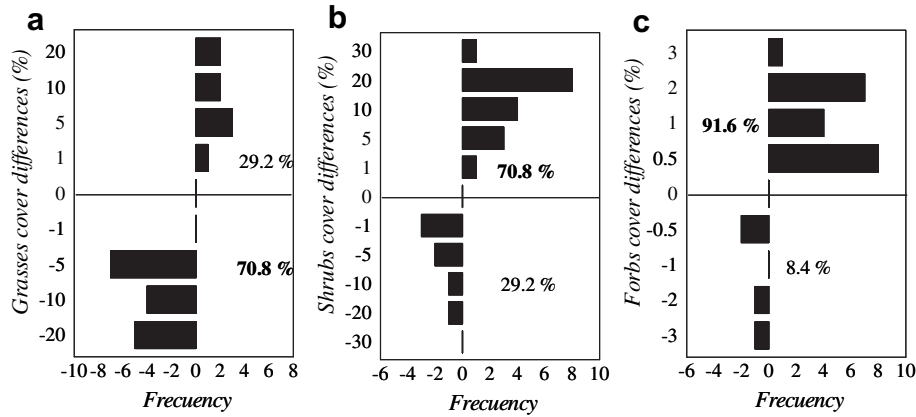

Fig. 1. Number of sites that present positives (top) and negative (bottom) differences between ungrazed and grazed site (cover UG − cover G). a) Total cover, b) green material and c) dead material. Numbers highlighted indicated significant differences; proportion expected 50% (χ^2, $p < 0.05$).

Fig. 2. Number of sites that present positives (top) and negative (bottom) differences between ungrazed and grazed site (cover UG − cover G). a) Grasses cover, b) Shrubs cover and c) Forbs cover. Numbers highlighted indicated significant differences, proportion expected 50% (χ^2, $p < 0.05$).

different sites) tried to minimize these effects. Differences in grazing intensity, soils, presence of additional herbivores, age of the exclosures, etc, would contribute to the experimental error.

At each site we randomized the starting point of transect using fence poles. The 3 transects (30 m) were set <4 m from each side of the fence, 1 m apart. Measurements were performed in the same soil type. We measured the basal cover of each item (a plant species or dead material) according the line intercept method (Canfield, 1941). For grasses and forbs we considered basal cover, for shrubs we measured canopy projection. In addition to those intercepted by the lines we listed all species within the area defined by the first and third line surveyed.

2.2. Data analysis

We calculated total cover, dead material cover, green cover (total cover − dead material), PFT cover and mean height as the sum of cm of each item along the transect. PFT were defined at two levels. At a coarse level plant species were grouped into grasses, forbs and shrubs (Soriano and Sala, 1983). The more detailed level is presented in Appendix 2 "electronic version only".

Because our study was included sites with total cover varying from 98% to 26%, attribute averages may not necessarily reflect the differences between ungrazed and grazed sites. The differences between grazed (G) and ungrazed (UG) sites were, analyzed using

a χ^2 approximation. We compared the number of sites with absolute positive differences (UG − G) to the number expected by random (50% of cases) with a 95% of confidence. To show the magnitude of change we expressed also the differences in relative terms ((UG−G)/UG). For those attributes with data for less than 10 sites the analysis was performed including Yates correction. To analyze differences in plant functional type height we used Welch ANOVA (SAS 8.2© 1999−2001).

Species richness (S') was calculated from the total number of species recorded (those intercepted by the lines plus those observed within the area defined by the first and third line surveyed). To calculated diversity and evenness were considered only the species intercepted by the line. Diversity was calculated using Shannon Index (H' = −∑pi ln pi, where pi is the cover of each species) and Evenness as: J' = H'/ln S. Richness, diversity and evenness were also calculated for grasses, shrubs and forbs. Differences between ungrazed and grazed areas were analyzed using χ^2.

The relationship between the relative cover (total cm of each item/total cm of green cover) of species and PFT in grazed and ungrazed areas was analyzed for items present in at least seven sites (25%). We determine the correlation (r) and also compared the slope and Y-intercepts of the regression model fitted to relationship between the cover of the entities (species of PFT) in grazed areas and ungrazed areas. A slope of 1 and a Y-intercept of 0 correspond to no differences between grazed and ungrazed sites.
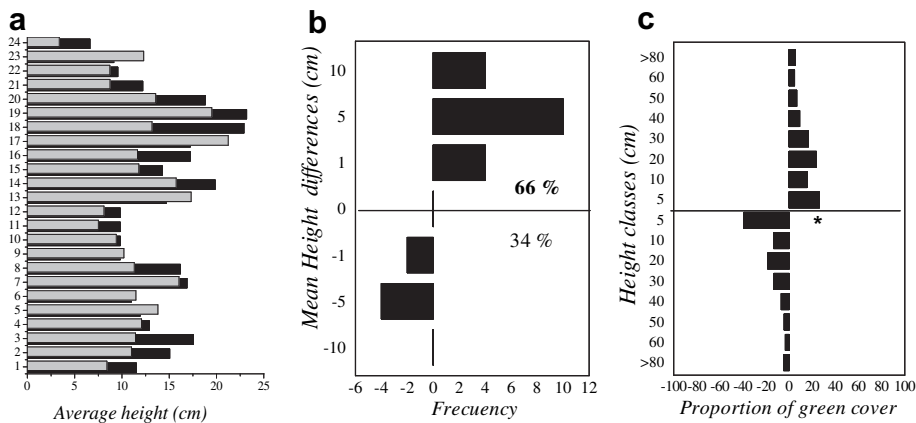
Fig. 3. Vertical distribution of cover. a) Average height (cm) in each sites (black: ungrazed, grey: grazed); b) Number of sites that present positives (top) and negative (bottom) differences between UG and G site (height in ungrazed site − height in grazed site) and c) Proportion of cover in each class of height. Numbers highlighted and asterisk indicated significant differences, proportion expected 50% (χ^2, $p < 0.05$).
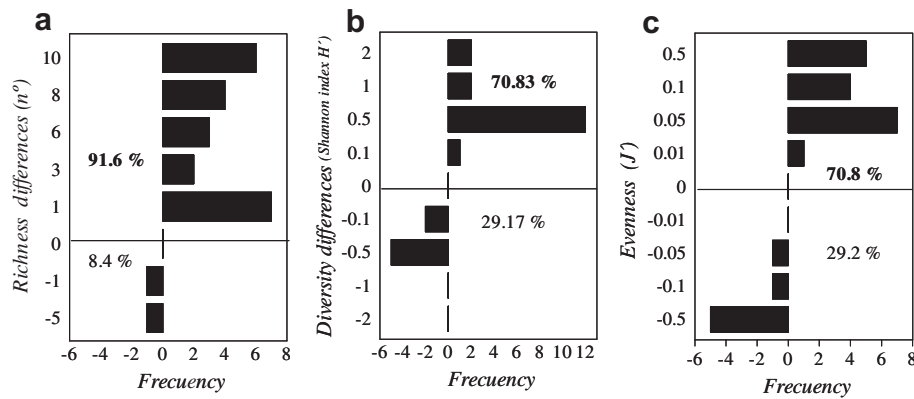
Fig. 4. Number of sites that present positives (top) and negative (bottom) differences between ungrazed and grazed site (value UG − value G). a) Richness (n°), b) Diversity (Shannon index H′) and c) Evenness (J′). Numbers highlighted indicated significant differences, proportion expected 50% (χ^2, $p < 0.05$).

3. Results

3.1. Change in vertical and horizontal distribution of cover

Grazing regime modified total and green cover (Fig. 1a and b). Most of the ungrazed plots presented a higher total (17:7; $\chi^2 = 4.16$, $p < 0.05$) and green (19:5, $\chi^2 = 8.16$, $p < 0.05$) cover than the paired grazed areas. The proportion of dead material was higher in ungrazed than in grazed plots in 79.2% of the cases ($\chi^2 = 8.16$, $p < 0.05$) (Fig. 1c). The absolute differences observed translate into broader differences in relative terms. The sites that showed positive differences had a 22%, 23% and 42% more total cover, green cover and proportion of dead material in ungrazed than in grazed plots. Grass, shrub and forbs covers were also modified by the grazing regime (Fig. 2). Grass cover was higher in grazed than in ungrazed conditions in most the sites (7:17, $\chi^2 = 4.16$, $p < 0.05$). The opposite pattern was observed for shrubs and forbs (17:7, $\chi^2 = 4.16$ and 20:4, $\chi^2 = 8.16$, $p < 0.05$). As it was described for total cover and green cover, relative differences in grass, forbs and shrubs cover were higher than the absolute ones. Forbs relative cover was 681% higher in ungrazed than in grazed sites. Similarly, relative differences in shrub and grass cover resulted 129% higher and 43% lower in ungrazed sites than in grazed sites.

Grazing regime did not modify the number and size of bare ground patches: the number of sites with positive difference in these attribute did not differ from those expected by chance (10:14, χ^2 0.66). Ungrazed sites showed in average 82 patches of 43 cm (ranging from 14 to 149 cm) as a mean size. Grazed sites presented, 91 patches as average and in grazed 46.6 cm (5−227 cm). In a significant proportion of the ungrazed sites the vegetation was

taller than in grazed sites (Fig. 3, 19:5, χ^2: 8.16, $p < 0.05$). In both situations, vegetation cover was concentrated below 30 cm. Grazed sites had 84.3% total cover below this height and ungrazed 78%. The proportion of the total cover concentrated in the first 5 cm of the profile was higher in grazed plots (21:3, χ^2: 13.5, $p < 0.05$; Fig. 3c) on the other hand cover concentrated on 20−80 cm was higher in ungrazed sites (17:7, χ^2: 4.16, $p < 0.05$).

3.2. Richness, diversity and evenness

Total number of species (S′) was affected by grazing. Over 24 sites, 22 show more species in ungrazed than in grazed areas (22:2, χ^2 16.6 $p < 0.05$). Differences in one specie was founded in 32% of the cases and in 22% differences were over 10 species. Diversity (H′) and evenness (J′) showed a similar pattern, both attributes were higher in ungrazed sites in 70.8% cases (Fig. 4). Average relative differences between grazing regimes were 20% for richness and 4% for evenness, indicating that changes in diversity were mainly due to differences in the number of species. Grazed and ungrazed sites differed significantly in shrubs and grasses richness; in grasses evenness and in diversity of forbs. Differences in forbs diversity were associated to changes in evenness between grazing systems (Table 1).

3.3. Functional types and species cover

Relative cover in grazed and ungrazed sites was significantly correlated for 6 out of 9 PFT (Table 2). In 4 cases, the linear model fitted has a slope significantly lower than 1 and a negative intercept indicating a lower cover in grazed sites. For the Xerophytic Grasses, the slope was lower than 1, but the Y-intercept was over 10% of cover in grazed sites. Its shows 20 sites over the 1:1 line, meaning that the cover in grazed sites was higher than in ungrazed ones (Table 2). Mesophytic Grasses, Evergreen Forbs and Short Deciduous Shrubs showed the highest differences in slope and showed.

At the species level, grazing regime generated different responses (Table 3). We found a significant correlation between the relative cover of ungrazed and grazed sites for 10 out of 21 species. For a group of 11 species relative cover in grazed and ungrazed plots showed no significant correlation (*Ephedra frustillata*, *Rodophiala elwessii*, *Valeriana clarionifolia* and *Jarava humilis*, *Acaena pinatifida*, *Euphorbia collina*, *Cerastium arvense*, *Sisyrinchium junceum*, *H. comosum*, *B. pictus* and *J. speciosa*). Six of these species (*Acaena pinatifida*, *E. collina*, *C. arvense*, *S. junceum*, *H. comosum*, *B. pictus*), though, showed higher cover in ungrazed than in grazed sites in

Table 1
Richness (S′), Diversity (Shannon index H′) and Evenness (J′) by life form (shrubs, grasses and forbs). Table contains the number of sites with positive and negative differences (UG−G), χ^2 value to 50% expected, p value, means and standard deviations.

| PFTs | Attribute | Number of site with differences | | | | Means | |
		+	−	χ^2	p	UG	G
Shrubs	S′	16	6	4.54	0.03	3.5	2.95
	H′	13	11	0.16	0.68	0.75	0.68
	J′	11	13	0.16	0.68	0.62	0.64
Grasses	S′	17	7	4.16	0.041	6.29	5.58
	H′	21	3	13.5	0.001	1.23	0.81
	J′	20	4	10.6	0.001	0.68	0.52
Forbs	S′	21	3	13.5	0.001	5.8	3.5
	H′	21	3	13.5	0.001	1.057	0.57
	J′	12	12	0	1	0.69	0.59

Table 2
Results model comparison. Adjusted model correspond to relationship between relative cover in UG vs G for PFT. Null model correspond to 1:1 line, equal cover in both sites. Table contains: the number of sites where each FT was present; correlation value, slope value; Y value; p value for slope comparison, p value for origin comparison and the number of site below line 1:1. Highlighted numbers show significant values.

Functional type	N	Relative cover					
		r	Slope value	Y value	Slope (p value)	Y-intercept (p value)	N° under line 1:1
Short deciduous shrubs	21	0.63	0.64	−7.90	**0.038**		**15**
Perennial mesophytic grasses	24	0.57	0.61	−0.47	**0.040**		**20**
Perennial xerophytic grasses	24	0.49	0.52	16.54	**0.020**		**6**
Evergreen forbs	14	0.79	0.47	−0.14	**0.007**		**12**
Perennial deciduous forbs	24	0.85	0.24	−0.90	**0.001**		**16**
Annual forbs	17	0.82	0.74	−0.44	0.120	**0.005**	14
Short evergreen shrubs	24	0.90	0.93	−0.75	0.460	0.22	11
Tall deciduous shrubs	7	0.87	1.16	−0.20	0.760	0.54	4
Graminoids	7	0.01					

75% of the cases (χ^2: 6.0, $p < 0.05$) and one (*J. speciosa*) shows the opposite pattern with higher cover in grazed sites (χ^2: 18.3, $p < 0.05$). A second group of species (*A. campestris*, *Festuca argentina*, *F. pallescens* y *Relbunium richardianum*) showed a positive relationship between cover in grazed vs ungrazed site, but without differences in slope or Y-intercept. Five species (*S. filaginoides*, *Rumex acetocella*, *P. ligularis*, *P. lanuginosa* and *M. spinosum*), showing also a significantly relationship between grazed and ungrazed sites cover, presented a slope significantly lower than 1. Finally one specie (*Acaena splendens*) showed a Y-intercept significantly different than 0, was higher under grazing.

4. Discussion and conclusions

Sheep grazing modified vegetation structure in the Patagonian steppes. Areas where grazing was excluded had higher total cover, richness, diversity and the vegetation was taller than in grazed areas. In the two areas studied (north and south) the variables recorded presented the same pattern of response to grazing. The results presented did not support, though, our predictions on the effect of grazing on diversity. Diversity was lower in grazed areas. As it was observed in different semiarid and sub-humid sites, grazed areas presented a lower cover of both green and dead tissues (Bertiller, 1996; Bisigato and Bertiller, 1997; Xie et al., 2007). However the number and size of bare soil patches did not change between grazing treatments. Bare soil patches play a critical role in the recruitment of new individuals in the Patagonian steppe (Aguiar and Sala, 1997). A lack of change in the distribution of bare soil patches would result in null effect of grazing on recruitment and colonization. The vertical distribution of the biomass may also affect recruitment by modifying roughness and wind profiles and, consequently, seed dispersal (Aguiar et al., 1996; Rotundo and Aguiar, 2004). Secondary dispersion is an important factor in the recruitment dynamics of Patagonian species (Aguiar and Sala, 1997).

We did not find either evidence for our second prediction: grazed areas would have a higher relative abundance of shrubs. In the exclosures the relative abundance of shrubs was higher than in grazed areas. These results contradict the common paradigm of grazing-induced shrub encroachment in arid and semiarid areas (Walker et al., 1981; Weber et al., 1998). For Patagonia shrub encroachment was described for the western grass steppes (Bertiller and Bisigato, 1998; León and Aguiar, 1985). Perelman et al. (1997) also described an increase in shrub cover in the grass-shrub steppes of the Occidental district of Patagonia. However, this analysis was based on an indirect gradient analysis instead on a paired comparison of grazed and ungrazed sites. A detailed analysis of shrub density in grazed and ungrazed areas of the Occidental district showed that shrub abundance was higher in areas where large herbivores were excluded (Cipriotti et al., 1999).

Table 3
Results model comparison. Adjusted model correspond to relation between relative cover in UG vs G sites for each species. Null model correspond to 1:1 line, equal cover in both sites. Table contains: 21 more constant species, PFT; number of sites where it is present; significance of correlation UG vs UG relative cover, differences in slope or origin, situation where cover was higher and the number of sites under the 1:1 line.

Species	PFT	N°	Relationship between relative cover in UG vs G sites	Differences in slope	Differences in origin	Side where cover is higher	N° under line 1:1 (χ^2 $p < 0.05$)
Ephedra frustillata	SES	7	No significant				
Rodophiala elwessii	PDE	8					
Valeriana clarionifolia	PEF	6					
Jarava humilis	PMG	14					
Acaena pinatifida	PDE	14				Ungrazed	9
Euphorbia collina	PDE	11				Ungrazed	8
Cerastium arvense	PDE	12				Ungrazed	10
Sisyrinchium junceum	PDE	13				Ungrazed	11
Hordeum comosum	PMG	22				Ungrazed	14
Bromus pictus	PMG	23				Ungrazed	17
Jarava speciosa	PXG	22				Grazed	2
Adesmia campestris	TDS	8	Significant	No significant			
Festuca argentina	PXG	13					
Festuca pallescens	PXG	19					
Relbunium richardianum	PDE	13				Ungrazed	10
Senecio filaginoides	SES	21		Significant		Grazed	8
Rumex acetosella	ANF	14				Ungrazed	8
Poa ligularis	PMG	22				Ungrazed	14
Poa lanuginosa	PMG	11				Ungrazed	7
Mulinum spinosum	SDS	22				Ungrazed	14
Acaena splendens	TES	13			Significant	Grazed	5

High shrub cover in ungrazed areas was common in sub-humid grasslands of Uruguayan Campos (Altesor et al., 2006).

The balance between shrubs and grasses motivated a profound debate (Sala et al., 1997; Soriano and Sala, 1983; Walker et al., 1981). Fire, grazing and water partitioning has been proposed as the major controls of the relative abundance of the two PFT (Noy-Meir, 1973; Paruelo et al., 2000). In the Occidental district of Patagonia fire is almost absent due to the lack of thunderstorms (Paruelo et al., 1998). Shrubs concentrate their roots below 40 cm and grasses in the upper layer (Fernandez and Paruelo, 1988). Grasses by absorbing water from the upper layers reduce drainage and hence water availability in the lower layers affecting shrub absorption and productivity (Sala et al., 1989). The observed increases in xerophytic grasses cover in grazed areas may result in a reduction in water availability in the layers where shrubs concentrate their roots, explaining then the decrease in shrub cover in these areas. In addition to water dynamics grazing *per se* may play a role in determining changes in shrubs abundance. Shrub response to grazing is not uniform among shrub species. In general deciduous species (*M. spinosum* and *A. campestris*) are more consumed by sheep than evergreen species. Deciduous shrubs (mainly *M. spinosum*) decreased in grazed areas while evergreen species (mainly *S. filaginoides*) increased. Changes in competition ability mediated by grazing among shrubs may also contribute to explain the observed changes in cover between grazed and ungrazed areas.

Forbs presented the greatest differences among grazing regimes. Though their total cover was always lower than 5%, forbs accounted for most of the differences in richness, diversity and evenness between grazed and ungrazed areas. As shown by many authors for arid and semiarid environments, exclosures presented higher diversity and richness of forbs (Pastor et al., 1998; Schlichter et al., 1978). Differences in richness between grazing regimes were higher than in evenness. The lost of forbs species, with low cover, in grazed areas would explain this patterns.

Our results showed that grazing-induced subtle changes in the physiognomy of the steppe. The 13 PFT defined were present in both grazing conditions. Possibly our definition of PFTs it was not sensitive enough to detect the effect of grazing. Xerophytic grasses did not show major changes, however, the response of the species pertaining to the PFT varied widely. For example *F. pallescens* decreased under grazing, while *J. speciosa* increased. Grouping species based on attributes related to water use and drought tolerance (Solbrig et al., 1977), was not able to detect differences in grazing response (Cingolani et al., 2005; Díaz et al., 2007). Although many attributes related to drought tolerance (as leaf thickness, leaf tensile strength, cuticular wax) may represent exaptations to grazing (Coughenour, 1985) additional factors such as tussock structure or relative availability of forage items would generate differences in the response of species pertaining to the same PFT. The reduction in cover of the species most preferred by sheep (*F. pallescens*, *P. ligularis*, *B. pictus*, *P. lanuginosa* and *M. spinosum*) in grazed conditions determines a sharp decline in forage quality. Moreover, such reduction may determine the local extinction of some species. Aguiar et al. (unpublished) showed the genetic erosion and the local extinction of *P. ligularis* under grazing conditions. However, the impact of grazing on other structural attributes was relatively low determining small physiognomic changes. Verón (2008) showed for the Occidental district that the structural changes associated to grazing has relatively minor effects on ecosystem functioning, particularly on water dynamics.

Despite the uncertainties related to stock density, age of exclosures, etc., our experimental design allowed us to detected a clear signal of the "grazing–no grazing" factor. Though we recognize that the perception of the impact of grazing may varied depending on the age of the exclosure or the stocking density, in our analysis the uncertainty associated to this factor did not mask the effect of grazing exclusion *per se*. The analysis of paired grazed and ungrazed sites across the shrub-grass steppes of Patagonia highlight some important characteristics of the vegetation response to a major disturbance factor:

- Shrub encroachment is not a generalized response of the steppe to grazing. The increase of shrub would be restricted to the western grass steppes.
- Grazed areas presented lower richness and diversity than exclosures. Such differences were explained mainly by forb species.
- Physiognomic changes (as describe by PFT relative abundance) were less important than those observed at the species level.

These results showed that the status of the shrub-grass steppes of the Occidental district of Patagonia not can be characterized in terms of contrasting physiognomic states as in the case of the grass steppes of the Subandean district. Forbs and a few mesophytic and xerophytic grasses are the key elements to identify the condition of the steppe. Monitoring programs should focus on the relative abundance of these elements. The low impact of grazing on the major structural features of the steppe may represent an advantage in terms of management and/or restoration. The target species in a management or restoration plan are, in general, the more dynamics component due to the high relative growth (Oyarzabal et al., 2008) or recruitment rates (Rotundo and Aguiar, 2004).

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Appendix. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.jaridenv.2011.04.003.

References

Aguiar, M.R., Sala, O.E., 1997. Seed distribution constrains the dynamics of the patagonian steppe. Ecology 78 (1), 93–100.
Aguiar, M.R., Paruelo, J.M., Sala, O.E., Lauenroth, W.K., 1996. Ecosystem responses to changes in plant functional type composition: an example from Patagonian steppe. Journal of Vegetation Science 7, 381–390.
Allen, R.B., Wilson, J.B., Mason, C.R., 1995. Vegetation change following exclusion of grazing animals in depleted grassland, Central Otago, New Zealand. Journal of Vegetation Science 6, 615–626.
Altesor, A.I., Piñeiro, G., Lezama, F., Jackson, R.D., Sarasola, M., Paruelo, J.M., 2006. Ecosystem changes associated with grazing removal in sub-humid grasslands of South America. Journal of Vegetation Science 17, 323–332.
Angassa, A., Oba, G., 2007. Effects of management and time on mechanisms of bush encroachment in southern Ethiopia. African Journal of Ecology. doi:10.1111/j.1365-2028.2007.00832.x Online Early Articles, Published article online: 5-Sep-2007.
Archer, S., 1989. 'Have Southern Texas savannas been converted to woodlands in recent history?'. American Naturalist 134, 545–561.
Ares, J.O., Beeskow, A.M., Bertiller, A.M., Rostagno, C.M., Irisarri, M.P., Anchorena, J., Defossé, G.E., Merino, A.C., 1990. Structural and dynamic characteristics of overgrazed grassland of northern Patagonia, Argentina. In: Breymeyer, A. (Ed.), Managed Grasslands. Elsevier, Amsterdam, pp. 149–175.
Bertiller, M.B., 1996. Grazing effects on sustainable semiarid rangeland in Patagonia: the state and dynamics of the soil seed bank. Environmental Management 20 (1), 123–132.
Bertiller, M.B., Bisigato, A., 1998. Vegetation dynamics under grazing disturbance. The state-and-transition model for the Patagonian steppes. Ecología Austral 8, 191–199.

Bisigato, A.J., Bertiller, M.B., 1997. Grazing effects on patchy dryland vegetation in northern Patagonia. Journal of Arid Environments 36, 639–653.

Borelli, P., Anglesio, F., Baetti, C., Iacomini, M., Ramstrom, A., 1988. Condición de pastizales en el sudeste de Santa Cruz (Patagonia), II: Sitio "Santacrucense". Revista Argentina de Producción Animal 3, 201–213.

Canfield, R.H., 1941. Application of the line interception method in sampling range vegetation. Journal of Forestry 39, 388–394.

Chambers, J.C., MacMahon, J.A., 1994. A day in the life of a seed: movements and fates of seeds and their implications for natural and managed systems. Annual Review of Ecological Systems 25, 263–292.

Cingolani, A.M., Noy-Meir, I., Díaz, S., 2005. Grazing effects on rangeland diversity: a synthesis of contemporary models. Ecological Applications 15 (2), 757–775.

Cipriotti, P.A., Aguiar, M.R., 2005. Effects of grazing on patch structure in a semi-arid two-phase vegetation mosaic. Journal of Vegetation Science 16, 57–66.

Cipriotti, P., Aguiar, M.R., Batista, W., 1999. Diferencias en la respuesta al pastoreo en especies de arbustos dominantes de la estepa Patgónica. Abril 1999. XIX Reunión Argentina de Ecología, San Miguel de Tucumán, Tucumán, Argentina, p. 221.

Coughenour, M.B., 1985. Graminoid Responses to Grazing by Large Herbivores: Adaptations, Exaptations and Interacting Processes. Annual Missouri Botanical Garden Press, 72: pp. 852–863.

Díaz, S., Lavorel, S., McIntyre, S., Falczuk, V., Casanovess, F., Milchunas, D.G., Skarpe, C., Rusch, G., Sternberg, M., Noy-Meir, I., Landsberg, J., Zhnag, W., Clarkss, H., Campbell, B.D., 2007. Plant trait responses to grazing – a global synthesis. Global Change Biology 13, 313–341.

Elissalde, N., Buono, G., Escobar, J.M., Nakamatsu, V., Behr, S., Llanos, E., 2008. Disponibilidad de forraje para el ganado ovino de los pastizales naturales de las zonas áridas y semiáridas del Chubut. INTA. www.inta.gov.ar/chubut, p. 12.

Fernandez, A.R.J., Paruelo, J.M., 1988. Root systems of two Patagonian shrubs: a quantitative description using a geometrical method. Journal of Range Management 41 (3), 220–223.

Golluscio, R.A., León, R.J.C., Perelman, S., 1982. Caracterización fitosociológica de la estepa del oeste de Chubut: su relación con el gradiente ambiental. Boletín de la Sociedad Argentina de Botánica 21 (1–4), 299–324.

Hadar, L., Noy-Meir, I., Perevolotsky, A., 1999. The effect of shrub clearing and grazing on the composition of a Mediterranean plant community: functional groups versus species. Journal of Vegetation Science 10, 673–682.

Hoffman, M.T., Cowling, R.M., 1990. Vegetation change in the semi-arid eastern Karoo over the last 200 years: an expanding Karoo - fact or fiction? South African Journal of Science 86, 286–294.

Jobbágy, E.G., Paruelo, J.M., Leon, R.J.C., 1995. Estimación de la precipitación y de su variabilidad interanual a partir de información geográfica en el NW de Patagonia, Argentina. Ecología Austral 5, 47–53.

León, R.J.C., Aguiar, M.R., 1985. El deterioro por uso pasturil en estepas herbáceas patagónicas. Phytocoenologia 13 (2), 181–196.

León, R.J.C., Bran, D., Collantes, M., Paruelo, J.M., Soriano, A., 1998. Grandes unidades de vegetación de la Patagonia. Ecología Austral 8, 125–143.

McNaughton, S.J., 1979. Grazing as an optimization process: grass-ungulate relationships in the Serengeti. The American Naturalist 113 (5), 691–701.

Milchunas, D.G., Lauenroth, W.K., 1993. A quantitative assessment of the effects of grazing on vegetation and soils over a global range of environments. Ecological Monograph 63, 327–366.

Noy-Meir, I., 1973. Desert ecosystems: environments and producers. Annual Review of Ecology and Systematic 4, 25–51.

Oesterheld, M., Loreti, J., Semmartin, M., Paruelo, J.M., 1999. Grazing, fire and climate effects on primary productivity of grasslands and savannas. In: Walker, L. (Ed.), Ecosystems of Disturbed Ground. Elsevier, Amsterdam.

Olff, H., Ritchie, M.T., 1998. Effects of herbivores on grassland plant diversity. Trends in Ecology and Evolution 13 (7), 261–265.

Oyarzabal, M., Paruelo., J.M., del Pino, F., Oesterheld, M., Lauenroth, W.K., 2008. Trait differences between grass species along a climatic gradient in South and North America. Journal of Vegetation Science 19, 183–192.

Paruelo, J.M., Sala, O.E., 1995. Water losses in the Patagonian Steppe: a modelling approach. Ecology 76, 510–520.

Paruelo, J.M., Beltrán, A., Jobbágy, E., Sala, O.E., Golluscio, R.A., 1998. The climate of Patagonia: general patterns and controls on biotic processes. Ecología Austral 8, 85–101.

Paruelo, J.M., Sala, O.E., Beltrán, A.B., 2000. Long-term dynamics of water and carbon in semi-arid ecosystems: a gradient analysis in the Patagonian steppe. Plant Ecology 150, 133–143.

Pastor, J., Dewey, B., Moen, R., Mladenoff, D.J., White, M., Cohen, Y., 1998. Spatial patterns in the moose forest soil ecosystem on isle Royale, Michigan, USA. Ecological Application 8 (2), 411–424.

Perelman, S., León, R.J.C., Bussacca, J.P., 1997. Floristic changes related to grazing intensity in a Patagonian shrub steppe. Ecography 20, 400–406.

Rotundo, J.L., Aguiar, M.R., 2004. Vertical seed distribution in soil constrains regeneration processes of Bromus pictus in a Patagonian steppe. Journal of Vegetation Science 15, 515–522.

Sala, O.E., Golluscio, R.A., Lauenroth, W.K., Soriano, A., 1989. Resource partitioning between shrubs and grasses in the Patagonian steppe. Oecologia 81, 501–505.

Sala, O.E., Lauenroth, W., Golluscio, R.A., 1997. Functional types in temperate semi-arid regions. In: Smith, T.M., Shugart, H.H., Woodward, F.I. (Eds.), Plant Functional Types – Their Relevance to Ecosystem Properties and Global Change. Cambridge University Press, Cambridge, pp. 217–233.

Schlichter, T.M., León, R.J.C., Soriano, A., 1978. Utilización de índices de diversidad en la evaluación de pastizales naturales en el centro-oeste del Chubut. Ecología 3, 125–132.

Solbrig, O.T., Barbour, M.A., Cross, J., Golsdtein, G., Lowe, C.H., Morello, J., Young, T.W., 1977. The strategies and community patterns of desert plants. In: Orians, G.H., Solbrid, O.T. (Eds.), Convergent Evolution in Warm Deserts, Dowden. Hutchinson and Ross, Inc., Stroudsburg, PA, pp. 67–106.

Soriano, A., Sala, O.E., 1983. Ecological strategies in Patagonian arid steppe. Vegetatio 56, 9–15.

Verón, S., 2008. El impacto de la desertificación sobre el funcionamiento de la estepa patagónica. Tesis para optar al Título de Doctor en Ciencias Agropecuarias, EPG-FAUBA, Director: PhD J.M. Paruelo.

Walker, B.H., Ludwig, D., Holling, C.S., Peterman, R.M., 1981. Stability of semi-arid savanna grazing systems. Journal of Ecology 69, 473–498.

Weber, G.E., Jeltsch, F., Van Rooyen, N., Milton, S.J., 1998. Simulated long term vegetation response to grazing heterogeneity in semi arid rangelands. Journal of Applied Ecology 35, 687–699.

Xie, Y., Becker, U., Witting, R., 2007. Vegetation of the Stipa loess steppe un Ningxia (northern China) in relation to grazing intensity. Grassland Science 53, 143–154.

Yahdjian Laura, Osvaldo E. Sala, Amy T. Austin, 2006. Differential controls of water input on litter decomposition and nitrogen dynamics in the Patagonian Steppe. Ecosystems 9, 128–141.

Further reading

Aguiar, M.R., Premoli, A.C., Cipriotti, P. After half a century of exclosure, native grass species recover demographically but not genetically from grazing by exotic sheep. Conservation Biology, submitted for publication.

Bertiller, M.B., Sain, C.L., Carrera, A.L., Vargas, D.N., 2005. Patterns of nitrogen and phosphorus conservation in dominant perennial grasses and shrubs across an aridity gradient in Patagonia, Argentina. Journal of Arid Environments 62, 209–223.