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ARTICLE



The impact of livestock grazing on the spatial pattern of vegetation in north-eastern Patagonia, Argentina

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Background: The occurrence of shrub patches, alternating with either bare soil or low herbaceous cover, is a common feature in arid and semi-arid shrublands throughout the world. This patchy pattern of vegetation may result from water limitation, modulated by plant interactions; grazing (offtake and trampling) by livestock may cause further patchiness vegetation structure.

Aims: We hypothesised that vegetation patchiness in the semi-arid shrublands of north-eastern Patagonia would be increased by livestock grazing, but not by positive interactions between adult plants of shrubs and grasses.

Methods: We compared vegetation cover and pattern at three grazing intensities (exclosure, light and heavy grazing) and measured the growth of a representative shrub and grass in the presence and absence of the other to quantify the role of plant-to-plant interactions and its interaction with grazing for vegetation structure.

Results: In the grazing exclosure and in moderately grazed areas, vegetation cover among shrub patches was larger, whereas the top cover of shrubs was lower than in the heavily grazed areas. We did not find any evidence of positive interactions between shrub and grass life forms.

Conclusions: Our results were consistent with the hypothesis that livestock grazing increased the formation of patchy vegetation cover in arid and semi-arid shrublands.

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Desertification; livestock grazing; Patagonia; shrub–grass interactions; vegetation patchiness; vegetation spatial distribution

Introduction

In arid and semi-arid shrublands throughout the world, the vegetation is commonly arranged in dense shrub patches that alternate with either bare soil or thin herbaceous cover, the latter determining the degree of vegetation patchiness. This heterogeneous spatial distribution of the vegetation may result from ecosystem water limitation that results in a discontinuous plant cover (Noy-Meir 1985; Tongway and Ludwig 1994; Aguiar and Sala 1999) and any resultant patchiness may be further reinforced by livestock grazing (Schlesinger et al. 1990; Fuls 1992; Kellner and Bosch 1992; Augustine 2003). For example, selective grazing of herbaceous vegetation can lead to the invasion of grasslands by shrubs (Archer 2010), which, in turn, changes the distribution of soil resources (Allington and Valone 2014). The concentration of grazing and trampling among shrub patches (less preferred by grazers) may

decrease vegetation cover and compact the soil, which reduces water infiltration and increases water run-off (Rostagno 1989). At the same time, wind and water erosion results in removing soil from these open areas and concentrate it under the shrubs (Ridolfi et al. 2008), leading to soil mounding. Once begun, the increased spatial heterogeneity in soil resources is likely to develop a positive feedback that will reinforce the clumped spatial pattern of vegetation distribution.

In semi-arid environments with such spatial heterogeneity, greatest biomass and highest species diversity are found in shrub patches, mainly because they concentrate resources (water and nutrients), act as sink for seeds dispersed from open areas and facilitate biotic interactions that promote microbial processes under the shrubs (West 1989; Stavi et al. 2009). In grazed semi-arid grasslands, positive interactions (facilitation) between adult shrubs and seedlings of herbaceous species may happen (Bertness

and Callaway 1994). For instance, shrubs can ameliorate physical stress (Aguilar and Sala 1994) and herbivore pressure (Milchunas and Noy-Meir 2002) on grass seedlings, contributing to patch formation. However, competitive interactions between shrub and grasses at adult stages are likely to prevail (Aguilar and Sala 1994; Callaway and Walker 1997). For example, the benefit grasses derive from reduced evapotranspiration demands under a shrub canopy (Callaway 1995) may be offset or overcome by interception of precipitation by the shrub canopy (Branson et al. 1981) and competition for water in the upper soil layers (Kröpfl et al. 2002; Rodríguez et al. 2007). Competition between shrubs and grasses at adult stages may decrease their biomass production, though not necessarily results in structural changes to the patches (Aguilar and Sala 1998).

In semi-arid north-eastern Patagonia, Argentina, the amount of precipitation should allow the development of a higher cover of herbaceous plants between shrub patches than that observed at present. Historical documents (D'Orbigny 1945; Villarino 1972), circumstantial evidence from long-term grazing protection (Kröpfl et al. 2013), post-fire transitions from shrubland to grassland (Rostagno et al. 2006) and simulation modelling (Bisigato et al. 2002) have all suggested a potentially higher cover of herbaceous plants among shrub patches. However, today's vegetation, after ca. 100 years of livestock grazing history, is highly patchy, composed of a mosaic of shrub patches with high plant cover in an open herbaceous matrix (Bisigato and Bertiller 1997; Bertiller et al. 2004; Kröpfl et al. 2007).

We hypothesised that vegetation patchiness in the semi-arid ecosystems of north-eastern Patagonia was attributable to increased livestock grazing, rather than to positive interactions between adult shrubs and grasses. We tested the following predictions: (1) there would be a greater inter-patch herbaceous cover, and less shrub cover and soil mounding, in areas with low as opposed to high grazing intensity; and (2) there would be a similar or greater growth of both adult shrubs and grasses in the absence of the other in areas without grazing and thus leading to a more closed yet patchy vegetation structure than in the presence of grazing.

Materials and methods

Study area

The study was conducted in north-eastern Patagonia, Argentina (40° 41'–40° 46' S, 64° 06'–64° 30' W). The climate is temperate and semi-arid; mean monthly air temperatures ranged from 7°C in July to 24°C in January, with an annual mean of 14°C. Mean annual rainfall is 270 mm (CV = 40%), with peaks in autumn and spring, and the mean annual potential evapotranspiration is 800 mm (Godagnone and Bran 2009). In the two years preceding the study period (2007–2008), and during the study period (2009–2012), the annual mean precipitation was markedly below (2007–2009, multi-year drought conditions) or close (2010–2012) to the long-term historical average precipitation (Figure 1). The dominant soils are Haplargids and Haplocalcids, the former is characterised by the presence of an argillic horizon at 20–30 cm depth, while the latter by the presence of a calcic horizon at variable soil depth.

The vegetation of the study area is a shrubland dominated by *Chuquiraga erinacea* and *Condalia microphylla* in the Monte phytogeographical province (Cabrera 1976). Perennial grasses are mainly represented by *Nassella tenuis* and to a lesser extent by *Jarava plumosa*, *Nassella longiglumis*, *Pappostipa speciosa*, *Piptochaetium napostaense* and *Poa ligularis*. The most abundant annual grasses are *Bromus hordeaceus* and *Schismus barbatus*, and the most abundant forb is *Erodium cicutarium*, exotic species introduced from the Mediterranean. All

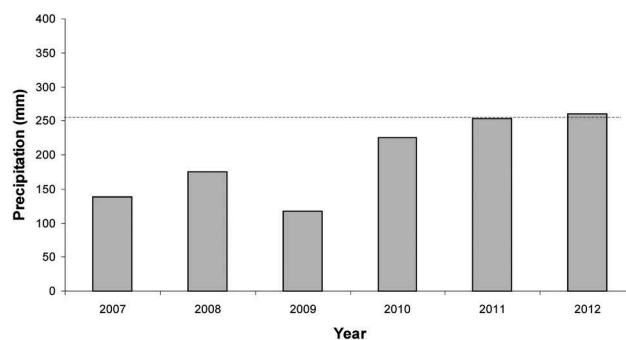


Figure 1. Annual rainfall in the study area, north-eastern Patagonia, 2007–2012, during the two years preceding the beginning of the study and over the study period. The horizontal broken line represents the historical annual average rainfall (255 mm, period 1900–1994; Godagnone and Bran 2009).

scientific names follow Flora Argentina (2015). There is also a cryptogamic layer composed of cyanobacteria, bacteria, algae, bryophytes and lichens.

Today, after about 100 years of livestock grazing, shrub patches alternating with either bare soil or low herbaceous plant cover make up the vegetation (Figure 2). For the purpose of this study, we defined a shrub patch as a discrete unit in the spatial pattern of vegetation with an upper shrub layer and a lower layer composed of perennial grasses, annual species and cryptogams, associated with soil mounding. Inter-patch areas have little vegetation cover and have low species diversity on degraded soil (i.e. soil affected by erosion, soil compaction, soil crusting, reduced water infiltration and increased water run-off).

Livestock grazing in the study area began at the beginning of the twentieth century. At that time, plant cover appeared to have been more homogeneous in space than today, and the main large herbivore was the guanaco (*Lama guanicoe*); summer fires occurred frequently (D'Orbigny 1945; Villarino 1972). Since the arrival of sheep and afterward cattle, the vegetation has been heavily grazed because the density of domestic livestock has surpassed the carrying capacity of the system (Oesterheld et al. 1992; Cecchi and Kropfl 2002). Sheep and cattle have very different impact on vegetation since they markedly differ in feeding habits; sheep have narrower mouths and more flexible lips than cattle, which allow them to be more selective and browse on woody plants (Huston and Pinchak 1991).

Sampling sites

In March 2009, we selected three sampling sites, each on a different commercial ranch. The sites

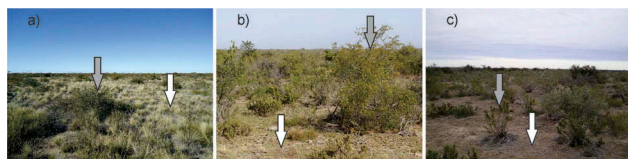


Figure 2. Spatial distribution of the vegetation in the study area with no grazing (a), moderate grazing (b), and heavy grazing (c), north-eastern Patagonia. The grey arrows indicate the shrub patches and the white arrows indicate the grass covered or bare soil patches.

were separated from one another by no more than 30 km. They had a similar grazing history (with an average stocking rate of ca. 0.36 sheep equivalent ha^{-1}), soil type and plant community type in common. Each sampling site comprised a square paddock of 625 ha, with a water source located at one corner. Within each paddock, we sampled at two distances from the water source: 600 and 2500 m. We assumed that these distances represented different grazing intensities and thus impacts, based on the creation of piosphere effects, which determine a decreasing intensity of grazing radiating out from the water source (Andrew and Lange 1986; Jeltsch et al. 1997). We also sampled grazing exclosures of 1 ha, adjacent to each paddock, which had not been grazed for 10 years or more. In this way, we arbitrarily defined three grazing intensities: heavy grazing up to 600 m from the water source, moderate grazing between 600 and 2500 m from the water source and no grazing in the exclosures.

Spatial vegetation pattern

In the autumn and spring of 2009, 2010, 2011 and 2012, we measured the basal cover (the area outline of a plant near the ground surface; Mueller-Dombois and Ellenberg 1974) of perennial grasses, annual species (grasses and dicots), perennial dicots, shrubs, cryptogams, plant litter and bare ground at all sampling sites at each grazing intensity. In each case, we randomly placed five 20-m line transects on which the length of each intercepted variable was measured with a precision of 1 cm. We also measured the vertical projection of the shrub canopy on each transect. Thereby, the size of the inter-patch area and the number of the shrub patches were determined for each line transect.

In autumn 2009, we evaluated soil mounding by measuring soil elevation at 20-cm intervals along each transect. Measurements from the soil surface to a tight levelled cord, held at the top of metal rods inserted up to 1 m above the soil surface at each extreme of the transect, were taken with a ruler placed perpendicularly to the soil. In spring 2010, we also measured shrub density at all sampling sites along the grazing gradient. In each case, we randomly selected five plots (10 m \times 10 m) in which we counted the number of shrubs.

Shrub–grass interactions

In spring 2010, we selected nine shrub patches in each grazing enclosure at the three sampling sites. The shrub patches were similar in size, mound height and floristic composition where *C. erinacea* and *P. ligularis* were the dominant species in the shrub layer and understorey, respectively. Subsequently, the nine selected shrub patches in each enclosure were randomly assigned to one of the three treatments ($n = 3$): intact (control patch), grass removal (*Chuquiraga* patch) or shrub removal (*Poa* patch). Grass or shrub individuals were carefully removed at ground level to prevent disturbance to the rest of the patch components. Subsequent regrowth of either shrubs or grasses was periodically removed.

Immediately after the treatments, we randomly selected one individual of *C. erinacea* in each *Chuquiraga* patch and permanently marked five branches. Next, we measured each branch length and counted the number of current season twigs per branch. These measurements were repeated in spring and autumn 2011 and 2012 and autumn 2013. In each *Poa* patch, we randomly selected and permanently marked three established plants of *P. ligularis*, and we measured the basal cover and counted the number of panicles on each selected individual on the same dates as the measurements in the *Chuquiraga* patches. The same measurement protocol was followed on the shrub and grass plants in the control patches. The growth of *C. erinacea* and *P. ligularis* was calculated as the sum of cumulative positive changes between the measurement dates.

At the end of the measurement period (autumn 2013), we harvested the above-ground biomass of both *C. erinacea* and *P. ligularis* target individuals. The samples were sorted into live and dead fractions and then oven-dried at 70 °C for 48 h. We used the proxy live to dead ratio to compare the aerial biomass between treatments, to minimise the variation due to differences in plant size. We also measured the soil moisture content by the gravimetric method in the three treatments (Reynolds 1970).

Data analysis

For the analysis of the spatial pattern of the vegetation, basal cover data were analysed by split-plot

ANOVA that included treatment, site nested within year, treatment \times year and year (year was considered the main factor and grazing intensity as the split factor). Prior to analysis, data were transformed (arcsine square root for the cover of shrubs, perennial grasses, plant litter and bare ground or rank for the cover of cryptogams, annual species and perennial dicots) to fulfil the requirements of normality and homogeneity of variance. Data from the shrub patches and inter-patches were analysed separately. Data on shrub density and soil mound height, which corresponded to a single sample date, were analysed by ANOVA in a randomised complete block design. Tukey's multiple comparison was used to test the significance of the differences between means.

In the shrub–grass interaction experiment, the data were analysed by repeated-measures ANOVA, except for data on the live to dead ratio of the aerial biomass and soil moisture measured at the end of the study period, which were analysed by ANOVA in a randomised complete block design.

All statistical analyses were carried out using InfoStat version 2009 (Di Rienzo et al. 2009). The results presented are based on untransformed data.

Results

Spatial vegetation pattern

Grazing intensity influenced five of the seven response variables measured in the inter-patch areas and two of the eight response variables measured in the shrub patches (Table 1). There was no grazing intensity \times year interaction ($P > 0.05$) for any response variable measured either in the shrub patches or between them. In the inter-patch areas, the total basal cover of vascular plants and that of perennial grasses was higher in the enclosures and moderately grazed areas than in the heavily grazed areas, whereas the cover of cryptogams was higher under no grazing than under grazing. Moreover, bare ground cover was higher under heavy grazing than in the enclosure. On the other hand, in the shrub patches, the cover of perennial grasses was higher at no grazing and moderate grazing than at heavy grazing. In both the shrub patches and among them, the cover of

Table 1. Vegetation and bare ground cover in shrub patches and in areas among patches (inter-patches) at different grazing intensities, north-eastern Patagonia.

Response variable	No grazing	Moderate grazing	Heavy grazing	P-value
	%			
Inter-patches				
Bare ground	58.2 ± 3.2a	65.8 ± 1.1ab	73.0 ± 2.6b	<0.01
Basal cover				
Plant litter	24.3 ± 1.8	23.2 ± 1.3	19.8 ± 2.0	0.1
Cryptogams	9.2 ± 2.0b	2.7 ± 1.1a	2.3 ± 0.7a	<0.05
Perennial grasses	6.4 ± 0.5b	5.6 ± 0.5b	2.9 ± 0.4a	<0.001
Annual species	0.6 ± 0.3a	1.8 ± 0.5b	1.0 ± 0.3ab	<0.05
Perennial dicot	0.6 ± 0.3	0.3 ± 0.1	0.2 ± 0.1	0.07
Total vascular plants	8.3 ± 0.7b	8.2 ± 0.7b	4.9 ± 0.4a	<0.001
Shrub patches				
Bare ground	34.4 ± 1.7	34.1 ± 2.2	33.5 ± 2.9	0.9
Basal cover				
Plant litter	44.5 ± 2.7	47.3 ± 1.7	50.9 ± 2.6	0.06
Cryptogams	9.1 ± 1.6	4.8 ± 1.8	4.2 ± 1.3	0.1
Perennial grasses	6.0 ± 0.7b	5.1 ± 0.6b	3.2 ± 0.5a	<0.001
Annual species	1.1 ± 0.5a	2.7 ± 1.1b	1.9 ± 0.7ab	<0.05
Perennial dicot	0.2 ± 0.1	0.2 ± 0.1	0.1 ± 0.1	0.2
Shrub	4.3 ± 0.4	5.3 ± 0.6	5.2 ± 0.7	0.5
Total vascular plant	12.0 ± 1.1	13.7 ± 1.6	11.4 ± 1.2	0.2
Shrub aerial cover	32.9 ± 1.9a	31.8 ± 2.3a	45.5 ± 2.7b	<0.01

Each value represents the mean of 12 measurements (three sites × four years) ± SE. Within row, means followed by the same letter are not significantly different ($P > 0.05$). Bold P -values indicate statistically significant differences.

annual species was higher at moderate grazing than at no grazing.

Shrub cover (Table 1) and soil mound height associated with shrub patches (Table 2) were higher at heavy grazing than under moderate grazing and no grazing conditions. The number of shrub patches was larger at no grazing than at moderate and heavy grazing (Table 2), whereas the mean size of the non-shrubby vegetation patches was larger at moderate grazing than at no grazing (Table 2). There was no significant difference in shrub density between the three grazing intensities (Table 2).

Shrub–grass interactions

Both the shrub (*C. erinacea*) and the grass (*P. ligularis*) grew similarly ($P > 0.05$) in the presence (control patches) and absence (*Chuquiraga* patches, *Poa* patches) of each other (Figure 3); however, the number of reproductive panicles per individual of

P. ligularis was higher ($P < 0.01$) in the absence than in the presence of *C. erinacea* in spring 2012 and autumn 2013 (Figure 3(d)). There was only a significant ($P < 0.05$) treatment × time interaction for the number of reproductive panicles of *P. ligularis*. Moreover, the presence or absence of a life form did not change ($P > 0.05$) the live to dead ratio of the aerial biomass ($4.4 ± 0.6$ vs. $5.5 ± 0.9$ for *C. erinacea*, respectively; and $5.9 ± 0.9$ vs. $5.4 ± 1.3$ for *P. ligularis*, respectively; mean ± 1 SE). The soil moisture content was higher ($P < 0.05$) in the *Poa* patches ($12.06 ± 1.45%$, mean ± 1 SE) than in the control or the *Chuquiraga* patches ($9.51 ± 1.18$ and $9.61 ± 1.36%$, respectively).

Discussion

Spatial vegetation pattern

Our results were consistent with our hypothesis that vegetation patchiness would increase by

Table 2. Attributes of shrub patches and areas between patches (inter-patches) at different grazing intensities, north-eastern Patagonia.

Response variable	No grazing	Moderate grazing	Heavy grazing	P-value
Shrub patches				
Soil mound height (cm)	7.7 ± 0.9a	8.4 ± 0.7a	11.8 ± 0.9b	<0.01
Shrub patch density (number/20-m linear transect)	7.7 ± 0.3b	6.4 ± 0.2a	6.4 ± 0.2a	<0.01
Shrub density (number/m ²)	0.8 ± 0.1	0.7 ± 0.1	0.6 ± 0.1	0.2
Inter-patches				
Mean size (cm)	178.8 ± 8.1a	221.9 ± 8.9b	200.4 ± 11.9ab	<0.01

Each value represents the mean of three sites ± SE. Within row, means followed by identical letters are not significantly different ($P > 0.05$). Bold P -values indicate statistically significant differences.

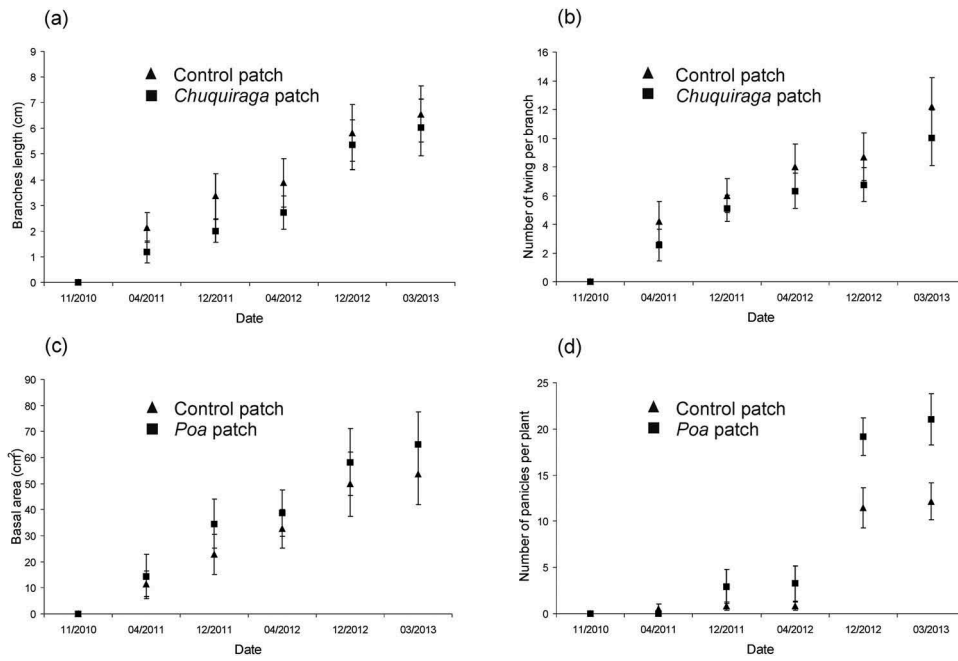


Figure 3. Cumulative branch length (a) and number of twigs per branch (b) for *Chuquiraga erinacea* in control patches (presence of grasses) or in *Chuquiraga* patches (absence of grasses) and cumulative basal area (c) and number of panicle per plant (d) for *Poa ligularis* in control patches (presence of shrubs) or in *Poa* patches (absence of shrubs). Bars represent ± 1 standard error.

livestock grazing in the semi-arid shrublands of north-eastern Patagonia. In areas with either no grazing or moderate grazing, the vegetation cover among patches was denser, whereas the shrub cover and associated soil mound height were lower than in areas with heavy grazing (Table 1). Thereby, although vegetation patchiness might primarily have resulted from water limitations in the ecosystem, our results showed that vegetation patchiness could be intensified by livestock grazing. However, we acknowledge the limitation for interpretation of our results arising from the low number of replicates, in view of the inherent spatial variability of vegetation in the study system.

In the areas not covered by shrubs, the cover of perennial grasses and cryptogams was reduced by livestock grazing (Table 1). Frequent and intense defoliation in combination with severe trampling under heavy grazing results in reduced grass and cryptogam growth and survival (Caldwell 1984; Salihi and Norton 1987; Evans and Johansen 1999). In addition, trampling causes the soil become compacted, leading to physical crusting, reduced water infiltration and a depleted organic matter content (Rostagno and Del Valle 1988; Rostagno 1989; Yates et al. 2000; Chartier and Rostagno 2006). Under

moderate grazing, the cover of annual species (e.g. *S. barbatus*, *Pelletiera verna* and *Herniaria cinerea*) was higher than at no grazing, which may be explained by their adaptation (rapid growth, prostrate habit and high reproductive effort) to disturbance (Grime 1977; Pugnaire and Lázaro 2000; Sternberg et al. 2003). In heavily grazed areas, the severity of disturbance may have negatively affected even ruderal species.

The more evident development of soil mounds in heavy grazing areas may have been due to the more compact grouping of the shrubs within patches since overall shrub density was similar along the grazing gradient and there was a lower number of large size patches under heavy grazing conditions. Enhanced grouping of shrubs and soil erosion between shrub patches under heavy grazing conditions in turn favour the development of soil mounds in shrub patches by concentrating sediments in them (Field et al. 2012), as observed in the present study.

Shrub–grass interactions

We did not find any evidence of positive interactions between adult individuals of one of the dominant shrubs (*C. erinacea*) and those of a dominant

perennial grass (*P. ligularis*). During 2010–2013, a period with an annual rainfall close to the long-term annual average, and in the absence of grazing, *P. ligularis* grew similarly or better in the absence of *C. erinacea*. This response suggests the predominance of neutral or negative interactions between the two species. Similar results have been obtained when comparing the water status and growth of the grass *Nassella tenuis* in the presence or absence of the shrub *Larrea divaricata* in north-eastern Patagonia (Kröpfl et al. 2002). The response of *P. ligularis* to the presence or absence of the shrub may be explained at least in part by compensation between the positive effect on the microclimate created by the presence of the shrub and the ensuing competition between the shrub and the grass. Competition for water between these two life forms probably explains the greater reproductive effort of *P. ligularis* in the absence of the shrub. This argument is consistent with the higher soil moisture measured in the absence of shrub individuals. Conversely, the similar growth of shrub individuals irrespective of the presence or absence of grass individuals may be due to the access by shrubs to deep soil water table, which is beyond the reach of the grasses (Sala et al. 1989).

Conclusion

Within the limits imposed by a low number of replicates, our results suggest that livestock grazing increases the degree of vegetation patchiness in the semi-arid shrublands of north-eastern Patagonia. Heavy grazing reinforces the clumpy distribution of plant cover, increasing the cover of bare soil and much decreasing herbaceous plant cover among shrub patches. However, it does not necessarily mean that grazing is the primary driver of patchiness. Importantly, we found that shrub–grass interactions can be predominantly neutral between adult individuals of shrubs and grasses under average rainfall conditions.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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