

Responses of vegetation to different land-use histories involving grazing and fire in the North-east Patagonian Monte, Argentina

Guadalupe Peter^{A,B,D}, Flavia Alejandra Funk^C and Silvia Susana Torres Robles^B

^ACentro Universitario Regional Zona Atlántica, Universidad Nacional del Comahue – CONICET, 8500 Viedma, Argentina.

^BSede Atlántica, Universidad Nacional de Río Negro, 8500 Viedma, Argentina.

^CCentro de Recursos Naturales Renovables de la Zona Semiárida – CONICET, 8000 Bahía Blanca, Argentina.

^DCorresponding author. Email: gpeter@unrn.edu.ar

Abstract. In arid and semiarid lands around the world, vegetation is distributed in patches within a bare soil matrix. Vegetation in the North-east Patagonian Monte, Argentina is a shrubland steppe, and patches are dominated by shrubs, with grasses, forbs and cryptogams under their canopy. It was hypothesised that grazing increases patchiness; and fires and wind erosion homogenise the distribution of vegetation. It was predicted that there would be: (1) greater cover, specific frequency and richness of shrubs in grazed sites; (2) greater cover, specific frequency and richness of herbs and preferred grasses in ungrazed sites; and (3) a random pattern of distribution in burnt areas. Aerial cover of all perennial species was measured at six sites with different land-use histories: heavily grazed, medium grazed, ungrazed, long enclosure from grazing followed by grazing, burnt and then ungrazed, and burnt and then grazed. Species were grouped into five functional types: shrubs, sub-shrubs, preferred grasses, non-preferred grasses and forbs. The results showed significant differences in the cover of preferred and non-preferred grasses, forbs and total cover with previous grazing but there was no evidence of shrub encroachment. Species frequency and richness decreased especially with increased grazing intensity. The pattern of spatial distribution changed from aggregated in grazed sites to random in ungrazed and burnt sites for all plant functional types. At the population level, the cover of the grass, *Poa ligularis*, was greatest on ungrazed sites whereas the cover of the shrub, *Chuquiraga erinacea*, was greatest on burnt sites. It is concluded that, after applying a heterogeneous patchwork of disturbance, such as grazing, or with fire, followed by periods of rest, the plant diversity is increased.

Additional keywords: distribution pattern, fire, grazing intensity, plant functional types, rangeland communities.

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Introduction

In arid and semiarid lands around the world, vegetation is distributed in patches within a bare soil matrix (Aguiar and Sala 1999); these vegetation patches have a greater concentration of sediments, nutrients, seed and water, and are classed as phytogenic mounds. In most arid drylands overgrazing by domestic livestock is the principal cause of desertification (Fleischner 1994; Whitford *et al.* 1997; Allington and Valone 2011) and of shrub encroachment (Puigdefàbregas 1998; Roques *et al.* 2001; Parizek *et al.* 2002; Villagra *et al.* 2009). Overgrazing can cause an increase in the cover of annual and shrub species and a decrease in the cover of perennial grasses (Milchunas and Lauenroth 1993; Bertiller and Bisigato 1998). These changes in cover are reflected in the structure of the vegetation patches. Thus, in areas with high grazing pressure, patches dominated by preferred grasses disappear and are replaced by shrub species with grasses under their canopy (Bertiller and Bisigato 1998; Aguilar and Sala 1999). This can lead to changes in the structure of the plant community from gramineous steppe to shrubland. The

magnitude of the grazing impact on these systems depends on the type of herbivore and grazing management (for example, see Bisigato and Bertiller 1997; Bertiller and Bisigato 1998; Olf and Ritchie 1998; Bertiller *et al.* 2002; Cingolani *et al.* 2005; Loydi *et al.* 2012).

Shrub encroachment has been recognised as one of the most important ecological and economic issues in semiarid rangelands (Rostagno *et al.* 2006). Fire can be a useful tool to reverse shrub encroachment and promote the recovery of grasses because post-fire wind-erosion processes redistribute nutrient resources accumulated by the shrubs in the phytogenic mounds and, hence, change the spatial patterns of vegetation (Hodgkinson and Harrington 1985; West and Hassan 1985; Wambolt and Payne 1986; Pfeiffer and Steuter 1994; Bóo *et al.* 1996; Rostagno *et al.* 2006; Ravi *et al.* 2007; Peláez *et al.* 2010). Moreover, it has been suggested that burning should be used in combination with grazing management, as high grazing rates can reduce grass cover and also facilitate enhanced shrub seed dispersal (Ravi *et al.* 2009).

In the semiarid province of Monte in the North-east Patagonian region of Argentina, the vegetation is distributed in patches dominated by shrubs, with grasses, forbs and cryptogams under their canopy (Bisigato and Bertiller 1997; Busso *et al.* 2012; Kröpfl *et al.* 2013). Patches have been described for some areas of Monte (Bertiller *et al.* 2004; Busso and Bonvissuto 2009) but the structural characteristics of vegetation in this ecological region have scarcely been studied. Overgrazing in the Patagonian rangelands can cause a reduction in plant cover (Bisigato and Bertiller 1997), changes in botanical composition (Bertiller and Bisigato 1998; Peter *et al.* 2012), an increase in shrub cover (Bertiller and Bisigato 1998), and reduction or even suppression of fires (Peláez *et al.* 2003; Cingolani *et al.* 2005, 2008; Tizón *et al.* 2010; Loydi *et al.* 2012).

It was hypothesised that grazing, with its associated trampling and selective foraging, increases the patchiness; and that fires and wind erosion homogenise the distribution of vegetation, through the redistribution of sediments. The present study was designed to test three predictions, arising from these hypotheses, namely that: (1) cover, frequency and richness of shrubs would increase in grazed sites; (2) cover, frequency and richness of herbs and preferred grasses would be greater in ungrazed sites; and (3) the distribution of vegetation would change from an aggregated pattern under livestock grazing to a random pattern following burning.

Methods

Study area

The study area was located in North-east Patagonia, in the Departments of Adolfo Alsina and San Antonio in Río Negro, Argentina (40°40'S, 64°10'W). Phytogeographically, it belongs to the Monte province, Southern District, Northern Patagonic sub-district (Roig *et al.* 2009). The area is characterised by a transition sub-temperate semiarid climate, with warm summers (mean temperature 21°C) and mild winters (mean temperature 7°C). Average annual precipitation is between 200 and 350 mm, with high intra-annual variability (Bran *et al.* 2000). The climate is windy, especially in spring and summer, which contributes to the soil moisture deficit. Soils are ustolic Natrargides on the plains and fluventic Haplocambides on hillocks (Godagnone and Bran 2009).

Vegetation is a shrubland steppe, with an herbaceous stratum of predominantly winter-growing grasses. The dominant shrub species are *Chusquea erinacea* D. Don, *Larrea divaricata* Cav., *L. cuneifolia* Cav., *Condalia microphylla* Cav. and *Prosopis alpataco* Phil. Among the dominant herbaceous species are *Nassella tenuis* (Phil.) Barkworth, *Poa ligularis* Nees. ex Steud., *Jarava plumosa* (Spreng.) S.W.L. Jacobs & J. Everett, *Pappostipa speciosa* (Trin. & Rupr.) Romasch., *Schismus barbatus* (L.) Thell. and *Erodium cicutarium* (L.) L'Hér. ex Aiton (Cabrera 1971; Godagnone and Bran 2009). The study site had been grazed by sheep for almost 100 years with a normal annual stocking rate in the region of ~0.18 sheep ha⁻¹.

Sites and field sampling

The topography in the study area was uniformly flat and is <100 m above sea level (Godagnone and Bran 2009). The area is grazed by native herbivores – the guanaco (*Lama guanicoe*) is the most

abundant species – and, as we mentioned above, domestic herbivores have been introduced for ~100 years. The area of the study was 30 × 10 km of a vegetation unit which comprised several ranches with different land uses. The vegetation unit was defined as a medium shrubby steppe, with some specific variation in relation with the soil texture (Godagnone and Bran 2009). A railway passes through the area, and an area of land 200 m wide along the railway was protected from grazing by fences, which provided an enclosure of 200 m × 30 km. Further, after a road was constructed, an area of 100 ha was isolated from grazing for 40 years because there was no permanent water point. It was then grazed by sheep at the normal stocking rate of ~0.18 sheep ha⁻¹ for 1 year.

Eight years before sampling, wild fires partially affected the study area. This fire event allowed the study of the role of grazing and fire on the vegetation community, because after the fire an area of 1 ha was excluded from grazing by fences.

Piosphere formation is common around permanent water points in arid areas (Bisigato *et al.* 2005), so a grazing intensity gradient, based on the distance from the water point, was studied.

Six sites were selected with different land-use histories (Table 1). Two sites with different grazing intensities due to distance from water were selected: ≤600 m from the water point (heavily-grazed area, site HG), ≥2500 m from the water point (medium-grazed area, site MG). A third site was located near the railway from which domestic livestock had been excluded for a long time (ungrazed area, site UG). A fourth site was located in the 100-ha enclosure, which was grazed by sheep for 1 year after 40 years of exclusion of (long ungrazed-grazed area, site LU). The final two sites were selected in burnt places: one in the 1-ha area in which livestock was excluded after fire (burnt ungrazed area, site BU); and the other in an adjacent site which remained grazed by sheep at the normal stocking rate (burnt grazed area, site BG).

We located 30 plots within the six land-use sites in the study area. Then, at each site, five plots of 10 × 10 m were randomly established. This plot number and size was determined from preliminary studies using the methods of Mueller-Dombois and Ellenberg (1974) and Mateucci and Colma (1982). In the spring of 2010 the aerial cover of all perennial species on each plot at all six sites was measured following the Braun-Blanquet method (Braun-Blanquet 1972). Species were grouped into five functional types: shrubs, sub-shrubs, preferred grasses, non-preferred grasses and forbs.

Table 1. Description of the land-use history of the six sites

Land-use history	Description of the site
Medium grazed (MG)	Grazed area with typical stocking rate for the region
High grazed (HG)	Highly grazed area at ≤600 m of the water point
Ungrazed (UG)	Enclosures generated by fencing of a railroad
Long ungrazed-grazed (LU)	Area excluded from grazing for 40 years of which was grazed the year before the data collection
Burnt-ungrazed (BU)	Area which was burnt in a wildfire, excluded for 10 years after the fire
Burnt-grazed (BG)	Area which was burnt in a wildfire, continuously grazed for 10 years after the fire

Statistical analyses

Vegetation attributes. The similarity between sites was determined using Principal Component Analysis (Digby and Kempton 1987). The similarity with respect to species frequency (number of plots where a species was present in each site), species richness (number of species of each plant functional type in each site) and aerial cover (m^2) of each species and of each plant functional type in each site were analysed. The data on vegetation cover (whether transformed or untransformed) did not follow a normal distribution (Shapiro–Wilks Normality Test) so the non-parametric Kruskal–Wallis test for multiple comparisons between sites was applied with a post-hoc paired comparison test (Balzarini *et al.* 2008). All the analyses were undertaken using InfoStat software (Di Rienzo *et al.* 2011).

Spatial distribution. To analyse species pattern, the aerial cover of each species was used. For functional group patterns, the cover of all species in each functional group in the plot was summed. For all six land-use sites the variance/mean for each species and functional type was calculated (Mateucci and Colma 1982), testing the significance with an χ^2 test (de la Cruz Rot 2008). If the variance/mean ($n - 1$) was lower than the critical value [$\chi^2_{(0.025;4)} = 0.484$], the distribution pattern was considered to be regular; if the rate was greater than the critical value [$\chi^2_{(0.975;4)} = 11.14$], the distribution pattern was classed as aggregated; and if the rate was between the critical values (0.484 and 11.14) then the pattern was considered to be random (de la Cruz Rot 2008).

Population level. For characterisation of spatial pattern at the population level, the data on the aerial cover for one preferred grass species, *Poa ligularis*, and the shrub, *Chuquiraga erinacea*, was used. These two species were selected to study the changes at population level because Peter *et al.* (2012) found that cover of *Poa ligularis* varied with grazing and they observed that

vegetation patches were dominated principally by *Chuquiraga erinacea*.

Results

Vegetation attributes in plant communities

Based on species frequency, PC1 of the Principal Components Analysis explained almost 42% of the variability and PC2 27%. Sites with different land-use histories were ordered in a disturbance gradient on PC1, principally by grazing intensity (Fig. 1). On PC2 the burnt sites were separated from the unburnt ones, particularly for the lower frequencies of *Larrea divaricata* and *Prosopidastrum globosum* on unburnt sites. Based on the frequency of each species on each site (Table 2, the frequency of some species of low frequency (shrubs: *Geoffroea decorticans*, *Larrea cuneifolia*, *Cyclolepis genistoides*, *Mulguraea ligustrina* and *Monttea aphylla*; sub-shrubs: *Acantholippia seriphioides* and *Baccharis crispa*; grasses: *Melica rigida*, *Piptochaethium napostaense* and *Jarava naei*; forbs: *Baccharis darwinii*, *Trichocline sinuata* and *Tweedia* sp.) and species of high frequency (shrubs: *Condalia microphylla*, *Lycium* spp. and *Prosopis alpataco*) did not change with land-use history. On the one hand, the frequency of some species decreased at higher grazing levels (i.e. *Chuquiraga erinacea*, *Schinus johnstonii*, *Senna aphylla*, *Margyricarpus pinnatus*, *Baccharis trimera*, *B. gilliesii*, *Poa ligularis*, *Senecio filaginoides* and *S. melanopotamicus*), while on the other hand the frequency of other species increased at higher grazing levels (*Baccharis ulicina*, *Nassella tenuis* and *Poa lanuginosa*). On burnt sites the frequency of one shrub decreased (*Larrea divaricata*) whereas the preferred grass, *Pappophorum caespitosum*, increased.

In respect of the species richness of each plant functional type, PC1 explained 70% of the variability and PC2 27% (Fig. 2).

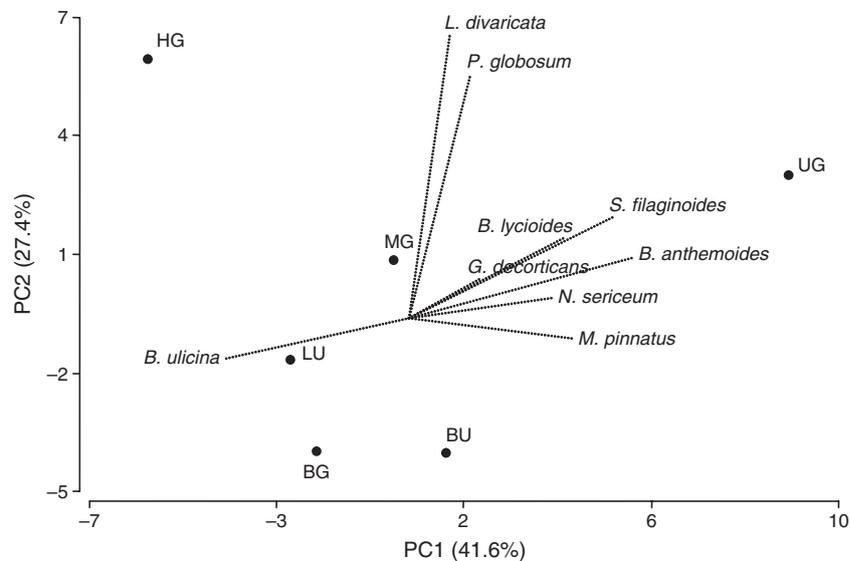
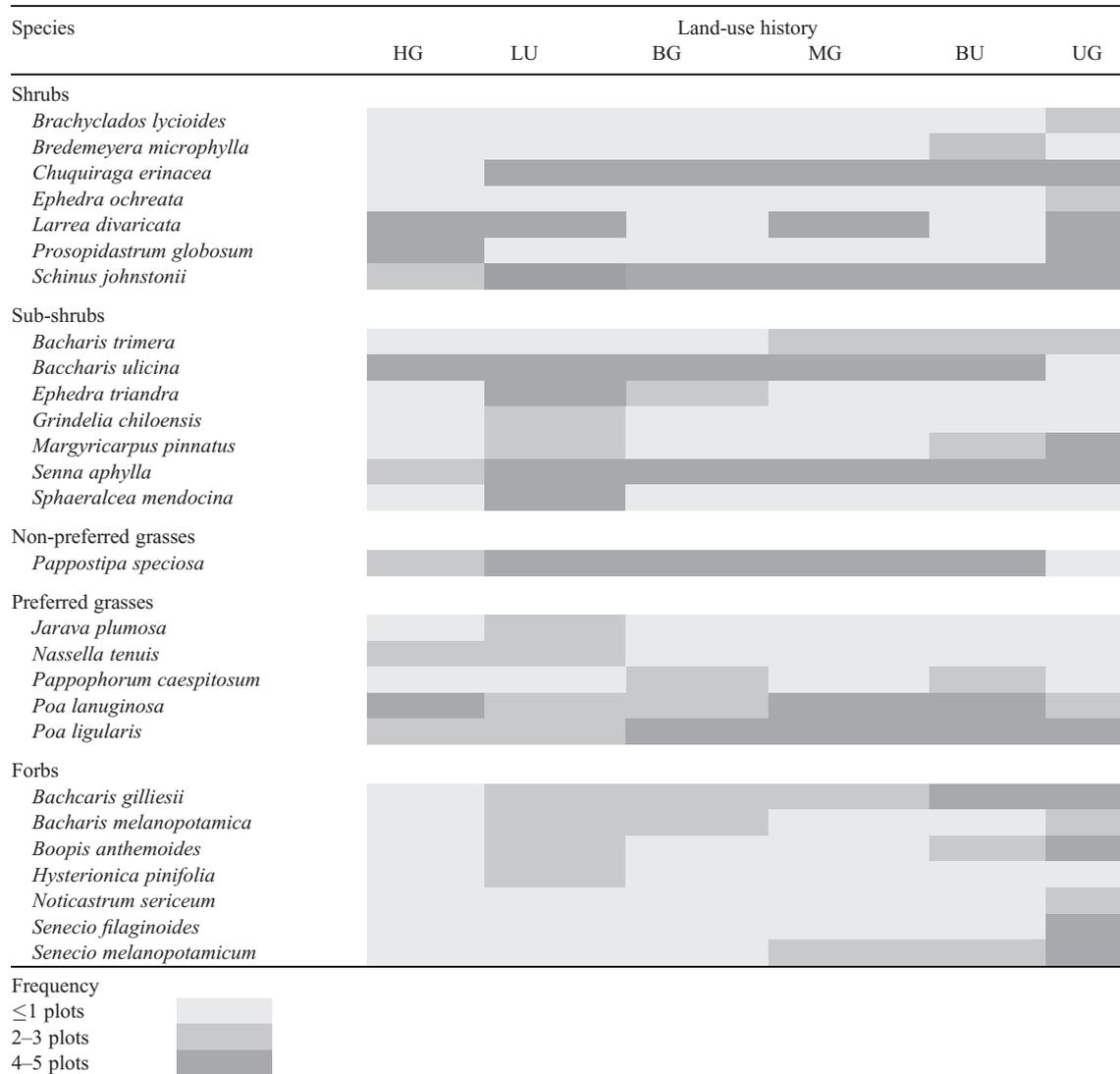


Fig. 1. Principal Components Analysis showing the relationships of similarities between the six sites with respect to species frequency. Only species with correlations greater than 0.80 are indicated. The six sites were: ungrazed site (UG), medium-grazed site (MG), heavily-grazed site (HG), ungrazed for a long period then grazed site (LU), burnt then ungrazed site (BU), and burnt and then grazed (BG).

Table 2. Changes in species frequency (number of plots where the species was present) in sites with different land-use histories
 The six sites were: ungrazed site (UG), medium-grazed site (MG), heavily-grazed site (HG), ungrazed for a long period then grazed site (LU), burnt then ungrazed site (BU) and burnt then grazed site (BG)



Again, the sites were ordered on the PC1 along a grazing intensity gradient with ungrazed sites having the greater richness of forbs and shrubs. The second axes separated the exclosures from grazing, which had been subject to previous burning or grazing (sites BU and LU) with their higher richness of preferred grasses and sub-shrubs.

Species aerial cover and plant functional type cover showed some differences in the ordination of sites. For species cover, PC1 explained 53% of the variability and PC2 35% (Fig. 3a). Site UG was very different from all other sites with a greater cover of *Poa ligularis* and *Noticastrum sericeum*. Burnt sites (sites BU and BG) and site LU were defined by a higher cover of *Chuquiraga erinacea*, while sites MG and HG principally consisted of *Larrea divaricata*.

In the case of cover per plant functional type, PC1 and PC2 explained 88 and 9% of the variability, respectively (Fig. 3b). Site

UG showed a higher cover of preferred grasses and forbs, and a higher total cover. However, some grazed sites (sites LU, HG and BG) were characterised by a lower cover of forbs and total cover. Site BU had medium cover for all plant functional types.

The results showed significant differences in the cover of preferred and non-preferred grasses, forbs and total cover between sites ($H = 16.98, P = 0.004$; $H = 17.05, P = 0.003$; $H = 18.26, P = 0.002$; $H = 11.94, P = 0.03$, respectively), and no significant differences were found in the cover of shrubs and sub-shrubs (Fig. 4). Significant differences were principally due to grazing intensity, because the burnt sites did not differ in the cover of any functional group. The site UG had the highest cover of preferred grasses, forbs and total plant species, and the grazed sites had a lower cover of the same elements. For non-preferred grasses, the highest cover was on the BU site, and the lowest on the UG site.

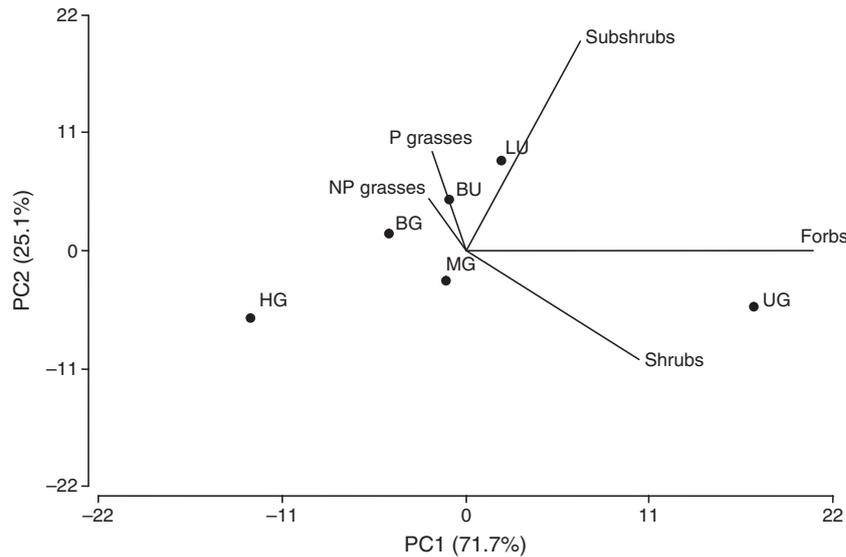


Fig. 2. Principal Components Analysis showing the relationships of similarities between sites with respect to the species richness of each plant functional type. The six sites were: ungrazed site (UG), medium-grazed site (MG), heavily-grazed site (HG), ungrazed for a long period then grazed site (LU), burnt then ungrazed site (BU) and burnt then grazed site (BG). P grasses are preferred grasses and NP grasses are non-preferred grasses.

Spatial distribution per plant functional type

The pattern of spatial distribution changed with land-use history in all plant functional types (Table 3). For shrubs the pattern changed from random in the ungrazed sites to aggregated in the grazed sites. The pattern of sub-shrubs was aggregated in HG and MG sites and random in the others. The forbs group showed the greatest changes; it was absent in site HG, regular in site LU, random in site BG and aggregated in the other sites. Preferred grasses presented an aggregated pattern except in site BU, where it was random. Among non-preferred grasses, the pattern was aggregated in sites UG and MG, random in site HG and absent in the other sites. This pattern was driven primarily by one species – *Pappostipa speciosa* – which was the principal non-preferred grass. In general, the ungrazed and burnt areas changed in pattern from aggregated to random, probably due to the removal of niches and the homogenisation of resources and propagules.

Cover and spatial distribution in grass and shrub populations

Cover of the preferred grass, *Poa ligularis*, was significantly different ($H = 20.01$; $P = 0.0011$) between sites (Fig. 5a), having the greatest cover values in site UG. Cover in ungrazed sites (sites UG and BU) was significantly greater than cover in the grazed sites (HG, LU, MG and BG). *Poa ligularis* showed an aggregated pattern in ungrazed and burnt sites, and a random pattern in grazed (HG and MG) and BU sites (Table 3).

Chuquiraga erinacea also varied significantly between land-use histories ($H = 17.79$; $P = 0.0027$) (Fig. 5b), with the greatest cover in sites BU and BG and the least in site HG. *Chuquiraga erinacea* showed a change in the pattern, being random in the BU site and aggregated in the rest (Table 3).

Discussion

The area of study was selected to be as representative as possible of the soil, topography and vegetation of the steppe on the North-east Patagonian Monte. In spite of the small size of the BU site and the lack of spatial replication of sites, it is considered that the observations of this study are important in understanding the role of fire and management in the sustainability of this productive system. They should also contribute to the design of future and more definitive studies. The following discussion highlights the significance of the recorded effects of past land-use on vegetation of the steppe, the observed interactions between grazing and fire, and the influence of distance from water on vegetation.

Vegetation attributes in plant communities

The results revealed that land-use history influenced all the vegetation attributes analysed (frequency, richness, cover and spatial pattern) in all functional groups.

Species frequency was especially influenced by grazing intensity, with fire as a lesser source of variability. Neither dominant nor rare species changed frequency. The frequency of the dominant species of the community, e.g. *Condalia microphylla* and *Prosopis alata*, did not vary significantly, indicating their ability to tolerate all levels of disturbance. Amongst the species that declined in frequency under higher grazing intensities, the only preferred species was *Poa ligularis*, so its decrease was probably due to the loss of individuals as a consequence of defoliation. In the case of non-preferred species (*Chuquiraga erinacea*, *Schinus johnstonii*, *Senna aphylla*, *Margyricarpus pinnatus*, *Baccharis trimera*, *B. gilliesii*, *Senecio filaginoides* and *S. melanopotamicus*), the diminished frequency could be due to the lack of optimal sites for recruitment as a result

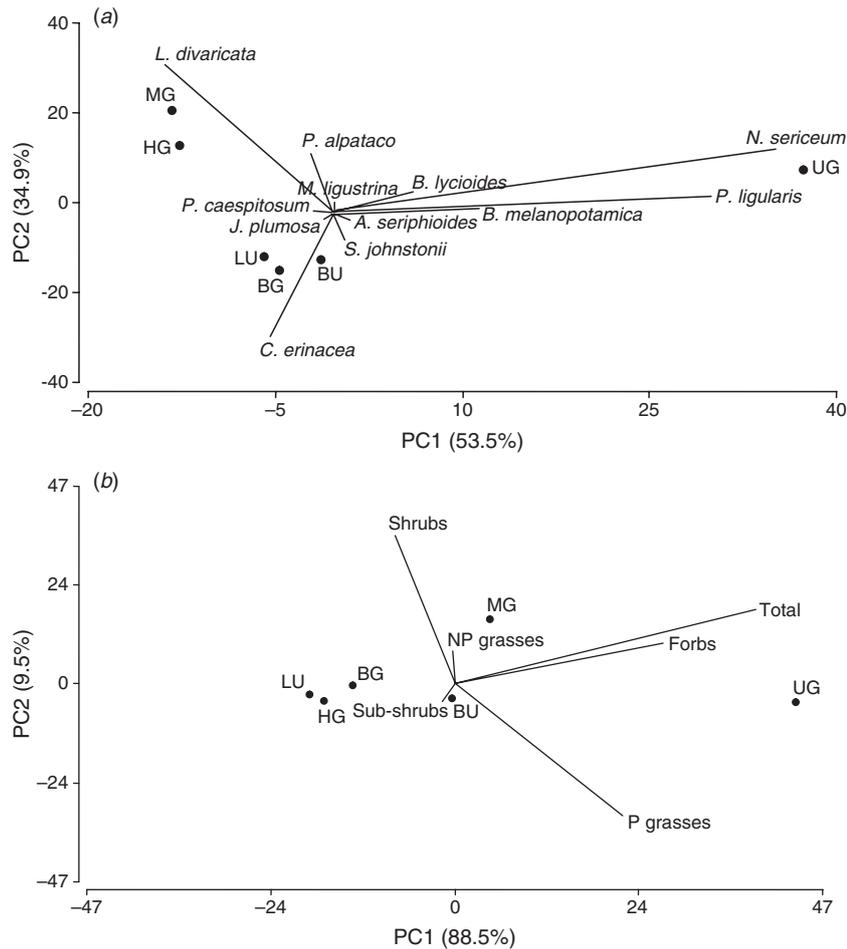


Fig. 3. Principal Components Analysis showing the relationships of similarities between sites with respect to the (a) specific cover and (b) cover of each plant functional type. Only species with a correlation of greater than 0.80 are indicated. The six sites were: ungrazed site (UG), medium-grazed site (MG), heavily-grazed site (HG), ungrazed for a long period then grazed site (LU), burnt then ungrazed site (BU) and burnt then grazed site (BG).

of trampling. At higher grazing pressures, the frequency of the preferred grasses, *Poa lanuginosa* and *Nassella tenuis*, increased. *Poa lanuginosa* is a rhizomatous grass, which has been reported as a coloniser of bare ground due to its vegetative reproduction (Busso and Bonvissuto 2009). It is possible that individuals that have survived grazing form new tillers from their rhizomes in sites without cover. Rostagno *et al.* (2006) reported that both these species are able to establish readily in mounds after fires, especially *Nassella tenuis*, which they found dominated the shrub interspaces which are characterised by a soil with low nitrogen and phosphorous contents. This did not occur in this study. Rather, these species decreased at the burnt sites. The lower frequency of the shrub, *Larrea divaricata*, in burnt sites might be due to its high mortality (~60%) after wildfires (Bóo *et al.* 1997). In contrast, the frequency of the preferred grass, *Pappophorum caespitosum*, increased in burnt sites as this species prefers open sites (Villagra 2000), and fire diminishes aerial cover and provides sites for recruitment.

Land-use histories affected the species richness of each plant functional type in a similar way. Ungrazed areas were

characterised by greater richness of forbs and shrubs, but the highest richness of grasses (preferred and non-preferred) was in the burnt areas, regardless of whether they were being grazed or not. Peláez *et al.* (2010) suggested that this response is explained, at least in part, by reduced competition of shrubs for light, water and/or nutrients after fire. On the other hand, this might be due to the provision of sites for recruitment which have inherently better growing conditions, enabling a large number of species to be recruited, thus reducing the effects of grazing. Previous work in semiarid woodlands showed that fires contribute to grasses re-sprouting and limit shrub growth, altering community composition from a shrubland to a grassland (Hodgkinson and Harrington 1985; West and Hassan 1985; Wambolt and Payne 1986; Pfeiffer and Steuter 1994; Bóo *et al.* 1996; Rostagno *et al.* 2006; Ravi *et al.* 2007; Peláez *et al.* 2010).

In general, the results suggest that grazing diminishes the cover of grasses, forbs and total cover. Ordination of sites in respect to specific cover supports the idea that shrubs of dense canopies, such as *Chuquiraga erinacea*, are replaced by open canopied shrubs, such as *Larrea divaricata*, under grazing

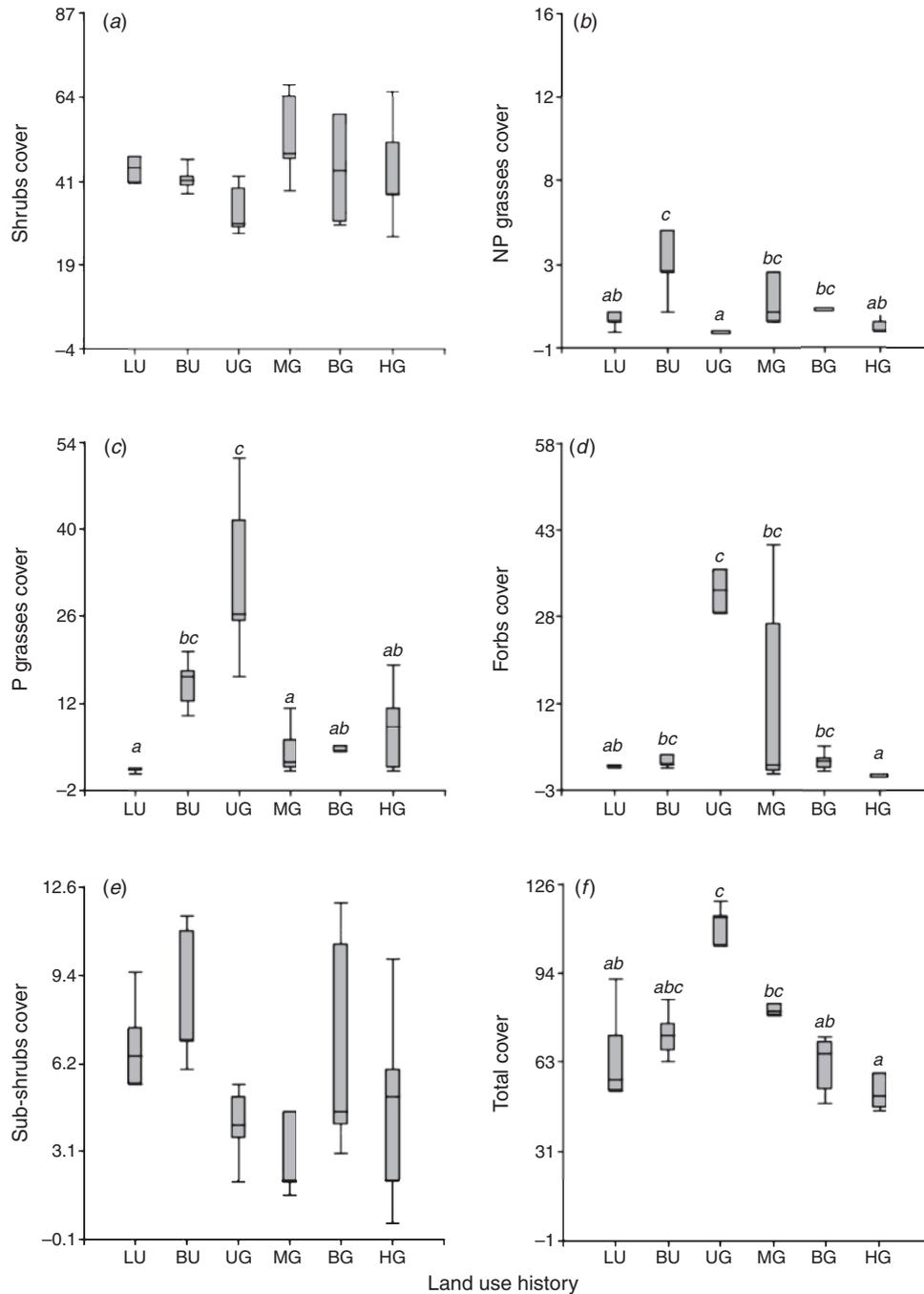


Fig. 4. Cover (m²) of each plant functional type: (a) shrubs; (b) non-preferred grasses; (c) preferred grasses; (d) forbs; (e) sub-shrubs; and (f) total cover. The solid line within each box represents the median. Horizontal hyphens at the top and bottom of vertical lines represent the maximum and minimum values, respectively. The lower Q1 and the upper Q3 quartiles are represented as the bottom and top horizontal lines of each box. Vertical bars indicate the distance between the minimum and maximum values. Different letters indicate significant differences ($P < 0.05$) in the cover of each plant functional type. The absence of letters indicates no detection of significant differences within a plant functional group. The six sites were: ungrazed site (UG), medium-grazed site (MG), heavily-grazed site (HG), ungrazed for a long period then grazed site (LU), burnt then ungrazed site (BU) and burnt then grazed site (BG).

(Bisigato *et al.* 2005; Fernández *et al.* 2009) because the latter favour the passage of cattle. Besides, *Larrea divaricata* has a greater recruitment in bare soil under grazing (Bisigato and

Bertiller 1999) and is more affected by fire (Bóo *et al.* 1997). Thus, differences found in the ordination of grazed and burnt sites with reference to species cover and cover of functional groups

Table 3. Spatial distribution of species and plant functional type (ran = random, abs = absent, agg = aggregated, reg = regular) at sites with different land-use histories

Data were obtained from the species cover and cover of each plant functional type. The six sites were: ungrazed site (UG), medium-grazed site (MG), heavily-grazed site (HG), ungrazed for a long period then grazed site (LU), burnt then ungrazed site (BU) and burnt then grazed site (BG)

Species	BG	BU	LU	HG	MG	UG
<i>Brachyclados lycioides</i>	abs	abs	abs	abs	ran	agg
<i>Bredemeyera microphylla</i>	ran	ran	ran	abs	abs	abs
<i>Chuquiraga erinacea</i>	agg	ran	agg	agg	agg	agg
<i>Condalia microphylla</i>	agg	ran	ran	ran	ran	ran
<i>Ephedra ochreata</i>	ran	abs	ran	abs	abs	ran
<i>Geoffroea decorticans</i>	abs	abs	abs	abs	abs	ran
<i>Larrea divaricata</i>	abs	agg	agg	agg	agg	ran
<i>Lycium</i> spp.	ran	ran	ran	agg	ran	ran
<i>Monttea aphylla</i>	abs	abs	abs	abs	ran	abs
<i>Mulguraea ligustrina</i>	abs	abs	abs	ran	ran	abs
<i>Prosopidastrum globosum</i>	agg	abs	abs	ran	ran	ran
<i>Prosopis alpataco</i>	ran	agg	agg	agg	agg	ran
<i>Schinus johnstonii</i>	agg	agg	ran	ran	ran	ran
Total shrubs	agg	ran	agg	agg	agg	ran
<i>Acantholippia seriphioides</i>	ran	ran	ran	abs	abs	ran
<i>Baccharis crispata</i>	abs	ran	abs	abs	ran	ran
<i>Baccharis ulicina</i>	ran	ran	ran	agg	ran	ran
<i>Ephedra triandra</i>	ran	ran	ran	abs	ran	ran
<i>Grindelia chilensis</i>	abs	abs	ran	abs	abs	abs
<i>Margyricarpus pinnatus</i>	ran	ran	ran	abs	ran	ran
<i>Senna aphylla</i>	agg	ran	ran	ran	agg	ran
<i>Sphaeralcea mendocina</i>	abs	ran	ran	abs	ran	ran
Total sub-shrubs	ran	ran	ran	agg	agg	ran
<i>Melica rigida</i>	abs	abs	ran	abs	abs	abs
<i>Pappostipa speciosa</i>	ran	ran	ran	ran	agg	ran
Total non-preferred grasses	ran	ran	ran	ran	agg	ran
<i>Jarava neaei</i>	abs	abs	ran	abs	abs	abs
<i>Jarava plumosa</i>	ran	ran	ran	abs	abs	abs
<i>Nasella longiglumis</i>	agg	agg	abs	ran	ran	ran
<i>Nassella tenuis</i>	abs	abs	ran	ran	abs	abs
<i>Pappophorum caespitosum</i>	ran	ran	ran	ran	ran	abs
<i>Piptochaetium napostaense</i>	abs	ran	ran	abs	abs	abs
<i>Poa lanuginosa</i>	ran	ran	ran	agg	agg	ran
<i>Poa ligularis</i>	agg	ran	agg	ran	ran	agg
Total preferred grasses	agg	ran	agg	agg	agg	agg
<i>Baccharis darwinii</i>	ran	abs	abs	abs	abs	ran
<i>Baccharis gilliesii</i>	ran	agg	ran	abs	agg	agg
<i>Baccharis melanopotamica</i>	ran	agg	ran	abs	ran	agg
<i>Boopis anthemoides</i>	abs	ran	ran	abs	ran	reg
<i>Hysterionica pinifolia</i>	abs	ran	abs	abs	abs	ran
<i>Noticastrum sericeum</i>	ran	ran	abs	abs	ran	agg
<i>Senecio filaginoides</i>	ran	ran	ran	abs	ran	ran
<i>Senecio melanopotamicum</i>	abs	abs	abs	abs	ran	ran
<i>Trichocline sinuata</i>	abs	abs	ran	abs	abs	abs
<i>Tweedia</i> sp.	abs	ran	abs	abs	abs	abs
Total forbs	ran	agg	reg	abs	agg	agg

could be explained by the replacement of species of the same functional group, for example *Chuquiraga erinacea* by *Larrea divaricata*. Contrary to our prediction, no differences were found in the cover of shrubs and sub-shrubs between the different sites.

Accordingly, there is no evidence of shrub encroachment in this system. This conclusion coincides with that of Cipriotti and Aguiar (2005, 2012) and Cesa and Paruelo (2011) and is partially coincident with that of Rostagno *et al.* (2006) who concluded that removal of livestock favours the recovery of grasses but does not change shrub dominance. Moreover, a previous study in the Monte region (Peláez *et al.* 2010) showed that the cover of some shrub species recovered 5 years after a fire, which could explain the absence of significant differences between the sites in this study. On the other hand, the BU site had the highest cover of non-preferred grasses, and had medium values for the other functional groups. In this context, Franzese and Ghermandi (2012) mentioned that burning positively affects the emergence of *Pappostipa speciosa*, the most important non-preferred grass in the area. This is in agreement with our hypothesis that fire attenuates the grazing effects on vegetation cover because with fire there is a non-selective removal of biomass and because fire promotes wind erosion of soil and redistribution of sediments and propagules. Besides, no difference was found in forbs, preferred grasses and total cover between the burnt site, excluded from grazing, and the ungrazed area, which might be because fire accelerates the recovery processes of grasses due to reduced competition from shrubs (Peláez *et al.* 2010), and the aerial cover of vegetation attained similar values to those of the sites excluded from grazing.

Considering changes in cover at the population level, *Poa ligularis* showed a predictable response to grazing, and fire did not seem to attenuate grazing effects. On the other hand, *Chuquiraga erinacea* was dominant in the burnt sites, and fire affected *Larrea divaricata* considerably as was previously mentioned by Bóo *et al.* (1997).

Spatial distribution

Consistent with our predictions, the spatial distribution pattern of some species and of all plant functional types was found to change in relation to land use. As mentioned in the Results section, the vegetation pattern changed from aggregated under ungrazed conditions to random in ungrazed and burnt areas. As in other arid shrubby systems of the world, fire tends to break the phytogenic mound and inter-mound pattern and to accelerate recovery of vegetation in areas of bare soil (Whicker *et al.* 2002; Ravi *et al.* 2009). This is probably due to the destruction of niches, which then allows the random recruitment of new plants.

In particular, the spatial patterning of *Poa ligularis* differed from its functional type because it showed an aggregated pattern in some grazed and burnt sites and a random pattern in other grazed sites, although differences in the latter sites are probably due to a low cover of *Poa ligularis*. Previous studies have demonstrated that grazing has not had a consistent effect on the spatial distribution of this native preferred grass. For example, the spatial distribution *Poa ligularis* was shown to be affected by grazing domestic herbivores in the study of Bertiller *et al.* (2002) but not in that of Pazos *et al.* (2007). With respect to shrubs, Cipriotti and Aguiar (2005) found that the patchy structure remained unchanged in areas that had been grazed for 100 years and they suggested that grazing did not affect processes that may be involved in the maintenance of spatial structure. Somewhat in contrast, changes from aggregated patterning in the grazed

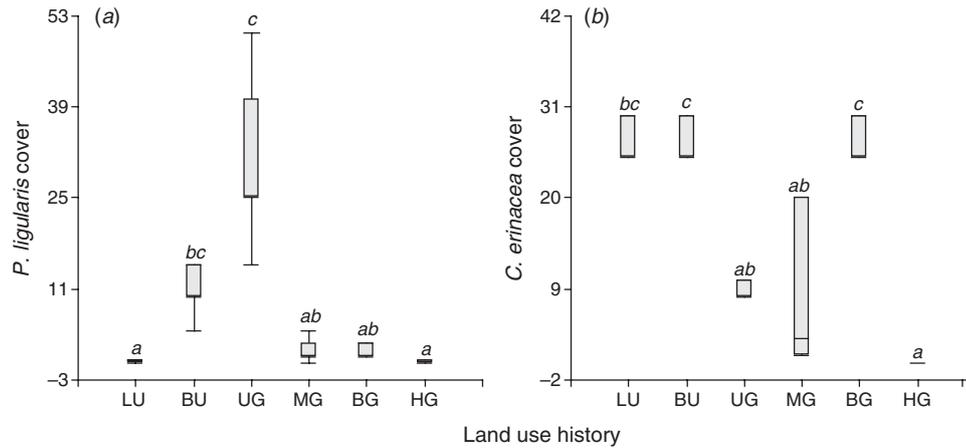


Fig. 5. Cover (m^2) of (a) *Poa ligularis* and (b) *Chuquiraga erinacea*. The solid line within each box represents the median. Horizontal hyphens at the top and bottom of vertical lines represent the maximum and minimum values, respectively. The lower Q1 and the upper Q3 quartiles are represented as the bottom and top horizontal lines of each box. Vertical bars indicate the distance between the minimum and maximum values. Different letters indicate significant differences ($P < 0.05$) in the cover of each species. The six sites were: ungrazed site (UG), medium-grazed site (MG), heavily-grazed site (HG), ungrazed for a long period then grazed site (LU), burnt then ungrazed site (BU) and burnt then grazed site (BG).

situations to random patterning in the ungrazed areas were detected. These could be the result of an absence of trampling by livestock in the inter-mound areas excluded from grazing, allowing recruitment and subsequent increase in shrub cover. In respect to *Chuquiraga erinacea*, the pattern is predominantly aggregated whereas fire and exclusion from grazing together generated new sites with the same probability of being colonised and the aggregated pattern changing to random. The effect of changes in the spatial pattern of shrubs on the susceptibility of grasses to grazing is relevant to the detection of degradation thresholds (Bisigato *et al.* 2005).

Conclusion

The results of this study support the view that this semiarid rangeland type is resilient to fire (Bóo *et al.* 1997) but not so to continuous grazing (Rostagno *et al.* 2006). In spite of not finding shrub encroachment, a positive response of the grasses to fire and exclusion was found, and previous studies (Bóo *et al.* 1997; Rostagno *et al.* 2006; Tizón *et al.* 2010) have suggested that repeated fires may be necessary to suppress woody plants and favour grass species. On the other hand, an intermediate level of disturbance from livestock grazing can promote a more heterogeneous landscape, providing greater opportunities for a variety of plant species (McNaughton 1983); that is, moderate grazing may sustain a greater diversity of native plant species. There are doubts about the efficacy of short-term removal of cattle for increasing plant diversity at a local scale and also about moderate grazing practices that may result in increased community heterogeneity (Loeser *et al.* 2007). According to Fuhlendorf and Engle (2001), landscape management which involves a heterogeneous patchwork of disturbance, such as grazing or fire, followed by periods of rest, is recommended for increasing forage production.

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