



Original article

Continuous feral horse grazing and grazing exclusion in mountain pampean grasslands in Argentina

A.E. de Villalobos*, S.M. Zalba

GEKKO (Grupo de Estudios en Conservación y Manejo), Departamento de Biología, Bioquímica y Farmacia, Universidad Nacional de Sur, San Juan 670, Bahía Blanca 8000, Argentina

ARTICLE INFO

Article history:

Received 6 May 2010

Accepted 13 July 2010

Published online 7 August 2010

Keywords:

Feral ungulates

Grazing

Plant functional groups

Invasion resistance

Grasslands restoration

ABSTRACT

This paper evaluates changes in the composition and structure of plant communities and plant functional groups associated with the continuous presence of feral horses in mountain pampean grasslands in Argentina in order to explore the potential effects of horse removal on vegetation restoration. Specific and functional richness, diversity, evenness, spatial heterogeneity and above-ground biomass were compared between areas subjected to ten years of intensive grazing by horses and exclusions of the same age. Forbs, shrubs and rosettes were more abundant after ten years of grazing, while the spatial heterogeneity of perennial grasses was higher in long-term grazed areas. Nevertheless, grasslands showed good recovery after horse removal, with greater species diversity and evenness, higher abundance of perennial grasses, greater above-ground biomass and lower percentages of exotic species. An understanding of the effect of feral animals on plant communities will lead to the design of a strategy of adaptive management and monitoring tools for measuring the condition of grasslands.

© 2010 Elsevier Masson SAS. All rights reserved.

1. Introduction

Grazing by large herbivores has an affect on grasslands (Dyer et al., 1993). Direct effects include selective defoliation that results in morphological and physiological alterations of plants and in the reduction of their reproductive capacity and competitive ability. Indirect effects include changes in soil characteristics, nutrient cycles and soil water availability (Archer and Smeins, 1991; Sternberg et al., 2000). Alterations in the distribution of plant species modify habitat diversity (Adler and Lauenroth, 2000; Wang et al., 2002) that might make an impact on the abundance and reproductive success of small mammals, birds and insects (Milchunas et al., 1998; Hobbs, 2001; Zalba and Cozzani, 2004), change interactions between coexisting species (Vázquez and Simberloff, 2003) and modify disturbance regimes, ecosystem resistance and resilience properties (Prieur-Richard and Lavorel, 2000; Holmgren, 2002).

The effect of introduced herbivores on the composition and structure of grasslands may vary, depending on the intensity and frequency of grazing and the evolutionary relationship between grasslands and grazers (Milchunas et al., 1988). Ecosystems that have evolved under low grazing pressure, like most South American

grasslands, are more vulnerable when they are overgrazed, compared with those that included large hooved congregating mammals, like bovids and sheep, in their evolutionary past (Milchunas et al., 1988; Mack, 1989; Cingolani et al., 2005). Native herbivores differ from domestic livestock and feral herbivores due to differences in their spatial and temporal patterns of plant resource-use (Archer and Smeins, 1991). Moreover, these alterations are more severe in the case of feral herbivores since they are free-ranging and non-managed, which differs from the typical situation of cattle ranching. Most exotic herbivores are artificially maintained at high concentrations in limited areas where fences prevent their emigration when the abundance of desirable forages decreases, resulting in the overgrazing of preferred plants (Archer and Smeins, 1991; Holmgren, 2002). As a result, self-sustained perpetuation of unmanaged exotic herbivore populations may result in ecological effects that are different to those extensively studied for cattle and which could pose serious concerns for the conservation of plant communities (Huntly, 1991; Loucougaray et al., 2004).

The presence of feral horses and donkeys is a common management problem in natural or semi-natural grasslands in many countries (Duncan, 1987; Beever and Brussard, 2000a; Department of the Environment and Heritage, 2004; Linklater et al., 2004; Rheinhardt and Rheinhardt, 2004) and efforts for restoring the structure and composition of affected communities are becoming more and more common (Dobbie et al., 1993; Olson-Rutz et al., 1996a; Bastian et al., 1999; Beever and Brussard, 2000b; Loucougaray et al., 2004; Dawson et al., 2006). It is important to evaluate the effects of

Abbreviations: CV, Coefficient of variation; ETPP, Ernesto Tornquist Provincial Park; NMDS, Non-parametric multidimensional scaling analysis.

* Corresponding author. Tel.: +54 291 4595100.

E-mail address: avillalo@criba.edu.ar (A.E. de Villalobos).

feral herbivores in wild-lands from this perspective and to assess the reversibility of their impacts once they are removed. Some studies have evaluated the effect of continuous intensive grazing by feral horses on the species composition of natural grasslands (Duncan, 1987; Rogers, 1991) and there is evidence that the presence of feral horses affects grass performance (Kristensen and Frangi, 1992; Loydi and Zalba, 2009) as well as bird communities (Zalba and Cozzani, 2004) in mountain pampean grasslands in Argentina. However, as far as we know, no previous study has considered the dynamics, abundance and distribution of plant species following horse removal.

An understanding of the responses of vegetation to long-term, continuous grazing and grazing cessation is critical in order to facilitate the management of mountain grasslands for both biological conservation and sustainable use. Therefore, the objective of this study was to evaluate the resulting changes in the composition and structure of plant communities and plant functional groups associated with continuous grazing by feral horses in mountain pampean grasslands and to explore the potential effects of vegetation restoration after the removal of exotic ungulates. We evaluated the composition (species richness and diversity), abundance and spatial patterns of plant functional types (life forms and growth forms) and the percentage cover of bare ground to clarify whether any changes occur in the grassland in response to the contrasting grazing histories and to improve the management of mountain pampean grasslands. In order to do this the vegetation composition of mountain grasslands was compared after ten years of intensive grazing (1993–2003), and also with that in exclosures (1997–2003), in a nature reserve invaded by feral horses.

2. Materials and methods

2.1. Study site description and grazing history

This study was carried out in the Ernesto Tornquist Provincial Park (ETPP), established in 1942, one of the last relicts of pampean grasslands in a relatively good state of conservation (Cabrera, 1976; Bilenca and Miñaro, 2004). ETPP is located in the Ventania mountain range in the central Pampas region, between 38° 00' and 38° 10' S, and 61° 45' and 62° 08' W. It has an area of ca. 6700 ha, and includes some of the highest peaks in the region, reaching up to 1200 m. Climate is temperate, with an average annual temperature of 14 °C (Burgos, 1968). Average precipitation is 800 mm, falling mostly in spring and autumn, with occasional snow-fall in the winter. The mean air temperature was 13.5 °C and mean annual precipitation 686 mm, ranging from 583.5 (1995) to 1154 mm (2001), over the period considered in this study (1993–2003). The region belongs to the Southern District of the Pampas Phytogeographic Region, where grass steppe is the dominant vegetation (Cabrera, 1976) and *Stipa*, *Piptochaetium*, *Festuca* and *Briza* are among the most common grass genera. There are also less frequent shrub communities dominated mainly by *Eupatorium bunifolium*, *Discaria longispina* and *Geoffroea decorticans* (Kristensen and Frangi, 1995; Long and Grassini, 1997). In pre-hispanic times native herbivores in this region included Pampas Deer (*Ozotoceros bezoarticus*) and Guanaco (*Lama guanicoe*). The former became extinct in the region early in the 20th century, while guanacos still remain but in extremely low numbers (Chébez, 1994). Cattle were introduced to the Pampas at the end of the 15th century and were rapidly adopted by the Indians, becoming abundant in the 18th century in some areas of the Pampas (Brailovsky and Foguelman, 2006). Other exotic herbivores of medium size were introduced to the area in the 19th century for hunting: Red deer (*Cervus elaphus*) and Fallow deer (*Dama dama*). Nevertheless, the main impact of exotic ungulates in the study area probably started much later: in 1942 five horses were released in the reserve with the aim of maintaining a “native” breed (*caballos criollos*). Since then, the

population has increased by 6% p.a. and horses have become the main herbivore in the area, reaching a population of 700 horses. However, the abundance of other exotic and native ungulates has decreased due to predation, sickness, migration and competition with horses and they have almost disappeared from the area (Scorolli, 2007). During our sampling period horse densities ranged from 0.20 horses ha⁻¹ (1993) to 0.35 horses ha⁻¹ (2003) (Scorolli, 2007).

2.2. Sampling

All study areas were located on adjacent piedmont grasslands, with 5–11% steepness of warmer, preferentially grazed, north-facing slopes, characterized by shallow soils and occasional rocky outcrops. Grazed areas included three valleys of 27, 23 and 18 ha under continuous intensive grazing by free-ranging feral horses. The three grazed areas were sampled in two sampling periods, the springs of 1993 and 2003. In 2003, two exclosure areas, where horses and others ungulates were excluded by perimeter fences, were added to the analysis. The exclosure areas were two sections, of 15 and 12 ha respectively, of the first two previously described valleys that have been protected from feral horses since the beginning of 1997. The exclosure areas were not sampled in 1997, so the records obtained in 1993 were used as a reference of the state of the grassland condition, as well as to evaluate 7 years of horse exclusion and 10 years of continuous grazing treatments. In spring (late November–early December) 1993 and 2003, 20 plots of 1 m² were randomly distributed each time in the study areas, and the frequency (presence/absence) of each plant species present in each plot was recorded. Species richness, Shannon's diversity (Krebs, 2001) and evenness (Pielou, 1975) were calculated for each study area in both sampling periods.

Species with similar biological traits, such as growth form (erect or prostrate) and life cycle (annual or perennial), that are notable for their response to grazing (Vesk and Westoby, 2001) were grouped together. The abundance of the resulting functional groups were calculated from the frequency of each species recorded in the 20 randomly distributed plots (1 m²) in each study area for both sampling periods. The corresponding coefficient of variation (CV) of each functional group was calculated for each grazing treatment: reference condition (grazed areas sampled in 1993), 10 years of continuous grazing (grazed areas sampled in 2003) and 7 years of horse exclusion (exclosure areas sampled in 2003) for both sampling periods. The CV was used as an indicator of the changes in spatial pattern for each functional group between grazing treatments (Sokal and Braumann, 1980; Sternberg et al., 2000; Veen et al., 2008).

Above-ground grass and forb biomass was estimated at the end of the rainy season in 2003 (spring) by drying and weighing the herbaceous standing crop clipped from five 1 m² randomly distributed plots in each study area. The percentage of bare ground was estimated in 20 plots (1 m²) randomly distributed in the exclosure and grazed areas sampled in 2003 using the canopy-cover method of Braun Blanquet (Mueller-Dombois and Ellenberg, 2003).

2.3. Data analysis

Patterns of variation in species composition in the studied areas were analyzed using the non-parametric multidimensional scaling test (NMDS) based on a matrix of Euclidean distance calculated from the frequency of each plant species in each grazing treatment, in which stress values were minimised. Species present in less than 5% of the plots were excluded from the analysis in order to reduce the influence of rare species (Legendre and Legendre, 1998; Legendre and Gallagher, 2001). We performed a Mantel test to determine whether the vegetation groups obtained from NMDS analysis were significantly different. We undertook a Spearman correlation

analysis between the NMDS results, the abundance of plant species and the functional groups recorded in each grazing treatment to evaluate whether the ordination-defined vegetation groups reflect the differential response of plants to grazing by feral horses (Legendre and Legendre, 1998).

Differences in species diversity and evenness, percentage of exotic species and relative abundance of functional groups between grazing treatments were analyzed by one-way analysis of variance for a completely randomized design (Sokal and Rohlf, 1979). Data were transformed to the square-root and means were then separated using the Tukey test (Zar, 1996). Tests of significant differences between the CVs calculated for the abundance of each functional group recorded in 1993 and 2003 were carried out according to Sokal and Braumann (1980). Differences in the percentage of bare ground and in above-ground biomass of grass and forb vegetation between grazed and ungrazed areas sampled in 2003 were assessed using Student *t*-test for unequal samples (Zar, 1996).

3. Results

3.1. Changes in richness, diversity and abundance of exotic species

There was a negative effect of continuous feral horse grazing on the species richness of mountain grasslands. Out of a total of 130 plant species that were recorded during this study, 57 species had been recorded in 1993 in areas grazed by feral horses. In 2003, 53 species were detected in the grazed areas, whereas 67 species were associated with ungrazed areas. Thirty species were only detected in the enclosures and 10 species were exclusive to the grazed areas. Species diversity, evenness and percentage of exotic species also were associated with contrasting histories of grazing by feral horses in these mountain grasslands. Significantly higher species diversity ($F_{2,5} = 5.8$, $p = 0.049$) and evenness ($F_{2,5} = 5.5$, $p = 0.05$) were recorded for ungrazed areas in comparison with the grazed ones, whereas the percentage of exotic species was significantly higher in areas under long-term continuous grazing by feral horses ($F_{2,5} = 6.4$, $p = 0.042$) (Table 1).

3.2. Changes in species composition

Three main clusters of vegetation samples became apparent on the NMDS ordination in two-dimensional space, with a stress value of 0.086 (Fig. 1). The three different vegetation clusters showed relatively clear and significant separation (Mantel statistic = 0.989; $p < 0.0001$) within the ordination space. The first axis separated the ungrazed areas from the groups consisting of grazed areas sampled in 1993 and 2003 and the second axis segregated the grazed groups from each other (Fig. 1). The first group defined on axis 1 (ungrazed areas) was positively correlated with the frequency of *Piptochaetium lepodum* ($r = 0.733$), *Piptochaetium hackelii*, *Stipa juncooides* ($r = 0.733$), *Stipa neesiana* ($r = 0.764$) and *Stipa tenuis* ($r = 0.764$); and negatively correlated with *Dichondra sericea* ($r = -0.822$) and *Discaria americana* ($r = -0.886$). The grazed areas sampled in 1993

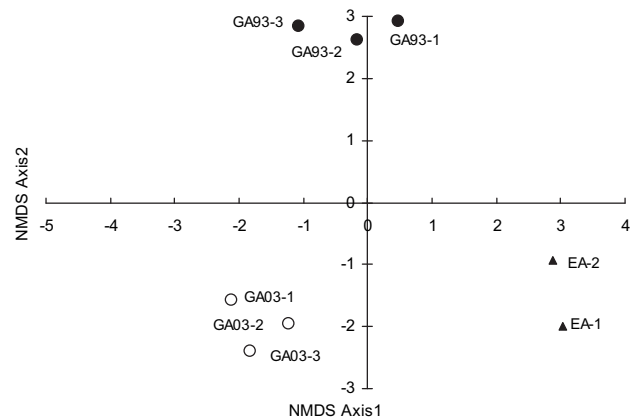


Fig. 1. Non-metric multidimensional scaling (NMDS) ordination of vegetation samples from enclosure areas sampled in 2003 (EA-1 and EA-2) (▲), grazed areas sampled in 1993 (GA93-1, GA93-2 and GA93-3) (●) and grazed areas sampled in 2003 (GA03-1, GA03-2 and GA03-3) (○).

were associated with *Margyricarpus pinnatus* ($r = 0.743$) and *Sida physocalix* ($r = 0.866$). Variables loaded onto axis 2 and correlated with grazed areas sampled in 2003 were the abundances of *Briza subaristata* ($r = -0.741$), *Daucus pusillus* ($r = -0.830$), *Echium plantagineum* ($r = -0.784$), *Mimosa rocae* ($r = -0.892$), *Modiola caroliniana* ($r = -0.722$), *Plantago lanceolata* ($r = -0.741$), *Plantago patagonica* ($r = -0.732$), *Plantago myosurus* ($r = -0.889$), and *Piptochaetium napostaense* ($r = -0.822$). Analysis of the correlation between the two NMDS axes and the abundance of functional groups revealed highly significant and positive correlations of grasses and graminoids and perennial tussock grasses with axis 1 and axis 2, but they were negatively correlated with rosettes and shrub species (Table 2).

3.3. Changes in functional groups and species abundances

The classification obtained using growth form and life cycle attributes of all the species recorded resulted in seven functional groups being defined: grasses and graminoids (including annual and rhizomatous perennial grasses and other monocotyledonous species), perennial tussock (caespitose) grasses, perennial forbs, annual forbs, shrubs and rosettes. After ten years of continuous grazing, the relative importance of the different plant functional groups had been modified. The abundance of annual forbs, shrubs and rosettes showed a significant increase ($p < 0.05$), while grasses and graminoids, and tall perennial grasses showed a decline (Fig. 2). The frequency of grasses and graminoids and tall perennial grass groups was significantly higher ($p < 0.05$) in the enclosures than in both groups of grazed areas. The frequency of shrubs, rosettes and annual forbs was significantly lower in the enclosures than in the grazed areas sampled in 2003, whereas no differences were seen in the same areas sampled in 1993. The abundance of perennial forbs

Table 1

Mean species diversity (Shannon index), evenness (Pielou index) and percentage of exotic species (\pm SE) in areas grazed by feral horses sampled in 1993 ($N = 3$) and in 2003 ($N = 3$) and in ungrazed areas ($N = 2$). Values followed by the same letter do not significantly differ ($p > 0.05$) for each variable.

	Grazed areas (1993)	Grazed areas (2003)	Ungrazed areas
Diversity	2.7 \pm 0.7 b	2.9 \pm 0.3 b	3.9 \pm 0.6 a
Evenness	0.67 \pm 0.06 b	0.60 \pm 0.05 b	0.85 \pm 0.09 a
Exotic species (%)	14.1 \pm 3.1 b	16.7 \pm 2.5 a	12.7 \pm 1.5 b

Table 2

Spearman correlation coefficients between the relative abundance of each functional group and the first two axes of non-parametric multidimensional scaling test (NMDS). Bold typing indicates significant correlations ($p < 0.05$).

Functional groups	Axis 1	Axis 2
Grasses and graminoids	0.580	0.010
Perennial tussock grasses	0.819	0.057
Shrubs	0.024	-0.730
Rosettes	0.008	-0.850
Perennial forbs	0.057	0.444
Annual forbs	0.046	0.413

does not seem to have been affected by the different grazing histories (Fig. 2).

The spatial patterns of the functional groups were also modified. The spatial heterogeneity of grasses significantly increased and this was particularly evident when comparing perennial grasses sampled in 1993 and 2003 in the grazed areas. On the contrary, shrubs and perennial and annual forbs showed less spatial heterogeneity in the later samples ($p < 0.05$). Ungrazed areas showed lower values in the spatial heterogeneity of grasses, whereas rosette growth forms and annual forbs were more heterogeneous than in grazed areas (Table 3).

3.4. Above-ground biomass and soil cover associated with contrasting grazing histories

The above-ground biomass measured in the enclosures was significantly higher than those measured in grazed areas ($t = 5.55$, $p = 0.005$). The effect of grazing history differed among forbs, grasses and graminoid species. Under enclosure conditions, accumulated grass biomass was eight times greater than forb biomass ($t = 9.97$, $p < 0.001$). In contrast, grazed areas showed that forb biomass was twice as great as for grasses ($t = 5.05$, $p < 0.001$) (Table 4). The percentage cover of bare ground was almost 30% greater in grazed areas than in ungrazed grasslands ($t = 8.5$, $p = 0.001$) (Table 4).

4. Discussion

Our results reflect significant changes in mountain grasslands associated with the history of grazing by feral horses. The continuous presence of feral horses was associated with alterations in the composition of species and functional groups, and with a reduction in plant diversity and evenness, as has been reported for prairies affected by domestic livestock (van de Koppel et al., 2002; Bullock et al., 2001; Hobbs, 2001). We also documented a significant recovery of grassland structure and an increase in species richness after seven years of horse exclusion. In contrast with our findings, Fahnestock and Detling (1999) found that the number of plant species was lower in enclosed areas than in other areas grazed by feral horses in midwest North American grasslands. In Río de la Plata grasslands (sensu Soriano, 1991), the results reported by Sala et al. (1986), Hongo et al. (1995), Rodríguez et al. (2003), Altesor et al. (2005) and Sternberg et al. (2000) contrast with ours in reporting higher species diversity and evenness in grazed ecosystems than in those excluded from grazers. These differences might correspond to variations in the intensity and persistence of grazing and in the type of herbivores. Horses exhibit grazing behaviour markedly different from that of domestic livestock which were the herbivores present in most of the studies on grazing effects in natural grasslands (Rook et al., 2004). There are important differences in the impacts of

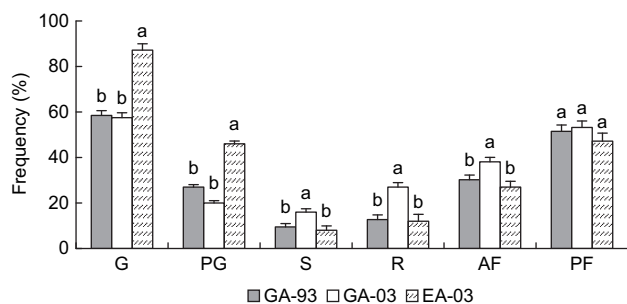


Fig. 2. Frequency (%) of grasses and graminoids (G), perennial tussock grasses (PG), shrubs (S), rosettes (R), annual forbs (AF) and perennial forbs (PF) in grazed areas sampled in 1993 (GA-93) and in 2003 (GA-03) and in enclosure areas (EA-03). Columns with the same letter do not significantly differ ($p > 0.05$).

Table 3

Coefficient of variation (CV) of the relative abundance of grasses and graminoids (G), perennial tussock grasses (PG), shrubs (S), rosettes (R), annual forbs (AF) and perennial forbs (PF) in grazed areas sampled in 1993 (GA-93) ($N = 3$) and in 2003 (GA-03) ($N = 3$) and in enclosure areas (EA-03) ($N = 2$). Numbers in bold indicate significant differences between surveys ($p < 0.05$).

	GA-93	GA-03	<i>t</i>	<i>P</i>	EA-03	<i>t</i>	<i>P</i>
G	16.7	29.4	17.1	0.003	5.6	25.5	0.001
PG	39.7	91.3	39.6	0.000	8.9	8.4	0.013
S	43.2	21.5	17.3	0.003	96.8	3.9	0.080
R	15.4	10.2	3.3	0.080	90.0	4.7	0.042
AF	49.1	21.7	9.5	0.010	23.0	7.7	0.016
PF	17.3	4.3	57.1	0.000	47.8	3.5	0.071

t: statistical index value.

P: probability value.

different grazing animal species on grazed communities. Cattle are more selective about the plant parts or species that they consume, while horses have an excellent ability to utilize herbage of variable quality with high fiber content and they are well-adapted to grazing a range of plant species and pasture types (Gudmundsson and Dyrmondsson, 1994). Moreover, feral horses are not managed in a way that would reduce the grazing impact whereas the grazing of domestic livestock is usually controlled in order to maintain the load capacity below that which would cause deterioration of the grassland. When the resistance threshold of grassland is exceeded, the diversity declines rapidly as mortality due to grazing becomes a greater force than competitive interactions in shaping the composition of the plant community (Milchunas et al., 1988). This process results in higher diversity at relatively low grazing intensities, but in plant communities with a short evolutionary grazing history, such as the Argentine pampas grasslands, the response of competitors in the herbaceous canopy to the removal of above-ground biomass dominated by grasses might create an increase in species that are usually subordinated, such as alien or opportunistic plants that displace the dominant vegetation.

The percentage of exotic plant species in our study area increased after ten years of continuous grazing and decreased in the areas closed to feral horses. Resource-use patterns and competition intensity are determinants of community invasibility (Levine and D'Antonio, 1999; Davis et al., 2000). This has led to the assumption that richer, more diverse communities may be less subjected to invasion because they offer fewer empty niches for the establishment of exotic plants and use resources more completely than poor or less diverse communities (Tilman, 1997; Shea and Chesson, 2002). In our case, grazing by feral horses might have prevented the competitive exclusion of alien plants by perennial grasses, decreasing community resistance, as proposed by Wardle (2001). Long-term grazing also resulted in an increase in the abundance of some invasive alien plants. *E. plantagineum*, an aggressive alien toxic weed (Grigulis et al., 2001; Nordblom et al., 2002), which was not recorded in 1993, was present in 50% of the grazed and 15% of the ungrazed plots in 2003. Invasion by exotic species could, in turn, disrupt competitive interactions and reduce the availability of appropriate micro-sites for the establishment of native seedlings,

Table 4

Total grasses and forbs above-ground biomass (g) and percentage of bare ground (%) in grazed ($N = 3$) and ungrazed areas ($N = 2$) sampled in 2003. Values followed by the same letter do not significantly differ ($p > 0.05$) for each variable.

	Grazed areas	Ungrazed areas
Total Biomass (g)	107.6 ± 16.0b	287.0 ± 25.7a
Grasses (g)	33.6 ± 7.8b	245.8 ± 33.0a
Forbs (g)	74.0 ± 5.3a	41.2 ± 9.5b
Bare ground (%)	32.4 ± 6.7a	4.0 ± 1.2b

which could lead to a positive feedback with the direct effects of grazing and trampling by feral horses. Whichever process was involved, it is an important lesson for management to note that these alien plants have spread in the grazed areas and even into exclosures in a good state of conservation in less than ten years, highlighting the pervasive effects of the interaction between exotic herbivores and exotic plants.

The abundance of plants with avoidance-of-grazing or tolerance-to-grazing strategies increased after ten years of continuous grazing by horses, whereas perennial grasses and palatable forbs were favored under feral horse exclosure. The observed changes in the abundance of functional groups after ten years of continuous horse grazing in ETPP clearly shows the loss of perennial grasses (*Piptochaetium* and *Stipa* spp.) and the increase of shrubs (*M. rocae*) and prostrate and rosette plants (i.e. *M. caroliniana* and *Plantago* spp.). Unpalatable (*B. subaristata*; Cabrera, 1967) and grazing tolerant grasses (*P. napostaense*; Loreti et al., 2001) replaced grasses that are preferred by horses. This response is in line with many other studies showing the reduction of palatable grasses and an increase of unpalatable plants, mostly forbs and shrubs (Altesor et al., 1998; Fahnestock and Detling, 1999; Chaneton et al., 2002; Rodríguez et al., 2003), and also an increase in the encroachment of woody plants, as a direct consequence of overgrazing by domestic herbivores (Brown and Archer, 1989; O'Connor, 1995; de Villalobos et al., 2005).

The exclusion of feral horses in ETPP resulted in a reversion of the described patterns of species and functional groups dominance in our study site. After seven years of feral horse exclusion in the ETPP grasslands, grasses that are typical of pristine communities, e.g. *Stipa* spp. and *Piptochaetium* spp. (Prieto, 2000), became abundant again and the abundance of annual forbs also increased. The recovery of grasslands after the exclusion of feral horses was very notable when the above-ground herbaceous biomass and the percentage of bare soil between ungrazed and grazed areas was analyzed. This recuperation is consistent with similar results described for other grasslands formerly affected by domestic herbivores (Noy-Meir et al., 1989; Olson-Rutz et al., 1996; Fahnestock and Detling, 1999; Todd and Hoffman, 1999; Sternberg et al., 2000).

Grazing by feral horses in our study site was also associated with a change in the spatial pattern of the vegetation that reverted after horse exclusion. The particularly high CV of perennial grass abundance in grazed areas in our study site was probably due to their vulnerability to defoliation by feral horses, resulting in a patchy distribution that could eventually result in the total exclusion of this group. Complementary to this, the decrease in the heterogeneity of forbs, shrubs and rosettes in the continuously, intensively grazed areas could be taken as a sign of their spatial dominance. On the contrary, the exclusion of feral horses for seven years reduced the spatial heterogeneity of grasses and graminoids and perennial tussocks, while increasing the CVs calculated for rosettes species. It is known that perennial grasses are usually able to close the vegetation matrix after herbivore exclusion, displacing species that are less competitive for light such as rosettes plants (Sternberg et al., 2000). This recovery of the spatial pattern of vegetation is a valuable sign of restoration, considering, for instance, the importance of vegetation structure for grassland birds nesting in the area (Zalba and Cozzani, 2004).

Grassland dynamics critically depends on the activity of grazing animals. Grazing in ETPP is started by feral, unmanaged horses, which have never been under any rotation cycles and whose densities have reached unusually high levels compared with the original grazing scenarios (Prieto, 2000). Nevertheless, our findings indicate that: 1- feral horses are responsible for severe changes in the composition and structure of grassland communities; 2- the relative abundances and spatial patterns of functional groups are variables that are sensitive to grazing history and easy to measure,

which could be used as indicators of grassland condition; and 3- the effect of grazing by feral horses promotes an increase in the abundance of invasive alien plants that might colonize areas in the vicinity, even if they are free of horses.

Conclusions from studies on the effect of domestic livestock on grasslands should not be applied uncritically for situations with feral animals. An understanding of the local effect of feral animals on plant communities and a strategy of adaptive management, including active monitoring actions, are the best alternatives for accompanying the control of feral ungulates.

Acknowledgements

This work was funded by CONICET (Consejo Nacional de Investigaciones Científicas y Técnicas) and SGCYT, Universidad Nacional del Sur, Argentina. We also wish to thank Paola Germain and Alejandro Loydi who kindly helped with field surveys, Andrea Long and Carlos Villamil for species determinations, Yannina Cuevas for providing monthly rainfall records, and Susana Bravo, Isabel Miranda and Franz-Xavier Dillier for comments on the manuscript, and two anonymous reviewers who gently revised our manuscript.

References

- Adler, P.B., Lauenroth, W.K., 2000. Livestock exclusion increases the spatial heterogeneity of vegetation in Colorado shortgrass steppe. *App. Veg. Sci.* 3, 213–222.
- Altesor, A., Di Landro, E., May, H., Ezcurra, E., 1998. Long-term species change in a Uruguayan grassland. *J. Veg. Sci.* 9, 179–180.
- Altesor, A., Oesterheld, M., Leoni, E., Lezama, F., Rodríguez, C., 2005. Effect of grazing on community structure and productivity of a Uruguayan grassland. *Plant Ecol.* 179, 83–91.
- Archer, S., Smeins, S., 1991. Ecosystem-level processes. In: Heitschmidt, R.K., Stuth, J.W. (Eds.), *Grazing Management. An Ecological Perspective*. Timber Press, Portland, Oregon, pp. 109–139.
- Bastian, C., Van Tassel, L.W., Cotton, A.C., Smith, M.A., 1999. Opportunity costs related to feral horses: a Wyoming case study. *J. Range Manage.* 52, 104–112.
- Beever, E.A., Brussard, P.F., 2000a. Charismatic megafauna or exotic pest? Interactions between popular perception of feral horses (*Equus caballus*) and their management and research. *Proceedings 19th Vertebrate Pest Conference, California*. pp. 413–418.
- Beever, E.A., Brussard, P.F., 2000b. Examining ecological consequences of feral horse grazing using exclosures. *West. N. Am. Nat.* 60, 236–254.
- Bilenca, D., Miñaro, F., 2004. Identificación de Áreas Valiosas de Pastizal (AVPs) en las Pampas y campos de Argentina, Uruguay y sur del Brasil. *Fundación Vida Silvestre Argentina*, Buenos Aires.
- Brailovsky, A.E., Fogelman, D., 2006. Memoria verde: historia ecológica de la Argentina. Editorial Sudamericana, Buenos Aires.
- Brown, J.R., Archer, S., 1989. Woody plant invasion of grasslands establishment of honey mesquite (*Prosopis glandulosa* var. *glandulosa*) on sites differing in herbaceous biomass and grazing history. *Oecologia* 80, 19–26.
- Bullock, J.M., Franklin, J., Stevenson, M.J., Silvertown, J., Coulson, S.J., Gregory, S.J., Tofts, R., 2001. A plant trait analysis of responses to grazing in a long-term experiment. *J. Appl. Ecol.* 38, 253–267.
- Burgos, J., 1968. El clima de la provincia de Buenos Aires en relación con la vegetación natural y el suelo. In: Cabrera, A.L. (Ed.), *Flora de la Provincia de Buenos Aires*. Colección Científica INTA, Buenos Aires, pp. 33–100.
- Cabrera, A.L., 1967. Flora de la Provincia de Buenos Aires. Colección Científica del INTA, Buenos Aires.
- Cabrera, A.L., 1976. Regiones fitogeográficas argentinas. *Enciclopedia Argentina de Agricultura y Jardinería. A C M E*, Buenos Aires.
- Chaneton, E.J., Perelman, S.B., Omacini, M., León, R.J.C., 2002. Grazing, environmental heterogeneity, and alien plant invasions in temperate pampa grasslands. *Biol. Inv.* 4, 7–24.
- Chébez, J.C., 1994. Los Que Se Van. *Especies Argentinas en Peligro*. Editorial Albatros, Buenos Aires.
- Cingolani, A.M., Noy Meir, I., Diaz, S., 2005. Grazing effects on rangeland diversity: a synthesis of contemporary models. *Ecol. Appl.* 15, 757–773.
- Davis, A.D., Grime, D.J.P., Thompson, K., 2000. Fluctuating resources in plant communities: a general theory of plant community. *J. Ecol.* 88, 528–534.
- Dawson, M.J., Lane, C., and Saunders, G., 2006. *Proceedings of the National Feral Horse Management Workshop*, Canberra, Australia.
- de Villalobos, A.E., Peláez, D.V., Elia, O.R., 2005. Factors related to establishment of *Prosopis caldenia* Burk. seedlings in central rangelands of Argentina. *Acta Oecol.* 27, 99–106.
- Department of the Environment and Heritage, 2004. Feral horse (*Equus caballus*) and feral donkey (*Equus asinus*). Invasive Species. <http://www.environment.gov.au/biodiversity/invasive/publications/horse/index.html> (accessed February 08).

- Dobbie, W.R., Berman, D., Braysher, M.L., 1993. Managing Vertebrate Pests: Feral Horses. Department of Primary Industries and Energy, Bureau of Resource Sciences. Australian Government Publishing Service, Canberra.
- Duncan, P., 1987. Horses and Grasses. The Nutritional Ecology of Equids and Their Impact on the Camargue. Springer, New York.
- Dyer, M.I., Turner, C.L., Seastedt, T.R., 1993. Herbivory and its consequences. *Ecol. Appl.* 3, 10–16.
- Fahnestock, J.T., Detling, J.K., 1999. The influence of herbivory on plant cover and species composition in the Pryor Mountain Wild Horse Range, USA. *Plant Ecol.* 144, 145–157.
- Grigulis, K., Sheppard, A.W., Ash, J.E., Groves, R.H., 2001. The comparative demography of the pasture weed *Echium plantagineum* between its native and invaded ranges. *J. Appl. Ecol.* 38, 281–290.
- Gudmundsson, O., Dyrmondsson, O., 1994. Horse grazing under cold and wet conditions: a review. *Livestock Prod. Sci.* 40, 57–63.
- Hobbs, R.J., 2001. Synergisms among habitat fragmentation, livestock grazing and biotic invasions in Southwestern Australia. *Conserv. Biol.* 15, 1522–1528.
- Holmgren, M., 2002. Exotic herbivores as drivers of plant invasions and switch to ecosystem alternative states. *Biol. Inv.* 4, 25–33.
- Hongo, A., Matsumoto, S., Takahashi, H., Houyan, Z., Jimin, C., Hengyi, J., Zhiyi, Z., 1995. Effect of enclosure and topography on rehabilitation of overgrazed shrub-steppe in the loess plateau of Northwest China. *Rest. Ecol.* 1, 18–25.
- Huntly, N., 1991. Herbivores and the dynamics of communities and ecosystems. *Annu. Rev. Ecol. Syst.* 22, 477–503.
- Krebs, C.J., 2001. *Ecological Methodology*. Addison-Wesley, California.
- Kristensen, M.J., Frangi, J.L., 1992. La Sierra de la Ventana: una isla de biodiversidad. *Ciencia Hoy* 5, 25–34.
- Kristensen, M.J., Frangi, J.L., 1995. Mesoclimas de Pastizales de la Sierra de la Ventana. *Ecol. Austral* 5, 55–64.
- Legendre, P., Gallagher, E.D., 2001. Ecologically meaningful transformations for ordination of species data. *Oecologia* 129, 271–280.
- Legendre, P., Legendre, L., 1998. *Numerical Ecology*, second ed. Elsevier Science, Amsterdam.
- Levine, J.M., D'Antonio, C.M., 1999. Elton revisited: a review of evidence linking diversity and invisibility. *Oikos* 87, 15–26.
- Linklater, W.L., Cameron, E.Z., Minot, E.O., Stafford, K.J., 2004. Feral horse demography and population growth in the Kaimanawa Ranges, New Zealand. *Wildl. Res.* 31, 119–128.
- Long, M.A., Grassini, C.M., 1997. Actualización del conocimiento florístico del Parque Provincial Ernesto Tornquist. Ministerio de Asuntos Agrarios Provincia de Buenos Aires y Universidad Nacional del Sur.
- Loreti, J., Oesterheld, M., Sala, O.E., 2001. Intraspecific variation in the resistance to defoliation in a grass that evolved under light grazing pressure. *Plant Ecol.* 157, 197–204.
- Loucougaray, G., Bonis, A., Bouzillé, J.-B., 2004. Effects of grazing by horses and/or cattle on the diversity of coastal grasslands in western France. *Biol. Conserv.* 116, 59–71.
- Loydi, A., Zalba, S.M., 2009. Feral horses dung piles as potential invasion windows for alien plant species in natural grasslands. *Plant Ecol.* 201, 471–480.
- Mack, R.N., 1989. Temperate grasslands vulnerable to plant invasions: characteristics and consequences. In: Drake, J.A., Mooney, H.A., Di Castri, F., Groves, R.H., Kruger, F.J., Rejmanek, M., Williamson, M. (Eds.), *Biological Invasions: A Global Perspective*. Wiley & Sons, Chichester, pp. 155–179.
- Milchunas, D.G., Sala, O.E., Lauenroth, W.K., 1988. A generalized model of the effect of grazing by large herbivores on grassland community structure. *Am. Nat.* 132, 87–106.
- Milchunas, D.G., Lauenroth, W.K., Burke, I.C., 1998. Livestock grazing: animal and plant biodiversity of shortgrass steppe and the relationship to ecosystem function. *Oikos* 83, 65–74.
- Mueller-Dombois, D., Ellenberg, H., 2003. *Aims and Methods of Vegetation Ecology*. The Blackburn Press, Caldwell.
- Nordblom, T.L., Smyth, M.J., Swirepik, A., Sheppard, A.W., Briese, D.T., 2002. Spatial economics of biological control: investing in new releases of insects for earlier limitation of Paterson's curse in Australia. *Agric. Econ.* 27, 403–424.
- Noy-Meir, I., Gutman, H., Kaplan, Y., 1989. Responses of Mediterranean grasslands plants to grazing and protection. *J. Ecol.* 77, 290–310.
- O'Connor, T.G., 1995. Acacia karroo invasion of grassland: environmental and biotic effects influencing seedling emergence and establishment. *Oecologia* 103, 214–223.
- Olson-Rutz, K.M., Marlow, C.B., Hansen, K., Gagnon, L.C., Rossi, R.J., 1996a. Packhorse grazing behavior and immediate impact on a timberline meadows. *J. Range Manage.* 49, 546–550.
- Olson-Rutz, K.M., Marlow, C.B., Hansen, K., Gagnon, L.C., Rossi, R.J., 1996b. Recovery of a high elevation plant community after packhorse grazing. *J. Range Manage.* 49, 541–545.
- Pielou, E.C., 1975. *Ecological Diversity*. J. Wiley & Sons, New York.
- Prieto, A.R., 2000. Vegetational history of the Late glacial-holocene transition in the grasslands of eastern Argentina. *Palaeog. Palaeoec.* 157, 167–188.
- Prieur-Richard, A.H., Lavorel, S., 2000. Invasions: the perspective of diverse plant communities. *Austral Ecol.* 25, 1–7.
- Rheinhardt, R.D., Rheinhardt, M.C., 2004. Feral horse seasonal habitat use on a coastal barrier spit. *J. Range Manage.* 57, 253–258.
- Rodríguez, C., Leoni, E., Lezama, F., Altesor, A., 2003. Temporal trends in species composition and plant traits in natural grasslands of Uruguay. *J. Veg. Sci.* 14, 433–440.
- Rogers, G.M., 1991. Kaimanawa feral horses and their environmental impacts. *N.Z. J. Ecol.* 15, 49–64.
- Rook, A.J., Dumont, B., Isselstein, J., Osoro, K., Wallis de Vries, M.F., 2004. Matching type of livestock to desired biodiversity outcomes in pastures – a review. *Biol. Conserv.* 119, 137–150.
- Sala, O.E., Oesterheld, M., León, R.J.C., Soriano, A., 1986. Grazing effects upon plant community structure in subhumid grassland of Argentina. *Vegetatio* 67, 27–32.
- Scorolli, A., 2007. Dinámica poblacional y organización social de caballos cimarrones en el Parque Provincial Ernesto Tornquist (PhD thesis), Universidad Nacional del Sur, Argentina.
- Shea, K., Chesson, P., 2002. Community ecology theory as a framework from biological invasions. *Trends Ecol. Evol.* 17, 170–176.
- Sokal, R.R., Braumann, C.A., 1980. Significance tests for coefficients of variation and variability profiles. *Syst. Zool.* 29, 50–66.
- Sokal, R.R., Rohlf, F.J., 1979. *Biometry*, first ed. W.H. Freeman and Co, New York.
- Soriano, A., 1991. Río de la Plata grasslands. In: Coupland, R.T. (Ed.), *Natural Grasslands. Introduction and Western Hemisphere*. Elsevier, pp. 367–407.
- Sternberg, M., Gutman, M., Perevolotsky, A., Ungar, E.D., Kigel, J., 2000. Vegetation response to grazing management in a Mediterranean herbaceous community: a functional group approach. *J. Appl. Ecol.* 37, 224–237.
- Tilman, D., 1997. Community invasibility, recruitment limitation, and grassland biodiversity. *Ecology* 78, 81–92.
- Todd, S.W., Hoffman, M.T., 1999. A fence-line contrast effects of heavy grazing on plant diversity and community composition in Namaqualand, South Africa. *Plant Ecol.* 142, 169–178.
- van de Koppel, J., Rietkerk, M., van Langevelde, F., Kumar, L., Klausmeier, C.A., Fryxell, J.M., Hearne, J.W., van Andel, J., de Ridder, N., Skidmore, A., Stroosnijder, L., Prins, H.H.T., 2002. Spatial heterogeneity and irreversible vegetation change in semiarid grazing system. *Am. Nat.* 159, 209–218.
- Vázquez, D.P., Simberloff, D., 2003. Changes in interaction biodiversity induced by an introduced ungulate. *Ecol. Lett.* 6, 1077–1083.
- Veen, G.F., Blair, J.M., Smith, M.D., Collins, S.L., 2008. Influence of grazing and fire frequency on small-scale plant community structure and resource variability in native tallgrass prairie. *Oikos* 117, 859–866.
- Vesk, P.A., Westoby, M., 2001. Predicting plant species' responses to grazing. *J. Appl. Ecol.* 38, 897–909.
- Wang, Y., Shiyomi, M., Tsuiki, M., Tsutsumi, M., Yu, X., Yi, R., 2002. Spatial heterogeneity of vegetation under different grazing intensities in the Northwest Steppe of China. *Agric. Ecosys. Environ.* 90, 217–229.
- Wardle, D.A., 2001. Experimental demonstration that plant diversity reduces invasibility: evidence of a biological mechanism or a consequence of sampling effect? *Oikos* 95, 161–170.
- Zalba, S.M., Cozzani, N.C., 2004. The impact of feral horses on grassland bird communities in Argentina. *Anim. Conserv.* 7, 35–44.
- Zar, J.H., 1996. *Biostatistical Analysis*. Prentice Hall, New Jersey.