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Feral horses and alien plants: effects on the structure and function of the Pampean Mountain grasslands (Argentina)

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ABSTRACT

Disturbances can affect the biotic resistance of plant communities and alterations could take place in the system, such as the appearance or increase in abundance of new components. To characterize the resistance to disturbance and the aptitude to limit the establishment of alien plants, it is necessary to know the functional and specific diversity of plant communities. The objective was to evaluate the effects of grazing by feral horses on the resistance of natural grasslands of Argentina to alien plant invasion by means of specific composition and functional structure. Two grasslands under continuous grazing by feral horses and two enclosures were studied. Species composition and functional structure were characterized using species richness, Shannon's diversity index, functional richness, functional evenness and functional divergence. Alien plant richness and abundance, as well as alien: native plants ratio were determined. Specific composition and functional structure were negatively affected by feral horse grazing and the distribution of alien species in the different functional groups differed in areas with contrasting grazing histories. The activity of feral horses can modify the abundance of dominant plants and functional diversity, thus providing niche opportunities for the establishment of alien plants, in turn affecting the function and structure of the system.

RÉSUMÉ

Les perturbations peuvent affecter la résistance biotique des communautés végétales et ainsi causer des modifications du système, telles que l'apparition ou l'augmentation de l'abondance de nouvelles composantes. Pour caractériser la résistance aux perturbations et la capacité à limiter l'établissement de plantes envahissantes, il est nécessaire de connaître la diversité spécifique et fonctionnelle des communautés végétales. L'objectif de cette étude était d'évaluer les effets du pâturage par les chevaux sauvages sur la résistance de prairies naturelles de l'Argentine à l'invasion par les plantes exotiques en mesurant la composition spécifique et la structure fonctionnelle. Deux prairies sous pâturage continu par des chevaux sauvages et deux exclos ont été étudiés. La composition spécifique et la structure fonctionnelle ont été caractérisées par la richesse spécifique, l'indice de diversité de Shannon, ainsi que la richesse, l'uniformité et la divergence fonctionnelles. La richesse des plantes exotiques, l'abondance et le rapport plantes exotiques: indigènes ont été déterminés. La composition spécifique et la structure fonctionnelle ont été affectées par le pâturage des chevaux et la répartition des espèces exotiques dans les différents groupes fonctionnels différait sur les sites avec différentes histoires de pâturage. L'activité des chevaux sauvages peut modifier l'abondance des plantes dominantes et la diversité fonctionnelle, favorisant ainsi l'établissement de plantes envahissantes et modifiant de ce fait la fonction et la structure du système.

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Introduction

The resistance of plant communities to biological invasions and their response to disturbances are determined by their specific composition and functional structure (Milberg and Lamont 1995). Disturbances are defined as any relatively discreet event in time that disrupts the structure of natural systems and changes resources availability and the physical

environment (Lozon and Mac Isaac 1997). Responses of plant communities to disturbances depend on the identity and abundance of plant species and functional groups. The compositional and functional characteristics of plant communities have significant impacts on the processes and dynamics of grassland ecosystems. Functional groups of plants are constituted of species that share morphological, phenological and physiological traits, and present similar responses to

environmental factors such as disturbances (Cornelissen et al. 2003). Plant functional groups have received attention when predictable patterns in response to disturbance have been sought (McIntyre et al. 1999). The functions of natural grasslands may be controlled more by the biological characteristics of the dominant species in the system than by species diversity (Tilman et al. 1997). The resistance of natural systems can be measured by their capacity to retain fundamental structure and processes, despite being subjected to disturbances (Chambers et al. 2014). When the resistance of plant communities is affected by a disturbance, such as overgrazing, alterations can take place in the system, such as the appearance or increase in abundance of new components like alien plants (Zimmermann et al. 2014). In this particular case, the biotic resistance of natural grasslands describes the ability of resident species to reduce the success of alien plant invasions (Levine et al. 2004). Therefore, to characterize the resistance to disturbance and the aptitude to limit the establishment of alien plants, it is necessary to know the functional diversity of a plant community. Functional diversity is defined by Diaz and Cabido (2001) as the quantity, type and distribution of functions performed by plants within a natural system and it can be characterized by means of the functional richness, functional evenness and functional divergence (Villéger et al. 2008). The joint interpretation of these three indexes allows the functional characterization of a system (de Bello et al. 2016).

Large ungulates are responsible for significant changes in the structure and composition of plant communities as a result of grazing, trampling and the deposition of urine and feces, affecting the abundance, distribution, and spatial and temporal heterogeneity of vegetation. In addition, they can facilitate the invasion of plant species by acting as selective agents on native plant communities (Nuñez et al. 2010). Vegetation and herbivores have shared a long evolutionary history reflected in the morphological, physiological and behavioral characteristics of the interacting species. These relationships can be altered by anthropogenic changes including a reduction in the density of native herbivores and their replacement by alien ungulates. The effect of introduced ungulates on plant communities is often quite different from that produced by native species due to differences in patterns of habitat use and in the type and quantity of resources that are consumed. Grasslands that have evolved under moderate levels of grazing, like South American savannas, are usually more vulnerable to overgrazing than those that share long evolutionary periods with large herds of gregarious ungulates (Cingolani et al. 2005), such as

in the case of Africa and North America (Anderson 2006; Linstädter et al. 2014). When native herbivores are replaced by cattle or horses, the grazing habits and behavior of these new species can be so different that this represents an unprecedented ecological situation (Milchunas et al. 1988). Introduced ungulates may affect the outcome of competition between native and alien plants through such direct mechanisms as feeding on the plants, soil disturbance, and also through indirect effects such as a reduction in competitive capacity leading to species replacement. One component of grazing by alien ungulates is the increased abundance of alien invasive plant species. Many invasive plants share low requirements for establishment, high reproductive capacity and rapid growth, which represent adequate abilities for growing under high grazing pressure (Rejmánek and Richardson 1996).

Natural grasslands are among the most disturbed natural ecosystems due to human activities (Hannah et al. 1995; Laurance 2010). There is, however, controversial evidence of the impact of introduced ungulates on species composition and functional diversity in natural grasslands (Vavra et al. 2007). Selective defoliation by some species could increase plant species richness and diversity due to reduction of the competitive capacity of dominant plants, favoring the appearance of species not previously present in the system or with very limited representation (Belsky 1992; Collins et al. 1998). However, high grazing intensity alters the composition and structure of grasslands by encouraging the establishment and persistence principally of those plants capable of avoiding or resisting grazing (Sternberg et al. 2000; Wardle et al. 2001). Natural grasslands of Central Argentina have been intensively transformed as a consequence of livestock production developed since the middle of the 19th century (Burkart et al. 1990). Before European colonization and the increase in cattle production, the level of grazing by native ungulates, such as the Pampean deer (*Ozotoceros bezoarticus*) and Guanaco (*Lama guanicoe*), was low, contributing to the maintenance of the structure and composition of natural grasslands (Medan et al. 2011). Livestock are usually artificially kept at high stocking rates in limited areas, where fences prevent their emigration when the abundance of desirable forage decreases, resulting in the overgrazing of preferred plants (Holmgren 2002). On the other hand, the action of feral ungulates differs to that of livestock as they form non-managed, free-ranging populations and their effects on natural grasslands can be more intense than those of native ungulates (Davies et al. 2014). As a result, self-sustained perpetuation of unmanaged introduced ungulate populations may result in ecological effects that are different from

those extensively studied for managed stock and which could pose serious concerns for the conservation of plant communities (Davies et al. 2014).

There is evidence that the activity of feral horses over long periods can precipitate changes in specific composition of natural grasslands in the southern Pampean mountains (de Villalobos and Zalba 2010; Loydi et al. 2012). However, the effects of the grazing by feral horses on the functional structure and their relationship to the resistance against alien plants have not yet been sufficiently evaluated. We hypothesize that continuous grazing by feral horses affect the functional structure and reduces the resistance of natural grasslands to alien plant invasion. Therefore, the aims of the present study were: (1) to assess the effects of grazing by feral horses on species composition and functional structure in remnants of natural grasslands in the Mountain Pampean grasslands of southern Argentina; (2) to describe the functional structure of grazed and ungrazed grasslands using the components of functional diversity; and (3) to evaluate grassland resistance to disturbance by feral horses through measurement of alien plant abundance and their distribution between functional groups.

Materials and methods

Study site

This study was carried out in the Ernesto Tornquist Provincial Park (ETPP), one of the last relicts of Pampean grasslands in a relatively good state of conservation (Cabrera 1976). ETPP is located in the Ventania mountain system, an area of 6700 ha range in the central Pampas region, between 38° 00' and 38° 10' S, and 61° 45' and 62° 08' W. 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. January is the warmest month (average temperature 21.9°C) and June is the coldest month (average temperature 7.2°C). Grass steppe is the dominant vegetation (Cabrera 1976) and *Nasella*, *Piptochaetium*, *Festuca* and *Briza* are among the most common grass genera. The shrub community is dominated by *Eupatorium buniifolium*, *Discaria longispina* and *Geoffroea decorticans* (Kristensen and Frangi 1995; Long and Grassini 1997). Native herbivores in this region included the Pampas Deer (*Ozotoceros bezoarticus*) and Guanaco (*Lama guanicoe*) that are now locally extinct or in extremely low numbers. Introduced ungulates are represented principally by feral horses that have become very abundant since their introduction

in 1942 and they are the main herbivore in the area, reaching a population of 700 horses or 0.35 horse ha⁻¹ (Scorolli and Lopez Cazorla 2010).

Experimental design and sampling

For this study were selected two experimental areas of natural grassland (23 and 27 ha, respectively) under continuous grazing by free-ranging feral horses and two experimental areas closed to alien herbivores for 20 years (12 and 15 ha, respectively). All experimental areas were located on the adjacent piedmont grasslands distant from each other by 2 and 5 km, with 5–15 degree slope on the warmer, north-facing slopes that are preferentially grazed and characterized by shallow soils with occasional rocky outcrops. In spring (late November, early December) 20 plots of 1 m² were randomly distributed directly in the field and separated from each other by about 50–100 m to assure that the experimental plots are independent and interspersed across each of the experimental areas (Quinn and Keough 2002; McDonald 2008).

The abundance of each species identified in each plot was recorded, expressed as the percentage of the surface cover. The percentage of bare soil was also noted. The compositional structure of each experimental area was characterized by means of the species richness, Shannon's diversity index (Krebs 2001) and an evenness index (Pielou 1975). Species with similar biological traits, such as taxonomic similarities (grasses or herbs), growth form (erect or prostrate) and life cycle (annual or perennial) were grouped together. Each identified plant species was included in only one functional group, considering their life story and growth form (Lavorel et al. 1997). The abundance of the functional groups in each experimental area was calculated as the percentage cover of each species recorded in the 20 randomly distributed plots (1 m²). The functional structure of the experimental areas was characterized by way of three components of functional diversity: functional richness (Mason et al. 2005), functional evenness (Mouillot et al. 2005) and functional divergence (Mason et al. 2003). Functional richness is defined as the abundance of the species included in each functional group, whereas functional evenness reflects the uniformity in the spatial distribution of the functional groups in the plant community (Mason et al. 2005; Mouillot et al. 2005), and functional divergence is defined as the spread in distribution of the abundance of each functional group in comparison with the average total abundance (Villéger et al. 2008). The indexes were calculated with the FDiversity software (Casanoves et al. 2010). In order

to evaluate the total and relative abundance of alien plants, the percentage of alien plants, alien plant richness and the alien:native plants ratio were determined for each experimental area with contrasting grazing histories.

Statistical analysis

Differences between species richness, diversity (Shannon index), and evenness (Pielou index), as well as functional richness, evenness and divergence were analyzed by means of two-way analyses of variance using a completely random design. The factors of analysis were grazing history and location of experimental areas (two locations for each grazed and ungrazed treatment). Following the analyses of variance, Tukey tests were used to identify the means that were significantly different (Zar 1999). The same analysis was performed in order to differentiate between the percentage of bare soil, alien plant cover, alien species richness and the alien:native plants ratio between areas with contrasting grazing histories. A paired Student's t-test was performed for the comparison of the number of species and the cover of each functional group between grazed and ungrazed areas. All data were previously root square transformed to improve normality and homoscedasticity. Pearson correlation tests were used to quantify the relationships between alien plant cover, alien species richness and the alien:native plants ratio with the compositional and functional indexes for each of the areas with contrasting grazing histories. Also, Z proportion comparison tests were performed to compare the values of the alien:native plants ratio calculated for each functional group inside the experimental areas with contrasting grazing histories (Zar 1999).

Results

Species composition and functional structure of natural mountain grasslands were affected by continuous feral horse grazing, independently of the location of the experimental area evaluated. There was no difference between experimental areas with the same grazing history ($F = 2.9$, $p > 0.10$) and no significant interaction between these two factors (grazing history \times experimental area) for any of the parameters analyzed ($F = 3.6$, $p > 0.05$). The absence of significant interactions indicated that the factors were independent of each other and not influenced by the location of the experimental area, therefore all experimental plots can be considered to be independent and were analyzed as replicates for the grazing history treatments (Hurlbert 1984; McDonald 2008). Species richness

and diversity ($F = 4.4$, $p < 0.05$ and $F = 5.6$, $p < 0.05$, respectively), specific evenness ($F = 5.2$, $p < 0.05$), functional richness, functional divergence and functional evenness ($F = 8.2$, $p < 0.01$; $F = 11.4$, $p < 0.005$ and $F = 6.5$, $p < 0.05$, respectively) were significantly higher for the ungrazed areas than for the grazed areas (Table 1), whereas the percentages of alien plant cover, alien richness, alien:native plants ratio and percentage cover of bare ground were significantly higher in the grazed areas ($F = 9.1$, $p < 0.01$; $F = 5.8$, $p < 0.05$ and $F = 8.7$, $p < 0.01$; $F = 15.8$, $p < 0.001$, respectively) (Table 1). We recorded 90 plant species in the ungrazed areas and 67 in the grazed areas; 52 species were present in both types of areas (Appendix). All the species recorded in the experimental areas were included in seven functional groups defined by the growth form and life story of the functional traits: grasses and graminoids (including annual and rhizomatous perennial grasses and other monocotyledonous species), perennial tussock (caespitoses) grasses, shrubs, rosettes, prostrate plants, annual and perennial herbs. Grazing condition affected significantly the composition and relative abundance of functional groups. Average percentage cover of grasses and perennial tussocks were significantly higher in the areas closed to feral horses ($t = 9.2$ and $t = 6.0$; both $p < 0.001$) (Figure 1), whereas shrubs, rosettes, prostrate plants, and annual herbs were strongly associated with feral horse grazing because they were more abundant in grazed areas ($t = 9.7$, $p < 0.001$; $t = 9.4$, $p < 0.000$; $t = 6.6$, $p < 0.001$; $t = 2.1$, $p = 0.04$) (Figure 1). The abundance of perennial herbs was apparently not affected by grazing by feral horses ($t = 1.6$, $p > 0.05$) (Figure 1).

The number of species recorded in each functional group also changed in relation to grazing history. Species of grasses and perennial tussocks were more

Table 1. Mean ($n = 40$) (\pm SE) species richness, species diversity (Shannon index), evenness (Pielou index), functional richness (index), functional evenness (index), bare ground (%), alien species cover (%), alien species richness and alien:native species ratio in grazed and ungrazed experimental areas. For each variable, values followed by different letters are significantly different ($p < 0.05$).

	Grazed Areas	Ungrazed Areas
Species richness	23.20 \pm 0.60 b	37.50 \pm 0.50 a
Species diversity	1.70 \pm 0.05 b	3.00 \pm 0.04 a
Species evenness	0.58 \pm 0.02 b	0.97 \pm 0.01 a
Functional richness	0.53 \pm 0.10 b	0.72 \pm 0.20 a
Functional evenness	0.25 \pm 0.07 b	0.42 \pm 0.04 a
Functional divergence	0.30 \pm 0.05 b	0.53 \pm 0.10 a
Bare ground (%)	45.0 \pm 1.5 a	5.00 \pm 0.7 b
Alien species cover (%)	17.0 \pm 1.50 a	5.80 \pm 0.30 b
Alien species richness	12.5 \pm 2.80 a	7.2 \pm 1.50 b
Alien:Native Species ratio	0.75 \pm 0.10 a	0.20 \pm 0.05 b

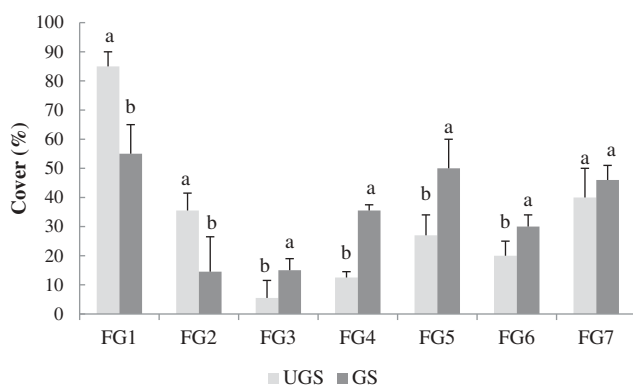


Figure 1. Cover percentages (%) (means \pm SE) of annual and rhizomatous perennial grasses and other monocotyledonous species (FG₁), perennial tussock grasses (FG₂), shrubs (FG₃), rosette plants (FG₄), prostrate plants (FG₅), annual herbs (FG₆) and perennial herbs (FG₇) in the ungrazed (UGS) and grazed (GS) experimental areas. For each functional group, columns with different letters are significantly different ($p < 0.05$).

numerous in the ungrazed than in the grazed areas ($t = 11.8$ and $t = 16.0$; both $p < 0.001$) (Figure 2), whereas the number of species of rosette plants and annual herbs were higher in the grazed than in the ungrazed areas ($t = 12.2$ and $t = 6.8$ both $p < 0.001$) (Figure 2). Grazing history did not affect the species richness of shrubs, prostrate plants or perennial herbs ($t = 1.3$; $t = 1.5$ and $t = 1.1$, all $p > 0.05$) (Figure 2). The relationships between the compositional and functional indexes and alien plant richness, abundance and alien:native ratio were influenced by grazing history. Alien

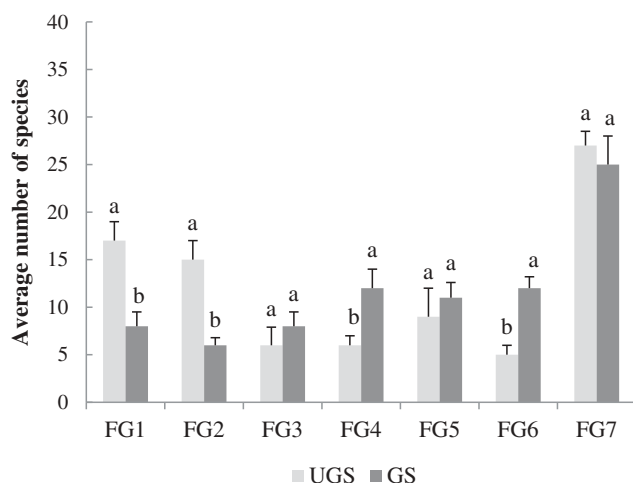


Figure 2. Number of species (means \pm SE) of annual and rhizomatous perennial grasses and other monocotyledonous species (FG₁), perennial tussock grasses (FG₂), shrubs (FG₃), rosette plants (FG₄), prostrate plants (FG₅), annual herbs (FG₆) and perennial herbs (FG₇) in the ungrazed (UGS) and grazed (GS) experimental areas. For each functional group, columns with different letters are significantly different ($p < 0.05$).

Table 2. Pearson's correlation coefficients and p values between alien plant cover (%), alien richness and alien:native ratio in grazed areas ($n = 40$) and species richness, species diversity (Shannon index), species evenness (Pielou index), functional richness (index), functional evenness (index) and functional divergence (index).

	Alien plant cover (%)	p	Alien richness	p	Alien:native	p
Species richness	0.20	> 0.05	0.42	< 0.05	0.15	> 0.05
Species diversity	-0.82	< 0.001	0.70	< 0.001	-0.35	< 0.05
Species evenness	-0.83	< 0.001	-0.32	< 0.05	-0.45	< 0.05
Functional richness	-0.73	< 0.001	-0.55	< 0.005	-0.62	< 0.001
Functional evenness	-0.80	< 0.001	-0.75	< 0.001	-0.80	< 0.001
Functional divergence	-0.75	< 0.001	-0.65	< 0.001	-0.70	< 0.001

plant cover was negatively correlated with species diversity and functional indexes, except for species richness in grazed areas (Table 2). In ungrazed areas, only the functional indexes were inversely correlated with alien plant abundance (Table 3). The richness of alien species was positively correlated with species richness and species diversity and negatively correlated with functional richness, and species and functional evenness, in both grazed and ungrazed areas (Tables 2 and 3). The alien:native species cover ratio had a high negative coefficient of agreement with the specific and functional indexes measured in grazed areas, except for species richness (Table 2). In ungrazed areas, this proportion was inversely related to the functional indexes (Table 3).

In areas with contrasting grazing histories, differences were found in the distribution of the cover of alien species between different functional groups. In

Table 3. Pearson's correlation coefficients and p values between alien plant cover (%), alien richness and alien:native ratio in ungrazed areas ($n = 40$) and species richness, species diversity (Shannon index), species evenness (Pielou index), functional richness (index), functional evenness (index) and functional divergence (index).

	Alien plant cover (%)	p	Alien richness	p	Alien:native	p
Species richness	0.12	> 0.10	0.35	< 0.05	0.25	> 0.05
Species diversity	-0.22	> 0.05	0.40	< 0.05	-0.25	> 0.05
Species evenness	-0.18	> 0.10	-0.32	< 0.05	-0.21	> 0.05
Functional richness	-0.47	< 0.05	-0.45	< 0.05	-0.52	< 0.01
Functional evenness	-0.50	< 0.01	-0.55	< 0.01	-0.60	< 0.001
Functional divergence	-0.60	< 0.001	-0.50	< 0.01	-0.65	< 0.001

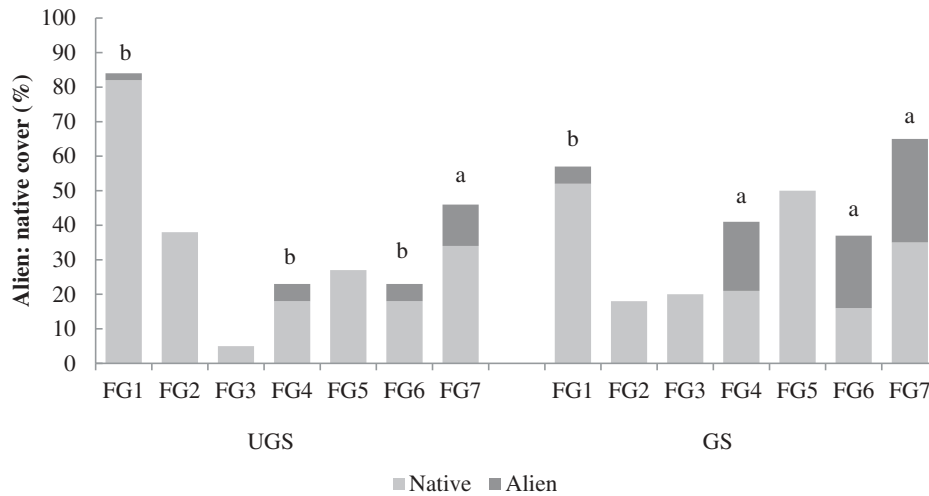


Figure 3. Percentage (%) of alien:native plants in annual and rhizomatous perennial grasses and other monocotyledonous species (FG₁), perennial tussock grasses (FG₂), shrubs (FG₃), rosette plants (FG₄), prostrate plants (FG₅), annual herbs (FG₆) and perennial herbs (FG₇) in the ungrazed (UGS) and grazed (GS) experimental areas. For each experimental area, columns with different letters are significantly different ($p < 0.05$).

grazed and ungrazed areas, the abundance of alien species was represented for grasses and graminoids, rosette plants, annual and perennial herbs. In ungrazed areas, the alien:native species cover ratio was significantly higher for perennial herbs than for other functional groups ($Z > 1.96$, $p < 0.01$), whereas in grazed areas, the alien:native species cover ratio was higher for rosette plants, and annual and perennial herbs ($Z > 1.96$, $p < 0.01$) (Figure 3).

Discussion

In line with the hypothesis, this work revealed significant reductions in species richness, diversity and uniformity in grasslands under continuous grazing by feral horses. Increases in the proportion of invasive alien plants and in the percentage cover of bare soil were also found to be associated with grazing. A better conservation status of grassland condition was recorded for areas free of feral horses. Ungulate exclusion improved the maintenance of the structural and compositional properties of the grassland community, limiting the abundance of alien plants. The presence of introduced ungulates has been involved in major natural shifts in the southern Pampean grasslands (Chaneton et al. 2002; Loydi et al. 2012), including a reduction in species richness, diversity and uniformity. These changes altered the functional structure, reducing the resistance of natural grasslands against the invasion of alien plants. Other studies have also found that feral horse grazing promoted a decline in species richness (Fahnestock and Detling 1999; Davies et al. 2014). Moreover, Beaver et al. (2008) found that

grazed and ungrazed areas, the abundance of alien species was represented for grasses and graminoids, rosette plants, annual and perennial herbs. In ungrazed areas, the alien:native species cover ratio was significantly higher for perennial herbs than for other functional groups ($Z > 1.96$, $p < 0.01$), whereas in grazed areas, the alien:native species cover ratio was higher for rosette plants, and annual and perennial herbs ($Z > 1.96$, $p < 0.01$) (Figure 3).

areas without horses in the North American Midwest Prairie had more shrubs and native grasses, as well as total plant cover and number of species, than sites with horses. In the same way, feral horse exclusion in the sagebrush steppe of southwest Oregon increased plant species diversity and promoted the recovery of important soil surface characteristics (Davies et al. 2014).

The introduction of horses in the Pampean grasslands about 70 years ago has apparently produced changes in plant species composition, where alien species tend to dominate in grazed sites. Previous reports of primary productivity for the same region (Pérez and Frangi 2000) suggest that these grasslands could be considered as sub-humid productive grasslands according to the ranking by Milchunas and Lauenroth (1993). Based on these analyses it would be expected that grazing promotes species richness, dominance by grazing tolerant or avoiding plant species, and no invasion by alien plants (Belsky 1992; Cingolani et al. 2005). Results of the present study do not confirm these predictions. Grazing by feral horses may increase diversity by reducing the dominance of superior competitors, or it may reduce diversity by eliminating grazing-intolerant species (Milchunas et al. 1988). The outcome is also likely to depend on the evolutionary history that shapes grazing tolerance. In general, grazing is expected to affect diversity positively in systems with a long history of grazing by ungulates, and negatively in systems without ungulate grazing. The absence of significant densities of large herbivores between the Pleistocene and the colonial period is a distinctive pattern of South American grasslands. According to McNaughton (1992), the Mountain Pampean grasslands have a short evolutionary history of

ungulates grazing. Therefore, the effects of introduced ungulates on this ecosystem could be severe.

The composition and relative abundance of functional groups responded differently to feral horses grazing. Positive responses by annual plants to grazing, and negative responses by perennial plants, were reported in the present study. Particularly, the abundance of perennial tussock grasses and that of other grasses and graminoids species were lower in grazed grasslands. These responses of functional groups also seemed to depend on the evolutionary history of herbivory by large ungulates. The greatest alterations in representation of plant functional groups were reported in systems with reduced grazing history (Milchunas et al. 1989; Diaz et al. 2006). According to our results, positive responses of short plants and negative responses of tall plants were also frequently reported in systems grazed by introduced ungulates, and positive responses of rosettes and stoloniferous plants and negative responses of tussock grasses were also reported frequently (Diaz et al. 2006).

The present study evaluated changes in the functional structure of Mountain Pampean grasslands as a consequence of feral horse activity. The presence of horses not only affected composition, but also distribution and abundance of functional groups. Grazed areas showed lower functional richness, evenness and divergence, and a higher abundance of alien plants. Therefore, feral horses also have the potential to reduce resistance to disturbance in plant communities and thus foster the invasion of alien plants, for instance, by preferentially foraging on the most palatable plants. Reduced abundance of perennial tussock grasses and other grasses and graminoids in grazed areas, together with the increased proportion of bare ground, left available resources for the development of populations of alien plants and other species that can grow and reproduce under heavy herbivore pressure, such as prostrate and rosette plants. A previous study revealed that grazing by feral horses modifies ecological processes, such as changes in the frequency of plant species (de Villalobos and Zalba 2010) and competitive interactions between native and alien plants, that also may affect the invasion success of *Pinus halepensis* in Mountain Pampean grasslands (de Villalobos et al. 2011). Invasion by alien plants in areas with introduced grazers have also been observed in other Pampean grasslands (Mazia et al. 2001; Chaneton et al. 2002; Zalba and Villamil 2002) and in grasslands of other regions of the world (Foxcroft et al. 2010).

The results obtained in this study are consistent with a growing body of evidence suggesting that high specific and functional diversity increase resistance against

alien plant establishment, possibly through preemption of available resources (Pokorny et al. 2005; Byun et al. 2013; Naeem et al. 2000). The grasslands not grazed by feral horses, that have greater functional richness, functional divergence and functional evenness, would be more heterogeneous systems with higher regularity in the distribution of functional groups (Frankow-Lindberg 2011). The more functionally diverse a system is, the more efficient and homogeneous it is in the use of resources and site occupation (Tilman et al. 1997; Veblen et al. 2015; Faison et al. 2016). James et al. (2008) affirmed that the key mechanism of invasion resistance within a system depends on the functional variation among coexisting species and how species abundance is distributed in the system. Increasing functional diversity in the Mountain Pampean grasslands has been shown to decrease invasion by alien plant invaders, probably through maximizing niche occupation and preempting resource use by invaders. Similarly, in California grasslands, Dukes (2001) found that high functional diversity decreased invader success, and Symstad (2000) found a negative relationship between functional group richness and invasion success in tall grass prairies.

Increasing evidence suggests that plant functional groups are more important for ecological integrity and resistance to invasion than plant species diversity or richness (Diaz and Cabido 2001). This affirmation is not completely supported by the results obtained in the present study, because both the specific and functional diversity indexes were negatively correlated with alien plant abundance, and therefore could be equally important for the resistance of grasslands. More efficient systems, with high specific and functional diversity, can respond faster and neutralize disturbance effects on plant communities. From a functional perspective, species-rich communities often result in high functional diversity when species show different functional traits and thereby, diverse strategies for acquiring resources. The higher the number of species with different functions, the more probable it is that the species will be able to survive in disturbed environments and the greater the probability will be of maintaining ecosystem stability (Diaz and Cabido 2001). Moreover, the functional groups represented in the natural systems allow more efficient use of resources and limit or restrict availability for alien plants (Von Holle and Simberloff 2004).

The distribution and abundance of alien species in different functional groups responded differently to grazing history. Not only was the average cover of alien plants higher in grazed than in ungrazed areas, their relative abundances were also determined by the

types of functional groups and grazing histories in the experimental areas. Feral horses acted as a selection factor on the different plant types in the Mountain Pampean grasslands and the grazing positively selected opportunistic species (short-lived, small-size, fast-growing) with grazing-avoidance strategies (shorter, rosette or prostrate stress-tolerant) (Briske 1996). Many alien plants recorded in the grazed montane Pampean grasslands, such as *Echium plantagineum*, *Medicago minima* and *Erodium cicutarium*, exhibit these characteristics (de Villalobos and Zalba 2010).

Functional group could be a good predictor of biotic resistance. The functional group of the resident plant species most similar to that of the invader species would offer higher resistance, suggesting fitness inequality as one of the key resistance mechanisms because competition may be more intense within similar functional groups (Lavorel et al. 1999; Lulow 2006; Sheley and James 2010). Functional trait similarity between resident, native and alien species is expected to lead to overlapping resource requirement and therefore competition (Funk et al. 2008). Nevertheless, this affirmation was not supported by the results obtained in this study. The relative abundance of alien plants belonging to groups with grazing-avoidance strategies, such as rosette and prostrate species, was higher in the grazed grasslands and the same functional groups were the most represented in the native flora (Figure 3). A similar tendency was observed in ungrazed areas, where the relative abundance of alien species was higher in perennial herbs, and grasses and graminoids, and both groups were well represented in the set of native plants (Figure 3). Rusch and Oesterheld (1997) also found that livestock grazing promotes short lived and low-stature alien herbs and grasses. Similar invasion patterns by functional groups were reported for other temperate grasslands under grazing, suggesting that alien plants exploited novel niche opportunities created by introduced herbivores (Dlugosch et al. 2015). These functional types are usually poorly represented in natural grasslands, which primarily consist of perennial grass species (Parker et al. 2006).

Certain functional groups, not just total species, and functional diversity, may be critical to plant community resistance and the perennial grasses play a critically important role in minimizing invasion (Sheley and James 2010). Davis et al. (2000) hypothesized that the lack of a key functional group in a resident community that is usually more abundant and with greater competitive capacity, will make that community more susceptible to invasion. In the Mountain Pampean grasslands, resistance against alien plant invasion could be related to the abundance of perennial grasses.

High cover of perennial grasses could imply less resource availability for alien plants, which could in turn lead to strong biotic resistance in ungrazed areas, while in grazed areas the abundance of perennial grasses and other grass and graminoid species was lower, leaving free resources for alien plants. In healthy grasslands, soil water and nutrient contents decreased with increasing grass density, and limited the space available for the establishment of alien seedlings (Corbin and D'Antonio 2004; Harrington 2011). Feral horses could affect the biotic resistance mechanisms of the grasslands, such as competition and recruitment limitation, by preferentially foraging on the most palatable plants, increasing bare ground or affecting physical soil properties and damaging biological soil crusts through hoof action (de Villalobos and Zalba 2010). In addition, reduction of the perennial grass cover increased the encroachment of woody plants, as a direct consequence of overgrazing in natural grasslands of Central Argentina (de Villalobos et al. 2002, 2011). Perelman et al. (2007) also found that regeneration of alien plants in flooded Pampean grasslands may be negatively affected by a well-developed canopy of summer grasses.

Conclusion

The findings of the present study show that reduced resistance of Mountain Pampean grasslands to alien plant invasion could be determined by several factors associated with grazing by feral horse. The evidence suggests that the identity of the functional groups, specific and functional diversity, would therefore be good predictors of biotic resistance of grasslands. Feral horse activity can modify the abundance of dominant plant species, as well as functional diversity within communities, providing niche opportunities for seed germination and seedling establishment of alien plants, in turn affecting the function and structure of the system. These results have important implications in the management of invasion-resistant grassland communities. Knowledge about plant community composition and functional groups that convey invasion resistance are central to developing sustainable management of introduced herbivores and preventing plant invasions in natural grasslands.

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Appendix

List of the plant species presents (x) in the grazed areas (GA), ungrazed areas (UGA) and both types of experimental areas (BTA).

	GA	UGA	BTA
<i>Abutilon terminale</i>		x	x
<i>Adesmia pampeana</i>		x	
<i>Alcornoque decumbens</i>		x	x
<i>Anemone decapetala</i>		x	
<i>Arenaria serpyllifolia</i>		x	
<i>Aristida multiramea</i>		x	
<i>Aristida spigazzini</i>	x		
<i>Astragalus argentinus</i>		x	
<i>Baccharis artemisioides</i>		x	x
<i>Baccharis articulata</i>		x	
<i>Baccharis trimera</i>		x	
<i>Bowlesia incana</i>	x		
<i>Briza brizoides</i>	x		x
<i>Briza subaristata</i>		x	x
<i>Bromus bonariensis</i>		x	
<i>Bromus brevis</i>	x		x
<i>Bromus catharticus</i>	x		
<i>Calystegia sepium</i>		x	x
<i>Capsella bursa-pastoris</i>	x		
<i>Cardus pycnocephalus</i>	x		

(Continued)

(Continued).

	GA	UGA	BTA
<i>Carduus acanthoides</i>	x		
<i>Cerastium glomeratum</i>		x	x
<i>Cerastium mollissimum</i>		x	
<i>Chaptalia integerrima</i>	x		
<i>Chervulella sarmentosa</i>	x		x
<i>Commelina erecta</i>		x	
<i>Conium maculatum</i>	x		
<i>Convolvulus arvensis</i>		x	x
<i>Convolvulus hermannaiae</i>		x	x
<i>Crepis vesicaria</i>	x		
<i>Cressa truxellensis</i>		x	x
<i>Cyclosporum leptophyllum</i>	x		
<i>Danthonia cirrata</i>	x		
<i>Daucus pusillus</i>	x		
<i>Deyeuxia sp</i>		x	
<i>Dichondra sericea</i>	x		x
<i>Discaria americana</i>	x		x
<i>Echinochloa crus galli</i>	x		
<i>Echium plantagineum</i>	x		
<i>Echium vulgare</i>	x		
<i>Eleusine indica</i>	x		
<i>Eleusine tristachia</i>	x		
<i>Eragrostis lugens</i>		x	
<i>Erodium cicutarium</i>	x		
<i>Erodium malacoides</i>		x	
<i>Eruca vesicaria</i>	x		
<i>Eryngium nudicaule</i>		x	X
<i>Eryngium paniculatum</i>		x	X
<i>Eupatorium saucechicoense</i>		x	
<i>Euphorbia caespitosum</i>		x	
<i>Euphorbia portulacoides</i>	x		
<i>Evolvulus sericeus</i>		x	X
<i>Facelis retusa</i>	x		
<i>Festuca pampeana</i>		x	
<i>Fumaria capreolata</i>	x		
<i>Gaillardia melanopotamica</i>		x	X
<i>Galium aparine</i>	x		
<i>Gamochoaeta filaginea</i>		x	X
<i>Gamochoaeta spicata</i>		x	X
<i>Geoblasta pennicillata</i>	x		
<i>Geranium albicans</i>		x	
<i>Geranium molle</i>	x		
<i>Gilia laciniata</i>		x	
<i>Glandularia dissecta</i>		x	X
<i>Glandularia flava</i>		x	
<i>Glandularia peruviana</i>		x	x
<i>Gomphrena pulchella</i>		x	x
<i>Grindelia cabreræ</i>		x	x
<i>Gymnocalycium gibbosum</i>		x	
<i>Gymnocalycium reductum</i>		x	
<i>Hedeoma medium</i>		x	x
<i>Helenium radianum</i>		x	
<i>Helianthemum brasiliense</i>		x	x
<i>Heliotropium amplexicaule</i>	x		
<i>Heliotropium curassavicum</i>	x		
<i>Heliotropium phyllicoides</i>		x	

(Continued)

(Continued).

	GA	UGA	BTA
<i>Hieracium chacoense</i>		x	
<i>Holocheilus brasiliensis</i>		x	
<i>Hordeum geniculatum</i>	x		
<i>Hybanthus parviflorus</i>		x	
<i>Hypochaeris glabra</i>	x		x
<i>Hypochaeris variegata</i>		x	
<i>Ipheion uniflorum</i>	x		
<i>Jaborosa bergii</i>	x		
<i>Koeleria ventanica</i>		x	
<i>Lamium amplexicaule</i>	x		
<i>Lathyrus tomentosus</i>		x	
<i>Lecanophora ecristata</i>		x	x
<i>Lepidium aletes</i>		x	
<i>Linum selaginoides</i>		x	
<i>Lucilia acutifolia</i>		x	x
<i>Lycium sp</i>		x	x
<i>Margyricarpus pinnatus</i>	x		x
<i>Marrubium vulgare</i>	x		
<i>Medicago arabica</i>	x		
<i>Medicago lupulina</i>	x		
<i>Medicago minima</i>	x		
<i>Medicago sativa</i>		x	
<i>Melica argyrea</i>		x	x
<i>Melica brasiliensis</i>	x		x
<i>Melilotus indica</i>	x		
<i>Mimosa rocae</i>	x		x
<i>Modiola caroliniana</i>		x	x
<i>Nasella neesiana</i>		x	
<i>Nasella tenuis</i>		x	
<i>Nasella trichotoma</i>		x	
<i>Nierembergia rivularis</i>		x	x
<i>Oxalis articulata</i>		x	x
<i>Oxalis conorrhiza</i>		x	x
<i>Oxalis cordobensis</i>		x	x
<i>Oxypetalum pratense</i>	x		
<i>Pavonia cymbalaria</i>	x		x
<i>Petrorraghia nanteulii</i>		x	
<i>Pfaffia gnaphalioides</i>		x	x
<i>Phyla canescens</i>		x	
<i>Piptochaetium hackelii</i>		x	
<i>Piptochaetium leopodium</i>		x	
<i>Piptochaetium montevidense</i>		x	
<i>Piptochaetium napostaense</i>		x	x
<i>Plantago berroi</i>		x	
<i>Plantago lanceolata</i>	x		
<i>Plantago myosurus</i>	x		
<i>Plantago patagonica</i>	x		
<i>Poa lanuginosa</i>		x	
<i>Podocoma hirsuta</i>		x	x
<i>Polygala sp</i>		x	
<i>Ranunculus muricatus</i>	x		x
<i>Rostraria (Lophochloa) cristata</i>	x		
<i>Salpichroa organifolia</i>	x		
<i>Schizachyrium microstachyum</i>	x		
<i>Scleranthus annus</i>		x	x
<i>Senecio burchellii</i>	x		

(Continued).

	GA	UGA	BTA
<i>Senecio madagascariensis</i>	x		
<i>Sherardia arvensis</i>	x		x
<i>Sida physocalyx</i>		x	x
<i>Silene gallica</i>	x		
<i>Sisyrinchium minus</i>		x	x
<i>Sisyrinchium platense</i>		x	x
<i>Solanum sisymbriifolium</i>	x		
<i>Sommerfeldia spinulosa</i>		x	x
<i>Sphaeralcea australis</i>		x	
<i>Sphaeralcea bonaerensis</i>		x	
<i>Stelaria media</i>	x		
<i>Stevia satuireifolia</i>		x	x
<i>Stipa juncooides</i>		x	
<i>Thelesperma megapotamicum</i>	x		
<i>Torilis nodosa</i>		x	
<i>Trifurcia lahue</i>	x		
<i>Turnera pinnatifida</i>	x		
<i>Urtica urens</i>	x		
<i>Veronica persica</i>	x		
<i>Vicia setifolia</i>		x	
<i>Viola arvensis</i>		x	
<i>Vulpia bromoides</i>		x	
<i>Vulpia myurus</i>		x	
<i>Wigginsia tephraantha</i>	x		x
<i>Xanthium sp</i>	x		

(Continued)