RESEARCH ARTICLE

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Large Herbivore Grazing and Non-native Plant Invasions in Montane Grasslands of Central Argentina

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ABSTRACT: Grazing by large herbivores has the potential to facilitate invasion of natural grasslands by non-native plant species. Often, both herbivore identity and plant community type modulate this effect. The objective of this study was to evaluate the impact of grazing on non-native plant species richness and cover in montane grasslands of central Argentina as related to herbivore identity (horse or cattle) and plant community type. The study was conducted in piedmont valleys of the Ventania Mountains. The area is occupied by two major types of plant communities: short-needlegrass and tall-tussock grasslands. Short-needlegrass grasslands occupy poor soils and have higher plant species diversity compared to tall-tussock grasslands which typically grow on rich soils. Part of the study area is devoted to cattle husbandry, part is inhabited by feral horses, and part has been free of grazing by large herbivores for the last 15 years. We compared non-native species richness and cover at three levels of grazing (horse grazing, cattle grazing, grazing exclusion) and two levels of plant community type (short-needlegrass grassland and tall-tussock grassland) at the end of the growing season in 2006 and 2007. Thirty-one non-native plant species were found growing in the study area. Grazing increased non-native species richness and cover and was highest under horse grazing and in communities on resource-rich soils. Our results are consistent with the hypothesis that grazing by large non-native herbivores can facilitate non-native plant species invasion of natural grasslands. They also suggest that herbivore identity and community type modulate the effect of large herbivore grazing on grassland invasion by non-native plant species.

Index terms: Argentina, cattle, disturbance, feral horses, non-native herbivores, non-native plants

INTRODUCTION

Non-native plant invasions are a threat to conservation of natural ecosystems in many regions of the world (Williamson 1996; Van Wilgen et al. 2001; Millenium Ecosystem Assessment 2005). Even when maintained below a damage threshold, non-native plant species present a risk of rapid colonization and expansion into plant communities (Stohlgren et al. 1999a). Many invasion-susceptible communities are those with high resource availability and/or are subject to frequent disturbance (Stohlgren et al. 1999b; Davis et al. 2000; Wardle 2001; Blumenthal 2005).

Non-native plant species invasions are often facilitated by positive interactions with other non-native species (Parker et al. 1999; Davis et al. 2000; Richardson et al. 2000; Callaway et al. 2005; Grosholz 2005; Parker et al. 2006; Paiaro et al. 2007; Walter and Levin 2008). For example, grazing by large non-native herbivores reduces competition for resources and increases spatial heterogeneity (McNaughton 1983; Olff and Ritchie 1998), which can facilitate invasion by non-native plant species (Hobbs and Huenneke 1992). The largest manifestation of this process is expected to occur in ecosystems that have evolved with low pressure of large herbivore grazing (Milchunas et al. 1988; Mack 1989). The process of facilitation would also depend on the type of herbivore (e.g., ruminant or monogastric species, native or non-native species, generalist or specialist species) (Parker et al. 2006) and characteristics of the invaded environment (e.g., low or high diversity of native species, resource-rich versus resource-poor sites) (Elton 1958; Davis et al. 2000).

In Argentina, as in other parts of the world, human activity has drastically changed the structure and function of natural grasslands (Bilenca and Miñarro 2004). Domestic livestock, such as cattle, sheep, and horses, have replaced native herbivores, reducing vegetation cover and promoting soil erosion in different parts of the country (Kristensen and Frangi 1992; Baldi et al. 2001; Puig et al. 2001; Vázquez 2002; Cingolani et al. 2003). Natural grasslands of central Argentina ("Pampa grasslands") in particular have become intensively transformed and degraded (Mazia et al. 2001; Chaneton et al. 2002). The objective of this study was to evaluate the impact of grazing on non-native plant species richness and cover in mountain grasslands of central Argentina as related to herbivore identity and plant community type.

METHODS

Study Area

The 190 ha study area is located in mid-eastern Argentina (between 38º 02' and

38º 04' S and 61º 57' and 62º 00' W) and includes parts of Ventania Provincial Park (VPP) (169 ha) and the privately owned Palo Alto Ranch (PAR) (21 ha). Piedmont valleys, with 3% to 11% slopes and occasional rocky outcrops, dominate the study area. Climate is temperate and subhumid (Burgos and Vidal 1951). Average annual air temperature is 14 ºC, and average annual precipitation is 80 cm. Snow occasionally falls during the winter (Burgos 1968). Annual precipitation in VPP during the study period was 86 cm in 2006 and 95 cm in 2007.

Two types of communities co-occur in piedmont valleys of the study area: short-needlegrass grasslands (hereafter needlegrass grasslands) and tall-tussock grasslands (hereafter tussock grasslands) (Lizzi et al. 2007). Both communities are dominated by herbaceous species, with low abundance of small shrubs. Needlegrass grasslands occur in shallow, resource-poor soils (Table 1). In the absence of livestock grazing, the grass canopy may reach 50 to 60 cm in height, dominated by *Piptochaetium haeckelii* (Arechav.) Parodi, *Stipa bonaerensis* Henrard and Parodi and *Briza subaristata* Lam. (Frangi and Bottino 1995). Tussock grasslands develop in areas of deeper soil and higher resource abundance (Table 1), where the soil is saturated with water during rainy periods. These communities are dominated by *Paspalum quadrifarium* Lam., which can represent 80% or more of total plant cover (Frangi and Bottino 1995). Height of P. quadrifarium tussocks can reach one meter or more, with few other plants species growing amongst them (Table 1).

Both VPP and PAR have a long history (> 50 years) of heavy (ca. 0.25 – 0.30 animal units per ha) continuous, year-around grazing by feral horses or domestic cattle, respectively. Grazing intensity estimated by indirect indicators (e.g., percentage of bare ground, vegetation height, dung percentage cover, and frequency) was similar in areas grazed either by horses or cattle (A. Loydi, unpubl. data). Cattle and horses use needlegrass grasslands and tussock grasslands for their daily activities (Scorolli 1999). Besides defoliation, disturbances in the study area include trampling and paths, and wallows and dung piles. VPP also includes an exclosure (28 ha) that has not been grazed by large herbivores for the last 15 years. Vegetation composition in the exclosure is similar to descriptions of the original communities in piedmont valleys of the study area (Frangi and Bottino 1995). Before the introduction of domestic livestock, the study area was grazed by native ungulates, especially the guanaco (*Lama guanicoe* Müller), a South American camelid (Hudson 1929; Bilenca and Miñarro 2004).

Sampling Design and Statistical Analysis

Sampling was done in 1-ha plots at the end of the growing season (December/January) in 2006 and 2007. We chose to sample at this time of year since this is when plant species richness peaks in the study area (Frangi and Bottino 1995). In 2006, eight plots were selected: two in the grazing exclosure area, four in VPP under horse grazing, and two in PAR under cattle grazing. In 2007, nine plots were selected resulting in three, four, and two plots in the grazing exclosure, horse-grazed, and cattle-grazed conditions, respectively. Selected plots in 2006 and 2007 were different. Within each treatment, plots were located far enough from each other and on similar topography and slope exposure, which imposed restriction on the number of plots for sampling. Plots were > 250 m away from each other to assure independence and avoid pseudoreplication and on same topography and slope exposure to assure similar soil properties and microclimatic (temperature, solar radiation) conditions (Cantón et al. 2004 and references therein). Sampled plots had 3% to 8% slope and northern exposure. Consequently, our results are limited to this particular topography and slope exposure. Each plot included both needlegrass grasslands and tussock grasslands, which are strong indicators of edaphic conditions in piedmont valleys of the study system (Frangi et al. 1980; Table 1). In every 1-ha plot, thirty 1 m^2 sub-plots size were selected in a stratified random manner: 15 in needlegrass grasslands and 15 in tussock grasslands. A total of 15 m^2 were sampled per community type and in each 1-ha plot. Preliminary sampling indicated that this number of sub-plots was sufficient to record most of the species present in each community type. In each subplot, we visually estimated non-native

Table 1. Soil and vegetation characteristics of needlegrass grasslands and tussock grasslands communities at Ventania Mountains (Buenos Aires Province, Argentina). Data are from Frangi et al. (1980) and Frangi and Bottino (1995).

	Needlegrass Grasslands	Tussock Grasslands
Soil depth (cm)	< 35	> 60
Soil total N (%) 0-20 cm depth	0.4	0.49
Soil organic matter (%) 0-20 cm depth	7.9	9.9
Canopy height (cm)	50 - 60	> 80
Plant species diversity	High	Low
Dominant plant species	*Piptochaetium haeckelii, Stipa bonaerensis , Briza subaristata*	*Paspalum quadrifarium*

plant cover to the nearest percent using a modified Braun-Blanquet scale (Sutherland 1996) with 10% cover classes. Richness and percent cover of non-native plants were used as an indicator of community invasibility (Stohlgren et al. 2003). Species nomenclature follows Zuloaga and Morrone (2007).

We used analysis of variance (ANOVA) to explore variation in non-native plant species richness and cover by herbivore identity, plant community type, and their interaction. Each sampling year was analyzed separately. Data were analyzed according to a split-plot design, with herbivore identity as the main plot factor with three levels (horse-grazed, cattle-grazed, and grazing exclosure) and community type as the within-plot factor with two levels (needlegrass grasslands and tussock grasslands). Species richness data were square root transformed, and cover data were square root-arcsine transformed prior to analysis to meet ANOVA assumptions (Zar 1999). Normality was tested with normal probability plots; homocedasticity was examined using Bartlett's test (Zar 1999). When interactions were not significant, the Tukey test ($\alpha = 0.05$) was used to identify individual differences in treatment means (Zar 1999). All analyses were done using Infostat Software (InfoStat 2008).

RESULTS

Thirty-one non-native plant species were found growing in tussock and needlegrass grasslands under horse or cattle grazing or in grazing exclosure conditions (Table 2). Grazing increased non-native plant richness and cover in both sampling years (Table 3). Non-native plant richness was higher under horse grazing than under cattle grazing or under grazing exclusion (Figure 1a). Total percent cover of non-native plants was higher under horse grazing than under grazing exclusion but did not differ between areas under cattle grazing and grazing exclusion (Figure 1b).

Non-native plant richness and percent cover were higher in tussock grasslands than in needlegrass grasslands in both sampling years, except for richness in 2007 which was similar in both community types (Table 3). Non-native plant richness (means ± 1 SE) for both years was 6.4 ± 1.2 SE versus 9.7 ± 1.4 SE species/15 m^2 in 2006, and 7.6 ± 1.0 SE versus 8.9 ± 1.2 SE species/15 m^2 in 2007, for needlegrass and tussock grasslands respectively. Percent cover of non-native plants was 2.5 ± 0.8 SE versus 12.0 ± 2.6 SE in 2006, and 2.7 ± 0.6 SE versus 9.7±1.6 SE in 2007, for needlegrass and tussock grasslands respectively. There was no interaction between herbivore identity and community type for non-native plant richness and cover in both years (Table 2, Figure 2).

DISCUSSION

Our results are consistent with the hypothesis that large herbivore grazing can facilitate invasion of non-native plants into natural grasslands. Similar results have been found in a variety of natural ecosystems subjected to grazing by large native or non-native herbivores (Richardson et al. 2000; Chaneton et al. 2002; Parker et al. 2006; Vavra et al. 2007). Easing of interspecific plant competition (McNaughton 1983; Olff and Ritchie 1998) and generation of gaps for colonization (Bakker and Olff 2003) have been indicated as key mechanisms facilitating invasions of non-native plants in grazed grasslands. We observed that non-native plant establishment occurred largely in gaps of the grass canopy, which likely facilitates colonization by ruderal species (e.g., Grime 1977, 2001).

Both herbivore identity and plant community type modulated the effect of grazing on non-native plant richness and cover, since invasibility was higher under horse grazing than under cattle grazing and in rich soil sites (tussock grassland communities) than in poor soil sites (needlegrass grassland communities). Variation in the effects of horse grazing and cattle grazing on non-native plant species can be in part attributed to differences in herbivore morphophysiology and size. For example, retention time of undigested residues is higher in cattle than in horses (Duncan et al. 1990), which is associated with higher levels of forage intake and longer daily grazing time in the later species (Fleurance et al. 2001). Horses have both top and bottom incisors (cattle lack top incisors), which allow them to graze much closer to the ground than cattle (Rook et al. 2004). Horses are also bigger and heavier than cattle, making a larger impact on the structure of the vegetation and on soil surface. These and other differences (e.g., dung piles that result from the marking behavior of stallions) between herbivore species may explain the more important role of horses as facilitators of non-native plant invasion in our study.

The plant communities we studied showed different levels of invasion by non-native plants regardless of herbivore identity. This result could be explained by variation in competitive interactions between communities due to differences in resource availability and/or diversity of native plant species. Increasing experimental evidence shows that species-rich communities are less invasible than species-poor communities (Elton 1958; Tilman 1997; but see also Lonsdale 1999), probably because competition intensity and resource-use efficiency are higher in species-rich than in species-poor communities (Shea and Chesson 2002). Concordantly, non-native plant species were more abundant and diverse in tussock grasslands, the community with a lower diversity of native plant species (Frangi and Bottino 1995). On the other hand, non-native plant invasion may be facilitated by high resource availability (Davis et al. 2000). Non-native plants are often opportunistic species, able to use resources efficiently in the short term (Funk and Vitousek 2007). We observed the highest abundance of non-native plant species in tussock grasslands, which are associated with rich soils. Therefore, both mechanisms (native plant species diversity and soil-resource availability) may contribute to explain the observed differences in invasibility between needlegrass and tussock grasslands in our study.

There may be additional, although we think less plausible, explanations for the observed pattern of non-native plant invasion in this study. For example, differences in non-native plant richness between needlegrass and tussock grasslands could simply result from life history traits (dis-

Table 2. Non-native plant species found in needlegrass and tussock grasslands communities in the study area under different grazing conditions. Ex: grazing exclusion; Ca: cattle grazing; Ho: horse grazing. Nomenclature follows Zuloaga and Morrone (2007).

	Needlegrass grasslands						Tussock grasslands					
	2006			2007			2006			2007		
Species	**Ex**	**Ca**	**Ho**	**Ex**	**Ca**	**Ho**	**Ex**	**Ca**	**Ho**	**Ex**	**Ca**	**Ho**
Apium leptophyllum			X	X		X			X		X	X
Arenaria serpyllifolia	X		X	X	X	X						X
Briza minor												X
Bromus hordeaceus						X	X	X	X		X	X
Centaurea calcitrapa			X					X	X		X	X
Cerastium glomeratum			X									
Chondrilla juncea								X				
Cirsium vulgare		X	X	X		X	X	X	X	X	X	X
Conium maculatum										X		
Cynodon dactylon								X				
Cynosurus echinatus			X			X			X			X
Echium plantagineum			X	X		X	X		X	X		X
Geranium molle	X	X	X	X	X	X			X	X	X	X
Hordeum murinum ssp. *leporinum*						X	X	X	X			
Hypochaeris radicata			X	X	X	X		X	X	X		X
Lactuca serriola									X			
Lolium perenne ssp. *multiflorum*				X		X	X	X	X	X	X	X
Medicago minima						X			X			X
Petrorhagia nanteuilii		X	X	X	X	X			X			X
Poa annua	X		X	X			X		X			
Polycarpon tetraphyllum			X									
Rosa spp.							X					
Rostraria cristata						X						
Rumex spp.									X			
Scleranthus annuus		X	X	X	X	X						X
Silene gallica	X	X	X			X			X			X
Sonchus asper				X		X	X		X	X	X	X
Sylibum marianum												X
Taraxacum officinale				X		X	X	X	X	X	X	X
Tragopogon dubius	X						X		X		X	X
Viola tricolor							X	X	X	X		X
Total richness	**5**	**5**	**14**	**12**	**5**	**17**	**11**	**10**	**20**	**9**	**9**	**20**
Mean richness per plot	**3.5**	**3.5**	**9.3**	**6**	**4.5**	**10.3**	**7.5**	**7.5**	**12.7**	**6.3**	**7.5**	**11.5**
Mean % cover per plot	**0.9**	**0.3**	**4.4**	**1.5**	**1.5**	**4.2**	**5.5**	**10.8**	**17.2**	**4**	**9.6**	**13.9**

Table 3. Influence of herbivore and plant community type on non-native plant species (NNP) percentage cover and richness, tested by split-plot ANOVA (P < 0.05).

	Herbivore		Community		Herbivore*Community	
			2006			
	$F_{(2,5)}$	*P*	$F_{(1,4)}$	*P*	$F_{(2,4)}$	*P*
NNP richness	11.75	**0.013**	8.54	**0.043**	0.19	0.832
NNP cover	6.36	**0.042**	92.23	< **0.001**	2.44	0.203
			2007			
	$F_{(2,6)}$	*P*	$F_{(1,6)}$	*P*	$F_{(2,6)}$	*P*
NNP richness	9.99	**0.012**	3.33	0.118	0.63	0.562
NNP cover	17.77	**0.003**	82.24	< **0.001**	4.54	0.063

persal ability, germination requirements, plant life-form) (Gross 1984; Pearson et al. 2002; Wang et al. 2008) of the non-native plant species present in the study site. If this were the case, different non-native plant species should be present in each community type. However, ca. 60% of non-native plant species co-occurred in needlegrass and tall-tussock communities. On the other hand, differences in cover of non-native plants between needlegrass and tussock grasslands could be, at least in part, due to differences in competitive ability between C3 grass species (dominants in needlegrass grasslands) and C4 grass species (dominant in tussock grasslands). However, C4 grasses commonly have high competitive ability, particularly in competing for light in resource-rich sites (Tilman 1982), which render this explanation less probable.

The results of our study highlight the potential impact of large non-native herbivores on non-native plant invasion with implications for conservation of natural grasslands. It has been recently suggested that large non-native herbivores can be used as ecological agents to mimic the effects of native herbivores, maximizing diversity of native plants (Hart 2001; Loucougaray et al. 2004), birds (Zalba and Cozzani 2004), and invertebrates (Dennis et al. 2001; Woodcock et al. 2005; Boschi and Baur 2007) at intermediate grazing levels. We have shown that uncontrolled grazing by large non-native herbivore species, particularly horses, facilitates non-native plant invasion in Argentinian grasslands. We suggest that programs which use non-native herbivores as surrogates for native grazers in grasslands, even at intermediate grazing levels, closely monitor their sites in order to prevent expansion of non-native plant populations. This is especially relevant in natural areas, where grazing by non-native herbivores is used as an ecological management tool.

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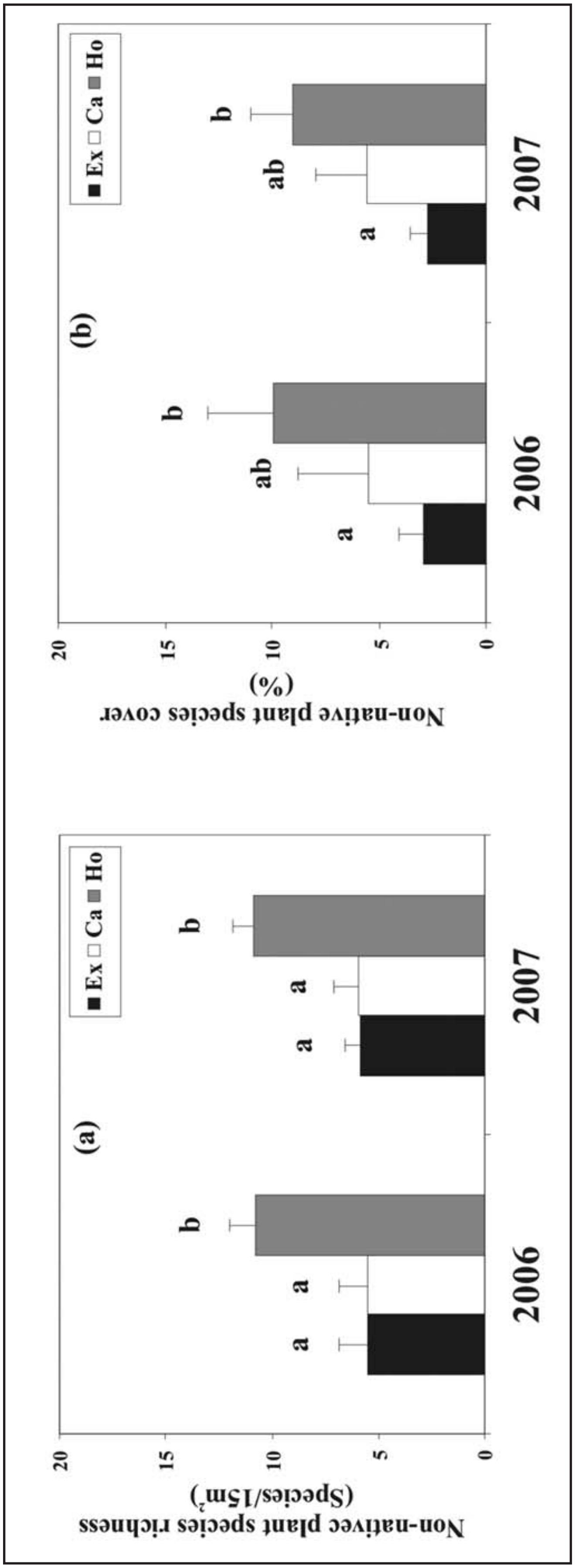

Figure 1. Non-native plant species richness (a) and cover (b) in 2006 and 2007. Ex: grazing exclusion; Ca: cattle grazing; Ho: horse grazing. Means ± 1 S.E. are displayed. Within each year, different letters mean significant statistical differences treatment between means (Tukey test, $P < 0.05$).

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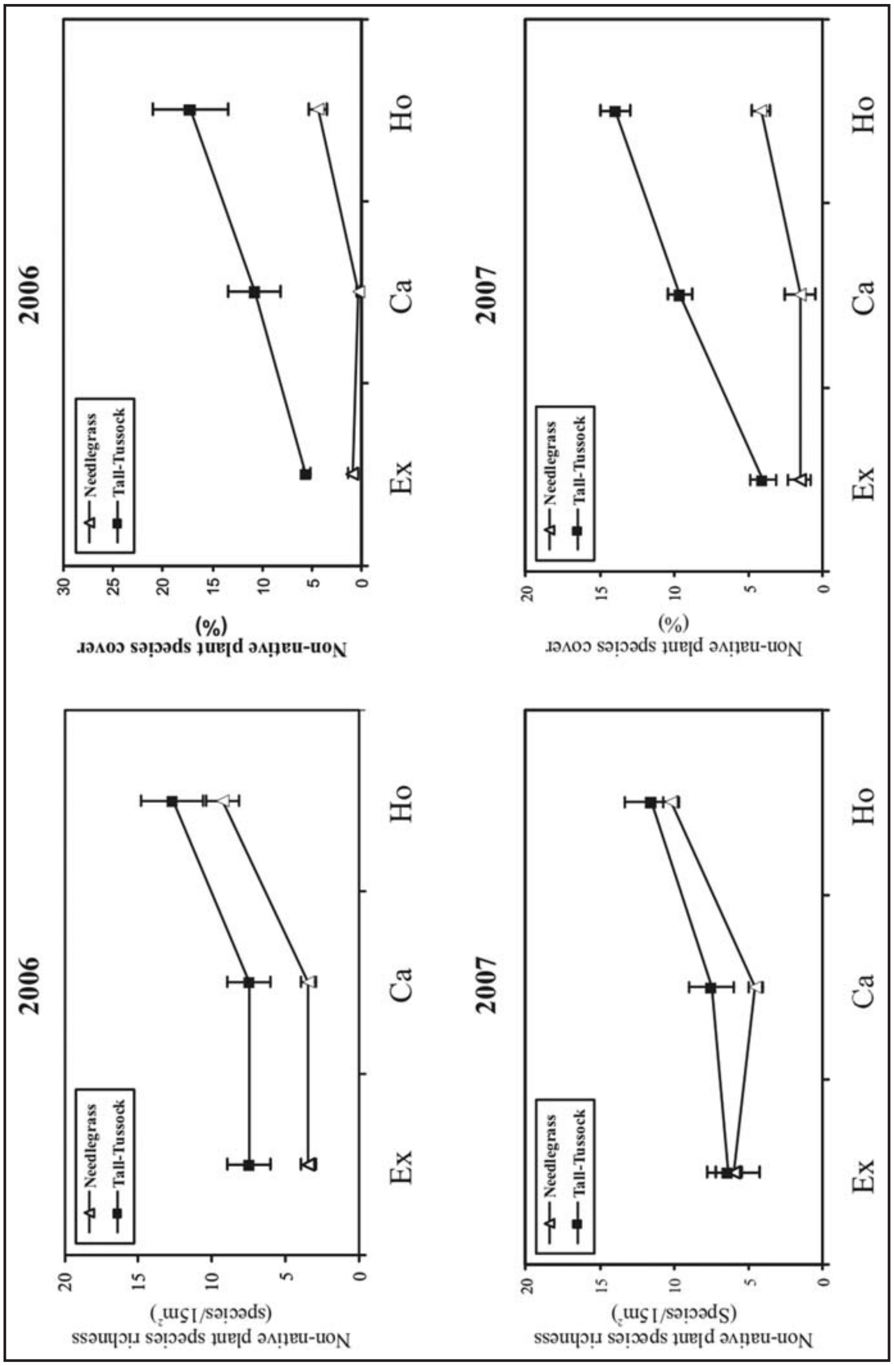

Figure 2. Interaction plot between the effects of herbivore and plant community type on non-native plant species richness and cover in 2006 and 2007. Ex: grazing exclusion; Ca: cattle grazing; Ho: horse grazing. Means ± 1 S.E. are displayed.

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