

Refuge effect of an unpalatable forb on community structure and grass morphology in a temperate grassland

Silvana E. Noëll Estapé · María Semmartin ·
José M. Paruelo

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Abstract The role of unpalatable plant species as biological antiherbivore refuges for palatable species is well-documented at community level particularly in harsh environments. In productive sub-humid temperate grassland subjected to domestic grazing, we examined the protective effect of *Eryngium horridum* on plant community structure and floristic composition, and evaluated whether these changes impacted on a number of morphological traits of grasses, related to grazing resistance. We also investigated, for a

palatable grass species (*Stipa neesiana*) the existence of morphological differences between protected and unprotected plants and if this eventual variation was either plastic or genetic. The study consisted of a field survey where we compared paired patches, with and without *E. horridum*, and a greenhouse experiment where we evaluated individuals of *S. neesiana* coming from both patch types over a 11 months period. Patches dominated by *E. horridum* had lower richness and cover of forbs than patches without the forb, and similar richness but greater cover of cool-season tussock palatable grasses, which suggests a protective role on the latter. Grasses in these patches also had longer blades and sheaths and lower specific leaf area. The morphological differences of *S. neesiana* individuals collected from both patch types disappeared after 11 months growth in a common environment which revealed significant phenotypic plasticity in this species. These results suggest the existence of plant-to-plant facilitation in a productive ecosystem not only at community level, through changes in species richness and the promotion of palatable grasses, but also at population level, through plastic changes in aboveground morphological traits. Both facilitation and plasticity, would contribute to the persistence of threatened palatable grasses in the heavy grazed productive ecosystems.

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S. E. Noëll Estapé (✉)
Facultad de Agronomía, Departamento de Producción
Animal y Pasturas, Estación Experimental
Dr. Mario A. Cassinoni, Universidad de la República,
Ruta 3 km 363, C.P. 60000 Paysandú, Uruguay
e-mail: silvana@fagro.edu.uy

M. Semmartin · J. M. Paruelo
Facultad de Agronomía, Instituto de Investigaciones
Fisiológicas y Ecológicas Vinculadas a la Agricultura
(IFEVA), Universidad de Buenos Aires, Consejo Nacional
de Investigaciones Científicas y Técnicas (CONICET),
Av. San Martín 4453, C1417DSE Buenos Aires,
Argentina

J. M. Paruelo
Laboratorio de Análisis Regional y Teledetección,
Departamento de Métodos Cuantitativos y Sistemas
de Información, Facultad de Agronomía, Universidad
de Buenos Aires, Buenos Aires, Argentina

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Introduction

Positive plant-to-plant interactions have been particularly documented in habitats exposed to severe environmental stress (e.g., desert, tundra, arctic, and subalpine forests) (Franco and Nobel 1989; Callaway et al. 2002; Cavieres et al. 2002). Moreover, greater positive interactions have also been documented for a given species, along an environmental stress gradient (Pugnaire and Luque 2001). In water-stressed ecosystems, nurse plants increase soil moisture and nutrient for seedlings (Cavieres et al. 2002; Rossi and Villagra 2003; Oosterheld and Oyarzábal 2004; Yu et al. 2006), and modify community structure. Conversely, in less stressful ecosystems these facilitative interactions are weaker than competitive interactions, which usually are major determinants of community structure (Bertness and Callaway 1994).

A widely recognized positive plant-to-plant interaction is that in which unpalatable plants provide protection to palatable plants, acting as a biotic refuge against large herbivores (McNaughton 1978; Callaway et al. 2000; Milchunas and Noy-Meir 2002; Fidelis et al. 2009; Boughton et al. 2011). In general spiny shrubs, cacti or even unpalatable grasses provide protection to palatable grasses (McNaughton 1978; Callaway et al. 2000; Rebollo et al. 2002; Oosterheld and Oyarzábal 2004). These biotic interactions that have been largely documented in stressful habitats, have implications for plant species at the community and population levels and, ultimately, influence the net impact of grazing on the plant community (Milchunas and Noy-Meir 2002). Unpalatable plants, particularly in overgrazed rangelands, assure the long-term viability of preferentially grazed populations (Callaway et al. 2000; Oosterheld and Oyarzábal 2004), and might strengthen intraspecific variability allowing the expression of phenotypic plasticity and/or ecotype differentiation. In non-stressful ecosystems there is much less evidence about biotic refuges, and it seems to be apparent only under heavy grazing pressure (McNaughton 1978; Bertness and Callaway 1994; Milchunas and Noy-Meir 2002; Fidelis et al. 2009; Boughton et al. 2011).

In many grassland species, morphological plant traits such as height and specific leaf area have been found to be strong indicators of plant ability to resist grazing by avoidance and tolerance, respectively (Díaz et al. 2001). Short plants are less probable to

be consumed by vertebrate herbivores, whereas plants with greater leaf area per unit of biomass have a better ability to re-grow after defoliation. In native temperate grasslands of South America, where C3 and C4 grasses account for most of the available forage, cattle grazing promotes a particular vegetation structure (Soriano 1992), with a low and dense stratum, often intensively grazed and dominated by short, prostrate grasses and forbs (Rosengurt 1979), and an upper stratum with tussock grasses and medium forbs and shrubs (Millot et al. 1987). During winter, low temperature determine the lowest annual forage production and heavy grazing may cause the disappearance of most productive and palatable cool-season grasses (Millot et al. 1987). Forbs and shrubs, and the palatable grasses growing in the vicinity of these plants, are usually avoided by large herbivores suggesting a plant-to-plant protection. Moreover, individuals of grasses growing close to unpalatable shrubs seem to be larger than those growing away from them.

Here we evaluated the protective role of an unpalatable native forb on community structure and morphology of grasses in a subhumid temperate grassland (Paysandú, Uruguay) subjected to grazing by sheep and cattle. We specifically investigated the role of *Eryngium horridum* (Malme) on plant species composition, diversity, and on morphological traits of grasses, particularly on *Stipa neesiana* (Trin. and Rupr.), a palatable grass. *Eryngium horridum* expanded in the region and is considered an important weed since it reduces the effective grazing area and, consequently, forage production. Most research has been focused on the design of strategies to reduce its density and cover (Montefiori and Vola 1990; Lallana et al. 2006), whereas its ecological role as refuge for other valuable or even threatened species has been barely considered. Recently, in the grasslands of Rio Grande do Sul (Brazil), Fidelis et al. (2009) found that *E. horridum* played an important role as facilitator of other species, either through physical protection from grazers, under heavy grazing, or through allowing greater light penetration, in ungrazed canopies. However, it is still unknown whether these structural changes of plant community are accompanied by morphological changes in plant populations. We hypothesized that, under grazing conditions, *E. horridum* will affect plant community structure and would exert a protective effect against herbivores particularly on the most

palatable grass species. We predicted that (1) the abundance and diversity of the most palatable species (largely cool-season grasses) will be promoted in patches dominated by *E. horridum* with respect to patches without it; (2) the different grass species composition of patches with *E. horridum* with respect to those without it will result in an average larger leaf size and a lower specific leaf area of grasses; (3) within a given palatable grass (*S. neesiana*), individuals growing in patches with *E. horridum* will exhibit larger leaves and lower specific leaf area than their counterparts in patches without *E. horridum*.

Materials and methods

Study species and system

Eryngium horridum is one of the most conspicuous non-palatable native species of Uruguay, southern Brazil and northeastern and central Argentina grasslands (Lombardo 1982; Lallana et al. 2006). It is a perennial Umbelliferae with numerous spiny leaves arranged in basal rosettes (Cabrera 1953; Rosengurtt 1979). Early studies of these grasslands concluded that *E. horridum* abundance was promoted in areas subjected to degradation processes triggered by frequent burning or overgrazing (Rosengurtt 1943, 1946; Fidelis et al. 2008). *Stipa neesiana* is a palatable, cool-season, C3 perennial tussock grass, widespread in the natural grasslands of Uruguay and the rest of South America (Rosengurtt et al. 1970). It has hairy flat leaves and multiflora lax panicles (Rúgolo de Agrasar et al. 2005) and is one of the most productive and palatable species, particularly during winter (Rosengurtt et al. 1970; Cadenazzi 1992). *Stipa neesiana* has been identified as one of the most conspicuous species whose abundance is dramatically reduced in grazed areas (Rodríguez et al. 2003).

The study was conducted at the Experimental Station Dr. Mario Cassinoni of the Faculty of Agronomy, University of the Republic (Uruguay) (32°22'41"S, 58°03'50"W). Climate is subhumid and temperate with an average annual rainfall of 1,200 mm and average annual temperature of 18 °C. Soils (Argiudolls) are deep and have a silt–clay texture (Duran et al. 2005). Mean annual aerial net primary productivity is approximately 4,000 kg ha⁻¹ y⁻¹ with a first peak of production during spring and a second peak during late summer

and autumn (Symonds and Salaberry 1978). The experimental site covered 35 ha of natural grassland dominated by C4 grasses grazed by sheep and cattle with a stocking rate equivalent of 1 cow ha⁻¹. Vegetation structure exhibits three layers: the highest one consisting of isolated individuals of native and exotic tree species (*Acacia caven*, *Prosopis affine* and *Eucalyptus* spp.) scattered on a matrix of grasses, and two herbaceous layers composed by shrubs, forbs, and grasses. The upper layer included shrub species like *Baccharis coridifolia*, *Baccharis trimera*, *Heimia salicifolia*, and tall forbs such as *E. horridum*, whereas the lower layer included a diverse set of grass species (*Paspalum notatum*, *Bothriochloa laguroides*, *Coelorhachis selloana*, *Schizachyrium microstachyum*, *Andropogon ternatus*, *Axonopus affinis*, *S. neesiana*, *Piptochaetium stipoides*, *Lolium multiflorum*, among others), and forbs (*Juncus* spp., *Chevreulia acuminata*, *Chaptalia piloselloidea*, etc.) (Cadenazzi 1992). In the experimental site, *E. horridum* covered 40 % of surface area, 21 % corresponded to grouped individuals and 19 % to isolated individuals. Its density was 6.6 plants m⁻² and the individual mean size was 0.06 m² (ranging from 0.002 to 0.47 m²).

Experimental design and data analysis

Field survey

In order to evaluate the effects of *E. horridum* on community and population traits, we randomly delimited a total of 36 paired patches, 18 of them included the presence of one individual of *E. horridum*, and the remaining 18 were outside its influence (each pair of patches was at least 10 m apart). Patches with *E. horridum* consisted of circular areas (the shape of *E. horridum* individuals) with a variable size which depended on the individual diameter; we selected isolated individuals of 35 to 60 cm in diameter (average diameter 0.45 cm) surrounded by an *E. horridum*-free area of at least 40 cm radius. The area of patches with *E. horridum* ranged between 0.1 and 0.28 cm², with an average area of 0.16 cm². Patches without *E. horridum* consisted of square 40 × 40 cm areas (average area 0.16 cm²). Since *E. horridum* patch size was variable, we evaluated its potential effects on grasses or forbs richness and cover by a linear regression and we found that none of these variables were significantly correlated with patch size

(grasses richness: $r^2 = 0.15$, $P = 0.11$, $n = 18$; forbs richness: $r^2 = 0.02$, $P = 0.54$, $n = 18$; grasses cover: $P = 0.45$, $r^2 = 0.05$, $n = 18$; forbs cover: $P = 0.89$, $r^2 = 0.0016$, $n = 18$).

The survey was performed during the Austral spring (September to December 2005). In both patch types, we recorded floristic composition, richness, aerial cover of plant species, cover of bare soil, and canopy height. In patches with *E. horridum*, we first carefully eliminated its leaves to have a full access to plants growing beneath the selected patch. On the basis of the species composition (presence–absence), we estimated the similarity between patches with and without *E. horridum* using the Sorensen index ($S = 2\cap/(U + \cap)$, ($\cap$ = shared species and U = total species), which ranges between 0 and 1, where $S = 1$ indicates complete similarity between plot types (i.e., both plot types have all species in common) and $S = 0$ indicates complete dissimilarity (i.e., both plot types do not have any species in common). The species were grouped as grasses or forbs, perennial or annual, tussock or prostrate (prostrate grasses were stoloniferous) and cool or warm season. Finally, we also classified the species according to their palatability for domestic herbivores (high, medium, and low palatability), adapted from Rosengurtt (1979), (see Appendix S1 in Supporting Information).

We estimated leaf length and width and specific leaf area of all grass species. In each plot, and for each grass species, we randomly selected two fully expanded leaves without signals of herbivory or senescence (Cornelissen et al. 2003). We recorded length and width of blades and the length of sheaths. Leaves were scanned and dried (dried at 55 °C for 48 h). Scanned leaves were analyzed with the image analysis program MultispecW32 (Purdue Research Foundation®) to determine leaf area. We estimated the specific leaf area as the quotient between leaf area and dry weight (Cornelissen et al. 2003). In summary, from each patch (replicate), for each morphological variable and plant species category (e.g., cool season, warm season, etc.), we obtained a single value that averaged those of each species integrating the corresponding category.

Data analysis to evaluate the differences in community composition between patch types was based on two principal component analyses of the presence–absence plant species and cover of grasses and forbs groups (Pcord4 software, Mc Cune and

Mefford 1999). We analyzed plant species richness with Wilcoxon's test for paired plots, and cover and morphological traits of grasses with t tests for paired plots.

Greenhouse experiment

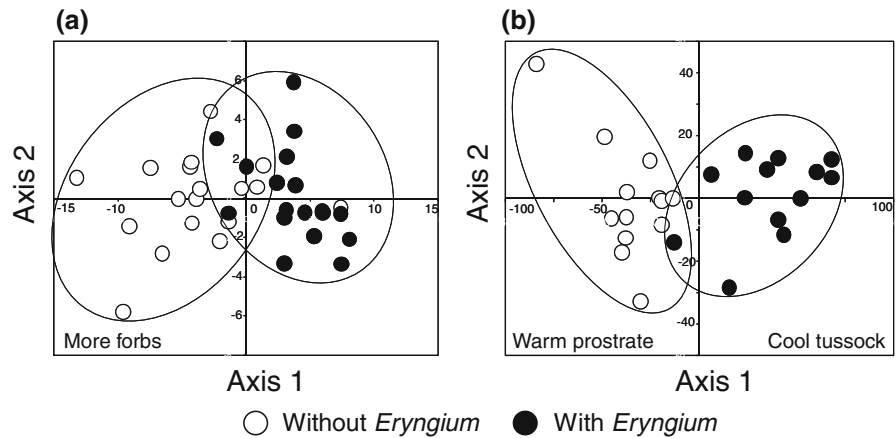
The experiment examined the existence of morphological differences in *S. neesiana* individuals from patches with and without *E. horridum* in a common environment. During the Austral spring of 2006 (October to December), we collected, in plots with and without *E. horridum*, individuals of *S. neesiana* with an average of 5 tillers. Plants were transplanted into individual 2.6-l pots, filled with a mixture of soil from the study site and sand (2:1) and, after a few weeks of acclimation, they were grown for 11 month period (from December 2006 to November 2007). Throughout this period, pot location in the greenhouse was randomly changed once every other week. Plants received natural photoperiod and radiation intensity and were periodically watered. At month 9 (September 2007), after a complete leaf turnover, there were 14 individuals from each different patch (with and without *E. horridum*, total 28 individuals), and each plant was divided into two equal portions. One was used for destructive measurements and the other one was replanted, defoliated at 4 cm height and cultivated for two additional months. For both plant groups, in months 9 and 11, we recorded tiller number, blade width, length and biomass, and sheath length and biomass in two, randomly selected, tillers per plant, and calculated the specific leaf area following the same procedure described for the field survey. We also recorded the biomass removed during the defoliation.

We analyzed individual leaf area, specific leaf area, blade-length and width- and sheath length for the field survey and the greenhouse (after 9 and 11 months of growing), and tiller weight only in greenhouse by single comparisons of each variable with independent t tests. The statistical package used was InfoStat (2008).

Results

Species composition differed between patches with and without *E. horridum* (Fig. 1). The first axis of the principal component analysis of the presence-absence

Fig. 1 Ordination of the patches with and without *Eryngium horridum* plants according to **a** presence–absence of species, and **b** cover of grasses and forbs groups



of species accounted for 76.6 % of the total variance, largely explained by number of forb species (Fig. 1a), whereas the first axis of the analysis including plant cover accounted for 66.2 % of the total variance, largely explained by cool-season perennial tussocks and warm-season prostrate grasses (Fig. 1b).

Out of the total 69 species, 34 were present in both situations, 6 only occurred in patches with *E. horridum*, and 29 were confined to patches without *E. horridum* (see List of species Appendix S1 in Supporting Information). The 6 species exclusively associated with *E. horridum* were perennial and included grasses, forbs, and one shrub (*Sporobolus indicus*, *Calamagrostis montevidensis*, *Cuphea glutinosa*, *Tragia geranifolia*, *Rhynchosia* sp., and *Baccharis coridifolia*). In contrast, most of the species exclusively found in patches without *E. horridum* were prostrate grasses, forbs, and annuals. The average Sorensen similarity index between patches with and without *E. horridum* was 0.66 when considering all the species. It reached 0.89 when only grasses were considered (patches were more similar) and, conversely, it dropped to 0.52 when only forbs were considered (patches were more dissimilar).

Total richness was lower in patches with *E. horridum* ($P = 0.006$) due to a significant reduction in forbs ($P = 0.002$), while grass richness was similar between plot types ($P = 0.27$; Fig. 2). Within grasses, the warm-season perennial prostrate grasses had greater richness in patches without *E. horridum* ($P < 0.0001$).

Relative plant cover was high in both plot types but patches with *E. horridum* had a slightly higher cover than those without *E. horridum* (97 vs. 91 %, $P = 0.03$). Grasses also showed the highest cover in

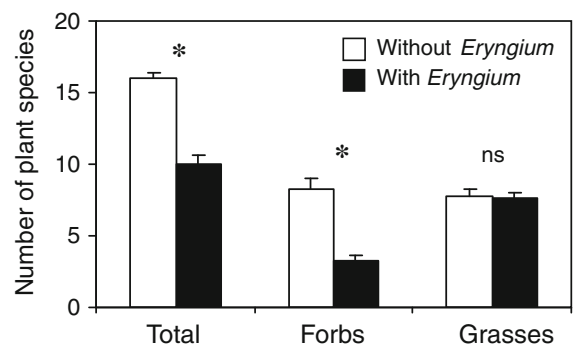


Fig. 2 Number of plant species recorded in field corresponding to total species, forbs, and grasses, in patches with and without *E. horridum*. Bars represent ± 1 standard error. Asterisks indicate significant differences within each group of species and *ns* indicates non-significant differences

patches with *E. horridum*, whereas forbs cover was five-fold greater in patches without *E. horridum* (Fig. 3a). Both cool-season perennial tussock and warm-season perennial prostrate grasses were particularly sensitive to the presence or absence of *E. horridum*. Cool-season tussock grasses had significantly greater cover in patches with *E. horridum*, whereas prostrate grasses had the opposite response (Fig. 3b). As examples of the first group, three species classified as highly palatable accounted for most changes: *Piptochaetium bicolor* (11.8 and 3.1 %, $t = 1.99$, $P = 0.069$), *Piptochaetium stipoide* (20.5 and 7.9 %, $t = 1.83$, $P = 0.09$), and *S. neesiana* (28.5 and 12.4 %, $t = 2.95$, $P = 0.012$) (mean cover in patches with and without *E. horridum*, respectively). As an example of the second group, *Paspalum notatum* (also a highly palatable grass) had a cover of 2.4 and 20.3 % in patches with and without

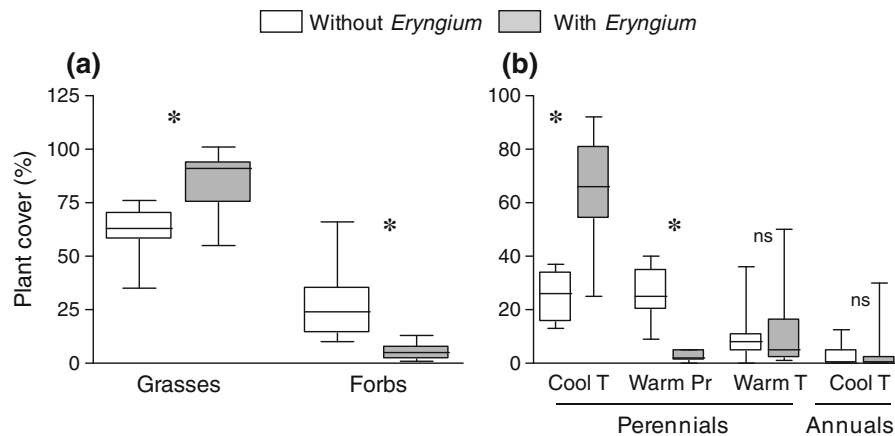


Fig. 3 **a** Cover of grasses ($P = 0.0007$) and forbs ($P = 0.0006$) of patches with and without *E. horridum* plants. **b** Cover of the different groups of perennial and annual grasses. Among perennials, classes are: Cool Tussock (Cool T), $P < 0.0001$; Warm Prostrate (Warm Pr), $P < 0.0001$; and Warm Tussock

(Warm T), $P = 0.7$. Annuals has a single class: Cool Tussock (Cool T), $P = 0.5$. Boxes extend from 25th to 75th percentile, lines indicate the medians and whiskers the lowest and highest values. Asterisks indicate significant differences within each group of species and *ns* indicates non-significant differences

E. horridum, respectively ($t = -5.35$, $P = 0.0002$). Conversely, cover of cool-season annual and warm-season perennial tussocks did not differ between plot types (Fig. 3b). According to preference by domestic grazers, the highly palatable species (mainly cool-season perennial tussocks), had greater cover in patches with *E. horridum* than in patches without *E. horridum* (71.8 vs. 48.7 %, $t = 3.39$, $P = 0.005$). Canopy height was higher in patches with *E. horridum* than in patches without *E. horridum* ($t = 17.36$, $P < 0.0001$) (8.35 vs. 2.26 cm).

Grass individuals growing in patches with *E. horridum*, in general, had a greater leaf area, and longer blades and sheaths than those growing in patches without *E. horridum* (Fig. 4). The specific leaf area of all grasses analyzed together and the cool-season grasses in particular, was greater in patches without *E. horridum* (Fig. 4). Blade width was less sensitive to *E. horridum* presence and the analysis by groups showed that it only varied for cool-season grasses which had wider blades in patches with *E. horridum* (Fig. 4).

When we analyzed morphological traits in *S. neesiana*, in the field, plants from patches with and without *E. horridum* markedly differed in all traits except in specific leaf area, where differences were marginal ($t = -2.16$, $P = 0.07$, $n = 8$) (Fig. 5). Conversely, after 9 months of growing in a common environment, three of the five traits were not statistically different between patch types and the other two

showed smaller differences than in the field. After 11 months, all traits were statistically similar (Fig. 5). In addition, the mean weight per tiller, only documented at months 9 and 11 of the greenhouse experiment, was higher in plants from patches with *E. horridum* ($t = -2.69$, $n = 14$, $P = 0.01$) after 9 months, and similar after 11 months ($t = -1.23$, $n = 14$, $P = 0.23$) (data not shown).

Discussion

As we hypothesized, our results revealed the influence of *E. horridum* on palatable grasses in particular, and on plant community structure in general. Suggesting its protective role on palatable grasses, patches with *E. horridum* had a high cover of palatable grass species, and overall, grasses in these patches had longer blades and sheaths and lower specific leaf area than those growing away from *E. horridum* plants. However, the absence of differences in morphological traits of individuals of *S. neesiana* from different patch types after growing in a common environment for several months, indicates that the morphological variation of grasses documented in the field was accounted for by both variation in species composition and plasticity of individuals of the same population. Patches with *E. horridum* had also lower total plant species richness due to lower forb richness. Canopy

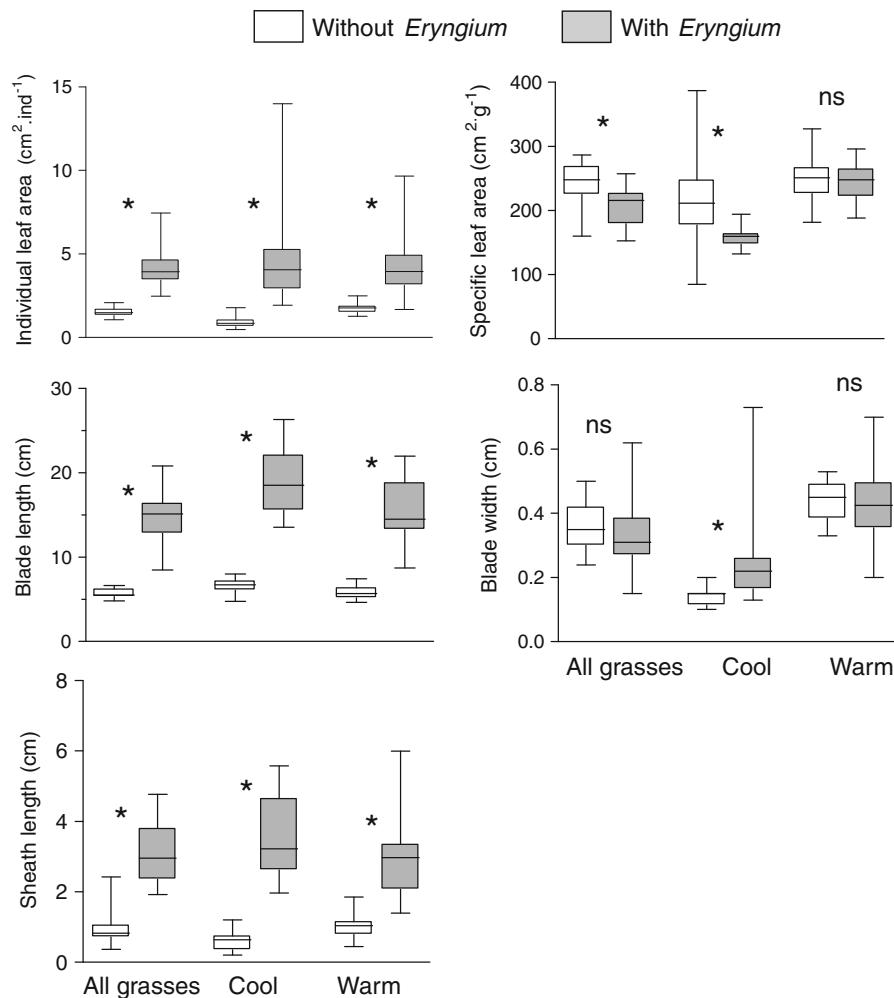


Fig. 4 Morphological traits of total grass species and classified according to their seasonality, cool- and warm-season, of patches with and without *E. horridum*. Boxes extend from 25th to 75th percentile, lines indicate the medians and whiskers the

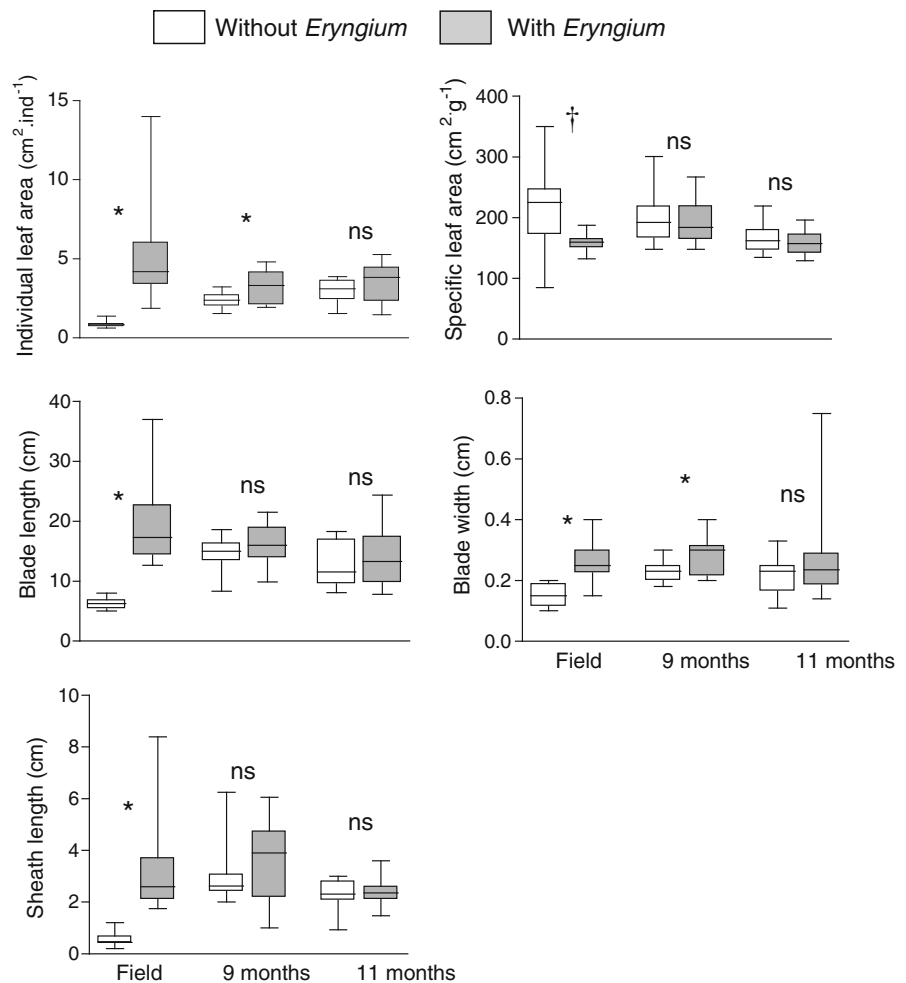
lowest and highest values. Asterisks indicate significant differences ($P \leq 0.05$) within each group of species and *ns* indicates non-significant differences

height of patches with *E. horridum* was higher than without *E. horridum*. The opposite effects on grasses and forbs suggest the combination of a protective role of *E. horridum* on palatable and intensively consumed grass species, and a negative effect on prostrate species, less able to compete for light, similar to grazing exclusion contrasts (Noy-Meir et al. 1989; Díaz et al. 1992; Rodríguez et al. 2003; Altesor et al. 2006).

The role of certain non-palatable plant species on community structure as a refuge against herbivores is a relatively well-described interaction in arid and semi-arid ecosystems, in contrast to the evidence gathered in subhumid and humid ecosystems (Milchunas and

Noy-Meir 2002; Rebollo et al. 2002, 2005; Oesterheld and Oyarzábal 2004; Graff et al. 2007). In arid and semiarid environments, the refuge plants usually promote plant species diversity at the patch scale (Callaway et al. 2000; Rebollo et al. 2005), and particularly the growth of highly palatable species (Oesterheld and Oyarzábal 2004; Graff et al. 2007). Our results partially agree with these findings since we found a reduction of forbs and total plant richness associated with the refuge plants but we also documented an increase of palatable grasses cover. Even though the evidence in mild ecosystems is limited, our results agree with two recent studies, one from a similar subtropical grassland in southern Brazil, where *E. horridum*

Fig. 5 Morphological traits of *S. neesiana* collected from patches with and without *E. horridum* plants, at three stages of evaluation: during field survey; after 9 months of growing in a common environment (greenhouse) and after 11 months of growing in the greenhouse, after being defoliated at month 9 (see “Materials and methods” section for more details). Boxes extend from 25th to 75th percentile, lines indicate the medians and whiskers the lowest and highest values. Asterisks and cross indicate significant differences ($P \leq 0.05$ and $P \leq 0.1$, respectively) within each stage of evaluation and *ns* indicates non-significant differences



presence was associated with lower forb and total plant diversity under grazed conditions (Fidelis et al. 2009) and the second one documented in grazed wetlands of south central Florida (USA), where *Juncus effusus* plays an antiherbivore refuge role by improving the cover of palatable grass species (Boughton et al. 2011). Since our study only evaluated the role of *E. horridum* on grazed sites we cannot conclude that the observed differences in plant species composition and morphology are exclusively due to the antiherbivore role of *E. horridum*. However, the consistent pattern particularly observed for palatable species provides strong and convincing evidence. Furthermore, since we did not evaluate the impact of these structural and morphological differences in terms of fitness (e.g., seeds production), we are cautious with interpretation of our results.

Differences in plant richness and abundance of different functional groups that we observed in patches

with and without *E. horridum* are similar to those induced by grazing on plant community structure. In sub-humid grasslands, grazing exclosure reduces diversity, species richness and evenness compared to grazed areas (Sala et al. 1986; Rusch and Oesterheld 1997; Chanton et al. 2002; Altesor et al. 2005, 2006). Moreover, our results agree with those obtained by Rodríguez et al. (2003) who found that patches protected from grazing favoured cool-season tussock grasses whereas continuous grazing favoured warm-season prostrate grasses. The presence of *E. horridum* produced the same effects on plant community structure to grazing exclosures. More important, our results provide evidence of facilitation as a mechanism that operates as a reservoir of palatable grass species in grazed areas since our study showed that *E. horridum*, usually perceived by range managers as an obnoxious weed species, generates patches that act as small grazing exclosures that benefit

highly valuable forage grass species. Nevertheless, we are aware that the beneficial role of *E. horridum* must be compensated by the reduction in area accessible for forage and the negative impact on forbs.

The different morphology of individuals growing in patches with and without *E. horridum* was consistent with the results found by previous studies (Noy-Meir et al. 1989; Díaz et al. 1992; Rebollo et al. 2002; Oesterheld and Oyarzábal 2004). Patches with *E. horridum* had a higher canopy height, grasses with bigger leaves (longer blades and sheaths), and a lower specific leaf area than patches without *E. horridum*. The cool-season grasses, *S. neesiana* included, exhibited a considerable plasticity in the traits evaluated. This plasticity coincides with that found for *Paspalum dilatatum*, a valuable warm-season grass of the Flooding Pampa, with large variability in blade to sheath ratio, tillering rate, and tiller insertion angle in response to different grazing, water availability and light-quality conditions (Loreti et al. 2001). Studies conducted by Díaz et al. (1992, 2001) found important differences in plant size and specific leaf area of individuals growing in paired grazed and ungrazed sites. Grazing morphotypes, in general, were associated with a greater ability to produce new leaves after defoliation (Westoby 1999; Cornelissen et al. 2003) as well as to resist grazing by avoidance (Briske 1999).

In summary, our results suggest the existence of plant-to-plant facilitation in a productive ecosystem and the impact that this relationship has not only on community structure but also on morphological traits for the most palatable grass group. In fact, our results suggest that mechanisms like facilitation and plasticity might contribute to the persistence of threatened palatable grasses in heavy grazed productive ecosystems. In addition, our results modify the general negative perception of the functional role of non-consumed plant species in grasslands, as we show that they can act as a diversity reservoir of more palatable native species. For these ecosystems it is still necessary to identify the equilibrium between facilitation and competition in order to design a new range management strategy that optimize the role of *E. horridum* and other unpalatable species in these grasslands rather than seeking their eradication.

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