

Habitat stress, species pool size and biotic resistance influence exotic plant richness in the Flooding Pampa grasslands

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Summary

1 Theory and empirical evidence suggest that community invasibility is influenced by propagule pressure, physical stress and biotic resistance from resident species. We studied patterns of exotic and native species richness across the Flooding Pampas of Argentina, and tested for exotic richness correlates with major environmental gradients, species pool size, and native richness, among and within different grassland habitat types.

2 Native and exotic richness were positively correlated across grassland types, increasing from lowland meadows and halophyte steppes, through humid to mesophyte prairies in more elevated topographic positions. Species pool size was positively correlated with local richness of native and exotic plants, being larger for mesophyte and humid prairies. Localities in the more stressful meadow and halophyte steppe habitats contained smaller fractions of their landscape species pools.

3 Native and exotic species numbers decreased along a gradient of increasing soil salinity and decreasing soil depth, and displayed a unimodal relationship with soil organic carbon. When covarying habitat factors were held constant, exotic and native richness residuals were still positively correlated across sites. Within grassland habitat types, exotic and native species richness were positively associated in meadows and halophyte steppes but showed no consistent relationship in the least stressful, prairie habitat types.

4 Functional group composition differed widely between native and exotic species pools. Patterns suggesting biotic resistance to invasion emerged only within humid prairies, where exotic richness decreased with increasing richness of native warm-season grasses. This negative relationship was observed for other descriptors of invasion such as richness and cover of annual cool-season forbs, the commonest group of exotics.

5 Our results support the view that ecological factors correlated with differences in invasion success change with the range of environmental heterogeneity encompassed by the analysis. Within narrow habitat ranges, invasion resistance may be associated with either physical stress or resident native diversity. Biotic resistance through native richness, however, appeared to be effective only at intermediate locations along a stress/fertility gradient.

6 We show that certain functional groups, not just total native richness, may be critical to community resistance to invasion. Identifying such native species groups is important for directing management and conservation efforts.

Key-words: abiotic stress, diversity, environmental heterogeneity, functional groups, grasslands, invasibility, niche overlap, recruitment limitation, spatial scales, species pool size

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Introduction

Exotic plant species have become conspicuous elements of ecosystems around the world (Mack *et al.* 2000). However, ecologists have struggled to pinpoint both the roles of biotic and abiotic drivers of invasion (Lonsdale 1999; Davis *et al.* 2000; Shea & Chesson 2002), and the contribution of exotic species to diversity patterns at various scales (Sax & Gaines 2003). Species richness has received most attention as a potential factor controlling community invasibility, although evidence in favour of Elton's (1958) diversity–invasion resistance hypothesis has been controversial (Levine & D'Antonio 1999; Wardle 2001). Studies emphasizing local processes of biotic resistance to invasion (see Levine *et al.* 2004) tend to neglect the role of large-scale factors, notably species pool sizes and physical stress/disturbance gradients, in driving patterns of exotic plant richness (Lonsdale 1999; Von Holle 2005).

A comprehensive understanding of exotic invasions may require a pluralistic approach to accommodate patterns observed at different scales. Recently, Shea & Chesson (2002) proposed a model that attempts to reconcile conflicting evidence on the relationship between invasion magnitude and native species diversity. Their model predicts an overall positive correlation between exotic and native species richness over broad spatial scales, at which extrinsic factors are expected to drive diversity gradients across different habitats (Levine & D'Antonio 1999). This pattern has been supported by observational studies (Lonsdale 1999; Stohlgren *et al.* 1999, 2002; Pysek *et al.* 2002; Brown & Peet 2003; Gilbert & Lechowicz 2005), reflecting the likely influence of dispersal processes, disturbance regimes and abiotic stress (or productivity) on exotic and native richness alike (Huston 1999). In addition, Shea & Chesson's (2002) model posits that a negative correlation between exotic and native richness may be expected over narrow ranges of environmental variation. At small scales, extrinsic factors should not change systematically and biotic resistance mechanisms such as competition and recruitment limitation would control the extent of invasion (Tilman 1997; Levine 2000; Naeem *et al.* 2000). In this light, species-rich communities are regarded as being more 'saturated' than species-poor ones (Moore *et al.* 2001; Stachowicz & Tilman 2005), thus offering reduced niche opportunities for the establishment of exotic species (Shea & Chesson 2002).

Empirical support for a negative effect of native plant diversity on invasion success has been elusive. Small-scale experiments often indicate that resident species richness may limit invasion (e.g. Levine 2000; Naeem *et al.* 2000; Prieur-Richard *et al.* 2000; Hector *et al.* 2001; Kennedy *et al.* 2002; Fargione *et al.* 2003; Zavaleta & Hulvey 2004). However, while some of these studies tested for diversity effects on native rather than exotic invaders, others showed that in stressful habitats native richness did not affect, and sometimes even facilitated, non-native invasions (Dethier & Hacker 2005; Von

Holle 2005). On the other hand, relatively few studies have examined the scale dependence of exotic vs. native richness relations using observational data of sufficient extent and biological detail. Those testing for scale effects found mixed results when analyses were constrained to small plots or narrow habitat ranges (Stohlgren *et al.* 1999, 2002; Brown & Peet 2003; Cully *et al.* 2003; Davies *et al.* 2005; Gilbert & Lechowicz 2005). Such discrepancies might be due, in part, to the plant variables used as proxies of biotic resistance and invasion success.

Specifically, correlations between *overall* richness measures may not adequately reflect potential interference from native residents on exotic invaders. If the exotic species pool were dominated by a particular functional group, biotic resistance would be better measured by the presence of native species with greater chances of interacting with exotics in that group (Fargione *et al.* 2003; Von Holle & Simberloff 2004). Thus, other descriptors reflecting potential niche overlap based on species' functional identities (e.g. richness of specific functional groups) may be useful when seeking evidence that native diversity affects invasion success (Symstad 2000; Prieur-Richard *et al.* 2002; Ortega & Pearson 2005).

In this study we examine patterns of exotic and native species richness in the Flooding Pampa grasslands of Argentina. Increasing modification of native pampean grasslands over four centuries of human activity has been followed by massive invasions by alien species, which today account for *c.* 23% of all species in the regional herbaceous flora and have colonized all extant community types (Chaneton *et al.* 2002). Here, we evaluate the role of various drivers of community diversity and look for observational evidence consistent with the hypothesis that native diversity reduces invasion success (Levine & D'Antonio 1999; Shea & Chesson 2002). Although correlational analyses cannot establish causal mechanisms, they are indispensable for assessing multiscale patterns of invasion.

We use data from vegetation surveys conducted at different latitudes within the study region (Perelman *et al.* 2001) to test for exotic richness correlates with landscape species pools, major habitat gradients and native richness over broad and narrow ranges of environmental heterogeneity. First, we analyse changes in local plant richness *across* different habitat types covering the entire range of Flooding Pampa grasslands. At this scale, invasion levels would be driven by species dispersal from landscape pools and dominant abiotic gradients (Brown & Peet 2003). Secondly, we focus on native and exotic richness *within* grassland habitat types. At this scale, biotic interference from native species would contribute to limit invasion success (Shea & Chesson 2002). To enhance the latter analysis, we assess potential niche overlaps (or complementarity) between exotic and native species by looking at the functional composition of their respective landscape pools in each grassland type. Lastly, we examine the relationship between exotic richness and specific functional groups of native species.

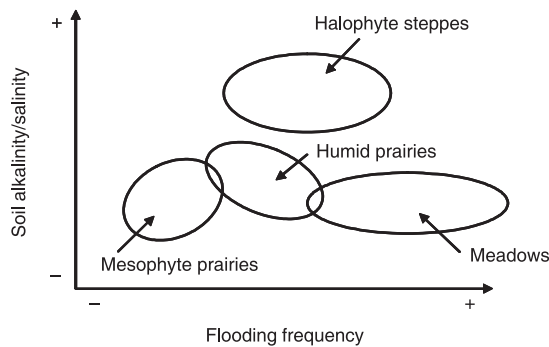


Fig. 1 Distribution of grassland types along major environmental gradients in the Flooding Pampa. Each ellipse comprises a subset of the 749 samples used in the present study, as shown by ordination analysis in Perelman *et al.* (2001).

Methods

STUDY SYSTEM

The Flooding Pampas comprise 90 000 km² of grassland-dominated landscapes, extending between 35° and 38° S in eastern Argentina (Soriano 1992; Perelman *et al.* 2001). The climate is temperate subhumid; mean annual precipitation varies between 1000 mm in the north and 850 mm in the southernmost plains. Mean annual temperatures range from 15.9 °C (north) to 13.8 °C (south). Soils are Mollisols and Alfisols, varying from slightly acidic (pH = 6.2–6.8) to alkaline (pH = 8.1–8.7) in the top horizon. The topographic relief is extremely flat, except for a few elevated zones with arable soils. Soil water drainage is impeded by the lack of slope and reduced infiltration, causing periodic floods of varied magnitude throughout the year (Soriano 1992). Less than 20% of the region has been cultivated; the natural grassland vegetation has been used for cattle grazing since Spanish settlers arrived in the mid-1600s (Vervoort 1967; León *et al.* 1984).

Phytosociological surveys conducted at different latitudes (Vervoort 1967; León *et al.* 1979; Batista *et al.* 1988; Burkart *et al.* 1990, 1998) indicated that species composition changes along environmental gradients, reflecting differences in landscape topography and soil salinity. Four major grassland habitat types have been described (Perelman *et al.* 2001; Fig. 1): (i) *mesophyte prairies*, which dominate on deep, well-drained soils located at elevated landscape positions; (ii) *humid prairies*, covering extensive flatlands at intermediate elevations; (iii) *meadows*, occurring on acidic soils in flood-prone lowland areas; and (iv) *halophyte steppes*, which dominate frequently flooded areas with saline/alkaline soils. As habitat heterogeneity is relatively fine grained, stands of all four grassland types co-occur, forming intricate landscape mosaics throughout the region (Perelman *et al.* 2001). Grasslands are grazed year round by cattle at moderate stocking rates (*c.* 0.5 cow ha⁻¹). Despite existing variation in primary production, continuous grazing regimes tend to homogenize the grazing pressure among grassland habitat types.

VEGETATION AND SOIL DATA

The present analysis was based on two data sets of different size and spatial extent. The first data set comprised a region-wide survey including 749 grassland *relevés* from four phytosociological inventories, each carried out at a different latitudinal belt within the study region. A full description of the sampling protocol is given in Perelman *et al.* (2001); only essential details are summarized here. Each of the four vegetation surveys encompassed an area of *c.* 500 km²; distance between surveyed latitudinal belts was > 100 km (Perelman *et al.* 2001). Vegetation sampling excluded sites with signs of recent agricultural use (< 10 years since last crop).

In each site we noted all vascular plant species present in a 0.25-ha stand of grassland, with a search effort of 1 h (two to three people). The percentage aerial cover of individual species was visually estimated within one 25-m² plot located at the centre of each stand, using a modified Braun-Blanquet abundance scale (Mueller-Dombois & Elleberg 1974). Sampling was always conducted in early summer (December to January), when both cool- and warm-season species were present and readily identifiable through their flowering structures. Perelman *et al.* (2001) employed these data to synthesize landscape-scale patterns of vegetation heterogeneity for the whole Flooding Pampas (Fig. 1). For the present work, we used information on the total number (richness) of native and exotic species in each site (*relevé*) to investigate the correlates of invasion magnitude across and within grassland habitat types. Nomenclature and species origin (native or exotic) followed Zuloaga *et al.* (1994) and Zuloaga & Morrone (1996, 1999). Species were regarded as exotic if they were not original from southern South America. Most exotics were of Eurasian origin, particularly from the Mediterranean zone.

The second data set comprised another 60 grassland sites surveyed within a 1000-ha study area located at the centre of the Laprida Basin in the southern Flooding Pampa (Batista *et al.* 1988). These sites were selected to encompass a wide range of topo-edaphic conditions corresponding to different grassland types (Batista 1991). In each site, during early summer, paired vegetation and soil samples were obtained from one 200-m² plot marked within a relatively homogeneous grassland stand. The vegetation was sampled to determine individual species frequencies and overall plant richness using 25 0.1-m² quadrats regularly distributed within each plot. A hole was dug at the centre of each plot to measure depth of the topsoil layer (A1 horizon), and to extract a sample for determination of soil salinity (electrical conductivity, dS/cm) and percentage organic carbon (Walkley-Black method). Topsoil depth was used as a surrogate for relative topographic elevation and flooding frequency, flood-prone lowlands having the shallower soils (Batista & León 1992). These plant and soil data were used here to examine patterns in native and exotic

species richness along the dominant habitat gradients in the system.

DATA ANALYSIS

The relationship between the richness of native and exotic species per site was tested through simple regression analysis. Regressions were performed for each full data set ($n = 749$ and 60 sites) and within each of the four grassland habitat types ($n = 173$ –202 and 12–21 sites, for the large and small data sets, respectively). The mean number of exotic and native species per site was compared among grassland types using Welch's one-way ANOVA, which is robust to departures from the assumption of equal within-group variances (Weerahandi 1995). Differences in mean proportion of exotic species were tested through one-way ANOVA on arcsin square-root transformed data. When ANOVA yielded significant results, the Bonferroni method was used to evaluate *post hoc* differences between grassland types.

To explore relationships between landscape processes on local species richness (Zobel 1997; Huston 1999), exotic and native species pool sizes were estimated separately for each grassland habitat type within each of the four regional inventories. The first-order jackknife estimator (Palmer 1990) was used to compute the total number of exotic and native species in each subset of grassland sites. This procedure assumed that, for a given inventory, the number of plant species observed in a particular habitat type was smaller than its actual total plant richness. The jackknife estimator was computed as $J = S + r_1(n-1)/n$, where S equals the observed number of species, r_1 is the number of species occurring in one site, and n equals the total number of sites. Step-wise multiple regression (backwards) was used to examine changes in native and exotic richness along major environmental gradients using the small data set ($n = 60$) from the Laprida basin. All three measured habitat variables (topsoil depth, salinity and organic carbon) were included in the initial regression models but only those having a significant fit ($P = 0.05$) were retained. The correlation structure of habitat variables was examined to determine whether they reflected orthogonal habitat axes or if they conformed to a composite environmental gradient. A simple linear regression was then fitted through the residuals corresponding to the best 'habitat models' obtained for exotic and native richness, respectively. This analysis evaluated the relationship between exotic and native richness after adjusting for the variance accounted for by habitat differences among grassland types.

In theory, resident communities containing many species of a given functional group should be less prone to invasion by exotics from that same guild, as native and exotics would then be more likely to have overlapping resource-use patterns (Fargione *et al.* 2003; Von Holle & Simberloff 2004). To examine potential

functional overlaps between the exotic and native floras, all species recorded in each grassland type were grouped according to their life history (annual vs. perennial), growth form (forbs vs. grasses) and phenology (cool season vs. warm season). Forbs comprised all dicotyledonous herbs, including legumes, which represented only 6% of the whole flora and generally had very low cover (< 1%). Grasses comprised species in the *Poaceae*, as well as sedges, rushes and other monocot herbs, which together accounted for 5% of all species (18% of 'grasses'). These broad groupings have been used previously to assess exotic invasions and grassland responses to major disturbances in this system (Sala *et al.* 1986; Chaneton *et al.* 1988; Rusch & Oosterheld 1997) and elsewhere (Mack & Thompson 1982; Mack 1989; Ortega & Pearson 2005). Species phenologies were considered as a means of distinguishing between broad patterns of resource use over the growing season (Sala *et al.* 1981; Soriano 1992). The number of annual and perennial species was compiled for each of the following functional groups: cool-season forbs (CSF), cool-season grasses (CSG), warm-season forbs (WSF), and warm-season grasses (WSG). The percentage representation of each functional group was computed separately for the native and exotic species pools (observed richness) in each grassland type.

To search for possible evidence of biotic resistance while accounting for the functional composition of exotic and native species pools, we tested the relationship between exotic richness and that of different native functional groups. Simple linear regressions were performed within grassland types using Bonferroni adjusted P -values. As these analyses revealed that exotic richness was negatively associated with native grass richness only across humid prairie sites (see Results), we examined other descriptors of invasion in this grassland habitat. Associations with native richness were tested for (i) the richness and total cover of exotic annual CSF, the functional group best represented in the exotic flora and which is also known to increase in heavily grazed sites (León *et al.* 1984; Sala *et al.* 1986); and (ii) the cover of *Lolium multiflorum*, a widely naturalized, exotic annual CS grass occurring in all four grassland types. Dependent variables were transformed as required to enhance linearity and reduce variance heterogeneity in regression analyses.

Results

REGIONAL PATTERNS OF INVASION

The numbers of exotic and native species were positively correlated across the whole set of sampled grassland sites ($r^2 = 0.24$, $P < 0.0001$, $n = 749$, Fig. 2). The same pattern was found for the smaller data set from the Laprida Basin in the southern Flooding Pampa ($r^2 = 0.81$, $P < 0.0001$, $n = 60$). Mean species richness of native and exotic plants varied significantly among grassland habitat types (Table 1). Both native and

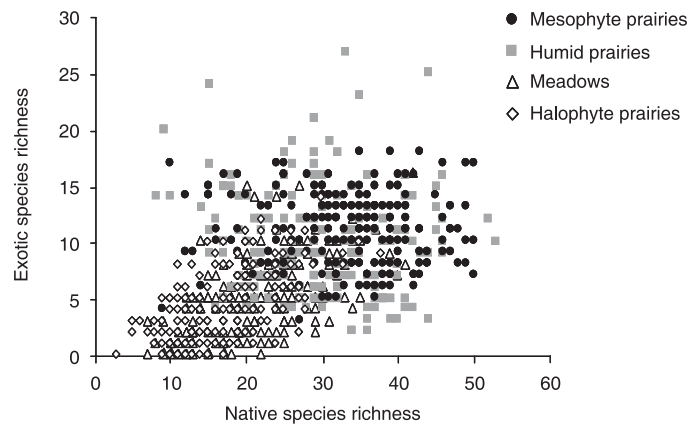


Fig. 2 Region-wide relationship between exotic and native plant species richness in the Flooding Pampa grasslands. Symbols denote different grassland habitat types. Linear regression: exotics = 0.23 natives + 1.89 ($n = 749$).

Table 1 Native and exotic richness (number of species per site) in the four grassland habitat types. Data show means \pm 1 SD ($n =$ number of sites). Different superscript letters indicate significant differences within columns (Bonferroni test, $P = 0.05$)

| Grassland type | n | Natives | Exotics | Exotics (%) |
|--------------------|-----|------------------------------|------------------------------|-------------------------------|
| Mesophyte prairies | 202 | 33.7 \pm 8.38 ^a | 11.1 \pm 3.26 ^a | 25.4 \pm 9.8 ^a |
| Humid prairies | 173 | 29.1 \pm 8.94 ^b | 9.9 \pm 4.73 ^b | 25.9 \pm 12.2 ^a |
| Meadows | 180 | 22.5 \pm 7.51 ^c | 5.1 \pm 3.62 ^c | 16.7 \pm 10.06 ^b |
| Halophyte steppes | 194 | 16.3 \pm 5.43 ^d | 4.4 \pm 3.34 ^c | 18.9 \pm 10.72 ^b |

exotic richness decreased from mesophyte through humid prairies to meadows or halophyte steppes, following the two main gradients represented in Fig. 1. Mean exotic richness did not differ between the latter two grassland types (Table 1). In addition, the mean proportion of exotic species per site was significantly higher in mesophyte and humid prairies (Table 1). Sampled sites free of exotic species represented 10% of the halophyte steppes (19 sites), 11% of the meadows (18 sites), and none of the mesophyte and humid prairies.

Across the four grassland inventories, the mean number of exotic species present in a local community increased with the size of the landscape pool of exotic species that invaded the corresponding habitat type ($r^2 = 0.74$, $P < 0.001$, $n = 16$, Fig. 3a). Thus meadows and halophyte steppes not only had lower exotic richness per site (Table 1), but encompassed smaller pools of exotic species than mesophyte and humid prairies (Fig. 3a). In addition, meadow and halophyte steppe sites contained a smaller proportion of their corresponding species pools (15.6 \pm 0.01%, $n = 8$) than prairie habitat sites (29.0 \pm 0.01%, $n = 8$). A similar overall positive relationship between regional and local richness held for native plant species ($r^2 = 0.81$, $P < 0.001$, $n = 16$, Fig. 3b).

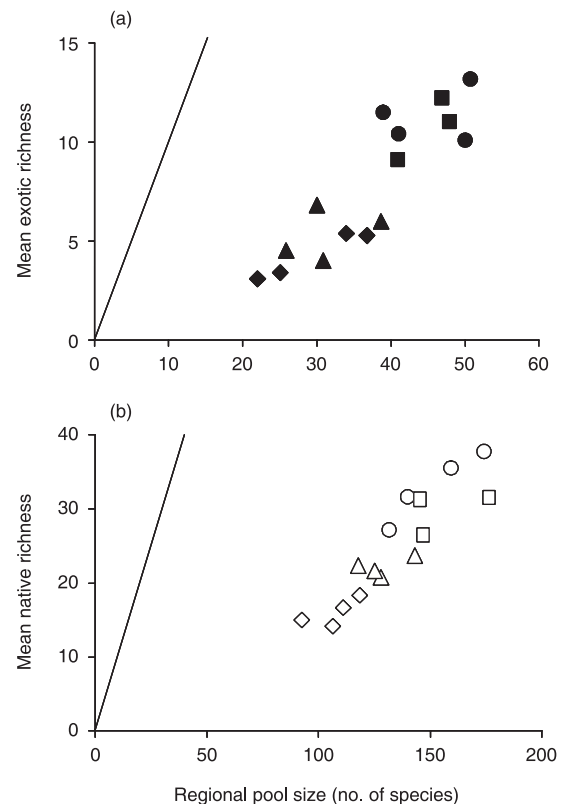


Fig. 3 Mean richness of exotic (a) and native (b) plant species per site in relation to their regional species pool sizes (first-order jackknife estimator) for mesophyte prairies (circles), humid prairies (squares), meadows (triangles) and halophyte steppes (diamonds), at four different latitudes across the Flooding Pampas. The diagonal shows the 1 : 1 equality line.

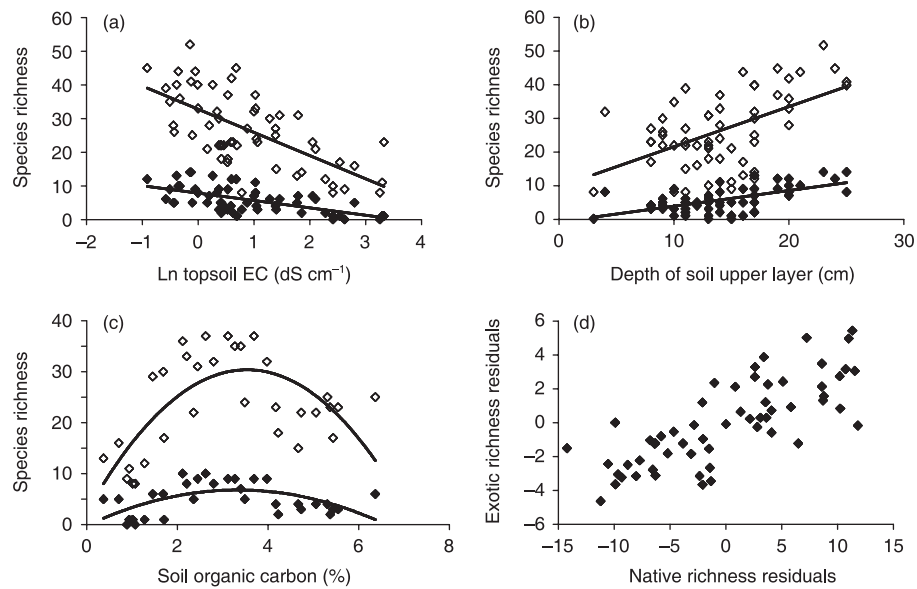


Fig. 4 Relationship of native (empty symbols) and exotic (solid symbols) species richness with (a) topsoil electrical conductivity (\log_e -transformed), (b) depth of topsoil layer, and (c) topsoil organic carbon content. All regressions are significant at $P < 0.001$. (d) Residuals of exotic and native species richness from best multiple regressions on habitat variables (see Table 2).

Table 2 Multiple regression models for the relationship of (a) native and (b) exotic species richness with major habitat factors across the four grassland types (southern Flooding Pampa, $n = 60$). (c) Simple regression between residuals from the above models. Standard errors are shown in brackets. A1 depth = depth of topsoil horizon (cm); EC = electrical conductivity of topsoil horizon (dS cm^{-1})

| Dependent variable | Model term | b_x | t | P | R^2 |
|---------------------|---------------------|-------------------|----------|---------|-------|
| Native richness | Intercept | 23.84 (3.58) | 6.65 | < 0.001 | 0.49 |
| | A1 depth | 0.63 (0.22) | 2.85 | 0.006 | |
| | ln (soil EC) | -6.15 (1.03) | -5.94 | < 0.001 | |
| Exotic richness | Intercept | 4.03 (1.34) | 3.02 | 0.004 | 0.42 |
| | A1 depth | 0.26 (0.08) | 3.17 | 0.002 | |
| | ln (soil EC) | -1.79 (0.39) | -4.65 | < 0.001 | |
| Exotics (residuals) | Intercept | 10^{-16} (0.22) | < 0.0001 | c.1 | 0.68 |
| | Natives (residuals) | 0.309 (0.03) | 11.26 | < 0.001 | |

increased with depth of topsoil layer (Fig. 4a,b). In addition, species numbers showed a unimodal relationship with soil organic carbon (Fig. 4c), a variable indicative of soil fertility level (Chaneton *et al.* 2002). Native and exotic richness were both highest in sites with intermediate soil carbon levels and declined towards both ends of the gradient (low-fertility halophyte steppes at one end, and the most fertile but frequently flooded meadows at the other). However, multiple regression showed that the best 'habitat models' for plant richness included only topsoil depth and salinity as explanatory variables (Table 2). Soil organic carbon did not account for a significant amount of variance (P -values > 0.30, for linear and quadratic terms) in either native or exotic richness after controlling for effects of soil depth and salinity. Measured habitat properties did not fully explain the positive relationship between exotic and native richness, as residuals from the corresponding habitat models still showed a strongly significant positive correlation (Table 2, Fig. 4d).

INVASION PATTERNS WITHIN HABITAT TYPES

The overall positive association between exotic and native richness observed across the whole study region (Fig. 2) did not always hold when the analysis was constrained to each grassland habitat type. The relationship between exotic and native richness was still significantly positive for meadows and halophyte steppes, whereas no relationship was found at this scale within mesophyte and humid prairie habitats (Fig. 5). Similar results were obtained for exotic vs. native richness relations within the small data set from the Laprida basin (meadows, $r^2 = 0.76$, $P < 0.0001$, $n = 21$; halophyte steppes, $r^2 = 0.57$, $P = 0.005$, $n = 12$; mesophyte prairies, $r^2 = 0.16$, $P = 0.15$, $n = 14$; humid prairies, $r^2 = 0.37$, $P = 0.09$, $n = 13$).

NATIVE AND EXOTIC FUNCTIONAL GROUPS

In all four grassland types, native and exotic species belonged to broadly contrasting functional groups

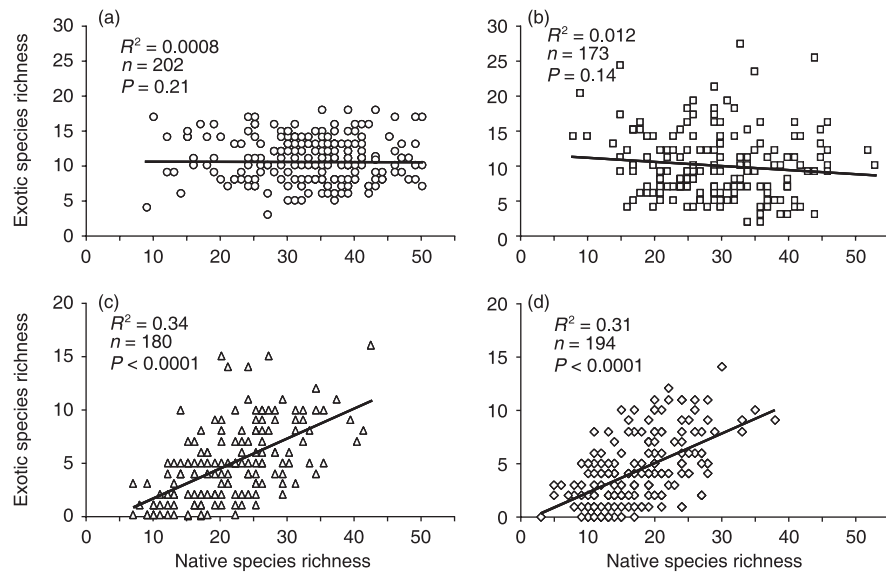


Fig. 5 Relationship between exotic and native plant richness within each grassland habitat type. (a) mesophyte prairies, (b) humid prairies, (c) meadows, and (d) halophyte steppes. Data show numbers of exotic and native species per site.

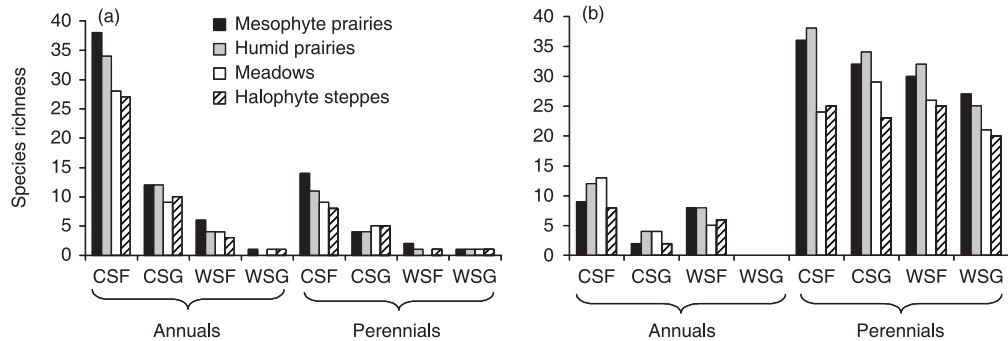


Fig. 6 Functional group composition of exotic (a) and native (b) floras in the four grassland types. Each bar represents the total number of species per functional group. CSF, cool-season forbs; CSG, cool-season grasses; WSF, warm-season forbs; WSG, warm-season grasses.

(Fig. 6). Among the natives, 85% were perennial species, which were evenly distributed among cool- and warm-season grasses and forbs (Fig. 6b). In contrast, 74% of all exotic species were annuals (Fig. 6a), especially cool-season forbs (50%) and grasses (17%), two functional groups poorly represented (8% and 2%, respectively) in the native flora. The third most important group among the exotics was perennial cool-season forbs (16%), which accounted for 23% of all native species.

Functional group distributions were quite similar among grassland types (Fig. 6). Differences in native species richness across grassland types were explained in a similar proportion by the richness of different functional groups. In contrast, differences in exotic richness among grassland types were largely due to differences in forb species numbers. The observed total richness of exotic forbs was 64 in mesophyte prairies, 53 in humid prairies, 43 in meadows, and 40 in halophyte steppes, while exotic grass richness ranged from 16–18 species.

FUNCTIONAL GROUPS AND INVASION PATTERNS

We found remarkable changes in the sign and strength of correlations observed in each habitat type between exotic richness and the species richness of different groups of native perennial plants (Table 3). Annual species contributed little to native richness (Fig. 6b) and were unrelated to the magnitude of invasion (data not shown). Exotic richness was not significantly correlated with the richness of any native plant group across mesophyte prairie sites. In meadows and halophyte steppes exotic richness showed a weak, yet significant, positive correlation with the richness of some native plant groups. Conversely, local exotic richness significantly decreased with the number of native warm-season grasses across humid prairie sites (Table 3). Other descriptors of invasion magnitude produced similar patterns consistent with the potential for biotic resistance in humid prairies. The richness and cover of exotic annual cool-season forbs (Fig. 7a,b) and the cover of

Table 3 Regression analyses for the relationship between exotic species richness and the richness of various functional groups of native perennial plants within each grassland type. WSG, warm-season grasses; CSG, cool-season grasses; WSF, warm-season forbs; CSF, cool-season forbs. NS, non-significant regression slope after Bonferroni's correction ($P = 0.05$). Number of sites per grassland type as in Table 1

| Grassland type | Independent variable | b_x | R^2 | F | P |
|--------------------|----------------------|-------|-------|--------|---------|
| Mesophyte prairies | CSF | -0.16 | 0.02 | 4.04 | NS |
| | CSG | -0.07 | 0.006 | 1.22 | NS |
| | WSF | -0.07 | 0.002 | 0.38 | NS |
| | WSG | -0.07 | 0.006 | 1.21 | NS |
| Humid prairies | CSF | -0.06 | 0.001 | 0.16 | NS |
| | CSG | -0.06 | 0.002 | 0.29 | NS |
| | WSF | -0.62 | 0.07 | 12.60 | < 0.001 |
| | WSG | -1.33 | 0.41 | 117.80 | < 0.001 |
| Meadows | CSF | 0.82 | 0.34 | 91.96 | < 0.001 |
| | CSG | 0.24 | 0.02 | 4.13 | NS |
| | WSF | 0.16 | 0.005 | 0.86 | NS |
| | WSG | 0.40 | 0.12 | 24.53 | < 0.001 |
| Halophyte steppes | CSF | 0.59 | 0.09 | 20.39 | < 0.001 |
| | CSG | 0.75 | 0.20 | 47.79 | < 0.001 |
| | WSF | 0.64 | 0.16 | 36.30 | < 0.001 |
| | WSG | 0.30 | 0.04 | 7.89 | 0.02 |

Lolium multiflorum (Fig. 7c) decreased as the richness of native warm-season grasses increased in the local community. Other functional groups of exotics (Fig. 6a) showed no consistent relationship with native grass richness across humid prairie sites (r^2 values < 0.001).

Discussion

Our analysis shows that patterns of exotic vs. native richness may depend both on the range of habitat heterogeneity and the identity of functional groups involved. Native and exotic richness were positively correlated across sites when analyses encompassed the whole range of landscape heterogeneity in the Flooding Pampa grasslands. At this broad scale, covarying abiotic factors and species pool sizes seemed to constrain local community richness and invasion success (Huston 1999; Shea & Chesson 2002). When we searched for exotic–native richness relations *within* different grassland habitats, however, positive relationships only held for the more stressful habitats. Moreover, for one grassland type cross-site differences in exotic richness were negatively associated with the richness of a particular functional group of native species, instead of total richness. These findings indicate that not only the spatial scale of inquiry (Stohlgren *et al.* 1999; Brown & Peet 2003; Davies *et al.* 2005) but also the level of biological detail (Ortega & Pearson 2005) matters in looking for evidence consistent with diversity–invasion resistance hypotheses (Levine & D'Antonio 1999; Shea & Chesson 2002).

The overall association between richness of exotic and native species was found to be positive over a broad range of grassland habitats. This result parallels those reported for other systems (Lonsdale 1999; Stohlgren *et al.* 1999, 2002; Levine 2000; Pysek *et al.* 2002; Brown & Peet 2003; Gilbert & Lechowicz 2005). Such patterns are consistent with Shea & Chesson's (2002) model,

which suggests that composite abiotic gradients may drive invasion patterns at broad scales of environmental heterogeneity. We found that native and exotic richness similarly changed along physical stress gradients associated with topsoil depth and salinity (Table 1, Fig. 4). It appears that site conditions favouring high native diversity also increase the chances for successful establishment of exotic invaders (Lonsdale 1999; Stohlgren *et al.* 1999; Shea & Chesson 2002). Conversely, stressful habitats would limit both native and exotic richness. This could have resulted in flood-prone meadows and halophyte steppes being less invaded than mesophyte and humid prairies. Yet, because native and exotic richness were still positively related after adjusting for the influence of habitat variables (Fig. 4d), other large-scale factors may have also driven the pattern of invasion among grassland types.

Indeed, exotic richness was higher in those grassland habitats having a larger landscape pool of exotic species, a trend also found for native richness (see Fig. 3). These patterns may be expected under a regional species-pool size limitation of local richness (Zobel 1997; Partel & Zobel 1999). Interestingly, grasslands typical of more stressful habitats contained, on average, a smaller fraction of their corresponding exotic pools than those located in the least stressful, prairie habitats. This is consistent with the proposal that species dispersal from landscape pools would be a more important determinant of invasion success at intermediate locations along major stress/fertility gradients (Huston 1999). Following this rationale, limited dispersal and/or ecological resistance (biotic or abiotic) might place additional restrictions on invasion of meadows and halophyte steppes by exotics pre-adapted to conditions in those habitats. The fine-grained mosaic of landscape heterogeneity in the study region (Batista *et al.* 1988; Perelman *et al.* 2001), coupled with cattle movement across

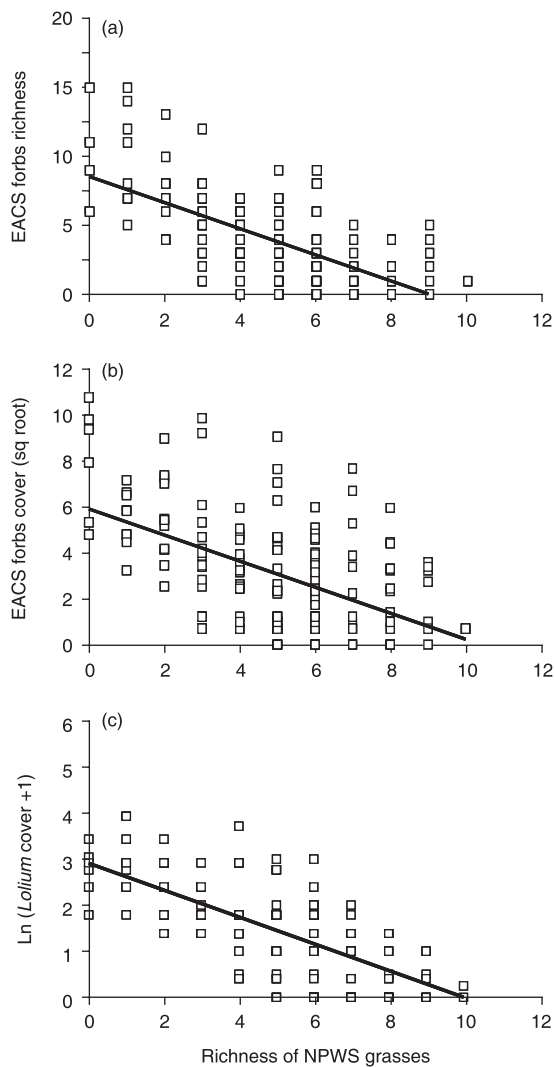


Fig. 7 Change in (a) species richness and (b) cover of exotic annual cool-season forbs (EACS), and (c) cover of the exotic grass *Lolium multiflorum*, in relation to richness of native perennial warm-season (NPWS) grasses across humid prairies. Regression lines: (a) $y = -0.95x + 8.51$, $r^2 = 0.42$; (b) $y = -0.56x + 6.04$, $r^2 = 0.32$; (c) $y = -0.27x + 2.89$, $r^2 = 0.48$ (all $P < 0.0001$, $n = 173$).

habitats, would argue against a differential role for dispersal limitation in different grassland types. Instead, increased invasion resistance is likely to occur in meadows and halophyte steppes, which characterize physically stressful environments (Perelman *et al.* 2001). In these grassland types, abiotic constraints imposed by frequent flooding and elevated soil salinity may limit community invasibility (Chaneton *et al.* 1988; Greiner La Peyre *et al.* 2001; Dethier & Hacker 2005; Von Holle 2005).

Several studies have reported negative exotic–native richness correlations after reducing the spatial scale of analysis (e.g. Stohlgren *et al.* 1999; Brown & Peet 2003; Davies *et al.* 2005), a result consistent with models discussing the scale-dependency of diversity–invasibility relations (Moore *et al.* 2001; Shea & Chesson 2002; Byers & Noonburg 2003). Here, we did not find a negative association between the total numbers of native and

exotic species per site within any of the four grassland types (Fig. 5). By focusing on each grassland habitat, and without changing the unit sample size (cf. Brown & Peet 2003), we reduced the effective range of environmental heterogeneity involved in analyses of invasion patterns across sites. However, contrary to predictions from Shea & Chesson (2002), exotic and native richness were either positively associated or showed no consistent relationship at the within-grassland habitat scale. Furthermore, the strong positive correlations observed in meadows and halophyte steppes (Fig. 5c,d) were robust to changes of biological detail incorporated in the analyses (Table 3). This finding fits the notion that in stressful habitats biotic resistance mechanisms (Tilman 1997; Levine *et al.* 2004) might become relatively less important in limiting exotic species establishment (Huston 1999; Dethier & Hacker 2005; Von Holle 2005). Indeed, facilitative interactions between native and exotic species should not be discarded as a factor potentially influencing diversity patterns in stressful sites (Bruno *et al.* 2005; Von Holle 2005).

We observed no significant association between native richness and invasion success across mesophyte prairies, the richest grassland communities in the region (Fig. 5a, Table 3). This result could reflect the frequent and relatively intense anthropogenic disturbances affecting these grasslands (Davis *et al.* 2000). Mesophyte prairies occupy elevated topographic positions with deep soils and are rarely affected by flooding or salinity (Batista & León 1992). As a result, they are subjected to periodic cultivation and are always grazed by livestock (León *et al.* 1984; Batista *et al.* 1988; Burkart *et al.* 1998). These perturbations are likely to relax competition from native perennial grasses, thus maintaining a high richness of exotic and native ruderal species commonly found in croplands and early successional old fields (Oesterheld & León 1987; Omacini *et al.* 1995). Patterns of exotic richness in this grassland habitat would be more likely to reflect differences in propagule pressure, and the site history of anthropogenic disturbance.

It has been argued that a more accurate interpretation of community invasibility may be gained by considering species' functional attributes rather than total species numbers (Symstad 2000; Prieur-Richard *et al.* 2002; Von Holle & Simberloff 2004; Zavaleta & Hulvey 2004). Nonetheless, studies looking for correlative evidence of invasion resistance usually neglect the functional aspects of diversity (Ortega & Pearson 2005). Our results showed that native and exotic species largely belong to different functional groups (Fig. 6), with exotics being overwhelmingly represented by annual cool-season forbs. Cattle grazing has been found to promote short-lived and low-stature exotic forbs and grasses (Sala *et al.* 1986; Rusch & Oesterheld 1997; Jacobo *et al.* 2006). These functional types are poorly represented in the native flora, which is primarily made up of perennial species. Similar invasion patterns by functional group were reported for other temperate grasslands under domestic grazing, suggesting that exotics exploited novel

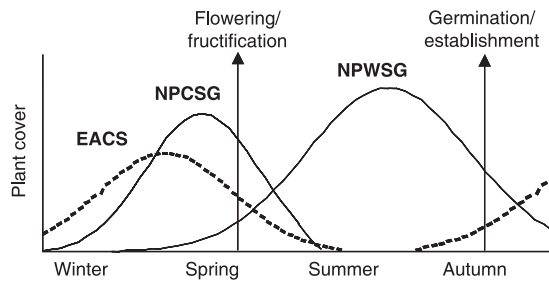


Fig. 8 Schematic representation of phenological patterns for major native and exotic plant functional groups. EACS, exotic annual cool-season species; NPCSG, native perennial cool-season grasses; NPWSG, native perennial warm-season grasses. The vertical lines highlight two critical periods for the regeneration of common exotic species, and how they overlap with native species growth patterns. We suggest that the negative response of exotic richness to native warm-season grasses found in humid prairies chiefly reflects interference of summer grasses with seedling recruitment of exotic annuals during autumn. Gradients in native warm-season grass abundance would result from cross-site differences in grazing pressure.

niche opportunities created by introduced herbivores (Mack & Thompson 1982; Parker *et al.* 2006). In contrast, the predominance of cool-season species among the exotics cannot be attributed to their rarity in the native flora (see Fig. 6). The phenological niche occupied by alien species may in part reflect the history of invasions (Mack 1989), as most exotic herbs in the Flooding Pampas originated from temperate Europe. However, as warm-season exotics do occur frequently in cropland habitats, their rarity in grasslands might result from either competition with a native flora rich in warm-season grasses or lack of adaptation to flooding or salinity.

When we focused on different native functional groups, a clear pattern emerged consistent with the hypothesis that native diversity may limit invasion success in some habitats but not others. In humid prairies, total exotics richness and annual cool-season forb richness both decreased with increasing richness of native perennial warm-season grasses (Table 3, Fig. 7). Invasion resistance associated with high resident richness depends on the mechanisms controlling local coexistence, e.g. niche complementarity and recruitment limitation (Tilman 1997; Moore *et al.* 2001). As the peak growing seasons of native warm-season grasses and exotic cool-season species do not overlap, one might, in principle, assume they have complementary resource-use patterns (Fig. 8). However, the persistence of annual exotic species in these grasslands depends strongly on seedling recruitment during late summer–autumn (Oosterheld & Sala 1990; Deregibus *et al.* 1994; Jacobo *et al.* 2000, 2006). We thus hypothesize that regeneration of exotics may be negatively affected by a well-developed canopy of summer grasses (Fig. 8). Across humid prairie sites, the total cover and local richness of native warm-season grasses were directly related ($r = 0.67$, $P < 0.0001$). Humid prairies with higher numbers of warm-season grasses would present harsher microsite conditions for

the seedlings of cool-season exotics like the widespread invasive *L. multiflorum* (Fig. 7). Native perennial grasses have been found to limit germination and survival of exotic annuals in other systems (Corbin & D'Antonio 2004). The proposed influence of warm-season grasses on community invasibility suggests that biotic resistance through native richness may critically depend on specific interactions between certain sets of native and exotic species (Fig. 8).

What 'extrinsic' factors could underpin the within-habitat pattern of native–exotic diversities found in humid prairies? Evidence suggests that grazing by domestic herbivores may indirectly drive native diversity–invasion resistance relations (Parker *et al.* 2006). A previous survey of humid prairies (León *et al.* 1984) showed that livestock grazing creates spatially explicit floristic gradients involving the replacement of native perennial grasses by low-growing annual species. Long-term exclosure studies have demonstrated that grazing drastically reduces the biomass of native grasses, while increasing the cover and richness of exotics through gap-colonization dynamics (Sala *et al.* 1986; Oosterheld & Sala 1990; Rusch & Oosterheld 1997; Chaneton *et al.* 2002; Jacobo *et al.* 2006). Conversely, cattle removal results in the recovery of native tall grasses and a rapid decline of exotic forbs, many of which go locally extinct. We thus contend that differences in grazing management history may generate natural gradients of native grass-species richness, and thus invasion magnitude.

In conclusion, our findings support previous claims that both physical and biotic factors operating at various scales influence community invasibility (Lonsdale 1999; Levine 2000; Naeem *et al.* 2000; Shea & Chesson 2002). In the Flooding Pampas, broad-scale patterns of exotic invasions were associated with habitat stress gradients, species pool sizes, and native species richness. The expected negative relationship between exotic and native richness could be detected only in one grassland habitat. Moreover, evidence suggests that the diversity of a particular group of native plants, not total richness, may provide invasion resistance. While this hypothesis remains open to experimental testing, identifying such key native functional groups may be crucial to inform management and conservation efforts.

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