Functional traits of alien plants across contrasting climatic and land-use regimes: do aliens join the locals or try harder than them?

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Summary

1. Two main views have been put forward to explain whether coexisting alien and resident plant species should show converging or diverging functional attributes. According to the 'try-harder' hypothesis, successful aliens should differ from resident species with traits that allow them to deal better with the local conditions than resident species. On the other hand, the 'join-the-locals' hypothesis stresses the importance of filtering by environmental factors and predicts strong functional trait similarities between alien and native species, especially among the dominants.

2. On the basis of a functional trait comparison between native and alien species of central-western Argentina across five contrasting ecosystems and four land-use regimes, we tested these hypotheses over a broad range of habitats. We built a data set with common measurement methods and biogeographical factors but strongly varying environmental conditions, ranging from mesic to extremely dry, and from nearly pristine to heavily disturbed.

3. When considering all species together, the main trend of variation in trait syndromes was between acquisitive (tender, large leaves, with high specific area) and conservative (tough, small leaves, with low specific area and low nutrient content). Although both native and alien species appeared to be well spread across the whole range of trait variation, woody alien species showed a significantly more acquisitive set of attributes (higher specific leaf area, larger and thinner leaves, lower wood density) than native species. No significant difference was detected between herbaceous alien and native species. These general trends were maintained under contrasting climatic and land-use conditions.

4. *Synthesis*. The patterns detected for herbaceous species were in line with the 'join-the-locals' hypothesis. In contrast, those found for woody species, with woody alien species showing more acquisitive attributes than native species in more resource-rich habitats, provide partial support for the 'try-harder' hypothesis. Overall, our findings reinforce the idea that a universal suit of attributes is unlikely to explain alien plant distribution. They also stress the need for caution when mixing major life-forms in comparative plant trait analysis.

Key-words: acquisitive strategy, biological invasions, central-western Argentina, conservative strategy, exotic species, functional attributes, herbaceous species traits, trait syndromes, woody species traits

Introduction

Invasions by alien plant species are an important component of human-caused global environmental change, often resulting in significant biodiversity, cultural and economic losses in the invaded ecosystems (Mack *et al*. 2000; Pimentel *et al*. 2000; Pimentel, Zuniga & Morrison 2005). Therefore, the identifica-

tion of potentially invasive alien species before they spread over the landscape has long been a major goal (Hulme 2003). However, it has so far proved elusive. While it is well known that the success of alien plants in new environments greatly depends on their functional attributes, to date we have failed to identify a set of attributes associated with invasiveness that applies to all vascular plants across the world (Richardson & Pyšek 2006). Major obstacles include (i) biogeographical differences among floras; (ii) environmental differences among

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invaded habitats; (iii) the lack of distinction between alien species typical of agricultural or urban habitats (agricultural weeds) and those that can establish in more pristine ecosystems (environmental weeds); and (iv) a lack of systematic, empirically based enquiries across contrasting habitat conditions.

The success of alien species is often associated with a high ability to capture and retain resources. Attributes associated with this ability are strongly habitat-dependent (Theoharides & Dukes 2007). Attributes related to rapid resource acquisition and growth (i.e. thin, soft and nutrient-rich leaves, high specific leaf area, short lifespan) tend to be associated with alien success in resource-rich environments (Leishman & Thomson 2005; Rejmánek, Richardson & Pyšek 2005; Burns 2006; Leishman *et al.* 2007). On the other hand, aliens possessing attributes associated with resource conservation and slow growth (i.e. long-lived, thick, tough leaves with high concentrations of defence compounds and low nutrient content) tend to succeed in resource-poor habitats (Grime 1973; Funk & Vitousek 2007). The same general principles tend to apply to resident species, however (Grime *et al.* 1997; Díaz *et al.* 2004; Wright *et al.* 2004). Therefore, a theoretically and practically relevant question is whether coexisting alien and resident species should show converging or diverging functional attributes. Two main views have been put forward in this respect. On the one hand, the 'try-harder' view, initially presented by Crawley, Harvey & Purvis (1996), maintains that successful aliens should be able to deal better with the local conditions than resident species. According to this view, aliens should show more conservative functional trait syndromes than resident species in low-resource environments and more acquisitive syndromes in resource-rich environments. This view has been supported by the work of e.g. Leishman *et al.* (2007) for resource-rich habitats, and that of Funk & Vitousek (2007) for resource-poor habitats (see also Grime 1973; Leishman & Thomson 2005; Rejmánek, Richardson & Pyšek 2005; Burns 2006; Pyšek & Richardson 2007). On the other hand, the 'join-the-locals' view stresses the importance of filtering by environmental factors (local climate, soil resources, disturbance regime) and therefore expects strong functional trait similarities between alien and native species, especially the dominant ones (Thompson, Hodgson & Rich 1995; Duncan & Williams 2002; Thompson & McCarthy 2008). To our knowledge, no empirical test of these ideas has been carried out beyond local habitats, encompassing different climatic and land-use conditions.

Here, we explore the general links between functional traits linked to resource use and alien species success (Díaz *et al.* 2004; Wright *et al.* 2004) in contrasting habitats. By building a new data set, we kept measurement methods and biogeographical factors constant, while strongly varying the environmental conditions, which ranged from mesic to extremely dry, and from nearly pristine to heavily disturbed.

Under the 'try-harder' hypothesis, we expected aliens to differ from native species by showing more extreme trait syndromes. Specifically, they should show more conservative attributes than resident species in drier and colder ecosystems (arid Monte and mountain grasslands) and in less-disturbed habitats (i.e. undisturbed and moderately grazed sites), but they should show more acquisitive attributes in milder climates (xerophytic and mesic Chaco woodlans and xerophytic Espinal woodlands) and highly disturbed habitats (i.e. roadsides and post-agricultural fields). Under the 'join-the-locals' hypothesis, alien and native species growing in the same habitat should not show significant trait differences. At the broad regional scale (i.e. considering all ecosystems and contrasting land uses together), we expected no significant difference between alien and native species under both hypotheses, although for different reasons. Under the 'try-harder' hypothesis, this should be the result of averaging the more extreme syndromes of aliens at resource-rich and resource-poor habitat extremes. Under the 'join-the-locals' hypothesis, this should be the result of strong similarities between alien and native species at each habitat.

Materials and methods

STUDY AREA

We studied five different ecosystems along a climatic gradient in central-western Argentina: Monte arid shrublands, xerophytic lowland Chaco woodlands, xerophytic Espinal woodlands, mesic mountain Chaco woodlands and temperate subhumid mountain grasslands (Table S1, Supporting Information). This gradient starts with a warm and dry shrubland (19.6 °C and 326 mm mean annual temperature and precipitation, respectively), continues across three woodlands with increasing precipitation (612, 682 and 847 mm, respectively) and ends at a cold and wet mountain grassland (8.1 °C and 951.5 mm). Dominant vegetation and main climatic, edaphic and biogegraphical characteristics of the five ecosystems are summarized in Table S1. Four types of land use were considered within each ecosystem: (i) undisturbed plots, (ii) plots with moderate grazing and selective logging, (iii) roadsides, and (iv) post-cultivation plots with approximately 1 year of abandonment. Undisturbed plots were located within protected areas whenever possible (Monte, mountain Chaco and mountain grassland). When this was unfeasible, satellite images and local information were used to identify sites with the lowest possible disturbance (lowland Chaco and Espinal). Due to human activities such as livestock grazing, logging and burning, the original vegetation of the woodland ecosystems has been almost completely transformed into a mosaic of grassland, shrubland and open woodland (Zak & Cabido 2002). In particular, our grazed and logged plots were restricted to moderately grazed and selectively logged areas, which are widespread in the region and should be considered as most representative of the remaining natural vegetation. Selective logging was present in the grazed plots in all ecosystems except the mountain grasslands. Grazing pressure (i.e. livestock units per hectare) was 0.05 LU ha^{-1} (Monte shrubland), 0.11 LU ha^{-1} (lowland Chaco), 0.2 LU ha^{-1} (Espinal woodland), 0.17 LU ha^{-1} (mountain Chaco) and 0.14 LU ha^{-1} (mountain grassland). Roadside vegetation was surveyed along roads with moderate use and all post-cultivation plots except those of the driest ecosystem (Monte) had no history of irrigation. The field sites were chosen on the basis of previous detailed vegetation studies (Cabido *et al.* 1991, 1993, 1994; Díaz & Cabido 1997; Díaz, Cabido & Casanoves 1998; Cabido & Zak 1999; Díaz *et al.* 1999; Martinez Carretero 1999) and regional maps obtained from the integration of remote-sensing and field vegetation surveys (Zak & Cabido 2002; Zak 2008). Six plots (replicates) were considered for each land use. Thus, a total of 120 plots were surveyed.

VEGETATION SURVEY

We recorded all vascular plant species growing in each plot, following the guidelines of Cabido *et al.* (1992) and Díaz *et al.* (1999), Díaz, Cabido & Casanoves (1998). The size of the plots was defined by the minimum area at which the species–area curve became stabilized (20 × 20 m in forests and shrublands; 5 × 5 m in grasslands; 10 × 10 m in post-cultivation sites), and bands at least 10 m long and 4 m wide on roadsides, following previous studies by the authors (Cabido *et al.* 1993, 1997, 1998, 2008; Díaz *et al.* 1999; Díaz, Acosta & Cabido 1994; Funes & Cabido 2008). Nomenclature and origin of species (native or alien) follow Zuloaga *et al.* (1994) and Zuloaga & Morrone (1996, 1999), with species counted as alien if they were not of South American origin. Only naturalized species, i.e. those sustaining populations without direct intervention of humans (Richardson *et al.* 2000; Pyšek, Richardson & Williamson 2004), were included in the database (see Appendix S1). Among these species, those categorized as cosmopolitan (i.e. wide global distribution) by Cabrera (1970) and Cabrera & Zardini (1978) were excluded.

FUNCTIONAL TRAIT CHARACTERIZATION OF SPECIES

We measured functional traits on a total of 116 vascular plant species belonging to 32 families (Appendix S1). We included all locally common (species with a mean relative cover higher than 1% in the local community) native and alien species, covering a wide range of growth forms, families and habitats. Our species selection was not clade-based, but rather community-based. This is the most appropriate sampling strategy considering that one of our major aims was to assess consistency of patterns across species assemblage, land uses and ecosystems and that our questions were much more in the field of present-day community and ecosystem ecology, than in that of evolutionary ecology (Ackerly 2000; Westoby *et al.* 2002).

We considered 10 vegetative traits (Table 1), all of them with direct functional implication for resource capture, retention and release for adult plants under different environmental conditions (Weiher *et al.*

Table 1. Traits measured on 116 vascular plant species from five ecosystems and four types of land use in central-western Argentina. See Hendry & Grime (1993) and Cornelissen *et al.* (2003) for their ecological interpretation and measurement protocols

Trait	Type of variable and units
Leaf area	Continuous (mm^2)
Specific leaf area	Continuous (mm^2 leaf area mg^{-1} leaf mass)
Leaf thickness	Continuous (mm)
Leaf toughness	Continuous (= leaf tensile strength; Newton mm^{-1} leaf width)
Lifespan	Binary: 0 = annual or biennial; 1 = perennial
Wood density	Continuous (g mL^{-1}) measured on woody species; tertiary branch
Canopy height	Continuous (cm)
Clonal spread	Binary: 0 = no evident clonal expansion; 1 = clonal expansion
Leaf nitrogen content	Continuous (g N × 100 g dry weight leaf sample)*
Leaf phosphorous content	Continuous (g P × 100 g dry weight leaf sample)*

*Measured only on 55 species, and thus not included in the PCA

1999; Westoby *et al.* 2002; Cornelissen *et al.* 2003; Díaz *et al.* 2004; Lloret *et al.* 2005). These traits are known not to be trivially correlated among themselves, i.e. each trait considers a different plant property (Díaz *et al.* 2004), and therefore offer a time- and labour-efficient way to characterize the general resource use strategy of high numbers of species (Cornelissen *et al.* 2003). We also measured leaf nitrogen and phosphorus on a representative subset of species (55 species, of which 34 were native and 21 were alien, Appendix S1). All traits were measured in the field on healthy, sexually mature plants growing in unshaded habitats and reported values are the average of at least six replicates per species. Wood density was measured only on those species that have secondary growth (34 species, of which 23 were native and 11 were alien).

DATA ANALYSIS

To detect general trends in functional attributes of native and alien plant species across the five ecosystems and four land uses, we first organized the dataset into a single seven traits (variables) × 116 species (cases) matrix, on which we carried out a principal component analysis (PCA) based on the correlation matrix of variables (Jongman, ter Braak & van Tongeren 1987). Wood density, nitrogen and phosphorus were excluded because they had been measured in only a subset of species (see above). In order to test for overall differences in attributes of alien and native species of herbaceous and woody growth forms, we compared their scores along PCA axes 1 and 2, using ANOVA and Tukey test (Di Rienzo *et al.* 2002). A second PCA was run considering only woody species. This more-targeted analysis allowed us to test whether trends detected within the whole dataset were consistent when wood density (relevant only to woody plants) was included, and lifespan (constant for all woody species) was excluded. Continuous traits were log-transformed before carrying out both ordination analyses.

To evaluate whether the PCA axes obtained from these seven traits were associated with leaf nutrient content (foliar nitrogen and phosphorus), we performed Pearson correlations between PCA axes 1 and 2 and nutrient content across a subset of 55 species highly representative of the taxonomic, growth-form and habitat range covered by the whole dataset.

Differences between native and alien species in terms of individual continuous traits were assessed using the Mann–Whitney test (Siegel 1983). This analysis was feasible only in the case of (i) all characterized species within each ecosystem regardless of the land use and (ii) all species within each land use regardless of the ecosystem. Reductions in sample size imposed limitations to statistical comparisons between co-occurring species within each land use and ecosystem. Therefore, such comparisons are not reported here, but trends of trait differentiation were similar to those reported at broader scales of the analysis. Many species occurred in more than one habitat, so the sum of the sampling units (i.e. number of species) considered in the comparisons across different conditions (Tables 2 and 3) is higher than the total number of species. All the analyses were performed separately for herbaceous and woody species in order to avoid bias associated to differences between these two major life-forms.

Results

OVERALL COMPARISON OF ALIEN VS. NATIVE SPECIES

When considering all species together (Fig. 1a), the main trend of variation (PCA axis 1) was between acquisitive (tender,

Table 2. Trait comparison between native and alien species within five ecosystems of central-western Argentina. Means of each variable are provided for alien and native species and asterisks indicate statistically significant differences (*$P < 0.05$ and **$P < 0.001$, Mann–Whitney test). Number of species (N) considered in the analysis within ecosystems is provided for alien and native species, respectively. No data on woody species is shown for Monte arid shrubland and Mountain grassland due to absence of woody alien species in both situations

| | Ecosystem | | | | | | | | | | | | | | |
| | Monte arid shrubland | | | Lowland Chaco woodland | | | Espinal woodland | | | Mountain Chaco woodland | | | Mountain grassland | | |
	N	Alien	Native	N	Alien	Native	N	Alien	Native	N	Alien	Native	N	Alien	Native
Herbaceous species															
SLA (mm² mg⁻¹)	10;12	18.66	12.49*	14;21	19.63	17.57	12;28	20.83	19.14	17;26	19.67	22.47	10;17	15.18	16.1
Leaf thickness (mm)		0.42	0.43		0.47	0.29		0.5	0.31		0.46	0.29		0.46	0.28
Leaf area (mm²)		1976.11	813.21		2277.16	1659.4		3559.75	1331.32*		3011.4	1402.14*		1361.54	310.81
Leaf toughness (N mm⁻¹)		0.93	3.77		0.72	2.22		0.72	1.98		0.74	1.84		2.33	4.14
Plant height (cm)		74.52	70.26		81.08	83.71		81.08	87.27		67.35	91.06		39.49	26.88
Phosphorous (%)	4;5	0.23	0.17	9;7	0.25	0.26	8;9	0.28	0.27	9;9	0.26	0.25	4;8	0.15	0.15
Nitrogen (%)		3.4	2.3		3.49	2.74		3.79	2.89		3.77	3.09		2.59	2
Woody species															
SLA (mm² mg⁻¹)				2;15	30.83	9.68*	3;9	23.26	9.39	11;11	17.57	10.77*			
Leaf thickness (mm)					0.18	0.33*		0.24	0.33		0.23	0.33*			
Leaf area (mm²)					13971.88	734.9*		10323.84	844.61*		9135.93	938.91**			
Leaf toughness (N mm⁻¹)					0.36	2		0.54	2.09		0.63	1.51			
Plant height (cm)					739.17	470.21		737.22	417.94		549.25	364.82*			
Wood density (g mL⁻¹)					0.5	0.77*		0.54	0.74*		0.54	0.73**			
Phosphorous (%)				2;12	0.26	0.18	3;7	0.21	0.21	9;8	0.23	0.22			
Nitrogen (%)					3.26	2.91		2.68	3.06		2.75	2.89			

Table 3. Trait comparison between native and alien species of central-western Argentina within four land uses. Means of each variable are provided for alien and native species, and asterisks indicate statistically significant differences (*$P < 0.05$ and **$P < 0.001$, Mann–Whitney test). Number of species (N) considered in the analysis within ecosystems is provided for alien and native species, respectively. Trait comparison between woody species was not possible in the post-cultivation condition due to presence of only one woody alien species

	Land use												
	Undisturbed			Moderate grazing/logging			Roadsides			Post-cultivation			
	N	Alien	Native	N	Alien	Native	N	Alien	Native	N	Alien	Native	
Herbaceous species													
SLA (mm² mg⁻¹)	8;25	18.81	18.15	17;34	18.7	16.83	25;33	19.04	17.61	22;36	19.7	19.91	
Leaf thickness (mm)		0.56	0.3		0.42	0.29		0.39	0.33		0.44	0.29	
Leaf area (mm²)		3162.4	1120.11*		2511.71	959.94		2374.28	1486.62		2320.68	1307.01	
Leaf toughness (N mm⁻¹)		0.67	3.77		0.74	3.12		1.42	2.35		0.95	2.14	
Plant height (cm)		56.21	75.84		72.41	74.15		54.05	81.49		72.78	66.33	
Phosphorous (%)	5;12	0.27	0.19	10;16	0.24	0.22	12;13	0.24	0.24	10;11	0.25	0.26	
Nitrogen (%)		3.33	2.36		3.34	2.49*		3.49	2.61		3.81	2.94	
Woody species													
SLA (mm² mg⁻¹)	8;22	20.28	10.47**	9;22	18.03	10.71*	6;9	18.27	14.92	1;8	18.31	15.02	
Leaf thickness (mm)		0.22	0.37**		0.24	0.36*		0.23	0.33		0.17	0.39	
Leaf area (mm²)		11416.45	730.78***		6500.89	739.69***		8746.45	861.46**		13276.5	970.01	
Leaf toughness (N mm⁻¹)		0.57	1.64*		0.67	1.63		0.7	1.69		0.84	1.79	
Plant height (cm)		650.63	385.16*		619.75	397.87*		597.51	227.49*		840.00	223.06	
Wood density (g mL⁻¹)		0.56	0.76**		0.59	0.76**		0.52	0.66		0.70	0.62	
Phosphorous (%)	6;15	0.25	0.18	8;15	0.22	0.18	6;5	0.21	0.22	1;4	0.21	0.22	
Nitrogen (%)		3.00	2.84		2.73	2.84		2.61	3.21		2.87	3.44	
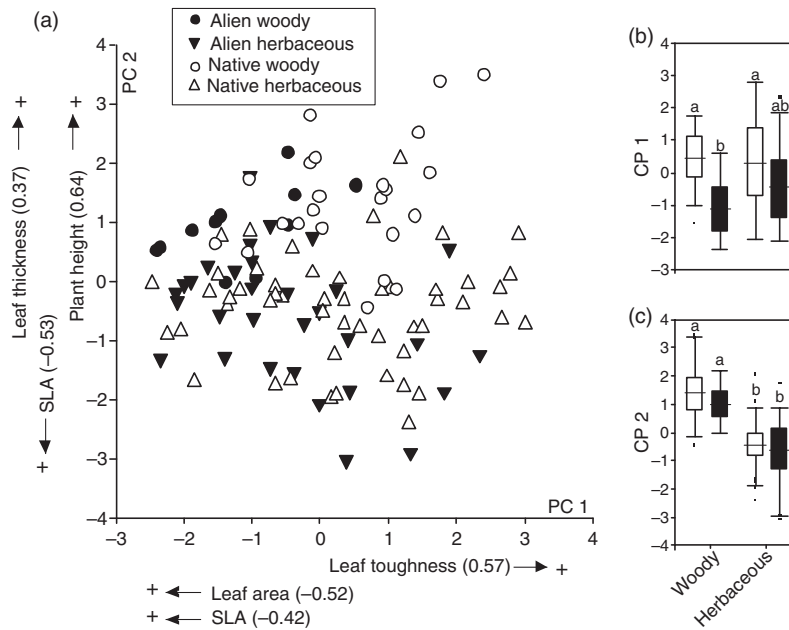
Fig. 1. (a) PCA ordination of 116 vascular plant species from central-western Argentina on the basis of seven traits (49% of the variance explained by the two-first PC axes; eigenvalues $\lambda_1 = 0.27$ and $\lambda_2 = 0.22$). Labels display traits with the highest eigenvector scores on PCA axes 1 and 2, with the respective score in brackets. Box plots on the right illustrate the distribution of native (in white) and alien (in black) woody and herbaceous species along PCA axes 1 (b) and 2 (c). Score mean distribution was significantly different between some of the four groups of species as indicated by the letters (ANOVA and Tukey LSD test; $P < 0.001$ for both axes). Box = interquartile range; line across box = mean.
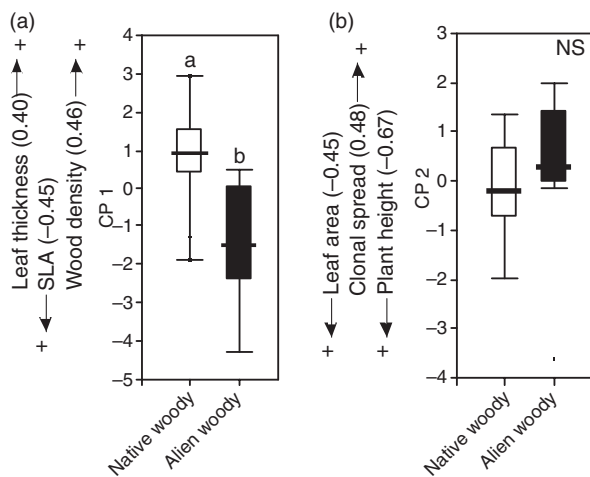
Fig. 2. PCA ordination of 34 native and alien woody species present in central-western Argentina on the basis of their functional traits (66% of the variance explained by the two-first PC axes; eigenvalues $\lambda_1 = 0.45$ and $\lambda_2 = 0.21$). (a) Score mean distribution was significantly different between alien and native woody species along the first axis ($T = -4.5$, $P < 0.0001$ for axis 1). (b) No significant difference was found between native (white) and alien (black) mean scores along the second axis ($T = 1.09$, $P = 0.2837$ for axis 2). Labels display traits with the highest eigenvector scores on PCA axes 1 and 2, with the respective score in brackets. Box = interquartile range; line across box = mean.

large leaves, with high specific area) and conservative (tough, small leaves, with low specific area) plant trait syndromes. This axis was significantly associated to leaf nutrient content ($r = -0.60$ for leaf N_{mass}, $r = -0.52$ for leaf P_{mass};

$P < 0.0001$; Pearson correlation test). A secondary trend of variation (PCA axis 2) tended to separate herbaceous plants from woody plants. This axis was significantly associated with plant size and, to a lesser degree, with leaf thickness and specific leaf area (Fig. 1a) as well as with leaf nutrient content ($r = -0.26$ for leaf N_{mass}, $r = -0.32$ for leaf P_{mass}; $P < 0.05$). Although both native and alien species appeared to be well spread across the range of trait variation, alien species were significantly clustered on the more acquisitive end of PCA axis 1 ($T = -4.00$, $P = 0.0001$, irrespective of growth form). PCA axis 2, on the other hand, separated woody and herbaceous species ($T = -8.99$, $P < 0.0001$, irrespective of species origin). No significant difference was detected between herbaceous alien and native species (Fig. 1b,c). In the case of woody plants, however, alien species showed a significantly more acquisitive set of attributes than native species (Fig. 1b). These patterns were consistent despite differences in species abundance across communities. Very abundant (i.e. with a mean relative cover higher than 5% of the mean total local abundance) alien species did not significantly differ in PCA scores from less abundant (i.e. mean relative cover between 1% and 5% of the mean total local abundance) alien species ($T = -0.165$, $P = 0.87$ and $T = -0.238$, $P = 0.813$, for axes 1 and 2 respectively; data not shown).

The trend observed among woody species became stronger in a second analysis, focused on woody species only and thus including wood density (Fig. 2). Alien species significantly differed from native species through a combination of lower wood density, higher specific leaf area and thinner leaves (Fig. 2a). The position of alien species along PCA axis 1 was

significantly associated with higher leaf nutrient content ($r = -0.45$ and $r = -0.62$ for leaf N_{mass} and P_{mass}, respectively; $P < 0.05$, Pearson correlation test).

Native and alien woody species did not significantly differ in their scores along PCA axis 2 (Fig. 2b), which was most strongly associated with height, leaf size and capacity for clonal spread.

COMPARISON BETWEEN ALIEN AND NATIVE SPECIES UNDER DIFFERENT CLIMATIC CONDITIONS

The general trends described above were maintained under contrasting climatic conditions (Table 2). Across a wide range of temperatures, humidity and soil conditions, herbaceous alien and native species did not differ in terms of functional attributes (only three exceptions out of 35 cases). In contrast, woody alien species differed from woody native species in a number of attributes in all habitats. In general, woody aliens showed higher specific leaf area, larger and thinner leaves or lower wood density than native species.

COMPARISON BETWEEN ALIEN AND NATIVE SPECIES UNDER DIFFERENT LAND USES

The functional attributes of woody alien species also differed from those of native species when considering different land-use regimes (Table 3). This was particularly evident in the absence of major disturbances (undisturbed and moderately grazed and logged plots), where they differed in most of the measured traits. High specific leaf area, large, soft and thin leaves, low wood density and high canopy height characterized woody aliens in these situations.

In line with the results described above, herbaceous native and alien species showed few trait differences with only two exceptions (Table 3). In general, functional differentiation between alien and native species seemed more consistent in undisturbed and moderately grazed plots than along roadsides and formerly cultivated fields.

Discussion

A considerable amount of research has been devoted to the relevance of plant functional traits in controlling success in new environments (Thompson, Hodgson & Rich 1995; Rejmánek 2000; Richardson & Pyšek 2006; Morrison & Mauck 2007; Pyšek & Richardson 2007; Theoharides & Dukes 2007; Moles, Gruber & Bonser 2008), and the inclusion of wide spectra of environmental conditions and biomes is essential (Vázquez & Aragón 2002; Lake & Leishman 2004; Pyšek *et al.* 2008). Our findings, spanning different climatic and land-use situations in central-western Argentina, lend support to the idea that a universal suit of attributes is unlikely to explain alien plant success (Thompson, Hodgson & Rich 1995; Pyšek 1998; Rejmánek 2000; Lloret *et al.* 2005; Richardson & Pyšek 2006; Lambdon, Lloret & Hulme 2008).

Overall, our results indicate that in central-western Argentina alien species tend to differ from native species in their func-

tional attributes among woody species but not among herbaceous species. The attributes that appeared most consistently associated with woody alien species – large, soft, thin, nutrient-rich leaves, and low-density wood – have been previously identified by Díaz *et al.* (2004) as key elements of an acquisitive syndrome of resource use, retention and release, consistent across a wide range of floras, regions and ecosystems. In agreement, in the present study woody alien species with an acquisitive strategy were only present in the less-stressful ecosystems (see below).

Going back to the initial hypotheses, we found that, across all ecosystems and land uses, herbaceous alien and native species growing in the same habitat did not show significant functional attribute differences. This is in line with the 'join-the-locals' hypothesis. However, this was not the case for most of the surveyed woody alien species, in which functional attributes differed from those of woody native species in all ecosystems and land uses. The fact that woody alien species exhibited more acquisitive attributes than native species in the less-stressful ecosystems partially supports the 'try-harder' hypothesis. However, in more stressful (drier, colder) and less-disturbed habitats, we did not observe more conservative attributes in alien than in native woody species, as would have been expected under the 'try-harder' hypothesis. Moreover, and in contrast to our expectations, differentiation towards more acquisitive traits was stronger in less-disturbed habitats. At the regional scale (i.e. considering all ecosystems and contrasting land uses together), we expected no significant difference between alien and native species under both hypotheses, although for different reasons (see Introduction). Herbaceous alien and native species indeed did not differ. The consistency of this pattern with those found at more local scales of analysis suggests that this is the overall result of strong similarities between alien and native species at each habitat, which again is in line with the 'join-the-locals' hypothesis. In contrast, overall regional patterns among woody species did not follow our prediction, since their differentiation towards more acquisitive attributes was observed even when considering all ecosystems and contrasting land uses together. All in all, the 'join-the-locals' hypothesis seems to be the best one to account for the functional trait patterns among herbaceous alien and native species of central-western Argentina. On the other hand, functional trait patterns among woody species seem satisfactorily explained by the 'try-harder' hypotheses at the less-stressful extreme of the gradient. These markedly different patterns among herbaceous and woody species stress the need for caution when mixing major life-forms in comparative plant trait analyses (Lavorel *et al.* 1997).

FUNCTIONAL SIMILARITY BETWEEN NATIVE AND ALIEN HERBACEOUS SPECIES

In line with the 'join-the-locals' hypothesis, there were strong functional trait similarities between alien and native herbaceous species, supporting the filtering by environmental factors (local climate and disturbance regime) as a major influence leading to converging functional attributes among coexisting

alien and native species. Similar patterns were reported for closed plant communities of relatively cool, damp climates of NW Europe, both seminatural (Thompson, Hodgson & Rich 1995) and urban (Thompson & McCarthy 2008), where dominant alien and native species were similar in terms of resource use strategy. In central-western Argentina this functional similarity seems to hold not only in the temperate subhumid mountain grasslands (that are the most similar to NW European moist grasslands) but also in the drier and warmer woody ecosystems. Interestingly, in our study both native and alien herbaceous species showed higher specific leaf area, foliar nitrogen and phosphorous (N_{mass} and P_{mass}) than those observed by Leishman *et al.* (2007) for invasive species both in Australia and in a global data set. This suggests that in central-western Argentina, like in NW Europe (Thompson, Hodgson & Rich 1995), both native and alien herbaceous species share the strategy of rapid growth ability and low investment in conservative tissues (Cornelissen *et al.* 2003), being a feature of the whole growth form rather than a strategy of the novel species.

FUNCTIONAL DIFFERENCES BETWEEN NATIVE AND ALIEN WOODY SPECIES

The more acquisitive attributes of woody alien species as compared to coexisting native species found in the more mesic ecosystems (lowland Chaco, Espinal and mountain Chaco woodlands) is consistent with predictions for resource-rich habitats under the 'try-harder' hypothesis. However, no woody alien species was found in the most stressful ecosystems (i.e. Monte and mountain grassland), where alien species were expected to show more conservative attributes under this hypothesis (Funk & Vitousek 2007). This stops us from drawing definitive conclusions about the relevance of a 'conservative strategy' among woody species in these systems. The possibility that woody alien species with highly conservative traits are not present in the more stressful habitats simply because of dispersal limitations cannot be ruled out. However, this seems unlikely, considering the long history of European settlement in both ecosystems. Notably, a small set of the woody alien species screened in this study fell at the more conservative extreme of the woody alien trait spectrum (*Ligustrum lucidum*, *Ligustrum sinense*, *Pyracantha angustifolia*), are widely used as ornamental trees and hedgerows all over central-western Argentina, and are effectively dispersed by native birds (Delucchi 1991; Montaldo 1993, 2000; Aragón & Groom 2003). *Pyracantha angustifolia* has even been reported as a conservative invader in Hawaii (Funk & Vitousek 2007) with low leaf nutrient contents similar to those observed in our study (1.91% vs. 1.83% of N_{mass}, respectively). However, none of these species were observed in the most stressful ecosystems in our study. This suggest that support for the 'try-harder' hypothesis among woody alien species in central-western Argentina depends on which extreme of the resource gradient is considered. Although with our methodology we cannot completely rule it out at the least productive extreme, the supporting evidence is much stronger at the most productive extreme.

Despite the overall tendency of woody alien species to show more acquisitive resource use strategies than native species, some overlap existed between both groups (Figs 1 and 2) indicating that there is not a clear-cut functional syndrome exclusive to woody aliens. Rather, they showed a more restricted combination of attributes within one extreme of the spectrum defined by native species. This is in line with previous findings suggesting that alien and native species do not have fundamentally different resource use strategies but fall instead at different ends of a common spectrum of variation in leaf economics (Leishman *et al.* 2007). The existence of extreme values for some traits in alien floras, like those described for woody invaders in this study, might enable the novel species to benefit from resources that are permanently or temporarily unavailable or underused by the resident species (Crawley, Harvey & Purvis 1996; Davis, Grime & Thompson 2000; Gurvich, Tecco & Diaz 2005).

It has been suggested that trait differences between natives and aliens (i.e. ecological novelty) would be partially gauged by relatedness of the invaders to natives, as novel genera seem more successful in new ranges than genera with native species representatives (Strauss, Webb & Salamin 2006). Although a phylogenetic analysis was beyond the objectives and the practical sampling design of this study, some overlap was observed between native and alien species in terms of family affiliation (i.e. half of the 22 families with alien species also had native members). However, it is worth mentioning that certain families were only represented by alien species, particularly among woody aliens (e.g. Aceraceae, Meliaceae, Moraceae, Oleaceae; Appendix S1). Whether phylogenetic relatedness explains part of the differences between woody natives and aliens found here or the impact of aliens on these ecosystems (Strauss, Webb & Salamin 2006) certainly deserves further study with specific assessment.

It has been shown that specific leaf area is the most influential trait on relative growth rate (Lambers & Poorter 1992; Swanborough & Westoby 1996; Grime *et al.* 1997; Grotkopp, Rejmánek & Rost 2002) and consistently facilitates invasiveness in disturbed and peri-urban habitats (Lake & Leishman 2004). In our study high specific leaf area was one of the attributes that consistently differentiated alien from native woody species across ecosystems and even within undisturbed habitats (Figs 1 and 2 and Tables 2 and 3). Species with high specific leaf area values are expected to benefit more rapidly from any increment in resource availability, such as light, soil nutrients or moisture.

Our approach, based on vegetative traits directly relevant to resource use, storage and release (Díaz *et al.* 2004), provides useful insight into the possible mechanisms behind the persistence of alien species at the regional scale and also into their likely consequences on an ecosystem-level. This does not imply, however, an underestimation of regenerative traits (Rejmánek & Richardson 1996), differential below-ground competition and soil biota interaction (Kueffer *et al.* 2007; Mangla & Callaway 2008), resource-enemy release (Blumenthal 2006), novel biochemical weapons (Callaway & Ridenour 2004) or other biotic interactions such as invasional meltdown (Simberloff &

Von Holle 1999; Simberloff 2006), which we did not investigate here as possible factors influencing alien presence in some ecosystems, including the ones studied by us. For instance, some of the alien woody species present in undisturbed and moderately grazed and logged areas of the mountain Chaco woodland benefit from seasonally uncoupled dispersal in relation to that of most native woody species (Gurvich, Tecco & Diaz 2005; Tecco *et al.* 2006; Ferreras, Torres & Galetto 2008), or by positive interaction among invaders (Tecco *et al.* 2006, 2007). However, detailed exploration of such traits and interactions is not feasible in large-scale comparative approaches like the one taken in this paper, but is more suitable for studies focusing on single species or small numbers of species.

PRACTICAL IMPLICATIONS

Woody species have been suggested as the most successful invaders of natural communities (Cronk & Fuller 1995; Panetta & Sparkes 2001). The ecosystem consequences of their presence are expected to increase in proportion to the functional differences with the resident community (Chapin, Lubchenco & Reynolds 1995; Strauss, Webb & Salamin 2006), particularly when these differences affect resource availability (Vilà 2000; Levine *et al.* 2003). The fact that most woody alien species present in undisturbed and moderately disturbed woodlands of central-western Argentina show a combination of attributes consistent with an acquisitive strategy may have important implications, particularly in the face of the consistent trend of increase in precipitation observed during the last 50 years in some areas of the region (Viglizzo *et al.* 1995; Minetti *et al.* 2003; Zak *et al.* 2008). It is tempting to speculate that, through their acquisitive attributes, woody alien species will differentially benefit from any increment in resource availability, such as soil moisture, as compared to woody native species (presumably better adapted to seasonal drought). In turn, their expansion might increase the input of high-quality litter (i.e. large, thin and soft leaves with high nutrient content) to the system, change decomposition dynamics, further increasing resource availability and thus ultimately resulting in an overall synergy towards favouring alien species expansion (invasional meltdown, *sensu* Simberloff & Von Holle 1999). All these speculations represent fruitful venues for experimental exploration.

Overall, considering the functional differences between native and alien woody species and the evidence for the negative impacts of some of the alien species in our study area (Tourn *et al.* 1999; Aragón & Morales 2003; Lichstein, Grau & Aragón 2004; Chaneton *et al.* 2004; Tecco *et al.* 2006, among others), we suggest that regional efforts to monitor, control and manage plant invasions should focus on woody invaders as a main priority.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. List of species surveyed. A total of 128 species were originally characterized in terms of vegetative traits, but 12 of them were later excluded because they are considered cosmopolitan.

Table S1. Geographical location, climatic, soil and floristic general description of the five ecosystems of central-western Argentina considered in this study.

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