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Contrasting functional trait syndromes underlay woody alien success in the same ecosystem

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Abstract We performed a comprehensive comparative study of functional traits in coexisting alien and native woody species in order to examine the strategies related to resource use and dispersion underlying alien success in mountain Chaco woodlands of central Argentina. Our approach integrated seemingly contrasting pieces of evidence in the region. We specifically assessed whether (i) the 'functional acquisitive trend' previously observed along a broad environmental gradient accounts for woody alien naturalization when considering a single mesic ecosystem; or (ii) more than one trait syndrome is important among alien species, which would be more in line with the context-dependent nature of biological invasions at a local scale. Fifteen vegetative and regenerative traits were measured on the most common 14 native and 11 alien woody species. We compared the attributes of (i) native and alien species and (ii) between native species and two contrasting groups of alien species identified in the previous analysis. The overall trait comparison (i) showed that, in terms of vegetative attributes, woody alien species tend to be on average more acquisitive than native species. However, (ii) two contrasting syndromes were revealed among alien species: a group of seven deciduous species with acquisitive attributes; and a group of four evergreen species showing markedly more conservative attributes than the first group. The functional attributes of 'conservative aliens' completely overlapped with the range observed for native species, except for an exclusive dispersal phenology and a stronger tendency to clonal spread. Acquisitive aliens, in turn, proved to be beyond the range of attributes of native species, at the acquisitive extreme, as they did in previous comparisons. Despite their importance, general trends in plant functional attributes across regions and ecosystems can sometimes obscure trends at more local scales that are nevertheless important for the understanding and management of particular systems. Our study concurs with previous general trends when looking at the overall comparison between native and alien species, but unveils contrasting functional strategies among alien species when examining their attributes more closely, even within the same ecosystem.

Key words: acquisitive species, central–western Argentina, conservative species, plant functional trait, woody invader.

INTRODUCTION

Considerable effort has been devoted to identify the mechanisms by which organisms become invasive outside their natural range of distribution (Richardson & Pyšek 2006; van Kleunen *et al.* 2010), and to why certain ecosystems are more invasible than others (Milbau *et al.* 2008). Two main views have been put forward to explain whether coexisting alien and resident plant species should show converging or diverging functional attributes related to resource acquisition and conservation (Grime 2006; De Bello *et al.* 2009; Pillar *et al.* 2009). According to the first one, successful aliens should differ from resident species in attributes that allow them to deal better with the local conditions than resident species do (Funk & Vitousek 2007; Pyšek & Richardson 2007; Thuiller *et al.* 2010; van Kleunen *et al.* 2010). The second one stresses the importance of filtering by environmental factors. It predicts strong functional similarities in attributes (= trait values) related to resource acquisition and conservation (*sensu* Grime *et al.* 1997; Díaz *et al.* 2004; Wright *et al.* 2004), especially among the dominants (Thompson *et al.* 1995; Thompson & McCarthy 2008). Both hypotheses were recently tested by Tecco *et al.* (2010) by comparing vegetative functional attributes between native and locally common alien species of central–western Argentina across five contrasting ecosystems and four land use regimes. These authors found functional convergence among herbaceous species whereas functional divergence among woody species. Woody aliens showed more acquisitive attributes than natives, particularly at the less stressful – and more invaded –

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extreme of the gradient (mountain Chaco woodlands). These attributes refer to a strategy of rapid resource acquisition and growth ('acquisitive syndrome' *sensu* Díaz *et al.* 2004) generally expressed by soft, thin, nutrient-rich leaves, high specific leaf area (SLA) and low wood density. In contrast, the 'conservative syndrome' refers to resource conservation and slow growth, reflected by thick, tough, long-lived leaves with high concentration of defences and low nutrient content (Díaz *et al.* 2004). The general pattern of alien woody species being on average more acquisitive than native ones was consistent across a number of species in Tecco *et al.* (2010). However, there were two notable exceptions: the woody aliens *Ligustrum lucidum* and *Pyracantha angustifolia*, which were markedly similar to native species in terms of vegetative attributes. Both species are notorious invaders (Tecco 2006; Hoyos *et al.* 2010; Giorgis 2011; Giorgis *et al.* 2011) and their success has been ascribed to regenerative attributes (i.e. bird dispersal seasonally decoupled from most native species; Gurvich *et al.* 2005; Tecco *et al.* 2006). These seemingly contrasting pieces of evidence in the region lead us to extend our investigation to include functional traits beyond those above-ground vegetative traits considered by Tecco *et al.* (2010). Specifically, we aimed to test for functional divergence over a wider set of functional traits, including some known to be at least partially decoupled from the traits that determine resource acquisition strategy (Leishman & Westoby 1992; Westoby 1998). To this end, we measured 15 functional traits relevant to the regenerative and established phases of the plant life cycle, including above- and below-ground traits, on the most common native and alien woody species coexisting in the mountain Chaco woodlands of central–western Argentina.

METHODS

Study area

The study was carried out in the surroundings of the Reserva Hídrica Natural 'Parque La Quebrada' in Córdoba mountains, central Argentina (31°23′S, 63°35′W, 800–900 m a.s. l.). Mean annual temperature is 14°C, with frosts from May to September. Mean annual rainfall is about 800 mm, mainly from November to March. According to climate the vegetation should be mountain Chaco woodland dominated by *Lithraea molleoides*, *Celtis ehrenbergiana*, *Acacia caven* and *Condalia buxifolia* (Luti *et al.* 1979). Because of livestock grazing, logging and frequent burning, the original woodland has been largely transformed into a mosaic of grasslands, shrublands and open woodlands (Zak & Cabido 2002). This study corresponded to open woodlands which are widespread in the region and should be considered as most representative of the remaining natural vegetation.

Species characterization

A total of 25 woody species were characterized (Appendix S1), including 14 of the most frequent native woody species in the mountain woodlands of Córdoba, central Argentina and the 11 most frequent woody aliens found in these systems (Tecco 2006; Giorgis *et al.* 2011). The alien species considered here sustain populations without deliberate human assistance (i.e. they are naturalized aliens) and are the most frequent aliens in the study area (Giorgis *et al.* 2011). However, they are not necessarily invasive (i.e. dominant in terms of biomass or having an obvious ecosystem-level impact). Both alien and native species were well distributed among several taxonomic families and co-occur along the landscape. That is, all alien species selected here are found occupying woodland patches intermingled with natives (Giorgis 2011). Those aliens that are naturalized but restricted to particular habitat conditions were excluded (e.g. *Salix babylonica* because of its riparian habitat and *Pinus* spp. that are closely associated with grasslands from forestation surroundings).

We considered 15 above- and below-ground functional traits (Table 1), all of them with direct functional implications to the regenerative and established phases of plant life and to plant responses to the environment. A brief description about the ecological context for these functional traits recognized as critical for tackling ecological questions of plant strategies is provided in Appendix S2. Most of the traits measured in this study are considered 'soft traits', that is, traits that are ecologically meaningful and at the same time relatively easy, low-tech and inexpensive to measure (Hodgson *et al.* 1999; Cornelissen *et al.* 2003). Three 'hard' traits (i.e. more directly related to plant physiology or ecosystem functioning) were also considered as a complement of the 12 soft traits: leaf nitrogen and phosphorus concentration, expressed as percentage nitrogen or phosphorus on a leaf dry mass basis (hereafter N_{mass} and P_{mass}) and potential decomposition rate (see below). These traits were measured on a representative subset of species: 20 species (11 native and nine alien) in the case of leaf N_{mass}, P_{mass}, and 13 species (seven native and six alien) in the case of decomposition rate. The subset of species included the most frequent native and alien species (see Appendix S1). All traits were measured on healthy, sexually mature plants growing in unshaded habitats of the study site and are the average of six replicates per species (Cornelissen *et al.* 2003; Díaz *et al.* 2004). Most leaf and whole-plant traits data were taken from Díaz *et al.* (2004) and Tecco *et al.* (2010), whereas some others were measured anew and are first reported here (Appendix S2). All species were measured in the field and/or the laboratory using the same standard protocols of Cornelissen *et al.* (2003). In the case of mycorrhizal status, data were obtained through field collection and laboratory analysis of roots and complemented with information from the literature (Wang & Qiu 2006; Brundrett 2009). Although plant responses to mycorrhizal fungi can vary according to environmental conditions, the mycorrhizal type per se is not expected to change when plants are established outside their native range (Richardson *et al.* 2000). Data on fruiting phenology and dispersal mode were obtained from field observation and regional literature (Caziani & Protomastro 1994; Montaldo 2000; de Noir *et al.* 2002; Demaio *et al.* 2002; Astegiano 2003; Hurrell

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Table 1. Traits measured on the most representative native and alien woody species of the montane woodland of central–western Argentina

Trait	Type of variable
Leaf area	Continuous (mm^2)
Specific leaf area	Continuous (mm^2 leaf area (mg leaf mass)$^{-1}$)
Leaf thickness	Continuous (mm)
Leaf toughness	Continuous (= leaf tensile strength; newton (mm leaf width)$^{-1}$)
Leaf phenology	Ordinal: 1 = deciduous; 2 = evergreen and semi-deciduous
Leaf nitrogen (N_{mass} %)	Continuous (foliar N concentration per unit leaf mass)
Leaf phosphorous (P_{mass} %)	Continuous (foliar P concentration per unit leaf mass)
Mycorrhizal status	Nominal: 1 = arbuscular mycorrhizal species; 2 = non-mycorrhizal species
Potential litter decomposition rate	Continuous (% of dry mass loss)
Stem-specific density	Continuous (oven dry mass of a section of a plant third main stem divided by the volume of the same section when still fresh; g mL^{-1}).
Plant height	Continuous (cm)
Clonal spread	Binary: 0 = no evident clone expansion; 1 = clone expansion
Seed mass	Continuous (mg)
Dispersal mode	Nominal: 1 = unassisted; 2 = wind; 3 = mammals; 4 = birds
Fruiting phenology	Ordinal: 1 = spring, spring–summer, summer; 2 = summer–autumn, autumn; 3 = autumn–winter, winter, winter–spring

The source of the data and a brief description about its ecological meaning is provided in Appendix S2 (see Cornelissen *et al.* 2003) for further details).

& Bassano 2003; Lahitte *et al.* 2004; Ferreras & Galetto 2010). Potential decomposition rate was defined as the percentage of litter dry weight loss after incubation in an experimental garden under natural climatic conditions (Cornelissen 1996; Cornelissen *et al.* 1999; Pérez-Harguindeguy *et al.* 2000, 2007; Vaieretti *et al.* 2005). In this study, potential leaf litter decomposition data were obtained from previous work by the authors where selected species were incubated together under standard conditions. Incubations were done in decomposition beds within mountain woodland sites. Incubation period varied from 10 weeks, in summer decomposition beds (Pérez-Harguindeguy *et al.* 2000; Giorgis 2004; Vaieretti *et al.* 2005), to 16 weeks, in winter decomposition beds (P. Tecco, unpubl. data, 2004). Mass loss values were calibrated across experiments through shared species (see Cornelissen 1996 and Cornelissen *et al.* 1999 for details on litter collection, processing and incubation).

Data analysis

To detect general trends among native and alien species, we organized the data into a single 12 traits × 25 species matrix and performed a Principal Coordinates Analysis (PCoA). The PCoA was based on a matrix of species compared by the Gower index. Decomposition rate, N_{mass} and P_{mass} were excluded because they had been measured in only a subset of species (see above). Main loading traits of the ordination were identified by performing correlation analyses between PCoA axes and trait values (continuous variables) and by contingency analyses in the case of categorical variables.

The PCoA allowed us to identify two major combinations of attributes (i.e. different trait syndromes) among alien species along the PCoA 1. One combination overlapped with natives and the other was differentially distributed towards an extreme of the ordination. We then tested the differences between native species and these two identified groups of alien species by comparing their scores along the PCoA axes 1 and 2 using ANOVA and Tukey test. In this way, we assessed whether (i) the overall attributes of alien species (summarized by axis 1 and axis 2 scores) were significantly different between the two identified groups, or (ii) alien species attributes were exclusive or fell within the attribute range of native species.

We evaluated whether the PCoA axes obtained from soft traits were associated with the hard traits leaf N_{mass}, P_{mass} and decomposition rate. This was achieved by performing correlation analyses of PCoA axes 1 and 2 with these three variables across the subset of species for which we had decomposition and/or leaf nutrient data. Differences in terms of individual traits between natives and both groups of alien species were assessed using ANOVA on rank data and Tukey test for the continuous data. Chi-squared analysis (χ^2–Fisher's exact test) was performed to detect differences among the three groups of species in terms of the categorical traits (i.e. leaf phenology, mycorrhizal status, clonal spread, dispersal mode and fruiting phenology). All analyses were carried out with the Infostat sofware package (DiRienzo *et al.* 2008).

RESULTS

Overall trait differences between native and alien species

The first PCoA axis was identified as an axis of resource capture, usage and release, accounting for 24% of the total variance (Fig. 1). The main trend of variation was between acquisitive and conservative vegetative trait syndromes. Native species were concentrated towards the conservative extreme of this attribute range, characterized by low SLA, small, tough and thick mostly evergreen leaves, and high stem-specific density (SSD). In addition they tended to be dispersed by animals. Although alien species appeared well spread across the whole range of trait variation, their mean score distribution was significantly clustered towards the more acquisitive end of PCo1 as compared with natives ($t = 2.62$, $P = 0.0154$; Fig. 1B). This extreme of the axis

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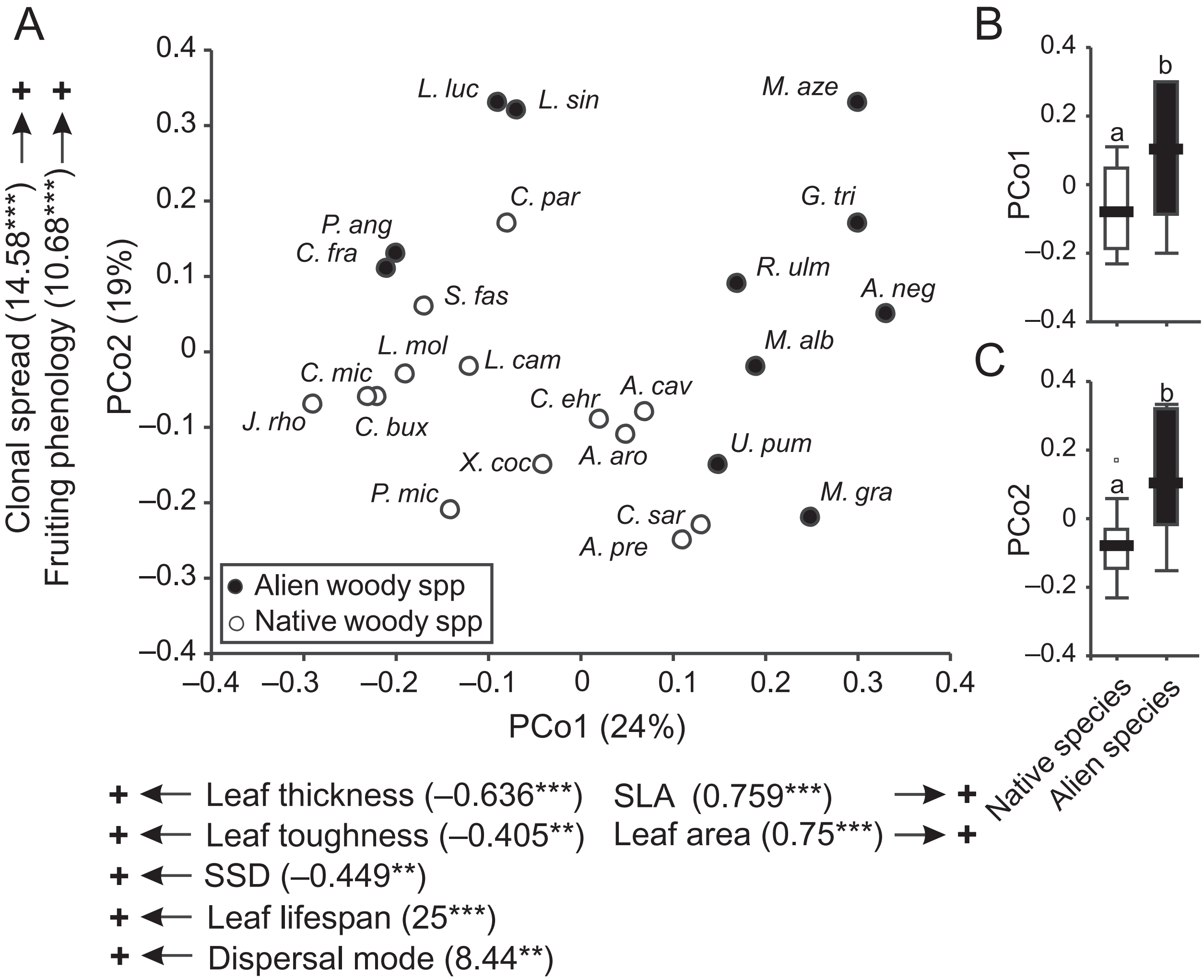

Fig. 1. (A) PCoA ordination of the most representative native and alien woody species of the mountain Chaco woodlands of central–western Argentina on the basis of 12 vegetative and reproductive traits. Labels display traits that characterize the main trend of variation of the ordination, with the corresponding score in brackets (Pearson *r* coefficient and Pearson–χ^2 for continuous and categorical variables, respectively). Asterisks indicate level of significance of these main loading traits along PCoA axes (**$P < 0.001$ and ***$P < 0.0001$). Species' identity is indicated in the ordination with the first letter of the genera and first three letters of the species epithet (see legend of Fig. 2 for full names). Box plots on the right of the ordination illustrate mean score distribution of native and alien species along PCo1 (B) and PCo2 (C) axes. Box = interquartile range; line across box = mean; whiskers = highest and lowest values. SLA, specific leaf area; SSD, stem-specific density.

was characterized by a combination of large, soft, thin, deciduous leaves with high SLA and low SSD. In line with the acquisitive-to-conservative trend of variation, species positions along the first axis were correlated with leaf nitrogen content ($r = 0.569$, $P = 0.009$ for N_{mass}, Pearson correlation test).

The mean score distribution along the PCo2 axis also differed between natives and aliens ($t = 3.1$, $P = 0.005$; Fig. 1C). This second axis accounted for a further 19% of the total variance and appeared to be associated to reproduction. That is, aliens tended to show higher frequency of species with clonal expansion and fruiting phenology spread between autumn and spring. This axis was also correlated with species' decomposition rates ($r = –0.61$, $P = 0.027$, Pearson correlation test).

Two different syndromes among woody aliens

With respect to alien species distribution along the ordination, two distinct clouds of species were found associated to opposite extremes of PCo1 (Fig. 1). One was clustered towards the left side of PCo1 (i.e. conservative extreme), overlapping with the distribution range of native species. The other was concentrated

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towards the right side, that is, the acquisitive side of the axis. This last group (hereafter 'acquisitive aliens') comprised the attribute combination described for all the alien species in previous analysis of Tecco *et al.* (2010). The other group (hereafter 'conservative aliens') showed most of the attributes previously described for native species (but see below).

The mean distribution of scores of the native species as well as both groups of alien species differed both along PCo1 ($F = 22.19$, $P < 0.0001$; ANOVA and Tukey test) and PCo2 ($F = 7.942$, $P = 0.003$; Fig. 2). 'Conservative alien' species fell inside the attribute range of the native woody species along PCo1 but not along PCo2. That is, while sharing an overall combination of conservative attributes, this group of aliens showed in addition an exclusive autumn–winter fruiting phenology and a stronger tendency to show clonal expansion than native species (Fig. 2B). In contrast, native species' position along the first axis was significantly different from the 'acquisitive aliens' (Fig. 2A) though overlapping along the second PCo axis associated with the already mentioned reproductive attributes. It is worth mentioning that although acquisitive aliens were not generally different from natives along PCo2 (Fig. 2B), several of the individual species in Figure 1 certainly are.

The similarities between native and 'conservative aliens', and their differences with the 'acquisitive aliens' along the main axis, were also observed when comparing the individual traits between the three groups of species (Table 2). Moreover, the lack of differences between native species and 'conservative aliens' remained consistent for most of the individual traits when excluding the 'acquisitive aliens' from the analysis ($P > 0.1$ in 12 of the 15 traits; Mann–Whitney test and χ^2–Fisher exact test for continuous and categorical traits, respectively). The exceptions were N_{mass}, seed mass and fruiting phenology. N_{mass} and seed mass were significantly lower in conservative aliens than in native species ($P = 0.002$ and $P = 0.046$, respectively). In line with the differences along PCo2 (Fig. 2B), all 'conservative aliens' dispersed their fruits in the cold season, while 11 of the 14 native species (78.6%) dispersed theirs in the warm season ($P < 0.0001$).

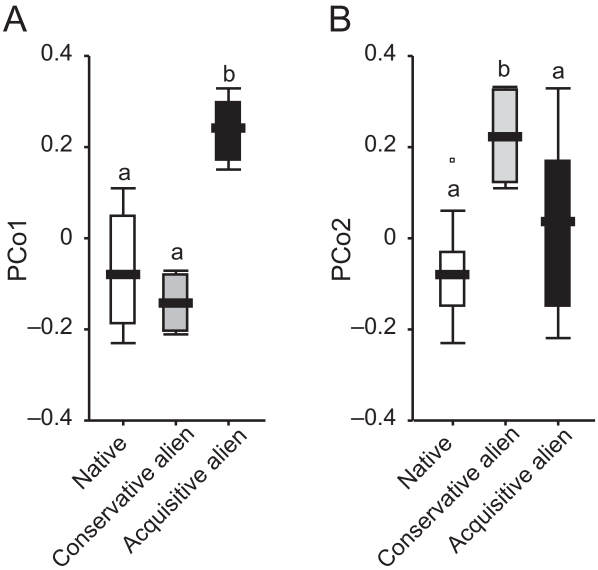

Fig. 2. Box plot illustrating the distribution of groups of species along PCo1 (A) and PCo2 (B) axes. Letters indicate significant differences in mean score distribution. Box = interquartile range; line across box = mean; whiskers = highest and lowest values. Species' identity of each group as follows. Native woody species: *Acacia aroma, A. caven, A. praecox, Celtis ehrenbergiana, Cestrum parqui, Condalia buxifolia, C. microphylla, Croton sarcopetalus, Jodina rhombifolia, Lantana camara, Lithrea molleoides, Porlieria microphyll*a, *Schinus fasciculata* and *Zanthoxylum coco*. Conservative alien species: *Ligustrum lucidum, L. sinensis, Pyracantha angustifolia* and *Cotoneaster franchetii*; Acquisitive alien species: *Acer negundo, Gleditsia triacanthos, Manihot grahamii, Melia azederach, Morus alba, Rubus ulmifolius* and *Ulmus pumila*.

DISCUSSION

General trends in plant functional attributes across regions and ecosystems can sometimes obscure trends at more local scales. Our study unveils contrasting functional strategies among alien species when examining their attributes within a single ecosystem. Both functional divergence and convergence with residents appear to underlie woody alien success in Chaco woodlands.

Revisiting previous findings

Our previous findings, considering vegetative functional traits across a broad spectrum of species and habitat conditions in several ecosystems of central–western Argentina, supported functional divergence among woody species (Tecco *et al.* 2010). It suggested that woody alien species differ from resident species in attributes that allow them to deal better with the local conditions by being on average more acquisitive than natives (Tecco *et al.* 2010). In this study, we considered a single ecosystem in more detail, included a broader set of traits, and focused on alien features alone and within the attribute range of native species. The overall trait comparison between native and alien species confirmed that woody aliens tend to be on average more acquisitive than natives in this ecosystem (Fig. 1B). However, our new results revealed that at least two contrasting functional trait syndromes underlie alien species success in mountain woodlands of central–western Argentina (Fig. 2). On the one hand, there was a group of seven deciduous woody alien species (*Acer negundo*, *Gleditsia triacanthos*,

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Table 2. Trait comparison between the native species and the two groups of alien species described by the PCoA analysis (Fig. 1)

Species attributes	*n*	Acquisitive alien spp.	*n*	Conservative alien spp.	*n*	Native spp.	*P*
Specific leaf area (mm^2 mg^{-1})	7	21.64 (a)	4	10.45 (b)	14	11.79 (b)	**0.010**
Leaf area (mm^2)	7	1 3717.17 (a)	4	1118.76 (b)	14	1716.43 (b)	**0.001**
Leaf thickness (mm)	7	0.19 (a)	4	0.3 (b)	14	0.36 (b)	**0.002**
Leaf toughness (N mm^{-1})	7	0.47 (a)	4	0.9 (b)	14	1.16 (ab)	**0.037**
Plant height (cm)	7	581.52	4	492.76	14	355.81	0.107
Stem-specific density (g mL^{-1})	7	0.49	4	0.62	14	0.70	0.101
Leaf P_{mass} (%)	6	0.28 (a)	3	0.14 (b)	11	0.23 (ab)	**0.016**
Leaf N_{mass} (%)	6	3.23 (a)	3	1.78 (b)	11	3.03 (a)	**0.028**
Decomposition (%)	3	61.37	3	50.67	7	74.66	0.196
Seed mass (mg)	7	114.95	4	12.52	14	47.94	0.268
Clonal spread (% spp.)	7	57	4	50	14	7	**0.020**
Leaf phenology (% deciduous spp.)	7	100	4	0	14	36	**0.001**
Mycorrhizal status (% spp.)	7		4		14		0.673
Arbuscular mycorrhizal spp.		100		100		86	
Non-mycorrhizal spp.		0		0		14	
Dispersal mode (% spp.)	7		4		14		0.289
Wind		29		0		0	
Mammals		14		0		14	
Birds		43		100		57	
Unassisted		14		0		29	
Fruiting phenology (% spp.)	7		4		14		**0.001**
Spring, spring–summer, summer		71.4		0		79	
Summer–autumn, autumn		14.3		0		21	
Autumn–winter, winter		14.3		100		0	

Means (continuous variables) and relative species frequency (categorical variables) are provided for each group. *P*-values in bold and letters in brackets indicate significant differences between groups (ANOVA on rank data and Tukey test for continuous variables; χ^2–Fisher's exact test for categorical variables). Group 1: *Acer negundo*, *Gleditsia triacanthos*, *Manihot grahamii*, *Melia azederach*, *Morus alba*, *Rubus ulmifolius* and *Ulmus pumila*; Group 2: *Ligustrum lucidum*, *L. sinensis*, *Pyracantha angustifolia* and *Cotoneaster franchetii*. Natives: See Fig. 1. *n*, number of species considered in the analysis.

Manihot grahamii, *Melia azederach*, *Morus alba*, *Rubus ulmifolius* and *Ulmus pumila*), with acquisitive attributes. This group of species appeared to support our previous findings on functional divergence (Tecco *et al.* 2010). These alien species may be thriving in the invaded ecosystems through faster resource acquisition and growth than other members of the community. Particularly in circumstances of increased resource availability (e.g. light, soil nutrients and moisture) often associated with land use. On the other hand, there was a group of four evergreen species (*L. lucidum, L. sinensis, Pyracantha angustifolia* and *Cotoneaster franchetii*) completely overlapping with natives' range of attributes (Fig. 1A) and showing markedly more conservative attributes than the first group (Fig. 2A). These 'conservative alien' species, like native woody species, appear hardier in the face of the seasonal droughts that characterize the Chaco region. However, conservative aliens might benefit from having a seemingly exclusive combination of autumn–winter bird dispersed fruits (Fig. 2B, Table 2). That is, despite their overall similarity in vegetative attributes with native species, this regenerative difference might trigger their success (Gurvich *et al.* 2005).

According to our results, two of the four most abundant alien species invading mountain Chaco woodlands (Giorgis *et al.* 2011, see Appendix S1), belonged to the acquisitive group (*G. triacanthos* and *M. alba*), whereas the other two belonged to the conservative group (*L. lucidum* and *P. angustifolia*). This suggests that both strategies are involved in woody alien success in the study region. Our analysis also showed that evergreen species were generally more conservative and deciduous species were more acquisitive (Lambers & Poorter 1992; Aerts & Chapin 2000). However, deciduous aliens did not overlap with deciduous native species along the main trend of variation and significantly differed from them in most traits (data not shown). The observed patterns could thus not be exclusively explained by deciduousness.

It is worth mentioning that in the case of 'conservative aliens', two species belonged to the same genera and the other two to the same family. Both families (i.e. Oleaceae and Rosaceae) are, however, highly unrelated (Stevens 2008). This suggests that the suite of attributes shared by this conservative group of four species cannot be solely explained by phylogenetic affiliation.

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Regenerative and phenological traits of resident plant communities have been shown to be relatively independent from the general acquisitive–conservative trend across a wide range of floras, regions and ecosystems (Díaz *et al.* 2004). However, in the studied ecosystem, 'conservative aliens' appear to combine vegetative hardiness with reproductive opportunism by offering ripe fleshy fruits to birds in the cold season, unlike the acquisitive aliens and most native species (Aragón & Groom 2003; Gurvich *et al.* 2005; Tecco *et al.* 2006; Ferreras *et al.* 2008). It is also worth mentioning that while the 'acquisitive aliens' covered all variety of dispersal modes, the 'conservative aliens' were all bird dispersed (Table 2). This is in line with some previous findings on invaders of natural or semi-natural communities (Cronk & Fuller 1995; Lloret *et al.* 2005). Clonality was present in both conservative and acquisitive aliens though poorly represented among natives. The ability to form a bud bank might aid in recovery and persistence of these aliens after environmental disturbances (Bond & Midgley 2001).

Whether functional differences between native and alien species result in differential litter qualities (Ehrenfeld 2004) and therefore differential decomposability patterns, is still a matter of debate (Liao *et al.* 2008; Kurokawa *et al.* 2010; Davis *et al.* 2011). In our study, decomposability did not differ between species groups, nor was it associated with the main trend of trait variation (PCo1). This suggests that attributes underlying the acquisitive and conservative syndromes of resource acquisition may not always be coupled with attributes related to resource release or nutrient cycling (Ehrenfeld 2003).

General trends might mask particular syndromes

Numerous studies have addressed the question of whether alien success is mediated by functional differences or by high similarities with resident species (i.e. 'try harder' *vs.* 'join the locals' hypotheses in Tecco *et al.* 2010). Sound evidence has been found supporting both hypotheses, although the try harder one apparently predominates in recent reviews and meta-analyses (e.g. Leishman *et al.* 2007; Ordonez *et al.* 2010; van Kleunen *et al.* 2010). Both Leishman *et al.* (2007) and van Kleunen *et al.* (2010) found that invasive plants are, in contrast to the majority of coexisting native and non-invasive plants, at a position along the global multi-trait leaf economics spectrum that favours fast growth. Accordingly, Ordonez *et al.* (2010) stressed that, when compared at a community scale, the more dissimilar (functionally and/or phylogenetically) an alien species is to the native species pool, the greater are the chances to be successful when introduced. Assessing general trends among regions, ecosystems and communities is extremely important for theoretical and practical reasons. However, some trends and processes occurring at particular contexts or scales might be overlooked when taking these general approaches. For instance, our study concurs with previously reported general trends when looking at the overall comparison between native and aliens, but reveals contrasting functional strategies among alien species when examining their attributes separately from those of native species. Woody aliens in mountain woodlands of central–western Argentina appear to enter and persist in the community through two alternative syndromes. Some species benefit by being different than natives in attributes that allow faster growth and resource acquisition (as reported by e.g. Lake & Leishman 2004; Ordonez *et al.* 2010; van Kleunen *et al.* 2010). Others succeed by being similar to the resident species in many ways (as reported by e.g. Thompson *et al.* 1995), particularly in showing an overall conservative vegetative syndrome. They though differ in some key regenerative trait combination (termed 'triggering attributes' by Gurvich *et al.* 2005). While the first group still supports the 'try harder' hypothesis, the conservative alien group might be capitalizing 'the best of both worlds'. They might benefit by matching the environmental requirements of residents ('join the locals'), but achieve fast spread across the landscape by differing in a key aspect such as dispersal. It is tempting to say that these 'conservative aliens' species 'join but trick the locals'.

Invasion ecology is currently striving for a synthesis by searching for general principles that apply widely across taxonomic groups and floras. To this elusive end, detailed understanding of the ecology of individual species is still indispensable (Pyšek *et al.* 2008). Our present findings, together with previous ones (Gurvich *et al.* 2005; Tecco *et al.* 2010), illustrate the importance of complementing comparative synthetic approaches with comprehensive studies of specific systems.

Conservation implications

The evidence so far suggests that there is no universal suite of traits that make a species or set of species successful invaders everywhere (Pyšek & Richardson 2007). This is in part because the relevance of specific attributes for invasion is strongly system-dependent. Our data further suggest that even within the same ecosystem, alien species may fall in distinct syndromes that may be showing different strategies according to local conditions. It is tempting to speculate that presence and spread of these contrasting groups will become major drivers of woodland dynamics in the region: One group, the 'acquisitive aliens', might be early successional invaders. They may be successful in the face of human disturbances such as forest fragmentation, logging and urban sprawl (Zak *et al.* 2008). The other group, the 'conservative with opportunistic dispersal', might spread and dominate in communities

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without severe disturbances. They may act as aggressive late-successional invaders, as recently observed for *L. lucidum* (Hoyos *et al*. 2010). Overall, this study suggests that in conservation initiatives there should not be a unique strategy to prevent woody alien invasion given the contrasting functional syndromes that may be underlying their success.

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SUPPORTING INFORMATION

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

Appendix S1. List of all species considered in this study.

Appendix S2. Traits measured on representative native and alien woody species.

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