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 –
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 1440 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 Nmass and Pmass) 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 Nmass, Pmass 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 & Qui 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
Table 1. Traits measured on the most representative native and alien woody species of the montane woodland of central-western Argentina

<table>
<thead>
<tr>
<th>Trait</th>
<th>Type of variable</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leaf area</td>
<td>Continuous (mm²)</td>
</tr>
<tr>
<td>Specific leaf area</td>
<td>Continuous (mm² leaf area (mg leaf mass)⁻¹)</td>
</tr>
<tr>
<td>Leaf thickness</td>
<td>Continuous (mm)</td>
</tr>
<tr>
<td>Leaf toughness</td>
<td>Continuous (= leaf tensile strength; newton (mm leaf width)⁻¹)</td>
</tr>
<tr>
<td>Leaf phenology</td>
<td>Ordinal: 1 = deciduous; 2 = evergreen and semi-deciduous</td>
</tr>
<tr>
<td>Leaf nitrogen (Nmass %)</td>
<td>Continuous (foliar N concentration per unit leaf mass)</td>
</tr>
<tr>
<td>Leaf phosphorous (Pmass %)</td>
<td>Continuous (foliar P concentration per unit leaf mass)</td>
</tr>
<tr>
<td>Mycorrhizal status</td>
<td>Nominal: 1 = arbuscular mycorrhizal species; 2 = non-mycorrhizal species</td>
</tr>
<tr>
<td>Potential litter decomposition rate</td>
<td>Continuous (% of dry mass loss)</td>
</tr>
<tr>
<td>Stem-specific density</td>
<td>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).</td>
</tr>
<tr>
<td>Plant height</td>
<td>Continuous (cm)</td>
</tr>
<tr>
<td>Clonal spread</td>
<td>Binary: 0 = no evident clone expansion; 1 = clone expansion</td>
</tr>
<tr>
<td>Seed mass</td>
<td>Continuous (mg)</td>
</tr>
<tr>
<td>Dispersal mode</td>
<td>Nominal: 1 = unassisted; 2 = wind; 3 = mammals; 4 = birds</td>
</tr>
<tr>
<td>Fruiting phenology</td>
<td>Ordinal: 1 = spring, spring–summer, summer; 2 = summer–autumn, autumn; 3 = autumn–winter, winter, winter–spring</td>
</tr>
</tbody>
</table>

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.

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, Nmass and Pmass 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 Nmass, Pmass 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 (χ²–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 software 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...
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 $N_{\text{mass}}$, 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...
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 

*CONTRASTING SYNDROMES AMONG COEXISTING ALIENS 5*

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, Manihot grahamii, Melia azederach, Morus alba, Rubus ulmifolius and Ulmus pumila*).
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.

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

<table>
<thead>
<tr>
<th>Species attributes</th>
<th>n</th>
<th>Acquisitive alien spp.</th>
<th>n</th>
<th>Conservative alien spp.</th>
<th>n</th>
<th>Native spp.</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Specific leaf area (mm² mg⁻¹)</td>
<td>7</td>
<td>21.64 (a)</td>
<td>4</td>
<td>10.45 (b)</td>
<td>14</td>
<td>11.79 (b)</td>
<td>0.010</td>
</tr>
<tr>
<td>Leaf area (mm²)</td>
<td>7</td>
<td>13717.17 (a)</td>
<td>4</td>
<td>11187.56 (b)</td>
<td>14</td>
<td>1716.43 (b)</td>
<td>0.001</td>
</tr>
<tr>
<td>Leaf thickness (mm)</td>
<td>7</td>
<td>0.19 (a)</td>
<td>4</td>
<td>0.3 (b)</td>
<td>14</td>
<td>0.36 (b)</td>
<td>0.002</td>
</tr>
<tr>
<td>Leaf toughness (N mm⁻²)</td>
<td>7</td>
<td>0.47 (a)</td>
<td>4</td>
<td>0.9 (b)</td>
<td>14</td>
<td>1.16 (ab)</td>
<td>0.037</td>
</tr>
<tr>
<td>Plant height (cm)</td>
<td>7</td>
<td>581.52</td>
<td>4</td>
<td>492.76</td>
<td>14</td>
<td>355.81</td>
<td>0.107</td>
</tr>
<tr>
<td>Stem-specific density (g mL⁻¹)</td>
<td>7</td>
<td>0.49</td>
<td>4</td>
<td>0.62</td>
<td>14</td>
<td>0.70</td>
<td>0.101</td>
</tr>
<tr>
<td>Leaf Pₘₐₓ (%)</td>
<td>6</td>
<td>0.28 (a)</td>
<td>3</td>
<td>0.14 (b)</td>
<td>11</td>
<td>0.23 (ab)</td>
<td>0.016</td>
</tr>
<tr>
<td>Leaf Nₘₐₓ (%)</td>
<td>6</td>
<td>3.23 (a)</td>
<td>3</td>
<td>1.78 (b)</td>
<td>11</td>
<td>3.03 (a)</td>
<td>0.028</td>
</tr>
<tr>
<td>Decomposition (%)</td>
<td>3</td>
<td>61.37</td>
<td>3</td>
<td>50.67</td>
<td>7</td>
<td>74.66</td>
<td>0.196</td>
</tr>
<tr>
<td>Seed mass (mg)</td>
<td>7</td>
<td>114.95</td>
<td>4</td>
<td>12.52</td>
<td>14</td>
<td>47.94</td>
<td>0.268</td>
</tr>
<tr>
<td>Clonal spread (% spp.)</td>
<td>7</td>
<td>57</td>
<td>4</td>
<td>50</td>
<td>14</td>
<td>7</td>
<td>0.020</td>
</tr>
<tr>
<td>Leaf phenology (% deciduous spp.)</td>
<td>7</td>
<td>100</td>
<td>4</td>
<td>0</td>
<td>14</td>
<td>36</td>
<td>0.001</td>
</tr>
<tr>
<td>Mycorrhizal status (% spp.)</td>
<td>7</td>
<td>4</td>
<td>14</td>
<td>0</td>
<td>0</td>
<td>0.673</td>
<td></td>
</tr>
<tr>
<td>Arbuscular mycorrhizal spp.</td>
<td>100</td>
<td>100</td>
<td>86</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Non-mycorrhizal spp.</td>
<td>0</td>
<td>0</td>
<td>14</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dispersal mode (% spp.)</td>
<td>7</td>
<td>29</td>
<td>4</td>
<td>0</td>
<td>14</td>
<td>29</td>
<td>0.289</td>
</tr>
<tr>
<td>Wind</td>
<td>29</td>
<td>0</td>
<td>0</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mammals</td>
<td>14</td>
<td>0</td>
<td>14</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Birds</td>
<td>43</td>
<td>100</td>
<td>57</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Unassisted</td>
<td>14</td>
<td>0</td>
<td>29</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fruiting phenology (% spp.)</td>
<td>7</td>
<td>71.4</td>
<td>4</td>
<td>0</td>
<td>14</td>
<td>79</td>
<td>0.001</td>
</tr>
<tr>
<td>Spring, spring–summer, summer</td>
<td>71.4</td>
<td>0</td>
<td>0</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Summer–autumn, autumn</td>
<td>14.3</td>
<td>0</td>
<td>21</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Autumn–winter, winter</td>
<td>14.3</td>
<td>100</td>
<td>0</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

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; χ²–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.

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
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.

**ACKNOWLEDGEMENTS**

Research leading to this paper was supported by Universidad Nacional de Córdoba, CONICET, FONCyT (PICT-2008-953), SECyT-UNC, Agencia Córdoba Ciencia S.E., CYTED Project XII.5 (Spain), Darwin Initiative (DEFRA-UK) and the Inter-American Institute for Global Change Research (CRN II 2015 and CRN II 2005; supported by the US National Science Foundation Grant GEO-0452325). We are grateful to D.E. Gurvich, H. Cornelissen, the Associated Editor, the Managing Editor and an anonymous reviewer for useful comments on the manuscript. We also thank A. Mangeaud and F. Casanoves for statistical advices; and several members of the Plant Ecology and Phytogeography Group (IMBIV-UNC) for field assistance and discussions. All data are now deposited by the authors in the ecological database CORDOBASE. This database is a resource of Núcleo DiverSus (http://www.nucleodiversus.org) and is part of the TRY Worldwide Plant Trait Initiative (IGBP-DIVERSITAS-QUEST Jena Max Planck Institute; http://www.try-db.org).

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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.