

Do alien and native tree species from Central Argentina differ in their water transport strategy?

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Abstract In this study we assessed the water transport strategies and the abundance of alien and native tree species at a regional scale in Córdoba Mountains, Central Argentina. The aims of this study were: (i) to analyse whether alien and native tree species show divergent water transport strategies; and (ii) to explore whether species abundances of alien and natives are associated with specific trait attributes. Eight alien species and 12 native species were recorded in 50 complete vascular plant vegetation relevés. Water transport strategies were assessed through the following functional traits: minimum leaf water potential, potential water content of wood, effective leaf area, leaf area per sapwood area and wood density. Also, resource use strategies were assessed throughout the measurement of specific leaf area. We found that alien species had a higher efficiency in water transport (i.e. higher minimum leaf water potential and lower wood density values) and faster resource acquisition and use (higher specific leaf area values) than native species. We did not find evidence suggesting that the relative abundance of species was associated to water transport strategies and faster resource acquisition and use. Alien species seem to differ from natives in specific functional attributes that are absent in the resident community and might allow aliens to use more resources and at a higher rate than native species. Finally, our results show the potential of a trait-based predictive framework for alien species, and the possible effects on ecosystem functions.

Key words: alien woody species, biological invasions, functional ecology, leaf area per sapwood area, species abundance.

INTRODUCTION

Biological invasions are one of the most important worldwide factors that threaten global biodiversity (Sala *et al.* 2000; Mooney 2005) and affect ecosystem functioning (Zavaleta 2000; Crooks 2002; Le Maitre 2004). The success of alien species is often associated with a faster resource acquisition and use compared to native species (Leishman *et al.* 2007; Thompson & Davis 2011). Therefore, research focused on the differences in resource acquisition and use between alien and native species should contribute to the understanding of the mechanisms behind the invasion processes. However, until now these studies have reported contrasting results and have failed to develop general rules for explaining the mechanisms behind the invasion process (Daehler 2003; Pyšek & Richardson 2007; Thompson & Davis 2011).

In the last decades, several studies comparing alien and native species involving the leaf economics spectrum have reported that both groups of species may share a common strategy of carbon fixation (Leishman *et al.* 2007; Ordóñez & Olff 2013). That is, aliens and natives are located along the same trait–trait relation-

ships (Leishman *et al.* 2010). Nonetheless, alien species are at the fast return end of the relation, with higher leaf nutrient content and specific leaf area (SLA) than native species (Leishman *et al.* 2007, 2010; Ordóñez *et al.* 2010). Furthermore, Ordóñez and Olff (2013) have suggested that this pattern is mainly driven by non-woody species and that perhaps some different traits could explain some aspects of the invasiveness of alien woody species. Thereby, given the great importance of water in the physiology and performance of woody plants (Reich *et al.* 2003; Sperry *et al.* 2008; Poorter *et al.* 2010; Manzoni *et al.* 2013), when comparing alien and native woody species it might be fruitful to explore traits related to water conductance through the xylem (Funk 2013; Ordóñez & Olff 2013).

Several studies have found that an efficiency–safety trade-off in the hydraulic transport capacity of woody species exists (Zimmermann 1983; Tyree *et al.* 1994; Hacke & Sperry 2001b; Reich *et al.* 2003). This spectrum of variation summarizes a trade-off between traits that allow either for maximum rates of water uptake and use (efficient species with high leaf water potential (Ψ_1) and low wood density (W_d)) or a high resistance to water stress which confers a safe hydraulic system at the expense of low rates of water uptake and use (secure species with low Ψ_1 and high W_d ; Hacke *et al.* 2006;

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Sperry *et al.* 2008; Manzioni *et al.* 2013). Nonetheless, fewer studies have focused on the comparison of water transport traits between alien and native woody species (Stratton *et al.* 2000; Pratt & Black 2006; Caplan & Yeakley 2010). Pratt and Black (2006) compared five pairs of alien and native woody species from different regions in the USA, testing the hypothesis that alien species have a more secure water transport system than native species due to a higher cavitation resistance and lower hydraulic efficiency. However, they did not find differences among the alien and native species under comparison. In contrast, Stratton *et al.* (2000) have reported that native tree species in Hawaii show characteristics related to a more secure water transport system (i.e. lower hydraulic efficiency and Ψ_1), in comparison to the alien *Schinus terebinthifolius*, which has an efficient water transport system (i.e. higher hydraulic efficiency and Ψ_1). Besides, Cavaleri and Sack (2010) have found strong differences in water variables (i.e. stomatal conductance, pre-dawn leaf water potential, etc.) between specific paired alien and native species and, moreover, they reported a general tendency for a higher water use by alien species (i.e. higher daily sap flow rates per ground area). These results highlight not only that alien species may differ in water transport functional traits from native species, but also that studying these kinds of functional traits may be crucial to identify the potential impact of alien species in water cycling and ecosystem functioning (Le Maitre *et al.* 2000; Jobbágy *et al.* 2008, 2013; Boyce *et al.* 2012).

Most of the studies that compare functional traits between alien and native species do not account for the abundance of aliens in the community or are restricted to the dominant species (i.e. Thompson *et al.* 1995; Leishman *et al.* 2010; Ordonez *et al.* 2010; Tecco *et al.* 2010). This issue is noteworthy since species abundance is not only the result of a series of solely stochastic events (Adler *et al.* 2007), but it is also influenced by specific plant traits that might increase the probability of species success (Chesson 2000; Shipley *et al.* 2006; Cingolani *et al.* 2007). Consequently, if alien and native species with different abundance status were compared, specific functional traits related to their success could be detected (van Kleunen *et al.* 2010).

Cordoba Mountains in Central Argentina have been under an increasing invasion process by alien woody species for the last three to four decades (Giorgis *et al.* 2011a,b). Previous studies by Gurvich *et al.* (2005) and Tecco *et al.* (2010, 2013) have compared functional strategies between alien and native woody species in the area. Tecco *et al.* (2010) have found that most alien species possessed traits which enhance rates of resource capture and use, such as high SLA and leaf nitrogen content. Interestingly, none of these studies has considered water transport traits despite the fact that plants

must coordinate water conduction and photosynthetic systems in order to maximize growth rate and competitive ability of species (Brodribb & Feild 2000; Santiago *et al.* 2004; McDowell *et al.* 2008; McDowell & Sevanto 2010; Poorter *et al.* 2010; Sala *et al.* 2010; Reich 2014). On this basis, we expect that alien woody species that have successfully established in our study area will not only have a faster resource acquisition and use (i.e. throughout high SLA values), but will also have a more efficient water transport system (i.e. higher Ψ_1 and lower W_d) than native woody species. Additionally, and since an efficient water transport system might confer a higher competitive ability to species, we expect that the most abundant species both aliens and natives will have a more efficient water transport system. Based on the above, this study is aimed to (i) analyse whether alien and native tree species show divergent water transport strategies; and (2) identify whether tree species abundance of aliens and natives is associated with specific trait attributes.

MATERIALS AND METHODS

Study area and species selection

The study was carried out in xerophytic woodlands and shrublands close to the city of Salsipuedes (31°07'18"W, 64°19'13"S) in Córdoba Mountains, Central Argentina. The study area is located in the eastern slope of the Sierras Chicas range with an altitude around 750 m a.s.l. The mean annual temperature and precipitation are 15°C and 750 mm, respectively (De Fina 1992). Rainfall is concentrated in the warm season, from October to April. The original seasonally dry Chaco woodlands have been converted into a complex mosaic of vegetation, with small patches of closed forests in a matrix of open woodlands and shrublands (Zak & Cabido 2002; Gavier-Pizarro & Bucher 2004). As in other sites in Córdoba Mountains (Giorgis *et al.* 2011b) and Argentina (Speziale *et al.* 2012), this area has traditionally been occupied by European immigrants, who planted alien woody species as ornamentals. Some of these have spread from gardens and are now widely distributed in natural and semi-natural areas.

Tree species selection was based on 50 complete vascular vegetation relevés performed in the study area by Giorgis *et al.* (2011b) comprising an area of about 7000 ha. Each relevé comprised one plot of 400 m² with at least a 1% tree cover; all tree species were recorded and their percentage cover was visually estimated. The relative abundance was calculated for all species based on the percentage cover in each of the 50 plots (see Table 1). Species nomenclature follows Zuloaga *et al.* (2008) and plant status was defined following Richardson *et al.* (2000) and Pyšek *et al.* (2004). We considered as natives, those species that belong to the Chaco Serrano District within the Chaco Phytogeographical Province (Cabrera 1976), while alien species were those outside this region (as defined in Richardson & Rejmánek 2011, and Rejmánek & Richardson 2013). Besides, aliens were those

Table 1. List of species names, family, origin, relative abundance and mean values of each functional trait for 20 tree species found in the 50 complete vascular vegetation surveys in the Córdoba Mountains, Central Argentina

	Family	RA	Ψ_1	LA	SLA	LA/SA	W_d	WC_{sat}
Alien species names								
<i>Ligustrum lucidum</i> W.T. Aiton	Oleaceae	25.7	-2.4	2768.7	8.1	7304.5	0.69	80
<i>Morus alba</i> L.	Moraceae	2.9	-1.2	3771.7	24.5	4147.9	0.59	96
<i>Gleditsia triacanthos</i> L.	Fabaceae	2.6	-2.9	85.7	24.1	5006.1	0.58	80
<i>Melia azederach</i> L.	Meliaceae	1.5	-2.4	745.7	22.0	4398.6	0.5	108
<i>Manihot grahamii</i> Hook.	Euphorbiaceae	1.5	-1.3	967.6	21.3	8506.2	0.32	221
<i>Acer negundo</i> L.	Aceraceae	1.3	-2.1	2138	27.8	5391.3	0.48	111
<i>Ulmus pumila</i> L.	Ulmaceae	0.1	-2.1	1273.2	15.9	3150.3	0.5	97
<i>Jacaranda mimosifolia</i> D. Don	Bignoniaceae	0.1	-1.7	23.01	9.9	7959.8	0.51	125
Native species names								
<i>Lithraea molleoides</i> (vell.) Engl.	Anacardiaceae	27.5	-2.6	430.3	6.2	2015.2	0.58	57
<i>Condalia buxifolia</i> Reissek	Rhamnaceae	14.7	-4.9	74.8	5.9	2033.7	0.87	50
<i>Celtis ehrenbergiana</i> (Klotzsch) Liebm.	Celtidaceae	7.4	-3.7	409.6	8.8	2668.1	0.64	76
<i>Zanthoxylum coco</i> Gillies ex Hook. f & Arn.	Rutaceae	5.1	-2.6	275.1	11.5	2633.4	0.43	141
<i>Ruprechtia apetala</i> Wedd.	Poligonaceae	3.8	-2.6	1099.7	7.1	1400.1	0.7	69
<i>Aspidosperma quebracho-blanco</i> Schlttdl.	Apocynaceae	2.1	-3.6	248.7	5.1	3017.5	0.77	57
<i>Boungainvillea stipitata</i> Griseb.	Nyctaginaceae	1.4	-2.5	910.3	17.4	2072.3	0.48	120
<i>Kageneckia lanceolata</i> Ruiz & Pav.	Rosaceae	1.1	-2.6	431.3	11.5	4128.3	0.62	74
<i>Sebastiania commersoniana</i> (Baill.) L.B. Sm & B.J. Downs.	Euphorbiaceae	0.7	-2.4	403.3	8.5	1660.6	0.63	70
<i>Prosopis alba</i> Griseb.	Fabaceae	0.4	-3.7	25.2	8.5	2399.7	0.58	82
<i>Geoffroea decorticans</i> Gillies ex Hook. & Arn.	Fabaceae	0.1	-4.6	40.7	11.2	1349.8	0.64	73
<i>Jodina rhombifolia</i> (Hook. & Arn.) Reissek	Santalaceae	0.01	-3.3	531.4	1.2	2508.8	0.65	78

RA, relative abundance; Ψ_1 , minimum leaf water potential (Mpa); LA, leaf area (mm^2); SLA, specific leaf area ($\text{mm}^2 \text{mg}^{-1}$); LA/SA, leaf area per sapwood area ($\text{mm}^2 \text{mm}^{-2}$); W_d , wood density (g mL^{-1}); WC_{sat} , potential water content of wood (%).

species in a given area whose presence there is due to intentional or accidental introduction as a result of human activity (Richardson *et al.* 2000; Pyšek *et al.* 2004). A total of 20 tree species from 17 families and 20 genera were recorded in the 50 surveys; 8 species were aliens and 12 were natives (Table 1).

Trait measurements

The measurement of the selected functional traits was performed from February to March, and was based on standard protocols (Pérez-Harguindeguy *et al.* 2013). For all trait measurements, six individual plants per species were sampled. All the individuals were mature and without any evidence of damage by pathogens or herbivores. Only sun exposed leaves/branches were sampled.

To assess the efficiency and safety hydraulic transport trade-off we measured Ψ_1 , potential water content of wood (WC_{sat}), leaf area (LA) and leaf area per sapwood area (LA/SA). Wood density was considered as a functional trait associated with the efficiency-safety trade-off since it has an effect in determining the vulnerability of xylem conduits to cavitation (Hacke *et al.* 2001a). All these traits have been reported as good predictors of water transport strategies (Zimmermann 1983; Tyree *et al.* 1994; Ackerly 2004; Bhaskar & Ackerly 2006; Wright *et al.* 2006; Mitchell *et al.* 2008). We also measured SLA, a widely used trait that has been reported as an indicator of resource use strategies in relation to the leaf carbon economics spectrum (Westoby *et al.* 2002; Wright *et al.* 2004).

Minimum leaf water potential (MPa) was measured with a pressure chamber (Scholander *et al.* 1965). Measurements

were made at midday on sunny days (samples were collected from 12.30 to 13.00 h). Two leaves or short twigs were collected from each individual. Samples were placed and sealed in plastic bags and transferred promptly to the pressure chamber for measurement. All samples were measured within 60 min after collection.

For LA (mm^2) measurements, 10 leaves per individual were scanned and their area was calculated with Leaf Area© software (University of Sheffield, UK). For compound-leaved species, leaf size refers to the average size of leaflets. Then the samples were oven-dried (48 h at 70°C) and weighed to calculate SLA ($\text{mm}^2 \text{mg}^{-1}$). For W_d and WC_{sat} , one wood sample was taken per individual from the main trunk at a height of 1.5 m (diameter at breast height) using an increment borer. Wood cores were weighted after soaking them for 24 h (saturation mass), and then their volumes were calculated with the Archimedes' principle using a graduated test tube (10: 0.1 mL). Afterward, the samples were oven-dried (48 h at 70°C) and weighed. Wood density was determined as the dry mass per volume (g mL^{-1}) (Jacobsen *et al.* 2007, 2008), and WC_{sat} (%) was calculated as: [(saturation mass - dry mass) per dry mass] \times 100 (Borchert 1994). For the measurement of LA/SA ($\text{mm}^2 \text{mm}^{-2}$), the inverse of Huber value, two terminal branches per individual were cut at the level where the twigs had a diameter of approximately 1 cm. Sapwood-cross sectional area was calculated using the diameter of the twig from where it was cut and was measured with a digital caliper after the bark had been removed. All the leaves of each twig were oven-dried (48 h at 70°C) and weighed, and then the total LA per twig was calculated, multiplying total leaf dry mass per SLA (Wright *et al.* 2006).

Data analysis

In the first place, a principal components analysis (PCA) was used to examine the similarity relationships of tree species in terms of their water transport and resource use traits. For this purpose, an 6 trait \times 20 tree species matrix was subjected to PCA. Then, a general linear model (GLM) was performed with plant status as fixed effect and relative abundance of species as covariate. This was done in order to test differences between alien and native tree species regarding their functional traits and to identify whether tree species abundance of aliens and natives was related to specific trait attributes. Interactions were tested and included in the final model only when significant. In order to achieve normality and homoscedasticity requirements, LA, SLA, LA/SA and WC_{sat} were natural log transformed. All analyses were performed using the *vegan* and *stats* packages in R 2.15.1 (R Development Core Team 2012).

RESULTS

The first PC axis accounted for 59.12% of the variance, and was mainly explained by W_d (4.49; in brackets the eigenvector scores of the traits), which had a positive loading, and by Ψ_1 (-4.59), WC_{sat} (-4.50), SLA (-4) and LA/SA (-3.94), which had negative loadings (Fig. 1). PC axis 2 (18.19% of the variance) was mainly related to LA and W_d , which had positive loadings (6.10 and 3.94 respectively), and by WC_{sat} , which had a negative loading (-3.95). Tree species separation was observed only along axis 1 (Fig. 1). At one end of this axis we observed tree species with higher hydraulic conductivity (higher Ψ_1 and lower W_d)

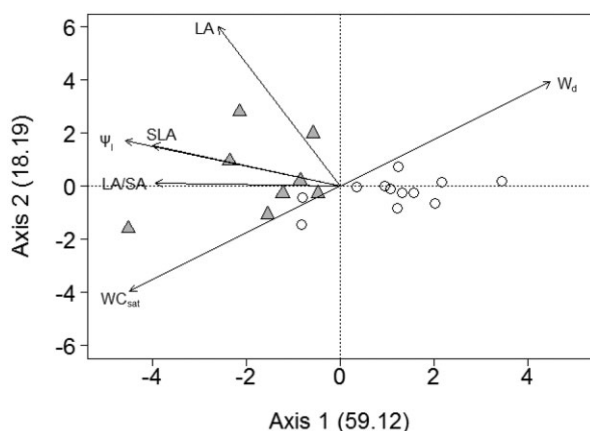


Fig. 1. PCA biplot ordination of 20 alien and native tree species on the basis of six functional traits (77.31% of the variance explained by the two-first principal components) from Córdoba Mountains, Central Argentina. Abbreviations: Ψ_1 , minimum leaf water potential (Mpa); SLA, specific leaf area ($\text{mm}^2 \text{mg}^{-1}$); LA/SA, leaf area per sapwood area ($\text{mm}^2 \text{mm}^{-2}$); LA, leaf area (mm^2); W_d , wood density (g mL^{-1}); WC_{sat} , potential water content of wood (%). Each dot is a species. Triangles are alien tree species; circles are native tree species.

and a faster resource acquisition (higher SLA; Fig. 1). On the other end, we observed tree species with a higher resistance to cavitation (lower Ψ_1 and higher W_d) and a slower resource acquisition (lower SLA; Fig. 1). Aliens and natives showed a clear separation along axis 1 (Fig. 1), reflecting divergence in their water transport and resource use traits. This trend was confirmed through the second analysis (GLM; Fig. 2). Aliens showed higher values for Ψ_1 ($F_{2,17\ 20} = 5.65$; $P = 0.01$, Fig. 2A), LA/SA ($F_{2,17\ 20} = 16.8$; $P = 0.001$; Fig. 2B), WC_{sat} ($F_{2,17\ 20} = 5.6$; $P = 0.01$; Fig. 2C) and SLA ($F_{2,17\ 20} = 5.8$; $P = 0.01$; Fig. 2D); and lower values for W_d ($F_{2,17\ 20} = 3.54$; $P = 0.05$; Fig. 2E), than natives. The relative abundance of aliens and natives was not associated with the functional traits attributes (Appendix S1). Furthermore, because to the interaction term (plant status \times relative abundance) was not significant (Appendix S1), it was not taken into account when we performed the GLM.

DISCUSSION

Our study showed that alien and native tree species not only have contrasting water transport strategies, but also are located at different ends of the leaf economic spectrum. Also, we did not find any relationship between the abundance of species and the occurrence of certain functional traits attributes. Our results also show that alien species presented a strategy towards a more efficient water transport system in which they optimized higher water conduction at the expense of becoming more vulnerable to cavitation. This strategy may promote higher transpiration and growth rate (Vander Willigen & Pammenter 1998; Manzoni *et al.* 2013). In contrast, native species showed a strategy towards a more secure water transport with a higher cavitation resistance but with lower water conduction capacity. This functional strategy derives in low transpiration and growth rates (Reich *et al.* 2003). Consequently, alien species do not seem to be physically constrained in resource acquisition and use as native ones are. Therefore, under the same supply of resource alien species could allocate more resources to leaf biomass and photosynthetic system than native species (Keane & Crawley 2002), with an enhancement of their competitive ability.

In agreement with previous studies (Leishman *et al.* 2007, 2010; Ordonez & Olff 2013), we found that along the leaf economics spectrum alien tree species present a faster growth strategy than native tree species. The highest values in SLA and the lowest values in W_d , observed in alien species, have been linked to an acquisitive strategy that might confer aliens higher resource capture ability and growth rates (Enquist *et al.* 1999; Vendramini *et al.* 2002; Nascimento *et al.* 2005; King *et al.* 2006; Poorter *et al.*

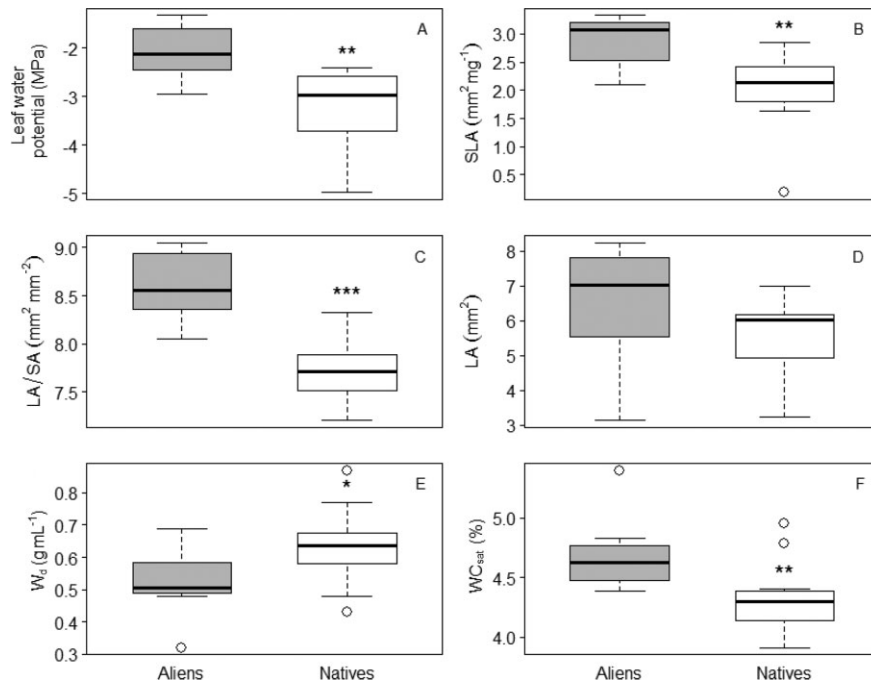


Fig. 2. Box plots of functional traits of alien and native species. (A) Ψ_1 , leaf water potential (MPa); (B) SLA, specific leaf area ($\text{mm}^2 \text{mg}^{-1}$); (C) LA/SA, leaf area per sapwood area ($\text{mm}^2 \text{mm}^{-2}$); (D) LA, leaf area (mm^2); (E) W_d , wood density (g mL^{-1}); (F) WC_{sat} , potential water content of wood (%). Gray boxes are alien tree species; White boxes are native tree species. Asterisk means significant differences: * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.

2010). This result is in line with previous findings reported for the study area (Tecco *et al.* 2010, 2013) and other places of the world (Ordonez *et al.* 2010; Godoy *et al.* 2011; Shen *et al.* 2011), in which it has been found that alien species have an acquisitive strategy. Overall, these characteristics and those reflecting an efficient water transport system, could confer a higher growth rate to alien trees and hence a higher competitive ability than native tree species (Stratton & Goldstein 2001; Díaz *et al.* 2004; Allred *et al.* 2010; Shen *et al.* 2011). In consequence, this competitive ability may facilitate the establishment and spread of alien tree species into new areas.

In a seasonal ecosystem like our study area, the alien success could be promoted by LA/SA differences between alien and native tree species. That is, aliens may allocate more resource to leaf biomass through a higher leaf quality (high SLA) than native species. Therefore, this attribute might allow alien species not only to have a fast foliage recovery in the wet season, but also to reach higher leaf biomass than native trees with a direct impact on growth rate (Grady *et al.* 2013). On the contrary, during the dry period this trait confers a water stress tolerance to species. That is, plants can rapidly adjust to changes in environmental conditions by shedding or producing leaves (Bhaskar & Ackerly 2006). Therefore, species might maintain a constant water supply in order to mitigate the increase of transpiration rate, caused by a high vapour pressure deficit or by a decrease in soil water content (Bhaskar

& Ackerly 2006). Consequently, the higher LA/SA values of alien species could allow them to have a higher plastic response to changes in environmental conditions than native species.

Despite the functional traits divergence reported in this study between alien and native tree species, we did not find any evidence suggesting that the relative abundance of species could be associated with water transport strategies and the leaf economics spectrum. This result highlighted that despite the fact that alien establishment and spread could be related to their functional traits attributes (Dietz & Edwards 2006; Schlaepfer *et al.* 2010), their abundance was not related to alien invasiveness through the functional traits attributes measured. In addition, Cingolani *et al.* (2007) found that trait attributes which determine the probability of a species to be present in a given community are not necessarily the same as those which determine its probability of becoming abundant. Furthermore, we cannot discard other ecological processes like habitat requirements and propagules pressure (Colautti *et al.* 2006; Simberloff 2009), which could be important in determining the success of aliens.

Although our study was focused mainly on understanding some aspects of the mechanisms behind invasion processes, our findings may also provide insights into the effects of alien trees on ecosystem processes (Lavorel & Garnier 2002). One of the major ecosystem services that mountains provide is water yield (Viviroli & Weingartner 2004; Brown *et al.* 2005; Brauman *et al.*

2007; Mark & Dickinson 2008). Furthermore, most of the rivers in Central-Western Argentina originate in mountain systems (Cingolani *et al.* 2010), and the water yielded is the main source for the population surrounding the mountains (around 3 million people in Córdoba province). Our results report that alien trees present trait attributes (i.e. higher Ψ_1 and lower W_d) that suggest a higher growth rate and daily sap flow rates per unit of sapwood area than native tree species, which in turn suggest that the replacement of native by alien trees would alter the water balance by increasing evapotranspiration (Jackson *et al.* 1999; Zhang *et al.* 1999; Jobbágy *et al.* 2008, 2013; Boyce *et al.* 2012).

In conclusion, alien species seem to differ from natives in specific functional trait attributes that are absent in the resident community and might allow aliens to use more resources and at a higher rate than native species (Gurvich *et al.* 2005; Funk & Vitousek 2007). Following the patterns described in this paper and because variability of resource acquisition and use vary in space and time, it is likely that alien trees may increase their competitive ability over natives during the wet season (Gavier-Pizarro *et al.* 2012). Furthermore, alien species have the potential to use more water than native species during the wet season, with deep effects on the water cycle. Also, the establishment of alien species in our study area indicates that drought tolerance is not a prerequisite for alien success (Stratton *et al.* 2000; Caplan & Yeakley 2010). Finally, our results highlight the huge potential of a trait-based predictive framework to understand some aspects behind the mechanisms involved in the invasion process by alien trees and also could be useful to predict possible ecosystem effects of biological invasions (Cavaleri & Sack 2010).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. General linear model (GLM) results for plant status and relative abundance of each functional trait.