Original article

The importance of native and exotic plant identity and dominance on decomposition patterns in mountain woodlands of central Argentina

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ABSTRACT

Exotic species can have a strong influence on ecosystem processes, especially when exotic invaders differ from natives in key morpho-functional features. We explored whether exotic species, especially those forming monospecific patches in Chaco montane woodlands, differ from natives in leaf attributes and decomposability. We then evaluated how exotic monospecific patches in that region alter litter decomposability, by weighting leaf trait values and decomposability by species abundance in the communities. In general, native and exotic species from Córdoba Chaco montane woodlands did not differ in leaf attributes (specific leaf area, leaf toughness, and leaf water content), or decomposability. Because of similar trait values and decomposability, we expected to find no differences in litter decomposability between plots dominated by exotic species and those of Native woodland. However, individual species decomposability weighted by species abundance in the communities showed that litter from exotic monospecific plots had slower decomposition than native ones. This pattern was confirmed by the higher decomposability and higher quality of the naturally mixed litter collected from native plots, compared to those collected from exotic plots. Despite the general similarities between most native and exotic species inhabiting Chaco montane woodlands, the overwhelming dominance of some exotic invaders in monospecific stands (and the consequent weight of their attributes on the litter each woodland produces) might be driving differences in decomposition patterns between woodland types. Our results indicate that when estimating the impact of exotic species on ecosystem processes, we should include their relative abundance in the community, as well as the relevance of the traits influencing those processes. Otherwise, we may draw erroneous conclusions.

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1. Introduction

There is now consensus that species identity, abundance, and leaf attributes affect ecosystem processes — such as decomposition and nutrient cycling — in terrestrial ecosystems around the world (Chapin et al., 2002; Garnier et al., 2004; Wardle et al., 2004; Díaz et al., 2005, 2007). Accordingly, the presence of exotic species in an ecosystem can produce not only profound changes in community structure, but also in ecosystem functioning (Mack et al., 2000; Liao et al., 2008; Godoy et al., 2010).

It has been proposed that exotic plants may have a strong influence on ecosystem processes, particularly when exotic invaders differ from natives in key morpho-functional features, such as physical and chemical properties of their leaves (Wilsey and Polley, 2006; Litton and Giardina, 2008; Peltzer et al., 2010; Wardle et al., 2011). In turn, according to the biomass ratio hypothesis (i.e., "the extent to which a plant species affects ecosystem functions is likely to be closely predictable from its contribution to total plant biomass"; Grime, 1998), the impact of exotic species may be much stronger if they account for a high proportion of the ecosystem biomass (Metcalfe et al., 2011). If so, differences in morpho-functional features may be reflected in differences in community litter quality and nutrient-cycling rates (Ehrenfeld, 2003, 2004; Liao et al., 2008; Kurokawa et al., 2010; Metcalfe et al., 2011). Up to the present, most studies that link plant invasion with decomposition

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have dealt with a low number of species, focused on particular regions, or included some functional groups more frequently than others (Godoy et al., 2010; Wardle et al., 2011). In a recent meta-analysis, Liao et al. (2008) found that plant invasions generally increase litter decomposition rates, probably because of higher nitrogen concentration in invasive plants than in native ones (Allison and Vitousek, 2004). Higher decomposition in exotic species was also found in Mediterranean ecosystems, where the specific leaf area of invaders was larger than that of native species (Castro-Díez et al., 2009). By contrast, slower decomposition of invasive exotics in grasslands and other ecosystems of North America was associated with higher polyphenolic content, higher lignin content and higher carbon to nitrogen ratio (Drenovsky and Batten, 2007; Knight et al., 2007). These contradictory findings suggest that it is still necessary to deal with general principles to improve our ability to predict the impact of exotic species on real ecosystems through field experiments (Davis et al., 2011; Wardle et al., 2011; Moles et al., 2012). We agree with Wardle et al. (2011) that a trait-based framework (Lavorel and Garnier, 2002; Hooper et al., 2005; Suding et al., 2008) integrated to the predictions of the biomass ratio hypothesis (Grime, 1998) is crucial for the assessment of invader impact from a functional perspective (Davis et al., 2011).

Several exotic plants have established in natural and suburban communities in the Córdoba mountains of central Argentina (Tecco, 2006; Giorgis et al., 2011a, 2011b). Among them, some exotic woody species (Ligustrum lucidum, Gleditsia triacanthos and Pinus spp.) are currently spreading and generating large monospecific patches (Gavier and Bucher, 2004; Hoyos et al., 2010; Giorgis et al., 2011a, 2011b; Gavier-Pizarro et al., 2012). In a screening of exotic species from different ecosystems in central-western Argentina, Tecco et al. (2010) found morpho-functional similarities in living leaf attributes of native and exotic herbaceous species, as well as significant differences between native and exotic woody species. Whether functional differences between natives and exotics result in different litter quality (Ehrenfeld, 2004) and, therefore, different decomposability, is still a matter of debate (Leishman et al., 2007; Liao et al., 2008; Kurokawa et al., 2010; Davis et al., 2011; Metcalfe et al., 2011).

The goal of our work was to assess if exotic species, especially those that form monospecific patches, differ from natives in decomposability (Cornelissen, 1996). We also analysed if such differences could be attributed to living leaf attributes of the species in question (species level analysis). Based on this information and by weighting decomposability values by species abundance in the communities, we evaluated how the presence of exotic monospecific patches in Córdoba Chaco montane woodlands would alter litter decomposability (plot level analysis). We hypothesised that differences in morpho-functional features between exotic and native species would result in differences in litter quality (Ehrenfeld, 2004), and therefore in litter decomposability. Additionally, if decomposability of natural litter mixtures depends on dominant species decomposability (Grime, 1998; Garnier et al., 2004), decomposability of naturally mixed litter produced in each woodland type (exotic monospecific and native woodlands) will also be different.

2. Methods

2.1. Study area

The study was conducted in Sierras Chicas of Córdoba mountains, central Argentina. We selected experimental plots in the surroundings of the localities of La Granja (31°00′S 64°16′W), Salsipuedes (31°08′S 64°19′W) and Unquillo (31°14′S 64°19′W), at approximately 700 m asl. Mean annual precipitation in the area is about 950 mm (concentrated in summer) and mean annual temperature is 17.5 °C (De Fina, 1992). Vegetation in the area is typical of Chaco montane woodlands and is dominated by Lithraea molleoides (Vell.) Engl., Celtis ehrenbergiana (Klotzsch) Liebm., Acacia caven (Molina) Molina, and Condalia buxifolia Reissek (Luti et al., 1979). However, livestock grazing, logging and frequent burning have largely transformed the original woodland into a mosaic of open woodlands (hereafter Native woodland), secondary shrublands, and grasslands (Zak and Cabido, 2002; Gavier and Bucher, 2004). Recently, the spread of exotic woody species introduced for ornamental or forestry purposes has added monospecific patches of exotic woodlands to the previously described mosaic (Hoyos et al., 2010; Giorgis et al., 2011a, 2011b; Gavier-Pizarro et al., 2012).

We selected three monospecific types of exotic woodlands patches (1 ha), each one dominated by one of the most important invasive species in the region: L. lucidum W. T. Aiton (Glossy privet), G. triacanthos L. (Honey locust), and Pinus elliottii Engelm (Pine). For each type of exotic woodland, we randomly selected three 20 × 20 m plots. Additionally, we selected three plots of Native woodland. All plots were located along a fringe (5 km wide, 15 km long) on the eastern slope of the Sierras Chicas mountain range, to keep edaphic conditions and slope aspect constant. Because of high species heterogeneity in the Native woodlands, we randomly selected three subplots (20 × 20 m) within each Native plot. To compare native and exotic woodlands, all floristic censuses and litter measurements (see below) were performed in each Native woodland subplot and then averaged to obtain a single value per plot.

We recorded all vascular plant species growing in each plot and estimated their relative percent cover. Those measurements were used to weight species decomposability values based on the abundance of each species within each type of woodland (see below). Nomenclature and origin (native or exotic) of species followed Zuloaga et al. (1994) and Zuloaga and Morrone (1996, 1999), with species counting as exotic when not of South American origin.

2.2. Species selection and litter preparation

Based on Tecco (2006), we selected 29 plant species representative of the vegetation of the study area. We included 17 woody species (12 exotic and 5 native), 8 herbaceous dicots (2 exotic and 6 native) and 4 graminoids (2 exotic and 2 native; see Appendix A). We collected 10 litter replicates per species and air-dried the material. Each replicate consisted of freshly senesced, undecomposed leaves from at least one individual. Additionally, to characterize the naturally mixed litter produced in each woodland type, we obtained a composite litter sample by collecting all litter present in three 50 × 50 cm quadrats randomly placed in each forest plot (hereafter Honey locust woodland litter mixture, Glossy privet woodland litter mixture, Pine woodland litter mixture and Native woodland litter mixture). Naturally mixed litter samples were mainly composed of leaves, branches and bark, as well as of a small percentage (less than 10%) of seeds, fruits and mosses. Naturally mixed litter from exotic monospecific patches was dominated by the leaf litter of dominant exotic species, whereas there were no dominant species in Native woodland mixtures.

Decomposition experiments were carried out following the methodology used by Cornelissen (1996). We weighed samples of each species (1.0 ± 0.1 g, 10 replicates), and then sealed each one into tube-shaped nylon bags of 0.3 mm mesh (i.e., 10 litterbags per species). We used this mesh size to avoid the loss of small litter fragments. Although this mesh size precludes the access of mesofauna, its contribution to decomposition is relatively small

compared with the activity of bacteria, protozoa and fungi (Anderson et al., 1983; Cornelissen, 1996; Pérez Harguindeguy et al., 2000). We also prepared litterbags with the naturally mixed litter occurring in each woodland type (i.e., 3 litterbags per plot, 9 litterbags per woodland type). These litterbags contained 2 ± 0.1 g of each sample. To estimate true dry mass before litterbag burial we first calculated air-dried water content. We air-dried a sub-sample of each species and of each naturally mixed litter, and then oven-dried it at 50 °C during 48 h. Water content (%) was calculated from the mass loss in samples after drying.

2.3. Litter incubation

We incubated all litterbags (containing litter of a single species or naturally mixed litter) simultaneously during summer (January and February 2009) in a decomposition bed constructed at the study area. All samples were under the same incubation conditions (soil, temperature, humidity, soil decomposer communities) to ensure that decomposition values obtained were solely driven by litter quality (Cornelissen, 1996; Cornelissen et al., 1999). The decomposition bed consisted of a 9-m^2 portion of soil, cleaned of plant material and litter. We randomly placed all litter samples in the decomposition bed with one side of the litterbag in contact with soil. We covered all litterbags with the plant litter material that was previously removed. Finally, we covered the decomposition bed with a galvanized wire mesh to protect litterbags from animals. Despite this, some litterbags were lost before harvest.

Litterbags were harvested after 6 weeks of incubation, when mass loss was 60% or less. After harvesting, samples were stored at −14 °C until processing. Once samples were defrosted, we removed adhered soil, soil micro-fauna and other extraneous material (like small roots) from the decomposed leaf litter by gentle brushing. Then, all samples were oven-dried at 50 °C during 3 days and weighed with a precision balance to estimate litter mass loss. Since litterbags can be contaminated with soil, we corrected litter mass loss for ash content to determine decomposability as the effective loss of organic matter (ash free dry mass). We randomly selected three (out of 10) samples of decomposed and undecomposed litter of each species, and determined ash content by burning the samples in an oven at 500 °C for 4 h (Harmon and Lajtha, 1999; Vivanco and Austin, 2006). The percentage of ashes obtained was subtracted from dry weight to correct for contamination. We followed the same procedure to correct for soil contamination in all woodland litter mixtures (three mixtures per woodland type).

2.4. Leaf morpho-functional traits

To evaluate if differences in litter decomposability among species are related to morpho-functional features of their green leaves, we characterized the 29 species selected in terms of three vegetative leaf traits: specific leaf area (SLA) (i.e., one-sided area of a fresh leaf divided by its oven-dry mass), leaf tensile strength (LTS) (i.e., force needed to tear apart a fragment of leaf of known width), and leaf water content (LWC) (i.e., percentage of water in relation to total leaf weight). These traits were reported as strong predictors of species decomposition in species of the study area (Vaieretti et al., 2005) as well as in other ecosystems (Cortez et al., 2007). We obtained trait data from Tecco (2006), in which all traits were measured following the procedures described by Cornelissen et al. (2003) on green leaves of healthy, sexually mature plants, growing in unshaded habitats of the study site. The values used were the average of at least five replicates per species (see Appendix A for mean trait values).

2.5. Litter chemical quality

We analysed a subsample of naturally mixed litter of each forest (three replicates per woodland type) to determine its Carbon (C), Nitrogen (N), Lignin, Cellulose and Hemicellulose content. Total C was estimated as 50% of ash-free biomass (Schlesinger, 1977; McClaugherty et al., 1985; Gallardo and Merino, 1993). Total N was measured using an Autoanalyser (RFA 300-Alpken, Wilsonville, OR, USA). Lignin, Cellulose and Hemicellulose contents were measured following the technique of Goering and Van Soest (1970) at the Chemical Analyses Laboratory of INTA Bariloche. We calculated two indices that reflect the chemical quality of the litter samples: (1) *total fibre content of litter* (LCH = lignin + cellulose + hemicellulose) and (2) *holocellulose: lignocellulose ratio* (HLQ = (cellulose + hemicellulose)/LCH) (Berg, 1984; McClaugherty and Berg, 1987; Vaieretti et al., 2005).

2.6. Data analysis

To describe floristic composition of plots, we performed a detrended correspondence analysis (DCA, Legendre and Legendre, 1998) of the census data matrix (160 species × 12 plots). We calculated species richness within each plot (Magurran, 1988) and differences in species richness between woodland types by ANOVA and LSD Fisher test (Sokal and Rohlf, 1995).

For all analyses, we calculated decomposability (of litter from single species and of naturally mixed litter) as *percentage of litter mass loss* (i.e., difference between ash-free initial litter dry weight and litter dry weight after incubation, hereafter %LML; see 2.3 for a detailed explanation of ashes correction). At the *species level*, we assessed differences in %LML between native and exotic species using ANOVA with a nested structure design of the treatment (i.e., status: native vs. exotic) to maintain intraspecific variability. Then we evaluated differences in green leaf traits (means of SLA, LWC, and LTS) between native and exotic species using Mann–Whitney test. The relationship between species %LML and species leaf morpho-functional features was assessed with Spearman Rank correlations. At the *plot level*, we calculated the aggregated plot decomposability, as proposed by Garnier et al. (2004), based on species decomposability weighted by its abundance in each plot. We used cover as a measure of abundance. We calculated aggregated values (hereafter weighted values) using the general equation proposed by Garnier et al. (2004):

$$\text{trait}_{agg} = \sum_{i=1}^{n} p_i \times \text{trait}_i$$

where trait$_{agg}$ is the weighted %LML in each plot, p_i is the relative abundance (% cover) of species i, n is the number of species studied, and trait$_i$ is the decomposability of species i. We then evaluated differences in weighted %LML between woodlands using ANOVA, with woodland type as main effect. We applied an *a posteriori* LSD-Fisher test to identify differences among woodland means. We used the same analysis to assess differences in decomposability between natural woodlands mixtures. We analysed the relationship between weighted% LML values of plots and the decomposability of forest litter mixtures (in the decomposition bed) with Spearman Rank correlations. We used the same analysis to evaluate the relationship between decomposability of litter mixtures and chemical quality (N and non-labile compounds).

In all cases %LML data did not show normal distribution or homogeneous variances, and we could not apply log or any other transformations. Hence, we rank-transformed the data and conducted ANOVAs (same models as above) on rank data (Zar, 1999).
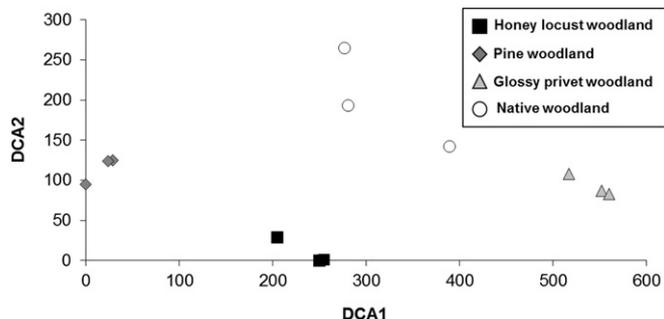
Fig. 1. Detrended correspondence analysis (DCA) of the 12 experimental plots (four types of forests) on the basis of their floristic composition (33.3% of the variance explained by the two first axes; DCA1 = 25.2 and DCA2 = 8.1). Dot symbols and grey scale indicate the type of forest of each plot (see reference in the figure).

Results of these non-parametric analyses were similar to those of parametric ANOVAs run on the non-transformed data, indicating that the analysis used had enough power (Zar, 1999). All statistical analyses were performed with *Infostat* Version 2011 (Di Rienzo et al., 2011) and PCord software (McCune and Mefford, 2011).

3. Results

The distribution of the plots along both DCA axes (Fig. 1) confirmed our assumption of differences in floristic composition among different types of woodland. The eigenvalues were 0.841 and 0.272 for DCA axis 1 and 2, respectively. The broader distribution of native plots than of exotic plots along DCA axes suggests higher floristic heterogeneity in the Native woodlands than in any of the exotic woodland types. Accordingly, we found significant differences in species richness among woodland types ($F = 10.12$, $p = 0.0043$). Native woodland and Honey locust woodland showed the highest number of species (about 50 and 44 species, respectively), followed by Pine woodland (34 species). Glossy privet woodland had the lowest richness value of all woodland types (16 species).

3.1. Do native and exotic species differ in decomposability and leaf traits in the Chaco montane woodland?

At the species level, in general, decomposability (%LML) did not differ between native and exotic species ($F = 1.30$, $p = 0.2648$). This trend was also observed within herbaceous species (native vs. exotic), as well as within woody species ($F = 0.23$, $p = 0.6427$; and $F = 1.71$, $p = 0.2107$, respectively). Percentages of litter mass loss of exotic species were interspersed with those of natives. Despite this, decomposability values of woody exotics that form monospecific

patches (*G. triacanthos*, *L. lucidum* and *P. elliottii*) tended to be lower than those of most natives (Fig. 2).

Native and exotic species also did not differ in their leaf trait values (SLA: $p = 0.5060$ $W = 16.00$; LWC: $p = 0.3390$ $W = 240.00$; LTS: $p = 0.7214$ $W = 209.00$). This trend was also non-significant when comparing native and exotic species within herbaceous or woody species separately. Litter decomposability (%LML) was significantly correlated with all morpho-functional traits measured in green leaves. Regardless of species origin (exotic vs. native), species with high leaf litter decomposability had leaves with high SLA, high LWC and low LST (Spearman correlation: $r_s = 0.43$, $r_s = 0.57$ and $r_s = -0.40$, respectively, $p < 0.05$ in all cases).

3.2. Do native and exotic forest patches differ in decomposability and litter quality?

Plot level analysis (i.e., leaf litter decomposability weighted by its abundance in the plot), showed that litter from Native woodlands had the highest decomposability, whereas that from Pine woodlands had the lowest litter decomposability (Fig. 3). Both Glossy privet and Honey locust woodlands had intermediate values (Fig. 3). Plot weighted decomposability was significantly correlated with that of naturally mixed litter of each woodland type (Spearman index: $r_s = 0.66$, $p = 0.03$).

The analysis of decomposability of naturally mixed litter of each woodland type also showed higher decomposability in mixtures from Native woodland than in Pine woodland and Honey locust woodland mixtures (Fig. 4). However, in this analysis, Native woodland did not differ from Glossy privet woodland (Fig. 4). The high decomposability of Native woodlands (and Glossy privet woodland) was associated with a high nutrient content and a low content of recalcitrant compounds (Spearman correlation indices: $r_s = 0.73$ and $r_s = -0.78$ for N and LCH, respectively; $p < 0.05$ in both cases). See appendix B for details on litter quality parameters.

4. Discussion

Our first goal was to assess possible differences in decomposability among exotic species and if those differences could be attributed to the living leaf attributes of the species. We found that, in general, native and exotic species from Córdoba Chaco montane woodlands did not differ in the leaf attributes measured (specific leaf area, leaf toughness and leaf water content) and, therefore, did not differ in decomposability. We only found a trend for those woody exotic species that form monospecific patches to decompose slowly (Fig. 2).

Both leaf toughness and leaf water content (or its counterpart, leaf dry matter content) have been reported as fundamental drivers of species decomposability in the study region (Pérez-Harguindeguy
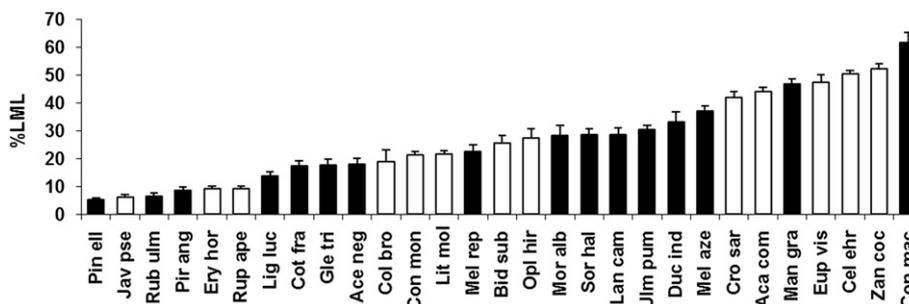

Fig. 2. Decomposability measured as percentage of litter mass loss (%LML) of all native (white) and exotic (black) species included in this study. Bars indicate means of litter mass loss after 43 days of incubation in common garden experiment. Scientific names are abbreviated using the first three letters of the genus and species (see full name in Appendix A).
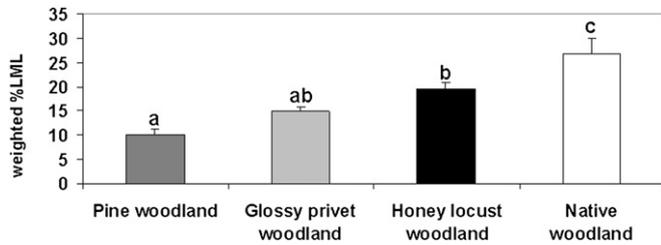
Fig. 3. Differences in potential decomposability among woodland types ($F = 25.93$, $p = 0.0002$) considering species individual decomposability (in a common garden experiment) weighted by its plot abundance (see equation in Methods section). Bars provide means of weighted percentages of litter mass loss within each plot of each type of forest. Letters indicate significant differences (LSD-Fisher test, $p < 0.05$).

et al., 2000; Vaieretti et al., 2005) as well as in other systems (Cornelissen et al., 1999; Cortez et al., 2007; Fortunel et al., 2009). The similarities in decomposability patterns between native and exotic woody species found in the present work are therefore consistent with the similarities in leaf attributes.

The functional likeness among herbaceous species, regardless of origin, is consistent with previous findings in the region (Tecco et al., 2010), as well as in other systems (Thompson et al., 1995). For woody species, a recent survey in mountain woodlands (Tecco et al., 2012) showed both divergence and convergence in functional leaf traits (including SLA, nutrient content and leaf toughness) between exotics and natives. Indeed, some of the woody exotics analysed in that survey showed softer, thinner, nutrient-richer leaves, and higher specific leaf area than natives. In turn, other woody exotics had, as natives, thick, tough, long-lived leaves with low nutrient content. Our study, together with the results presented by Tecco et al. (2012), confirm the existence of contrasting functional strategies among exotic species, even within the same ecosystem.

Differences and similarities in species attributes in relation to invasiveness and success of exotics have been widely documented in the literature (Callaway and Ridenour, 2004; Strauss et al., 2006; among others). Much less attention, however, has been paid to the effect of attributes on ecosystem processes (Davis et al., 2011). In a meta-analysis including 94 experimental studies, Liao et al. (2008) found that invasion of woody species had greater impact on carbon and nitrogen cycles than invasion of herbaceous species. However, Kurokawa et al. (2010) reported exceptions to that pattern. Based on the general similarities in trait values and decomposability found in our experiment, we expected to find no differences in decomposability between plots dominated by exotic species and those of Native woodland. Nevertheless, when we weighted individual species decomposability by species abundance in the communities, we found lower decomposability in exotic
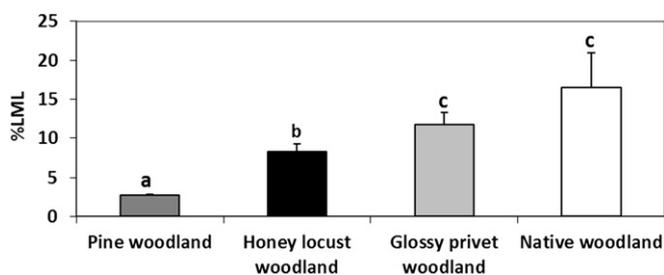
monospecific plots than in native ones, particularly in Pine plots. Despite the general likeness in decomposability between native and exotic species, Native woodlands had overall higher decomposability than exotic woodlands at the plot level (when compared through the weighted means of their component species). This pattern was not an artefact of the weighting procedure, as it was confirmed by the higher decomposability and litter quality of the natural mixtures collected from native plots than of those collected from exotic plots (particularly Pine and Honey locust woodland).

Our study shows that even in the absence of important differences in trait values between native and exotic species, small differences in decomposability (i.e., a trend of lower decomposability in those woody exotics that form mono-specific patches) can be increased by big differences in their abundance. Consequently, those highly dominant species can significantly change ecosystem decomposability, and therefore may strongly alter nutrient cycling.

The influence of exotic species on community dynamics and ecosystem function has been recognized as associated with the novelty of their attributes relative to those of natives (Callaway and Ridenour, 2004; Wardle et al., 2011). Up to the present, however, conclusive evidence for this is scarce (Davis et al., 2011). In the present study, exotic species, especially those that form monospecific patches, do not clearly differ from natives in their trait values. Yet, the analysis at the plot level and from an ecosystem perspective did show differences. This result indicates that a trait-based framework integrated to the biomass ratio hypothesis (Grime, 1998; Garnier et al., 2004; Kazakou et al., 2006; De Deyn et al., 2008; Fortunel et al., 2009; Pakeman et al., 2011) would be essential to understand the effects of exotic species on ecosystem processes and properties (see Wardle et al., 2011). Despite the general trait similarities between most native and exotic species in this study, the overwhelming dominance of the exotic invaders in their respective monospecific stands and their major contribution to litter stocks and overall litter quality would be driving the differential patterns of decomposition between woodland types. It is still not known whether decomposition rates could also be affected by differences in micro-environmental conditions associated with variations in stand structure (Belyea, 1996; Hector et al., 2000; Martínez-Yrízar et al., 2007; Furey, 2010). The effects and interactions of micro-environment, decomposers and decomposability on the different woodland types are still difficult to predict and represent an interesting research avenue.

5. Conclusions

This study suggests that exotic status itself may not be a good indicator of potential effect of exotic species on natural ecosystems (Davis et al., 2011), unless plant trait values are weighted relative to plant abundance. Invasive woody species (i.e., species capable of structural dominance over large mono-specific stands) might be promoting changes in key processes, such as decomposition, consequently affecting nutrient cycling and productivity of the invaded system. These changes would be associated with small differences in litter quality between native and exotic species, which translate into changes in plot-level litter decomposability due to strong dominance of exotic species. Inferring the impact of exotic species on ecosystem processes, without considering their relative abundance in the community and the traits that are relevant to ecosystem processes might lead to erroneous conclusions. In Córdoba Chaco montane woodlands, the dominance of woody invaders is likely to have a strong influence on ecosystem-level decomposition rates, and therefore on nutrient cycling, via changes in litter quality and decomposability mediated by changes in community floristic identity and abundance.

Fig. 4. Differences in decomposability of naturally mixed litter between woodland types incubated at a common garden experiment ($F = 16.57$, $p < 0.0001$). Bars indicate means of litter mass loss within each plot of each woodland type. Letters indicate significant differences (LSD-Fisher test, $p < 0.05$).

Acknowledgements

Appendix A

Complete name and family affiliation of all native and exotic species considered in our study. Mean values of leaf traits and mean cover in plots of each type of woodland is also provided. A total of 29 species were considered: 17 woody species (12 exotic and 5 native); 8 herbaceous dicots (2 exotic and 6 native) and 4 graminoids (2 exotic and 2 native). Specific leaf area (SLA), leaf tensile strength (SLT) and leaf water content (LWC) values were obtained from Tecco (2006). Woodland type names are abbreviated as HL (Honey locust woodland), GP (Glossy privet woodland), P (Pine woodland) and N (Native woodland).

Species	Family	Origin	SLA (mm^2/g)	LST (Nmm-1)	LWC (%)	Species cover (%)			
						HL	GP	*P*	*N*
Woody species									
Acer negundo L.	Aceraceae	Exotic	13.24	0.53	0.69	0.33	3.50	0	0.44
Cotoneaster franchetii Bois	Rosaceae	Exotic	9.52	0.62	0.50	1.33	0	0	2.28
Gleditsia triacanthos L.	Fabaceae	Exotic	10.03	0.84	0.63	80.00	0	0	0
Lantana camara L.	Verbenaceae	Exotic	10.74	0.38	0.68	0.17	0	0	1.00
Ligustrum lucidum W. T. Aiton	Oleaceae	Exotic	5.76	0.76	0.69	0.33	92.67	1.33	2.22
Manihot grahamii Hook.	Euphorbiaceae	Exotic	19.89	0.46	0.70	0	0.17	0	0
Melia azedarach L.	Meliaceae	Exotic	9.25	0.43	0.66	0.50	0	0	0
Morus alba L.	Moraceae	Exotic	10.70	0.28	0.60	0.50	0	0	0.11
Pinus elliottii Engelm.	Pinaceae	Exotic	2.88	9.39	0.53	0	0	70.83	0
Pyracantha angustifolia (Franch.) C.K. Scheind.	Rosaceae	Exotic	7.98	1.31	0.48	12.83	0.17	0	0
Rubus ulmifolius Schott[a]	Rosaceae	Exotic	14.84	0.42	0.58	0	0	0	0
Ulmus pumila L.	Ulmaceae	Exotic	6.90	0.26	0.57	0	0	1.67	0
Celtis ehrenbergiana (kltzsch) Liebm.	Celtidaceae	Native	6.36	0.63	0.66	1.33	1.83	0	10.33
Condalia montana A. Cast.	Ramnaceae	Native	8.28	0.92	0.45	10.33	0	0	0.67
Lithraea molleoides (Vell.) Engl.	Anacardiaceae	Native	6.50	0.83	0.55	12.67	1.33	0.33	47.78
Ruprechtia apetala Wedd.	Polygonaceae	Native	5.31	0.30	0.55	0	0	0	2.00
Zanthonxylum coco Gillies ex Hook. F. & Arn.	Rutaceae	Native	9.91	0.58	0.71	0	0	0.67	8.00
Herbaceous dicots									
Conium maculatum L.	Apiaceae	Exotic	32.27	0.560	0.83	0	0	0	0.33
Duchesnea indica (Andrews) Focke	Rosaceae	Exotic	24.01	0.390	0.73	0.83	0.33	0.17	0.39
Acalypha communis Müll. Arg.	Euphorbiaceae	Native	8.04	0.670	0.70	0	0	0.67	0.39
Bidens subalternans DC.	Asteraceae	Native	23.07	0.321	0.88	0.33	0	15.00	3.00
Cologania broussonetii (Balb.) DC.	Fabaceae	Native	28.50	0.378	0.74	2.00	0.17	3.17	0.33
Croton sarcopetalus Müll. Arg.	Euphorbiaceae	Native	12.38	0.446	0.76	3.33	0	0.50	1.56
Eryngium horridum Malme	Apiaceae	Native	3.08	4.690	0.73	0	0	1.00	0
Eupatorium viscidum Hook. & Arn.	Asteraceae	Native	21.35	0.253	0.75	0.33	0.17	0	3.72
Graminoids									
Melinis repens (Willd.) Zizka[a]	Poaceae	Exotic	23.88	2.71	0.64	0	0	0	0
Sorghum halepense (L.) Pers.[a]	Poaceae	Exotic	17.86	0.99	0.68	0	0	0	0
Jarava pseudoichu (Caro) F. Rojas	Poaceae	Native	4.80	22.35	0.44	3.33	0	2.67	11.39
Oplismenus hirtellus (L.) P. Beauv.	Poaceae	Native	44.33	0.46	0.72	19.00	1.00	0	18.17

[a] Absent in the study plots, but present in surroundings of the study site. According to Giorgis et al. (2011a,b), the percentage of relative frequency of these three species are: 0.69 for *Rubus ulmifolius*, 2.52 for *Melinis repens*, and 0.69 for *Sorghum halepense* (based on floristic surveys in 471 plot (20 × 20 m) distributed among mountain Chaco woodlands of central-western Argentina).

Appendix B

Chemical quality of naturally mixed litter. Carbon (C), Nitrogen (N), Lignin, Cellulose and Hemicellulose content. Two indexes that reflect the chemical quality of the litter samples are also provided: (1) *total fibre content of litter* (LCH = lignin + cellulose + hemicellulose) and (2) *holocellulose: lignocellulose ratio* (HLQ = (cellulose + hemicellulose)/LCH).

Woodland	Carbon (%)	Nitrogen (%)	Lignin (%)	Cellulose (%)	Hemicellulose (%)	LCH	HLQ
Native	44.22	1.78	29.14	24.39	4.66	58.18	0.50
Honey locust	43.45	1.13	29.37	25.10	4.30	58.77	0.50
Pine	48.55	0.56	38.31	25.53	0.00	63.84	0.40
Glossy privet	44.41	1.21	22.62	16.77	3.53	42.92	0.47

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