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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 morphofunctional 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 metaanalysis, 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; Hovos 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 \times 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 meso-fauna, its contribution to decomposition is relatively small

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