

# Direct and indirect effects of invasion by the alien tree *Ailanthus altissima* on riparian plant communities and ecosystem multifunctionality

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**Abstract** Most existing studies addressing the effects of invasive species on biodiversity focus on species richness ignoring better indicators of biodiversity and better predictors of ecosystem functioning such as the diversity of evolutionary histories (phylogenetic diversity). Moreover, no previous study has separated the direct effect of alien plants on multiple ecosystem functions simultaneously (multifunctionality) from those indirect ones mediated by the decrease on biodiversity caused by alien plants. We aimed to analyze direct and indirect effects, mediated or not by

its effect on biodiversity, of the invasive tree *Ailanthus altissima* on ecosystem multifunctionality of riparian habitats under Mediterranean climate. We measured vegetation attributes (species richness and phylogenetic diversity) and several surrogates of ecosystem functioning (understory plant biomass, soil enzyme activities, available phosphorous and organic matter) in plots infested by *A. altissima* and in control (non-invaded) ones. We used structural equation modelling to tease apart the direct and indirect effects of *A. altissima* on ecosystem multifunctionality. Our results suggest that lower plant species richness, phylogenetic diversity and multifunctionality were associated to the presence of *A. altissima*. When analyzing each function separately, we found that biodiversity has the opposite effect of the alien plant on all the different functions measured, therefore reducing the strength of the effect (either positive or negative) of *A. altissima* on them.

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Soraya Constán-Nava and Santiago Soliveres have contributed equally to this work.

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This is one of the few existing studies addressing the effect of invasive species on phylodiversity and also studying the effect of invasive species on multiple ecosystem functions simultaneously.

**Keywords** Biodiversity · Ecosystem function · Invasive species · Path analysis · Phylodiversity · Riparian forests

## Introduction

Invasive plant species are a major threat to biodiversity and ecosystem functioning in many ecosystems around the world (Vitousek et al. 1997; Liao et al. 2008; Vilà et al. 2011). In recent years, there has been increasing interest on the effects of invasive species on species composition, community structure and ecosystem functioning of invaded habitats (Williamson 1998; Simberloff et al. 2003; Cantero et al. 2003). Previous research shows that plant invasions reduce the diversity of plants (Vilà et al. 2011) and animals (Pyšek et al. 2012), modify soil properties and alter nutrient cycles, native microbial communities and their associated ecosystem processes (Ehrenfeld 2003; Wolfe and Klironomos 2005; Weidenhamer and Callaway 2010).

Most existing studies deal with these effects of invasive plants separately, focusing either on biodiversity or on ecosystem functioning, thus ignoring the well-known relationship that exists between both ecosystem properties. Many ecosystem functions (*sensu* Reiss et al. 2009; Jax 2010) are known to be enhanced with greater species richness (e.g., Tilman et al. 1997; Zavaleta et al. 2010; Maestre et al. 2012a). Therefore, reduced diversity or alterations in the composition and structure of vegetation, often documented in invaded ecosystems, can result in indirect changes of ecosystem functioning. The presence of invasive species can also directly affect ecosystem functions through a variety of mechanisms, such as by

releasing allelopathic compounds, altering nutrient availability, or by soil salinisation (e.g., Vitousek 1986; Levine et al. 2003). Thus, we are still far from achieving a full mechanistic understanding of the effect that alien plants have on ecosystems. It is unclear if their effect on ecosystem functioning is direct or indirect, mediated or not by their effect on biodiversity. Insight into the nature of the effects of invasive species on ecosystem functions and services may help to improve the body of theory regarding the ecology of invasions. Although seldom applied to the effects of plant invasions, assessing the directness or indirectness of its effect has proven very useful to guide management aimed to minimize the impacts of anthropogenic changes on ecosystem functioning (Isbell et al. 2013). Along these lines, including this framework in the assessment of the effect of alien plants could increase the efficiency of management and restoration plans by providing insights of the main factors driving ecosystem degradation.

Most of the existing studies regarding the effect of invasive plants on biodiversity focus solely on the number of species as a measure of biodiversity ignoring other indicators of biodiversity which are more closely related to ecosystem functioning, such as the diversity of evolutionary histories or phylogenetic diversity (Forest et al. 2007; Maherali and Klironomos 2007; see also Santoro et al. 2012; Hejda and de Bello 2013; Bennett et al. 2014). Numerous important ecological traits, such as co-evolved relationships with N-fixing bacteria or other soil organisms, are preserved through evolutionary times (Flynn et al. 2011; Milcu et al. 2013). Therefore, phylogenetic diversity (hereafter phylodiversity) is thought to be a good surrogate for the diversity of functional forms present in a given community (Prinzing et al. 2001; Webb et al. 2002). Species assemblages containing phylogenetically diverse species are more likely to provide a greater range of different ecosystem functions and services than communities formed by functionally similar species (Forest et al. 2007; Maherali and Klironomos 2007; Flynn et al. 2011). This is so because mechanisms often invoked to justify the relationship between species diversity and ecosystem functions, such as complementarity in the use of resources, interspecific positive interactions or the existence of trade-offs in important ecological traits featuring different species (Cardinale et al. 2007; Zavaleta et al. 2010) are more likely to occur between phylogenetically distant species

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(Burns and Strauss 2011; Soliveres et al. 2012). As a result, phylodiversity can provide critical information to help understand the functional effects of biodiversity loss (Forest et al. 2007; Maherali and Klironomos 2007; Cadotte et al. 2008).

While the study of ecosystem functions and the services they provide has been a major topic in ecology in recent years (reviewed in Hooper et al. 2005), most of these studies focus on single functions or processes. However, we must study the effect of a given factor (e.g., invasive species) on ecosystem functioning whilst considering multiple ecosystem functions simultaneously (multifunctionality: Hector and Bagchi 2007; Gamfeldt et al. 2008; Zavaleta et al. 2010; Maestre et al. 2012a). Studying multiple ecosystem functions simultaneously is crucial, since different ecosystem processes or services may be affected by a given factor, but in different ways (Zavaleta et al. 2010). Hence, analyzing single functions could result in contradictory results and misleading conclusions of the role of a given factor in ecosystem processes and services. For instance, due to their high growth rates, invasive species could enhance C-sequestration through increases in plant productivity, and reduce soil erosion in the midterm (Liao et al. 2008; Vilà et al. 2011). However, they may also simultaneously slow down nutrient cycling, or reduce soil fertility or ecosystem resilience due to their elevated nutrient uptake or the release of allelopathic compounds, reducing ecosystem functionality (Liao et al. 2008; Godoy et al. 2010; Weidenhamer and Callaway 2010). This is especially relevant considering the reduction of species richness (Gaertner et al. 2009; Vilà et al. 2011), functional diversity (Hejda and de Bello 2013) or phylodiversity (Bennett et al. 2014) found in ecosystems affected by the invasion of alien species. The minimum number of species required to maintain ecosystem functioning increase with the number of functions considered (Hector and Bagchi 2007; Gamfeldt et al. 2008; Zavaleta et al. 2010). Therefore, the indirect impact of alien species on ecosystem functioning could be much higher than previously suggested by studies that focus solely on single functions or processes.

We aimed to analyze the direct and indirect effects, mediated or not by its effect on biodiversity, of the invasive tree *Ailanthus altissima* on the ecosystem multifunctionality of riparian habitats under Mediterranean climate. We measured vegetation and soil attributes,

together with different ecosystem functions in invaded and non-invaded riparian forests. Our main hypotheses were (1) *A. altissima* reduces not only species richness, but also the phylodiversity of neighboring vegetation (Bennett et al. 2014), (2) the effect on ecosystem multifunctionality caused by *A. altissima* is direct through its known effects on nutrient cycles and soil properties, and 3) the effects of *A. altissima* on vegetation diversity indirectly alter ecosystem multifunctionality.

## Materials and methods

### Study area

The study was conducted in riparian forests at water courses and streams located in the Site of European Community Importance (Directive 92/43/CEE) SCI Serres de Mariola i el Carrascar de la Font Roja, in South-East Spain (38°40'46"N, 0°31'19"W). This is one of the Mediterranean Basin's most important areas regarding diversity since it has acted as flora refuge after climatic change in the Mediterranean since the Pleistocene (Serra et al. 2003; Médail and Diadema 2009). The climate is Mediterranean, with a mean annual precipitation and temperature of 647 mm and 14.7 °C, respectively (Bocairent meteorological station located in the study area, at 641 m.a.s.l.; Data from the period 1985–2006 for temperature and 1966–2006 for precipitation). Soils are xerorthents on limestone, with the presence of impermeable clays. Vegetation in riparian ecosystems is especially important for numerous ecological processes, such as providing habitat for wildlife, stabilizing riverbanks, filtering sediments and nutrients into streams and influencing soil properties (see Forman and Godron 1986; Décamps 1993; Tabacchi et al. 2000). The presence of invasive species in such ecosystems, therefore, is likely to alter ecosystem functions indirectly by reducing the high levels of plant diversity they hold. Moreover, invasive plants can alter ecosystem multifunctionality directly by bank destabilization, lowering water tables, soil salinisation, changing channel capacity for flood flow or altering nutrient cycling (e.g., Mooney and Drake 1986; Tu 2003; Hulme and Bremner 2006; Follstad Shah et al. 2010).

*Ailanthus altissima* (Mill.) Swingle (Simaroubaceae), our target species, is a deciduous tree from China and North Vietnam that has become an

invasive species since the eighteenth century because of its use both for ornamental and landscape restoration purposes (Kowarik and Säumel 2007). It has occupied numerous ecosystems in the Mediterranean Basin, such as disturbed urban areas, old fields, pine and oak forests and riparian communities (Kowarik 1983; Constán-Nava et al. 2007; Kowarik and Säumel 2007). *A. altissima* is known to affect ecosystem functioning and vegetation composition, structure and dynamics (Lawrence et al. 1991; Vilà et al. 2006; Motard et al. 2011). Previous research has shown that *A. altissima* enhances or diminishes, in comparison with control (uninvaded) areas, different ecosystem attributes. It is known that *A. altissima* reduces plant diversity (Vilà et al. 2006; Motard et al. 2011), alters N cycling (Castro-Díez et al. 2009), slows down litter decomposition, and increases the total N, organic C, C/N ratio and pH in the soils it colonizes (Vilà et al. 2006; Gómez-Aparicio and Canham 2008; Godoy et al. 2010; but see Castro-Díez et al. 2012). The importance of plants for multiple ecosystem functions and the sensitivity of riparian ecosystems to invasion, together with the well-known effects on both diversity and several ecosystem functions caused by *A. altissima*, make both this study area and this species suitable targets for studying both direct and indirect effects of invasive plants on ecosystem multifunctionality.

### Study set-up

We established ten 10 m × 10 m control plots (without *A. altissima*) and ten 10 m × 10 m plots infested with the invasive species [canopy cover of *A. altissima* (young and adults trees) >85 %] in riparian forests in July 2008 and 2009 (Fig. S1). Distance to the closer water course was always similar among all our plots (20–10 m). Thus we do not think that differences in flooding or soil saturation, very infrequent events under the climate of our study area, would affect our results. We acknowledge that this is an observational study and that we cannot be certain of the causal relationship between *Ailanthus*' invasion and the changes in ecosystem properties registered. However, two evidences support the notion that *A. altissima* invasion is the cause of changes in diversity and multifunctionality registered and not the other way around: (1) management and disturbance levels of

both invaded and non-invaded plots have remained exactly the same as the study area has been protected for over 30 years (Natural Protected Area staff, personal comm.), and (2) the difference in the degree of invasion between control and invaded plots is more likely to be caused by dispersal limitation rather than by initial differences among the plots. In support of this latter statement, invaded plots were closer than control plots to roadsides (one way ANOVA,  $F_{1,19} = 4.8$ ;  $P = 0.042$ ; Table 1), a well-known dispersal corridor for this species (Kowarik and von der Lippe 2006, 2011). It must be noted, however, that *A. altissima*, can also disperse by water (Säumel and Kowarik 2010, 2013).

Plant communities in both control and invaded plots were dominated by mature populations formed by relatively large (10–15 m) trees. We randomly placed forty 0.5 × 0.5 m quadrats within each plot and we visually estimated percentage of plant cover according to species. To complete the species richness sampling, we then searched the whole plot for any other species present in the plot but not encountered within the quadrats. In half of the sampled quadrats ( $n = 20$ ), we also visually estimated the percentage of soil surface covered by litter. In five quadrats per plot, we removed all the plant biomass of shrubs and herbs and transported it to the laboratory where it was oven-dried at 50 °C until constant weight was achieved. Tree biomass was not removed because of the important ecological role and conservation value that riparian trees hold in the study area. We were only interested in the effect of *A. altissima* on soils at the plot-level scale and not in the within-plot heterogeneity. Thus, we took a composite sample, implicitly including this within-plot heterogeneity, from five different randomly located soil cores of 30 cm depth. Since both invaded and non-invaded plots were dominated by trees, distances from the soil sample to a tree were always <2 m. We acknowledge that most plant limiting resources are concentrated in the top 20 cm of the soil (Jobbágy and Jackson 2000). However, we sampled slightly deeper (30 cm) as we wanted to account for the potential effect on soil salinization predicted for some alien plants in riparian systems (e.g., Vitousek 1986; Levine et al. 2003), and salt accumulation is known to occur at deeper soil profiles (Jobbágy and Jackson 2001). Although it is likely that our decision makes us to under-estimate soil nutrient concentrations, we do not see any reason for it to affect their response to plant

**Table 1** Characteristics of the studied plots; UTM coordinates (X, Y), distance to nearest road (m), distance to nearest building (m), species richness, and the phylogenetic species evenness (PSE) of Control and *Ailanthus* plots

	X	Y	Distance to nearest road (m)	Distance to nearest building (m)	Species richness	PSE
Control plots						
1	709597	4294362	375	370	24	0.25
2	709626	4294321	430	350	23	0.23
3	709834	4294518	315	180	35	0.37
4	709770	4294609	210	160	32	0.31
5	705060	4286873	90	25	32	0.35
6	705394	4287098	495	350	22	0.29
7	706046	4287571	1,300	1,150	17	0.23
8	705927	4287486	1,140	1,030	19	0.33
9	706478	4288288	2,105	1,960	23	0.25
10	706508	4288480	2,280	2,140	24	0.30
Average			874	771.5	25.1	0.29
<i>Ailanthus</i> plots						
1	709608	4294743	8	115	27	0.20
2	716414	4285184	26	219	14	0.17
3	715063	4286121	11	19	13	0.17
4	704655	4286858	33	45	17	0.15
5	709587	4294775	25	77	16	0.20
6	706296	4288086	1,810	1,700	19	0.20
7	717407	4284810	30	6	22	0.21
8	704687	4286882	3	75	9	0.06
9	716138	4285412	7	16	5	0.01
10	707970	4293597	17	1,900	6	0.07
Average			197	417.2	14.8	0.14

invasion. Both control and invaded sites are dominated by trees and, therefore, no major changes in soil nutrient re-distribution across the soil profile are expected (Jobbágy and Jackson 2000).

Soil samples were oven-dried at 50 °C during 72 h in the laboratory and sieved to obtain the fraction <2 mm, which was used for the analyses described below. Soils were collected after removing the litter layer and during the dry period of summer, as this minimizes experimental noise due to microbial growth flushes as a consequence of rain pulses (see Maestre et al. 2012a, b for example). For all the statistical analyses described below, each one of the 20 plots was our sample size as this was the scale of our interest. Samples within each site could not be considered independent and we were not interested in *A. altissima* effects on intra-site heterogeneity, therefore, the average of the subsamples taken in each one of these plots was used.

#### Analysis of soil functions and attributes

We measured variables representing indirectly ecosystem functions (sensu Jax 2010; soil organic matter, soil enzymes, biomass). We measured  $\beta$ -glucosidase and acid phosphatase soil enzymatic activities, soil organic matter and available phosphorous, and the understory plant dry biomass (described above). Both enzyme activities were estimated using the methodology described in Tabatabai (1982;  $\beta$ -glucosidase) and Tabatabai and Bremner (1969; acid phosphatase). Organic matter (OM) was measured using the Walkley–Black acid digestion method (CMA 1973). The available phosphorus was analyzed by  $\text{NaHCO}_3$  extraction (Watanabe and Olsen 1965). The functional variables measured in this study are known to be strongly related to key ecosystem processes, such as ecosystem productivity (plant biomass: Tilman 1988; Flombaum and Sala 2008), Carbon cycling ( $\beta$ -

glucosidase: Tabatabai 1982), Phosphorus cycling (phosphatase, available phosphorous: e.g., Sinsabaugh et al. 2008; Maestre and Puche 2009) or water infiltration and water holding capacity (organic matter: Maestre et al. 2012a).

To characterize soil attributes at each site, we also analyzed pH, electric conductivity (EC) and litter cover as soil attributes. EC and pH were measured in 1:2.5 mass:volume soil and water suspension (CMA 1973). We acknowledge that both pH and EC are crucial for many ecosystem processes and probably should be included as functional variables. However, they could confound our multifunctionality measure (see below) since high values of such variables do not necessarily mean high levels of particular ecosystem functions. On the other hand, litter cover *per se* cannot be regarded as a functional measure, since litter chemistry, but not litter amount, can play a key role in several ecosystem functions (Reich et al. 2005). Hence, we analyzed the effect of *A. altissima* invasion on such variables but did not include them in our index of multifunctionality.

#### Measurement of evolutionary relationships

We assembled a phylogenetic tree for the 115 species included in this study (see species list in Table S1 and phylogenetic tree in Fig. S2), using the Phylomatic function available at Phylocom 4.1 software (Webb et al. 2008). All families in the dataset matched the family names of the angiosperm megatree used in Phylomatic (R20100701.new), which was based on the APG III phylogenetic classification of flowering plant orders and families (Angiosperm Phylogeny Group 2009). Phylogenetic relationships were further resolved based on data from various published molecular phylogenies [Apiaceae (Downie et al. 2000), Asteraceae (Funk et al. 2009), Dipsacales (Winkworth et al. 2008), Lamiids (Bell et al. 2010), Fabaceae (Steele et al. 2010), Poaceae (Bouchenak-Khelladi et al. 2008), Rosaceae (Potter et al. 2007)].

After assembling the phylogenetic tree, we adjusted its branch lengths using the Phylocom BLADJ algorithm, which fixes the age of internal nodes based on clade age estimates, whereas undated internal nodes in the phylogeny are spaced evenly (Webb et al. 2008). Thus, BLADJ is a simple tool that fixes the root node of a phylogeny at a specified age, as well as other nodes for which age estimates are available. It sets all

other branch lengths by placing the nodes evenly between dated nodes, as well as between dated nodes and terminals (of age 0). We search for divergence time estimations in the TimeTree database (Hedges et al. 2006; <http://www.timetree.org>). TimeTree uses a hierarchical tree-based system to identify all published molecular time estimates bearing on the divergence of two chosen taxa (e.g., species), to compute summary statistics and to present the results. We mainly used this database to fix the ages of internal nodes on our phylogenetic hypothesis, completing TimeTree results with other published sources when this database did not provide any date (Lavin et al. 2005; Besnard et al. 2009; Bremer and Eriksson 2009; Bell et al. 2010; Bouchenak-Khelladi et al. 2008; Torices 2010; Wang et al. 2010). The procedure described above resulted in the fixation of 80 nodes (representing more than 70 % of our tree's internal nodes; Figure S2).

#### Data reduction

We avoided conducting an elevated number of analyses on the high number of response variables obtained by using different methodologies to summarize the dataset. Firstly, we organized soil variables not included in our multifunctionality index (pH, EC, litter cover) and reduced these to a single synthetic variable by using principal component analysis (PCA). Prior to the PCA, we standardized (*sensu* Anderson et al. 2008) the three variables, subtracting the mean and dividing by its standard deviation. With this a priori data transformation, we homogenized units for all the variables. Therefore the greater influence of a given variable was diminished, simply by using different units (i.e., parts per million instead of percentage). The first axis of the PCA explained 79.1 % of the variation in the data (eigenvalue = 8.98) and so this first axis was used to infer the effects of *A. altissima* on soil attributes (hereafter, this first PCA axis will be referred to as “soil attributes”). This “soil attributes” axis was highly related to litter cover (eigenvector = 0.803) and pH (eigenvector = -0.530), but not to EC (eigenvector = -0.273).

Secondly, to summarize variables related to ecosystem functioning, we calculated the multifunctionality index recently proposed by Maestre et al. 2012b (see below). The use of this index improved two aspects of the results: (1) reduce the five variables (understory biomass,  $\beta$ -glucosidase and acid

**Table 2** Summary of the standardized direct and total effects for the separate SEM analyses performed for each of the ecosystem functions studied. Control versus invaded = values of a given variable in the control versus invaded plots (mean  $\pm$  SE,  $n = 10$ ). Results for both functional variables and soil attributes are given

Soil variable	<i>Ailanthus altissima</i> effect		Control versus invaded	Percentage of change
	Direct	Total (direct + indirect)		
<i>Functions</i>				
Soil organic matter (%)	-0.46	-0.23	7.1 $\pm$ 1.0 versus 5.9 $\pm$ 0.4	-17 %
Available phosphorus (ppm)	0.42	0.24	11.7 $\pm$ 1.5 versus 15.9 $\pm$ 3.8	+36 %
Phosphatase activity ( $\mu\text{mol PnP g}^{-1} \text{h}^{-1}$ )	0.64	0.32	0.9 $\pm$ 0.1 versus 1.4 $\pm$ 0.3	+56 %
$\beta$ -Glucosidase activity ( $\mu\text{mol PnP g}^{-1} \text{h}^{-1}$ )	-0.73	-0.35	2.2 $\pm$ 0.2 versus 1.9 $\pm$ 0.1	-14 %
Understorey biomass (g 0.5 m <sup>2</sup> )	-0.79	-0.86	45.6 $\pm$ 5.3 versus 5.6 $\pm$ 1.7	-88 %
<i>Attributes</i>				
Ph	0.07	0.13	7.6 $\pm$ 0.0 versus 7.7 $\pm$ 0.0	+0.5 %
Electrical conductivity (mS/cm)	-0.01	-0.31	3.5 $\pm$ 0.3 versus 3.5 $\pm$ 0.7	+0.2 %
Litter cover (%)	-0.31	-0.33	88.4 $\pm$ 6.3 versus 87.6 $\pm$ 4.0	-1 %

phosphatase activities, soil available phosphorous and organic matter) to one, therefore reducing multiple testing, and (2) allow us the assessment of the effect of *A. altissima* on the ecosystem's ability to maintain multiple functions simultaneously. To calculate this multifunctionality index, we first found the maximum level of a given function within the 20 study plots. Then, we calculated the percentage of this maximum level achieved by each of the 20 studied plots and for each of the five studied functions. The average of these percentages for all the functions was used as our index of multifunctionality for each plot (Zavaleta et al. 2010; Maestre et al. 2012b). Since this averaging can mask the effect of *A. altissima* or biodiversity on each individual function, we also provide the results of the effect of *A. altissima* on each ecosystem function separately (Table 2). None of the functional variables were correlated ( $P$  values  $> 0.2$  in all cases) with the exception of understorey biomass versus phosphatase activity ( $\rho = -0.44$ ;  $P = 0.05$ ; Table S2).

A substantial number of indices have been proposed to evaluate different aspects of phylogenetic diversity (see Helmus et al. 2007; Vamوسي et al. 2009; Pausas and Verdú 2010 for recent reviews), including the most widely-used and accepted of these: the mean phylogenetic distance (MPD), the mean nearest taxon distance (MNTD), the phylogenetic species variability (PSV) and the phylogenetic species evenness (PSE; see Webb et al. 2002; Helmus et al. 2007; Kraft et al. 2007). In this study, all of these indices were strongly correlated ( $r > 0.5$  in all cases) and yielded

qualitatively similar results regarding the effect of *A. altissima* invasion and their relationships with ecosystem multifunctionality. For simplicity, only the results regarding PSE are shown here. This value incorporates both phylogenetic and species abundance information; its variability is less sensitive to sample size and it does not depend on species richness (Helmus et al. 2007). The maximum value of PSE (maximum phylogenetic diversity) is 1, corresponding to a community formed by evolutionarily independent species (referred to as "star phylogeny") and to equal abundances of those species (complete evenness).

#### Statistical analyses

We used structural equation modelling (SEM; Grace 2006) to test for the effect of *A. altissima* on biodiversity and multifunctionality. In this technique, an a priori theoretical model describing the causal relationships among variables is established allowing the partition of the direct and indirect effects among variables in a systems context (Shipley 2000). These relationships are expressed as standardized path coefficients, which range between 0-1 and are mathematically related to a regression weight or partial correlation coefficient. These path coefficients estimate the influence that one variable has on another. Probability tests for these path coefficients are employed to test for significant departures from zero. Our a priori model predicted the existence of both a direct and indirect (mediated by its effect on biodiversity) effect of *A. altissima* [introduced

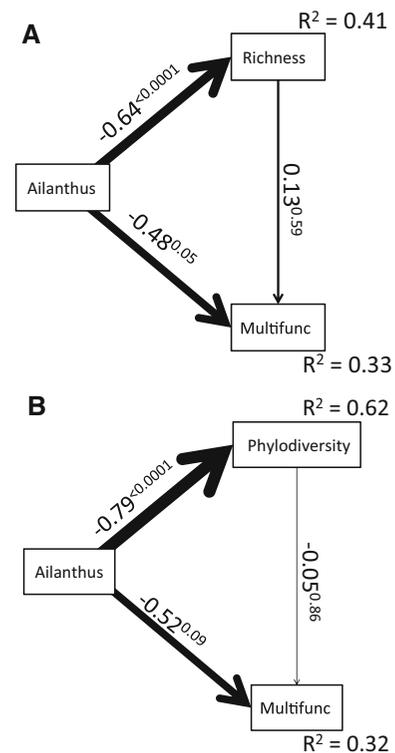
as a binomial variable (present/absent) on multifunctionality. We included *A. altissima* invasion as a binomial variable rather than as continuous (i.e., *A. altissima*'s abundance) as we considered it more statistically correct. *A. altissima*'s cover had two contrasted levels [very high (>85 %) and very low (<5 %)] and introducing it as a continuous variable would not be correct.

Separate analyses were carried out to test the effect of *A. altissima* invasion on species richness or phylodiversity (PSE). Since our a priori models were saturated (i.e., with all possible causal pathways considered), no overall goodness-of-fit test is provided. Separate SEMs, following exactly the same a priori model described above, were performed for each individual functional measure. Due to the relatively low sample size, we could not perform more complex models including more variables and paths, so we also used ANOVAs to test the effect of *A. altissima* invasion (included as a two-level fixed factor: control and invaded) on the “soil attributes” PCA axis. To aid with the interpretation of the SEM results, an evaluation of the relationship between multifunctionality (dependent variable) and either species richness or PSE (predictors) was undertaken using linear regressions.

All the variables fulfilled analyses assumptions and no transformations were needed. We performed SEMs with AMOS 7.0 (2007 SPSS Inc.). PCA was conducted using the Primer v. 6 statistical package for Windows (PRIMER-E Ltd., Plymouth Marine Laboratory, UK). We calculated the PSE index using the Picante package (Kembel et al. 2010) for R version 2.10.1 (R Development Core Team 2009). The rest of analyses were carried out using SPSS 13.0 for Windows (Chicago, IL, USA).

## Results

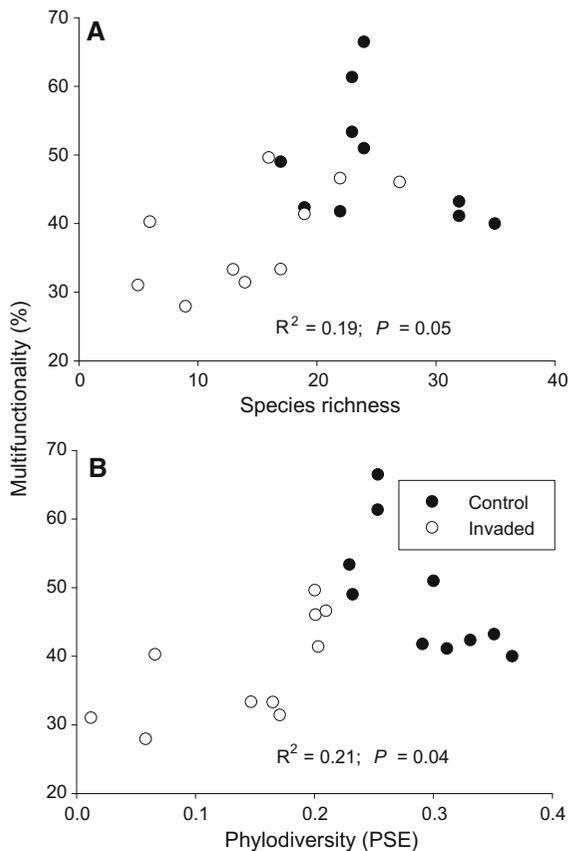
We found a significant and direct relationship between invasion of *A. altissima* and the loss of species richness, phylodiversity and ecosystem multifunctionality (Fig. 1). After accounting for the effect of the alien plant on both ecosystem attributes, the relationship between biodiversity and multifunctionality, and therefore, the indirect effect of *A. altissima* on ecosystem multifunctionality, was very low and not statistically different from zero. The invasion of *A. altissima* was



**Fig. 1** Path analyses for the effects of *A. altissima* on species richness and multifunctionality (a) or phylodiversity and multifunctionality (b). Path coefficients and their associated *P* values and the total amount of variance explained for each response variable are shown. Arrows width are proportional to the size of the path coefficients

significantly related to lower species richness ( $25 \pm 2$  vs  $15 \pm 2$  plant species in control vs invaded plots, respectively; Figs. 1, 2) and phylodiversity (PSE =  $0.29 \pm 0.02$  vs  $0.14 \pm 0.02$  in control vs invaded plots, respectively). The latter results show an increase in phylogenetic clustering in the invaded communities. The effects of *A. altissima* on phylodiversity were mainly driven by the loss of dominant species from three different families [*Trifolium repens* (Fabaceae), *Agrimonia eupatoria* (Rosaceae), *Scabiosa atropurpurea* (Caprifoliaceae)]. These species were very abundant (present in at least 50 % of the sites) at control plots, but became absent after the invasion of *A. altissima* (Fig. S2). It must be noted that rare species of interest for conservation were only encountered within control plots (Table S1; see “Discussion”).

The negative effects of *A. altissima* on richness and phylodiversity also extended to ecosystem multifunctionality (multifunctionality index =  $48.9 \% \pm 2.9$



**Fig. 2** Relationships between species richness (a) and phylodiversity (b) and ecosystem multifunctionality. Results from the linear regressions are shown in each panel ( $n = 20$ ). To aid interpretation, the particular relationships for control and invaded plots are, for species richness versus multifunctionality,  $R^2 = 0.13$ ;  $P = \text{ns}$  and  $R^2 = 0.49$ ;  $P = 0.02$ , respectively. For the relationship between phylodiversity and multifunctionality results were:  $R^2 = 0.39$ ;  $P = 0.05$  for control and  $R^2 = 0.42$ ;  $P = 0.04$  for invaded plots

vs  $38.0\% \pm 2.4$  in control vs invaded plots, respectively) but soil attributes were unrelated to *A. altissima* invasion (ANOVA:  $F_{1,18} = 0.44$ ;  $P = 0.83$ ). Separate ANOVA analyses for each of the three soil attributes (pH, CE and litter cover) also supported these latter results with  $P > 0.4$  in all cases. *A. altissima* effects differed depending on the ecosystem function studied (Table 2); in short, these effects were positive for functions related to the Phosphorus cycle (available P and acid phosphatase activity) and negative for the rest. Interestingly, the total effects (direct + indirect) of *A. altissima* on the five different functions studied were, in all but one case (understory biomass), lower than its direct effect (Table 2). The fact that the total

effects of *A. altissima* were generally lower than its direct effects suggests that biodiversity indirectly dampened the effect of the alien plant on the different ecosystem functions studied.

Both species richness and phylodiversity were positively related to ecosystem multifunctionality (Fig. 2). The SEMs conducted, however, suggest that this positive relationship was mainly driven by the effect of *A. altissima* on both indicators of biodiversity.

## Discussion

This is one of the few existing studies addressing the effect of invasive species on biodiversity indicators other than species richness and also studying the effect of invasive species on multiple ecosystem functions simultaneously. To the best of our knowledge, this is also the first study to separate direct and indirect (mediated by their effect on biodiversity) effects of invasive plants on ecosystem functioning.

The results of this study support our first hypothesis since *A. altissima* reduced not only species richness, but also the phylodiversity of neighboring vegetation (see also Bennett et al. 2014). Previous results reported in this regard are controversial, with negative, nil, or even positive effects of invasive species on biodiversity (e.g., Sax and Gaines 2003; Meffin et al. 2010). However, the results in this paper are along the lines of those studies analyzing the effect of alien plants in riparian habitats, or with *A. altissima* as their target species; such studies have found important decreases in species richness after the invasion (Vilà et al. 2006; Gaertner et al. 2009; Motard et al. 2011). A more detailed view of the results obtained in this study suggests an even more important reduction of plant biodiversity related to the invasion of *A. altissima* than suggested just by looking at species richness or even phylodiversity. For example, it was observed that other invasive species, such as *Robinia pseudoacacia* L. (which is a N-fixer), were present in the plots invaded by *A. altissima* but not in the control plots (Table S1). It is known that the presence of invasive species accelerates invasions by other alien species and amplifies their effects on native communities (*invasional meltdown*: see Simberloff and Von Holle 1999). Moreover, rare species of high conservation interest, such as *Cephalanthera damasonium* (Mill.)

Druce, a protected species with one of its biggest populations in the area (Decreto 70/2009; Serra et al. 2006) were only present in the control plots. It must be noted that our results are very unlikely to be driven by invasive species other than *A. altissima*. Other invasive species (i.e., *R. pseudoacacia*, *Celtis australis*) were present but only in one and two sites, respectively, and with low abundances (cover < 5 %); thus, it is unlikely that they substantially affected our results.

Our SEM analyses suggest a direct reduction of ecosystem multifunctionality with the presence of *A. altissima*. *A. altissima* has a rapid growth (Zasada and Little 2002), increases soil fertility and alter soil C and N cycling, reducing the C/N ratio (Vilà et al. 2006; Gómez-Aparicio and Canham 2008). Our results, however, show that this increase in soil fertility does not translate to a higher productivity of the neighbouring plants. In spite that *A. altissima* enhanced total P in our study, it reduced productivity, water retention and decomposition in comparison with the control sites. The existence of direct effects of *A. altissima* on several ecosystem functions and soil attributes has been demonstrated in previous experimental studies (litter decomposition, Godoy et al. 2010; N cycle, Castro-Díez et al. 2012), and has also been suggested by observational studies (organic C, C/N ratio, Vilà et al. 2006; Gómez-Aparicio and Canham 2008). Our study, however, is the first one suggesting the dominance of these direct effects, regarding the indirect effects mediated by the reduction of the alien species on biodiversity, when studying multiple ecosystem functions simultaneously.

Our results, however, are based on an observational study and therefore should be taken cautiously. The degree of invasion by *A. altissima* could be the consequence, rather than the cause of, differences in plant composition and ecosystem functioning (Levine et al. 2003). Indeed, it is known that habitat characteristics and the phylogenetic structure of the host community can influence the invasion of alien plants (e.g., Traveset et al. 2008; Vacher et al. 2010; but see Bennett et al. 2014). However, we believe that this problem is unlikely in our study as the difference in the degree of invasion between control and invaded plots is more likely to be caused by dispersal limitation rather than by initial differences among the plots (see “Materials and methods” above). Nevertheless, future research based on manipulative approaches is required

to conclude if the invasive species directly or indirectly alters ecosystem functioning.

Interestingly, when analyzing single functions separately (Table 2), our results were different from those obtained with the multifunctionality index (Fig. 1). It was found that the (direct) effect of *A. altissima* on single functions was partially moderated when biodiversity was included in the analyses (total effect). The difference between the results found when analyzing single or multiple functions arose due to the differential sign found for the effects of both biodiversity and *A. altissima* on the different functions studied. While *A. altissima* and biodiversity affected negatively and positively variables related to C cycling and productivity, respectively, the contrary happened with variables related to P cycling. The former set of results is easily explained by the well-known reduction of plant productivity and C storage and cycling in less diverse communities (Tilman et al. 1997; Hooper and Vitousek 1998; Cardinale et al. 2007), and the reduction of litter decomposition rate of leaves of *A. altissima* in comparison with native species (Godoy et al. 2010). Although we did not measure any variable directly related to N cycling, results from previous research have shown a positive effect of this invasive species on N cycling (Vilà et al. 2006; Gómez-Aparicio and Canham 2008; but see Castro-Díez et al. 2012). Nitrogen availability is tightly related to the activity of the acid phosphatase enzyme and may explain the positive effect found on P cycling and availability. The only explanation we might think of for the negative effect of biodiversity on the P cycle is that P was depleted from the soil and captured by the greater understory plant biomass found in the more diverse communities. Unfortunately, our data do not allow us to be certain about the latter. An interesting finding was the correlation between soil enzymatic activities and the amount of resources to which they are related to. While this is commonly observed in the case of beta-glucosidase and soil C (Sinsabaugh et al. 2008; Maestre et al. 2012a), it was unexpected in the case of phosphatase and P availability (e.g., Burns et al. 2013). We can only speculate about two potential explanations for this latter result: (1) excessive enzymatic activity can generate accumulation in soil P, as observed in other stressful environments (Weintraub and Schimel 2005), or (2) although more P is available in the soil, *A. altissima* might be more efficient than the

microorganisms taking this nutrient, and therefore that would cause a pulse in phosphatase enzymatic activity. Regardless of the mechanisms behind, the contrasting results found (contrary effects on different functions, different results drawn from the analyses of single functions vs multiple functions simultaneously) clearly illustrate the interest of studying multiple ecosystem functions to avoid misleading conclusions and gain insights on the overall effect of alien plants on ecosystem functionality.

### Concluding remarks

Our main findings show that plant species richness, phylodiversity and ecosystem multifunctionality were reduced in the presence of *A. altissima*. The indirect effect of the alien plant on multifunctionality was negligible, mainly because the strong effects of *A. altissima* on biodiversity and multifunctionality obscured the relationship between both ecosystem properties. However, when addressing single functions, we found that biodiversity reduced the strength of the direct effects of *A. altissima* on such functions.

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