

Do the invasive trees, *Ailanthus altissima* and *Robinia pseudoacacia*, alter litterfall dynamics and soil properties of riparian ecosystems in Central Spain?

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Abstract

Aims To assess the impacts of *Ailanthus altissima* and *Robinia pseudoacacia* on the whole litterfall process and on soil properties of riparian ecosystems of Central Spain by comparing invaded and non-invaded forests.

Methods We selected 3–4 plots of four different types of forests: invaded by *A. altissima* or *R. pseudoacacia*, or dominated by the native *Fraxinus angustifolia* or *Populus alba*. In each plot we collected the litter monthly over 2 years and separated the litter from different plant organs. We calculated annual inputs of litter, nitrogen (N) and phosphorus (P) to soil. We also analyzed soil pH, organic matter (OM), N and P.

Results Most litter fractions from the two invasive trees contained over twice as much N as those from the native

P. alba. Although not significantly different, the annual inputs of N in invaded forests were 1.7–2.2 times higher than in native forests. In the invaded forests, extra litterfall peaks were found in summer and/or late-spring (June), corresponding to reproductive and/or leaf litter fractions. The percentage of annual litter represented by these peaks was over twice those in native forests. Soil OM, N and P were higher in invaded than in *P. alba* forests. In addition, forests invaded by *R. pseudoacacia* had higher soil OM and N than *F. angustifolia* forests. **Conclusions** This study showed the capability of *A. altissima* and *R. pseudoacacia* to alter soil properties and litterfall dynamics in riparian ecosystems.

Keywords Litterfall timing · Nitrogen · Phosphorus · Soil organic matter · Litter fractions · Exotic trees

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Introduction

Litterfall is a key process for nutrient cycling and energy transfer from plants to soils in terrestrial ecosystems (Vitousek 1984). The quality and quantity of plant litter play an important role in structuring the communities of plants and detritivorous invertebrates living in the soil (Facelli and Pickett 1991; Ponge et al. 1993; Xiong and Nilsson 1999), and the aquatic food webs when the litter falls into aquatic ecosystems (Wallace 1997). In addition, litterfall dynamics, i.e., the timing of abscission of different plant organs (e.g., leaves, flowers, branches), determines the period of food availability for detritivores, as well as the microclimatic conditions for

litter decomposition (Abelho and Graça 1996; Singh et al. 1999; Kirschbaum 2010). The chemical composition of the litter, particularly nutrient content, largely determines the rate of litter decomposition (Simons and Seastedt 1999; Wang et al. 2008), as well as soil properties, such as organic matter (OM), nutrient concentrations and pH (Witkowski 1991; Rice et al. 2004; Yelenik et al. 2004). Given that litter production, litterfall dynamics and chemical composition of plant tissues vary across species (Bray and Gorham 1964; Facelli and Pickett 1991; Abelho 2001; Martin et al. 2009; González 2012), a change in the species composition of the plant community, e.g., by an exotic plant invasion, may alter the ecosystem processes and soil properties affected by litter properties.

Riparian ecosystems are highly vulnerable to exotic plant invasion in part due to their high frequency of disturbance as well as habitat heterogeneity, which provides more opportunities for exotic plants to find appropriate conditions to establish and persist (Hobbs and Huenneke 1992; Hood and Naiman 2000; Chytrý et al. 2008). The invasion by exotic plants implies changes in plant community composition, which in turn may affect the quantity, quality, and dynamics of litterfall and therefore the functioning of both aquatic and terrestrial ecosystems (Bray and Gorham 1964; Facelli and Pickett 1991; Abelho 2001). The magnitude and direction of the effect of exotic invasive trees on litterfall may depend on the invasive species and the invaded community (Witkowski 1991; Ellis et al. 1998; Rice et al. 2004; Martin et al. 2009; Lee et al. 2011). Litter production in riparian forests can depend on soil properties, community structure and distance to the river (González et al. 2010). However, the link between invasion and soil properties through alteration of litterfall patterns remains largely unexplored.

Ailanthus altissima Mill. Swingle (Simaroubaceae) and *Robinia pseudoacacia* L. (Fabaceae) are two exotic invasive trees natives to China and North America, respectively (Sanz Elorza et al. 2004). They are found invading temperate ecosystems worldwide and are considered among the 100 worst invasive species in Europe (Kowarik and Sämel 2007; DAISIE 2009; Cierjacks et al. 2013). In Spain they were introduced during the 18th century for ornamental purposes, and they are now spreading through riparian areas, among other habitats, being considered among the 20 most harmful species in Spain (Sanz Elorza et al. 2004; GEIB 2006). Both invaders are deciduous and in Central Spain they coexist

with other riparian deciduous trees such as *Populus alba* L. (Salicaceae), *Populus nigra* L. (Salicaceae), or *Fraxinus angustifolia* Vahl. (Oleaceae) (De la Cruz and Peinado 1996; Castro-Díez et al. 2009). *R. pseudoacacia* is a N₂-fixing species capable of increasing N pools and speeding up N cycling in nutrient-poor invaded ecosystems (Rice et al. 2004; Von Holle et al. 2013). *A. altissima* can also increase soil N and pH in a range of different soils (Vilá et al. 2006; Gómez-Aparicio and Canham 2008). In contrast, *Robinia pseudoacacia* is able to decrease soil pH due to enhanced nitrification (Vítková et al. 2015). In riparian ecosystems of Central Spain, *A. altissima* produced higher quantities of fast-decomposing leaf litter than coexisting native trees, while *R. pseudoacacia* had the contrary effect (González-Muñoz et al. 2013; Castro-Díez et al. 2009, 2012). Phenological studies indicated that both invasive species displayed later flowering and fruit set and earlier leaf abscission than most of the coexisting native trees in Central Spain (Castro-Díez et al. 2014). Because other plant organs can be important sources of nutrients to soil (e.g., Lee et al. 2011), studies of litterfall that exclusively consider the leaf fraction provide only a partial understanding of the impact of plant invaders on soil inputs. Moreover, seasonal variation of litterfall may be essential, but it is rarely studied because of the frequent and sustained sampling required. No one has yet estimated the effects of *A. altissima* and *R. pseudoacacia* on soil properties through the whole litterfall process, taking into account all plant organs, their nutrient content and the time when they fall.

The aim of this study was to assess the impacts of *A. altissima* and *R. pseudoacacia* on the whole litterfall process and on soil properties of riparian ecosystems of Central Spain by comparing invaded and non-invaded forests. Specifically we tested the effects of the invasive species on: 1) the annual quantity of litterfall from different plant organs and their temporal dynamics 2) nitrogen (N) and phosphorus (P) inputs to the soil from litterfall and their temporal dynamics 3) soil N and P concentration, OM and pH. We expected litter production in invaded forests to be greater than in non-invaded forests, given the higher growth rates and lower N use efficiency reported for these invaders as compared to the coexisting native trees (Kowarik and Sämel 2007; Cierjacks et al. 2013; González-Muñoz et al. 2013; Castro-Díez et al. 2014). Associated with

increased litter production, we expected higher inputs of nutrients and higher levels of soil nutrients and OM in invaded forests. We also expected different litterfall dynamics between invaded and native forests due to the contrasting phenologies of these exotic and native trees (Castro-Díez et al. 2014). This study provides valuable data to understand the impacts produced by *A. altissima* and *R. pseudoacacia* in riparian Mediterranean forests on the whole litterfall process and thus on soil properties and the detritivore communities that rely on litter.

Materials and methods

Study plots

The study was carried out within the riparian forest (along 80-km stretch) of the Henares River (Tagus Basin, Central Spain). In this area, the climate is continental Mediterranean, with a mean annual precipitation of 341 mm and mean annual temperature of 13 °C during the two study years, and an arid period of at least 2 months (Fig. 1). Native vegetation is dominated by *P. alba*, *P. nigra*, *F. angustifolia*, *Salix alba* and *Ulmus minor*. Some areas are invaded by *A. altissima* and *R. pseudoacacia*, which may grow in pure stands or mixed with native species. We selected

four forest types, i.e., patches of forests dominated by four different tree species: *A. altissima*, *R. pseudoacacia*, *F. angustifolia* and *P. alba*, occurring under similar environmental conditions (Xerotherm + Xerofluvent soils (Fernández et al. 2012, 2013)). For each forest type, we delimited three or four 300 m² plots where the target species was dominant (see Table 1). Plots were all found within 100 m of the Henares River and within 80 km of each other. Plots had rectangular shape, with the wider side parallel to the river, except one *A. altissima* plot (AA1) which had triangular shape. In spring 2012 we measured in each plot the diameter at breast height (DBH) of all adult trees (DBH > 7 cm and height > 1.30 m) and calculated the total tree basal area (TTBA) ($\Pi(\frac{DBH}{2})^2$) and the percentage of TTBA belonging to the dominant species of each plot (DomTBA). In all plots, DomTBA represented more than 50 % of TTBA (Table 1). Average DBH was similar among forest types (Table 1).

Litterfall collection

Eighteen litterfall traps were distributed within each plot. To collect different plant materials, we used three types of traps: 1) Four traps made of mosquito net (1 mm mesh) forming a square (0.30 m² surface) and fixed to the ground with spikes; 2) ten “pot” traps

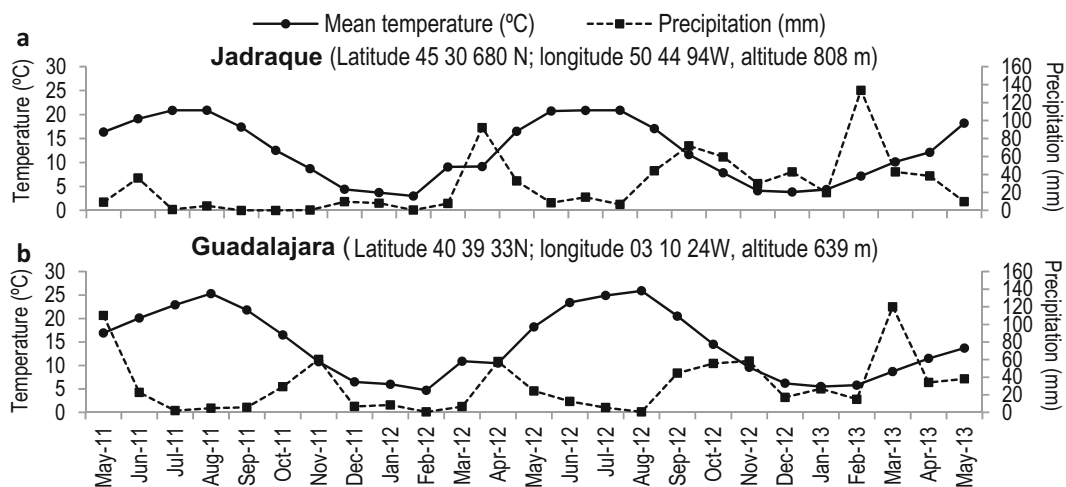


Fig. 1 Mean monthly temperature and precipitation from the meteorological stations of Jadraque (**a**) and Guadalajara (**b**) during the study period (May 2011–May 2013). Data from the Ministry of Agricultura Alimentación y Medio Ambiente of Spain (<http://www.aemet.es/es/serviciosclimaticos/datosclimatologicos/valoresclimatologicos> and <http://portal.magrama.gob.es/websiar/SeleccionParametrosMap.aspx?dst=1>)

[aemet.es/es/serviciosclimaticos/datosclimatologicos/valoresclimatologicos](http://portal.magrama.gob.es/websiar/SeleccionParametrosMap.aspx?dst=1) and <http://portal.magrama.gob.es/websiar/SeleccionParametrosMap.aspx?dst=1>)

Table 1 Summary of the community structure of adult trees in the study plots

Plot name	Location	Dominant tree species (number of adults)	Other tree species (number of adults)	TTBA (m ²)	Mean DBH (Mean (cm))	DomTBA (% from TTBA)
AA1	40° 34' 31.1" N 3° 13' 46.6" W	<i>A. altissima</i> (39)		7.1	14.2±0.9	100.0
AA2	40° 34' 27.4" N 3° 13' 46.4" W	<i>A. altissima</i> (31)	<i>Populus nigra</i> (2)	3.5	10.4±0.9	75.1
AA3	40° 39' 53.2" N 3° 10' 23.9" E	<i>A. altissima</i> (53)	<i>P. nigra</i> (1)	12.0	14.5±1.1	97.8
FA1	40° 57' 18.0" N 2° 55' 20.2" W	<i>F. angustifolia</i> (15)		6.3	19.9±3.2	100.0
FA2	40° 57' 16.2" N 2° 55' 50.4" W	<i>F. angustifolia</i> (25)	<i>Juglans regia</i> (1) <i>R. pseudoacacia</i> (5) ^a	8.0	15.7±1.7	56.0
FA3	40° 30' 57.3" N 3° 18' 13.8" W	<i>F. angustifolia</i> (23)	<i>Morus spp.</i> (1) <i>P. alba</i> (4) ^a <i>P. nigra</i> (3)	3.3	11.0±0.7	56.4
PA1	40° 56' 49.2" N 2° 56' 19.2" W	<i>P. alba</i> (11)		11.8	36.0±2.7	100.0
PA2	40° 43' 29.8" N 3° 9' 21.1" W	<i>P. alba</i> (24)		12.2	24.1±1.7	100.0
PA3	40° 57' 19.3" N 2° 55' 43.1" W	<i>P. alba</i> (59)		6.8	11.6±0.4	100.0
PA4	40° 36' 43.9" N 3° 12' 23" W	<i>P. alba</i> (41)		2.9	9.3±0.3	100.0
RP1	40° 56' 48.4" N 2° 56' 15.7" W	<i>R. pseudoacacia</i> (26)	<i>F. angustifolia</i> (3) ^a	4.7	13.4±1.0	94.0
RP2	40° 56' 57.9" N 2° 56' 1.3" W	<i>R. pseudoacacia</i> (21)	<i>P. nigra</i> (1)	1.4	8.5±0.7	74.4
RP3	40° 56' 48.0" N 2° 56' 17.2" W	<i>R. pseudoacacia</i> (16)	<i>Juglans regia</i> (1) <i>F. angustifolia</i> (4) ^a	6.5	18.5±1.6	77.1

For each plot, total number of adult trees (height ≥ 1.30 m and diameter at breast height (DBH) ≥ 7 cm) from dominant and non-dominant species (in brackets), total tree basal area (TTBA), mean (± SE) DBH of all adult trees, and the percentage of TTBA represented by the basal area of the dominant tree species (DomTBA) are presented

^a The contribution of these species was summed to that of the dominant species to calculate per-plot monthly/annual input of mass and nutrients

consisting of poly-vinyl chloride (PVC) circular pots (0.02 m² surface) fixed on the ground with spikes and containing a nylon bag (<1 mm mesh); 3) four hanging traps consisting of nylon bags (<1 mm mesh) fixed to a wire circle of 0.18 m² at 1 m above the ground. Overall, traps covered a total collection surface of 2.12 m² per plot and were evenly distributed within each plot.

We collected the contents of each trap monthly from 15th June 2011 to 15th May 2013. Once in the lab, the contents of each sample were separated by tree species and plant litter fraction (leaves, bark and branches, flowers, fruits and unidentifiable debris). Then, samples were oven dried at 60 °C for at least 48 h and weighed (Balance Sartorius BP211D, 0.0001 g). We pooled all the data across the different traps for each plot to calculate monthly (g m⁻² month⁻¹) and annual (g m⁻² year⁻¹) litterfall for each fraction and for all litter.

Litter nutrients

The litter collected during the 1–3 month period of maximum litterfall in 2012 was reserved for nutrient analyses. We only analyzed the litter of the four target species and the main litter fractions (i.e., the “unidentifiable debris” fraction, which was on average 9±2 % of the total litter, was not analyzed because its composition changes over time). We used only the samples collected by hanging and pot traps because they were not in direct contact with the soil, reducing the risk of fungal colonization. All samples from the same plot, species and plant litter fraction were pooled into a single compound sample and ground with a Cullati mill (0.7 mm particle size). N and P concentration were determined with a segmented flux auto-analyzer (Skalar San⁺⁺) after digestion with H₂SO₄ and Cu-KSO₄. To calculate N and P inputs per

month, we used a single estimate of the N and P concentration of each plant organ for each selected species, then multiplied by the grams of litter of each plant organ supplied by the dominant species, plus any of the additional studied species if present (see Table 1). In each plot, annual N and P inputs were estimated as the sum of N and P inputs in each of the 12 months (June–May).

Soil collection and soil properties

From each plot, in March (spring) and December (autumn) 2012 we collected a mixed soil sample, from around each of the four hanging traps. Each mixed sample consisted of three soil cores (7×7 cm×11 cm deep) collected and pooled together. Soil samples were carried to the lab in polyethylene bags, spread on filter paper and allowed to air dry. Afterwards, soil samples were sieved with a 1 mm mesh, homogenized, and kept at 4 °C until analysis.

To analyze total N and P concentrations, 0.5 g of soils were digested with H₂SO₄ and Cu–KSO₄. The digested solution was analyzed with a segmented flux autoanalyzer (Skalar San⁺⁺). We determined soil OM following a modification of the method described by Nelson and Sommers (1996). We weighed 5–10 g of soil previously dried at 105 °C for 48 h. Then the soil was burned at 400 °C for 2 h, cooled in a desiccator to room temperature and reweighed. OM (%) was calculated as the proportion of weight loss. We measured pH in a slurry of 20 g of soil with 40 ml of deionized water using a pH meter (micropH 2001, Crison Instruments, Barcelona, Spain) (Allen et al. 1974).

Statistical analysis

Since TTBA (m²) varied across plots, and the litter mass and nutrient inputs at plot level tend to increase with TTBA (Online resource 1), we expressed all litterfall variables per unit of surface area and TTBA (g m⁻⁴) to make them comparable across plots. Similarly, we expressed soil N, P and OM per TTBA unit (m²), since they also tended to increase with TTBA (Online resource 2). This approach is consistent with other studies that found significant positive correlations between litterfall and tree size (Negash and Starr 2013) or between litterfall and TTBA (Williams and Wardle 2007; González et al. 2010).

For each plant fraction, differences across species in N and P concentrations were assessed by one-way

ANOVA followed by Tukey HSD test. Data were log or square-root transformed when appropriate to attain normality and/or homoscedasticity. To assess differences in the percentage of each litter fraction, the total and per fraction annual litter mass and N and P inputs across forest types and years, we used linear mixed models with forest type and year as fixed factors and plot nested within forest type as a random factor. After 3 months of sampling, one *P. alba* plot (PA3, Table 1) had to be moved to another location because of a timber harvest in the original plot. This plot therefore is missing data for the first 3 months. The model using the interaction term between year and forest type did not significantly differ ($P>0.05$) from the model without the interaction, so we did not include the interaction.

To compare differences in total and per-fraction monthly input of litter mass, N and P produced by the dominant species, we used linear mixed models with dominant species and month as fixed factors and plot nested within dominant species as a random factor. We concluded that the temporal patterns of litterfall, N or P varied across species when the interaction term “dominant species x month” was significant. The model using the interaction term between year and dominant species did not significantly differ ($P>0.05$) from the model without the interaction, so we did not include this interaction.

Differences in soil N, P, OM and pH across forest types were analysed using generalized linear mixed models (family = gamma) (Bolker et al. 2009), with forest type and season (March vs. December) as fixed factors and plot nested within forest type as a random factor. Tukey’s all pairwise comparisons were conducted in R package with the *glht* function in the software package *multcomp* (Hothorn et al. 2008). We used R package 2.14.0 (R Development Core Team 2011) for all data analyses.

Results

Annual quantity and dynamics of litterfall

In the study plots, the different litter fractions included flowers (6 % of the total annual litter), fruits (10 %), leaves (69 %), bark and branches (16 %), and unidentifiable debris (9 %), with no significant differences among forest types ($F_{3;21}<0.83$, $P>0.05$ in all cases).

The peak of flower abscission in the exotic trees occurred in June, 2–3 months later than in the natives (April for *P. alba* and March–April for *F. angustifolia*) (Fig. 2a). *P. alba* fruits fell in May and June, but the remaining species extended fruit dispersal throughout the year (Fig. 2b). The shedding of bark and branches did not show any clear temporal pattern (Fig. 2c). All species showed their main peak of litterfall during autumn (October–December), coinciding with the period of leaf shedding of deciduous trees (Fig. 2d and e). However, exotic species showed extra litterfall peaks, which were absent in the natives (significant interaction between dominant species and month, $F_{69, 243}=2.13$, $P<0.0001$) (Fig. 2e). *R. pseudoacacia* showed

additional peaks in summer (August 2011 and September 2011; Fig. 2e) corresponding to a late-summer leaf abscission (Fig. 2d) and another extra peak in late spring (June 2012) due to the shedding of flowers and fruits (Fig. 2a and b). *A. altissima* also showed a late-spring peak (June 2011) due to early leaf shedding (Fig. 2d and e). Flowers represented a large proportion of the litter at their time of maximum floral abscission; flowers made up 34 % of the total litter for *A. altissima*, 43 % for *R. pseudoacacia*, 56 % for *F. angustifolia* and 48 % for *P. alba* during the month of maximum flower fall for each tree species. The proportion of total annual litter fallen in summer 2011 (July to September) was 47 % in forests invaded by *R. pseudoacacia* but only 24 % and

Fig. 2 Mean flower (a), fruit (b), bark and branch (c), leaf (d) and total litter (e), provided by the dominant species (*Ailanthus altissima*, *Robinia pseudoacacia*, *Fraxinus angustifolia* and *Populus alba*) in each month (from Jun 2011 to May 2013). Arrows represent litterfall peaks from the invasive species almost absent in the natives. Standard errors were not shown for better clarity

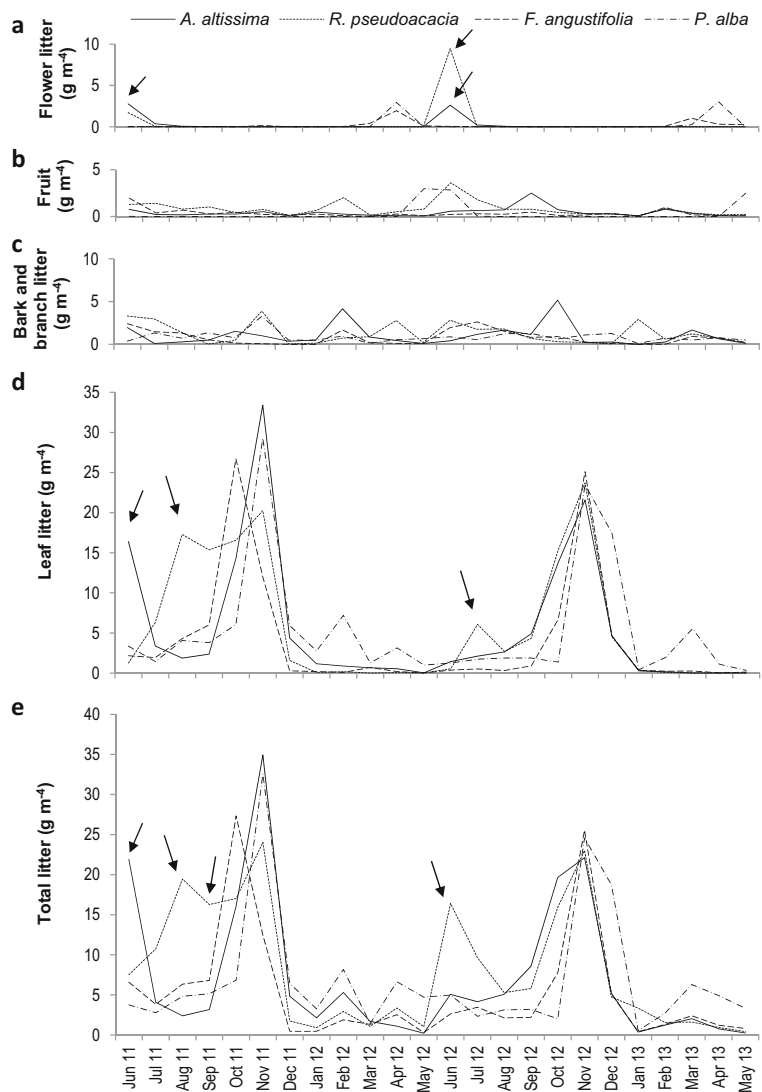


Table 2 Mean (\pm SE) total and per fraction (flowers, fruits, leaves and bark and branches) annual litter ($\text{g m}^{-2} \text{ year}^{-1}$) collected in different forest types (*Ailanthus altissima*, *Robinia pseudoacacia*,*Fraxinus angustifolia* and *Populus alba* forest) and the F and P values for linear mixed models assessing the effects of forest type and year on annual litterfall variables

Litter fractions	Litter production ($\text{g m}^{-2} \text{ year}^{-1}$)								Fixed effects			
	Exotics				Natives				Forest type		Year	
	<i>A. altissima</i>		<i>R. pseudoacacia</i>		<i>F. angustifolia</i>		<i>P. alba</i>					
	Year 1 (n=3)	Year 2 (n=3)	Year 1 (n=3)	Year 2 (n=3)	Year 1 (n=3)	Year 2 (n=3)	Year 1 (n=3)	Year 2 (n=4)	F	P	F	P
Flowers	3.2 \pm 1.5	2.8 \pm 1.2	12.3 \pm 8.0	8.2 \pm 3.5	3.5 \pm 0.4	3.0 \pm 0.4	3.9 \pm 1.6	3.8 \pm 2.8	1.30	0.334	2.05	0.180
Fruits	3.7 \pm 1.7	11.2 \pm 6.6	14.0 \pm 2.7	17.1 \pm 5.0	6.1 \pm 3.4	5.5 \pm 2.3	4.0 \pm 2.5	5.6 \pm 2.6	2.08	0.173	1.69	0.220
Leaves	68 \pm 26	47 \pm 17	87 \pm 32	66 \pm 20	60 \pm 20	40 \pm 12	64 \pm 31	61 \pm 29	0.29	0.834	22.76	0.0001
Bark and branches	11.9 \pm 4.6	12.4 \pm 5.4	14.8 \pm 9.1	14.5 \pm 6.1	7.6 \pm 2.4	8.4 \pm 3.2	13.1 \pm 2.2	10.7 \pm 0.5	0.40	0.758	0.14	0.713
Total litter	80 \pm 22	78 \pm 19	113 \pm 37	114 \pm 31	73 \pm 23	64 \pm 14	76 \pm 32	84 \pm 27	0.55	0.661	0.01	0.919

Significant P-values are indicated in bold

12 % in forests dominated by *F. angustifolia* and *P. alba*, respectively. The late-spring peaks of *A. altissima* and *R. pseudoacacia* accounted for 21 and 16 % of total annual litter, respectively. By contrast, this proportion was less than 10 % in non-invaded forests.

There was no significant difference among forest types either in the total annual litter mass or in the annual litter by fractions (flowers, fruits, leaves, bark and branches), but forests invaded by *R. pseudoacacia* showed a non-significant tendency to produce more litter than the other forests (1.4–1.7 times more; Table 2). The annual leaf litter was

significantly greater in the first than in the second year in all forest types (Table 2).

Litter nutrients

P. alba litter showed low N and P concentrations in most fractions (Tables 3 and 4). The remaining species had similar N concentrations in their different fractions, except *R. pseudoacacia* fruits, which had the highest N and P concentrations (Tables 3 and 4). *F. angustifolia* had the highest P concentration in bark and branches of

Table 3 Mean (\pm SE) of nitrogen (N) concentration contained in flowers, fruits, leaves, and bark and branches of each species (*Ailanthus altissima*, *Robinia pseudoacacia*, *Fraxinus angustifolia*and *Populus alba*) assessed at the time of the maximum abscission in 2012 for each plot

Litter fractions	Nitrogen (%)			
	Exotics		Natives	
	<i>A. altissima</i> (n=3)	<i>R. pseudoacacia</i> (n=3)	<i>F. angustifolia</i> (n=3)	<i>P. alba</i> (n=4)
Flower	4.90 \pm 0.52 ^a	4.95 \pm 0.13 ^a	5.09 \pm 0.40 ^a	2.33 \pm 0.61 ^b
Fruits	4.80 \pm 0.31 ^b	11.70 \pm 0.27 ^a	4.05 \pm 0.25 ^b	2.36 \pm 0.35 ^c
Leaves	3.64 \pm 0.35 ^a	3.86 \pm 0.34 ^a	3.73 \pm 0.31 ^a	1.42 \pm 0.14 ^b
Bark and branches	1.78 \pm 0.17 ^{ab}	2.29 \pm 0.10 ^{ab}	2.71 \pm 0.60 ^a	0.86 \pm 0.17 ^b

Different letters in a row indicated significant differences among species for N ($P < 0.05$, one way-ANOVA, Tukey HSD test)

Table 4 Mean (\pm SE) of phosphorus (P) concentration contained in flowers, fruits, leaves, and bark and branches of each species (*Ailanthus altissima*, *Robinia pseudoacacia*, *Fraxinus angustifolia*

and *Populus alba*) assessed at the time of the maximum abscission in 2012 for each plot

Litter fractions	Exotics		Natives	
	<i>A. altissima</i> (n=3)	<i>R. pseudoacacia</i> (n=3)	<i>F. angustifolia</i> (n=3)	<i>P. alba</i> (n=4)
Flower	0.70 \pm 0.11 ^a	0.45 \pm 0.01 ^{ab}	0.44 \pm 0.02 ^{ab}	0.29 \pm 0.08 ^b
Fruits	0.72 \pm 0.08 ^b	1.29 \pm 0.14 ^a	0.61 \pm 0.09 ^b	0.37 \pm 0.08 ^b
Leaves	0.28 \pm 0.04 ^a	0.14 \pm 0.03 ^a	0.49 \pm 0.25 ^a	0.15 \pm 0.04 ^a
Bark and branches	0.14 \pm 0.04 ^{ab}	0.10 \pm 0.03 ^b	0.33 \pm 0.07 ^a	0.13 \pm 0.05 ^{ab}

Different letters in a row indicated significant differences among species for P ($P < 0.05$, one way-ANOVA, Tukey HSD test)

all studied species, and *A. altissima* had the highest P concentration in flowers (Table 4).

The temporal pattern of N and P input differed among species (significant interaction between forest type and month; $F_{69,243}=2.22$, $F_{69,243}=2.04$ for N and P inputs, respectively; $P < 0.0001$). The additional summer leaf peak of *R. pseudoacacia* resulted in an additional peak of N but not of P (Fig. 3a and b), because *R. pseudoacacia* leaf litter had low P concentration (Table 4). The additional late-spring peaks of *A. altissima* and *R. pseudoacacia* resulted in additional peaks of N and P (Fig. 3a and b).

Total N and P inputs did not significantly differ among forest types because of the high variability, although average N inputs were 1.7–2.2 times higher in

invaded than in non-invaded forests (Tables 5 and 6). Annual N inputs from fruits were marginally different among forest types, tending to be greater in forests invaded by *R. pseudoacacia* than in the other forests (Table 5). However, annual N inputs from other litter fractions did not significantly differ among forest types. Due to greater quantities of leaf litter, both N and P inputs from leaf litter were significantly greater in the first year than in the second year (Tables 5 and 6).

Soil properties

Forests invaded by *R. pseudoacacia* had the highest OM and soil N concentrations, while *P. alba* forests had the lowest soil OM, N and P (Fig. 4). *A. altissima* and

Fig. 3 Mean total phosphorus (P) (a) and nitrogen (N) (b) inputs estimated from total litter produced in each community (*Ailanthus altissima*, *Fraxinus angustifolia*, *Populus alba* and *Robinia pseudoacacia*) per month (from Jun 2011 to May 2013). Arrows represent litterfall peaks from the invasive species almost absent in the natives. Standard errors are not shown for better clarity

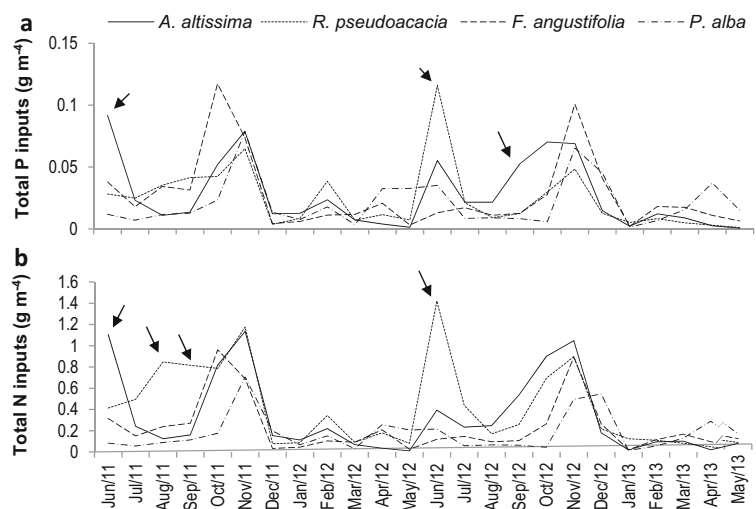


Table 5 Mean (\pm SE) nitrogen (N) inputs from total and per fraction (flowers, fruits, leaves, and bark and branches) annual litter ($\text{g m}^{-4} \text{ year}^{-1}$) collected in different forest types (dominated by *Ailanthus altissima*, *Robinia pseudoacacia*, *Fraxinus angustifolia* and *Populus alba*) and the F and P values for linear mixed models assessing the effects of forest type and year on annual N input variables

Litter fractions	Nitrogen inputs ($\text{g m}^{-4} \text{ year}^{-1}$)										Fixed effects							
	Exotics			Natives			Natives			Natives			Forest type			Year		
	<i>A. altissima</i>			<i>R. pseudoacacia</i>			<i>F. angustifolia</i>			<i>P. alba</i>			F			P		
	Year 1 (n=3)	Year 2 (n=3)	Year 1 (n=3)	Year 2 (n=4)	Year 1 (n=3)	Year 2 (n=3)	Year 1 (n=3)	Year 2 (n=3)	Year 1 (n=3)	Year 2 (n=4)	Year 1 (n=3)	Year 2 (n=3)	Year 1 (n=3)	Year 2 (n=3)	F	P	F	P
Flowers	0.17 \pm 0.10	0.15 \pm 0.08	0.09 \pm 0.06	0.48 \pm 0.25	0.12 \pm 0.06	0.09 \pm 0.05	0.12 \pm 0.08	0.12 \pm 0.12	0.89	0.481	0.50	0.496						
Fruits	0.17 \pm 0.08	0.33 \pm 0.21	0.36 \pm 0.04	0.37 \pm 0.06	0.20 \pm 0.09	0.14 \pm 0.11	0.10 \pm 0.07	0.14 \pm 0.07	3.57	0.060	0.69	0.423						
Leaves	1.79 \pm 0.9	1.14 \pm 0.51	1.53 \pm 0.48	1.12 \pm 0.30	1.25 \pm 0.24	0.90 \pm 0.11	0.88 \pm 0.41	0.71 \pm 0.26	0.93	0.464	58.68	<0.001						
Bark and branches	0.21 \pm 0.08	0.24 \pm 0.11	0.31 \pm 0.23	0.26 \pm 0.12	0.20 \pm 0.13	0.28 \pm 0.22	0.08 \pm 0.01	0.08 \pm 0.01	0.79	0.530	0.04	0.836						
Total litter	2.33 \pm 0.75	1.86 \pm 0.67	2.58 \pm 0.55	2.30 \pm 0.69	1.53 \pm 0.21	1.15 \pm 0.07	1.18 \pm 0.34	1.06 \pm 0.18	2.66	0.112	10.01	0.009						

Significant P-values are indicated in bold

Table 6 Mean (\pm SE) total and per fraction (flowers, fruits, leaves, and bark and branches) annual litter ($\text{g m}^{-4} \text{ year}^{-1}$) collected in different forest types (dominated by *Ailanthus altissima*, *Robinia pseudoacacia*, *Fraxinus angustifolia* and *Populus alba*) and the F and P values for linear mixed models assessing the effects of forest type and year on annual P input variables

Litter fractions	Phosphorus inputs ($\text{g m}^{-4} \text{ year}^{-1}$)										Fixed effects							
	Exotics			Natives			Natives			Natives			Forest type			Year		
	<i>A. altissima</i>			<i>R. pseudoacacia</i>			<i>F. angustifolia</i>			<i>P. alba</i>			F			P		
	Year 1 (n=3)	Year 2 (n=3)	Year 1 (n=3)	Year 2 (n=4)	Year 1 (n=3)	Year 2 (n=3)	Year 1 (n=3)	Year 2 (n=3)	Year 1 (n=3)	Year 2 (n=3)	Year 1 (n=3)	Year 2 (n=3)	Year 1 (n=3)	Year 2 (n=3)	F	P	F	P
Flowers	0.026 \pm 0.015	0.023 \pm 0.012	0.008 \pm 0.006	0.041 \pm 0.020	0.012 \pm 0.005	0.008 \pm 0.004	0.015 \pm 0.011	0.016 \pm 0.015	1.05	0.416	0.10	0.762						
Fruits	0.025 \pm 0.014	0.045 \pm 0.026	0.030 \pm 0.004	0.031 \pm 0.004	0.032 \pm 0.015	0.023 \pm 0.018	0.016 \pm 0.011	0.024 \pm 0.013	0.73	0.559	0.69	0.425						
Leaves	0.113 \pm 0.041	0.072 \pm 0.023	0.049 \pm 0.010	0.036 \pm 0.006	0.160 \pm 0.095	0.117 \pm 0.069	0.106 \pm 0.050	0.078 \pm 0.033	0.39	0.761	56.23	<0.001						
Bark and branches	0.018 \pm 0.010	0.022 \pm 0.014	0.012 \pm 0.008	0.010 \pm 0.004	0.023 \pm 0.013	0.030 \pm 0.022	0.009 \pm 0.002	0.012 \pm 0.004	0.09	0.964	0.00	0.962						
Total litter	0.18 \pm 0.03	0.16 \pm 0.04	0.15 \pm 0.02	0.14 \pm 0.02	0.18 \pm 0.08	0.14 \pm 0.03	0.15 \pm 0.04	0.13 \pm 0.02	0.26	0.854	2.24	0.163						

Significant P-values are indicated in bold

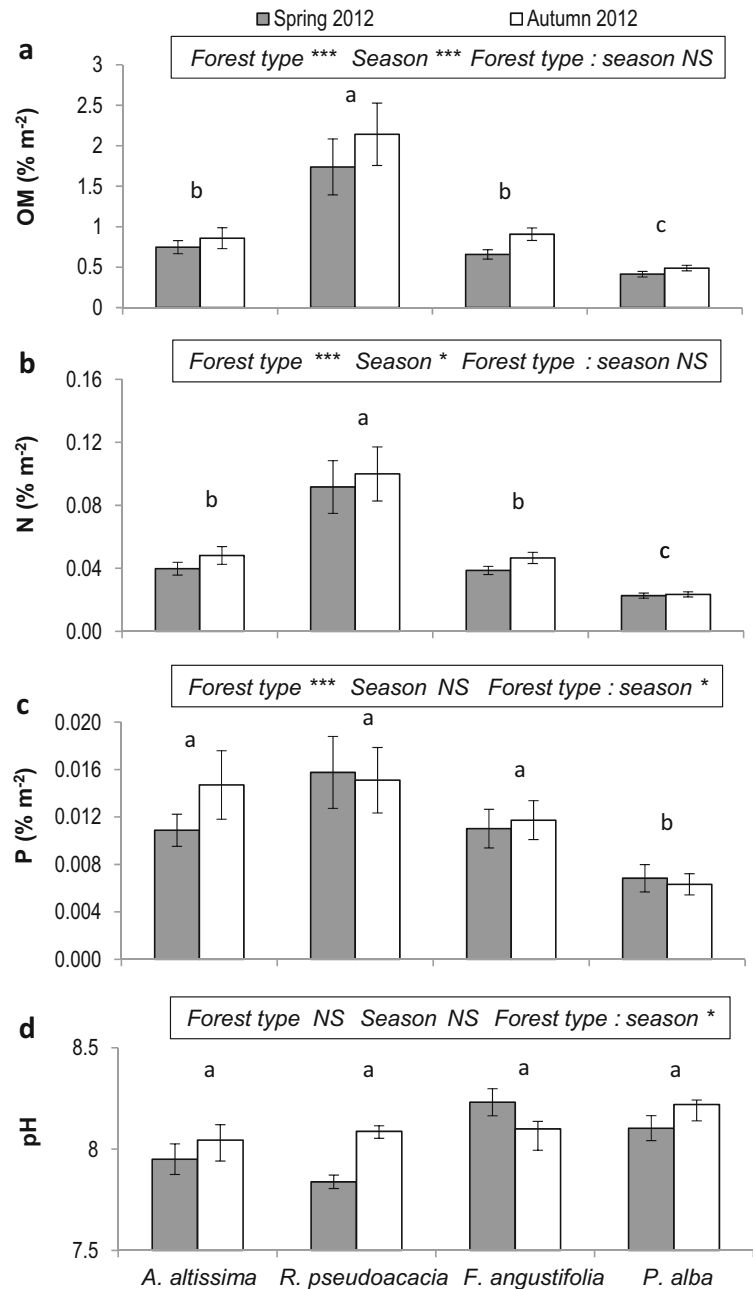
F. angustifolia forests showed intermediate and similar values of soil OM and N (Fig. 4a and b). Soil OM and N were greater in autumn than in spring (Fig. 4a and b). However, soil P tended to decrease from spring to autumn in *A. altissima* and *F. angustifolia* forests and increase in *P. alba* and *R. pseudoacacia* forests (Fig. 4c). Soil pH did not significantly differ among forest types, but it was higher in autumn than in spring in all forests

except in *F. angustifolia* forests, where it was higher in spring than in autumn (Fig. 4d).

Discussion

In our study, forests invaded by *R. pseudoacacia* had the greatest soil OM, N and P, while native forest dominated

Fig. 4 Mean (\pm SE) soil organic matter (OM) (a), nitrogen (N) (b) and phosphorus (P) concentration (c), per unit of total tree basal area (m^2), and pH (d) in two seasons (spring and autumn 2012) in *Ailanthus altissima*, *Robinia pseudoacacia*, *Fraxinus angustifolia* and *Populus alba* forests. Different letters mean significant differences among forest types (Tukey HSD test). The significance of forest type, season and their interaction is shown in each chart (NS No significant; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$)



by *P. alba* showed the lowest values. This result is consistent with patterns of the N and P content of litter, which was greatest in *R. pseudoacacia* and lowest in *P. alba* in most litter fractions, even though we failed to find differences in total N or P inputs or in the quantity of litter among forest types. The capacity of *R. pseudoacacia* to fix N, and its low N use efficiency (González-Muñoz et al. 2013) may explain the higher N concentration of some of its senescent tissues. Additions of N-rich litter from trees have been reported to increase soil N (Johanson 1995). Litter from different plant organs of both invasive species had higher N content than that of *P. alba*, which likely led to greater soil N in invaded than in *P. alba* soils. In addition, greater quantities of litter usually increase total soil N and OM (Martin et al. 2009), and we found a (non-significant) trend for *R. pseudoacacia* to produce more annual litter (up to 44 % more) and N inputs (up to 56 % more) than the remaining species (Tables 2 and 5). This trend likely reflects the high growth rates and poor N use efficiency of *R. pseudoacacia* (González et al. 2010; Cierjacks et al. 2013; González-Muñoz et al. 2013; Castro-Díez et al. 2014).

Soil OM depends not only on the quantity and quality of litter inputs, but also on the decomposability of the litter, the root exudates of organic carbon, the persistence of the different OM compounds, and the soil microbial biomass and activity (Schmidt et al. 2011). In the case of *R. pseudoacacia*, previous studies in Central Spain have pointed to the potential of *R. pseudoacacia* to accumulate recalcitrant OM and N in the soil due to its high lignin content and the consequent slower leaf litter decomposition than coexisting native species (Castro-Díez et al. 2009, 2012). Moreover, flowers from the exotic species fell in June, at the beginning of the dry season (2–3 months later than those from the natives), when microbial and plant activity declines due to water shortage. These arid conditions may slow down decomposition and the uptake of the derived nutrients, enlarging the period when OM and nutrients remains in the soil.

The summer and late-spring inputs from the exotic species were mostly due to leaf abscission and probably reflect the adjustment of these species to reduce water loss during the arid period. Neither *A. altissima* nor *R. pseudoacacia* evolved in regions with strong summer water stress, and they may have fewer adaptations than native species to tolerate water shortage. In fact, the time of the additional leaf litter peaks displayed by exotics

match the times of lowest precipitation and highest temperature (Figs. 1 and 2d). The leaf litter that falls in summer could decay more slowly, due to water shortage during the summer. This would enlarge the time when organic nutrients remain in the soil and contribute to the increment in soil nutrients and OM in invaded forests (Kirschbaum 2010).

Given that N and P concentration may vary in plant tissues across the year, measuring nutrients only at the peak of each fraction fall may introduce errors into the calculation of the annual input of nutrients in the soil, particularly in the case of *R. pseudoacacia* and *A. altissima*, which showed early peaks of leaf abscission (Fig. 2). Given that pre-senescent leaf litter can have greater nutrient content due to a more limited nutrient resorption (Killingbeck 1996), our calculation may have underestimated the amount of N and P input to the soil in the sites invaded by the two exotic species. In the remaining species, we believe that the potential error was lower because 1) the fraction of flowers, fruits and leaves that fell out of the period of maximum fall was lower; 2) *P. alba* leaves have been found to have similar N concentrations whether they fall in summer or autumn (González-Muñoz et al. 2013), and 3) annual changes in N and P of branches of Mediterranean phanerophytes in general have been found to be quite low (Milla et al. 2005).

The additional litterfall peaks produced in late spring by the invasive species may generate additional soil litter layers, which may act as physical barriers for germination, establishment and growth of species that shed their seeds in spring and do not form soil seed banks (Facelli and Pickett 1991). This is the case for *P. alba*, whose seeds disperse in May–June and are viable for only a few weeks (Prada and Arizpe 2008). Germination of small seeds, such as those of *P. alba*, may be more hindered by litter layers than that of bigger seeds, such as those of *A. altissima* and *R. pseudoacacia* (Facelli and Pickett 1991; Seiwa and Kikuzawa 1996). Therefore, the re-colonization of invaded forests by the native *P. alba* could be hindered by the accumulation of spring litter layers from exotic trees. At the same time, seed germination of these exotics species could be less affected by their own summer and spring litter since they shed their fruits throughout the year (Castro-Díez et al. 2014).

Additional litter inputs with different quality from invasive species may affect abundance and composition of detritivore communities, which are in synchrony with

litterfall processes (Takeda 1987; Ponge et al. 1993). Some detritivores may not be adapted to feed on recalcitrant leaf litter (Bastow et al. 2008), such as that of *R. pseudoacacia*, which may lead to a longer persistence of *R. pseudoacacia* litter layers. However, the abundance of some arthropod species may also increase with additions of high quality litter (Cesarz et al. 2007), such as *A. altissima* litter with its high nutrient content and rapid decomposition (Castro-Díez et al. 2009, 2012). In fact, soils invaded by *A. altissima* host altered soil arthropod communities compared to non-invaded soils (Gutiérrez-López et al. 2014; Motard et al. 2015).

In conclusion, our study highlighted the potential of the invasive trees, *A. altissima* and *R. pseudoacacia*, to alter soil properties even when we did not find significant differences in the annual quantities of litterfall and nutrient inputs between invaded and native forests. *R. pseudoacacia* tended to produce more annual litter and N inputs than the remaining species, likely due to its high growth rate and poor N use efficiency. Forests invaded by *R. pseudoacacia* had higher concentrations of soil nutrients and OM than native riparian forests. These soil variables were also elevated in *A. altissima* forests, but only when compared with *P. alba* forests. Finally, invasive trees altered litterfall dynamics by producing additional litterfall peaks and N and P inputs in summer and late-spring, which may modify soil nutrients, the activity of detritivores, as well as seed germination success.

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Conflict of interest The authors declare that they have no conflict of interest.

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