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REGULAR ARTICLE

Chemical composition rather than plant geographic origin drives the breakdown of riparian plant litter with changes in associated invertebrate diversity

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Abstract

Background and aims The study aimed to assess the effects of the potential replacement of dominant native plants by co-occurring exotic invasives on organic matter degradation in a riparian area. The questions were: *i*) Is there a relationship between the litter breakdown rate and species origin? *ii*) Is the chemical composition more relevant than species origin? *iii*) Does species origin influence the associated saprophagous invertebrate community?

Methods Within the riparian zone of the Garonne River (France), we conducted a litterbag experiment using pairs of native and exotic species selected in the stages of the successional gradient.

Results Native and exotic species did not differ in their primary chemical composition and breakdown rate. Litter breakdown rates were primarily driven by the C:N ratio with no influence of species origin. The abundance and diversity of saprophagous invertebrates of exotic and native species did not differ, but the composition did. Only one plant litter was completely degraded much earlier than expected (next litterfall) while remnant litter were still present at this time for the other species.

Conclusions The replacement of a dominant native by an exotic invasive plant species does not generally result in noticeable changes in the litter breakdown rate, which mainly depends on litter composition. Litter from quickly degrading exotic species may cause a resource discontinuity in invaded areas stabilized by river regulation.

Keywords Invasive plant · Species replacement · River bank · Litter bag experiment · Leaf litter invertebrates · Resource discontinuity

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Introduction

Riparian ecosystems are sensitive to invasion by introduced exotic plants which can represent more than 20% of the species pool (Hood and Naiman 2000; Tabacchi and Planty-Tabacchi 2005; Richardson et al. 2007). Following recurrent hydrological disturbances, diverse mosaics of habitats become available to exotic plants in riparian areas of the middle courses of river systems (Planty-Tabacchi et al. 1996, Schnitzler et al. 2007). Invasive species may replace native plants with consequent changes in community structure and ecosystem functioning (Vitousek et al. 1996; Ehrenfeld 2010). Such replacement may result from competitive exclusion or niche shift and changes in habitat properties, especially following human activities. As mild temperatures and high levels of soil and air moisture enhance litter decomposition, temperate riparian areas are likely to represent singular ecosystems when considering a functional switch in organic matter processing following biological invasions.

Within a wide range of terrestrial and aquatic ecosystems, more than 50% of net primary production directly enters food webs as detritus, with terrestrial ecosystems tending to channel more detritic matter than aquatic ecosystems (Cebrian and Lartigue 2004). Thus, plant litter breakdown is a key process that regulates the availability of most nutrients and, in turn, organic matter production (Webster and Benfield 1986; Xiong and Nilsson 1999). Microbial litter decomposition enhances the quality and attractiveness of plant detritus to saprophagous invertebrates which can degrade 20-30% of the annual litter input into terrestrial ecosystems depending on abiotic and biotic factors (Cummins and Klug 1979; Petersen and Luxton 1982).

In invaded areas, possible differences between the exotic and native litter breakdown rate relate to the biological and ecological characteristics of these two categories of plants. On the one hand, invasive exotic plants can better compete for resources and thus produce nutrient-rich biomass that decomposes faster than that from native plants (Ehrenfeld 2003, Ashton et al. 2005). On the other hand, native microorganisms and invertebrates may have to face unusual secondary compounds produced by exotic plants (Ehrenfeld 2006). Such higher sensitivity to plant secondary compounds could slow down exotic litter degradation. However, results vary considerably among studies comparing litter breakdown rates between exotics and natives. No difference was found when comparing species that were selected based on litter quality (Hladyz et al. 2009). In sampling designs, phylogenetic proximity may help to evaluate the effect of being an invasive compared with being a native because evolutionary processes reduce exogenous variability in individual ecological responses. Higher (Ashton et al. 2005) as well as lower (Godoy et al. 2009) breakdown rates have been reported for exotic plant litter when comparing several species pairs that were selected using a phylogenetic criterion. When targeting the functional consequences of invasions, the ecological relationships between exotics and natives as well as their biological traits appear to be more relevant criteria in case of species displacement (Emery and Perry 1996) or replacement (Harner et al. 2009). Hence, the question of the relevance of species origin for the decomposability by microorganisms and degradability by invertebrates of leaf litter is still being debated (Bottollier-Curtet et al. 2011).

We aimed to evaluate the implications of the potential replacement of dominant native plants by co-occurring invasive exotic plants for organic matter breakdown in a riparian area. Based on field co-occurrence and abundance data, we selected five pairs of native and exotic species in the herbaceous and woody strata of the main successional stages developed in the riparian area of a large river.

We addressed three questions: *i)* Is there a directional relationship between litter breakdown rates and species origin when exotics and natives are selected based on ecological criteria? *ii)* Is the primary chemical composition more relevant than species origin? *iii)* Does the species origin of plant litter influence the associated invertebrate community structure and/or composition?

Materials and methods

Study species

Disturbance effects of floods in floodplain ecosystems decrease laterally in the margins of the active river channel (Appendix A1). Hence, herbaceous plants generally dominate close to the river channel while shrubs and then trees become dominant in more and more stable habitats. This drives a successional maturity gradient from the river channel (low elevation) to the floodplain (Naiman and Décamps 1997). We compared invasive exotics with dominant natives as these two categories share some similar biological traits in similar habitats (Smith and Knapp 2001; Alpert 2006) that distinguish them from species of low abundance (Thompson 1994).

We selected the paired species on an ecological basis from the data reported by Tabacchi and Planty-Tabacchi (2005) using mainly two criteria: *(i)* the co-occurrence of the exotic and the native in the same stage of the vegetation successional gradient of the riparian area and *(ii)* the species relative abundance in the stage where both the exotic and native species were the most abundant (Appendix 2). The potential replacement of a native species by an exotic species may be related to a higher growth rate with similar morphological attributes, or, when morphological attributes or lifespan differ, to a higher fitness within a changing environment. Evidences of such species-specific replacements were supported by data from: Beerling and Perrins (1993), Beerling et al. (1994), Kendle and Rose (2000), Child and Wade (2000), Tickner et al. (2001), Tabacchi and Planty-Tabacchi (2003), Hejda and Pysek (2006) and Bernez et al. (2006). All the selected exotics are neophytes that are recognized as highly invasive in Europe (DAISIE 2010), and “species origin” refers here to the native or exotic status of the species in this continent.

Experimental site

The studied riparian area of the Garonne River (stream order 6; SW France) is located downstream from the confluence with the Ariège River, *ca.*10 km upstream from the city of Toulouse. We conducted a litterbag experiment from November 2007 to November 2008 in the surrounding of a pond (Bottolier-Curtet et al., 2011) within a *Populus nigra*-dominated riparian forest (43°31’36.96” N, 1°25’38.24” E, 147 m a.s.l.) that corresponds to the post-pioneer - mature stage (stage 3-4a and b in Appendix A1 and Table 1) of the successional gradient. The 10 selected paired species were all dominant in one stage of the successional gradient and exhibited variable mean cover percentage in the other strata/successional stages (Appendix A2). To analyse specifically the overall effect of the geographical origin of the species (exotic *vs* native) and the potential effect of species replacement among each pair, we placed all the bags in the same post-pioneer - mature stage (stages 3–4).

During the study, we recorded air temperature at the litter level using Tinytalk (Gemini-Orion™) data loggers (mean 10.9°C, min=−2.4°C, max=29.9°C). We analysed four replicates of the first 10 cm of the soil for grain size distribution (laser particle size analyser, CILAS 1090; clay=16.7±2.5%, silt=58.7±9.4%, sand=23.7±6.9%), pH (Isis 20 000, Tacussel™; pH=7.41±0.09) and total carbon and nitrogen content (CHN analyser, NA 2100, CE Instruments™; C=2.9±0.1% and *N*=0.23±0.01%,).

Leaf bag experiment

In October 2007, we collected leaf litter in the study site from litter traps and air-dried them at ambient temperature (*ca.* 20°C). *Agrostis stolonifera* and *Paspalum distichum* litter comprised leaves and stems, without stolons. *Impatiens glandulifera* and *Urtica dioica* litter comprised the distal end of the main stems. *Buddleja davidii, Fallopia japonica*, *P. nigra* and *Salix alba* litter comprised leaves and petioles while *Acer negundo* and *Rubus caesius* litter included leaflets, petiolules, rachises and petioles. Petiolules, rachises, petioles and stems are throughout this study referred to as refractory material. We weighed 20 litter packs of 5±0.05 g per species and then sprayed them with deionized water to prevent break-up when introduced into 10 mm mesh bags, adapting the method of Baldy et al. (2007) to terrestrial environments. To avoid site-specific variation, we placed four replicate blocks of five bags per plant litter species *ca.* 10 m apart in November 2007. We anchored the bags to an iron bar driven into the soil such that the bags were at the level of the pre-existing litter layer, which was dominated by *P. nigra*. The riparian substrate was sandy and the upper organic layer was limited because most of the litter was decomposed during the current year and the soil surface was exposed to leaching by floods (return period: approximately 2.5 years in the sampled zone). We retrieved one bag per replicate block after 48, 90, 148, 229 and 357 days of exposure.

In the laboratory, we rinsed leaf litter onto a 200 μm sieve to remove mineral particles and exogenous organic matter. We collected invertebrates (>200 μm) and preserved them in 70% ethanol. We dried litter samples at 105°C until constant weight, weighed them to the nearest 0.01 g, and then ground and passed them through a 0.5 mm mesh screen. We ashed a 250 mg sample of the ground portions at 550°C for 6 h and weighed it to the nearest 0.01 mg to determine the organic matter content (ash-free dry mass, AFDM).

Table 1 Pairs of exotic invasive and native species studied in the four main stages (bold numbers, see Appendix 1) of the riparian succession gradient of the river Garonne

Gradients		Successional stage	Exotic species	Native species
Disturbance	Maturity	1. Pioneer (low elevation) (132.7±35.2 d.yr^{-1})	*Paspalum distichum* L. (creeping bentgrass), herbaceous, perennial	*Agrostis stolonifera* L. (water couch), herbaceous, perennial
↑	↓	2. Pioneer (top bank) (15.1±7.1 d.yr^{-1})	*Fallopia japonica* Houtt. (giant knotweed), herbaceous, perennial	*Rubus caesius* L. (european dewberry), woody
		3. Post-pioneer (intermediate) (5.2±3.2 d.yr^{-1})	*Buddleja davidii* Franch. (butterfly bush) woody	*Populus nigra* L. (black poplar), woody
		4a. Mature (tree layer) (2.1±1.6 d.yr^{-1})	*Acer negundo* L. (boxelder) woody	*Salix alba* L. (white willow) woody
		4b. Mature (understory) (2.1±1.6 d.yr^{-1})	*Impatiens glandulifera* Royle (Himalayan basalm), herbaceous, annual	*Urtica dioica* L. (stinging nettle), herbaceous, perennial

Arrows indicate either the increasing intensity of hydrological disturbance or the increasing maturity of the plant community along the riparian transect. Long-term mean flood duration are given for each stage

Litter composition

For each species, we dried four additional litter packs at 105°C and determined the initial dry litter mass by weighing them to the nearest 0.01 g. We then obtained the initial %C and %N, %P, and lignin content of three ground litter subsamples using a CHN analyser (NA 2100, CE Instruments), the method of digestion by acid of Flindt and Lillebø (2005) and the detergent method of Van Soest (1963) with the Fibersac 24 Ankom™, respectively.

Invertebrate processing

The invertebrates were counted under a stereomicroscope and identified to the lowest possible taxonomic level. Phytophagous, predaceous, fungivorous and detritivorous guild assignments were made according to various references including Coleman *et al.* (2004) and Schneider et al. (2004), and from morphological attributes of the buccal organ. A polyphagous species was placed in each group with fuzzy assignment in proportion to its estimated activity within each group. We carried out most statistical analyses on saprophagous (fungivorous and detritivorous) invertebrates associated with litter, but we also included other groups (phytophagous and predaceous) in specific analyses as their abundance may be litter-dependent because of cascading effects.

Data analysis

The most frequently used model to fit litter mass loss data is the single exponential decay function discussed by Olson (1963). However, the fit of refractory material decay for a few species at the end of the experiment required a regression model with two exponentials (Wieder and Lang 1982). Over the one-year experiment, the slope of the second exponential was not significantly different from 0 and we thus replaced it with a constant for regression analysis:

$$M_t = M_0 * exp(-kt) + c$$

where M_t is the remaining AFDM of the litter at time *t*, M_0 is the initial mass, *k* is the breakdown rate and *c* is a constant.

We compared litter breakdown rates using a nested analysis of covariance (ANCOVA) with log-transformed AFDM used as a response variable, species origin (exotic *vs* native) and leaf species as nested categorical factors, and time of exposure as a covariate while Tukey's test was used for *post hoc* pairwise comparisons. A second ANCOVA model was performed to test the effect of species growth form (herbaceous *vs* woody), which was considered to be a proxy of the dominant structure of the successional gradient (Table 1).

We analysed differences in the litter's primary chemical composition between total exotic and native species, all species, and growth forms with a nested analysis of variance (ANOVA) followed by Tukey's test for *post hoc* pairwise comparisons. We used simple exponential regression models to describe the relationship between litter breakdown rate and primary chemical components as indicated by best-fit modelling based on the R^2 criterion. We performed a Mann–Whitney test on regression residuals of exotic and native species to assess differences because of species origin when the regression relationship was significant. We did not use the C:P ratio as a predictor of degradability because of its co-linearity with the C:N ratio.

We performed the invertebrate community analysis using the invertebrate density (number of individuals per gram of litter AFDM). We performed a nested ANOVA with log-transformed densities as the response variable to assess differences in saprophagous invertebrate density. We used nested ANCOVA to assess differences in the taxonomic richness of saprophagous invertebrates, with log-transformed abundances as covariates. We compared the saprophagous invertebrate community composition using analysis of similarity (ANOSIM) with 1000 permutations. We grouped sampling dates to test differences among species because the number of replicates did not allow for the processing of ANOSIM among species for each sampling date. We performed a detrended correspondence analysis on the density of each group of invertebrates summed for the first four dates for each plant species to visualize differences in invertebrate community composition. Because remarkably little litter remained in the bags at the fifth date and because the invertebrates could be attracted to recently fallen litter from the surrounding vegetation, we performed the invertebrate analyses on the first four dates.

We used TableCurve 2D (version 5.1, Systat Software Inc.) to perform non-linear regression modelling of litter breakdown and best-fit modelling of the relationships between the litter breakdown rate and litter primary chemical components. We performed nested ANOVA, nested ANCOVA and multiple regressions with Statistica (version 6.0, Edition 98, Statsoft). We carried out ANOSIM using PRIMER (version 5.2.2, Edition 2001, Primer-E Ltd). We used type II sum of squares for ANOVA and ANCOVA analyses. We graphically verified normality and homogeneity of variance assumptions and when it was necessary to reach them, we used the mathematical transformation indicated above.

Results

Primary litter quality

No effect of plant origin was observed when separately considering the initial percentage of carbon, nitrogen, phosphorus and lignin (P=0.12–0.86) or the C:N (P=0.60) and C:P (P=0.14) ratios as revealed by nested ANOVA (Appendix A3), while a species effect was found with each of these parameters (all P<0.0001). *P. distichum* (exotic, stage 1) litter had the highest C:N ratio (39.5±0.1) and the lowest phosphorus content (0.10±0.00%). *U. dioica* (native, stage 4b) and *I. glandulifera* (exotic, stage 4b) litter displayed the highest phosphorus content (both 0.28±0.00%) and the lowest C:N ratio (11.4±0.2 and 14.0±0.1 respectively). This pair of species also had a remarkably similar litter chemical composition, a feature shared with the selected *S. alba* (native) / *A. negundo* (exotic) pair in stage 4a. The carbon content of woody species was significantly higher (7.7%) than that of herbaceous species (F=6.2, P=0.04) (Appendix A3).

The C:N ratio significantly explained 67% of the variance in litter breakdown rates with a value of about 20 corresponding to a slow-down threshold (Fig. 1). There was no statistical difference between exotic and native species based on the statistical dispersion of the regression residuals (Mann–Whitney test; U=11, P=0.8). Separate non-linear regressions with the other chemical parameters, in particular lignin content, showed no significant relationship with litter breakdown.

Leaf litter breakdown rate

The litter breakdown rate was not significantly different between exotic and native litters across all the studied

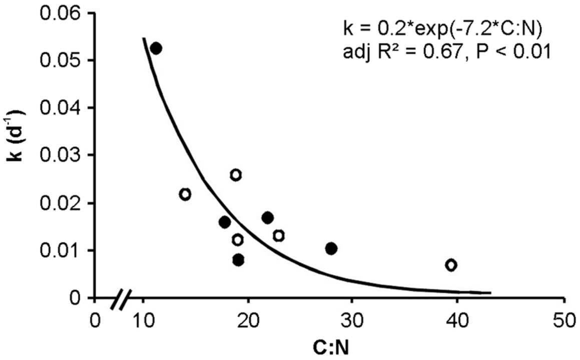

Fig. 1 Breakdown rates as a function of initial litter C:N ratio. Close circles, natives; open circles, exotics. Line, exponential regression with corresponding curve equation, with adjusted partial determination coefficient and *P*-value

species pairs (Fig. 2 top, Table 2, $P=0.92$). No effect of species growth form was detected (ANCOVA, F=0.4, $P=0.55$).

U. dioica (native, stage 4b) litter was the less refractory of all the studied litters and degraded twofold faster than that of *I. glandulifera* (exotic, stage 4b) and *B. davidii* (exotic, stage 3), while these three litter types degraded significantly faster than that of all other species (Fig. 2, Table 2, $P<0.0001$). Less than 20% AFDM remained for all species after the one-year experiment (Fig. 2). The high breakdown rates of *U. dioica* and *I. glandulifera* resulted from the fast degradation of the leaves whereas the residual mass corresponding to refractory material remained fairly constant at 229 and 357 days (Fig. 2), resulting in values of the constant *c* that were significantly different from zero in the regression model (4.1 and 15.3, respectively; both $P<0.03$; Table 1). Within the selected species pairs, comparisons showed that only the breakdown rate of *B. davidii* (exotic, stage 3) litter was significantly higher (2.5-fold) than that of its native counterpart *P. nigra* (native, stage 3) (Fig. 2, $P<0.0001$). By contrast, *P. distichum* (exotic, stage 1), the most refractory litter, and *F. japonica* (exotic, stage 2) litter degraded more slowly than their paired native species *A. stolonifera* and *R. caesius,* respectively (Fig. 2, Table 2, $P<0.01$ and $P<0.005$, respectively). In contrast with all other species, no *B. davidii* (exotic, stage 3) and *R. caesius* (native, stage 2) leaflets and refractory material remained in the bags after the end of April (Fig. 2; the calculated *c* in Table 2 is not significantly different from zero). This was 6 months before the next autumn litterfall (Miller 1984; Tabacchi E., unpublished data)(Table 3).

Litter-associated invertebrate communities

The invertebrate communities present in the experimental environmental conditions may have been somewhat different from that we could observe in each stage from which the paired species were originally selected. However, the observations remain relevant because most litter species studied can be removed by floods and trapped under mature stages. The mean percentage of saprophagous individuals (88.35±1.85%) or saprophagous species (85.20±1.45%) did not show any significant difference (ANOVA, $P>0.05$) among litter origins or species. These percentages decreased from dates 1 to 4. No significant difference was detected between the litter species within a given pair.

Maximum saprophagous invertebrate densities occurred at 148 days with *R. caesius* (native, stage 2)> *B. davidii* (exotic, stage 3)>*I. glandulifera* (exotic, stage 4b) >>all other species (Fig. 3). We observed an expected negative relationship between remaining AFDM and saprophagous invertebrate abundance (R=0.28; $P<0.0001$). We found no effect of litter species origin on the saprophagous invertebrate assemblage densities (ANOVA, F=0.6, $P=0.47$) and taxonomic richness (ANCOVA, F=0.0, $P=0.83$). All 'date' * 'species' interactions were significant ($P<0.0001$).

Acari, *Collembola* and *Trichoniscidae* Isopods numerically dominated the invertebrate assemblages. *Collembola* and *Diptera* (mostly *Chironomidae* and *Sciaridae*) maximum proportions occurred at the first date and then decreased with AFDM. *Isopoda* and *Myriapoda: Diplopoda* dominated at dates 2 and 3, and 3 and 4, respectively. *Collembola* especially dominated the *S. alba* (native, stage 4a) litter (67%), but were also well represented in *B. davidii* (exotic, stage 3), *A. stolonifera* (native, stage 1) and *P. distichum* (exotic, stage 1) litter, with more than 45% of the individuals (Appendix 3). While *Acari* represented around 20% of the individuals found in most litter species, their percentage was lower than 10% in the *S. alba* (native, stage 4a) and *U. dioica* (native, stage 4b) litter. *Acari* (mainly *Cryptostigmata*) peaked in relative abundance at the fourth date. Isopods were overall more abundant (30%) in *R. caesius* (native, stage 2) litter whereas they represented less than 5% in *P. distichum* (exotic, stage 1) and *S. alba* (native, stage 4a) litter. Significant effects in 'date'*'origin' were detected for the relative abundance of springtails in the following pairs: *A. stolonifera*/ *P. distichum* (stage 1; $P<0.001$), *P. nigra*/*B. davidii*

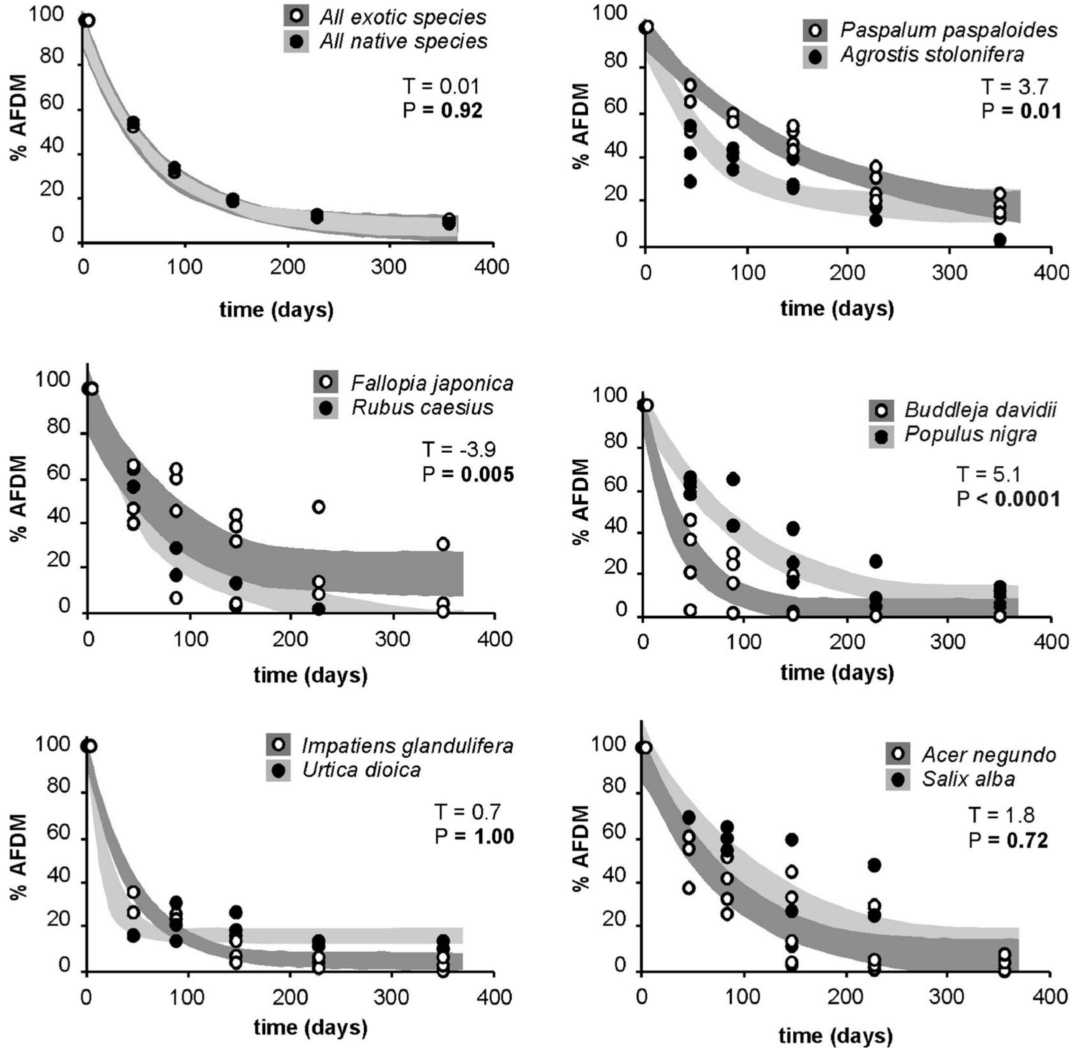

Fig. 2 Time course of ash-free dry mass remaining (AFDM) in litter bags (n=4). Closed circles; native species, open circles, exotic species. Light and dark grey areas show 95% confidence intervals calculated with the regression model for natives and exotics, respectively. ANCOVA *post-hoc* Tukey's test value (T) and associated P-value

(stage 3; P>0.001) and *U. dioica*/*I. glandulifera* (stage 4b; P=0.004). They were only detected in the *P. nigra*/*B. davidii* pair (stage 3; P<0.001) for *Acari*, and for all pairs (P<0.03) except *A. stolonifera*/*P. distichum* (stage 1) for Isopoda. AFDM was overall significantly positively correlated with the relative abundance of *Collembola* (R=0.498, P<0.0001) and *Diptera* (R=0.265, P=0.002). The correlation between *Collembola* relative abundance and AFDM was slightly higher for native litters (R=0.517, P<0.001) than for exotic litters (R=0.483; P<0.001). Such a correlation with AFDM was also significant and positive for *Diptera* (R=0.349, P=0.006) when considering exotic litters, and significant and negative for Isopoda (R=−0.306, P=0.03) when considering native litters. At the species level, such a correlation between the relative abundance of invertebrates and AFDM was observed for *B. davidii* (exotic, stage 3) with *Diptera* (R=0.692, P=0.01), for *I. glandulifera* (exotic, stage 4b) with *Collembola* (R=0.783, P=0.01) and for *S. alba* (native, stage 4a) with *Collembola* (R=0.628, P=0.046).

The composition of invertebrate species assemblages associated with exotic litter always differed from those associated with native litter on the first four dates (ANOSIM, P<0.03), with a significant effect of plant species (R=0.18, P=0.001). We observed the largest

Table 2 Initial C:N ratio, lignin percentage of litters and parameters of the breakdown model

	C:N	Lignin (%)	k (days-1)	c (%)
P. distichum	39.5 (0.1)	1.4 (0.1)	0.0068 (0.0005)	10.9 (6.4)
A. stolonifera	21.9 (0.3)	3.6 (0.1)	0.0169 (0.0009)	16.9 (3.4)
F. japonica	21.2 (0.3)	9.1 (0.2)	0.0130 (0.0023)	13.0 (7.3)
R. caesius	17.9 (0.2)	4.8 (0.1)	0.0159 (0.0005)	0.0 (3.3)
B. davidii	18.9 (0.1)	6.2 (0.2)	0.0258 (0.0013)	1.9 (3.1)
P. nigra	27.9 (0.5)	6.8 (0.1)	0.0104 (0.0005)	4.3 (4.7)
A. negundo	18.5 (0.1)	8.7 (0.3)	0.0120 (0.0008)	3.7 (5.1)
S. alba	19.1 (0.1)	7.9 (0.2)	0.0079 (0.0012)	0.0 (10.4)
I. glandulifera	14.0 (0.1)	7.0 (0.2)	0.0219 (0.0003)	4.1 (1.8)
U. dioica	11.4 (0.2)	7.0 (0.1)	0.0524 (0.0041)	15.3 (1.6)
Exotics	22.5 (5.7)	6.5 (1.8)	0.0153 (0.0004)	9.5 (2.7)
Natives	19.6 (3.5)	6.0 (1.0)	0.0142 (0.0002)	7.9 (2.5)

k, litter breakdown rate. *c*, constant. Mean (± SE), (n=4). Grey-highlighted, exotic species

differences between three species, *B. davidii* (exotic, stage 3), *I. glandulifera* (exotic, stage 4b) and *R. caesius* (native, stage 2), and almost all other species (Tukey test, all P<0.05). In particular, *R. caesius* litter was associated with significantly higher crustacean (*Isopoda: Trichoniscidae*) densities (ANOVA, P<0.006). Axes 1 and 2 of the detrended correspondence analysis displayed 85% and 13% of inertia, respectively (Fig. 4). The projection of the data points showed that exotic and native litter species were not clearly discriminated by their associated invertebrate communities or by specific invertebrate groups. Axis 1 distinguished between *R. caesius/U. dioica/I. glandulifera* and *A. stolonifera/P. distichum/B. davidii/S. alba* plant species. The two exotic litters of *A. negundo* and *F. japonica* were among the most representative of the dominant invertebrate groups (*Acari*, *Collembola* and *Diptera*). These species-specific differences resulted in overall differences in the invertebrate community composition between exotics and natives (Appendix A4).

Discussion

Effect of species origin on litter breakdown

We observed no overall influence of species origin on the breakdown rate of litter dominant native and co-occurring exotic invasive species in a temperate riparian forest. In a mixed forest and a common-garden experiment, Ashton et al. (2005) and Godoy et al. (2009) showed that the breakdown of exotic species was slightly faster and slower than the native species, respectively.

Table 3 Nested ANCOVAs on remaining AFDM in litter bags (n=4). “Origin” refers to the species origin (exotic *vs* native) and “Time” to harvest dates

Source of variation	df	SS	MS	F	P
Origin	1	0.05	0,05	0.01	0.92
Species(origin)	8	32.8	4.1	12.3	**<0.0001**
Time	1	90.3	90.3	271.1	**<0.0001**
Origin*time	1	0.1	0.1	0.2	0.67
Species(origin)*time	8	10.6	1.3	4.0	**<0.0001**
Error	180	60.0	0.3		
Total	199	204.1			

Bold refers to a significant result (P<0.05)

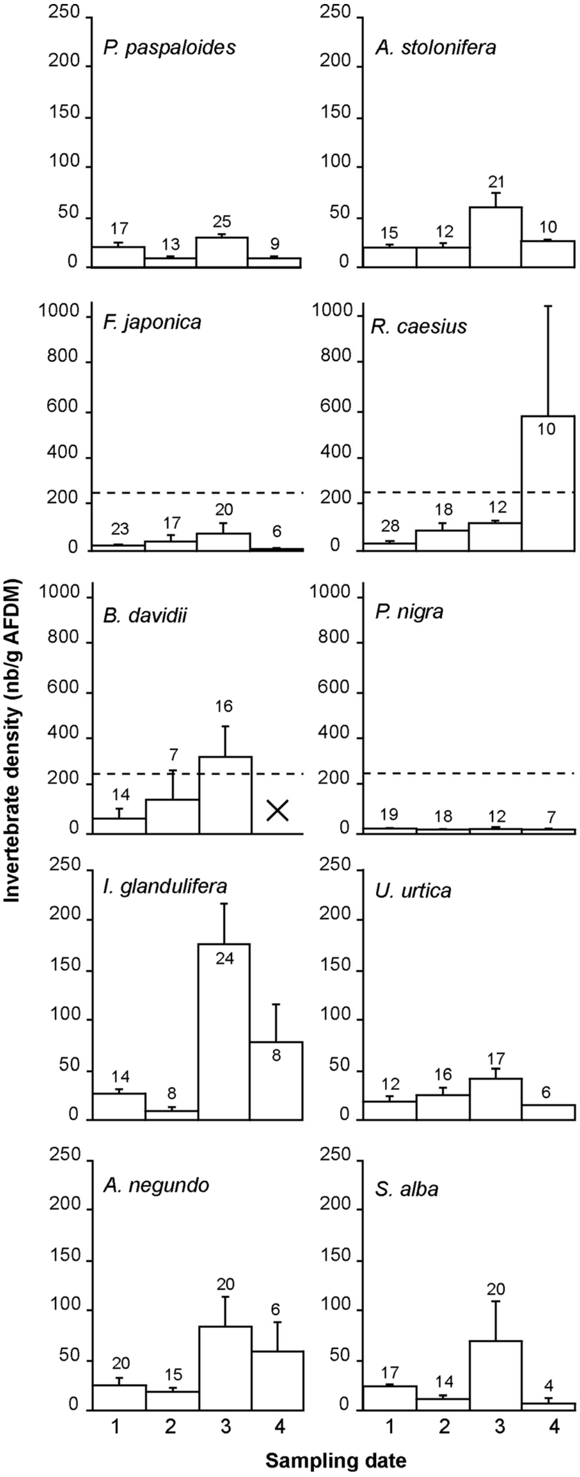

Fig. 3 Mean densities of saprophagous (detritivorous and fungivorous) invertebrates. Crosses, no more litter in bags. Error bar, SE. Numbers in bars are mean taxonomic richness (SE comprised between 1 and 3). Because scales are not the same between species pairs, the horizontal dashed line corresponds to 250 individuals/g AFDM in each of the graphs

The small difference in mass loss (8 and 10%) observed between exotics and natives was partly explained by species origin as well as by higher N litter content (Ashton et al. 2005) or higher lignin content (Godoy et al. 2009). In these studies, paired plant species were selected based on phylogenetic proximity, which limits interspecific variability in biological traits and helps to evaluate the effect of being an invasive compared with being a native (Godoy et al. 2009). As we selected the native and exotic species based on ecological criteria (co-occurrence and abundance in each of the successional stages), additional within-pair variability in litter quality might exist because of different evolutionary processes. For this reason, a minor effect of species origin may have been hidden in our results. In a previous study, we reported that breakdown rates were similar between exotic and native species in an aquatic environment of the same riparian area (Bottollier-Curtet et al. 2011). However, this study shows that, within a given pair, the breakdown of the exotic species can be either significantly faster (one pair) or slower (two pairs) than the native species, or not significantly different (two pairs). Taken together, the results obtained with the 28 pairs of exotic and native plants selected in these four studies (two terrestrial, including the present one, and two aquatic environments) suggest that there is no critical directional relationship between litter breakdown rate and species origin.

Our results are in agreement with those obtained by Hladyz et al. (2009) who observed no overall difference in lotic breakdown rates between several exotic and native dicots that were selected based on litter quality and palatability. Whether the selection of several paired species was based on litter quality (Hladyz et al. 2009), on phylogenetic proximity (Ashton et al. 2005; Godoy et al. 2009) or on ecological successional status (Bottollier-Curtet et al. 2011), all the studies strongly suggest that the breakdown rate of exotic litter is primarily driven by primary chemical composition. Our sampling design based on a single experimental condition (stage 3–4) may have slightly modified the results as the literature suggests that the breakdown process of the species selected in the other stages could have been slightly driven through the influence of environmental conditions on microbial activity (as related to moisture and temperature, Langhans 2006), the microbial adaptation to litter types (Ayres et al. 2006; Strickland et al. 2009) and the abundance of macroinvertebrate (Langhans 2006)..

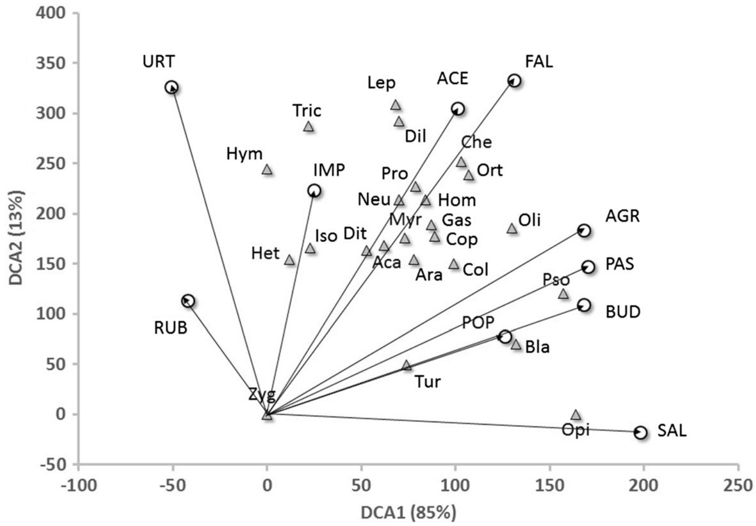

Fig. 4 Detrended Correspondence Analysis (first projection plane, %inertia indicated on each axis) based on invertebrate abundance. Open circles, litter species; triangles, invertebrate groups. Litter species: ACE: *Acer negundo*; AGR: *Agrostis stolonifera*; BUD: *Buddleja davidii*; FAL: *Fallopia japonica*; IMP: *Impatiens glandulifera*; PAS: *Paspalum distichum*; POP: *Populus nigra*; RUB: *Rubus caesius*; SAL: *Salix alba*; URT: *Urtica dioica*. Invertebrate groups: Col: *Collembola*; Aca: *Acari*; Iso: *Isopoda*; Dit: *Diptera*; Gas: *Gastropoda*; Myr: *Myriapoda*; Hym: *Hymenoptera*; Oli: *Oligochaeta*; Ara: *Araneae*; Col: *Coleoptera*; Che: *Chernetes*; Dil: *Diplura*; Hom: *Homoptera*; Pso: *Psocoptera*; Het: *Heteroptera*; Opi: *Opilionida*; Tur: *Turbellata*; Tri: *Trichoptera*; Zyg: *Zygentoma*; Ort: *Orthoptera*; Lep: *Lepidoptera*; Bla: *Blattoptera*; Pro: *Protura*

Litter breakdown and litter quality

The replacement of dominant natives by invasive exotics is expected to impact ecosystem functioning from a simple quantitative effect. As riparian areas are subject to differential litter mixing by floods, the consequences of the redistribution of litter within the riparian areas following invasions constitutes a major issue in functional studies. As no data on litter production by the selected species were available, we determined the litter quality that is known to controls the breakdown rate (Hladyz et al. 2009) and could therefore impact the organic matter recycling in case of species replacement.

In this study, litter breakdown of both exotic invasive and native species was mainly driven by the C:N ratio rather than by lignin content. In both terrestrial (Melillo et al. 1982) and aquatic environments (Gessner and Chauvet 1994; Ostrofsky 1997), the breakdown rates of woody dicots were negatively related to lignin content. The absence of a relationship between breakdown rate and lignin content in our study, which deals with a majority of ligneous dicots may be related to two factors. Firstly, we determined the lignin content of the whole litter while some species comprised various proportions of both easy- and difficult-to-degrade material of low and high lignin content, respectively. As the slope of the second exponential of the difficult-to-degrade material was not significant for several species, the overall breakdown rate mainly corresponded to the first exponential of the easy-to-degrade material that most probably contains less lignin than the whole litter. Secondly, we studied species from distinct botanical groups (monocots *vs* dicots). Compared with that of dicots, the chemical structure of the lignin in monocots slows down the decomposition process by microorganisms (Carpita 1996; Buranov and Mazza 2008). The lowest breakdown rate for *P. distichum* has to be related to its C:N ratio (Fig. 1) and low P content, but can also be partly related to the lignin composition in monocots (cf. above). Compared with *P. distichum*, the higher breakdown rate observed for *A. stolonifera* litter may be accounted for by its lower C:N ratio, as previously pointed out (Aerts 1997, Aerts et al. 2003). We could not predict the fast breakdown of *B. davidii* (exotic, stage 3) from its initial primary chemical composition. The fast breakdown of *B. davidii* may be accounted for, at least in part, by the physical distribution of lignin within the cell wall biomass of this species (Pan et al. 2006; Hallac et al. 2010). The high soil moisture prevailing in the riparian area studied could also have sped up microbial litter decomposition and/or the chemical degradation of the antimicrobial compounds still present in decomposing litter. In this line, the breakdown rates we report here are higher than those reported in non-riparian terrestrial environments by Cornelissen (1996). At last, an effect of 2-methyl-1,4-naphthoquinone, which is mainly responsible for the antibacterial and antifungal properties of *I. glandulifera* (Chapelle 1974, Lobstein et al. 2001), may account for its breakdown rate which is half as fast as that of its co-occurring native *U. dioica*.

Saprophagous invertebrate communities and their drivers

Saprophagous invertebrate abundances were not related to the plants' species origin. This result is in accordance with other studies (Pereira et al. 1998; Bailey et al. 2001; Braatne et al. 2007; Kappes et al. 2007; Lecerf et al. 2007), although Gutiérrez-López et al. (2014) showed in a single pair comparison study that most invertebrate groups were more abundant in native litter than in exotic litter. However, the exotic plant species in the study of Guttierrez-Lopez et al. is known to produce allelopathic and highly repellent compounds. We also found no difference in invertebrate taxonomic richness between native and exotic litter as reported in other previous studies (Bailey et al. 2001; Braatne et al. 2007; Lecerf et al. 2007). In contradiction with the production of unusual secondary compounds by exotic plants (Ehrenfeld 2006) that could affect native invertebrate development, we did not find lower invertebrate abundances or diversity in *F. japonica* (stage 2), *I. glandulifera* (stage 4b) and *B. davidii* (stage 3) litter. Native invertebrates may have been insensitive to these compounds, which alternatively may have been degraded earlier and/or leached. At higher taxonomic levels, the dominance of *Collembola* and *Diptera* in the early stage of the breakdown process, followed by *Acari* and *Myriapoda*, is a frequently observed pattern (Irmler 2014, Keiser et al. 2014). Such patterns could be related to a reaction of the exposed invertebrate community to litter chemical (primary and secondary composition), biological (colonization by microorganisms) and physical (fragmentation) patterns. The overall positive correlation of springtail proportions with AFDM observed for both native and exotic litters remains significant only for *I. glandulifera* (exotic, stage 4b) and *S. alba* (native, stage 4a) at the species level, while no clear discriminating pattern among litters appears when examining the invertebrate succession during the breakdown of both native and exotic litter. Similarly to Rusterholz et al. (2014), we did not observe specific patterns for *Collembola* abundance or species richness, but a pattern was observed for the invertebrate community composition associated with *I. glandulifera* (exotic, stage 4b) litter.

As the 10 different litters were exposed to the same pool of invertebrate species (*P. nigra*-dominated forest), differences among litter species could have been smoothed by the experimental protocol. Simultaneously, the pattern showed that all litter (species origin and successional stage confounded) could be favourable for colonization by invertebrates. The invertebrate assemblage composition exhibited highly variable grouping patterns that were significantly linked to the plant species. In particular, we recorded more abundant and frequent *Collembola, Coleoptera* and *Nematoda* species associated with exotic litter. Bailey et al. (2001) found fewer *Chironomidae* larvae associated with exotic compared with native litter and suggested an effect of habitat and/or resource quality. In our study, the difference between exotics and natives was because of species-specific differences. Because litter presented diverse species-specific morphologies, an overall habitat effect of exotic *vs* native litter seems unlikely. Besides, we cannot rule out that the species effect we observed on all the measured litter components is responsible for the differences we observed in the invertebrate assemblage composition at the species level (ANOSIM analysis). As an easier-to-degrade litter species compared with the others, *R. caesius* (native, stage 2) tends to increase the overall discriminations among invertebrate communities. The assemblage composition was also not specifically different between *B. davidii* (exotic, stage 3), *I. glandulifera* (exotic, stage 4b) and *R. caesius* (native, stage 2) and the other plant species. As such, we cannot suspect an effect of their specific secondary compounds. Although these distinct patterns are not associated with a lower biodiversity in the exotic litter and had no influence on breakdown rates, we cannot rule out an overall long-term effect on the breakdown process.

Species replacement and ecosystem function

All the selected exotic species are known to be highly invasive at the European scale and could represent more than 80% of the local vegetation according to the literature (e.g., Aguiar et al., 2005; Hejda and Pysek 2006) . As such, a deep modification of ecosystem processes can be expected when an invasive exotic replaces a co-occurring dominant native. This would be related to the ecological similarity between the invasive species and the natives they replace. There were no differences between the breakdown rates of exotic and native species from mature successional stages (4a: *S. alba*/*A. negundo*; 4b: *U. dioica*/*I. glandulifera*). Thus, the integrity of organic matter turnover should be maintained in this stage, although the litter-associated invertebrate communities could be impacted. In the pioneer (low elevation; stage 1) plant communities, *P. distichum* displayed a lower breakdown rate than, but exhibited the same remaining AFDM as *A. stolonifera* at the end of the experiment. In addition, in the pioneer (top bank) stage 2, *F. japonica* showed a slightly lower breakdown rate than the co-occurring native *R. caesius* in the riparian area studied. Within these two stages, a replacement of the native by its paired exotic species should have rather limited consequences on organic matter turnover. By contrast, in the post-pioneer stage 3, the fast *B. davidii* breakdown observed here and in other aquatic environments (Cornelissen 1996; Hladyz et al. 2009) is of noteworthy ecological interest because it is notably higher than that of the co-occurring native species, *P. nigra*, a result also reported in a pond located within the same site (Bottollier-Curtet et al. 2011).

Our study pointed out that *U. dioica* and *I. glandulifera* litter from the mature stage (4b) displayed fast breakdown rates. The slow disappearance of refractory material of these litter and the additional production of refractory material by the woody species surrounding the herbaceous strata would sustain the organic matter supply between consecutive litterfalls. By contrast, *B. davidii* litter from post-pioneer stage 3 disappeared 6 months before the next autumn litterfall. The local replacement of *P. nigra* by *B. davidii* can make the latter litter species almost the only one present. Hence, a resource discontinuity could occur during summer in both riparian terrestrial and lentic aquatic systems, when no flooding redistributes various litters throughout the floodplain (Xiong and Nilsson 1997; Langhans 2006; Bottollier-Curtet et al. 2011). Thus, the disappearance of *B. davidii* litter could be critical in the case of massive invasion, especially in temperate areas exhibiting low hydraulic connectivity with possible consequent erosion of specific invertebrate diversity and change in ecosystem functioning because of a cumulative year-to-year decrease in organic matter availability.

Conclusions

In a riparian forest, the study of five pairs of co-occurring invasive exotic and dominant native plants showed no influence of species origin on litter breakdown, which is instead primarily driven by resource quality. Therefore, the effects of the replacement of native plant species by exotic species mainly depend on the chemical composition of the litter of each species rather than species origin. The abundance and species richness within invertebrate communities did not differ between exotics and natives, while the abundance of a few groups associated with particular native and exotic species varied extensively. Species-specific effects of fast degradable litter on nutrient cycling, such as for *B. davidii*, can be buffered by hydrological connectivity in temperate riparian areas. In accordance with other studies of several species, we can conclude that an exotic invasive species will not systematically alter the litter breakdown process.

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References

Aerts R (1997) Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: a triangular relationship. Oikos 79:439–449

Aerts R, De Caluwe H, Beltman B (2003) Plant community mediated vs. nutritional controls on litter decomposition rates in grasslands. Ecology 84:1398–3208

Aguiar FC, Ferreira MT, Albuquerque A, Bernez I (2005) Invasibility Patterns of Knotgrass (Paspalum distichum) in Portuguese Riparian Habitats. Weed Technology, 19(3):509–516

Alpert P (2006) The advantages and disadvantages of being introduced. Biol Invasions 8:1523–1534

Ashton IW, Hyatt LA, Howe KM, Gurevitch J, Lerdau MT (2005) Invasive species accelerate decomposition and litter nitrogen loss in a mixed deciduous forest. Ecol Appl 15: 1263–1272

Ayres E, Dromph KM, Bardgett RD (2006) Do plant species encourage soil biota that specialise in the rapid decomposition of their litter? Soil Biol Biochem 38:183–186

Bailey JK, Schweitzer JA, Whitham TG (2001) Salt cedar negatively affects biodiversity of aquatic macroinvertebrates. Wetlands 21:442–447

Baldy V, Gobert V, Guerold F, Chauvet E, Lambrigot D, Charcosset JY (2007) Leaf litter breakdown budgets in streams of various trophic status: effects of dissolved inorganic nutrients on microorganisms and invertebrates. Freshw Biol 52:1322–1335

Beerling DJ, Perrins JM (1993) *Impatiens glandulifera* royle (*impatien roylei* walp.). J Ecol 81:367–382

Beerling DJ, Bailey JP, Conolly AP (1994) *Fallopia Japonica* (Houtt.) Ronse Decraene. J Ecol 82:959–979

Bernez I, Aguiar F, Violle C, Ferreira T (2006) Invasive river plants from Portugese floodplains: what can species attributes tell us? Hydrobiologia 570:3–9

Bottollier-Curtet M, Charcosset JY, Planty-Tabacchi AM, Tabacchi E (2011) Degradation of native and exotic riparian plant leaf litter in a floodplain pond. Freshw Biol 14:1445–1458

Braatne JH, Mažeika S, Sullivan P, Chamberlain E (2007) Leaf decomposition and stream macroinvertebrate colonisation of japanese knotweed, an invasive plant species. Int Rev Hydrobiol 92:656–665

Buranov AU, Mazza G (2008) Lignin in straw of herbaceous crops. Ind Crop Prod 28:237–259

Carpita NC (1996) Structure and biogenesis of the cell wall of grasses. Annu Rev Plant Physiol Plant Mol Biol 47:445–476

Cebrian J, Lartigue J (2004) Patterns of herbivory and decomposition in aquatic and terrestrial ecosystems. Ecol Monogr 74: 237–259

Chapelle JP (1974) 2-Methoxy-1,4-naphthoquinone in *Impatiens glandulifera* and related species. Phytochemistry 13:662

Child LE, Wade M (eds) (2000) The Japanese knotweed manual: the management and control of an invasive alien weed. Packard Publishing, Chichester, 123 pp

Coleman DC, DA Crossley J, Hendrix PF (2004) Fundamentals of soil ecology. Elsevier, Burlington

Cornelissen JHC (1996) An experimental comparison of leaf decomposition rates in a wide range of temperate plant species and types. J Ecol 84:573–582

Cummins KW, Klug KW (1979) Feeding ecology of stream invertebrates. Annu Rev Ecol Syst 10:147–172

DAISIE 2010. European Invasive Alien Species Gateway. Available at http://www.europe-aliens.org. Accessed 6 November 2013

Ehrenfeld JG (2003) Effects of exotic plant invasions on soil nutrient cycling processes. Ecosystems 6:503–523

Ehrenfeld JG (2006) A potential source of information for screening and monitoring the impact of exotic plants on ecosystems. Biol Invasions 8:1511–1521

Ehrenfeld JG (2010) Ecosystem consequences of biological invasions. Annu Rev Ecol Syst 41:59–80

Emery SL, Perry JL (1996) Decomposition rates and phosphorus concentrations of purple loosestrife (*Lythrum salicaria*) and cattail (*Typha* spp.) in fourteen Minnesota wetlands. Hydrobiologia 323:129–138

Flindt MR, Lillebø AI (2005) Determination of total nitrogen and phosphorus in leaf litter. In: Graça MAS, Bärlocher F, Gessner MO (eds) Methods to study litter decomposition: a practical guide. Springer, Berlin, pp 45–50

Gessner MO, Chauvet E (1994) Importance of stream microfungi in controlling breakdown rates of leaf litter. Ecology 75: 1807–1817

Godoy O, Castro-Díez P, Van Logtestijn RSP, Cornelissen JHC, Valladares F (2009) Leaf litter traits of invasive species slow down decomposition compared to Spanish natives: a broad phylogenetic comparison. Oecologia 162:781–790

Gutiérrez-López M, Ranera E, Novo M, Fernández R, Trigo D (2014) Does the invasion of the exotic tree *Ailanthus altissima* affect the soil arthropod community? The case of a riparian forest of the Henares River (Madrid). Eur J Soil Biol 62:39–48

Hallac BB, Ray M, Murphy RJ, Ragauskas AJ (2010) Correlation between anatomical characteristics of ethanol organosolv pretreated *Buddleja davidii* and its enzymatic conversion to glucose. Biotechnol Bioeng 107:795–801

Harner MJ, Crenshaw CL, Abelho M, Stursova M, Shah JJF, Sinsabaugh RL (2009) Decomposition of leaf litter from a native tree and an actinorhizal invasive across riparian habitats. Ecol Appl 19:1135–1146

Hejda M, Pysek P (2006) What is the impact of Impatiens glandulifera on species diversity in invaded vegetation? Biol Conserv 132:143–152

Hladyz S, Gessner MO, Giller PS, Pozo J, Woodward G (2009) Resource quality and stoichiometric constraints on stream ecosystem functioning. Freshw Biol 54:957–970

Hood WG, Naiman RJ (2000) Vulnerability of riparian zones to invasion by exotic vascular plants. Plant Ecol 148: 105–114

Irmler U (2014) Changes in the fauna and its contribution to mass loss and N release during leaf litter decomposition in two deciduous forests. Pedobiologia 44(2):105–118

Kappes H, Lay R, Topp W (2007) Changes in different trophic levels of litter-dwelling macrofauna associated with giant knotweed invasion. Ecosystems 10:734–744

Keiser AD, Keiser DA, Strickland MS, Bradford MA (2014). Disentangling the mechanisms underlying finctional differences among decomposer communities. Journal of Ecology, doi: 10.1111/1365-2745.1222

Kendle AD, Rose JE (2000) The Aliens have landed! What are the justifications for 'native only' policies in landscape plantings? Landsc Urban Plan 47:19–31

Langhans SD (2006) Riverine floodplain heterogeneity as a controller of organic matter dynamics and terrestrial invertebrate distribution. PhD Thesis, Swiss federal institute of technology, Zurich.

Lecerf A, Patfield D, Boiche A, Riipinen MP, Chauvet E, Dobson M (2007) Stream ecosystems respond to riparian invasion by Japanese knotweed (*Fallopia japonica*). Can J Fish Aquat Sci 64:1273–1283

Lobstein A, Brenne X, Feist E, Metz N, Weniger B, Anton R (2001) Quantitative determination of naphthoquinones of *Impatiens* species. Phytochem Anal 12:202–205

Melillo JM, Aber JD, Muratore JF (1982) Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. Ecology 63:621–626

Miller A (1984) The distribution and ecology of *Buddleja davidii* Franch in Britain, with particular reference to conditions supporting germination and the establishment of seedlings. Ph.D. Dissertation, CNAA, Oxford Polytechnic

Naiman RJ, Décamps H (1997) The ecology of interfaces: Riparian zones. Annu Rev Ecol Syst 28:621–658

Olson JS (1963) Energy storage and the balance of producers and decomposers in ecological systems. Ecology 44:322–331

Ostrofsky ML (1997) Relationship between chemical characteristics of autumn-shed leaves and aquatic processing rates. J N Am Benthol Soc 16:750–759

Pan XP, Gilke N, Kadla J, Pye K, Saka S, Gregg D, Ehara KX, Lam D, Saddler J (2006) Bioconversion of hybrid poplar to ethanol and co-products using an organosolv fractionation process: optimization of process yields. Biotechnol Bioeng 94:851–861

Pereira AP, Graça MAS, Molles M (1998) Leaf litter decomposition in relation to litter physico-chemical properties, fungal biomass, arthropod colonization, and geographical origin of plant species. Pedobiologia 42:316–327

Petersen H, Luxton M (1982) A comparative analysis of soil fauna populations and their role in decomposition processes. Oikos 39:288–388

Planty-Tabacchi AM, Tabacchi E, Naiman RJ, Deferrari C, Décamps H (1996) Invasibility of species-rich communities in riparian zones. Conserv Biol 10:598–607

Richardson DM, Holmes PM, Esler KJ, Galatowitsch SM, Stromberg JC, Kirkman SP, Pysek P, Hobbs RJ (2007) Riparian vegetation: degradation, alien plant invasions, and restoration prospects. Divers Distrib 13:126–139

Rusterholz H.P., Salamon J. P., Rucklia R., Baura B. (2014). Effects of the annual invasive plant Impatiens glandulifera on the Collembola and Acari communities in a deciduous forest. Pedobiologia, in press.

Schneider K, Migge S, Norton RA, Scheu S, Langei R, Reineking A, Maraun M (2004) Trophic niche differentiation in soil microarthropods (Oribatida, Acari): evidence from stable isotope ratios (^{15}N/^{14}N). Soil Biol Biochem 36(11):17769–1774

Schnitzler A, Hale BW, Aslum EM (2007) Examining native and exotic species diversity in European riparian forests. Biol Conserv 138:146–156

Smith MD, Knapp AK (2001) Physiological and morphological traits of exotic, invasive exotic, and native plant species in tallgrass prairie. Int J Plant Sci 162:785–792

Strickland MS, Osburn E, Lauber C, Fierer N, Bradford MA (2009) Litter quality is in the eye of the beholder: initial decomposition rates as a function of inoculum characteristics. Funct Ecol 23:627–636

Tabacchi E, Planty-Tabacchi AM (2003) Recent changes in riparian vegetation: possible consequences on dead wood processing along rivers. River Res Appl 19:251–263

Tabacchi E, Planty-Tabacchi AM (2005) Exotic and native plant community distributions within complex riparian landscapes: A positive correlation. Ecoscience 12:412–423

Thompson K (1994) Predicting the fate of temperate species in response to human disturbance and global change. In: Boyle TJB, Boyle CEB (eds) NATO advanced research workshop on biodiversity, temperate ecosystems and global change. Springer, Berlin, pp 61–76

Tickner DP, Angold PG, Gurnell AM, Mountford JO, Sparks T (2001) (2001) Plant invasions: Species Ecology and Ecosystem Management. In: Brundu G, Brock J, Camarda I, Child L, Wade M (eds) Hydrology as an influence on invasion: experimental invezstigations on the copmpetition between the alien *Impatiens glandulifera* and the native *Urtica dioica* in the UK. Backhuys Publ, The Netherlands, pp 158–168

Van Soest PJ (1963) Use of detergents in the analysis of fibrous feeds II. A rapid method for the determination of fiber and lignin. J Assoc Off Anal Chem 46:829–835

Vitousek PM, D'antonio CM, Loope LL, Westbrooks R (1996) Biological invasions as global environmental change. Am Sci 84:468–478

Webster JR, Benfield EF (1986) Vascular plant breakdown in freshwater ecosystems. Annu Rev Ecol Syst 17:367–394

Wieder RK, Lang GE (1982) A critique of the analytical methods used in examining decomposition data obtained from litter bags. Ecology 63:1636–1642

Xiong S, Nilsson C (1997) Dynamics of leaf litter accumulation and its effects on riparian vegetation: a review. Bot Rev 63: 240–264

Xiong S, Nilsson C (1999) The effects of plant litter on vegetation: a meta-analysis. J Ecol 87:984–994