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Degradation of native and exotic riparian plant leaf litter in a floodplain pond

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SUMMARY

1. A litter-bag experiment was undertaken in a pond on the margins of a large temperate floodplain in south-western France to assess the potential influence of the replacement of native by exotic riparian species on organic matter degradation. We determined initial litter chemical composition, breakdown rates and the invertebrate assemblages associated with the litter for five pairs of native dominant and exotic invasive species co-occurring at different stages along a successional gradient.

2. Litter chemical composition, breakdown rates and abundance and diversity of detritivorous invertebrates were similar for the exotic and native species overall. No overall changes in organic matter degradation can thus be predicted from the replacement of dominant natives by exotic invasives. Breakdown rates were primarily driven by the C/N ratio.

3. One invasive species (*Buddleja davidii*) showed significantly higher breakdown rates than its native counterpart (*Populus nigra*), resulting in the disappearance of leaf litter 6 months prior to the next litterfall. In some cases, therefore, invasion by exotic species may result in discontinuity of resource supply for decomposers.

Keywords: decomposition, floodplains, invasive species, invertebrates, ponds

Introduction

Plant litter breakdown is a fundamental ecological process that affects nutrient cycling, nutrient availability and consequently organic matter production in both aquatic and terrestrial ecosystems (Swift, Heal & Anderson, 1979; Webster & Benfield, 1986; Xiong & Nilsson, 1999). In riparian zones, litter produced by terrestrial plants is an important source of organic matter for the associated freshwater environments through direct input (Cummins *et al.*, 1989; Thorp & Delong, 1994; Langhans, 2006) or terrestrial litter

redistribution by recurrent flooding (Xiong & Nilsson, 1997; Langhans, 2006). Litter breakdown is mainly controlled by climate (Hanson *et al.*, 1984; Coûteaux, Bottner & Berg, 1995), litter chemical quality (Cadish & Giller, 1997; Ostrofsky, 1997) and microbes and detritivorous animals (Petersen & Luxton, 1982; Hieber & Gessner, 2002). Microbial decomposition of litter enhances the attractiveness of leaf detritus to detritivores that can degrade up to 50% of the annual litter input into lotic ecosystems (Cuffney, Wallace & Lugthart, 1990; Hieber & Gessner, 2002). In temperate ecosystems, seasonal litterfall results in a sharp decrease in breakdown activity from autumn to the end of summer. However, late leaf abscission of some plant species and the persistence of slowly degrading litter can maintain resource continuity for microbes and detritivores until the next autumn (Staelens *et al.*, 2011).

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As a result of worldwide transport by humans, coupled with hydrological disturbance and high landscape connectivity, exotic plants can represent on average more than 20 % of plant species inhabiting temperate riparian ecosystems (Planty-Tabacchi *et al.*, 1996; Stohlgren *et al.*, 1998; Richardson *et al.*, 2007). The highly diverse mosaic of habitats that characterises riparian areas of floodplains may support a wide diversity of invasive species (Planty-Tabacchi *et al.*, 1996; Schnitzler, Hale & Aslum, 2007). Such invasive species can be responsible for marked changes in community structure and ecosystem functioning (Vitousek *et al.*, 1996; Ehrenfeld, 2010). Two main hypotheses have been proposed to account for differences in breakdown rates among native plants and the exotic species that may replace them. The first hypothesis relates to the distinctive traits of invasives that makes them more efficient in resource uptake and in the production of biomass with higher nutrient concentrations, especially of N and P (Alpert, 2006; Leishman *et al.*, 2007; Liao *et al.*, 2008). Thus, it has been suggested that litter from exotic species will degrade faster than that from natives (Ehrenfeld, 2003; Ashton *et al.*, 2005). The second hypothesis refers to the lack of co-evolution between exotic species and the organisms in the recipient communities. In this context, the "Novel Weapons Hypothesis" (Callaway & Ridenour, 2004) and further developments (Cappuccino & Arnason, 2006; Ehrenfeld, 2006) suggest that secondary chemical compounds produced by exotic invasive species could act as antimicrobial agents or invertebrate repellents in their areas of introduction, because these organisms have not had yet the opportunity to adapt to these compounds. Among secondary metabolites, polyphenols are both ubiquitous and diverse from one species to another (Haslam, 1989). They could be important modulators of breakdown processes, in particular through the inhibition of spore germination and hyphal growth of saprotrophic fungi (Grime *et al.*, 1996; Hättenschwiler & Vitousek, 2000). Polyphenols could also influence invertebrate activity that most often contributes substantially to litter breakdown (Cuffney *et al.*, 1990; Hieber & Gessner, 2002).

Current studies consider three criteria to select litter species in comparative studies of exotic and native plants: litter quality, phylogenetic or ecological proximity. Studies based on litter quality in low-

order wooded streams have shown comparable breakdown rates among native and exotic species (Lecerf *et al.*, 2007; Hladyz *et al.*, 2009). Using phylogenetic proximity for 19 species pairs in a terrestrial environment, Godoy *et al.* (2009) found lower breakdown rates related to higher lignin litter concentration in exotic species. However, recognising that species co-occurrence and replacement are based on ecological niche similarity, in other studies exotic and native species have been selected according to ecological proximity in single pair experiments (Emery & Perry, 1996; Bailey, Schweitzer & Whitham, 2001; Harner *et al.*, 2009). In the riparian areas of large rivers, hydrological disturbance generates contrasting environmental conditions resulting in a gradient of plant successional maturity that is overall organised from the river channel to the floodplain (Gregory *et al.*, 1991; Naiman & Décamps, 1997). It seems particularly appropriate for studies that focus on the ecological impact of plant invasions to select exotic and native species that have similar ecological characteristics and occur in the same successional stages.

Therefore, to assess the effect of a potential species replacement on organic matter degradation, we selected one pair of co-occurring native and exotic plant species in each of the four main successional stages identified within the riparian vegetation of a large river. Considering the ecological importance of herbaceous understory in the most mature successional stage (Malanson, 1993; Naiman, Décamps & McClain, 2005), we selected a fifth pair of species in the understory plant formation. The selected natives were dominant species, the exotics being invasive ones. Indeed, Thompson, Hodgson & Rich (1995) and Smith & Knapp (2001) suggested that these two categories share similar biological traits that distinguish them from natives and exotics that occur at low occurrence (Thompson, 1994). Litter breakdown rates were determined in a natural pond, using an experimental design that allowed free access to invertebrates. We addressed two questions: (i) do litter degradation rates differ between exotic and native species with respect to their primary chemical composition and (ii) is detritivorous invertebrate community structure influenced by the geographical origin (exotic versus native) of the leaf litter with which they are associated?

Methods

Study species

We selected five pairs of exotic and native plant species along the vegetation maturity gradient in the middle Garonne River (SW France, Fig. 1). Exotic species were chosen according to their high co-occurrence frequency and the closeness of their ecological characteristics to those of their native counterparts (Tabacchi & Planty-Tabacchi, 2005). For each pair of exotic and native species, we assumed that the native is likely to be replaced by its ecologically related exotic counterpart. Selected exotics are neophytes (*sensu* Pyšek, 1995) and recognised as highly invasive in Europe (Daisie, 2010). Species were designated geographically as exotic or native in the context of their status in Europe.

Experimental site

We conducted litter-bag degradation experiments from November 2007 to November 2008 in a pond in the Garonne River floodplain downstream from its confluence with the Ariège River and upstream from the city of Toulouse [43°31'36.96"N, 1°25'38.24"E, 147 m a.s.l.; about 150 m length (north–south orientation) 25 m width]. The pond is groundwater-fed and

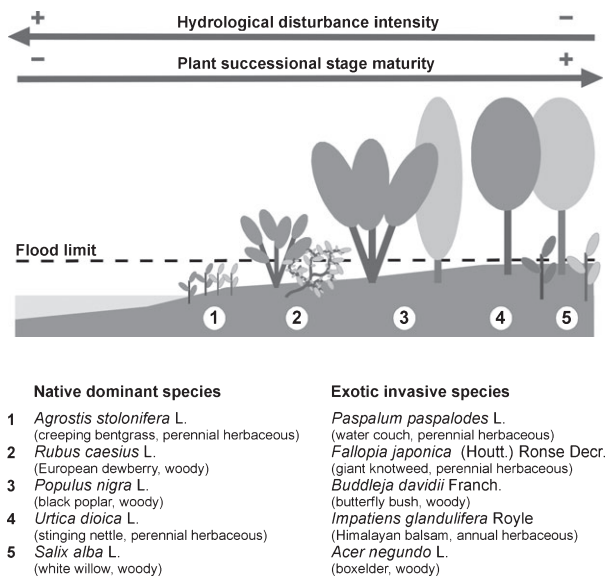


Fig. 1 Distribution of exotic and native species along gradients of hydrological disturbance and successional stages occurring within the riparian area. Flood limit corresponds to a flooding frequency of 1–3 years.

surrounded by a *Populus nigra*-dominated riparian forest. Riparian ponds and similar gravel-pits represent 31% of the waterbody's surface area within the studied middle Garonne River stretch. We chose this pond among four similar ones with comparable physicochemical characteristics because the vegetation on one bank allowed us to optimally set the bags and manipulate them without disturbing the benthos. Preliminary measurements showed that a gradient of oxygen, soluble reactive phosphorus (SRP), NO₃-N and NH₄-N concentration existed along the major axis of the pond. To encompass this gradient, we carried out *in situ* measurements and water sampling at the two extremities of the pond. We recorded water temperature every hour using Tinytalk (Gemini-Orion, Chichester, UK) data loggers. We monitored pH (pH 320; WTW GmbH, Weilheim, Germany), oxygen saturation (Oxi 330i; WTW GmbH) and conductivity (HI 98311; Hanna instruments, Woonsocket, RI, U.S.A.) at the beginning of experiments and at each of the five litter-bag retrieval dates, at 09h00–09h30 AM (GMT 1.00). We also collected water samples for alkalinity determination by titration at pH 4.5 ± 0.05 (precision: 2%). We filtered an aliquot of water in the field on a GF/F glass fibre filter (retention 0.7 μm; Whatman International Ltd, Florham Park, NJ, U.S.A.) for soluble reactive phosphorus (SRP) determination (Motomizu, Wakimoto & Tōei, 1983; precision 5%). We measured nitrate concentration by UV spectral deconvolution (Thomas *et al.*, 1993) using an Anthelie 70MI instrument (precision: 2%; Secomam, Ales, France). We carried out ammonium determination by the indophenol blue method (Apha, 1998; precision 5%).

Litter-bag experiment

We collected plant leaves from litter traps in October 2007 and air-dried them at ambient temperature (20 °C). *Rubus caesius*, *Fallopia japonica*, *Populus nigra*, *Buddleja davidii*, *Salix alba* and *Acer negundo* litter consisted of leaves including petioles while *Agrostis stolonifera*, *Paspalum distichum*, *Urtica dioica* and *Impatiens glandulifera* litter included leaves and stems. We weighed 20 litter packs of 5 ± 0.05 g per species and sprayed them with deionised water to prevent break-up when we placed them into 10-mm-mesh bags. We placed four replicate blocks of five bags per plant litter species at regular intervals along the pond

margin in November 2007. In order not to disturb the benthic layer, we anchored the bags to an iron bar driven into the bank and we carefully submerged the weighted bags at the bottom of the pond. We retrieved one bag per replicate block after 22, 55, 91, 203 and 359 days of exposure. During the retrieval, we placed a 150- μm -mesh net beneath the litter bag to collect material losses. Both the litter bag and the collected material were introduced into a zip-lock plastic bag containing filtered pond water. We estimated leaching of soluble compounds for each plant species from separate bags after 24 h of submersion (Gessner & Schwoerbel, 1989).

In the laboratory, we gently rinsed leaves with demineralised water over a 200- μm -mesh sieve to remove sediment. We identified leaf and stem parts of the studied species thanks to their morphological characteristics, and we removed exogenous organic matter. We collected invertebrates (>200 μm) and preserved them in 70% ethanol. We dried litter samples at 105 °C until constant weight and weighed to the nearest 0.01 g and ground. We ashed a 250-mg sample of the ground portions at 550 °C for 6 h and weighed to the nearest 0.01 mg to determine organic matter content (ash-free dry mass, AFDM). We expressed remaining AFDM as percentage of the initial ADFM.

Litter composition

For each species, we dried four additional litter packs at 105 °C and weighed to the nearest 0.01 g to determine the initial dry litter mass. We used three subsamples of 0.5-mm mesh ground litter to determine the contents of carbon, nitrogen (CHN analyser, NA 2100; CE Instruments, Milan, Italy), phosphorus (acid digested litter ash method; Flindt & Lillebø, 2005) and lignin (detergent method; Van Soest, 1963; Fibersac 24 Ankom, La Chapelle-sur-Erdre, France).

Invertebrate processing

We sorted invertebrates under a stereomicroscope, identified to the lowest possible taxonomic level (mainly species level) and counted individuals in each litter bag (Tachet *et al.*, 2000). We assigned taxa to functional feeding groups (shredders, scrapers,

filterers, gatherers and predators) according to the method described by Tachet *et al.* (2000). For species whose feeding behaviour spanned more than one feeding group, we allocated the number in each group in proportion to the corresponding activity estimated in the Tachet *et al.*'s fuzzy classification.

Data analysis

In contrast to the classical simple exponential model (Olson, 1963) that usually describes leaf litter breakdown kinetics, we used an additional constant to take refractory material at the end of the experiment into account:

$$\text{AFDM}_t = \text{AFDM}_0 \times \exp(-kt) + c$$

where AFDM_t is the remaining mass of litter at time t , AFDM_0 is the initial mass, k is the breakdown rate and the constant c corresponds to the remaining mass at the end of the experiment. As leaching is very short and distinct from the organism-mediated breakdown process, we did not include it in the model that starts at 24 h with measured AFDM after leaching. The statistical regression method allows the calculation of 95% intervals. We compared litter breakdown rates using a nested analysis of covariance (ANCOVA), followed by Tukey's test for *post hoc* pairwise comparisons. Log-transformed remaining AFDM was used as a response variable, species geographical origin (native versus exotic) and species as nested categorical factors, and time of exposure as a covariate. We performed a second ANCOVA model to test the effect of species growth form (herbaceous versus woody).

We analysed differences in chemical litter 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. Following a best-fit screening (Table curve 2D, version 5.1; Systat Software Inc., Chicago, IL, U.S.A.), we used simple exponential regression models ($y = a \times \exp(b \times x)$) to describe the relationship between litter breakdown rates and litter primary chemical composition. The difference because of exotic *vs.* native origin was tested by applying a Mann-Whitney's test on regression residuals when the regression models were significant. As a predictor of degradability, we used the C/N ratio as

it is relevant to microbial activity (Herbert, 1976). The C/P ratio was co-linearly related with the C/N ratio.

We used invertebrate density (number of individuals g AFDM⁻¹) in each sample for invertebrate community analysis. We performed nested analysis of variance (ANOVA) to assess the differences in density of detritivorous invertebrates associated with litter, with log-transformed densities as the response variable. We used nested analysis of covariance (ANCOVA) to assess the differences in taxonomic richness of saprophytic invertebrates, with log-transformed abundances as covariates. We compared invertebrate community composition using analysis of similarity (ANOSIM with 1000 permutations). The number of replicates did not allow processing of ANOSIM among litter species for each sampling date, because of the low number of possible permutations, and we tested differences among species without distinguishing between sampling dates. We used the first four dates because very little litter remained in the bags at the fifth (autumnal) date and the invertebrate communities were expected to be attracted to recently fallen litter from the surrounding vegetation.

We modelled litter breakdown using TableCurve 2D (version 5.1; Systat Software Inc.), and we performed nested ANOVA, nested ANCOVA and multiple regressions with Statistica (version 6.0, Edition 98; Statsoft, Tulsa, OK, U.S.A.). We used PRIMER (version 5.2.2, Edition 2001; Primer-E Ltd, Ivybridge, U.K.) to carry out ANOSIM. We used type II sum of squares for ANOVA and ANCOVA analysis. We graphically verified normality and homogeneity of variance assumptions. When data transformation was necessary to approach normal distribution and homogeneity of variance, the nature of the transformation is specifically indicated earlier.

Results

Leaf litter breakdown rate

Water physicochemical characteristics indicated low oxygen saturation (41 and 15%) and notably high NH₄-N concentrations (43 and 99 µg L⁻¹) in both south and north extremities of the pond (Table 1). Although we recorded a difference in site descriptors between the two extremities, no effect of the replicate samples on breakdown rate was observed (ANCOVA, $F = 1.2$, $P = 0.33$). Leaching resulted in 12.5–30.3%

Table 1 Physical and chemical characteristics of water at the pond extremities. Mean (minimum, maximum) are shown for hourly temperature and oxygen saturation and mean (\pm SE) for other parameters ($n = 6$)

Parameters	South extremity	North extremity
Temperature (°C)	9.6 (3.0, 27.9)	9.3 (2.8, 28.3)
Oxygen saturation (%)	41 (18, 76)	15 (7, 26)
pH	7.48 (0.10)	7.55 (0.08)
Conductivity at 25 °C (µS cm ⁻¹)	858 (20)	801 (20)
Alkalinity (mg CaCO ₃ L ⁻¹)	365 (6)	328 (9)
SRP (µg L ⁻¹)	4.0 (2.3)	12.1 (5.4)
NO ₃ -N (µg L ⁻¹)	552 (114)	26 (18)
NH ₄ -N (µg L ⁻¹)	43 (16)	99 (28)

mass loss and was similar for exotic and native litter (nested ANOVA, $F = 0.2$, $P = 0.6$) (Table 2). Less than 20% of AFDM, corresponding to leaf veins and stems, remained for all species after the 1-year experiment (Fig. 2). The overall litter breakdown rate for exotic litter was not significantly higher than that for native litters (Fig. 2, Tables 2 & 3).

I. glandulifera, *U. dioica* and *B. davidii* degraded significantly faster than all other species (Fig. 2, Table 2). For *I. glandulifera* and *U. dioica*, the residual mass at the end of the experiment ($6.7 \pm 1.7\%$ and $15.0 \pm 2.0\%$) resulted in significant values for the constant c in regression models (Table 2, all $P < 0.03$) that correspond to the mass percentage of refractory stems. It is noteworthy that in contrast to other species, whether native or exotic, no *B. davidii* litter remained in bags 6 months prior to the next litterfall.

Table 2 Parameters of the breakdown model for the ten species in this study (grey highlighting indicates exotic species).

Leaching, per cent litter ash-free dry mass loss after leaching; k , litter breakdown rate; c , constant. Mean (\pm SE), ($n = 4$)

	Leaching (%)	k (days ⁻¹)	c (%)
<i>P. distichum</i>	13.2 (1.0)	0.0060 (0.0013)	0.0 (8.8)
<i>A. stolonifera</i>	17.6 (1.9)	0.0083 (0.0019)	10.1 (5.6)
<i>F. japonica</i>	12.5 (0.9)	0.0064 (0.0012)	0.0 (6.8)
<i>R. caesius</i>	21.8 (1.0)	0.0069 (0.0016)	0.0 (7.2)
<i>B. davidii</i>	27.7 (2.2)	0.0230 (0.0019)	0.0 (1.7)
<i>Populus nigra</i>	21.8 (1.3)	0.0066 (0.0016)	0.1 (7.6)
<i>I. glandulifera</i>	30.3 (1.6)	0.0575 (0.0085)	6.7 (1.7)
<i>U. dioica</i>	24.2 (0.6)	0.0463 (0.0078)	15.0 (2.0)
<i>A. negundo</i>	23.6 (1.2)	0.0103 (0.0020)	8.2 (3.9)
<i>S. alba</i>	27.4 (2.3)	0.0069 (0.0019)	0.0 (8.1)
Exotics	21.5 (8.2)	0.0116 (0.0020)	5.0 (3.8)
Natives	22.5 (3.6)	0.0074 (0.0011)	1.0 (4.3)

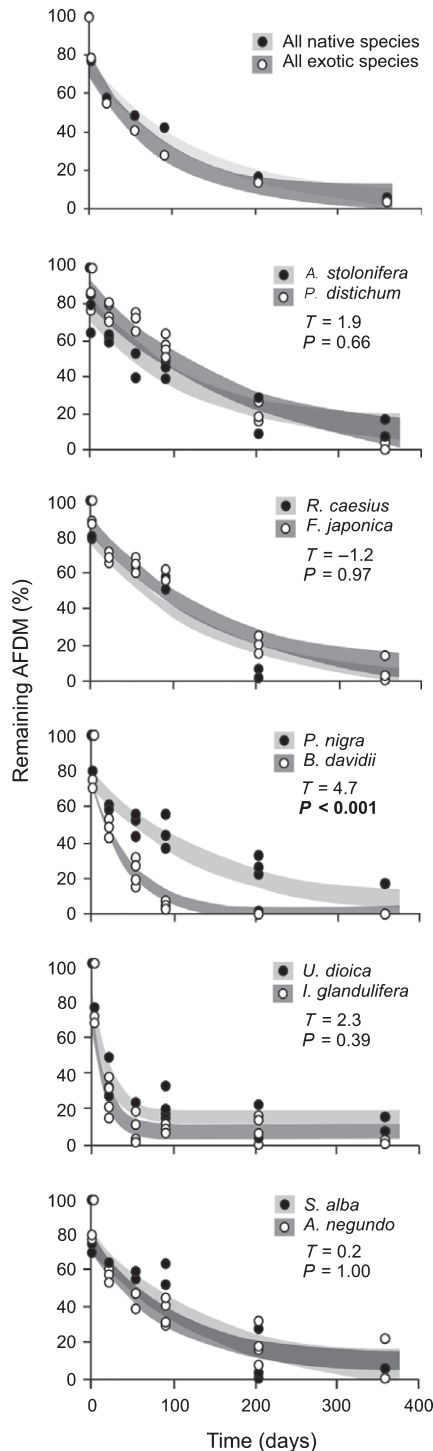


Fig. 2 Patterns ($n = 4$) in remaining ash-free dry mass (AFDM) of litter for the ten selected species (black circles native, open circles exotic). Dark and light shaded areas show 95 % confidence intervals for exotic and native species, respectively (intervals between data points were calculated with the regression model). ANCOVA *post hoc* Tukey's test (T) and associated *P*-value (*P*) are given.

Table 3 Nested ANCOVAs on remaining AFDM. "Origin" and "Time" refer to litter from exotic or native species and harvest date, respectively. $n = 4$

Source of variation	d.f.	SS	MS	<i>F</i>	<i>P</i>
Origin	1	0.5	0.5	0.1	0.79
Species(origin)	8	57.7	7.2	18.6	<0.0001
Time	1	274.8	274.8	708.2	<0.0001
Origin*time	1	0.02	0.02	0.05	0.83
Species(origin)*time	8	13.6	1.7	4.4	<0.0001
Error	220	85.4	0.4		
Total	239	428.6			

Bold text indicated significant effect.

Comparisons among paired species showed that only the breakdown rate of *B. davidii* litter was significantly 3.5-fold higher than that of the native counterpart *P. nigra* (Fig. 2, Table 2). No effect of species growth form was found (ANCOVA, $F = 0.01$, $P = 0.91$).

Leaf litter quality

No effect of plant species geographical origin was observed, whether in relation to initial percentage of carbon (nested ANOVA, $F = 0.03$, $P = 0.86$), nitrogen ($F = 0.2$, $P = 0.63$), phosphorus ($F = 3.1$, $P = 0.12$), lignin ($F = 0.1$, $P = 0.77$) or the ratios of C/N ($F = 0.3$, $P = 0.60$) and C/P ($F = 2.7$, $P = 0.14$), whereas a species effect was found with each of these parameters (all $P < 0.0001$) (Table 4). *P. distichum* litter appeared to be the most refractory to degradation with respect to its low phosphorus content ($0.10 \pm 0.00\%$) and high C/N ratio (39.5 ± 0.1). *U. dioica* and *I. glandulifera* litter had the highest phosphorus contents (both $0.28 \pm 0.00\%$) and the lowest C/N ratios (11.4 ± 0.2 and 14.0 ± 0.1 respectively). Litter from two plant species pairs, *U. dioica*/*I. glandulifera* and *S. alba*/*A. negundo*, had a very similar chemical composition. The litter of woody species had 3% more carbon than those of herbaceous species ($F = 6.2$, $P = 0.04$).

Separate nonlinear regressions showed that only the C/N ratio explained a significant proportion of variance in litter breakdown rates (Fig. 3). There were no differences in the statistical dispersion of the regression residuals for exotic and native species (Mann-Whitney test; $U = 4$; $P = 0.1$). There was no relationship between litter breakdown rate and lignin content. The litter of the two herbaceous plants *P. distichum* and *A. stolonifera* displayed low lignin contents and degraded with breakdown rates close to

Table 4 Initial chemical composition of litters. Species are sorted by increasing C/N ratio. Mean values ($n = 3$) of per cent ash-free dry mass are shown (\pm SE). An identical italic letter means no significant difference (nested ANOVA and Tukey's *post hoc* test; $P < 0.05$). Grey-highlighted species are exotics. GF, growth form

	C (%)	N (%)	P (%)	C/N	C/P	Lignin (%)
<i>U. dioica</i>	36.8 (0.1)	3.2 (0.1)	0.28 (0.00) <i>a</i>	11.4 (0.2)	133.0 (1.2) <i>a</i>	7.0 (0.1) <i>ad</i>
<i>I. glandulifera</i>	39.0 (0.1)	2.8 (0.0)	0.28 (0.00) <i>a</i>	14.0 (0.1)	138.7 (0.3) <i>a</i>	7.0 (0.2) <i>a</i>
<i>R. caesius</i>	43.7 (0.1) <i>cd</i>	2.4 (0.1)	0.21 (0.00)	17.9 (0.2) <i>a</i>	201.6 (0.7)	4.8 (0.1)
<i>A. negundo</i>	41.4 (0.1) <i>a</i>	2.2 (0.1) <i>a</i>	0.19 (0.00)	18.5 (0.1) <i>ac</i>	221.8 (2.7)	8.7 (0.3) <i>bc</i>
<i>B. davidii</i>	43.3 (0.1) <i>bc</i>	2.3 (0.0) <i>a</i>	0.18 (0.00) <i>b</i>	18.9 (0.1) <i>ac</i>	241.9 (1.7) <i>b</i>	6.2 (0.2) <i>a</i>
<i>S. alba</i>	43.8 (0.1) <i>de</i>	2.3 (0.0) <i>a</i>	0.18 (0.00) <i>b</i>	19.1 (0.1) <i>c</i>	245.0 (2.1) <i>b</i>	7.9 (0.2) <i>cd</i>
<i>F. japonica</i>	43.1 (0.1) <i>b</i>	2.0 (0.1)	0.16 (0.00)	21.2 (0.3) <i>b</i>	270.7 (1.6)	9.1 (0.2) <i>b</i>
<i>A. stolonifera</i>	41.1 (0.1) <i>a</i>	1.9 (0.1)	0.37 (0.01)	21.9 (0.3) <i>b</i>	111.3 (2.6)	3.6 (0.1)
<i>Populus nigra</i>	44.3 (0.1) <i>e</i>	1.6 (0.0)	0.25 (0.00)	27.9 (0.5)	176.6 (1.3)	6.8 (0.1) <i>a</i>
<i>P. paspaloides</i>	41.4 (0.1) <i>a</i>	1.1 (0.1)	0.10 (0.00)	39.5 (0.1)	422.9 (2.6)	1.4 (0.1)
Exotics	41.6 (1.0)	2.1 (0.3)	0.18 (0.00)	22.5 (5.7)	259.2 (1.7)	6.5 (1.8)
Natives	41.9 (1.9)	2.3 (0.3)	0.26 (0.00)	19.6 (3.5)	173.5 (1.3)	6.0 (1.0)
Herbaceous	40.2 (0.6)	2.2 (0.2)	0.22 (0.03)	21.3 (2.5)	262.6 (4.5)	5.8 (0.7)
Woody	43.3 (0.3)	2.2 (0.1)	0.21 (0.01)	20.5 (1.0)	210.9 (9.3)	6.9 (0.4)
Origin effect	$F = 0.03$ $P = 0.86$	$F = 0.2$ $P = 0.63$	$F = 3.1$ $P = 0.12$	$F = 0.3$ $P = 0.60$	$F = 2.7$ $P = 0.14$	$F = 0.1$ $P = 0.77$
Species effect	$F = 784.3$ $P < 0.0001$	$F = 470.1$ $P < 0.0001$	$F = 770.7$ $P < 0.0001$	$F = 1203.7$ $P < 0.0001$	$F = 1974.3$ $P < 0.0001$	$F = 209.4$ $P < 0.0001$
GF effect	$F = 6.2$ $P = 0.04$	$F = 0.0$ $P = 0.92$	$F = 0.0$ $P = 0.90$	$F = 0.02$ $P = 0.89$	$F = 0.6$ $P = 0.47$	$F = 0.6$ $P = 0.47$

Bold text indicated significant difference.

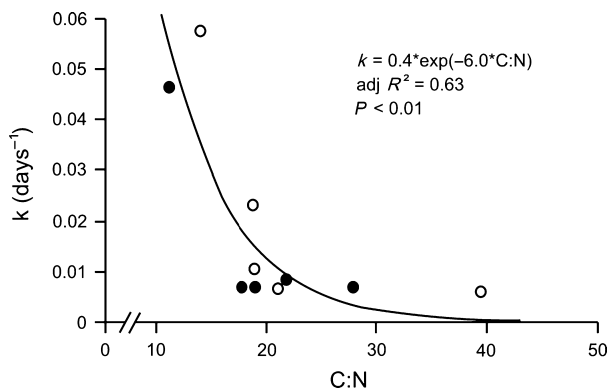


Fig. 3 Breakdown rates as a function of initial litter C/N ratio. Black circles, natives; open circles, exotics. The line shown is the nonlinear regression with corresponding curve equation, adjusted partial determination coefficient and P -value.

those of the woody *S. alba* and *A. negundo*, which displayed high lignin contents (Tables 2 & 4). The high breakdown rates of *I. glandulifera* and *U. dioica* resulted from the fast degradation of the leaves whereas the lignin content was determined on the sampled mix of leaves and stems. Finally, phosphorus content showed a positive, but non-significant relationship with breakdown rates (adjusted $R^2 < 0.0001$; $P > 0.35$).

Detritivorous invertebrate communities

Invertebrate abundance was not related to remaining AFDM, whether the relationship was constructed using total detritivorous invertebrate abundance ($P = 0.58$) or shredder abundance ($P = 0.63$).

No effect of exotic versus native litter was found on the invertebrate assemblage (ANOVA, $F = 0.0$, $P = 0.98$ for densities; ANCOVA, $F = 0.1$, $P = 0.81$ for taxonomic richness). A significant effect was observed in the interaction "date" * "species" ($P < 0.0001$ for all analyses). Maximum densities of total invertebrates occurred at 203 days with values in decreasing order for *B. davidii* > *I. glandulifera* > *P. nigra* > *R. caesius* > *F. japonica* >> all other species (Fig. 4). Filterers represented the major proportion of invertebrates, except at 203 days, when gatherers were predominant.

The analysis of detritivorous invertebrate assemblage composition showed that shredders were dominated by *Asellus aquaticus*, *Proasellus meridianus* and Chironomidae, while several species of Cladocera were dominant in the filterer group. ANOSIM analysis showed that the composition of invertebrate assemblages associated with exotic litter was similar to that associated with native litter ($R = 0.14$, $P = 0.1$).

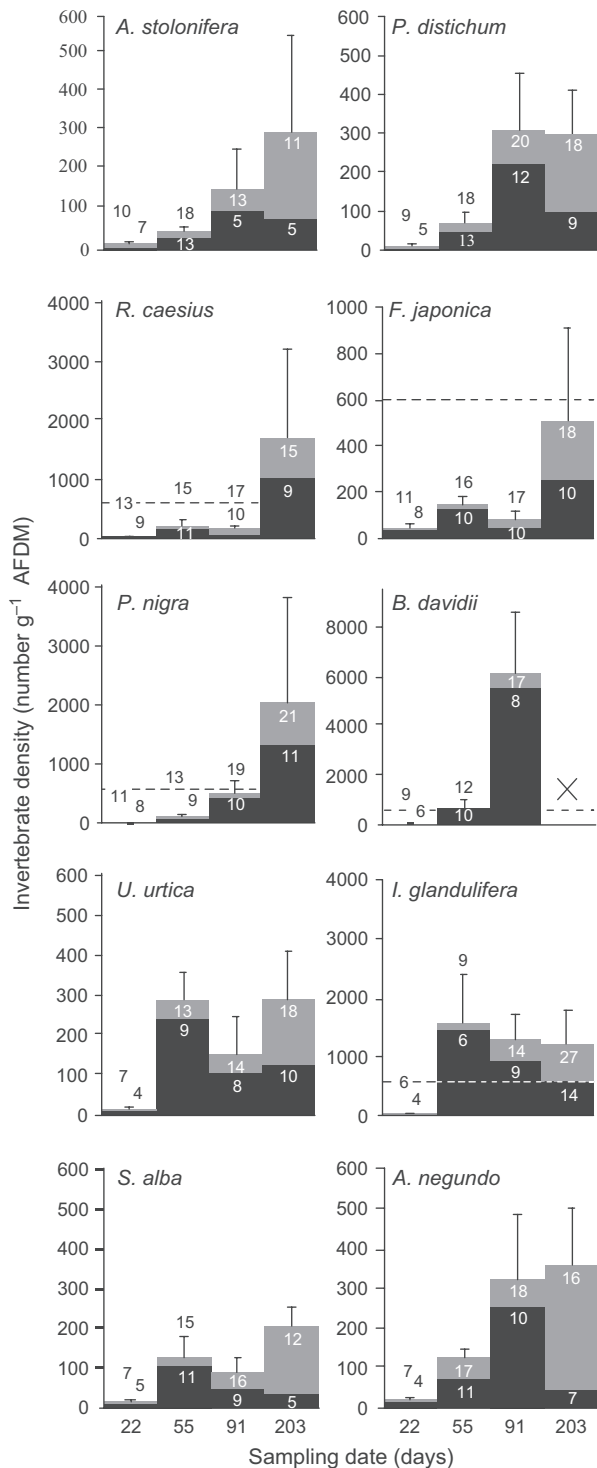


Fig. 4 Mean densities of detritivorous invertebrates. Black bars, filterer densities; grey bars all detritivorous invertebrates. Cross, no litter remaining in bags. Standard errors shown. Numbers in bars are mean taxonomic richness. The horizontal dashed line corresponds to 600 individuals.g⁻¹ AFDM.

A strong effect of plant species was demonstrated ($R = 0.07$, $P = 0.001$). *Post hoc* comparisons showed that this was mainly attributed to differences between *B. davidii*, *I. glandulifera* and other species. Among selected pairs, differences were only detected for the *U. dioica*/*I. glandulifera* pair, but with low statistical significance ($R = 0.09$, $P = 0.049$).

Discussion

Litter breakdown rate and species geographical origin

Our comparison of dominant native and co-occurring exotic invasive species has shown that litter breakdown rates of ecologically related plants in a temperate lentic ecosystem were primarily driven by the C/N ratio, with no influence of plant geographical origin. Among pairs of selected ecologically related species, one native species had a lower breakdown rate than its exotic counterpart (*P. nigra* /*B. davidii*), but we did not observe differences within any of the other species pairs. Based on species ecological proximity, our selection of plant species produced results that are congruent with those of Hladysz *et al.* (2009). These authors observed no overall difference in a wooded stream between breakdown rates of several exotic and native species selected on the basis of litter quality and palatability. Studying phylogenetically paired species in terrestrial environments, Ashton *et al.* (2005) and Godoy *et al.* (2009) found that breakdown rates were partly driven by species geographical origin, through its influence on litter chemical composition. However, these studies showed opposite trends with, respectively, higher breakdown rates for exotic species, probably related to higher N litter content (Ashton *et al.*, 2005), and lower ones, related to higher lignin litter content (Godoy *et al.*, 2009). Moreover, breakdown differences were only 8 and 10% mass loss, indicating that, when observed, neither tendency is marked.

The growth form of the selected species only slightly influenced initial carbon content, with higher values for woody species, but had no influence on C/N ratios and thus on litter breakdown rates. This apparently contrasts with the results of Godoy *et al.* (2009) who found growth form was the most influential factor in litter breakdown rates in a terrestrial environment. However, these authors found much

higher lignin content in woody species (up to 46%) compared with herbaceous species (down to 3%) whereas the range displayed by our selected species was smaller (1.4–9.1%). Given the range in our study, we did not find the previously observed negative relationship between litter breakdown rate and lignin content in woody species (Melillo, Aber & Muratore, 1982; Gessner & Chauvet, 1994; Ostrofsky, 1997). In particular, the low lignin contents of the herbaceous *P. distichum* and *A. stonolifera* were not associated with high breakdown rates. However, our results are consistent with those of Middleton *et al.* (1992) who showed that the breakdown rate of *P. distichum* was among the lowest of ten species in a tropical wetland. Here, the absence of a relationship between breakdown rate and lignin content may be related to the use of species from distinct botanical groups (monocots *vs.* dicots) and life forms (herbaceous *vs.* woody) that have different chemical compositions (Cornelissen, 1996; Cornelissen & Thompson, 1997; Buranov & Mazza, 2008).

Detritivorous invertebrate communities and their drivers

Invertebrate abundance and taxonomic richness associated with native and exotic plants were quite similar, in accordance with previous studies (Pereira, Graça & Molles, 1998; Bailey *et al.*, 2001; Braatne *et al.*, 2007; Kappes, Lay & Topp, 2007; Lecerf *et al.*, 2007). Contrary to the “Novel Weapons Hypothesis” (Callaway & Ridenour, 2004), we did not find lower invertebrate abundance or diversity in litter from species known to produce secondary chemical compounds that could act as invertebrate repellents (*F. japonica*: Beerling, Bailey & Conolly, 1994; *I. glandulifera* : Lobstein *et al.*, 2001; *B. davidii*: Houghton *et al.*, 2003). Perhaps leaching has induced a loss of a significant proportion of these inhibitory compounds. In this context, other studies have also found comparable macroinvertebrate assemblages and breakdown rates between *F. japonica* and native woody species in lotic systems (Braatne *et al.*, 2007; Lecerf *et al.*, 2007).

The lack of a relationship between invertebrate abundance and remaining litter AFDM can be explained by the low level of shredder abundance because of constraining environmental conditions, mainly low oxygen and high $\text{NH}_4\text{-N}$ concentrations. Ammonium-ammonia (NH_3) equilibrium depends on

temperature and pH. In the pond, the calculated mean $\text{NH}_3\text{-N}$ concentration (Emerson *et al.*, 1975) was $0.72 \mu\text{g L}^{-1}$, which is above the one recorded in streams where this toxic compound has been strongly suspected to be responsible for the absence of *Gammarus* (Lecerf *et al.*, 2006; Baldy *et al.*, 2007). As *Asellus aquaticus* is more resistant to ammonia than *Gammarus pulex* (Maltby, 1995), it is not surprising that the former species was the main shredder associated with litter in the pond. Beside the effect of low oxygen concentration *per se*, we cannot rule out additive or synergistic effects of high ammonia and low oxygen concentrations on invertebrate abundance and community structure. The low abundance of shredders also supports the hypothesis of dominance of microbial decomposition in the breakdown process as observed by Lecerf *et al.* (2006) and Baldy *et al.* (2007) in highly eutrophic and hypertrophic streams. Microbial activity produces fine particulate organic matter (Findlay & Arsuffi, 1989) that is consumed by collector or filterer invertebrates (Cummins & Klug, 1979). A related emerging pattern in our study is the early and large increase of filterer densities associated with plant species with fast litter breakdown, *B. davidii* and *I. glandulifera*, suggesting important microbial decomposition activity. High levels of fungal biomass and invertebrate abundance have already been observed in association with *B. davidii* litter (Hladyz *et al.*, 2009). As observed in that study and ours, initial primary chemical composition did not clearly favour the high breakdown rates observed. However, the specific jelly-like litter mass observed during *B. davidii* litter degradation strongly suggests a particular polymer structure and/or organisation in this species, which in turn could be related to fast breakdown. Conversely, the low C/N ratio and the high phosphorus content of *I. glandulifera* litter was expected to allow fast microbial decomposition accompanied by intense filterer activity. Finally high invertebrate densities associated with *F. japonica* and *P. nigra* litter could result in a habitat effect, as we preferentially found Chironomidae and *Asellus* individuals in numerous folds of *F. japonica* litter.

Fast leaf litter breakdown and resource discontinuity

In temperate ecosystems, breakdown of litter of various quality generally provides resource continuity until the next autumn’s litterfall (Staelens *et al.*, 2011).

Although in our study *I. glandulifera* and *U. dioica* leaf litter exhibited high breakdown rates, the longer persistence of stem litter and the additional production of relatively refractory leaf litter from the surrounding canopy of woody species, notably *S. alba*, was able to maintain resource availability until the next autumn. In contrast, *B. davidii* leaf litter degraded 3.5-fold faster than its native counterpart *P. nigra*, resulting in the disappearance of litter 6 months before the next litterfall. As we have also observed this result in the terrestrial environment (data not shown), leaf litter resource continuity is expected to be broken where *B. davidii* is the only species present, or is very strongly dominant, in temperate riparian areas. In these ecosystems, under a natural or moderately modified flow regime and strong floodplain connectivity, recurrent flooding allows for litter of various types to be redistributed repeatedly within the habitat mosaic of the floodplain (Xiong & Nilsson, 1997; Langhans, 2006). In such situations, overall litter turnover and consequent matter and energy transfers are expected to be altered only weakly by *B. davidii* inputs. In contrast, in areas showing natural or human-induced physical stability, the lack of litter transport by floods would result in dramatic reductions in inputs of slowly-degrading litter produced by other species. More generally, large stands of rapidly degrading leaf litter species would have limited effects when surrounding plant diversity is high and litter redistribution by floods is occurring. When either one or other condition is lacking, the induced discontinuity of plant litter resource would decrease niche opportunities for rare and specialised detritivores, with cumulative effects from year to year and a possible result of loss of biodiversity. We may also expect large consequences of invasions by exotic species that produce poor leaf quality litter, as a very slow breakdown rate would result in limited nutrient cycling (Dassonville, 2008; Hladyz *et al.*, 2009). Invasions by plants producing litter subject to extreme breakdown rates have to be considered a potential threat for biodiversity.

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