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PLANT-MICROBE-ANIMAL INTERACTIONS – ORIGINAL RESEARCH

Exotic tree and shrub invasions alter leaf-litter microflora and arthropod communities

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Abstract

Approximately 90% of all annual net primary productivity in temperate deciduous forests ends up entering the detritus food web as leaf litter. Due to chemical and physical differences from native litter, inputs from invasive species may impact the litter-dwelling community and ecosystem processes. We compared leaf-litter nutritional quality and decomposition rates from two invasive shrubs, *Lonicera maackii* and *Rhamnus davurica*, and the invasive tree *Ailanthus altissima* to litter from native oak-hickory forest in the Shenandoah Valley of Virginia, USA. We sampled litter from both invaded and uninvaded habitats and conducted litter colonization experiments to test for effects on microflora and the litter-dwelling arthropod communities. Litter from all three invasive species decomposed more rapidly than native litter, with native habitats averaging two to nearly five times as much litter by June. Invasive litter had higher nitrogen concentration and lower C:N ratios than native litter. Invasive litter supported greater growth of bacteria and fungi. Higher numbers of arthropods colonized invasive litter than native litter, but litter arthropod numbers on the forest floor of invaded habitats dropped in the early summer as litter decomposed. Litter had no effect on arthropod richness. Over short time scales, our results indicate that these invasive species represent beneficial, novel resources for the litter-dwelling community. However, the short-lived nature of this resource resulted in a crash in the abundance of the litter-dwelling organisms once the litter decomposed. As a whole, native habitat seems to support a larger, more stable litter-dwelling community over the course of a growing season.

Keywords *Ailanthus altissima* · Decomposition · Detritus · *Lonicera maackii* · *Rhamnus davurica*

Introduction

Approximately 90% of the net primary production of temperate deciduous forests and shrublands enter into detrital food webs as leaf litter (Cebrian 1999), and its decomposition serves as a major pathway for nutrient cycling (Gessner et al. 2010; Handa et al. 2014). Litter fall provides an enormous resource pulse for bacteria, fungi, and invertebrates that facilitate its decomposition, but changes in litter quantity and quality can alter the detrital food webs and nutrient cycling (Uetz 1979; Bultman and Uetz 1984; Chen and Wise 1999; Antvogel and Bonn 2001). Because litter from non-native plants can differ substantially from native litter, we expect novel detrital food webs and patterns of nutrient cycling to emerge in heavily invaded habitats (Lee et al. 2017), but studies have tended to focus on only one or two components of the web. Here, we examine leaf properties of native and invasive litter, decomposition rates, and detrital communities including bacteria, fungi, and arthropods in

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invaded and uninvaded deciduous forests and shrublands in the Shenandoah Valley of Virginia.

The replacement of native litter with litter from invasive species has the potential to create effects that propagate through the detrital food web. Native and non-native leaf litters can differ in their functional traits such as C:N ratio (Liao et al. 2008), leaf secondary chemistry (Bassett et al. 2011), leaf toughness, and specific leaf area (Liu et al. 2018; Lopez-Rojo et al. 2018), leading to changes in the microflora, the types and numbers of arthropods supported by the leaf litter, and ultimately in rates of decomposition and nitrogen mineralization in the soil (Arthur et al. 2012; Rodrigues et al. 2015; Bray et al. 2017). Arthropods likely respond to leaf litter directly based on its habitat quality, nutritional quality, and secondary chemicals, and indirectly based on the colonization by micro-organisms. The population response of trophic groups such as fungivores and detritivores can carry the effects of the invasive litter to their predators, thereby affecting most or all of the detritus food web (Gutiérrez-López et al. 2014; Rusterholz et al. 2014; Motard et al. 2015).

The potential importance of invasive litter in altering forest ecosystem processes and detrital trophic webs has received a great deal of attention in the recent years. Most of these studies, however, have focused only on effects at a single trophic position or process in the web. Many recent studies have compared the rates of decomposition and nitrogen cycling for invasive and native litter (Standish et al. 2004; Poulette and Arthur 2012; Schuster and Dukes 2014; Stokdyk and Herrman 2014; Lanta et al. 2015; Jo et al 2017; Aerts et al. 2017). Others have examined the effects on fungal or bacterial communities (Elgersma et al 2012; Stokdyk and Herrman 2016). Still others have documented effects on invertebrate communities by comparisons of native and invaded habitats (Christopher and Cameron 2012; Motard et al. 2015; Nguyen et al. 2016) or by experimental manipulations (Tuttle et al. 2009; Gutiérrez-López et al 2014; Rusterholz et al. 2014; Lewis et al. 2017). Some studies have looked at two trophic levels (Belnap et al. 2005; Tuttle et al. 2009; Arthur et al. 2012; Bottollier-Curtet et al. 2015; Bray et al 2017), but to our knowledge, no study has attempted to examine leaf litter quality, supply, and decomposition, litter microflora, and litter arthropods.

The goal of this study was to determine what effects invasive species have on litter decomposition and the leaf litter-dwelling communities of a forest ecosystem using both observational and experimental approaches. We compared the nutritional quality and decomposition rates of native and invasive litter, and investigated the effects of these species on the bacteria, fungi, and arthropods in the litter in both uninvaded hardwood forest habitat and habitats already invaded by these species. We focused on the three most common invasive woody plants at our study site in the Shenandoah Valley of Virginia, USA: two invasive shrubs, *Lonicera maackii* (Rupr.) Herder (Caprifoliaceae) and *Rhamnus davurica* Pall. (Rhamnaceae), and the invasive tree *Ailanthus altissima* (Mill) Swingle (Simaroubaceae). We examined the effects of litter source (native vs. invasive litter) and habitat (native sites vs. invaded sites) using both litter naturally on the ground in each habitat and packets of native or invasive litter that were introduced into invaded and uninvaded habitats. We expected that litter sources with high nutrient concentration would promote higher abundance of litter-dwelling organisms (bacteria, fungi, and arthropods) with possible changes in taxonomic richness.

Materials and methods

Study site

This study took place at Blandy Experimental Farm in the northern Shenandoah Valley in Clarke County, VA, USA (39.06º N, 78.06º W). Blandy's 285 hectares includes shrubland and mature forest fragments ranging in size from 1.5 to 18 ha (Fig. S1). Annual mean precipitation is 99.6 cm with mean January and July high/low temperatures of 6.2º/-4.5ºC and 31.4º/17.5º C, respectively. Soils (Poplimento-Timberville) are well drained, with subsoils formed from weathered limestone (Edmonds and Stiegler 1982).

We studied four types of communities: forests dominated by native deciduous trees and shrubs and habitats heavily invaded by one of three non-native species: Dahurian buckthorn (*R. davurica*, bush honeysuckle (*L. maackii*), and tree of heaven (*A. altissima*). Five plots of each community type were included in the study. Native plots were located in forest fragments (each at least 100 years old) ranging from 5 to 18.6 ha and dominated by a mixed canopy of red oak (*Quercus rubra* L.), white oak (*Q. alba* L.), Mockernut hickory (*Carya tomentosa* (Lam.) Nutt.), hackberry (*Celtis laevigata* Willd.), and black walnut (*Juglans nigra* L.) with an understory of flowering dogwood (*Cornus florida* L.) and spicebush (*Lindera benzoin* (L.) Blume). The forest is typical of the valley floors of the Ridge and Valley section of Virginia (Braun 1950). Plots invaded by Dahurian buckthorn (hereafter, *Rhamnus*) were located in dense 5.0 and 11 ha shrublands where this species has formed near monocultures for the past 14–30 years. Plots invaded by bush honeysuckle (hereafter *Lonicera*) were located in a 14-year-old shrubland and four forest fragments ranging from 5 to 18.6 ha. A large *Lonicera* cut in one of the fragments dated to 1989, suggesting a minimum time since invasion of 25 years. Tree of heaven (hereafter, *Ailanthus*) plots were placed in areas with dense clusters of canopy-sized *Ailanthus*. A large *Ailanthus* cut at one of the sites dated to 1984, setting a minimum time

since invasion of 30 years. Plots of the same community type were never located closer than 100 m apart.

Each of these three invasive species was an abundant component of either the understory or canopy in parts of the forest fragments at Blandy Experimental Farm, replacing or displacing native trees and shrubs. For the *Ailanthus* and *Rhamnus* species, we selected sites where these species dominated the area (29–284 m^2 and 155–6782 m^2, respectively), such that almost all leaf litter came from these species. This was done to get the best estimate of the effects of the invasive litter, although there may be some confounding effects of land use (or other variables), because these sites were likely more recently disturbed. Only one *Lonicera* site was a pure stand (56 m^2). The others (82–366 m^2) were located in the forest fragments and had a native hardwood canopy over a dense honeysuckle canopy, so the litter at these sites was a mix of *Lonicera* and native canopy trees.

Leaf-litter density, chemical properties, and decomposition

To measure changes in the density of litter cover on the forest floor, we collected leaves from each of the five plots in all four habitats monthly from 22-Mar to 20-Jun-2014. We randomly placed a 0.25 m^2 frame at each plot and collected all litter within the frame. All samples were dried for at least 48 h at 60º C and were weighed to get dry mass. The dry mass 0.25 m^{-2} was then multiplied by 4, so that litter density was represented as g dry litter m^{-2} for each site.

To measure the leaf-litter nutrient concentrations, we oven-dried leaf-litter samples for 48 h at 70 °C from October 2013 for 48 h. We measured carbon (g C g^{-1} leaf) and nitrogen content (g N g^{-1} leaf) from 2 to 5 mg of ground samples with a Thermo Fisher Flash 2000 Organic Elemental Analyzer. We analyzed four replicate samples of each of the four litter types.

Decomposition rates of the different litter types were compared by placing leaf samples into nylon mesh bags (3 × 3 mm mesh) containing 45–50 g freshly fallen litter. We obtained fallen leaves from each habitat in the late October 2013 by raking from under native mixed hardwoods in uninvaded forest fragments, from monospecific stands of *Rhamnus* and *Ailanthus*, and by collecting *Lonicera* leaves with a tarp underneath several individuals of this species (the leaves never touched the ground). We dried ten representative freshly collected samples of each litter type (45–50 g each) for 48 h at 60 °C to obtain a conversion factor (the ratio of the dry mass/fresh mass, averaged for all ten samples of each litter type) to estimate the dry weight of litter placed in each packet at the beginning of the experiment. We placed six packets of native litter and six packets of each of the three invasive species into each of the five native plots on 29-Nov-2013. On the first of each month beginning on 1-Feb-2014, we collected one packet of each litter type from each native plot, for a total of 6 months. We weighed dried samples (48 h at 60 °C) and calculated the mean proportion of dry mass litter loss.

Statistical analyses

We conducted all analyses with SAS (v 9.4). We evaluated differences among the four habitats in litter density using a repeated-measures ANOVA using the mixed procedure, with the plot within habitat as the sampling unit and the log-transformed mass of litter (g m^{-2}) present in the study sites the dependent variable. Habitat, sampling date, and their interaction were treated as fixed effects. An "unstructured" variance–covariance structure assumption provided the best fit to the data based on AIC (Littell et al. 2006).

We tested for differences in decomposition rates among the four litter types placed in bags into native habitats using a randomized block ANOVA, with the remaining litter mass as a proportion of the initial litter mass as the dependent variable. Litter type, collection date, and their interaction were treated as fixed independent variables, and plot was included as a random effect. A one-way ANOVA tested for differences among the litter types in nutrient concentration. Carbon, nitrogen, and the C:N ratios were the dependent variables, and the litter source was the independent variable.

Arthropod communities in native and invaded habitats

To determine the abundance of arthropods naturally occurring in the leaf litter in each of the four habitats, we collected "fresh" litter at each site each month beginning 22-Mar through 20-Jun-2014. The goal was to collect approximately 50 g of dry litter at each collection, but due to variable environmental conditions, we collected 60–100 g of fresh litter to achieve this. We sampled all intact and fragmented litter in the sampling area until only bare ground remained. Our sampling technique almost certainly undersampled or missed some groups of arthropods (e.g., fast-moving or flying species), but we assume that these sampling errors were unbiased with respect to habitats. We immediately transferred the litter to the laboratory for arthropod collection using Berlese–Tullgren funnels. After 10 days, we then removed the litter and dried it at 60 °C for an additional 24 h to obtain a dry mass. We preserved all arthropods in ethanol and identified the lowest taxon possible (most commonly family). To control for differences in the amount of litter sampled and the differences among plots in litter density, we used our data on litter density (see previous subsection) to standardize arthropod abundances for each plot as numbers of arthropods m^{-2} of dry litter.

Statistical analyses

We tested for differences in arthropod abundance m^{-2} and arthropod richness (the number of identified arthropod taxa) among the four study habitats using a repeated-measures generalized linear mixed model ANOVA. We identified the most appropriate distribution and link function based on pseudo-AICc scores. For total abundance m^{-2}, the best fit was an exponential distribution and a log link, and for arthropod richness, the best fit was a Poisson distribution with a log link. Habitat, sampling date, and their interaction with time were included as fixed effects. Sampling date was treated as a repeated variable for the random subject effect, plots nested within habitat.

Leaf-litter colonization experiments

Leaf packets

To test for differential microorganism and arthropod colonization of different types of leaf litter, we placed leaf-litter packets in each of the four habitats. We deployed packets in late November and characterized colonization throughout the following spring. We did this for 2 consecutive years.

Specifically, we collected leaf litter from native and invasive species in November of 2012 and October 2013 as described in the earlier decomposition experiment. We used a representative mixture of native species rather than focusing on a single species, so that we could compare the properties of the invasive species litter to the litter in the habitats that they were invading. We air-dried leaves in the lab for at least a week to eliminate most of the arthropods that may have colonized the litter prior to collection. We feared that harsher treatment of leaves (e.g., high heat) could alter chemical composition. We created litter packets in 38 cm × 25 cm bags with 3 × 3 mm^2 mesh containing three "doses" of litter: 100% invasive, 50–50% invasive-native mix, or 100% native. Each packet contained 90–100 g of the air-dried litter. To test for the effect of habitat on colonization, we deployed packets in native habitats and in each of the three invaded habitats on 24-Nov-2012 and again on 29-Nov-2013. In year one, samples were collected beginning 27-Apr-2013, and packets were then retrieved at approximately 10-day intervals until 12-Jun-2013. In year two, we collected samples beginning 1-Mar-2014 and retrieved monthly until 4-Jul-2014.

In each invaded habitat, we placed three different litter packets at each site: one pure packet of the respective invasive litter, one native, and one mixed. In each native habitat, we placed seven packets: a packet of pure native litter, one pure packet of each of the three invasive species, and three mixed packets of each of the three invasive species with the native litter. On each collection date, we collected one representative packet of each type from each of the four habitats (*Ailanthus* invaded, *Lonicera* invaded, *Rhamnus* invaded, and native) by randomly selecting one plot from each habitat type and collecting all packets from those plots (3 packets × 3 invaded habitat plots + 7 packets from native habitat = 16 total packets per sampling date).

Microflora

In year one of the experiment, bacterial and fungal abundance was estimated using Acridine Orange Direct Counting (AODC), a microscopic enumeration technique (Hobbie et al. 1977). The advantage of this technique is that it is a direct measure of the cell number or hyphal length convertible to biovolume with relatively simple assumptions. We took two 1 g samples of litter from each pure species packet (100% native or invasive litter) on their collection date and stored them in 4% formalin. We omitted the mixed packet, because we were unable to determine the leaf species composition of a 1 g sample. Within 1 week of storing the samples in formalin, we homogenized each sample in 100 mL of a 2% formaldehyde solution in preparation for staining. For the staining procedure, 10 mL of deionized water was placed in a filter column, followed by an aliquot of sample, and then 1.0 mL Acridine Orange. We adjusted the volume of the sample aliquot to produce between 20 and 200 bacterial cells per microscope field. Prepared slides were viewed through a fluorescence microscope (bacteria under 1000×, fungi: 400×), and counted in accordance with the general AODC guidelines (Hobbie et al. 1977). Bacterial abundance is reported as the number of cells g^{-1} dry weight of litter material. Fungal abundance estimates are reported as hyphal length g^{-1} dry litter material using the hyphal intersection approach of Jones and Mollison (1948). To estimate biovolume of the microbiota, we took digital images of five random fields per sample for both bacteria and fungi. We measured the length and width of 20 bacteria cells and the mean diameter of hypha from each field using ImageJ 1.49. Bacterial biovolume was estimated using:

$$V = \left(\frac{\pi}{4}\right) w^2 \left(\frac{l - w}{3}\right), \quad (1)$$

where V = biovolume (μm^3); w = width of the bacterial cell (μm); and l = length of the cell (μm) (Krambeck et al. 1981). Fungal hypha volume was determined by treating hyphae as cylinders for biovolume conversion.

Arthropods

We collected arthropods from the leaf-litter packets with Berlese–Tullgren funnels as described previously. Ants occasionally nested under packets, but because their presence in the litter packets seemed to be an artifact of the

packet providing structural cover, we excluded ants from the arthropod abundance estimates. Tests on the abundance of ants separately indicated no differences between litter mixtures or habitats (Supplemental table S1).

Statistical analyses

Because the experiment was not established as a full factorial (litter from each invasive species was never placed in the habitat of another invasive species), we ran separate analyses for each invasive species (*Ailanthus*, *Lonicera*, and *Rhamnus*). Each analysis included the litter packets (100% invasive, 50% invasive, and 100% native) collected from the invaded habitat and the corresponding litter packets collected from the native habitat. The effects of leaf-litter type (invasive or native) and habitat (invaded or native) on the abundance of bacterial cells (cells g^{-1} dry litter), length of fungal hyphae, and the biovolume of bacterial cells and fungal hyphae (μm^3 g^{-1} dry litter) were analyzed by a factorial ANOVA with litter type, habitat, and their interaction as fixed effects. All response variables were log-transformed to meet normality and homogeneity of variance assumptions. Sampling date was included in the model as a random effect, but because only one sample of each litter type was collected from each habitat at each sampling date, two-way and three-way interactions involving time were not included in the model.

The effects of litter type and habitat on total arthropod abundance and richness were analyzed by a generalized linear mixed model ANOVA, with litter type (native, invasive, or mixed), habitat (native or invaded), and their interactions as fixed effects. The year of collection (2013 or 2014) and Julian day nested within year were included as random effects. Based on pseudo-AICc scores, we selected a Poisson distribution with a log link as the best assumption for all analyses except for the analysis of arthropod abundance for *Rhamnus* litter, which had a best fit using an exponential distribution with a log link.

Results

Leaf-litter density, chemical properties, and decomposition

Leaf-litter density on the ground differed significantly among habitats (Fig. 1; $F_{3,16} = 8.07$, $P < 0.0017$), and the rates of litter loss differed significantly among the four habitats (habitat × time: $F_{9,16} = 3.19$, $P < 0.0207$). Native and *Lonicera* habitats began with more than twice the litter than in both Ailanthus and *Rhamnus* habitats in March. By June, native habitats had 4.8 times more litter than *Ailanthus* habitats, 2.9 times more litter than *Rhamnus*, and 2.0

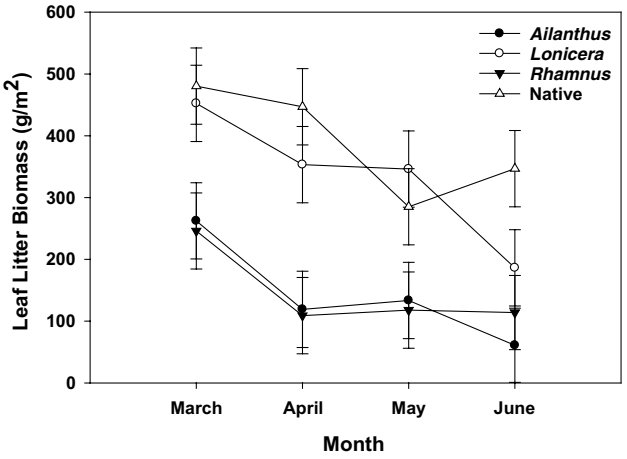

Fig. 1 Changes in mean litter cover (g m^{-2}) in *Ailanthus altissima*, *Lonicera maackii*, *Rhamnus davurica*, and native habitats. Error bars represent one standard error

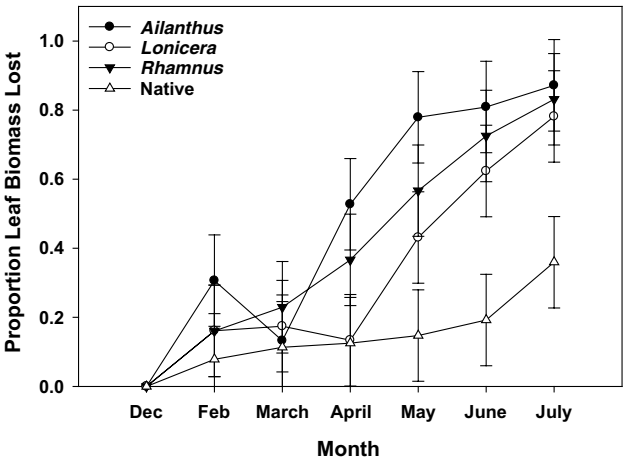

Fig. 2 Mean proportion of litter mass (± 1 s.e.) lost over 6 months for packets of *Ailanthus altissima*, *Lonicera maackii*, *Rhamnus davurica*, and native leaf litter placed in native habitat

times more litter than *Lonicera*. Litter decomposition within the mesh bags also showed a significant interaction between litter type and time (Fig. 2; $F_{15,60} = 3.31$, $P = 0.0005$), with the three invasive species losing mass at a higher rate than the native litter. By July, 78–87% of the invasive litter had decomposed, compared to only 36% of native litter.

Litter from invasive species showed significantly higher nitrogen concentration ($F_{3,12} = 116.57$, $P < 0.0001$), lower carbon concentration ($F_{3,12} = 47.81$, $P < 0.0001$), and lower C:N ratios ($F_{3,12} = 428.49$, $P < 0.0001$). Litter nitrogen concentrations in *Ailanthus* (2.4% ± 0.1), *Lonicera* (2.1% ± 0.1), and *Rhamnus* (1.5% ± 0.1) were 2.4, 2.1, and 1.5 times greater, respectively, than in native litter (1.0% ± 0.1). As a result, native litter had a higher C:N ratio (48.2 ± 1.4) than any of the invasive litters (*Ailanthus* 18.8 ± 1.4; *Lonicera*

22.1 ± 1.4, and *Rhamnus* 25.8 ± 1.4). These results indicate that the nitrogen content of invasive litter is potentially more readily available to decomposers than that of native litter.

Arthropod communities in native and invaded habitats

A single outlying plot (an unusually wet plot that contained exceptionally high numbers of mites and springtails) greatly inflated the variance in the *Ailanthus* samples. When we omitted this plot from the analysis, habitats differed significantly in mean arthropod abundance (Fig. 3a; $F_{3,15}=6.52$, $P=0.0049$), with both *Ailanthus* and *Rhamnus* habitats having significantly lower arthropod densities than native habitats (See Fig. S2 for an analysis with all plots). The temporal pattern of arthropod abundance throughout the sampling period varied only marginally (Fig. 3b; $F_{9,45}=1.88$, $P=0.0798$). Arthropod abundance in native habitat exceeded the invaded habitats in all months, but

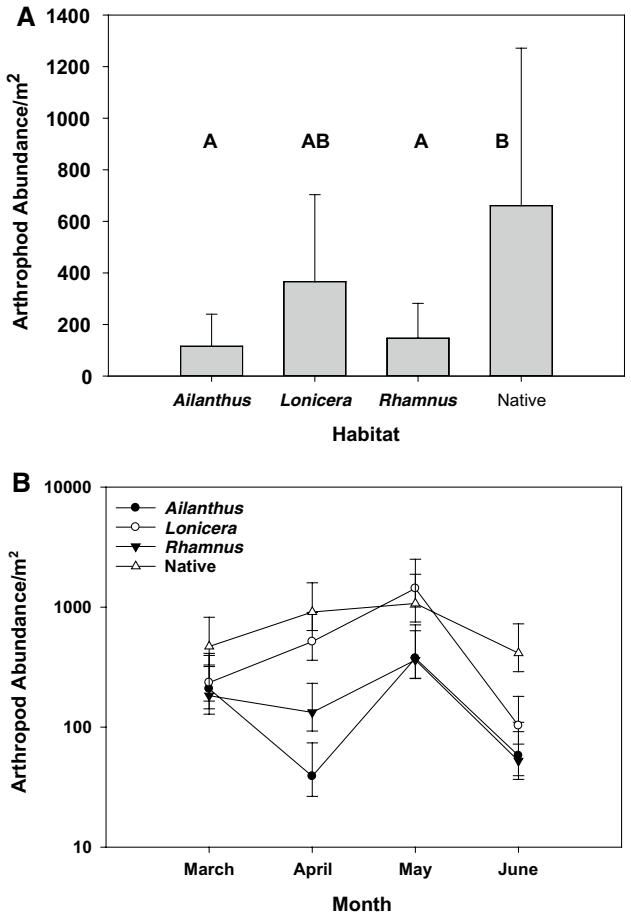

Fig. 3 Mean abundance of arthropods m^{-2} of litter naturally present in each habitat. **a** Mean abundance m^{-2} (and 95% confidence intervals) by habitat, pooled across sampling period. **b** Mean abundance m^{-2} (± 1 s.e.) for each habitat across collection dates

May. *Lonicera* climbed to a peak of 1431 arthropods m^{-2} in May before dropping to a low of 103 in June. *Ailanthus* and *Rhamnus* habitats had consistently low arthropod abundance, each peaking in May with 376 and 363 arthropods m^{-2}, respectively. Mean arthropod richness did not differ significantly among habitats (11.2–14.6 taxa, $F_{3,16}=0.9$, $P=0.4648$) and showed no temporal patterns.

Leaf-litter colonization experiments

Microflora colonization

Our various measures of the size of the bacterial and fungal communities tended to show much greater microflora loads on the litter of the invasive species. Mean bacterial abundance (cells g^{-1} dry leaf) in the three invasive species was two to nearly four times higher than in native litter (Table 1; *Ailanthus*: $F_{1,12}=24.81$, $P=0.0003$, *Lonicera*: $F_{1,12}=48.92$, $P<0.0001$; *Rhamnus*: $F_{1,12}=9.6$, $P=0.0092$). Bacterial biovolume (μm^3 g^{-1} dry leaf) did not differ between *Ailanthus* and native litter packets (Table 1; $F_{1,9}=2.28$, $P=0.1651$), but cell biovolume on *Lonicera* litter was 8.9 times greater than on native litter, and *Rhamnus* litter was 3.4 times greater than on native litter (Table 1; *Lonicera*: $F_{1,9}=9.89$, $P=0.0016$; *Rhamnus*: $F_{1,9}=6.98$, $P=0.0268$).

Mean fungal hyphae length in *Lonicera* and *Rhamnus* litter was 1.9 and 1.7 times greater, respectively, than native litter, but fungal hyphae length did not differ between native and *Ailanthus* litter (Table 1; *Lonicera* $F_{1,12}=5.54$, $P=0.0365$; *Rhamnus*: $F_{1,12}=4.07$, $P=0.0667$; *Ailanthus*: $F_{1,12}=2.35$, $P=0.1513$). There were no differences in the mean fungal biovolume (μm^3 g^{-1} dry leaf) between invasive litter packets and native litter (Table 1; *Ailanthus*: $F_{1,9}=0.01$, $P=0.9335$; *Lonicera*: $F_{1,9}=1.24$, $P=0.2936$; *Rhamnus*: $F_{1,9}=3.04$, $P=0.1153$).

Differences in microflora among habitats were not pronounced. The sole exception was that mean fungal biovolume (μm^3 g^{-1} dry leaf) was 1.9 times greater in native habitats relative to litter placed in *Ailanthus* habitats ($F_{1,9}=6.83$, $P=0.0281$). Fungal biovolume for litter placed in *Lonicera* or *Rhamnus* habitats did not differ from biovolume in native habitats (all $P>0.10$), and there were no differences among habitats in mean fungal hyphae length or in any measure of bacterial growth (all $P>0.14$).

Arthropod colonization

Arthropod colonization of leaf packets tended to be higher in native habitat. Regardless of habitat, however, colonization tended to be higher in invasive leaf packets. Total arthropod abundance in litter packets placed in native habitats was 1.6 times greater than in *Ailanthus* and 1.6 times greater than *Lonicera* habitats (Fig. 4a, b; *Ailanthus*: $F_{1,40}=484.2$,

Table 1 Means (and 95% confidence intervals) of bacterial and fungal responses to invasive and native litter (data pooled across habitats)

Microbial response	Invasive species	Litter type	
		Invasive litter	Native litter
Bacterial cell abundance (cells g^{-1} dry leaf)	*Ailanthus*	1.29×10^{10} ***	6.34×10^{9}
		(1.09–1.49)	(4.31–8.37)
	Lonicera	1.77×10^{10} ***	4.64×10^{9}
		(1.48–2.06)	(1.77–7.52)
	Rhamnus	1.27×10^{10} **	5.16×10^{9}
		(0.89–1.64)	(1.41–8.90)
Bacterial biovolume (μm^3 g^{-1} dry leaf)	*Ailanthus*	2.43×10^{8}	1.14×10^{8}
		(0.98–4.87)	(0.51–2.54)
	Lonicera	6.06×10^{8} **	6.79×10^{7}
		(2.77–13.3)	(3.10–14.9)
	Rhamnus	2.28×10^{8} *	6.80×10^{7}
		(1.10–4.74)	(3.27–14.1)
Fungal hyphae length (mm g^{-1} dry leaf)	*Ailanthus*	1.77×10^{8}	2.46×10^{8}
		(1.08–2.46)	(1.77–3.15)
	Lonicera	4.71×10^{8} *	2.46×10^{8}
		(3.24–6.18)	(0.99–3.94)
	Rhamnus	3.60×10^{8}	2.17×10^{8}
		(2.51–4.69)	(1.07–3.26)
Fungal biovolume (μm^3 g^{-1} dry leaf)	*Ailanthus*	8.37×10^{8}	8.20×10^{8}
		(5.69–12.3)	(5.58–12.1)
	Lonicera	1.11×10^{9}	5.93×10^{8}
		(0.45–2.73)	(2.41–14.6)
	Rhamnus	1.80×10^{9}	7.20×10^{8}
		(0.78–4.19)	(6.27–33.8)

Confidence intervals are of the same order of magnitude as the means. Means marked with asterisks (*) indicate significant differences between means from invasive and native leaf litter (*$P<0.05$, **$P<0.01$, ***$P<0.001$)

$P<0.0001$; *Lonicera*: $F_{1,40}=620.34$, $P<0.0001$). Total arthropod abundance in litter packets in *Rhamnus* habitats did not differ from native habitat (Fig. 4c; $F_{1,40}=0.83$, $p=0.3688$). In contrast, total arthropod abundance was significantly higher in all three invasive species litter packets relative to native packets (Fig. 4; *Ailanthus*: $F_{2,40}=1654.98$, $P<0.0001$; *Lonicera*: $F_{2,40}=2863.81$, $P<0.0001$; *Rhamnus*: $F_{2,40}=3.76$, $P=0.0318$), with *Ailanthus*, *Lonicera*, and *Rhamnus* litter containing 4.3, 5.1, and 2.5 times greater abundances, respectively. We detected significant interactions between litter mixture and habitat for the *Ailanthus* and *Lonicera* analyses, but not for *Rhamnus* (Fig. 4; *Ailanthus*: $F_{2,40}=7.3$, $P=0.002$; *Lonicera*: $F_{2,40}=248.51$, $P<0.0001$; *Rhamnus*: $F_{2,40}=0.24$, $P=0.7915$). More arthropods colonized *Ailanthus* (1.6×) and mixed-*Ailanthus* (1.8×) litter packets in native habitat than in the *Ailanthus* habitat. Similarly, in native habitat, more arthropods colonized *Lonicera* (1.9×) and mixed-*Lonicera* (2.4×) litter packets than in *Lonicera* habitat.

Total arthropod richness in native habitat was 1.2 times greater than in *Rhamnus* habitat, but it did not differ from *Ailanthus* or *Lonicera* and native habitat (Supplemental Table S2; *Ailanthus*: $F_{1,40}=2.87$, $P=0.0981$; *Lonicera*: $F_{1,40}=2.95$, $P=0.0934$; *Rhamnus*: $F_{1,40}=4.71$, $P=0.036$). Total arthropod richness was significantly greater in *Ailanthus* litter (1.2×) than native litter, but not for any other litter mixture compared to native litter (Supplemental Table S2; *Ailanthus*: $F_{2,40}=3.94$, $P=0.0274$; *Lonicera*: $F_{2,40}=2.8$, $P=0.0725$; *Rhamnus*: $F_{2,40}=1.82$, $P=0.1748$). There was no interaction between litter mixtures and invaded or uninvaded habitats for arthropod richness (*Ailanthus*: $F_{2,40}=0.23$, $P=0.7918$; *Lonicera*: $F_{2,40}=0.04$, $P=0.9597$; *Rhamnus*: $F_{2,40}=0.88$, $P=0.424$).

Discussion

We observed a higher nitrogen concentration and a lower C:N ratio in the litter from the three invasive species in this study. Higher nitrogen in invasive litter is a common pattern and is likely attributable to the rapid growth rates of invasive species (Leishman et al. 2007; 2010;

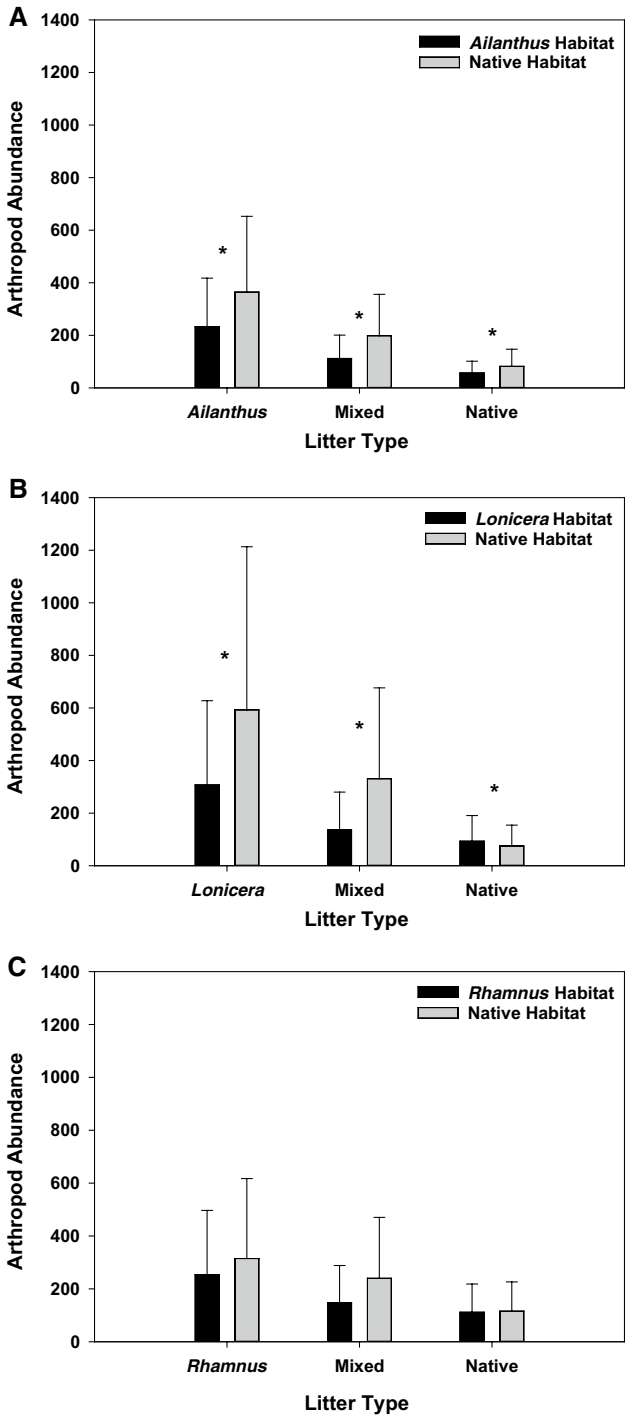

Fig. 4 Mean abundance of arthropods (and 95% confidence intervals) colonizing litter bags of three types (pure invasive, mixed, or pure native) for **a** *Ailanthus altissima*, **b** *Lonicera maackii*, and **c** *Rhamnus davurica* litter. Means are shown for bags placed in invaded (black bars) and native habitats (gray bars). Asterisks (*) indicate a significant difference between habitats ($P < 0.05$) based on a priori orthogonal contrasts

van Kleunen et al. 2010). Meta-analyses suggest that the greatest opportunity for shifts in ecosystem function occur when invasive species differ greatly in leaf traits (e.g., leaf nitrogen concentration, decomposition rates, and specific leaf area) from the native plant community (Castro-Díez 2014; Lee et al. 2017). It is likely that the large differences in leaf-litter nitrogen concentration and C:N ratio drove partly our observed biotic changes in the bacterial, fungal, and arthropod communities in this eastern deciduous forest community.

Invasive litter was associated with greater bacterial and, for *Lonicera*, fungal growth. Previous studies suggest that two of three invasive species in this study also promote shifts in the composition of the microbial community that may facilitate more rapid decomposition. Litter from *Lonicera* supports a microbial community prior to leaf senescence that is distinct from native litter and appears to drive the higher rate of decomposition compared to native litter (Arthur et al. 2012). *Rhamnus* litter increases the relative abundance of nitrogen-cycling bacteria in the soil (Rodrigues et al. 2015). A denser microflora was not universal across our invasive species, however. *Ailanthus* and *Rhamnus* did not differ from native litter in fungal abundance or biovolume. Antimicrobial secondary chemicals in *Ailanthus* leaves can lower soil microbial activity (Motard et al. 2015), and this may have been a factor here.

The greater bacterial load of the invasive litters compared to native litter is likely responsible, in part, for their faster decomposition rates, which likely results in accelerated nitrogen cycling (Liao et al. 2008; Schuster and Dukes 2014; Jo et al. 2017; Lee et al. 2017). Accelerated nitrogen cycling may produce a positive feedback for the establishment of the invading species, because invasive species benefit disproportionally from higher nitrogen availability (Elgersma et al. 2012; Schuster and Dukes 2014). We speculate that poor structural integrity of *Ailanthus* litter (noted by Swan et al. 2008) contributes its high rate loss from our mesh bags and from the forest floor.

A faster decomposition rate also likely creates summer discontinuities in resource and shelter availability for the arthropods that depend on leaf litter (Heneghan et al. 2002; Bottollier-Curet et al. 2015). From March to June *Rhamnus, Lonicera*, and *Ailanthus* habitats lost 75%, 59%, and 57% of their leaf-litter mass, respectively, compared to only 28% litter loss in the litter native habitats. By June, there was over five times more litter remaining in the native habitats compared to *Rhamnus* habitats and three times more than in the *Ailanthus* habitats. *Lonicera* habitats had slightly more than half the litter that native habitats had, but this was likely because most of our *Lonicera* plots were under native canopies and, therefore, included a substantial amount of native litter. The more reliable availability of litter in native habitats may contribute to our finding of higher arthropod

densities in the litter and that arthropod colonization rates were consistently higher in native habitats.

Although the invasive litter was much more ephemeral than the native litter, it appeared to be a superior resource for arthropods in the short term. Arthropod colonization was higher in all three invasive litter types relative to native litter, and most trophic groups showed higher numbers in the invasive litter than native litter. Arthropod abundance in packets containing a mix of native and invasive litter were almost always intermediate, suggesting a "dosage" response to litter quality. Previous studies have suggested that explanations for arthropod community responses to invasive litter may include microclimate changes such as litter or soil moisture content (Rusterholtz et al. 2014; Nguyen et al. 2016), so factors beyond the nitrogen and carbon composition of the litter may also be important. Previous work has shown that litter arthropods benefit from the biofilms on decaying leaves (Horváthová et al. 2015), so the more abundant microflora supported by invasive leaves may have also played a role. The greater attractiveness of the invasive litters may have played a role in their high rates of decomposition.

Interestingly, we did not find a dosage effect on arthropod richness in the mixed litter bags, suggesting that the different litter types were not attracting widely different arthropod taxa. The coarseness of our taxonomic classification may have limited our power, however. Previous studies have shown that by inhibiting or promoting the growth of the consumer populations, litter from exotic species has the potential to propagate effects through the food webs of the invaded community (Chen and Wise 199; Negrete-Yankelevich et al. 2008; Poulette and Arthur 2012).

In the long term, however, the greater loss of invasive litter due to higher decomposition rates was accompanied by lower densities of arthropods by late spring. The *Lonicera* habitat supported higher densities of arthropods than the native habitat in its peak month (May), but showed a steep decline into June. *Ailanthus* and *Rhamnus* habitat never supported densities higher than native habitat. Litter bags placed in native habitats generally were colonized by more arthropods than the litter bags in invaded habitats, regardless of the type of litter contained in the bags. This adds support for the conclusion that native habitats support a greater abundance of arthropods, but the proportionally higher colonization of invasive litter in native habitats is consistent with the conclusion that the invasive litter is a superior nutritional resource (higher N and lower C:N), though other factors (e.g., secondary chemistry) may play a role. Many studies have demonstrated that greater complexity in the litter layer (via biomass and/or litter depth) increases the abundance of arthropods and affects predator–prey interactions across trophic levels by improving the microclimate for arthropods, providing refuge from intraguild predation, and providing access to the other resources (Bultman and Uetz 1984; Langellotto and Denno 2004; Castro and Wise 2010; Sayer et al. 2010; Morice et al. 2013). It is possible that in the early stages of invasions into native communities, the abundance and perhaps diversity of leaf-litter arthropods could benefit from the introduction of a high-quality resource, but if these invasive species largely replace native litter, the reduced litter volume will likely cause arthropod abundance to suffer.

Invasive species can provide substantial increases in the primary productivity in some ecosystems (Trammell et al. 2012), much of which ends up entering the detrital food web (Cebrian 1999; Gessner et al. 2010). The three exotic species in our study represent a novel, high nutrient resource for the litter-dwelling communities of eastern deciduous forests, leading to a short-term increase in the abundance of a wide range of organisms at multiple trophic levels in this community. However, this resource is short-lived relative to native litter, which supported a more stable litter-dwelling community over the course of a growing season. Our study suggests that replacement of native litter by exotic litter can result in substantial changes in ecosystem functioning and result in substantial differences in the dynamics of the biotic communities that depend on this primary resource.

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Author contribution statement GRW and DEC designed the studies and analyses. GRW and JNW collected and processed samples. GRW wrote the first draft of the manuscript, and all authors contributed to the final version.

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