Biol Invasions
DOI 10.1007/s10530-008-9315-1

ORIGINAL PAPER

Tree leaf litter composition and nonnative earthworms influence plant invasion in experimental forest floor mesocosms

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Received: 29 May 2008 / Accepted: 16 June 2008

Abstract Dominant tree species influence community and ecosystem components through the quantity and quality of their litter. Effects of litter may be modified by activity of ecosystem engineers such as earthworms. We examined the interacting effects of forest litter type and earthworm presence on invasibility of plants into forest floor environments using a greenhouse mesocosm experiment. We crossed five litter treatments mimicking historic and predicted changes in dominant tree composition with a treatment of either the absence or presence of nonnative earthworms. We measured mass loss of each litter type and growth of a model nonnative plant species (*Festuca arundinacea*, fescue) sown into each mesocosm. Mass loss was greater for litter of tree species characterized by lower C:N ratios. Earthworms enhanced litter mass loss, but only for species with lower C:N, leading to a significant litter × earthworm interaction. Fescue biomass was significantly greater in treatments with litter of low C:N and greater mass loss, suggesting that rapid decomposition of forest litter may be more favorable to understory plant invasions. Earthworms were expected to enhance invasion by increasing mass loss and removing the physical barrier of litter. However, earthworms typically reduced invasion success but not under invasive tree litter where the presence of earthworms facilitated invasion success compared to other litter treatments where earthworms were present. We conclude that past and predicted future shifts in dominant tree species may influence forest understory invasibility. The presence of nonnative earthworms may either suppress of facilitate invasibility depending on the species of dominant overstory tree species and the litter layers they produce.

Keywords *Ailanthus altissima* · *Castanea dentata* · Decomposition · Earthworms · Invasional meltdown · Leaf litter · *Lumbricus terrestris* · Plant invasions

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Introduction

Dominant species control many community and ecosystem processes (Wardle 2002). In forests, leaf litter inputs to the forest floor serve as an important mechanism by which trees regulate ecosystem functions including nutrient and energy cycling, tree regeneration, and the maintenance of biological diversity (Gilliam and Roberts 2003; Sayer 2006). The type and quality of dominant leaf litter controls these processes by mediating temperature, moisture, and nutrient inputs, and serving as a physical barrier to plant establishment (Facelli and Pickett 1991; Beatty 2003). Therefore, when humans directly or indirectly alter dominant tree species via disturbance, climate change, extinction, or facilitation of various biological invasions, additional biological invasions may be facilitated or resisted, depending on the properties of the dominant trees' litter. An understanding of how dominant tree species influence forest invasibility could prove very useful for land managers interested in minimizing nonnative plant invasions.

Several well-known changes in dominant tree species have taken place in the temperate forests of eastern North America. American chestnut (*Castanea dentata* (Marsh.) Borkh.) was once a dominant canopy tree (Russell 1987), but experienced widespread mortality when the nonnative chestnut blight fungus (*Cryphonectria parasitica*) was introduced to eastern North America. The functions that American chestnut provided within ecosystems are not fully understood, but it may have served as a "foundation species" by controlling the composition of understory species and mediating nutrient dynamics in soils and streams (Ellison et al. 2005). Other ongoing changes in these forests include the introduction of nonnative, invasive trees such as tree-of-heaven (*Ailanthus altissima* (P. Mill.) Swingle, hereafter Ailanthus), and disturbance-driven shifts in native species compositions favoring early successional species (Johnson et al. 2002). For example, timber harvesting can shift an oak (*Quercus* spp.) dominated to a yellow-poplar (*Liriodendron tulipifera* L.) dominated forest on mesic upland sites (Loftis and McGee 1992). Additional changes in dominant species composition are predicted in the future because of changes in climate, further invasions, growing demands for timber resource extraction, fire suppression, and potential interactions between these factors (Reich and Frelich 2002). These shifts in dominant tree composition will also change the litter layers of forests.

Changes in litter can also occur through the action of animals. Earthworms in particular have gained much attention because of their dramatic effects on litter layers and subsequent changes to structure and function of terrestrial ecosystems (Bohlen et al. 2004; Hobbie et al. 2006; Hendrix 2007). Earthworms are considered ecosystem engineers because of their ability to modify habitats, alter pools and fluxes of nutrients, and change understory community species composition (Jouquet et al. 2006). The introduction of nonnative earthworms into forested habitats that naturally lack them often dramatically changes the composition and diversity of the forest floor by removing the litter layer and exposing mineral soil (Hale et al. 2005; Frelich et al. 2006). Observational studies suggest that nonnative earthworms may be introduced following disturbance (Kalisz and Dotson 1989) and may facilitate nonnative plants through "invasional meltdown"—the process where invasion by one species facilitates additional invasions (Simberloff and Von Holle 1999; Heneghan et al. 2007). Mechanistic experiments that test this hypothesis are lacking.

The direct effects and potential interactions between changes in dominant tree species (through "extinction", invasions, and disturbance) and invasions of nonnative earthworms on the invasibility of temperate deciduous forests are poorly understood. While whole-stand manipulations to test the influence of changes in dominant species and earthworm invasions on ecosystem function or community composition are difficult, and impossible for certain species (e.g., American chestnut), it is possible to experimentally investigate these changes by manipulating leaf litter and monitoring subsequent changes in forest floor function and recruitment of plant species.

After considering historic, ongoing, and potential future changes to dominant species of forested ecosystems, we formulated and tested several hypotheses in a study using experimentally created forest floor mesocosms. First, we hypothesized that litter from different species (representing dominant tree compositional changes) would have different impacts on invasibility because of variation in litter quality (e.g., N content) leading to differences in decomposition rate and subsequent differences in physical barriers to plant establishment (Sayer 2006). Second, we hypothesized that plant invasion would also depend on the presence of nonnative earthworms because earthworms consume and bury litter (Frelich et al. 2006) or seeds (Milcu et al. 2006). Finally, we hypothesized that litter type and earthworm presence would have interacting effects on plant invasion reflecting variation in earthworm consumption or burial of different litter types.

Methods

To test our hypotheses, we conducted a greenhouse study between 16 April and 16 June 2007. Simulated forest floor mesocosms were established by filling 18 liter plastic tubs with silt loam soils (classified as a Typic Dystrudepts) collected from the A and AB horizons of forested areas located in Montgomery County, Virginia, USA. Soil was sieved with a coarse metal screen (5 mm) to remove rocks, large root fragments, and macro-invertebrates (including earthworms) prior to filling the tubs. We filled the soil to a depth of 17 cm, leaving a 10 cm barrier to prevent earthworm escape from the top of the mesocosms. Each mesocosm included five drainage holes screened to allow drainage but prevent soil loss and earthworm escape. We added 0.5 l of water to each mesocosm every day for the first 4 weeks, and then reduced the watering frequency to every other day for the last half of the study. Average greenhouse temperature was maintained at 21°C throughout the experiment.

We collected senesced leaves from American chestnut, Ailanthus, yellow-poplar, and northern red oak (*Quercus rubra* L.) in October of 2006. Litter was collected from at least 12 individuals per species after senescence and before or immediately after abscission. American chestnuts still occur as stump sprouts in its native range and can overtop other tree species following canopy disturbance on certain sites before the blight induces mortality of the stem and tree crown (McCament and McCarthy 2005). We took advantage of one of these sites (a 10-year-old clearcut in Craig County, VA, USA where $\sim$4 m tall trees were relatively abundant) to collect litter of American chestnut trees. To mimic litter mass of typical hardwood forests of the area (Grigal and Grizzard 1975), we added 18.25 grams of air-dried litter to each mesocosm. These litter treatments represent past, current, and possibly future changes in dominant tree species and litter composition of the forest floor. A fifth treatment included the absence of litter as a control.

We added the nonnative anecic earthworm, *Lumbricus terrestris* to half of the mesocosms to cross litter treatments with presence or absence of earthworms. Earthworm densities of three individuals per mesocosm were chosen to mimic densities observed in earthworm-invaded habitats (Kalisz and Dotson 1989). Mesocosms were randomly relocated on the greenhouse bench every 2 weeks during the experiment. At experiment termination, we investigated each mesocosm containing earthworms for the presence of castings on the soil surface and burrows below the soil surface to ensure that earthworms were active where they were added. Each treatment combination was randomly assigned to mesocosms and replicated 5 times resulting in a fully crossed multi-factorial completely randomized design (5 litter treatments $\times$ 2 earthworm treatments $\times$ 5 reps $=$ 50 mesocosms).

To investigate how litter and earthworm treatment combinations influenced invasibility, 1000 seeds of a model invasive plant species (*Festuca arundinacea* Schreb., hereafter fescue) were sown into each of the mesocosms by evenly scattering onto soil surface prior to adding leaf litter and earthworms. We determined end of season production of fescue by harvesting above and belowground biomass as our measurement of invasion success. To test the prediction that decomposition would vary among treatment combinations, we collected litter from the soil surface at experiment termination and calculated per cent mass loss from initial litter mass. To investigate potential species-specific chemical characteristics of litter that might influence decomposition, five litter samples per species were drawn prior to establishing mesocosms and analyzed for initial percent C and N using a FlashEA 1112 Series Elemental Analyzer (CE Elantech, Lakewood, NJ); we used these data to calculate C:N ratios.

Statistical analysis

We used a two-way analysis of variance (PROC GLM; SAS 9.1) to test for main and interactive effects of litter treatment and earthworm treatment on two response variables, litter mass loss and fescue biomass. Data were tested for normality and homogeneity of variance using Shapiro-Wilk's W statistic and Levene's test, respectively (Levene 1960; Shapiro and Wilk 1965). Data not meeting assumptions were log or arc-sin square root transformed. Post-hoc mean comparisons within treatments were performed using least square mean contrasts. One litter and earthworm control mesocosm (i.e., no litter or earthworms present) was eliminated from analyses because it was a statistical outlier where fescue grew very poorly, the result of clogged drainage holes causing standing water. To investigate how litter C:N, mass loss, and invasion success were related we performed three pairwise regressions. Specifically, we regressed mass loss on litter C:N ratios, fescue biomass on C:N, and fescue biomass on mass loss rates. Because we did not measure percent C and N of litter in each mesocosm, the two regressions involving C:N were conducted using mean values per treatment combination; for the remaining regression, individual data points for each mesocosm were included. We employed a critical alpha value of 0.05 for statistical significance.

Results

Earthworm castings and burrows were observed in all of the mesocosms where we added earthworms. Litter mass loss depended on an interaction between species of litter and the presence of nonnative earthworms (Fig. 1). Specifically, percent mass loss tended to be higher in litter of invasive Ailanthus and early-successional yellow-poplar than in American chestnut or northern red oak. Percent mass loss of Ailanthus and yellow-poplar were nearly twice as much and 1.4 times greater in the presence versus absence of earthworms, respectively, but mass loss rates of American chestnut and northern red oak did not differ between earthworm treatments (Fig. 1). Litter mass loss tended to be lower for litter of species with lower percent leaf N and higher C:N ratios (Table 1; Figs. 1 and 2).

Successful invasion by fescue was mediated by an interaction between the litter treatments and earthworm presence (Fig. 3). Biomass of fescue tended to

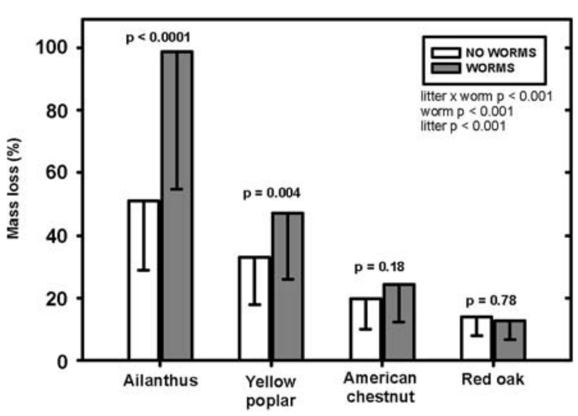

Fig. 1 Mean percent mass loss of litter (−SE) from four species in mesocosms with or without nonnative earthworms, *Lumbricus terrestris*. *P*-values above graphs indicate contrasts between earthworm treatments within each litter treatment

be highest in the absence of litter and under Ailanthus and yellow-poplar litter and lower under chestnut and red oak litter (Figs. 3 and 4). Earthworms decreased the success of fescue in the absence of litter and presence of yellow-poplar litter, but had no significant effect in the other three treatments. In the presence of earthworms, the greatest fescue biomass occurred under litter of the invasive tree Ailanthus (Table 2; Fig. 3). The effect of litter on invasion success (i.e., biomass of fescue) was related to litter C:N ratios and mass loss (Fig. 2). Specifically, invasion success increased with increasing litter mass loss.

Discussion

Results of this study supported all three of our hypotheses; i.e., that litter, earthworms, and their interactions can influence success of nonnative plant invasion into forest understories. The quality of the litter appeared to be driving these results. The effect of litter quality and recalcitrance from dominant species is known to influence multiple community and ecosystem components across diverse habitats (Facelli and Pickett 1991; Wardle 2002; Hättenschwiler et al. 2005; Sayer 2006). In our study, results suggest that litter layers of forests dominated by species with recalcitrant litter (i.e., slow decomposition rates) and high C:N ratios may be more resistant to understory plant invasions even if nonnative earthworms are introduced. Alternatively, forested stands with rapidly decomposing litter (and lower C:N ratios) may be particularly vulnerable to invasions by understory plant species. These results confirm predictions that changes in litter layers simulating historic, ongoing, or future shifts in tree composition may influence the resistance of forest floor ecosystems to invasions by nonnative plant species.

Recent studies suggest that “functionally extinct” American chestnut trees were a foundation species and that their litter played an important role in stream and soil nutrient dynamics (Ellison et al. 2005; Rhoades 2007). Our study suggests that chestnut litter may have served as a barrier to nonnative understory plant species compared to litter from species with faster decomposition rates. However, in many forests, oak species likely replaced chestnuts following blight mortality (Abrams et al. 1997) and we detected no

Table 1 Mean percent C, N, and C:N ratios (±SE, $n = 5$ samples) from initial litter prior to addition to mesocosms, and notes on ecology and abundance, for species used in a greenhouse test of invasibility of forest understories

Species	Common name	C (%)	N (%)	C:N	Current or historic trends
Ailanthus altissima	Tree-of-heaven	49.2 ± 0.2^a	2.24 ± 0.04^a	22.0 ± 0.4^a	Invasive in disturbed habitats
Liriodendron tulipifera	Yellow-poplar	47.9 ± 0.4^b	0.77 ± 0.02^b	62.4 ± 1.7^b	Early successional and dominant, can replace *Q. rubra* on mesic upland sites following disturbance
Castanea dentata	American chestnut	50.9 ± 0.2^c	0.62 ± 0.01^c	82.8 ± 0.7^c	Functionally extinct because of blight invasion, mostly replaced by oak and other hardwood species
Quercus rubra	Northern red oak	51.7 ± 0.6^c	0.69 ± 0.02^d	75.1 ± 1.6^d	Dominant canopy tree; local abundance can decline because of harvesting and gypsy moth defoliation; can be replaced by *L. tulipifera* following disturbance

Means with different letters represent significant differences ($P < 0.05$)

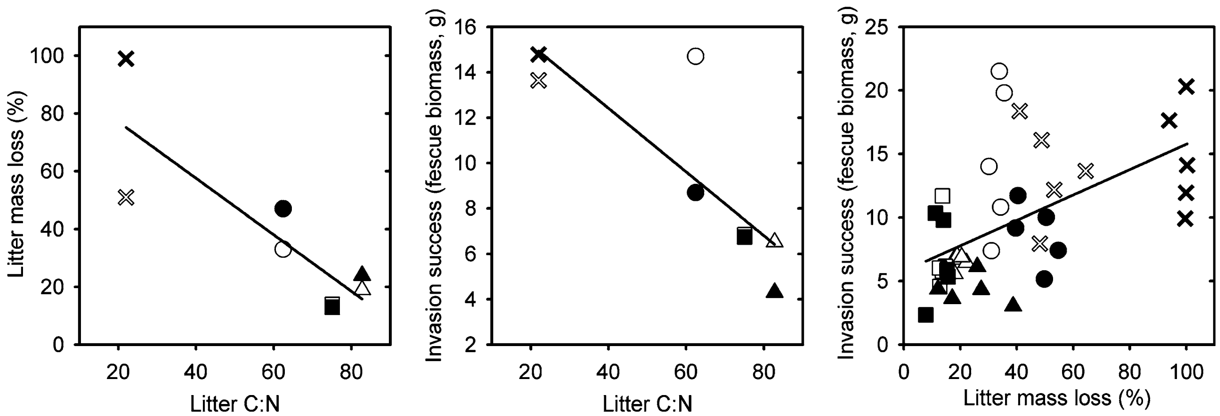

Fig. 2 Pairwise regressions between litter C:N and mass loss ($R^2 = 0.73$, $P = 0.007$), litter C:N and invasion success ($R^2 = 0.70$, $P = 0.01$), and litter mass loss and invasion success ($R^2 = 0.30$, $P < 0.001$). Square symbols represent values of litter of northern red oak, triangles are values for litter of American chestnut, circles are values for litter of yellow-poplar, and × represents values from litter of Ailanthus. Filled symbols indicate values for mesocosms that included additions of nonnative earthworms; open symbols are values where earthworms were absent. C:N values were estimated based on litter sampled from the leftover pool of litter and not from litter used in each mesocosm

significant difference between the main effects of chestnut litter and red oak litter on invasion success. This study also confirms personal observations that oak-dominated forests, which may be declining in abundance due to low rates of oak regeneration, altered disturbance regimes, and timber harvesting practices (Loftis and McGee 1992; McShea et al. 2007), appear particularly resistant to understory plant invasions, while forest stands dominated by yellow-poplar or invasive Ailanthus may be more vulnerable to understory plant invasions.

Nonnative earthworms had mixed effects on the success of plant invasions in this study. Earthworms typically reduced fescue biomass within litter treatments, but tended to have no negative influence under Ailanthus or northern red oak litter. Within litter treatments, earthworms likely buried or consumed seeds or new sprouts of fescue (Brown et al. 2004; Eisenhauer and Scheu 2008), which reduced its overall success. However, earthworms consumed or buried nearly 100% of the N-rich Ailanthus litter, which removed the physical barrier that litter creates.

This led to fescue biomass tending to be greater under Ailanthus litter than other litter treatments where earthworms were present. Under highly recalcitrant northern red oak litter and where overall invasion success was lowest (main effect of litter), earthworms did not have a negative effect on invasion success. The fact that earthworms preferentially consume or bury litter of certain species is well known (Darwin 1881; Perel and Sokolov 1964; Curry and Schmidt 2007). Litter from oak species has been observed to be relatively unpalatable to *Lumbricus terrestris* (Satchell 1983; Heneghan et al. 2007).

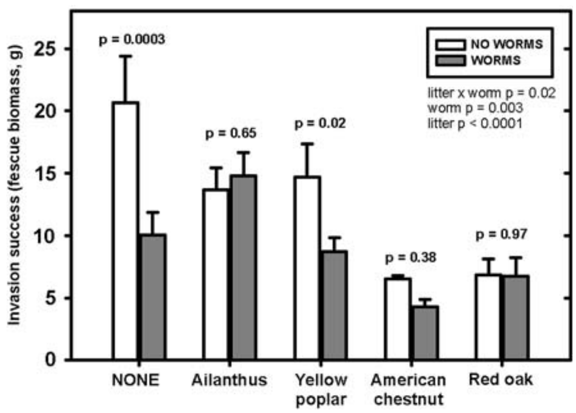

Fig. 3 Invasion success of fescue (grams of biomass per mesocosm +SE) in mesocosms receiving crossed treatments of litter and earthworms. *P*-values above graphs indicate contrasts between earthworm treatments within each litter treatment. *P*-values for contrasts between litter treatments within earthworm treatments are in Table 2

Ecologists have often observed that nonnative earthworms and nonnative plants frequently occupy the same habitats, suggesting potential facilitation between earthworm and plant invaders (Kourtev et al. 1999; Heneghan et al. 2007). However, understanding causality of these patterns has been limited by the observational nature of the studies. Some ecologists have suggested that nonnative plants may change soil characteristics, which allows for nonnative earthworms to invade (Ehrenfeld et al. 2001). Other hypotheses suggest that earthworms facilitate plant invasions, or that both nonnative earthworms and nonnative plants respond similarly to covarying factors such as disturbance or proximity to agricultural land use (Kalisz and Dotson 1989). While we did not test the hypothesis that plant invasions facilitate earthworm invasion, results from our study do suggest that invasion by a nonnative tree and the litter layer it produces, coupled with invasion by nonnative earthworms might directly facilitate further understory plant invasions.

The long-term effects of litter differences on earthworm populations or nonnative plants is

Fig. 4 Sample photos of mesocosms showing main effects of each litter treatment on invasion success of fescue. Photos were taken during the last week of the experiment

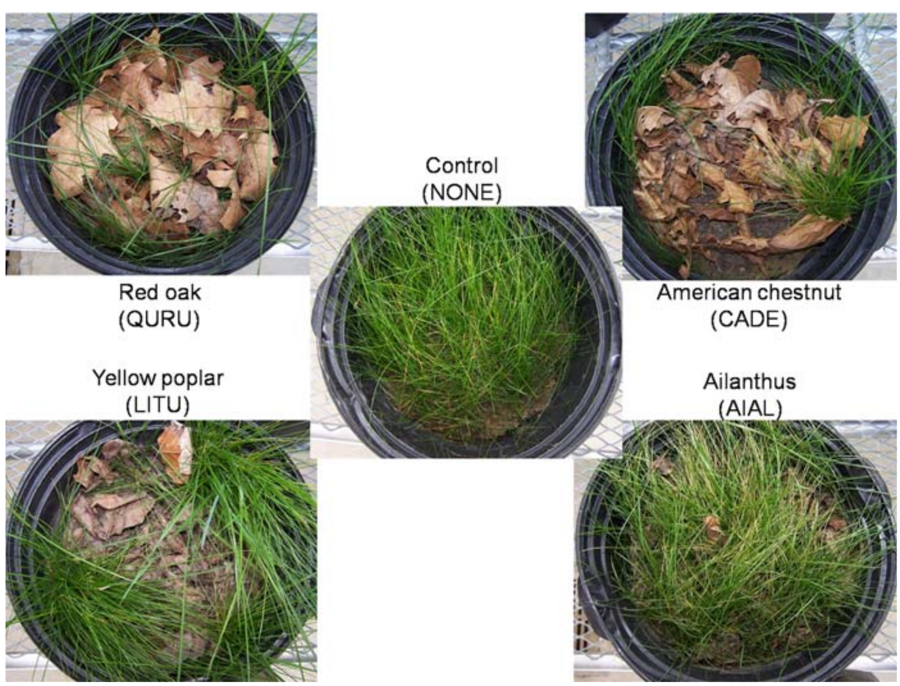

Table 2 *P*-values for least square means contrasts of invasion success (fescue biomass) between the 5 litter treatments within earthworm treatments

	Earthworms absent				Earthworms present			
	NONE	AIAL	LITU	CADE	NONE	AIAL	LITU	CADE
NONE								
AIAL	0.01				0.07			
LITU	0.03	0.67			0.59	0.02		
CADE	<0.0001	0.007	0.002		0.03	0.0002	0.09	
QURU	<0.0001	0.01	0.003	0.90	0.19	0.003	0.44	0.33

Litter treatments are: NONE = no litter, control; AIAL = *Ailanthus altissima*, Ailanthus; LITU = *Liriodendron tulipifera*, Yellow poplar; CADE = *Castanea dentata*, American chestnut; QURU = *Quercus rubra*, Northern red oak

not clear. Our experiment lasted only 2 months, which was insufficient to investigate treatment effects on humic and mineral soil layers and composition. Differences in humic layers and mineral soil chemical characteristics under litter layers may have longer term effects on invasibility and direct effects on earthworm populations. Moreover, while each tree species represented in our litter treatments can dominate forests on similar sites, the abundance and likelihood of dominance of the tree species in a particular area may depend on soil and site characteristics, which can also influence invasive plant establishment and nonnative earthworm abundance (Frelich et al. 2006). For example, yellow-poplar typically replaces red oaks following disturbance only on mesic upland sites, but not on drier, less productive sites (Carmean and Hahn 1983). The same environmental factors that influence shifts in tree composition may also influence earthworm abundance and behavior.

The application of this study to natural systems is somewhat limited because it was conducted in a high light greenhouse environment using a model invasive species not typical of an understory plant invader. Our aim was to test specific mechanisms based on how changing litter layers may interact with earthworms to influence invasive plant establishment. However, differences in litter layers likely have important effects on native understory species as well (Gilliam and Roberts 2003). The effects of nonnative earthworms on native understory species depend on the traits or plant functional groups (Hale et al. 2005). Additionally, natural litter layers contain mixtures of litter from various species and support complex detrital foodwebs (Facelli 1994; Wardle 2002), which could also influence litter decomposition and understory invasibility. Clearly, more studies are needed to investigate the complex interaction between litter quality, earthworm invasions, native species, and nonnative plant invasions.

Acknowledgements We thank Debbie Wiley and Aaron Teets for assistance in the greenhouse and lab. Bobbie Niederlehner helped with the carbon and nitrogen analysis. Erik Nilsen provided greenhouse space and helpful comments on earlier drafts. Jessica Homyack, Aimeé Classen, and Martin Nuñez provided helpful comments during manuscript preparation. Cindy Hale, Carola Haas, Tom Fox, Nate Sanders, and Dan Simberloff provided helpful comments and ideas during project conception. The work was supported by NSF-DBI grant # 0400684, USDA-NRI grant # 2005-35101-15363 and a Virginia Tech WPI Environmental Fellowship.

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