Leaf Litter Disappearance in Earthworm-Invaded Northern Hardwood Forests: Role of Tree Species and the Chemistry and Diversity of Litter

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ABSTRACT

Earthworm invasion in North American temperate forest reduces forest floor mass, yet the interactions between litter composition, invasive earthworm community composition, and forest floor structure and composition are not well understood. For 2 years, we compared disappearance of leaf litter in field mesocosms in which we manipulated litter composition (monocultures of *Quercus rubra*, *Acer saccharum*, and *Tilia americana* litter, and an equal mixture of all three) and thereby the initial litter chemistry (C, C fractions, N, Ca) in sites with and without the major litter-feeding invasive earthworm species. The disappearance of litter mass followed the same ranking at both the sites: *T. americana* > equal mixtures > *A. saccharum* ≥ *Q. rubra*. However, differences in disappearance rate between the sites depended on litter composition and time. The differences in mass loss among litters of different compositions were greatest at the site invaded by the large litter-feeding earthworm, *Lumbricus terrestris*, and especially for *T. americana* and the mixture. Similarly, observed disappearance of the litter mixture was faster than predicted by an additive model at the site with *L. terrestris*, especially for the higher quality litter component in early summer. Initial litter calcium content was the best predictor ($R^2 \geq 0.90$) of overall litter mass remaining each year, supporting the idea of the importance of calcium in forest floor dynamics, especially in the presence of calciferous, invasive earthworms.

Key words: decomposition; earthworm invasion; northern hardwood forest; *Acer saccharum*; *Quercus rubra*; *Tilia americana*; *Lumbricus terrestris*; calcium; lignin; litter mesocosms.

INTRODUCTION

The forest floor serves many roles in hardwood forests. It regulates nutrient cycling and water infiltration, provides a seedbed and rooting zone, and is habitat for a variety of fungi, arthropods, small vertebrates, and other organisms (Bormann and Likens

1979). It shapes plant-community composition and structure by affecting germination, establishment, and competition and ecosystem functioning by influencing decomposition and nutrient mineralization rates (Facelli and Pickett 1991; Hättenschwiler and others 2005). Furthermore, the forest floor is an important zone for understanding how ecosystems will respond to global changes including land-use change, increasing CO_2 concentrations, nitrogen deposition, and species invasions (Hättenschwiler and Bretscher 2001; Liu and Zou 2002; Tietema 1998; Vitousek and Walker 1989).

One of the more significant changes that can alter the forest floor is earthworm invasion (Bohlen and others 2004b; Hendrix and others 2008), especially in the several million km^2 of North American temperate and boreal forests previously devoid of earthworms (Bohlen and others 2004a; Frelich and others 2006). The overall effects of Eurasian earthworm invasion on the litter layer are becoming relatively well documented. They include reduction in litter layer depth and mass (Gundale 2002; Hale and others 2005; Nielson and Hole 1964; Suárez and others 2006) as well as the accompanying redistribution and loss of carbon (Alban and Berry 1994; Bohlen and others 2004a). These impacts are also accompanied by changes in the distribution and retention of nitrogen and phosphorous (Bohlen and others 2004a; Hale and others 2005; Suárez and others 2004), microbial biomass (Groffman and others 2004), microarthropod and microfungal communities (Eisenhauer and others 2007; McLean and Parkinson 1998, 2000; Straube and others 2009) and fine root distributions (Fisk and others 2004). Although the overall reduction of the litter layer by invasive earthworms is well documented, the interactions between litter of different tree species and invasive earthworms and the consequences of these interactions for the structure and composition of the litter layer are less well known. An experimental study in native European systems shows strong effects of tree species on forest floor litter dynamics as a consequence of litter calcium chemistry that are mediated by the effects of earthworms (Hobbie and others 2006; Reich and others 2005), leading us to posit that differences in litter Ca among North American tree species would have predictable effects on litter dynamics as well.

The removal of the forest floor by invasive earthworms is one of the major hypothesized mechanisms for earthworm-induced plant-community change (Frelich and others 2006). In the absence of earthworms, understory plants of northern temperate forests are rooted in a well-developed organic horizon (Hale and others 2006). Earthworm invasion in northern hardwood forests can lead to declines in the abundance of most herbaceous layer plants, often transforming a diverse community of forbs and tree seedlings into a community dominated by *Carex* species (Hale and others 2006; Holdsworth and others 2007a) or invasive plant species (Nuzzo and others 2009). Given the influence of the litter layer on plant communities (Facelli and Pickett 1991), understanding temporal changes in the structure and composition of the litter layer under earthworm invasion could improve understanding of mechanisms of earthworm-induced changes in forest plant communities.

The structure and composition of the litter layer is shaped by aboveground and belowground conditions. The quality and quantity of leaf litter inputs to the litter layer are directly related to stand composition and productivity (Aber and Melillo 1980; Frelich and others 1993; Pastor and others 1982, 1984; Reich and others 1997). The spatial distribution of these inputs within forest stands is heterogeneous (Ferrari 1999) and is further influenced by water and wind (Orndorff and Lang 1981) and microtopography (Beatty and Sholes 1988), contributing to a forest floor of varying mass, thickness, and composition. Within given climate conditions, the rate at which this litter layer decomposes is largely determined by the quality of the litter and the decomposer community (Cadish and Giller 1997; Coûteaux and others 1995; Hättenschwiler and others 2005).

The species composition of the macro-faunal decomposer community can influence the litter layer and ecosystem processes (Edwards and Lofty 1977). For instance, *Lumbricus terrestris* is one of the major invasive litter-feeding earthworm species in North America and has distinct litter preferences (Bohlen and others 1997; Curry and Schmidt 2007; Hendriksen 1990). Although the other major invasive litter-feeding earthworm species, *L. rubellus* is the most responsible for the loss of the O_a/O_e sub-horizons (Gundale 2002; Hale and others 2005), *L. terrestris* removes large quantities of surface litter in the O_i sub-horizon (Raw 1962) by selectively dragging whole leaves of lower C:N ratio into its burrows leaving behind litter with higher C:N ratios (Bohlen and others 1997; Bohlen and others 2004b). Litter disappearance is significantly greater where *L. terrestris* is present (Suárez and others 2006) and can be so high in some stands with large *L. terrestris* populations that the litter layer almost completely disappears by autumn (Eisenhauer and others 2007; Knollenberg and others 1985). Thus, the presence of *L. terrestris* in invaded temperate forests could have significant effects beyond those of other earthworm species

present. Additionally, litter inputs are an important driver of litter-consuming earthworm populations (Hendriksen 1990; Nordström and Rundgren 1974) and can positively or negatively affect their populations (Cothrel and Kost 1997; Judas 1990).

The composition of litter and soil organisms and the interactions between them can influence decomposition (Hättenschwiler and Gasser 2005; Hättenschwiler and others 2005; Zimmer and others 2005). However, most studies of decomposition use single species study units and exclude macro-fauna (Gartner and Cardon 2004). Of the studies that examine decomposition of mixed litters, the degree to which litter diversity has additive or synergistic effects on litter decomposition rates is highly variable from study to study (Gartner and Cardon 2004). Furthermore, most litter mixture studies only measure changes in total litter mass and not changes of the individual species within the mixture. Such studies cannot determine how individual species' responses to being in a mixture affect decomposition (Hättenschwiler and others 2005).

The objective of our study was to explore the relationships between litter composition and disappearance from the forest floor in forests with and without the major litter-feeding earthworm species, *L. terrestris*. We hypothesized that litter disappearance would depend on initial litter composition and the presence of *L. terrestris*. We expected that low-quality (for example, as measured by C:N, calcium concentration, lignin or other carbon fractions, or lignin:N) litter would disappear more slowly than high-quality litter. Disappearance of high-quality litter would be faster overall, but especially where *L. terrestris* has invaded. We also hypothesized that mixtures of high- and low-quality litter would disappear faster than would be predicted based on disappearance rates of litter "monocultures". Given *L. terrestris'* preferences for high-quality litter, we expected that disappearance of high-quality litter within mixtures would be greater where *L. terrestris* is present.

METHODS

Study Sites

We chose four sites that had similar climate, soils, and vegetation, but different invasive earthworm communities (Table 1). All the four sites are high-quality, old-growth remnants of the "Big Woods" ecosystem (Grimm 1984; MNDNR 1999) and have never been plowed. The sites range from 50–90 ha and are within 3–100 km of each other in a region centered at 45.31 N, 93.97 W. All the sites have

mull, sandy-loam, or loam soils with pH of about 6.4 and C:N ratio of around 12 (Table 1). Two sites, Wood-Rill (WORI) and Wolsfeld Woods (WOLS), have a larger proportion (~50%) of oak (*Quercus rubra* and *Q. alba*) whereas Mary-Schmidt Crawford Woods (MASC) and Partch Woods (PAWO) have a larger proportion of *Acer saccharum* (Table 1). There are equal proportions of basswood (*Tilia americana*). Other tree species at the sites include *Fraxinus pennsylvanica*, *Acer rubrum*, *Ulmus rubra*, *Carya cordiformis*, *Prunus serotina*, and *Ostrya virginiana*.

There is one major difference in the invasive earthworm community composition between the four sites. The largest litter-feeding species, *L. terrestris*, is present and dominant at the WORI and WOLS sites, but absent at the MASC and PAWO sites. This determination of absence is based on hand and liquid mustard sampling (Lawrence and Bowers 2002) and searches for its middens (Nielson and Hole 1964) between 2001 and 2004. At the WORI and WOLS sites, *L. terrestris* adults and juveniles of *L. terrestris* and *L. rubellus* constitute 87% of total earthworm ash-free dry mass (AFDM) (Table 1). At the WORI site, *L. terrestris* adults constitute one-third (36%) of AFDM and coexist with juvenile *L. terrestris* and *L. rubellus* (51%), *Aporrectodea caliginosa* and *A. rosea* (9%), *Octolasion tyrtaeum* (3%), and *L. rubellus* adults (1%). At the MASC site where *L. terrestris* is absent, *L. rubellus*, *A. caliginosa*, *Dendrobaena octaedra*, and *O. tyrtaeum* constitute 43, 32, 17, and 8% of total AFDM, respectively. Earthworm composition between the two *L. terrestris* sites is comparable and is comparable between the two sites without it (Appendix 1 of Supplementary material). See Table 1 for methods used to describe site conditions.

Experimental Design, Installation, and Sampling

We established mesocosms containing different litter compositions and quantities accessible to microflora and micro-, meso-, and macro-fauna and measured litter layer changes during 2 years. These mesocosms were used in two simultaneous experiments: (1) a two-site litter composition experiment and (2) a four-site comparison experiment. The two-site composition experiment consisted of six litter composition treatments at each of the two sites, MASC where *L. terrestris* is absent, and WORI, where *L. terrestris* is present (Table 1). The litter composition treatments were *A. saccharum*, *T. americana*, *Q. rubra*, an equal mixtures of the three, the resident litter mixture, and a control

Table 1. Earthworm, Soil, and Vegetation Conditions at the Four Study Sites: MASC (Scientific and Natural Area), PAWO (SNA), WORI (SNA), and WOLS (SNA)

	Site			
	MASC	PAWO	WORI	WOLS
Earthworms[1] (g/m²) (±SE)				
L. terrestris	0 (0)	0 (0)	5.2 (2.1)	4.5 (1.9)
L. juveniles	1.0 (0.3)	1.1 (0.2)	7.3 (1.2)	7.0 (1.3)
Others	3.1 (0.4)	2.7 (0.7)	1.7 (0.3)	1.7 (0.4)
Climate[2]				
Temp. (mean monthly min./max. °C)	1.1/11.6	2.0/13.0	2.1/12.6	2.1/12.6
Precip. (cm/year)	80	84	79	79
Soils[3]				
Sand (%)	45	63	58	60
Silt (%)	38	26	27	28
Clay (%)	17	11	15	12
pH	6.4	6.1	6.3	6.6
Total carbon (%)	2.75	2.84	2.99	2.46
Total nitrogen (%)	0.24	0.22	0.24	0.23
Litterfall[4]				
Total (g/m²)	411.4	–	408.2	–
Quercus (%)	1	–	50	–
A. saccharum (%)	88	–	45	–
T. americana (%)	5	–	5	–
Litter chemistry				
Equal mixture[5]				
Nitrogen (%)	1.0	1.3	0.9	1.0
Lignin	15.8	22.0	17.6	16.8
Lignin/N	15.8	16.9	19.6	16.8
Calcium (%)	2.8	2.4	2.3	2.4
Q. rubra				
Nitrogen (%)	0.8	–	0.7	–
Lignin	16.1	–	23.3	–
Lignin/N	20.1	–	33.3	–
Calcium (%)	1.4	–	1.2	–
A. saccharum				
Nitrogen (%)	0.7	–	0.7	–
Lignin	10.2	–	11.2	–
Lignin/N	14.6	–	16.0	–
Calcium (%)	2.7	–	2.2	–
T. americana				
Nitrogen (%)	1.6	–	1.6	–
Lignin	19.4	–	18.4	–
Lignin/N	12.1	–	11.5	–
Calcium (%)	4.1	–	3.7	–

[1]*Earthworm data are AFDM (Hale and others 2004) of 2 years (October 2002, 2004) of five replicate liquid mustard samples (Lawrence and Bowers 2002) from each site.*
[2]*Climate data are for the study period 2001–2003 (Climatology Working Group, http://climate.umn.edu).*
[3]*Soil data are based on five soil cores from the top 10 cm. Composited samples were analyzed at the University of Minnesota's Research Analytical Laboratory.*
[4]*Litterfall (oven-dry) measured using twelve 0.24 m² litter traps at MASC and WORI between August and November 2002. Quercus includes Q. rubra and Q. alba.*
[5]*Data are means of 2001 and 2002 mixture treatment (1/3 A. saccharum, 1/3 Q. rubra, 1/3 T. americana) using litter from the respective site at time of installation.*

(described below). All the litters were applied at 1× mean autumn litterfall of the two sites. The four-site comparison experiment consisted of the equal mixture treatment applied at two sites without *L. terrestris* (MASC and PAWO) and two sites with *L. terrestris* (WORI and WOLS).

All the litter treatments were replicated five times and applied in November 2001 to mesocosms in a completely randomized design. Litter application quantities were determined using three 0.12 m² oven-dried samples of the O$_i$ horizon from each of the two main sites. This estimate of litterfall

was 95% of litterfall measured in 2002 using 12 litter traps at each site (Table 1). *A. saccharum*, *T. americana*, and *Q. rubra* were chosen because they are the three most common tree species among the four sites and represent a range of litter qualities in terms of carbon, nitrogen, and calcium.

At each of the four sites we sorted freshly fallen whole leaves of *A. saccharum*, *T. americana*, and *Q. rubra* for application to plots at the respective site. Plots consisted of 0.5 m^2 (87.4 $\times$ 57.2 cm) by 9-cm high rectangular wooden mesocosms capped with 6 mm^2 metal mesh and staked to the ground. These mesocosms held litter treatments on the soil while not impeding soil dwelling biota from accessing the litter. Mesocosms were placed 35–50 cm apart and at least 50 cm from trees larger than 10 cm in diameter. Before application of each litter treatment, existing litter was gently raked from each plot leaving only small (<1 cm^2) litter fragments. Although understory vegetation is sparse ($<10\%$) at the sites, any herbaceous matter was hand-pulled from mesocosms. Prior to field installation sub-samples of each litter type were weighed and oven-dried to determine fresh-oven-dry conversions. The 1$\times$ litter treatments were approximately 450 g/m^2 (dried). As litter was weighed during field installation, a second set of sub-samples was collected to estimate oven-dry mass of each plot. Litter treatments were randomly assigned to each mesocosm. As a control on the disturbance caused by raking litter away, five randomly chosen plots had a mesocosm placed over the undisturbed litter layer. After the first growing season of the experiment (2002), the litter treatments were re-applied over the remaining litter of the same plots for a second growing season (2003). As an indicator of the abundance/activity of the major litter-feeding earthworm, *L. terrestris*, we counted its middens prior to litter application in a 0.12 m^2 area at the center of each plot. A midden was defined as litter protruding from a vertical burrow with diameter larger than 4 mm (Nielson and Hole 1964). Midden counts occurred in November 2001, 2002, and at the completion of the experiment in October 2003.

We measured changes in litter mass during the growing season by extracting litter cores four times between June and November in 2002 and 2003. Litter cores were extracted using a 10 cm (1.6% of the mesocosm area) diameter rotating metal corer that held the litter sample in place while cutting accurately through the litter layer. All the litter fragments were >5 mm in diameter and most 3–5 mm were removed. One core was removed from each plot for the first three harvests and two

cores were removed for the last harvest. The second core was necessary to provide a sufficiently large sample for processing, especially for the plots that had less than 5% of their litter remaining. In this study, litter disappearance includes the consumption, physical alteration, and burial of litter by earthworms in addition to the effects of microbes and other decomposers.

Laboratory Analysis

For the purposes of comparing the initial litter qualities of each site for each year, we measured total carbon, nitrogen, calcium, and carbon fractions of 3–9 composited sub-samples of litter from all composition treatments. Oven-dried initial litter samples were ground and analyzed for carbon and nitrogen using a Costech ECS4010 Element Analyzer (COSTECH Analytical, Valencia, California) at the University of Nebraska, Lincoln. Calcium was measured using inductively coupled argon plasma emissions spectroscopy (Applied Research Laboratory ICP 3560) after digestion in 10% HCl at the University of Minnesota Research Analytical Laboratory. Although other elements were measured besides calcium using ICP, we only present calcium because it is strongly correlated with earthworm biomass and litter decomposition (Reich and others 2005) and was better correlated with litter disappearance in this study (A. Holdsworth, unpublished data). Carbon fractions (cell solubles, hemicellulose + bound protein, cellulose, and lignin + other recalcitrants, determined on an AFDM basis) were analyzed using an ANKOM Fiber Analyzer (Ankom Technology, Macedon, New York).

Litter core samples were dried (70°C), weighed, and corrected to AFDM. AFDM corrections were calculated by ashing (4 h at 500°C) a sub-sample of three of the five replicates of each treatment for each harvest. As the range in the proportion of mass that was ash-free for the three sub-samples was relatively small (typically $<10\%$), we applied the mean proportion to each replicate. Initial litter samples were also corrected for AFDM.

To better track changes in litter composition during the second year, we hand sorted all the samples into their litter components. We sorted all the mixture treatment samples into *A. saccharum*, *T. americana*, and *Q. rubra* litter based on color, venation pattern, and texture. Unrecognized petioles and litter fragments were also sorted and accounted for 2–7% of initial sample mass. Each component was weighed separately and corrected to AFDM using the whole sample correction factor.

Statistical Analysis

Treatment effects on the percent of initial litter mass remaining were analyzed using repeated measures ANOVA with litter mesocosm within site as the subject, litter treatment (replicated five times) as the between-subject effect, and harvest as the within-subject effect using SAS PROC Mixed (Littell and others 1996). Proportion litter mass remaining was arc sine square-root transformed. A completely balanced design was not possible in 2003 because 1–2 replicates per treatment were not sampled in October 2003 due to weather conditions. In general, PROC Mixed is relatively insensitive to missing values as long as they are randomly distributed (Littell and others 1996) which they were in this study. A spatial power correlation structure was applied for the repeated harvest factor (time) to each plot within each site. This structure has decreasing correlation with time and is appropriate for unequal time intervals between harvests (Littell and others 1996). Satterthwaite's method was used to calculate the appropriate denominator degrees of freedom for contrasts involving linear combinations of variables (Littell and others 1996). Estimate and contrast statements in PROC Mixed were used to compare individual site–treatment–time combinations when the overall model showed significance ($P < 0.05$) for the relevant main effects. Homogeneity of variances was verified for each model.

An effect of plot establishment-associated disturbance on litter disappearance was tested by comparing the resident mix treatment with the control treatment (mesocosm placed over undisturbed resident litter) at each site of the two-site experiments. As there was no treatment or treatment × time effect for either site each year (for example, MASC 2002, treatment: $F_{1,8} = 0.02$, $P = 0.90$; treatment × time: $F_{3,24} = 0.95$, $P = 0.43$; WORI 2002, treatment: $F_{1,8} = 0.52$, $P = 0.49$; treatment × time: $F_{3,24} = 0.59$, $P = 0.63$), the resident mix and control treatments were excluded from subsequent analyses because the litter composition of these treatments was substantively different between the two main sites (Table 1). For the two-site composition experiment separate models were fit for the effect of (1) litter composition (A. saccharum, Q. rubra, T. americana, equal mixture), (2) litter context one (as recorded by observed % litter remaining in mixture vs. predicted % litter remaining based on monocultures in 2003), and (3) litter context two (as recorded by % litter remaining each of A. saccharum, Q. rubra, and T. americana within the equal mixture but weighed

individually vs. each litter in its respective monoculture in 2003). Predicted % litter mass remaining for the litter context one model was calculated according to an additive model based on the % mass remaining of each species in monoculture (sensu Blair and others 1990). For example, for each harvest predicted % litter remaining was calculated as

$$[(A1 + Q1 + T1)/3 + (A2 + Q2 + T2)/3 \\ + (A3 + Q3 + T3)/3 + (A4 + Q4 + T4)/3 \\ + (A5 + Q5 + T5)/3]/5,$$

where A1 is the % remaining A. saccharum in monoculture replicate 1, Q1 is the % remaining Q. rubra in monoculture replicate 1, T1 is the % remaining T. americana in monoculture replicate 1, and so forth for replicates 2–5.

We used ANCOVA as implemented in JMP (SAS Institute Inc. 2002) to analyze the response of overall mean % litter mass remaining (arc sin square-root transformed) to site, year, site × year, and an initial litter chemistry covariate. Separate models were fit for calcium, % carbon, % nitrogen, C:N, and carbon fractions as covariates and best models were selected by backwards elimination of terms with $P > 0.05$, which yielded identical results to choosing models by AIC. Litter chemistry was based on initial litter samples for each site in 2002 and 2003, composited for each of five litter treatments (all monocultures, and equal and resident mixtures). Litter treatment effects on density of L. terrestris middens at the main site (WORI) with L. terrestris present were analyzed in JMP using matched pairs of midden density at the beginning (2001) and end of the experiment (2003) for the six 1× litter composition treatments.

RESULTS

Litter Composition and Litter Layer Change

The two-site litter composition experiment tested the effect of litter composition on litter disappearance in sites with and without L. terrestris. Litter composition, site, and time affected litter mass remaining in both the years (Table 2; Figure 1). The relative order of mean remaining mass of each litter composition treatment for all harvests was similar at the two sites in 2002 and 2003: Q. rubra > A. saccharum ≥ mixture > T. americana. The difference between the sites depended on litter composition and time. In 2002, there was no difference between the sites in overall mean %

Table 2. ANOVA Table of F Values for the Response of % Litter Mass Remaining to Site, Litter Composition, and Time for 2002 and 2003 in the Two-site Litter Composition Experiment

Treatment	df[1]		F values	
	2002	2003	2002	2003
Site (S)	1, 32	1, 32	35.2***	54.1***
Litter comp. (LC)	3, 32	3, 32	58.6***	50.6***
Time (T)	3, 96	3, 94	91.8***	18.6***
S × LC	3, 32	3, 32	4.8**	3.9*
S × T	3, 96	3, 94	1.3	0.7
LC × T	9, 96	9, 94	1.5	0.6
S × LC × T	9, 96	9, 94	2.8**	0.8

[1]*Denominator df are different in 2003 because of two plots that were not sampled at the last harvest due to weather-imposed time constraints.*
*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.*

Q. rubra remaining (72 vs. 68% at MASC and WORI, respectively) or % *A. saccharum* remaining (42 vs. 35%), but there was a significant difference between sites for the mixture (53 vs. 27%) (contrasts: $F_{1,128} = 26.6$, $P < 0.0001$) and for *T. americana* (32 vs. 12%) (contrasts: $F_{1,128} = 20.6$, $P < 0.0001$). Unlike *Q. rubra* and *A. saccharum*, the change in *T. americana* and mixture mass through time was different at the two sites (Figure 1A, B) in 2002. In 2003, the pattern of litter disappearance was similar to that in 2002 until the second harvest (July) when the rate of litter loss declined or leveled off (Figure 1C, D) resulting in higher residual litter mass. At the end of the season in 2003 the overall mean litter mass was 39 and 27% at MASC (without *L. terrestris*) and WORI (with *L. terrestris*), respectively, versus 16 and 10% in 2002.

The four-site comparison experiment allowed us to see if the results of the two main sites were similar at two other sites with and without *L. terrestris*. The sites with *L. terrestris* were similar in litter mass remaining both the years (contrasts: 2002: $F_{1,35} = 1.6$, $P = 0.22$; 2003: $F_{1,61} = 2.4$, $P = 0.12$) and the sites without *L. terrestris* were similar in 2002 (contrasts: $F_{1,35} = 0.0$, $P = 0.98$). Although in 2003, the PAWO site (without *L. terrestris*) had % litter remaining in between that of MASC and the other two sites, for both the years there was a highly significant difference between litter remaining at the sites without *L. terrestris* (MASC and PAWO combined) and the sites with *L. terrestris* (WORI and WOLS combined) (contrasts: 2002: $F_{1,35} = 45.5$, $P \le 0.0001$; 2003: $F_{1,61} = 69.0$, $P \le 0.0001$).

Chemistry of the four litter compositions differed most in calcium concentration and lignin/nitrogen ratio. *T. americana* litter had the highest calcium concentrations (3.9%) (mean across sites) and the lowest lignin/nitrogen ratio (11.8), whereas *Q. rubra* had the lowest (1.3%) calcium concentration and highest lignin/nitrogen ratio (26.7) (Table 1). Except for lignin, *A. saccharum* had moderate and similar chemistry to the equal mixture (Table 1).

Chemical attributes of litter, when added one at a time to models including site and year, were able to explain a considerable portion of total litter disappearance variance. Initial litter calcium concentration of the litter treatments in addition to site produced the best fit ($R^2 = 0.90$) of annual mean % litter remaining for both the years combined followed by a model including initial litter lignin/N, site and year ($R^2 = 0.67$) (Table 3; Figure 2). Other carbon fractions (cell solubles, hemicellulose + bound protein, and cellulose) were not significantly related to % litter remaining. In addition, a model that started with all litter chemistry traits tested above, site, and year, reduced to the same calcium and site sub-model cited above. Litter calcium was positively correlated with litter disappearance at both the sites, but mass remaining was higher at any given calcium concentration at the site without *L. terrestris* (MASC) (Figure 2). In plots of annual mean % litter remaining versus initial litter calcium concentrations, the data points from the WOLS site (*L. terrestris* present) plot next to those of WORI and the PAWO (*L. terrestris* absent) points plot between those of WORI and MASC (Figure 2). This provides additional evidence of a similarity between the two sites with *L. terrestris* (WOLS and WORI) and the two sites without *L. terrestris* (PAWO and MASC) in one of the two years.

Litter Disappearance in Mixtures versus Monocultures

The litter mixture in the two-site composition experiment disappeared faster than predicted by an additive model, but this difference depended on site and harvest time in 2002 and site in 2003 (Table 4; Figure 3). In 2002, observed % litter remaining was similar to predicted at the site without *L. terrestris*, MASC (contrasts: $F_{1,64} = 1.9$, $P = 0.1722$), but significantly lower at the site with *L. terrestris*, WORI (contrasts: $F_{1,64} = 11.1$, $P = 0.0014$). Differences in % litter remaining were most pronounced in June when the mixture was 27% points higher than predicted at MASC and 26% points lower than predicted at WORI. The similarity of observed and predicted litter remaining persisted at MASC in 2003 and the differences persisted longer at WORI.
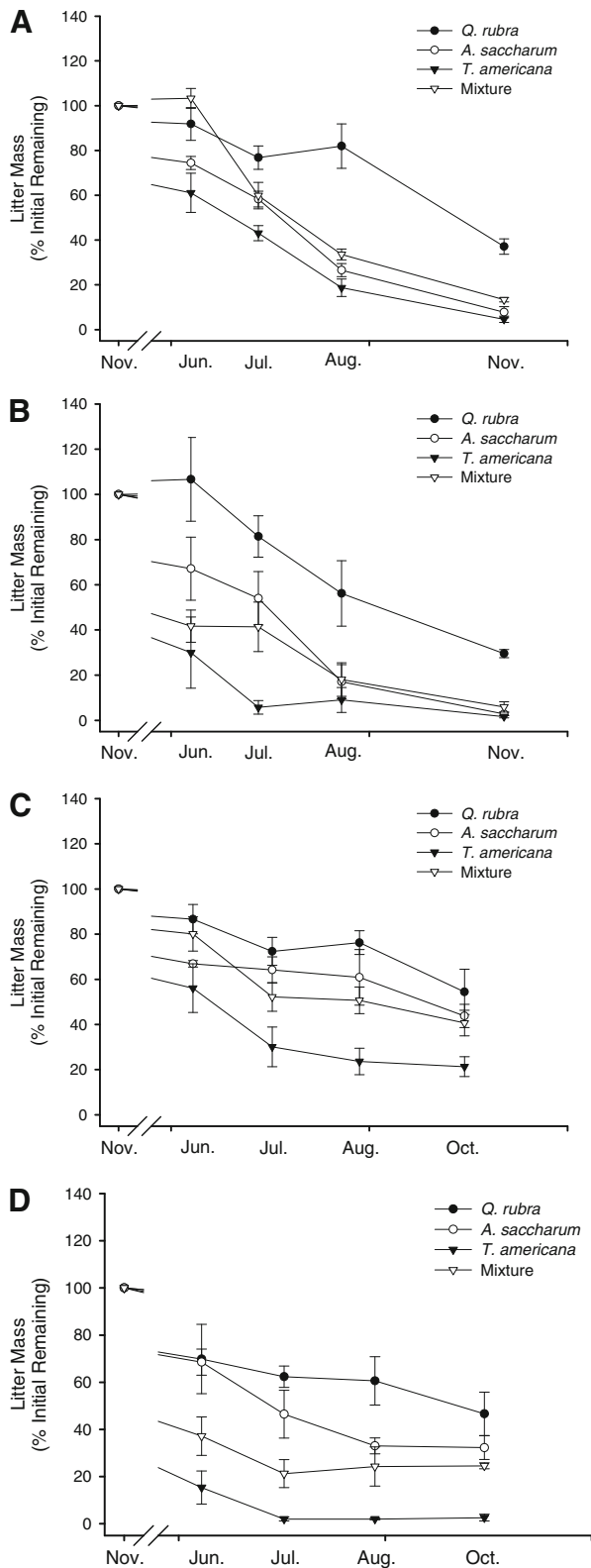
◄ **Figure 1.** % Initial litter mass remaining (±SE) in mesocosms of *Q. rubra*, *A. saccharum*, and *T. americana* litter and the equal mixture of the three litters in the two-site litter composition experiment at MASC (*L. terrestris* absent) and WORI (*L. terrestris* present). **A** MASC, 2002; **B** WORI, 2002; **C** MASC, 2003; **D** WORI, 2003. The *x*-axis is scaled by days since litter application and labeled with month of installation and harvest. Values above 100% for *Q. rubra* are likely due to it being in the accumulation stage of decomposition where mass has increased due to microbial colonization but litter mass loss has been negligible compounded by the heterogeneity in the litter layer created by the activity of *L. terrestris* at WORI.
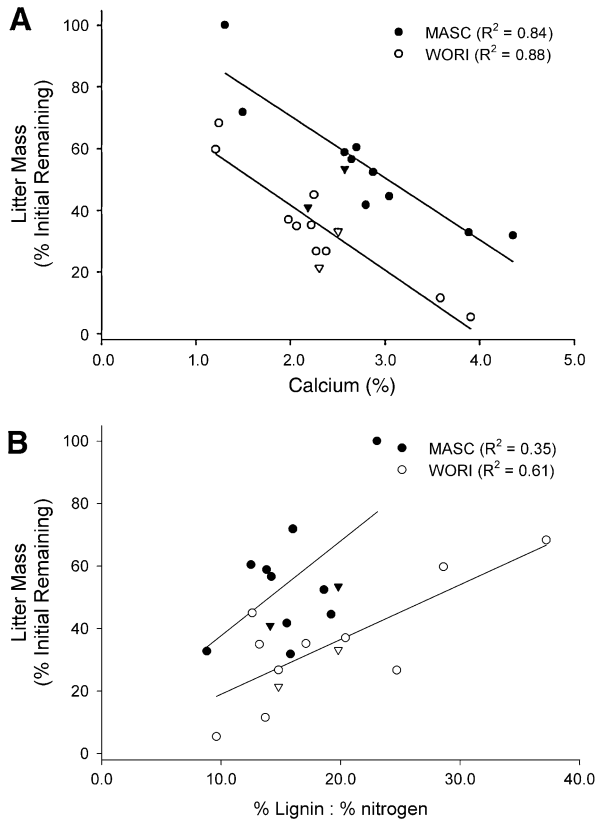
Table 3. *F* and R^2 Values of ANCOVA Models for the Response of Mean % Litter Remaining versus Site, Year, Site × Year and Calcium, % Nitrogen, % Lignin (and recalcitrants) and Lignin/N of Initial Litter from All Litter Composition Treatments

	Model covariate			
	Ca	Lignin/N	% N	Lignin
Overall model	73.7***	11.0***	13.0***	2.4
R^2	0.90	0.67	0.61	0.22
Site	72.6***	19.8***	10.0**	4.8*
Year		4.5*		
Site × year				
Covariate	111.6***	22.1***	16.7***	0.1

Terms with blank cells were removed from the model during backwards elimination (P > 0.05).
*P < 0.05, **P < 0.01, ***P < 0.001.

In 2003, we sorted each harvest by litter species to investigate how *Q. rubra*, *A. saccharum*, and *T. americana* lost mass within the mixture compared to in monoculture (litter context two). Besides each species disappearing faster overall at the site with *L. terrestris*, WORI, *A. saccharum* and *T. americana* disappeared faster in mixture (Table 5; Figure 4). The difference was the greatest for *A. saccharum* and depended on site. At WORI, *A. saccharum* had a significantly lower (32% points) overall remaining mass in mixture (contrasts: $F_{1,27} = 34.0$, $P \leq 0.0001$) (Figure 4B). Although *A. saccharum* had 12% points lower than overall remaining mass in mixture at MASC, this was not significant (contrasts: $F_{1,28} = 3.6$, $P = 0.0685$) (Figure 4A). If the petiole and mass of other unknown fragments is assumed to be all *A. saccharum* (a reasonable assumption since *A. saccharum* litter fragments much more readily compared to *Q. rubra* and *T. americana*) there is still a highly significant 21% point difference between the mixture and the monoculture at WORI while the difference at MASC disappears. *T. americana* decomposed faster

Observed litter remaining in the mixture at WORI was 14, 16, 8, and 3% points lower than predicted in the four harvests (Figure 3B).

Table 4. ANOVA Table of *F* Values for the Response of % Litter Mass Remaining to Site, Context (Context One: Observed in Mixture versus Predicted from Monoculture), and Time for 2002 and 2003 in the Two-Site Litter Composition Experiment

Treatment	df[1]		*F* values	
	2002	2003	2002	2003
Site (S)	1, 64	1, 62	39.9***	64.2***
Context (C)	1, 64	1, 62	1.9	1.7
Time (T)	3, 64	3, 62	82.8***	16.0***
S × C	1, 64	1, 62	11.1**	6.0*
S × T	3, 64	3, 62	3.6*	1.8
C × T	3, 64	3, 62	0.9	0.9
S × C × T	3, 64	3, 62	5.9**	0.9

[1]*Denominator df are different in 2003 because of two plots that were not sampled at the last harvest due to weather-imposed time constraints.*
$*P < 0.05$, $**P < 0.01$, $***P < 0.001$.

Figure 2. % Initial litter mass remaining versus initial calcium (**A**) and lignin/nitrogen (**B**) for the three monoculture and two mixture treatments. Data points are mean % litter remaining of all the four harvests of each composition treatment for 2002 and means for 2003 at MASC (*L. terrestris* absent) and WORI (*L. terrestris* present). However, as there was no significant difference between years, the regression lines are fit for both the years combined. Calcium and lignin/nitrogen values are based on composited initial litter samples of each treatment for each site in 2002 and 2003. 2002 and 2003 data for the additional sites used in the four-site comparison experiment, PAWO (▼) (*L. terrestris* absent) and WOLS (∇) (*L. terrestris* present), are plotted for comparison with the MASC and WORI sites.

in mixture at both the sites (Table 5; Figure 4). *Q. rubra* did not decompose faster in mixture at either site (Table 5; Figure 4).
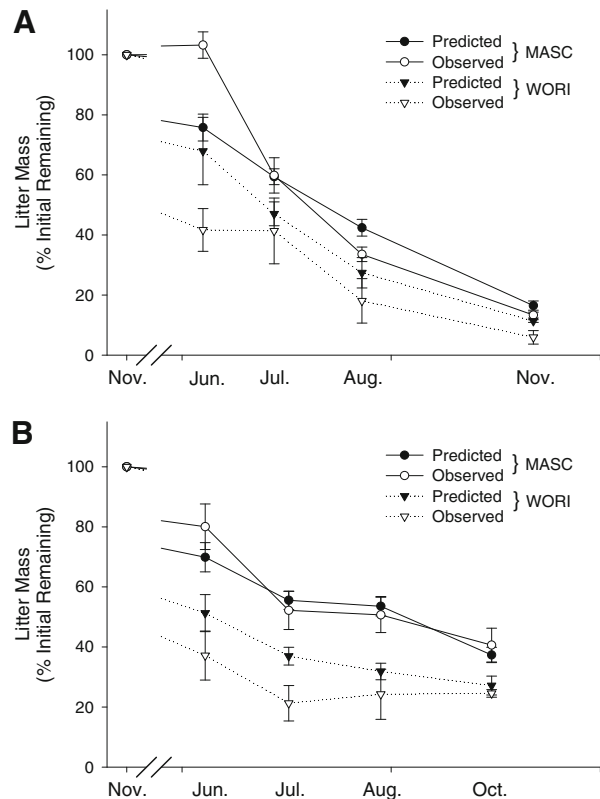
Litter Composition and *L. terrestris* midden density

Litter composition did not have a significant effect on *L. terrestris* midden density at WORI between the beginning and the end of the experiment (fall 2001, fall 2003). At the beginning of the experiment, WORI midden density did not differ between litter composition treatments ($F_{5,44} = 1.2$, $P = 0.31$)

Figure 3. Predicted based on additive model of monocultures and observed % initial litter mass remaining (±SE) in mesocosms of an equal mixture of *Q. rubra*, *A. saccharum*, and *T. americana* litter in the two-site litter composition experiment (context one) at MASC (*L. terrestris* absent) and WORI (*L. terrestris* present). **A** 2002 and **B** 2003.

Table 5. ANOVA Table of *F* Values for the Responses of % *Q. rubra*, *A. saccharum*, *T. americana* Remaining to Site, Context (Context Two), and Time in 2003 for the Two-Site Litter Composition Experiment

Treatment	*Q. rubra*		*A. saccharum*		*T. americana*	
	df	*F*	df	*F*	df	*F*
Site (S)	1, 16	13.0**	1, 16	41.0***	1, 16	28.2***
Context (C)	1, 16	3.8	1, 16	29.7***	1, 16	7.5*
Time (T)	3, 46	2.8	3, 47	12.1***	3, 47	14.8***
S × C	1, 16	0.2	1, 16	7.6*	1, 16	0.0
S × T	3, 46	1.1	3, 47	1.4	3, 47	3.5*
C × T	3, 46	1.0	3, 47	0.9	3, 47	2.0
S × C × T	3, 46	0.7	3, 47	0.6	3, 47	2.4

Litter context two refers to measurement for each of A. saccharum, Q. rubra, and T. americana incubated within the equal mixture but weighed individually versus each litter in its respective monoculture.
[1]Denominator df are different for each species because of one (in the case of A. saccharum and T. americana) or two (Q. rubra) plots that were not sampled at the last harvest due to weather-imposed time constraints.
*P < 0.05, **P < 0.01, ***P < 0.001.
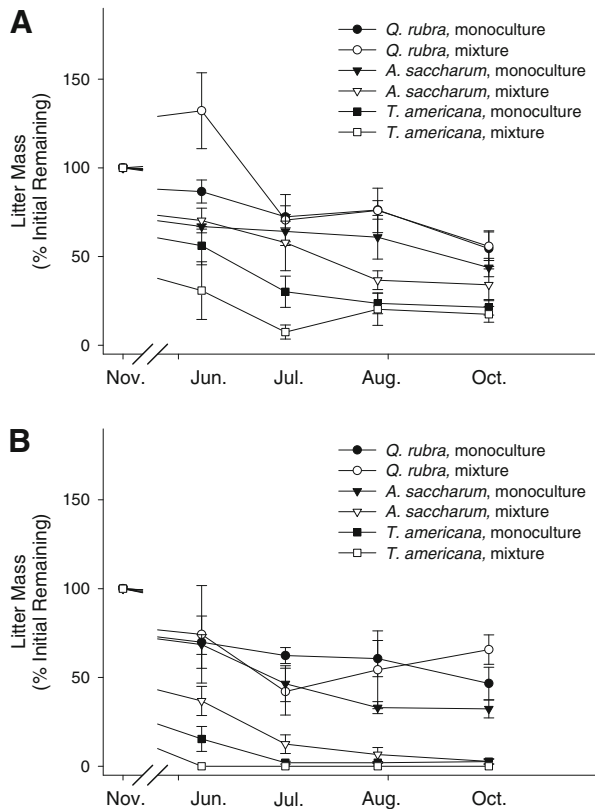
Figure 4. % Initial *Q. rubra*, *A. saccharum*, and *T. americana* mass remaining (±SE) in monoculture and in mixture in the two-site litter composition experiment (context two) at MASC and WORI in 2003. **A** MASC (*L. terrestris* absent) and **B** WORI (*L. terrestris* present).

and was a mean of 33.1 (±2.1) middens/m². Midden density under *T. americana* was the only treatment that exhibited an increase during the experiments (mean increase of 4.8 middens/m²)

and midden density decreased the most under *Q. rubra* (mean decrease of 12.8 middens/m²); however, there was not a significant litter composition effect (matched pairs $t_{29} = -1.4$, $P = 0.18$).

DISCUSSION

Litter Composition and Site Effects

Litter composition and site (in particular the presence of *L. terrestris*) exhibited a strong influence on litter disappearance in mesocosms fully accessible to soil dwelling macro-fauna. The relative order of mean remaining litter mass was similar in both the years at the two main sites: *Q. rubra* > *A. saccharum* ≥ mixture > *T. americana*. This order is similar to other studies of litter disappearance (Bocock and Gilbert 1957; Côté and Fyles 1994; Heath and others 1966) and can be largely explained by litter chemistry. In this study, initial litter calcium content was the best predictor of overall litter mass remaining each year (Figure 2). Many predictors of decomposition and litter disappearance rates have been tested including litter C/N ratio, lignin, lignin/nitrogen ratio, holocellulose to lignocellulose quotient, and litter toughness (Côté and Fyles 1994; Hendriksen 1990; McClaugherty and Berg 1987; Meentemeyer 1978; Melillo and others 1982; Swift and others 1979). However, in some ecosystems calcium may be a much better predictor, especially for earlier stages of decomposition (Staaf 1987). A common-garden study of 14 tree species growing in the European range of the earthworm species in this study also found that litter calcium was strongly related to forest floor removal rates, *L. terrestris* biomass, and a variety of soil properties (Hobbie and others 2006; Reich and others 2005).

As palatability of litter with high phenolic compounds increases as decomposition progresses, changes in the concentrations of phenols may be better predictors of decomposition even for low calcium litter (Hendriksen 1990; Satchell 1967). One explanation for the importance of calcium to *Lumbricus'* species is their high calcium demands to supply their well-developed calciferous glands which produce calcium carbonate (Canti and Piearce 2003; Robertson 1936) that could moderate blood CO_2 levels and pH when soil pCO_2 levels are elevated (Crang and others 1968; Robertson 1936).

By autumn of the first year there was substantial loss of litter mass at both sites (Figure 1). *T. americana*, *A. saccharum*, and the mixture had all lost 87–98% of their mass and *Q. rubra* 30–43%. This large overall loss of litter mass is similar to other studies on relatively rich sites where macro-fauna were permitted full access (Nielson and Hole 1964; Staaf 1987). The present study is the first to our knowledge to document the loss of litter treatments of a variety of types and mixtures through the growing season. Our total litter mass loss was larger compared to decomposition studies using litter bags at these sites and in other studies. In a related study at our sites, the same litter mixture in litterbags had 37–44 fewer percentage points of mass loss than in the mesocosms (Holdsworth and others 2008). In another study, using litter bags at a site of relatively comparable climate and soils in south-central Wisconsin (Pastor and others 1982), *A. saccharum* lost 55% mass in 1 year (McClaugherty and others 1985) compared to 92–97% in this study and *Q. alba* lost 40% compared to 63–70% for *Q. rubra* in this study. Although, the decomposition rate of litter removed from mesocosms is not known, allowing soil macro-fauna, especially earthworms, access to litter likely explains much of the large difference in total litter mass lost between our mesocosm study and litterbag studies (Heath and others 1966; Suárez and others 2006). Furthermore, in one of the most comprehensive tests of litter bag-based decomposition rates versus mass balance-based forest floor turnover rates, Hobbie and others (2006) found no correlation between the two approaches and they attributed the lack of correlation to differences in the accessibility of litter contained or not contained in litter bags to earthworms.

The differences in mass loss between treatments of different compositions were greatest at the site invaded by the large litter-feeding earthworm, *L. terrestris*, especially for the higher calcium litter in June and July (Figure 1). For litter monocultures, there was no difference among sites in mean %

remaining mass of *Q. rubra* or *A. saccharum* litter whereas there was significantly less mixture and *T. americana* litter remaining at the site with *L. terrestris*. Furthermore, just as monocultures of higher calcium litter disappeared faster in the site with *L. terrestris*, mixtures also disappeared significantly faster than predicted at this site, but not at the site without *L. terrestris* (Figure 3). This faster than predicted disappearance was due to accelerated loss of *A. saccharum* and *T. americana* but not *Q. rubra* (Figure 4B). Given that virtually all the *T. americana* had disappeared at WORI by June or July, our sampling schedule missed the majority of the disappearance sequence. However, the majority of this rapid loss of *T. americana* at WORI is likely due to the presence of *L. terrestris*. The tops of *L. terrestris* middens consisted of nearly 100% *T. americana* litter within weeks of litterfall in the fall (A. Holdsworth, personal observation). It is well documented that *L. terrestris* selectively removes high-quality litter and leaves low-quality litter (Blair and others 1997; Satchell and Lowe 1966).

Field and lab experiments on the effects of litter and detritivore diversity on litter decomposition substantiate the preferential effect of litter-feeding earthworms on high-quality litter. In a field microcosm experiment in an old-growth beech forest in Switzerland, Hättenschwiler and Gasser (2005) found that the addition of the litter-feeding earthworm *Aporrectodea longa* increased decomposition of high-quality *Tilia*, *Prunus*, and *Carpinus* litter but not relatively low-quality *Quercus* and *Fagus* litter. Similarly, in a laboratory microcosm experiment of detritivore and litter diversity, Zimmer and others (2005) found that decomposition of two species mixtures was principally additive (as in the MASC site of this study). However, with the litter-feeding earthworm *L. rubellus* present, mixtures decomposed non-additively, as in WORI.

L. terrestris as an Important Site Factor

Another study of litter disappearance in earthworm-invaded hardwood forests attributed large site differences in litter disappearance to *L. terrestris* and its feeding behavior (Suárez and others 2006). Our study supports their conclusions. Patterns of litter disappearance in our study follow those found in other studies (Bohlen and others 1997; Satchell and Lowe 1966; Staaf 1987; Suárez and others 2006) and observations of litter selection by *L. terrestris* in the field. Within weeks of litterfall, middens in the vicinity of the mesocosms were predominantly full of *T. americana* litter when *A. saccharum* and *Q. rubra* were more available.

During the first harvest in June when *T. americana* was almost completely removed from the mixtures, middens were predominantly *A. saccharum* and finally at the end of the season when *A. saccharum* was almost completely gone, *Q. rubra* was pulled into middens (A. Holdsworth, personal observations). Furthermore, disappearance of the equal mixture placed at all the four sites was similar at the two sites with *L. terrestris* and significantly faster than the two sites without *L. terrestris*. Although, lack of replication at the site level prevents inference on the significance of *L. terrestris'* effect, the sites of this study provide examples of how litter disappearance can differ with and without *L. terrestris* and suggest the importance of gaining a better understanding of the effects of earthworm invasion with and without *L. terrestris*.

Ecosystem Implications

There are important aboveground–belowground interactions between forest plant-community composition, earthworm community composition, and changes in the structure and composition of the forest floor. Our study provides evidence for the importance of litter calcium to litter layer dynamics, especially when *L. terrestris* is a member of the invasive earthworm community. Assuming suitable soil conditions, we posit that forest types dominated by tree species that have higher leaf litter calcium concentrations (that is, *T. americana*, *A. saccharum*, *Populus tremuloides*) will generally undergo the greatest degree of change in the litter layer upon invasion by *Lumbricid* earthworms.

The geographical extent of invasion by *L. terrestris* is the most limited of all the litter-feeding species in the upper Midwest of North America (Holdsworth and others 2007b), yet its addition to the invasive earthworm community could have important ecosystem consequences (Nielson and Hole 1964). Where the earthworm community includes the anecic species *L. terrestris*, the litter layer will lose more of the O_i litter component earlier in the growing season, especially of species with high litter calcium levels. This *L. terrestris*-induced seasonality of litter loss could have bearing on the mechanisms underlying some of *L. terrestris'* community and ecosystem effects. For instance, *L. terrestris'* activities can influence microbial and microfungal communities (Bohlen and others 2002; Orazova and others 2003), contribute to increased nitrogen leaching (Domínguez and others 2004), affect phosphorous cycling (Suárez and others 2004) and carbon budgets (Suárez and others 2006). Its activities can also increase the risk

of erosion (Hazelhoff and others 1981), and could contribute to the dominance of sedges in heavily invaded forests. By significantly reducing litter depth and exposing mineral soil it could increase likelihood of species invasions by species such as *Rhamnus cathartica* (Frelich and others 2006; Holdsworth and others 2007a), and reduced density and nest survival of ground-dwelling forest songbirds (Loss and Blair 2011). The ecological changes associated with the addition of *L. terrestris* merit more research as its relatively limited distribution expands in northern hardwood forests invaded by other invasive earthworms.

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