Contributed Paper

Earthworm Invasion as the Driving Force Behind Plant Invasion and Community Change in Northeastern North American Forests

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Abstract: *Identification of factors that drive changes in plant community structure and contribute to decline and endangerment of native plant species is essential to the development of appropriate management strategies. Introduced species are assumed to be driving causes of shifts in native plant communities, but unequivocal evidence supporting this view is frequently lacking. We measured native vegetation, non-native earthworm biomass, and leaf-litter volume in 15 forests in the presence and absence of 3 non-native plant species (*Microstegium vimineum, Alliaria petiolata, Berberis thunbergii*) to assess the general impact of non-native plant and earthworm invasions on native plant communities in northeastern United States. Non-native plant cover was positively correlated with total native plant cover and non-native earthworm biomass. Earthworm biomass was negatively associated with cover of native woody and most herbaceous plants and with litter volume. Graminoid cover was positively associated with non-native earthworm biomass and non-native plant cover. These earthworm-associated responses were detected at all sites despite differences in earthworm species and abundance, composition of the native plant community, identity of invasive plant species, and geographic region. These patterns suggest earthworm invasion, rather than non-native plant invasion, is the driving force behind changes in forest plant communities in northeastern North America, including declines in native plant species, and earthworm invasions appear to facilitate plant invasions in these forests. Thus, a focus on management of invasive plant species may be insufficient to protect northeastern forest understory species.*

Keywords: *Alliaria petiolata*, *Berberis thunbergii*, earthworm invasion, facilitation, forest soils, invasive plants, leaf litter, *Microstegium vimineum*

Invasión de Lombrices de Tierra como la Fuerza Conductora detrás de la Invasión de Plantas y Cambios en la Comunidad en Bosques del Noreste de América del Norte

Resumen: *La identificación de factores que conducen los cambios en la estructura de la comunidad de plantas y que contribuyen a la declinación y puesta en peligro de especies de plantas nativas es esencial para el desarrollo de estrategias de manejo adecuadas. Se asume que las especies introducidas son las causas de cambios en comunidades de plantas nativas, pero frecuentemente se carece de evidencia inequívoca que soporte este punto de vista. Medimos la vegetación nativa, la biomasa de lombrices de tierra no nativas y el volumen de hojarasca en 15 bosques con la presencia y ausencia de tres especies de plantas no nativas (*Microstegium vimineum, Alliaria petiolata, Berberis thunbergii*) para evaluar el impacto general de plantas no nativas e invasiones de lombrices de tierra sobre comunidades de plantas nativas en el noreste de Estados Unidos. La cobertura de plantas no nativas se correlacionó positivamente con la cobertura total de plantas nativas y la biomasa de lombrices de tierra no nativas. La biomasa de lombrices de tierra se asoció negativamente con la cobertura de plantas nativas leñosas y la mayoría de plantas herbáceas y con el volumen de hojarasca. La*

cobertura de graminoides se asoció positivamente con la biomasa de lombrices no nativas y con la cobertura de plantas no nativas. Estas respuestas asociadas a lombrices de tierra fueron detectadas en todos los sitios no obstante las diferencias en especies de lombrices y abundancia, composición de la comunidad de plantas nativas, identidad de las especies de plantas invasoras y región geográfica. Estos patrones sugieren que la invasión de lombrices de tierra, y no la invasión de plantas no nativas, es la fuerza conductora detrás de los cambios en las comunidades de plantas de bosque en el noreste de Norte América, incluyendo declinaciones en especies de plantas nativas, y las invasiones de lombrices de tierra aparentemente facilitan las invasiones de plantas en estos bosques. Por lo tanto, el enfoque en el manejo de especies de plantas invasoras puede ser insuficiente para proteger especies del sotobosque de bosques nororientales.

Introduction

Plant communities worldwide are changing rapidly, often resulting in altered ecosystem processes (Levin et al. 2006) and an accelerated loss of rare and endangered species (Wilcove et al. 1998). Among the leading causes of plant community changes are habitat alteration and destruction and introduction of non-native plants (Vitousek et al. 1996; Burgman et al. 2007). Invasions by non-native plant species are generally considered a threat to native species diversity and abundance (Mack et al. 2000; D'Antonio et al. 2004); however, support for this assessment is equivocal (e.g., Stohlgren et al. 2003; MacDougall & Turkington 2005; Kumar et al. 2006).

The question of whether change in native plant communities is a result of habitat alteration or the result of non-native plant invasion is not simply academic. Effective protection and conservation of native species, their habitats, and evolutionary potential requires identification of the underlying causes of environmental change and implementation of practices to manage those changes (Burgman et al. 2007). Increases in abundance or diversity of native plants following removal of an invasive species (D'Antonio & Mahall 1991; McCarthy 1997; Hulme & Bremner 2006), are often used as evidence that observed differences in species richness and community composition are caused by the invasive plant and, by extrapolation, by invasive plants in general. Although this approach provides substantial support for negative impacts of invasive plants, it cannot rule out associated factors, such as initial vegetation differences, different land-use histories, herbivory, and interactions with other invasive organisms, as causative or contributing factors.

Deer herbivory and non-native earthworm invasions also have been implicated in changes in native plant community structure (Cote et al. 2004; Hale et al. 2006), including population reductions of perennial herbs (McGraw & Furedi 2005) in North America. White-tailed deer (*Odocoileus virginianus*) selectively browse preferred species, and detrimental impacts of increased deer browse on understory herbaceous vegetation are well documented (e.g., Horsley et al. 2003; Ruhren & Han-

del 2003; Knight 2004; Kraft et al. 2004). Deer herbivory may also promote non-native plant invasion by reducing competition from native species and increasing exposed soil suitable for invasion (Vavra et al. 2007). The spread of many non-native earthworms has been directly linked to declines in a rare fern (Gundale 2002) and woodland herbs (Hale et al. 2006), and indirectly linked to declines in sugar maple (*Acer saccharum*) through alteration of soil mychorrizal colonization and abundance (Lawrence et al. 2003).

The changing plant communities and effects of many individual stressors on individual species are widely recognized; however, few studies have examined multiple threats simultaneously. For example, we are not aware of any studies that considered plant and earthworm invasions simultaneously for their impact on native plants or that tested whether these invasions are linked. We repeatedly surveyed plant communities in invaded and uninvaded habitats across invasion fronts of 3 non-native plant species in 15 deciduous forests in the northeastern United States to test the following hypotheses: increased non-native plant cover is associated with reduced diversity and cover of native plant species and increased non-native earthworm biomass is associated with reduced cover of native plant species and positively associated with non-native plant cover. Ecological change directly associated with invasive species may be detectable by working across invasion fronts. To reduce the potential for site-specific differences (e.g., site history, native plant community, climate) to confound results and to improve our ability to identify conditions that facilitate or are the result of non-native plant invasions, we worked across multiple, independent invasion fronts.

Methods

Study Sites and Plant Species

We selected 3 common non-native plants that invade northeastern forests in North America as target plant species. These plant species represent 3 distinct

functional groups and 2 different regions of origin: the biennial herb *Alliaria petiolata*, the perennial shrub *Berberis thunbergii*, and the annual grass *Microstegium vimineum* (hereafter referred to as *Alliaria*, *Berberis*, and *Microstegium*, respectively, and collectively as target plant species). Each species is implicated in declines in native plant diversity or abundance (e.g., McCarthy 1997; Kourtev et al. 1998; Cole & Weltzin 2004; Stinson et al. 2006) and is generally assumed to be a "strong" invader (sensu Ortega & Pearson 2005). *Alliaria* is an obligate biennial herb introduced from Europe in the 1800s that has spread throughout the eastern and central United States (Nuzzo 1993). It germinates in early spring, forms a low-growing rosette by summer and overwinters as a rosette. Second-year plants produce 0.5- to 1-m-tall flower stalks in midspring, seed in summer, and then die. The 2 life stages overlap for approximately 3 months.

Berberis is a 2- to 3-m-tall thorny perennial shrub introduced from Asia in 1875 as an ornamental that has spread through the northeastern United States, forming very dense stands in the eastern part of this range (Ehrenfeld 1999; Silander & Klepeis 1999). *Berberis* germinates in May, forms a single-stemmed plant, and after one or more years produces shoots from the root base to form a multiple-stemmed plant. Plants are long-lived and mortality is rare once shrubs have ≥3 stems (Ehrenfeld 1999).

Microstegium is an annual C_4 grass introduced from Asia that has spread throughout southeastern and much of northeastern United States since it was first collected in 1919 (Barden 1987). *Microstegium* germinates in spring, grows rapidly to up to 1 m tall, flowers in summer, and produces seeds in late summer or early autumn. *Microstegium* and *Berberis* frequently co-occur (Ehrenfeld et al. 2001; Kourtev et al. 2002), and both have been associated with increased earthworm density and changes in ecosystem properties, including loss of leaf litter, increased soil pH, and increased soil nitrogen (Kourtev et al. 1998; Ehrenfeld et al. 2001).

We located 15 hardwood forest sites in New York State and Pennsylvania (5 sites invaded by each of the target plant species). We selected sites on the basis of presence of a single target species with a clearly defined invasion boundary, visual estimates of approximately 30% cover by target plant species in the invaded area, and absence of apparent site, vegetational, or land-use differences between the invaded and uninvaded areas. We defined *invasion front* as the leading edge of invasion, with the target species absent ahead of the front and present at and behind the front. Although we anticipated invasion fronts progressing during our study, we observed only minor advances of plants at few sites within the study period. Sites invaded by *Alliaria*, *Berberis*, and *Microstegium* were clustered in south-central New York, northeastern Pennsylvania, and southeastern Pennsylvania, respectively, creating an unavoidable bias in distribution of sites among the plant types. Sugar maple (*Acer sacchar-*

rum) dominated the tree canopy at the *Alliaria* sites and oaks (*Quercus* sp.) dominated the canopy at the *Berberis* and *Microstegium* sites. Sites were established over several years: 3 *Alliaria* sites in 2000; 1 *Alliaria* site in 2001; 1 *Alliaria*, 5 *Berberis*, and 3 *Microstegium* sites in 2002 (all plots sampled through 2003); and 2 *Microstegium* sites in 2003 (sampled through 2004).

Assessment of Plant Communities

At each site we established 30 study plots, 15 in the invaded habitat and 15 in the uninvaded habitat. On each side of the invasion front, plots were located ≥5 m apart, beginning approximately 10 m from the invasion front. All plots in the uninvaded habitat were randomly located, whereas plots in the invaded habitat were randomly located with the requirement that the plots meet the following criteria: *Alliaria* plots contained adult or seedling plants; *Berberis* plots contained or were immediately adjacent to shrubs; and *Microstegium* plots had seedlings or senescent plants present. Because plots were located near the invasion front, all plots contained <80% cover of the target species, and some contained as little as 3% cover.

Each plot consisted of a permanently marked 1-m² quadrat that we used for monitoring vegetation and leaf litter. We sampled vegetation communities at 3 *Alliaria* sites 4 times in 2000 (early spring, late spring, midsummer, autumn) to determine optimal sampling time to detect peak cover of dominant species. Thereafter, we conducted sampling at all sites once in late spring and once in autumn at the same phenological time at each site. We estimated the percent cover for each species <1 m tall and for leaf litter, soil, rock, and downed wood in 17 cover categories (midpoints: 0.01%, 0.2%, 0.5%, 1%, 3%, 5%, 10%, 20%, 30%, 40%, 50%, 60%, 70%, 80%, 90%, 98%, and 100%). We identified all species present, including seedlings. Additionally, we scored each species for presence or absence of deer herbivory and measured leaf-litter depth (cm) at 4 locations within each plot. We later calculated leaf-litter volume by multiplying the mean of all nonzero measurements of litter depth by the percent area of the plot covered by leaf litter.

Assessment of Earthworm Biomass

Each study plot was bounded by 2 coverboards (100 × 25 × 6 cm boards made from rough-cut and untreated maple) used for monitoring earthworm abundance. The use of coverboards is not a standard technique for quantifying earthworm abundance or biomass. Generally, earthworms are extracted from the soil through the application of mustard solution or formalin. This was not an option for our study because we could not use removal sampling or add compounds to plots that might affect plant or animal communities. The use of artificial cover is routinely used to quantify the abundance of other types

of soil fauna (Heyer et al. 1994; Monti et al. 2000). Coverboards were checked every 2–3 weeks from early April through early November in 2001 and 2002 and thereafter from early April through early June and early September through early November. Each time we counted the number of earthworms in each of 3 size classes (small, <5 cm; medium, 5–10 cm; large, >10 cm) for each of 3 guilds: epigeic (surface-dwelling species that feed on leaf litter), anecic (vertically burrowing earthworms that feed on leaf litter), and endogeic (worms that live in mineral soil and feed on soil organic matter). (For a detailed description of non-native earthworm guilds, their specific constituents, ecology, and habits see reviews by Hendrix [1995], Hendrix and Bohlen [2002], and Hale et al. [2006]). At each site we also collected specimens of each size class and guild from areas around our study plots. In the lab, we identified these specimens to determine earthworm assemblages at each site, and we weighed them to determine the mean fresh weight for each earthworm size class.

Our passive measure of earthworm abundance was dependent on earthworm surface activity, so it may better represent active abundance rather than total abundance. Furthermore, we do not know how our measure compares with more traditional worm-extraction methods, Because our method was standardized across habitats and sites, however, we could produce a comparative index of "active fresh biomass" of earthworms. To estimate mean annual fresh biomass of active earthworms, we first estimated fresh biomass for each plot by multiplying count data from plots by the mean fresh mass of earthworms for that guild and size class for each visit. We then averaged this estimate for all observations for 1 year for each plot (hereafter the term *earthworm biomass* refers to active fresh weight).

Statistical Analyses

We compared means between plant-invaded and uninvaded habitats. For plant cover we used the maximum cover observed for each plant species in each quadrat over the entire monitoring period as the percent cover for that species. This provided a correction for species that peaked in cover at different times within plots, for variation across years due to phenology or climatic factors such as drought, and for differences among sites in the number of years monitored (2, 3, or 4 years, depending on when each site was established). We summed the maximum cover values to determine total native and non-native plant cover and total cover of different plant functional groups (graminoids [sedges and grasses], ferns, annual and biennial herbs, perennial herbs [including ephemerals], and woody species [trees and shrubs]).

When possible, we used paired or dependent analyses to test hypotheses, but some analyses (e.g., principle components analysis, PCA) required us to treat the invaded and uninvaded habitats within sites as independent replicates. We used one-way repeated measures analysis of variance (ANOVA) to test the hypothesis that percentage of native plants is lower in habitats invaded by non-native plants. Target plant species was included as a fixed factor, and the invaded and uninvaded habitats were treated as dependent (repeated) measures. We used the same ANOVA model to test the hypotheses that estimated active earthworm biomass is greater and leaf litter volume is lower in habitats invaded by non-native plants. Finally, to examine the relationships between earthworms, plant invasions, and the cover of different native plant functional groups, we conducted a PCA with cover of non-native plants, various native plant functional groups, and estimated active earthworm biomass. We also used Pearson's correlation coefficients to test for correlations between plant functional group cover, invasive plant cover, leaf-litter volume, and earthworm biomass. Analyses were conducted with Statistica (version 6.0; StatSoft, Tulsa, Oklahoma).

Results

Earthworm Assessments

Estimated annual active earthworm biomass (Fig. 1a) and leaf-litter volume (Fig. 1b) differed consistently between invaded and uninvaded habitats, regardless of identity of the plant invader. Eleven earthworm species (all non-native) were recorded, with 3 to 9 species occurring at each site (Table 1). Although the number of species differed among sites, generally earthworm communities were similar among sites in that they were comprised of a large anecic (*Lumbricus terrestris*) or endoanecic (*Aporectodea calignosa* complex) species, a medium-large (*Lumbricus rubellus* or *Amynthas* sp.) and small (*Dendrobaena* spp.) epigeic species, and a medium endogeic species (*Octolasion tyrtaeum*). *L. terrestris* and *L. rubellus* were the most common species. Earthworm biomass was significantly greater in invaded than in uninvaded habitats (mean square [MS] = 110.208, $F_{2,12}$ = 21.402, $p < 0.001$; Fig. 1a). At individual sites earthworm biomass was significantly greater in invaded habitats at 12 of 15 sites, similar between habitats at 3 sites, and never lower in the invaded habitat (Fig. 1a). Earthworm biomass varied significantly among the 3 target plant regions (MS = 54.799, $F_{2,12}$ = 4.008, $p = 0.046$): biomass was similar among *Alliaria* and *Berberis* sites ($p = 0.607$) and significantly lower among *Microstegium* sites compared with *Alliaria* ($p = 0.045$) and *Berberis* ($p = 0.045$) sites (Fig. 1a).

Among all habitats across all sites, earthworm biomass was significantly negatively correlated with leaf-litter volume ($r = −0.579$, $p < 0.001$; Fig. 2). Across all forests leaf-litter volume was significantly lower in invaded than
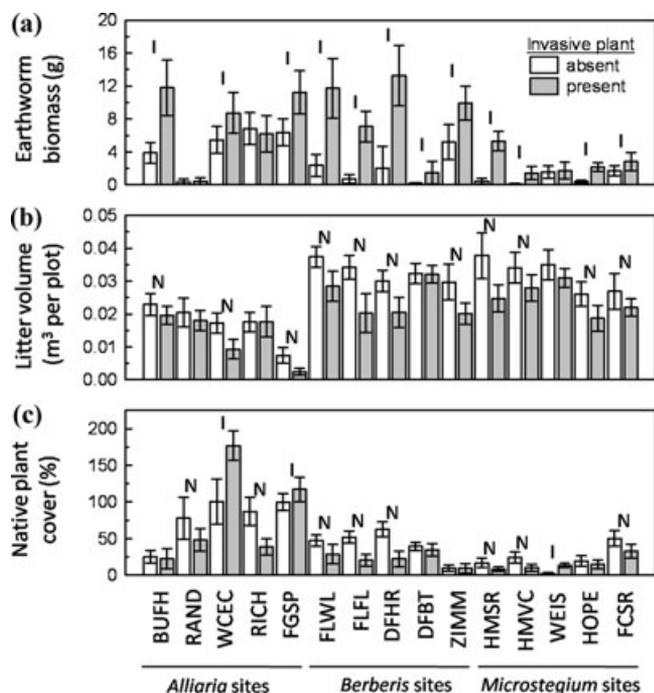
Figure 1. Mean (a) annual "active" earthworm biomass, (b) leaf-litter volume, and (c) cover by native understory plants in adjacent habitats invaded and uninvaded by non-native A. petiolata, B. thunbergii, *or* M. vimineum. *Bars show means, and error bars show 2 SE. For each site, a letter indicates a statistically significant difference (p < 0.05) between habitats (N, uninvaded > invaded; I, invaded > uninvaded).*

in uninvaded habitats (MS = 0.031, $F_{1,12}$ = 40.112, p < 0.001; Fig. 1b. Within sites leaf-litter volume was significantly lower in invaded habitats at 13 of 15 sites (Fig. 1b). Leaf litter volume varied significantly among the 3 target-plant regions (MS = 0.058, $F_{2,12}$ = 11.096, p = 0.002) and was significantly lower in maple-dominated *Alliaria* sites compared with oak-dominated *Berberis* sites (p = 0.001) and *Microstegium* sites (p = 0.001; Fig. 1b). There was no significant difference in leaf-litter volume between *Berberis* and *Microstegium* sites (p = 0.966; Fig. 1b), and the difference in leaf-litter volume between habitats did not differ among the 3 target-plant regions (target plant × habitat interaction: MS = 0.015, $F_{2,12}$ = 1.958, p = 0.184).

Plant Community Assessments

Cover of the target non-native plant varied significantly among the 3 plant regions (MS = 1688, $F_{2,12}$ = 23.495, p < 0.001). *Microstegium* sites averaged (SE) 5.6% (2.0) cover per plot, whereas *Alliaria* and *Berberis* sites had similar (p = 0.905) and significantly higher mean cover per plot (*Alliaria* sites 38.6% [SE 5.2], Tukey's honest significant difference test, p < 0.001; *Berberis* sites 36.0%

Table 1. Earthworm species present at 15 study sites (sexually mature voucher specimens for all sites).

	Sites by focal non-native plant species														
	A. petiolata					B. thunbergii					M. vimineum				
Guild and species	BUFH	WCEC	RICH	FGSP	RAND	FLFL	FLWL	DFBT	DFHR	ZIMM	HMSR	HMVC	WEIS	FCSR	HOPE
Anecic species															
Lumbricus terrestris	+	+	+	+	+	+	+	+	+	+	+			+	+
Epigeic species															
Amynthas sp.	+	+		+	+						+	+			
Dendrobaena octaedra		+			+	+	+	+			+		+	+	
D. rubida										+				+	+
Eisenoides carolinensis	+														
L. rubellus	+	+	+	+	+	+	+	+	+		+	+		+	+
L. castaneus				+							+		+		
Endogeic species															
Aporrectodea rosea	+			+							+			+	
A. calignosa complex*	+	+				+	+	+	+	+	+			+	+
Bimastos longicinctus		+		+							+				
O. tyrtaeum	+	+	+							+		+			

*Aporrectodea calignosa is often used to refer to a complex of 3 species: A. trapezoides, A. tuberculata, and A. turgida. Although classified as endogeic, these species are relatively anecic in habit, often forming extensive burrows and feeding on surface litter.
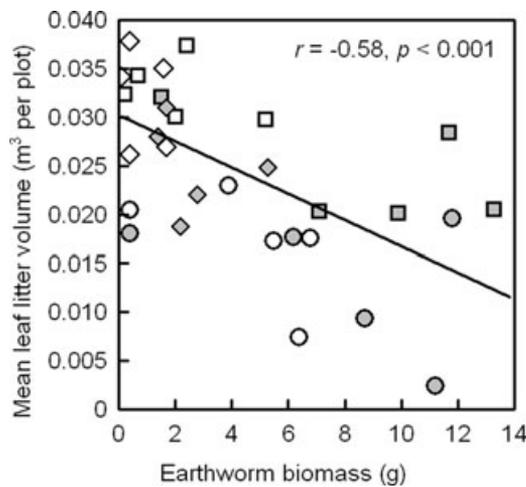
Figure 2. Correlation between mean 'active' earthworm fresh biomass (grams per coverboard pair) and mean leaf-litter volume among adjacent habitats uninvaded (open symbols) and invaded (shaded symbols) by non-native A. petiolata *(circles),* B. thunbergii *(squares), or* M. vimineum *(diamonds) (n = 30; 2 habitats per site for 15 sites).*

Table 2. Loadings, eigenvalues, and cumulative percent variance explained for factors identified in principle component analysis of earthworm 'active' fresh biomass and percent cover of non-native and native plant functional groups.*

Biomass or percent cover	Factor 1	Factor 2	Factor 3
Non-native earthworm	−0.727	0.521	0.242
Non-native plants	−0.740	0.269	−0.059
Native graminoids	−0.680	0.533	0.317
Native ferns	−0.495	−0.571	0.016
Native annual herbs	−0.729	−0.503	−0.103
Native perennial herbs	−0.894	−0.602	−0.031
Native woody plants	0.309	−0.406	0.839
Eigenvalue	2.897	1.733	0.878
Cumulative variance explained (%)	41.4	66.1	78.7

Factors are composite variables, derived from a larger number of variables, that collectively reflect the strongest linear correlation structure. Negative loading values indicate a negative relationship and positive values indicate a positive relationship between each biomass or cover variable and the associated factor. Each eigenvalue represents a portion of the original total variance, corresponding to a particular axis. The size of the eigenvalue indicates how much variance is explained by each axis or factor. These relationships are presented visually in Fig. 3.

[5.2], $p < 0.001$). Other non-native species were absent or rare at all sites and composed 0–4% of total vegetation cover.

Native plant cover did not differ significantly between invaded and uninvaded habitats (MS = 457, $F_{2,12} = 0.998$, $p = 0.337$), but did vary significantly among the 3 target-plant regions (MS = 9982, $F_{2,12} = 6.339$, $p = 0.013$; Fig. 1c). Native cover was significantly higher at the *Alliaria* (mean [SE] 78.8% [9.2]) sites in central New York compared with the *Berberis* (34.2% [3.9]) sites in northeastern Pennsylvania ($p = 0.006$) and the *Microstegium* (19.2% [3.0]) sites in southeastern Pennsylvania ($p < 0.001$; Fig. 1c). Native cover did not differ significantly between *Berberis* and *Microstegium* sites ($p = 0.596$; Fig. 1c). At individual sites, native plant cover was significantly greater in uninvaded than invaded habitats at 8 sites (2 *Alliaria* sites, 3 *Berberis* sites, and 3 *Microstegium* sites), similar in both habitats at 4 sites (1 *Alliaria* site, 2 *Berberis* sites, and 1 *Microstegium* site), and significantly lower in uninvaded habitats at 3 sites (2 *Alliaria* sites and 1 *Microstegium* site; Fig. 1c). Across all 15 sites, native plant cover in invaded and uninvaded habitats was significantly positively correlated ($r = 0.776$, $p < 0.001$), supporting our assertion that habitats were similar except for the presence of the non-native target plant species.

The PCA of percent cover of non-native target plants, non-native earthworm biomass, and native plant functional groups (graminoids, perennial herbs, annual herbs, ferns, and woody plants) revealed 2 factors that explained 66% of the variation in plant community com-

position (Table 2). The PCA revealed a strong positive association between non-native earthworm biomass, non-native plant cover, and native graminoid cover, and all 3 measures were strongly negatively correlated with native woody cover (Fig. 3). Cover of native perennial herbs, annual herbs, and ferns were all strongly positively
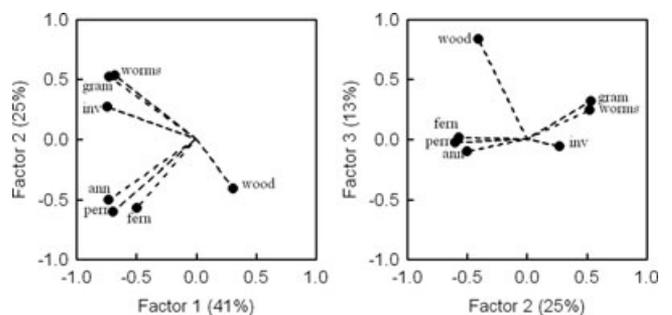

Figure 3. Principle component analysis projection plots for non-native plant cover, cover of different native plant functional groups, and non-native earthworm biomass. Percent values indicate proportion of total variance explained by that factor. Groups are inv, non-native plants; gram, native graminoids; fern, native ferns; perr, native perennial herbs; ann, native annual herbs; wood, native shrubs and tree seedlings; and worms, non-native earthworms. Projections in the same direction indicate a positive correlation between variables, and projections in the opposite direction indicate negative correlations.

associated and collectively were negatively associated with all other factors (non-native earthworm biomass, non-native plant cover, and native graminoid woody cover; Fig. 3).

Discussion

Our results provide compelling evidence that earthworm invasions are facilitating non-native plant invasions in the temperate forests of northeastern North American and are probably the cause of many of the changes in these forest understories publicly attributed to plant invasions. This pattern was robust for 3 different non-native plant species in 3 different regions. Although other researchers have noticed a positive association between non-native earthworms and non-native plant species, including *Berberis* and *Microstegium* in New Jersey (Kourtev et al. 1999; Ehrenfeld et al. 2001) and *Myrica faya* in Hawaii (Aplet 1990), and have documented higher soil nitrogen (Aplet 1990; Kourtev et al. 1999), higher soil pH (Kourtev et al. 1999), and faster litter decomposition (Ehrenfeld et al. 2001) when both life forms are present, our results are the first to imply causality in a broad relationship across multiple invasive species. Other recent studies report similar shifts in native plant communities (including declines in native woody and perennial herbaceous cover) in response to earthworm invasion in the *absence* of non-native plant invasions (Hale et al. 2006).

We found no consistent relationship between non-native plant invasions and the cover of native plants. This result conflicts with the hypothesis that non-native plant invasions are associated with (i.e., cause) reduced cover of native plant species. We suggest 2 reasons for this apparent lack of impact. First, we worked at invasion fronts where the non-native plants had low cover and a short invasion history. Second, different plant functional groups exhibit different responses to non-native plant and earthworm invasion, and decline in one or more groups is compensated for by increases in other groups. In our study native perennial and annual herb, fern, and woody shrub and tree seedling cover was negatively associated and native graminoid (sedge and grass) cover was strongly positively associated with non-native plant cover and earthworm biomass. These results are consistent with other studies of earthworm invasion effects on the plant communities of temperate forests (Bohlen et al. *2004c*; Hale et al. 2006; Holdsworth et al. 2007). Hale et al. (2006) and Holdsworth et al. (2007) found that most native plant species decline with increasing non-native earthworm biomass; however, in some areas where earthworm biomass is high, the native sedge *Carex pensylvanica* increases in abundance and becomes the dominant understory plant. The change in the native-plant community reported by these authors is highly similar to our findings, but occurred in the absence of invasion by a non-native plant species. Therefore, we hypothesize that shifts in understory plant communities, including shifts among native plant functional groups and invasion by non-native plants, are the direct result of non-native earthworm effects on forest soils.

Most northern forests of North America lacked earthworms prior to European settlement, and earthworms of both European and Asian origin are now rapidly invading these forests (Bohlen et al. 2004*c*). Non-native earthworm biomass was greater in habitats with invasive plants and was positively correlated with loss of the litter layer. The negative effects of non-native earthworm invasions on northeastern forest litter layers are well documented and include rapid incorporation of leaf litter into the soil, alteration of soil chemistry, change in soil pH, mixing of soil layers, and increased soil disturbance due to burrowing and cast deposition (Gundale 2002; Bohlen et al. 2004*a,c*; Hale et al. 2005; Suarez et al. 2006). In particular, *L. terrestris* and *L. rubellus*, the most common and abundant species in our study sites, are associated with rapidly depleted leaf litter (Gundale et al. 2005; Suarez et al. 2006) and loss of most native herbaceous and woody vegetation (Hale et al. 2006).

There are a number of ways in which earthworms may directly or indirectly promote invasion by non-native plants and affect native plant communities. Earthworm-induced changes in soil nutrients alter competitive relationships among native plant species and between native and non-native plant species (Scheu 2003). For example, non-native earthworms increase soil nitrogen levels (Bohlen et al. 2004*b*), creating conditions that facilitate invasions by species such as *B. thunbergii* into forests (Cassidy et al. 2004). Earthworm burrowing can disrupt plant mycorrhizae to the detriment of native species (Lawrence et al. 2003). Most of the plants in northern forest understories in North America are mycorrhizal, so earthworm invasions may disadvantage those species in favor of amycorrhizal species such as the native sedge *C. pensylvanica* and the 3 non-native species in our study (*A. petiolata*, *B. thunbergii* and *M. vimineum*). which are either nonobligate or amycorrhizal (Bohlen et al. 2004*c*).

The observed decline in native plants in many northeastern forests has been attributed to excessive deer herbivory (e.g., Rooney et al. 2004; McGraw & Furedi 2005*b*; Webster et al. 2005) in addition to invasion by non-native plants (Stinson et al. 2006) and non-native earthworms (Bohlen et al. 2004*c*). We suggest that for many species, a combination of these factors limits growth of native vegetation. Hale et al. (2006) speculated that earthworm impacts may be amplified by excessive deer herbivory: herbaceous vegetation declines with earthworm invasion and the remaining species are then subjected to more intense herbivory and subsequently decline in abundance.

Rooney and Waller (2003) found similar shifts in ground-layer composition (increased gramininoids and decreased perennial herbs) in Wisconsin forests that were linked directly to deer herbivory. At our study sites, we recorded little to no browse activity except on one annual herb at one site (unpublished data).

Non-native plants are widely believed to threaten natural communities. Nevertheless, it is the impact and not the presence of the invader that threatens natural communities (Levine et al. 2003). We hypothesize that plant invasions of northeastern forest understories are symptomatic of larger plant-community shifts in response to non-native earthworm invasions. Invasive plants are conspicuous and are often assumed to be the agents of change; however, our study in conjunction with the work of others indicates that much of the change is occurring belowground and that invasive plants are the beneficiaries, rather than the agents, of this change. In light of the accumulating evidence for the importance of factors other than introduced plants, land managers and conservation scientists may need to revisit priorities for the protection of native species. Controlling introduced plants alone may not achieve the desired effects of protecting native biota from further declines.
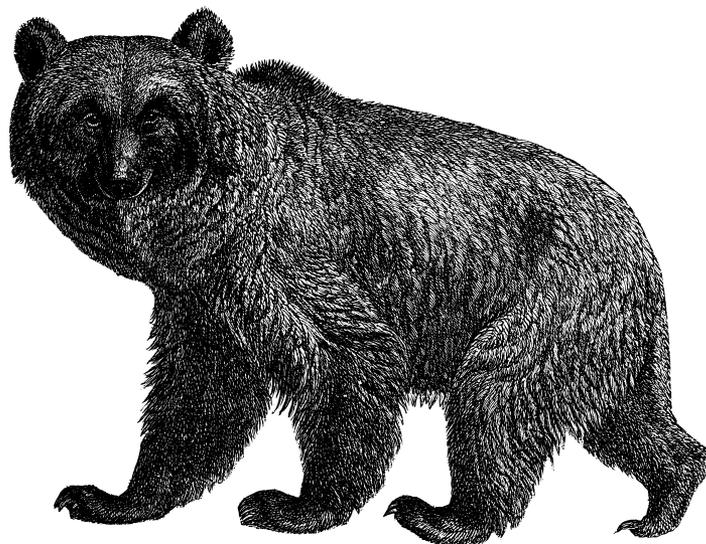
Acknowledgments

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