

Invasive Earthworms and Plants in Indiana Old- and Second-Growth Forests

Kevin D. Gibson, Patricia M. Quackenbush, Nancy C. Emery, Michael A. Jenkins, and Eileen J. Kladvik*

Hardwood forests in eastern North America are being colonized by multiple nonnative plant and animal species. Colonization rates can be affected by stand structure and distance from edge. We sampled earthworm densities and understory plant species cover in transects located in paired old- and second-growth forests in Indiana. Two 100-m transects were established within each forest stand during late April to early May in each year. One transect was placed parallel to and within 5 m of a south- or west-facing edge. The second transect was placed parallel to the first but at no less than 100 m from any edge. Nonnative earthworms and plants were found in forest edge and interior regardless of structural stage (second-growth vs. old-growth). The number of native plant species decreased linearly as the densities of adult *Lumbricus* and *Aporrectodea* earthworms and the percent cover of multiflora rose (an invasive plant species) increased. Densities of *L. terrestris* and *Aporrectodea* earthworms and percent cover of multiflora rose cumulatively explained 39% of the variation in the number of native plant species found in transects across the state. However, multivariate analyses suggested that the species composition of Indiana understory plant communities was affected more by geography than by earthworm densities. Our results suggest that nonnative earthworms and plants are ubiquitous in Indiana hardwood forests and that they may reduce the number of native plant species.

Nomenclature: Multiflora rose, *Rosa multiflora* Thunb. ex Murr. ROSMU; nightcrawler, *Lumbricus terrestris* L.

Key words: Edge effects, hardwood forest, invasion, *Lumbricus rubellus*, plant community, *Rosa multiflora*.

European earthworms (Family Lumbricidae) which are not native to eastern temperate and boreal forests in North America, have been linked to changes in forest soils and to declines in native plant diversity in invaded areas (Addison 2009). Nonnative earthworms can deplete organic horizons and forest floor litter, accelerate organic matter decomposition, and increase the availability of nutrients such as nitrogen and phosphorus (Bohlen et al. 2004a,b; Filley et al. 2008; Hale et al. 2005; Szlavecz et al. 2011). Nonnative earthworms also appear to reduce arbuscular mycorrhizal fungi (AMF) populations at invaded sites (Lawrence et al. 2003; Szlavecz et al. 2011). Because many native woody

and herbaceous forest species require AMF associations, researchers have speculated that nonnative earthworms might indirectly limit the growth of native plant species by limiting their ability to form AMF associations (Brundrett 2002; Frelich et al. 2006; Lawrence et al. 2003). Nitrogen availability has been positively correlated with plant invasions (Howard et al. 2004), and researchers have speculated that increased nitrogen (N) availability associated with earthworms might facilitate plant invasions and vice versa (Addison 2009; Heimpel et al. 2010). Population densities of introduced earthworms appear to be greater under several invasive plant species—Japanese barberry (*Berberis thunbergii* DC.), Japanese stiltgrass [*Microstegium vimineum* (Trin.) A. Camus], and common buckthorn (*Rhamnus cathartica* L.)—than under native plant species (Heneghan et al. 2007; Kourtev et al. 1998). Nuzzo et al. (2009) measured native vegetation and nonnative earthworm biomass in fifteen northeastern hardwood forests and found that earthworm biomass was positively associated with nonnative plant cover and negatively associated with native woody species, perennial and annual herbs, and ferns. The authors suggested that nonnative earthworms rather than nonnative plant species were the “driving force” behind reductions in native plant species in northeastern North American forests, and that earthworm invasions appear to facilitate the invasion of those forests by nonnative plant species.

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* Associate Professor, Department of Botany and Plant Pathology, Purdue University, 915 West State Street, West Lafayette, IN 47907; Graduate Student, Department of Forestry, University of Missouri, 203 Anheuser-Busch Natural Resources Building, Columbia, MO, 65211; Assistant Professor, Department of Botany and Plant Pathology and Department of Biology, Purdue University, 915 West State Street, West Lafayette, IN 47907; Associate Professor, Department of Forestry and Natural Resources, Purdue University, 715 West State Street, West Lafayette, IN 47907; Professor, Department of Agronomy, Purdue University, 915 West State Street, West Lafayette, IN 47907. Corresponding author's E-mail: kgibson@purdue.edu

Management Implications

European earthworms, which are not native to eastern temperate and boreal forests in North America, have been linked to changes in forest soils and to declines in native plant diversity in invaded areas. Earthworm densities appear to be greater under several invasive plant species and researchers have speculated that these earthworms might facilitate plant invasions and vice versa. We sampled six old- and second-growth pairs in Indiana for earthworms and understory plants in 2009 and 2010. The number of native plant species decreased as the densities of adult *Lumbricus* and *Aporrectodea* earthworms and the percent cover of multiflora rose (an invasive plant species) increased. We found little evidence that stand structure or distance from edge strongly affected earthworm distributions (with the possible exception of *L. rubellus*). It seems apparent from this study that nonnative earthworms and plants can establish in the interior of old-growth forest. Consequently, land managers should anticipate changes in nutrient availability, organic matter decomposition, and arbuscular mycorrhizal fungi populations that are associated with earthworms in hardwood forests irrespective of stand age. These changes, which constitute a substantial disturbance to North American hardwood forest ecosystems, seem likely to promote the further colonization of hardwood forests by nonnative plant species. It is unlikely that earthworm invasions can be prevented or reversed and in some areas, such as Indiana, the colonization of forests by introduced earthworms might be largely complete. This study highlights the importance of invasive plant management within the context of multiple plant and animal invaders.

Site invasibility has been linked to current and historical land-use, species diversity, disturbance, site size, and edge effects (Davies et al. 2007; McDonald and Urban 2006; Shea and Chesson 2002; Tanentzap et al. 2010; Vilà and Ibáñez 2011). Studies have found that the frequency and abundance of nonnative and invasive plant species are directly associated with the intensity of land use (Chytrý et al. 2008; Pyšek et al. 2010; Vilà and Ibáñez 2011). Highly fragmented forest sites that are surrounded by human activity, such as agriculture or recreation, are more prone to invasion by nonnative species along forest edges than large, continuous forests that are relatively free of human influence (Borgmann and Rodenwald 2005; Duguay et al. 2007; Guirado et al. 2006; McDonald et al. 2008; McKinney 2006). Fraver (1994) found that this edge effect could extend up to 50 m from south-facing edges and between 10 to 30 m from north-facing edges. Forest fragmentation in Indiana has contributed to the invasion of nonnative plant species along forest edges (Brothers and Spingarn 1992). Brothers and Spingarn (1992) found that nonnative species richness in old-growth forests was higher along forest edges than in interior transects, and that nonnative plant species showed a preference for south and west edges, which were warmer and drier, than for north and east edges.

Parker (1989) defined old-growth forests in the Central Hardwood Region of the United States as > 150 yr old

with little human disturbance in the previous 80 to 100 yr, an all-aged multilayered structure with large (80 to 160 cm [31.5 to 63.0 in] diameter at breast height [dbh]) canopy trees and a shade-tolerant understory. Old-growth stands typically have lower light availability at the forest floor outside of canopy gaps, greater woody debris, and can have lower plant species richness than younger forests (Hale et al. 1999; Scheller and Mladenoff 2002). Several researchers have attributed relatively low abundances of invasive plant species in old-growth forests to low light availability and have suggested that older stands might be less susceptible to invasion than younger stands (Brothers and Spingarn 1992; McCarthy et al. 2001; Mosher et al. 2009; Weber and Gibson 2007). However, few studies have directly compared invasive plant densities in old- and second-growth forests. Flory and Clay (2006) examined the effect of stand age and distance to roads on invasive shrubs in Indiana. Densities for four of the seven shrub species decreased with increasing distance from the nearest road and greater shrub densities were found in young and midsuccessional stands than in mature forest. Nonnative earthworms have been negatively associated with distance to roads (Hale et al. 2008; Holdsworth et al. 2007) but the effect of stand age and associated changes in forest structure on earthworm abundance is unclear. Filley et al. (2008) found that earthworm biomass and densities in Maryland forests, primarily influenced by *Lumbricus rubellus* Hoffmeister and *Octolasion lacteum* Orley, were four to five times greater in younger forests than in more mature sites. However, the effect of stand structure and distance from edge on earthworm densities has not been specifically addressed for forests in the midwestern United States.

In this paper we assess (1) the effect of forest structure and distance from forest edge on the abundance of exotic earthworms and introduced plants in Indiana forests and (2) examine relationships among earthworms and understory plant species in Indiana forests. We predicted that nonnative earthworms and invasive plants would be more abundant along forest edges and in second-growth forest stands than in the forest interior or in old-growth stands.

Methods

A complete randomized block design with stand pairs treated as blocks (six blocks total) and stand structure—old- and second-growth as defined by Parker (1989)—and distance to edge as the main factors was used. We sampled six old- and second-growth pairs in Indiana for a total of 12 hardwood stands (Figure 1). All of the old-growth stands meet the definition of old-growth forest suggested by Parker (1989); five of the stands are listed as old growth and designated as Nature Preserves by the Indiana Department of Natural Resources (IDNR). The sixth stand is located at the Davis Purdue Agricultural Center



Figure 1. Location of paired old- and second-growth forest stands sampled in Indiana during 2009 and 2010. The old-growth stand is listed first within each stand pair.

forest, which is owned and managed by Purdue University. We refer to this old-growth stand as “Davis” and the second-growth stand as “DPAC” throughout the paper. Indiana has relatively few old-growth stands (we sampled 5 of the 11 old-growth stands listed by Indiana as Nature Preserves and these stands are embedded in a highly fragmented agricultural landscape (IDNR; Spetich et al. 1997). The old-growth stands vary in size, shape, internal fragmentation due to paths and roads, and proximity to landscape features such as roads, agricultural fields, and other forests (Spetich et al. 1997). Second-growth stands were chosen based on proximity (less than 32 km [20 mi] between stand pairs), approximate age since last human disturbance (< 80 yr), and on land ownership. With the exception of the Davis Purdue Agricultural Center, the second-growth stands sampled in this project are dedicated Indiana State Parks. The State Parks sampled in this study were primarily established before 1950; the exception is Potato Creek State Park, which was formally designated as a State Park in 1969 (IDNR). Stand pairs (old- and second-growth, respectively) were located in northern (Bendix Woods and Potato Creek, McClue and Pokagon State Park), central (Davis and DPAC, Rocky Hollow and

Turkey Run) and southern (Donaldson’s Woods and Spring Mill, Dogwood and Versailles) Indiana. Personnel working for Indiana State Parks and Indiana Nature Preserves were consulted to ensure that transects were not placed in areas where invasive plants had been managed. Bendix Woods, Potato Creek, Davis, Rocky Hollow, and Turkey Run were sampled in 2009; the remaining stands were sampled in 2010. Two 100-m transects were established within each forest stand during late April to early May in each year. One transect was placed parallel to and within 5 m of a south- or west-facing edge. South- and west-facing edges in Indiana have higher light levels than north and east edges and favor colonization by nonnative plant species (Brothers and Spingarn 1992). The second transect was placed parallel to the first but at no less than 100 m from any edge.

Earthworm species can be placed into three main ecological groups: epigeic, anecic, and endogeic (Bouche 1977). Epigeic species are typically small, pigmented, and live and feed in the leaf litter and upper soil surface (Bouche 1977; Brown et al. 2000). Endogeic species are lightly pigmented or nonpigmented and live and feed in the mineral horizon, whereas anecic species such as

Lumbricus terrestris L. often form deep vertical burrows and incorporate surface litter into the soil (Brown et al. 2000). Although generally useful for characterizing earthworm ecology, not all species fit neatly into these categories. For example, *Lumbricus rubellus* has been characterized as an “epi-endogeic” species (Hale et al. 2005; Addison 2009). Although *Aporrectodea longa* Ude is typically considered an anecic species, Eisenhauer et al. (2008) suggested that the behavior of *A. longa* was more consistent with that of an endogeic species.

Earthworms were counted and percent cover of plant species recorded within 5-m-diam circular quadrats located at 10-m intervals along each transect (10 quadrats were sampled per transect). Two approaches were used to subsample worm densities within each quadrat. First, a pit (0.33 m by 0.33 m (0.1 m²) by 0.10 m deep) was excavated and the soil hand-sifted to capture earthworms. Second, a mustard solution (10.6 g [0.37 oz.] ground mustard seed L⁻¹ deionized water) was poured within a 0.1 m² quadrat placed at least 1 m from the excavated pit. The mustard solution irritates earthworms, causing them to surface soon after pouring on the solution (Hale 2007). Earthworms were anesthetized in isopropyl alcohol, preserved in formalin (neutral buffered, 10%), and transported to the lab for identification using Hale (2007). The mustard extract method was used to calculate densities for *L. terrestris* earthworms because this method accounted for 76% of all *L. terrestris* individuals collected. The digging method was used to calculate densities for *Lumbricus* juveniles and *L. rubellus* individuals because this method accounted for 96% of all *Lumbricus* juveniles and *L. rubellus* earthworms collected. Both methods were used to estimate densities for endogeic species. Endogeic species included *Allolobopha chlorotica* Savigny, *Octolasion cyaneum* Savigny, *O. trytaeum* Savigny, and species in the *Aporrectodea* genus. The *Aporrectodea* species are morphologically similar, variable in the field, and can be difficult to identify to species; thus, we present data and conducted analyses using the genus rather than individual species (Hale et al. 2006; Holdsworth et al. 2007). Transects were sampled for earthworms in spring (late April to early June) and fall (late September through October). Data were combined for spring and fall sampling; earthworms collected in the fall comprised 23% to 55% of all earthworms collected, depending on ecological class. Although earthworms were collected within the same 5-m circular area as in the spring, areas subsampled in the spring were not resampled in the fall. Soil temperature was measured with a soil thermometer before collecting worms; worms were only collected if soil temperatures were within a biologically active range of 10 to 20 C (50 to 68 F).

The understory vegetation was sampled in the spring within 24 h of collecting worms. Percent cover was estimated for herbaceous species and for tree seedlings/

saplings less than 1 m in height within 1-m² quadrats placed at 10-m intervals along each transect. Quadrats used for vegetation sampling were located within the 5-m-diam circular areas used to sample earthworms. The following cover classes were used: 0%, 1 to 5%, 6 to 25%, 26 to 50%, 51 to 75%, and 76 to 100% (Goldsmith et al. 1986). The midpoint for each cover class was used for data analyses. Plants were identified to species in the field when possible but occasionally specimens were collected and identified in the laboratory; in some cases identification could only be made to genus.

Species found on fewer than two transects were dropped from all analyses to reduce the noise effect of rare species (Peck 2010). This decreased the number of plant species included in the analyses from 120 to 86. Earthworm densities, percent plant cover, and species presence/absence were calculated from quadrat data for each transect ($n = 24$). The fit of residuals to normal distribution and homogeneity of residual variance were improved if necessary by square-root transformations of count data and arcsine of the square-root transformations for percent data. Means and standard errors presented were calculated from back-transformed data. A mixed model analysis of variance was used to analyze the effect of stand structure and distance from edge on earthworm densities and the number of native and introduced species. Blocks were treated as a random effect, and stand structure, distance to edge, and their interaction were treated as fixed effects. ANOVA and regression analyses were conducted with the SAS 9.1.3 software package (SAS Institute Inc., Cary, NC).

A combination of simple and multiple linear regression analyses were used to examine relationships between introduced species—earthworm densities and percent cover for garlic mustard [*Alliaria petiolata* (M. Bieb.) Cavara and Grande] and multiflora rose (*Rosa multiflora* Thunb. ex Murr.) and the number and percent cover of introduced, native, and total plant species. Garlic mustard and multiflora rose were included as independent variables in the analyses because they were the only plant species found on more than two transects that are considered invasive in Indiana (INPAWS 2003). Optimal subsets of independent variables were obtained by using the SELECTION=ADJRSQ (adjusted r -square) option in PROC REG in SAS (Freund and Littell 2000). The Akaike Information Criterion was then used to select among models (models with the smallest values were chosen) and variance inflation factors (VIF) were examined to detect multicollinearity (Freund and Littell 2000). Influential data points were identified using the DFFITS option for both simple and multiple regression models; values greater than 1 were considered influential (Neter et al. 1990).

We used agglomerative cluster analysis in Version 6 of the PC-ORD software (MjM Software, Gleneden Beach, OR,) with the group average method and Sorenson's

Table 1. Effects of stand age and transect location on European earthworm frequencies and densities in Indiana old- and second-growth forests. Values are means; parentheses enclose standard errors. Means with the same letter were not significantly different ($P < 0.05$) between old- and second-growth stands or between edge and interior transects, according to analyses of variance.

	Stand age		Transect location	
	Old-growth	Second-growth	Edge	Interior
Frequency of occurrence (%)				
<i>Lumbricus</i> juveniles	83 (11.2)a	100 (0.0)a	83 (11.2)a	100 (0.0)a
<i>L. rubellus</i>	42 (14.8)b	75 (13.0)a	58 (14.9)a	58 (14.9)a
<i>L. terrestris</i>	50 (15.1)a	67 (14.2)a	58 (14.9)a	58 (14.9)a
<i>Aporrectodea</i> juveniles	83 (11.2)a	92 (8.3)a	92 (8.3)a	83 (11.2)a
<i>Aporrectodea</i> adults	67 (14.2)a	67 (14.2)a	67 (14.2)a	67 (14.2)a
Endogeic ^a earthworms	83 (11.2)a	92 (8.3)a	83 (11.2)a	92 (8.3)a
Total earthworms	92 (8.3)a	100 (0.0)a	92 (8.3)a	100 (0.0)a
Density (individuals m ⁻²)				
<i>Lumbricus</i> juveniles	37 (13.7)a	45 (15.3)a	36 (11.4)a	45 (17.1)a
<i>L. rubellus</i>	2 (0.9)b	8 (3.4)a	5 (2.3)a	5 (2.9)a
<i>L. terrestris</i>	3 (1.0)a	2 (0.6)a	3 (0.8)a	2 (0.9)a
<i>Aporrectodea</i> juveniles	14 (4.6)a	21 (6.5)a	18 (4.5)a	17 (6.7)
<i>Aporrectodea</i> adults	7 (3.5)a	9 (3.7)a	7 (2.9)a	8 (4.3)
Endogeic earthworms	7 (2.9)a	7 (1.8)a	10 (2.9)a	3 (1.0)b
Total earthworms	68 (19.6)a	91 (28.4)a	80 (18.1)a	80 (29.8)a

^a *Octolasion* and *Allobophoa* species.

distance measure to identify groups of transects with similar plant species based on percent cover (McCune and Grace 2002). Species indicator analysis was then used in PC-ORD to calculate indicator values for groups identified in cluster analysis for all plant species based on percent cover. The indicator value is a synthetic measure of the specificity and fidelity of a species to a particular group (Peck 2010). Nonmetric multidimensional scaling (NMS) was used to assess the plant community in relation to earthworm densities in PC-ORD. NMS is a type of ordination that uses an iterative technique to move objects in ordination space based on rank orders of their similarities (distances) to minimize stress (McCune and Grace 2002). Stress is a measure of the departure from the distances among objects in the original many-dimensional space and distance in the reduced-dimensional space (McCune and Grace 2002). Data were placed into main and secondary matrices. The main matrix contained presence/absence data or percent cover for each plant species. The secondary matrix contained earthworm densities. The preliminary ordination was performed using the autopilot mode with 250 runs with real data and 250 runs with randomized data (Peck 2010). A Sorenson distance measure was used and a Monte Carlo test of significance conducted to identify an optimal number of ordination dimensions based on the lowest stress achievable with the fewest number of dimensions (Peck 2010). A three dimensional solution was recommended and a series

of NMS analyses, each with 250 runs with real data constrained to three-dimensional solutions, were conducted (Peck 2010). Pearson's correlation and Kendall's tau coefficients were calculated to assess relationships between the main and secondary matrices and ordination axes. Pearson correlation coefficients provide a measure of the linear relationship between two variables, whereas Kendall's tau is nonparametric and can be more robust when relationships are not linear. Once a final NMS solution was chosen, joint plots were overlaid and significant earthworm effects ($R^2 \geq 0.30$) were superimposed as vectors in the resulting ordination (Hale et al. 2006; Peck 2010). Vector length and direction indicate the strength and direction of relationships with environmental axes.

Results and Discussion

Nonnative earthworms were found on all 24 transects, spanning edge and interior habitats and old- and second-growth stands (Table 1). *Lumbricus rubellus* individuals were found less frequently and at lower densities in old- than in second-growth stands and more endogeic earthworms (*Octolasion* and *Allobophoa* species) were found in edge than in interior stands (Table 1). *Lumbricus rubellus* has been implicated in extirpation of the rare fern *Botrychium mormo* W. H. Wagner in the Chippewa National Forest (Gundale 2002) and associated with major changes in plant communities in Minnesota (Hale et al.

Table 2. Effects of stand age and transect location on the number of plant species and plant percent cover in Indiana old- and second-growth forests. Values are means; parentheses enclose standard errors. Means with the same letter were not significantly different ($P < 0.05$) between old- and second-growth stands or between edge and interior transects, according to analyses of variance.

	Stand age		Transect location	
	Old-growth	Second-growth	Edge	Interior
Percent cover (%)				
Nonnative plants	10.6 (3.3)a	14.8 (4.0)a	14.2 (4.2)a	11.3 (6.7)a
Native plants	55.6 (4.7)a	54.0 (4.7)a	54.4 (4.9)a	55.2 (4.4)a
Total plants	66.2 (5.6)a	68.9 (3.4)a	68.5 (5.1)a	66.5 (4.1)a
Number of plant species transect ⁻¹				
Nonnative plants	3.0 (0.5)a	4.3 (0.6)a	4.0 (0.6)a	3.3 (0.4)a
Native plants	19.3 (1.7)a	18.4 (1.4)a	18.8 (1.6)a	18.9 (1.5)a
Total plants	22.3 (2.0)a	22.7 (1.1)a	22.8 (1.6)a	22.2 (1.6)a

2006). *Lumbricus rubellus* can substantially reduce or even eliminate forest floor horizons and facilitate site colonization by *L. terrestris* (Frelich et al. 2006; Suarez et al. 2006). No other differences were detected for stand age or transect location among the remaining earthworm groups.

Lumbricus and *Aporrectodea* juveniles accounted for more than half of all earthworms collected. Total earthworm densities averaged between 68 and 91 earthworms m^{-2} (Table 1). Similar earthworm densities (< 200 individuals m^{-2}) have been reported for nonnative earthworms in conventionally managed agricultural fields in Indiana (Kladivko et al. 1997), for nonnative earthworms in heavily invaded areas within south central New York (Suarez et al. 2006), and for native earthworms in eastern Kentucky (Kalisz and Dotson 1989). However, our densities were considerably lower than those reported for introduced earthworms in Canadian forests during early stages of invasion (Addison 2009). For example, Dymond et al. (1997) reported densities up to 2,500 individuals m^{-2} for an epigeic species, *Dendrobaena octaedra* Savigny, in forests in Alberta, Canada. In contrast, only 14 epigeic earthworms, all from the genus *Eisenia*, were collected from all 24 transects in our study. Earthworm invasions typically follow a pattern in which epigeic worms arrive first at a site and are followed by endogeic and anecic species (Addison 2009; Suarez et al. 2006). Eisenhauer et al. (2007) suggested that epigeic earthworm populations might peak early in the invasion process and decline as anecic and endogeic earthworms arrive and consume the resources required by epigeic earthworms. The near absence of epigeic earthworms and the ubiquity of endogeic and anecic species in sampled areas suggest that Indiana forests are in the later stages of earthworm invasion.

Stand age and transect location did not affect percent cover or the number of native plant species (Table 2). Species richness in our stands (22 to 23 plant species, depending on stand age and location) was similar to that

reported by Jenkins and Parker (1999) who sampled ground-layer vegetation in southern Indiana forests and found 27 plant species in the older stands (> 80 yr old). Nonnative plant species were found on all transects, and stand age and transect location did not affect the percent cover or number of nonnative plant species (Table 2). Thirty-two nonnative plant species were detected; however, a third of these species were present on only one transect and averaged less than 2% cover (Table 3). Most of the nonnative species are considered common weeds in agricultural fields, pastures, or roadsides (Bryson and DeFelice 2010). Only five of the nonnative plant species—common periwinkle (*Vinca minor* L.), garlic mustard, Amur honeysuckle [*Lonicera maackii* (Rupr.) Herder], multiflora rose, and tree-of-heaven [*Ailanthus altissima* (Mill.) Swingle]—are considered invasive in Indiana forests (INPAWS 2003). Garlic mustard and multiflora rose were the only invasive plant species found on more than two transects (Table 3). Multiflora rose and garlic mustard are widely distributed in Indiana forests and are able to establish in forest interiors (Brothers and Spingarn 1992; Flory and Clay 2006; Weber and Gibson 2007). Percent cover was less than 9% for individual nonnative plant species and less than 2% for more than half of the introduced species (Table 3).

No significant relationship was detected between earthworm densities and the percent cover of introduced or native plant species (data not shown). However, the number of native plant species decreased linearly with adult *Aporrectodea*, *L. rubellus*, and *L. terrestris* densities and the total number of plant species decreased linearly with adult *Aporrectodea* and *L. terrestris* densities (Figure 2). It should be noted that the regression of native plant species and *L. rubellus* was influenced ($DFFITS > 1$) by the transects at Potato Creek State Park which had high *L. rubellus* densities (Figure 2). The relationship between *L. rubellus* and native plant species was not statistically significant

Table 3. Presence and cover of nonnative plant species in Indiana old- and second-growth forests. Presence is the number of transects on which the species was found. Values for percent cover are the average for transects on which the species was found. Parentheses enclose standard errors.

Species	Habit	Presence	Percent cover
<i>Alliaria petiolata</i> (M. Bieb.) Cavara and Grande	Biennial	14	4.5 (1.40)
<i>Rosa multiflora</i> Thunb. ex Murr.	Woody	13	6.8 (1.66)
<i>Polygonum persicaria</i> L.	Annual	11	2.5 (1.95)
<i>Daucus carota</i> L.	Biennial	6	1.3 (0.23)
<i>Dactylis glomerata</i> L.	Perennial	5	3.6 (1.27)
<i>Rumex crispus</i> L.	Perennial	4	1.5 (0.83)
<i>Setaria faberi</i> Herrm.	Annual	4	2.9 (1.90)
<i>Taraxacum officinale</i> G. H. Webber ex Wiggers	Perennial	4	0.3 (0.00)
<i>Barbarea vulgaris</i> W. T. Aiton	Biennial	3	0.6 (0.00)
<i>Elytrigia repens</i> (L.) Desv. ex B. D. Jackson	Perennial	3	0.8 (0.38)
<i>Ailanthus altissima</i> (P. Mill.) Swingle	Woody	2	2.2 (1.90)
<i>Convolvulus arvensis</i> L.	Perennial	2	1.6 (0.00)
<i>Conyza canadensis</i> (L.) Cronq.	Annual	2	5.9 (4.08)
<i>Echinochloa crus-galli</i> (L.) P. Beauv.	Annual	2	1.2 (0.93)
<i>Lactuca serriola</i> L.	Annual	2	2.5 (0.92)
<i>Lamium amplexicaule</i> L.	Annual	2	0.5 (0.15)
<i>Lonicera maackii</i> (Rupr.) Herder	Woody	2	8.6 (7.07)
<i>Mollugo verticillata</i> L.	Annual	2	7.7 (2.00)
<i>Ranunculus repens</i> L.	Perennial	2	2.5 (2.18)
<i>Vinca minor</i> L.	Perennial	2	6.0 (5.68)
<i>Avena fatua</i> L.	Annual	1	6.9 (0.00)
<i>Digitaria sanguinalis</i> (L.) Scop.	Annual	1	1.6 (0.00)
<i>Festuca</i> spp.	Perennial	1	0.3 (0.00)
<i>Ipomoea hederifolia</i> L.	Annual	1	1.6 (0.00)
<i>Lamium purpureum</i> L.	Annual	1	0.3 (0.00)
<i>Leonurus cardiaca</i> L.	Perennial	1	0.3 (0.00)
<i>Leucanthemum vulgare</i> Lam.	Perennial	1	0.3 (0.00)
<i>Plantago lanceolata</i> L.	Annual	1	1.6 (0.00)
<i>Setaria viridis</i> (L.) P. Beauv.	Annual	1	0.3 (0.00)
<i>Stellaria media</i> (L.) Vill.	Annual	1	1.6 (0.00)
<i>Verbascum thapsus</i> L.	Biennial	1	1.6 (0.00)
<i>Veronica officinalis</i> L.	Perennial	1	0.3 (0.00)

when the Potato Creek transects were removed from the regression. Potato Creek State Park is the most recently created of the state parks included in this study and contains a 132-ha (327-ac) man-made lake. Earthworms are used as bait for fishing and can be introduced to an area if disposed of improperly (Addison 2009; Hale 2008). Thus the presence of a lake might explain the relatively high densities of *L. rubellus* at Potato Creek State Park. No significant relationships between endogeic or juvenile *Lumbricus* or *Aporrectodea* densities and the number of plant species were detected (data not shown).

The number of native plant species was not affected by garlic mustard percent cover. Multiflora rose percent cover explained 16% of the variation ($P = 0.05$) in the number of native plant species (Figure 3). The regression of native plant species richness and multiflora rose percent cover was

not affected by influential points ($DFFITs < 1$). Multiflora rose is a shrub native to eastern Asia but now is reported as invasive in over 30 states, including Indiana. Yurkonis et al. (2005) reported that multiflora rose reduced plant species richness, but Banasiak and Meiners (2009) found evidence for both positive and negative correlations with associated species during a 40-yr study of abandoned agricultural fields in the Piedmont region of New Jersey. Banasiak and Meiners (2009) suggested that the major influence on multiflora rose population dynamics during late succession was reduced light availability associated with forest canopy cover. However, Ashton et al. (2005) reported accelerated decomposition and N turnover rates in forested areas with invasive plants, including multiflora rose.

A greater percentage of the variation in the number of native plant species was explained by multiple regression

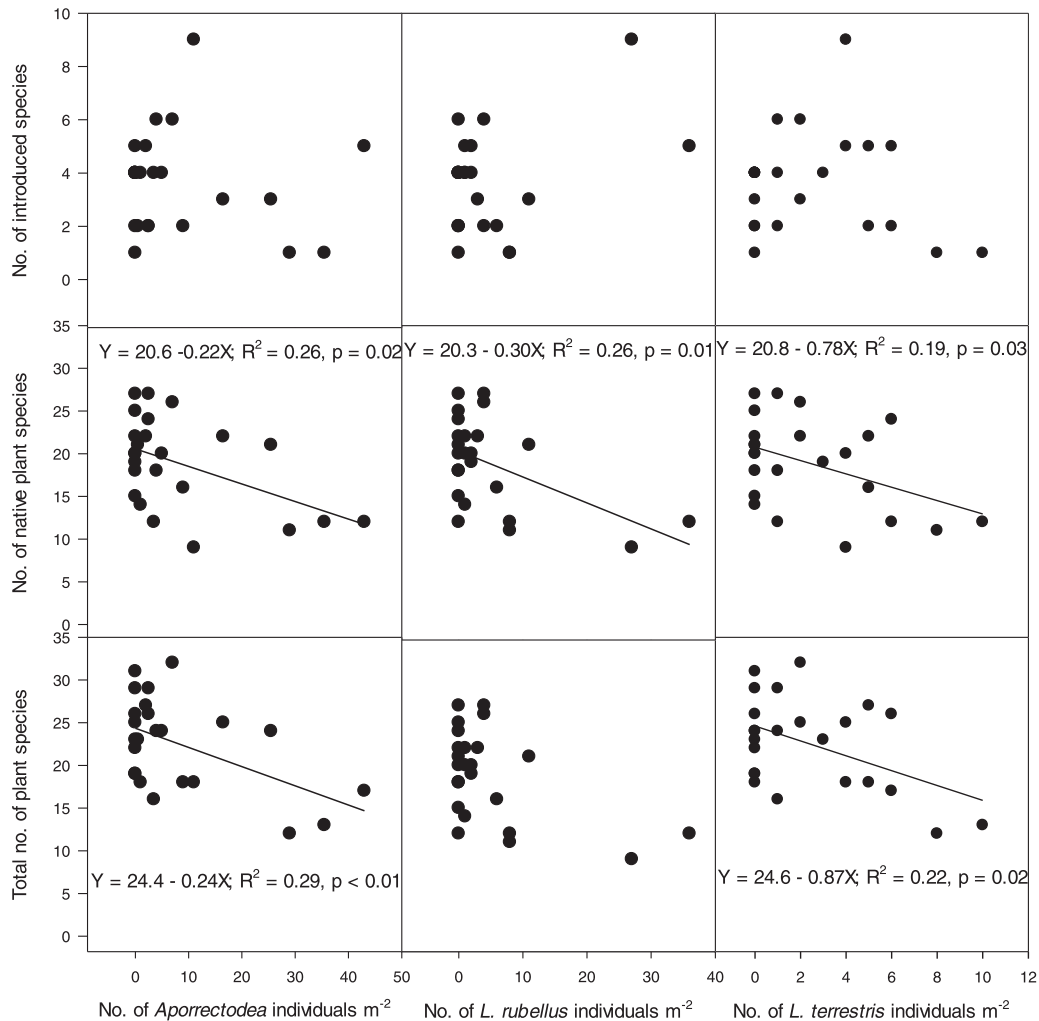


Figure 2. Relationships between adult *Lumbricus* and *Aporrectodea* densities and the number of introduced, native, and total plant species in old- and second-growth forests in Indiana. Values represent transect means.

models that included multiflora rose percent cover and *L. terrestris* or the *Aporrectodea* densities than by simple regressions (Table 4). When multiflora rose and both *Lumbricus* species were included in a model, they cumulatively explained 39% of the variation in the number of native plant species. Multiflora rose percent cover and *Aporrectodea* densities explained 33% of the variation in the total number of plant species (Table 4). Multiple regression models did not explain more of the variation in the number of introduced plant species than simple models (data not shown). Variance inflation factors were less than 3 and DFFITS were no greater than 1 for all presented multiple regression models. Our results support the hypothesis that nonnative earthworms affect native plant species richness, but suggest that including both nonnative earthworms and nonnative plant species can more fully explain native plant species richness in Indiana hardwood forests.

Cluster analysis was used to objectively identify groups of similar transects. The resulting dendrogram was pruned

to four groups with 20.1% of information remaining (Figure 4). Transects from northern and central Indiana, with the exception of the transects at the DPAC site and the Bendix Woods : Potato Creek pair, were placed into a single group, and the southern transects and the transects at DPAC were grouped together (Figure 4). The Bendix Woods : Potato Creek pair was split into two groups (Figure 4). Introduced plant species characterized the Potato Creek site (Table 5) according to indicator species analysis, further supporting the positive association of *L. rubellus* with nonnative plant species. White trillium [*Trillium grandiflorum* (Michx.) Salisb.] and wild ginger (*Asarum canadense* L.) were indicator species for Bendix Woods (Table 5). *Trillium* species and wild ginger were found as part of a diverse community of herbaceous plants in Minnesota hardwood forests in the absence of *L. rubellus* (Hale et al. 2006). The authors reported a reduction in the presence of these species where *L. rubellus* biomass was greatest (Hale et al. 2006).

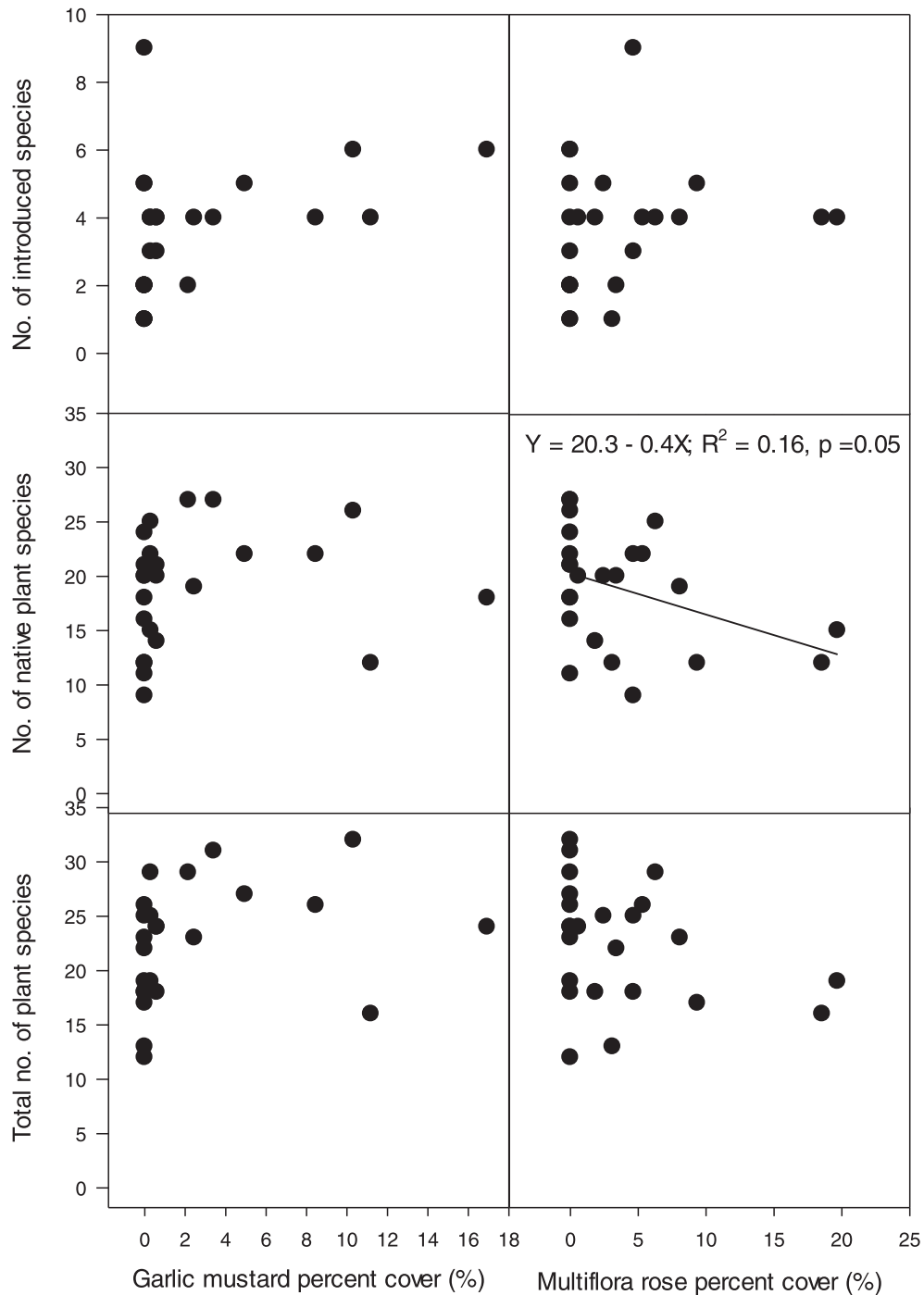


Figure 3. Relationship between the percent cover of two introduced plant species—multiflora rose and garlic mustard—and the number of introduced, native, and total plant species in old- and second-growth forests in Indiana. Values represent transect means.

NMS ordination of plant species percent cover data resulted in a three-dimensional solution with a final stress of 13.7 and instability < 0.0001. The cumulative R^2 value for the three dimensional solution was 0.79 with R^2 values of 0.36, 0.34, and 0.09 for axes one, two, and three, respectively. The first axis represents a shift in understory plant communities from southern Indiana to northern and

central Indiana (Figure 5) and therefore supports the clustering of transects in these areas into distinct groups (Figure 4). The location of Bendix Woods along the second axis supports the cluster analysis and suggests that the plant community at Bendix Woods differs from plant communities at the other sites (Figure 5). Correlations between earthworm densities and the axes were below the

Table 4. Relationships between the number of plant species and earthworm densities and invasive plant percent cover.^a Parentheses enclose standard errors for the intercept and regression coefficients.

Y ^b	Intercept	Regression coefficient			Standardized regression coefficient			Adj. R ²	P value
		Multiflora rose ^c	<i>L. terrestris</i>	<i>A. longa</i>	Multiflora rose	<i>L. terrestris</i>	<i>A. longa</i>		
Native	23.14 (1.38)	-15.52 (5.84)	-0.44 (0.39)	-0.15 (0.09)	-0.44	-0.25	-0.34	0.39	< 0.01
		Multiflora rose		<i>A. longa</i>	Multiflora rose		<i>A. longa</i>		
Total	25.83 (1.34)	-11.51 (6.21)		-0.23 (0.07)	-0.32		0.53	0.33	< 0.01

^a Independent variables were percent cover for invasive plants (garlic mustard and multiflora rose) and density (individuals m⁻²) for earthworms. Models with the lowest Akaike's Information Criterion values are presented.

^b The number of plant species and plant percent cover was modeled. Significant (P ≤ 0.05) relationships between the independent variables and native, introduced, or total percent cover were not detected. Significant relationships between the independent variables and the number of introduced species were not detected.

^c Data for multiflora rose were arcsine square-root transformed.

cutoff ($R^2 \geq 0.30$) for the percent cover ordination. NMS ordination of plant species presence/absence data (not shown) resulted in a similar three-dimensional ordination (final stress of 13.9, instability < 0.0001, and cumulative $R^2 = 0.77$). *Lumbricus rubellus* densities were correlated with the first axis in the presence/absence ordination, but only when the Potato Creek transects were included in the analysis (data not shown). This suggests that the ordination of these transects based on both plant percent cover and plant species presence/absence primarily reflects geography rather than the influence of earthworms. Potential explanations for differences in plant communities among

north/central and southern Indiana sites include climatic differences and differences in soil substrate. The north/central sites are located on glaciated soils and the southern sites are on unglaciated soils.

Considerable evidence exists that introduced earthworms are altering plant communities and reengineering soil structures and processes in hardwood forests in the United States and Canada (Addison 2009; Heimpel et al. 2010; Szlavecz et al. 2011). Several studies have evaluated the effect of earthworms along invasion fronts and found marked differences in plant communities between invaded and uninvaded areas (Hale et al. 2005; Nuzzo et al. 2009).

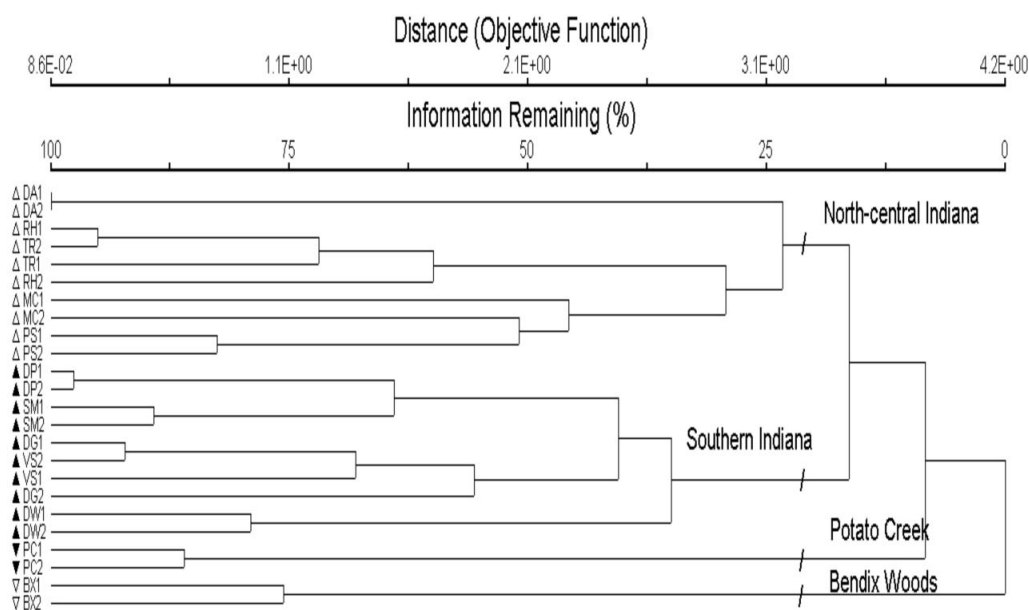


Figure 4. Cluster analysis of transects based on percent cover of plant species. Two-letter codes represent forest stands and numbers at the end of each code indicate the location of transects relative to the forest edge (1 = edge and 2 = interior). The dendrogram was pruned to four groups with 20.1% of information remaining.

Table 5. Indicator species for groups identified by cluster analysis.

Species	Common name	Life history	Group ¹	Observed indicator value	P value
<i>Geranium maculatum</i> L.	Wild geranium	Native perennial herb	1	68.3	> 0.01
<i>Galium aparine</i> L.	Sticky bedstraw	Native annual herb	1	56.0	0.02
<i>Vitis</i> spp.	Wild grape	Native perennial vine	2	79.4	> 0.01
<i>Ailanthus altissima</i> (P. Mill.) Swingle	Tree of heaven	Introduced tree	2	100	> 0.01
<i>Conyza canadensis</i> (L.) Cronq.	Marestail	Introduced annual	2	100	> 0.01
<i>Lonicera maaackii</i> (Rupr.) Herder	Amur honeysuckle	Introduced perennial shrub	2	100	> 0.01
<i>Taraxacum officinale</i> G. H. Weber ex Wiggers	Dandelion	Introduced perennial herb	2	83.3	0.04
<i>Rubus</i> spp.	Wild raspberry	Native perennial herb	2	77.8	0.02
<i>Claytonia virginica</i> L.	Spring beauty	Native perennial herb	3	80.0	> 0.01
<i>Cardamine concatenata</i> (Michx.) Sw.	Cutleaf toothwort	Native perennial herb	3	94.7	> 0.01
<i>Geum canadense</i> Jacq.	Yellow avens	Native perennial herb	3	90	> 0.01
<i>Asarum canadense</i> L.	Wild ginger	Native perennial herb	4	82.5	0.02
<i>Hydrophyllum virginianum</i> L.	Virginia waterleaf	Native perennial herb	4	86.2	> 0.01
<i>Maianthemum racemosum</i> (L.) Link	False Solomon's seal	Native perennial herb	4	86.7	> 0.01
<i>Trillium grandiflorum</i> (Michx.) Salisb.	White trillium	Native perennial herb	4	94.0	> 0.01

^a Groups identified by cluster analyses where 1 = all transects in northern and central Indiana except the DPAC transects, 2 = Potato Creek, 3 = all transects in southern Indiana and the DPAC transects, and 4 = Bendix Woods.

We did not sample near invasion fronts; with the possible exception of epigeic earthworms, European earthworms were ubiquitous in Indiana forests. Thus it is perhaps not surprising that earthworms did not appear to strongly affect the species composition of plant communities in Indiana forests.

We found little evidence that stand structure or distance from edge strongly affected earthworm distributions (with the possible exception of *L. rubellus*). However, we did not sample within young stands (< 30 yr) and it is possible that differences in earthworm densities would have been detected if younger stands had been included in our study. We did not attempt to exhaustively sample plant species at the sites and cannot comment on potential effects of earthworms on rare plant species, although other studies have suggested that rare plants might be at risk from earthworms (Gundale 2002). It should also be noted that we did not attempt to characterize sites from a landscape perspective, i.e., we did not include factors such as distance to nearest neighboring forest, road, cropland, urban area, etc., which might have influenced plant communities in our edge and interior transects. With that caveat, it seems apparent from this study and others that nonnative earthworms and plants can establish in the interior of old-growth forest.

Efforts to prevent the introduction of earthworms into new areas might delay their spread, but it is likely that most hardwood forests in Canada and the northern United States will be colonized by nonnative earthworms. In some

areas, e.g., Indiana, the colonization of hardwood forests by introduced earthworms might be largely complete. Our research suggests that European earthworms can colonize forest interior in both old-growth and younger forests. Consequently, land managers should anticipate increases in nutrient availability and organic matter decomposition accompanied by reductions in leaf litter depth, AMF populations, and O horizon thickness that are associated with earthworms in hardwood forests irrespective of stand age and structural development. These changes, which constitute a substantial disturbance to North American hardwood forest ecosystems, seem likely to promote the further colonization of hardwood forests by nonnative plant species. Our research suggests that a substantial percentage of the variation in the number of native understory plant species observed across sites in our study could be explained by variability in earthworm densities and percent multiflora rose cover. If additional nonnative plant species, particularly those that can increase earthworm densities (Heneghan et al. 2007; Kourtev et al. 2002), invade these sites, then it seems reasonable to believe that native plant diversity would be even further affected by introduced species.

The long-term response of eastern deciduous forests to introduced earthworms is unclear; given sufficient time it is possible that native plant forest species might adapt to their new environment. However, the effect of European earthworms on eastern forests in North America should be viewed in context of multiple invaders that include the

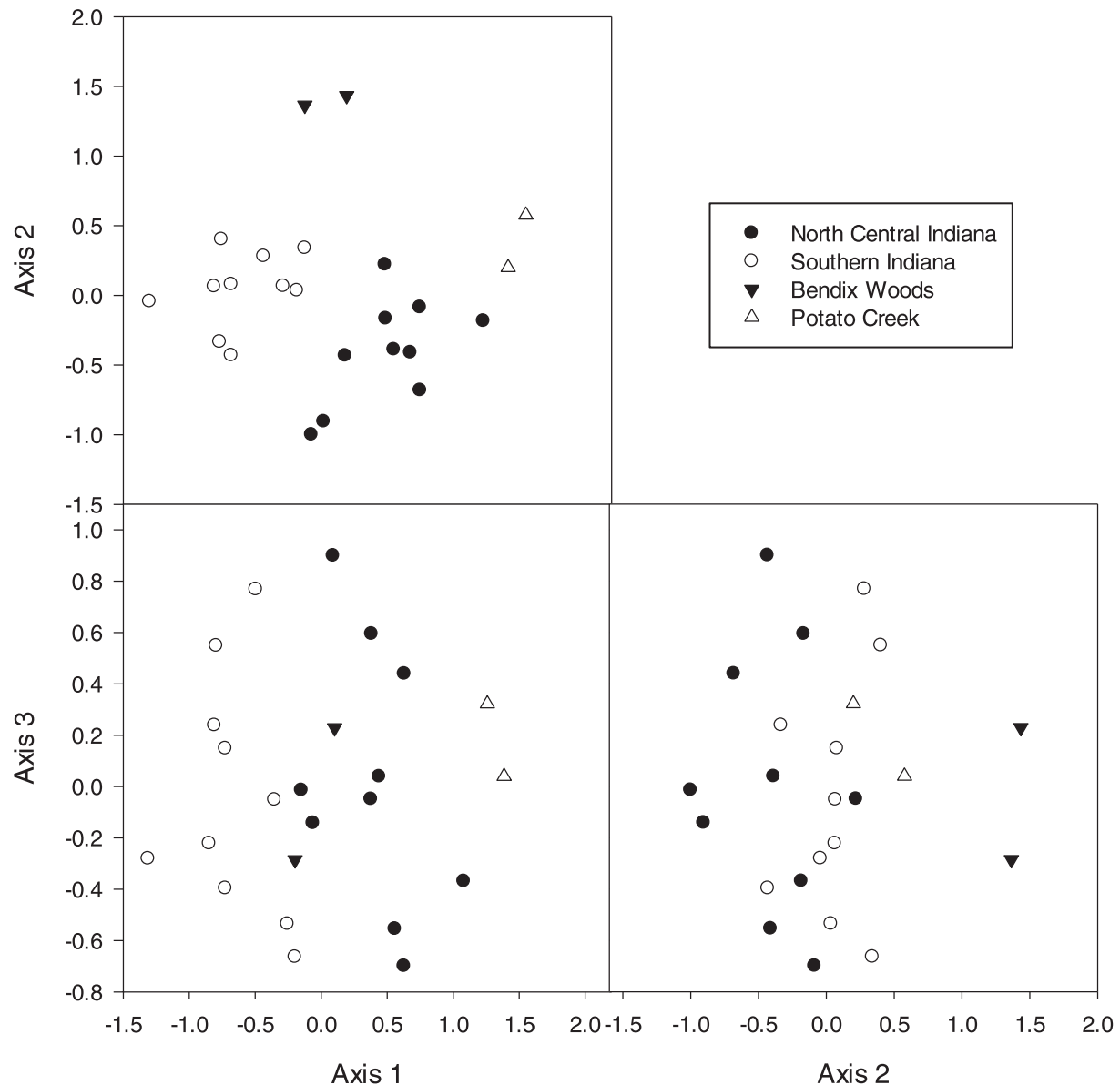


Figure 5. Nonmetric multidimensional scaling ordination of transects ($n = 24$) based on plant species percent cover data. A three-dimensional solution with a final stress of 13.7 and instability < 0.0001 is presented in two dimensions. Symbols indicating group membership correspond to transect groups identified through cluster analysis. A joint plot overlay of earthworm densities is not presented because the earthworm vectors did not meet cutoff values ($R^2 > 0.30$).

gypsy moth (*Lymantria dispar* L.), beech scale (*Cryptococcus fagisuga* Lind.), the hemlock woolly adelgid (*Adelges tsugae* Annand), emerald ash borer (*Agrilus planipennis* Fairmaire), the Asian longhorned beetle (*Anoplophora glabripennis* Mostschulsky), Dutch elm disease (*Ophiostoma ulmi*), and other invasive insects and diseases that have the potential to reshape forest communities (Eschtruth et al. 2008; Gandhi and Herms 2010; Lovett et al. 2006). The cumulative impact of multiple plant, animal, and pathogen invasions is unknown but might overwhelm the ability of native plant communities to adapt to any single invader.

Manipulative field experiments to assess the cumulative impact of multiple invaders and to more fully characterize interactions among invaders are needed.

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