Effects of Earthworm Invasion on Plant Species Richness in Northern Hardwood Forests

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Abstract: *The invasion of non-native earthworms (*Lumbricus *spp.) into a small number of intensively studied stands of northern hardwood forest has been linked to declines in plant diversity and the local extirpation of one threatened species. It is unknown, however, whether these changes have occurred across larger regions of hardwood forests, which plant species are most vulnerable, or with which earthworm species such changes are associated most closely. To address these issues we conducted a regional survey in the Chippewa and Chequamegon national forests in Minnesota and Wisconsin (U.S.A.), respectively. We sampled earthworms, soils, and vegetation, examined deer browse in 20 mature, sugar-maple-dominated forest stands in each national forest, and analyzed the relationship between invasive earthworms and vascular plant species richness and composition. Invasion by* Lumbricus *was a strong indicator of reduced plant richness in both national forests. The mass of* Lumbricus *juveniles was significantly and negatively related to plant-species richness in both forests. In addition,* Lumbricus *was a significant factor affecting plant richness in a full model that included multiple variables. In the Chequamegon National Forest earthworm mass was associated with higher sedge cover and lower cover of sugar maple seedlings and several forb species. The trends were similar but not as pronounced in Chippewa, perhaps due to lower deer densities and different earthworm species composition. Our results provide regional evidence that invasion by* Lumbricus *species may be an important mechanism in reduced plant-species richness and changes in plant communities in mature forests dominated by sugar maples.*

Keywords: deer herbivory, earthworm invasion, herbaceous layer, invasive species, Lumbricidae, northern hardwood forests, plant-species richness, regional survey

Efectos de la Invasión de Lombrices de Tierra sobre la Riqueza de Especies de Plantas en Bosques Deciduos del Norte

Resumen: *La invasión de lombrices de tierra (*Lumbricus *spp.) no nativas en un pequeño número de sitios estudiados intensivamente en bosques deciduos del norte ha sido relacionada con declinaciones en la diversidad de plantas y con la extirpación local de una especie amenazada. Sin embargo, se desconoce si estos cambios han ocurrido en regiones más extensas de bosques deciduos, cuales especies de plantas son más vulnerables o con cual especie de lombriz de tierra se asocian más estrechamente los cambios. Para abordar estos temas, realizamos un muestreo regional en los bosques nacionales Chippewa y Chequamegon en Minnesota y Wisconsin (E.U.A.), respectivamente. Muestreamos lombrices de tierra, suelos y vegetación, examinamos el ramoneo de venados en 20 sitios dominados por arce en cada bosque nacional, y analizamos la relación entre lombrices invasoras y la riqueza y composición de especies de plantas vasculares. La invasión por* Lumbricus *fue un indicador robusto de una reducción en la riqueza de especies de plantas en ambos bosques nacionales. La masa de* Lumbricus *juveniles se correlacionó significativa y negativamente con la riqueza de especies de plantas en ambos bosques. Adicionalmente,* Lumbricus *fue un factor que afectó significativamente la riqueza*

de especies en un modelo total que incluyó múltiples variables. En el Bosque Nacional Chequamegon, la masa de lombrices se asoció con una mayor cobertura de juncia y una menor cobertura de plántulas de arce y varias especies de hierbas. Las tendencias fueron similares, pero no tan pronunciadas en Chippewa, probablemente debido a menores densidades de venado y una composición de especies de lombrices diferente. Nuestros resultados proporcionan evidencia regional de que la invasión por especies de Lumbricus *puede ser un mecanismo importante en la reducción de la riqueza de especies de plantas y en los cambios en comunidades de plantas en bosques maduros dominados por arces.*

Palabras Clave: bosques boreales del norte, especies invasoras, estrato herbáceo, herbivoría de venados, invasión de lombriz de tierra, Lumbricidae, muestreo regional, riqueza de especies de plantas

Introduction

Predicting which invasive species will have significant impacts on native biodiversity and ecosystem function is an important area of inquiry (Vitousek 1990; Byers et al. 2002). The scope of the effects of invasive species varies with species, from population- and community-level to ecosystem-level effects. Ecosystem effects can include alteration of nutrient cycling, altered trophic structure, and altered disturbance regimes (Vitousek 1990). In general, invasive species that are ecosystem engineers (sensu Jones et al. 1994) have the potential to transform entire ecosystems and their associated communities.

Earthworms are ecosystem engineers that are invading regions with native species of earthworms and regions previously devoid of earthworms (Bohlen et al. 2004; James & Hendrix 2004). In the northern portion of the temperate eastern deciduous forest biome of North America postglacial colonization by North American earthworm taxa has not occurred (Hendrix & Bohlen 2002). These deciduous, and especially maple (*Acer*)-dominated, forests have experienced greater intensity of European earthworm invasion than other cold-temperate forests (Tiunov et al. 2006), likely because of the strong affinity of these earthworms for the calcium-rich litter of maple and other deciduous tree species (Ponge et al. 1999; Reich et al. 2005). The majority of the plant diversity of this biome is in the herbaceous layer, and all species spend at least part of their lives in this layer (Gilliam & Roberts 2003). In the absence of earthworms the plants of this layer are rooted in the well-developed organic horizon that constitutes the forest floor (Hale et al. 2006). Declines in native plant species have been attributed to many drivers, including land-use change (Flinn & Vellend 2005), logging (Gilliam & Roberts 2003), and overabundant deer populations (Augustine & Frelich 1998; Côté et al. 2004). There has been an average 18.5% decline in the density of native species over the past 50 years (Rooney et al. 2004). The well-documented overabundance of white-tailed deer (*Odocoileus virginianus* Boddaert) is an important driver of this change (Rooney et al. 2004). We argue that earthworm invasion may also play a role. The extensive yet incomplete nature of the European earthworm invasion (Gundale et al. 2005; Holdsworth et al. 2007) offers a good opportunity to study its ecological effects.

Results of intensive stand-scale studies of earthworm invasions in the western Great Lakes region (U.S.A.) link local extirpation of one rare plant species and reduced plant species richness to the early stages of invasion. Invasion by *L. rubellus* is strongly associated with the removal of the forest floor and local extirpation of the rare goblin fern (*Botrychium mormo* W.H. Wagner) (Gundale 2002). Earthworm invasions also transform diverse herb-layer plant communities to simplified and sparser communities dominated by a few species (Hale et al. 2006). Although significant reductions in the forest floor and plant species abundance and richness have been documented at Hale's (2006) intensively studied sites during the early stages of invasion, it is unknown whether these changes occur across larger landscapes of hardwood forests.

We conducted a regional survey of mature sugar-maple-dominated forest stands in two national forests of the western Great Lakes region of North America to answer the following questions: (1) Is earthworm invasion associated with reduced plant-species richness? (2) Is earthworm invasion associated with declines in particular plant species? (3) Which earthworm species or species assemblage is associated with observed shifts in plant species composition or richness?

Methods

Study Regions and Site Selection

This study included a total of 40 forest stands in the Chequamegon National Forest in Wisconsin (46°N, 91°W) and the Chippewa National Forest in Minnesota (47°N,94°W). Both regions predominantly occupy glacial till and outwash plains punctuated with hundreds of lakes. Soils are generally deep, well-drained fragiorthods and haplorthods in the Chequamegon, and deep, well-drained boralfs in the Chippewa (Albert 1995) that in the absence of earthworms are characterized by a thick forest floor composed of O_i (L), O_e (F), and O_a (H) layers.

Additional information on the study regions is in Holdsworth (2006).

We chose 20 forest stands of similar forest type, soils, and management history in each national forest. We identified stands that met the following criteria: upland mesic hardwood forest type, >60 years old, on sandy-loam or loamy-sand soils, bordering on lakes >4 ha, extending >400 m from lake shore, and with no logging activity in the last 40 years. Mature upland mesic hardwoods were chosen to complement the intensive studies in the same forest and soil types by Hale et al. (2005*a*, 2005*b*, 2006). We used recent (>1990) aerial photographs to examine candidate stands for canopy conditions. Stands with significant canopy loss (>50%) due to wind or other disturbance were eliminated because earthworms are affected by canopy gaps (Nachtergale et al. 2002) as are herb communities (Gilliam & Roberts 2003). We placed a transect in each of the remaining stands such that most transects were >1000 m apart. To meet all other stand-selection criteria, 11 of 40 transects had to be placed 500–1000 m from one other transect. The coordinates and bearing of each transect were measured on the aerial photo and used to locate it in the field.

Vegetation, Earthworm, and Soil Sampling

We sampled vegetation and earthworms in 5–10 (median = 8) nested plots spaced every 50 m along transects that ranged from 300 to 550 m (median = 400). Transect length varied based on the number of plots that could be sampled in 1–2 d. Sampling occurred once in June or July of 2001 or 2002 in Chequamegon and August or September of 2001 or 2002 in Chippewa. We sampled the herb layer with four 1-m-radius subplots (3.1 m^2 each) evenly centered 2.5 m from the main plot center. We identified all vascular plants, including woody plants <50 cm tall (Gleason & Cronquist [1991] taxonomic authority), and placed each plant species in one of six cover classes (0–1, 1–5, 5–25, 25–50, 50–75, and 75–100%). Browsing intensity by white-tailed deer was estimated in each subplot with a sugar maple browse index based on the proportion of sugar maple seedling twigs browsed by deer (Frelich & Lorimer 1985). We recorded total number of tree saplings (>50 cm tall and <5.0 cm diameter at breast height [dbh]) in a 3.5-m-radius plot (38.5 m^2). Trees ≥5 cm dbh within a 10-m-radius plot (314.2 m^2) were identified and counted in 5-cm dbh classes. We measured percent canopy openness at the plot center with a densiometer.

At each plot trained technicians sampled earthworms with a combination of hand sifting and liquid extraction (Bouché & Gardner 1984; Lawrence & Bowers 2002) when soil moisture was sufficient for earthworm activity and when earthworms were active. Hand sifting occurred in a 0.12 m^2 (35.4 × 35.4 cm) × 30 cm deep subplot placed 1 m from the main plot center. We applied liquid-mustard extraction to a 0.12-m^2 subplot 2 m from where we did the hand sifting. A trained technician sampled the upper 30 cm of soil at one hand-sifted plot along every one-third of each transect and described soil texture and horizons. We oven dried soil samples at 100° C for 48 h and sifted them through a 1.7-mm sieve. We measured soil texture with the hydrometer method and pH with a 240 pH meter (Corning, Corning, New York).

Analyses

We aggregated the four herb-layer subplots (3.1 m^2) to calculate species richness of all species in the herb layer and richness by growth form (forbs, graminoids, woody plants, and ferns/fern allies) at the plot scale. To analyze herb-layer species richness at the transect scale, we aggregated six sets of plots with four adjacent subplots. For transects with more than six plots, we randomly chose six sets of four subplots. The aggregation of plots at the transect scale meant there was less replication in the plot scale analyses. Because this could generate inconsistencies of "scale" that are really artifacts of statistical power, we noted this in our presentation of the results. We did not analyze exotic plant species separately from native species because they were few in number (three and two in the Chequamegon and Chippewa, respectively), uncommon (≤8% of plots), and were not abundant (<1% mean cover). Given that soil descriptions made at each plot revealed substantial similarity between adjacent plots, we applied soil texture and pH data from the soil plots to the nearest plot without soil samples. Analyses with transect mean values also produced the same results.

We used the same earthworm groups as Hale et al. (2005*a*) and Holdsworth et al. (2007): *Dendrobaena, Lumbricus rubellus, Lumbricus* juveniles*, Lumbricus terrestris, Aporrectodea* spp., and *Octolasion tyrtaeum*. The *Lumbricus* juveniles group consisted of the juveniles of *L. rubellus* and *L. terrestris* because it can be difficult to distinguish among juvenile *Lumbricus*. We calculated plot ash-free dry mass (AFDM) of plots (following Hale et al. 2004) for each earthworm group as the mean AFDM of the liquid extraction and hand-sifted samples at each plot. In another study with the same plots we found two major earthworm assemblages indicative of different intensities of invasion (Holdsworth et al. 2007). The *Dendrobaena* assemblage indicated lightly invaded plots and was dominated by *Dendrobaena octaedra*, a species that has negligible effect on plant communities (Hale et al. 2006). The *Lumbricus-Aporrectodea* assemblage indicated heavily invaded plots and was associated with significantly thinner forest floors (Holdsworth 2006). *Lumbricus* juveniles and *Aporrectodea* species dominated this assemblage, which also includes *L. rubellus* and *L. terrestris* (Holdsworth et al. 2007).

We fit mixed-effects models (PROC MIXED, SAS 8.0) (Littell et al. 1996) to analyze the relationships between earthworm invasion and herb-layer plant species

richness. We fit a primary model with AFDM of individual earthworm groups as predictors and an alternative model with earthworm invasion intensity (lightly vs. heavily invaded) as a categorical predictor for each national forest. These models also included the following initial predictors: proportion soil sand, clay, pH, tree basal area, sapling density, canopy openness, browse index, and browse index × *Lumbricus* juveniles mass or browse index × earthworm invasion intensity (in the case of the invasion-intensity-based alternative model) (Table 1). Starting with this initial set of predictors, we sequentially removed variables with the highest *p* values from the model and chose the models with the lowest AIC (Akaike information criterion). We used *Lumbricus* juveniles mass for the browse index × earthworm mass interaction because *Lumbricus* juveniles are the most frequent and highest mass group of earthworm species responsible for removal of the organic horizon (Hale et al. 2005*b*; Holdsworth et al. 2007). Subsequent models also included interactions between other earthworm groups and browse index, but these did not contribute to model fit. The alternative model with invasion intensity instead of individual earthworm groups led to similar output. For brevity we show only the analyses by groups, except for contrasting plant richness between plots classified as lightly versus heavily invaded. Plant-species richness was not transformed because it was normally distributed.

We used a random effect on transect to permit the application of results to the larger population of transects (Littell et al. 1996). Because species richness of herb-layer plants tends to be autocorrelated beyond our 50-m inter-plot distance (Scheller & Mladenoff 2002), we used a repeated-measures model with an autoregressive (AR[1]) correlation structure on within-transect interplot distance.

We analyzed herb-layer species composition of plots with nonmetric multidimensional scaling (Kruskal 1964) in PC-ORD (McCune & Mefford 1999, v. 4.20). Analyses excluded species occurring in fewer than 5% of plots in each national forest and plots with average Sørensen distance >2.5 SD (3 and 2 plots in Chequamegon and Chippewa, respectively). We relativized species cover to the maximum cover attained by each species in each national forest. Compositional differences between plots were evaluated with Sørensen's distance calculated from species' mean cover of the four 3.1-m^2 subplots. Starting with a random configuration and stepping down from a 6 to 1 dimensional solution, we assessed final dimensionality with 50 runs with real data, 50 runs of randomized data, and a Monte Carlo test of significance (McCune & Grace 2002). We chose the final number of dimensions that minimized stress with the fewest dimensions. From a second set of ordinations with this dimensionality, we chose the stable ordination with the lowest final stress to present here. We used environmental variable overlays to evaluate relationships between herb-layer species composition, earthworms, and soil and vegetation environmental variables.

The relationship of earthworm invasion to individual herbaceous species was analyzed with DuFrêne and Legendre's (1997) method of indicator species analysis in PC-ORD (McCune & Mefford 1999, version 4.20). We tested all plant species present in at least 20 plots in each national forest for their association with either lightly invaded plots or heavily invaded plots. A perfect indicator of a particular group is always present and only present in that group. Based on this standard and the relative species abundance and frequency, this method calculates an indicator value for each species. Tests for statistical significance used 1000 Monte Carlo randomizations (McCune & Grace 2002). For nonmetric multidimensional scaling and indicator species analysis, we evaluated statistical significance at $\alpha = 0.05$.

Results

Earthworm Invasion and Plant Species Richness

All analyses indicated that *Lumbricus* was significantly related to decreased plant species richness in both forests and at both plot and transect scales. Simple bivariate correlations showed that *Lumbricus* juveniles' mass was negatively related to richness in both forests (Figs. 1a & 1b). Additionally, the mixed effects models with multiple variables had at least one measure of *Lumbricus* mass as a significant factor negatively associated with richness in both Chippewa and Chequamegon at both the plot scale (four adjacent 3.1-m^2 plots) and the transect scale (six

Table 1. Mean (±SD) of predictors of plant species richness used in analysis for Chequamegon and Chippewa national forests.

Predictor	Chequamegon	Chippewa
Dendrobaena mass[a]	0.2 ± 0.2	0.2 ± 0.2
Lumbricus rubellus mass	0.1 ± 0.3	0.2 ± 0.4
Lumbricus juveniles mass	1.0 ± 1.4	0.7 ± 1.0
L. terrestris mass	0.6 ± 1.2	0.4 ± 1.3
Aporrectodea mass	2.9 ± 3.5	2.3 ± 2.6
Octolasion mass	0.1 ± 0.6	0.0 ± 0.2
Total earthworm mass[b]	4.8 ± 5.1	3.9 ± 3.9
Soil pH	4.3 ± 0.2	5.5 ± 0.3
Sand (proportion)[c]	0.67 ± 0.16	0.55 ± 0.12
Clay (proportion)	0.10 ± 0.04	0.09 ± 0.02
Tree basal area (m^2/ha)	32.5 ± 8.1	29.7 ± 10.4
Sapling density (no./plot)	15.0 ± 14.4	26.9 ± 25.5
Canopy openness (proportion)	0.04 ± 0.02	0.04 ± 0.03
Browse index	1.1 ± 0.6	0.7 ± 0.5

[a]*AFDM (ash-free dry mass) in grams per square meter.*
[b]*Total mass and mass of separate earthworm groups were used in separate models.*
[c]*Silt was not used in models because it is highly negatively correlated with sand (R^2 ≥ 0.95).*
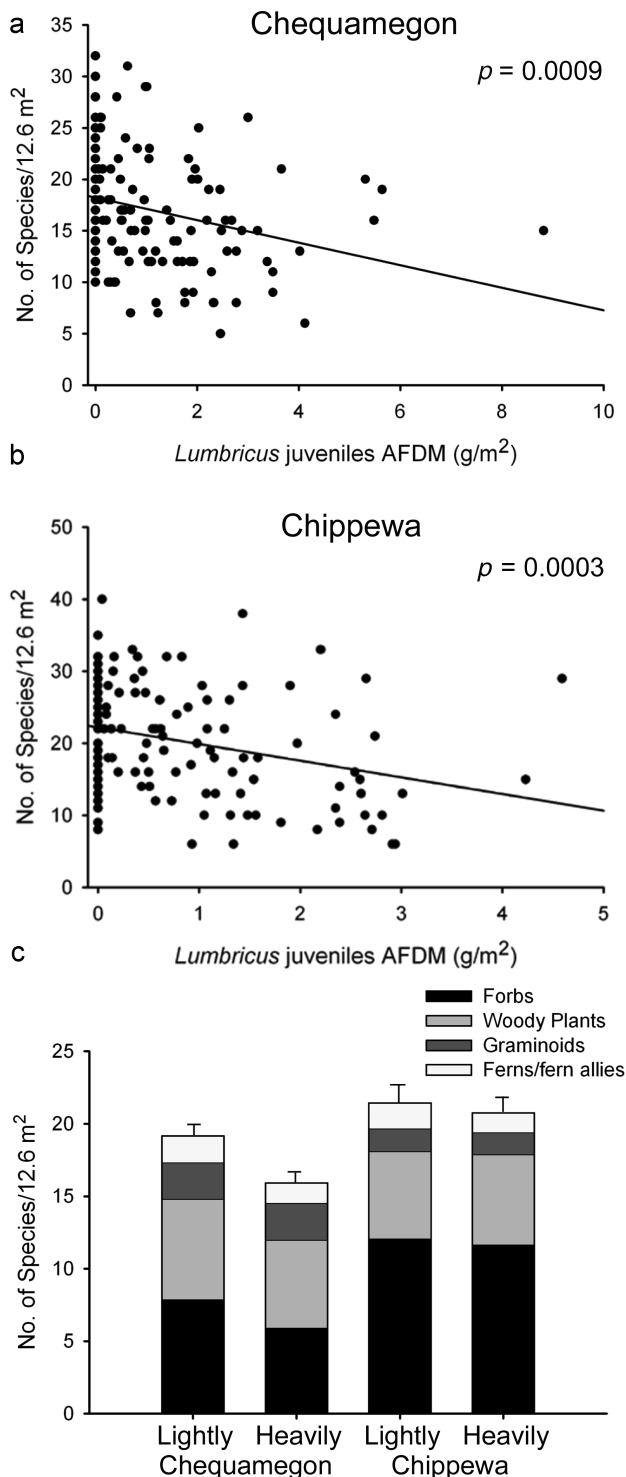
Figure 1. Plant species richness of the herb layer in relation to (a) Lumbricus *juveniles mass in the Chequamegon National Forest, (b)* Lumbricus *juveniles mass in the Chippewa National Forest, and (c) lightly and beavily invaded plots and plant growth form in both national forests (mean richness ±SE). Scales are different in each panel, and AFDM is ash-free dry mass.*

sets of four adjacent 3.1-m^2 plots) (Table 2). The one measure of *Lumbricus* mass with a positive relationship to plant species, *Lumbricus* juveniles, occurred at the transect scale and may have been an artifact of its smaller sample size, which reduced the power of the data. Additionally, some other earthworm groups had positive relationships with species richness. At the plot scale *Dendrobaena* mass was positively related to richness in the Chequamegon, largely due to the effect of *Lumbricus* invasion on *Dendrobaena* mass. At the transect scale *Aporrectodea* mass was positively related to richness in both forests as was *Octolasion* mass in Chippewa (Table 2).

Other variables also contributed to model fit of plant species richness including sand, canopy openness, and browse index. Browse index had significant, but contrasting effects in the two national forests. In Chequamegon it had a negative effect at the plot scale, whereas it had a positive effect at both scales in Chippewa (Table 2). Interactions between browse index and *Lumbricus* juveniles mass and between browse and other earthworm groups did not contribute to model fit (Table 2). Although canopy openness had a positive effect on species richness in Chippewa (Table 2), there was no significant interaction between it and mass of other earthworm groups in each model.

The results of the alternative model that contrasted sites classified as lightly versus heavily invaded (with earthworm assemblages rather than species groups) were similar in Chequamegon. In Chequamegon heavily invaded plots had a mean of three (17%) fewer species ($p = 0.0049$), whereas in Chippewa species richness was not significantly lower (Fig. 1c). The total reduction in richness in Chequamegon included a 25% and 12% decline in forb and woody species, respectively (Fig. 1c).

Earthworm Invasion and Plant-Community Composition

Herb-layer community composition differed between lightly and heavily invaded plots by varying degrees in the two national forests. A three-axis solution resulted in significant ordination axes ($p = 0.02$) that cumulatively represented 59–60% of the variance in the original n-dimensional space for each forest. Axes 1 and 2 represented the majority of this variance (35% and 47% in Chequamegon and Chippewa, respectively). Given the importance of *Lumbricus* juvenile mass, we rotated the axes so that axis 1 corresponded to a gradient of its mass (McCune & Grace 2002). In Chequamegon, plots segregated by invasion intensity. Ninety-one percent of lightly invaded plots were on the left half of axis 1, and 64% of heavily invaded plots were along the right half (Fig. 2a). Axis 1 represented an earthworm mass—soil sand gradient, with the largest positive correlation (Pearson's r) for *Aporrectodea* mass ($r = 0.52$) and the largest negative correlation for sand ($r = -0.54$) (Table 3;

Table 2. Model summary of plot-level (13 m^2) and transect-level (75 m^2) species richness in the Chequamegon and Chippewa national forests by mass of the earthworm group and environmental variables.[a]

| | Chequamegon | | | | | | Chippewa | | | | | |
| | plot | | | transect | | | plot | | | transect | | |
Model effect[b]	eff-rel	F	p	eff-rel	F	p	eff-rel	F	p	eff-rel	F	p
Mass												
Dendrobaena	+	4.40	0.0381									
Lumbricus rubellus				−	12.15	0.0051						
L. juveniles	−	8.65	0.0039	+	2.76	0.1246	−	8.19	0.0051	−	23.17	0.0004
L. terrestris				−	6.22	0.0298						
Aporrectodea				+	5.88	0.0337				+	22.45	0.0005
Octolasion										+	7.30	0.0192
pH												
sand				−	5.72	0.0358						
clay							+	1.28	0.2600			
Tree basal area												
sapling density												
canopy openness							+	20.90	<0.0001	−	6.33	0.0271
browse index	−	4.82	0.0302	+	2.56	0.1380	+	5.66	0.0191	+	10.933	0.0063
Brwse I*L. juv. mass												

[a]*Blank cells indicate variables removed during model selection; eff-rel is effect relationship (+/−).*
[b]*Denominator df are 116 and 108 for all effects in the Chequamegon and Chippewa, respectively, at the 13-m^2 plot scale and 11 and 12 at the 75-m^2 scale.*

Fig. 2c). Axis 2 best represented a gradient in browse index ($r = 0.44$) (Table 3; Fig. 2c). Herb-layer plant species with the strongest negative correlations ($r \leq -0.2$) with axis 1 were sugar maple seedlings, wild sarsaparilla (*Aralia nudicaulis* L.), big-leaved aster (*Aster macrophyllus* L.), rose twisted stalk (*Streptopus roseus* Michx.), hairy solomon's seal (*Polygonatum pubescens* [Willd.] Pursh), princess pine (*Lycopodium obscurum* L.), and false solomon's seal (*Smilacina racemosa* [L.] Desf.) (Fig. 2c; Supplementary Material). A sedge, *Carex pensylvanica* Lam., reached its highest abundances in heavily invaded plots and was strongly positively associated with axis 1 ($r = 0.78$) (Fig. 2a,e; Supplementary Material) as were jack-in-the-pulpit (*Arisaema triphyllum* [L.] Schott.) ($r = 0.46$) and ash (*Fraxinus spp.*) seedlings ($r = 0.45$) (Fig. 2c).

Lightly invaded and heavily invaded plots in Chippewa did not segregate in the ordination as much as in Chequamegon. Nevertheless, the trend was similar with the majority (79%) of the lightly invaded plots on the left half of axis 1 (Fig. 2b). Axis 1 represented a pH and earthworm—browse index and soil sand gradient with the largest positive correlations with pH ($r = 0.42$) and *Lumbricus* juveniles mass ($r = 0.35$) and the largest negative correlations with browse index ($r = -0.35$) and sand ($r = -0.25$) (Table 3; Fig. 2d). None of the measured environmental variables explained notable variance in axis 2. Herb-layer plant species with the strongest negative correlations ($r \leq -0.2$) for axis 1 included woody plant seedlings of sugar maple, basswood (*Tilia americana* L.), red oak (*Quercus rubra* L.), and herbaceous species, in-

cluding wild ginger, big-leaved aster, rose twisted stalk, wild oats (*Uvularia sessilifolia* L.), round-lobed hepatica (*Hepatica americana* [D.C.] KerGawler), Canada mayflower (*Maianthemum canadense* Desf.), starflower (*Trientalis borealis* Raf.), and early meadow rue (*Thalictrum dioicum* L.) (Fig. 2d; Supplementary Material). In contrast to Chequamegon, the sedge *Carex pensylvanica* was strongly negatively correlated ($r = -0.58$) with axis 1. Species with the strongest positive correlations with axis 1 ($r \geq 0.2$) included wood nettle (*Laportea canadensis* [L.] Wedd.) ($r = 0.68$), wild ginger (*Asarum canadense* L.), ostrich-fern (*Matteucia struthiopteris* [L.] Todaro), blue cohosh (*Caulophyllum thalictroides* [L.] Michx.), bloodroot (*Sanguinaria canadensis* L.), jack-in-the-pulpit, Virginia waterleaf (*Hydrophyllum virginianum* L.), and jewel-weed (*Impatiens pallida* Nutt.) ($r = 0.21$) (see Supplementary Material).

Indicator Species

Analysis of indicator species identified more indicator species associated with lightly invaded plots than heavily invaded plots in each national forest. There were 11 indicator species of lightly invaded plots (5 forbs, 5 trees, and 1 club moss) in Chequamegon and 7 in Chippewa (4 forbs, 2 trees, and 1 fern) (Table 4). Two of these species were indicators of lightly invaded plots in both national forests, wild sarsaparilla and rose twisted stalk. There were only three indicators of heavily invaded plots in Chequamegon, jack-in-the-pulpit, *Carex pensylvanica*,
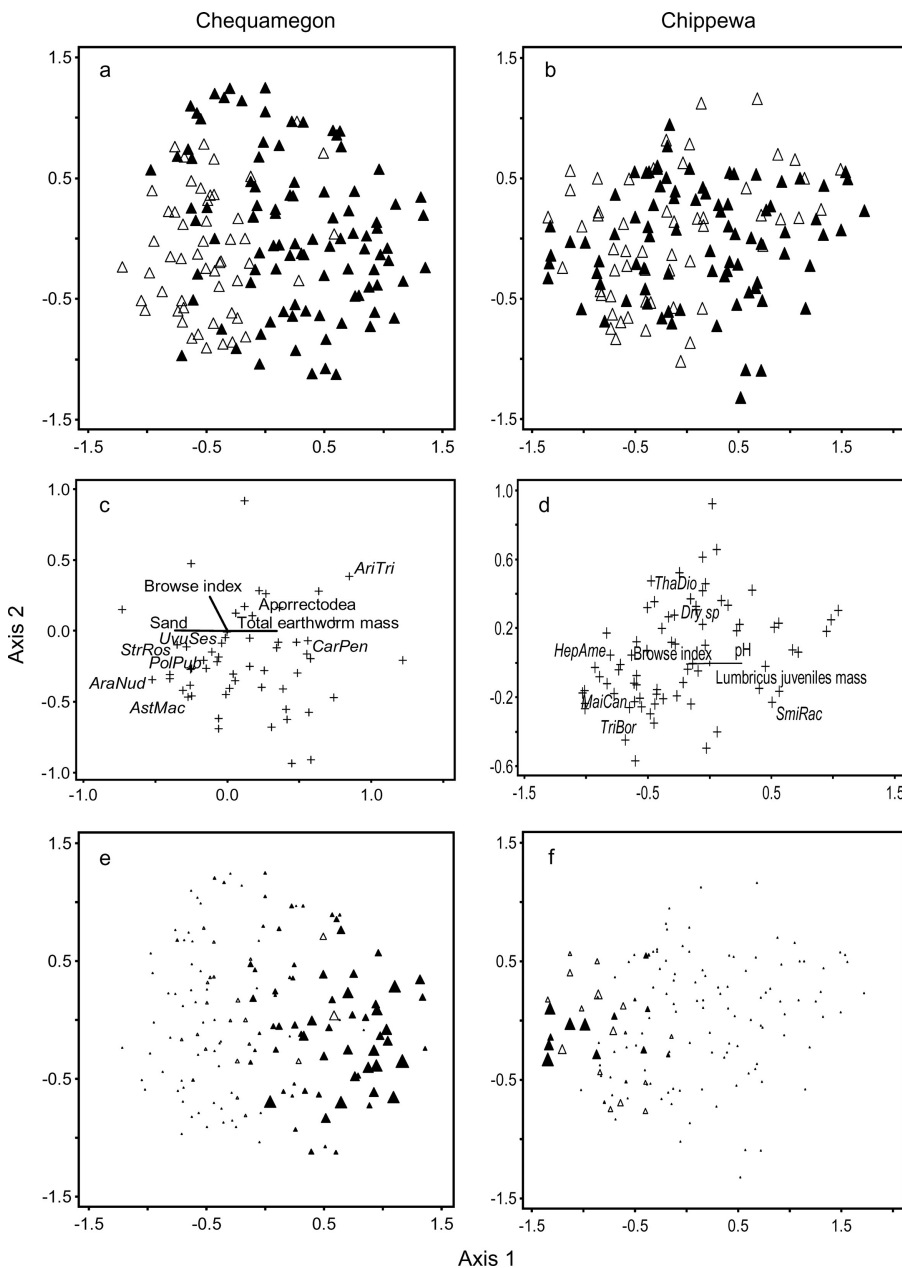
Figure 2. Axes 1 and 2 from nonmetric multidimensional scaling ordination of the (a, b) plots and (c, d) herb-layer species in the Chequamegon (a, c, e) and Chippewa (b, d, f) national forests ([a, b]: △, lightly invaded plots; ▲, heavily invaded plots; [c, d]: +, with major environmental variables [forb indicator species from Table 4 are labeled]; [e, f]: relative abundance of Carex pensylvanica, symbol size proportionate to abundance; △, lightly invaded plots; ▲, heavily invaded plots). All axis labels are raw scores.

and ash seedlings, whereas false solomon's seal was the single indicator in Chippewa (Table 4).

Discussion

In an intensive 4-year study of plant community change during earthworm invasion at four sites, Hale et al. (2006) found declines in most herbaceous species resulting in communities of low diversity dominated by a few species. Findings such as this (e.g., Gundale 2002) led Frelich et al. (2006) to suggest that this might be a general effect of earthworm invasion. The results of our broader regional surveys provided additional evidence for earthworm in-

vasion as an important mechanism of decline for several species of forest forbs.

Earthworm Invasion and Changes in the Plant Community

The removal of the forest floor by invasive earthworms is a function of the litter chemistry (Reich et al. 2005; Hobbie et al. 2006) and has been linked to reduced plant species richness (Gundale 2002; Hale et al. 2006). Removal of the forest floor by invasive earthworms increases with the litter calcium concentration (Reich et al. 2005; Hobbie et al. 2006; Holdsworth 2006), which tends to be highest in maple and basswood species and results in partial or complete uprooting of herbaceous plants and tree seedlings (Hale 2003). Heavily invaded plots in our study

Table 3. Correlation (Pearson's *r*) of earthworm and other environmental variables with nonmetric multidimensional scaling axes (where *r* ≥ 0.2 for axis 1) for Chequamegon and Chippewa national forests.

Forest	Variable	*Pearson's r*		
		axis 1	axis 2	axis 3
Chequamegon	*Aporrectodea* mass	0.52	−0.001	−0.11
	total earthworm mass	0.46	0.05	−0.13
	clay	0.32	0.08	−0.13
	canopy openness	0.28	−0.19	−0.08
	Lumbricus juveniles mass	0.25	0.09	−0.09
	L. terrestris mass	0.21	0.07	−0.01
	tree basal area	−0.20	0.15	−0.04
	browse index	−0.32	0.44	0.17
	sand	−0.54	0.04	−0.03
Chippewa	pH	0.42	0.01	−0.07
	Lumbricus juveniles mass	0.35	−0.02	0.03
	L. rubellus mass	0.26	−0.01	−0.08
	sand	−0.25	0.03	−0.06
	browse index	−0.35	−0.04	0.24

had comparable earthworm mass to the plots studied by Hale et al. (2005) and had approximately half the forest floor mass compared with lightly invaded plots in both national forests (Holdsworth 2006). As in Gundale (2002) and Hale et al. (2006), the earthworm genus associated with reduction in forest floor, *Lumbricus,* also was significantly associated with reduced plant species richness in both national forests (Table 2; Figs. 1a & 1b).

In addition to the negative relationships of *Lumbricus* earthworm species, there were some positive statistical relationships between plant species richness and non-*Lumbricus* species (Table 2). The positive relationship between the exclusively litter-dwelling *Dendrobaena* group at the plot scale in the Chequamegon was largely due to the effect of *Lumbricus* invasion on *Dendrobaena*. *Dendrobaena* is most abundant in thick forest floors, where plant species richness also tends to be higher, but *Dendrobaena* declines as *Lumbricus* species invade and reduce the forest floor (Hale et al. 2005*a*, 2005*b*). The positive relationship with soil-dwelling (endogeic) earthworm species at the transect scale could be due to confounded effects of endogeic mass and soil texture on richness. *Aporrectodea* species were most abundant in finer textured soils, and these soils tended to be more species rich in Chequamegon. Additionally, the relationship between *Aporrectodea* mass and richness in both national forests was different for finer versus coarser textured soils, whereas it did not differ for *Lumbricus* species. Although there is evidence that *Aporrectodea* can influence plant competition (Wurst et al. 2005), additional research is necessary to better understand its effects on plant community composition and richness.

Composition of plant communities in heavily invaded plots of Chequamegon differed most from lightly invaded plots (Fig. 2a) and was similar to changes in plant community documented during the early stages of invasion in several intensively studied stands (Hale et al. 2006). In our large regional survey, ordination axes were correlated with some environmental variables besides earthworm mass, suggesting potentially confounding effects of soil pH, sandiness, or browse index (Table 3). Given this, we focus our discussion on earthworm-plant compositional patterns consistent between this study and the multiyear study of plant compositional change during earthworm invasion of Hale et al. (2006). As in Hale et al. (2006), sugar maple seedlings, wild sarsaparilla, rose twisted stalk, hairy solomon's seal, and false solomon's seal were associated with lightly invaded plots and *Carex pensylvanica* and jack-in-the-pulpit were associated with heavily invaded plots (Fig. 2c). Of these species, sugar maple seedlings, wild sarsaparilla, rose twisted stalk, and jack-in-the-pulpit also showed the same relationships to earthworm invasion in Chippewa. The former group of species associated with lightly invaded plots are all species that are successful in thick forest floors and tend to have larger seeds, have more complex dormancy and germination strategies, and are more shade tolerant than species favored by thin forest floors (Harper et al. 1965; Baskin & Baskin 1998).

There are several ways earthworm invasion could favor the two species commonly found in heavily invaded areas with thin forest floor, *Carex pensylvanica* and jack-in-the-pulpit. Most herb-layer species of sugar-maple-dominated forests are strongly mycorrhizal (Brundrett & Kendrick 1988), and earthworm invasion can alter the abundance and structure of soil fungal communities (Johnson et al. 1992; McLean & Parkinson 1998*a*; McLean & Parkinson 2000; Lawrence et al. 2003). *Carex pensylvanica* is one of the few nonmycorrhizal species in sugar maple forests (Brundrett & Kendrick 1988) and thus could gain a competitive advantage with earthworm-altered mycorrhizal fungi communities. Because *Carex pensylvanica* is nearly twice as common as the next most common sedge in both national forests (see Supplementary Material), it is well positioned to take advantage of earthworm invasion-induced conditions in many forest stands. Finally, deer herbivory could contribute to increased abundances of *Carex pensylvanica* and jack-in-the-pulpit. Deer are selective browsers and avoid such unpalatable species as jack-in-the-pulpit, which has high levels of secondary compounds, and *Carex pensylvanica*, which has a high silica content (Augustine & McNaughton 1998).

Earthworm Invasion and Deer Herbivory

There could be synergistic effects of invasive earthworms and herbivory by white-tailed deer (Frelich et al. 2006).

Table 4. Herb-layer indicator species of plots lightly invaded and heavily invaded by earthworms in the Chequamegon and Chippewa national forests.[a]

Invasion degree	Species	Chequamegon[b]	Chippewa[b]	Concordance with Hale et al. (2006)
Light	forbs			
	Streptopus roseus	53**	40**	yes
	Aralia nudicaulis	49**	40*	yes[c]
	Uvularia sessilifolia	49**		yes[d]
	Polygonatum pubescens	42**		yes
	Aster macrophyllus	53**		
	Thalictrum dioicum		27**	yes
	Maianthemum canadense		43**	no
	Trientalis borealis		27**	
	Hepatica Americana		24**	
	tree seedlings			
	Acer saccharum	57[e]	61*	yes
	Acer rubrum	64**		
	Ostrya virginiana	56**		
	Quercus rubra	48*		
	Tilia americana	36*		
	Amelanchier spp.	26**		
	Populus spp.		17*	
	fern/fern ally			
	Lycopodium obscurum	63**		
	Dryopteris spp.		39**	
Heavy	forbs			
	Arisaema triphyllum	27**		yes
	Smilacina racemosa		41**	no
	tree seedlings			
	Fraxinus spp.	62**		
	graminoid			
	Carex pensylvanica	72**		yes

[a] *Numbers for each national forest are indicator values (% of perfect indication) from indicator species analysis (Dufrêne & Legendre 1997). The p values are from 1000 Monte Carlo randomizations. Concordance with an intensive study of plant community changes during earthworm invasion (Hale et al. 2006) is also noted (blank cells indicate species that were absent or occurred in numbers too low for analysis).*
[b]*$p < 0.05$, **$p < 0.01$.*
[c] *Hale et al. (2006) found earthworm-related declines for* A. nudicaulis *and even stronger declines for the congeneric* Aralia racemosa.
[d] *Hale et al. (2006) found earthworm-related declines in a Chippewa congeneric of* Uvularia sessilifolia, U. grandiflora.
[e] *Acer saccharum was a marginally significant (*$p = 0.056$*) indicator of lightly invaded plots in the Chequamegon.*

Abundance of white-tailed deer has increased substantially in the region, recently reaching densities 2–12 times that of estimated presettlement densities (Rooney 2001; Rooney et al. 2004). Herbivory by white-tailed deer has been linked to declines in native plant density at the community and species level (Augustine & Frelich 1998; Côté et al. 2004; Rooney et al. 2004). Wiegmann (2006) found a significant interaction between browse index and total earthworm density but not significant main effects on changes in plant diversity. Although we found individual negative effects of deer browse in some analyses, there was no significant interaction between the intensity of earthworm invasion and the index of deer browse in Chequamegon (Table 2). Because *Lumbricus* juveniles *and L. rubellus* have the strongest negative effects on plant communities (Hale et al. 2006; [this study]), the use of total earthworm density by Wiegmann (2006)

instead of earthworm-group specific masses could explain the differences in our results. The positive effect of deer browse on species richness in Chippewa (Table 2) was somewhat surprising. Navertheless, deer densities in Chippewa are 30% lower than in Chequamegon (Minnesota and Wisconsin Departments of Natural Resources, unpublished data), and Rooney and Waller (2003) found evidence of nonlinear relationships between seedling density and deer density. Furthermore, this interpretation assumes a deer-to-plants direction of causality. Other factors such as the forage quality of plant communities in the larger area can influence the effects of deer on plant communities (Augustine & Jordan 1998). Results from ongoing research with deer exclosures across different intensities of earthworm invasion should provide additional insights into this potentially important interaction.

Differences between the National Forests

The differences in herb-layer species richness and composition in heavily versus lightly invaded plots were more pronounced in Chequamegon than in Chippewa (Figs. 1c & 2). The degree of plant-community change following earthworm invasion might be greater if deer densities were high enough to consume more plant biomass than plants can recover each year (Augustine et al. 1998; Frelich et al. 2006). With 30% lower deer densities in Chippewa, the degree or rate of plant-community change during earthworm invasion may be lower. Furthermore, the distribution of the largest bodied earthworm species, *L. terrestris*, is much more limited in Chippewa. *L. terrestris* was well established throughout the transect in four Chequamegon stands, whereas it was well established in only one stand in Chippewa. Although *L. terrestris'* effects on forest herbs are not well known, we found a significant negative relationship between it and plant species richness at the transect scale (Table 2). *L. terrestris'* feeding habits create an even thinner forest floor than where *L. rubellus* and *Aporrectodea* species occurred without *L. terrestris,* and it may further plant-community change (Hazelhoff et al. 1981; Holdsworth 2006).

Earthworm-Sensitive Plant Species

Given the multiple mechanisms through which earthworm invasion could reduce plant species richness (Frelich et al. 2006), predicting which plant species may have contributed to declines in richness is difficult. Multiple interacting factors in any given stand could influence which species decline or are locally extirpated including land-use history (Flinn & Vellend 2005), disturbance history (Gilliam & Roberts 2003), deer herbivory (Rooney et al. 2004), and plant population condition upon invasion (Augustine et al. 1998). Nevertheless, our results from two national forests and the results of the earlier intensive multiyear study suggest some species whose occurrence and abundance show sensitivity to earthworm invasion. Wild sarsaparilla and rose twisted stalk were significant indicators of lightly invaded plots in both national forests in this study and negatively associated with heavy earthworm invasion in the study of Hale et al. (2006). Hairy solomon's seal was a significant indicator of lightly invaded plots in the Chequamegon and was strongly negatively associated with heavy earthworm invasion in Hale et al. (2006). *Uvularia sessilifolia* was also a significant indicator of lightly invaded plots in the Chequamegon and its Chippewa congener, *U. grandiflora*, was strongly negatively associated with heavy earthworm invasion in Hale et al. (2006). It is also important to note that these effects of earthworm invasion on specific species will be regulated by the affinity of earthworms for different litter types (and hence forest types), with the calcium-rich lit-

ter of maple and basswood particularly advantageous for earthworms (Reich et al. 2005; Holdsworth 2006).

In a resurvey of northern Wisconsin plots after 50 years, the species discussed above (except *Uvularia grandiflora*) were among the 21 "losers" that suffered the greatest declines in abundance, and earthworm invasion and increased deer herbivory were cited as two possible mechanisms (Wiegmann & Waller 2006). In additional analyses with logistic normal models of presence and absence of these species, we found significant negative effect of *Lumbricus* juveniles or *L. rubellus* on the presence of these species but no effect of browse index. These species in particular, and the other species associated with lightly invaded plots in Table 4 or that showed contradictory responses to that of Hale et al. (2006) (Canada mayflower and false solomon's seal), merit further study with regard to the relative contribution of earthworm invasion and other factors influencing their population status. Furthermore, because the timing of this study excluded spring ephemeral plant species, future studies should include them.

Earthworm invasion could also influence the successional trajectory of the canopy (Frelich et al. 2006). Our data on tree seedlings suggest that earthworm invasion may favor tree species such as ash over maple, ironwood, oak, and basswood (Table 4). Changes in the composition of canopy species following earthworm invasion will be complex because tree species respond differently to the multiple ecosystem effects of earthworm invasion, deer herbivory, and climate change (Frelich et al. 2006).

Conclusions

Invasive earthworms are important agents of ecosystem change in previously earthworm-free northern hardwood forests (Bohlen et al. 2004). Besides contributing to reduced abundances of many native plant species (Gundale 2002; Hale et al. 2006), earthworm invasion can contribute to a shift in herb-layer state from forb and tree seedling dominance to *Carex* dominance (this study; Powers 2005). Earthworm invasion also affects other organisms of the forest floor, including microarthropods (McLean & Parkinson 1998*b*) and small vertebrates (Maerz et al. 2005).

In previously earthworm-free hardwood forests, lightly invaded areas (areas without *Lumbricus-Aporrectodea* invasion) should be identified and protected as earthworm-free refugia. Often these are large roadless areas, but finding these areas requires stand-level surveys that can be easily done by forest technicians (Holdsworth et al. 2007). Although almost all hardwood forests are susceptible to earthworm invasion (Gundale et al. 2005), colonization rates of earthworms are relatively slow at 5–10 m/year (Marinissen & van den Bosch 1992; Hale et al.

2005*a*) and will vary with canopy type because of litter effects on earthworm abundance and diversity (Reich et al. 2005). Thus, targeted education campaigns (e.g., http://www.nrri.umn.edu/worms/) and policies can help prevent introduction of earthworms so that these areas remain free of earthworms or lightly invaded for as long as possible (Hendrix & Bohlen 2002).

Acknowledgments

Supplementary Material

Frequency, mean cover, and nonmetric multidimensional-scaling axis correlation coefficients of vascular plant species in the herbaceous layer of Chequamegon National Forest (Appendix S1) and Chippewa National Forest (Appendix S2) are available as part of the on-line article from http:/www.blackwell-synergy.com. The author is responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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