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Abstract The National Wildlife Refuge System is the world's largest network of lands set aside specifically for wildlife conservation. For refuge planners and managers tasked with maintaining ecological integrity and wildlife habitat, many uncertainties exist. In forests in the Upper Midwest, for instance, exotic earthworms are impacting ecosystem structure and function, but their community composition and effects on refuges is unknown. We examined the association of earthworm functional group abundance and community composition within upland forests of refuges with broad scale patterns of anthropogenic land use and local scale differences in forest characteristics. Patterns of anthropogenic land cover, including

proportion of the land, mean patch area, and largest patch index, were strongly correlated with the biomass of epi-endogeic earthworms. Earthworm community diversity, however, was inversely related to patterns of dominating anthropogenic land cover, and increased under high ratios of natural to anthropogenic lands in the surrounding ecoregion. Within forests, earthworm community composition could be partially explained by variables representing both dispersal opportunities and habitat suitability. In general, heavily-invaded forests had low conifer dominance, high silt content, high basal area, greater amounts of anthropogenic cover within 500 m, and were closer to roads and farther from agriculture. However, the relationship between local forest characteristics and biomass differed greatly among earthworm functional groups and between refuges dominated by natural lands and those dominated by anthropogenic lands. For refuges with high earthworm loads and well developed earthworm communities, managers may be confounded in restoring historic conditions and may need to look at multiple tools, including artificial regeneration, to mitigate for current earthworm effects. In refuges seemingly in earlier stages of earthworm invasion, future planning and management should be tempered by potential effects observed in those refuges in more anthropogenic landscapes.

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Introduction

Many exotic species have been shown to alter ecosystem structure and function. The presence of exotic earthworms in forests of the Upper Midwest region of the United States, for example, has been linked to decreased native plant species richness, changes in plant community composition, altered forest floor and soil conditions, shifts in tree regeneration and nutrient cycling, and indirect impairments to wildlife habitat (Alban and Berry 1994; Bohlen et al. 2004b; Suarez et al. 2006; Holdsworth et al. 2007a). Most regional studies of earthworms have focused on cascading impacts in deciduous forest communities (Bohlen et al. 2004a; Hale et al. 2005; Frelich et al. 2006; Maerz et al. 2009; Heimpel et al. 2010; Loss and Blair 2011), with fewer studies considering potential drivers of earthworm invasion patterns (Gundale et al. 2005; Holdsworth et al. 2007b; Sackett et al. 2012). Furthermore, previous studies have generally been confined to a limited geographic area or a specific forest type, thereby reducing the ability to make inferences across space and forest ecosystem types.

Initial research on European earthworms in North America came primarily from agricultural systems, where earthworms were found to be abundant and thought to be beneficial, particularly to soil and plant productivity (Hendrix and Bohlen 2002; Scheu 2003). In forest ecosystems, the impacts of earthworms depend largely on their feeding and burrowing activities, and earthworms have been categorized into functional groups based on these differences (Bouché 1977; Edwards and Bohlen 1996). Epigeic (litter and surface dwelling) earthworms are small-bodied, feeding mainly on microorganisms and other organic matter at the soil surface. This activity contributes to breakdown and mixing of organic matter into the mineral soil and associated changes in the forest floor and soil structure (Edwards and Bohlen 1996). Epigeic earthworms can tolerate poor-quality litter, coarse-textured soil, and acidic sites (Tiunov et al. 2006). Endogeic (soil dwelling) earthworms feed on soil organic matter and create horizontal, non-permanent burrows within the mineral soil. These actions can disrupt fungal communities and alter soil nutrient cycling, which may have cascading ecosystem effects such as decreased native plant productivity (Bohlen et al. 2004b). Anecic (deep burrowing) earthworms

form deep, permanent burrows, yet feed on fresh surface litter. Permanent burrows can be identified by the presence of a midden, a mound of residual plant material and earthworm castings with a central plug composed of leaf litter. Anecic earthworms transport organic material to and from the mineral soil, mixing soil horizons and altering biogeochemical cycling (Subler et al. 1997; Suarez et al. 2003). Their burrowing activity also increases soil porosity and leads to greater nutrient leaching (Subler et al. 1997). In addition to these functional groups, some earthworms are considered to be epi-endogeic because they feed in the organic horizons, but live mainly in the mineral soil. Juveniles of the anecic species *Lumbricus terrestris* can also be considered epi-endogeic, as they usually live within the soil and feed on litter material similar to other epi-endogeic earthworms (Asshoff et al. 2010). Litter-feeding epi-endogeic and anecic earthworms prefer soils and litter rich with calcium and nitrogen and with low concentrations of phenols and tannins (Hendriksen 1990; Reich et al. 2005). They are thought to be constrained by soil properties such as low pH, coarse texture, or low moisture (Tiunov et al. 2006). High earthworm functional group diversity tends to result in increased site alteration and impact due to synergistic effects (Lavelle 1997; Hopfensperger et al. 2011), and may be more important than earthworm biomass alone (Hale et al. 2006).

Anthropogenic landscape features (e.g., roads, urban development, and agriculture) may cause the introduction and spread of invasive species (Lodge and Shradler-Frechette 2003; Shartell et al. 2011). Not surprisingly, therefore, the dispersal of exotic earthworms into native ecosystems is often associated with human activity (Gundale et al. 2005; Tiunov et al. 2006; Cameron et al. 2007; Holdsworth et al. 2007b; Sackett et al. 2012). Despite the potential benefit to forest ecosystem management and planning, few studies have considered broad-scale patterns of anthropogenic land cover and other landscape features as potential drivers of earthworm invasion.

The impact of broad and local patterns of anthropogenic activity and local forest and soil characteristics on earthworm abundance and community composition is an important consideration for future forest ecosystem management decisions. Understanding patterns of earthworm abundance and existing stages of invasion will aid forest managers in evaluating the limitations and potential consequences of

habitat restoration and the impacts of nearby anthropogenic development. To evaluate potential drivers of exotic earthworm abundance and community composition in upland forests of the Upper Midwest, we studied earthworm communities in National Wildlife Refuges across the region. At nearly 60 million ha the National Wildlife Refuge System (NWRS), managed by the U.S. Fish and Wildlife Service, is the world's largest network of lands specifically designated for wildlife conservation. The mission of the NWRS is to conserve, preserve, and restore lands for the wildlife that they support. Overall, NWRS land managers have been encouraged to favor ecologically-based wildlife habitat management, with restoration to historic conditions where and when possible (Schroeder et al. 2004; Scott et al. 2004; Meretsky et al. 2006). However, planners and land managers must assess both the opportunities and limitations to restoration before conducting costly management activities. Earthworms may limit the ability to restore lands to historic conditions, and considering the potentially adverse impacts noted above, their presence should be considered in management decisions. With this need, we addressed the following research questions:

1. How do broad-scale anthropogenic land use patterns influence the distribution and community composition of exotic earthworms? We hypothesize that earthworm abundance and community diversity will be higher at sites with greater amounts of anthropogenic lands both within the refuge and in the surrounding ecoregion;
2. What are the characteristics of heavily earthworm-invaded forests, and how do these characteristics influence the presence of differing earthworm functional groups? We hypothesize that variables related to habitat suitability and dispersal opportunity will be correlated with earthworm biomass, and that these variables will vary among earthworm functional groups;
3. How do local-scale influences of earthworm communities differ between refuges located within ecoregions dominated by natural land covers compared to those within ecoregions dominated by anthropogenic covers? We hypothesize that those refuges in ecoregions dominated by more natural land covers will be at an earlier stage of invasion and will have earthworm communities that are driven more by dispersal

mechanisms than by forest composition and soil characteristics.

Methods

Study area

Sampling occurred within upland forests in six National Wildlife Refuges (NWRs) found within different ecoregions as defined by Cleland et al. (1997) (Fig. 1, Table 1). Based on rapid ecological assessment (REA) findings of Petrillo and Corace (2011) and the work of Corace et al. (2012) that documented the variability in existing and pre-European land cover and landscape patterns found in a subsample of these refuges and their ecoregions, we placed these six refuges in two categories a posteriori: natural and anthropogenic, based on the amount of land in anthropogenic cover types (Table 1). Differences in land use among refuges and ecoregions provides a novel opportunity to describe the range of variation in both earthworm communities and associated landscape and land cover patterns found across the Upper Midwest. Three of the refuges (Rice Lake, Seney, and Tamarac) are located within ecoregions where natural forest land covers predominate (Corace et al. 2012). The remaining three refuges (Horicon, Shiawassee, and Ottawa) are found in ecoregions much more impacted by agriculture and human development. Climate across the refuges is relatively similar, characterized by large seasonal differences in temperature. With the exception of Tamarac, which has a more continental climate, the refuges are strongly influenced by their proximity to the Great Lakes, which acts to moderate temperature and increase precipitation.

Ecoregional analysis

Landscape metrics describing the pattern and predominance of anthropogenic lands were calculated for refuges and their associated ecoregion(s). Metrics were calculated using the spatial analysis program FRAGSTATS (McGarigal et al. 2002) and included refuge total area, patch richness, land cover Shannon's diversity, and specific to anthropogenic cover types only, proportion of landscape, mean patch area, largest

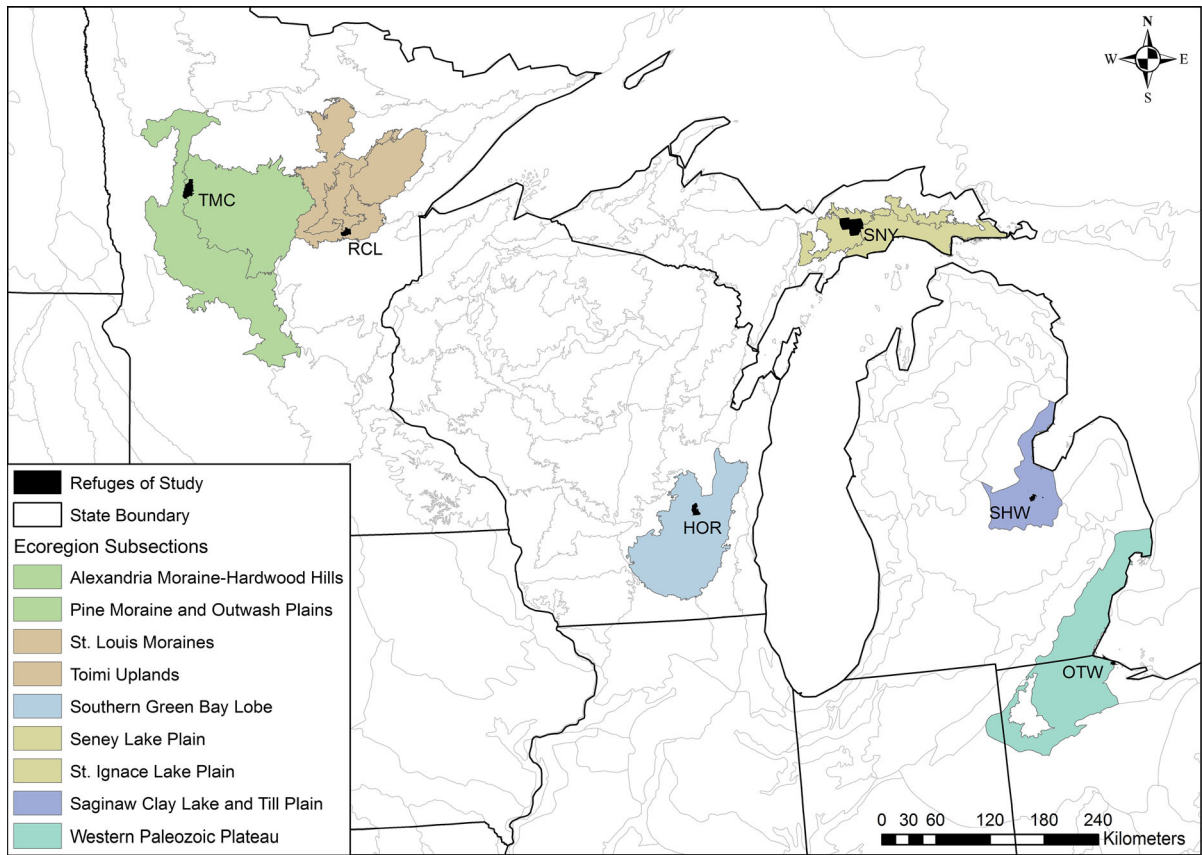


Fig. 1 Refuges of study and associated ecoregion subsections, located within the Upper Midwest region of the United States. Background polygons indicate different ecoregion subsections (Cleland et al. 1997). When a refuge boundary overlapped two

ecoregions, both were combined in the analyses. Codes used for each National Wildlife Refuge (from west to east) were: *TMC* Tamarac, *RCL* Rice Lake, *HOR* Horicon, *SNY* Seney, *SHW* Shiawassee, *OTW* Ottawa

Table 1 Characteristics of six National Wildlife Refuges in the Upper Midwest and amount of anthropogenic cover in the associated ecoregion(s) and within the refuge

Refuge	Area (ha)	Dominant land cover	Dominant forest type	Dominant forest soil type	Climate	Dominant ecoregion land use	Ecoregion % anthropogenic cover	Refuge % anthropogenic cover
Horicon	8842	Wetland	Deciduous	Mesic sands/loam	Lacustrine-influenced	Agriculture	75	8
Ottawa	2401	Upland	Deciduous	Mesic clay/loam	Lacustrine-influenced	Agriculture-urban	87	13
Rice Lake	7406	Upland	Deciduous	Mesic sands/loam	Lacustrine-influenced	Forest products	9	3
Shiawassee	3868	Upland	Deciduous	Mesic clay/loam	Lacustrine-influenced	Agriculture-urban	73	28
Seney	38,541	Wetland-upland	Coniferous	Xeric sands	Lacustrine-influenced	Forest products	4	2
Tamarac	17,295	Upland	Deciduous	Mesic sands/loam	Continental	Forest products	39	2

Table 2 Descriptions for selected landscape metrics used to describe landscape patterns for refuges and their associated ecoregions in the Upper Midwest

Metric	Description	Units	Index
Patch richness	Number of patch types on a landscape	–	Landscape composition
Shannon's diversity	The sum of proportional abundance of each land cover multiplied by that proportion	–	Landscape diversity
Mean patch area	Mean patch size of all patches on a landscape	ha	Landscape fragmentation
Largest patch index	Percentage of the landscape comprised of the largest patch	%	Landscape fragmentation
Landscape shape index	Total length of edge divided by the minimal length of class edge possible for a maximally aggregated class	%	Landscape fragmentation

patch index (LPI), and landscape shape index (LSI) (Table 2). We considered six 2006 National Land Cover Data (NLCD, USGS 2011) cover types to be anthropogenic (classification classes derived by NLCD): (1) developed open space, (2) developed low intensity, (3) developed medium intensity, (4) developed high intensity, (5) hay-pasture, and (6) cultivated crops. The ratio of natural land cover types to anthropogenic land cover types was calculated using those cover types occupying >1 % of the refuge or ecoregion from all NLCD classification types available.

Forest sampling

Forest REA plots ($n = 413$) were established along transects ($n = 64$) within upland forests as part of the work of Petrillo and Corace (2011). Transects were randomly placed within forest stands, with the first plot being located at least 20 m from the edge. Circular plots 0.01 ha in area were established every 40 m (2010 data) or 20 m (2011 data) along each transect, with overall transect length dependent upon stand size (plots per transect ranged from 3 to 21, with an average of 6). Total number of transects sampled at each refuge was dependent on forest dominance at that refuge and ranged from 7 to 14. At refuges with extensive forest cover (i.e., Seney and Tamarac) a selection of stands was sampled that was representative of the existing variability in forest types. At smaller refuges, sampling occurred in all stands >4 ha and constituted a nearly complete sampling of the forests at these refuges.

Forest REA methods were developed by Petrillo and Corace (2011) to quantify composition and structure using procedures similar to the U.S. Department of Agriculture Forest Service Forest Inventory

and Assessment Program (Bechtold and Patterson 2005; Waddell 2002). Within each plot, diameter at breast height (dbh) and basal area were measured for each overstory tree by species. In addition, coarse woody debris (CWD) >10 cm in diameter and at least 1.5 m in length was measured and assigned a decay class. CWD was sampled along three sub-transects running from plot center to plot edge at 0°, 135°, and 225° per the line-intercept guidelines of Waddell (2002). Groundcover was sampled within one 1 m² subplot placed along each of the three sub-transects. Distance from center point to subplot edge was staggered along the three transects at 1, 2, and 4 m. Three metrics from the REA dataset were used as potential correlates with earthworm communities and two additional metrics were calculated from the REA data: (1) total overstory basal area, (2) overstory species richness, (3) presence of coarse woody debris, (4) overstory basal area of tree species preferred by litter-feeding earthworms (Reich et al. 2005), and (5) percent of overstory basal area composed of coniferous species. Tree species preferred by litter-feeding earthworms and encountered at sample plots included boxelder (*Acer negundo*), black maple (*A. nigrum*), red maple (*A. rubrum*), sugar maple (*A. saccharum*), white ash (*Fraxinus americana*), black ash (*F. nigra*), green ash (*F. pennsylvanica*), hop-hornbeam (*Ostrya virginiana*), and basswood (*Tilia americana*).

Earthworm and soil sampling

Earthworms were sampled adjacent to the three groundcover subplots. Earthworm community composition and abundance were quantified using the mustard extraction method (Gunn 1992; Lawrence and Bowers 2002) within an area of 0.11 m² (33 cm × 33 cm). The mustard solution consisted of

10 g ground yellow mustard (*Sinapis alba*) powder per 1 L of water. The amount of mustard solution applied in each subplot varied depending on soil moisture and drainage patterns, with a maximum of 3.8 L of solution used per subplot. Earthworms that emerged within 5 min were collected and preserved in 70 % isopropyl alcohol. Earthworms were identified to genus or species and the length (mm) of each individual was measured within 24 h of collection. Earthworm biomass was calculated as ash-free dry mass (AFDg) using earthworm lengths and allometric equations developed by Hale et al. (2004).

Soil sampling was conducted concurrent with earthworm sampling. Soil cores approximately 27 cm deep were taken immediately adjacent to each earthworm plot for assessment of soil pH, organic matter content, and texture. Prior to collecting the sample loose litter was cleared from the soil surface. Soils were dried to a constant mass at 105 °C (a minimum of 48 h, maximum of 72 h in the oven) and then ground and passed through a 2 mm (#10 mesh) sieve. The hydrometer method (Bouyoucos 1962) was used to determine the proportion of sand, silt, and clay in determining soil texture. The pH of a 1:1 soil-to-water solution was measured using a benchtop pH meter. Organic matter content was determined by loss on ignition (LOI) over 4 h at 500 °C.

Statistical analysis

All statistical analyses, except where noted below, were performed using R (R Development Core Team 2011), and significance was determined at $\alpha = 0.05$. Subplot data were averaged to create plot-level data for all variables. In addition to those variables measured in the field, road and agriculture distances were calculated by determining Euclidean distance to each plot using a geographic information system (GIS). Agricultural land was identified using 2006 NLCD, with the land cover types hay-pasture and cultivated crops being considered agricultural. Percent anthropogenic cover within a 500 m buffer surrounding each transect was calculated using 2006 NLCD and the six anthropogenic land cover types used above. Variables were assessed for normality and transformed where necessary; a square root transformation was used for road distance, log transformation for agriculture distance, and arcsine square root transformation for data expressed as proportions. Following

transformation, all variables were relativized by the maximum (i.e., divided by the maximum value) to standardize variation across variables. Proportion clay was excluded from analysis due to correlation with sand and silt content. Analysis of variance (ANOVA) was used to test overall differences in total earthworm biomass among refuges, and multivariate analysis of variance (MANOVA) was used to test overall differences in community composition among refuges based on earthworm functional groups.

Two spatial scales of analysis (i.e., broad-scale consisting of ecoregions with refuges as the experimental unit and local-scale using transects within forests as the experimental unit) were used to assess the influence of vegetation, soils, and landscape metrics on earthworm abundance and community composition. Transect data for earthworm biomass were pooled and averaged by refuge ($n = 6$) at the broad scale. Shannon's diversity for earthworm communities was calculated for each refuge based on biomass by earthworm functional group. Biomass and diversity were tested as response variables with broad-scale landscape metrics describing patterns of anthropogenic activity within refuges and associated ecoregions as indicators. Due to low sample size at this scale ($n = 6$ refuges), landscape metrics were assessed using individual linear regressions rather than multiple regression to identify variables correlated with earthworm biomass and community diversity.

Each transect ($n = 64$) represented an individual forest stand at a given refuge at the local scale. Twelve forest characteristics (environmental variables) were related to total earthworm biomass and biomass by earthworm functional group as potential drivers of invasion patterns (Table 3). Stepwise multiple linear regression, using Akaike information criterion (AIC) values, was used to identify the best model explaining earthworm biomass. Analyses were first performed with all refuges pooled, and then by grouping transects at those refuges located within ecoregions dominated by anthropogenic land covers (for the purpose of this study >73 % anthropogenic land, $n = 27$ transects) and those at refuges in more natural ecoregions (>61 % natural land, $n = 37$) (Table 1). To explore differences in earthworm communities and forest characteristics between refuges in anthropogenic and natural landscapes canonical correspondence analysis (CCA) was performed in PC-ORD (McCune and Mefford 1999) using earthworm functional group

Table 3 Description of environmental variables assessed in association with earthworm abundance and community composition data in refuges of the Upper Midwest

Variable	Units	Description
Basal area	m ² /ha	Basal area of live overstory species
Preferred species	m ² /ha	Basal area of earthworm preferred live overstory species
Overstory species richness	#	Number of overstory species present
Conifer dominance	%	Percent of basal area consisting of coniferous species
Coarse woody debris	P/A	Presence of coarse woody debris
Soil pH	pH	Soil pH
Organic matter	%	Percent loss on ignition from soil
Sand	%	Percent sand content
Silt	%	Percent silt content
Road distance	m	Distance to the nearest road
Agriculture distance	m	Distance to nearest agricultural land
Anthropogenic cover	%	Percent of land within 500 m buffer comprised of anthropogenic cover

biomass and 12 environmental variables (Table 3). CCA is a direct gradient analysis that is useful when there is a priori knowledge about major factors that might be influencing the patterns of the dependent variable in space. The results of the CCA were evaluated using a Monte Carlo randomization test with 200 runs. Ordinations were plotted using a biplot vector cutoff value of 0.20.

Results

Earthworms were found at 92 % of the sampled forests (transects) and 77 % of the sampled plots. Seven earthworm taxa were identified and assigned to the following functional groups: epigeic (*Dendrobaena octaedra*, *Dendrodrilus rubidus*, *Eiseniella tetraedra*), endogeic (*Aporrectodea* spp.), epi-endogeic (*L. rubellus* and *Lumbricus* juveniles), and anecic (*L. terrestris*). Each earthworm functional group was present at all refuges, with the exception of anecic earthworms, which were not found at Rice Lake. Total earthworm biomass differed across the six refuges (ANOVA, $F_{5,58} = 3.77$, $P < 0.01$), with mean biomass of all functional groups ranging from 0.40 AFDg/m² at Seney to 2.14 AFDg/m² at Horicon (Fig. 2). Earthworm community composition based on functional groups also differed among refuges (MANOVA, $F_{20,183} = 10.17$, Wilks $\lambda = 0.08$, $P < 0.001$), with pairwise comparisons indicating specific differences between refuges (Table 4). The dominant

functional group at each refuge varied, with endogeic dominant at Tamarac, anecic at Horicon, and epi-endogeic dominant at the remaining four refuges.

Broad-scale analysis

At the broad-scale of refuges within ecoregions, total earthworm biomass was explained by a positive relationship with mean patch area of anthropogenic cover within refuges ($R^2 = 0.74$, $P = 0.03$), with all other metrics being unrelated and not included in further analyses. In some cases however, metrics of anthropogenic land cover within the surrounding ecoregion were important drivers of earthworm

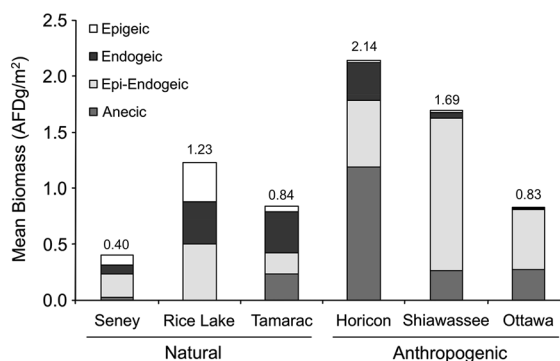


Fig. 2 Mean earthworm biomass by functional group within upland forests of six National Wildlife Refuges in the Upper Midwest. Refuges are arranged in ranked order based on the proportion of anthropogenic cover in the surrounding ecoregion. Values above bars represent mean earthworm biomass across all refuge stands for all earthworm functional groups

Table 4 Mean earthworm biomass (AFDg/m² ± 1 SE) totaled and by functional group within sampled upland forest stands (transects; sample size follows refuge name)

Refuge	Total	Epigeic	Endogeic	Epi-endogeic	Anecic
Horicon (10)	2.14 (±0.52)a	0.01 (±0.01)b	0.34 (±0.09)a	0.59 (±0.17)b	1.19 (±0.28)a
Ottawa (10)	0.83 (±0.14)ab	0.01 (±0.01)b	<0.01 (±0.01)a	0.53 (±0.13)b	0.27 (±0.09)b
Rice Lake (12)	1.23 (±0.20)ab	0.36 (±0.06)a	0.37(±0.05)a	0.51(±0.15)b	–
Shiawassee (7)	1.69 (±0.17)ab	0.01 (±0.01)b	0.05 (±0.01)a	1.36 (±0.20)a	0.27 (±0.09)b
Seney (11)	0.40 (±0.21)b	0.09 (±0.03)b	0.07 (±0.05)a	0.21 (±0.11)b	0.03 (±0.03)b
Tamarac (14)	0.84 (±0.38)b	0.05 (±0.02)b	0.36 (±0.15)a	0.19 (±0.11)b	0.23 (±0.16)b
F	3.77	19.42	3.35	7.15	8.74
P	0.005	<0.001	0.01	< 0.001	< 0.001

Differing letters indicate significant differences in pairwise comparisons among refuges (ANOVA)

abundance when analyzed by functional group. Endogeic biomass was best explained by land cover Shannon's diversity in the surrounding ecoregion ($R^2 = 0.66$, $P = 0.05$). Epi-endogeic biomass was explained by the proportion of anthropogenic cover on the refuge ($R^2 = 0.89$, $P < 0.01$), refuge mean patch area ($R^2 = 0.69$, $P = 0.04$), and refuge largest patch index ($R^2 = 0.92$, $P < 0.01$). No relationships were found among landscape metrics and the biomass of epigeic or anecic earthworms.

Overall refuge earthworm community diversity (Shannon's diversity index) was also related to the ecoregional anthropogenic land cover patterns, including a negative relationship with both ecoregion largest patch index ($R^2 = 0.88$, $P < 0.01$) and proportion of anthropogenic cover across the ecoregion ($R^2 = 0.89$, $P < 0.01$). Earthworm community diversity was also positively correlated with the ratio of natural to anthropogenic cover types ($R^2 = 0.94$, $P < 0.01$).

Local-scale analysis

At the scale of individual transects within refuges, total earthworm biomass was positively correlated with low conifer dominance, high silt content, high anthropogenic cover within 500 m, high basal area, sites closer to roads, and sites more distant from agriculture (Table 5, $R^2 = 0.36$, $P < 0.001$). With the exception of endogeic earthworms, models improved and variables explaining biomass differed when analyzed by functional group (Table 5). Epigeic biomass was best explained by a model including soil pH, agriculture distance, organic matter, road distance, silt content, coarse woody debris,

anthropogenic cover within 500 m, and overstory species richness ($R^2 = 0.52$, $P < 0.001$). Soil pH and agriculture distance were the most important explanatory variables for epigeic biomass, with increased biomass being associated with low pH and close proximity to agriculture. Endogeic biomass was weakly explained by conifer dominance and agriculture distance ($R^2 = 0.10$, $P < 0.05$), with higher biomass being associated with low conifer dominance and sites distant from agriculture. Epi-endogeic biomass was best explained by soil pH, conifer dominance, basal area, organic matter, anthropogenic cover within 500 m, road distance, and overstory species richness ($R^2 = 0.51$, $P < 0.001$), with high soil pH being the most important explanatory variable of high biomass. Anecic biomass was explained by anthropogenic cover within 500 m, soil pH, basal area, agriculture distance, conifer dominance, and overstory species richness ($R^2 = 0.39$, $P < 0.001$), with high biomass being most explained by high anthropogenic cover.

Grouping refuges into anthropogenic and natural landscapes resulted in differing effects of variables in explaining total biomass and biomass by functional groups. We were better able to explain total biomass for natural ecoregions ($R^2 = 0.65$, $P < 0.001$, Table 6) than for anthropogenic ($R^2 = 0.42$, $P < 0.001$, Table 7), but both analyses resulted in better models than that for total earthworm biomass at all refuges combined. Epigeic biomass in natural ecoregions was better explained than when all refuges were pooled ($R^2 = 0.70$, $P < 0.001$, Table 6), but we were unable to develop a significant model for epigeic biomass in anthropogenic ecoregions. Models were found for

Table 5 Stepwise multiple regression modeling results describing variables influencing total earthworm biomass and earthworm biomass by functional groups within upland forests of six refuges

Response	Variable	F	P	R ²
Total biomass	<i>Model</i>	5.35	<0.001	0.36
	Conifer dominance	-2.89	<0.01	0.11
	Silt content	1.98	0.05	0.08
	Anthropogenic cover	2.04	<0.05	0.07
	Basal area	2.85	<0.01	0.06
	Road distance	-1.55	0.13	0.02
	Agriculture distance	1.92	0.05	0.02
Epigeic biomass	<i>Model</i>	7.48	<0.001	0.52
	Soil pH	-3.49	<0.001	0.15
	Agriculture distance	-3.91	<0.001	0.13
	Organic matter	-1.84	0.07	0.08
	Road distance	-1.86	0.07	0.05
	Silt content	3.12	<0.01	0.04
	Coarse woody debris	-2.20	0.03	0.03
	Anthropogenic cover	-2.26	0.03	0.03
	Overstory species richness	1.53	0.13	0.01
	<i>Model</i>	3.23	<0.05	0.10
Endogeic biomass	Conifer dominance	-2.40	0.02	0.07
	Agriculture distance	1.68	0.10	0.03
Epi-endogeic biomass	<i>Model</i>	7.17	<0.001	0.51
	Soil pH	1.99	0.05	0.07
	Conifer dominance	-1.73	0.09	0.07
	Basal area	2.96	<0.01	0.06
	Organic matter	-1.87	0.07	0.05
	Anthropogenic cover	1.41	0.16	0.05
	Road distance	-2.07	0.04	0.05
	Overstory species richness	1.53	0.13	0.04
Anecic biomass	<i>Model</i>	6.06	<0.001	0.39
	Anthropogenic cover	4.44	<0.001	0.16
	Soil pH	1.63	0.11	0.07
	Basal area	3.01	<0.01	0.07
	Agriculture distance	2.90	<0.01	0.04
	Conifer dominance	-1.53	0.13	0.03
	Overstory species richness	-2.13	0.04	0.02

endogeic biomass at both natural ($R^2 = 0.37$, $P < 0.01$) and anthropogenic ($R^2 = 0.34$, $P = 0.02$) ecoregions, though the variance explained still remained low. Epi-endogeic biomass was better predicted for natural ecoregions ($R^2 = 0.64$, $P < 0.001$) than with all refuges combined, but not for anthropogenic ecoregions ($R^2 = 0.43$, $P = 0.01$). Anecic biomass was better explained for both natural ($R^2 = 0.49$, $P < 0.01$) and anthropogenic ($R^2 = 0.40$, $P = 0.04$) ecoregions. Despite some improvement, the variance explained

for both epi-endogeic and anecic biomass remained relatively low.

Canonical correspondence analysis (CCA) explained 27 % of the cumulative variance in earthworm community composition across three axes and showed clear separation between natural and anthropogenic (Monte Carlo $P < 0.01$). The first axis of the CCA ordination explained 16 % of the variance in earthworm community composition (Table 8). This axis was most strongly correlated with soil pH, organic

Table 6 Stepwise multiple regression modeling results describing variables influencing total earthworm biomass and earthworm biomass by functional groups within upland forests at those refuges within natural ecoregions

Response	Variable	F	P	R ²	
Total biomass	<i>Model</i>	6.42			
		<0.001	0.65		
		Soil pH	5.17		
		<0.001	0.22		
		Road distance	-3.50	<0.01	0.11
		Basal area	3.21	<0.01	0.06
		Anthropogenic cover	1.96	0.06	0.05
	Agriculture distance	-1.62	0.12	0.05	
	Organic matter	-1.42	0.17	0.02	
	Epigeic biomass	<i>Model</i>	14.27		
		<0.001	0.70		
		Agriculture distance	-4.08		
		<0.001	0.30		
		Sand content	-3.46	<0.01	0.14
		Road distance	-2.82	<0.01	0.12
Silt content		-3.35	<0.01	0.10	
Overstory species richness		1.51	0.14	0.04	
Endogeic biomass		<i>Model</i>	4.79	<0.01	0.37
			Soil pH	4.08	
		<0.001	0.25		
		Agriculture distance	-2.53	0.02	0.06
		Sand content	1.65	0.11	0.04
Road distance	-1.84	0.07	0.03		
Epi-endogeic biomass	<i>Model</i>	6.34			
		<0.001	0.64		
		Road distance	-3.82		
		<0.001	0.17		
		Conifer dominance	-2.09	<0.05	0.11
		Soil pH	3.88		
		<0.001	0.10		
		Basal area	4.15		
		<0.001	0.10		
	Anthropogenic cover	2.49	0.02	0.08	
Sand content	-1.41	0.17	0.04		
Silt content	-1.48	0.15	0.03		
Organic matter	-1.31	0.20	0.02		
Anecic biomass	<i>Model</i>	4.86	<0.01	0.49	
		Soil pH	4.96		
		<0.001	0.24		
		Organic matter	-3.24	<0.01	0.07
		Basal area	3.12	<0.01	0.06
		Anthropogenic cover	2.71	0.01	0.06
		Overstory species richness	-1.64	0.11	0.04
	Road distance	-1.38	0.18	0.02	

Table 7 Stepwise multiple regression modeling results describing variables influencing total earthworm biomass and earthworm biomass by functional groups within upland forests at those refuges within anthropogenic ecoregions

Response	Variable	F	P	R ²
Total biomass	<i>Model</i>	3.09	0.03	0.42
	Anthropogenic cover	2.69	0.01	0.14
	Silt content	1.58	0.13	0.09
	Basal area	1.58	0.13	0.08
	Agriculture distance	1.79	0.09	0.07
	Sand content	1.39	0.18	0.04
Epigeic biomass	<i>Model</i>	1.35	0.28	–
Endogeic biomass	<i>Model</i>	3.88	0.02	0.34
	Agriculture distance	3.19	<0.01	0.20
	Organic matter	2.57	0.02	0.10
	Sand content	2.00	0.06	0.04
Epi-endogeic biomass	<i>Model</i>	4.13	0.01	0.43
	Silt content	3.52	<0.01	0.23
	Basal area	2.38	0.03	0.09
	Overstory tree species	1.94	0.07	0.08
	Road distance	–1.40	0.17	0.03
Anecic biomass	<i>Model</i>	2.77	0.04	0.40
	Anthropogenic cover	2.19	0.04	0.10
	Silt content	2.88	<0.01	0.10
	Sand content	2.65	<0.01	0.08
	Soil pH	–2.52	<0.01	0.06
	Basal area	1.62	0.12	0.06

No significant model was found for epigeic biomass

matter, and conifer dominance, as well as with the type of ecoregion (natural or anthropogenic). Refuges located within anthropogenic ecoregions were associated with high pH, high organic matter, low conifer dominance, high basal area of all tree species, and high anthropogenic cover (Fig. 3). Axis two explained an additional 8 % of the variance, and was most closely correlated with overstory tree species and distance to agriculture (Table 8; Fig. 3).

Discussion

Broad-scale patterns of earthworm distribution

We found that refuges in ecoregions with a high proportion of anthropogenic lands generally had greater earthworm biomass and more biomass of what are considered the more impactful functional groups for forest ecosystems (i.e., epi-endogeic and anecic).

Although based on a relatively small sample of six refuges, our broad-scale analyses suggest that earthworm invasion patterns may be correlated with broad patterns of anthropogenic land use within and surrounding invaded areas. Refuges and associated ecoregions less dominated by anthropogenic land covers, such as Seney and Tamarac, had considerably lower mean earthworm biomass. Conversely, greater earthworm biomass was encountered at refuges (Horicon and Shiawassee) which had more anthropogenic cover types and were associated with ecoregions in which these cover types predominated. Examining earthworm invasion by functional group indicated that this relationship was mainly driven by epi-endogeic earthworms. Epi-endogeic earthworms were most strongly associated with anthropogenic lands, and abundance tended to increase as anthropogenic cover patch size increased and comprised more of the refuge. There were, however, some exceptions (Fig. 2). First, Rice Lake, which had

Table 8 Summary statistics for the canonical correspondence analysis (CCA) of local level earthworm community composition related to environmental variables

CCA summary	Axis 1	Axis 2	Axis 3
Eigenvalue	0.291	0.151	0.064
Variance in community data			
% of variance explained	15.5	8.1	3.4
Cumulative % explained	15.5	23.6	27.0
Pearson correlation	0.825	0.717	0.647
Inter-set correlations			
Soil pH	-0.603	0.054	0.179
Organic matter	-0.537	0.084	-0.041
Conifer dominance	0.438	-0.080	-0.208
Basal area	-0.381	0.152	-0.207
Anthropogenic cover	-0.378	0.095	-0.270
Silt content	-0.352	0.222	0.001
Sand content	0.308	-0.301	0.013
Preferred species	-0.263	0.190	0.070
Coarse woody debris	-0.168	0.026	0.073
Road distance	-0.120	-0.218	0.185
Overstory species richness	-0.009	0.371	-0.004
Agriculture distance	-0.004	-0.335	0.305

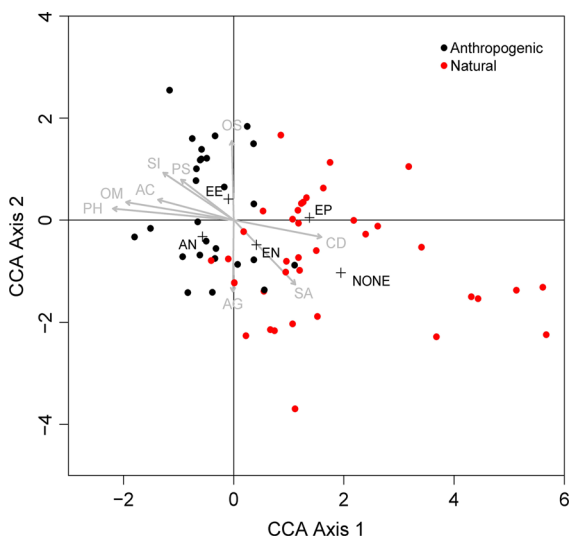


Fig. 3 Canonical correspondence analysis (CCA) biplot explaining earthworm community composition by functional group within upland forests at refuges within anthropogenic and natural ecoregions. Environmental variables: AC anthropogenic cover, AG agriculture proximity, CD conifer dominance, OM organic matter, OS number of overstory species, PH soil pH, PS basal area preferred species, SA sand content, SI silt content. Functional groups: EP epigeic, EN endogeic, EE epi-endogeic, AN anecic, NONE no earthworms present

relatively low amounts of anthropogenic cover within the refuge and surrounding ecoregion, had greater earthworm biomass than Seney or Tamarac, but interestingly lacked *L. terrestris*. This may indicate that the introduction of later successional earthworm groups is limited by surrounding ecoregional land use, but that Rice Lake contains natural lands capable of supporting larger earthworm populations. Secondly, at Ottawa, the low earthworm biomass encountered was unexpected since there is a high proportion of anthropogenic land within and surrounding the refuge, but this result may be related to seasonal flooding and standing water conditions (saturated soils) that occurred in the spring before earthworm sampling took place. Furthermore, across the whole region in which these refuges reside, it is unclear how climate might affect earthworm biomass or functional groups. Anthropogenic activity, particularly agriculture, is somewhat driven by climate, so this relationship should be examined further and may be confounding in our study.

In contrast to the relationship with earthworm biomass, and contradictory to our hypothesis, the presence of anthropogenic lands in the refuge and

surrounding ecoregion had no effect or tended to decrease earthworm functional group *diversity*. In fact, a high ratio of natural to anthropogenic cover types within the ecoregion was associated with greater diversity of earthworms. Similar results were found in Europe, where high earthworm diversity is promoted for the benefit of agricultural lands (Nieminen et al. 2011). Earthworm diversity was found to be lower in agricultural lands than in adjacent field margins that consisted of natural land covers (Smith et al. 2008; Nieminen et al. 2011). A potential explanation for this finding is that anthropogenic lands promote epi-endogeic and anecic earthworms, while restricting epigeic and endogeic earthworms. Further supporting this was the finding that endogeic earthworm biomass was greater where ecoregional land cover diversity was high. Thus a mosaic including natural and anthropogenic land cover types may result in a greater diversity of food resources and other habitat conditions or niches, thereby allowing all earthworm functional groups to occur simultaneously.

Characteristics of heavily invaded forests

Heavily-invaded forests (as denoted by greater earthworm biomass) had relatively lower conifer dominance, higher silt content, higher anthropogenic cover within and immediately surrounding the stand, higher basal area, and were closer to roads and farther from agriculture. These results, with the exception of distance from agriculture, support the findings of other studies determining drivers of earthworm distribution (Edwards and Bohlen 1996; Holdsworth et al. 2007b; Tiunov et al. 2006). Forests heavily invaded by epigeic earthworms tended to have lower soil pH, higher silt content, little coarse woody debris, lower amounts of anthropogenic cover, higher overstory species richness, and occurred within close proximity to agriculture and roads. This was most strongly explained by soil pH, with epigeic being the only group to be associated with lower pH sites. The ability to tolerate lower pH allows this group to dominate at these sites, while their absence from other sites may be due to their eventual replacement by other earthworm groups and the reduction of leaf litter caused by these groups (Hale et al. 2005; Holdsworth et al. 2007b). Endogeic biomass was only minimally explained by lower conifer dominance and sites distant from agriculture, suggesting that their habitat preferences

may be more wide-ranging and that they are better able to co-exist with epi-endogeic and anecic earthworms. Epi-endogeic and anecic earthworms were both associated with sites that had higher soil pH, higher anthropogenic cover, higher basal area, and lower conifer dominance. Anecic earthworms, however, occurred at greater biomass in sites with lower overstory tree species richness, often those stands dominated by one or two highly preferred species (such as maple), while epi-endogeic species were in sites with higher overstory species richness. Contradictory to what was hypothesized, epi-endogeic earthworms were associated with lower organic matter, which could be an impact of the feeding activity of this group rather than a driver of distribution and abundance.

Influence of natural versus anthropogenic ecoregions

The differing results between natural and anthropogenic lands suggest that anthropogenic factors are correlated with earthworm invasion patterns and that forest characteristics are of secondary importance. At refuges where anthropogenic land use dominated the ecoregion, anthropogenic cover was the best explanatory variable. Anthropogenic cover and agriculture distance were both significant variables in predicting overall earthworm abundance even in natural ecoregions. Where anthropogenic lands were lacking, other characteristics, particularly soil pH, took importance in predicting overall and functional group biomass.

Forests at refuges within anthropogenic ecoregions differed from those within natural ecoregions in both their environmental characteristics and their degree of association with earthworm functional groups. Transects within anthropogenic ecoregions were associated with sites commonly thought to be more preferable to earthworms, such as those with high soil pH and increased organic matter, and these were more closely associated with epi-endogeic and anecic earthworms. Epigeic earthworms were associated with low pH, low organic matter, low anthropogenic cover, and high conifer dominance sites, conditions that were also associated with stands at refuges within natural ecoregions. Where earthworm-free sites occurred, they were associated with forests only at refuges within natural ecoregions rather than anthropogenic. These results are consistent with the findings that

anthropogenic lands promote earthworm invasion, that epi-endogeic earthworms are most strongly associated with anthropogenic land covers, and that natural land covers may offer opportunities for epigeic and endogeic earthworms.

Study limitations

Overall, the earthworm biomass values we found among our refuges tended to be lower than reported elsewhere (Hale et al. 2004, 2005; Gundale et al. 2005; Frelich et al. 2006). Although this may indicate that our study refuges have lower loads of earthworms than forests previously studied elsewhere in the Upper Midwest, other possible explanations may include the timing of our sampling and the fact that we sampled across forest types. Sampling during drier conditions and within conifer stands (albeit a small part of our overall sample) may have reduced our earthworm numbers compared to studies conducted in the spring and focused on deciduous forests. Nonetheless, we believe the *pattern* of biomass and community composition we observed among the sampled refuges is of more interest to refuge planners and managers than purely the magnitude of the response. Other potential limitations of our study include our small sample size of six refuges, our focus on functional groups and not species of earthworm, our a posteriori categories of natural and anthropogenic, and the lack of resolution in our analysis of anthropogenic cover types. Our functional groups did not represent all possible earthworm species, which may limit inference in other regions and in areas with other species present. Further exploration of differences in the influence of agricultural and other anthropogenic lands on earthworm populations between native habitats and invaded areas is needed and may provide insight into the success and spread of exotic earthworms in the Upper Midwest.

Management implications

Ecosystem conservation and restoration occurs at multiple scales and in multiple phases (George and Zack 2001). The planning phase often includes using remotely-sensed data across broad landscapes to provide context for work at finer spatial scales (i.e., stands or patches). Past work on these Upper Midwest refuges provided forest restoration context based upon

the dominance of current forest types relative to pre-European coverage (Corace et al. 2012). Because the 1997 *Refuge Improvement Act* prioritizes restoration within the NWRS, the study herein described identifies potential opportunities and limitations for forest restoration on the sampled refuges. In particular, the increased dominance of maple and other deciduous tree species previously described by Corace et al. (2012) may have fostered the spread of earthworms, along with agriculture, road developments, and other factors we have described in this paper.

Thus, we suggest our findings indicate that land use patterns should be considered when determining future forest management opportunities on these refuges. In the past many refuges have incorporated anthropogenic agricultural cover types into their lands for wildlife forage or cover, which may have aided the introduction and spread of earthworms. The linkage between anthropogenic and agricultural land covers and earthworm patterns suggests a potential benefit to reducing the dominance of anthropogenic features across the landscape. Further support for removal of agricultural lands comes from an assessment of post-agricultural forests that found few agricultural legacies remained, and that soil physical and chemical properties were similar to that of undisturbed forests (Flinn and Marks 2007). Although some earthworms were present, earthworm communities did not differ between post-agriculture and undisturbed forests (Flinn and Marks 2007).

Previous studies have suggested that exotic earthworm invasion proceeds in succession beginning with epigeic earthworms, followed by endogeic, epi-endogeic, and finally anecic earthworms (Hale et al. 2005; Holdsworth et al. 2007b). Based on the presence and absence of various earthworm functional groups, our findings suggest that the successional development of earthworm communities in forests across the Upper Midwest is not yet complete. For instance, Rice Lake, which had no anecic earthworms present, had higher biomass of epigeic earthworms than any other refuge. In contrast, Horicon, the refuge with the greatest earthworm biomass, had very low biomass of epigeic earthworms and the highest biomass of anecic earthworms. Forests with no earthworms encountered were found at Seney and Tamarac, and many stands sampled were not invaded by the full suite of earthworm groups. This lends support to the use of strategies to prevent further introduction and spread of

earthworms, such as restricting soil movement between sites by equipment or vehicles and limiting the use of earthworms as fishing bait (Cameron et al. 2007; Hale 2008). These strategies also have merit at invaded sites, as multiple introductions have been shown to increase genetic variability and may be linked to increased impacts (Hale 2008).

Earthworm removal in invaded sites is difficult, if not impossible. There has been some evidence that removal of invasive plants may reduce earthworm biomass, and could potentially be used as a method for earthworm control (Madritch and Lindroth 2008). Understanding the potential association between invasive plants and earthworms is critical for forest management and is an important area of future research (Nuzzo et al. 2009). Forest management should also incorporate consideration for both short and long term and synergistic effects of earthworms on ecosystem patterns and processes and explore methods for mitigating these impacts. For instance, earthworms and white-tailed deer (*Odocoileus virginianus*) browse may have cumulative negative effects on natural plant communities (Frelich et al. 2006). Reducing deer browse in areas with high earthworm abundance may be a mitigating action that could be taken, and is being taken, by some National Wildlife Refuge System land managers. Furthermore, a better understanding of the differing ecology of earthworm functional groups is also important, since the later successional epi-endogeic and anecic earthworms contribute most to changes seen in the forest floor and understory community, while endogeic and epigeic earthworms exhibit less influence (Frelich et al. 2006). Along with changes in land use, other potential stressors, including climate change (Griffith et al. 2009), should be expected to further exacerbate the impacts of earthworms and other exotic species in the Upper Midwest in the future.

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