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# Predicting exotic earthworm distribution in the northern Great Lakes region

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**Abstract** Identifying influences of earthworm invasion and distribution in the northern Great Lakes is an important step in predicting the potential extent and impact of earthworms across the region. The occurrence of earthworm signs, indicating presence in general, and middens, indicating presence of *Lumbricus terrestris* exclusively, in the Huron Mountains located in the Upper Peninsula of Michigan were modeled using generalized linear models and stepwise regression to identify important environmental variables. Models were then applied to earthworm occurrence data from Seney National Wildlife Refuge, also located in the Upper Peninsula of Michigan to validate results. Occurrence of earthworm signs was associated with high soil pH, high basal area of earthworm preferred overstory species, and north facing aspects. Middens of *L. terrestris* were associated with high soil pH, high basal area of preferred species, and close proximity to roads. The resulting model for *L. terrestris* was incorporated into a geographic information system (GIS) to map the expected distribution, both current and potential, across the study area. Results indicate that *L. terrestris* has not yet fully saturated its potential habitat, as it is currently found close to roads and has yet to establish in most interior forests sampled. Comparing field measured data to GIS layers revealed limitations in the precision of publicly available spatial data layers that should be addressed in future attempts to predict the extent of earthworm invasion across the larger Great Lakes region. However, within the Huron Mountains, it is predicted that the distribution of *L. terrestris* will cover, at minimum, 41 % of the area.

**Keywords** Distribution prediction · European earthworms · Great Lakes · *Lumbricus terrestris* · Spatial modeling

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## Introduction

The invasion of European earthworms (family Lumbricidae) in the Great Lakes region is expected to have detrimental impacts on forest ecosystems (Bohlen et al. 2004; Frelich et al. 2006). Exotic earthworms have been shown to decrease the thickness of the forest floor, and increase soil compaction, erosion, and nutrient leaching (Scheu and Parkinson 1994; Bohlen et al. 2004; Hale et al. 2008). They also have the potential to cause declines in native plants, arthropods, salamanders, ground-nesting birds, and small mammal populations (Hale 2008; Maerz et al. 2009; Loss and Blair 2011). As ecosystem engineers (Jones et al. 1994), earthworms influence the major processes that underlie ecosystems and their health, making invasion a concern for the persistence of forest ecosystems as they are now (Frelich et al. 2006). Identifying influences of earthworm invasion and distribution is of interest for predicting the potential extent and impact of exotic earthworms in the Great Lakes.

The introduction of European earthworms has been both intentional, such as for use in gardening and agriculture, and accidental, in soils used for ballast in ships (Barley 1961). Further spread of earthworms, both short and long distances, has been facilitated by human activity. Human-mediated spread occurs through the release of earthworms used as fishing bait and in the movement of soil containing earthworms and/or cocoons (Hendrix and Bohlen 2002). Earthworm cocoons, or egg capsules, are able to survive cold temperatures and desiccation over long periods of time (Holmstrup and Westh 1995). Consequently any movement of soil, including unintentional movement on shoes, tire treads, and other equipment, can spread earthworms via cocoons. Thus it is thought that the transport of cocoons on vehicles is an important mechanism for the spread of earthworms into relatively undisturbed forested ecosystems (Cameron et al. 2008). Furthermore, cocoons can be transported in waterways, facilitating spread along lakes and streams or in conjunction with floodwaters (Schwert and Dance 1979). These mechanisms exert a dynamic influence on the patterns of earthworm invasion across the landscape, and offer opportunities for multiple introductions, which can increase the genetic diversity of earthworm populations potentially increasing success (Cameron et al. 2008). While anthropogenic dispersal can have a substantial effect on introduction, autogenic dispersal processes complete the saturation of suitable habitat as invasion proceeds to later stages, particularly as earthworms move into areas where human-mediated dispersal mechanisms are lacking.

While anthropogenic activity is known to accelerate short and long distance dispersal, exotic earthworm presence and abundance at later stages of invasion is dependent primarily on site conditions such as soil and litter properties (Tiunov et al. 2006). These habitat characteristics can be considered static because they define the maximum extent of the potentially invasible area, unlike the dynamic role that dispersal mechanisms play in invasion. Forest composition is particularly important for litter feeding earthworm species, which prefer materials that are calcium-rich, with a low C:N ratio and low concentration of phenols and tannins (Hendriksen 1990; Reich et al. 2005). For example, species in the genus *Lumbricus* were found to prefer litter from basswood (*Tilia*), ash (*Fraxinus*) and alder (*Alnus*) to litter from oak (*Quercus*) and beech (*Fagus*) (Hendriksen 1990). Earthworm populations can also be limited by unfavorable soil conditions, such as low pH, low moisture, and/or coarse texture (Tiunov et al. 2006). These soil conditions in turn influence forest composition, and thus litter and organic matter availability. In addition, topographical characteristics such as aspect and slope are expected to influence forest composition and soils, as well as natural dispersal ability, ultimately affecting earthworm occurrence across the landscape.

Of the European earthworms identified in the Great Lakes, *Lumbricus terrestris* (an anecic species, commonly known as the night crawler) has had a relatively large impact on forested ecosystems (Frelich et al. 2006). This is partly attributable to their large size (adults range from 80 to 150 mm), and thus high consumption of litter and substantial alteration of the soil structure from burrowing. In forests, *L. terrestris* preferentially feeds on fresh leaf litter and large populations have the potential to consume all litter accumulated each season (Hale et al. 2005). Their use of deep vertical burrows also results in transport of surface organic matter into the mineral soil and potential for increased macropore water flow. It is thought that the presence of *L. terrestris* in combination with other earthworm species, whose feeding and burrowing habits have differing effects, will contribute to increased alteration of the forest floor, soil, and ultimately the flora and fauna of forests (Hale et al. 2008). For example, the commonly associated species *Lumbricus rubellus* feeds on older organic matter that has accumulated on the soil surface, while *L. terrestris* feeds on fresh litter, together rapidly decreasing all components of the forest floor.

The objectives of this research were to identify factors influencing the distribution of earthworms in northern Great Lakes forested landscapes, using the land of the Huron Mountain Club (hereafter referred to as the Huron Mountains) in the Upper Peninsula of Michigan as a target for detailed modeling efforts. We hypothesized that earthworm signs and middens (unique to *L. terrestris*) would be positively related to the following characteristics favoring earthworm dispersal and survival: proximity to human activity (distance to roads and water bodies), forest composition (basal area of earthworm preferred species), and soil and site conditions (warm, mesic, slightly acidic to calcareous soils on flat sites at low elevation). After determination of the importance of these variables, a predictive model was created to identify high risk areas for earthworm invasion and to determine the potential distribution of earthworms across the study area.

## Study area

Earthworm invasion was assessed within the Huron Mountains located in Marquette County in the Upper Peninsula, Michigan, USA. The land is a limited access private club set aside as a nature reserve and used primarily as a remote area for hunting, fishing, and recreation. According to 2006 National Land Cover Data (NLCD, USGS 2011), the area is dominated by forested land, consisting of 27 % evergreen forest, 24 % mixed forest, 19 % deciduous forest, and 12 % woody wetlands. The site contains a series of inland lakes and streams (12 % of the area) and is bordered by Lake Superior to the north. Terrain is highly variable, ranging from an elevation of 183 m above sea level at Lake Superior to a maximum elevation of approximately 510 m inland. There is currently very little developed land (3 % of the area), and thus relatively limited human activity beyond a small network of cabins, roads, trails, and fishing access points. Some portions of the area, however, have been logged or farmed in the past creating non-natural ecosystem types, such as open meadows that are dominated by European weed species (Simpson et al. 1990). Variable soil conditions exist across the area, ranging from excessively drained sandy soils to very poorly drained muck and peat (Soil Survey Geographic data, SSURGO, NRCS 2006). Soil pH averages 4.5, however areas with pH values as low as 3.0 and as high as 7.0 are present (SSURGO, NRCS 2006).

## Methods

Field sampling took place at random points generated within the study area boundary (excluding open water) using ArcGIS (ESRI 2011). Actual GPS coordinates were recorded in the field and updated for spatial analyses. At each plot, site characteristics of slope and aspect were measured. Forest composition was assessed from plot center using a basal area factor 2 metric prism to count trees by species. Overstory species were ranked by their suitability as a food source for earthworms based on available assays and literature (Reich et al. 2005; Yatso and Lilleskov unpublished). Preferred species present in the study area were basswood (*Tilia americana*), maple (*Acer* spp.), ash (*Fraxinus* spp.), and balsam fir (*Abies balsamea*). While not commonly mentioned as a species preferred by exotic earthworms in the Great Lakes region, balsam fir was included based on the association of high earthworm abundance with the related European species silver fir (*Abies alba*; Reich et al. 2005). Using this information the basal area ($m^2$/ha) of preferred trees was calculated for each point. Plots in wetlands were identified, as these conditions may limit earthworm presence due to acidic and saturated soil conditions (Tiunov et al. 2006). A mineral soil core from 0 to 10 cm was collected, from which soil pH was determined using both the $H_2O$ and $CaCl_2$ methods (Thomas 1996) for verification (pH $CaCl_2$ results were more consistent and are presented hereafter).

Earthworm presence was confirmed without extraction by documentation of signs of earthworm activity. This included mixing of organic and mineral soil layers (e.g., admixture of Oa and E horizons), missing organic soil layers (Oa or Oe horizons), earthworm castings, and presence of earthworms. Presence of *L. terrestris*, specifically, was confirmed by identifying middens, recognized by the distinct mounding of residual plant material, castings, central plug composed of leaf litter, and underlying burrow. Identification of middens is a rapid and non-destructive way to estimate the presence and abundance of *L. terrestris* (Clapperton et al. 2008). Previous investigations have confirmed the presence of *L. terrestris*, *L. rubellus*, *Aporrectodea* spp., and *Dendrobaena octaedra* in the Huron Mountains (Karberg and Lilleskov 2009; Lilleskov unpublished report to the Huron Mountain Wildlife Foundation).

Additional landscape characteristics were obtained using spatial GIS data layers. Roads and hydrologic features were obtained from Michigan Geographic Framework data (State of Michigan 2009). Private roads within the study area were digitized based on aerial photographs and ground-truthing. Distances to roads and hydrologic features (excluding Lake Superior) were calculated in ArcGIS (ESRI 2011) using Euclidean distance. Elevation was extracted from a digital elevation model (DEM). Finally, drainage index, a measure of the soil water availability that incorporates aspects of soil taxonomy including moisture regime, drainage class, water table depth, soil volume, and secondarily, soil texture, was obtained for the study area (Schaetzl et al. 2009).

To assess patterns of earthworm distribution, site and landscape characteristics (referred to as environmental variables, Table 1) were related to the presence or absence of earthworm signs, as well as to the presence or absence of middens (indicating patterns specific to *L. terrestris*). Statistical analyses were performed using R (R Development Core Team 2011). Pearson's correlation was used to test environmental variables for multicollinearity. Correlations were considered significant at $P < 0.01$. A generalized linear model (GLM) using a binomial distribution and logit link function was applied to explain the presence of earthworm signs and middens based on influential environmental variables. The best model was selected using a stepwise procedure based on Akaike's Information Criterion (AIC) and maximization of area under the receiver operator characteristic (ROC) curve (AUC, Hanley and McNeil 1982). AUC values represent the probability that the model correctly predicts presence and absence, such that a value of 1 represents prefect agreement and a value of 0.5 represents random chance agreement (Pearce and Ferrier 2000). The resulting models were assessed for significance using a likelihood ratio test. Model performance was assessed using accuracy (the proportion of both presence and absence points correctly predicted), sensitivity (the proportion of presence points correctly predicted), and specificity (the proportion of absence points correctly predicted). These measures were calculated using an optimal threshold, determined as the value where the ROC curve was closest to perfect fit. The results were validated further by applying the models and performance measures to 112 earthworm sampling plots at Seney National Wildlife Refuge (Shartell et al. 2012) also located in the Upper Peninsula of Michigan.

Following statistical analysis, the resulting models were applied to the entire study area to create maps of invasion probability. A spatial resolution (pixel size) of 30 m was used for inputted GIS layers and model outputs. Euclidean distance was used to calculate the distance to nearest road from the center of each 30 m pixel across the study area. Available GIS data were substituted for basal area of earthworm preferred species and soil pH in order to determine results across the Huron Mountains. Preferred species was represented by the Integrated Forest Monitoring, Assessment, and Prescription (IFMAP) Gap Land Cover dataset (MI DNR 2001). Each land cover type was assigned a value based on its inferred potential to provide favorable habitat (moderate soil pH, texture, and moisture) and palatable litter for earthworms (Reich et al. 2005; Tiunov et al. 2006; Yatso and Lilleskov unpublished; Table 2). Soil pH was represented by SSURGO soil data (NRCS 2006). In addition, due to limitations of the SSURGO dataset, soil pH was interpolated across the study area using ordinary kriging (ArcGIS 10 Spatial Analyst, ESRI 2011) based on the complete set of sample points

**Table 1** Environmental variables selected to describe the occurrence of earthworm signs and middens

| Variable | Code | Units | Description |
|---|---|---|---|
| Basal area | BA | $m^2$/ha | Basal area of all overstory species |
| Preferred species | PS | $m^2$/ha | Basal area of earthworm preferred species |
| Soil pH | PH | pH | Soil pH ($CaCl_2$) |
| Wetlands | WT | binary | Presence of wetlands/saturated soils |
| Aspect | AS | ° | Deviation from north |
| Slope | SL | % | Percent slope |
| Elevation | EL | m | Elevation at plot center |
| Drainage index | DI | | Drainage index (Schaetzl et al. 2009) |
| Road proximity | RD | m | Distance to the nearest road |
| Hydrology proximity | HY | m | Distance to nearest waterway |

**Table 2** Values assigned to IFMAP (MI DNR 2001) land cover types within the Huron Mountains. Larger values indicate higher potential to provide favorable habitat (moderate soil pH, texture, and moisture) and palatable litter for earthworms (Reich et al. 2005; Tiunov et al. 2006; Yatso and Lilleskov unpublished)

| Cover type | Assigned value |
|---|---|
| Northern Hardwood Association | 5 |
| Lowland deciduous forest | 5 |
| Roads and corridors | 5 |
| Mixed upland deciduous | 4 |
| Upland shrub/low density trees | 4 |
| Low intensity urban | 4 |
| High intensity urban | 4 |
| Upland mixed forest | 3 |
| Lowland mixed forest | 3 |
| Lowland shrub | 3 |
| Lowland coniferous forest | 2 |
| Mixed upland conifers | 2 |
| Forage crops | 2 |
| Other upland conifers | 2 |
| Aspen Association | 2 |
| Herbaceous Openland | 2 |
| Pines | 1 |
| Oak Association | 1 |
| Mixed non-forest wetland | 1 |
| Emergent wetland | 1 |
| Sand/soil | 1 |
| Bare/sparsely vegetated | 1 |
| Water | 1 |

(N = 235). Pearson's correlation was used to compare field measured environmental data to GIS layers. In doing so, limitations of available spatial datasets were identified, as well as potential concerns for extrapolation beyond the study area.

The performance of the GIS based models was assessed using the same methods applied to the models derived from field data. In addition to mapping the "current" model of earthworm invasion, a "potential" predictive map was created by removing road and water body proximity from the models, thus incorporating only static variables as opposed to dynamic. The remaining variables were those expected to have a consistent effect (whether constraining or promoting) on earthworm populations without regard to stage of invasion, unlike dispersal mechanisms which are most influential at earlier stages of invasion. The potential predictive map indicates all those areas expected to be suitable for earthworm invasion. Using the current and potential models, invasion progress was quantified by calculating the difference in percent occupancy between the models and sampled presence.

## Results

Significant correlations between environmental variables were found in some cases (Table 3), and inclusion of collinear variables was avoided during modeling. Earthworm sampling took place at 235 plots distributed across the Huron Mountains study area. Signs of earthworm activity were observed at 58 % of plots visited (N = 135). The best model describing the distribution of earthworm signs included basal area of earthworm preferred species, soil pH, and aspect ($\chi^2 = 19.8$, $P < 0.001$). This model, however, performed somewhat poorly as a predictive model (AUC = 0.67). The model accuracy, sensitivity, and specificity values were also <0.70, using an optimal threshold value of 0.59 (Table 4). Of the 112 data points from Seney National Wildlife Refuge, 64 % had earthworms present (N = 72). Applying the model at Seney resulted in an accuracy of 0.66, a sensitivity of 0.63, and a specificity of 0.73 based on an optimal threshold of 0.49.

Middens (exclusive to *L. terrestris*) were observed at 20 % of plots (N = 47). The best model describing the distribution of middens included the environmental variables road proximity, basal area of earthworm preferred species, and soil pH ($\chi^2 = 41.38$, $P < 0.001$). As a predictive model, the model performed well (AUC = 0.79), and had an accuracy of 0.74, a sensitivity of 0.77, and a specificity of 0.73 based on an optimal threshold of 0.21 (Table 4). Midden occurrence at Seney National Wildlife Refuge was limited to 8 % of all sampled points (N = 9). Applying the model from the Huron Mountains to midden occurrence at Seney resulted in an accuracy of 0.57, a sensitivity of 0.78, and a specificity of 0.55 based on an optimal threshold of 0.42.

The resulting models were applied to the entire study area, where possible. The presence of earthworm signs could not be interpolated due to a strong lack of correlation between aspect measured in the field and that derived from a DEM (correlation coefficient = 0.004,

**Table 3** Correlation matrix showing Pearson's correlation coefficients for environmental variables

| | BA | PS | PH | WT | AS | SL | EL | DI | RD |
|---|---|---|---|---|---|---|---|---|---|
| PS | 0.23* | | | | | | | | |
| PH | −0.10 | 0.05 | | | | | | | |
| WT | −0.07 | −0.13 | −0.03 | | | | | | |
| AS | 0.17 | −0.03 | 0.03 | −0.03 | | | | | |
| SL | 0.02 | −0.20* | 0.15 | −0.19* | 0.08 | | | | |
| EL | −0.04 | −0.11 | 0.14 | −0.11 | −0.09 | 0.37* | | | |
| DI | −0.02 | 0.03 | 0.10 | 0.18* | −0.03 | −0.14 | −0.01 | | |
| RD | −0.16 | 0.06 | −0.07 | 0.08 | −0.10 | 0.01 | 0.17* | 0.15 | |
| HY | −0.11 | 0.18* | −0.14 | 0.08 | −0.29* | −0.13 | −0.11 | 0.07 | 0.24* |

For code descriptions see Table 2. * Significant correlation ($P < 0.01$)

**Table 4** Comparison of performance measures for models predicting the occurrence of earthworm signs and middens

| Model | AUC | Threshold | Accuracy | Sensitivity | Specificity |
|---|---|---|---|---|---|
| Earthworm signs | | | | | |
| *pH + PS + ASP* | 0.67 | 0.59 | 0.64 | 0.62 | 0.66 |
| Middens | | | | | |
| *RD + pH + PS* | 0.79 | 0.21 | 0.74 | 0.77 | 0.73 |
| *RD + SSpH + IF* | 0.73 | 0.23 | 0.69 | 0.64 | 0.70 |
| *RD + KpH + IF* | 0.76 | 0.21 | 0.69 | 0.77 | 0.68 |
| *KpH + IF* | 0.66 | 0.20 | 0.61 | 0.64 | 0.60 |

Independent variables are: *PS* preferred species, *pH* measured soil pH, *ASP* aspect, *RD* distance to road, *SSpH* pH derived from SSURGO data, *IF* habitat preference derived from IFMAP land cover data, *KpH* kriged soil pH

$P = 0.95$). For this reason, predictive maps are only presented for *L. terrestris* based on midden occurrence. To apply the model for *L. terrestris* to the entire study area, corresponding GIS layers were necessary for preferred species and soil pH. Basal area of preferred species was significantly positively correlated with the values assigned to IFMAP land cover classes (correlation coefficient = 0.40, $P < 0.001$), demonstrating that the IFMAP layer was somewhat satisfactory in representing the basal area of preferred species. Field sampled pH values were weakly correlated with SSURGO soil pH values (correlation coefficient = 0.15, $P = 0.02$), apparently due to high variability in soil pH across the Huron Mountains that was not perceptible in SSURGO data. For this reason, soil pH values interpolated across the study area were used. Kriged soil pH values showed a stronger correlation with pH values measured in the field (correlation coefficient = 0.44, $P < 0.001$). Using these values, the model was significant ($\chi^2 = 30.65$, $P < 0.001$), and performed better than that incorporating SSURGO pH in predicting the presence of middens (Table 4).

Applying the best performing GIS model (incorporating kriged soil pH), a current invasion map for *L. terrestris* was created (Fig. 1). Removing the dynamic variable of road proximity and taking into account only the static variables soil pH and land cover produced a model that was currently less accurate (Table 4), but indicated the potential distribution of *L. terrestris* across the Huron Mountains (Fig. 2). For the current invasion model 37 % of those points expected to have middens present were invaded, and for the potential invasion model 29 % of points were invaded. Using the threshold value (0.20) based on current midden presence and absence among sample points, the potential model predicts that 41 % of the Huron Mountains study area (excluding open water) is expected to be invaded by *L. terrestris*.

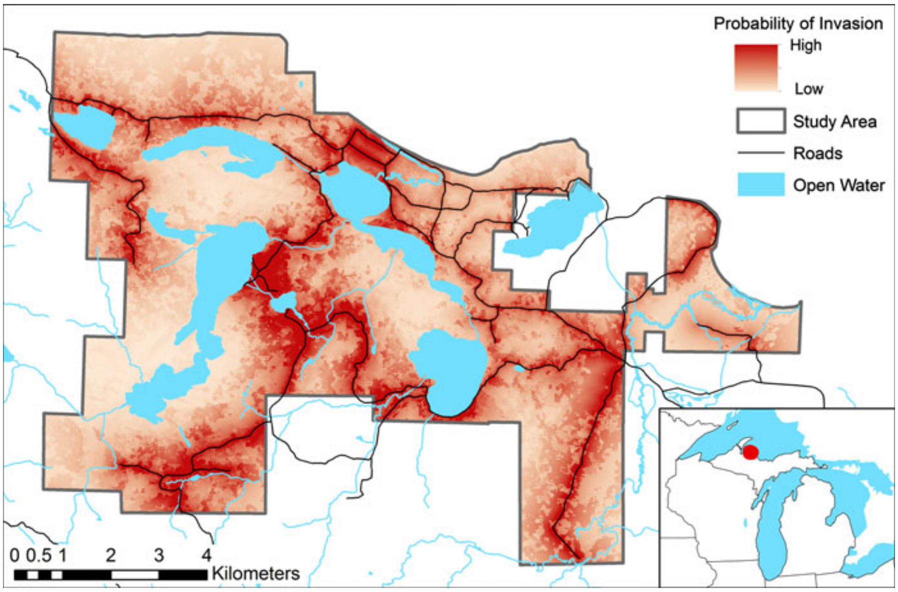


**Fig. 1** Current predicted probability of invasion for *L. terrestris* across the study area in the Huron Mountains, Upper Peninsula, Michigan. Model parameters include road proximity, soil pH, and land cover

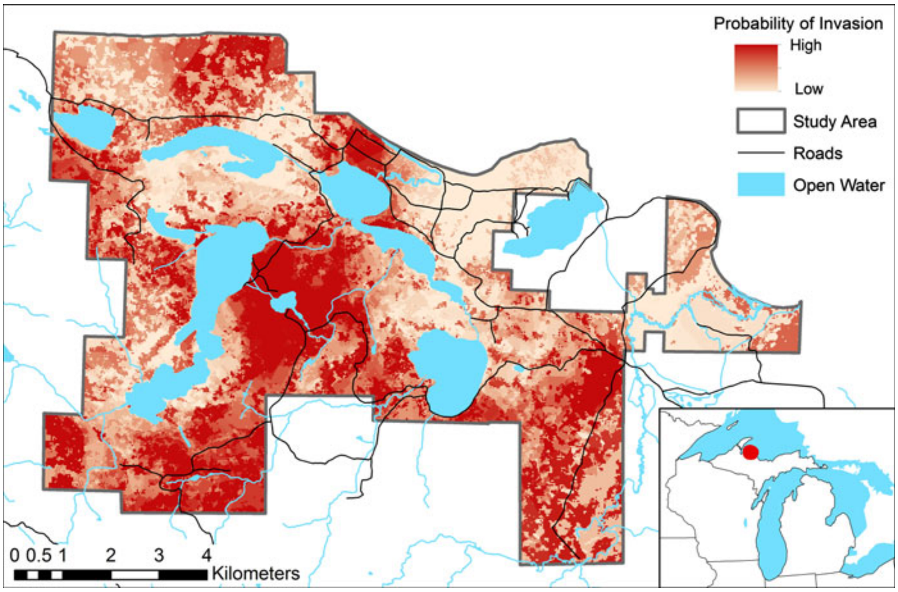


**Fig. 2** Potential predicted probability of invasion for *L. terrestris* across the study area in the Huron Mountains, Upper Peninsula, Michigan. Model parameters include soil pH and land cover

## Discussion

Our results have shown that the existing distribution of earthworms, particularly *L. terrestris*, can be predicted using environmental variables. Basal area of earthworm preferred species and soil pH were found to be significant in predicting both earthworm signs and *L. terrestris* midden presence. These factors are both commonly known to be drivers of earthworm distribution at a coarse scale (Lee 1985; Edwards and Bohlen 1996, Tiunov et al. 2006). Basal area of earthworm preferred tree species was higher in plots with earthworms, which is attributable to both the availability of palatable food and the associated suitability of other habitat conditions (e.g. soil pH, moisture, texture). Soil pH is known to limit earthworm activity for most species, particularly in low pH conditions. In the Huron Mountains, earthworm signs (including middens) were rarely present in soils with pH ($CaCl_2$) less than 3.5 and were nearly always present in soils with pH above 4.0.

Consistent with this, a recent study showed no effect of soil pH on earthworm distribution in areas where pH values exceeded 4.1 (Sackett et al. 2012). In general, studies of earthworm distributions have taken place in forests dominated by hardwood species associated with higher pH soils, as opposed to forests dominated by coniferous species associated with lower pH, as can be found in the Huron Mountains. Despite the link between forest composition and soil pH, there was no significant correlation between basal area of earthworm preferred species (i.e., basswood, maples, ash, and balsam fir) and soil pH in our study. This might be due to the mixed composition (containing both hardwood and coniferous species) of many forests sampled within the Huron Mountains or may be an indication that some other factor, rather than litter and organic matter content, may be driving soil pH.

The lower predictive ability for earthworm signs as opposed to *L. terrestris* midden presence may be due to the variation in feeding preferences among earthworm species. Those species that feed on microorganisms or partially decomposed organic matter would be less influenced by basal area of preferred species, since this ranking was developed specifically for *L. terrestris*, which feeds on fresh leaf litter. Furthermore, earthworm species differ in their tolerance of extremes in soil pH, soil moisture, and other conditions. For example, *D. octaedra*, an epigeic earthworm present within the Huron Mountains, is known to invade low pH, conifer-dominated stands in the Great Lakes region that lack other earthworm species (Tiunov et al. 2006; Shartell 2012).

Road proximity was also important in explaining the current distribution of *L. terrestris*, but was not associated with earthworm signs in general. This may indicate that other species of earthworms (in aggregate) are at a later stage of invasion than *L. terrestris*. Similarly, Holdsworth et al. (2007) found that *L. terrestris* distribution in the Chequamegon National Forest in Wisconsin was associated with roads, while *D. octaedra* distribution was not. These findings are consistent with the theory of invasion waves, in which there is an orderly procession of earthworm species and/or functional group invasion, beginning with epigeic species such as *D. octaedra*, and ending with *L. terrestris* (James and Hendrix 2004; Hale et al. 2005). Accordingly, *D. octaedra* is by far the most widespread species in the Huron Mountains (Lilleskov, personal observation), and may be at or approaching steady-state distribution patterns, limiting the predictive ability of roads, which are associated with invading species. It is important to understand how the effect of variables as predictors differs depending on whether they are static constraints on earthworm distribution or dynamic variables related to stage of invasion. The ability to identify current stage of invasion would help explain the importance of dynamic variables such as road proximity in predictive models, and justify their removal in models predicting potential or future distributions.

Many of the environmental variables assessed in relation to earthworm distribution were not significant despite having reasonable theoretical associations. In this study, proximity to lakes or streams was not related to earthworm distribution. This finding was also true of earthworm distributions described in a temperate hardwood forest in south-central New York (Suarez et al. 2006). However, other studies have shown contradictory results, indicating that boat launches, fishing sites, and streams can be important sources of introduction, particularly for *Lumbricus* species (Hale et al. 2005; Holdsworth et al. 2007; Cameron et al. 2008; Sackett et al. 2012). It was also hypothesized that earthworms would be more common on south-facing, low, flat areas because of their tendency to be warmer, more accessible for dispersal, and generally wetter sites. Suarez et al. (2006) found that exotic earthworms were more likely to occur on low lying, flat sites rather than more remote, steep sites. In our study, none of the topographic characteristics (aspect, slope, or elevation) were significantly related to *L. terrestris* midden presence. Earthworm signs, however, were associated with north facing sites, a finding that was contradictory to our hypothesis, but could indicate the importance of soil moisture.

Because predicting the occurrence of earthworms as a whole is difficult due to differences in both habitat preferences and stage of invasion, focusing on a single species should produce a more successful model, as was the case for predicting the occurrence of *L. terrestris* middens. This model was validated by the similar high sensitivity found for sample points at Seney National Wildlife Refuge (0.78 compared to 0.77 within the Huron Mountains). Occurrence of *L. terrestris* at Seney was less common, perhaps indicating an earlier stage of invasion across the site or a greater abundance of unsuitable habitat. Forest composition data from Seney National Wildlife Refuge indicate that while many plots were dominated by coniferous species, not all hardwood dominated plots were invaded by earthworms (Petrillo and Corace 2011; Shartell et al. 2012). Furthermore, those stands invaded by *L. terrestris* at Seney were in close proximity to agricultural sites or old fields (Shartell personal observation). At an earlier stage of invasion the predictive model would be expected to have many false positives where the probability of occurrence is high but because of limitations in the speed of dispersal earthworms have not yet reached. Thus the low overall accuracy and low specificity observed at Seney are not of concern at this time, and would be expected to increase as the species spreads further across the site. Similarly, *L. terrestris* invasion has not yet fully progressed within the Huron Mountains, with only 29 % of the area expected to become invaded being currently occupied.

Using the statistical model based on field data to predict the distribution of *L. terrestris* across the entire Huron Mountains revealed limitations in the precision of available spatial data. Aspect and soil pH as measured in the field were not strongly correlated with values derived from widely available datasets. Because soil pH was interpolated across the study area, this limited the predictive map to the Huron Mountains and prevented further extrapolation. However, the model including SSURGO data had only slightly lower AUC, accuracy, specificity, and sensitivity values than the model using kriged soil pH, and could prove useful for estimating potential earthworm distributions on a larger scale, despite its lower predictive ability. These considerations should be addressed in future attempts to predict the extent of earthworm invasion across the northern Great Lakes region. A further concern is spatial autocorrelation of model inputs. Using Moran's I (ArcGIS 10 Spatial Statistics, ESRI 2011) significant clustering was identified for the environmental variables included in the model predicting *L. terrestris* midden occurrence (soil pH, road proximity, and preferred species, $P < 0.01$ in all cases). A geographically weighted approach, such as geographically weighted logistic regression (necessary for presence/absence data) or autologistic regression could benefit modeling efforts, however these methods are less common and require further examination of applicability and validity before application (Dormann 2007).

It is expected that the potential distribution of exotic earthworms, in general, will cover much of the Huron Mountains. According to the model predictions and calculated threshold value, *L. terrestris* is expected to occur on 41 % of the land. It should be noted, however, that this is based on current presence and absence of middens at sample points, and thus, the actual proportion of the landscape invaded is expected to be greater. Other studies of earthworm distribution tend to predict high rates of invasion, some exceeding 90 % of the landscape, though these studies are usually limited to northern hardwood forest cover types (Gundale et al. 2005; Suarez et al. 2006). A lower invasion potential for *L. terrestris* within the Huron Mountains might be expected because of the abundance of coniferous forests that should prove unsuitable for *L. terrestris* populations. Other earthworm species, however, are expected to occur across a much larger proportion of the landscape. Over time, these species might alter soil and forest floor conditions in ways that facilitate invasion by *L. terrestris* (Hale et al. 2005), allowing this species to reach a greater potential across the Huron Mountains and Great Lakes region.

## Conclusions

Earthworm invasion within the Huron Mountains appears to be at varying stages dependent upon species. A lack of correlation between measures of dispersal and the presence of earthworm signs suggests that epigeic and endogeic species in aggregate have reached a further stage of invasion than the anecic species *L. terrestris*, which was closely associated with roads. For both earthworm signs and *L. terrestris* middens specifically, high soil pH and high basal area of earthworm preferred tree species were important predictive variables. Thus, high pH sites with a substantial basal area of basswood, maples, ash, and/or balsam fir have the highest likelihood for invasion. Likewise, these conditions within close proximity to roads are most likely to contain earthworm species at earlier stages of invasion, such as was the case for *L. terrestris* within the Huron Mountains. Because of the high variability in site characteristics at a fine scale, specifically soil pH, using existing spatial datasets to expand these models beyond the Huron Mountains may present difficulties. While there is optimism for management approaches to prevent earthworms from invading earthworm-free or minimally invaded forests (Hale 2008), implementation will rely on identification of current populations and can be further focused using predictive modeling to determine invasion potential.

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