

# Invasions of non-native earthworms related to population declines of ground-nesting songbirds across a regional extent in northern hardwood forests of North America

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Received: 19 August 2011 / Accepted: 30 January 2012  
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**Abstract** Non-native invasive earthworms (*Lumbricus* spp.) substantially change previously earthworm-free hardwood forests of North America by consuming the leaf litter layer, reducing cover and richness of herbaceous plants, and increasing dominance of sedges and grasses. These changes have been associated with reduced density of Ovenbirds (*Seiurus*

*aurocapilla*) and Hermit Thrushes (*Catharus guttatus*) in 10–20 ha forest stands, and with reduced Ovenbird nesting success. Whether earthworms reduce songbird populations across a regional extent is unclear. We investigated relationships among *Lumbricus*, vegetation structure, landscape patterns of forest cover, and density of four ground-nesting songbird species at points scattered across the Chequamegon-Nicolet (Wisconsin) and Chippewa (Minnesota) National Forests, USA. In both national forests, Ovenbird density was significantly lower at invaded points than *Lumbricus*-free points, but only in sugar maple (*Acer saccharum*) and sugar maple/basswood (*Tilia americana*) (hereafter, maple-basswood) woodlands. Density of the Hermit Thrush, Black-and-white Warbler (*Mniotilta varia*), and Veery (*Catharus fuscescens*) did not differ in relation to *Lumbricus*. In maple-basswood forests, *Lumbricus* biomass was the best predictor of Ovenbird density, with greater biomass associated with reduced density. Vegetation structure and landscape pattern variables received weak support as density predictors. Across all forest types, Ovenbird density was most strongly related to forest cover within 500 and 1,000 m radii. Our results suggest that earthworm invasions may pose a regional threat to Ovenbirds within maple-basswood forests of the U.S. northern Midwest.

**Electronic supplementary material** The online version of this article (doi:10.1007/s10980-012-9717-4) contains supplementary material, which is available to authorized users.

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**Keywords** Hermit Thrush · Invasive earthworms · *Lumbricus* · Minnesota, USA · Ovenbird · Wisconsin, USA

## Introduction

Invasions of non-native species are a leading threat to the persistence of native species and the functioning of ecosystems (Wilcove et al. 1998; Mack et al. 2000). Birds are thought to be particularly vulnerable, with 68% of population declines of endangered North American species partially attributed to biological invasions (Gurevitch and Padilla 2004). Elucidating the impacts of invasives to populations and ecosystems requires local-scale research to be complemented by regional and continental-scale investigations (Crowl et al. 2008). Whereas the spread of invasive diseases has been linked to regional and continental population declines of North American birds (Hochachka and Dhondt 2000; LaDeau et al. 2007), incomplete information about distributions of many invasives has limited most research of effects on birds to relatively small spatial scales (e.g. study areas <100,000 ha).

In north-temperate and boreal North America, invasive European earthworms (*Lumbricus* spp.) are causing substantial ecosystem-level changes to historically earthworm-free forests (Bohlen et al. 2004) to the extent that earthworm invasions are among the top emerging concerns for the conservation of biodiversity (Sutherland et al. 2010). Invasive earthworms alter soil structure and consume the leaf litter layer (Alban and Barry 1994; Hale et al. 2005). These changes affect seedbed conditions, which reduces richness and cover of herbaceous plants, increases dominance by sedges and grasses (Hale et al. 2006; Holdsworth et al. 2007a), and reduces tree regeneration and growth (Lawrence et al. 2003; Larson et al. 2010).

Indirect effects of invasive earthworms on vertebrates are beginning to come to light. Earthworm-caused reductions of litter depth and arthropod food supplies reduce abundance of salamanders (Maerz et al. 2009), and ground-nesting songbirds have been observed to be absent from heavily invaded forests (Fox et al. 2010). The only study designed to explicitly assess associations between invasive earthworms and songbirds found that *Lumbricus* invasions were related to reduced abundance of Ovenbirds (*Seiurus aurocapilla*) and Hermit Thrushes (*Catharus guttatus*) in sugar maple (*Acer saccharum*)/basswood (*Tilia americana*) forest stands of 10–20 ha (Loss and Blair 2011). This study also found reduced nesting success of Ovenbirds relative to earthworm-caused reductions

in litter depth and increases in sedge cover that likely reduce nest concealment and increase predation rates.

Regional-scale studies indicate that a vast majority of northern U.S. hardwood forests are invaded by *Lumbricus* (Gundale et al. 2005; Holdsworth et al. 2007b). The broad regional extent of invasions cannot be explained solely by natural dispersal, which is slow (5–15 m/year, Marinissen and van den Bosch 1992). Instead, invasion patterns are consistent with human-assisted dispersal. Remaining earthworm-free forests are in wilderness areas receiving minimal human use, and invasions emanate from roads, boat launches, and agricultural areas (Suarez et al. 2006; Cameron et al. 2007; Holdsworth et al. 2007b; Cameron and Bayne 2009).

Whether relationships between earthworms and songbirds exist across the broad spatial extent of invasions is unclear. Determining the extent of this association is crucial because songbird population declines in the northern Midwest, a region thought to provide a surplus of songbirds that colonize other regions (Robinson et al. 1995), could affect populations across the mid-continent (Temple and Cary 1988; Donovan et al. 1995). In previous work by two of the authors (Loss and Blair 2011), relationships between *Lumbricus* invasions and songbird density and between *Lumbricus* and Ovenbird nesting success were assessed at 12 sites in a portion of the Chequamegon-Nicolet National Forest (CHEQ) in Wisconsin, USA covering approximately 70,000 ha in area. The current study expands the scope of inference by using a broad-scale (>1.2 million ha) and non-overlapping data set from points scattered across the CHEQ and the Chippewa National Forest (CHIP) in Minnesota, USA to investigate relationships among *Lumbricus* invasions, vegetation structure, landscape patterns of forest cover, and ground-nesting songbird populations. We sought to determine whether earthworms pose a regional threat to ground-nesting forest songbirds by: (1) comparing densities of four species—the Ovenbird, Hermit Thrush, Veery (*Catharus fuscescens*), and Black-and-white Warbler (*Mniotilta varia*)—between points invaded by *Lumbricus* spp. and points that were earthworm-free or only contained *Dendrobaena octaedra*, a species with minimal adverse effects in the region (Hale et al. 2006, 2008); and (2) clarifying the contribution of *Lumbricus* relative to vegetation structure and landscape

patterns of forest cover for predicting density of the Ovenbird.

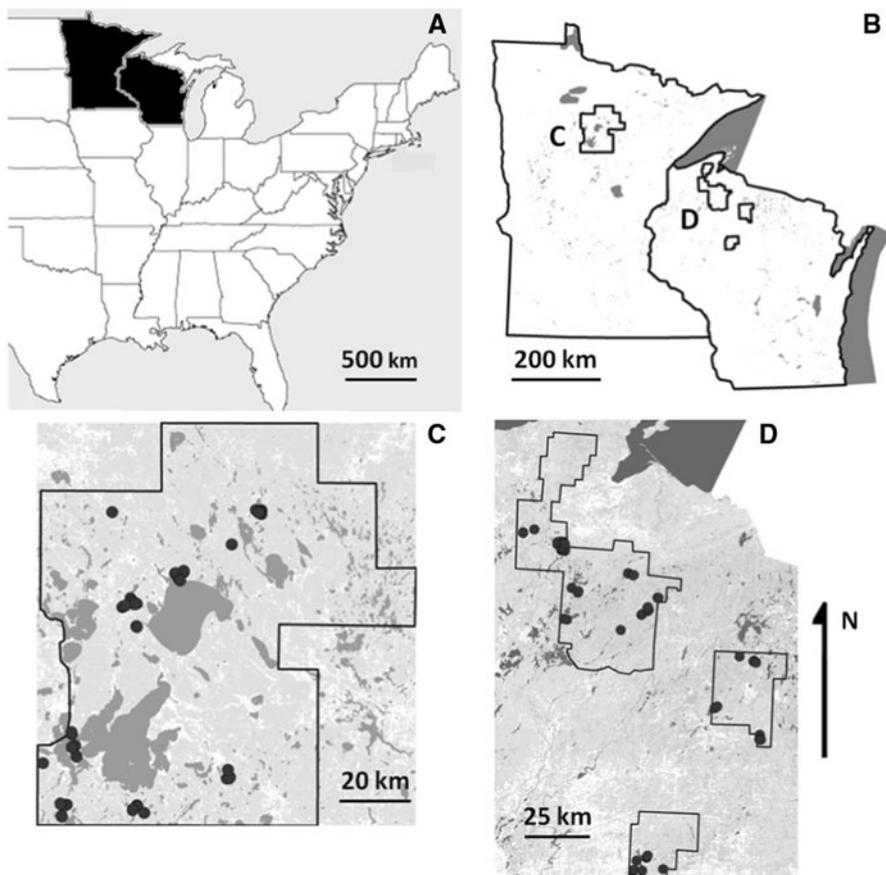
## Methods

### Study area

The study was conducted at 100 m-radius survey points that partially constitute the Forest Birds of the Western Great Lakes monitoring program (Hanowski et al. 2005). Points were located throughout the CHIP in northern Minnesota (47°N, 94°W) and the Chequamegon unit of the CHEQ in northwest Wisconsin (46°N, 91°W; Fig. 1). For details about the national forests, including climate, glacial history, forest cover, and soils, see Holdsworth et al. (2007b).

From 283 points that were in hardwood or mixed hardwood-coniferous forests, we randomly selected 124 points, with roughly half in the CHEQ ( $n = 65$ ) and half in the CHIP ( $n = 59$ ). We stratified selection by forest district so that points were scattered across each forest, and we stratified by distance from the nearest road, because this factor provides a first-order predictor of earthworm invasion in the study area (Holdsworth et al. 2007b). The selection approach was designed to provide broad spatial coverage of both national forests and to capture *Lumbricus*-free and *Lumbricus*-invaded sites.

The 124 points were characterized by varying species and age of canopy trees and different timber removal histories. Hardwood forest types (Table 1), as classified by dominant canopy tree species following the U.S. Forest Service Forest Inventory and Analysis



**Fig. 1** Location of Minnesota and Wisconsin in the USA (a), study area within Minnesota and Wisconsin (b), and survey points (black circles) in the Chippewa National Forest (c), and

Chequamegon-Nicolet National Forest (d). Black polygons indicate national forest boundaries (b–d), dark gray and light gray shading indicate water and forest cover, respectively (c, d)

**Table 1** *Lumbricus* invasion status by forest type at 124 points in the Chequamegon-Nicolet (Wisconsin) and Chippewa National Forests (Minnesota), USA

Forest type	Total	Number of points	
		With <i>Lumbricus</i>	Without <i>Lumbricus</i>
Sugar maple	21	15	6
Sugar maple/basswood	32	20	12
Red oak	11	7	4
Quaking aspen	28	12	16
Paper birch	7	1	6
Aspen/paper birch	4	1	3
Ash/elm/red maple	15	11	4
Aspen/paper birch/fir	6	2	4
Total	124	69	55

Program (Woudenberg et al. 2010), included sugar maple (*Acer saccharum*), sugar maple/basswood (*Tilia americana*), red oak (*Quercus rubra*), quaking aspen (*Populus tremuloides*), paper birch (*Betula papyrifera*), aspen/paper birch, and ash/elm/red maple (*Fraxinus* spp./*Ulmus* spp./*A. rubrum*). The single mixed hardwood-coniferous forest type was aspen/paper birch/fir (*Abies balsamea*).

#### Bird point surveys

We conducted bird surveys at all points, with the majority of points ( $n = 110$ ) surveyed once in both 2009 and 2010. Some points were sampled only once in 2009 ( $n = 13$ ) or 2010 ( $n = 1$ ) due to logistical constraints or inclement weather. We conducted all surveys between 1 June and 4 July. The minimum distance between points was 220 m; however, most points were  $>0.5$  km apart. Because of large distances between points, and because surveyors were trained to avoid double-counting, it is unlikely that individual birds were counted at more than one point.

We conducted 10-min point surveys according to previously published methods (Etterson et al. 2009). Trained bird surveyors recorded each Ovenbird, Hermit Thrush, Veery, and Black-and-white Warbler that was seen or heard within 10, 25, 50, and 100 m radii. Surveys were conducted between 0.5 h before sunrise and 4 h after sunrise (0445–0930 local time) on relatively calm days (winds  $<19$  kph) with little or no precipitation. To minimize observer effects within

forest types and at each point, each surveyor sampled the same number of points within each forest type, and no point was surveyed by the same person in subsequent years.

#### Earthworm sampling

Trained technicians collected earthworms at all points between 15 September and 10 October of 2009 ( $n = 59$ ) or 2010 ( $n = 65$ ), with roughly half of each year's samples collected in each national forest. Sampling dates corresponded to a period of moisture conditions favorable for earthworm activity and during which most earthworms were adults, and therefore identifiable to species. Sampling during bird surveys was not possible due to fieldwork-related time constraints. Moreover, because low soil moisture reduces earthworm activity (C. Hale personal communication), sampling during the drier summer months could have led to sampling of a comparatively low proportion of earthworms. It is unclear whether earthworm populations experience substantial intra-annual fluctuations; however, the slow natural rate of earthworm dispersal makes it unlikely that species composition and abundance changed greatly between spring and summer of each year. We assume that fall sampling results represent summer earthworm populations.

We used the liquid mustard extraction technique (Hale 2007) to collect earthworms from three  $33 \times 33$  cm sub-plots randomly located within 100 m of each point, the radius within which we surveyed birds. We cleared all vegetation and leaf litter, poured a mustard-water mixture (40 g ground yellow mustard dissolved in 4 L water) on the soil, and collected all earthworms until no earthworms emerged for 2 min. Earthworms were preserved in the field using 70% isopropyl alcohol and were stored in buffered 10% formalin. We used a dissecting microscope to count, identify, and measure earthworm length. We identified adult earthworms to species, except for *Aporrectodea* spp., which we identified to genus, owing to morphological similarities (Hale 2007). Most juvenile earthworms were only identifiable to genus. We used length measurements and allometric relationships to estimate biomass (Hale et al. 2004), and we averaged biomass across sub-plots for each point.

## Quantification of vegetation structure

Due to the large number of points (>1,200) in the Forest Birds of the Western Great Lakes monitoring program and the substantial effort required to collect data, vegetation quantification occurs every 3–4 years immediately before or after bird surveys are conducted. Thus, for most vegetation variables (see exceptions below), data were collected during 2005, 2006, or 2007. However, because surveyors noted in 2009 and 2010 that none of the points had experienced recent timber harvest, had openings created by disturbances, or had changed forest type, major structural changes between 2005–2007 vegetation surveys and 2009–2010 bird and earthworm surveys are unlikely.

Within a 100 m radius of each point, we visually estimated (in 10% increments) high canopy cover (vegetation >3.7 m in height), understory canopy cover (vegetation 0.9–3.7 m in height), and ground cover (vegetation <0.9 m in height). Within a 10 m radius, we estimated shrub density by counting the number of woody plants with diameter at breast height <2.5 cm. Immediately before bird surveys in 2009 and 2010, we measured litter depth and cover of

sedges and grasses, variables that have been found to significantly decrease and increase, respectively, with *Lumbricus* invasions (Hale et al. 2006; Holdsworth et al. 2007a), and that have been related to Ovenbird nesting success (Loss and Blair 2011). We based average litter depth on measurements from two random locations within 10 m of the point and estimated by pushing a metal skewer through the litter until meeting resistance from rock or mineral soil. We visually estimated sedge/grass cover (in 10% increments) within 100 m of the point.

## Quantification of landscape patterns of forest cover

We quantified landscape patterns of forest cover using ArcMap (version 9.3, ESRI 2008). The seven landscape variables we selected included distance to forest edge, distance to water, and percentage of core (i.e., forest >100 m from open land) hardwood and mixed hardwood/coniferous forest in five concentric circles centered on each point. These variables have been related to density, nesting success, pairing success, and territory size of ground-nesting forest songbirds, and of Ovenbirds in particular (Table 2). Ovenbirds

**Table 2** Candidate variables for analysis of Ovenbird density in the Chequamegon-Nicolet (Wisconsin) and Chippewa (Minnesota) National Forests, USA

Variables	Justification/citations <sup>a</sup>
Shrub density	Ovenbird distribution associated with low (1) and intermediate (2) shrub density
Canopy cover	Ovenbird habitat characterized by high (60–90%) canopy closure (1,3,4,5,6)
Understory cover	Ovenbird density (7) and occupancy probability (8) inversely related to understory cover
Ground cover	Ovenbird distribution associated with low ground cover (1); relationship varies regionally (9)
Litter depth	Ovenbird selects territories with thick leaf litter (5,10,11,12,13)
Sedge cover	Ovenbird nest success inversely related to cover of sedges (13)
Distance to forest edge	Inverse relationship between distance to edge and pairing success (14), availability of nest sites (10), and nest success (15,16)
Distance to water <sup>b</sup>	Ovenbird presence inversely related to distance to nearest water (17)
Core forest (w/i 100 m)	Ovenbird occurrence related to understory vegetation density at 3 ha extent (100 m radius) (8)
Core forest (w/i 200 m)	Ovenbird occurrence related to understory vegetation density at 12 ha extent (200 m radius) (8)
Core forest (w/i 500 m)	Corresponds to intermediate scale between other well-supported scales
Core forest (w/i 1,000 m)	Corresponds to intermediate scale between other well supported scales
Core forest (w/i 2,000 m)	Ovenbird nest success positively related to core forest cover within 2,000 m (11)
<i>Lumbricus</i> biomass	Ovenbird density lower in invaded versus <i>Lumbricus</i> -free forests and nesting success affected by <i>Lumbricus</i> -related habitat changes (13)

<sup>a</sup> Numbers refer to citations: (1) Smith and Shugart (1987); (2) James (1971); (3) Smith (1977); (4) Collins (1983); (5) Van Horn (1990); (6) Thompson and Capen (1988); (7) Crawford et al. (1981); (8) Smith et al. (2008); (9) Van Horn and Donovan (1994); (10) Burke and Nol (1998); (11) Mattsson and Niemi (2006); (12) Fox et al. (2010); (13) Loss and Blair (2011); (14) Van Horn et al. (1995); (15) Flaspohler et al. (2001); (16) Manolis et al. (2000); (17) Mitchell et al. (2001)

<sup>b</sup> Removed from analysis because of correlation with “distance to forest edge”

are known to require large tracts of forest for successful reproduction (Van Horn and Donovan 1994), respond to landscape patterns of forest cover at multiple spatial extents (Burke and Nol 1998; Mattsson and Niemi 2006; Smith et al. 2008), and experience reduced nest success probability near forest edges, even in relatively un-fragmented forests (Manolis et al. 2000).

We analyzed land cover using the 2001 National Land Cover Database (Homer et al. 2007) which provides data at 30-m resolution. We constructed five circular buffers around each survey point (radius = 100, 200, 500, 1,000, and 2,000 m), and within each buffer we calculated percentage of core forest. For this calculation, we only considered upland hardwood and mixed hardwood/coniferous forest types because Ovenbirds do not commonly occur in lowland forests. We defined open land to consist of all non-forested cover types, including water, wetland, grassland, shrubland, and barren, agricultural, and other human-developed areas. We also calculated average distance of survey points to water and to nearest forest edge. For distance to edge, we defined open land to consist of the same cover types used for the core forest calculation, including water. Distance variables were calculated as an average for the 100 m radius around points.

#### Data analysis

We used the observed distance to each bird to develop species-specific detectability functions and to estimate density for each species in both 2009 and 2010 using program Distance 6.0 (Thomas et al. 2010). For the following analyses, we used the 2-year average density for each species at each point.

All of the following analyses were repeated for: (1) all forest types combined ( $n = 124$ ), and (2) points in sugar maple and sugar maple/basswood forests (hereafter; maple-basswood,  $n = 53$ ), because earthworm effects in the study region have been documented to be most substantial in these forest types (Hale et al. 2006; Holdsworth et al. 2007a, b), and a previous study found significant associations between *Lumbricus* and songbirds in these forest types (Loss and Blair 2011). We used independent samples *t*-tests to compare density of each bird species, as well as litter depth, ground cover, and sedge cover, between *Lumbricus*-free and invaded sites. We conducted univariate linear

regression for the same three vegetation variables with *Lumbricus* biomass as the dependent variable.

We used linear regression and Akaike's Information Criteria, corrected for small sample sizes ( $AIC_c$ ; Burnham and Anderson 2002), to assess the relative contribution of *Lumbricus* biomass, vegetation structure, and landscape pattern variables to explaining variation in Ovenbird density. We initially selected 14 variables (*Lumbricus* biomass, six vegetation structure, and seven landscape pattern variables) based on published relationships and the questions of the current study. We used Pearson's correlation to identify highly correlated variable pairs ( $r > 0.4$ ), and we removed one variable from correlated pairs to reduce multicollinearity within models. This resulted in a final set of 13 variables (Table 2).

We conducted univariate linear regression for each variable with Ovenbird density as the dependent variable, and we constructed an intercept-only (null) model and a global model with all variables. We used  $AIC_c$  to compare models, and we considered single-variable models to receive initial support if they had  $\Delta AIC_c$  between 0–2 and  $\Delta AIC_c$  at least 2 lower than the null model. Variables meeting initial criteria were combined in two-variable additive models. Final assessment of variable support was based on the complete set of one and two-variable models, the difference in  $AIC_c$  between the top model and every other model ( $\Delta AIC_c$ ), and the relative weight of support for each model ( $\omega_i$ ). We identified variables receiving strong support (appearing in  $>1$  model with  $\Delta AIC_c$  between 0 and 2 and single-variable  $\Delta AIC_c$  between 0 and 2), moderate support (appearing in  $>1$  model with  $\Delta AIC_c$  between 0 and 2 and single-variable  $\Delta AIC_c$  between 2 and 4), or weak support (not meeting criteria for strong or moderate support) (Loss and Blair 2011). For strongly supported variables, we calculated model-averaged  $\beta$ -coefficients by weighing coefficient estimates from all models by the model  $\omega_i$  (Burnham and Anderson 2002).

## Results

### Density comparison between *Lumbricus*-free and invaded points

We collected *Lumbricus* from 69 (56%) of 124 points and from 35 (66%) of 53 maple-basswood points

(see Table 1 for invasion by forest type). Point-scale *Lumbricus* biomass was variable (all points 0–9.44 g/m<sup>3</sup>; maple-basswood points 0–6.50 g/m<sup>3</sup>). We concluded that our selection approach resulted in samples of both *Lumbricus*-free and *Lumbricus*-invaded points.

When considering all forest types, there was no difference in Ovenbird density between invaded points and *Lumbricus*-free points ( $t = -0.42$ ,  $df = 122$ ,  $p = 0.69$ ); however, in maple-basswood forests, Ovenbird density was significantly lower at invaded points compared to *Lumbricus*-free points ( $t = 2.03$ ,  $df = 51$ ,  $p = 0.05$ ; Fig. 2a). To test the robustness of this result, we separately analyzed maple-basswood forests in each national forest and found similar significant decreases in Ovenbird density in each forest (CHEQ  $t = 2.21$ ,  $df = 34$ ,  $p = 0.03$ ; CHIP  $t = 2.40$ ,  $df = 15$ ,  $p = 0.03$ ). The magnitude of density decrease with invasion in each forest was similar to that found in the analysis across both forests

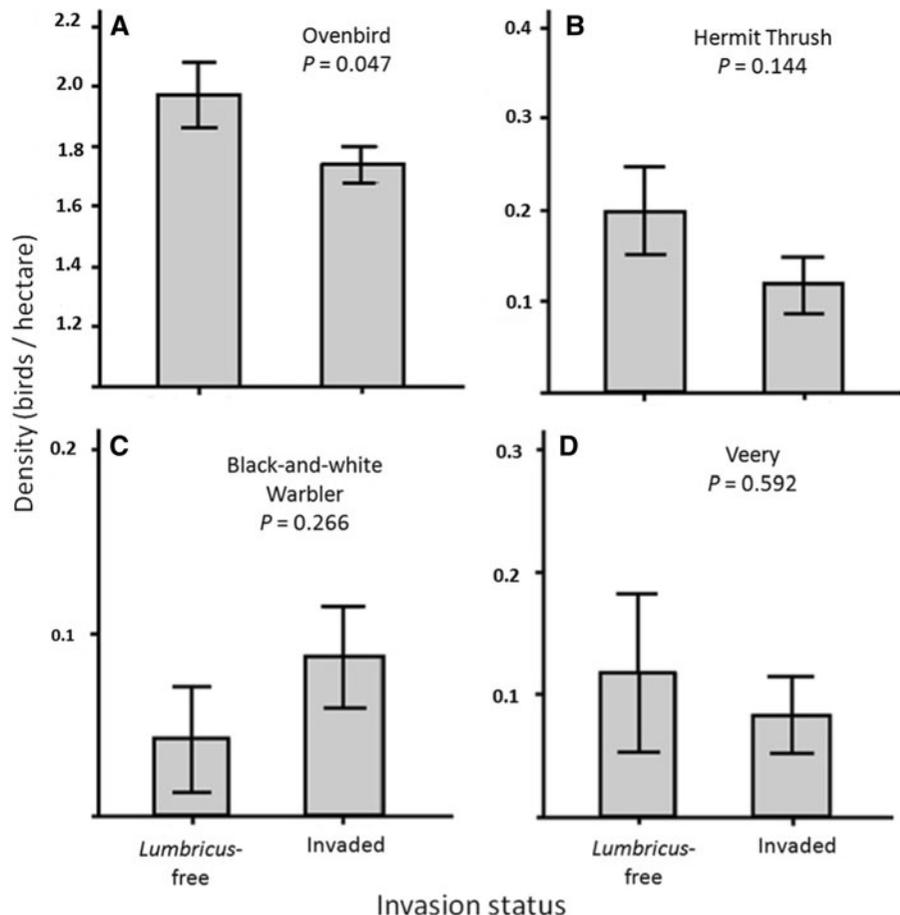
(0.23 and 0.48 fewer birds/ha on average in the CHEQ and CHIP, respectively, compared to 0.28 fewer birds/ha across both forests).

We found no significant difference in density between *Lumbricus*-free and invaded points for Hermit Thrush (all points  $t = 0.88$ ,  $df = 122$ ,  $p = 0.38$ ; maple-basswood points  $t = 1.42$ ,  $df = 51$ ,  $p = 0.14$ ; Fig. 2b), Black-and-white Warbler (all points  $t = -0.28$ ,  $df = 122$ ,  $p = 0.82$ ; maple-basswood points  $t = -1.13$ ,  $df = 51$ ,  $p = 0.27$ ; Fig. 2c), or Veery (all points  $t = 0.91$ ,  $df = 122$ ,  $p = 0.36$ ; maple-basswood points  $t = 0.54$ ,  $df = 51$ ,  $p = 0.59$ ; Fig. 2d).

#### Relative contribution of *Lumbricus* biomass to explaining Ovenbird density

Across all forest types, the model containing *Lumbricus* biomass received weak support for explaining variation in Ovenbird density (Online Supplementary Table 1), and the two strongly supported variables

**Fig. 2** Comparison of mean density of Ovenbird (a), Hermit Thrush (b), Black-and-white Warbler (c), and Veery (d) between *Lumbricus*-invaded ( $n = 35$ ) and *Lumbricus*-free ( $n = 18$ ) maple-basswood forests in the Chequamegon-Nicolet (Wisconsin) and Chippewa (Minnesota) National Forests, 2009–2010. Units on y-axis are different for each species

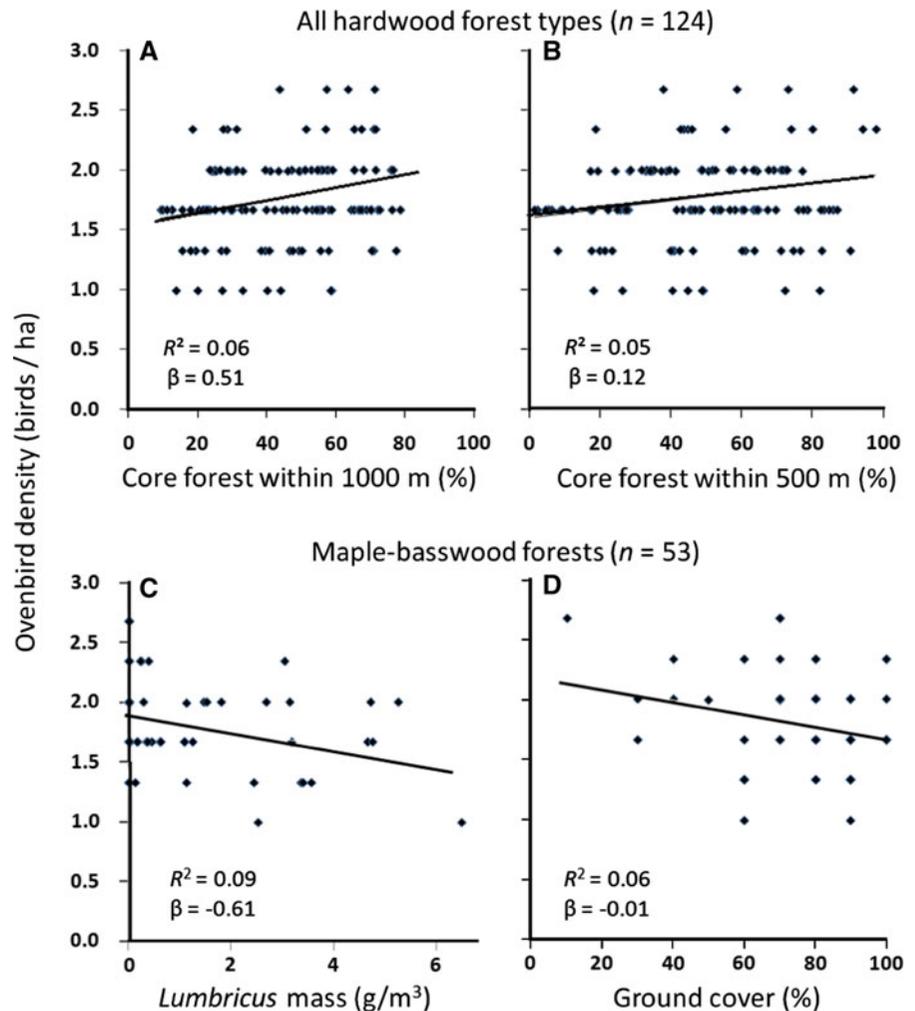


were core forest cover within 500 and 1,000 m. The model containing core forest within 1,000 m received the greatest support, and this variable appeared in two of the top three models and displayed a positive relationship with Ovenbird density ( $\beta \pm SE = 0.51 \pm 0.25$ ,  $p = 0.01$ , Fig. 3a). The model containing core forest within 500 m received the second greatest support. This variable appeared in two of the top three models, but displayed a relatively weak relationship with Ovenbird density ( $\beta \pm SE = 0.12 \pm 0.13$ ,  $p = 0.02$ ; Fig. 3b).

In maple-basswood forests, the *Lumbricus* model received strong support for predicting Ovenbird density, ranking above all other models (Online Supplementary Table 2). *Lumbricus* biomass was in the top two models and displayed an inverse relationship with Ovenbird density such that density was

modeled to decline by 25% across observed biomasses ( $\beta \pm SE = -0.61 \pm 0.29$ ,  $p = 0.03$ ; Fig. 3c). Ground cover received moderate support as a predictor of Ovenbird density in maple-basswood forests. This variable appeared in two of the top three models; however, the inverse relationship between ground cover and Ovenbird density was comparatively weak ( $\beta \pm SE = -0.01 \pm 0.004$ ,  $p = 0.09$  Fig. 3d). To test the robustness of the relationship between *Lumbricus* biomass and Ovenbird density in maple-basswood forests, we separately analyzed data from each national forest and found significant inverse relationships in both (CHEQ  $\beta \pm SE = -0.46 \pm 0.27$ ,  $p < 0.01$ ; CHIP  $\beta \pm SE = -2.32 \pm 1.09$ ,  $p = 0.05$ ). Density was modeled to decline by 42 and 11% across observed biomasses in the CHEQ and CHIP, respectively.

**Fig. 3** Relationships between Ovenbird density and core forest cover within 1,000 m (a) and 500 m (b) across all 124 points, and between Ovenbird density and *Lumbricus* biomass (c) and ground cover (d) at 53 maple-basswood points, Chequamegon-Nicolet (Wisconsin) and Chippewa (Minnesota) National Forests, 2009–2010



When comparing invaded and *Lumbricus*-free points, we found no differences in litter depth (all points  $t = 0.54$ ,  $df = 122$ ,  $p = 0.59$ ; maple-basswood points  $t = 1.29$ ,  $df = 51$ ,  $p = 0.20$ ) or ground cover (all points  $t = 1.71$ ,  $df = 122$ ,  $p = 0.09$ ; maple-basswood points  $t = 1.20$ ,  $df = 51$ ,  $p = 0.24$ ). Sedge cover was greater at invaded points in both analyses (all points  $t = -3.21$ ,  $df = 122$ ,  $p < 0.01$ ; maple-basswood points  $t = -2.43$ ,  $df = 51$ ,  $p = 0.02$ ). Regression analyses also indicated no relationships between biomass and litter depth (all points  $\beta \pm SE = -0.49 \pm 1.01$ ,  $p = 0.63$ ; maple-basswood points  $\beta \pm SE = -0.18 \pm 1.81$ ,  $p = 0.92$ ) or ground cover (all points  $\beta \pm SE = 7.67 \pm 9.07$ ,  $p = 0.40$ ; maple-basswood points  $\beta \pm SE = 13.67 \pm 14.89$ ,  $p = 0.36$ ). There was a significant positive relationship between *Lumbricus* biomass and sedge cover in maple-basswood forests ( $\beta \pm SE = 41.96 \pm 18.72$ ,  $p = 0.03$ ) but not across all forest types ( $\beta \pm SE = 17.64 \pm 11.76$ ,  $p = 0.13$ ).

## Discussion

Across two national forests, we found reduced Ovenbird density relative to *Lumbricus* invasions in maple-basswood stands. In this forest type, *Lumbricus* biomass received the greatest support for predicting Ovenbird density among the vegetation and landscape pattern variables assessed. Given the broad spatial extent of earthworm invasions in maple-basswood woodlands of the northern U.S., our results suggest that earthworms may be a region-wide threat to Ovenbirds in these forests. We found no evidence for similar associations across all hardwood forest types or for other ground-nesting species.

Density comparison between *Lumbricus*-free and invaded points

Mechanisms for the relationship between *Lumbricus* invasion and Ovenbird density are unclear; however, we provide three hypotheses for the observed patterns. First, *Lumbricus*-caused habitat changes reduce nest concealment resulting in elevated nest predation rates, increased cumulative mortality, and reduced abundance. This hypothesis is supported by research finding an association between *Lumbricus* and predation of Ovenbird nests via sedge cover increasing at

the expense of herbaceous species (Loss and Blair 2011), and by the observation of increased sedge cover with increasing *Lumbricus* biomass in the current study. Second, habitat changes reduce arthropod food supplies, and Ovenbirds compensate by establishing larger territories that are more widely spaced than in *Lumbricus*-free forests. Reduced litter depth has been related to reduced invertebrate abundance (e.g. Haskell 2000), and this could cause density changes; however, more research of *Lumbricus* effects on arthropod populations is needed to provide strong support for this hypothesis. Third, forests with heavy *Lumbricus* invasions are perceived by Ovenbirds to be sub-optimal habitat and are avoided in favor of less impacted areas. In agreement with this hypothesis, Ovenbirds are known to select territories and nest sites with deep leaf litter (Van Horn and Donovan 1994; Mattsson and Niemi 2006) and at least some herbaceous ground cover and shrubs for nest concealment (James 1971; Smith and Shugart 1987), conditions that are characteristic of *Lumbricus*-free and lightly invaded forests (Hale et al. 2006; Holdsworth et al. 2007a; Nuzzo et al. 2009). All three hypothesized mechanisms could mediate *Lumbricus*-associated declines; however, further research is required to determine the importance of each.

We observed no statistically significant differences in density of Hermit Thrush, Black-and-white Warbler, or Veery between invaded and *Lumbricus*-free points. Because these species had widely spaced territories (e.g. densities an order of magnitude lower than Ovenbirds), density differences may have been undetectable at the 100 m radius of survey points. Previous work found lower Hermit Thrush density in invaded sites compared to *Lumbricus*-free sites at the scale of 10–20 ha sites (Loss and Blair 2011), and similar patterns may exist for Veery and Black-and-white Warbler density. Alternatively, these three species may possess life history traits making them less vulnerable to invasions than Ovenbirds. For example, differences in use of vegetation for concealment of ground nests may determine whether *Lumbricus*-caused habitat changes elevate predation rates. Furthermore, Black-and-white Warblers, which rarely forage on the ground (Kricher 1995), may experience minimal effect of any earthworm-caused changes to forest floor arthropod populations. Investigation of ground-nesting songbird populations across different spatial scales and whether invasions affect

nest predation of species other than Ovenbirds will clarify these uncertainties. Finally, our results show an apparent increase in Black-and-white Warbler density with invasion, but this result should be interpreted cautiously, given the statistical non-significance of the relationship and small sample of points at which the species occurred ( $n = 36$ ).

Because we collected a small sample of bird observations at each point, we did not calculate point-level detection probabilities and compare detectability between invaded and *Lumbricus*-free points. We cannot completely overrule the possibility that density comparisons were affected by detectability differences between categories. However, since *Lumbricus* invasions reduce cover of plants, shrubs, and tree seedlings (Lawrence et al. 2003; Hale et al. 2006; Holdsworth et al. 2007a; Nuzzo et al. 2009), we would expect visual and auditory detection of songbirds to increase in “thinned out” invaded forests compared to *Lumbricus*-free forests. The magnitude of Ovenbird decline that we report would be conservative if this were the case.

#### Relative contribution of *Lumbricus* biomass to explaining Ovenbird density

Ovenbird density, nesting success, and pairing success have been correlated to vegetation features, including litter depth (Burke and Nol 1998; Rodewald and Yahner 2000; Mattsson and Niemi 2006), openness of the ground and understory layers (Crawford et al. 1981; Smith and Shugart 1987, Smith et al. 2008), canopy closure (Van Horn and Donovan 1994), and to landscape patterns of forest cover (Manolis et al. 2000; Flaspohler et al. 2001; Smith et al. 2008). *Lumbricus* invasions cause substantial changes to the litter layer and forest floor plant communities, and large-scale invasion patterns are related to patterns of land cover and use. Our finding that *Lumbricus* biomass was related to Ovenbird density in maple-basswood forest—with greater biomass associated with reduced density—suggests that *Lumbricus* invasions could be a mechanism for some of the above correlations.

The relatively weak relationship between ground cover and Ovenbird density and the lack of support for sedge cover are unexpected given previous research indicating a response of Ovenbirds to ground layer vegetation (Smith and Shugart 1987) and an apparent effect of sedge cover on nest concealment and

predation (Loss and Blair 2011). A possible explanation for this result is the time lag between vegetation surveys in 2005–2007 and bird and earthworm surveys in 2009–2010. Although we controlled for major forest structure changes during this period, ground-layer and understory plant communities may have experienced minor changes that obscured relationships between vegetation structure and bird density and between ground cover and *Lumbricus* invasion. Our finding of no relationship between *Lumbricus* and litter depth also contradicts previous research findings. This negative result cannot be explained by sampling time lags because litter depth and sedge cover were measured in 2009–2010. However, a possible explanation is that we did not control for all confounding factors within each forest type (e.g. soil type/texture, forest age, productivity) that could affect litter depth. Despite this limitation, we documented a highly significant positive relationship between *Lumbricus* and sedge cover, suggesting that this invasion effect occurs across a diversity of environmental conditions.

We found little support for *Lumbricus* biomass as a predictor of Ovenbird density across all hardwood forest types. Instead, we documented a positive association between Ovenbird density and core forest cover within 500 and 1,000 m radii. This finding was not unexpected, because impacts of *Lumbricus* in North America have been most commonly documented in maple-basswood forests, both within our study region (Gundale et al. 2005; Hale et al. 2005, 2006; Holdsworth et al. 2007a, b) and in the northeastern U.S. (Lawrence et al. 2003; Fox et al. 2010). Studies finding *Lumbricus* impacts in other forest types are less common (but see Alban and Barry 1994; Nuzzo et al. 2009). The greater magnitude of earthworm effects in maple-basswood forests may be caused by preference of *Lumbricus* for the calcium-rich leaf litter of sugar maple and basswood (Holdsworth et al. 2008). This preference leads to more rapid decomposition of the litter layer (Reich et al. 2005; Heneghan et al. 2007) and likely to a more rapid cascade of effects to understory plant communities in maple-basswood forests.

#### Regional implications for Ovenbird populations

We found a statistically significant association between *Lumbricus* invasions and Ovenbird density in maple-basswood woodlands, and our results suggest

that abundance may decline by as much as 25% in heavily invaded forests. Nonetheless, it is unclear whether this level of decline has biological significance for regional Ovenbird populations, especially since analyses across all forest types indicated that Ovenbird density is most strongly related to the amount of forest cover in the landscape. Although we lack the data needed to conduct a population analysis to clarify the relative impact of earthworms compared to other drivers of demographic rates, we outline four lines of evidence suggesting that, at least within maple-basswood forests, *Lumbricus* invasions may be a regional concern for Ovenbird populations.

First, maple-basswood forests: (1) are among the preferred Ovenbird habitats in the region (Van Horn and Donovan 1994), (2) comprise a considerable portion of the region's woodlands, including ~620,000 ha (10% of all woodland) in Minnesota (Miles et al. 2004) and ~490,000 ha (8% of all woodland) in Wisconsin (Vissage et al. 2004), and (3) are experiencing *Lumbricus* invasions across most of the northern Midwest. Therefore, a non-trivial portion of the regional Ovenbird population is likely exposed to invasions and their adverse effects. Second, because *Lumbricus* invasions have an apparent adverse effect on nest survival probability (Loss and Blair 2011), Ovenbird density declines of 25% (or even less) relative to *Lumbricus* invasion may contribute to significant reductions in productivity. Third, our finding of an apparent adverse effect of *Lumbricus* on Ovenbirds is notable, given the possibility that invasive earthworms may provide a food benefit to ground-foraging songbirds. Direct support for this benefit has yet to be documented, but our results suggest that *Lumbricus*-caused habitat changes outweigh any benefits, resulting in a net negative effect of invasions. Salamanders have been found to experience such an over-riding negative effect of earthworm-caused habitat changes, despite their utilization of earthworms for food (Maerz et al. 2005, 2009).

Fourth, North American Breeding Bird Survey results indicate that northern Minnesota and Wisconsin contain exceptionally high abundance of Ovenbirds (Sauer et al. 2011). Forest songbirds—including Ovenbirds—in the relatively un-fragmented forests of this region have been found to experience relatively low nest predation and parasitism rates and positive net population growth. This region may serve as a source of colonists that sustain smaller sink

populations in fragmented woodlands of the central U.S. (Robinson et al. 1995; Lloyd et al. 2005). *Lumbricus*-related declines across the northern Midwest region could therefore contribute to population declines across broader spatial scales.

This study provides further evidence for the far-reaching adverse effects of earthworm invasions in forested ecosystems of north temperate North America. Effects of invasive earthworms on forest songbirds via degradation of the litter layer and plant communities are only beginning to be studied, but earthworms may have a negative effect on ground-dwelling songbirds in other historically earthworm-free regions currently experiencing invasions (e.g. the northeastern U.S. and southern Canada). Negative effects of *Lumbricus* on vertebrates have been documented in other regions. Fox et al. (2010) observed that ground-nesting songbirds were absent from a heavily invaded sugar maple forest in southern Indiana, and Maerz et al. (2009) documented exponential declines of woodland salamanders in response to earthworm-caused reduction of litter depth in the northeastern U.S. More research is needed to clarify whether additional vertebrate species, such as small mammals, amphibians, reptiles, and other ground-nesting and ground-foraging birds, are affected by earthworm invasions and associated habitat changes. Furthermore, future research should address how potentially at-risk species are affected by interactions between earthworms and other stressors, including climate change, plant invasions, herbivory by over-abundant deer populations, and shifts in disturbance regimes (e.g., Frelich and Reich 2009).

Currently, no methods exist to remove invasive earthworms across the broad extent of existing invasions. Minimizing further effects requires preventing earthworm introductions into remaining earthworm-free areas and of additional earthworm species into areas invaded by only one or a few species. Such efforts will be especially important given the emergence of earthworm taxa that are new to North America and that have unknown effects on forest ecosystems (e.g. the Asian *Amyntas* spp.). Our results suggest that, in *Lumbricus*-invaded maple-basswood forests, management and conservation plans for the Ovenbird, and perhaps other ground-dwelling vertebrates, may benefit from recognition of earthworm effects to forest floor habitat.

**Acknowledgments** Research was funded by the American Museum of Natural History, Bell Museum of Natural History, Dayton-Wilkie Foundation, The Explorers Club, Minnesota Ornithologists' Union, U.S. Department of Agriculture (Chequamegon-Nicolet National Forest), and Wisconsin Society for Ornithology. S.R.L. was supported by a University of Minnesota Graduate School Fellowship and National Science Foundation Interdisciplinary Graduate Education and Research Traineeship: Risk Analysis for Introduced Species/Genotypes (NSF-DGE-0653827). We thank C. Hakseth, L. Raab, and K. Bennett for earthworm sampling assistance, J. Bednar, P. Dolan-Linne, A. Bracey, J. Bailley, C. Lapin, D. Ostrowski, H. Seeland, and J. Smith for conducting bird surveys, and A. Grinde for compiling vegetation and bird data. We thank L.E. Frelich, D.E. Andersen, P. Bolstad, A. Holdsworth, and C. Hale for guiding the study's development. Work was conducted with appropriate permits and approval by the University of Minnesota Institutional Animal Care and Use Committee.

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