

Effects of native deer on invasive earthworms depend on earthworm functional feeding group and correlate with earthworm body size

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ABSTRACT

Above and belowground interactions between animals can influence species abundances, biological invasions, and ecosystem processes. A deeper understanding of above and belowground interactions among animals might benefit from considering functional groups or functional traits, yet most studies have focused on plant functional traits. Here, we consider the possible role of functional group and body size for interactions between invasive earthworms and deer. White-tailed deer are overabundant and are often times considered ecosystem engineers within many forest communities, while invasive earthworms have become an emerging threat to forest communities. We therefore asked a series of questions determine if there were any connections between these two species, with the first being: Do white-tailed deer influence invasive earthworm populations? Because invasive earthworms are divided into different functional groups based on their placement in the soil column and feeding mode, we asked if each of the earthworm functional groups would respond differently to the presence of deer. Finally, we asked if earthworm body size might correlate with the effects of white-tailed deer. We sampled earthworms across 44 paired deer enclosure and control sub-plots across four spatial regions in Ohio, USA. Our analysis controlled for phylogenetic relationships among invasive earthworms, to ensure that confounding effects of evolutionary history did not obscure our ability to detect trait correlations. We found that control sub-plots had more than twice as many endogeic, or soil-dwelling earthworms (e.g. *Octolasion tyraeum*) than paired deer enclosure sub-plots, in the three regions in which they were found. Smaller earthworms were more likely to have higher abundance in the presence of deer, including in phylogenetically corrected tests. If deer overpopulation has a positive effect on some functional groups of invasive earthworms, this suggests that managing deer is important, not only for their aboveground effects on plant communities, but also for their belowground effects on invasive earthworms. More generally, studies of above and belowground interactions might benefit from considering animal functional traits, such as body size, which correlates with functional feeding group.

1. Introduction

There has been a recent surge of studies that have focused on above and belowground interactions involving both plants and animals (Porazinska et al., 2003, Bardgett and Wardle, 2003, Wardle et al., 2004, Wardle, 2006, Kardol and Wardle, 2010, Deyn, 2017). Incorporating information about functional groups and functional traits adds nuance to the study of above and belowground interactions, and generates new, testable predictions for future work. There are thousands of studies that focusing on functional traits (Fig. 1) (Mougi and Kishida, 2009, Salgado-Luarte and Gianoli, 2012), and plant functional traits have informed our understanding of interactions with herbivores and mutualists (Barber et al., 2012), ecosystem functioning (Diaz et al., 2007, Aguirre-Gutiérrez, 2016), and above- and belowground

interactions (Deyn, 2017). However, there are still relatively few studies of above- and belowground interactions that focus on animal functional feeding groups or traits, such as those of earthworms (Fig. 1).

Invasive earthworms have substantial negative effects on native plant communities and ecosystem processes by altering the nutrient availability (Hale et al., 2008), consuming seeds from the seed bank (Nuzzo et al., 2015), and breaking up root and mycorrhizae hyphal networks (Lawrence et al., 2003). Invasive earthworms are likely to be influenced by deer populations because deer have large effects on soil structure and nutrient profiles (e.g. Murray et al., 2013). There has been recent support of this prediction by Dávalos and colleagues, who found greater earthworm abundance in plots where deer had access when compared to plots where deer had been excluded (Dávalos et al., 2015b). Further, abundance of a native earthworm (*Eisenoides*

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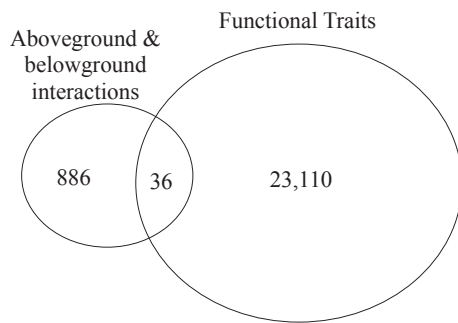


Fig. 1. Number of publications in web of science (24 July 2017) with topic: above and belowground interactions OR aboveground and belowground interactions AND functional trait*, following (Deyn, 2017).

carolinensis) was greater in plots where deer were found compared to plots where deer were excluded for three years (Rearick et al., 2011), consistent with the prediction that deer may increase earthworm populations.

Earthworms are categorized into four functional groups based on their feeding and burrowing traits as well as their size. The anecic functional group contains large earthworms (9–15 cm) that create long vertical burrows from the soil surface to as deep as a meter below-ground. These earthworms pull leaf litter down into the soil from the surface and can rapidly increase nutrient cycling (Fahey et al., 2013). Endogeic earthworms are usually small (1–7 cm) non-pigmented worms that are found within the top soil horizons. These worms have been shown to alter both the microarthropod community as well as the rate of nutrient cycling (Eisenhauer, 2010). Uniquely, endogeic earthworms feed primarily within the soil column, and depend on plant root and soil fungi, unlike the other functional groups, which feed largely on leaf litter. Epigeic earthworms primarily feed within the upper organic layer of soil; due to their relatively small size (2–4 cm) they are thought to have a limited effect on mixing the soil layers. Lastly the epi-endogeic earthworms, most commonly *Amyntas* sp., are large (4–20 cm) soil dwelling species. Epi-endogeic earthworms have large negative effects on native communities by consuming the soil organic layer and breaking up mycorrhizae hyphal networks (Lawrence and Bowers, 2002). Because different functional groups of earthworms use different components of the soil horizon, they might vary in their response to deer. Earthworm body size correlates with functional group and soil horizon usage, and might be an especially useful trait, because it is very easy to measure.

While interactions between the belowground biota, such as invasive earthworms, and native deer are possible (Lessard et al., 2012; Bressette et al., 2012), most deer studies have focused on aboveground interactions. Ungulate overpopulation is a global problem because of increasing urbanization and decreasing predator populations, and their effects on tree regeneration and forest understory plants have been well documented and often dramatic (Côté et al., 2004). There have been numerous long term studies that focus on plant communities in the absence of deer through the use of deer exclosures, tall fences that keep out deer (e.g. McGarvey and Bourg, 2013). For example, deer negatively affect native forbs such as *Trillium grandiflorum* (Knight et al., 2009b). White-tailed deer preferentially feed on the flowering and large non-flowering stages of this plant, thereby stymieing reproduction (Knight et al., 2009b). White-tailed deer also facilitate invasive plant success in forest understories (Knight et al., 2009a), allowing species such as *Alliaria petiolata* and *Microstegium vimineum* to exploit the open patches created by reduced native cover (Knight et al., 2009a). However, whether deer differentially influence different species of earthworms is largely unknown.

To compare multiple species of earthworms, we conducted a comparative study. Comparative studies across multiple species should consider the phylogenetic relationships among species, because species

are not statistically independent sampling units (Felsenstein, 1985). For example, we ask whether there is a correlation between earthworm body size and response to deer presence. If closely related earthworms have similar body sizes, a pattern called phylogenetic signal (Blomberg et al., 2003), then body size would be confounded with phylogenetic relatedness. Further, most statistical tests assume that the residuals of the model are independently and identically distributed, an assumption that can be violated in comparative data sets, even in the absence of phylogenetic signal (Symonds and Blomberg, 2014). Thus we compare analyses with and without controlling for phylogeny, using phylogenetic generalized least squares analysis (Symonds and Blomberg, 2014), to ensure that any correlations we observe accurately describe the relationship between earthworm body size and response to deer.

Previous research has suggested that earthworms' responses to environmental change may be species specific (Zicsi et al., 2011; Wandeler et al., 2016), but whether species specific patterns are idiosyncratic, or might be predicted by functional group or body size, is largely unknown (Karberg and Lilleskov, 2009; Zicsi et al., 2011; Dávalos et al., 2015c). We sampled invasive earthworm abundance across a long-running (5–15 years) large-scale field experiment with 44 deer exclosures and paired control (deer-access) plots. We used experimental field data to ask whether the effects of deer exclusion differ for earthworms in different functional feeding groups or across body sizes. Further, we used phylogenetic comparative methods to ensure that correlations between earthworm body size and deer exclusion were not confounded by relatedness (Felsenstein, 1985). We predicted differences in response to deer across functional feeding groups or body size, which leads to more nuanced hypotheses about deer-earthworm interactions.

2. Methods

2.1. Study system

Our study site in northeastern Ohio, USA, encompassed 44 different plots, each of which contained both a deer exclosure and pre-established paired control sub-plot that were between 3 and 5 m of each other. This allowed sub-plots to be within the same microhabitat but also avoid any edge effects that might be caused from the exclosure. The maximum distance between any two given plots was 71 km, and the closest distance between any two plots was 0.1 km. The spatial location of each plot was recorded with a Garmin GPSmap 60 Cx GPS with a resolution of 10 m. All of the plots have been established between five and twenty years ago (Appendix A: Table S1). Soil characteristics consisted of a silt-loam substrate, with the exception of Little Mountain at Holden Arboretum, which consisted of a sandy silt-loam substrate (Web Soil Survey, USDA: 7/12/2016).

2.2. Study design

We collected earthworms in the exclosure and control sub-plots between late August to early October in both 2013 and 2014. This was done so that most of the earthworms would have reached maturity by that point in the season. Two random locations within each sub-plot were sampled for earthworms (Fig. 2). The earthworm sampling was conducted using the hot mustard extraction technique (Chan and Munro, 2001; Lawrence and Bowers, 2002). This method has been demonstrated to be biased towards sampling greater numbers of anecic earthworms compared to endogeic earthworms (Chan and Munro, 2001). Thus, absolute differences in abundance among functional groups should be interpreted with caution. For the purpose of this study, we were interested in comparing relative earthworm abundance between control and exclosure sub-plots. Thus, the mustard extraction method is appropriate for answering the key question in this study: does earthworm abundance differ between subplots with and without deer access, including within different functional groups? Leaves were first

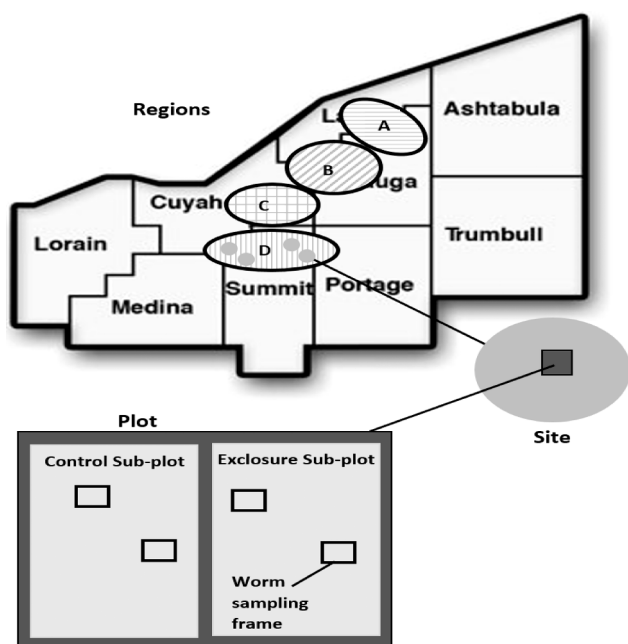


Fig. 2. The experimental design of the paired control and deer exclosure sub-plots in Northeastern Ohio, USA. Earthworm populations were sampled across 4 regions: Lake Metroparks (A), Holden Arboretum (B), Cleveland Metroparks (C), and Metroparks Serving Summit County (D). Each plot contained two sub-plots: a control sub-plot, which was open to deer, and a fenced deer exclosure sub-plot. Earthworms were randomly sampled in two locations within each sub-plot.

carefully removed and hand sorted for any earthworms that may be present within the leaf litter from the 0.09 m^2 area within the sample frame. One gallon of water was mixed with 80 mL of hot mustard powder (Penzeys Spices, Wauwatosa, WI) and poured into the 0.09 m^2 frame. Earthworms were collected from within the frame until they no longer surfaced for ten minutes, then preserved in a 15 percent formalin solution until they could be identified and weighed.

We identified each individual adult earthworm to species, while each juvenile earthworm was identified to genus, because juvenile worms cannot typically be identified to species using morphological characteristics. Keying of each earthworm was based on the earthworm identification field guide provided by Great Lakes Worm Watch (Hale, 2007). *Amyntas* sp. were only identified to genus as they are all almost indistinguishable from each other without the use of molecular techniques.

To determine the biomass of the earthworms, we aggregated all individuals for each species within each sub-plot and dried them in a 60°C oven for a minimum of 24 h. Once they were dry, we weighed the aggregated sample to the nearest 0.0001 g for each species. Then biomass was placed in a 500°C incinerator for a minimum of 4 h to ash the earthworms and remove all organic material, leaving only the stomach contents of the earthworms. We then weighed the ash free remains to the nearest 0.0001 g and took the difference between the dry and ash-free weight to determine the earthworm biomass (Hale et al., 2004).

Because previous studies have suggested that pH is correlated with the deer-earthworm interaction (Dávalos et al., 2015c), we measured the pH of the soil within both the control and exclosure sub-plots. Soil was collected along three transects that were spaced every 2.5 m within the sub-plot. Each of the transects contained three sampling points, spaced every two meters, that were then pooled into one sample. The pH was then recorded for each transect within each sub-plot using a Sartorius PP-20 pH meter. We then took the average of the three transects to determine the pH for each sub-plot.

2.3. Statistical analyses

To determine whether the abundance of earthworms differed between deer exclosure and control sub-plots, we compared earthworm count and biomass data across the 44 paired sub-plots. We summed earthworm counts across the two earthworm sampling frames for each sub-plot (Fig. 2). Earthworm counts were both spatially autocorrelated and zero-inflated and no single analysis method addressed both of these features of the data. Following the methods of similar studies, we split the earthworm count data into two separate response variables: presence/absence and earthworm count when present (Zuur et al., 2009, Wandeler et al., 2016). For the earthworm count response variable, we retained 37 paired sub-plots that had relevant zeros. For example, if we found an anecic earthworm in the control sub-plot but not its paired exclosure sub-plot, the zero from that exclosure was included to maintain the split-plot design of this experiment.

To test for an effect of deer exclosure treatment on invasive earthworm presence, we used a generalized linear model (glm) with a binomial error distribution on earthworm presence/absence as a function of treatment (control vs. deer exclosure), earthworm functional group, a treatment by functional group interaction, and year the plots were established. To address the possible role of functional groups, we constructed planned contrasts within functional groups to compare the control to the exclosure treatments. While this model does not account for potential spatial autocorrelation in earthworm presence, based on visual inspection of a semivariogram, the residuals showed only a slight correlation when compared to the fitted values.

To test for an effect of deer exclosure treatment on earthworm counts and biomass, we used a generalized least squares (gls) model incorporating spatial autocorrelation in the nlme library (Pinheiro et al., 2017). Square-root transformed earthworm count or untransformed biomass were initially modeled as a function of treatment (control vs. deer exclosure), earthworm functional group, year the plots were established, and average pH, and all possible interactions. We then reduced this model by removing any interactions that were not significant ($p > 0.25$) following Bancroft (1964). We inspected semivariograms, which suggested that there was a significant amount of spatial autocorrelation in earthworm counts. Latitudes and longitudes were jittered by adding a small value ($< 0.0000001 \text{ s}$), in order to incorporate sub-plots that did not have unique locations. We compared models using different correlation structures (corGaus, corSpher, corExp) with AIC, to determine the best method for modeling spatial autocorrelation. Although this method assumes that residuals are normally distributed, and residuals of this model were right skewed, least squared approaches are highly robust to violations of the distributional assumption (Ives, 2015), and diagnostic plots suggested that autocorrelation was well-modeled with this approach.

To determine the robustness of the gls results to alternative methods, we conducted a second analysis on earthworm counts when present. We used a generalized linear mixed effects model (glmer) in the lme4 library (Bates et al., 2015) with a Poisson error structure and untransformed earthworm count as a function of treatment (control vs. deer exclosure), earthworm functional group, a treatment by functional group interaction, and year the plots were established. Plot was also included as a random effect in the model. Diagnostics of this model suggested that not incorporating spatial autocorrelation in this glmer was a more severe violation of model assumptions, compared to the diagnostics of the gls.

To explore a possible correlation between earthworm body size and earthworm response to deer exclusion, we calculated earthworm species and site-specific experimental effect sizes. The effect size of the deer exclusion treatment was calculated for earthworm densities across experimental treatments, following Dávalos et al., 2015c.

Effect size = (exclosure – control)/maximum(exclosure, control)

The resulting effect sizes range from -1 to 1 , where 0 indicates no

effect of deer exclusion, negative values indicate more earthworms in the control treatments than in the deer exclusion treatments, and positive values indicate greater earthworm densities in enclosure plots. The sample size for this species comparison was 10. We used a linear model to quantify the correlation between deer enclosure effect size and average adult earthworm body size, log transformed. We examined Q-Q plots and standardized residual plots, and model assumptions were well-met.

To determine whether the relationship between body size and experimental deer exclusion effect size was robust to including phylogenetic information (Felsenstein, 1985), we conducted a phylogenetic analysis amongst the 11 earthworm species sampled in this study (Supplemental Information, Phylogenetic Methods). We tested for phylogenetic signal on body size using Pagel's λ (Pagel, 1999) with the `phylosig` function in the `phytools` package in R, with 1000 replicates (Revell, 2012). We compared gls models for effect size as the response variable and log transformed body size as the predictor variable, for models with and without phylogeny using AIC and a likelihood ratio test. The phylogenetic gls (PGLS) analysis incorporated phylogeny in the error structure of the model as a variance-covariance matrix (Martins and Hansen, 1997) assuming a Brownian motion model of evolution using the `corBrownian` function in the `ape` package in R (Paradis et al., 2004).

All analyses were conducted in the R statistics program (version 3.1.1, R Core Development Team 2014).

3. Results

3.1. Earthworm functional groups

The presence of invasive earthworms was a function of the year the enclosure was established, soil pH, functional group, and experimental treatment (Table 1). There was no interaction between control/exclosure treatment and pH or between control/exclosure treatment and the year the enclosure was established (Appendix A: Table S2). Earthworms were more likely present in the control rather than the enclosure sub-plots, and this was true for six out of ten of the adult taxa (Appendix A: Table S5). This was also true for eight out of nine juvenile taxa (Appendix A: Table S6).

The number of earthworms depended on the control/exclosure treatment by functional group interaction (Table 2). Within endogeic earthworms there were over twice as many earthworms within control sub-plots as there were within enclosure sub-plots (Table 2, Fig. 3a), and this pattern was consistent across spatial regions (Fig. 3b). Three out of four of the regions sampled had been invaded by endogeic earthworms, the fourth (Cleveland Metroparks) had no endogeic earthworms sampled. The other functional groups had similar numbers of earthworms between control and enclosure sub-plots (Table 2, Fig. 3a). The different functional groups of earthworms responded differently to variation in soil pH, but this interaction did not depend on the experimental deer exclusion treatment. The year the experimental deer exclusion fence was established was not a significant covariate on the number of earthworms found (Table 2).

We found five endogeic species amongst the adults, all of which had more earthworms in the control when compared to the enclosure sub-

Table 2

A generalized least squares model with square root transformed earthworm abundance as a function of control and deer enclosure treatments, earthworm functional group, the interactions between treatment and functional group, and functional group by average pH, with the year of enclosure establishment and pH as covariates. Latitude and longitude were used in a `corSper` correlation structure to model spatial autocorrelation. Contrasts within functional groups compared control to deer enclosure treatments.

	NumDF	DenDF	F-value	p-value
Control/Enclosure (C/E)	1	81	7.05	0.009
Functional Group	3	81	3.96	0.009
Average pH	1	81	1.44	0.23
Year Enclosure Established	1	81	0.00	0.99
C/E \times Functional Group	3	81	3.12	0.03
Functional Group \times Average pH	3	81	7.15	0.0002
Contrasts	Estimate	Std Error	z-value	p-value
Anecic	-0.003	0.41	-0.009	1.00
Endogeic	1.08	0.31	3.47	0.002
Epigeic	0.67	0.33	2.02	0.13
Epi-endogeic	0.10	0.36	0.27	1.00

plots (Appendix A: Table S4). Amongst the juveniles, there were four taxa, only two of which had more earthworms within control rather than enclosure sub-plots (Appendix A, Table S5). *Lumbricus terrestris* adults were relatively abundant where they were found, on average 1.5 earthworms in control sub-plots and 5.75 earthworms in enclosure sub-plots but were found across relatively few sub-plots (Appendix A: Table S4). *Amyntas* sp. were found in about a quarter of the sub-plots, with an average of 5.4 earthworms per control sub-plot and 7.73 per enclosure sub-plot (Appendix A: Table S4).

The amount of earthworm biomass per sub-plot varied across the functional groups (Appendix A: Table S2). Amongst adult earthworms, *Lumbricus terrestris* and *Amyntas* sp. contributed the largest amount towards earthworm biomass (Appendix A: Table S4). Amongst juveniles *Lumbricus* sp., *Aporrectodea* sp., and the *Amyntas* sp. contributed the largest amount towards earthworm biomass. There was a marginally significant treatment effect on earthworm biomass per sub-plot ($p = 0.09$), and no interaction between treatment and functional group ($p = 0.52$).

3.2. Earthworm body size

Earthworm adult average body size correlated positively with the experimental effect size of deer enclosure (slope = 0.13, $F_{1,8} = 5.13$, $p = 0.05$) (Fig. 4). *Dendrobaena octaedra* was the smallest earthworm in this sample, with an average body size of 0.013 g and a negative experimental effect size (average effect size = -0.11). *Aporrectodea rosea* was similar in size (0.014 g) with a negative effect size (-0.084). The largest earthworms in our sample were *Lumbricus terrestris* (0.30 g) with a positive effect size (0.39) and *Amyntas* sp. (0.15 g) with a positive effect size (0.28).

We found no phylogenetic signal on earthworm body size ($\lambda < 0.01$, $P = 1.00$; Appendix A: Fig. S1). The model without phylogeny had a higher likelihood and lower AIC (log likelihood = 0.56, AIC = 4.88) than a model with phylogeny (log likelihood = -0.39,

Table 1

A generalized linear model with binomial error distribution on the presence/absence of earthworms as a function of control and deer enclosure treatments, earthworm functional group, and the interaction between treatment and functional group with pH and the year of enclosure establishment as covariates.

	DF	Deviance	Residual DF	Residual deviance	p-value
Control/Enclosure (C/E)	1	6.13	397	522.97	0.01
Functional Group	3	19.59	394	497.25	0.0002
C/E \times Functional Group	3	6.29	389	465.38	0.09
Average pH	1	6.55	393	490.70	0.01
Year Enclosure Established	1	19.03	392	471.67	< 0.0001

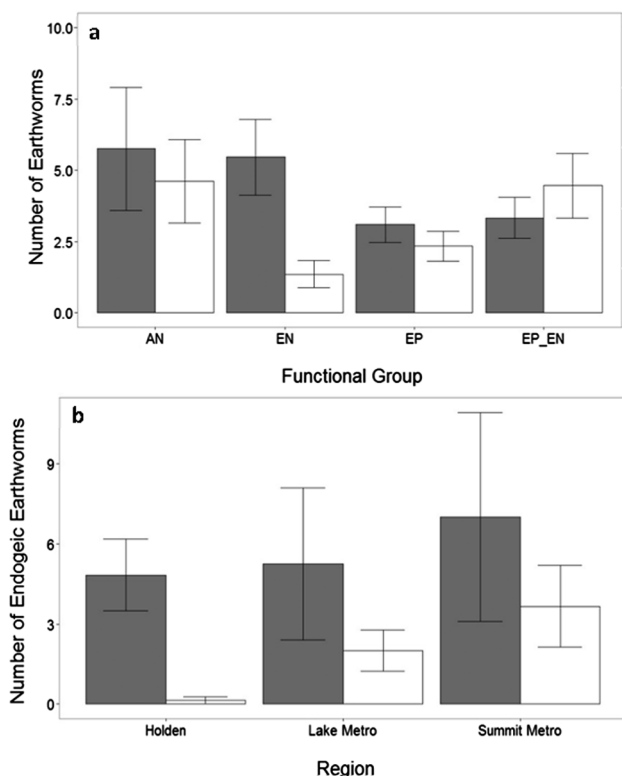


Fig. 3. (a) The number of invasive earthworms was twice as high in control compared with deer exclusion sub-plots for endogeic (EN) earthworms across 44 plots in northeastern Ohio ($p = 0.002$). Anecic (AN), epigeic (EP), and epigeic-endogeic (EP_EN) earthworms did not differ in abundance between treatments (Table 2). Grey bars represent control sub-plots and white bars represent deer exclusion sub-plots. (b) The number of endogeic, soil-dwelling, earthworms were greater in the presence of deer (grey bars) than when deer were experimentally excluded (white bars) for three out of four regions sampled, the other region (Cleveland Metroparks) had no endogeic earthworms (means per sub-plot ± 1 SE).

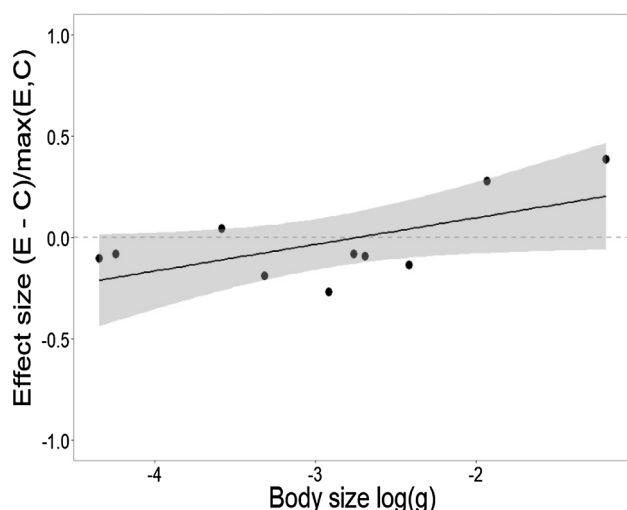


Fig. 4. The standardized experimental effect size of deer exclusion (E), compared with control (C) sub-plots, correlated with earthworm species average adult body size (note log scale). Effect sizes of zero (dashed line) indicate no effect of deer exclusion on earthworm count; negative values indicate greater earthworm count in control sub-plots, and positive values indicate greater earthworm count in exclusion sub-plots.

AIC = 6.77), and the statistical relationship between experimental effect size and body size was robust to incorporating phylogeny ($F_{1,8} = 5.41$, $p = 0.049$).

4. Discussion

While above- and belowground interactions for deer are less well studied than the aboveground effects of deer, our study and several others (Frelich et al., 2012; Dávalos et al., 2015a, 2015b; Dobson and Blossey, 2015) suggest that deer interact with invasive earthworms. Because these interactions are species-specific (Dobson and Blossey, 2015), a consideration of functional groups might enhance our understanding of this species-level variation. Our data suggest that the effects of deer on invasive earthworms depend on earthworm functional group. Other studies have also found that categorizing earthworms by functional group is crucial when understanding both above- and belowground ecological processes (Eisenhauer, 2010; Wandeler et al., 2016). Different species of earthworms affect ecological processes such as nutrient cycling (Eisenhauer et al., 2007; Hale et al., 2008; Straube et al., 2009), seed consumption (Nuzzo et al., 2015), mutualistic associations (Lawrence and Bowers, 2002; Scheu, 2003), and aboveground species (Dávalos et al., 2015b), in diverse ways. Our study suggests that soil-dwelling endogeic earthworms might be more responsive to the effects of deer than other functional groups.

Anecic, epigeic, and epi-endogeic earthworms feed largely on leaf litter, which in these forests is composed mostly of tree litter. Endogeic earthworms exclusively feed in the soil column where the roots of most of the forests herbaceous layer are located. Because the tree community responds so slowly to deer exclusion, and the herbaceous community so quickly, indirect effects of deer mediated by plant community structure are more likely for earthworms that are influenced by the herbaceous layer. This could help explain why endogeic earthworms are more responsive to deer presence than the other functional groups, and additional work could test this putative mechanism.

There are several other potential mechanisms that could influence deer and earthworm interactions, and they are not mutually exclusive. First, deer could facilitate earthworm population growth, if deer pellets contain nutrients that are beneficial to earthworms. Deer fecal pellets can lead to an increase in nutrient availability for earthworms through direct consumption of the pellets or through nutrients leaching from the pellets into the soil, and as a result lead to increases in earthworm mass and population size (Karberg and Lilleskov, 2009; Rearick et al., 2011). For example, a laboratory study found that both native earthworms and the invasive earthworm *Lumbricus terrestris* density and biomass increased more from consuming deer pellets than just leaf litter alone (Rearick et al., 2011). Therefore, nutrients leaching from the pellets might be beneficial to earthworm population growth. Deer could also be increasing earthworm populations through soil disturbance, as they have been shown to physically alter the soil column through scrapes (the pawing of the ground to clear a large area of leaf litter) and trampling (Kumbasli et al., 2010). Further studies are needed to test these potential mechanisms influencing the relationship observed between deer and invasive earthworm populations.

Our data also suggest that earthworm body size correlates with the experimental effect size of deer exclusion. Earthworm species with smaller body sizes, such as *Dendrobaena octaedra* and *Aporrectodea rosea*, were more abundant where deer were present. Larger earthworms, such as *Lumbricus terrestris* and *Amyntas* sp. were somewhat more abundant where deer were experimentally excluded, though not significantly so. Body size is an important functional trait in animals, which correlates strongly with metabolic rate across a wide variety of taxa, including invertebrates (Brown et al., 2004). Body size also correlates with other important functional characteristics, such as desiccation tolerance in frogs (Tracy et al., 2010). In invasive earthworms, body size and functional group are correlated with each other (Bouche, 1977), suggesting that body size may serve as a proxy for functional

group. However, the strong correlations between body size and metabolic rates (Brown et al., 2004), latitudinal clines (e.g. in birds: Olson et al., 2009), and temperature (Gardner et al., 2011), suggest that body size is a widely useful functional trait in animals, and our data suggest that body size in earthworms might correlate with the strength and direction of above and belowground interactions.

We found that both pH and the year the plots were established affected whether earthworms were present or absent. However, contrary to Dávalos et al., (2015c) we found no interaction of deer exclusion and pH on the presence of earthworms despite there being a similar range in pH (3.6–6.4). Also, we found no effect of pH on differences in earthworm abundance between control and enclosure treatments. The main effect of year the plots were established could be an artifact of the experimental design. For example, plots at Holden Arboretum were established between 2005 and 2009, plots at Lake County Metroparks were established between 1994 and 2001, thus we cannot distinguish between effects of year established and regional variation in earthworm abundances. In addition, we also acknowledge that earthworm populations are known to be very patchy and that our sampling methods might have missed some of the population numbers within each of the sub-plots. However, prioritizing a larger spatial scale and increasing plot replications over sampling replications within sub-plots allows us to better detect the effects of deer presence on earthworm populations. We recognize that there is not a large body of literature that has focused on edge effects of deer enclosures in regards to resource availability outside enclosures. Further studies on this topic will provide insight into the spatial extent and magnitude of these effects. We also note that there might be variation in deer density across the different sites; however, the paired sub-plot design should control for spatial variation in deer density.

There is currently no known practical way of controlling earthworm invasions into forest ecosystems (Hendrix, 2006). Our study shows that managing white-tailed deer populations could have an unexpected additional benefit of reducing endogeic invasive earthworm populations. Managing global ungulate populations has been a major topic of discussion for conservation biologists (Côté et al., 2004), and strategies like controlled hunting, culling, exclusion, and female sterilization have been successfully implemented (Côté et al., 2004). While completely excluding deer is not realistic, reducing overabundant deer populations closer to historical densities could help to control some invasive earthworm populations. Further research needs to be conducted to explore mechanisms governing above- and belowground interactions between deer and earthworms, including effects that depend on functional feeding group and body size.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2019.01.003>.

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