ECOSYSTEMS

CrossMark

Non-consumptive Effects of Native Deer on Introduced Earthworm Abundance

Andrea Dávalos,[1]* Elizabeth Simpson,[1] Victoria Nuzzo,[2] and Bernd Blossey[1]

[1]Department of Natural Resources, Cornell University, Ithaca, New York 14853, USA; [2]Natural Area Consultants, 1 West Hill School Road, Richford, New York 13835, USA

ABSTRACT

Chronic ungulate herbivory impacts are well documented, consistently showing changes in plant community dynamics. In contrast, indirect ungulate effects on soil biota and processes are less well understood and idiosyncratic. Evidence suggests that increased deer abundance in northeastern North American forests may facilitate invasions by non-native earthworms and non-native plants through indirect non-consumptive processes. We sampled earthworm abundance using paired open and fenced plots (experimentally excluding deer) from 2008 to 2011 at 12 sites at West Point, NY and in 2013 at 21 additional sites across four states that varied in exclosure size and age since establishment. Fencing decreased earthworm abundance at West Point and in regional surveys. At West Point, negative effects of fencing on earthworm abundance decreased with soil pH and were stronger at sites dominated by native than non-native understory vegetation. Sites dominated by native vegetation had more acidic soils and lower earthworm abundance compared to sites dominated by non-native vegetation. In the regional survey, negative effects of fencing on earthworm abundance increased with time since fences were established, but effects were not affected by exclosure size or site location. We show unforeseen indirect effects of deer exclusion on earthworm populations. Results illustrate the need to account for complex interactive effects among co-occurring stressors, such as deer, earthworms, and non-native plants. Failures to account for these interactions will result in hidden treatments, will complicate interpretation of ecological experiments, and will create difficulties in designing appropriate management strategies aimed at reducing stressor effects.

Key words: deer; deciduous forest; earthworms; invasive plants; invasion; multiple stressors; non-consumptive effects; soil pH.

INTRODUCTION

Ungulate herbivory can result in profound and long-lasting ecosystem effects including changes in plant community composition and dynamics as well as impacts on associated fauna, soil properties, and nutrient availability (Wardle and others 2001; Côté and others 2004; Tanentzap and others 2011; Murray and others 2013). Across northeastern North America, the effects of white-tailed deer

(*Odocoileus virginianus*) on plant composition and population dynamics are well documented and evidence consistently shows detrimental deer impacts on forest tree regeneration and understory plant diversity (Alverson and others 1988; Miller and others 1992; Anderson and Katz 1993; Porter and Underwood 1999; Horsley and others 2003; Rooney and Waller 2003; Ruhren and Handel 2003; Kraft and others 2004; Webster and others 2005). Intense selective deer herbivory creates a shift in plant species composition towards browse resistant or unpalatable species (Horsley and others 2003; Tanentzap and others 2011). Detailed studies consistently show that species in certain functional groups such as grasses, sedges, and some ferns increase under intense deer herbivory, while overall herb diversity declines (Horsley and others 2003; Rooney and Waller 2003). Furthermore, deer herbivory may facilitate expansion of non-native plant species (Eschtruth and Battles 2009; Kuebbing and others 2013; DiTommaso and others 2014; Kalisz and others 2014).

On the other hand, deer effects on soil-dwelling fauna have only recently been recognized and evidence indicates positive, negative, or neutral effects (Wardle and others 2001; Nuttle 2011; Bressette and others 2012). Deer may indirectly affect soil-dwelling fauna by altering plant composition and successional dynamics (De Jager and others 2013; Thomas-Van Gundy and others 2014) or by affecting plant resource allocation and hence the quantity or quality of plant tissue (Mason and others 2010). In addition, herbivores may affect soil-dwelling fauna through soil-mediated processes. Individual deer consume 3–5 kg of vegetation a day (Marquis and Brenneman 1981) and their feeding and activity patterns may increase soil compaction and alter mycorrhizal colonization (Heckel and others 2010; Kardol and others 2014). Moreover, increased return of organic matter and nutrients through deposition of urine and feces (Rooney and Waller 2003) may increase microbial activity and consequently accelerate decomposition rates (Harrison and Bardgett 2003). Lastly, by changing vegetation composition, deer may also affect leaf litter quality and quantity (Harrison and Bardgett 2003; Nuttle and others 2011; Bressette and others 2012). For example, in New Zealand, deer activity reduced soil macrofauna, but this reduction was not correlated with the magnitude of understory plant diversity reduction but to levels of litter layer habitat diversity (Wardle and others 2001). Considering that soil-mediated processes can produce positive or negative effects on detritivore food webs, it is not surprising that deer effects

on soil fauna are idiosyncratic (Wardle and others 2004) and that our knowledge of their impacts is still limited.

White-tailed deer, non-native earthworms, and non-native plants are major agents of change throughout northeastern North American forests (Mack and others 2000; Côté and others 2004; Hale and others 2006; Vilá and others 2011; Fisichelli and others 2013). Although their individual impacts have been widely documented (Mack and others 2000; Côté and others 2004; Hale and others 2006; Vilá and others 2011), we lack information about potential interactive effects. Strong links between above- and below-ground food webs (van der Putten and others 2013) indicate that these widespread and co-occurring stressors may produce complex non-additive interactive effects. Interactive effects could occur through a modification of stressor mode of action (functional process) or through population facilitation (numerical process) (Didham and others 2007). For example, deer and earthworms may produce interactive effects if leaf litter depletion by earthworms results in increased plant visibility and higher likelihood of deer consumption (Frelich and others 2006) (a functionally mediated process, sensu Didham and others 2007). But interactive effects can also occur if deer presence facilitates earthworm populations (a numerically mediated process, sensu Didham and others 2007). Although both processes may result in similar effects, they arise from different mechanisms and may require distinct management strategies.

A beneficial effect of deer on non-native earthworm abundance has been proposed (Frelich and others 2006), but we lack field or experimental data to confirm such patterns. A Web of Science © search (8 July 2014) using key words ''deer'' and ''earthworm'' yielded 22 citations: Only four assessed effects of deer on earthworms (Karberg and Lilleskov 2009; Rearick and others 2011; Seki and Koganezawa 2013; Shelton and others 2014) and three of those found a positive effect of deer on earthworm abundance. Earthworms appear to benefit from high nutrient deer fecal pellets, especially in areas with acidic soils and low-quality leaf litter input such as in hemlock (*Tsuga canadensis*) stands (Karberg and Lilleskov 2009). Comparisons of earthworm populations between open and fenced plots that manipulated deer access indicate higher earthworm abundance in open plots in two studies (Rearick and others 2011; Seki and Koganezawa 2013) and no difference between open and fenced plots in a third study (Shelton and others 2014). Overall, albeit limited, evidence

indicates facilitative effects of deer on earthworms (Karberg and Lilleskov 2009; Rearick and others 2011; Seki and Koganezawa 2013) and non-native forest plant invasions (Eschtruth and Battles 2009; Kalisz and others 2014), which themselves are facilitated by earthworm invasions (Nuzzo and others 2009; Roth and others 2015). Reported links among these organisms suggest that their populations are intricately connected through a network of indirect pathways, likely driven by soil-mediated effects produced by deer (Wardle and others 2004; Kardol and others 2014) and earthworm activity (Bohlen and others 2004).

Here we report on the effects of experimental deer exclusion (through fencing) on earthworm community composition, density, and biomass at 12 forested sites at US Army Garrison West Point, New York State, USA (hereafter referred to as West Point) from 2008 to 2011. Sites at West Point varied in abundance of three non-native plant species (*Alliaria petiolata, Berberis thunbergii,* and *Microstegium vimineum*) allowing us to also assess effects of non-native plant invasion on earthworm abundance, measured as both number of organisms and total biomass. Based on previous results, we expected higher earthworm abundance at sites dominated by non-native plant species (Nuzzo and others 2009) but had no a priori expectation for the effect of deer

exclusion on earthworm communities. In order to assess fencing effects over a larger geographical area and timescale, we conducted a complementary regional study covering 21 locations in the northeastern deciduous forest region of North America (Figure 1). We selected sites with established deer exclosures of different size and age since establishment, and compared earthworm abundance inside fenced plots to earthworm abundance in adjacent paired unfenced (open) plots with otherwise similar site characteristics. Based on preliminary results from our West Point study, we hypothesized that deer exclusion will result in lower earthworm abundance compared to earthworm abundance in deer accessible areas. Furthermore, we expected deer exclusion effects to accumulate over time, such that the difference in earthworm abundance between open and fenced (deer excluded) plots will increase with years since fences were established.

MATERIALS AND METHODS

Annual Surveys at West Point

West Point, a 65 km² facility located on the west bank of the Hudson River, NY, USA is located within the Hudson Highlands Province, characterized by rugged hilly terrain with rocky outcrops
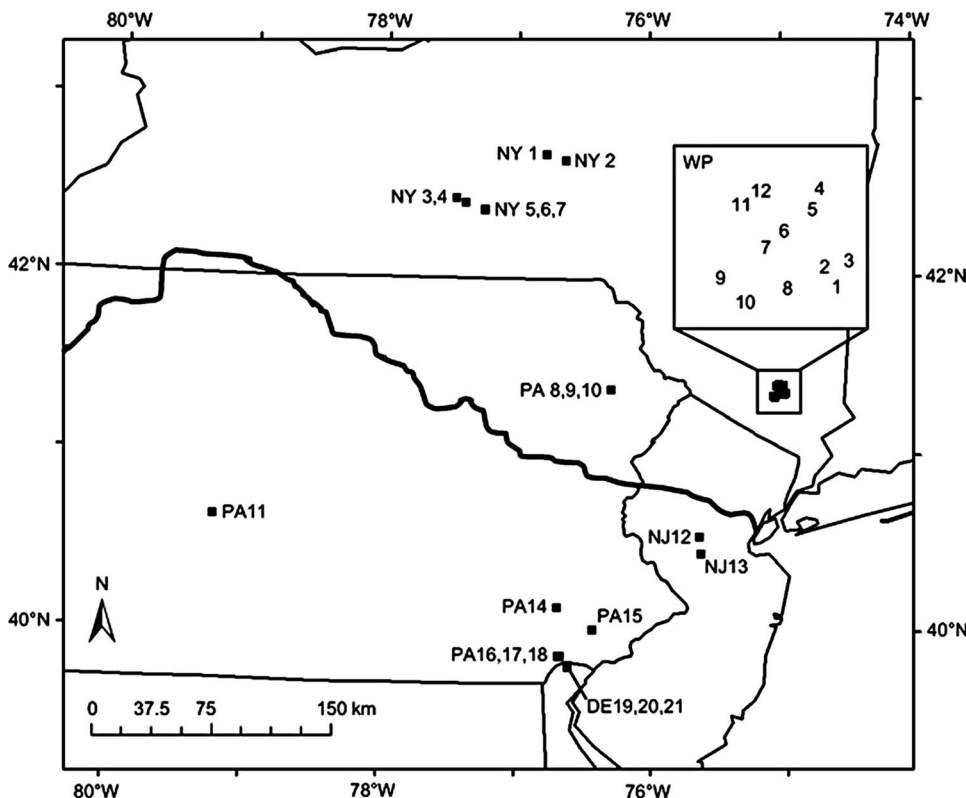

Figure 1. Study locations to assess earthworm abundance in the Northeastern USA. For reference, the approximate extent of the Wisconsinan Glaciation is represented by the east–west wavy line (Pennsylvania Bureau of Topographic and Geologic Survey—Deparment of Conservation and Natural Resources 1995). For site characteristics please see Tables 1 and 2.

and frequently thin soils. We selected 12 upland deciduous forested sites greater than 1 km apart avoiding areas with high military training intensity and/or restricted access (Figure 1). Study sites are dominated by oak (*Quercus rubra* and *Q. prinus*) and/or sugar maple (*Acer saccharum*) but differ in land use history, aspect, soil, and understory plant species composition. We selected 6 sites based on the presence and abundance of three non-native plant species (*A. petiolata, B. thunbergii, M. vimineum*; 2 sites each) and 6 sites with few or no non-native plant species present (Table 1). At each site, we established two 30 m × 30 m plots situated 5–50 m apart. One plot of each pair was randomly selected to be an open plot accessible to deer, and the other a fenced plot to exclude deer. We constructed deer-proof exclosures with black polypropylene fencing (2.6 m high, 3.8 cm × 5 cm cell size, 408 kg breaking strength, Deer Busters, Frederick MD) from 7 to 11 July 2008.

We removed leaf litter and collected soil samples (7 cm in diameter, 5 cm deep) at 10 random locations in each open or fenced plot in October 2008. We homogenized soils and removed all roots and rocks before submitting samples for analyses of pH, C, P, and Ca (extracted through the Modified Morgan procedure) at the Cornell Nutrient Analysis Laboratory Ithaca NY).

We collected vegetation data in May and July 2008–2012 in 10 1-m^2 permanent quadrats located at random in each fenced and open plot. We estimated cover of each native and non-native plant species in 17 cover categories (midpoints: 0.01, 0.2, 0.5, 1, 3, 5, 10, 20, 30, 40, 50, 60, 70, 80, 90, 98, and 100%) and leaf litter volume by measuring the depth of the litter at four equi-distant locations within each quadrat, and then multiplying by the proportion of the quadrat covered by leaf litter. We estimated vegetation height by measuring the average height of vegetation at four locations within each quadrat, and then averaging these heights for each quadrat. Leaf litter and height estimates included all vegetation present in the quadrat (native and non-native).

Regional Survey

We selected 21 forested sites with existing deer exclosures ranging in size (100–2,428,000 m^2) and years since fence establishment (2–21 years; Table 2). We chose sites in 2013 based on availability of an adjacent unfenced area with comparable soil type, vegetation, and former land use conditions. Existing fences (metal or plastic) were 2–3 m high and excluded deer but allowed access by small mammals such as rodents. At two sites, Flintwood Preserve Blowdown and Beaver Meadow State

Table 1. Characteristics of the 12 Study Sites at West Point, NY

Site[1]	Vegetation and soil				Earthworms		
	Vegetation type[2]	Non-native cover (%)[3]	Species richness	Soil pH	Density[4]	Biomass (g)[4]	Dominant genus
4	Native	0	27	3.6	0.33 ± 0.13	0.02 ± 0.01	*Dendrobaena*
2	Native	0	21	3.8	2.48 ± 0.81	0.44 ± 0.22	*Dendrobaena*
9	Native	0.10 ± 0.023	59	4.3	14.08 ± 1.43	5.30 ± 0.99	*Dendrobaena*
8	Native	0.01 ± 0.01	58	4.6	7.60 ± 2.25	3.36 ± 1.29	*Dendrobaena*
11	Native	0.20 ± 0.06	36	4.7	1.13 ± 0.47	0.44 ± 0.21	*Lumbricus*
10	Native	0.01 ± 0.005	31	4.7	11.63 ± 2.37	4.57 ± 1.23	*Lumbricus*
12	*Microstegium vimineum*	81.01 ± 7.2	25	4.8	9.15 ± 2.79	4.56 ± 1.58	*Aporrectodea*
6	*Berberis thunbergii*	80.14 ± 3.92	9	4.9	12.10 ± 1.73	7.48 ± 1.44	*Lumbricus*
7	*Alliaria petiolata*	3.14 ± 0.38	32	5.1	12.50 ± 3.84	8.49 ± 2.76	*Amynthas*
3	*Microstegium vimineum*	31.12 ± 2.85	61	5.2	9.80 ± 2.46	5.17 ± 1.15	*Aporrectodea*
5	*Alliaria petiolata*	2.30 ± 0.42	42	5.2	13.60 ± 4.09	9.51 ± 2.99	*Amynthas*
1	*Berberis thunbergii*	26.81 ± 1.29	44	6.4	1.98 ± 0.40	1.19 ± 0.37	*Amynthas*

[1]*Sites are ordered according to soil pH and understory vegetation type.*
[2]*Indicates site classification according to understory vegetation type (native/non-native). Sites with non-native vegetation were selected based on the presence and abundance of three target non-native plant species (A. petiolata, B. thunbergii, and M. vimineum; 2 sites each). All sites with non-native species had higher soil pH than native sites and hence are grouped in the lower section of the table.*
[3]*Plant cover in May (for A. petiolata) and July (remaining sites) 2008 (%; mean at start of study, n = 20 1-m^2 permanent quadrats/site). We estimated vegetation cover in 17 categories (midpoints: 0.01, 0.2, 0.5, 1, 3, 5, 10, 20, 30, 40, 50, 60, 70, 80, 90, 98, and 100%).*
[4]*Earthworm density (number per 0.25 m^2; mean ± SD) and wet biomass (g per 0.25 m^2) (n = 10 quadrats/site) in July 2008–2011. We extracted earthworms by pouring 3.79 l of mustard solution at 15 g l^{-1} per quadrat.*

Table 2. Study Site, Exclosure Size (m²), Years Since Fence was Established at the Time of Sampling, Earthworm Density and Biomass per Year (mean ± 1SE), and Dominant Earthworm Genus Found at 21 Sites in Regional Survey

Site	Location	Size (m²)	Years since fencing	Earthworm density[1]	Earthworm biomass (g)[2]	Dominant genus
Bucks Brook State For. (NY1)	Otselic, NY	2230	7	0	0	
Beaver Meadow State For. (NY2)	Smyrna, NY	8100	6	5.2 ± 3.48	2.22 ± 1.48	*Lumbricus*
Mundy Wildflower Preserve (NY3)	Ithaca, NY	24,281	5	20 ± 3.18	10.81 ± 1.45	*Amynthas*
Polson Preserve (NY4)	Ithaca, NY	114	21	2.6 ± 1.83	0.96 ± 0.94	*Lumbricus*
Red Trillium, W. Hill School Rd (NY5)	Richford, NY	2770	5	16.4 ± 3.36	5.35 ± 1.32	*Lumbricus*
Meadow, W. Hill School Rd (NY6)	Richford, NY	7500	4	12.5 ± 3.46	2.56 ± 1.09	*Dendrobaena*
Driveway, W. Hill School Rd (NY7)	Richford, NY	1170	6	31.4 ± 2.42	5.92 ± 1.19	*Lumbricus*
Lacawac Sanctuary New (PA8)	Lake Ariel, PA	6380	2	0.9 ± 0.27	0.31 ± 0.15	*Aporrectodea*
Lacawac Sanctuary Old Oak (PA9)	Lake Ariel, PA	6500	19	0.7 ± 0.26	0.20 ± 0.16	*Lumbricus*
Lacawac Sanctuary Old Hemlock (PA10)	Lake Ariel, PA	6500	19	0.6 ± 0.31	0.44 ± 0.32	*Aporrectodea*
Plummer's Hollow (PA11)	Tyrone, PA	12,820	12.5	0	0	
Duke Farms Migration For. (NJ12)	Hillsborough, NJ	2,428,000	5	5.7 ± 1.09	6.31 ± 0.95	*Lumbricus*
Duke Farms Research For. (NJ13)	Hillsborough, NJ	121,406	10	4.2 ± 1.25	4.72 ± 1.61	*Lumbricus*
Welkinweir Old (PA14)	Pottstown, PA	100	12	9.3 ± 1.29	11.85 ± 2.04	*Amynthas*
Waterloo Mills Preserve (PA15)	Chadds Ford, PA	100	10	1.5 ± 0.58	2.6 ± 0.99	*Amynthas*
Kendal-Crosslands Communities (PA16)	Kennett Square, PA	100	8	10.4 ± 1.65	7.9 ± 1.41	*Amynthas*
Longwood For. (PA17)	Kennett Square, PA	195	4.5	14.7 ± 1.88	14.12 ± 2.72	*Amynthas*
Longwood Garden (PA18)	Kennett Square, PA	195	4.5	5.1 ± 0.64	3.37 ± 0.42	*Amynthas*
Flintwood Preserve Blowdown (DE19)	Centreville, DE	4187	8	11.5 ± 2.26	9.52 ± 1.97	*Amynthas*
Flintwood Preserve Diversity (DE20)	Centreville, DE	2689	9	8.2 ± 1.75	5.35 ± 1.21	*Amynthas*
Flintwood Preserve Former Field (DE21)	Centreville, DE	4351	10	10.3 ± 4.45	7.75 ± 2.23	*Amynthas*

Sites are abbreviated as the two-letter state abbreviation followed by sequential numbers from North to South.
Sites in bold indicate sites excluded from analyses because we found no earthworms (NY1, PA11), collected < 10 earthworms across all samples (PA8, PA9, PA10), or earthworm invasion front had not reached both plots (NY2).
[1]*Earthworm density (number per 0.25 m²; mean ± 1SE) and wet biomass (g per 0.25 m²) (n = 10 quadrats/site).*
[2]*We extracted earthworms by pouring 3.79 l of mustard solution at 15 g l⁻¹ per quadrat on one occasion per site in Jul–Sep 2013.*

Forest, tree blowdowns in the past year had damaged the fence and we observed limited evidence of deer presence in the enclosed area; however, this was minimal compared to the considerable deer browse we observed in the paired open plots.

Earthworm Sampling

At all sites, we sampled for earthworms in five randomly located 0.25 m² quadrats in each open and fenced plot. Samples were located at least 3–5 m from the fence to avoid potential edge effects. At each sampling location, we pushed a metal frame into the topsoil, removed, and manually searched all leaf litter for earthworms, and then poured 3.79 l of mustard solution at 15 g l⁻¹ (Frontier Natural Products Co-op, Norway, IA) onto the soil to extract earthworms (Lawrence and Bowers 2002). Mustard extraction is a non-destructive method that, like most non-destructive methods, is sensitive to soil moisture and earthworm activity patterns (Eisenhauer and others 2008). We fixed specimens in 10% formalin, transferred them to 70% ethyl alcohol for storage, and identified each individual to species when possible (only sexually mature worms can reliably be identified to species). We obtained individual earthworm biomass for West Point 2009–2011 and total earthworm biomass per sample (0.25 m²) for West Point 2008 and regional survey samples. At West Point, we annually assessed earthworm abundance in late July from 2008 to 2011. We collected regional survey samples on one occasion per site July through November 2013 (for exact dates please see Supplemental Table 1). We collected samples in paired open and fenced plots per site on the same day.

Statistical Analyses

We conducted separate analyses for West Point and regional surveys. For West Point data, we evaluated effects of fencing and study year (2008–2011) on percent cover of the three focal non-native plant species and on leaf litter volume via independent repeated measures linear models, including site and plot within site as random factors. We arcsine square-root transformed cover values to meet model assumptions.

We also evaluated effects of year (2008–2011) and vegetation origin (dominated or not by non-native plant species) on earthworm density and biomass at West Point with linear mixed models, including site and plot within site as random factors. We log transformed biomass data to meet assumptions of normal distribution and constant variance. We averaged data from five samples taken per plot each year to correct for lack of independence among samples.

We compared earthworm diversity between sites dominated by European earthworms to sites dominated by the Asian genus *Amynthas* using the Shannon Diversity Index (Spellerberg and Fedor 2003). We estimated the Shannon Index for each site and ran Analyses of Variance to compare the index between *Amynthas*-dominated and European-dominated sites. We performed separate analyses for West Point and the regional survey.

To evaluate effects of fencing on earthworm abundance (density and biomass) across sites in the West Point study and the regional survey, we estimated the magnitude of fencing effects at each study site (and year for West Point) as the difference in mean earthworm density (number per 0.25 m^2, N = 5 samples per plot) or biomass (g per 0.25 m^2, N = 5 samples per plot) between paired open and fenced plots relative to the plot with the higher earthworm abundance in the pair [fencing effect = (fenced − open)/max(fenced, open)]. The denominator was included to avoid potential bias towards negative values (Markham and Chanway 1996). Estimated fencing effects vary from −1 to 1 with a value of zero indicating no fencing effects, negative values indicating negative effects of fencing, and positive values indicating positive effects of fencing on earthworm density or biomass.

For West Point data, we applied linear mixed models to evaluate effects of year (2008–2011), soil pH, Ca and P concentration, understory species richness, leaf litter volume, and their two-way interactions on fencing effects. We included soil and vegetation characteristics in the model in order to account for differences among sites that may potentially affect earthworm communities or earthworm response to fencing. We evaluated effects of fencing on earthworm density and biomass with separate models. Models included site as a random factor to account for repeated measures. We excluded site 4 from all analyses because we captured <10 earthworms per year (Table 1).

We tested for correlation of fixed factors using Spearman's rank correlation test. Soil pH was significantly correlated with Ca (Spearman's rank correlation = 0.61, $P < 0.001$). Sites dominated by native vegetation had lower pH ($F_{1,10} = 10.25$, $P < 0.01$) and Ca ($F_{1,10} = 4.24$, $P = 0.06$) than sites dominated by non-native vegetation. To avoid problems in model building due to multicollinearity, we excluded Ca concentration from the models and fitted a second set of models that did not include soil pH to evaluate effects of site vegetation status (native or non-native).

For the regional survey, we applied linear models to evaluate effects of site latitude, exclosure size, years since fencing was established, and their interactions on the relative difference in mean earthworm density between open and fenced plots. We ran a second set of models to evaluate effects of all factors and interactions on relative differences in mean earthworm biomass. Earthworms were absent (2 sites), present in low abundance (<10 at 3 sites), and their invasion front only reached one of the plots (1 site) at 6 sites, which we therefore excluded from further analyses (Table 2).

We also evaluated fencing effects on the most abundant earthworm genera (*Amynthas, Aporrectodea, Dendrobaena,* and *Lumbricus*) at our study sites, fitting independent models for each genus and survey (West Point or regional). Given the uneven distribution of earthworm genera across sites, we only included sites at which the genus was present (>10 individuals) in genera models. For West Point data, we evaluated year (2008–2011) effects with mixed linear models, including site as a random factor. For the regional survey, we evaluated effects of exclosure size and years since fencing was established with linear models.

Starting with the full model, we evaluated the explanatory power of competing models with Akaike Information Criterion corrected for small samples sizes (AICc) and selected the best-fit model based on minimum AICc (Burnham and Anderson 2002). We conducted all tests in R 2.14 (R Core Team 2014) and fitted mixed models with the lme4 package (Bates and others 2014).

RESULTS

Annual Surveys at West Point

Soil characteristics varied across sites, but did not differ between paired open and fenced plots at the start of the study. Soil pH ranged from 3.7 to 6.4, with lowest pH recorded at sites with low earthworm abundance (sites 2 and 4; Table 1). Soil pH was not correlated with total earthworm density (Spearman rank correlation = 0.12, $P = 0.24$) but positively correlated with earthworm biomass (correlation = 0.21, $P = 0.04$).

Across the 12 sites, cover of target non-native vegetation ranged from 0 to 81% and was higher at *B. thunbergii* (27 and 80%) and *M. vimineum* (31 and 81%) sites than at *A. petiolata* sites (3% at each site; Table 1). Non-native vegetation cover did not differ between paired open and fenced plots in 2008 when fences were erected. By 2011 (4 years after fencing), cover of *A. petiolata* and *M. vimineum* was significantly lower in fenced than open plots ($P < 0.05$), but *B. thunbergii* cover remained similar between open and fenced plots ($P > 0.05$). Leaf litter volume was not significantly different between years or between open and fenced plots ($P > 0.05$).

Mean earthworm density (0.33 to 14.08 earthworms per 0.25 m^{-2} per site) and biomass (0.02 to 9.51 g per 0.25 m^{-2} per site) varied among sites and sampling years. Earthworm biomass was significantly higher at sites dominated by non-native than native understory vegetation throughout the study period, whereas earthworm density was significantly higher at sites dominated by non-native vegetation in 2008 and 2011 only (Figure 2, Supplemental Table 2).

We recorded 13 non-native earthworm species in eight genera with the genera *Amynthas*, *Aporrectodea*, *Dendrobaena*, and *Lumbricus* being most abundant. The epigeic *Amynthas* spp. (mean individual biomass 0.63 g) was present at eight sites, dominant at three sites, and at two sites accounted for 95 and 98% of earthworms we collected (Supplemental Figure 1). *Amynthas* spp. consisted of a mixture of mature and immature *A. agrestis* and *A. hilgendorfi*. The endogeic *Aporrectodea* spp. (mean individual biomass 0.15 g) and the epigeic *Dendrobaena octaedra* (mean individual biomass 0.05 g) were dominant at two and four sites each, accounting for 45–85% and 41–49% of earthworms, respectively. We identified two *Aporrectodea* species: *A. caliginosa* species complex and *A. rosea*. The anecic *Lumbricus terrestris* (mean adult biomass 2.4 g) was present at six sites in relatively low abundance (1–17%). However, juveniles of this genus were
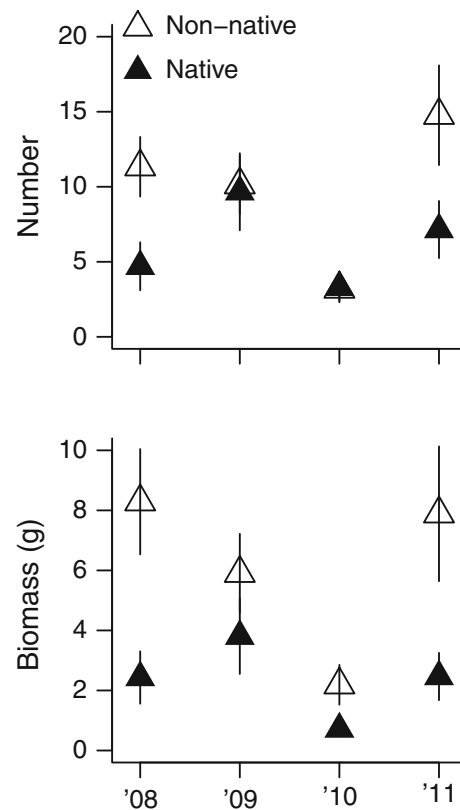

Figure 2. Number (per 0.25 m^2) and biomass (g per 0.25 m^2) of earthworms captured at sites dominated by native and non-native vegetation ($N = 6$ per vegetation type) at West Point, NY from 2008 to 2011. Data are untransformed means $\pm$ 1 SE. Note different scales on number and biomass y-axes.

common and accounted for 23% of all captured earthworms and for 15–27% of earthworms captured at each site (Supplemental Figure 1). *Lumbricus castaneus* and *L. rubellus* were restricted to few sites and occurred at lower abundance. We recorded no native earthworms.

Sites dominated by European earthworm species exhibited higher earthworm species diversity (Shannon diversity index = 1.08 ± 0.11; $N = 9$) than sites dominated by the Asian earthworm genus *Amynthas* (Shannon diversity index = 0.27 ± 0.18; $N = 3$; $F_{1,10} = 12.73$, $P = 0.005$).

Fencing effects (estimated as the relative difference between paired fenced and open plots) on earthworm density and biomass were significantly and similarly affected by an interaction between study year and soil pH (Table 3, Supplemental Table 3). Although at the beginning of the study fencing effects did not differ from zero and were unaffected by soil pH, by 2010 fencing effects were positively correlated with soil pH (Figure 3).

Table 3. Model Results for the Effects of Study Year and Soil pH on the Effects of Fencing on Earthworm Density and Biomass at 12 Sites at West Point, NY from 2008 to 2011

Factor[1]	Density				Biomass			
	Estimate	SE	X^2	P	Estimate	SE	X^2	P
Intercept	0.60	0.96			−0.55	1.26		
Year	−1.26	0.35			−0.75	0.30		
pH	−0.14	0.19			0.07	0.26		
Year x pH	0.25	0.07	10.72	0.001	0.17	0.06	6.54	0.01

[1]*Estimates and standard errors are reported from the model fitted with restricted maximum likelihood. Chi-squared statistics and P values are from likelihood ratio tests with each parameter removed from the maximum likelihood-based model, with all other parameters retained. It was not possible to test the significance of all terms because of higher order interactions.*
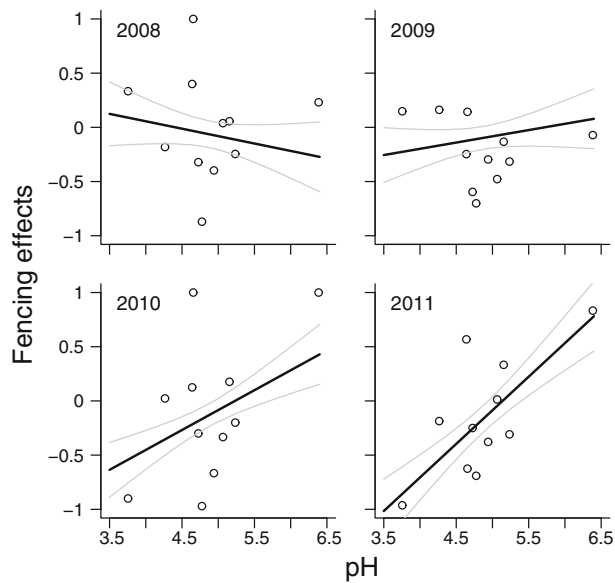*Models included site as random factor.*

Figure 3. Relationship between study year, soil pH, and fencing effect on density of earthworms captured in paired open and fenced plots at West Point, NY from 2008 to 2011. Fences were erected 3 weeks prior to 2008 earthworm sampling. Estimated fencing effects vary from −1 to 1 with a value of zero indicating no fencing effects, negative values indicating negative effects of fencing and positive values indicating positive effects of fencing on earthworm density. Lines represent predicted and 95% confidence intervals from Linear Mixed Model with site included as random factor.

Vegetation height, leaf litter volume, and understory species richness had no significant effect and dropped from the final model. Models excluding an outlier site that has higher soil pH than remaining study sites (Site 1) indicated a significant interaction between year and soil pH for the effect of fencing on earthworm density (Supplemental Table 4), but no effect of fencing on biomass (best model included random term only).
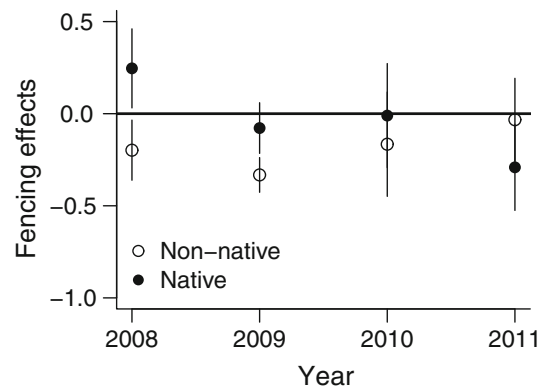

Figure 4. Relationship between vegetation origin (native or non-native) and effect of fencing on density of earthworms captured in open and fenced plots at 12 sites (N = 6 of each vegetation type) at West Point, NY from 2008 to 2011. Estimated fencing effects vary from −1 to 1 with a value of zero indicating no fencing effects, negative values indicating negative effects of fencing, and positive values indicating positive effects of fencing on earthworm density.

The second set of models in which we evaluated the effect of vegetation origin (dominated by native or non-native vegetation) rather than soil pH indicated a significant interaction between year and vegetation origin on the effects of fencing on earthworm density (likelihood ratio test: X^2 = 4.79, P = 0.03). At sites dominated by native vegetation (with more acidic soil pH), the effect of fencing on earthworm density significantly decreased over time, whereas at sites dominated by non-native vegetation fencing effects were negative but tended to increase throughout the study period (Figure 4). The effect of fencing on earthworm biomass was not significantly affected by vegetation origin.

Analyses by genus indicated that fencing effects on density of the four most abundant genera did not vary with year and were significantly lower
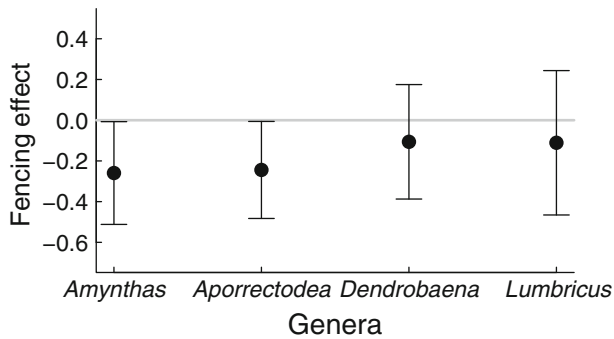
Figure 5. Relative effects of fencing on density of most abundant earthworm genera captured in fenced and open plots at West Point, NY from 2008 to 2011. Estimated fencing effects vary from −1 to 1 with a value of zero indicating no fencing effects, negative values indicating negative effects of fencing, and *positive values* indicating positive effects of fencing on earthworm density or biomass. Data represent estimated mean effects and 95% confidence intervals (Wald method) estimated from Linear Mixed Model with site included as random factor.

than zero (95% confidence interval estimated via Wald method) for *Amynthas* (present at 3 sites) and *Aporrectodea* (present at 4 sites) genera only (Figure 5) indicating lower earthworm abundance of these genera inside exclosures. We found no significant fencing effects on biomass of any of the four genera.

Regional Survey

We collected 1638 earthworms at 15 of 21 study sites. Mean earthworm density (1.5 to 31.4 earthworms per 0.25 m^{-2}) and biomass (0.96 to 14.12 g per 0.25 m^{-2}) varied among sites (Table 2). We recorded 12 non-native earthworm species in six genera with *Amynthas* (54%; 9 sites) being most abundant followed by *Lumbricus* (23%; 8 sites), *Dendrobaena* (12%; 3 sites), *Aporrectodea* (6%; 4 sites), and *Octolasion* (3%; 4 sites). We recorded no native earthworm species.

Amynthas spp. dominated sites south of the last glacial (Wisconsinan glacier) line extent (Figure 1), but were present and dominant at one site north of this border (Mundy Wildflower Garden, Ithaca, NY; Supplemental Figure 2) in the regional survey, and were also present at West Point. Sites included in the regional survey and dominated by European earthworm species exhibited higher earthworm species diversity (Shannon diversity index = 0.92 ± 0.26; N = 6) than sites dominated by the Asian earthworm genus *Amynthas* (Shannon diversity index = 0.11 ± 0.06; $F_{1,13} = 13.27$; $P = 0.002$; N = 9), a pattern also found at West Point.
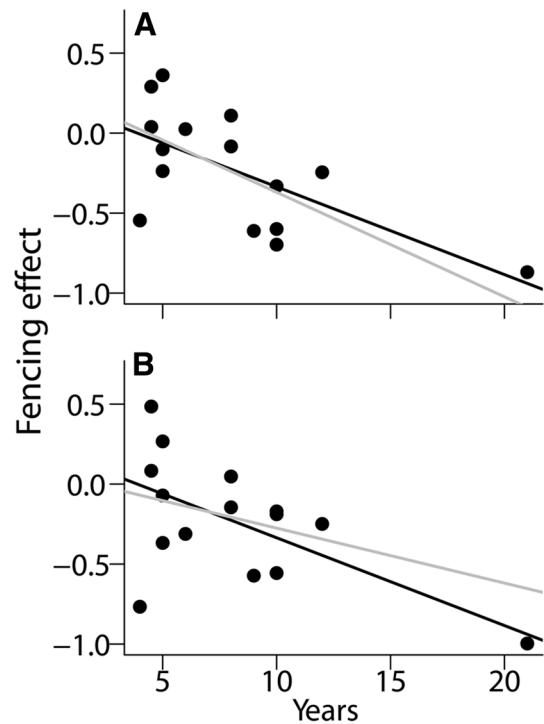

Figure 6. Relationship between age since establishment of the fenced plot and fencing effect on density (**A**) and biomass (**B**) of earthworms captured in paired fenced and open plots at 15 sites in four states in July–September 2013. *Lines* depict predictions from linear regression models including all sites (*black*) and excluding the site with the oldest fenced plot (Polson Preserve, age 21; *gray*).

Fencing effects (estimated as the relative difference between paired fenced and open plots) were significantly <0 for earthworm density (95% CI −0.44 to −0.03; $t = -2.43$; $P = 0.02$) and earthworm biomass (95% CI −0.45 to −0.02; $t = -2.35$; $P = 0.03$), indicating a negative effect of fencing on earthworm abundance. Across the 15 study sites, fencing effects on density ($F_{1,13} = 9.43$, $P = 0.008$) and biomass ($F_{1,13} = 6.45$, $P = 0.02$) were inversely correlated with fence age (years since establishment of fences; Figure 6). Size of the fenced plot, site latitude, and interactions were not significant and dropped from the final model. Models excluding the oldest site in the sample to account for an outlier site (Polson Preserve, age 21) also found a negative correlation between fencing effects and age of the fenced plot on earthworm density ($F_{1,13} = 4.27$, $P = 0.06$), but not on earthworm biomass ($F_{1,13} = 0.95$, $P = 0.35$). Although total earthworm abundance decreased inside fences, analyses by genus indicated no significant effects of fencing on density of individual genera in the regional survey.

DISCUSSION

Our findings that deer exclusion results in lower earthworm abundance in fenced areas and that this effect becomes stronger over time, add important new insights into multi-trophic interactions between above- and below-ground organisms and processes. Despite some recent advances, impacts of mammalian herbivores on plant and decomposer communities as well as nutrient cycling are still poorly understood (Cherif and Loreau 2013). Empirical studies have found a range of effects (Wardle and others 2001), and this low predictability, in part, is thought to be a function of the varying effects and interactions of different herbivores with the varying productivity and fertility of different ecosystems (Wardle and others 2004). Previously, most studies failed to account for potential interactive effects among the myriad of biotic components in the studied systems that may account for the reported differences. We are aware of only two other studies reporting similar effects of deer exclusion on earthworms in Virginia, USA (Rearick and others 2011) and Japan (Seki and Koganezawa 2013). Earthworms and deer in the studies from Virginia and Japan were native, whereas in our case we only detected non-native earthworms, suggesting that origin of earthworms does not affect their interaction with deer.

At West Point, soil pH, non-native plant cover, and non-native earthworm abundance were intricately related, such that sites with higher pH (and Ca concentration) had higher earthworm abundance and higher non-native plant cover. Positive associations between earthworms and higher soil pH and Ca availability had been reported before (Holdsworth and others 2007; Bernard and others 2009; Holdsworth and others 2012; Fisichelli and others 2013), as well as associations between earthworms and non-native plants (Nuzzo and others 2009; Roth and others 2015). We cannot establish if earthworms and non-native plants both benefited from similar site conditions or to what extent these organisms altered site characteristics to their benefit. Regardless of the cause for such association, experimental exclusion of deer results in different effects according to soil pH (and hence non-native plant cover): at sites with lower pH earthworms benefited from deer presence, whereas at sites with higher soil pH earthworms were negatively affected by deer presence. Beneficial effects of deer at sites where earthworm expansion is limited by low soil pH suggest deer play an important role in facilitating earthworm expansion into otherwise unsuitable sites.

Interestingly, different earthworm genera showed variable responses to fencing. While fencing was negative for all genera combined at West Point and in the regional survey, it was only significantly different from zero for *Amynthas* and *Aporrectodea* at West Point when analyzing the response of individual genera. These variations in response may be partially due to uneven distribution of genera across sites, which reduced overall replication of the study, or to confounding effects of species grouped into the same genus but which have distinct ecological behaviors (Zicsi and others 2011). As an alternative, earthworms are often classified into ecological feeding groups (anecic, epigeic, and endogeic); however, these groups are not necessarily a cohesive assemblage of species with common behaviors (Edwards and Bohlen 1996; Zicsi and others 2011). Therefore, detailed behavioral studies of individual species are needed in order to understand why some earthworm species are positively associated with deer while others do not seem to respond.

In both surveys (West Point and regional), earthworm diversity at sites dominated by the Asian genus *Amynthas* was lower than at sites dominated by European genera. At many sites, *Amynthas* was the only represented genus, suggesting an ability to outcompete European earthworms, potentially through dietary flexibility (Zhang and others 2010). *Amynthas* spp. were widespread south of the extent of the last glaciation, although their presence north of this line in our survey and at other northern locations (Görres and Melnichuk 2012) indicates that climate conditions do not prevent *Amynthas* invasion. Southern sites were closer to large population centers or botanical gardens, suggesting that these may constitute invasion hubs from which the genus is expanding northward and westward. Both observations highlight the need to perform detailed assessments of *Amynthas* impacts, spread rate, and interactions with other soil biota.

The effect of deer exclusion at West Point persisted despite wide fluctuations in earthworm abundance during the study period. Earthworm abundance varied across sampling years and was significantly lower in 2010 at all twelve sites when our sampling coincided with a drought. While dry periods can affect earthworm recruitment, survival, activity, and also sampling efficacy (Eisenhauer and others 2008), the relationship of earthworm response to deer was not affected by the low abundance during drought.

As in any field study, vegetation and soil characteristics varied across our study sites potentially

affecting local earthworm abundance. Earthworm populations are affected by many factors, including leaf litter quality, soil chemical content (Hale and others 2005; Holdsworth and others 2007), forest successional age (Szlavecz and Csuzdi 2007; Crow and others 2009), and proximity of sites to human-modified environments, especially roads and agricultural fields (Holdsworth and others 2007). Our design of paired open and fenced plots allowed us to evaluate deer exclusion as well as to include soil and vegetation characteristics of each site that may affect local earthworm abundance or their response to deer. Notably, except for soil pH, inclusion of these variables did not change our results or importance of the fencing effect on earthworm abundance at West Point. As past land use and vegetation composition may affect soil pH (Koerner and others 1997; Flinn and others 2005), this measure is likely encompassing multiple site characteristics and processes. Our results highlight the importance of deer as one of many factors that may affect earthworm distribution and abundance, in addition to habitat characteristics and anthropogenic influences.

Although non-consumptive impacts of deer have received less attention than impacts produced by herbivory, mounting evidence indicates that deer activity may exert non-consumptive effects on native and non-native flora (Knight and others 2009; Heckel and others 2010; Dávalos and others 2014; Kalisz and others 2014) and soil-dwelling fauna (Wardle and Bardgett 2004). Results suggest that deer affect earthworm populations through a soil-mediated process, by which deer activity either increases soil pH or releases constraints imposed on earthworms by low soil pH.

Soil-mediated effects, including changes in soil physical properties, mycorrhizal infection rate, and nutrient availability (Heckel and others 2010; Murray and others 2013; Kardol and others 2014), constitute important pathways by which deer may exert ecosystem impacts. Although there is no evidence indicating that deer can significantly affect soil pH over short-term experiments (Kuebbing and others 2013; Kardol and others 2014; Relva and others 2014), deer may affect decomposition and decomposer communities including alterations in the quantity, quality, or composition of resources returned to the brown food web that in turn may affect soil microbial communities (Bardgett and Wardle 2003; Kardol and others 2014). Furthermore, changes in microbial composition, abundance, and activity may follow if plants respond to deer herbivory by altering root exudates, secondary chemistry, or other defense traits (Bardgett and Wardle 2003).

In addition, large ungulate trampling and potential compaction of soils may affect nutrient dynamics, decomposition, and decomposer communities as well as fitness of certain plant species (Heckel and others 2010; Kumbasli and others 2010; Gass and Binkley 2011; Bressette and others 2012; Schrama and others 2013). Over time, deer herbivory, particularly at elevated levels, can have strong sorting effects on plant communities, shifting plant communities from highly palatable to less palatable (Côté and others 2004; Wardle and others 2004), often favoring introduced species (Eschtruth and Battles 2009; Knight and others 2009; Abrams and Johnson 2012; Kalisz and others 2014), which, as our results and previous reports (Heneghan and others 2007; Nuzzo and others 2009) indicate, are associated with increased earthworm abundance. Increase of understory native cover with associated decrease of non-native cover in the fenced plots at West Point, only occurred after 4 years of fence establishment, yet the effect of deer exclusion on earthworms preceded these vegetation changes (Nuzzo and others unpublished data). Therefore, changes in vegetation cover cannot explain the differences in earthworm abundance recorded earlier in the study.

Herbivores change net primary productivity and thus overall litter production through consumption but also return partially, often more easily decomposable resources in the form of urine and feces to the litter that further stimulate soil biota (Hobbs 1996; Schrama and others 2013). While the fertilizing effect of ungulates at the landscape scale appears trivial compared to aerial deposition, actual measurements show the importance of herbivore feces and urine to localized (Hobbs 1996; Murray and others 2013) and landscape nutrient dynamics (Seagle 2003; Abbas and others 2012). These results are consistent with previous reports indicating that the earthworm *L. terrestris* benefits from nutrient subsidies provided by fecal pellets on deer winter ranges (Karberg and Lilleskov 2009). This overall fertilization effect and stimulation of microbial decomposition benefits earthworms by increasing the palatability of plant litter as well as increasing microbial communities, which constitute an important yet variable component of earthworm diets.

Both deer and introduced earthworms are considered ecosystem engineers (Côté and others 2004; Hale and others 2006), important agents of environmental change, and major problems for conservation of native biota (Côté and others 2004; Maerz and others 2009). Our results show that their populations are linked through a rather

intricate network of interactions (although we do not know if earthworms affect deer abundance in reciprocal ways) and it is likely that the status of plant, herbivore, and earthworm as native or introduced, as well as their abundance will affect the outcome of these interactions. These interactions are likely facilitated through abiotic changes, soil microbial communities, and legacy effects. But the ultimate mechanisms responsible for the documented patterns currently elude us. We expect these relationships to play out over a multi-decadal time frame, while our own assessment spans only two decades and with few truly old exclosures in our sample set.

Studies investigating ecosystem effects of earthworms, deer, below-ground microbial communities, and invasive plants and their interactions are a recently emerged phenomenon with enormous potential to further our ecological understanding. Much more detailed work capturing more components of ecosystems and their responses will be needed and more and novel assessment protocols using interdisciplinary approaches will be required to further understand these interactions. Deer effects are frequently quantified by installation of a deer-proof fence, while earthworm effects are typically studied without manipulation of ungulate populations. Our results clearly show the shortcomings of either approach due to the interactions of deer, earthworms, and introduced plant species. It is of considerable importance to recognize these interactions, as they constitute a ''hidden treatment'' (Huston 1997) with important consequences for interpretation of experiments aimed at understanding deer or earthworms (or invasive plant) impacts. However, our results also emphasize the critical role of white-tailed deer in forest ecosystems. Reducing deer densities may have multiple benefits beyond protecting vegetation (Baiser and others 2008; Christopher and Cameron 2012), including decrease of other stressor populations, such as earthworms and non-native plants.

ACKNOWLEDGMENTS

REFERENCES

Abbas F, Merlet J, Morellet N, Verheyden H, Hewison AJM, Cargnelutti B, Angibault JM, Picot D, Rames JL, Lourtet B, Aulagnier S, Daufresne T. 2012. Roe deer may markedly alter forest nitrogen and phosphorus budgets across Europe. Oikos 121:1271–8.

Abrams MD, Johnson SE. 2012. Long-term impacts of deer exclosures on mixed-oak forest composition at the Valley Forge National Historical Park, Pennsylvania, USA. J Torrey Botanical Soc 139:167–80.

Alverson WS, Waller DM, Solheim SL. 1988. Forests to deer: edge effects in northern Wisconsin. Conserv Biol 2:348–58.

Anderson RC, Katz AJ. 1993. Recovery of browse-sensitive tree species following release from white-tailed deer *Odocoileus virginianus* Zimmerman browsing pressure. Biol Conserv 63:203–8.

Baiser B, Lockwood JL, La Puma D, Aronson MFJ. 2008. A perfect storm: two ecosystem engineers interact to degrade deciduous forests of New Jersey. Biol Invasions 10:785–95.

Bardgett RD, Wardle DA. 2003. Herbivore-mediated linkages between aboveground and belowground communities. Ecology 84:2258–68.

Bates D, Maechler M, Bolker B, Walker S. 2014. lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-7. http://CRAN.R-project.org/package=lme4.

Bernard MJ, Neatrour MA, McCay TS. 2009. Influence of soil buffering capacity on earthworm growth, survival, and community composition in the western Adirondacks and Central New York. Northeast Nat 16:269–84.

Bohlen PJ, Groffman PM, Fahey TJ, Fisk MC, Suarez E, Pelletier DM, Fahey RT. 2004. Ecosystem consequences of exotic earthworm invasion of north temperate forests. Ecosystems 7:1–12.

Bressette JW, Beck H, Beauchamp VB. 2012. Beyond the browse line: complex cascade effects mediated by white-tailed deer. Oikos 121:1749–60.

Burnham KP, Anderson DR. 2002. Model selection and multi-model inference: a practical information-theoretic approach. New York: Springer-Verlag.

Cherif M, Loreau M. 2013. Plant—herbivore—decomposer stoichiometric mismatches and nutrient cycling in ecosystems. Proc R Soc B 280:20122453.

Christopher CC, Cameron GN. 2012. Effects of invasive amur honeysuckle (*Lonicera maackii*) and white-tailed deer (*Odocoileus virginianus*) on litter-dwelling arthropod communities. Am Midl Nat 167:256–72.

Côté SD, Rooney TP, Tremblay J-P, Dussault C, Waller DM. 2004. Ecological impacts of deer overabundance. Annu Rev Ecol Syst 35:113–47.

Crow SE, Filley TR, McCormick M, Szlavecz K, Stott DE, Gamblin D, Conyers G. 2009. Earthworms, stand age, and species composition interact to influence particulate organic matter chemistry during forest succession. Biogeochemistry 92:61–82.

Dávalos A, Nuzzo V, Blossey B. 2014. Demographic responses of rare forest plants to multiple stressors: the role of deer, invasive species and nutrients. J Ecol 102:1222–33.

De Jager NR, Cogger BJ, Thomsen MA. 2013. Interactive effects of flooding and deer (*Odocoileus virginianus*) browsing on floodplain forest recruitment. For Ecol Manag 303:11–19.

Didham RK, Tylianakis JM, Gemmell NJ, Rand TA, Ewers RM. 2007. Interactive effects of habitat modification and species invasion on native species decline. Trends Ecol Evol 22:489–96.

DiTommaso A, Morris SH, Parker JD, Cone CL, Agrawal AA. 2014. Deer browsing delays succession by altering aboveground vegetation and belowground seed banks. Plos One 9:e91155.

Edwards CA, Bohlen PJ. 1996. Biology and Ecology of Earthworms. 3rd edn. London: Chapman and Hall.

Eisenhauer N, Straube D, Scheu S. 2008. Efficiency of two widespread non-destructive extraction methods under dry soil conditions for different ecological earthworm groups. Eur J Soil Biol 44:141–5.

Eschtruth AK, Battles JJ. 2009. Acceleration of exotic plant invasion in a forested ecosystem by a generalist herbivore. Conserv Biol 23:388–99.

Fisichelli NA, Frelich LE, Reich PB, Eisenhauer N. 2013. Linking direct and indirect pathways mediating earthworms, deer, and understory composition in Great Lakes forests. Biol Invasions 15:1057–66.

Flinn KM, Vellend M, Marks PL. 2005. Environmental causes and consequences of forest clearance and agricultural abandonment in central New York, USA. J Biogeogr 32:439–52.

Frelich LE, Hale CM, Scheu S, Holdsworth AR, Heneghan L, Bohlen PJ, Reich PB. 2006. Earthworm invasion into previously earthworm-free temperate and boreal forests. Biol Invasions 8:1235–45.

Gass TM, Binkley D. 2011. Soil nutrient losses in an altered ecosystem are associated with native ungulate grazing. J Appl Ecol 48:952–60.

Görres JH, Melnichuk RDS. 2012. Asian invasive earthworms of the genus *Amynthas* Kinberg in Vermont. Northeast Nat 19:313–22.

Hale CM, Frelich LE, Reich PB. 2006. Changes in hardwood forest understory plant communities in response to European earthworm invasions. Ecology 87:1637–49.

Hale CM, Frelich LE, Reich PB, Pastor J. 2005. Effects of european earthworm invasion on soil characteristics in northern hardwood forests of Minnesota, USA. Ecosystems 8:911–27.

Harrison K, Bardgett R. 2003. How browsing by red deer impacts on litter decomposition in a native regenerating woodland in the Highlands of Scotland. Biol Fertil Soils 38:393–9.

Heckel CD, Bourg NA, McShea WJ, Kalisz S. 2010. Nonconsumptive effects of a generalist ungulate herbivore drive decline of unpalatable forest herbs. Ecology 91:319–26.

Heneghan L, Steffen J, Fagen K. 2007. Interactions of an introduced shrub and introduced earthworms in an Illinois urban woodland: impact on leaf litter decomposition. Pedobiologia 50:543–51.

Hobbs NT. 1996. Modification of ecosystems by ungulates. J Wildl Manag 60:695–713.

Holdsworth A, Frelich L, Reich P. 2012. Leaf litter disappearance in earthworm-invaded northern hardwood forests: role of tree species and the chemistry and diversity of litter. Ecosystems 15:913–26.

Holdsworth AR, Frelich LE, Reich PB. 2007. Regional extent of an ecosystem engineer: Earthworm invasion in northern hardwood forests. Ecol Appl 17:1666–77.

Horsley SB, Stout SL, DeCalesta DS. 2003. White-tailed deer impact on the vegetation dynamics of a northern hardwood forest. Ecol Appl 13:98–118.

Huston MA. 1997. Hidden treatments in ecological experiments: Re-evaluating the ecosystem function of biodiversity. Oecologia 110:449–60.

Kalisz S, Spigler RB, Horvitz CC. 2014. In a long-term experimental demography study, excluding ungulates reversed invader's explosive population growth rate and restored natives. Proc Natl Acad Sci 111:4501–6.

Karberg NJ, Lilleskov EA. 2009. White-tailed deer (*Odocoileus virginianus*) fecal pellet decomposition is accelerated by the invasive earthworm *Lumbricus terrestris*. Biol Invasions 11:761–7.

Kardol P, Dickie IA, St. John MG, Husheer SW, Bonner KI, Bellingham PJ, Wardle DA. 2014. Soil-mediated effects of invasive ungulates on native tree seedlings. J Ecol 102:622–31.

Knight TM, Dunn JL, Smith LA, Davis J, Kalisz S. 2009. Deer facilitate invasive plant success in a Pennsylvania forest understory. Nat Areas J 29:110–16.

Koerner W, Dupouey JL, Dambrine E, Benoit M. 1997. Influence of past land use on the vegetation and soils of present day forest in the Vosges mountains, France. J Ecol 85:351–8.

Kraft LS, Crow TR, Buckley DS, Nauertz EA, Zasada J. 2004. Effects of harvesting and deer browsing on attributes of understory plants in northern hardwood forests, Upper Michigan, USA. For Ecol Manag 199:219–30.

Kuebbing S, Rodriguez-Cabal MA, Fowler D, Breza L, Schweitzer JA, Bailey JK. 2013. Resource availability and plant diversity explain patterns of invasion of an exotic grass. J Plant Ecol 6:141–9.

Kumbasli M, Makineci E, Cakir M. 2010. Long term effects of red deer (*Cervus elaphus*) grazing on soil in a breeding area. J Environ Biol 31:185–8.

Lawrence AP, Bowers MA. 2002. A test of the 'hot' mustard extraction method of sampling earthworms. Soil Biol Biochem 34:549–52.

Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. Ecol Appl 10:689–710.

Maerz JC, Nuzzo VA, Blossey B. 2009. Declines in woodland salamander abundance associated with non-native earthworm and plant invasions. Conserv Biol 23:975–81.

Markham JH, Chanway CP. 1996. Measuring plant neighbour effects. Funct Ecol 10:548–9.

Marquis DA, Brenneman R. 1981. The impact of deer on forest vegetation in Pennsylvannia. USDA Forest Service General Tech. Rep. NE-65, Northeast For. Exp. Stn.

Mason NWH, Peltzer DA, Richardson SJ, Bellingham PJ, Allen RB. 2010. Stand development moderates effects of ungulate exclusion on foliar traits in the forests of New Zealand. J Ecol 98:1422–33.

Miller SG, Bratton SP, Hadidian J. 1992. Impacts of white-tailed deer on endangered and threatened vascular plants. Nat Areas J 12:67–89.

Murray B, Webster C, Bump JK. 2013. Broadening the ecological context of ungulate–ecosystem interactions: the importance of space, seasonality, and nitrogen. Ecology 94:1317–26.

Nuttle T, Yerger EH, Stoleson SH, Ristau TE. 2011. Legacy of top-down herbivore pressure ricochets back up multiple trophic levels in forest canopies over 30 years. Ecosphere 2:art 4.

Nuzzo VA, Maerz JC, Blossey B. 2009. Earthworm invasion as the driving force behind plant invasion and community change in northeastern North American forests. Conserv Biol 23:966–74.

Pennsylvania Bureau of Topographic and Geologic Survey—Department of Conservation and Natural Resources. 1995. DCNR Glacier 500 k 1995. Version 1. Pennsylvania Bureau of Topographic and Geologic Survey, Harrisburg, PA. http://www.pasda.psu.edu/.

Porter WF, Underwood HB. 1999. Of elephants and blind men: deer management in the US National Parks. Ecol Appl 9:3–9.

R Core Team. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/.

Rearick D, Kintz L, Burke KL, Ransom TS. 2011. Effects of white-tailed deer on the native earthworm, *Eisenoides carolinensis*, in the southern Appalachian Mountains, USA. Pedobiologia 54:S173–80.

Relva MA, Castan E, Mazzarino MJ. 2014. Litter and soil properties are not altered by invasive deer browsing in forests of NW Patagonia. Acta Oecol 54:45–50.

Rooney TP, Waller DM. 2003. Direct and indirect effects of white-tailed deer in forest ecosystems. For Ecol Manag 181:165–76.

Roth A, Whitfeld TS, Lodge A, Eisenhauer N, Frelich L, Reich P. 2015. Invasive earthworms interact with abiotic conditions to influence the invasion of common buckthorn (Rhamnus cathartica). Oecologia 178:219–230.

Ruhren S, Handel SN. 2003. Herbivory constrains survival, reproduction and mutalisms when restoring temperate forest herbs. J Torrey Botanical Soc 130:34–42.

Schrama M, Heijning P, Bakker JP, van Wijnen HJ, Berg MP, Olff H. 2013. Herbivore trampling as an alternative pathway for explaining differences in nitrogen mineralization in moist grasslands. Oecologia 172:231–43.

Seagle SW. 2003. Can ungulates foraging in a multiple-use landscape alter forest nitrogen budgets? Oikos 103:230–4.

Seki Y, Koganezawa M. 2013. Does sika deer overabundance exert cascading effects on the raccoon dog population? J For Res 18:121–7.

Shelton AL, Henning JA, Schultz P, Clay K. 2014. Effects of abundant white-tailed deer on vegetation, animals, mycorrhizal fungi, and soils. For Ecol Manag 320:39–49.

Spellerberg IF, Fedor PJ. 2003. A tribute to Claude Shannon (1916–2001) and a plea for more rigorous use of species richness, species diversity and the 'Shannon–Wiener' Index. Glob Ecol Biogeogr 12:177–9.

Szlavecz K, Csuzdi C. 2007. Land use change affects earthworm communities in Eastern Maryland, USA. Eur J Soil Biol 43:S79–85.

Tanentzap AJ, Bazely DR, Koh S, Timciska M, Haggith EG, Carleton TJ, Coomes DA. 2011. Seeing the forest for the deer: do reductions in deer-disturbance lead to forest recovery? Biol Conserv 144:376–82.

Thomas-Van Gundy M, Rentch J, Adams MB, Carson W. 2014. Reversing legacy effects in the understory of an oak-dominated forest. Can J For Res 44:350–64.

van der Putten WH, Bardgett RD, Bever JD, Bezemer TM, Casper BB, Fukami T, Kardol P, Klironomos JN, Kulmatiski A, Schweitzer JA, Suding KN, Van de Voorde TFJ, Wardle DA. 2013. Plant-soil feedbacks: the past, the present and future challenges. J Ecol 101:265–76.

Vilá M, Espinar JL, Hedjda M, Hulme PE, Jarošik V, Maron JL, Pergl J, Schaffner U, Sun Y, Pyšek P. 2011. Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. Ecol Lett 14:702–8.

Wardle DA, Bardgett RD. 2004. Human-induced changes in large herbivorous mammal density: the consequences for decomposers. Front Ecol Environ 2:145–53.

Wardle DA, Bardgett RD, Klironomos JN, Setala H, van der Putten WH, Wall DH. 2004. Ecological linkages between aboveground and belowground biota. Science 304:1629–33.

Wardle DA, Barker GM, Yeates GW, Bonner KI, Ghani A. 2001. Introduced browsing mammals in New Zealand natural forests: Aboveground and belowground consequences. Ecol Monogr 71:587–614.

Webster CR, Jenkins MA, Rock JH. 2005. Long-term response of spring flora to chronic herbivory and deer exclusion in great Smoky Mountains national Park, USA. Biol Conserv 125:297–307.

Zhang W, Hendrix PF, Snyder BA, Molina M, Li J, Rao X, Siemann E, Fu S. 2010. Dietary flexibility aids Asian earthworm invasion in North American forests. Ecology 91:2070–9.

Zicsi A, Szlavecz K, Csuzdi C. 2011. Leaf litter acceptance and cast deposition by peregrine and endemic European lumbricids (Oligochaeta: Lumbricidae). Pedobiologia 54:145–53.