Earthworm invasion, white-tailed deer and seedling establishment in deciduous forests of north-eastern North America

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Summary

1. Earthworm invasions and high deer populations are among many stressors threatening long-term population viability of forest understorey plants in north-eastern North America. Stressor effects are typically tested one at a time; however, stressors often co-occur and plants respond to effects of multiple stressors simultaneously.

2. We used a factorial design to test independent and combined effects of non-native earthworms and native white-tailed deer on survival of seedling transplants of 15 native understorey plants in five forests in New York State.

3. Earthworm biomass was negatively correlated with survival of 12 of 15 species. We found no interactive effect of deer and earthworms, but did find a positive, non-consumptive effect of deer on *Geranium maculatum* and *Polygonum virginianum* survival.

4. Deer and earthworm presence/absence indirectly influenced other trophic levels: earthworm presence increased the likelihood of insect attack, and deer exclusion increased the likelihood of rodent disturbance of transplants.

5. *Synthesis.* Invasive earthworms negatively affected seedling survival of many understorey plants, including species previously thought to benefit from earthworm associations. This effect was a function of earthworm biomass, a surrogate for earthworm activity. We expect deer herbivory to increase in importance, including indirect effects, as seedlings grow into browse height over the next years. Investigations of co-occurring stressors can result in 'ecological surprises' including previously overlooked non-consumptive effects or effects on other trophic levels.

Key-words: conservation, deciduous forests, indirect effects, invasion ecology, invasive species, multiple stressors, plant–soil below-ground interactions, seedling establishment

Introduction

Eastern North American forests have undergone major transformations in response to land-use changes, species gains and losses, climate change, pollution and habitat fragmentation (De Schrijver *et al.* 2011; Fisichelli, Frelich & Reich 2013; Suarez-Rubio *et al.* 2013; Hanberry, Kabrick & He 2014). Local biodiversity in contemporary forests is changing as a result of rapidly advancing invasive species (Liebhold *et al.* 2013; Lovett *et al.* 2013) and a disproportionate reduction of species with short dispersal distances, limited reproduction and growth, long generation times and obligate mycorrhizal associations (Gundale 2002; Hale, Frelich & Reich 2006; Kain *et al.* 2011). Negative effects of introduced species have been well documented (Boag & Yeates 2001; Heneghan, Steffen & Fagen 2006; Dávalos *et al.* 2013; Lovett *et al.* 2013),

and they may interact with local climates, land-use history and native species in many intricate and unpredictable ways to ultimately shape plant performance and demography (Herms & McCullough 2014). However, the role of introduced species as drivers of negative ecosystem impacts has been questioned recently (Didham *et al.* 2005; MacDougall & Turkington 2005; Davis *et al.* 2011). Protecting and conserving species, habitats and ecosystem processes for the future will require identification and, where appropriate, local management of processes and stressors that are considered major threats to native species.

Amidst a changing assembly of ecological drivers, earthworm invasions and browse pressure from native white-tailed deer (*Odocoileus virginianus* Zimmerman, 1780) are two of the most important contemporary stressors to forest plant populations in eastern North America (Augustine & DeCalesta 2003; Lawrence *et al.* 2003; Rooney & Waller 2003; Bohlen *et al.* 2004a,c; Kraft *et al.* 2004; Hale, Frelich & Reich 2006;

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Maerz, Nuzzo & Blossey 2009; Nuzzo, Maerz & Blossey 2009; Greiner, Kashian & Tiegs 2012; Loss 2012; Fisichelli *et al.* 2013). These forests developed in the absence of earthworms after the last glaciation (James 1995). Although deer are native to eastern North America, land-use changes, supplemental feeding, climate change and insufficient predation and hunting pressure have facilitated a build-up of unprecedented populations in the 20th and 21st centuries (Rooney 2001; Shelton *et al.* 2014; Waller 2014). Following widescale agricultural abandonment, active reforestation efforts and species re-arrangements, forests have regrown and canopies matured, allowing little light to penetrate into the forest floor. Seedlings in these closed-canopy forests grow slowly and have an extended juvenile stage, where their roots are shallow and sensitive to changes to forest floor dynamics, and above-ground biomass remains in the 'molar' zone, where it may be repeatedly browsed by deer (Waller 2014).

Although earthworm species with different life histories and feeding strategies have different impacts on soils, the result is a myriad of physical, biological and chemical changes. Earthworm invasions favour bacterial over fungal decomposition and increase decomposition of the forest floor, which can lead to soil compaction, changes to soil structure, alteration of below-ground food webs and nutrient translocation (Bohlen *et al.* 2004b; Edwards 2004; Suarez *et al.* 2004; Szlavecz *et al.* 2011). These changes can affect plant growth-influencing and plant growth-regulating compounds, foliar chemistry, pest, parasite and pathogen communities, fine root abrasion and ingestion, and seed burial (Stephens *et al.* 1994; Bohlen *et al.* 2004c; Edwards 2004; Suarez *et al.* 2004; Eisenhauer *et al.* 2009). Whereas uninvaded forest soils often build up a thick leaf-fermenting humus (LFH) layer, earthworm-dominated forests are characterized by bare mineral soil and can completely lack stratified soil profiles (Bohlen *et al.* 2004a).

Given the complex ecosystem changes following earthworm invasions, we expect that some plant species may benefit while others suffer negative consequences. Many native plants require unique forest floor conditions for germination, nutrient and water retention, access to mycorrhizal symbionts and temperature buffering (Lawrence *et al.* 2003; Groffman *et al.* 2004; Hale, Frelich & Reich 2006). Indeed, surveys of plant community composition show that earthworm invasions promote grasses, sedges, non-mycorrhizal and non-native plants at the expense of native, herbaceous understorey plants (Hale, Frelich & Reich 2006; Nuzzo, Maerz & Blossey 2009; Fisichelli *et al.* 2013). Furthermore, the influence of earthworms has ripple effects extending to other taxa on the forest floor such as invertebrates, salamanders and ground-nesting birds (Bohlen *et al.* 2004a; Maerz, Nuzzo & Blossey 2009; Ransom 2011; Loss, Niemi & Blair 2012).

Increased deer browse pressure in eastern North America is decreasing diversity and richness of forest understorey communities, altering succession, restricting regeneration and causing local plant extinctions (Alverson, Waller & Solheim 1988; Anderson 1994; Côté *et al.* 2004; Shelton *et al.* 2014).

Particularly affected are browse-sensitive species such as spring ephemerals and herbaceous perennials in the order Liliales (i.e. *Trillium* spp.) (Webster, Jenkins & Rock 2005), while graminoids and ferns are released from competition (Horsley, Stout & deCalesta 2003; Rooney & Waller 2003). Deer browse impacts are compounded in slow-growing perennials, as preferential browsing of the largest individuals has severe negative consequences for plant demography (Rooney & Gross 2003; Knight 2004; McGraw & Furedi 2005). Direct effects of deer browse are well documented, yet strong, indirect, non-consumptive effects on unpalatable species are increasingly reported (Côté *et al.* 2004; Heckel *et al.* 2010; Kalisz, Spigler & Horvitz 2014). Furthermore, introduced species appear to be favoured by high deer abundance and continue to thrive due to their reduced palatability compared to native species (Eschtruth & Battles 2009; Fisichelli *et al.* 2013; Kalisz, Spigler & Horvitz 2014; Waller 2014). And similar to ripple effects of earthworm invasion, deer browse can affect birds, insects and mammals and their predators that rely on vegetation for food and shelter (deCalesta 1994; Nuttle *et al.* 2011; Parsons, Maron & Martin 2013).

Deer and earthworm impacts are well studied independently, but these stressors often co-occur in fragmented forests and heavily human-influenced environments that can support large populations of both (Alverson, Waller & Solheim 1988; Tiunov *et al.* 2006; Addison 2009). Deer and earthworms may also interact; for example, earthworms may benefit from supplementary N, Ca and C in deer urine and faecal pellets (Seagle 2003). The resulting nutrient subsidy may in turn benefit invasive and fast-growing plants at the cost of slow-growing native perennials. Where browse pressure is sufficiently high, deer accelerate nutrient cycling by rapidly transferring carbon and nutrients from green plant material to faeces and urine, potentially further reducing green forest food webs based on primary production to detritus-based brown food webs (Waller 2014). Finally, deer can increase compaction, promoting bare ground and decreasing litter depth (Heckel *et al.* 2010; Bressette, Beck & Beauchamp 2012).

Conservation and management for particular species or ecosystems must be guided by recognition and knowledge of independent and multiplicative effects of multiple stressors (Didham *et al.* 2007), but such studies are rarely done. Testing for interactions between multiple stressors and plant communities may reveal additive effects, but may also illuminate 'ecological surprises', such as sub-additive or synergistic effects (Darling & Côté 2008). Positive and negative feedbacks are widespread where herbivore–plant–decomposer dynamics are studied with an integrated above- and below-ground approach (Bardgett & Wardle 2003; Shelton *et al.* 2014). Non-additive effects could also occur if declining genotypic diversity in response to increasing earthworm abundance makes plants more susceptible to insect, rodent and deer browse (Wurst & Jones 2003; Parker, Salminen & Agrawal 2010).

We created a long-term experiment to assess how earthworm invasions, white-tailed deer and their interactions may

affect survival and growth of seedlings of 15 native forest understorey species. Because earthworm and deer impacts on seedlings are net effects of beneficial and detrimental forces acting on species traits, we selected species with a range of traits and in different functional groups (Table 1). We expected that (i) earthworm presence will negatively affect survival of slow-growing species with high mycorrhizal dependency; (ii) earthworm presence will enhance seedling survival of grasses, sedges and fast-growing species; (iii) deer exclusion will increase survival of species heavily browsed by deer; and (iv) when seedlings are simultaneously exposed to deer and earthworms, reductions in survival rates will be larger than the sum of individual stressor effects (i.e. they are synergistic). To capture potential fencing effects on interactions with other organisms, we monitored insect and rodent attack on our seedlings, two factors considered important for survival and performance of many forest plants.

Materials and methods

STUDY AREAS

We selected five forested sites (Bobolink Hill, BOB; Connecticut Hill Game Management Area, CON; Hammond Hill State Forest, HAM; Ringwood Preserve, RIN; and Yellow Barn State Forest, YEL) in Tompkins and Tioga counties in the Finger Lakes Region of New York State. The study area lies within the Allegheny section of the Appalachian Plateau, at approximately 42°N, 76°W (Fig. 1). Nearly 80% of forested land was cleared for agriculture in the 19th century, but following widespread farm abandonment in the 20th century, forest cover greatly increased. Present forests remain highly fragmented and include significant agriculture-adjacent edge habitat. While land-use history among sites ranges from actively (CON, YEL) to passively (HAM, BOB) reclaimed farmland to uncleared land with a history of timber harvest (RIN), we ensured that all plots within a site had similar land-use history.

Table 1. Species traits, functional group and expected (+ = positive; – = negative; and ? = unknown) response to deer herbivory and earthworm invasions of 15 plant species

| Species	Deer	Earthworm	Functional group	Time to germination (years)	Mycorrhizal colonization	Growth rate
Actaea pachypoda	±	–	Herb	2+	High	Slow
Allium tricoccum	–	+	Herb	1–2	High	Slow
Agrimonia gryposepala	–	+	Herb	1	?	Fast
Brachyelytrum erectum	+	+	Grass	1	Low	Moderate
Carex radiata	+	+	Sedge	1	None/low	Moderate
Caulophyllum thalictroides	?	+	Herb	2+	Moderate	Slow
Fraxinus americana	–	–	Tree	1	High	Fast
Geranium maculatum	–	+	Herb	1	Moderate	Fast
Geum canadense	–	+	Herb	1	High	Fast
Polygonatum biflorum	–	–	Herb	1–3	Moderate	Slow
Polygonum virginianum	–	+	Herb	1	Low	Fast
Sanguinaria canadensis	?	?	Herb	1	Moderate	Slow
Thalictrum dioicum	–	–	Herb	1	Moderate	Moderate
Tiarella cordifolia	–	–	Herb	1–2	Moderate	Moderate
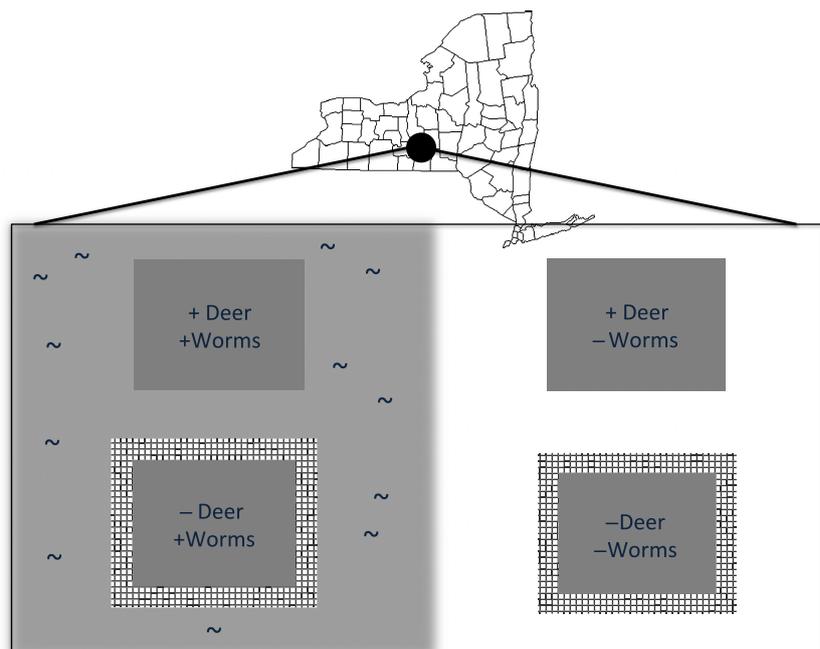
Fig. 1. Location and experimental design assessing individual and combined effects of deer and earthworms on native plants in five forests in central New York.

EXPERIMENTAL DESIGN

We created a 2 × 2 factorial design to assess individual and combined effects of white-tailed deer and earthworms on native seedlings in our five forests (Fig. 1). We selected two locations in each forest, one with an existing earthworm invasion and a second in an earthworm-free area (0.5–2 km between locations). At each location, we established two treatment plots (50 × 50 m each) and randomly assigned one to a fence treatment to exclude deer and the other to allow deer access. To prevent deer access, we erected a 2.5-m-high plastic mesh fence (deerbusters.com, Standard perimeter fencing) attached to two strands of plastic cabling. We then randomly established 20 permanent belt transects in each plot, 2 m wide and 10 m long, divided into 20 planting cells (1 × 1 m).

ENVIRONMENTAL MEASUREMENTS

To account for potential abiotic, biotic and land-use history differences between plots that may affect seedling survival, we measured pH, % soil organic matter (SOM), leaf area index (LAI), soil suborder, slope and tree species richness. We pooled soils from five pits (10 cm diameter, 10 cm deep) randomly located in each plot. For each sample, we first removed the O-horizon and dug the pit to 10 cm below the surface. We homogenized soils and removed all roots and rocks. We air-dried soils for 48 h and measured pH in deionized water (Vision 6071 microcomputer pH; Markson LabSales, Henderson NC, USA). We dried soils at 60 °C for 48 h, followed by grinding (DynaCrush; Customer Laboratory Inc., Orange City, FL, USA) and sieving (1.18 mm). Finally, to measure % organic matter (SOM), we ignited 5 g of soil at 360 °C for 2 h in a muffle furnace to combust organic material, while maintaining inorganic soil constituents followed by reweighing.

Since we could not capture light measurements across all plots simultaneously, we measured light by determining the LAI. Leaf area index estimates the total one-sided surface area of the canopy and is inversely related to the amount of light penetrating into the forest floor (Watson 1947). We measured photosynthetically active radiation (PAR) on the forest floor under clear skies at five locations within each plot using an AccuPAR-LP80 ceptometer (Decagon Devices, Pullman, WA, USA). The ceptometer transforms multiple PAR measurements to an average LAI using an algorithm that incorporates GPS location, time of day, date, etc. We obtained soil sub-order using SoilWeb (USDA-NRCS & UC Davis California 2010). We chose to compare sub-order because this grouped plots into three categories. We obtained plot slopes using a clinometer (M0003; Forestry Suppliers, Jackson, MS, USA). Finally, we measured tree species richness by recording tree species identity and richness of trees with a d.b.h. > 5 cm in each plot.

EARTHWORM SAMPLING

We sampled earthworms at 10 locations along two diagonal transects within each plot before fence construction in autumn 2011 and again in autumn 2012 using liquid mustard extraction (3 g powdered mustard 3.79 L^{-1} water poured into a 0.5 × 0.5 m sampling frame) (Lawrence & Bowers 2002). We collected all surfacing earthworms and preserved them in formalin for 48 h before transferring them into ethanol for storage. We weighed and, wherever possible, identified each earthworm to species (Reynolds 1977; Hale 2007). We then pooled all 10 samples from within each plot and dried them at 60 °C for 72 h to determine dry biomass.

TRANSPLANTS

We selected 15 forest understorey plant species representing a spectrum of expected susceptibility to deer browse and earthworm presence (Table 1) based on information provided by previous studies (Brundrett & Kendrick 1988; Williams, Mosbacher & Moriarity 2000; Lawrence *et al.* 2003; Kraft *et al.* 2004; Hale, Frelich & Reich 2006) and local observations (V. Nuzzo and K. Boys, pers. comm.). These species represent a diversity of traits in different functional groups, growth and germination rates and mycorrhizal associations (Brundrett & Kendrick 1988; Berliner & Torrey 1989).

We harvested seeds locally in the Finger Lakes Region between 2008 and 2012 and germinated them in 2011 and 2012 according to their specific requirements. We transferred germinants to 4 × 3.7 × 6 cm cells (*Caulophyllum thalictroides* germinants in 6 × 5.5 × 5.8 cm cells) filled with potting soil (Pro-Mix® BX Mycorrhizae®; Premier Tech Ltd, Rivière-du-Loup, QC, Canada) inoculated with *Glomus intaradices* Schenck & Sm. mycorrhizas and grew them outdoors in elevated cages to restrict access of deer and earthworms. We transferred seedlings germinated in 2011 to cold storage from November–April. Just prior to transplanting, we randomly assigned plants to treatments and compared species-specific measurements using an ANOVA (*P* > 0.05 for all species) to ensure that each treatment had similarly sized seedlings.

Between May and June 2012, we transplanted 20 individuals each of *Actaea pachypoda, Allium tricoccum, Agrimonia gryposepala, Carex radiata, C. thalictroides, Fraxinus americana, Geum canadense, Polygonatum biflorum, Polygonum virginianum, Sanguinaria canadensis* and *Trillium erectum* into each plot. We planted *Brachyelytrum erectum, Geranium maculatum, Thalictrum dioicum* and *Tiarella cordifolia* in September 2012 (Gleason & Cronquist 1991). For six species with low germination or overwinter survival in cold storage, we planted fewer individuals in each plot (Table S1, Supporting information). We planted each transect with one of each species in a randomized design and individually labelled each transplant.

Approximately 2 weeks after spring planting, we surveyed seedlings and replaced seedlings that had died from apparent transplant shock. We also noted presence/absence of rodent disturbances and insect attack. We could not determine transplant shock, insect attack or rodent disturbance in fall transplants because many seedlings had begun to senesce. In June 2013, we assessed seedling survival, presence of insect damage (defoliation, phloem feeding, etc.), deer browse and rodent disturbance (browse, digging, etc.). We assessed all planting locations, including those where a seedling was not present in 2012, and indeed, several species dormant in summer 2012 were present in spring 2013 (Table S1). A seedling was considered present if any green part was visible above the leaf litter.

STATISTICAL ANALYSES

We modelled survival of each individual plant species separately using generalized linear mixed models (GLMM) with logit link function and binomial distribution. We included random effects of plot and plot within site in all models to account for the experimental design. Using information theory, we evaluated the effect of fencing, earthworms and their interaction on seedling survival with two sets of models: (i) in all plots (*n* = 20) according to earthworm presence/ absence and (ii) in all plots with at least one earthworm present (*n* = 13), using earthworm density and biomass as predictors. We included initial plant measurements and environmental variables in models. In all cases, we selected the most parsimonious models using corrected Akaike's information criterion (AICc) to determine the best-

supported model for survival of each species (Burnham, Anderson & Burnham 2002).

Starting with the null model, which included plot and plot within site as random effects, we added fixed effects one at a time and compared subsequent models with the previous, up to the full model. We included random effects to account for the experimental design, as well as underlying differences in site-specific factors. In addition, we tested for correlation of fixed effects using Spearman's rank correlation coefficient. We did not include correlated fixed effects ($P > 0.05$) in the same model, opting to include our treatments (earthworm invasion and fencing) above environmental variables. Earthworm biomass, density and presence were positively correlated with SOM, as well as pH and soil sub-order, which were subsequently correlated with each other (Table 2). We removed environmental variables correlated with our treatments, including SOM, pH and soil sub-order, to avoid problems and inconsistencies in model building due to high degrees of multicollinearity (Burnham, Anderson & Burnham 2002). There was also a moderate correlation between LAI and slope; however, since they did not correlate with our treatments, we retained them as candidate factors in the model.

We used GLMM with binomial errors to assess effects of treatments and location on presence/absence of rodent disturbance and insect attack in summer 2012 and fall 2013. We pooled plant species, types of rodent disturbance (browse, digging, etc.) and insect attack (defoliation, phloem feeding, etc.). All models included plot and plot within site as random effects. We included year as a fixed effect because both dependent variables are likely to change with time since transplanting. We adjusted incidents of insect attack to account for differences in survival rates by dividing the number of attacks for each species in each plot by the proportion of that species surviving at the time of assessment. However, because rodents dug both surviving and dead transplants at similar frequencies, we did not adjust rodent browse numbers to reflect survival.

To test the similarity of earthworm populations in fenced and unfenced plots, we compared dry earthworm biomass using a paired *t*-test.

We used R version 3.0.1 (R Core Team 2013) and the add-on packages 'lme4'(Bates *et al.* 2013) for all mixed models and 'AICcmodavg' (Mazerolle 2013) for model selection.

Results

We identified 10 earthworm species from five genera, all of European origin in the family Lumbricidae, at our experimental sites (Fig. 2). These included *Lumbricus terrestris* L.,
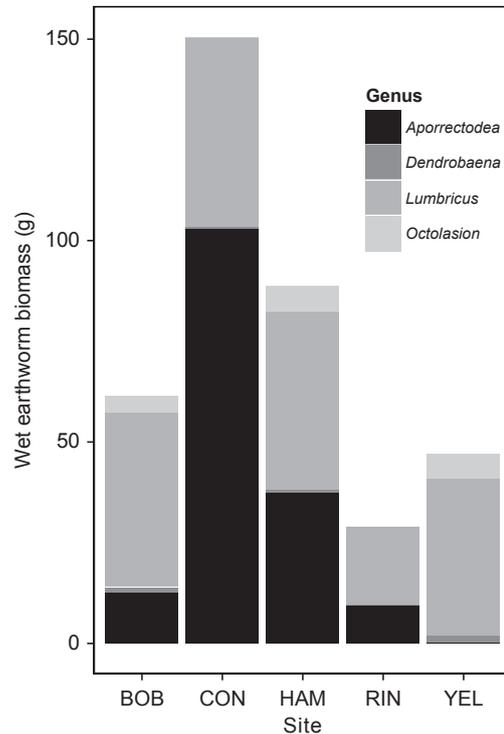

Fig. 2. Earthworm community composition and wet biomass (g) at five forests in autumn 2012 (Bobolink Hill, BOB; Connecticut Hill Game Management Area, CON; Hammond Hill State Forest, HAM; Ringwood Preserve, RIN; and Yellow Barn State Forest, YEL). Data represent total earthworm biomass of 40 0.25 m^2 quadrats/site.

Lumbricus rubellus Hoffmeister, *Octolasion tyrtaeum* Savigny, *Octolasion cyaneum* Savigny, *Apporectodea tuberculata* Eisen, *Apporectodea calignosa* Savigny, *Apporectodea rosea* Savigny, *Apporectodea trapezoids* Duges, *Dendrobaena octaedra* Savigny and *Dendrodrillus rubidus* Savigny. Earthworm density, biomass and community composition varied among sites (Fig. 2); however, *L. terrestris, D. octaedra* and *Aporrectodea* spp. occurred at all sites. The fenced and open plots at each site had similar biomass ($t = 0.704$, d.f. $= 9$, $P = 0.75$). Interestingly, anecic (*L. terrestris*), epigeic (*D. octaedra* and *D. rubidus*) and epi-endogeic (*L. rubellus*) species had similar biomass and frequency across sites, while endogeic species (*Aporrectodea* spp., *Octolasion* spp.) contributed the most to variability

Table 2. Correlation matrix of treatments and environmental variables

	Earthworm presence (W)	Dry earthworm biomass (B)	Earthworm density (D)	Fencing (F)	pH	% SOM (O)	Light (L)	Slope (S)	Soil suborder (T)
Earthworm presence (W)									
Dry earthworm biomass (B)	0.73***								
Earthworm density (D)	0.73***	0.90***							
Fencing (F)	0.14	0.14	−0.02						
pH	0.73***	0.83***	0.75***	0.29					
% SOM (O)	0.59*	0.62*	0.64*	0.37	0.57*				
Light (L)	0	−0.33	−0.48	0.12	−0.12	−0.43			
Slope (S)	−0.24	−0.26	−0.16	−0.23	−0.23	−0.12	−0.55*		
Soil suborder (T)	−0.64*	−0.73***	−0.53*	−0.09	−0.65*	−0.19	0.01	0.19	
Tree species richness (R)	0.42	−0.04	0	0	0.03	−0.18	0.20	0.38	−0.31

*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

between sites. We found no earthworms in the designated 10 earthworm-free plots in 2011; however, three plots had one or two *D. octaedra* individuals in 2012.

Transplant survival varied widely across species, treatments and sites. At the plot level, survival ranged from 100% for *P. virginianum*, *T. dioicum* and *T. cordiformis* in multiple plots to 0% for *G. maculatum* and *G. canadense* in the same fenced, uninvaded plot. The first set of GLMMs including all plots showed a negative effect of earthworm presence, with it appearing as an important covariate in the best models for predicting survival of 5 of 15 species (Table S2a). In the subset of plots with at least one earthworm present, seedling survival declined with increasing earthworm density and biomass for 9 and 12 of 15 species, respectively (Table S2b,c; Fig. 3; Table 3). Due to redundancy in the models, we present parameter estimates for earthworm biomass models only.

Survival of the species not affected by earthworms was best predicted by several other variables, with initial size being
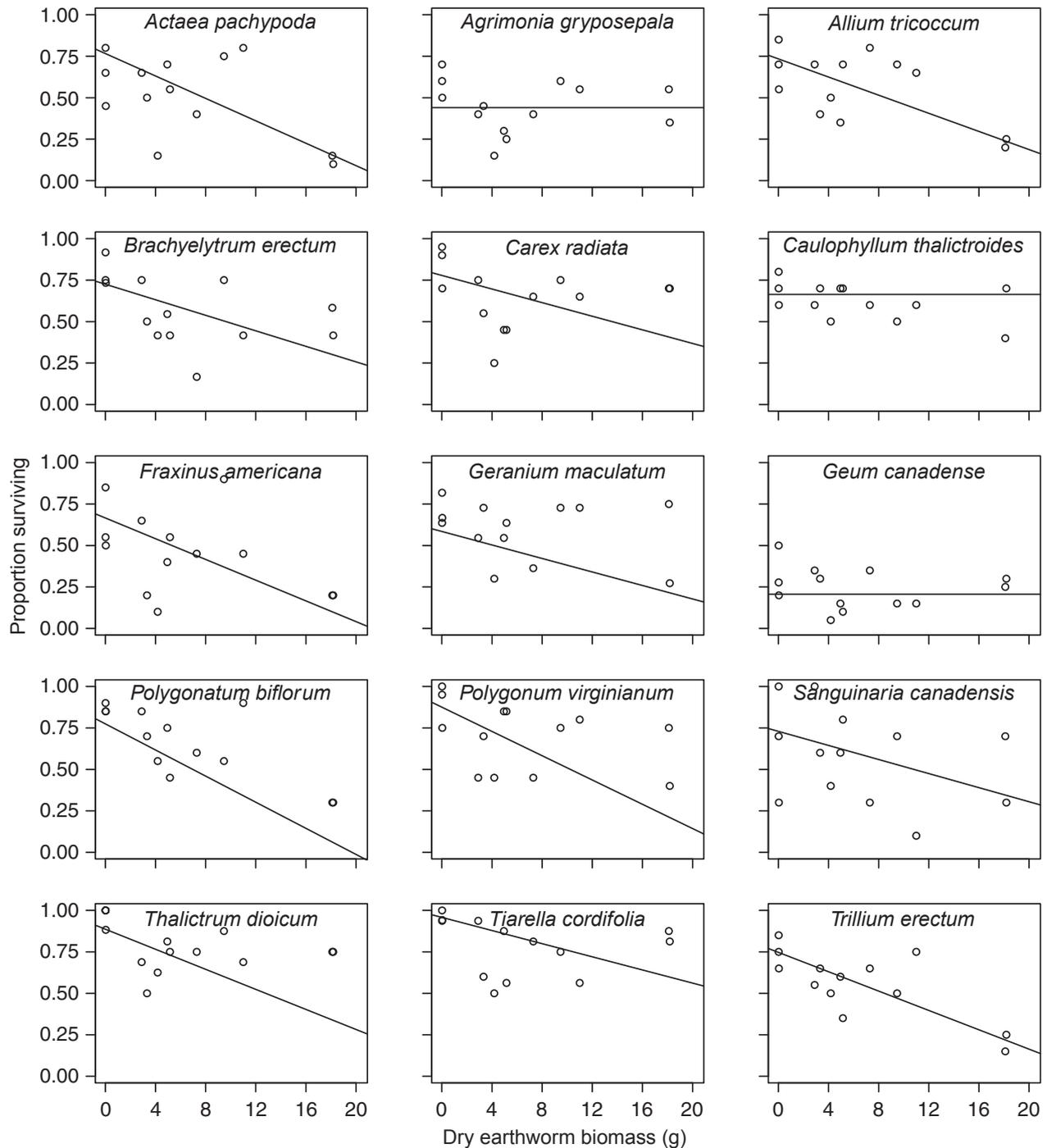

Fig. 3. Proportion of seedlings surviving after one year in plots where earthworms were present ($n = 13$), as a function of earthworm dry biomass (g) (see Supplementary material 2c for detailed model selection results).

Table 3. Parameter estimates for predictors of seedling survival of 15 plant species. Results obtained by generalized linear mixed models with binomial distribution using site and plot nested within site as random effects in all models

Species	Parameter	Estimate	SE	Z
Actaea	Intercept	0.40	0.54	0.74
pachypoda	Earthworm biomass	−0.16	0.03	−5.12***
	Initial size	0.28	0.10	2.76**
Agrimonia	Intercept	−0.24	0.20	−1.20
gryposepala				
Allium	Intercept	−0.08	0.57	−0.13
tricoccum	Earthworm biomass	−0.12	0.03	−4.47***
	Initial size	0.09	0.04	2.47*
Brachyelytrum	Intercept	−1.95	0.73	−2.66**
erectum	Earthworm biomass	−0.10	0.03	−2.87**
	Initial size	0.41	0.10	4.18***
Carex radiata	Intercept	0.35	0.55	0.65
	Earthworm biomass	−0.09	0.03	−2.92**
	Initial size	0.19	0.07	2.68**
Caulophyllum	Intercept	−2.45	0.57	−4.26***
thalictroides	Initial size	0.49	0.09	5.30***
Fraxinus	Intercept	6.84	2.20	3.11**
americana	Earthworm biomass	−0.16	0.03	−4.91***
	Leaf area index	−1.03	0.36	−2.86**
Geranium	Intercept	5.02	2.09	2.40*
maculatum	Earthworm biomass	−0.09	0.04	−2.11*
	Fencing (open)	1.13	0.42	2.71**
	Initial size	0.26	0.07	3.92***
	Leaf area index	−0.94	0.34	−2.74**
Geum	Intercept	−3.00	0.50	−5.94***
canadense	Initial size	0.68	0.16	4.31***
Polygonatum	Intercept	1.81	0.38	4.70***
biflorum	Earthworm biomass	−0.22	0.04	−4.86***
	Slope	−0.57	0.43	−1.31
Polygonum	Intercept	8.34	2.49	3.34***
virginianum	Earthworm biomass	−0.18	0.04	−4.33***
	Leaf area index	−1.07	0.40	−2.70**
Sanguinaria	Intercept	0.99	0.45	2.18*
candense	Earthworm biomass	−0.09	0.04	−2.44*
Thalictrum	Intercept	7.01	2.18	3.22**
dioicum	Earthworm biomass	−0.15	0.04	−3.21**
	Initial biomass	0.13	0.05	2.41*
	Leaf area index	−0.96	0.34	−2.85**
Tiarella	Intercept	8.02	3.22	2.49*
cordifolia	Earthworm biomass	−0.15	0.06	−2.59**
	Initial size	0.86	0.29	2.95**
	LAI	−0.70	0.37	−1.88
	Richness	−0.29	0.11	−2.70**
Trillium	Intercept	1.08	0.27	4.03***
erectum	Earthworm biomass	−0.13	0.03	−4.89***

*P < 0.05, **P < 0.01, ***P < 0.001.

among the most important (Tables 3 and 4; Table S2). In all instances where size at planting was an important predictor, large plants were more likely to survive (Tables 3 and 4). A greater LAI (i.e. lower light level) was associated with reduced survival in *A. gryposepala*, *F. americana*, *G. maculatum*, *P. virginianum*, *T. cordifolia* and *T. dioicum*. Tree species richness and slope affected the survival of species; however, the effect varied in direction between species and types of models (Tables 3 and 4).

We observed little evidence of direct deer effects on seedlings in any plot, with one individual each of *P. biflorum* and

Table 4. Summary of the number of plant species affected by fixed effects (rows) in earthworm presence/absence, density and biomass models (columns). A (+) indicates a fixed effect associated with higher seedling survival, (−) indicates an association with lower survival, and (±) indicated that the direction of the effect varied among plant species

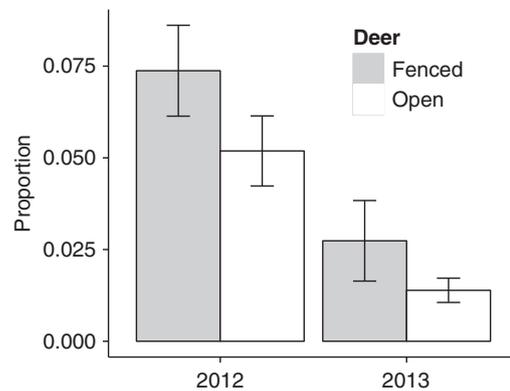|	Presence	Density	Biomass
Earthworm effect	5 (−)	9 (−)	12 (−)
Fence (open)	1 (+)	2 (−)	1 (−)
Earthworm × Fence (open)	0	0	0
Slope	6 (−)	5 (±)	1 (+)
Initial seedling size	11 (+)	9 (+)	9 (+)
Leaf area index	5 (−)	4 (−)	5 (−)
Tree species richness	4 (±)	1 (−)	1 (−)

Fig. 4. Proportion of seedlings showing rodent disturbance in summer 2012 (*n* = 160) and spring 2013 (*n* = 260) in fenced and open plots in 5 forests in NYS. Data are means (±1SE) pooled across all 15 plant species.

F. americana showing evidence of browse. Surprisingly, we found survival of *G. maculatum* was higher in unfenced plots (70 vs. 50%), suggesting a positive non-consumptive effect of deer (*z* = −2.71, *P* = 0.007). *Polygonum virginianum* had a similar positive association with unfenced plots (*z* = 2.94, *P* = 0.003); however, fencing was only included in the best models for earthworm density (Table S2b). No other species were significantly affected by fencing. And despite individual species responses to earthworm invasion and fencing, we found no interactive effect of these co-occurring stressors on transplant survival.

Seedlings in fenced plots exhibited slightly higher incidences of rodent disturbance (*z* = −1.836, *P* = 0.066) (Fig. 4; Table 5; Table S3). Although the best model included only year and the random term (*k* = 4, AICc = 150.38, ΔAIC = 0.16, AIC weight = 0.23; Table 5), several models fall within 2AIC, and the next best model included year and fencing (*k* = 5, AICc = 150.54, ΔAIC = 0.9, AIC weight = 0.22). The incidence of rodent disturbances declined in the year after transplanting, but the difference between fenced and unfenced plots remained.

Insect attack was best fit to the full model, which included a Deer × Earthworm × Year interaction (*k* = 10, AICc = 459.19, ΔAIC = 3.46, AIC weight = 0.2; Table 6).

Due to the high level of interaction, it is difficult to interpret the individual effects of deer and earthworms; however, seedlings growing in earthworm-invaded plots tended to have a higher incidence of insect attack ($z = -8.894$, $P < 2 \times 10^{16}$; Fig. 5).

Discussion

Our seedling transplant experiment revealed strong negative consequences of introduced earthworms on 12 of 15 native

Table 5. Model results for the effect of fencing on rodent disturbance (chewing, digging) pooled across 15 experimental plant species. Data were analysed using a generalized linear mixed model (GLMM) with binomial distribution using plot and plot nested within site as random effects

Fixed effects	Estimate	SE	Z
Rodent disturbance model 1			
Intercept	2347.41	248.762	9.436***
Year	−1.168	0.124	−9.449***
Rodent disturbance model 2			
Intercept	−2.592	0.204	−12.686***
Fence (open)	−0.41	0.223	−1.836
Year (2013)	−1.168	0.124	−9.45***

*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

Table 6. Model results of effects of deer access and earthworm invasion on insect attack using pooled browse on all plant species, with adjusted values to account for seedling survival. Data were analysed using a generalized linear mixed model (GLMM) with binomial distribution using plot and plot nested within site as random effects

Fixed effects	Estimate	SE	Z
Intercept	−1.722	0.189	−9.114***
Fence (open)	0.126	0.189	0.668
Year (2013)	−0.344	0.11	−3.137**
Worm (uninvaded)	−1.061	0.119	−8.894***
Fence (open) × Year (2013)	−0.435	0.153	−2.842**
Fence (open) × Worm (uninvaded)	0.415	0.162	2.561*

*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

plant species. These negative impacts materialized across a diversity of growth forms among experimental plants exposed to different earthworm communities. Reductions in seedling survival were a function of earthworm biomass – a novel insight of our experiment. In contrast to other reports suggesting positive effects of earthworm invasion on graminoids (Hale, Frelich & Reich 2006; Eisenhauer *et al.* 2007; Holdsworth, Frelich & Reich 2007), the two species included in our experiment were negatively affected, although the magnitude of the effect was lower than for other herbaceous species.

Our reports of earthworm-associated declines in plant survival are not by themselves surprising, since declines in native plant cover, overall plant diversity and perennial herb abundance have been reported previously (Lawrence *et al.* 2003; Gundale, Jolly & Deluca 2005; Hale, Frelich & Reich 2006; Hale *et al.* 2008). We add to this body of knowledge by establishing a link between seedling survival and earthworm biomass, but mechanisms underlying these declines have yet to be demonstrated. Earthworm effects materialize despite site-specific biotic and abiotic conditions (i.e. moisture, pH, leaf litter, pathogens) that may interact and may shape or be shaped themselves by earthworm invasion.

It has been proposed that earthworms stress certain plant species through negative effects on fungi (Lawrence *et al.* 2003; Hale, Frelich & Reich 2006), particularly for species highly colonized by mycorrhizae. However, this is not likely the most important driver of seedling survival at our research sites, as negative effects of earthworms were also observed in graminoids that rarely have mycorrhizal associations, including *C. radiata* and *B. erectum* (Brundrett & Kendrick 1988).

Our observations during frequent site visits suggest that mortality occurred during both summer and winter months. Most summer mortality appeared to be due to desiccation, suggesting moisture stress as an important factor for seedling survival. Without moisture buffering effects of a well-developed O-horizon in heavily earthworm-invaded sites, drought effects can be exacerbated (Frelich *et al.* 2006). In addition, we observed dramatic erosion patterns in earthworm-invaded sites, causing seedlings to be washed away with major precipitation events. Earthworm-free sites were able to absorb similar rain events and show no erosion on similar slopes. Winter mortality in earthworm-invaded sites appeared to be a result of freeze–thaw cycles uprooting seedlings, particularly for
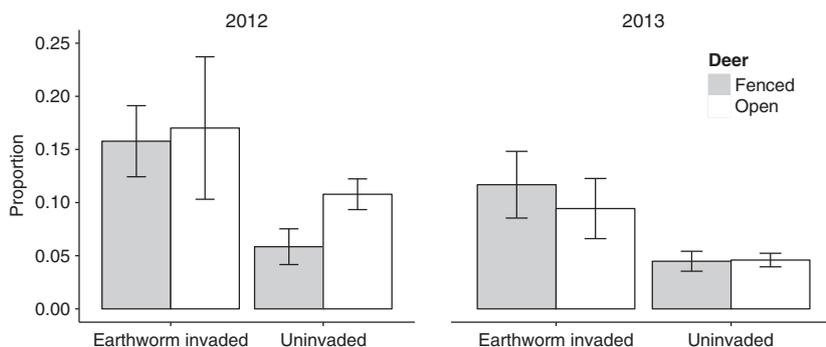

Fig. 5. Proportion of seedlings exhibiting signs of insect attack in 2012 ($n = 160$) and 2013 (260) in fenced and open plots, with and without earthworm invasion located in 5 forest sites. Data were pooled for all 15 plant species, with adjusted values to account for seedling survival, and analysed using a generalized linear mixed model with binomial distribution. (Data are plot means ± 1SE).

C. radiata. This may account in part for its surprising decline as earthworm biomass increased. Our observations suggest that earthworm invasion and particularly earthworm biomass affecting moisture retention are important mechanisms, at least for young seedlings, in determining native plant survival.

Contrary to our expectations, we saw no benefit to any of our 15 experimental species from increased earthworm biomass. Our observations suggesting that moisture stress, erosion and frost heave are more important than other earthworm-induced biotic changes in soil communities question the hypothesis that graminoids benefit from earthworm invasion (Hale, Frelich & Reich 2006; Holdsworth, Frelich & Reich 2007; Eisenhauer *et al.* 2009; Nuzzo, Maerz & Blossey 2009; Loss & Blair 2011). We suggest a need to re-examine this generalization in the light of new evidence: Corio *et al.* (2009) observed a negative association between earthworms and the rare sedge *Carex deweyana,* and Dávalos *et al.* (2013) observed diminished growth rates in *C. radiata* and *C. retroflexa* when *L. terrestris* was present. Corio *et al.* (2009) also observed that higher *C. pensylvania* cover was only associated with invasion of *Allobophora* spp. and *Aporrectodea* spp., and not in areas invaded by earthworms in the genera *Dendrobaena, Octolasion* or *Lumbricus*. In contrast to the cespitose growth form of *C. pensylvanica*, *C. radiata* is rhizomatous, had lower survival in earthworm-invaded plots (70 vs. 90–95% in uninvaded plots) and was negatively correlated with increasing earthworm density ($z = 2.95$, $P = 0.0032$) and biomass ($z = -2.92$, $P = 0.0035$). This further supports the conclusion that unique traits of *C. pensylvanica* may allow the species to benefit from earthworm invasion, but attributing this response to all graminoids is a problematic generalization.

Three species unaffected by earthworm biomass in our experiment (*G. canadense, A. gryposepala,* and *G. maculatum*) share many traits; all tend to grow quickly and have relatively broad habitat requirements that include younger forests and more disturbed areas (Table 1). Conversely, *C. thalictroides* is relatively slow to germinate and grow, but has a unique root morphology that is lignified, unbranching, and extends into deeper soil horizons (Brundrett & Kendrick 1988). Deep roots may make this species less vulnerable to loss of forest floor buffering capacity (Lawrence *et al.* 2003). Furthermore, there is mounting evidence that earthworms are not functioning merely as detritivores, but are consuming a substantial volume of live fine roots (Fisk *et al.* 2004; Gilbert *et al.* 2014). The high lignin content, minimal branching and low annual turnover of *C. thalictroides* roots may make the roots unpalatable to earthworms (Brundrett & Kendrick 1988).

Our experimental species vary in their habitat requirements; therefore, it was not surprising that less shade-tolerant species (*A. gryposepala, F. americana, G. maculatum, P. virginianum* and *T. dioicum*) showed reduced survival in plots with a high LAI, with an effect size 2–10 times that of earthworm biomass. These species are often found in urban forests heavily invaded by earthworms. Surprisingly, our experiment revealed that earthworms reduced early seedling survival of *F. americana, G. maculatum, P. virginianum* and *T. dioicum*, potentially indicating that earthworm impacts are underestimated for shade-intolerant plants.

Several environmental variables including pH, SOM and soil sub-order correlated closely with each other and with earthworm measurements. Patterns connecting earthworm activity and abundance with pH, organic matter and other soil parameters are well documented and are often interconnected in feedback loops (Burtelow, Bohlen & Groffman 1998; Raty & Huhta 2003; Bohlen *et al.* 2004c; Ammer *et al.* 2006). Therefore, it is important to consider (and further assess) how declines in seedling survival are affected by earthworm activity and site-specific conditions that occur in earthworm-invaded ecosystems.

Causality between stresses and declines in understorey plant communities is notoriously difficult to discern because stressors often co-occur (Didham *et al.* 2007; Evans, Possingham & Wilson 2011). For this reason, it is critically important to study stressors together in field settings to separate drivers and passengers of ecosystem change (MacDougall & Turkington 2005). At the beginning of our experiment, we considered deer herbivory to be a major driver of forest understorey plant communities (Rooney & Waller 2003; Côté *et al.* 2004). Despite apparently high deer densities at our research sites (indicated by abundant browse on non-experimental individuals), we observed deer browse only once on *P. biflorum* and once on *F. americana*. We attribute this lack of consumption to the small stature of our seedlings, and we expect consumptive deer effects to become increasingly important in this ongoing investigation as slow-growing perennials reach the browsable 'molar zone' (> 10 cm). However, we observed a significant non-consumptive deer effect, with higher *G. maculatum* and *P. virginianum* seedling survival in unfenced plots, an effect we are unable to explain at this time. Traits expected to confer a benefit from deer browse are usually attributed to chemical or physical defences and low nutrient quality, none of which are associated with palatable species such as *G. maculatum* and *P. virginianum* (Wrazen & Svendsen 1978; Waller & Maas 2013). Nutrient addition from deer or an indirect effect of reduced above- and below-ground competition from other plant species browsed by deer is a possible explanation (Seagle 2003), but these effects should similarly extend to other species in our experiment. Possible species-specific effects involving changes in microbial communities and decomposition processes in response to presence or absence of deer (Wardle & Bardgett 2004; Kardol *et al.* 2014) will require further study. This surprising result could suggest that benefits to younger or shorter individual palatable plants may be passing unnoticed in field surveys.

In our experiment, we measured three factors to capture potential indirect effects of earthworm invasion and deer herbivory. We observed significant correlations between background tree richness and seedling survival; however, these effects were both negative and positive. These results are difficult to interpret within the scope of the current experiment, but suggest that abiotic factors and land-use history are extremely important for seedling survival. Furthermore, more rig-

orous, experimental analysis would be required to determine whether it is richness or dominance of certain tree species that are associated with higher seedlings survival.

The higher frequency of rodent disturbance in fenced plots suggests that deer could be displacing other herbivores through either competition or habitat alteration. The scope of this experiment was to assess changes of rodent disturbance to native plant seedlings, but it illuminates questions about the relative abundance and behaviour of rodents as a function of deer abundance and impact. Such effects usually take time to develop (Parsons, Maron & Martin 2013) and may be restricted to specific species (Buesching *et al.* 2011) yet at the very least, exclosure experiments should be conducted with the assumption that multiple species and trophic levels will be impacted.

Insect attack was affected by both fencing and earthworm invasion, suggesting changes in leaf chemistry or morphology, which may ultimately influence plant community dynamics (Shimazaki & Miyashita 2002; Wurst & Jones 2003), factors we plan to assess in the future. Earthworms may also impact insect herbivores indirectly by acting as subsidiary prey, thus sustaining higher predator populations (Scheu 2003). However, the degree and type of impact depend on earthworm size, feeding guild and location in the soil profile (Ransom 2012). Relationships of earthworms and leaf herbivores, phloem feeders, microphagous organisms and parasitoids have gained some attention in agricultural systems (Scheu, Theenhaus & Jones 1999; Setälä 2002; Wurst & Jones 2003; Salmon 2004), but different studies show earthworms stimulating, reducing or having no effect on herbivore fitness (Scheu 2003). We plan to conduct further experiments to assess the importance of these effects in forest habitats.

Our study shows important negative impacts of earthworm biomass (a surrogate for earthworm activity) on native forest understorey species, yet our results suggest that for many species, the observed mortality may not be catastrophic (Mottl, Mabry & Farrar 2006). We will need full demographic models for species to assess the various beneficial and deleterious effects of earthworms on different life stages of plants to gain a full understanding of impacts. Most deleterious effects of earthworms on plant communities are observed at the leading edge of an invasion as roots of established plants are exposed (Hale, Frelich & Reich 2006). Our results offer hope for long-term survival of herbaceous understorey plants and potential restoration of invaded sites.

Acknowledgements

Data accessibility

Seedling survival, environmental measurements, insect and rodent attack: Data available from the Dryad Digital Repository (Dobson & Blossey 2014).
Total seedling survival: uploaded as Table S1.
Model selection: uploaded as Tables S2 and S3.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Seedling survival in August 2012 and June 2013, and number of rodent disturbances (dig and attack), and insect attack on all seedlings.

Table S2. Model selection results for generalized linear mixed model analyses of seedling survival at five experimental sites according to earthworm presence/absence (a), earthworm density (b) and earthworm biomass (c).

Table S3. Model selection results for generalized linear mixed model analyses of rodent disturbance and insect attack at five forests in NYS.