



Single and interactive effects of deer and earthworms on non-native plants



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ABSTRACT

Understanding drivers of plant invasions is essential to predict and successfully manage invasions. Across forests in North America, increased white-tailed deer (*Odocoileus virginianus*) abundance and non-native earthworms may facilitate non-native plant invasions. While each agent may exert independent effects, earthworms and deer often co-occur and their combined effects are difficult to predict based solely on knowledge of their individual effects. Using a network of twelve forested sites that differ in earthworm density, we evaluated deer exclusion effects (30 × 30 m; with an adjacent similar sized unfenced control plot) on cover, growth and reproduction of three non-native plant species: *Alliaria petiolata*, *Berberis thunbergii* and *Microstegium vimineum*. In addition, we assessed interactive effects of deer exclusion and earthworm invasions on *B. thunbergii* ring-growth. Five years after fence construction, *A. petiolata* frequency and density, *B. thunbergii* height, and *M. vimineum* cover were all significantly lower in fenced compared to open plots. In addition, *B. thunbergii* ring-growth was significantly lower in fenced compared to open plots, and ring-growth was positively correlated with earthworm density. Moreover, deer access and earthworm density synergistically interacted resulting in highest *B. thunbergii* ring-growth in open plots at sites with higher earthworm density. Results indicate facilitative effects of deer on non-native plant species and highlight the importance of understanding interactions among co-occurring factors in order to understand non-native species success. Successful long-term control of invasive plants may require a reduction in deer abundance, rather than just removing invasive plant species.

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1. Introduction

Local biotic and abiotic interactions are central drivers of community structure (Levine, 2000) and may affect spread and success of invasive species. These interactions, involving both native and non-native organisms, may hinder (Davis et al., 2000; Yang et al., 2011) or facilitate (Simberloff and Von Holle, 1999; Flory and Bauer, 2014; Martorell and Freckleton, 2014) plant invasions. Understanding how these interactions affect species composition, community structure and invasion success or failure is central to ecology (Agrawal et al., 2007) and vital to increase prevention and management success of invasive species (Hulme et al., 2013).

Among species interactions, herbivory has been recognized as a vital factor shaping plant communities (Agrawal et al., 2012) and invasion success. Some generalist herbivores cause significant damage to non-native plants in their introduced range (Agrawal and Kotanen, 2003). Other generalist herbivores, in particular

white-tailed deer (*Odocoileus virginianus* Zimmermann), often avoid non-native species, thereby releasing them from herbivory in their introduced range (Wiegmann and Waller, 2006). In addition, chronic deer herbivory on native species may release non-native plants from competition and deer provide a nutrient subsidy through return of partially, often more easily decomposable resources in the form of urine and feces (Hobbs, 1996; Schrama et al., 2013). Indeed, evidence indicates that high deer density has a positive effect on cover, abundance and population growth rate of several non-native forest plant species (Eschtruth and Battles, 2009a; Kuebbing et al., 2013a; Kalisz et al., 2014).

In addition to benefiting from deer herbivory, non-native plants may also benefit from interactions with other non-native species (Simberloff and Von Holle, 1999). Positive associations between invasive earthworms and invasive plants (Heneghan et al., 2007; Nuzzo et al., 2009; Whitfield et al., 2014) suggest facilitative interactions between both groups. Studies at invasion fronts indicate that earthworm invasion precedes and facilitates invasion by three non-native forest plants [*Alliaria petiolata* (M. Bieb.) Cavara & Grande, *Berberis thunbergii* DC, and *Microstegium vimineum* (Trin.)

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A. Camus] (Nuzzo et al., 2009). However, experimental removal of non-native *Rhamnus cathartica* L.P. Mill and *Lonicera x bella* reduced non-native earthworm abundance (Madritch and Lindroth, 2009), suggesting non-native plants facilitate earthworm invasions. Facilitation is likely mediated through changes in soil quality and structure (Kourtev et al., 2002; Bohlen et al., 2004) and associated effects in microbial communities as a result of earthworms and non-native plant invasions alike (Eisenhauer et al., 2011; Elgersma et al., 2011). Additionally, nutrient rich leaf litter from non-native plants may provide a nutritional subsidy for earthworms, as occurs with *R. cathartica* (Heneghan et al., 2007). Leaf litter depletion by earthworms may facilitate non-native plant emergence for species that show higher germination rates and seedling survival in bare soil, such as *M. vimineum* (Warren et al., 2012) or *R. cathartica* (Roth et al., 2014).

White-tailed deer (native) and earthworms (non-native) are both considered major threats to forest plant populations across northeastern North America (Côté et al., 2004; Hale et al., 2006; Fisichelli et al., 2013; Dobson and Blossey, 2014). Both stressors have been associated with non-native plant invasions and recognized as major drivers of plant composition in natural communities (Fisichelli et al., 2013), yet knowledge of their concurrent effects on plant invasions is still incipient. Combined effects are difficult to predict based solely on knowledge of their individual effects (Darling and Côté, 2008). This requires an increased research emphasis to better understand combined effects, especially on the extent and magnitude of effects on native vegetation (Côté et al., 2004; Dobson and Blossey, 2014) and soil processes (Bohlen et al., 2004; Wardle and Bardgett, 2004; Wardle et al., 2004; Murray et al., 2013).

In this study we evaluate effects of deer exclusion on cover and growth of three target non-native forest species: the biennial herb *A. petiolata*, the perennial shrub *B. thunbergii* and the annual grass *M. vimineum*. We also examine interactive effects of deer exclusion and earthworm abundance on growth of *B. thunbergii*. These non-native plant species introduced from Europe (*A. petiolata*) and Asia (*B. thunbergii* and *M. vimineum*) are widespread in eastern North American forests and are considered major threats to native communities (Silander and Klepeis, 1999; Rodgers et al., 2008; Flory and Clay, 2010). They are associated with human dominated habitats but are also shade tolerant and able to invade mature forests (Silander and Klepeis, 1999; Flory and Clay, 2010; Warren et al., 2011). These species cause a myriad of ecosystem impacts including displacement of native vegetation (Flory and Clay, 2010), disruption of arbuscular mycorrhizal fungi growth (Barto et al., 2011), changes in nutrient cycling and microbial communities (Ehrenfeld et al., 2001; Kourtev et al., 2002; Lee et al., 2012) as well as changes in arthropod abundance and diversity (Simao et al., 2010).

The three target non-native species are not browsed by deer and consequently are likely to have a competitive advantage over deer-palatable understory plant species. In the presence of deer, unpalatable species produce higher biomass or show increased population growth rates (Eschtruth and Battles, 2009a; Kalisz et al., 2014). Target non-natives are also positively associated with earthworms (Nuzzo et al., 2009; Whitfeld et al., 2014) and, in fact, rarely occur at high densities at sites with low earthworm abundance (personal observation). Considering that these stressors co-occur and that mounting evidence indicates that populations and impacts of invasive plants, earthworms and deer are characterized by complex non-additive interactions (Waller and Maas, 2013; Dávalos et al., 2014; Flory and Bauer, 2014) it is paramount to quantify their combined effects.

Non-additive or interactive effects of deer and earthworms could potentially arise from two non-excluding mechanisms: (1) stressors modulate each other's impact or (2) stressors influence local

abundance of one another (Didham et al., 2007). For instance, earthworms may increase deer herbivory by depleting the leaf litter layer and hence increasing plant exposure (Frelich et al., 2006), which in turn may lead to a decrease in plant diversity (potentially resulting in reduced biotic resistance) or an increase in available resources that could facilitate plant invasions (Elton, 1958; Davis et al., 2000; Keane and Crawley, 2002). It is also likely that deer may increase local earthworm abundance, as earthworms benefit from high nutrient deer pellets, especially in areas with low quality leaf litter input such as in hemlock stands (Karberg and Lilleskov, 2009).

We experimentally manipulated deer access (paired open and fenced plots) in twelve forested sites in New York State that differ in earthworm density and biomass, allowing us to effectively disentangle deer and earthworm effects, as well as assess potential interactive effects. We also evaluated effects of climate variables, as *B. thunbergii* growth responds to precipitation and temperature in current and previous years (Li et al., 2008). *Berberis thunbergii* has clear annual growth rings that are cross-datable, and effects of local climate dynamics on *B. thunbergii* growth have been successfully evaluated using a dendroecological approach (Li et al., 2008). In addition, ring-width growth allows long-term assessment of herbivory effects (Chauchard et al., 2006; Speed et al., 2011) and invasive earthworms (Larson et al., 2010) on woody species. We were guided in our investigation by the following hypotheses: (1) in the presence of deer, cover and growth of the three target non-native species is higher than in the absence of deer; and (2) deer and earthworms synergistically interact to increase *B. thunbergii* ring-growth. *Berberis thunbergii* was the only target non-native species that was present at sites with low and high earthworm density, thus allowing us to test for the interactive effects of deer and earthworms.

2. Methods

2.1. Study sites

We conducted the study at 12 forested sites located 1–8 km apart within US Army Garrison West Point, New York, USA. West Point is located within the Hudson Highlands Province and is characterized by rugged hilly terrain with rocky outcrops and frequently thin soils. Forests are dominated by oak (*Quercus rubra* L. and *Q. prinus* L.) and/or sugar maple (*Acer saccharum* Marshall), and differ in land use history, aspect, soil, and plant species composition. Sites also vary in percent cover of non-native plant species and invasive earthworm density and biomass (Appendix A.1). Soil pH ranged from 3.7 to 6.4, with lowest pH recorded at sites with low earthworm abundance (sites 2 and 4; Appendix A.1). Deer hunting is allowed at nine of our study sites and while precise deer density estimates are not available for our study locations, deer harvest in 2013 within a large region including West Point averaged 5.3 per square kilometer (DEC, 2013). Our study sites are used occasionally for military training exercises and are otherwise not actively managed.

We established six sites in areas dominated by native species, and six in areas with large populations of non-native plants (*A. petiolata*, *B. thunbergii*, and *M. vimineum*). Each focal non-native species was dominant at two sites, but species also occurred at lower densities at additional sites. At each site we established two 30 m × 30 m paired plots situated 5–50 m apart from each other. We randomly assigned plots to a deer exclusion treatment (open or fenced) and erected deer-proof fences from 7 to 11 July 2008 (Trident extruded deer fence, 2.3 m high, www.deerBusters.com, MD). Within sites, paired plots had similar overstory vegetation, slope, and management regime. We had no *a priori* information about the timing of earthworm invasions or previous land use history at our study sites.

We sampled earthworms in mid-July 2008–2011 at 5 random 0.25 m² quadrats per plot per year. We extracted earthworms by pouring 3.79 l of mustard solution (Frontier Natural Products Co-op, Norway, IA) at 15 g l⁻¹ per quadrat (Lawrence and Bowers, 2002). We preserved earthworms in 70% ethanol, identified mature individuals to species and then obtained ethanol-dried weight.

2.2. *Alliaria petiolata*

We randomly established 10 1-m² permanent quadrats in each fenced and open plot and annually estimated percent cover 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%) in mid-May 2009–2012. We recorded *A. petiolata* in 3 of the 12 sites (sites 5, 7 and 12).

In mid-June 2012 we recorded *A. petiolata* presence/absence, density, stem height and number of siliques and seeds of each individual in 20 randomly located 1 m radius circular quadrats/plot at the three sites containing *A. petiolata*. Where *A. petiolata* occurred in low density (<25 plants in the 20 quadrats) we collected additional data by walking random transects until encountering a plant. We then established an additional 1 m radius circular quadrat centered on that individual, and measured each *A. petiolata* within the quadrat until we reached our minimum target goal of 25 plants/plot (6, 5 and 3 additional quadrats at each study site). We then added the same number of additional quadrats (similarly located along random transects) in the paired open or fenced plots to ensure equal sampling effort. Thus, we recorded frequency and density in the initial 20 1 m radius quadrats, and size and reproductive measurements in both the initial and additional quadrats.

2.3. *Berberis thunbergii*

In mid-July 2009–2012 we measured *B. thunbergii* cover (following the same methodology detailed for *A. petiolata* cover, Section 2.2) and height in 10 1-m² permanent quadrats per open and fenced plot (N = 2 sites, Sites 1 and 6). Both sites had large populations of *B. thunbergii* allowing us to accurately collect these measurements.

In June 2012, we searched all sites for presence of *B. thunbergii* and randomly sampled 232 individuals at eight of 12 study sites (Table 1). We selected shrubs at least 1 m tall and separated from other individuals by >1 m and then collected a basal stem disc from the widest stem. We dried and sanded each core with sand paper of progressively finer grit until obtaining a polished cross section of each sample. We measured ring width along two radii (three times along each radius) from the pith and outward to the nearest 0.001 mm over a measuring platform set under a dissecting microscope. We checked for presence of incomplete rings (2012 growth),

but did not include their measurement in the radial sequence. To account for asymmetrical growth around the stem, we estimated a mean chronology along both radii of each stem sample. We conducted all measurements using Tellervo© application (Brewer, 2011).

To evaluate interactive effects of earthworms and fencing on *B. thunbergii* growth, we first converted radial ring widths to basal area increment (BAI). Assuming circular growth pattern, BAI represents tree growth better than a linear measurement (Biondi and Qeadan, 2008). To evaluate quality of *B. thunbergii* ring-growth data, we first constructed a correlation matrix for all pairs using Pearson's method, and then calculated mean correlation for all *B. thunbergii* shrubs, for all shrubs within each deer exclusion treatment, and for all shrubs within each site. We standardized age trend (ring width decreased with age) via a ln regression of BAI on age: $\ln(\text{BAI}) = a + b \times \ln(\text{Age})$ (Fig. 1) and performed all statistical analyses on the residuals of this model (see Section 2.5).

2.4. *Microstegium vimineum*

We collected *M. vimineum* cover data in mid-July 2008–2012 at sites 3 and 12, following the same methodology detailed for *A. petiolata* (Section 2.2). We collected *M. vimineum* plants (shoots and roots) in 10 random quadrats (0.25 m²) per open and fenced plot

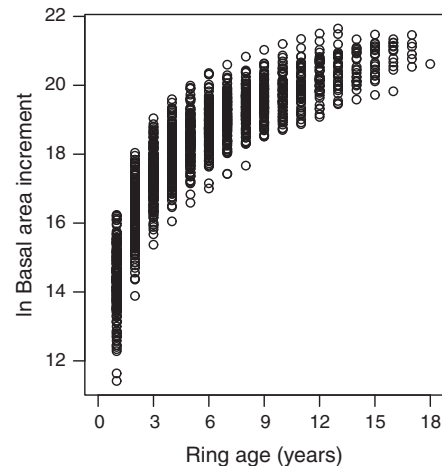


Fig. 1. Basal area increment (BAI) according to age (years) of *B. thunbergii* collected from open and fenced plots at eight sites at West Point, NY. BAI were age-standardized using parameters estimated from a linear regression: $\ln(\text{BAI}) = 14.63 + 2.30 \times \ln(\text{age})$, $R^2 = 0.88$, $P < 0.001$. Data for open and fenced plots are aggregated.

Table 1
Summary of tree-ring series from *B. thunbergii* collected in paired open and fenced plots at eight sites at West Point NY in June 2012. N = number of *B. thunbergii* stems sampled/plot.

Site	Fenced					Open				
	Earthworm density (SD) ^a	N	Time span ^b	Mean age (SD)	Mean r ^c	Earthworm density (SD)	N	Time span	Mean age (SD)	Mean r
	1	2.65(0.25)	15	1995–2012	10.87(4.49)	0.35	1.30(1.32)	16	1995–2012	9.57(3.55)
3	9.85(6.76)	17	1994–2012	6.30(4.36)	0.64	9.75(8.2)	16	1999–2012	7.50(3.07)	0.47
5	11.40(9.97)	15	1997–2012	7.67(3.40)	0.68	15.80(14.14)	15	1999–2012	9.00(3.17)	0.65
6	9.0(3.90)	15	1995–2012	8.59(4.50)	0.46	15.20(3.89)	16	1996–2012	8.50(3.92)	0.81
8	8.40(6.91)	10	1996–2012	6.11(3.96)	0.87	6.80(6.73)	10	2001–2012	5.20(2.42)	0.86
10	8.45(2.36)	12	1998–2012	10.70(2.85)	0.75	14.80(8.50)	15	1996–2012	9.40(3.84)	0.72
11	1.55(1.71)	15	1997–2012	9.00(3.68)	0.68	0.70(0.82)	15	1995–2012	7.40(3.96)	0.65
12	3.55(3.24)	15	2001–2012	4.73(2.59)	0.89	14.75(7.14)	15	2002–2012	5.07(2.27)	0.85

^a Average 2008–2011 from five 0.25 m² random quadrats per plot and year.

^b All stems were alive in 2012. Incomplete growth from 2012 was not included in radial sequence.

^c Correlation among *B. thunbergii* shrubs within the same plot and site.

in late August 2012. We subsequently dried all *M. vimineum* material for 48 h at 72 °C before weighing samples.

2.5. Statistical analyses

We evaluated effects of fencing and study year on percent cover of the three focal non-native species and on *B. thunbergii* height via independent repeated measures linear models, the effect of fencing on *M. vimineum* biomass and *A. petiolata* height in 2012 with linear models (including site as a fixed factor and plot within site), and the effect of fencing on *A. petiolata* density with non-parametric Kruskal–Wallis tests. We arcsine square root transformed cover values to meet model assumptions. We evaluated effects of fencing (within each site) and plant height on number of *A. petiolata* siliques and seeds in 2012 with independent Generalized Linear Models with Poisson errors for each metric, including site and plot within site as fixed factors. We did not test for the effect of earthworm abundance or its interaction with fencing on the above metrics as we only included sites at which the target non-native species were dominant. Sites dominated by non-native plant species had high earthworm abundance, except for site 1 (Appendix A).

We evaluated the effect of deer exclusion (open or fenced), earthworm density or biomass (mean per plot over the four year study periods), and climate variables on *B. thunbergii* ring-growth (age-standardized BAI) with a linear mixed model. Models included site, plot within site, and stem within plot and site as random factors, and only included data for the period with at least 10 individuals in each treatment (1999–2011). We assumed that all measurements prior to 2008 correspond to the open treatment.

We obtained mean monthly temperature and precipitation at West Point, NY weather station (41.391° N, 73.961° W) from the National Climatic Center (NCDC, 2014) and evaluated the following variables: mean annual temperature, mean winter temperature (December–February, December from the previous year), mean spring temperature (March–May), mean summer temperature (June–August), mean fall temperature, temperature seasonality (coefficient of variation in temperature among months), total annual precipitation and precipitation seasonality (coefficient of variation in precipitation among months). We also included mean annual temperature and total precipitation from the previous year because climate conditions in the current and previous year may affect growth. Mean annual and summer temperatures from the current ($r = 0.75$; $P < 0.001$) and previous year ($r = 0.75$; $P < 0.001$) were correlated; and therefore, we only included mean summer temperatures in the full model, as summer is the season when most growth occurs.

We evaluated the explanatory power of competing models with Akaike Information Criterion corrected for small samples sizes (AICc) (Burnham and Anderson, 2002). We ranked candidate models according to ΔAICc (difference between model's AICc and min AICc) and evaluated the explanatory power of each model using Akaike weights (w_i), which represent the probability that a candidate model is the best, given the data and the set of candidate models. We conducted all analyses in R 3.0.2 (R Core Team, 2014), used dpLR library to conduct dendrochronological analyses (Bunn, 2008; Bunn et al., 2012) and package lme to conduct linear mixed models (Bates et al., 2014).

3. Results

3.1. Earthworms

Earthworm communities (abundance and species composition) varied among sites (Table 1, Appendix A.1). Four sites (three dominated by native vegetation and one by non-native vegetation) had

low earthworm abundance (mean \pm 1SE: 1.48 ± 0.47 in 2011) and eight sites (three dominated by native vegetation and five by non-native plants) had high earthworm abundance (mean \pm 1SE: 15.7 ± 2.91 in 2011). Non-native *A. petiolata* and *M. vimineum* were present and dominant only at sites with high earthworm abundance, whereas *B. thunbergii* was present at sites with low and high earthworm abundance (Table 1, Appendix A.1). Earthworm populations were composed solely of non-native species, including *Amyntas* spp., *Dendrobaena octaedra* Savigny, *Lumbricus terrestris* L. and *Lumbricus* spp. juveniles.

3.2. *Alliaria petiolata*

Cover of *A. petiolata* varied among years ($F_{3,228} = 6.25$, $P < 0.001$) and by 2012 (five years after fence construction) was significantly higher in open compared to fenced plots (significant year \times fencing interaction $F_{3,228} = 3.91$, $P = 0.01$; Fig. 2).

Alliaria petiolata frequency was significantly higher in open than in fenced plots at two sites (Fisher's exact test, site 5: $P = 0.006$ and site 7: $P = 0.05$), whereas at the third site it did not significantly differ (site 12, $P = 0.34$; Fig. 3A). Stem density of this species was also higher in open than in fenced plots at two of three study sites (Kruskal Wallis tests, $P = 0.002$, sites 5 and 7), but did not differ at the third site ($P = 0.50$, site 12; Fig. 3B).

Stem height varied significantly among sites ($F_{2,453} = 12.03$, $P < 0.001$) and between open and fenced plots ($F_{3,453} = 15.66$, $P < 0.001$), with significantly taller stems at the open compared to the fenced plot of one study site only (site 12; Fig. 3C). At sites 5 and 7, stem height did not significantly differ between open and fenced plots. Thus, sites 5 and 7 presented an opposite pattern than site 12. At site 5 and site 7 frequency and density were higher in the open than fenced plot, but stem height did not differ. Conversely, at site 12 we found no significant difference in density

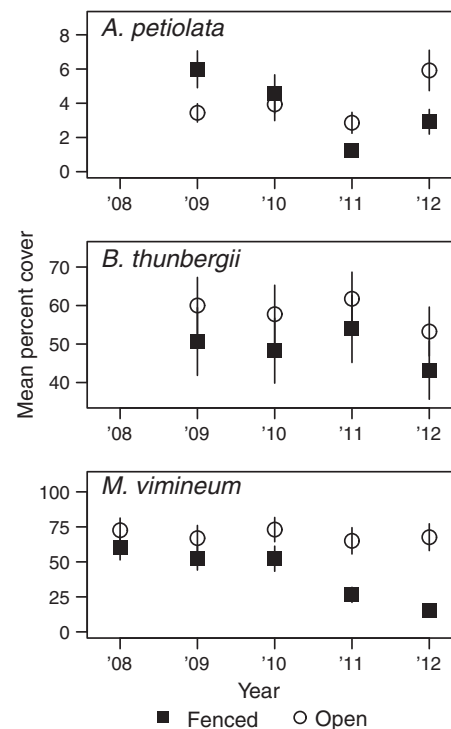


Fig. 2. Cover (%) of *A. petiolata*, *B. thunbergii* and *M. vimineum* in open and fenced plots (N = 10 quadrats/plot) in May (*A. petiolata*) and July (*B. thunbergii* and *M. vimineum*) at West Point, NY from 2008/9–2012 (N = 3 sites for *A. petiolata*; N = 2 for *B. thunbergii*; N = 2 for *M. vimineum*; please note different y-axes for different species). Data are means \pm 1SE.

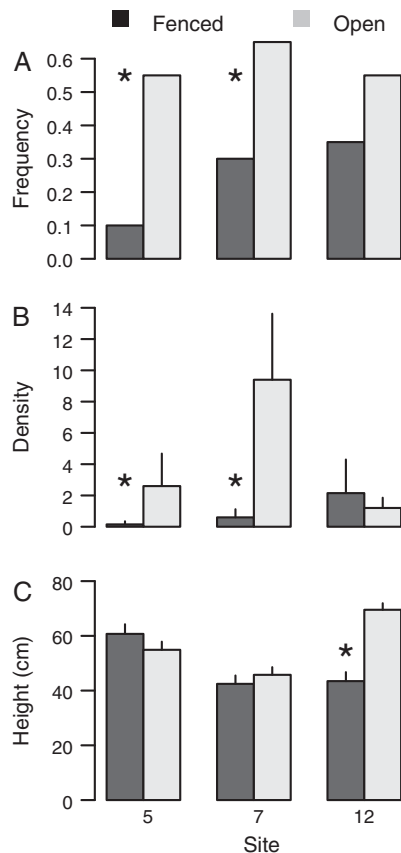


Fig. 3. Frequency (A), density per 0.25 m² (B) and height (cm) (C) of *A. petiolata* in open and fenced plots at three sites at West Point, NY in June 2012. Asterisks denote significant differences. Data are means \pm 1SE (please note different y-axes for different measures).

and frequency between open and fenced plots, but stem height was significantly lower in the fenced than open plot.

Silique and seed number were significantly and positively correlated with plant height and the effect of fencing varied among sites: silique and seed number were significantly lower at the open than fenced plot at site 5, significantly higher at the fenced than open plot at site 7 and did not differ significantly between the open and fenced plots at site 12 (significant site \times fencing interaction; Appendix Table B.1, Fig. C.1).

3.3. *Berberis thunbergii*

Cover of *B. thunbergii* varied among sites (mean: 26% and 80% at sites 3 and 6, respectively) but not among years or between open and fenced plots ($P > 0.05$, Fig. 2). Mean vegetation height per quadrat did not vary among years ($F_{3,150} = 1.84$, $P = 0.14$) and was significantly higher in open compared to fenced plots ($F_{1,150} = 9.53$, $P = 0.002$; 87.15 ± 4.36 vs. 77.88 ± 4.36 cm in open and fenced plots, respectively). We found no significant interaction between year and fencing ($F_{3,150} = 0.49$, $P = 0.69$).

Berberis thunbergii stem ages ranged from 1 to 18 years (1994–2011, 2012 incomplete growth excluded), with a mean of 7.90 ± 3.98 years (Table 1). Mean correlation between all *B. thunbergii* stems was $r = 0.60$; within fenced plots $r = 0.57$ and within open plots $r = 0.72$. Correlation within study plots ranged from $r = 0.35$ to $r = 0.89$ (Table 1).

Climate, fencing and earthworm density interactively affected *B. thunbergii* annual ring growth (expressed as age-detrended BAI). Results for models including earthworm biomass or density were similar; therefore, here we present earthworm density results

Table 2

Effects of climate variables, deer exclusion (open or fenced) and earthworm density on *B. thunbergii* age-standardized ring growth (expressed as basal area increment) according to Linear Mixed Models. Models included site, plot within site, and stem within plot and site as random factors.

Factor	Estimate	SE	<i>t</i>	X ²	<i>P</i>
Intercept	0.58	0.21	2.80		
Summer temperature	−0.02	0.01	−3.09	9.56	0.002
Precipitation _(<i>t</i>−1)	−5.41E−05	2.74E−05	−1.98	3.90	0.048
Fencing (open)	0.26	0.06	4.28		
Earthworm	0.17	0.04	3.80		
Earthworm Q	−0.01	0.00	−4.13		
Fencing \times Earthworm	−0.11	0.03	−4.14		
Fencing \times Earthworm Q	0.01	2.08E−03	4.61	21.14	<0.001

Q quadratic.

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.

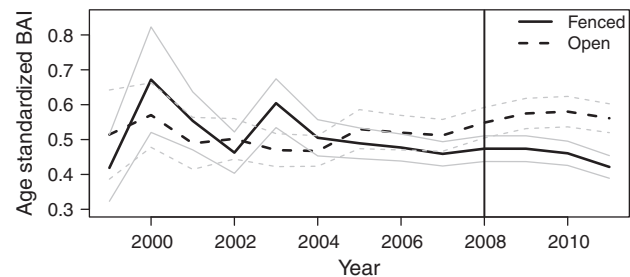


Fig. 4. Trend in age-standardized basal area increment (BAI) of *B. thunbergii* stems collected in open and fenced plots at eight sites at West Point, NY. Data are shown for the period with at least 10 individuals in each treatment (1999–2011). Vertical line shows the start of experimental deer fencing. Black lines show the mean and grey lines \pm 1SE according to model predictions (Table 2).

only. The model with greatest explanatory power ($w_i = 0.25$, Appendix Table B.2) included a negative effect of summer temperature, a positive effect of precipitation in the previous year, and an interactive effect between fencing and earthworm density (Table 2). The next best model (Δ AICc = 0.14, $w_i = 0.12$, Appendix Table B.2) included all terms from the previous model plus a negative effect of winter temperature and of summer temperature in the previous year. All models in the candidate set included an interaction between fencing and earthworm density (Appendix Table B.2).

Before fence construction in 2008 ring growth did not differ significantly between open and fenced plots (BAI = 0.051 in both plot types) but by 2011 (four years after fencing) ring growth was 33% greater in open than fenced plots (Fig. 4). There is an apparent divergent trend between open and fenced plots starting in 2005, but the rate of growth in the fenced plot significantly decreased only after fencing in 2008. We found a significant second order polynomial effect of earthworm density and a significant interaction between fencing and earthworm density. In the open plots *B. thunbergii* growth increased with earthworm density, whereas in the fenced plots growth reached a peak at intermediate densities (Fig. 5). Notably, we recorded higher earthworm density values (>11 individuals per 0.25 m²) in open plots only.

3.4. *Microstegium vimineum*

Microstegium vimineum cover varied among years ($F_{4,188} = 6.46$, $P < 0.001$) and at both sites *M. vimineum* cover decreased in fenced but not in open plots over the five year study period (significant year \times fencing interaction $F_{4,188} = 3.78$, $P = 0.005$; Fig. 2). *Microstegium*

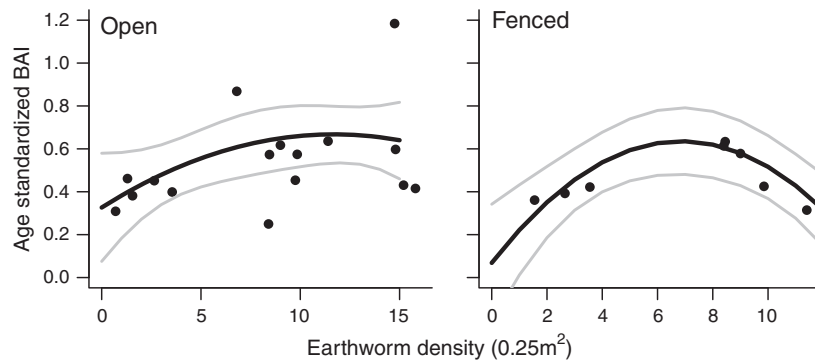


Fig. 5. Age-standardized basal area increment (BAI) according to earthworm density of *B. thunbergii* stems collected in open and fenced plots at eight sites at West Point, NY. Data are shown for the period with at least 10 individuals in each treatment (1999–2011). Black lines show predicted values from linear mixed model (Table 2) and grey lines \pm 1SE (please note different x-axes for open and fenced plots).

vimineum biomass differed between sites ($F_{1,36} = 84.96$, $P < 0.001$) and between open and fenced plots ($F_{1,36} = 130.18$, $P < 0.001$). Biomass was significantly lower in the fenced compared to the open plot of one site (3.30 ± 0.96 vs. 80.98 ± 5.35 g), but was similar in both plots of the second site (10.26 ± 2.93 vs. 10.81 ± 2.99 g in fenced and open plot respectively; significant site \times fencing interaction $F_{1,36} = 126.51$, $P < 0.001$).

4. Discussion

We found a strong positive correlation between deer, earthworm abundance and non-native plants at our study sites. Deer are major drivers in our study system, affecting native flora directly through herbivory (Dávalos et al., 2014) and indirectly through facilitation of earthworm (Dávalos et al., 2015) and non-native plant populations. Invasive earthworms and invasive plants are also linked, such that our target non-native plant species (*A. petiolata*, *B. thunbergii* and *M. vimineum*) occur at significant abundances only at sites with high earthworm density. Moreover, we found clear evidence to support our hypothesis that deer activity and earthworm abundance have a positive synergistic effect on *B. thunbergii* ring-growth demonstrating that populations of these major stressors in northeastern North America forests are connected through an intricate network of interactions.

Our results corroborate previous findings of deer facilitation of target non-native plants. Deer exclusion experiments and studies along a deer density gradient show higher cover and biomass of non-native plants in presence of deer (Eschtruth and Battles, 2009a,b; Knight et al., 2009). Furthermore, long term demographic studies of *A. petiolata* show that populations are expected to decline after deer exclusion (Kalisz et al., 2014).

At our sites *A. petiolata* was less affected by fencing than *M. vimineum* and *B. thunbergii*, in contrast with results from Eschtruth and Battles (2009b). These contrasting results may be due to differences in *A. petiolata* invasion stage among sites. At the time of site selection in 2008, *A. petiolata* was past peak abundance at two sites (sites 5 and 7), and populations further declined rapidly to very low abundance, whereas at the third site (site 12) *A. petiolata* abundance increased over the course of the study. At sites at or past peak abundance, fencing had a negative effect on frequency and density and no effect on height; conversely, at the site with increasing abundance fencing had no effect on frequency or density but a negative effect on height. *Alliaria petiolata* declines have been observed in long term monitoring studies (Blossey et al., unpublished data), suggesting that density dependent processes, facilitated through negative soil feedbacks, control *A. petiolata* populations. Our results suggest that high deer populations may reduce or slow down negative soil feedbacks.

Reported effects of fencing on target non-native plants are limited by sample size ($N = 2$ or 3 sites per target species), except for *B. thunbergii* ring-growth ($N = 8$ sites). However, our results show a similar and strong positive effect of deer on the three target non-native plant species. All plant measures were either unaffected or negatively affected by fencing, and in no case did we find a positive effect of fencing. However, the magnitude of fencing effects varied from site to site and by plant performance measure, highlighting the need to conduct replicated studies over a larger geographical area and along a deer density gradient.

Our approach allowed us to effectively separate the role of deer, earthworms and climate on *B. thunbergii* growth, and demonstrates that non-consumptive effects of deer and earthworms can be observed in the dendrochronological record. Before deer exclusion (through fencing) *B. thunbergii* ring-growth did not differ between plots, although a non-significant trend is apparent, but after fence construction ring-growth was significantly higher in open plots (Fig. 3). Moreover, ring-growth was positively correlated with earthworm density, and deer and earthworms synergistically interacted to favor growth, underscoring the importance of interactions among co-occurring agents in driving forest dynamics. While *B. thunbergii* individuals at our sites were relatively young (18 years; 1994–2011), when compared to shrubs dated at nearby locations which span 34 years (1971–2004) (Li et al., 2008), mean annual correlation among *B. thunbergii* ring series was high, as expected among shrubs of the same species growing within the same region (~ 65 km²). Correlation between plants growing in open plots was higher than correlation between plants in fenced plots, suggesting that variation in yearly growth decreases in presence of deer activity, likely a result of plant community homogenization due to intense deer activity (Holmes and Webster, 2011).

Climate variables influenced *B. thunbergii* growth in a pattern consistent with reports by Li et al. (2008). Growth was negatively associated with summer temperatures but unaffected by spring temperatures, although a positive trend with spring temperature was detected in both studies (Li et al., 2008). A negative association with summer temperature and a minor positive association with precipitation indicate that predicted warmer conditions in Northeastern North America due to climate change may limit *B. thunbergii* growth, whereas predicted wetter conditions may be favorable (IPCC, 2013). However, temperature effects on *B. thunbergii* ring-growth were stronger than precipitation effects suggesting that invasion trajectories of *B. thunbergii* may be more limited by future warmer conditions than favored by higher precipitation. Experimental manipulation of both climate variables is required to accurately predict *B. thunbergii* response to climate change.

We did not attempt to date earthworm invasion as it likely occurred well before 1994, most likely shortly after initial clearing of areas for agriculture, potentially well over 100 years ago. In Minnesota, using tree-ring analyses, earthworm invasion at two sites was dated back to 1960 and 1970 (Larson et al., 2010). Although we could not estimate time of earthworm colonization, ring growth was positively correlated with current earthworm density. Given our study design, we cannot determine if the association between earthworms and *B. thunbergii* is a result of facilitation between both species or if both species are responding positively to underlying site conditions. However, previous studies at plant-invasion fronts indicate that earthworm invasion precedes *B. thunbergii* invasion (Nuzzo et al., 2009), suggesting earthworm facilitation of *B. thunbergii*.

While the positive association between earthworms and *B. thunbergii* growth was consistent through time, the correlation was stronger after deer exclusion in 2008. Interactive effects between earthworms and fencing occurred rather quickly, as they were detectable after just four years since fence construction. A short lag phase after deer exclusion indicates that short-term (ex. nutrient addition through feces) rather than long-term (ex. reduction of plant competition) impacts are likely causing positive effects on *B. thunbergii* ring-growth.

Deer and earthworm effects on *B. thunbergii* ring-growth are indirect and both factors may be acting through similar mechanisms. Positive indirect effects of deer on ring-growth of oak trees has been attributed to increased nutrient inputs through deer excreta (Lucas et al., 2013), as deer can add a substantial quantity of nutrients through feces and urine (Jensen et al., 2011). Similarly, earthworm depletion of top soil layers (O horizon) may lead to nutrient pulses that benefit *B. thunbergii* growth. Furthermore, deer and earthworm impacts on soil microbial communities may indirectly alter above- and below-ground trophic interactions (Bardgett et al., 1998; Eisenhauer et al., 2011; Lessard et al., 2012; Dempsey et al., 2013; Kardol et al., 2014). In addition, both deer and earthworms have detrimental effects on native understory plant communities (Côté et al., 2004; Hale et al., 2006), likely reducing competition with palatable plant species and favoring growth of non-palatable *B. thunbergii*. At our sites, native plant cover was significantly higher in fenced plots only after five years of deer exclusion (Nuzzo et al. unpublished data), indicating that beneficial effects of deer on *B. thunbergii* growth were not driven by decreased interspecific competition in open plots, at least not in the first years after fencing.

Complex and unpredictable interactions among multiple factors indicate that impacts and subsequent management of invasive plant species cannot be adequately studied and managed without consideration of the myriad other influences on forest ecosystems, including other co-occurring non-native species (Rauschert and Shea, 2012; Kuebbing et al., 2013b; Roth et al., 2014), that may directly or indirectly confound experimental results or obscure interpretations. Taken together, our results emphasize the critical role of white-tailed deer in forest ecosystems and highlight the need to concurrently study multiple factors in order to understand mechanisms of plant and earthworm invasion success.

Our results have important management implications. Strong synergistic effects between deer and earthworms indicate that reducing either deer or earthworm populations might be sufficient to reduce populations of these non-native plant species to acceptable levels. There is at this time no effective way to reduce earthworm populations, therefore reducing deer densities may be the appropriate management approach to reduce non-native plants in areas with high earthworm density. While fencing to exclude deer may protect small areas or specimens of special concern, deer are key components of northeastern North American forests and their complete exclusion from the system is not desirable. We

therefore suggest that reducing, but not eliminating, deer density is necessary at the landscape level to both decrease non-native plant abundance and protect native species.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2015.04.026>.

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