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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.

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; Whitfeld 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. Mil 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 arbuscural 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.