



# Interactive effects of deer, earthworms and non-native plants on rare forest plant recruitment



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## ABSTRACT

Multiple biotic and abiotic factors, operating at several stages may affect plant demography and recruitment. Across forests in North America increased white-tailed deer (*Odocoileus virginianus*) abundance, non-native earthworms and non-native plant invasions are likely to generate single and interactive effects. We evaluated effects of these stressors on recruitment of three rare plants (*Aristolochia serpentaria*, *Carex retroflexa* and *Trillium erectum*). We conducted a multiple year seed addition experiment using paired open and fenced plots (experimentally excluding deer) at 12 forested sites that differ in earthworm density and non-native plant cover. We found strong microsite limitations for *C. retroflexa*, which completely failed to establish after a 3-year period despite successful germination in greenhouse trials. Addition of *A. serpentaria* and *T. erectum* seed resulted in successful seedling emergence; however, *A. serpentaria* recruitment steadily decreased over the study period. We found no significant effects of non-native *Alliaria petiolata* or *Berberis thunbergii* on seedling recruitment but surprisingly, we found strong positive effects of non-native *Microstegium vimineum* on *A. serpentaria* and *T. erectum*. Deer exclusion resulted in increased *T. erectum* emergence and seedling survival. Earthworm abundance negatively affected survival of *T. erectum* seedlings, and the effect manifested itself through interactive effects with fencing and non-native plants. Comparing recruitment through seeding addition to recruitment through transplants in a parallel study, we identified strong potential for *T. erectum* restoration using seed addition, but this will be dependent upon a significant reduction of deer impacts. Restoration of *A. serpentaria* and *C. retroflexa* will require manipulation of microsite conditions to promote recruitment.

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## 1. Introduction

Long-term conservation of currently declining or rare, threatened and endangered plant species will depend upon increasing their population growth rates at many locations to ensure local and regional population viability and to prevent demographic bottlenecks (Rodríguez-Pérez and Traveset, 2007; Rother et al., 2013). To achieve this goal, conservation practices should focus on reinstating ecological processes important for plant recruitment. Management may, for example, involve increasing the size of adult populations by managing stressors deemed responsible for poor performance of reproductive individuals. Depending on the species, this may involve management of herbivores, invasive species, anthropogenic disturbances, pollution or harvesting (Mooney and McGraw, 2009; Thomson, 2005; Wall et al., 2012). But increasing the reproductive output of remaining individuals may not always

be sufficient to achieve overall population viability. Furthermore, reestablishing populations through translocation of new individuals or seed addition into apparently suitable habitats is challenging (Holl and Hayes, 2006), often due to a lack of understanding of plant demography (Kwit et al., 2004) and specific habitat requirements.

Successful plant recruitment is determined by the combined effects of multiple biotic and abiotic factors affecting seed production, seed dispersal, seed bank presence, seed germination and seedling establishment (Bricker and Maron, 2012; DiTommaso et al., 2014; Maron et al., 2014; Olsen and Klanderud, 2014). Consequently, recruitment limitations may arise through the interplay of both seed and microsite limitations (Clark et al., 2007; Turnbull et al., 2000). Seed limitation may also occur due to stochastic events, such as dispersal processes, and through deterministic mechanisms that limit seed production, including herbivory and competition (Caughlin et al., 2013; Núñez-Ávila et al., 2013). Microsite limitation refers to biotic and abiotic filters that limit seedling emergence and establishment after seed arrives at

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a given location, such as local habitat characteristics (Maron and Simms, 1997). If the net effect of these interactions limits recruitment, plant species persistence is at risk with important consequences for overall community structure and composition (Bricker and Maron, 2012; Bruna, 2003; Rodríguez-Pérez and Traveset, 2007).

Seed addition experiments indicate that most plant populations are both seed and microsite limited (Clark et al., 2007; Turnbull et al., 2000), with microsite limitations of overriding importance in minimally disturbed environments (Clark et al., 2007). Notably, the relative importance of the multiple processes that cause recruitment limitations may vary in space and time (Lortie et al., 2004), are affected by species traits (Moles and Westoby, 2002) and are modulated by interactions of concurrent processes (Maron et al., 2014; Maron and Simms, 1997).

Record high deer densities, non-native earthworm invasions and non-native plants constitute major agents of change in forests in northeastern North America (Côté et al., 2004; Fisichelli et al., 2013; Hale et al., 2006; Mack et al., 2000). The single and combined effects of these stressors may impose local filters that result in recruitment limitations. For example, seed limitation may be the result of chronic deer herbivory reducing flowering probability and seed set of highly palatable species (Knight et al., 2009). Similar effects arise if stressors decrease plant survival or seed production (Clark et al., 2007; Turnbull et al., 2000), likely causing many herbivore-affected populations to be seed limited. Similarly, plant invasions may reduce species richness (Vilá et al., 2011) and reproductive effort of vulnerable species (Levine et al., 2003; Miller and Gorchov, 2004), while negative effects of earthworm abundance on seedling survival (Dobson and Blossey, 2014) may result in fewer flowering individuals and seed set.

These stressors may also increase microsite limitations through habitat alteration. For example, long-lasting changes in forest vegetation composition and structure (Amatangelo et al., 2011; Aukema et al., 2010) due to deer herbivory, earthworm activity or non-native plant invasions (Côté et al., 2004; Hale et al., 2006; Tanentzap et al., 2011; Vilá et al., 2011), may affect abiotic and biotic conditions, including changes in microclimate, light availability, amount and quality of leaf litter, leaf litter invertebrate abundance and composition, as well as soil microbial communities (Eisenhauer et al., 2011; Holdsworth et al., 2012; Suarez et al., 2006). At local scales, deer and earthworms can alter microsite conditions through changes in soil compaction (Kardol et al., 2014; Nuttle et al., 2011), nutrient availability (Bohlen et al., 2004; Ewing et al., 2014; Murray et al., 2013) and mycorrhizal infection rates (Kardol et al., 2014; Lawrence et al., 2003). Similarly, non-native plants may reduce recruitment through allelopathic effects (Cipollini and Flint, 2013; Corbett and Morrison, 2012; McEwan et al., 2010) and reductions in mycorrhizal infection rates (Barto et al., 2011).

The net effect of stressors on demography depends on their effects at each demographic transition. For example, positive earthworm effects on seed germination due to leaf litter depletion and exposure of bare soil (Warren et al., 2012) may be outweighed by negative earthworm effects on seed and seedling survival (Dobson and Blossey, 2014), caused by seed predation (Eisenhauer et al., 2010), seed burial (Lawton, 1994) or fine root consumption (Gilbert et al., 2014). Therefore, to properly assess the role of these factors on recruitment, it is important to conduct long-term seed addition experiments, where the single and combined effect of each stressor can be quantified at different stages of the plant life cycle. However, most seed addition experiments are short-term, following seedlings only during the first year of their emergence (Clark et al., 2007; Turnbull et al., 2000). Moreover, despite a recognized need to quantify interactions among multiple concurrent processes in order to understand the

underlying mechanisms shaping plant populations (Didham et al., 2007), few studies experimentally assess effects of multiple stressors on plant demographic parameters (Crone et al., 2011).

Here we explore the single and interactive effects of deer exclusion, earthworm abundance and non-native plant cover on recruitment of three rare forest understory species: *Aristolochia serpentaria* L., *Carex retroflexa* Muhl. ex Willd and *Trillium erectum* L. (hereafter referred to as *Aristolochia*, *Carex* and *Trillium*). We conducted a five-year seed addition experiment using a network of 12 forested sites that differ in earthworm abundance and cover of three non-native focal plant species [*Berberis thunbergii* DC, *Alliaria petiolata* (M. Bieb.) Cavara & Grande and *Microstegium vimineum* (Trin.) A. Camus]. All native understory target species were present in the region, but absent from our study sites (no extant individuals or presence in the seed bank (Nuzzo et al., 2015)). We addressed the following questions: (1) How is recruitment of *Aristolochia*, *Carex* and *Trillium* affected by the interaction of deer, non-native earthworms and non-native plants? (2) How do these stressors affect the relative importance of microsite limitation on recruitment? (3) Do effects of seedling emergence persist over time resulting in differences in seedling survival and growth? (4) Would restoration be more effective through seeding or seedling transplanting? We addressed the latter question by comparing recruitment success in this experiment to success of transplanted seedlings in a parallel study conducted at the same sites during the same study period (Dávalos et al., 2014).

## 2. Materials and methods

### 2.1. Study sites

We conducted the study at US Army Garrison West Point (hereafter West Point); a 65 km<sup>2</sup> facility located some 80 km north of New York City within the Hudson Highlands Province of New York State, USA. West Point is covered by upland deciduous forests dominated by oak (*Quercus rubra* L. and *Q. prinus* L.) and/or sugar maple (*Acer saccharum* Marshall). We selected 12 forested sites 1–8 km apart with different percent cover of native and non-native plant species; six sites were located in populations of three focal non-native plant species (*B. thunbergii*, *A. petiolata* and *M. vimineum*; 2 sites each) and six sites were located in mixed native understory plant communities. All 12 sites vary in invasive earthworm density and biomass (Dávalos et al., 2014). Based on earthworm monitoring results (see Section 2.3 and Dávalos et al., 2015), we classified sites into low and high earthworm abundance categories (measured as function of earthworm density and biomass).

### 2.2. Study species

We selected three rare herbaceous species based on their occurrence in the study region and conservation status: *Aristolochia serpentaria* (Aristolochiaceae), *Carex retroflexa* (Cyperaceae) and *Trillium erectum* (Liliaceae).

*Aristolochia* is a perennial herb that grows from a short rhizome with multiple fibrous roots. Stems usually grow singly, reaching 15–60 cm tall, with up to 6–10 alternate leaves per stem. Leaves are hastate shaped, 1–5 cm wide and 1–6 cm long. Maroon s-shaped flowers (1–2 cm long) have a ‘trap’ design to facilitate insect cross-pollination (Oelschlägel et al., 2009) and are produced singly on short basal stems at or under the leaf litter. Plants rarely have more than two flowers and few plants flower in any given year. The majority of flowers are chasmogamous, but occasionally cleistogamous flowers are produced (Barringer, 1997; Pfeifer, 1966). In our region, flowers are produced June–July and fruits

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