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RESEARCH ARTICLE

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Deer Facilitate Invasive Plant Success in a Pennsylvania Forest Understory

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ABSTRACT: Invasive species impose severe biological and economic costs worldwide. In forested ecosystems, invasive species supplant native species, resulting in decreased biodiversity. Furthermore, human-mediated disturbances may stress native forest species and benefit invasive species that thrive in disturbed habitats. Anthropogenic changes to the landscape have caused unprecedented increases in white-tailed deer (*Odocoileus virginianus*) numbers, which has resulted in the degradation of understory native plant communities. We suggest that deer-mediated disturbance to understory communities facilitates the success of invaders in forests. Many North American forests experience both exotic plant invasion and deer overabundance, but the two problems have never been empirically linked. In this paper, we quantify deer effects on native and exotic understory herbs in a western Pennsylvania forest. We show that the percentage of bare ground and the relative abundances of the invasive herbs, *Alliaria petiolata* and *Microstegium vimineum* are significantly greater, while native plants are significantly smaller with a lower proportion flowering in deer access vs. deer exclusion plots. Our data support the idea that invader success is due in part to both preferential foraging by deer on native herbs that reduces their size and flowering status and the creation of open patches when deer are present. We conclude that deer overabundance facilitates the success of invasive species in forested ecosystems and that management will benefit by considering these factors jointly.

Index terms: Alliaria petiolata, deer exclusion experiment, deer overabundance, invasive specie, *Microstegium vimineum*

INTRODUCTION

Invasive species are one of the largest threats to global biodiversity (Vitousek et al. 1996; Williamson 1996) and impose severe biological and economic costs worldwide (Pimentel et al. 2005). To maintain biodiversity and manage natural resources, it is essential to discover the mechanisms that allow invasive species to invade and then dominate specific habitats, while other habitats are able to resist invasion. Invasion research takes varied approaches. Some studies consider how the characteristics of the community might influence the community's susceptibility to invasion (MacDougall and Turkington 2005) and why some are prone to invasion while others appear to resist invaders. For example, communities with high species diversity are proposed to be more difficult to invade because the invader faces more potential competitors (Kennedy et al. 2002; Levine et al. 2003) or because native species use the available resources in the habitat more completely (Stachowicz et al. 1999; Levine et al. 2003). In addition, invasive species are hypothesized to invade and dominate habitats that receive different levels of disturbance (i.e., either higher or lower) than they experienced during their evolutionary past (e.g., Hobbs 1996; Gross et al. 2005). Additionally, some studies consider the characteristics of the exotic species to determine if the key traits can be identified that make it a good invader (e.g., Crawley et al. 1996; Callaway and Ridenour 2004; Sutherland 2004) or if the species has evolved in the novel habitat (e.g., Blossey and Notzold 1995). For example, the success of the exotic plant *Alliaria petiolata* in North America is attributed to its short lifespan, allelopathy, and autogamous breeding system (Nuzzo 1999). Clearly, community and exotic species characteristics both can contribute to the likelihood of invasion.

In addition to exotic plant invasion, the increase in the abundance of white-tailed deer (*Odocoileus virginianus, Zimmermann*) is a biotic disturbance challenging understory plant species in many forests throughout eastern North America. Deer increases are directly linked to human actions. Specifically, habitat fragmentation, agriculture, and eradication of large carnivores have resulted in a four-fold increase in the abundance of white-tailed deer throughout eastern North America over the past 50 years (McShea et al. 1997; Russell et al. 2001). These unprecedented numbers of deer are now occupying a wide range of habitats, including those not historically inhabited by deer, and are rapidly altering mature forest native understory plant abundance, biodiversity, community composition (Augustine and deColesta 2003; Rooney and Waller 2003; Côté et al 2004), and ecosystem function (Russell et al. 2001; Wardle et al. 2001; Côté et al. 2004). Managing for deer and invasive species are both top priorities for managers interested in preserving diversity of natural forests (McShea et al. 1997; National Invasive Species Council http://www.invasivespeciesinfo.gov/council/nmp.shtml), but heretofore, the two problems have not been linked.

Because increased deer densities are expected to impact the biotic and abiotic conditions within forests (McShea and Rappole 1997; Côté et al. 2004; Varva et al. 2007), deer are also suspect in creating conditions amenable to exotic plant invasions. Published data on the impacts of deer exclusion/deer access on exotic weeds invasion are scarce, difficult to compare due to differences in habitats and invader species (Vavra et al. 2007), and provide mixed results. In two studies, deer-browsing effects on invader abundance was found to be invader species-specific, but had no overall effect on the proportion of invaders in a community (Bowers 1993 [old-field]; Webster et al. 2005 [cove forest]). Likewise, exotic plants were more abundant in deer exclusion plots in one old-field but had no effect in a second old-field that differed in time since abandonment (Cadenasso et al. 2002). Finally, deer browsing had no effect on the species richness of exotic invaders in a beech-oak (*Fagus-Quercus)* forest in Maryland but decreased the abundance of oriental bittersweet, *Celastrus orbiculatus* (Rossell et al. 2007).

Here we address the potential interaction of elevated deer densities and the relative abundance of invasive herbs at the Trillium Trail Wildflower Reserve located in Fox Chapel, a borough of Pittsburgh, Pennsylvania. Its diverse spring flowering display has made Trillium Trail a wildflower hike destination since the land was donated to Fox Chapel in 1949. Trillium Trail is an ideal site for our research because we know the year when the local deer impact in the site changed. In 1992, an influx of deer into this area resulted in a nearly complete defoliation of the spring ephemeral understory at Trillium Trail; the carpet of wildflowers preferred by deer disappeared literally overnight due to browsing.

Since that time, field work in the understory demonstrates sustained levels of deer browse on the spring ephemerals (detailed below) while annual aerial censuses of the deer herd size in Fox Chapel reveal sustained deer densities of 25-40 deer/km^2. These deer abundance values are two to four times greater than their historical abundance in eastern North America and more than six times greater than the recommended 4-6 deer/km limit for sustainable forest plant community health (Witmer and deCalesta 1991; Anderson 1994).

In this study, we quantify the percent cover, reproductive status, and sizes of native and invasive herbaceous species growing in a set of paired control (deer access) vs. fenced (deer exclusion) plots and in a large fenced area in Trillium Trail to test the general hypothesis that deer facilitate exotic plant success in forests. We focus on change in abundance and average plant size across the two treatments.

METHODS

Study site and species

Trillium Trail is a 16-ha wildflower reserve embedded in a large tract (>125 ha) of forest and parkland associated with Squaw Run in Allegheny County, Pennsylvania (40° 52' 01.40" N; 79° 90" 10.75" W). Since 1949, the preserve has been owned and stewarded by the Borough of Fox Chapel. The Borough was dedicated as a wildlife sanctuary in 1970. Habitats at Trillium Trail range from the floodplain of Squaw Run to dry hilltops (280-315 m elevation range). The overstory at Trillium Trail consists of mature red oak (*Quercus rubra* L.), white oak (*Quercus alba* L.), beech (*Fagus americana* Ehrh.), sugar maple (*Acer saccharum* Marsh.), and tulip trees (*Liriodendron tulipifera* L.). The herbaceous understory is a diverse mixture of native species: white trillium (*Trillium grandiflorum*), wakerobin (*T. erectum* L.), toadshade (*T. sessile* L.), false mermaid (*Floerkea proserpinacoides* Willd.), two-leaved toothwort (*Cardamine diphylla* (Michx.) Alph. Wood), wild ginger (*Asarum canadense* L.), touch-me-not (*Impatiens capensis* Meerb. and *I. pallida* Nutt.), Solomon's seal (*Polygonatum biflorum* (Walter) Elliott), mayapple (*Podophyllum peltatum* L.), Jack-in-the-pulpit (*Arisaema triphyllum* L.), Virginia waterleaf (*Hydrophyllum virginianum* L.), and bloodroot (*Sanguinaria canadensis* L.) are common at the site.

Two exotic and invasive herbaceous species are also now common at the study site, garlic mustard (*Alliaria petiolata* ((M. Bieb.) Cavara & Grande))) and Asian stiltgrass (*Microstegium vimineum* (Trin.) A. Camus), but were rare or absent before 1992 (*A. petiolata*) and 2002 (*M. vimineum*), respectively. *Alliaria petiolata* is a biennial native to Europe. It was first documented in New York in 1868 and has recently become a rampant invader in woodlands throughout eastern North America (Nuzzo 1999). *Microstegium vimineum* is an annual grass native to Asia. It was first reported in Knoxville, Tennessee, in 1919 and has recently expanded its range east of the Mississippi River and into Texas (Gibson et al. 2002).

Paired Plots

We conducted our initial deer exclusion experiment using three paired 10-m^2 deer exclusion and deer access plots. Fences are 2.5 m tall with a mesh size of 6 cm effectively eliminating access by deer, but allowing free movement of other interacting species such as birds, small mammals, pollinators, and herbivorous insects. The fences were erected in 1994 and data collection continued until 2003, when a large deer exclusion fence was erected (see below).

Vegetation censuses were conducted four times in each growing season (April to September) every year. In each plot, we identified all herbaceous plants to species, visually estimated percent cover for each species and percent of bare ground, and counted the number of flowering individuals for each species. This allowed us to document the maximum percent cover and the number of flowering individuals for each species, since species differ in their phenology. We also calculated the sum of the percent cover values for each species for each treatment. To compare the relative rankings of species percent cover in the deer exclusion vs. deer access treatments, we summed the relative rankings across the three plots and calculated the average rank for each treatment. We used a Kruskal-Wallis rank test to compare the relative ranking of species with respect to percent cover in deer exclusion and control treatments after five years (1999) and a paired t-test to compare the average percent bare ground at the beginning of the experiment (1994) and nine years later.

10-hectare deer exclusion study

To protect the integrity of the wildflower preserve from the sustained deer browsing in Trillium Trail, in the late fall of 1999, the Borough of Fox Chapel enclosed a 10.06-ha area ranging from floodplain to steep hillside with a 2.5 m tall fence; thus, deer were excluded from portions of all habitat types found at the site. The construction of this fence provided us with a unique opportunity to test if the plant responses observed in the small plot deer exclusion experiment were repeatable at this larger spatial scale. Because there is only one large fenced area, the issue of statistical non-independence (Hurlbert 1984) can be raised (but see, Oksanen 2001). However, we expect that if deer are important drivers of invader success, then the outcome of the two experiments will be similar and support the same conclusions. Thus, taken together, the results from the two studies can provide strong evidence of the role of deer in exotic species invasion and in shaping the forest understory herbaceous community structure.

We established five sampling transects in the 10-ha deer exclusion area that spanned the elevation gradient of Trillium Trail. Transects were parallel to each other and adjacent transects were separated by ~15 meters. To determine if there were any pre-treatment differences in understory species composition between the deer exclusion and deer access sample plots described below, we surveyed 117 1-m^2 plots along five parallel transects in early spring 2000. Each 100 m transect was perpendicular to the southwest side of the fence, with 50 m inside the fence and 50 m outside the fence and plots inside and outside of the fence. Transects were 30 m apart on an elevation gradient. In each plot, we documented presence or absence of all plant species. We used a Mantel test (10,000 permutations) on the Euclidean distance on community composition between each plot. We found that the similarity of plots in their community composition did not depend on location inside or outside the large fence ($P > 0.10$). This remains true even when we correct for spatial distances between plots ($P > 0.10$). Thus, there were not any pretreatment differences in community composition.

In 2004, along each of the five transects, six 5-m^2 subplots were marked, three of which were inside the fence and three of which were arranged as the mirror image outside the fence. The first subplot was 20 m from the fence and adjacent subplots along each transect were separated by a distance of 10 m. The percent cover of each herbaceous species in the subplots was quantified in 2004, after five years of deer exclusion. As in the paired plots, vegetation censuses were conducted four times in each growing season (April to September). This allowed us to document the maximum percent cover and reproduction throughout the growing season for each species. The summed percent cover for each species was calculated for each treatment and transect in the final year (2004), for a total of five sample values for each treatment (one sample per transect). For each sample, we also calculated proportional percent cover of invasive species [(% cover of invasive species)/(Σ% cover for all species)]. In addition, we counted the number of reproductive individuals for each species at each census. This allowed us to calculate the total number of reproductive herbaceous plants for each sample – and the proportion of reproductive plants that were native and invasive species [(# reproductive stems of invasive species)/(# reproductive stems for all species)]. Finally, for seven focal species in the sample plots along the five transects – (the invasive species, *Alliaria petiolata* and the native species, *Arisaema triphyllum* (L.) Schott, *Asarum canadense* (L.), *Hydrophyllum virginianus* (L.), *Polygonatum biflorum* (Walter) Elliott, *Sanguinaria canadensis* (L.), and *Trillium grandiflorum* (Michx.) Salisb.) – we measured individual plant size and the incidence of deer herbivory. These focal species were chosen because they are abundant and well represented across our sample plots. We used t-tests to compare the proportional percent cover of herbaceous invaders and the proportion of herbaceous invasive reproductive plants in the two treatments. We used Wilcoxon paired sign-rank tests to examine mean differences between deer exclusion and deer access treatments in focal native plant size and paired one-tailed t-test to test for focal native reproduction.

RESULTS

Paired plots

A total of 46 herbaceous species were identified in our plots. After five years of the deer exclusion treatment, the plant community composition diverged significantly between the deer exclusion and deer access plots (Kruskal-Wallis rank test; P=0.001; Figures 1 and 2). In the deer exclusion plots, species abundances were more evenly distributed and the native wildflower, *T. grandiflorum,* was dominant. Conversely, in deer access plots, the majority of native species were rare or absent, and the invasive herb, *A. petiolata,* was dominant (Figure 1). Further, in 1999 only six individuals of all the native spe-

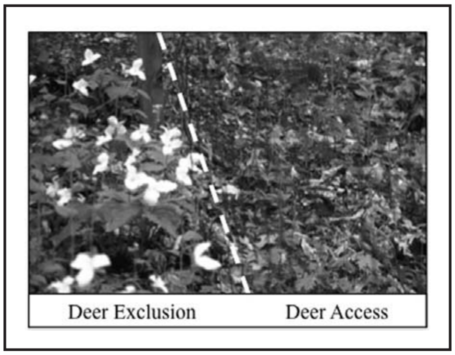

Figure 1. Photo taken at the boundary of a fenced 10-m^2 deer exclusion and a 10-m^2 deer access plot 5-years after the fence treatment was established. The dashed white line highlights the fence boundary. The area to the left of the line is inside the fence, where reproductive *Trillium grandiflorum* is the most abundant species. The area to the right of the line is part of the paired deer access plot, where *Alliaria petiolata* is the most abundant species.

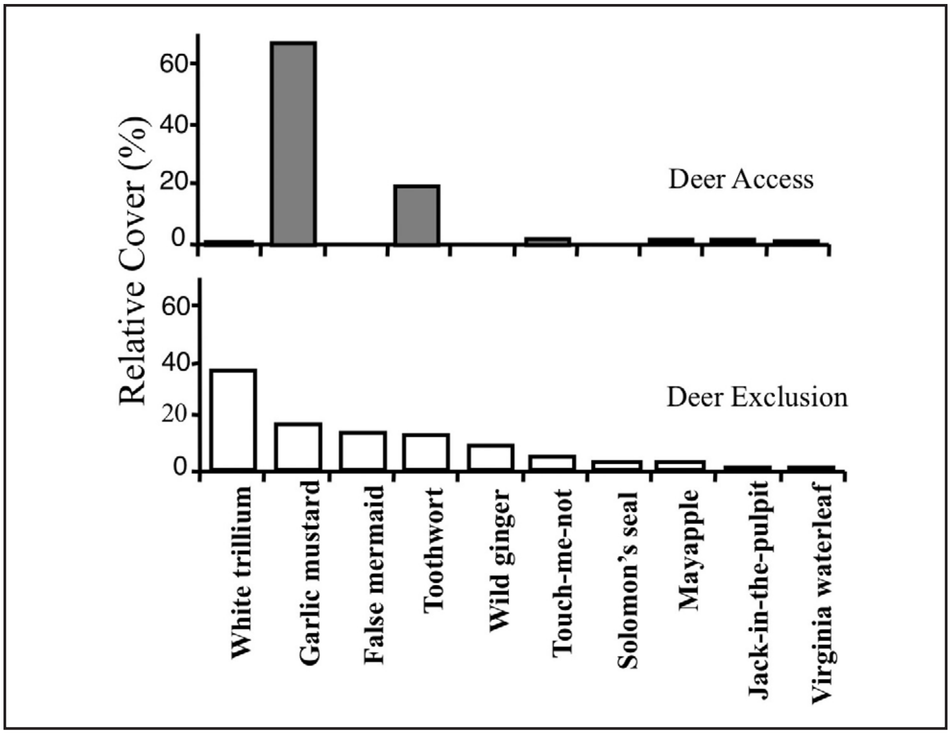

Figure 2. The relative percent cover of the ten most abundant plant species in our deer exclusion and control plots. All plant species are native, except garlic mustard. After five years of deer exclusion, community composition significantly diverged between treatments (Kruskal-Wallis rank test; $P = 0.001$).

cies present flowered across the three deer access plots, whereas in the deer exclusion plots, there were 145 flowering individuals counted for the native species. This is more than a 25-fold increase in the number of native flowering individuals in the absence of deer. Similarly, the percent bare ground diverged significantly in deer access vs. deer exclusion plots. Plots did not differ at beginning of the experiment (1994), but the percent bare ground decreased significantly in deer exclusion plots ($p < 0.0005$, t-test, $t = 3.73$, Figure 3).

10-hectare deer exclusion study

As with the paired plots, we found that the proportional abundance of invasive plants was significantly greater in deer access sample plots than in deer excluded sample plots (t-test results: $t = 3.06$, $df = 3$, $P = 0.03$). Similarly, the proportion of reproductive invasive plants [(# invasive reproductive stems)/(total # reproductive stems)] was significantly higher in the deer access sample plots than in the deer exclusion sample plots (t-test results: $t = 2.34$, $df = 3$, $P = 0.05$). All six focal native species were significantly smaller on average in the control sample plots than in the deer excluded sample plots ($P < 0.03$, Wilcoxon sign rank) and were less likely to be reproductive in control relative to deer excluded sample plots (paired one-tailed t-test, $t = 2.28$, $df = 3$, $P < 0.06$). Across all six native focal plant species, only nine individuals flowered in 2004 in the control sample plots, while 236 individuals flowered in the deer excluded sample plots. The mean plant size of the invader, *A. petiolata*, did not differ in size in the presence or absence of deer (t-test: number of branches, $F_{1,97} = 0.80$, $P = 0.37$; number of leaves, $F_{1,97} = 1.09$, $P = 0.30$). (Note: the invasive species *M. vimineum* was found in the deer access plots, but did not occur in the deer exclusion plots.)

On average, deer consumed 14% of the flowering stems of the native focal plant species in our sample plots (species ranges: 5%-33%) while no deer herbivory was observed in the deer exclusion sample plots. In contrast, neither of the invasive exotics, *A. petiolata* nor *M. vimineum*, experienced any deer herbivory.

DISCUSSION

Taken together, the results of the two experiments show that the abundance of the two exotic invasive species in this forest understory community is attributable to the presence of deer. Three mechanisms could have combined to produce this result: (1) greater tolerance of invasive species to herbivory; (2) direct consumption of native species and avoidance of invasive species; and/or (3) greater tolerance of invasive species to non-browsing effects of deer. We address each of these in turn.

First, our data provide no support for the idea that invasive species tolerate herbivory through re-growth and more rapid reproduction (Stowe et al. 2000). Neither invader was observed to experience any deer herbivory during this study or in other studies on *Alliaria* and *Microstegium* conducted at this site from 2002-2008 (S. Kalisz, unpubl. data). Both invasive species in our study are weedy short-lived herbs (i.e., *M. vimineum* is an annual and *A. petiolata* is a biennial) with rapid reproduction and high population growth rate (e.g., Davis et al. 2006; Morrison et al 2007; Cole and Weltzin 2008). In contrast, the native herbaceous understory species in our study are long-lived and slow-growing perennials (e.g., Bierzychudek 1982; Hanzawa and Kalisz 1993) that are likely to be more sensitive to herbivory (Knight 2004) than the short-lived invaders.

Second, we found strong support for the idea that deer preferentially consumed native plant species, with no evidence of herbivory on either invasive species *A. petiolata* or *M. vimenium*. The observed, intense herbivory by deer on the native perennials dramatically altered their population structure. Our data show that fewer native plants flowered and they were on average significantly smaller in size in the presence of deer relative to the deer exclusion plots. The changes in population structure seen in the native herbs can significantly alter population dynamics and long-term stability. For example, in the perennial native species, *Trillium grandiflorum*, flowering is size-dependent (Hanzawa and Kalisz 1993). Deer are known to preferentially consume flowering individuals over non-

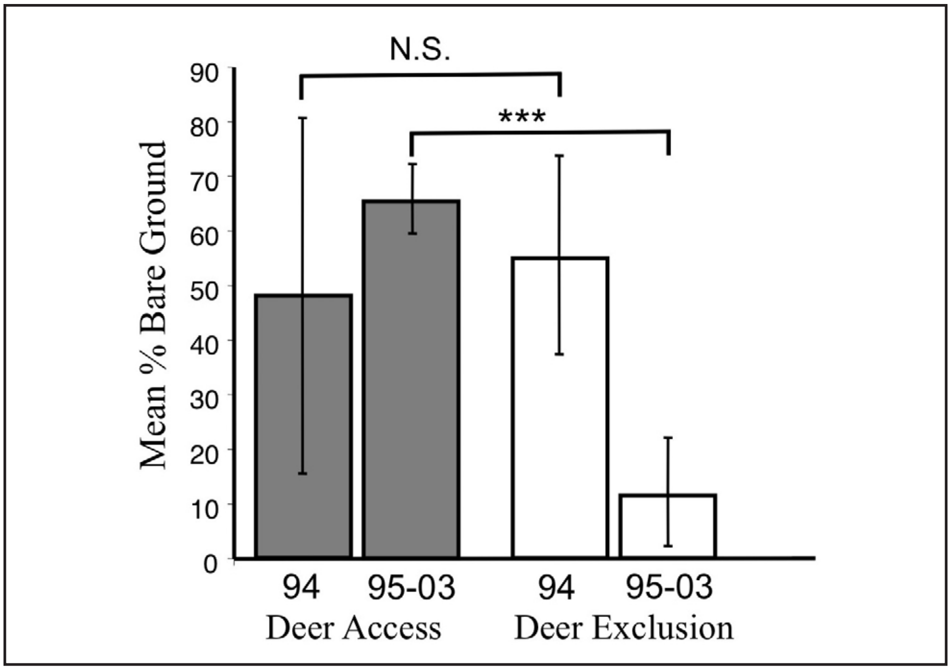

Figure 3. Percent bare ground (mean ± SE) is significantly greater in deer access vs. deer exclusion plots. Plots did not differ at beginning of the experiment (1994), but % bare ground decreased significantly in deer exclusion plots (grand mean of plots 1995-2003; *** p<0.0005, t-test, t = 3.73)..

flowering (Anderson 1994). Loss of photosynthetic biomass to herbivory causes individual plants to regress to a smaller, non-reproductive stage in the following year (Knight 2003; Rooney and Gross 2003). In addition, the loss of flowering individuals to deer browsing reduces the potential for regeneration by seed. Further, because the population growth rate of *T. grandiflorum* is sensitive to changes in the vital rates of reproductive individuals (Knight 2004), high levels of deer herbivory threaten population persistence for this species (Knight 2004; Knight et al., in press). It is unknown, but likely, that the demographic responses of other native plant species browsed by deer are similar to that of *T. grandiflorum*, and the reduction in plant size of all native species suggests that this will be the case. Significantly lower percent cover and greater percent of bare ground, significantly smaller individual plant sizes, and significantly lower numbers of reproductive individuals of native species are all evidence of the negative effects of current deer levels at our study site that could result in reduced competitive ability of the native plants.

Herbivory was not observed for either invader in our study. Although it is unclear why deer do not consume *M. vimenium* plants, this species has been shown to be less palatable to insects than *A. petiolata* (Morrison et al. 2007). *Alliaira petiolata* plants are known to possess chemicals that likely make them less palatable to deer (Haribal and Renwick 1998, 2001; Vaughn and Berhow 1999; Cipollini and Gruner 2007) and thus avoided. Therefore, our results are similar to a wetland study, where deer selectively browsed native plants and avoided the invasive grass, *Phalaris arundinacea* (Kellogg and Bridgeman 2004). Preferential browsing on natives may confer a competitive advantage to these invaders. Indeed, *A. petiolata* did not differ significantly in size or frequency of flowering between treatments in the 10-ha fence study.

One prominent hypothesis for why many exotic species become invasive is the ‘enemy release hypothesis’ (Williamson 1996; Mitchell and Power 2003), which posits that introduced species escape from *specialist* enemies when they colonize a new habitat and, as a result, have a competitive advantage over the native species. Further, a recent meta-analysis examining native and exotic species experiencing a wide range of native and invasive herbivore types in herbivore exclusions found that exotics are, in general, susceptible to novel, generalist herbivores (Parker et al 2006). In contrast, here we show that the exotic species *A. petiolata* and *M. vimineum* appear to be unpalatable to a native, *generalist* herbivore. This lack of herbivory by deer may contribute to the maintenance of their abundance in the presence, but not absence, of deer.

Finally, the effects of deer on understory communities could also be due to non-browsing effects of deer, such as soil and leaf litter disturbance that create bare soil areas, trampling, or soil compaction, which affect plant growth rates or seedling establishment (Wardle et al. 2001). Indeed, all native plants, whether browsed or not, were smaller when deer were present. While some size regression of the species deer browse regularly is undoubtedly due to herbivory, even Jack-in-the-pulpit, a native species that rarely experiences deer herbivory, showed a trend towards smaller vegetative size in the presence of deer after five years ($P < 0.07$; paired sample plots of the large fenced area). In contrast, *A. petiolata* did not decrease in size in the presence of deer in these same plots, which suggests that it may be more tolerant of soil compaction, trampling, or other indirect effects of deer. Interestingly, *M. vimenium* was only found outside the fence where deer had access. Leaf litter disturbance has been shown to facilitate the spread of *M. vimenium* (Oswalt and Oswalt 2007), and deer activity in the deer access portions of our study site had significantly more bare ground, which could facilitate this invasive species’ success. Thus, non-browsing effects of deer may also be contributing to native species decline.

Taken together, our results suggest that current, historically unprecedented densities of native white-tailed deer are causing changes in the forest understory community, likely through a combination of both selective foraging on palatable native species and the non-browsing effects that favor invaders. It is well known that deer can dramatically diminish the abundance and richness of native understory species (Russell et al. 2001; Côté et al. 2004). In this study we have shown an additional effect—the current effects of deer at this site appear to make the forest understory more hospitable to invaders of non-native species. Thus, two previously unconnected problems in land management, deer overabundance and invasive species, appear to be intimately linked.

Why some species become invasive and some communities are more easily invaded remain poorly understood and hotly debated topics in ecology (Shea and Chesson 2002; Levine et al. 2003). We suggest that the multi-trophic-level dynamics between a native herbivore and native and invasive plants changes in competition between native and invasive plants, and abiotic disturbance may all play important roles in the facilitation of these invaders. Specifically, herbivory by overabundant populations of white-tailed deer appear to create and sustain conditions for invasive species to dominate understory communities, while deer exclusion reverses this trend. These results may be general to other ecosystems with overabundant ungulate browsers. Further studies that link changes in abundance with the population growth rates of the invaders are required to assess if the invaders will, in fact, decline.

CONCLUSION

Our results suggest that management programs to reduce the abundance of deer and their effects on native plant communities will also help to curb the spread and dominance of invasive species.

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LITERATURE CITED

Anderson, R.C. 1994. Height of white-flowered trillium (*Trillium grandiflorum*) as an index of deer browsing intensity. Ecological Applications 4:104-109

Augustine, D.J., and D. DeCalesta. 2003. Defining deer overabundance and threats to forest communities: from individual plants to landscape structure. Ecoscience10:472-486.

Bierzychudek, P. 1982. The demography of Jack-in-the-pulpit, a forest perennial that changes sex. Ecological Monographs 52:335-351.

Blossey B., and R. Notzold. 1995. Evolution of increased competitive ability in invasive nonindigenous plants: a hypothesis. Journal of Ecology 83:887-889.

Bowers, M.A. 1993. Influence of herbivorous mammals on an old-field plant community: years 1-4 after disturbance. Oikos 67:129-141.

Callaway, R.M., and W.M. Ridenour. 2004. Novel weapons: invasive success and the evolution of increased competitive ability. Frontiers in Ecology and the Environment 2:436-443.

Cadenasso, M.L., S.T.A. Pickett, and P.J. Morin. 2002. Experimental test of the role of mammalian herbivores on old field succession: community structure and seedling survival. Journal of the Torrey Botanical Society 129:228-237.

Cipollini, D., and B. Gruner. 2007. Cyanide in the chemical arsenal of garlic mustard, *Alliaria petiolata*. Journal of Chemical Ecology 33:85-94.

Cole, P.G., and J.F. Weltzin. 2005. Light limitation creates patchy distribution of an invasive grass in eastern deciduous forests. Biological Invasions 7:477-488.

Côté, S.D., T.P. Rooney, J.P. Tremblay, C. Dussault, and D.M. Waller. 2004. Ecological impacts of deer overabundance. Annual Review Ecology Evolution and Systematics 35:113-147.

Crawley, M.J., P.H. Harvey, and A. Purvis 1996. Comparative ecology of the native and alien floras of the British Isles. Philosophical Transactions of the Royal Society of London, Series B – Biological Sciences 351:1251-1259.

Davis, A.S., D.A. Landis, V. Nuzzo, B. Blossey, E. Gerber and H.L. Hinz. 2006. Demographic models inform selection of biocontrol agents for garlic mustard (Alliaria petiolata). Ecological Applications 16:2399-2410.

Gibson, D.J., G. Spyreas, and J. Benedicta. 2002. Life history of *Microstegium vimineum* (Poaceae), an invasive grass in southern Illinois. Journal of the Torrey Botanical Society 129:207-219.

Gross, K.L., G.G. Mittelbach, and H.L. Reynolds. 2005. Grassland invasibility and diversity: responses to nutrients, seed input, and disturbance. Ecology 86:476-486.

Hanzawa, F.M., and S. Kalisz. 1993. The relationship between age, size and reproduction in *Trillium grandiflorum*. American Journal of Botany 80:405-410.

Haribal, M.J., and A.A. Renwick. 1998. Isovitexin 6''-O-ß-D-glucopyranoside: a feeding deterrent to *Pieris napi oleracea* from *Alliaria petiolata*. Phytochemistry 47:1237-1240.

Haribal, M.J., and A.A. Renwick. 2001. Seasonal and population variation in flavonoid and alliarinoside content of *Alliaria petiolata*. Journal of Chemical Ecology 27:1585-1594.

Hobbs, T.N. 1996. Modification of ecosystems by ungulates. The Journal of Wildlife Management 60:695-713.

Hurlbert, S.H. 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs 54:187-211.

Kellogg, C.H., and S.D. Bridgham. 2004. Disturbance, herbivory, and propagule dispersal control dominance of an invasive grass. Biological Invasions 6:319-329.

Kennedy, T.A., S. Naeem, K.M. Howe, J.M.H. Knops, D. Tilman, and P. Reich. 2002. Biodiversity as a barrier to ecological invasion. Nature 417:636-638.

Knight, T.M. 2003. Effects of herbivory and its timing across populations of *Trillium grandiflorum* (Liliaceae). American Journal of Botany 90:1207-1214.

Knight, T.M. 2004. The effects of herbivory and pollen limitation on a declining population of *Trillium grandiflorum*. Ecological Applications 14:915-928.

Knight, T.M., H. Caswell, and S. Kalisz. In press. Population growth rate of a common understory herb decreases non-linearly across a gradient of deer herbivory. Forest Ecology and Management.

Levine, J.M., M. Vila, C.M. D'Antonio, J.S. Dukes, K. Grigulis, and S. Lavorel. 2003. Mechanisms underlying the impacts of exotic plant invasions. Proceedings of the Royal Society of London, Series B – Biological Sciences 270:775-781.

MacDougall, A.S., and R. Turkington. 2005. Are invasive species the drivers or passengers of change in degraded ecosystems? Ecology 86:42-55.

McShea, W.J., and J.H. Rappole. 1997. Herbivores and the ecology of forest understory birds. Pp. 298-309 *in* W.J. McShea, H.B. Underwood, and J.H. Rappole, eds., The Science of Overabundance: Deer Ecology and Population Management. Smithsonian Institution Press, Washington, D.C.

McShea, W.J., H.B. Underwood, and J.H. Rappole. 1997. The Science of Overabundance: Deer Ecology and Population Management. Smithsonian Institution Press, Washington, D.C.

Mitchell, C.E, and A.G. Power. 2003. Release of invasive plants from fungal and viral pathogens. Nature 421:625-627.

Morrison, J.A., H.A. Lubchansky, K.E. Mauck, K.-M. McCartney, and B. Dunn. 2007. Ecological comparison of two co-invasive species in eastern deciduous forests: *Alliaria petiolata and Microstegium vimineum.* The Journal of the Torrey Botanical Society 134:1-17.

National Invasive Species Council. National management plan 2008-2012 draft document. Available online <http://www.invasivespeciesinfo.gov/council/nmp.shtml>.

Nuzzo, V.A. 1999. Invasion pattern of the herb garlic mustard (*Alliaria petiolata*) in high quality forests. Biological Invasions 1:169-179.

Oksanen, L. 2001. Logic of experiments in ecology: is pseudoreplication a pseudoissue? Oikos 94:27-38.

Oswalt, C.M., and S.N. Oswalt. 2007. Winter litter disturbance facilitates the spread of the nonnative invasive grass Microstegium vimineum (Trin.) A. Camus. Forest Ecology and Management 249:199-203.

Parker, J.D., D.E. Burkepile, and M.E. Hay. 2006. Opposing effects of native and exotic herbivores on plant invasions. Science 331:1458-1460.

Pimentel, D., R. Zuniga, and D. Morrison. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. Ecological Economics 52:273-288.

Rooney, T.P., and K. Gross. 2003. A demographic study of deer browsing impacts on *Trillium grandiflorum*. Plant Ecology 168:267-277.

Rooney, T.P., and D.M. Waller. 2003. Direct and indirect effects of white-tailed deer in forest ecosystems. Forest Ecology and Management 181:165-176.

Rossell, C.R., S. Patch, and S. Salmons. 2007. Effects of deer browsing on native and nonnative vegetation in a mixed oak-beech forest on the Atlantic coastal plain. Northeastern Naturalist 14:61-72.

Russell, F.L., D.B. Zippin, and N.L. Fowler. 2001. Effects of white-tailed deer (*Odocoileus virginianus*) on plants, plant populations and communities: a review. American Midland Naturalist 146:1-26.

Shea, K., and P. Chesson. 2002. Community ecology theory as a framework for biological invasions. Trends in Ecology and Evolution 17:170-176.

Stachowicz, J.J., R.B. Whitlatch, and R.W. Osman. 1999. Species diversity and invasion resistance in a marine ecosystem. Science 286:1577-1579.

Stowe, K.A., R.J. Marquis, C.G. Hochwender, and E.L. Simms. 2000. The evolutionary ecology of tolerance to consumer damage. Annual Review of Ecology and Systematics 31:565-595.

Sutherland, S. 2004. What makes a weed a weed: life history traits of native and exotic plants in the USA. Oecologia 141:24-39.

Vavra, M., C.G. Parks, and M.J. Wisdom. 2007. Biodiversity, exotic plant species, and herbivory: the good, the bad, and the ungulate. Forest Ecology and Management 246:66-72.

Vaughn S.F., and M.A. Berhow. 1999. Allelochemicals isolated from tissues of the invasive weed garlic mustard. Journal of Chemical Ecology 25:2495-2504.

Vitousek, P.M., C.M. D'Antonio, L.L. Loope, and R. Westbrooks. 1996. Biological invasions as global environmental change. American Scientist 84:218-228.

Wardle, D.A., G.M. Barker, G.W. Yeates, K.I. Bonner, and A. Ghani. 2001. Introduced browsing mammals in New Zealand natural forests: aboveground and belowground consequences. Ecological Monographs 71:587-614.

Webster, C.R., M.A. Jenkins, and J.H. Rock. 2005. Long-term response of spring flora to chronic herbivory and deer exclusion in Great Smoky Mountains National Park, USA. Biological Conservation 125:297-307.

Williamson, M. 1996. Biological Invasions. Chapman and Hall, London.

Witmer, G.W., and D.S. deCalesta. 1991. The need and difficulty of bringing the Pennsylvania deer herd under control. Proceedings of the Eastern Wildlife Damage Control Conference 5:130-237.