

Special Issue: Interactions Between White-Tailed Deer and Invasive Plants in North American Forests

Research Article

Interactive effects of deer exclusion and exotic plant removal on deciduous forest understory communities

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Received: 3 September 2016 **Editorial decision:** 16 August 2017 **Accepted:** 1 September 2017 **Published:** 7 September 2017

Guest Editor: Bernd Blossey

Citation: Bourg NA, McShea WJ, Herrmann V, Stewart CM. 2017. Interactive effects of deer exclusion and exotic plant removal on deciduous forest understory communities. *AoB PLANTS* 9: plx046; doi: 10.1093/aobpla/plx046

Abstract. Mammalian herbivory and exotic plant species interactions are an important ongoing research topic, due to their presumed impacts on native biodiversity. The extent to which these interactions affect forest understory plant community composition and persistence was the subject of our study. We conducted a 5-year, 2 × 2 factorial experiment in three mid-Atlantic US deciduous forests with high densities of white-tailed deer (*Odocoileus virginianus*) and exotic understory plants. We predicted: (i) only deer exclusion and exotic plant removal in tandem would increase native plant species metrics; and (ii) deer exclusion alone would decrease exotic plant abundance over time. Treatments combining exotic invasive plant removal and deer exclusion for plots with high initial cover, while not differing from fenced or exotic removal only plots, were the only ones to exhibit positive richness responses by native herbaceous plants compared to control plots. Woody seedling metrics were not affected by any treatments. Deer exclusion caused significant increases in abundance and richness of native woody species >30 cm in height. Abundance changes in two focal members of the native sapling community showed that oaks (*Quercus* spp.) increased only with combined exotic removal and deer exclusion, while shade-tolerant maples (*Acer* spp.) showed no changes. We also found significant declines in invasive Japanese stiltgrass (*Microstegium vimineum*) abundance in deer-excluded plots. Our study demonstrates alien invasive plants and deer impact different components and life-history stages of the forest plant community, and controlling both is needed to enhance understory richness and abundance. Alien plant removal combined with deer exclusion will most benefit native herbaceous species richness under high invasive cover conditions while neither action may impact native woody seedlings. For larger native woody species, only deer exclusion is needed for such increases. Deer exclusion directly facilitated declines in invasive species abundance. Resource managers should consider addressing both factors to achieve their forest management goals.

Keywords: Exotic plants; forest management; herbivory; invasive species; species richness; temperate forest; ungulates; white-tailed deer.

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Introduction

Two major ecological factors influencing forest composition and structure in many parts of the world today are foraging by large herbivores and invasion by exotic plant species. In particular, the impacts of deer species (Cervidae) on forest structure and regeneration are an issue worldwide – e.g. in North America (McShea et al. 1997); British woodlands (Fuller and Gill 2001; Gill and Morgan 2010); Japanese broad-leaved forests (Koda et al. 2008; Takatsuki 2009); and southern beech (*Nothofagus*) and temperate rainforests of New Zealand (Bellingham and Allan 2003; Husheer et al. 2003).

In eastern North America, native white-tailed deer (hereafter, deer) have increased dramatically over the past 50 years (McCabe and McCabe 1997; McShea et al. 1997; Russell et al. 2001) due to the convergence of many factors, including the loss of natural predators, reduction of hunting, increases in favourable habitat in agricultural, rural and suburban areas, and forestry practices (Anderson 1997; Rooney and Waller 2003; Côté et al. 2004; McShea 2005; McShea 2012). Over the same period, exotic invasive species have emerged as great threats to native biodiversity worldwide; their ability to alter the structure, composition and function of native natural communities makes them major ecological drivers of global change (Vitousek et al. 1996; Wilcove et al. 1998; Mack et al. 2000; Pimentel et al. 2005). Whether phenomena such as competitive displacement of long-term resident species, changes in local (α) diversity or homogenization of global (β) diversity are due to alien species is controversial (Davis 2003, 2009). Although deer and exotic plants occupy different trophic levels, their presence can affect forest floor microenvironments for native plants in similar ways through alterations in soil attributes and changes in light levels (Ehrenfeld et al. 2001; Rooney 2001; Gilliam 2007; Heckel et al. 2010). Indeed, deer can cause evolutionary responses in traits of unpalatable species via such non-trophic indirect effects (Heckel and Kalisz 2016). Deer can directly affect the ecological community through selective browsing, while invasive plant species can reduce survival of native species due to competition for resources and changes in microenvironment (Ehrenfeld and Scott 2001; Maron and Vila 2001; Keane and Crawley 2002; Rodgers et al. 2008; Waller and Maas 2013). Vavra et al. (2007) have highlighted the compounding influence of invasive plant species and generalist herbivores on native plant communities.

Metanalyses have shown negative effects on invasive plant performance and biotic resistance to exotic plant invasion due to native herbivores (Levine et al. 2004; Parker et al. 2006), but these studies had limitations (e.g. little breadth in habitat types included (only

3 of 27 studies in forest) and inability to examine specific herbivores such as deer, respectively). Most recently, a meta-analysis of community-level effects of deer on North American understory plants by Habeck and Schultz (2015) determined that the woody plant community responded positively to deer exclusion while the herbaceous community did not, and suggested that non-native species replacement, legacy effects of chronic deer overabundance and inadequate diversity metrics might be responsible for the lack of response in the herb layer.

Invasive plant species are also more common in disturbed habitats (Hobbs 2000; Knight et al. 2009; Jauni et al. 2015), and deer may create disturbance microenvironments through their foraging and bedding activities. While deer herbivory may promote the invasion of exotic species (Relva et al. 2010), most exotic species are palatable to deer and compose some portion of their daily forage (Erickson et al. 2017, this issue). Indeed, Rossell et al. (2007) found deer foraging suppressed the abundance of both exotic and native vegetation at a site in Washington, DC, while Dávalos et al. (2014) showed that direct and indirect deer impacts overrode all other factors, including non-native vegetation, in affecting the demographic metrics of four rare herbaceous understory species. With disturbance promoting both increased numbers of deer and exotic plant species, forests become depleted of native species but experience increased biomass of deer and exotic species (Knight et al. 2009). Once exotic plants form a significant portion of the diet of deer, their removal does not remove the deer's forage requirements and can lead to increased foraging on native plants (Stromayer et al. 1998). Intentional reduction of deer populations is an increasingly common prescription within eastern forests to restore forest succession and re-establish valuable tree species such as oaks (*Quercus* spp.) (Morrissey et al. 2010), yet the extent to which such efforts can succeed without also controlling exotic invasive plants is uncertain. The conversion of basal area dominance within many eastern deciduous forests from oaks to red maple (*Acer rubrum*) is partly due to changes in fire policy and land use, but also to preferential browsing by deer (McShea et al. 2007; Nowacki and Abrams 2008; McEwan et al. 2011). Oak seedlings are slow growing and need high light levels to progress to the sapling stage, a condition not present in forests with closed canopies or abundant ground cover (Dey 2002), compounding the foraging impacts from deer. Maple seedlings are more tolerant of closed canopies and deer herbivory and are increasing in dominance in eastern forests (McEwan et al. 2011).

To test the interactive effects of deer and invasive plants on native forest plant communities, we performed an experiment over multiple (5) seasons at three study sites with chronic high densities of both white-tailed

deer and invasive plant species. We predicted that: (i) only deer exclusion and exotic plant removal in tandem would yield increases in native plant species richness and abundance; (ii) the short-term effect of deer exclusion alone on woody plant life stages would depend on invasive plant initial abundance levels – low initial invasive abundances would result in increases under deer exclusion, while high initial invasive abundances would not (the associational resistance hypothesis; see Palmer et al. 2003; Bee et al. 2009); (iii) reported shifts in abundance of two common tree species groups – decreases in oaks and increases in maples (specifically, red maple) – will be reversed by the experimental reduction of deer and invasive plants; and (iv) deer exclusion alone would decrease exotic plant abundance over time.

Methods

Study sites, plot selection and experimental design

The three study sites were distributed over 90 km and included the Smithsonian Conservation Biology Institute of the National Zoological Park in Front Royal, VA (SCBI),

Great Falls National Park, VA (GF) and the Goldmine tract of the Chesapeake and Ohio Canal National Historical Park, MD (CHOH) (Fig. 1). Autumn deer density surveys conducted annually using the distance-sampling technique (Buckland et al. 2005; Lovely et al. 2013) from 2004 to 2006 yielded means of 28.9 deer km⁻² at GF, 42.4 deer km⁻² at CHOH (Bates 2007) and 34 deer km⁻² at SCBI (Heckel et al. 2010; Bourg et al. 2013). Such population densities are substantially above the 20 deer km⁻² level whereby management actions are recommended to prevent detrimental ecological community impacts in this region, based on Tilghman (1989). Exotic invasive plants are common and pervasive throughout all three sites, with *Microstegium vimineum*, *Alliaria petiolata* (garlic mustard) and *Lonicera japonica* (Japanese honeysuckle) being the most frequently encountered species.

In May 2005, 323 plot locations were identified with a GIS-stratified random point generator: 130 plots in GF, 100 plots in CHOH and 93 plots in SCBI (Fig. 1). Criteria for eligible plot locations were slopes of <20 % within upland oak- or American beech (*Fagus grandifolia*)-dominated habitat, canopy coverages of 70 % or greater as

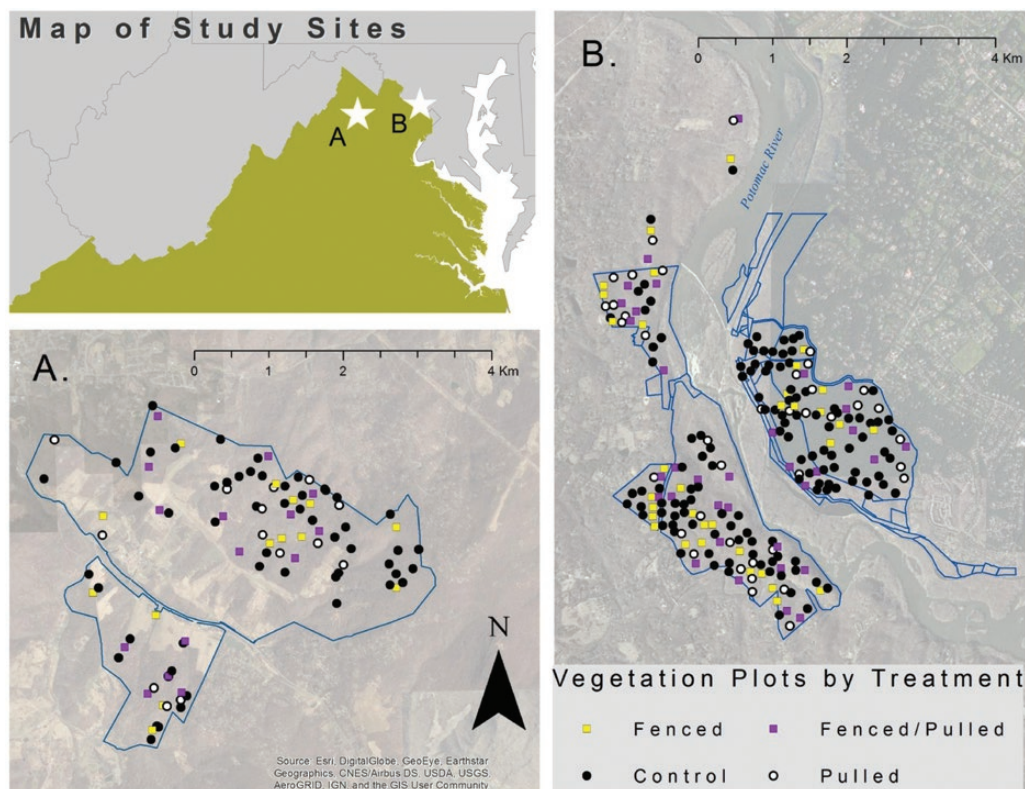


Figure 1. Map of the study sites, showing the general location of the SCBI (white star A) and the Great Falls National Park, VA (GF) and Goldmine tract of the Chesapeake and Ohio Canal National Historical Park, MD (CHOH) (white star B) sites in the upper left inset; and (A) distribution of study plots by treatment at SCBI; (B) distribution of study plots by treatment at GF (on left side of Potomac River) and at CHOH (right side).

estimated by densiometer measurements, lying at least 50 meters (m) from another plot, and not on a habitat boundary. Since Japanese stiltgrass was by far the most abundant invasive species in our study plots, we used its baseline survey values as a measure of initial invasive cover in this study; henceforth, initial invasive cover refers to per cent cover of Japanese stiltgrass, which was estimated with the same methods and cover categories as described for graminoids in the vegetation sampling section that follows below. However, in order to examine initial invasive cover as a variable in the analyses, these categories were condensed into two (i.e. low (≤ 25 % cover) and high (> 25 % cover)), so that we had an adequate number of plots distributed across all treatments. Furthermore, to strengthen the ability to detect differences in the manipulative treatments from the control plots, we intentionally assigned many more plots to the control group than the other treatments. Achieving adequate plot representation in all treatments also necessitated that we drop the threshold cut-off between the low and high categories to 25 %. This cover threshold was chosen due to the fact that a disproportionate share of the study plots had under 50 % initial invasive cover. This yielded the following distribution of plots to be used in examining the effect of initial invasive cover in the analyses: control – 176 plots (134 low, 42 high), fenced – 47 plots (23 low, 24 high), pulled – 53 plots (25 low, 28 high) and fenced/pulled – 47 plots (23 low, 24 high) for a total of 323 plots. At the end of the 2005 growing season, a 2×2 factorial experimental design was installed that assigned four treatments within each group: control, fenced only (fenced), invasive plant species hand-pulled only (pulled) and both fenced and invasive plant species hand-pulled (fenced/pulled). There were 60 control, 23 fenced, 24 pulled and 23 fenced/pulled at GF; 65 control, 10 fenced, 15 pulled and 10 fenced/pulled at CHOH; and 51 control, 14 fenced, 14 pulled and 14 fenced/pulled at SCBI. Fence integrity was maintained by twice yearly checks of all fenced plots through the 2009 growing season. In each year from 2006 to 2009, exotic plant species were hand-pulled from 100 plots (47 in GF, 25 in CHOH and 28 in SCBI). Early season invasive plants were removed in April and May and all plots were revisited in August to remove late season invasive plants. Thorough hand-pulling was first performed in late summer of the initial study year after the baseline vegetation surveys were completed.

Each plot contained an internal 4×4 m sapling square, within which four replicate 1×1 m quadrats, whose corners were located 1 m from the plot centre on each cardinal direction, were also placed. Five permanent stakes made from 1.25 cm diameter PVC pipe, marking the plot centre point and the proximal corner of each 1

m sampling quadrat, were installed at each plot. Plots that received the fencing treatment had their fences installed along the 4×4 m perimeter. Fencing was 2.4 m high plastic mesh (5×5 cm) that was anchored with zip-ties to 2.6 m metal t-bar posts on each corner. The bottom of the fence was staked to the ground but the mesh was sliced at ground level to allow access by small mammals < 1 kg in weight. Treatment manipulations were applied to an entire given 4×4 m plot, which was designated as the experimental unit.

Vegetation sampling

Baseline surveys for all vascular plants were conducted during the growing season of 2005 in the GF, CHOH and SCBI plots. Per cent tree canopy cover at each plot was estimated using a Forestry Suppliers spherical crown densiometer, convex Model A, at plot centre. During the 2007 and 2009 growing seasons, each plot was resurveyed once for all vascular plants. In all sampling years, the identity to species and abundance (number of individuals) of all forbs were recorded within each 1×1 m quadrat, except those with > 20 individuals, which were placed in abundance classes (i.e. 21–50; 51–100; and > 100 individuals). For ferns and graminoids (grasses and sedges), per cent cover in each 1 m^2 quadrat was ocularly estimated into one of four classes (1–10%; 11–25%; 26–75%; 76–100%). Woody seedlings were also surveyed in the 1 m^2 quadrats and were defined as any woody species ≤ 30 cm in height. Woody stems > 30 cm and < 2 m in height, which included tree saplings, shrubs and woody vines, were identified and counted in the entire 16 m^2 plot and hereafter will be termed collectively large woody species (LWS). Sapling counts were extracted from this group and defined as all species capable of assuming a tree form > 2 m in height. Plants that could not be identified to species were determined to genus, family or morphospecies. Those plants whose taxonomic identity could still not be determined were recorded as unknowns and not used in calculations of plant community metrics; these comprised 1038 of 29145 total records (3.6 %). Herbaceous species were defined as all forbs, graminoids and ferns. Data are stored at the Smithsonian Conservation Biology Institute and are available from authors N.A.B. or W.J.M. upon request.

Data analyses

Species richness, the number of stems for woody seedlings, LWS and saplings, respectively, and the number of stems of oak and maple individuals were calculated for all native species found in each plot in each survey year. To obtain values for herbaceous plants and woody species < 30 cm in height, the data for the four 1 m^2 quadrat samples in each plot were pooled for species richness and summed for species abundances;

therefore, analyses for these two plant groups apply to a 4 m² plot size. Abundance values for invasive plant species were compiled only for the control and fenced plots (where hand removal never occurred). For herbaceous species (forbs) where >20 individuals were counted, the minimum value of the estimated abundance class was scored to be conservative when testing for treatment differences. The per cent cover of Japanese stiltgrass, which was by far the most common (both in per cent cover and number of individuals) invasive species, was also estimated in the control and fenced plots by using the midpoint of its coverage class in each quadrat and calculating an average value for the plot.

A generalized linear model based on a negative binomial distribution (identified as fitting our count data better than the Poisson distribution by a goodness of fit test; function 'glm.nb' in R package 'MASS'; Venables and Ripley 2002) was used to confirm that species richness and abundance measurements did not differ between treatments at the beginning of the survey. Species richness or abundance was the dependent variable and treatment the fixed effect. The model was compared to its equivalent null model (no fixed effect) using a likelihood ratio test (LRT; function 'anova'). Chi-squared (X^2) values with degrees of freedom in parentheses followed by the *P*-value are reported.

For the analyses in this paper, the change in species richness or abundance between 2005 and 2009 was calculated as the response variable for each plant community group by simple subtraction (as per cent change would generate the loss of plots that had a species richness equal to zero at the beginning of the survey). Linear mixed models (function 'lmer' in R package 'lme4') were then fitted on the change values (response variable) using treatment only (TRT), initial invasive cover only (InvCov) and the interaction of treatment and invasive cover (TRT * InvCov) as fixed effects and site as a random effect. An LRT (using function 'anova' in R package 'stats') was performed to compare the models between each other as well as the equivalent null model (no fixed effect). The best model was chosen by examining the *P*-value of the test as well as the Akaike Information Criterion (AIC) of the models. Histograms and q-q plots were made to check normality of the residuals, keeping in mind that since the change was a discrete variable, the residuals could at best be approximately normal. When the AICs between two models were very close, we picked the model for which the distribution of the residuals was closer to normal, or if both distributions were close, the model with least number of parameters. The chi-squared values of the LRT along with degrees of freedom in parentheses followed by the *P*-value are reported in the text and the AICs are reported in the tables. When treatment had a significant effect on

change in species richness or abundance, Tukey–Kramer pairwise multiple comparison tests were performed (using functions 'lsmeans' and 'contrast' in R package 'lsmeans') to determine which of the treatments were responsible for the significance. When treatment and initial invasive cover were both significant factors, the effect of treatment for plots with low and high initial invasive cover was tested separately using linear mixed models and pairwise comparison in the manner described above.

Change in species richness was analysed for the following plant groups: native herbaceous species, native woody seedlings, native LWS and native saplings, and invasive species. Change in abundance was analysed for native woody seedlings, native LWS, native saplings, oak and maple stems, non-graminoid invasive species and Japanese stiltgrass. For stiltgrass, a binomial distribution gave the best fit and was therefore used for the baseline survey comparison ('glm' function). A significance level of 0.05 was used for all tests.

Results

Although the study sites differed in their overall species richness (SCBI – 25 sapling species, 18 large woody shrub and vine (LWS) species, 68 woody species detected at the seedling stage and 168 herbaceous species; GF – 27, 27, 74 and 107 species; and CHOH – 8, 12, 36 and 73 species, respectively), treatments responded similarly across sites over the course of the study and thus site was included as a random effect in our models. We focused the remaining description of results on significant treatment and initial invasive cover effects over time.

Initial survey conditions

Initial species richness or abundance in the study plots never significantly differed between treatments, except for (i) maple seedlings – abundance was significantly higher in control plots at the beginning of the survey; and (ii) Japanese stiltgrass – per cent cover was significantly higher in fenced plots at the beginning of the survey [see Supporting Information—Table S1]. However, for the latter, the significance was lost when plots with low and high initial invasive cover were analysed separately.

Native herbaceous species

The treatment by initial invasive cover interaction model best explained the change in native herbaceous species richness ($X^2 = 16.59$, $df = 4$, $P = 0.002$; Table 1). After separating plots by amount of initial invasive cover, treatment was a factor only in plots with high initial invasive cover (Table 2), where the increase in herbaceous richness was significantly greater in fenced/pulled plots than control plots ($P = 0.017$; Fig. 2). The fenced/

Table 1. Results of LRTs between mixed linear models to test if treatment only (TRT), initial invasive cover only (InvCov), the interaction of treatment and invasive cover (TRT * InvCov) or the null model (Null) explain change in species richness or abundance in study plots. Also given are the AIC and the AIC of the null models (AIC_{null}). When model without fixed effect (null model) is selected, the smallest *P*-value is reported.

Variable	Plant group	n	Fixed effect best model	AIC (AIC _{null})	Chi-squared (df)	<i>P</i>	
Species richness	Native herbaceous	323	TRT * InvCov	1516.8 (1540.1)	16.59 (4)	0.002	
	Native woody seedlings	323	InvCov	1532.7 (1558.6)	26.17 (1)	<0.0001	
	LWS	323	TRT	1166.6 (1237.8)	66.62(2)	<0.0001	
	Saplings	323	TRT * InvCov	860.73 (914.34)	10.99 (4)	0.027	
	Invasive species	163	Null	-----	-----	All > 0.33	
Species abundance	Native woody seedlings	323	InvCov	3084.7 (3092.4)	9.63 (1)	0.002	
	LWS	323	TRT	2309.9 (2335.0)	29.84 (2)	<0.0001	
	Saplings	323	TRT * InvCov	1733.4(1767.1)	11.59 (4)	0.020	
	Oak regeneration	135	TRT * InvCov	961.73 (986.44)	12.30 (4)	0.015	
	Oak seedlings	135	TRT * InvCov	953.4 (976.0)	12.16 (4)	0.016	
	Oak saplings	135	TRT	399.7 (401.90)	7.27 (2)	0.026	
	Maple regeneration	224	TRT	1503.8 (1507.9)	9.31 (2)	0.010	
	Maple seedlings	224	TRT	1502.5 (1506.4)	9.02 (2)	0.011	
	Maple saplings	224	Null	-----	-----	All > 0.17	
	Non-graminoid invasive species	163	InvCov	1902.6 (1914.2)	13.00 (0)	<0.0001	
	Per cent cover	Japanese stiltgrass	153	TRT * InvCov	-97.366 (-69.690)	18.89 (2)	<0.0001

Significant *P* values are in bold text.

Table 2. Results of LRTs for low and high initial invasive cover when best model was TRT * InvCov. Also given are the AIC and the AIC of the null models (AIC_{null}).

Variable	Plant group	Initial invasive cover	n	AIC (AIC _{null})	Chi-squared (df)	<i>P</i>
Species richness	Native herbaceous	L	205	899.49 (896.57)	3.07 (3)	0.38
		H	118	604.64 (608.08)	9.44 (3)	0.02
	Saplings	L	205	471.26 (491.67)	26.415 (3)	<0.0001
		H	118	374.36 (393.73)	25.364 (3)	<0.0001
Species abundance	Saplings	L	205	840.21 (859.49)	25.28 (3)	<0.0001
		H	118	736.5 (745.3)	15.10 (3)	0.002
	Oak regeneration	L	105	760.79 (784.35)	29.55 (3)	<0.0001
		H	130	194.59 (191.23)	2.64 (3)	0.45
	Oak seedlings	L	135	753.68 (775.42)	27.74 (3)	<0.0001
		H	30	194.47 (191.19)	2.71 (3)	0.44
Per cent cover	Japanese stiltgrass	L	98	-246.99 (-248.65)	0.23 (1)	0.63
		H	65	18.20 (24.40)	8.20 (1)	0.004

Significant *P* values are in bold text.

pulled treatment did not significantly differ from either the fenced only or pulled only treatments, however, and these latter two treatments were also not different from

the control plots. The number of species in all treatments and the control in this case increased significantly by 2009 ($P < 0.02$).

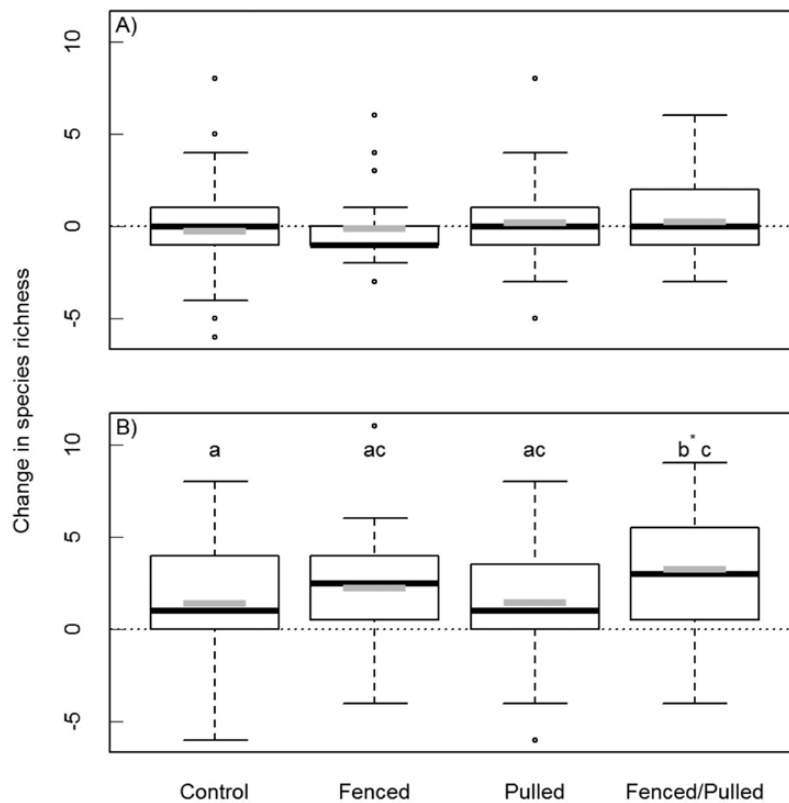


Figure 2. Change in native herbaceous species richness per plot for the four treatment types under low (A) and high (B) initial invasive species cover conditions. Box and whisker plot displays the median (bold black line), mean (gray bar), first and third quartiles (bottom and top of box), the lowest and highest datum still within 1.5 times the interquartile range below and above the quartiles (whiskers), and the outlier data points (open circles). Treatments without letters or sharing the same letters are not significantly different, and treatments not sharing the same letters are significantly different from one another. Asterisks following letters indicate significant difference levels of the respective treatment from other treatments; asterisk groups separated by commas refer to significant differences between treatments moving from left to right on the graphs. * $P < 0.05$.

In terms of functional group composition of the native herbaceous community, 84.1 % of the species recorded were perennials, 2.1 % were biennials, 9.0 % were annuals and 4.8 % could not be assigned because they were identified only to the genus level or above. Moreover, of the top 10 most frequently recorded native herbs at the beginning and end of the study, respectively, all but one species were perennials (Table 3). Only three of the species became less frequent, and control plots had a substantially lower average increase for these species (as measured by per cent change in number of plots recorded) than the other treatments (Table 3). Lastly, these species did not respond uniformly to the experimental manipulations: only 1 species (*Polystichum acrostichoides*) had its greatest positive per cent change in control plots, whereas 4 (*Circaea lutetiana*, *Arisaema triphyllum*, *Galium circaezans*, *Verbesina occidentalis*) responded most positively in the fenced plots, 3 (*Viola* sp. 1, *Oxalis* sp., *Polygonum virginianum*) in the pulled plots and 4 (*Pilea pumila*, *Galium triflorum*, *Stellaria*

pubera, *Botrypus virginianus*) in the fenced/pulled plots (Table 3).

Native woody seedlings

There was no effect of treatment on the change in native woody seedling species richness. However, there was an effect of initial invasive cover ($\chi^2 = 26.17$, $df = 1$, $P < 0.0001$; Table 1). Although woody species richness increased in plots that were lightly invaded initially (mean_{start} = 6.21 ± 2.82 (mean \pm SD); mean_{end} = 6.98 ± 3.13 ; estimated mean change = 0.85 ± 0.32 ; t -value = 2.67), the effect was stronger in plots that were highly invaded at the onset of the study (mean_{start} = 5.26 ± 2.74 ; mean_{end} = 7.92 ± 3.39 ; estimated difference in change = 1.69 ± 0.32 ; t -value = 5.23).

Similarly, analysis of the change in abundance of native woody seedlings showed no effect of treatment, yet there was once again a significant effect of initial invasive cover ($\chi^2 = 9.63$, $df = 1$, $P = 0.002$; Table 1). Woody seedling abundances increased significantly more in plots that

Table 3. The top native herbaceous species, as measured by the number of occurrence records in plots, in the survey years of 2005 and 2009, respectively. Seven species occurred in the top 10 in both survey years; those that were unique to the top 10 in only one of the years are listed with the year in superscript after their name, for a total of 13 species. Species are listed in decreasing order of abundance in the baseline survey year of 2005. Also shown are growth habit and the per cent change in occurrence between years in control and treatment plots.

Species	# Records 2005	# Records 2009	Growth habit	Per cent change				
				Control	Fenced	Pulled	Fenced/pulled	Mean change
<i>Viola</i> sp. 1	328	397	P	2.0	8.0	13.2	6.4	7.4
<i>Circaea lutetiana</i>	176	205	P	-2.4	11.2	2.8	10.1	5.4
<i>Arisaema triphyllum</i>	93	105	P	0.9	2.7	-1.4	2.1	1.1
<i>Oxalis</i> sp.	84	130	P	2.7	1.6	10.8	0.5	3.9
<i>Pilea pumila</i>	80	112	A	-0.3	-2.1	8.5	10.6	4.2
<i>Polystichum acrostichoides</i>	78	75	P	0.6	0.0	-1.9	-1.6	-0.7
<i>Galium circaeans</i>	71	114	P	0.7	7.4	7.1	4.8	5.0
<i>Galium triflorum</i> ²⁰⁰⁵	66	55	P	-1.7	-3.7	0.9	3.2	-0.3
<i>Verbesina occidentalis</i> ²⁰⁰⁵	53	55	P	-0.3	1.6	0.5	0.0	0.4
<i>Solidago</i> sp. 1 ²⁰⁰⁵	52	28	P	-2.1	-2.1	0.0	-2.7	-1.7
<i>Stellaria pubera</i> ²⁰⁰⁹	49	84	P	3.1	0.5	1.9	4.3	2.4
<i>Botrypus virginianus</i> ²⁰⁰⁹	48	73	P	1.0	2.7	1.9	4.8	2.6
<i>Polygonum virginianum</i> ²⁰⁰⁹	39	82	P	2.3	5.3	6.1	2.1	4.0
Mean change				0.5	2.5	3.9	3.4	

had high initial invasive cover (mean_{start} = 25.98 ± 27.11; mean_{end} = 45.83 ± 33.95) than in low initial invasive cover plots (mean_{start} = 30.24 ± 22.76; mean_{end} = 35.71 ± 30.62; estimated difference in change = 10.53 ± 3.4; *t*-value = 3.08).

Native LWS

The treatment model was significant for the change in species richness of native LWS ($\chi^2 = 66.62$, *df* = 2, *P* = 0.035; Table 1). The increases in species richness were significantly greater in the fenced and fenced/pulled treatments than in the control and pulled treatments, where changes were slight (Fig. 3A). There was no significant difference between the fenced and fenced/pulled treatments.

There was also a significant main effect of treatment on the change in native LWS abundance in plots ($\chi^2 = 29.84$, *df* = 2, *P* < 0.0001; Table 1). LWS stem numbers increased significantly more in the fenced and fenced/pulled treatments than in the control and pulled treatments (both *P* ≤ 0.003), where there was very little change (Fig. 3B). Again, the fenced and fenced/pulled treatments did not significantly differ from each other.

Separating out the native tree sapling component of the LWS data yielded similar results, with the treatment by initial invasive cover interaction model best explaining the change in native sapling species richness ($\chi^2 = 10.99$, *df* = 4, *P* = 0.027; Table 1). Treatment

was also significant for both initial invasive cover categories (Table 2), with only the fenced/pulled treatment having a significant increase in sapling species richness (mean_{start} = 0.40 ± 0.68; mean_{end} = 1.38 ± 1.42; mean change = 0.98 ± 0.38) over the control (mean_{start} = 0.30 ± 0.60; mean_{end} = 0.40 ± 0.82; mean change = 0.10 ± 0.79; *z*-value = 3.90, *P* < 0.001) and pulled treatments (mean_{start} = 0.19 ± 0.44; mean_{end} = 0.25 ± 0.59; mean change = 0.06 ± 0.72; *z*-value = 3.34, *P* = 0.004), where change was negligible.

The treatment by initial invasive cover interaction model also provided the best fit to the variation in the change in native sapling abundances ($\chi^2 = 11.59$, *df* = 4, *P* = 0.020; Table 1), and treatment was a significant factor for both initial invasive cover categories (Table 2). Only the fenced treatment had a significant increase in sapling abundance (mean_{start} = 0.51 ± 1.25; mean_{end} = 3.79 ± 7.10; mean change = 3.28 ± 7.18) over the control (mean_{start} = 0.47 ± 1.12; mean_{end} = 0.96 ± 2.49; mean change = 0.49 ± 2.51) and pulled treatments (mean_{start} = 0.38 ± 1.06; mean_{end} = 0.58 ± 1.38; mean change = 0.21 ± 1.72), in both low (*z*-value fenced vs. control = 2.60, *P* = 0.0442; *z*-value fenced vs. pulled = 2.66, *P* = 0.0381) and high (*z*-value fenced vs. control = 3.42, *P* = 0.0037; *z*-value fenced vs. pulled = 3.14, *P* = 0.0090) initial invasive cover.

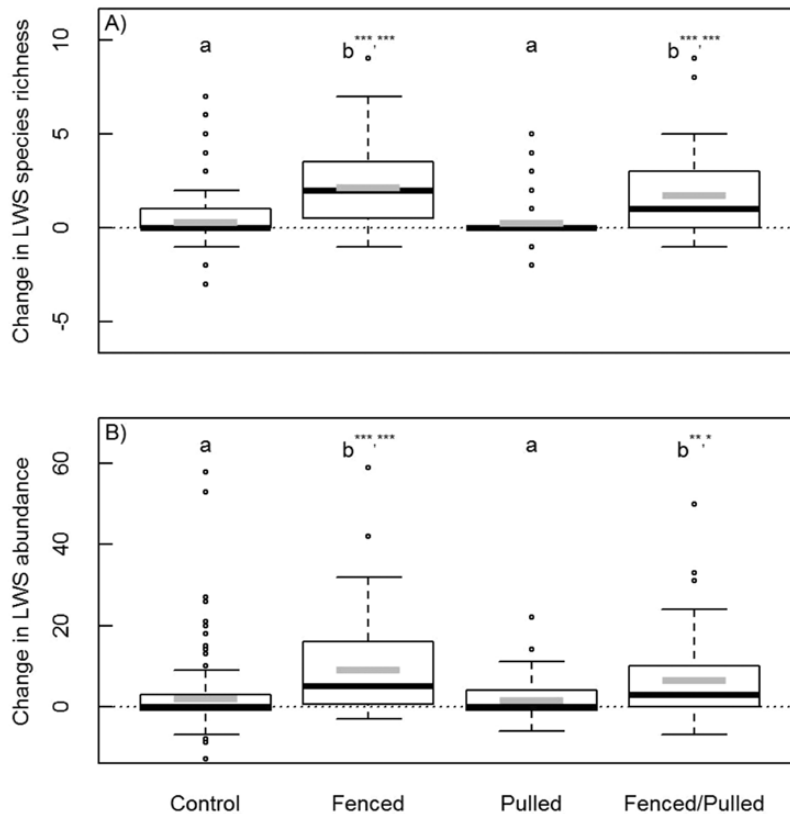


Figure 3. Change in (A) species richness and (B) abundance of native LWS per plot across treatments. Box-and-whisker plot display as described previously. Treatments without letters or sharing the same letters are not significantly different, and treatments not sharing the same letters are significantly different from one another. Asterisks following letters indicate significant difference levels of the respective treatment from other treatments; asterisk groups separated by commas refer to significant differences between treatments moving from left to right on the graphs. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Oak and maple regeneration

Change in the number of oak stems was best explained by the treatment by initial invasive cover interaction model ($\chi^2 = 12.30$, $df = 4$, $P = 0.015$; Table 1). Treatment was a significant factor only in plots with low initial invasive cover, where oak stem abundance increased in the fenced/pulled plots as compared to all other treatments (all $P \leq 0.05$; Fig. 4), which did not significantly differ from zero.

A treatment main effect model gave the best results for the change in maple stem numbers ($\chi^2 = 9.31$, $df = 2$, $P = 0.01$; Table 1); however, Tukey–Kramer pairwise comparison results indicated that all treatment pair tests were non-significant ($P > 0.05$). Stem numbers decreased slightly in the controls, increased slightly in the fenced plots and increased moderately in the pulled and fenced/pulled plots, but no changes were large enough to produce significant pairwise differences between treatments over the study period. Comparison of the AIC values for the treatment vs. null model showed that the treatment value was only slightly better, and this may explain why no significant differences

were detected in the multiple comparison tests. BIC (Bayesian Information Criterion) values were lower in the null model than the treatment model, since BIC uses a larger penalty term for adding variables to a model, i.e. overfitting (Schwarz 1978).

Invasive species

For invasive species, only control vs. fenced plots could be compared with each other. Treatment was not a significant factor in explaining changes in non-graminoid invasive plant species richness ($P > 0.33$; Table 1). Nevertheless, t -tests showed that invasive species richness increased in control plots (mean_{start} = 2.44 ± 1.91 ; mean_{end} = 2.82 ± 2.40 ; mean change = 0.38 ± 1.59 ; $t = 2.72$, $df = 127$, $P = 0.004$) but not in fenced plots (mean_{start} = 3.00 ± 1.37 ; mean_{end} = 3.09 ± 11.54 ; mean change = 0.09 ± 1.34 ; $t = 0.3338$, $df = 334$, $P = 0.35$).

Non-graminoid invasive plant abundances were also not affected by treatment, but rather initial invasive cover was a significant main effect ($\chi^2 = 13.60$, $df = 1$, $P = 0.0002$; Table 1). High initial invasive cover plots had

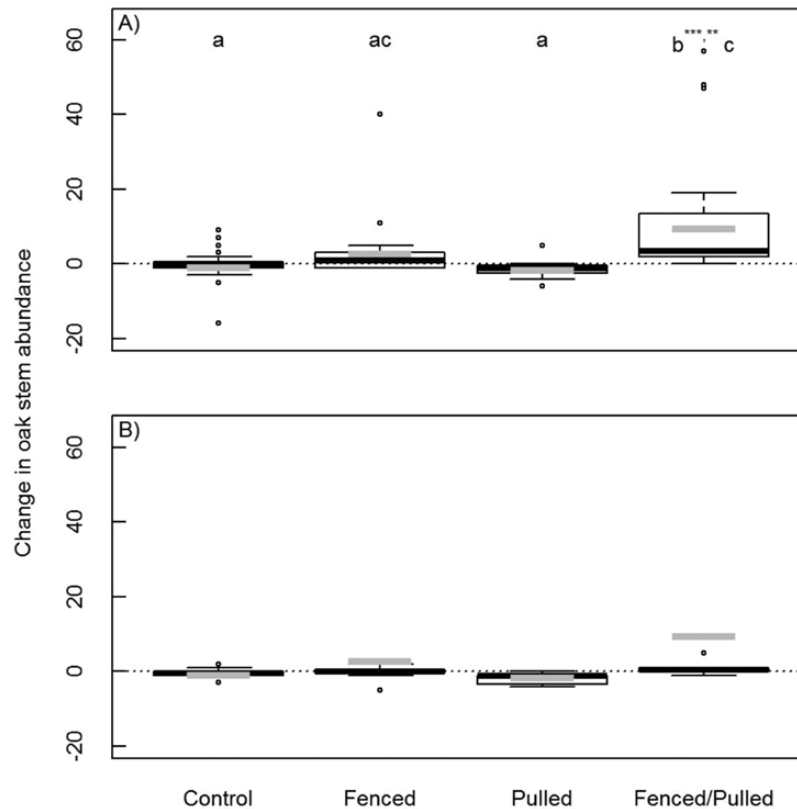


Figure 4. Change in oak stem abundances per plot across treatments, for plots in the low (A) and high (B) initial invasive cover category. Box-and-whisker plot display as described previously. Treatments without letters or sharing the same letters are not significantly different, and treatments not sharing the same letters are significantly different from one another. Asterisks following letters indicate significant difference levels of the respective treatment from other treatments; asterisk groups separated by commas refer to significant differences between treatments moving from left to right on the graphs. ** $P < 0.01$, *** $P < 0.001$.

significantly fewer non-graminoid invasive plant stems at the end of the study compared to the beginning (mean_{start} = 142.28 ± 151.14 ; mean_{end} = 61.28 ± 57.81 ; mean of change = -81.00 ± 126.2) than low initial invasive cover plots (mean_{start} = 38.44 ± 65.68 ; mean_{end} = 21.13 ± 33.82 ; mean of change = -17.31 ± 44.98 ; estimated difference = -48.37 ; SD = 12.99, t -value = -3.72).

The change in per cent cover of Japanese stiltgrass, the most common invasive species, was best explained by the treatment by initial invasive cover interaction model ($\chi^2 = 18.89$, $df = 2$, $P < 0.0001$; Table 1). The treatment effect was only significant when invasive cover was initially high, and by the end of the study there was significantly less per cent cover of Japanese stiltgrass in fenced plots than in control plots ($\chi^2 = 8.20$, $df = 1$, $P = 0.004$; Table 2 and Fig. 5).

Discussion

We designed our study to differentiate the effects of herbivores, competition from invasive exotic plants and the interaction of these two ecologically important

factors on the native understory forest plant community. We found the influence of each factor alone on native plants, as well as in combination, to be specific for different components of the plant community.

Species richness in the herbaceous plant community was impacted by both high herbivory levels and high invasive plant cover, with the combined treatment of fenced/pulled being the only one to yield significant increases over control plots. Although the fenced/pulled treatment did not differ from either the fenced or pulled treatments alone, it was the interactive effect of both excluding deer foraging and removing invasive plants that was needed to achieve increases in herbaceous species richness above the baseline, unmanipulated level in our study, since neither the fenced nor the pulled treatments differed significantly from this level (Fig. 2). This finding suggests that deer browsing and exotic plant invasion have acted in tandem to suppress native herb richness in these forests, whereas either stressor in isolation did not have a similar effect. It appears that competition with invasives inhibited species richness increases when only deer were removed, and deer herbivory did

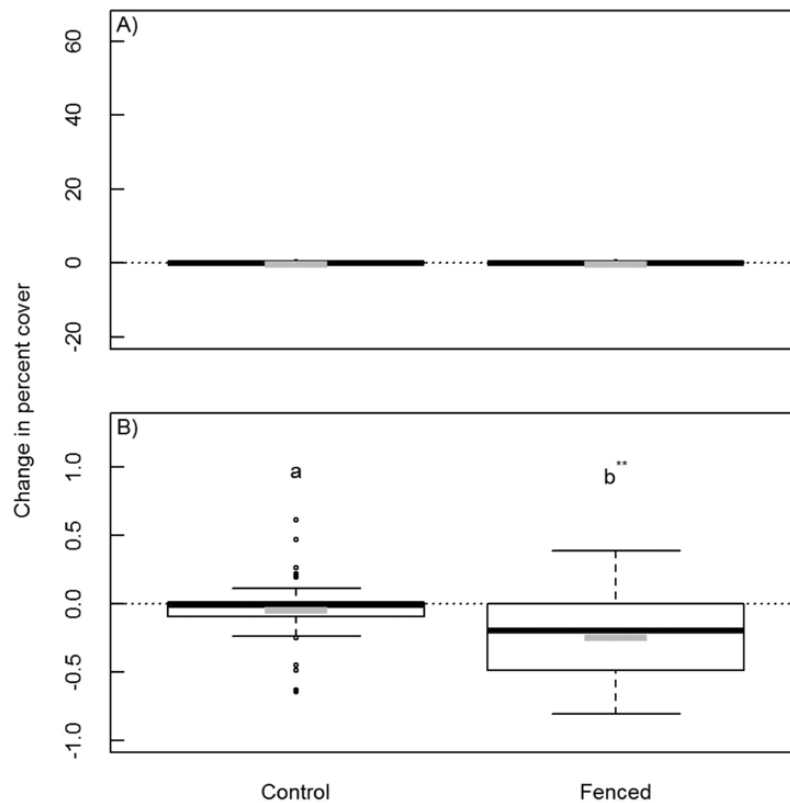


Figure 5. Change in Japanese stiltgrass abundance (measured as per cent cover) per plot across treatments under low (A) and high (B) initial invasive species cover conditions. Box-and-whisker plot display as described previously. Treatments without letters or sharing the same letters are not significantly different, and treatments not sharing the same letters are significantly different from one another. Asterisks following letters indicate significant difference levels of the respective treatment from other treatments; asterisk groups separated by commas refer to significant differences between treatments moving from left to right on the graphs. $**P < 0.01$.

the same when only invasive plants were removed from plots. Reduction in one factor did not result in significant increases in overall herb species richness at the plot level. Our assertion for the significance of the interaction of these two factors is given strong support for at least two reasons: (i) it was more than minimally significant ($P < 0.02$, rather than $P < 0.05$), and (ii) our study had nearly twice as many plots allocated to the high initial invasive cover control group (42 plots) as to the manipulative treatments of fenced (24), pulled (28) or fenced/pulled (24), thereby increasing the likelihood that any significant differences obtained against the control would be valid rather than due to a Type I error.

The above result is in contrast to earlier studies that found significant release of herbaceous plant communities in richness and diversity following removal of deer herbivory (Balgooyen and Waller 1995; Augustine et al. 1998; Webster et al. 2005; Goetsch et al. 2011; Begley-Miller et al. 2014), as well as with the findings of Aronson and Handel (2011) who showed that herb species richness increased significantly with the removal of *M. vimineum*, yet did not when it was combined

with deer exclusion. While a degree of caution should be taken with our herbaceous layer result, given that it was obtained over a relatively short study time frame (5 years) and with smaller plot sizes than some of these studies, our finding suggests that deer access and invasive plants interact to suppress the herb layer. This hypothesis was recently given strong support by Kalisz et al. (2014) who showed experimentally that overabundant deer enhanced invader's demographic success, and both interacted to depress native success.

Further examination of individual changes in the most common herbaceous species in the study plots showed that it was mainly perennial species, rather than short-lived annual or biennial species undergoing a flush of reproduction in response to invasive pulling and its associated soil disturbance, that accounted for much of the plot-level increases in species occurrences (Table 3). Additionally, responses among these most common native herbs to the treatments were species-specific, with some species responding best to deer exclusion (*C. lutetiana*, *A. triphyllum*, *G. circaeazans* and *V. occidentalis*), others having their greatest response to invasive

plant removal (*Viola* sp. 1, *Oxalis* sp. and *P. virginianum*), and still others responding best when both deer and invasive plants were removed (*G. triflorum*, *S. pubera* and *B. virginianus*). The one annual species in the group, *P. pumila*, did respond as expected, increasing most due to the pulling of invasives in the pulled and fenced/pulled plots while declining in both the control and fenced plots. Indeed, its positive response in the former two treatments over that in control and fenced plots was one of the two strongest, but it was also the only annual species to be present as one of the most common herbs in the study. [Dávalos et al. \(2014\)](#) obtained species-specific responses to deer and slug exclusion, non-native vegetation and earthworm densities, and nutrient addition in four rare native forest understory herbs. Although only two of these stressors were examined in this study, our findings of species-specific responses in common herbaceous species, as well as those of other researchers (e.g. [Meekins and McCarthy 1999](#); [Stinson et al. 2007](#); [Waller and Maas 2013](#)), may indicate that this is a more widely applicable phenomenon.

We observed no significant changes in the richness or abundances of woody seedling (i.e. ≤ 30 cm tall) species between treatments in our study including control plots, although plots which had initially high levels of invasive cover did show significant increases in this community component ([Table 1](#)). Other studies have documented positive effects on woody seedling richness and abundance after the removal of *A. petiolata* ([Anderson et al. 1996](#); [McCarthy 1997](#); [Hochstedler et al. 2007](#); [Stinson et al. 2007](#); [Rodgers et al. 2008](#)), and positive effects of Japanese stiltgrass removal on survival and growth of planted native woody seedlings have also been obtained ([Aronson and Handel 2011](#); [Johnson et al. 2015](#)). While our results were somewhat unexpected, previous studies have found that the small seedling community is regulated by annual variability in seed production and abiotic factors, particularly precipitation ([Hett and Loucks 1971](#); [Taylor and Aarssen 1989](#); [Boerner and Brinkman 1996](#)). It is possible that our high initial invasive cover plots, regardless of treatment assignment, had higher soil moisture levels or other abiotic differences that made them generally more favourable for woody seedling growth and survival. Other researchers have also shown a lack of direct impacts of deer on the small woody seedling community ([Horsley et al. 2003](#); [McGarvey et al. 2013](#)). These results were due in part to large annual variation in seedling production due to climatic conditions. In these studies, the pulse in seedlings following favourable conditions overrode other factors. Moreover, while introduced white-tailed deer in New Zealand forests have also been linked to increases in abundances of unpalatable woody species ([Bellingham and Allan 2003](#); [Husheer et al. 2003](#)),

competition and presence of local seed sources were additionally implicated in this result ([Bellingham and Allan 2003](#)), and we found no change in abundances of seedling spicebush (*Lindera benzoin*) and pawpaw (*Asimina triloba*), our two most common unpalatable woody species, between treatments in our study sites.

In terms of the above findings, recent workers have introduced the concept of the ‘recalcitrant understory’ to emphasize the impact of the formation of dense, persistent understory canopies by certain species on forest succession and diversity ([Royo and Carson 2006](#); [Young and Peffer 2010](#)). As originally developed by [Royo and Carson \(2006\)](#), such layers were defined as being composed of native understory species capable of rapid vegetative spread that become persistent and monodominant due to changes in forest disturbance and browsing regimes. [Young and Peffer \(2010\)](#) then refined this definition by highlighting that such species are typically clonal or thicket-forming with long life spans. While we acknowledge the importance of this conceptual advance, our study sites did not have a species that met the definition for a recalcitrant understory layer. Whereas more recent studies have applied this term to forests that have come to be dominated by *M. vimineum* in the herbaceous understory ([Baiser et al. 2008](#); [Webster et al. 2008](#)), similar to our study sites, we consider the process of *M. vimineum* invasion to be fundamentally different from that of the recalcitrant understory concept, as this species is a short-lived (annual) exotic grass that reproduces by seed and that undergoes abundance declines with reduction in deer densities ([Eschtruth and Battles 2009](#); [Knight et al. 2009](#); [Shen et al. 2016](#)).

In contrast to the results for the forest woody ground layer, the influence of invasive plants was insignificant once these species reached the LWS size class. Increases in LWS richness and abundance only occurred in the deer exclusion treatments ([Fig. 3](#)). Interestingly, neither LWS nor sapling measures increased in plots that only had invasive plants removed, and increases in the plots that had both treatments were less than the fenced plots. This is strong evidence that deer herbivory in our study sites was the predominant controlling factor on the LWS community. Given that the vast majority of exotic invasive plants at our study sites were short-lived herbaceous species of low stature, herbivory, and not competition with invasive plants for light, was the major limiting factor on such larger growth stages of woody species in these closed canopy forests. Our findings are supported by numerous studies that have shown the impacts of deer on saplings ([Tilghman 1989](#); [Russell et al. 2001](#); [Horsley et al. 2003](#); [Rooney and Waller 2003](#); [Côté et al. 2004](#); [Pedersen and Wallis 2004](#); [McGarvey et al. 2013](#)).

The generalized patterns we found in LWS had important nuances at the individual focal species level. Oak stem numbers increased significantly relative to controls as well as other treatments only in low initial invasive cover plots receiving both deer exclusion and invasive species removal treatments (Fig. 4). Oak seedlings are slow growing under closed canopy and spend multiple years within the lowest understory level where invasive species significantly impact light levels (Dey 2002). Our results indicate it is necessary to control both invasive plant species and deer when oak regeneration is a management goal. The importance of oaks as a keystone species group in the ecological functioning of eastern deciduous forests has been emphasized repeatedly (Dey 2002; Healy and McShea 2002; Abrams 2003; McShea et al. 2007), but present conditions in our study sites (e.g. closed canopy, lack of fire) were not ideal for oak regeneration, which potentially may have suppressed a similar response in deer-excluded high initial invasive cover plots via competition with the concurrent increased levels of native plants (e.g. herbs, woody seedlings, LWS and saplings) we obtained. Another possible explanation for the lack of response in high initial invasive cover plots and the pulled treatment is rodent herbivory on oak seedlings. Blossey et al. (2017) documented such a phenomenon for planted oaks in areas of high *M. vimineum* cover, and similar effects of rodent disturbance on numerous species of planted native herbs in deer-excluded plots in invaded forests have also been found (Dávalos et al. 2014; Dobson and Blossey 2015). Because our experimental plots were relatively small and located within larger areas of high *M. vimineum* cover (in the case of our high initial invasive cover category), it is possible that rodents finding cover in the surrounding invasive grass could readily find and browse the newly exposed oak stems in our treated plots.

For maple stem abundances, there were no significant differences detected between treatments. The overwhelming majority (88 %) of the 1316 maple stems recorded were *A. rubrum* (red maple), often called a ‘super-generalist’ (Abrams 1998) for its ability to thrive in a wide range of ecological conditions. Its increasing dominance in today’s deciduous forests has been implicated as one factor in the decline of oak species and shifts in forest tree community composition (Abrams and Downs 1990; Abrams 1998; McShea et al. 2007; McEwan et al. 2011).

Although we did not detect a strong effect of deer exclusion on the non-graminoid invasive plant community, there was a significant increase in richness in the control plots, and a significant decrease in abundance in high initial invasive cover plots. In summary, non-graminoid invasive plants became generally less dense over the course of the study but more of such species came into plots that

were not experimentally manipulated. Meanwhile, our most abundant invasive species, *M. vimineum*, substantially decreased (–38 % change) by the end of the study in the fenced plots where it was initially abundant (Fig. 5), which is strong evidence for facilitation of this species by deer. This result agrees with our previous finding of chronic high deer densities facilitating exotic plant invasions at one of this study’s sites (Shen et al. 2016), as well as with similar results in *Tsuga canadensis* forests (Eschtruth and Battles 2009) and in a western Pennsylvania deciduous forest (Knight et al. 2009; Kalisz et al. 2014). Indeed, at the Pennsylvania site, *M. vimineum* was never found inside a large deer enclosure even 5 years after its establishment (Knight et al. 2009).

Conclusions

This study demonstrates that under conditions of both high deer and exotic plant densities, impacts on the native forest plant community occur differentially. Invasive plant abundance interacted with deer herbivory to impact the species richness of native herbaceous plants, and thus exotic plant removal is important in addition to reduction of deer browsing to benefit this forest component. Over the somewhat limited duration of our study, our findings suggested that reductions in both stressors were needed to yield a significant positive change in herb species richness greater than that in control plots, even though this change was not significantly greater than that in plots that had only been fenced to exclude deer. In contrast, woody seedlings did not respond to our treatments and we infer that other mechanisms, such as abiotic factors or reproductive variation, may have more of a regulating influence on the small woody seedling community at our sites. However, for succession to occur seedlings must progress through the sapling stage and deer exclusion by itself was the primary factor causing significant increases in native LWS, including tree saplings. There were species-specific responses; individual native herb species responded variably, and oaks benefitted only when both invasive removal and deer exclusion occurred while shade-tolerant red maples showed no clear changes across treatments. This is likely due to oak seedlings being impacted by both competition for light with invasive plants as well as for resources with other native plants at the seedling stage, and subsequently suffering preferential herbivory from deer as they grow into the sapling stage. Based on declines in invasive species abundance over time in deer-excluded plots, we also infer that deer can facilitate invasion by exotic plant species, particularly Japanese stiltgrass. Concurring with Kalisz et al. (2014), we conclude that management to control deer numbers

(i.e. fenced exclusion or population reduction), in the absence of invasive plant removal, may be insufficient to promote restoration in many eastern temperate forests, and maintaining oak species in such forests where they have been historically dominant will rely on both invasive species and deer control actions.

Supporting Information

The following additional information is available in the online version of this article—

Table S1. Likelihood ratio test between two generalized linear models to test if treatment explains initial variability in species richness or abundance of study plots.

Sources of Funding

Funding for this research was provided by Cooperative Agreement Number H3097020003 of the National Capital Region of the U.S. National Park Service to W.J.M., and the Smithsonian Conservation Biology Institute.

Contributions by the Authors

The experiment was designed and maintained by W.J.M., C.M.S. and N.A.B. The field data were collected by N.A.B. Data analyses were performed by V.H., N.A.B. and W.J.M. N.A.B. led the writing and all authors contributed to writing the manuscript.

Conflicts of Interest

All authors had no conflicts of interest. Any use of trade, firm or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Acknowledgements

We thank S. Serchan, D. Rowan, X. Shen, M. Travaglini and many interns of the Smithsonian Conservation Biology Institute for their field and office assistance. Thanks also to B. Blossey and two anonymous reviewers, as well as D. E. Gill, A. Benthem and K. Breen for their helpful comments that improved the manuscript. N.A.B. extends thanks to C. R. Hupp for supporting his participation in the Botanical Society of America 2016 annual meeting.

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