The effects of deer and an invasive shrub, *Lonicera maackii*, on forest understory plant composition

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ABSTRACT

Overabundant generalist ungulates and invasive plants negatively impact forest plants, but few studies have investigated how these stressors interact. We tested the impacts after 5–6 years of exclusion vs. access of white-tailed deer and the presence or removal of an invasive shrub, *Lonicera maackii* (Amur honeysuckle), on forest understory plant composition in Ohio, USA. Exclusion of deer resulted in increased tree seedling density and species richness, and increased shrub basal area, but decreased species richness of the forest floor layer, as well as decreased cover of bare ground and annual plants. The removal of *L. maackii* resulted in impacts on a broader range of understory plants, including greater species richness and cover of the forest floor layer, and greater cover of graminoids and vines specifically. There were also interaction effects between deer and *L. maackii*. Where deer were excluded and *L. maackii* was removed, there was greater cover of tree seedlings, vines, and spring perennials, and a tendency for greater native species richness. These findings reveal that deer and invasive shrubs have synergistic effects on forest understories, indicating that management of both is warranted.

RÉSUMÉ

Les ongulés généralistes surabondants et les plantes envahissantes ont un impact négatif sur les plantes forestières, mais peu d'études se sont penchées sur les interactions entre ces facteurs. Nous avons testé les effets après 5 à 6 ans de l'exclusion du cerf de Virginie et de la présence ou l'élimination d'un arbuste envahissant, Lonicera maackii, sur la composition des plantes d'un sousbois forestier dans l'Ohio, aux États-Unis. L'exclusion des cerfs a entraîné une augmentation de la densité et de la richesse spécifique des plantules d'arbres, ainsi qu'une augmentation de la surface terrière des arbustes, mais une diminution de la richesse spécifique des plantes du tapis forestier, ainsi que la couverture du sol nu et des plantes annuelles. L'élimination de L. maackii a eu des effets sur une gamme plus étendue de plantes du sous-bois, notamment une plus grande richesse spécifique et une plus grande couverture de plantes du tapis forestier, ainsi qu'une plus grande couverture de graminoïdes et de lianes. Il y a eu aussi des effets d'interaction entre le cerf et L. maackii. L'exclusion des cerfs et l'enlèvement de L. maackii ont résulté en une plus grande couverture de plantules d'arbres, de lianes et de plantes vivaces de printemps, et une tendance à une plus grande richesse en espèces indigènes. Ces résultats montrent que les cerfs et les arbustes envahissants ont des effets synergiques sur les sous-bois des forêts, justifiant une gestion simultanée des deux éléments perturbateurs.

Introduction

Numerous studies have documented negative impacts on plant communities due to invasive plants (Vilà et al. 2011; Pyšek et al. 2012) or to high densities of ungulates (Habeck and Schultz 2015; Ramirez et al. 2018). With the recognition that many communities have both of these stressors, recent research has been carried out on the combined effects of both ungulates and invasive species, but their interactive effects are not well understood (Vavra et al. 2007; Knight et al. 2009; Waller and Maas 2013; Dávalos et al. 2015; Ward et al. 2017, 2018). Invasive plants impact native plant species and communities via competition, allelopathy, nutrient cycling, and changes to disturbance regimes (Vilà et al. 2011; Pyšek et al. 2012; Gioria and Osborne 2014). In temperate deciduous forests of North America, the impacts of invasive shrubs on understory plants are mostly attributed to shading by the invasive shrub (Gorchov and Trisel 2003; Kay and Hone 2016) although competition for nutrients and water, allelopathy, and indirect effects via herbivores and soil biota have also been documented (e.g., Warren et al. 2017). This shading impact is influenced by extended leaf phenology of the invasive shrub

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(Fridley 2012). One such shrub is Lonicera maackii (Rupr.) Herder (Amur honeysuckle), a species native to East Asia that has become widespread through many parts of the eastern United States (McNeish and McEwan 2016). Lonicera maackii has an extended leaf phenology, leafing out before many native plant species, and keeping its leaves later in the fall than natives. Experiments involving removal revealed that L. maackii reduces growth and reproduction of perennial herbs (Miller and Gorchov 2004), abundance of most growth forms of herbs (Christopher et al. 2014), and species richness of herbs (Peebles-Spencer et al. 2017). Comparative studies have revealed that species richness of herbs and tree seedlings are lower under L. maackii shrubs (Collier et al. 2002). Additionally, sites that are not invaded have greater densities and richness of seedlings and saplings, and higher richness of herbs, compared to sites invaded by L. maackii (Hartman and McCarthy 2008).

Impacts of high densities of ungulates are also well documented; e.g., in temperate forests, densities above a threshold of about 115 kg km⁻² generally negatively affect tree regeneration (Ramirez et al. 2018). Whitetailed deer (Odocoileus virginianus, hereafter 'deer') are overabundant in many parts of North America (> 10 km⁻², Rooney 2001), compared to pre-settlement abundances (estimated at 3.1-4.2 km⁻², McCabe and McCabe 1997). A meta-analysis by Habeck and Schultz (2015) found that woody plant diversity, cover, and abundance were higher where deer were excluded; the extent of the effects was dependent on the local deer density and the time since deer exclusion. Deer impact forest plant communities through preferential consumption of some plant species (impacting survival or growth and releasing less-preferred species from competition), seed predation and dispersal, trampling, and nutrient cycling (Rooney 2001; Russell et al. 2001; McGarvey et al. 2013; Nuttle et al. 2013; Bradshaw and Waller 2016).

Studies of the effects of both deer and invasive plants have revealed that in some cases their impacts are additive (e.g., Ward et al. 2017) and in other cases antagonistic (combined effects are less negative than the sum of the individual effects, e.g., Waller and Maas 2013). Two factorial experiments have examined the effects of both deer and *L. maackii* on understory plants, both in Ohio, USA. Christopher et al. (2014) found numerous direct effects of both factors, but significant interactions only on the densities of annuals and spring perennial herbs. Peebles-Spencer et al. (2017) also found primarily direct effects of deer exclusion and *L. maackii* removal, with the only significant interaction involving the cover of bare ground, which was greatest where deer had access and L. maackii was present (a synergistic response). However, there were trends for interactions in several other response variables, in many cases increasing in strength over the four years of this experiment. We hypothesized that these interactions would grow larger over time, due to lag effects and slow responses of perennial plants. For example, time since deer exclusion was a significant mediator of plant community richness, according to the meta-analysis by Habeck and Schultz (2015). Most studies of invasive plant control methods reviewed by Kettenring and Reinhardt Adams (2011) were ≤ 1 year, and the only study of deer and invasive shrub impacts > 4 years that we are aware of is Ward et al. (2017, 2018). To investigate longer-term responses, we returned to the plots investigated by Peebles-Spencer et al. (2017) after two additional years to re-assess the forest floor layer. Also, for the growth forms most impacted by deer – tree seedling and shrubs – we tested the direct and interactive effects of deer and L. maackii, on density, diversity, and basal area. The goal of this study was to determine the direct and interactive effects of abundant deer and an invasive shrub on different growth forms and individual species in the forest understory, including whether additional effects emerge as study duration increases.

Methods

Study site

For our study, we used the five paired deer exclosure and deer access study plots that were established in 2010 in the Miami University Natural Areas, Oxford, OH (39°29'-39°31'N, 84°42'-84°43'W) (Peebles-Spencer et al. 2017). The five sites were separated by ≥ 1 km and chosen to have closed-canopy mature deciduous forest, level topography, and a similar, moderate level of invasion by *L. maackii* (stem basal area $0.58-1.57 \text{ m}^2 \text{ ha}^{-1}$). Density of deer in the study area in late winter/early spring was estimated at 18.1 km⁻² in 2014 and 9.4 km^{-2} in 2017, and in summer at 11.2 km^{-2} in 2013 and 6.4 $\rm km^{-2}$ in 2017 (Barrett 2014; Peterson 2018). These densities were above the threshold density of 5.3 km⁻² expected to impact regeneration, based on Ramirez et al. (2018), and close to the threshold of $\sim 8 \text{ km}^{-2}$ for negative impacts on vegetation revealed by Horsley et al. (2003).

Each pair of plots consisted of a 20 m \times 20 m deer exclosure with 3 m fence, and a nearby 20 m \times 20 m control plot without fencing. One half of each plot had *L. maackii* removed by clipping stems at the base and then treating the stumps with Tordon RTU. All *L. maackii* in the *L. maackii* removed half-plots were cut and removed in 2010. Some stems resprouted in 2011 so this treatment was repeated and effectively killed all shrubs. Some new recruitment of *L. maackii* occurred in subsequent years, so in 2015 the treatment was again repeated.

Tree seedlings and shrubs

In summer 2015, in each half-plot, we identified and measured every tree and shrub stem between 30 cm and 2 m tall, as this is the typical deer browsing height range (Frelich and Lorimer 1985). These stem counts were used for analyses of density, but for analyses of Shannon diversity stems of a species within 10 cm of each other were counted as the same individual, as these were commonly connected below ground (e.g., ramets of the same genet). Plants were classified as either trees (hereafter 'tree seedlings') or shrubs. Shrubs were classified as native or non-native using Plants Database (2016). All tree seedlings were native species. Basal area (BA) of each tree or shrub stem was calculated from basal diameter measurements; these were summed to obtain the BA of tree seedlings and shrubs in each half-plot.

Forest floor layer

All plants < 1 m in height (hereafter 'forest floor') were sampled in spring (16-23 May) and summer (4-8 July). In each half-plot, we sampled 18 individual 0.1 m^2 (50 \times 20 cm) subplots (9 subplots, every 2 m along each of two transects) in a modified Daubenmire plot (Abrahamson et al. 2011), repeating the methods and locations sampled by Peebles-Spencer et al. (2017-2017). Percent cover < 1m of each species in leaf was estimated in each subplot using sample sheets of known areas. Bare ground, defined as ground without leaf litter, was also measured. Species were classified by growth forms: trees, shrubs, vines, ferns, graminoids, annuals, spring perennial forbs, summer perennial forbs, moss, and biennials. Perennial forbs were determined to be spring or summer based on classifications by Gleason and Cronquist (1991), Hochstedler et al. (2007), and Christopher et al. (2014). The species were also separately divided into native and non-native species.

Data analysis

For both tree seedlings and shrubs (2015 data) and forest floor layer (2016 data), variables were pooled

for each half-plot for analyses, and *L. maackii* data were not included in analyses. Separately for tree seed-lings and shrubs, we investigated treatment effects on abundance, species richness, Shannon diversity, and BA. For the forest floor layer we tested treatment effects on species richness (total, native, and non-native) and cover of bare ground and each of the growth forms.

For most of the above parameters, data were analyzed with a split-plot analysis, as the 'honeysuckle treatment' (*L. maackii* removed v. intact) was nested within each deer exclosure or deer access plot, which were paired across the five sites. For these nested analyses we used the lme4 (linear mixed-effects models using 'Eigen' and S4) package in R version 3.3.1 (Bates et al. 2017) of the R programming language (R Development Core Team 2017). We used lmer to perform a split-plot ANOVA, while assuming a linear, mixed-effects model. P-values were obtained by comparing the t statistic from each fixed-effects test to the t distribution with 16 df. Results were considered significant at $p \le 0.10$.

An indicator species analyses was performed using the package 'indicspecies' in R to examine the relationship between a species and the treatments. The mutipatt, IndVal.g approach was used to find indicator species, or species whose presence or abundance was indicative of a certain treatment (Cáceres and Legendre 2009; Cáceres et al. 2010), including combinations of a deer treatment and a honeysuckle treatment. Indicator species analyses were done for the 2015 tree seedlings and shrub data set using the number of stems of each species, and for the 2016 forest floor layer data using cover.

Results

Tree seedlings and shrubs

Species richness and stem density of tree seedlings were both greater where deer were excluded; neither parameter was affected by honeysuckle treatment or the deer*honeysuckle interaction (Figure 1, Supplemental Table 1). Tree seedling diversity and BA did not show effects of the honeysuckle or deer treatments, and showed no interaction effects. Shrub BA was greater where deer were excluded, but there were no honeysuckle or interaction effects. Shrub density, species richness and diversity were not affected by the honeysuckle, deer, or interaction treatments. When native and non-native shrubs were analyzed separately, none of the parameters were significantly affected by deer, honeysuckle, or their interaction.





Figure 1. Box-and-whiskers plot of species richness of woody tree seedlings, in half-plots where deer had access (AC) or were excluded (EX) and honeysuckle was removed or not, for the five study areas. Box-and-whiskers shows the five site values, with outliers being quantified if they are below or above the mean \pm 1.5*1QR (interquartile range = 3rd quartile-1st quartile). All tree seedlings were native species. There was a significant effect of deer treatment, but not honeysuckle treatment or the interaction (ANOVA statistics are in Supplemental Table 1).

Table 1. P-values from indicator species analyses of basal area of shrub species (indicated by *) and stem number for tree seedlings, reporting only species where P < 0.05. The indicator value is a measure of statistical significance of the species abundance and its relationship to a treatment, with higher values indicating a stronger significance (Cáceres et al. 2010).

		Indicator	
Indicator species	Indicator of	Value	P-value
Fraxinus spp.	deer excluded	0.926	0.001
Acer saccharum	deer excluded	0.872	0.007
Prunus serotina	deer excluded	0.825	0.016
*Euonymus alatus	deer excluded	0.812	0.017
Ostrya virginiana	honeysuckle removed	0.707	0.014
Acer saccharum	deer excluded, honeysuckle removed	0.801	0.044
*Euonymus alatus	deer excluded, honeysuckle removed	0.857	0.013

Indicator species

Tree seedlings *Fraxinus* spp., *Prunus serotina*, and *Acer saccharum*, and the non-native shrub, *Euonymus alatus*, were indicator species of deer exclusion, and the latter two were also indicators of the combination of deer exclusion and honeysuckle removal (Table 1). *Ostrya virginiana* was an indicator of honeysuckle removal (Table 1).

Forest floor layer

Species richness

Total species richness in spring was significantly greater where deer had access (Table 2, Figure 2(a),

Supplemental Table 2). Also, there was a marginally significantly deer*honeysuckle interaction, with lowest richness where deer were excluded and honeysuckle was present (Figure 2(a)). Total richness in summer was marginally significantly greater where deer were present, and was marginally significantly greater where L. maackii was removed, but there was no interaction (Figure 2(b)). Richness of native species in spring was greater where deer were present, but there was no honeysuckle effect or interaction (Figure 2(a)). In summer there was no effect of either treatment on native species richness. Richness of nonnative species in spring was not affected by either deer or honeysuckle. Non-native richness in summer was greater where deer were present, and was also greater where L. maackii was removed; there was also a marginally significant interaction: non-native richness was lowest where deer were excluded and honeysuckle was present (Figure 2(b)).

Cover

Total cover in spring was greater where *L. maackii* was removed, but there was no deer effect or deer*honeysuckle interaction (Figure 3(a), Table 2, Supplemental Table 3). There was no effect of either treatment in summer (Figure 3(b), Supplemental Table 4). Cover of native species in spring showed a marginally significant interaction, where native species cover was greater where deer were absent and *L. maackii* was removed (Figure 3(a)), but there was no deer or honeysuckle effect. In summer there was no effect of either treatment on native species cover (Figure 3(b)). Cover of non-native species showed no effects of deer or honeysuckle in spring and summer (Figure 3).

Bare ground

Where deer had access, there was significantly more bare ground cover in spring and marginally more in summer; there was no honeysuckle effect or interaction in either season (Figure 3, Table 2, Supplemental Tables 3 and 4).

Growth forms

There was a significant deer*honeysuckle interaction for cover of tree seedlings in spring – this was greatest where deer were excluded and *L. maackii* was removed – but there were no direct effects of deer or honeysuckle (Table 2, Supplemental Table 3). In summer there was no effect of either treatment (Figure 4, Supplemental Table 4). Vine cover in spring was marginally significantly greater where *L. maackii* was removed, but there was no effect of deer and no interaction. Vine cover in summer showed a significant

Table 2. P-values from nested split-plot two-way ANOVAs of each measure of the forest floor layer in half-plots subjected to two deer treatments (access, exclosure) and two honeysuckle treatments (removed, left intact) in Spring and Summer 2016. **Bold** indicates P < 0.05, *italics* indicates P < 0.10. SprPer are spring perennials, and SumPer are summer perennials. See Supplemental Tables 3 and 4 for ANOVA statistics.

		Spring		Summer			
		Deer Treatment	Honeysuckle Treatment	Interaction	Deer Treatment	Honeysuckle Treatment	Interaction
Richness	total	0.0248	0.5698	0.0665	0.0564	0.0672	0.4392
	native	0.0373	0.6525	0.1243	0.2869	0.1059	0.4986
	non-native	0.3118	0.4962	0.4709	0.0467	0.0483	0.0770
Cover	bare ground	0.0064	0.5422	0.8624	0.0843	0.9462	0.9444
	total	0.8123	0.0370	0.3495	0.9886	0.1165	0.4847
	natives	0.9955	0.2571	0.0620	0.9782	0.1779	0.5511
	non-natives	0.9851	0.1274	0.1977	0.4307	0.9286	0.9400
	trees	0.7552	0.8877	0.0193	0.9458	0.3408	0.3205
	shrubs	0.1476	0.8993	0.3465	0.1692	0.8231	0.5321
	vines	0.9334	0.0906	0.4887	0.3334	0.4639	0.0374
	ferns	0.9282	0.1625	0.9154	0.2446	0.7415	0.3338
	graminoids	0.1306	0.8657	0.3841	0.1879	0.0487	0.4935
	annuals	0.5994	0.3210	0.5017	0.0357	0.9704	0.7778
SprPer SumPe	SprPer	0.9694	0.2657	0.1698	0.4309	0.4732	0.0096
	SumPer	0.7956	0.7952	0.6588	0.6507	0.3674	0.9363
	moss	0.2285	0.2443	0.4053	0.2291	0.6600	0.7062
	biennials	0.3917	0.2860	0.4552	0.1161	0.7348	0.4467

interaction; it was greatest where deer were excluded and L. maackii was removed, but there were no main effects of deer or honeysuckle (Figure 4). Cover of graminoids showed no effect of either treatment in spring. However in summer graminoid cover was greater where L. maackii was removed, and there were no deer or interaction effects (Figure 4). Cover of annuals in summer was greater where deer had access (Figure 4), but there were no honeysuckle or interaction effects, and no effects in spring. Cover of spring perennials in spring showed no effect of either treatment, but in summer there was a significant interaction, where spring perennial cover was greatest where deer were excluded and L. maackii was removed (Figure 4). Cover of the other growth forms (shrubs, ferns, summer perennials, moss, and biennials) showed no effects of deer or honeysuckle, and no interactions, in either season.

Indicator species

Bare ground was an indicator 'species' for deer presence in both spring and summer (Table 3). Moss was an indicator species of deer presence in spring, but not in summer (Table 3). *Pilea pumila* and *Polygonum persicaria*, both annual herbs, were indicator species for deer presence in summer, but not in spring (Table 3). *Parthenocissus quinquefolia* and *Vitis* spp., both vines, were indicator species for honeysuckle removal in summer (Table 3). *Acer saccharum* was an indicator species in spring both for deer exclusion, and for the combination of deer exclusion and *L.maackii* removal. Additional indicator species for the interaction of deer exclusion and *L. maackii* removal in spring were *Euonymus fortunei*, a non-native vine, and *Fraxinus* spp. (Table 3). There were no indicator species for deer access or for *L. maackii* present.

Discussion

Effects of deer

Several findings together reveal an overall pattern of higher species richness and abundance of tree seedlings and shrubs where deer were excluded. Specifically, shrub basal area, as well as native tree seedling stem density and richness, were all greater where deer were excluded. These findings were likely due to deer browsing the woody seedlings once they reach the deer browse range of 0.3-2 m tall. Similarly, Ward et al. (2018) found that densities of both 30-90 cm tall and > 90 cm tree seedlings, and diversity of the taller seedlings, increased where deer were excluded in a study that also tested control of all invasive shrubs (primarily Berberis thunbergii). They attributed those results to release of browse pressure on relatively palatable species (Betula lenta, Liriodendron tulipifera, P. serotina). On our plots, woody species preferred by deer (Quercus spp., Ulmus spp.; all preferences for southwest Ohio based on Wright et al. 2019) were too sparse to have the potential to emerge as indicator species, which we attribute to decades of high deer density. Instead, the indicator species of the deer exclosure treatment were all species of intermediate preference: seedlings of the trees Fraxinus spp., P. serotina, A. saccharum, and shrubs of the invasive E. alatus.







Figure 2. Box-and-whiskers plots of species richness of native plants, non-native plants, and all plants (excluding *L. maackii*), in the spring (a) and summer (b) census, in half-plots designated as in Figure 1. In spring there was a significant effect of deer treatment on all three variables; in summer there were significant deer and honeysuckle effects on non-native plants (Table 2).

A different pattern emerges for the forest floor layer, where there was lower total species richness, as well as native and non-native richness, where deer were excluded. There was also lower bare ground cover and cover of annuals in deer exclosures. Indicators of deer access included both bare ground and moss, as well as the annuals *Pilea pumila* and *Polygonum persicaria*. This was opposite the findings of Christopher et al. (2014), whose experiment at another southwest Ohio site showed that annuals were less abundant where deer were present. Similarly, in Connecticut, cover of annuals/biennials and native vines were lower, but cover of graminoids was higher where deer had access, patterns attributed to differences in palatability to deer (Ward et al. 2017).

Our finding that deer increased bare ground was also apparent after four years of this study (Peebles-Spencer et al. 2017) and is comparable to other studies that found deer decreased leaf litter (e.g., Bressette et al. 2012); these are two measurements of the effects of deer impacting the decomposition of leaf litter and altering the amount of bare ground. Knight et al. (2009) measured bare ground directly, and also showed higher amounts of bare ground where deer had access. Investigation by M.B. Mahon and T.O. Crist (unpubl.) at this site revealed deer exclusion increased standing litter biomass over time, which they attribute to reduced activity by non-native earthworms. Deer exclusion decreased earthworm density and shifted earthworm community composition (Mahon and Crist, unpubl.). This positive correlation between deer and earthworm abundance has been documented across sites (Fisichelli and Miller 2018) and may be due deer fecal pellets serving as a high-quality food to earthworms (Karberg and Lilleskov 2009).

Our finding of greater cover of moss and annuals where deer had access is likely an indirect result of deer increasing bare ground cover. Reduced leaf litter and greater bare ground cover often promote seed germination or seedling establishment by allowing light to reach areas of bare ground, and by allowing dispersed seeds to contact the soil, although in some cases litter promotes germination or establishment (Facelli and Pickett 1991). Additionally, our finding that deer access plots had greater understory richness for both natives and non-natives could be due to bare ground promoting establishment of several species, regardless of whether the species is native or not. In previous studies, decreasing the amount of leaf litter in an area has been shown to increase the establishment of invasives such as L. maackii and the biennial Alliaria petiolata (Bartuszevige et al. 2007), as well as the annual grass Microstegium vimineum (Oswalt and Oswalt 2007).

Effects of L. maackii

Impacts of removal of *L. maackii* shrubs were manifest across numerous components of the forest floor layer, in contrast to deer exclusion, for which effects were largely confined to woody plants. While we did not detect effects on tree seedling or shrub density, species richness, diversity, or BA, we found greater total species richness, non-native richness, and total cover of plants in the forest floor layer where *L. maackii* was removed. Only the effect on richness had been detected after four years of the experiment





Figure 3. Box-and-whiskers plots of cover of bare ground, native species, non-native species (excluding *L. maackii*), and total cover (excluding *L. maackii*) in the spring (a) and summer (b) census, in half-plots designated as in Figure 1. In spring there was a significant effect of deer on bare ground, of honeysuckle on total cover, and of their interaction on tree seedling cover (Table 2). In summer there was a significant effect of deer on graminoids, and of their interaction on vines and spring perennials (Table 2).

(Peebles-Spencer et al. 2017), indicating that effects build over time. These experimental findings suggest competitive impacts by *L. maackii*; this competition is more likely for light than below-ground resources (Gorchov and Trisel 2003). Findings from comparative studies also indicate competitive impacts of *L. maackii*: plots under *L. maackii* shrubs had lower herb abundance and richness, and lower tree seedling richness and density, compared to plots away from *L. maackii* shrubs (Collier et al. 2002), and stands invaded by *L. maackii* had lower density and richness in the herb, tree seedling, and sapling layers than uninvaded stands in southwest Ohio (Hartman and McCarthy 2008). On the forest floor, several growth forms responded positively to *L. maackii* removal: graminoids and vines in this study (and Peebles-Spencer et al. 2017), similar to Christopher et al.'s (2014) finding that graminoids, annuals, spring perennials, and summer perennials increased where *L. maackii* was removed. Similarly, Ward et al. (2017) found that control of *B. thunbergii* and other invasive shrubs increased cover of perennial forbs, native shrubs, native and invasive vines, and density of tree seedlings.

The species we found to be indicators of *L. maackii* removal contrast those reported by Hartman and McCarthy (2008). While we found *Ostrya virginiana* tree seedlings and the vines *Parthenocissus quinquefolia* and *Vitis* spp. were indicators of removal plots, Hartman and McCarthy (2008) found numerous tree seedling and herb species were indicators of stands not invaded by *L. maackii*. Among vine species, Hartman and McCarthy found that *Vitis* spp. was an indicator of un-invaded sites, but *P. quinquefolia* showed the contrary pattern – it was an indicator of stands with a long history of this invasion.

Our finding that non-native richness was greater where *L. maackii* was experimentally removed seems contrary to Culley et al.'s (2016) finding that southwest Ohio sites where *L. maackii* had established had *lower* number, proportion, and diversity of other invasive species compared to sites in the same stands with *L. maackii*. These findings are not contradictory, however, as uncontrolled differences among sites in conditions or history may account for patterns in comparative studies, whereas the experimental studies reveal short-term responses to the release from competition.

Interactions

In addition to the above effects of deer exclosure and honeysuckle removal, we found that some parameters were significantly impacted by the interaction of these treatments. Most of these interactions were synergies – the combined effect of deer and *L. maackii* was greater than the sum of the individual main effects. Specifically, we found greater cover of natives, tree seedlings, vines, and spring perennials where deer were excluded and honeysuckle was removed; trends that were not significant after only four years of growth (Peebles-Spencer et al. (2017). Similarly, Christopher et al. (2014) found significantly greater densities of annuals and spring perennials where deer were excluded and *L. maackii* was

Indicator species	Indicator of	Season	Indicator Value	P-value
bare ground	deer access	spring	0.905	0.001
bare ground	deer access	summer	0.894	0.003
moss	deer access	spring	0.837	0.004
Pilea pumila	deer access	summer	0.775	0.009
Polygonum persicaria	deer access	summer	0.769	0.01
Acer saccharum	deer excluded	spring	0.815	0.043
Parthenocissus quinquefolia	honeysuckle removed	summer	0.849	0.027
Vitis spp.	honeysuckle removed	summer	0.804	0.045
Acer saccharum	deer excluded, honeysuckle removed	spring	0.790	0.008
Fraxinus spp.	deer excluded, honeysuckle removed	spring	0.686	0.036
Euonymus fortunei	deer excluded, honeysuckle removed	spring	0.756	0.048

Table 3. P-values from the indicator species analyses of forest floor layer cover data, reporting only those species where P < 0.05. Separate analyses were done on cover in spring and summer.

absent or removed. Ward et al. (2017, 2018) reported similar synergies; specifically greater volume and cover of native shrubs and cover of tall perennial forbs and invasive vines where shrubs were controlled and deer excluded. Those functional groups and species that share this positive response to the combination of deer exclusion and invasive shrub control appear to require both release from plant competition and deer browse; removing only shrubs likely exposes these to greater browse (Peebles-Spencer and Gorchov 2017), and exclusion only of deer may increase the growth and competitive effects of invasive shrubs such as *L. maackii* that are palatable and browsed by deer (Martinod and Gorchov 2017; Peebles-Spencer et al. 2018).

All of the species that were indicators of the interaction of deer exclosure and *L. maackii* removal were woody (native trees *A. saccharum* and *Fraxinus* spp., the invasive shrub *E. alatus*, and the invasive vine *E. fortunei*) The first three of these four species are of moderate browse preference to deer according to Wright et al. (2019). While highly palatable tree and shrub species would also be expected to thrive where deer are excluded and *L. maackii* removed, they were too sparse in the understory of these sites to emerge as indicator species. Tree and shrub species of low preference, such as *Asimina triloba*, do not benefit from deer exclusion. *Euonymus fortunei* is highly preferred by deer (Conover and Kania 1988), but can reach high cover where deer are abundant, likely because most stems form a mat near the ground (Mattingly et al. 2016) keeping most meristems too low for deer.

Most of the impacts on the forest floor layer that we found after six years of *L. maackii* removal and deer exclusion were not significant after the first four years (Peebles-Spencer et al. (2017). These delays in response reflect 'legacy effects' of deer and the invasive shrub, which in turn could be due to the gradual, cumulative growth responses of perennial plants to a new biotic environment, or to changes to the seed bank, soil biota, or soil structure (Nuttle et al. 2014; Pendergast et al. 2016). A review of the impacts of high ungulate populations concluded that more effects emerge with longer periods of time (Ramirez et al. 2018). This provides support for the argument that longer-term studies are



Figure 4. Box-and-whiskers plots of cover of growth forms in the forest floor layer (excluding *L. maackii*), in the summer census, in half-plots designated as in Figure 1. SprPer are spring perennials, and SumPer are summer perennials. Significance of treatments is shown in Table 2.

needed to detect impacts of the interaction between invasive plants and ungulates.

Conclusion

Forests with both high deer and *L. maackii* populations require reduction of both to restore understory plant communities, based on our findings that removal of both increased cover of native species and several specific growth forms, including trees, vines, and spring perennials, and greater abundance of sugar maple and ash seedlings. Reduction of only deer populations will likely result in lower overall plant species richness, and a decrease in moss and annuals. Removal of only *L. maackii* will probably result in increased richness of non-native plants, and increased vine and graminoid cover. However, lowering deer populations and removing *L. maackii* is likely to promote invasive *E. fortunei* and *E. alatus*, both indicator species of deer exclusion and *L. maackii* removal.

The low replication in this study (5 plots for each treatment combination) undoubtedly limited our ability to detect other impacts of deer or this invasive shrub species. Furthermore, this study examined the effects of deer using complete exclusion. Since deer are a natural component of this ecosystem, research is needed on the interactive effects of invasive shrubs and deer on understory plants across a gradient of deer densities, similar to how the direct effects of deer have been assessed in a handful of gradient experiments (e.g., Horsley et al. 2003).

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