Long-term interactive impacts of the invasive shrub *Lonicera maackii* and white-tailed deer (*Odocoileus virginianus*) on a deciduous forest understory

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Abstract

White-tailed deer (*Odocoileus virginianus*) (hereafter, 'deer') and invasive plants affect forest understories, but few studies have investigated their interaction. We investigated long-term (11-yr) effects of excluding deer and removing the invasive shrub, Amur honeysuckle [*Lonicera maackii* (Rupr.) Herder], on plants in southwest Ohio. Deer exclusion enhanced tree seedling richness and density, but reduced annual and bare ground cover. Vine density was reduced by *Lonicera*, especially where deer were excluded. Seedlings of several tree species, the invasive shrub, burning bush [*Euonymus alatus* (Thunb.) Siebold], and the invasive vine, winter creeper [*Euonymous fortunei* (Turcz.) Hand.-Maz.], were indicator species of the deer exclosure by *Lonicera* removal treatment combination. The effect of deer on cover of native species depended on *Lonicera* treatment: where shrubs were removed, cover was higher where deer were excluded, but where shrubs were present, cover was higher where deer had access. We attribute these interactions to the reduced growth of, and shading by, *Lonicera* where deer had access and browsed this invasive shrub. Some of these effects were evident in the first 6 yr, but are now larger. Other effects were not evident in the earlier evaluation. These findings inform management of areas with high densities of deer and invasive shrubs palatable to deer. Control of only invasive shrubs will reduce native cover and not improve tree regeneration. Managing only deer will increase woody plants but reduce native cover. Management of both stressors is needed to promote tree regeneration and restoration of plant communities.

Introduction

Forests in many regions are impacted by both high densities of native ungulates (Côté et al. 2004; Ramirez et al. 2018) and invasive nonnative plants (Liebhold et al. 2017; Riitters et al. 2018). In many parts of eastern North America, white-tailed deer (*Odocoileus virginianus*) (hereafter 'deer') occur at densities much higher than during pre-European settlement (Rooney 2001) with well-documented effects on forest understory plant composition and diversity (Averill et al. 2018; Bradshaw and Waller 2016; Habeck and Schultz 2015; Russell et al., 2001). In many of these same areas, invasive plants are impacting native plants (Bialic-Murphy et al. 2020; Boyce 2009; Waller et al., 2016). Both deer and invasive plants are implicated in regeneration failure (Miller and McGill 2019; Miller et al. 2023)—insufficient densities of juvenile trees to replace canopy trees.

While numerous studies, including replicated field experiments, have quantified the separate effects of high deer or invasive plant densities, relatively few have simultaneously quantified both. A recent review of deer-and-invasive plant studies found that deer impacts were more frequent and more consistently negative than invasive plant impacts (Gorchov et al. 2021), particularly on woody plants. In some cases, the effects of these two factors were additive, but in other cases, there were significant interactions between the effects of deer and of invasives. The most common interaction was a synergistic effect of deer exclusion and invasive removal—the response variable was higher in this treatment combination than expected based on additive effects (Gorchov et al. 2021). This can also be considered a "sub-additive" interaction of the negative effects of deer and invasives (Peebles-Spencer et al. 2017).

However, the majority of the publications (14 of 25) contributing to the above review reported data after only 1 to 4 yr of manipulation. There is a need for longer-term studies, because many vegetation responses to changes in deer density (Tanentzap et al. 2012) and invasive plants (D'Antonio and Flory 2017) are slow or lagged.

To determine longer-term effects of deer exclusion and invasive plant removal on forest understory plants, we evaluated a field experiment set up in 2010. This was a split-plot design, wherein all stems of an invasive shrub, Amur honeysuckle [*Lonicera maackii* (Rupr.) Herder],

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Management Implications

We found that tree seedlings responded more to exclusion of deer than to removal of the invasive shrub, *Lonicera maackii* (Amur honeysuckle), but that the combination of both measures results in the greatest tree seedling density and species richness. These findings inform management of deciduous forest areas with high densities of deer and invasive plants, a combination that is widespread in the eastern and midwestern United States. In particular, they are relevant where the dominant invasives are shrubs that are palatable to deer. In these forests, control of invasive shrubs without deer management will likely increase cover of annuals, but will likely reduce native cover and not improve tree regeneration. Only a few tree species not browsed by deer, such as pawpaw [*Asimina triloba* (L.) Dunal.], will regenerate.

Alternatively, managing deer without controlling invasive shrubs will likely increase tree seedlings, but will release the palatable invasive shrubs from deer browse, resulting in denser cover and greater shade. This in turn will reduce native species cover in the forest floor.

Managing both deer and invasive shrubs is necessary to realize the greatest improvement in tree seedling density and diversity and recruitment of trees from seedlings to the understory-size class, as well as cover of native plants. This will promote tree regeneration and facilitate recovery of plant diversity on the forest floor.

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were removed in half of each deer exclosure and access plot. *Lonicera maackii* was manipulated because it was, by far, the most abundant invasive plant in the study area. It is a large shrub native to East Asia that was introduced and has spread across much of the eastern United States (Luken and Thieret 1995). *Lonicera maackii* is known to negatively impact native woody vegetation in mature forest understories (reviewed by McNeish and McEwan 2016). It expands leaves earlier (McEwan et al. 2009) and retains them later (Wilfong et al. 2009) than native deciduous trees and shrubs, and this extended leaf phenology has been hypothesized to be important in shading native forest floor plants, particularly spring ephemerals that depend on light before canopy leaf-out (Miller and Gorchov 2004). Several studies have shown that *L. maackii* reduced growth, richness, and density of native plants (Gould and Gorchov 2000; Miller and Gorchov 2004; Shields et al. 2015b). Comparative studies revealed that areas invaded by *L. maackii* have lower richness and densities of tree seedlings as well as lower richness of herbs (Collier et al. 2002; Hartman and McCarthy 2008; Hutchinson and Vankat 1997; Shields et al. 2015a).

Materials and Methods

Study Site

This study was conducted across five sites located in the Miami University Natural Areas in Oxford, Ohio (39.48°–39.52°N, 84.70°–84.72°W). The Miami University Natural Areas consist of ~400 ha, most of which is early successional to mature eastern deciduous forest. At each site, two 20 by 20 m plots were established in 2010, 25 to 50 m apart at their closest corners, with one assigned to be a deer exclosure and the other a deer access plot (Peebles-Spencer et al. 2017). All site locations (College Woods, Western Woods, Bachelor Preserve, Kramer Preserve, Reinhart Preserve) were separated by ≥1 km and were chosen to have level topography, closed canopy deciduous forest, and intermediate

levels of *L. maackii* invasion (stem basal area [BA]: 0.58 to 1.57 m^2 ha^{-1}; Peebles-Spencer 2016). The forest canopy (trees > 10-cm diameter at breast height [DBH]) was mixed deciduous—in the vicinity of each plot the most common tree species was sugar maple (*Acer saccharum* Marshall) (Donoso 2022). Other common tree species, in order of abundance, were white oak (*Quercus alba* L.), bitternut hickory [*Carya cordiformis* (Wangenh.) K. Koch], chinquapin oak (*Quercus muehlenbergii* Engelm.), and northern red oak (*Quercus rubra* L.) (Donoso 2022). BA averaged 18.1 m^2 ha^{-1} in 2021 (Donoso 2022); it had been higher when plots were established in 2010, but emerald ash borer (*Agrilus planipennis*) subsequently killed all canopy *Fraxinus* spp. trees. Canopy cover, measured at 2 m (above most *L. maackii*), averaged 87% in 2021 and did not correlate with BA among plots (Donoso 2022).

Deer densities of all site locations had been estimated during winter and early spring in 2014 (Barrett 2014) and during spring and summer in 2017 (Peterson 2018) (Supplementary Table S1). At three of the sites, deer densities were greater than the ~8 deer km^{-2} expected to impact forest regeneration (Horsley et al. 2003; Nuttle et al. 2014; Tilghman 1989), while densities at the other two sites were sometimes above and sometimes below this threshold (Supplementary Table S1).

Exclosures were built in 2010, with 3-m-high fencing. One-half of each 20 by 20 m plot (exclosures and paired deer access plots) was randomly assigned to *L. maackii* intact or removed treatments (Peebles-Spencer et al. 2017). These 10 by 20 m areas are referred to as "half-plots." In *L. maackii* removed half-plots, removal involved clipping the base of stems that were >1 mm in diameter and treating the stumps with Tordon® RTU, a herbicide composed of a mixture of 5.4% picloram and 20.9% dicholorphenoxyacetic acid (Dow AgroSciences 2011). Resprouting and recruiting *L. maackii* stems were clipped and herbicide was applied to stumps in 2011, 2015, and in 2021 (following plot measurements in this study).

Findings based on early studies of these plots are summarized in the Supplementary File.

Field Measurements

Woody Stems Other Than Lonicera maackii

All woody stems taller than 0.3 m were identified and measured (basal diameter if ≤2 m and DBH if >2 m), counting stems of species within 10 cm of each other as the same individual (Haffey and Gorchov 2019). Species were classified as trees, shrubs, or vines. Trees were considered seedlings if between 0.3- and 2-m tall, the typical deer browse height (Frelich and Lorimer 1985); understory trees if >2 m and DBH <10 cm; and canopy trees if DBH >10 cm. Stems classified as understory trees in 2015 were also considered understory trees in this 2021 census, even if the DBH had increased to >10 cm.

Lonicera maackii shrubs

To determine the effects of deer on *L. maackii* growth, we measured the basal diameter of every *L. maackii* stem. We distinguished three size classes of *L. maackii* shrubs based on the basal diameter of the largest stem, using criteria in Peebles-Spencer et al. (2018). Shrubs with basal diameter of the largest stem ≥30 mm were considered large, as these diameters characterized shrubs with most of their leaves at a height taller than the typical deer browse height range. Shrubs with basal diameter of the largest stem ≤2 mm were considered recruits based on annual ring counts (Peebles-Spencer et al. 2018), while shrubs with basal diameter between the other size classes (3 to 29 mm) were considered

small. *Lonicera maackii* stems within 10 cm of each other were considered stems of the same individual.

Forest Floor Vegetation

Cover of each plant species in the forest floor layer (<1 m in height) was quantified in 20 by 50 cm (1,000 cm^2) "subplots" in each half-plot. Nine subplots were located at 2-m intervals along two transects, for a total of 18 subplots per half-plot, using the same methods and locations as Haffey and Gorchov (2019). Two surveys were done, the spring survey (May 27 to June 17) and the summer survey (July 20 to August 6) 2021. In each subplot, we used cards of known area to estimate the cover of each species and of bare ground (without leaf litter). Species were classified by growth form: trees, shrubs, vines, spring perennials, summer perennials, biennials, annuals, graminoids, moss, and unknown. Perennials were classified as either spring or summer based on classifications from Hochstedler et al. (2007), Christopher et al. (2014), and (Haffey and Gorchov 2019). Species were also classified as either native or nonnative (USDA-NRCS 2016).

Canopy Cover at 0.3 m

To investigate the effects of deer and *L. maackii* treatments on light availability, we took 16 photographs of the canopy at 0.3 m above the ground along two transects in each half-plot (figure 1 in Donoso 2022) from August 1 to 24. This height (0.3 m) was chosen because it was our height minimum for tree seedling census and it was below nearly all *L. maackii* foliage. Photographs were taken using a Samsung Galaxy S10 (Ridgefield Park, NJ, USA), which utilizes a 10-megapixel front facing camera module, ensuring that the device was level before each photograph. Images were analyzed using the GLAMA app (percent cover using Gap Light Analysis Mobile Application) (Tichý 2014, 2016). For this study, the modified canopy cover index value was used, as it accounts for various anomalies that are unaccounted for in the canopy cover index value. To calibrate the camera lens for accurate canopy cover estimation, a photograph of a circular object was taken to calculate diameter in pixels, which allowed the app to determine hemisphere diameter and the recommended horizon mask angle. Because a built-in camera lens was used, the polar projection option was chosen within the app. The level of preciseness chosen was All Pixels, and the color channels used was All RGB. Cut level was determined independently for each site by visually assessing images to ensure pixels were accurately defined as "white" (sky) or "black" (canopy). Photographs at 0.3 m from Western Woods were excluded from analysis, as *L. maackii* was mistakenly cut in the *L. maackii* present half-plot in the deer access plot, which influenced percent forest floor cover values at the site.

Data Analysis

Woody Plants Other Than Lonicera maackii

Change in understory tree variables (number, richness) from 2015 to 2021 for each half-plot was determined by subtracting its 2015 values from its 2021 value. Deer and *L. maackii* treatment effects on species richness and density were assessed for seedlings, shrubs, and understory trees. Only density was assessed for vines, as the number of species present was too low for species richness analysis. Data analyses for these response variables involved using split-plot analysis with both *L. maackii* removed and intact treatments nested within deer exclosure and access treatment plots, which were paired across each site. Data analysis was performed using the R programming language (R Development Core Team 2017)

utilizing the lme4 (linear mixed-effects models using 'Eigen' and S4; Bates et al. 2017) and lmerTest (provides P-values for ANOVA tables for linear mixed-effect models via Satterthwaite's degrees of freedom (df) method; Kuznetsova et al. 2017) packages. This analysis requires Gaussian (normal) distribution of residuals, which we tested using the Shapiro-Wilk test. Variables that failed this test were log-transformed. P-values were obtained via Satterthwaite's df method. Two variables (change in understory tree richness, vine density) failed the Shapiro-Wilk test after transformation, so for each of these two variables, we carried out a split-plot ANOVA on the ranks, using the ARTool package in R (https://CRAN.R-project.org/package=ARTool; Wobbrock et al. 2011).

Lonicera maackii

Basal diameter of each stem was converted to BA, then BAs were pooled for all *L. maackii* stems within each half-plot. To assess deer effects on BA (small shrubs, large shrubs, all) we utilized data only from half-plots where *L. maackii* was not removed, using a linear mixed-effect model with site as the random effect. To analyze deer and *L. maackii* treatment effects on the number of *L. maackii* recruits, we used counts from all treatment combinations, using glmer while assuming Poisson responses for density.

Forest Floor Vegetation

For each plant species and for bare ground, we pooled the area covered over all 18 subplots in each half-plot and divided by the sampled area (1.8 m^2) to determine percent cover. These values were summed for native species, nonnative species, and each of the growth forms (*L. maackii* was not included in analyses). Cover of mosses and biennials were not analyzed, as these were sparse in the half-plots. For each variable, we analyzed either the spring or the summer values, depending on which had the higher overall mean. Treatment effects for cover of each of these categories, as well as richness of native and nonnative species, were tested with split-plot ANOVAs using lme4 as described earlier for woody stems. Variables that did not have normal residuals (failed Shapiro-Wilk test) were log-transformed. Five variables failed the Shapiro-Wilk test after transformation, so for each of these two variables, we carried out a split-plot ANOVA on the ranks, using ARTool, as described earlier for woody stems.

Indicator Species Analyses

We used indicator species analysis to determine which species were indicative of certain combinations of deer and *L. maackii* treatments. Analyses used the indicspecies package (De Cáceres and Legendre 2009; De Cáceres et al., 2010) in R with the *multipatt*, *IndVal.g* function. For woody species (other than *L. maackii*), we used the number of stems of each woody species in each half-plot. For forest floor vegetation, we used the percent cover of each species in each half-plot, with separate indicator species analyses for spring and summer data sets.

Adjustment of P-Values to Minimize Type 1 Errors

Because the large number of tests with woody stem data ($n = 8$) and with the forest floor cover data ($n = 12$) increases the chance of Type 1 errors, we adjusted P-values using a procedure based on the false discovery rate (Pike 2011). In these adjustments, we considered each of the three factors (deer, *L. maackii*, and interaction) in each of the data sets (woody stems, forest floor) to be a separate "family" of P-values. We used the p.adjust command in R, specifying the 'BH' (Benjamini and Hochberg 1995)

Table 1. Adjusted P-values from nested split-plot two-way ANOVAs of richness and density (stems m^{-2}) of understory woody vegetation, and *Lonicera maackii* recruit counts, in summer 2021 in half-plots subjected to a combination of deer treatments (access, exclosure) and *L. maackii* treatments (present, removed).[a]

		Deer treatment	*L. maackii* treatment	Interaction
Richness	Tree seedlings	**0.002**	0.782	*0.056*
	Shrubs	*0.073*	0.707	0.345
	Δ Understory trees ##	*0.078*	0.264	0.828
Density	Tree seedlings #	**0.017**	0.960	*0.056*
	Shrubs #	*0.051*	0.520	0.828
	Δ Understory trees ##	0.736	0.662	0.828
	Vines ##	0.518	**0.032**	**0.040**
	L. maackii recruits	0.281	0.520	0.108
Modified canopy cover index	0.3m above ground	**0.015**	0.298	0.834

[a]For understory trees, variables are the change (Δ) in values in each half-plot from 2015 to 2021. P-values have been adjusted to control for the false discovery (type 1 error) rate (see " Materials and Methods"). Unadjusted P-values, as well as test statistics, are in Supplementary Tables S8 and S9. Additionally, P-values from nested split-plot two-way ANOVA of cover at 0.3 m above ground in half-plots subjected to same deer and *L. maackii* treatments in summer–fall 2021. # indicates log-transformed, ##indicates analysis of ranks. **Bold** indicates P < 0.05. *Italics* indicates P < 0.1.

adjustment, as was used by other studies of invasive shrub impact in forests (Owings et al. 2017; Shields et al. 2015b)

For all analyses, values of P ≤ 0.05 (after adjustments as per above) were considered significant.

Comparisons with 2015 to 2016

To illustrate how treatment effects have changed over time, for selected variables, we graphed values from 2015 or 2016 (5 to 6 yr after the start of the experiment) (Haffey and Gorchov 2019) alongside values from the present study (2021, 11 yr after the start).

Results and Discussion

Woody Stems Other Than L. maackii

Tree Seedlings and Shrubs
A total of 28 species with 2,137 tree seedlings (0.3 to 2 m height) were censused across the 20 half-plots. The most abundant species, accounting for 76.9% of seedlings, were white ash (*Fraxinus americana* L.; 843 stems), black cherry (*Prunus serotina* Ehrh.; 520), blue ash (*Fraxinus quadrangulata* Michx.; 177), and pawpaw [*Asimina triloba* (L.) Dunal.; 105] (Supplementary Table S2).

Deer significantly reduced seedling richness and density with no effect of *L. maackii* on either response (Table 1; Supplementary Table S3). There was also a marginally significant synergistic interaction between deer and *L. maackii* effects for both richness and density: each variable was much higher where deer were excluded and *L. maackii* removed than in the other three treatment combinations (Figure 1).

A total of 11 native and 8 nonnative (excluding *L. maackii*) shrub species were recorded in one or more plots (Supplementary Table S4). The most frequent native shrub species was blackhaw (*Viburnum prunifolium* L.) and the most frequent nonnative was border privet (*Ligustrum obtusifolium* Siebold & Zucc.) Deer marginally (P < 0.1) reduced shrub species richness and density, but there was no *L. maackii* effect on either variable (Figure 2A; Table 1; Supplementary Table S5).

While the negative effects of deer on tree seedlings and shrubs have been documented by numerous experimental and comparative studies (reviewed by Habeck and Schultz 2015; Russell et al. 2001), few studies have simultaneously assessed the effects of deer and invasive plants (Gorchov et al. 2021). A review of those two-factor experiments found deer exclusion effects to be more frequent than invasive removal effects across woody, herbaceous, and ecosystem responses and indicated that when the interaction of these main effects was significant, it was usually synergistic (Gorchov et al. 2021).

Our findings that shrubs and tree seedlings were suppressed by deer, and not by *L. maackii* after 11 yr is consistent with effects documented after 5 yr of treatment in these same plots (Haffey and Gorchov 2019). In Indiana, removal of *L. maackii*, as well as deer exclusion, improved survival of American chestnut [*Castanea dentata* (Marshall) Borkh.] and *Q. rubra* seedlings, with no interaction, and neither treatment affected the density or species richness of naturally regenerating seedlings (Owings et al. 2017). However, that was a short-term study, assessing responses after only 2 yr after shrub removal (4 yr after deer exclosure).

Deer exclusion, particularly where *L. maackii* was removed, not only greatly enhanced density and species richness of tree seedlings, but also affected their species composition. In the indicator species analysis of woody stems, four tree species (as seedlings) were indicators of the combination of deer exclusion and *L. maackii* removal treatments (in decreasing order of abundance: *P. serotina*, *C. cordiformis*, eastern redbud (*Cercis canadensis* L.), and *Q. rubra*) (Table 2). Each of these four species had more than five times higher density in this treatment than in any other treatment; in fact, all *Q. rubra* seedlings were in this treatment (Donoso 2022). Another tree, *A. saccharum*, was an indicator of this treatment combination in the cover data set.

Another tree, slippery elm (*Ulmus rubra* Muhl.), was an indicator of deer exclusion (*L. maackii* presence and removal) in the stem data set. This finding indicates *U. rubra* is sensitive to deer browse, but tolerant of shade from *L. maackii*.

The most abundant species in our samples, *F. americana*, accounted for the great majority of tree seedlings where deer had access but *L. maackii* was removed (Supplementary Table S2). However, even if seedlings of this and other species of *Fraxinus* overcome the repeated browsing by deer, they are not expected to pass 2.5 cm in diameter due to *A. planipennis* (Klooster et al. 2014). The density of this species in this treatment was more than half of its density in deer exclosure by *L. maackii* removal treatment and was much greater than in the plots where *L. maackii* was present. This suggests it is more tolerant of deer browse than the species listed above, but suppressed by shade of the invasive shrub. *Fraxinus americana* was considered of low/moderate browsing preference in spring/summer and high preference in fall/winter by Latham et al. (2005), but in southwest Ohio it had lower percent browsed and electivity than other common woody species (Wright et al. 2019). Transect surveys in the Miami University Natural Areas revealed that 6% to 19% of *F. americana* seedlings had
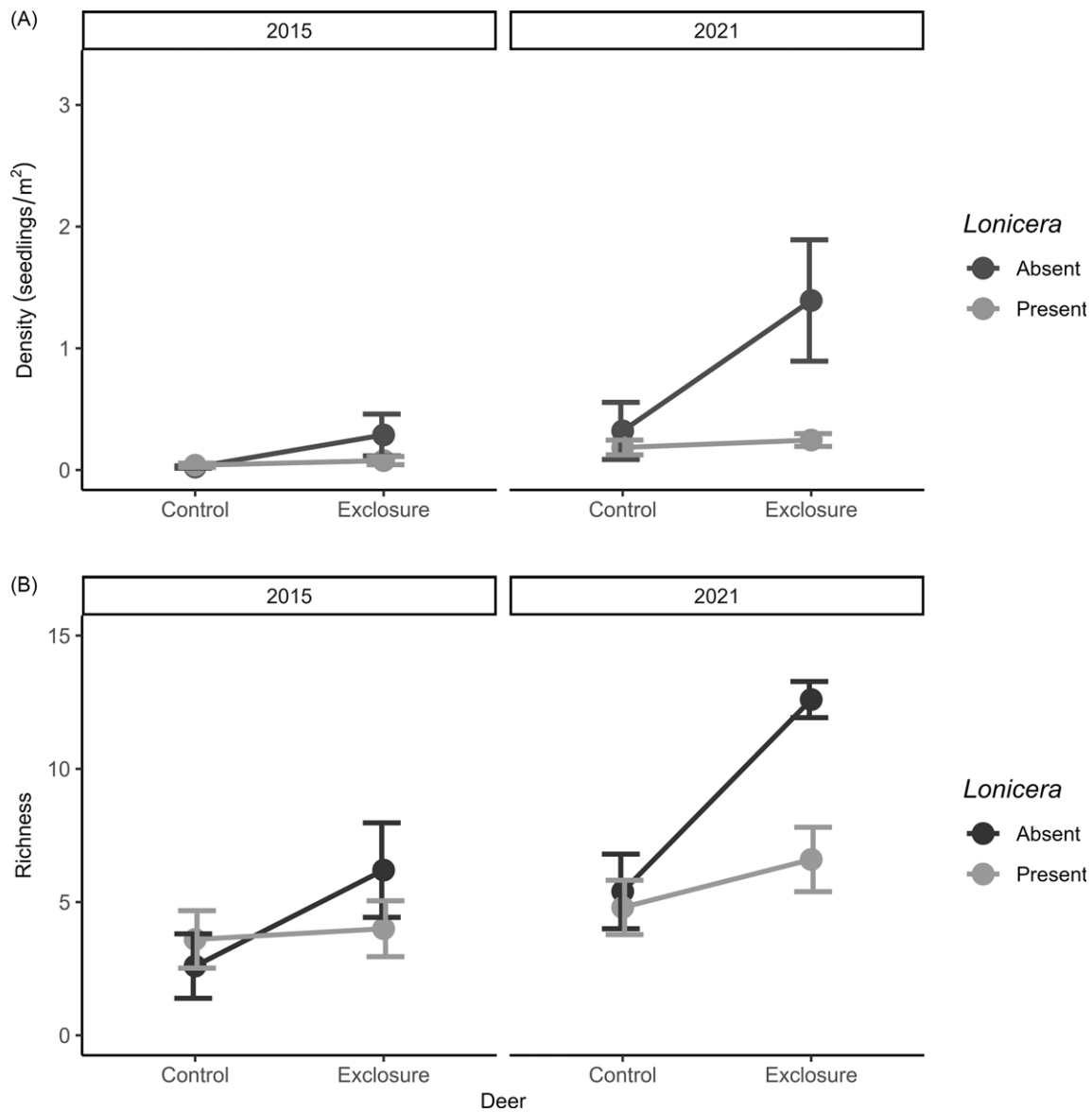
Figure 1. Interaction plots of (A) species richness and (B) density (seedlings/m²) of native tree seedlings for 2015 and 2021 in half-plots where deer had access or were excluded and where *Lonicera maackii* was present or removed (Absent). For each treatment combination, mean ± SE of the five sites is plotted. Data from 2015 are from Haffey and Gorchov (2019).

browse on apical shoots (E Cooper, unpublished data), but it appears that deer browse generally limits height growth, rather than causing mortality, of seedlings of this species.

The negative effect of deer on shrub species richness was due to reduction of nonnative shrubs; native shrub richness was not affected (Donoso 2022). The only shrub species to emerge as an indicator species, the nonnative shrub [*Euonymus alatus* (Thunb.) Siebold], was also an indicator of the deer exclusion and *L. maackii* removal treatment combination in the woody stem data set (Table 2).

Understory Trees

Ten tree species, all native, were represented as "understory trees" (>2 m in height, but <10 cm DBH) (Donoso 2022). *Acer saccharum* accounted for the majority of understory trees; other common species were Ohio buckeye (*Aesculus glabra* Willd.) and

A. triloba. The change in half-plot–level species richness of understory trees from 2015 to 2021 was marginally ($P = 0.078$) reduced by deer but was not affected by *L. maackii* (Table 1; Supplementary Table S6). Change in understory tree density was not affected by deer or *L. maackii* treatments. This tendency for deer to limit the diversity of trees recruiting into an intermediate size class is consistent with findings of other studies (Bradshaw and Waller 2016).

Vines

Five native and three nonnative vine species were recorded in the plots (Donoso 2022). The most frequently encountered vine species were the native bristly greenbrier (*Smilax tamnoides* L.) and the nonnative Oriental bittersweet (*Celastrus orbiculatus* Thunb.). Vine stem density was greater where *L. maackii* was removed, with a significant synergistic interaction: vine density was greatest
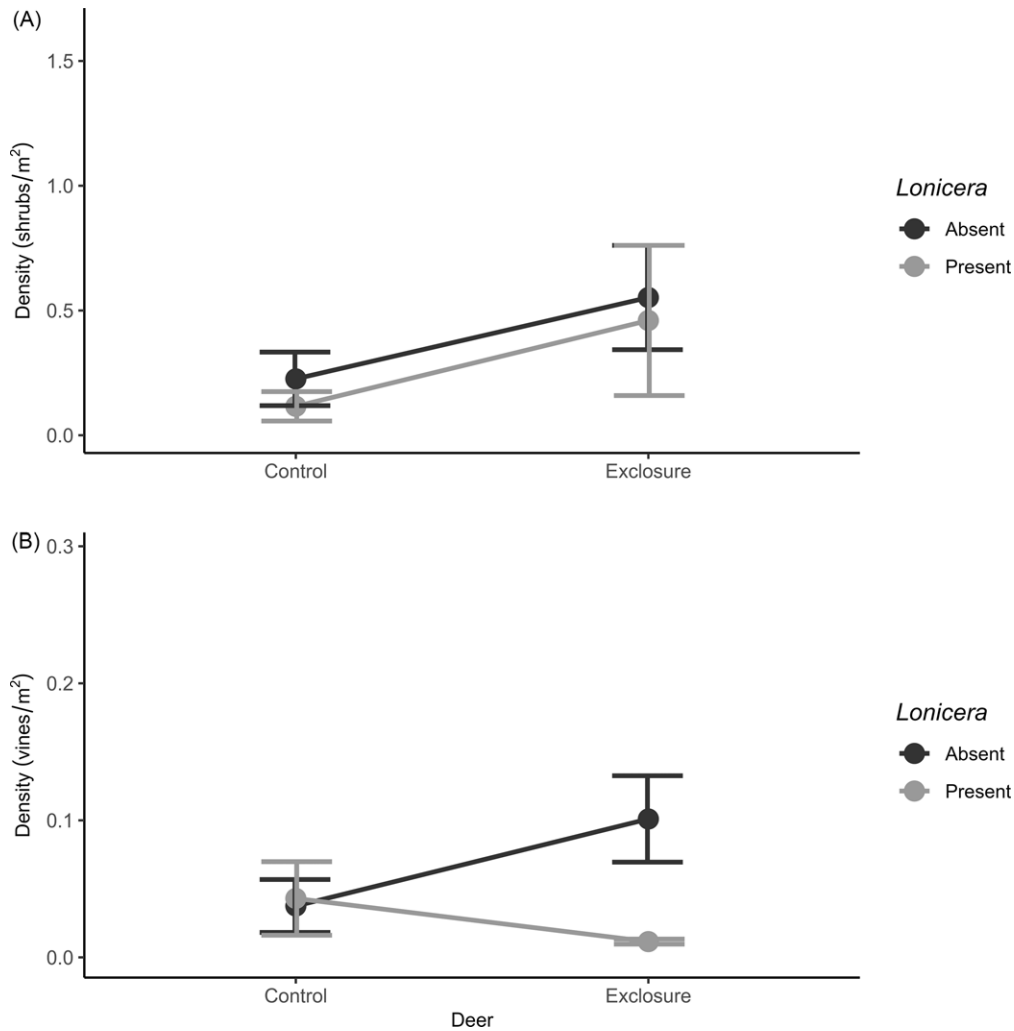
Figure 2. Interaction plot of density (A) shrubs and (B) vines per square meter for 2021 in half-plots where deer had access or were excluded and where *Lonicera maackii* was present or removed. For each treatment combination, mean ± SE of the five sites is plotted.

where deer were excluded and *L. maackii* was removed (Figure 2B; Table 1; Supplementary Table S7). These patterns were due largely to impacts on native vines; nonnative vines as a group were less impacted (Donoso 2022).

Deer effects on vines have not been studied as extensively as effects on tree seedlings and shrubs, but the native vines Virginia creeper [*Parthenocissus quinquefolia* (L.) Planch.] and poison ivy [*Toxicodendron radicans* (L.) Kuntze], and the nonnative vine Japanese honeysuckle (*Lonicera japonica* Thunb.) were indicators of deer exclusion plots in Averill et al.'s (2018) analysis across 23 research sites in the east-central and northeastern United States. In our indicator species analysis (Table 2), three vine species were associated with deer exclusion, but with different interactions with *L. maackii* removal. The nonnative winter creeper [*Euonymous fortunei* (Turcz.) Hand.-Maz.] was an indicator species (in the cover data set) of the combination of deer exclusion and *L. maackii* removal, revealing that release from herbivory was only consequential when not shaded by invasive shrubs. Stem density of *P. quinquefolia* was associated with the same treatment combination, but cover of this vine was an indicator of three of the treatment combinations (all except deer excluded and *L. maackii* present), suggesting that deep shade from unbrowsed

invasive shrubs limits leaf cover of this vine on the forest floor. Stem density of the native vine *S. tamnoides* was associated with three treatment combinations (deer exclosure both with and without *L. maackii* and deer access with *L. maackii* present), implying it is suppressed by deer browse and, in the presence of deer, is facilitated by this invasive shrub, perhaps through impeded browsing.

Lonicera maackii and Cover at 0.3 m

In plots where *L. maackii* was present, *L. maackii* BA was greater where deer were excluded (Table 3; Supplementary Figure S1). Where deer had access, BA showed limited growth from 2015 to 2021, but where deer were excluded, BA increased from 2015 to 2021 (Supplementary Figure S1). The greater BA of *L. maackii* where deer were excluded was due to greater BA of small *L. maackii* shrubs (Figure 3); there was no effect of deer treatment on density of recruits (Table 1) or BA of large shrubs (Table 3) that had crowns well above the height that deer browse (2.1 m).

Percent forest floor cover for photographs taken 0.3 m above the ground was significantly reduced by deer, but there was no effect of *L. maackii* (Figure 4; Table 1). We attribute this to reduced

Table 2. Results of indicator species analysis with P-values of species that are indicative of certain treatment combinations.[a]

Indicator species	Indicator of	Indicator value	P-value
Woody stems			
Prunus serotina	Deer excluded, *L. maackii* removed	0.949	0.0002
Carya cordiformis	Deer excluded, *L. maackii* removed	0.886	0.0016
Euonymus alatus[b]	Deer excluded, *L. maackii* removed	0.931	0.0091
Cercis canadensis	Deer excluded, *L. maackii* removed	0.846	0.0108
Parthenocissus quinquefolia	Deer excluded, *L. maackii* removed	0.829	0.0182
Quercus rubra	Deer excluded, *L. maackii* removed	0.775	0.0342
Ulmus rubra	Deer excluded, *L. maackii* removed + deer excluded, *L. maackii* present	0.770	0.0452
Smilax tamnoides	Deer excluded, *L. maackii* removed + deer excluded, *L. maackii* present + deer access, *L. maackii* present	0.912	0.0494
Spring forest floor % cover			
Acer saccharum	Deer excluded, *L. maackii* removed	0.900	0.0011
Euonymous fortunei[b]	Deer excluded, *L. maackii* removed	0.878	0.0108
Moss	Deer access, *L.* maackii removed + deer access, *L. maackii* present	0.880	0.0092
Polygonum virginianum	Deer access, *L. maackii* removed+ deer access, *L. maackii* present	0.837	0.0118
Carex aurea	Deer excluded, *L. maackii* removed + deer access, *L. maackii* removed + deer access, *L. maackii* present	0.947	0.0171
Parthenocissus quinquefolia	Deer excluded, *L. maackii* removed + deer access, *L. maackii* removed + deer access, *L. maackii* present	0.937	0.0300
Galium circaezans	Deer excluded, *L. maackii* removed + deer access, *L. maackii* removed + deer access, *L. maackii* present	0.856	0.0337
Summer forest floor % cover			
Acer saccharum	Deer excluded, *L. maackii* removed	0.912	0.0007
Euonymous fortunei[b]	Deer excluded, *L. maackii* removed	0.886	0.0056
Polygonatum biflorum	Deer excluded, *L. maackii* removed	0.775	0.0347
Polygonum persicaria	Deer access, *L. maackii* removed	0.759	0.0376
Pilea pumila	Deer access, *L. maackii* removed + deer access, *L. maackii* present	1.000	0.0001
Moss	Deer access, *L. maackii* removed + deer access, *L. maackii* present	0.943	0.0003
Polygonum virginianum	Deer access, *L. maackii* removed + deer access, *L. maackii* present	0.889	0.0037
Ageratina altissima	Deer access, *L. maackii* removed + deer access, *L. maackii* present	0.889	0.0037
Parthenocissus quinquefolia	Deer excluded, *L. maackii* removed + deer access, *L. maackii* removed + deer access, *L. maackii* present	0.958	0.0405
Carex aurea	Deer excluded, *L. maackii* removed + deer access, *L. maackii* removed + deer access, *L. maackii* present	0.931	0.0068
Alliaria petiolata[b]	Deer excluded, *L. maackii* present + deer access, *L. maackii* removed + deer access, *L. maackii* present	0.948	0.0328

[a]Only species where $P < 0.05$ are reported. Indicator values measure the statistical significance of species abundance and any relationship to a treatment(s), with a higher indicator value suggesting greater significance.
[b]Nonnative species.

Table 3. P-values from linear mixed models with site as the random effect of basal area (cm^2) of small *Lonicera maackii* shrubs, large *L. maackii* shrubs, and total *L. maackii* shrubs in summer 2021 in half-plots subjected to a combination of deer (access, exclosure) treatments.

		Deer treatment[a]
Basal area	*L. maackii* small	**0.0124**
	L. maackii large	0.8756
	L. maackii total	**0.0339**

[a]Bold indicates $P < 0.05$.

deer browse on *L. maackii*. Where deer were excluded, *L. maackii* grew more (both in BA [Supplementary Figure S1]) and in leaf cover within the deer browse range [Figure 5].

Although *L. maackii* in its invasive range in North America has been described as benefiting from escape from herbivory (Lieurance and Cipollini 2012), that study assessed only insect herbivores. *Lonicera maackii* does suffer substantial herbivory by deer, particularly in the early spring and late summer (Martinod and Gorchov 2017) and where it is sparse (Wright et al. 2019). Although *L. maackii* is the dominant shrub in these forests, twigs within the deer browse range show high levels of browse damage.

The negative effects of deer on growth of small, but not large, shrubs of *L. maackii* was already evident in 2015 (Peebles-Spencer et al. 2018) and is attributable, we believe, to loss of photosynthetic tissue to deer herbivory. Some other invasive shrubs in eastern North America (other species of *Lonicera*, as well as species of

Euonymus, *Elaeagnus*, *Ligustrum*, and *Rosa*; Averill et al. 2016) are also palatable to deer, and the deer impact on density of shrubs other than *L. maackii* in this study was due to impacts on nonnative species (see above under "Tree Seedlings and Shrubs"). Therefore, it would be compelling to investigate whether abundant deer limit the growth of these invaders and thus mitigate their negative effect on herbaceous plants, as they did with *L. maackii* in this study.

Forest Floor Vegetation

Species Richness
A total of 81 native and 13 nonnative species were identified in subplots in the forest floor layer (Leonard 2022). Neither richness of native species nor nonnative species was affected by treatments (Table 4).

Cover
Cover of native plants was significantly affected by deer treatment and the deer by *L. maackii* interaction (Table 4). Where *L. maackii* was removed, native cover was higher where deer were excluded, but where *L. maackii* was present, it was higher where deer had access (Figure 6). Cover of nonnative species was not affected by treatments (Table 4).

Our finding that deer exclusion reduced native cover where *L. maackii* was present but increased cover where *L. maackii* had been removed was diffuse, rather than attributable to a few common
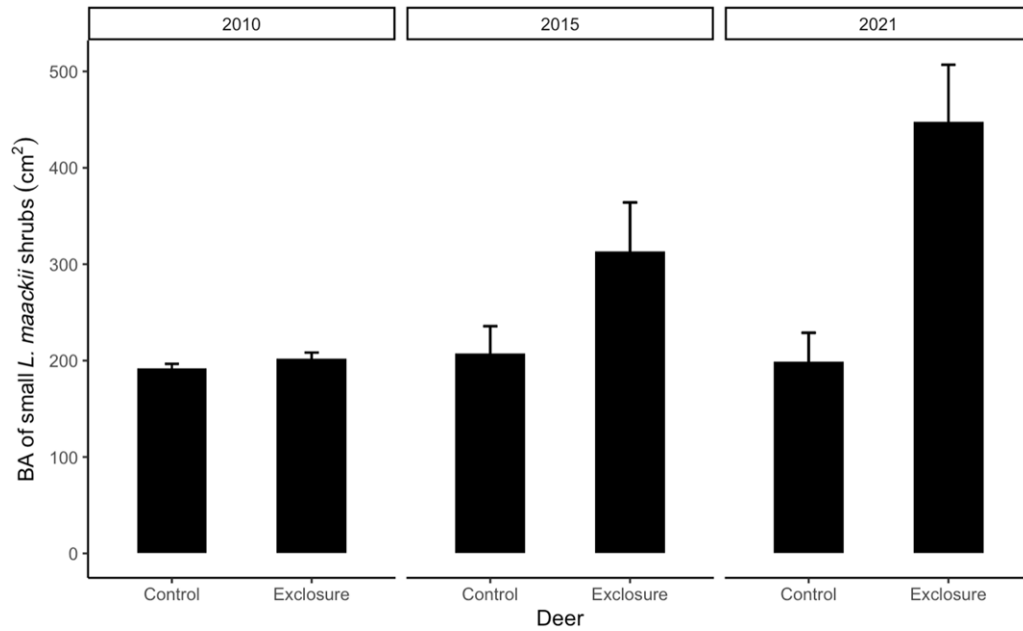
Figure 3. Mean + SE basal area (BA; cm^2) of small *Lonicera maackii* shrubs in 2010, 2015, and 2021 (shrubs with largest stem of basal diameter between 3 and 29 mm) in plots where *L. maackii* was left intact and where deer were excluded or had access. Data from 2010 and 2015 from Peebles-Spencer et al. (2018).
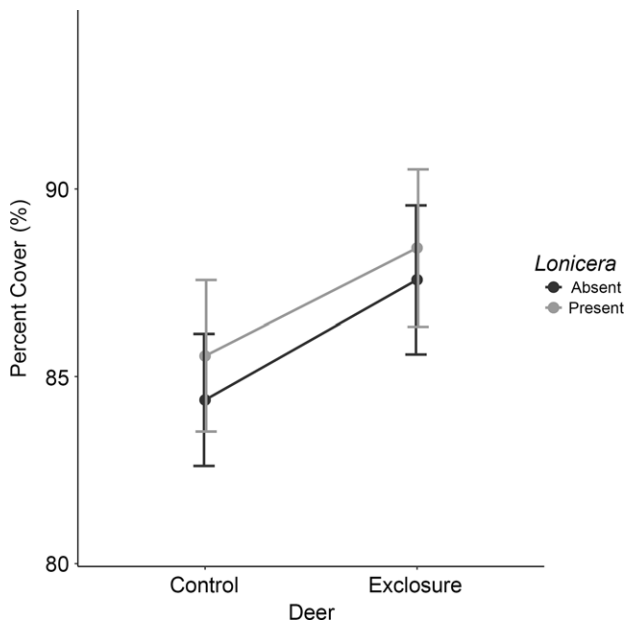

Figure 4. Interaction plot of mean modified percent forest floor cover index values from photographs taken in 2021 in half-plots at 0.3 m above the ground where deer had access or were excluded and where *Lonicera maackii* was present or removed. Data from Western Woods were excluded, as *L. maackii* was mistakenly removed in the deer exclosure × *L. maackii* present half-plot. For each treatment combination, mean ± SE of the four sites is plotted.

Figure 5. Contrasting cover of *Lonicera maackii* outside (left) and inside (right) the deer exclosure in Western Woods, July 7, 2022. When the exclosure was constructed in 2010, this nonnative shrub had the same abundance on both sides of the fence. Since 2010, *L. maackii* has greatly increased in basal area where deer are excluded (Figure 3). Where deer have access, basal diameter growth of this shrub has been lower, and foliage density within the deer browse height range has apparently declined.

species, as few species were indicators (see Table 2) of only the treatment combination of deer exclusion and *L. maackii* removal. We attribute these patterns to greater cover of *L. maackii* where it was released from deer browse, increasing its shading effect on the forest floor. Runkle et al. (2007) found *L. maackii* removal plots had greater ground-level cover than control plots after 8 yr, consistent

with our finding for deer exclosure plots, but contrasting with the lack of effect we saw where deer had access. This suggests deer browse intensity was not great at Runkle et al.'s (2007) study site.

Our finding that deer exclusion resulted in lower native cover (where *L. maackii* was present) was surprising and in contrast to Averill et al.'s (2018) finding that deer exclusion resulted in higher native richness and abundance. We think the negative effects of deer exclusion were due to the dense cover of *L. maackii* in the exclosures, which in turn was due to the high density of this invasive shrub in our study area, combined with 11 yr of growth without recurring browsing by deer.

Table 4. Adjusted P-values from split-plot two-way ANOVAs of species richness and percent cover of forest floor vegetation in half-plots with two deer treatments (access, exclosure) and two *Lonicera maackii* treatments (removed, present).[a]

		Season	Deer treatment	*L. maackii* treatment	Interaction
Richness	Native spp.	Spring	0.680	0.625	0.202
	Nonnative spp.	Spring	0.291	0.897	0.291
Cover	Bare ground	Summer	**0.014**	0.788	0.812
	Native	Spring	**0.014**	0.856	**0.020**
	Nonnative ##	Spring	0.519	0.278	0.283
	Trees ##	Spring	*0.060*	0.278	0.202
	Shrubs ##	Summer	0.217	0.278	0.436
	Vines #	Summer	0.217	0.552	0.202
	Graminoids	Spring	*0.060*	0.788	0.384
	Annuals ##	Spring	**0.015**	1.000	0.812
	SprPer #	Spring	0.519	0.788	0.291
	SumPer ##	Spring	0.519	0.278	0.812

[a]For each variable, we analyzed the season (spring or summer) with the higher overall mean. P-values have been adjusted to control for the false discovery (type 1 error) rate (see "Materials and Methods"). Unadjusted P-values, as well as test statistics, are in Supplementary Tables S8 and S9. **Bold** indicates P < 0.05. *Italics* indicates P < 0.1. # indicates log-transformed, ## indicates analysis of ranks. SprPer are spring perennials, and SumPer are summer perennials.
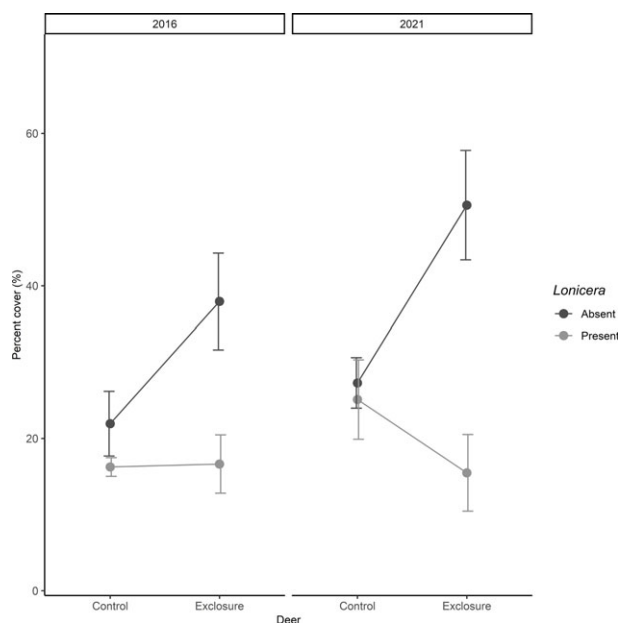

Figure 6. Interaction plots of percent cover of native species in spring 2016 and 2021 in half-plots where deer had access (control) or were excluded (exclosure) and *L. maackii* was removed (absent) or present. For each treatment combination, mean ± SE of the five sites is plotted.

Our finding that nonnative cover was not affected by deer contrasts with an analysis of 23 sites (Averill et al. 2018), which found greater nonnative cover in deer access plots. That pattern was due largely to Japanese stilt grass [*Microstegium vimineum* (Trin.) A. Camus] and garlic mustard [*Alliaria petiolata* (M. Bieb.) Cavara & Grande], species that are unpalatable to deer (Averill et al. 2016) that likely benefit from reduced competition with native plants where the latter are browsed. *Microstegium vimineum* was not present at our sites, and the greater cover of *A. petiolata* in deer access plots was countered by lower cover of woody nonnative species (*L. obtusifolium*, *L. japonica*, multiflora rose (*Rosa multiflora* Thunb.), and *E. alatus*). The only woody nonnative with higher cover in deer access plots was *C. orbiculatus* (Table 2).

Cover of Different Growth Forms and Indicator Species

Tree seedling cover tended to be higher in deer exclosures (P = 0.06) but was not affected by *L. maackii* treatment (Table 4;

Figure 7A). In contrast, annual cover was lower and graminoid cover tended to be lower (P = 0.06) in exclosures; neither was affected by the *L. maackii* treatment (Table 4; Figure 7B and 7C). Cover of shrubs, vines, spring perennials, and summer perennials showed no effects of either treatment (Table 4).

In the indicator species analysis based on cover, only the spring perennial smooth Solomon's seal [*Polygonatum biflorum* (Walter) Elliott] and the nonnative vine *E. fortunei* (discussed earlier) were indicators of the deer exclusion by *L. maackii* removal treatment combination (Table 2). The only species that was an indicator of only deer access by *L. maackii* removal was spotted ladysthumb (*Polygonum persicaria* L.); this species can grow as an annual or perennial and was classified as a summer perennial in this study. Moss, the native annual Canadian clearweed [*Pilea pumila* (L.) A. Gray], and the summer perennials jumpseed (*Polygonum virginianum* L.) and white snakeroot [*Ageratina altissima* (L.) R.M. King & H. Rob.] were indicators of deer access (*L. maackii* presence and removal). Three species were uncommon where deer were excluded and *L. maackii* was present; they were indicators of the other three treatment combinations: the graminoid golden sedge (*Carex aurea* Nutt.), the native vine *P. quinquefolia*, and the summer perennial licorice bedstraw (*Galium circaezans* Michx.). Although the nonnative biennial *A. petiolata* was an indicator of three treatment combinations in summer, we do not attach importance to this, as this species was not an indicator in spring, when it was at much higher cover.

Analysis of how different plant growth forms responded to treatments sheds light on how deer and *L. maackii* interact to shape forest floor vegetation. Our findings that cover of annuals and cover of the annual *P. pumila* were associated with the deer access treatment were similar to Averill et al.'s (2018) finding that *P. pumila*, as well as the annual common threeseed mercury (*Acalypha rhomboidea* Raf.), were among the few native species to be indicator species of deer access. We attribute the higher cover of annuals to the greater bare ground cover where deer had access (Table 4; Figure 7D), reasoning that germination and establishment of annuals is impeded by leaf litter (Facelli and Pickett 1991; Oswalt and Oswalt 2007). Consistent with this difference in bare ground, Mahon and Crist (2019) found greater litter biomass in these deer exclosures in 2015 to 2017. Lower litter biomass (and greater bare ground) are attributable to more rapid leaf decomposition where deer have access, which in turn was attributed to elevated abundance of nonnative earthworms
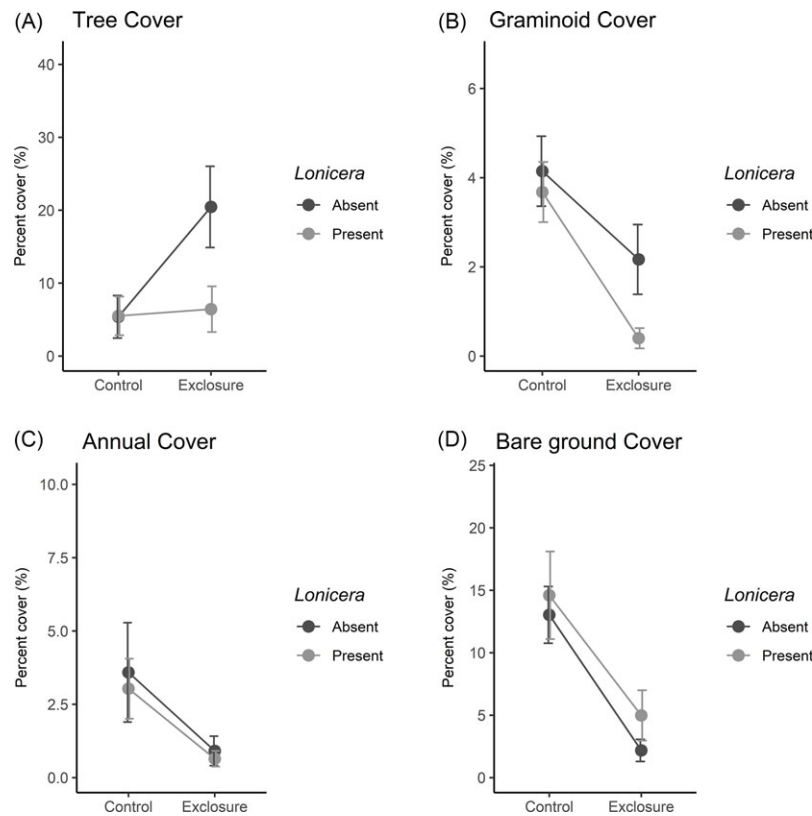
Figure 7. Interaction plots of (A) tree seedling, (B) graminoid, and (C) annual cover in the forest floor layer in spring 2021, and (D) bare ground cover in summer 2021, in half-plots where deer had access or were excluded and *Lonicera maackii* was present or removed.

(Mahon et al. 2020). Other studies have also reported deer elevating earthworm abundance (Cope and Burns 2019; Fisichelli and Miller 2018) and reducing litter depth (Lessard et al. 2012). Christopher et al. (2014) did not measure litter, but found that deer had the opposite effect on annuals, which were less abundant where deer had access.

Our finding that cover of graminoids tended to be higher where deer had access is consistent with previous studies (Rooney 2009) that found deer promote graminoids. Individual common graminoid species generally followed this same pattern of greater abundance where deer have access. The only graminoid among our indicator species, *C. aurea*, was an indicator of three treatments: both of the deer access treatments as well as the deer exclosure by *L. maackii* removal treatment. The most common graminoid in our plots, Virginia wildrye (*Elymus virginicus* L.), had three times higher cover in deer access versus deer exclosure plots (Leonard 2022). Similarly, the only native graminoid among the native species in Averill et al.'s (2018) indicator analysis, sweet woodreed (*Cinna arundinacea* L.), was an indicator of deer access. Christopher et al. (2014) found deer increased total graminoid abundance but had no effect on rosy sedge (*Carex rosea* Schkuhr ex Willd.).

Our finding that cover of spring perennials and summer perennials was not affected by deer or *L. maackii* contrasts with Christopher et al.'s (2014) finding that spring perennial cover was greatest where deer were excluded and *L. maackii* was removed. The lack of treatment effects on perennial cover may be due to (1) contrasting effects on different plant species within each growth form, depending on their palatability to deer and tolerance to shade from *L. maackii*; and/or (2) scarcity of browse-sensitive herbs at

this site. Of 26 common herb species considered palatable to deer in eastern deciduous forests (Rawinski 2014), only three were present in our samples. One of these, *P. biflorum* was an indicator species of the deer exclosure by *L. maackii* removal treatment, but the other two were sparse in our plots. Some summer perennials were not preferred by deer: *P. virginianum* and *A. altissima* were indicators of the deer access treatments, and *G. circaezans* was an indicator of both deer access treatments as well as the deer exclosure by *L. maackii* removal treatment.

Changes Subsequent to Earlier Assessment of This Experiment

Our findings on the effects of deer and *L. maackii* on the forest understory 11 yr into this experiment contrast with the findings after 5 to 6 yr (Haffey and Gorchov 2019). In general, deer effects became more prevalent, and *L. maackii* effects less prevalent, over this interval. Native cover showed a notable change in treatment effects over time (Figure 6). In 2016, this was not affected by treatments, but by 2021 it increased where deer were excluded and *L. maackii* was removed and was lowest where deer were excluded and *L. maackii* was present. We attribute this to the dense cover of *L. maackii* in the exclosures, due to the additional years of release from deer herbivory, with shading exceeding any direct positive effects of deer exclusion on native cover.

Although tree seedling richness and density already showed positive effects of deer exclusion in 2015, both increased substantially from 2015 to 2021 where deer were excluded and *L. maackii* was removed, while remaining low in the other treatments (Figure 1). We attribute the time lag in these synergistic

interactions to the years needed for large numbers of seedlings to reach the 30-cm height threshold when released from browse and shade.

This factorial experiment enabled us to distinguish the effects of exclusion of deer and removal of the invasive shrub *L. maackii* on all elements of the plant community, as well as the effects of the interactions of these treatments. Deer negatively affected woody plants, with *L. maackii* only reducing vine density, and only where deer were excluded. Deer and *L. maackii* had few direct negative effects on herbaceous plants, but deer impacts on native cover depended on *L. maackii* treatment: where this invasive shrub was present, deer increased native cover by reducing *L. maackii* cover, whereas where the invasive was removed, deer reduced native cover.

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