ABSTRACT

LONG-TERM INTERACTIVE IMPACTS OF THE INVASIVE SHRUB, *LONICERA MAACKII,* AND WHITE-TAILED DEER, *ODOCOILEUS VIRGINIANUS,* ON WOODY VEGETATION

By Marco Uriel Donoso

Direct effects of white-tailed deer (*Odocoileus virginianus*) and the invasive shrub *Lonicera maackii* on woody vegetation are well documented, but studies exploring their long-term interactive effects are limited. I investigated effects after 11 years of deer exclusion or access and *L. maackii* removal or presence on woody vegetation responses in the Miami University Natural Areas in Oxford, Ohio. Deer exclusion resulted in greater tree seedling richness, density, and basal area, native and non-native shrub richness, native vine density and basal area, change in understory tree richness since 2015, and cover at 0.3 m above ground. Deer exclusion also resulted in greater basal area growth of *L. maackii* shrubs. *Lonicera maackii,* in contrast, had no direct effects. Deer and *L. maackii* interactions impacted native tree seedling richness and density, and total vine density. All significant interactions revealed synergy between deer exclusion and *L. maackii* removal, most likely due to deer reducing *L. maackii* cover (via herbivory) and therefore mitigating its negative competitive effects on seedlings and vines Therefore, in areas with high deer densities and dense *L. maackii* stands, I recommend a reduction of both stressors to prevent tree regeneration failure.

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I. INTRODUCTION AND BACKGROUND

Invasive understory shrubs have demonstrated various negative impacts on native woody vegetation in forest understories (Boyce 2009). The presence of invasive shrubs can promote regeneration failure (Miller and McGill 2019), the inability of current tree species to regenerate, in forest understories via reduced native tree seedling diversity, modification of soil nutrient dynamics, competition for resources, and promotion of other invasive species (Merriam and Feil 2002; Ehrenfeld et al. 2001; Frappier et al. 2003; Hartman and McCarthy 2004; Boyce 2009; Shields et. al 2015).

One such invasive shrub is *Lonicera maackii* (Rupr.) Herder (Amur honeysuckle), a large shrub native to East Asia that was introduced and has spread across much of the eastern United States. *Lonicera maackii* is known to negatively impact native woody vegetation in mature forest understories (reviewed by McNeish and McEwan 2016). Several studies have shown that *L. maackii* reduced growth, richness, and density of native woody plants (Hutchinson and Vankat 1997; Shields et al. 2015). Miller and Gorchov (2004) proposed that because *L. maackii* has a long photosynthetic season, expanding its leaves earlier (McEwan et al. 2009) and retaining them later in the winter (McEwan et al. 2009; Wilfong et al. 2009), it successfully competes with native species for light (Shields et al. 2015). Comparative studies suggest that areas not yet invaded by *L. maackii* have greater richness and densities of tree seedlings as well as greater richness of herbs (Collier et al. 2002; Hartman and McCarthy 2008).

In addition to the negative impacts of invasive shrubs, negative impacts of certain ungulates on native woody vegetation in forest understories have been well recognized (Waller and Alverson 1997; Rooney and Waller 2003; Russell et al. 2017). *Odocoileus virginianus* (white-tailed deer, hereafter 'deer'), an ungulate, is a keystone species that has experienced drastic increases in population density in many parts of the United States (Rooney 2001). Deer are ungulate browsers that, in high densities, adversely affect woody species survival, recruitment and growth (Waller and Alverson 1997; Rooney 2001; Horsley et al. 2003; Rooney & Waller 2003; Habeck and Shultz 2015; Bradshaw and Waller 2016). Densities greater than ~20 deer/sq mi are expected to impact forest regeneration (Tilghman 1989; Horsley et al. 2003; Nuttle et al. 2014). As deer are selective herbivores, they directly seek out leaves and branches of highly palatable tree species, resulting in greater densities of lesser palatable species in forest understories (Frelich and Lorimer 1985; Tilghman 1989; Horsley et al. 2003; Bradshaw and Waller 2016; Ward et al. 2018). This intense deer browse pressure results in regeneration failure of highly palatable species, resulting in significant changes to overall forest structure, composition, and ecosystem services (Tilghman 1989; Rooney et al. 2002; Horsely et al. 2003; Rooney & Waller 2003; Bradshaw and Waller 2016; Ward et al. 2018).

Although the direct effects of deer and *L. maackii* are well documented in the literature, less is known of the interaction effects between the two stressors and different ways these stressors interact to impact vegetation. The effects of deer and the invasive plant may be additive, where both species directly impact native plant responses without any interactive effects (Fig. A1, top) (Peebles-Spencer et al. 2017; Gorchov et al. 2021), as deer and invasive plants impact plant communities in different ways. Sub-additive interactions occur if the joint negative effect of deer access and invasive plant presence on the native plant response are less negative than the additive response of the individual treatments (Fig. A1, bottom) (Peebles-Spencer et al. 2017; Gorchov et al. 2021). This interaction is also viewed as synergistic as the joint positive effect of excluding deer and removing the invasive plant is greater than the sum of the individual effects (Gorchov et al. 2021). This interaction results if deer do not browse in areas where the invasive plant is abundant as the shrubs act as a physical barrier, thereby mitigating the negative effect of deer browse on tree seedlings (Peebles-Spencer and Gorchov 2017). This sub-additive interaction also results if deer actively browse on *L. maackii* shrubs in the understory (Martinod and Gorchov 2017), reducing its overall cover (Peebles-Spencer et al. 2018) and diminishing negative impacts on native plants.

Knowledge of direct effects of invasive plants and deer browse on native plants is extensive, but there are limited long term studies focused on their interactions. Out of 25 publications in eastern North America investigating deer and invasive plant interactions experimentally, only ten publications involved studies greater than five years (Gorchov et al. 2021). Several of these studies found that deer and invasive plant interaction effects caused various deleterious effects on native plants. One long-term study (> 8 year) involving deer exclosures and the removal of *Alliaria petiolata* found interactive effects of deer and invasive plants on soil chemistry conditions, arbuscular mycorrhizae community structure, and *Trillium erectum* survival (Burke et al. 2019). Additionally, Waller and Maas (2013) identified synergistic interactive effects of deer exclusion and the removal of invasive *A. petiolata* on the growth of *Quercus rubra* (red oak) seedlings. Bourg et al. (2017) also found synergistic interactive effects on native herb richness after five years of deer exclusion and invasive plant removal. Alternatively, numerous studies have found no deer and invasive plant interactive effects on forest understories. Dornbush and Hahn (2013) found only additive deer and *A. petiolata* effects on native woody species after four years of deer exclusion and invasive removal. Aronson and Handel (2011) also found only additive effects of deer exclusion and *Microstegium vimineum* removal on growth and survival of native tree seedlings. Results from these and other related studies suggest that long-term deer and invasive plant interaction effects on native plants are variable. Based on these and other reviewed studies, Gorchov et al. (2021) concluded that deer were more impactful than invasive plants and that the interaction of deer and invasive plants on native plant species was infrequently significant. Where interactions were significant, they were usually synergistic in nature, where the removal of both stressors had greater combined impacts than removing only deer or only the invasive plant (Gorchov et al. 2021).

To better understand the long-term (>10 years) direct and interactive effects of the deer and *L maackii* treatments on richness, density, and basal area of woody vegetation, I reassessed the plots investigated from 2011 to 2014 by Peebles-Spencer et al. (2017) and in 2015 by Haffey and Gorchov (2019). The goal of this study was to investigate the effects of deer, *L. maackii,* and their interactions, including whether they have become more apparent over time. Given that previous studies at my site identified trends of sub-additive interactive effects of deer and *L. maackii* on certain response variables (Peebles-Spencer et al. 2017; Haffey and Gorchov 2019), I hypothesize that deer and *L. maackii* interact sub-additively to impact woody plants. I predicted that woody plant response variables would be much greater where deer were excluded and *L. maackii* was removed compared to the other treatment combinations. I also predicted that woody plant response variables would be greater after 11 years compared to 5 years of deer exclusion and *L. maackii* removal. In addition to identifying long-term direct and interactive effects of deer and *L. maackii* on woody vegetation, I also investigated the long-term treatment effects on light availability at 0.3 m above ground for all sites. Finally, to determine whether deer limited *L. maackii* growth, I measured the basal area of all *L. maackii* shrubs in 2021 and compared them to earlier values.

II. STUDY SITE AND PREVIOUS RESEARCH

Study Site

This study was conducted across five sites located in the Miami University Natural Areas in Oxford, Ohio (39°29'–39°31'N, 84°42'–84°43'). The Miami University Natural Areas consist of ~400 ha, most of which is early successional to mature eastern deciduous forest. Each site contains a deer exclosure and a paired deer access plot; these were established in 2010 (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 0.58–1.57 m^2 ha^{-1}, Peebles-Spencer 2016). Deer densities of all site locations were estimated during winter and early spring in 2014 (Barrett 2014) and during spring and summer in 2017 (Peterson 2018) (Table A1). Estimated densities across most sites in spring and summer remained below the ~20 deer/sq mi expected to impact forest regeneration (Tilghman 1989; Horsley et al. 2003). Western Woods and Bachelor Preserve were the only two sites to have deer densities above the ~20 deer/sq mi threshold (Table A1).

At each site, two 20 x 20 m plots were randomly assigned to deer access and deer exclosure treatments, with fencing 3 m high placed only around deer exclosures. One half of each plot (10 m x 20 m, exclosure and access) was randomly assigned as *L. maackii* intact or removed (Peebles-Spencer et al. 2017). 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, an herbicide composed of a mixture of 5.4% Picloram and 20.9% Dicholorphenoxyacetic acid (Dow AgroSciences 2011). Clipping and herbicide application of all *L. maackii* shrubs in removal half-plots occurred in 2010 and again in 2011 as resprouting had occurred (Peebles-Spencer et al. 2017). Clipping and reapplication of herbicide on new *L. maackii* recruits occurred again in 2015 (Haffey and Gorchov 2019) and in 2021.

Previous Research

In each half plot established in 2010, Peebles-Spencer et al. (2017) identified and measured cover of various growth forms twice per growing season from 2011 to 2014 using modified versions of Daubenmire plots (Abrahamson et al. 2011). Peebles-Spencer et al. (2017) then analyzed various plant responses for all treatments to investigate the direct effects of deer and *L. maackii* and their interaction on the forest floor. In spring and summer 2014, there was a significant positive effect of *L. maackii* removal on cover of tree seedlings, spring perennial forbs, vines, and graminoids (Peebles-Spencer et al. 2017). In summer of 2014, there was a significant positive effect of deer exclusion on tree seedlings and shrubs. Peebles-Spencer et al. (2017) identified one significant synergistic interaction between the deer access and *L. maackii* presence treatment on bare ground cover in spring 2013. Peebles-Spencer et al. (2017) also identified a trend for a sub-additive deer**L. maackii* interaction effect on species richness during summer seasons of the study.

Peebles-Spencer et al. (2017) also noted that deer browse on *L. maackii* may be sufficient to reduce its cover and therefore mitigate negative effects on certain growth forms. They found greater cover of *L. maackii* shrubs between 0.5 and 1.5 m tall where deer were excluded, evidence that deer actively suppressed the growth of *L. maackii.* Additionally, Peebles-Spencer et al. (2018) found that the basal area of small *L. maackii* shrubs (shrubs with largest stem between 3-29 mm in basal diameter) was greater where deer were excluded, providing evidence that deer reduced growth of *L. maackii* shrubs. This trend was also supported by Martinod and Gorchov (2017), who found that that deer actively browsed on *L. maackii* twigs throughout the year.

Haffey and Gorchov (2019) reassessed the forest floor in the paired plots at each site during spring and summer 2016 using the same methods as Peebles-Spencer et al. (2017). Haffey and Gorchov (2019) found that deer exclusion significantly increased understory richness, cover of annuals, and bare ground cover. Where *L. maackii* was removed, Haffey and Gorchov (2019) found greater total cover, greater non-native species richness, and greater total species richness. These results were only significant after the first four years of growth, emphasizing the need for more long-term studies (>4 years) to accurately determine how deer and *L. maackii* impact plant communities. In addition to the direct effects of deer and *L. maackii* on the forest floor, Haffey and Gorchov (2019) observed several significant synergistic deer and *L. maackii* interaction effects on spring tree seedling cover, summer vine cover, and spring perennial cover.

In addition to analyzing forest floor vegetation, Haffey and Gorchov (2019) identified and measured every tree seedling and shrub in 2015 in each half-plot between 0.3 m and 2 m tall, the typical deer browse height range (Frelich and Lorimer 1985). They found that deer exclusion significantly increased native tree seedling density, richness, and shrub basal area, results that were attributed to release of browse pressure. However, there were no *L. maackii* or interaction effects on woody plant responses.

III. METHODS

Woody Stems

To determine effects of deer exclusion and *L. maackii* removal, in summer 2021, within each half-plot at each site, I identified and measured the basal diameter of all woody stems taller than 0.3 m, counting stems of species within 10 cm of each other as the same individual (Haffey and Gorchov 2019). Stems were classified as trees, shrubs, or vines (i.e., all shrub response variables reported exclude *L. maackii*). Seedlings were classified as being between 0.3 and 2 m tall, the typical deer browse height (Frelich and Lorimer 1985). Shrubs and vines taller than 2 m were grouped with all other shrubs and vines. Tree stems taller than 2 m with diameter at breast height (DBH) <10 cm were considered understory trees while those with DBH >10 cm were considered overstory trees. Native and non-native status for shrubs and vines was determined using USDA (2016). All trees were native species. Within each half-plot, basal diameter measurements were used to calculate basal area (BA) for seedlings, shrubs, and vines. Basal diameter was used to determine BA for woody stems shorter than 2 m whereas DBH was used for stems taller than 2 m. For my analysis, stems ≥ 2 m with DBH<10 cm in 2015 were considered understory trees, even if the DBH had increased above 10 cm in 2021. Change in understory tree richness and BA was determined by subtracting 2015 values from 2021 across each plot. All vegetation sampling was performed prior to *L. maackii* removal.

L. maackii shrubs

To determine the effects of deer on *L. maackii* growth, I measured the basal diameter of every *L. maackii* shrub within each half-plot at each site to determine the basal area of all *L. maackii* shrubs and compared it to *L. maackii* measurements from earlier years. I distinguished three different size classes of *L. maackii* shrubs based on the basal diameter of the largest stem, using criteria that were used in 2015 by 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 (0.3 to 2.1 m, Frelich and Lorimer 1985). 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 of the largest stem between to the other size classes (3-29 mm) were considered small. *L. maackii* stems within 10 cm of each other were considered stems of the same individual.

Canopy Cover

To investigate deer and *L. maackii* impacts on light availability within half-plots, I took 16 photographs of the canopy at 0.3 m above ground along two transects established along the interior of each half-plot (Fig. 1) from August 1st to August 24th. Photographs were taken using a Samsung Galaxy S10 which utilizes a 10-megapixel front facing camera module. To ensure that all photographs taken were level, the Samsung Galaxy and an iPhone 11 were placed next to each other on a flat clipboard. The Measure application was open on the iPhone while every photograph was being taken to ensure a level surface at each location along the transect. The Measure app was tested to ensure accuracy using a beam level prior to being utilized in the field. The Measure app was used in lieu of the beam level due to greater visibility of level status under dense vegetation. All photographs taken were then analyzed using the mobile app GLAMA (percent cover using Gap Light Analysis Mobile Application) (Tichý 2014) available on the Android operating system to determine canopy openness, percent cover, canopy cover index, and modified canopy cover index. 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.

Site Differences

To determine differences in canopy tree composition, BA of large trees, and percent canopy cover among sites, I established a 40 x 40 m plot based on the center of 20 x 20 m treatment plots at each site. Plot size was determined by the maximum distance allowed without overlap between the paired deer treatment plots. Within each 40 x 40 m plot, I took 9 canopy photographs at 2 m above ground at each site inside each half-plot and around the exterior of each 20 x 20 m plot (Fig. 1). Within the 40 x 40 m plots at each site, I identified and measured all overstory trees in addition to those already sampled in the 20 x 20 m plots. All overstory trees were native species. Basal area (m^2/ha) of overstory trees, overstory tree composition, and modified canopy cover index values were used to determine differences among sites.

Data Analysis

For seedlings, shrubs, vines, and change in understory trees, response variables were pooled for each half-plot for analyses. For seedlings, shrubs (total, native, non-native), and understory trees, deer and *L. maackii* treatment effects on species richness, density, and basal area were assessed. For vines (total, native, non-native), only density and basal area were assessed 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 effects models via Satterthwaites' df method, Kuznetsova et al. 2017) packages. A split-plot ANOVA was performed using lmer while assuming Gaussian responses for richness, density, and basal area. P-values were obtained via Satterthwaites' degrees of freedom method. Values of $p \leq 0.05$ were considered significant.

For *L. maackii* analysis, I investigated treatment effects of deer on basal area of all shrubs as well as small shrubs in half-plots where *L. maackii* was not removed. I also investigated the effects of deer on recruitment of *L. maackii* using recruits in half-plots where the shrub was removed and where it remained intact. Analyses focused only on deer effects on *L. maackii* involved using a linear mixed effect model with site as the random effect. Analysis of *L. maackii* recruits involved used glmer while assuming Poisson responses for density. Analysis of small *L. maackii* shrubs used lmer, a linear mixed effects model with site as the random effect.

Deer and *L. maackii* treatment effects were also assessed for percent forest floor cover at 0.3 m above ground using the GLAMA app. Canopy cover for all canopy photographs was determined using the GLAMA app (Tichý 2014, 2016). 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. Since 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 above ground from Western Woods were excluded from analysis as I mistakenly cut *L. maackii* in the *L. maackii* present half-plot in the deer access plot, which influenced percent forest floor cover values at the site.

To determine if the presence of a certain species was indicative of certain combinations of treatments, indicator species analyses was also performed using the indicspecies package (De Cáceres and Legendre 2009, 2010) in R. I used the multipatt, IndVal.g function and the total number of stems of each woody species to investigate the relationship among species presence and deer and *L. maackii* treatments. Indicator species analysis was performed using abundances of each species of tree seedlings, shrubs, and vines for summer 2021.

Seedlings were grouped into deer palatability classes compiled by Koon 2022 (Master's Thesis). These deer palatability classes were based on deer preference during summer months that was investigated by Latham et al. (2005) and other sources. Seedlings were grouped into different deer palatability classes (high, moderate, low, no preference) and were then grouped by treatment to determine average seedling abundance in each treatment combination.

Seedlings were also grouped into shade tolerance classes based on Niinemets and Valladares (2006). Shade tolerance categories for seedlings were classified as high (>3.75), medium (2.75<x<3.75), and low (<2.75) (Fig. A2). Seedlings were then grouped by treatment to determine average abundance of seedlings of varying shade tolerance classes in each treatment combination.

IV. RESULTS

Site differences

Within all 40 x 40 m plots at all sites, there were 28 species and a total of 416 stems that were classified as overstory trees (Table A2). The five most common species were *Acer saccharum* (256 stems), *Quercus alba* (19 stems), *Carya cordiformis* (15 stems), *Quercus muehlenbergii* (15 stems), and *Quercus rubra* (14 stems). These five species represent 76.7% of all large stems. Western Woods had the lowest number of tree species (14); College Woods had the most tree species (23).

Basal area (m^2/ha) for overstory trees differed among sites, with greatest basal area at Bachelor Preserve, followed by (in decreasing order) College Woods, Reinhart Preserve, Kramer Preserve, and Western Woods (Table A3). For photographs taken at 2 m above ground, modified canopy cover was greatest at Reinhart Preserve, followed by (in decreasing order) Western Woods, Kramer Preserve, Bachelor Preserve, and College Woods (Appendix Table A3). Canopy cover showed no relationship to basal area (m^2/ha) of overstory trees across plots (Fig. 2, Table A3).

Tree seedlings

A total of 28 species with 2,137 individual stems were measured and identified as tree seedlings (0.3- 2 m height) across the 20 x 20 m study plots. Species with the greatest number of seedlings present included *Fraxinus americana* (white ash, 843 stems), *P. serotina* (black cherry, 520 stems), *Fraxinus quadrangulata* (blue ash, 177 stems), and *Asimina triloba* (pawpaw, 105 stems) (Table A4). These four tree species represented 76.9% of all seedlings encountered within the study plots.

Deer significantly reduced seedling richness and density with no effect of *L. maackii* on either response (Tables 1, A5). There was also a significant synergistic deer and *L. maackii* interaction effect, with greatest richness and density where deer were excluded and *L. maackii* was removed (Figs. 3, 4). Tree seedling basal area showed a weak negative effect of deer, but no effect of *L.*

maackii (Table 1). There was a weak synergistic deer and *L. maackii* interaction, with greatest basal area where deer were excluded and *L. maackii* was removed (Fig. 5, Table 1).

Shrubs

Deer significantly reduced total shrub species richness and non-native shrub richness, but there was no *L. maackii* or interaction effect on either variable (Figs. 6, 7, Tables 1, A6, A7, A8). Deer impacts on the BA of total and non-native shrubs were weak, but there was no *L. maackii* interaction effect (Table 1). There was no significant effect of deer, *L. maackii*, or their interaction on richness, density, or BA of native shrubs (Tables 1, A8, A9).

Vines

Species richness analysis was not performed on vines as the number of species per plot was too low, ranging only from 1 to 5 across treatments and sites. Total vine stem density showed no direct effect of deer or *L. maackii,* but there was a significant synergistic deer and *L. maackii* interaction effect, with greatest density where deer were excluded and *L. maackii* was removed (Fig. 8, Tables 1, A10). Total vine basal area showed no direct effect of deer or *L. maackii,* but there was a weak synergistic deer and *L. maackii* interaction effect, with greatest basal area where deer were excluded and *L. maackii* was removed (Tables 1, A10). Native vine density showed a weak negative effect of deer, no effect of *L. maackii*, and a weak synergistic deer and *L. maackii* interaction effect, with greatest density where deer were excluded and *L. maackii* was removed (Fig. 9, Tables 1, A11). Non-native vine density showed no direct deer or *L. maackii* effect, but there was a weak synergistic deer and *L. maackii* interaction effect, with greatest density where deer were excluded and *L. maackii* was removed (Tables 1, A12). There was no effect of deer, *L. maackii,* or their interaction on native or non-native vine basal area (Table 1).

Change in understory trees

Deer significantly affected change in understory tree richness from 2015 to 2021 (Fig. 10, Tables 1, A13), where deer exclusion resulted in greater understory tree richness. There were no *L. maackii* or interaction effects on change in understory richness. *L. maackii* contributions to change in understory tree basal area from 2015 to 2021 were weak (Fig. 11, Tables 1, A13), but there were no deer or interactive effects. There was no significant effect of deer, *L. maackii,* or their interaction on change in understory density from 2015 to 2021 (Tables 1, A13).

Lonicera maackii

In plots where *L. maackii* was present, total 2021 *L. maackii* basal area was greater where deer were excluded than where deer had access (Fig. 12, Table 2). Where deer had access, mean basal area showed limited growth from 2015 to 2021, but where deer were excluded, mean basal area increased from 2015 to 2021 (Fig. 12). At Bachelor Preserve, Reinhart Preserve, and Western Woods, *L. maackii* basal area was greater where deer were excluded than where deer had access for both 2015 and 2021 (Fig. 13). At Kramer Preserve, 2015 basal area was similar whether deer had access or were excluded, but greater where deer were excluded in 2021 (Fig. 13). At College Woods, basal area was greater where deer had access for both 2015 and 2021 (Fig. 13).

In plots where *L. maackii* was present, there was a significant negative effect of deer on basal area of small *L. maackii* shrubs (shrubs with largest stem 3-29 mm in basal diameter) (Fig. 14, Table 2), with lower basal area where deer had access than where deer were excluded. For the number of *L. maackii* recruits (shrubs with largest stem basal diameter ≤ 2 mm), there was no effect of deer or *L. maackii* but there was a weak interaction effect (Table 2), with lowest recruit counts where deer were excluded and *L. maackii* was removed (Fig. 15).

Forest floor Cover

Percent forest floor cover for photographs taken 0.3 m above ground was significantly reduced by deer, but there was no effect of *L. maackii* or their interaction (Fig. 16, Tables 1, 3). Western Woods was excluded from forest floor percent cover analysis due to accidentally removing *L. maackii* shrubs in the *L. maackii* present x deer access plot.

Indicator species

Indicator species of a combination of deer exclusion and *L. maackii* removal treatments included seedlings of *Prunus serotina, Carya cordiformis, Cercis canadensis*, *Quercus rubra, Ulmus rubra*; the non-native shrub *Euonymus alatus*; and the native vines *Parthenocissus quinquefolia* and *Smilax tamnoides* (Table 4). However, *U. rubra* and *S. tamnoides* seedlings were also indicator species of the combination of deer exclusion and *L. maackii* presence, with *S. tamnoides* also being an indicator species of the combination of deer access and *L. maackii* presence (Table 4).

Deer preference

Across all treatment combinations, tree seedlings of moderate palatability to deer were most abundant, followed by, in decreasing order, seedlings of low preference, not preferred, and seedlings of high preference (Table A14).

Shade tolerance

Among all treatment combinations, tree seedlings with low shade tolerance were most abundant, followed by, in decreasing order, seedlings with high shade tolerance and seedlings with medium shade tolerance. (Table A15).

V. DISCUSSION

I found that deer directly negatively impacted a greater number of woody plant responses than *L. maackii* at my site. This finding was consistent with Gorchov et al.'s (2021) review, which also found that deer impacts were more common than invasive plant impacts on herbaceous plants and ecosystem functions. Additionally, my results showed that where significant interactions occurred, the patterns were synergistic, as the exclusion of deer and the removal of *L. maackii* resulted in the greatest values. This pattern was found in most studies that found interactive effects of deer and invasive plants as reviewed by Gorchov et al. (2021).

I found that the combination of deer exclusion and *L. maackii* removal resulted in synergistic interaction effects, with the greatest woody plant response variables found in this treatment combination. This finding matched my prediction that woody plant response variables where deer were excluded and *L. maackii* was removed would be greater than response variables in other treatment combinations, therefore supporting my hypothesis that woody plants would be impacted by deer and *L. maackii* interactions. Additionally, when I compared my results to earlier studies conducted at my study site by Peebles-Spencer et al. (2017) and Haffey and Gorchov (2019), I found a greater number of woody plant responses that were impacted by deer and *L. maackii* interaction effects in 2021, a result that is most likely due to a combination of increased time since deer exclusion and a release from the competitive effects of *L. maackii.* This finding was consistent with my prediction that woody plant responses would be greater after 11 years compared to 5 years after the exclusion of deer and the removal of *L. maackii,* therefore supporting my hypothesis that the lack of browse pressure from deer and the lack of competition from *L. maackii* had the greatest impact on woody plants over time.

Deer effects

My findings that the exclusion of deer after 11 years resulted in greater richness, density, and basal area of native tree seedlings were consistent with other studies that found that the prolonged exclusion of deer resulted in greater seedling responses (Aronson and Handel 2011; Habeck and Schultz 2015). This direct negative effect of deer on tree seedlings was likely due to consistent deer herbivory of seedlings between 0.3 and 2 m tall, the typical deer browse height range (Frelich and Lorimer 1985). Direct deer effects were also only evident on the richness of total, native, and non-native shrubs, results that differed from the 2015 study at my site by Haffey and Gorchov (2019), who found only reduced BA of shrubs and no effect on shrub richness where deer were present. My result of a synergistic interaction effect of deer exclusion and *L. maackii* removal on total vine density was comparable to Haffey and Gorchov's (2019) finding of a similar synergistic interaction effect on vine cover.

I also found that the exclusion of deer directly resulted in increased richness of understory trees (> 2 m but < 10 cm DBH) from 2015 to 2021 (Fig. 10), a result that was unexpected, as most understory trees have foliage above the typical deer browse height range (0.3 to 2.1 m). To explore this, I examined which understory tree species were gained or lost from 2015 to 2021 in each site for each treatment combination. Where a plot gained or lost a tree species, I noted the DBH of the individual tree responsible for this gain or loss. I found that the trees responsible for a gain in richness within a plot had DBH <4 cm (Table A16). These trees had recruited into the understory most likely due to the lack of deer herbivory. Most of the understory trees responsible for the loss in richness within a plot in 2015 had between 3 – 6.3 cm DBH. As these understory trees that were lost were too tall for deer to browse on their twigs and leaves, mortality may have been induced via antler rubbing or bark stripping by deer (Gill 1992).

My results of negative deer effects on woody plants were consistent with the findings of Bradshaw and Waller (2016), who found that areas with high deer densities resulted in negative impacts on woody plant responses. Deer density estimates from 2018 at College Woods (spring), Western Woods, Bachelor Preserve, and Reinhart Preserve were at or above the threshold 7 deer km^{-2} (Table A1) where deer begin to negatively impact forest regeneration (Tilghman 1989). In a broad-scale comparative study, Bradshaw and Waller (2016) found that high deer densities (2.3 to 23 per km^{2}) impacted the regeneration of seedlings and saplings of high to intermediate palatability. At my study site, I found that seedlings of highly palatable tree species (*Liriodendron tulipifera, Ulmus alata,* *Quercus rubra*) (Koon Master's Thesis 2022) were extremely rare across all deer and *L. maackii* treatment combinations (Table A4), findings that were similar to those of Bradshaw and Waller (2016), who found that deer browse negatively impacted the densities of several highly palatable tree species in northern Wisconsin. Additionally, I found that the greatest abundance of seedlings of moderate and high deer palatability were found where both deer were excluded and *L. maackii* had been removed, conditions that are in line with Tilghman's (1989) finding that moderate and highly preferred seedlings are primarily targeted by deer over less preferred species.

In plots where both deer were excluded and *L. maackii* was removed in 2021, tree seedling densities were well above the estimated threshold of 0.25 seedlings/m^2 that was considered sufficient for forest regeneration by Miller and McGill (2019) (Fig. 4). In contrast, tree seedling densities in all other treatment combinations ranged from 0.2 to 0.3 seedlings/m^2, very close to that estimated threshold. However, in my study, seedlings were classified as being between 0.3 to 2 m tall while Miller and McGill (2019) classified seedlings as being taller than 0.3 m (for deciduous species) with DBH <2.54 cm. Given this difference in seedling classification, my 'seedling' class is a subset of Miller and McGill's 'seedlings', so the threshold for seedlings sufficient for regeneration at my site would be slightly lower than 0.25 seedlings/m^2. Based on these conditions, regeneration failure may be occurring in plots of all treatment combinations except for where both deer were excluded and *L. maackii* was removed.

In addition to the direct effect of deer on tree seedlings, I found that deer negatively impacted the richness of total and non-native shrubs (Table A7, A8, A9), but not native shrubs, results that contradict Averill et al.'s (2018) findings that deer negatively impacted native shrub richness. Deer also had a weak negative impacts on the density of total vines, whereas non-native vines were not impacted, a finding similar to that of Ashton and Lerdau (2008), who found that non-native vines were more tolerant to herbivory compared to native vines. Specifically, they found that the non-native vine *C. orbiculatus*, which was the most abundant vine in the plots, overcompensated for damage and therefore allocated more resources to growth following herbivory.

My analysis on *L. maackii* growth revealed a significant negative effect of deer on basal area across all sites in 2021 (Fig. 12, Table 2), a result that is most likely due to deer herbivory. I believe herbivory was the main cause of this negative effect as Martinod and Gorchov (2017) found that *L. maackii* was an important food source for deer in the Miami University Natural Areas. To understand the effect of deer herbivory on *L. maackii* shrubs in the study plots, I chose to investigate small *L. maackii* shrubs (basal diameter of largest stem between 3-29 mm), as large shrubs (basal diameter of the largest stem ≥ 30 mm) were typically too tall to have twigs within the deer browse height range of 0.3 to 2 m (Peebles-Spencer et al. 2018). I indeed found a pattern of negative effects of deer on basal area of small *L. maackii* shrubs (Table 2, Fig. 14), with greater basal area of small shrubs where deer had been excluded, results similar to those of Peebles-Spencer et al. (2018). Based on these findings, I can reasonably determine that deer actively limited the growth of *L. maackii* outside of deer exclosures via suppression of small, not large, *L. maackii* shrubs (Table 2). Further evidence for this is my finding that the difference in total *L. maackii* BA between deer treatments (Fig. 12) matched almost exactly with the difference in BA of small *L. maackii* shrubs (Fig. 14) for 2021.

The analysis on *L. maackii* recruitment (*L. maackii* shrubs with basal diameter between 0-2 mm) revealed a different pattern, as I found only a weak interactive effect of deer exclusion and *L. maackii* presence, resulting in the lowest recruit counts where deer were excluded and *L. maackii* was present (Fig. 15, Table 1). These results were most likely due to greater competitive effects from other, larger *L. maackii* shrubs and surrounding native and non-native vegetation. These results suggest that deer have no effect on recruitment of *L. maackii* and that the effects of deer on *L. maackii* were due to herbivory on small shrubs.

I found this pattern of lower *L. maackii* basal area where deer had access at Reinhart Preserve, Bachelor Preserve, and Western Woods (Fig. 13). This pattern did not apply at College Woods, which showed greater *L. maackii* BA where deer had access compared to where deer were excluded (Fig. 13). This distinctive pattern at College Woods could be due to a greater proportion of large, deer resistant *L. maackii* shrubs relative to other sites or to lower deer densities relative to other sites. I indeed found that College Woods contained the greatest proportion of *L. maackii* basal area in large rather than small shrubs, among all plots where deer had access (Table A18). As for my second explanation, deer densities at College Woods were not drastically different than deer densities of other sites (Table A1), making this possibility unlikely. Therefore, this interesting pattern at College Woods is most likely due to the greater proportion of *L. maackii* basal area consisting of shrubs too tall to be browsed.

L. maackii effects

There were no direct effects of *L. maackii* on richness, density, or basal area of seedlings, shrubs, or vines after 11 years of *L. maackii* removal (Table 1), results that were contrary to other investigations of *L. maackii* impacts on understory woody plants using comparative (Hutchinson and Vankat 1997; Collier et al. 2002; Hartman and McCarthy 2008) and experimental approaches (Gorchov and Trisel 2003; Hartman and McCarthy 2004; Runkle et al. 2007). Additionally, I found no significant effects on seedling, shrub, or vine responses as a result of *L. maackii* removal, results that were similar to those found in 2015 (Haffey and Gorchov 2019). Several studies have found that effects of *L. maackii* were primarily manifest on herbaceous plants as opposed to woody plants (e.g., Peebles-Spencer et al. 2017), while other studies that investigated *L. maackii* (Collier et al. 2002) have found impacts on woody plant responses, making my results of no direct impacts notable. However, I did find that the presence of *L. maackii* resulted in a weak positive effect on understory tree basal area growth from 2015 to 2021 (Fig. 11, Table 1). This result was surprising, as I expected that the presence of *L. maackii* would result in decreased basal area of woody vegetation via competitive effects. These results contradicted those of Hartman and McCarthy (2007), who found that the presence of *L. maackii* reduced the overall rate of basal area growth of large trees. This weak positive effect on understory tree BA occurred only where deer had access (Fig. 11) and may have been due to *L. maackii* acting as a barrier to deer (Gorchov and Trisel 2003), as the presence of the larger *L. maackii* shrubs that had not been removed may have made the understory trees less susceptible to deer herbivory. It was also possible that deer preferred to browse small *L. maackii* shrubs (Fig. 14) instead of the twigs and leaves of understory trees which would have been taller and more difficult to reach.

Although cover, as quantified by the GLAMA app, near the forest floor was slightly lower in half-plots where *L. maackii* had been removed, there was not a significant effect of the removal treatment. These results suggest that the removal of *L. maackii* alone would not result in impactful reductions in cover values at a height of 0.3 m above ground. Utilizing my measures of cover as a proxy to determine light availability at 0.3 m above ground, I infer that the removal of *L. maackii* had no impact on light availability at my specified height. My finding of no *L. maackii* removal effects on light availability contradicts that of Owings et al. (2017), who found that the removal of *L. maackii* resulted in greater levels of photosynthetically active radiation (PAR) at ~1 m above ground. Chen and Matter (2018) also found that *L. maackii* impacted light, as they found reduced light levels at 1 m above ground where *L. maackii* was present relative to native understory vegetation. However, they found no effect of *L. maackii* on light relative to native vegetation at ground level, providing evidence that measured height (ground level vs 1 m above ground) influences light levels measurements. These differing results between these studies and mine of *L. maackii* light impacts may be due difference in height of measurements (0.3 m compared to 1 m above ground). Differences in *L. maackii* abundance among sites may also explain these differences. The density of *L. maackii* shrubs >1 m in height at Owings et al.'s (2017) study sites ranged from 0.08 to 0.31 shrubs/m^2 (mean 0.17 (shrubs/m^2)) was lower than the density of *L. maackii* shrubs >1 m in height at my sites (range 0.09 to 0.52; mean 0.33 (shrubs/m^2)) (Table A18) (Chen and Matter (2018) provides no data on *L. maackii* abundance). Another possible explanation may involve my use of cover as a proxy for light while Owings et al. (2017) and Chen and Matter (2018) both measured light availability directly. *Lonicera maackii* may have a significant impact on light due to the shrub directly blocking incoming rays from being detected by the measuring device, whereas it can have no impact on percent forest floor cover if the sky is already being blocked by vegetation in the understory and canopy layers. This is most likely occurred at my site as evidenced by the high percent canopy cover at my sites at 2 m above ground (Table A3).

Although I did not find cover at 0.3 m above ground to be impacted by *L. maackii,* it was negatively impacted by deer (Fig. 16, Table 1). My result of lower forest floor cover where deer had access was similar to the finding of Walters et al. (2016), who noted that light availability for seedlings at 0.2 m above ground was greater where deer had access than where deer were excluded. They suspected that browsing of *Sambucus* shrubs by deer contributed to this increased light penetration, as *Sambucus* shrub density was greater where deer were excluded. My finding was also similar to the findings of Heberling et al. (2017), who reported greater light availability in plots where deer had access compared where they had been fenced off.

Deer and L. maackii Interactions

The synergistic pattern I found for tree seedling richness and density, as well as for total vine density, where values were highest where deer were excluded and *L. maackii* was removed, was in line with what was reported in the review by Gorchov et al. (2021), which found that this synergy was the most common type of interaction between deer and invasive plant effects. In my study, this synergy was most likely due to herbivory by deer on *L. maackii,* reducing its cover and therefore mitigating its negative competitive effects on seedlings and vines. I found evidence that deer actively suppressed *L. maackii* growth, as BA of small *L. maackii* shrubs was significantly lower where deer had access than where deer were excluded (Figs. 12, 14). In addition to deer mitigating the effects of *L. maackii,* there have been studies that have found that *L. maackii* mitigated the negative effects of deer. Specifically, *L. maackii* had positive impacts on tree seedlings (facilitation) where deer were present by conferring protection from deer herbivory. Gorchov and Trisel (2003), while studying *L. maackii* impacts on *A. saccharum* seedlings, found greater seedling mass where *L. maackii* was present. Additionally, in a one-year study, Peebles-Spencer and Gorchov (2017) found that *A. saccharum* seedlings planted under *L. maackii* shrubs where deer had access resulted in greater survival as well as leaf count, I found no evidence of this positive interaction between *L. maackii* and seedlings in my study, as seedling responses and vine density were not greater where *L. maackii* was present compared to where *L. maackii* was removed in plots where deer had access.

My results of greatest native tree seedling richness and density where deer were excluded and *L. maackii* was removed (Figs. 3, 4) were notable, as Haffey and Gorchov (2019) found no significant interaction effect on these responses in 2015, suggesting that interaction effects grew stronger as time since deer exclusion and *L. maackii* removal increased. These findings suggest that forests in the MU Natural Areas would require at least 6 years of both deer exclusion and *L. maackii* removal to experience increases in these seedling responses. This delayed response of seedlings was likely due to slow, gradual changes in seedling responses to an environment without constant deer browse pressure as well as competitive and allelopathic effects of *L. maackii* (Cipollini and Flint 2013). Tanentzap et al. (2011) noted that consumption of biomass by deer relative to plant growth rates as well as reductions in seed abundance can influence the time required for vegetation to respond to a release from herbivory.

Of all tree seedling species that were indicative of the deer exclusion and *L. maackii* removal treatment combination (Table 4), only *Q. rubra* was of high deer browse preference (Koon 2022), with other seedling species being of low or moderate deer browse preference (Table A4). This surprised me, as I expected that low or moderate preference seedlings would be indicative of treatments where deer had access. Additionally, I found that *U. rubra* (moderate deer preference) was indicative of treatment combinations where deer were excluded and *L. maackii* was present or absent (Table 4), indicating that it was sensitive to deer browse and was unaffected by the presence of *L. maackii*. The native vine *S. tamnoides* was indicative of all treatment combinations except for where deer had access and *L. maackii* was removed (Table 4), suggesting that this vine was sensitive to deer browse and was more vulnerable to browse due to the lack of *L. maackii* (Table A19). It should be noted that *Fraxinus americana* seedlings were not listed as an indicator species for any treatment combination as it was the most abundant seedling across all study plots.

Tree seedling composition

My findings on the species composition of tree seedlings provide evidence for regeneration mismatch, where current overstory tree composition differs from the juvenile composition (Miller and McGill (2019). Given the dominance of *A. saccharum* in the canopy (256 stems, 61.5% of all tress measured) (Table A2) and the low abundance of *A. saccharum* seedlings in all treatment combinations (70 seedlings, 3.28% of all seedlings measured) (Table A4), the Miami University Natural Areas are experiencing regeneration mismatch in all plots. This difference in composition between the overstory and understory layers and the seedling layer are a direct result of deer herbivory and a combination of deer and *L. maackii* interactions.

Out of the four most common seedlings present across all plots (*F. americana, F. quadrangulata, A. triloba, P. serotina;* Table A4), the two *Fraxinus* species will be unable to recruit into the overstory canopy due to the presence of the invasive emerald ash borer (EAB), an invasive insect introduced from Asia into the United States circa 2002 (Cappaert et al. 2005). After an adult EAB lays her eggs inside the bark of an ash tree, the larvae begin feeding on the xylem, girdling the tree until its eventual death (Poland et al. 2006). *Fraxinus* trees are highly susceptible to EAB attacks, with 99% of trees with ≥2.5 cm diameter experiencing mortality (Klooster et al. 2013).

Out of the most abundant seedling species, only *P. serotina* is capable of recruiting into the canopy as it is not susceptible to EAB and is able to grow tall enough, unlike the fourth most abundant species, *Asimina triloba*. *Prunus serotina* tree seedlings were also not highly preferred by deer as noted by Koon (2022). It should be noted, however, that the majority (99.6%) of all *P. serotina* seedlings identified in my study plots were found where both deer were excluded and *L. maackii* was removed (Table A4), indicating that *P. serotina* seedlings had low survivorship in plots where deer had access or where *L. maackii* was present, perhaps due to its low shade tolerance (Table A4). Because of this, I only expect *P. serotina* will become abundant in the overstory at my site where deer are excluded and *L. maackii* is removed, and to a lesser extent, where deer are excluded and *L. maackii* is present. I found only one *P. serotina* understory tree across all my study plots, suggesting that *P. serotina* seedlings did not successfully recruit into the understory layer due to high shade. If *L. maackii* alone were to be appropriately managed at my site, I would ultimately expect species with low shade tolerance, such as *P. serotina* and *Carya cordiformis* (Table A4) to successfully recruit into the canopy layer. If only deer were managed, it would be expected that there would be greater abundances of highly and moderately preferred species, such as *A. saccharum* and *Quercus* species (Table A4). If they are both managed appropriately, it would be expected that the forest would regenerate successfully with no regeneration mismatch, with *A. saccharum, Carya cordiformis,* and *Quercus* species successfully recruiting into the canopy.

VI. MANAGEMENT IMPLICATIONS

Based on my findings, I recommend that both deer and *L. maackii* be controlled simultaneously in order to achieve greater native tree seedling richness and density. However, given that high costs associated with the various methods of deer and *L. maackii* control (hunting deer, cutting and treating shrub with pesticide), if the control of only one stressor is feasible, I recommend controlling deer as they directly negatively impacted several growth forms (seedlings, shrubs, vines) in my study, whereas *L. maackii* had no significant impacts. If cost is not a concern, I have shown that the management of both deer and *L. maackii* will result in the greatest benefit for tree seedlings.

If resources allow, I also recommend that more invasive understory plants be controlled. The control of both deer and *L. maackii* would likely result in greater abundances of *E. alatus,* an invasive shrub that has negative impacts on forest floor plants (Swearingen et al. 2010), as this shrub was indicative of the deer exclusion and *L. maackii* removal treatment. The most common invasive shrub in my plots, *Ligustrum obtusifolium*, was not an indicator species for any of my treatment combinations, but it should still be controlled if resources allow due to its negative, competitive impacts on tree seedlings and herbs (Maynard-Bean et al. 2019).

VII. CONCLUSIONS

Given that my study utilized a small number of 20 x 20 m study plots (n=5) localized to a general area, I am cautious in applying my results to larger forested areas. However, my study makes clear that at least 6 years of both the exclusion of deer and the removal of *L. maackii* are required for tree seedling densities in the MU Natural Areas to reach and pass the threshold of 0.25 seedlings/m^2 estimated by Miller and McGill (2019) for successful forest regeneration. My study also makes clear that both stressors have caused regeneration failure as well as regeneration mismatch in the MU Natural Areas. Additionally, my finding of deer impacting the growth of *L. maackii* builds on Peebles-Spencer et al's (2018) findings and provides evidence that the effects of *L. maackii* on woody plants can be mitigated by deer. My study involved the complete exclusion of deer, which is not a realistic, practicable possibility in most forests. To better understand interactive impacts of realistic densities of deer and invasive plants, future studies should utilize other methods such as deer enclosures that include a certain density of deer or experiments that utilize variable deer densities in forests (Tilghman 1989; Horsley et al. 2003).

VIII. REFERENCES

Abrahamson, I. L., Nelson, C. R., & Affleck, D. L. (2011) Assessing the performance of sampling designs for measuring the abundance of understory plants. *Ecological Applications*, *21*(2), 452-464.

Anderson, R. C., & Katz, A. J. (1993). Recovery of browse-sensitive tree species following release from white-tailed deer *Odocoileus virginianus* (Zimmerman) browsing pressure. *Biological Conservation*, *63*(3), 203-208.

Aronson MFJ, Handel SN (2011) Deer and invasive plant species suppress forest herbaceous communities and canopy tree regeneration. Nat Areas J 31:400–407

Ashton, I. W., & Lerdau, M. T. (2008). Tolerance to herbivory, and not resistance, may explain differential success of invasive, naturalized, and native North American temperate vines. *Diversity and Distributions*, *14*(2), 169-178.

Barrett ML. 2014. Comparison of estimates of white-tailed deer (*Odocoileus virginianus*) population densities over two different seasonal periods in Miami University's natural areas. A practicum report, institute for environment and sustainability. Oxford (OH): Miami University.

Bates D, Maechler M, Bolker B, Walker S, Christensen RHB, Singmann H, Dai B, Grothendieck G, Green P. (2017) Linear mixed-effects models using 'Eigen' and S4, ver 1.1-8.

Bourg, N. A., McShea, W. J., Herrmann, V., Stewart, C. M., & Blossey, B. (2017). Interactive effects of deer exclusion and exotic plant removal on deciduous forest understory communities. *AoB Plants*, *9*(5).

Boyce, R. L. (2009). Invasive shrubs and forest tree regeneration. *Journal of sustainable forestry*, *28*(1-2), 152-217.

Bradshaw L, Waller DM (2016) Impacts of white-tailed deer on regional patterns of forest tree recruitment. *Forest Ecology and Management*, *375*, 1-11.

Burke, D. J., Carrino-Kyker, S. R., Hoke, A., Cassidy, S., Bialic-Murphy, L., & Kalisz, S. (2019). Deer and invasive plant removal alters mycorrhizal fungal communities and soil chemistry: Evidence from a long-term field experiment. *Soil Biology and Biochemistry*, *128*, 13-21.

Cáceres MD, Legendre P. (2009) Associations between species and groups of sites: indices and statistical inference. Ecology. 90:3566–3574.

Cáceres MD, Legendre P, Moretti M. (2010) Improving indicator species analysis by combining groups of sites. Oikos. 119:1674–1684.

Cappaert, D., McCullough, D. G., Poland, T. M., & Siegert, N. W. (2005). Emerald ash borer in North America: a research and regulatory challenge. *American Entomologist. 51 (3): 152-165.*, *51*(3).

Chen, H., & Matter, S. F. (2017). Quantification of changes in light and temperature associated with invasive Amur Honeysuckle (*Lonicera maackii*). *The American Midland Naturalist*, *177*(1), 143-152.

Cipollini, K. A., & Flint, W. N. (2013). Comparing allelopathic effects of root and leaf extracts of invasive *Alliaria petiolata, Lonicera maackii* and *Ranunculus ficaria* on germination of three native woodland plants. *The Ohio Journal of Science*, *112*(2), 37.

Collier MH, Vankat JL, Hughes MR (2002) Diminished plant richness and abundance below *Lonicera maackii*, an invasive shrub. Am Midl Nat 147:60–71

Dornbush ME, Hahn PG (2013) Consumers and establishment limitations contribute more than competitive interactions in sustaining dominance of the exotic herb garlic mustard in a Wisconsin, USA forest. Biol Invasions 15:2691–2706

Dow AgroSciences, 2011. Specimen label, Tordon® RTU

Ehrenfeld, J. G., Kourtev, P., & Huang, W. (2001). Changes in soil functions following invasions of exotic understory plants in deciduous forests. *Ecological applications*, *11*(5), 1287-1300.

Frelich LE, Lorimer CG (1985) Current and predicted long-term effects of deer browsing in hemlock forests in Michigan, USA. Biol Cons 34:99–120.

Gill RMA. (1992b). A review of damage by mammals in north temperate forests: 3. Impact on trees and forests. *Forestry* 65:363–88

Gorchov, D. L., Blossey, B., Averill, K. M., Dávalos, A., Heberling, J. M., Jenkins, M. A., ... & Waller, D. M. (2021). Differential and interacting impacts of invasive plants and white-tailed deer in eastern US forests. *Biological Invasions*, *23*(9), 2711-2727.

Gorchov DL, Trisel DE (2003) Competitive effects of the invasive shrub, *Lonicera maackii* (Rupr.) Herder (Caprifoliaceae), on the growth and survival of native tree seedlings. Plant Ecol 166:13–24

Habeck, C. W., & Schultz, A. K. (2015). Community-level impacts of white-tailed deer on understory plants in North American forests: a meta-analysis. *AoB plants*, *7*.

Haffey, C. M., & Gorchov, D. L. (2019). The effects of deer and an invasive shrub, *Lonicera maackii*, on forest understory plant composition. *Ecoscience*, *26*(3), 237-247.

Hartman KM, McCarthy BC (2004) Restoration of a forest understory after the removal of an invasive shrub, Amur honeysuckle (*Lonicera maackii*). Res Ecol 12:154–165

Hartman KM, McCarthy BC (2008) Changes in forest structure and species composition following invasion by a non-indigenous shrub, Amur honeysuckle (*Lonicera maackii*). J Torrey Bot Soc. 135:245–259

Heberling, J. M., Brouwer, N. L., & Kalisz, S. (2017). Effects of deer on the photosynthetic performance of invasive and native forest herbs. *AoB Plants*, *9*(2), plx011.

Horsley SB, Stout SL, DeCalesta DS (2003) White-tailed deer impact on the vegetation dynamics of a northern hardwood forest. Ecol Appl 13:98–118

Koon, K (2022). White-tailed deer impacts on tree regeneration and plant species composition in the Cincinnati Parks System. Master's Honors Thesis, Miami University.

Klooster, W. S., Herms, D. A., Knight, K. S., Herms, C. P., McCullough, D. G., Smith, A., ... & Cardina, J. (2014). Ash (*Fraxinus* spp.) mortality, regeneration, and seed bank dynamics in mixed hardwood forests following invasion by emerald ash borer (*Agrilus planipennis*). *Biological Invasions*, *16*(4), 859-873.

Latham, R. E., Beyea, J., Benner, M., Dunn, C. A., Fajvan, M. A., Freed, R. R., ... & Shissler, B. P. (2005, January). Managing white-tailed deer in forest habitat from an ecosystem perspective. In *Report by the Deer Management Forum for Audubon Pennsylvania and Pennsylvania Habitat Alliance; Audubon Pennsylvania: Harrisburg, PA, USA* (p. 340).

Leonard, H (2022). Long-term effects of an invasive shrub, Amur honeysuckle (*Lonicera maackii*), and white-tailed deer (*Odocoileus virginianus*) on Forest Floor Plant Composition. Undergraduate Honor's Thesis, Miami University.

Martinod, K. L., & Gorchov, D. L. (2017) White-tailed deer browse on an invasive shrub with extended leaf phenology meets assumptions of an apparent competition hypothesis. *AoB Plants*, *9*(2).

Maynard-Bean, E., & Kaye, M. (2019). Invasive shrub removal benefits native plants in an eastern deciduous forest of North America. *Invasive Plant Science and Management*, *12*(1), 3-10.

McEwan, R. W., Birchfield, M. K., Schoergendorfer, A., & Arthur, M. A. (2009). Leaf phenology and freeze tolerance of the invasive shrub Amur honeysuckle and potential native competitors. *The Journal of the Torrey Botanical Society*, *136*(2), 212-220.

McNeish RE, McEwan RW (2016) A review on the invasion ecology of Amur honeysuckle (*Lonicera maackii*, Caprifoliaceae) a case study of ecological impacts at multiple scales. *The Journal of the Torrey Botanical Society*, *143*(4), 367-385.

Merriam, R. W., & Feil, E. (2002). The potential impact of an introduced shrub on native plant diversity and forest regeneration. *Biological Invasions*, *4*(4), 369-373.

Michael, E. D. (1988). Effects of white-tailed deer on Appalachian hardwood regeneration. *Guidelines for regenerating Appalachian hardwood stands*, 219-225.

Miller KE, Gorchov DL (2004) The invasive shrub, *Lonicera maackii*, reduces growth and fecundity of perennial forest herbs. Oecologia 139:359–375

Miller, K. M., & McGill, B. J. (2019). Compounding human stressors cause major regeneration debt in over half of eastern US forests. *Journal of Applied Ecology*, *56*(6), 1355-1366.

Niinemets, Ü., & Valladares, F. (2006). Tolerance to shade, drought, and waterlogging of temperate northern hemisphere trees and shrubs. *Ecological monographs*, *76*(4), 521-547.

Nuttle, T., Ristau, T. E., & Royo, A. A. (2014). Long-term biological legacies of herbivore density in a landscape-scale experiment: forest understorys reflect past deer density treatments for at least 20 years. *Journal of Ecology*, *102*(1), 221-228.

Owings, C. F., Jacobs, D. F., Shields, J. M., Saunders, M. R., & Jenkins, M. A. (2017). Individual and interactive effects of white-tailed deer and an exotic shrub on artificial and natural regeneration in mixed hardwood forests. *AoB Plants*, *9*(4).

Peebles-Spencer, Jessica Rene. Interactions between invasive shrub, *Lonicera maackii*, and a generalist herbivore, White-tailed deer, in Southwestern Ohio forests. Diss. Miami University, 2016.

Peebles-Spencer, J. R., Gorchov, D. L., & Crist, T. O. (2017). Effects of an invasive shrub, Lonicera maackii, and a generalist herbivore, white-tailed deer, on forest floor plant community composition. *Forest Ecology and Management*, *402*, 204-212.

Peebles-Spencer, J. R., & Gorchov, D. L. (2017). Are native tree seedlings facilitated by an invasive shrub where white-tailed deer are abundant?. *Natural Areas Journal*, *37*(4), 540-548.

Peebles-Spencer, J. R., Haffey, C. M., & Gorchov, D. L. (2018). Browse by white-tailed deer decreases cover and growth of the invasive shrub, *Lonicera maackii*. *The American Midland Naturalist*, *179*(1), 68-77.

Peterson TE. 2018. Factors affecting densities of white-tailed deer (*Odocoileus virginianus*) in eastern deciduous forest: the roles of and surrounding land use, forest habitat edge, and invasive shrubs [master's thesis]. Oxford (OH): Miami University.

Plants Database. 2016. United States department of agriculture, natural resources conservation service; [accessed 2022 March 12].

Poland, T. M., & McCullough, D. G. (2006). Emerald ash borer: invasion of the urban forest and the threat to North America's ash resource. *Journal of Forestry*, *104*(3), 118-124.

R Development Core Team. (2017) The R foundation for statistical computing, ver 3.2.1. Vienna (Austria): Vienna University of Technology. http://www.r-project.org/.

Rooney TP (2001). Deer impacts on forest ecosystems: A North American perspective. Forestry 74:201–208

Rooney, T. P., Solheim, S. L., & Waller, D. M. (2002). Factors affecting the regeneration of northern white cedar in lowland forests of the Upper Great Lakes region, USA. *Forest Ecology and management*, *163*(1-3), 119-130.

Rooney TP, Waller DM (2003). Direct and indirect effects of white-tailed deer in forest ecosystems. For Ecol Manag 181:165–176

Russell, M. B., Woodall, C. W., Potter, K. M., Walters, B. F., Domke, G. M., & Oswalt, C. M. (2017). Interactions between white-tailed deer density and the composition of forest understories in the northern United States. *Forest Ecology and Management*, *384*, 26-33.

Shields, J. M., Jenkins, M. A., Saunders, M. R., Gibson, K. D., Zollner, P. A., & Dunning, J. B. (2015). Influence of intensity and duration of invasion by Amur honeysuckle (*Lonicera maackii*) on mixed hardwood forests of Indiana. *Invasive Plant Science and Management*, *8*(1), 44-56.

Swearingen, J., B. Slattery, K. Reshetiloff, and S. Zwicker (2010) Plant invaders of Mid-Atlantic natural areas, 4th ed. National Park Service and U.S. Fish and Wildlife Service. Washington, DC. 168.

Tichý, L. (2014). GLAMA-Gap Light Analysis Mobile Application.

Tichý, L. (2016). Field test of canopy cover estimation by hemispherical photographs taken with a smartphone. *Journal of vegetation science*, *27*(2), 427-435.

Tilghman, N. G. (1989). Impacts of white-tailed deer on forest regeneration in northwestern Pennsylvania. *The Journal of Wildlife Management*, 524-532.

Trisel, D. E. 1997. The invasive shrub, *Lonicera maackii* (Rupr.) Herder (Caprifoliaceae) factors leading to its success and its effect on native species. Dissertation, Miami University, Oxford, OH.

Waller, DM, Alverson WS (1997). The white-tailed deer: a keystone herbivore. *Wildlife Society Bulletin (1973-2006)*, *25*(2), 217-226.

Waller DM, Maas LI (2013). Do white-tailed deer and the exotic plant garlic mustard interact to affect the growth and persistence of native forest plants? For Ecol Manag 304:296–302

Walters, M. B., Farinosi, E. J., Willis, J. L., & Gottschalk, K. W. (2016). Managing for diversity: Harvest gap size drives complex light, vegetation, and deer herbivory impacts on tree seedlings. *Ecosphere*, *7*(8), e01397.

Ward, J. S., Williams, S. C., & Linske, M. A. (2018) Influence of invasive shrubs and deer browsing on regeneration in temperate deciduous forests. *Canadian Journal of Forest Research*, *48*(1), 58-67.

Wilcox, J., & Beck, C. W. (2007). Effects of *Ligustrum sinense* Lour. (Chinese privet) on abundance and diversity of songbirds and native plants in a southeastern nature preserve. *Southeastern Naturalist*, *6*(3), 535-550.

IX. TABLES

Table 1: *P-values* from nested split-plot two-way ANOVAs of richness, density (growth form/m^2), and basal area (cm^2) of understory woody vegetation in half plots subjected to a combination of deer treatments (access, exclosure) and *L. maackii* treatments (present, absent) in summer 2021. 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. *P-values* from split-plot two-way ANOVA of *L. maackii* recruit counts subjected to the same deer and *L. maackii* treatments are included. Bold and shaded indicates $P<0.05$, shaded only indicates $P<0.10$. Appendix contains statistics for each ANOVA.

		Deer treatment	*L. maackii* treatment	Interaction
Richness	seedlings	**0.0003**	0.6840	**0.0210**
	total shrubs	**0.0206**	0.4812	0.1558
	native shrubs	0.3011	0.6180	0.8961
	non-native shrubs	**0.0356**	0.7411	0.0799
	change in understory trees	**0.0440**	0.3630	0.5170
Density (vegetation/m^2)	seedlings	**0.0062**	0.6815	**0.0472**
	total shrubs	0.1420	0.3860	0.9180
	native shrubs	0.5835	0.1874	0.8738
	non-native shrubs	0.1510	0.7230	0.8830
	change in understory trees	0.7360	0.4140	0.6230
	total vines	0.1198	0.8381	**0.0178**
	native vines	0.0538	0.7160	0.0545
	non-native vines	0.3030	1.0000	0.0917
	L. maackii recruits	0.2104	0.2599	0.0542
Basal area (cm^2)	seedlings	0.0709	0.6599	0.0757
	total shrubs	0.0623	0.8837	0.1541
	native shrubs	0.9701	0.3292	0.6043
	non-native shrubs	0.0602	0.9853	0.1042
	change in understory trees	0.5370	0.0660	0.1570
	total vines	0.2948	0.8223	0.0718
	native vines	0.2677	0.7891	0.9195
	non-native vines	0.9550	0.9930	0.1240
Cover	0.3 m above ground	**0.0148**	0.2980	0.8338

Table 2: *P-values* from linear mixed models with site as the random effect of basal area of small *L. maackii* shrubs, large *L. maackii* shrubs, and total *L. maackii* shrubs subjected to a combination of deer (access, exclosure) treatments in summer 2021. Bold and shaded indicates *P*<0.05, shaded only indicates *P*<0.10

		Deer Treatment
Basal area (cm^2)	*L. maackii* small	**0.0124**
	L. maackii large	0.8756
	L. maackii total	**0.0339**

Table 3: Mean modified percent forest floor cover index values (%) for 2021 in half-plots where deer had access or were excluded and *Lonicera maackii* was present or absent. Photographs were taken at 0.3m above ground. See Fig. 25 for photograph locations within half-plots. Values for Western Woods were not used for analysis because *L. maackii* was inadvertently cut in the Access/Present treatment.

Mean Modified Percent Cover Index (%)

	Exclosure		**Access**	
Site	**Present**	**Absent**	**Present**	**Absent**
Reinhart	94.1	92.6	90.1	89.6
Western	90.2	88.6	85.8	87.2
Kramer	87.4	87.7	84.4	82.2
Bachelor	88.4	87.1	87.1	82.3
College	84.0	82.9	80.6	83.4
Mean	88.2	87.8	85.6	84.9

Table 4: Results of indicator species analysis. *P-values* of seedlings, shrubs (indicated by *), and vines (indicated by **) that are indicative of certain treatment combinations. Only reporting species where *P*<0.05. Indicator values measure the statistical significance of species abundance and any relationship to a treatment(s), with a higher indicator value suggesting greater significance.

Indicator Species	**Indicator of**	**Indicator Value**	***P-value***
Prunus serotina	deer excluded, *L. maackii* removed	0.949	0.0002
Carya cordiformis	deer excluded, *L. maackii* removed	0.886	0.0016
**Euonymus alatus*	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

X. FIGURES

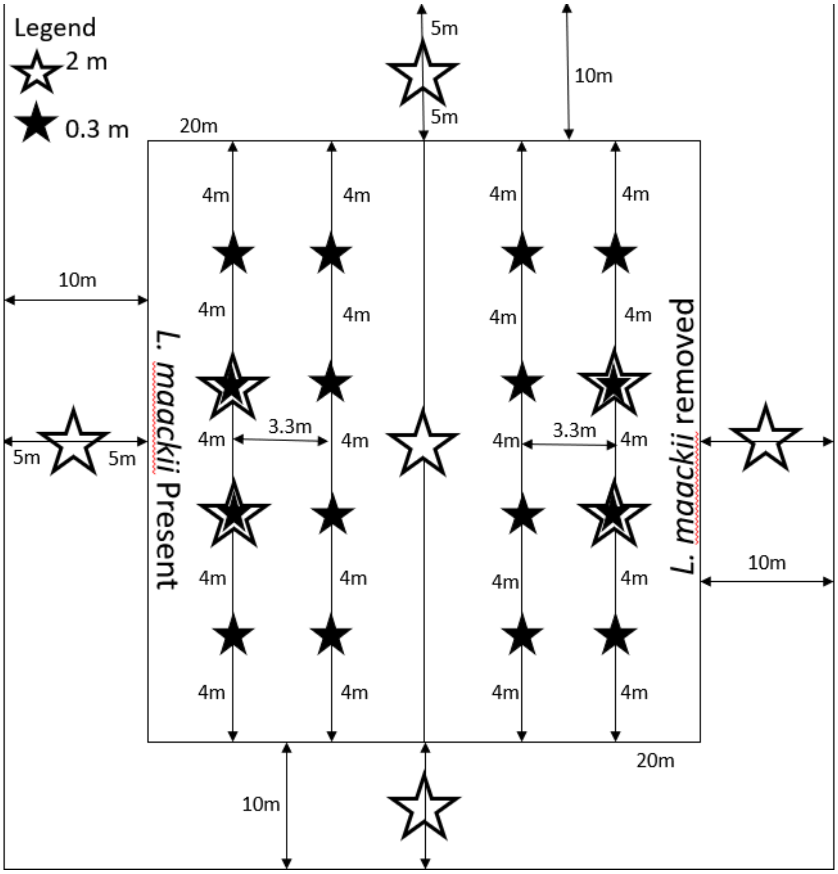


Figure 1: Diagram showing where canopy cover photographs were taken inside and around exterior of each 20 x 20 m plot at each site in 2021. Shaded stars represent photographs taken 0.3 m above ground and non-shaded stars represent photographs taken 2 m above ground. Non-shaded stars with shaded stars within them represent photographs taken at 0.3 m and 2 m above ground.

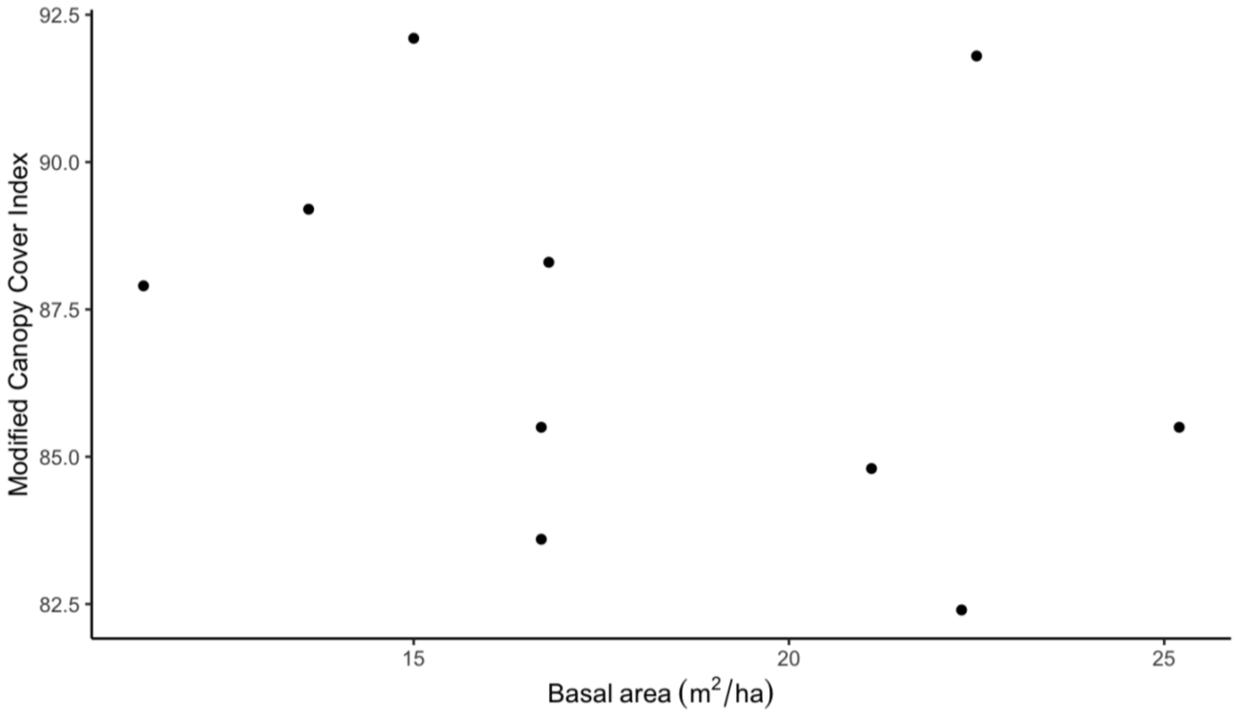


Figure 2: Mean modified canopy cover index values vs. basal area (m^2/ha) of trees taller than 2 m with DBH>10 cm for 2021. Canopy photographs and tree measurements were collected from 40-by-40 m plots at each site.

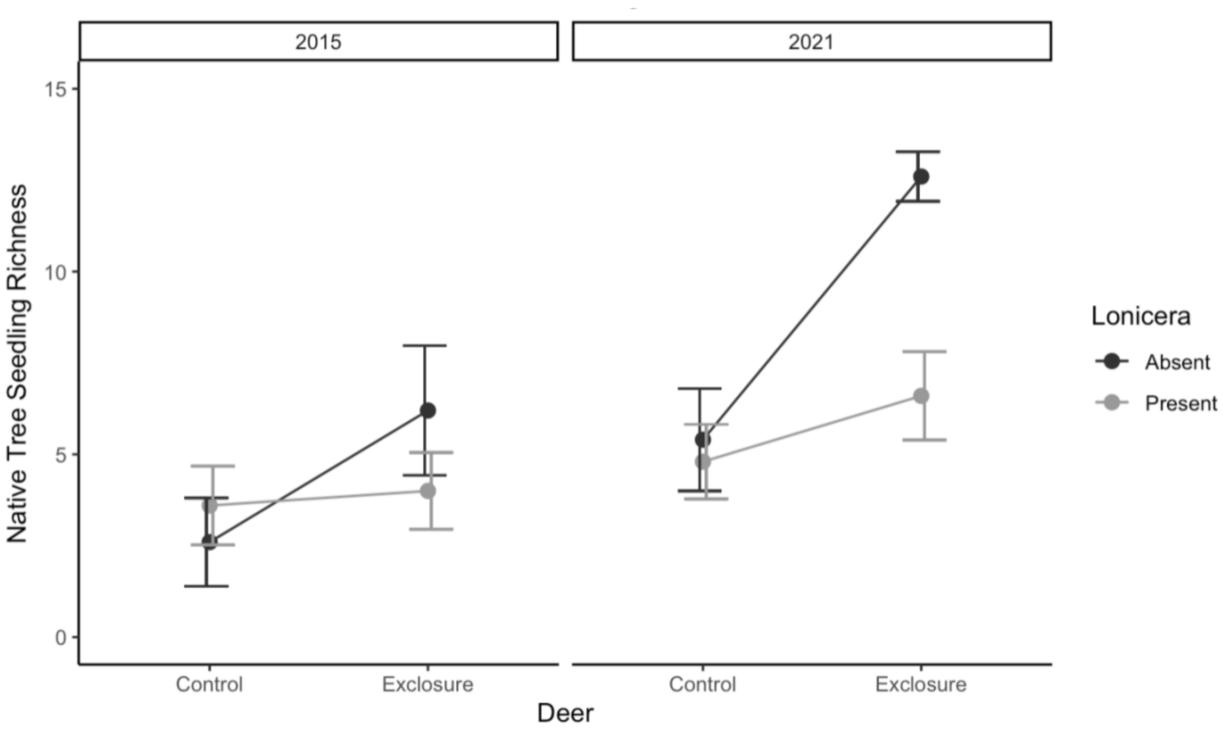


Figure 3: Interaction plots of species richness of native tree seedlings for 2015 and 2021 in half-plots where deer had access or were excluded and where *L. maackii* was present or absent. For each treatment combination, mean ± (SE) of the five sites is plotted. Data from 2015 are from Haffey and Gorchov (2019).

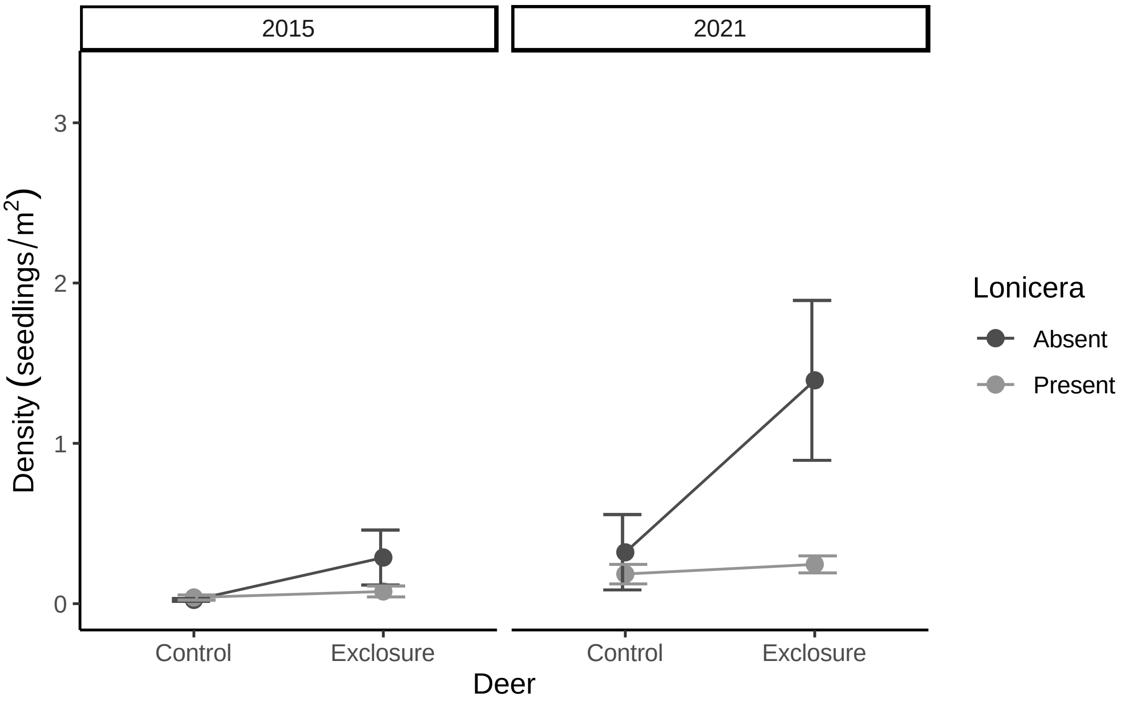


Figure 4: Interaction plots of density (seedlings/m^2) of native tree seedlings for 2015 and 2021 in half-plots where deer had access or were excluded and where *L. maackii* was present or absent. For each treatment combination, mean ± (SE) of the five sites is plotted. Data from 2015 are from Haffey and Gorchov (2019).

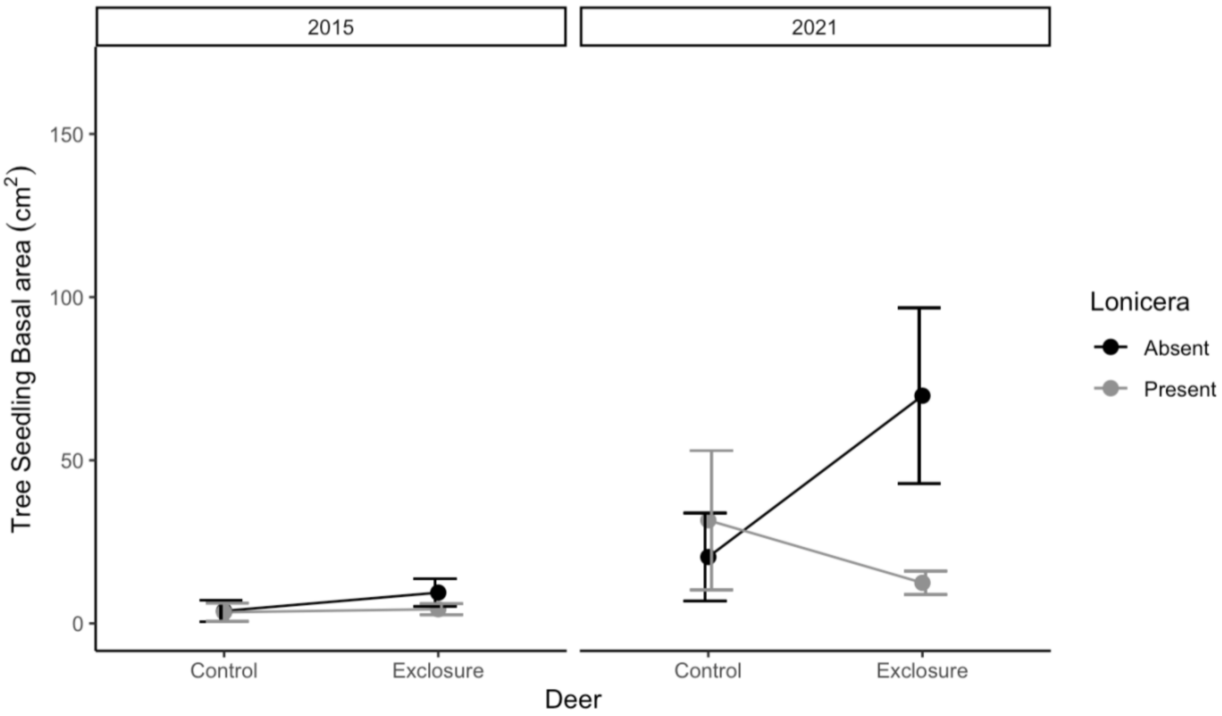


Figure 5: Interaction plots of basal area (cm^2) of native tree seedlings for 2015 and 2021 in half-plots where deer had access or were excluded and where *L. maackii* was present or absent. For each treatment combination, mean ± (SE) of the five sites is plotted. Data from 2015 are from Haffey and Gorchov (2019).

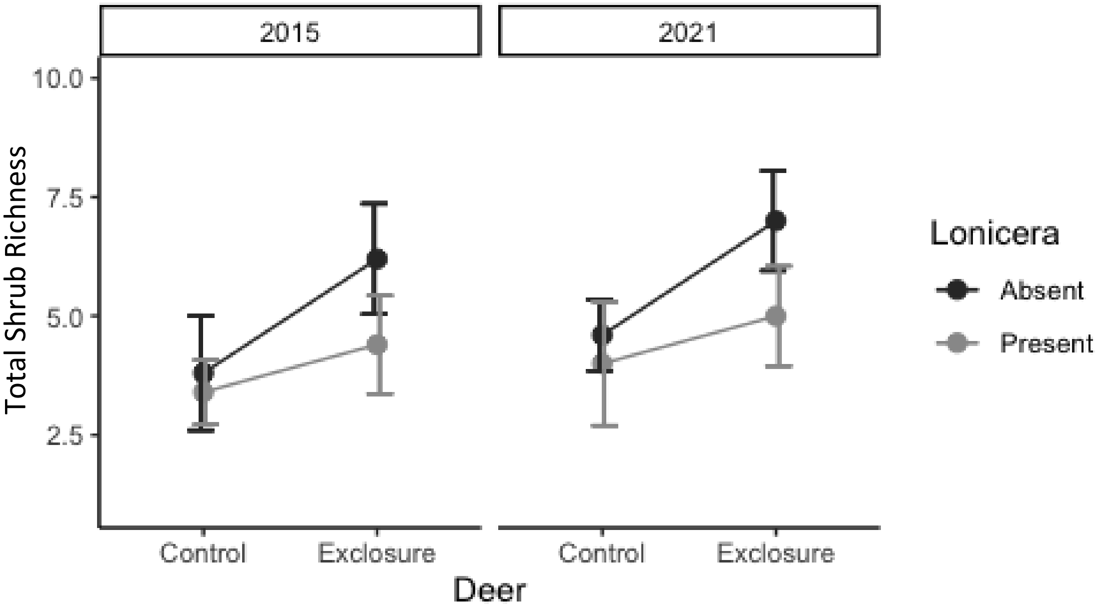


Figure 6: Interaction plots of species richness of all shrubs for 2015 and 2021 in half-plots where deer had access or were excluded and where *L. maackii* was present or absent. For each treatment combination, mean ± (SE) of the five sites is plotted. Data from 2015 are from Haffey and Gorchov (2019).

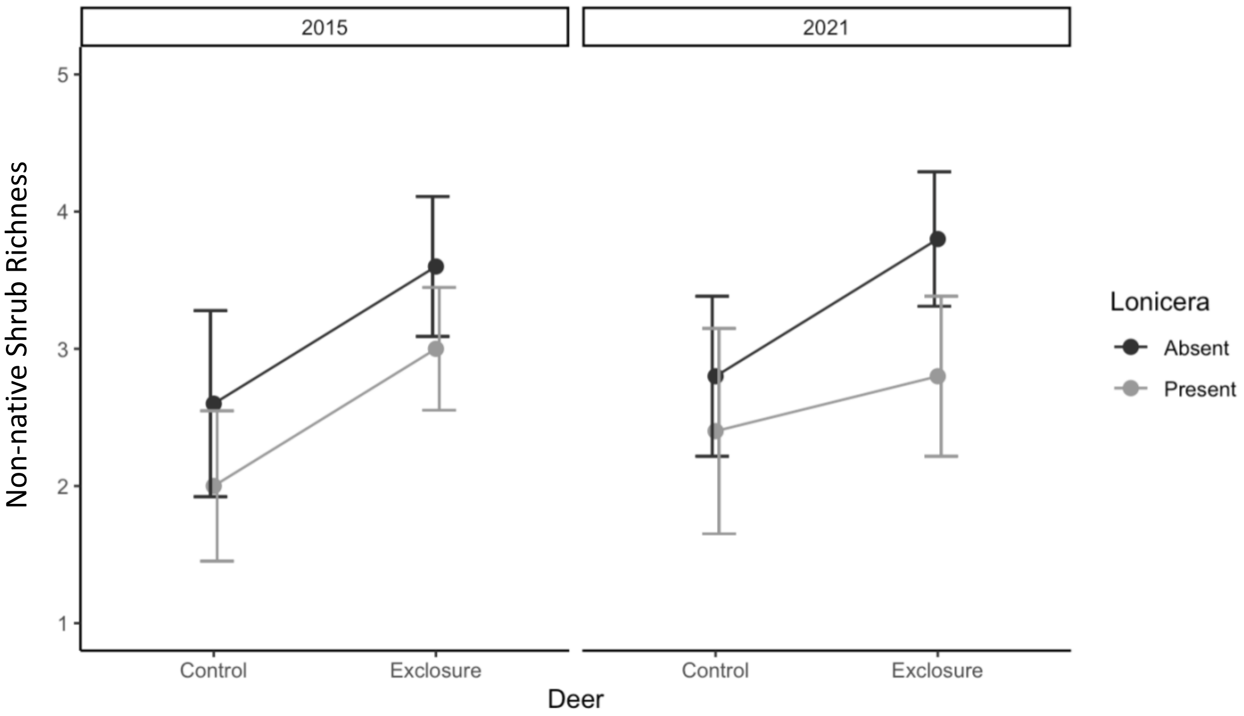
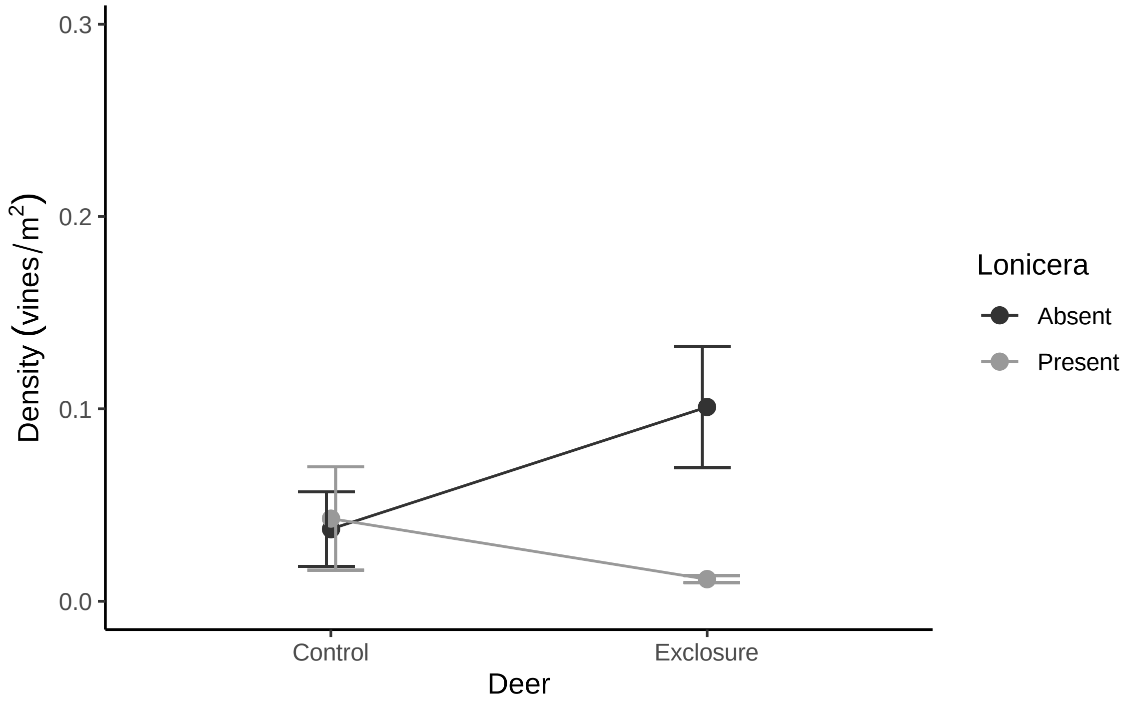


Figure 7: Interaction plots of species richness of non-native shrubs for 2015 and 2021 in half-plots where deer had access or were excluded and where *L. maackii* was present or absent. For each treatment combination, mean ± (SE) of the five sites is plotted. Data from 2015 are from Haffey and Gorchov (2019).



<u>Figure 8:</u> Interaction plot of density (vines/m^2) of all vines for 2021 in half-plots where deer had access or were excluded and where *L. maackii* was present or absent. For each treatment combination, mean ± (SE) of the five sites is plotted.

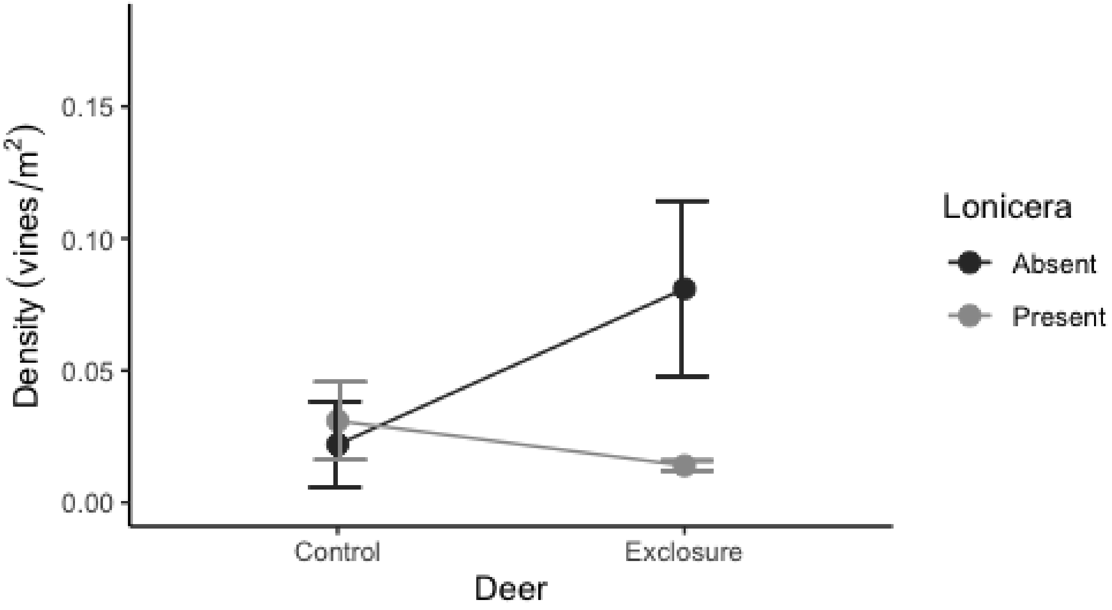


Figure 9: Interaction plot of density (vines/m^2) of native vines for 2021 in half-plots where deer had access or were excluded and where *L. maackii* was present or absent. For each treatment combination, mean ± (SE) of the five sites is plotted.

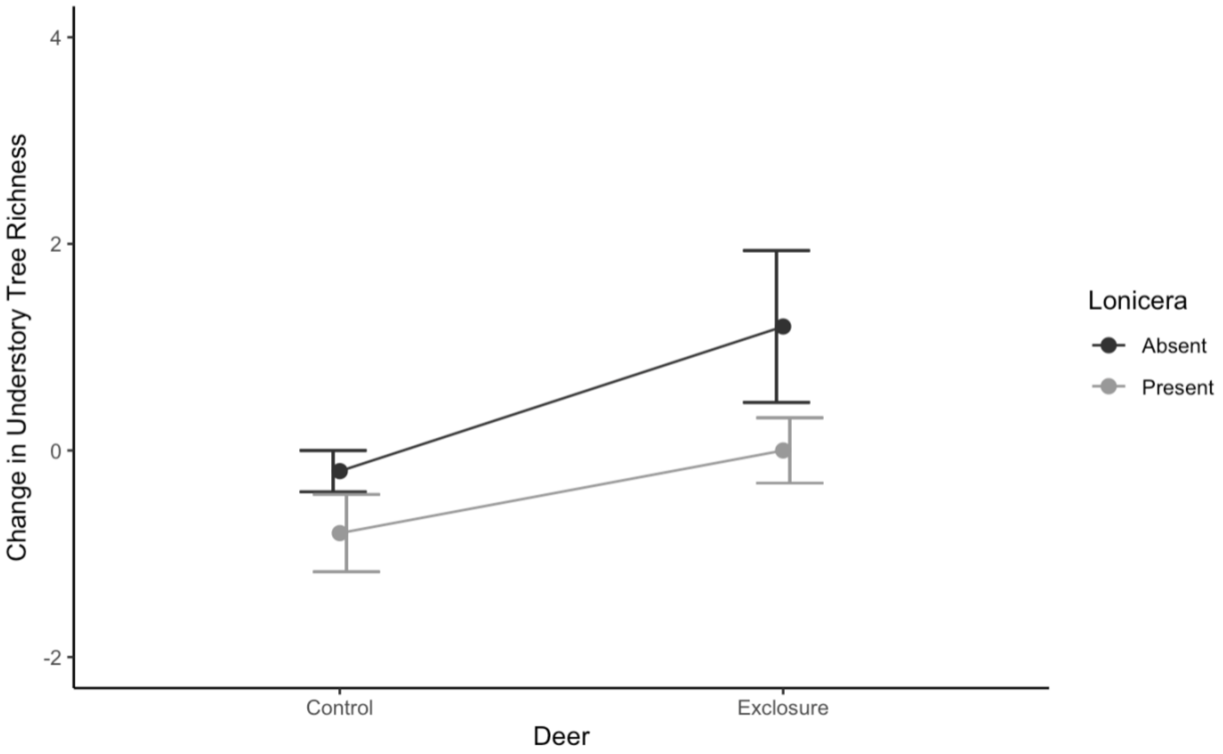


Figure 10: Interaction plot of change in richness of understory trees from 2015 to 2021 in half-plots where deer had access or were excluded and where *L. maackii* was present or absent. For each treatment combination, mean ± (SE) of the five sites is plotted.

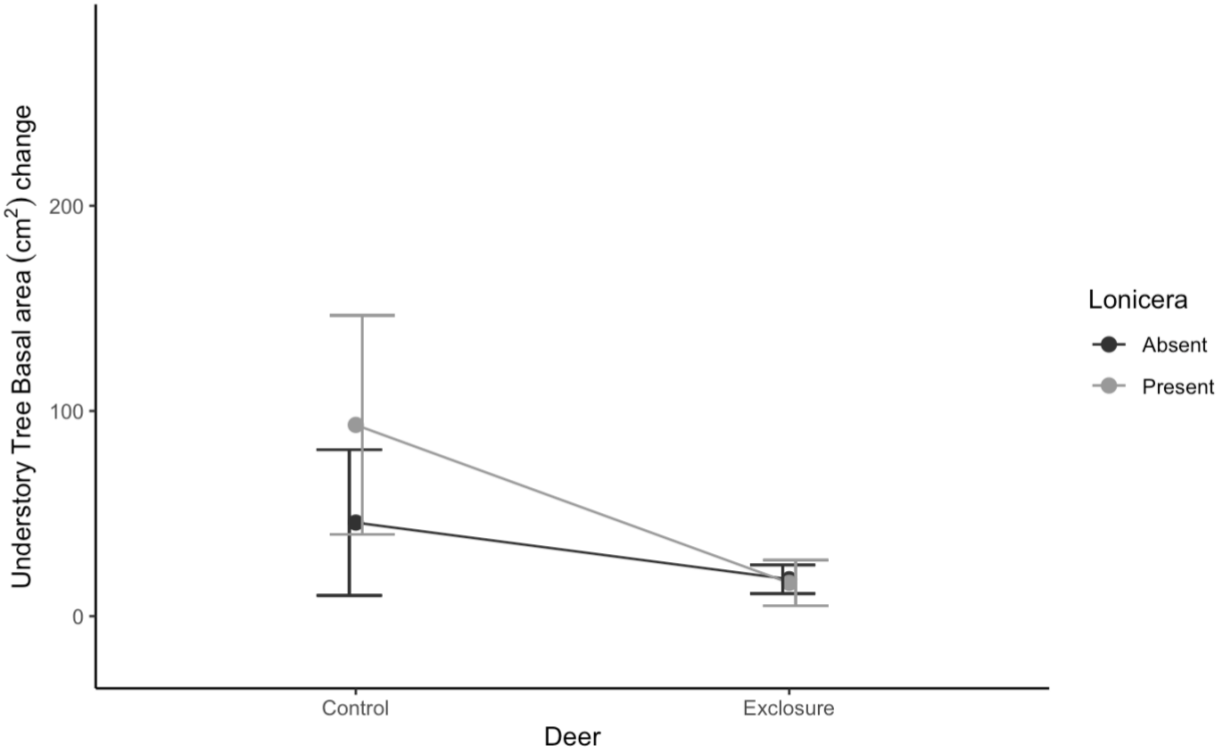


Figure 11: Interaction plot of change in basal area (cm^2) of understory trees from 2015 to 2021 in half-plots where deer had access or were excluded and where *L. maackii* was present or absent. For each treatment combination, mean ± (SE) of the five sites is plotted.

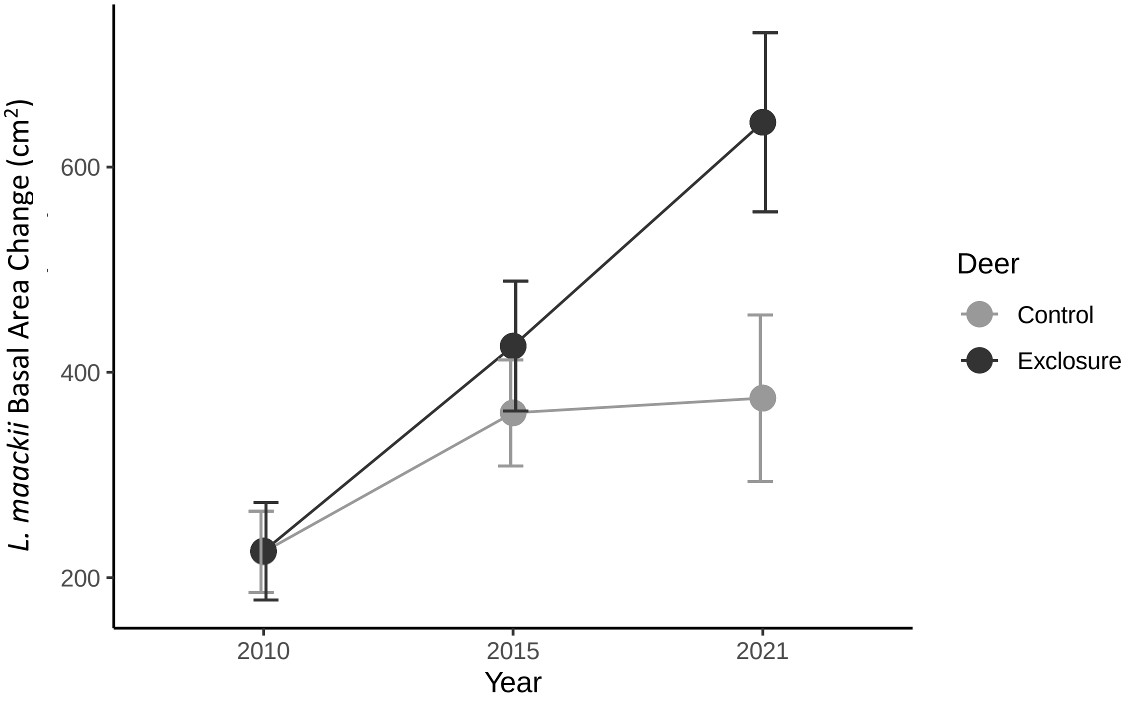


Figure 12: Plot of mean basal area (cm^2) of *Lonicera maackii* for 2010, 2015, and 2021 in half-plots where deer had access or were excluded and *L. maackii* was not removed. For each treatment combination, mean ± (SE) of the five sites is plotted.

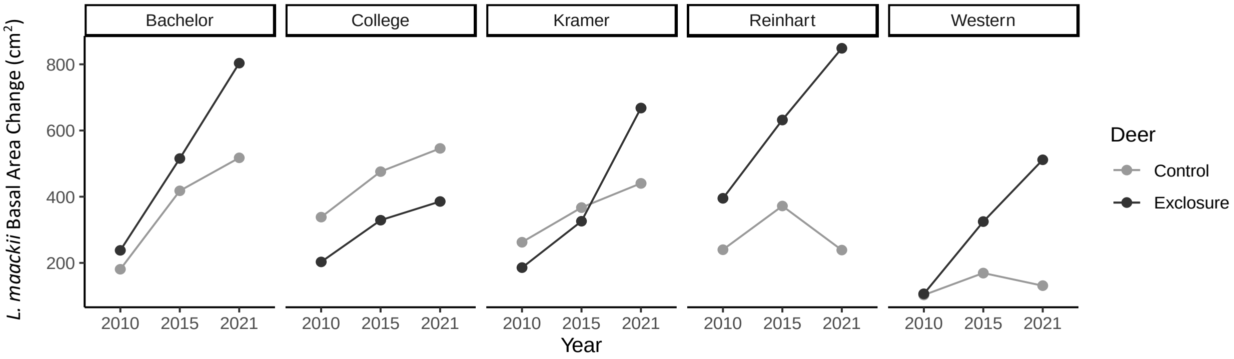


Figure 13: Plot of mean basal area (cm^2) of *Lonicera maackii* for 2010, 2015, and 2021 in half-plots at all sites where deer had access or were excluded and *L. maackii* was not removed. Data from 2010 are from Peebles-Spencer and Gorchov (2016). Data from 2015 are from Haffey and Gorchov (2019).

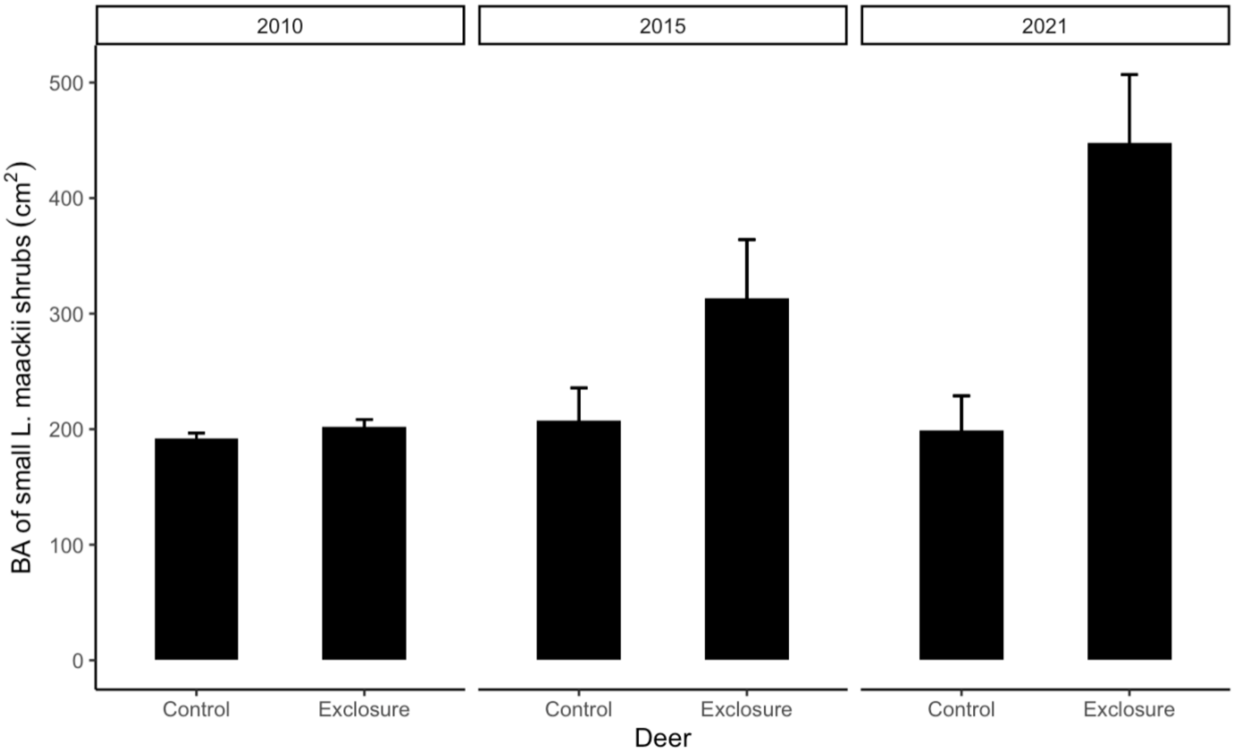


Figure 14: Mean (+SE) basal area (cm^2) of small *L. maackii* shrubs in 2010, 2015 and 2021 (shrubs with largest stem of basal diameter between 3-29 mm) in plots where *L. maackii* was left intact and where deer were excluded or had access. Data from 2015 Peebles-Spencer et al. (2018) and Haffey and Gorchov (2019).

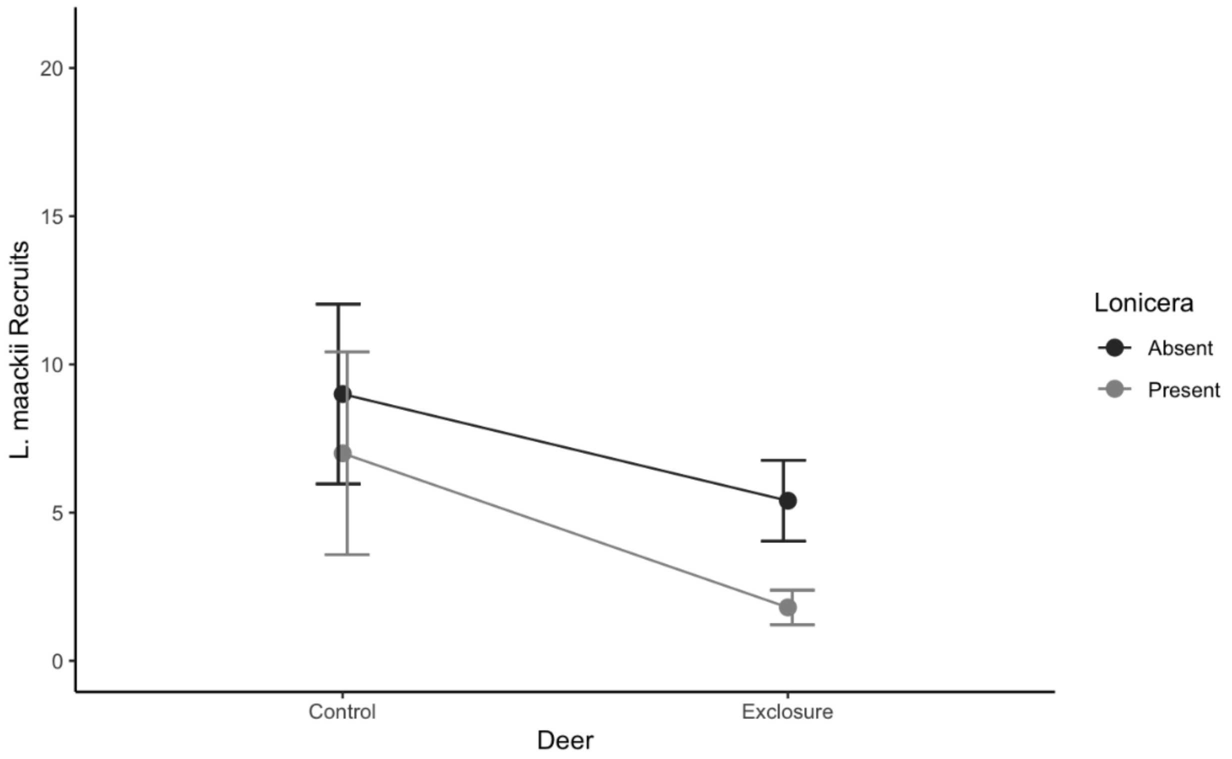


Figure 15: Interaction plot of *L. maackii* recruit count in 2021 (shrubs with largest stem basal diameter ≤ 2 mm) in half-plots where *L. maackii* was removed or left intact and where deer were excluded or had access.

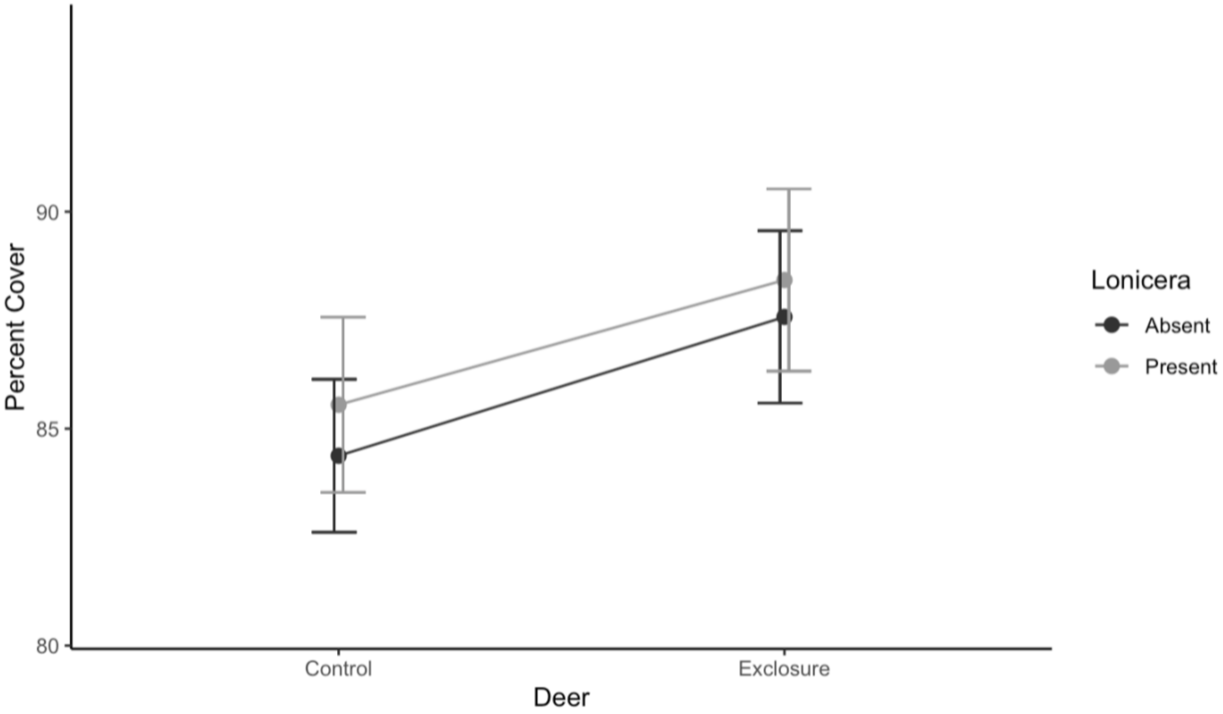


Figure 16: Interaction plot of mean modified percent forest floor cover index values from photographs taken in 2021 in half-plots at 0.3 m above ground where deer had access or were excluded and where *Lonicera maackii* was present or absent. Canopy photographs were taken every 4 m across two transects set 3.3m apart in each 10 x 20 m half-plot. Data from Western Woods was excluded as *L. maackii* was mistakenly removed in *L. maackii* present half-plots. For each treatment combination, mean ± (SE) of the five sites is plotted. See Fig. 1 for photograph locations within half-plots.

XI. APPENDIX

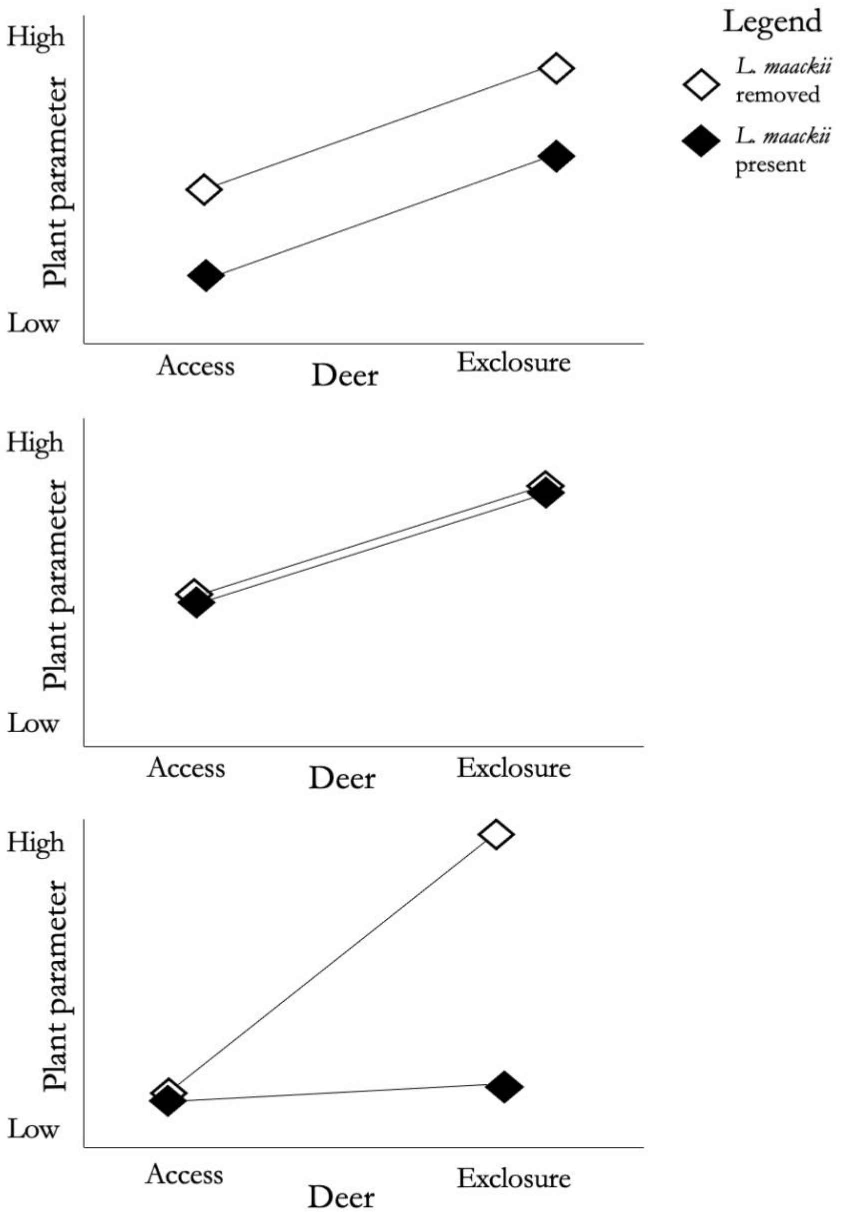


Figure A1: Projected plant response responses (abundance, richness, etc.) based on potential (top) additive effects of deer exclusion and *L. maackii* removal, (middle) direct deer effects and (bottom) sub-additive effect of deer access and *L. maackii* presence = (synergistic interactive effect of deer exclusion and *L. maackii* removal) (Peebles-Spencer et al. 2017).

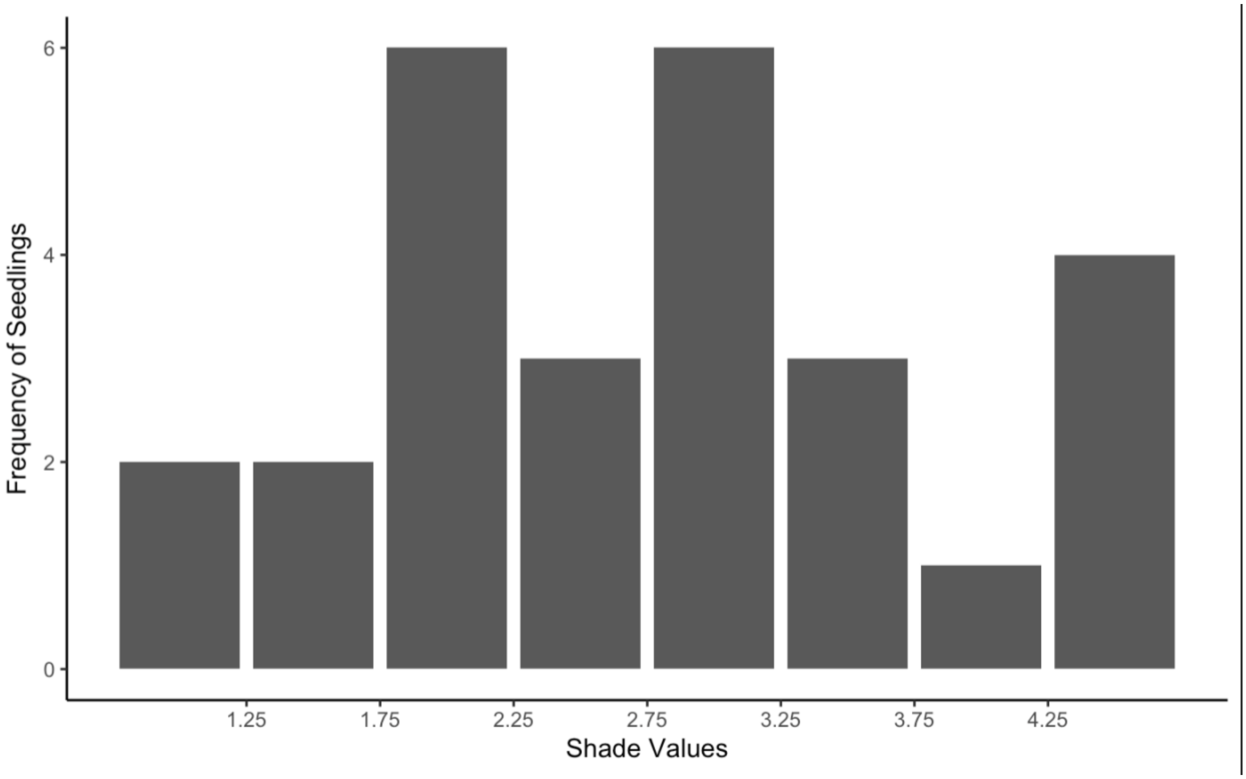


Figure A2: Frequency of shade tolerance values of tree species with seedlings across all study plots. Shade tolerance values were from Niinemets and Valladares (2006). This shade tolerance distribution was utilized to determine thresholds for shade tolerance classes for our study. Shade tolerance categories for seedlings were classified as high (>3.75), medium (2.75<x<3.75), and low (<2.75).

Table A1: Estimated white-tailed deer densities at five sites within the Miami University Natural Areas for summer and winter 2014 and spring and summer 2018 from Barret 2014 and Peterson 2018. Estimates were made using pellet-group distance sampling via transects.

	2014		2017	
Site Location	Summer Estimated Densities (deer km^{-2})	Winter Estimated Densities (deer km^{-2})	Spring Estimated Densities (deer km^{-2})	Summer Estimated Densities (deer km^{-2})
College Woods	11.3	6.8	8.0	5.0
Western Woods	12.1	25.8	13.6	8.8
Bachelor Preserve	13.0	13.7	18.2	9.5
Reinhart Preserve	9.6	30.0	7.9	7.8
Kramer Preserve	9.9	7.3	6.00	4.2

Table A2: Canopy tree composition for deer exclosure and control treatments across five sites in the Miami University Natural Areas. All canopy tree composition was recorded within the temporary 40 x 40 m plots established based on the center of each already established 20 x 20 m deer plots (Peebles-Spencer et al. 2017). All stems were taller than 2 m with DBH>10 cm. Basal area (BA) in cm^2 per $1600m^2$ plot are included.

	Bachelor Control		Bachelor Exclosure		College Control		College Exclosure		Western Control		Western Exclosure		Kramer Control		Kramer Exclosure		Reinhart Control		Reinhart Exclosure	
Tree Species	Stems	BA cm^2	Stems	BA cm^2	Stems	BA cm^2	Stems	BA cm^2	Stems	BA cm^2	Stems	BA cm^2	Stems	BA cm^2	Stems	BA cm^2	Stems	BA cm^2	Stems	BA cm^2
Acer saccharum	23	4763	30	8029	14	7000	16	8998	46	15367	44	21497	24	15579	17	13228	11	1463	31	14373
Quercus alba	4	2213	6	7237	5	5778	2	1455	-	-	1	1590	-	-	-	-	1	4963	-	-
Carya cordiformis	4	4673	4	5853	1	254	1	292	1	373	-	-	1	892	-	-	1	272	2	1315
Quercus muehlenbergii	2	695	-	-	7	9270	1	1158	1	1378	-	-	3	6589	1	2552	-	-	-	-
Quercus rubra	2	513	3	10191		10234	2	5509	-	-	-	-	1	5027	1	1878	-	-	5	6084
Ostrya virginiana	-	-	-	-	-	-	2	343	-	-	-	-	1	181	2	333	4	1898	4	376
Juglans nigra	-	-	-	-	-	-	-	-	-	-	1	572	1	1647	-	-	2	1423	7	5715
Liriodendron tulipifera	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7	11540	3	5714
Carya glabra	1	78	5	7168	-	-	1	463	1	572	-	-	-	-	-	-	1	1176	-	-
Acer nigrum	-	-	-	-	1	678	1	1562	1	526	-	-	-	-	1	222	-	-	3	908
Prunus serotina	-	-	2	409	-	-	-	-	1	2660	3	1243	1	1225	-	-	-	-	-	-
Acer platanoides	-	-	-	-	2	251	1	660	-	-	2	845	-	-	-	-	-	-	-	-
Carpinus caroliniana	-	-	1	213	2	223	-	-	-	-	-	-	-	-	-	-	2	164	-	-
Celtis occidentalis	2	434	1	81	-	-	-	-	1	814	-	-	-	-	-	-	1	471	-	-
Ulmus rubra	1	243	2	743	-	-	-	-	-	-	1	320	-	-	1	133	-	-	-	-
Fagus grandifolia	-	-	-	-	1	213	1	143	-	-	-	-	2	1160	-	-	-	-	-	-
Aesculus glabra	1	678	-		-	-	-	-	-	-	-	-	-	-	-	-	2	504	-	-
Platanus occidentalis	-	-	-	-	1	1359	-	-	-	-	-	-	-	-	-	-	-	-	2	1350
Carya tomentosa	-	-	-	-	-	-	2	1216	-	-	-	-	-	-	-	-	-	-	-	-
Quercus coccinea	1	12271	-		-	-	1	3653	-	-	-	-	-	-	-	-	-	-	-	-
Quercus bicolor	-	-	1	390	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Carya ovata	-	-	-	-	1	397	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Quercus imbricaria	-	-	-	-	-	-	1	1256	-	-	-	-	-	-	-	-	-	-	-	-
Fraxinus nigra	-	-	-	-	-	-	-	-	-	-	1	804	-	-	-	-	-	-	-	-
Populus deltoides	-	-	-	-	-	-	-	-	-	-	-	-	1	1626	-	-	-	-	-	-
Acer negundo	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	79	-	-
Cornus spp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	80
Acer rubrum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	141
Total	41	26561	55	40314	35	35657	30	26708	52	21690	53	26871	35	33926	23	18346	33	23953	59	36056

Table A3: Basal area (BA) of large trees (DBH>10cm) and canopy cover inside each 40 x 40 m plot created from the center of every 20 x 20 m treatment plot. BA in cm^2 per 1600m^2 plot and BA in m^2/hectare are included. Mean modified canopy cover index values (%) for each 40x40m plot were based on 9 photographs taken 2 m above ground in each plot. See Fig. 1 for photograph locations for plots.

Site	Deer	BA (cm^2)	BA (m^2/ha)	Mean ModifiedCaCo (%)
Bachelor	Access	26688	16.7	85.5
Bachelor	Exclosure	40322	25.2	85.5
College	Access	35664	22.3	82.4
College	Exclosure	26744	16.7	83.6
Kramer	Access	33929	21.2	84.8
Kramer	Exclosure	18258	11.4	87.9
Reinhart	Access	23952	15.0	92.1
Reinhart	Exclosure	36033	22.5	91.8
Western	Access	21703	13.6	89.2
Western	Exclosure	26875	16.8	88.3

Table A4: Native tree seedling species across all sites and deer treatments (exclosure or control) and *L. maackii* treatments (present or absent) in the Miami University Natural Areas. Includes all trees measured in the 20 x 20 m plots were between 0.3 to 2 m tall. Deer palatability classes are represented by N=No preference, L=Low, M=Moderate, and H=High based on Koon (2022). Shade tolerance classes are represented by L=Low, M=Medium, and H=High based on Niinemets and Valladares (2006) and Figure A2.

Deer Palatability Class			M	L	M	N	M	M	M	L	L	M	L	M	M	N	H	H	H	M	M	M	H	M	H	L	H	H	L	L
Shade Tolerance Class			L	L	L	H	M	H	H	L	M	H	L	M	M	M	L	M	H	L	H	M	L	L	L	L	M	H	L	H
Site	**Deer**	**Lonicera**	*Fraxinus americana*	*Prunus serotina*	*Fraxinus quadrangulata*	*Asimina triloba*	*Ulmus rubra*	*Acer saccharum*	*Fagus grandifolia*	*Celtis occidentalis*	*Aesculus glabra*	*Carpinus caroliniana*	*Carya cordiformis*	*Cercis canadensis*	*Acer nigrum*	*Acer negundo*	*Liriodendron tulipifera*	*Ulmus alata*	*Quercus rubra*	*Pyrus calleryana*	*Acer platanoides*	*Fraxinus nigra*	*Sassafras albidum*	*Morus rubra*	*Quercus muehlenbergii*	*Carya glabra*	*Quercus alba*	*Tilia americana*	*Maclura pomifera*	*Ostrya virginiana*
Bachelor	Control	Absent	218	2	8	-	-	1	-	12	6	-	1	-	-	-	-	1	-	1	-	-	-	-	1	-	-	-	-	-
College	Control	Absent	19	-	2	7	-	-	-	-	-	2	-	-	-	-	1	-	-	-	-	-	-	-	-	1	-	-	-	-
Reinhart	Control	Absent	9	-	2	-	-	-	-	-	3	7	1	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Western	Control	Absent	5	-	-	-	-	-	-	3	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-
Kramer	Control	Absent	3	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Bachelor	Control	Present	-	2	1	-	-	-	66	5	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
College	Control	Present	41	-	-	2	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Reinhart	Control	Present	18	-	3	-	-	3	-	-	11	4	-	-	-	3	-	-	-	-	-	-	-	-	-	1	-	-	-	-
Western	Control	Present	4	-	1	-	-	1	-	11	1	-	-	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Kramer	Control	Present	2	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Bachelor	Exclosure	Absent	221	306	52	-	-	26	1	15	2	-	7	1	10	-	-	7	-	3	-	1	-	2	2	-	-	-	1	-
College	Exclosure	Absent	113	34	81	8	-	23	-	4	-	1	7	8	-	-	1	-	5	-	-	2	4	1	-	-	-	-	-	-
Reinhart	Exclosure	Absent	9	17	-	34	20	8	-	-	2	20	4	4	1	7	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Western	Exclosure	Absent	17	49	7	-	19	-	-	2	1	-	3	4	-	-	5	-	2	-	3	-	-	-	-	-	-	-	-	1
Kramer	Exclosure	Absent	120	62	3	-	7	1	-	3	1	-	1	-	-	-	1	-	1	1	-	-	-	-	-	-	-	-	-	-
Bachelor	Exclosure	Present	-	26	10	-	-	3	-	-	16	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
College	Exclosure	Present	9	13	4	-	-	1	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Reinhart	Exclosure	Present	5	-	1	54	6	-	-	-	1	9	2	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
Western	Exclosure	Present	9	7	2	-	24	2	-	-	-	-	2	-	-	-	-	-	-	1	2	1	-	-	-	-	-	1	-	-
Kramer	Exclosure	Present	21	2	-	-	2	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-

Table A5: Seedling response variables across all sites and deer treatments (exclosure or control) and *L. maackii* treatments (present or absent) in the Miami University Natural Areas. Includes basal area (cm^2) (BA), density (seedlings/m^2), species richness, and abundance. All seedlings measured in the 20 x 20 m plots were between 0.3 to 2 m tall.

Site	Deer	Lonicera	BA	Density	Richness	Abundance
Bachelor	Exclosure	Present	18.2	0.29	5	58
Bachelor	Exclosure	Absent	168.3	3.26	15	657
Bachelor	Control	Present	13.7	0.38	5	75
Bachelor	Control	Absent	73.7	1.26	10	251
College	Exclosure	Present	4.7	0.14	5	28
College	Exclosure	Absent	85.8	1.46	13	291
College	Control	Present	15.2	0.22	3	44
College	Control	Absent	13.4	0.16	6	32
Reinhart	Exclosure	Present	23.1	0.42	9	83
Reinhart	Exclosure	Absent	31.6	0.65	11	129
Reinhart	Control	Present	116.3	0.22	7	43
Reinhart	Control	Absent	4.6	0.12	6	24
Western	Exclosure	Present	10.7	0.26	10	51
Western	Exclosure	Absent	22.6	0.57	12	113
Western	Control	Present	12.3	0.1	7	20
Western	Control	Absent	1.9	0.05	3	10
Kramer	Exclosure	Present	5.5	0.13	4	26
Kramer	Exclosure	Absent	40.6	1.02	12	203
Kramer	Control	Present	0.5	0.02	2	3
Kramer	Control	Absent	8.2	0.02	2	4

Table A6: Total shrub response variables across all sites and deer treatments (exclosure or control) and *L. maackii* treatments (present or absent) in the Miami University Natural Areas (excluding *L. maackii*). Includes basal area (cm^2) (BA), density ($shrubs/m^2$), species richness, and abundance. All shrubs measured in the 20-by20 m plots were taller than 0.3 m. Stems of species within 10 cm of each other were counted as being from the same individual shrub.

Site	Deer	Lonicera	BA	Density	Richness	Abundance
Bachelor	Exclosure	Present	8.6	0.13	3	26
Bachelor	Exclosure	Absent	67.4	0.11	5	22
Bachelor	Control	Present	9.2	0.06	2	11
Bachelor	Control	Absent	1.7	0.05	4	9
College	Exclosure	Present	2.9	0.06	3	11
College	Exclosure	Absent	107.9	0.68	6	136
College	Control	Present	5.8	0.09	3	17
College	Control	Absent	23.1	0.38	6	76
Reinhart	Exclosure	Present	258.1	1.63	7	326
Reinhart	Exclosure	Absent	292.1	1.28	9	255
Reinhart	Control	Present	55.6	0.35	9	69
Reinhart	Control	Absent	53.5	0.57	6	114
Western	Exclosure	Present	5.2	0.05	4	10
Western	Exclosure	Absent	38.4	0.18	5	36
Western	Control	Present	0.1	0.01	2	2
Western	Control	Absent	0.3	0.02	2	3
Kramer	Exclosure	Present	96.4	0.44	6	87
Kramer	Exclosure	Absent	60	0.52	10	103
Kramer	Control	Present	15.2	0.09	4	17
Kramer	Control	Absent	19.7	0.12	5	24

Table A7: Native shrub response variables across all sites and deer treatments (exclosure or control) and *L. maackii* treatments (present or absent) in the Miami University Natural Areas. Includes basal area (cm^2) (BA), density ($shrubs/m^2$), species richness, and abundance. See Table A6 for 'shrub' criteria.

Site	Deer	Lonicera	BA	Density	Richness	Abundance
Bachelor	Exclosure	Present	7.6	0.11	2	23
Bachelor	Exclosure	Absent	0.4	0.01	1	1
Bachelor	Control	Present	1.5	0.01	1	2
Bachelor	Control	Absent	0.4	0.02	1	4
College	Exclosure	Present	0.4	0.01	1	2
College	Exclosure	Absent	11.9	0.16	1	32
College	Control	Present	0	0	0	0
College	Control	Absent	8.3	0.27	2	54
Reinhart	Exclosure	Present	1.1	0.05	2	10
Reinhart	Exclosure	Absent	8.1	0.22	4	44
Reinhart	Control	Present	0.6	0.02	3	4
Reinhart	Control	Absent	0.5	0.02	2	3
Western	Exclosure	Present	2.4	0.02	2	4
Western	Exclosure	Absent	0.4	0.01	1	1
Western	Control	Present	0	0.01	1	1
Western	Control	Absent	0	0	0	0
Kramer	Exclosure	Present	14.4	0.07	4	13
Kramer	Exclosure	Absent	8.6	0.16	7	32
Kramer	Control	Present	13	0.05	2	10
Kramer	Control	Absent	19.7	0.12	4	23

<u>Table A8:</u> Number of native and non-native shrub species across all sites and deer treatments (exclosure or control) and *L. maackii* treatments (present or absent) in the Miami University Natural Areas. See Table A6 for 'shrub' criteria. For *L. maackii* only the number of recruits (basal diameter of the largest stem ≤ 2 mm; Peebles-Spencer et al. 2018) is reported in all plots for all treatments.

			Native											Non-native								
Site	Deer	Lonicera	*Viburnum prunifolium*	*Rubus allegheniensis*	*Lindera benzoin*	*Ribes* spp.	*Viburnum dentatum*	*Euonymus atropurpureus*	*Rubus occidentalis*	*Sambucus canadensis*	*Sambucus nigra*	*Sambucus racemosa*	*Viburnum nudum*	*Ligustrum obtusifolium*	*Euonymus alatus*	*Lonicera maackii*	*Rosa mutliflora*	*Lonicera morrowii*	*Elaeagnus umbellata*	*Berberis thunbergii*	*Rubus idaeus*	*Frangula alnus*
Bachelor	Control	Absent	-	4	-	-	-	-	-	-	-	-	-	1	1	7	3	-	-	-	-	-
College	Control	Absent	2	52	-	-	-	-	-	-	-	-	-	-	-	5	16	-	2	2	2	-
Reinhart	Control	Absent	1	-	-	2	-	-	-	-	-	-	-	88	3	7	9	-	10	-	-	-
Western	Control	Absent	-	-	-	-	-	-	-	-	-	-	-	2	-	21	1	-	-	-	-	-
Kramer	Control	Absent	1	10	11	-	1	-	-	-	-	-	-	1	-	5	-	-	-	-	-	-
Bachelor	Control	Present	-	-	-	2	-	-	-	-	-	-	-	9	-	0	-	-	-	-	-	-
College	Control	Present	-	-	-	-	-	-	-	-	-	-	-	13	2	3	2	-	-	-	-	-
Reinhart	Control	Present	2	-	-	1	-	-	-	-	-	-	1	42	2	10	5	9	3	-	-	2
Western	Control	Present	1	1	-	-	-	-	-	-	-	-	-	-	-	19	-	-	-	-	-	-
Kramer	Control	Present	-	1	9	-	-	-	-	-	-	-	-	5	-	0	2	-	-	-	-	-
Bachelor	Exclosure	Absent	-	-	-	-	-	1	-	-	-	-	-	11	5	5	-	-	1	-	-	-
College	Exclosure	Absent	32	-	-	-	-	-	-	-	-	-	-	32	63	9	4	-	2	-	2	-
Reinhart	Exclosure	Absent	-	-	-	18	22	-	3	-	-	-	-	164	3	3	15	13	1	-	-	-
Western	Exclosure	Absent	1	-	-	-	-	-	-	-	-	-	-	15	16	8	-	-	1	-	-	-
Kramer	Exclosure	Absent	14	5	4	-	2	1	-	-	2	-	-	-	63	2	4	-	-	7	1	-
Bachelor	Exclosure	Present	10	-	-	-	-	13	-	-	-	-	-	3	-	2	-	-	-	-	-	-
College	Exclosure	Present	2	-	-	-	-	-	-	-	-	-	-	1	8	1	-	-	-	-	-	-
Reinhart	Exclosure	Present	4	-	-	5	1	-	-	-	-	-	-	292	2	3	10	7	1	-	-	-
Western	Exclosure	Present	-	-	-	-	-	1	-	3	-	-	-	3	3	3	-	-	-	-	-	-
Kramer	Exclosure	Present	5	-	6	-	1	-	-	-	-	1	-	68	2	0	-	-	-	-	-	-

Table A9: Non-native shrub (excluding *L. maackii*) response variables across all sites and deer treatments (exclosure or control) and *L. maackii* treatments (present or absent) in the Miami University Natural Areas. Includes basal area (cm^2) (BA), density (shrubs/m^2), species richness, and abundance. See Table A6 for 'shrub' criteria.

Site	Deer	Lonicera	BA	Density	Richness	Abundance
Bachelor	Exclosure	Present	1	0.02	1	3
Bachelor	Exclosure	Absent	67	0.1	4	21
Bachelor	Control	Present	7.7	0.05	1	9
Bachelor	Control	Absent	1.2	0.03	3	5
College	Exclosure	Present	2.5	0.05	2	9
College	Exclosure	Absent	96	0.52	5	104
College	Control	Present	5.8	0.09	3	17
College	Control	Absent	14.8	0.11	4	22
Reinhart	Exclosure	Present	257	1.58	5	316
Reinhart	Exclosure	Absent	284	1.06	5	211
Reinhart	Control	Present	55	0.33	6	65
Reinhart	Control	Absent	53	0.56	4	111
Western	Exclosure	Present	2.75	0.03	2	6
Western	Exclosure	Absent	38	0.18	4	35
Western	Control	Present	0.1	0.01	1	1
Western	Control	Absent	0.4	0.02	2	3
Kramer	Exclosure	Present	82	0.37	2	74
Kramer	Exclosure	Absent	51.4	0.36	3	71
Kramer	Control	Present	2.2	0.04	2	7
Kramer	Control	Absent	0	0.01	1	1

Table A10: Total vine response variables across all sites and deer treatments (exclosure or control) and *L. maackii* treatments (present or absent) in the Miami University Natural Areas. Includes basal area (cm^2) (BA), density ($vines/m^2$), species richness, and abundance. All vines measured in the 20 x 20 m plots were taller than 0.3 m.

Site	Deer	Lonicera	BA	Density	Richness	Abundance
Bachelor	Exclosure	Present	1.3	0.03	2	6
Bachelor	Exclosure	Absent	3.8	0.24	4	48
Bachelor	Control	Present	0.7	0.05	3	9
Bachelor	Control	Absent	2.5	0.13	3	26
College	Exclosure	Present	1	0.03	3	6
College	Exclosure	Absent	5.3	0.47	5	93
College	Control	Present	0.1	0.01	1	1
College	Control	Absent	0	0	0	0
Reinhart	Exclosure	Present	0.2	0.02	3	4
Reinhart	Exclosure	Absent	0.8	0.07	6	13
Reinhart	Control	Present	0.3	0.02	3	3
Reinhart	Control	Absent	0.2	0.02	2	3
Western	Exclosure	Present	0.4	0.03	3	5
Western	Exclosure	Absent	2.9	0.11	4	21
Western	Control	Present	8.8	0.36	5	71
Western	Control	Absent	5.8	0.23	3	46
Kramer	Exclosure	Present	0.2	0.01	1	2
Kramer	Exclosure	Absent	4.9	0.14	2	27
Kramer	Control	Present	0	0.01	3	2
Kramer	Control	Absent	0	0	0	0

Table A11: Native vine response variables across all sites and deer treatments (exclosure or control) and *L. maackii* treatments (present or absent) in the Miami University Natural Areas. Includes basal area (cm^2) (BA), density (vines/m^2), species richness, and abundance. All vines measured in the 20 x 20 m plots were taller than 0.3 m.

Site	Deer	Lonicera	BA	Density	Richness	Abundance
Bachelor	Exclosure	Present	1	0.01	1	2
Bachelor	Exclosure	Absent	0.7	0.03	2	5
Bachelor	Control	Present	0.6	0.03	2	5
Bachelor	Control	Absent	0.5	0.02	2	4
College	Exclosure	Present	1	0.02	2	3
College	Exclosure	Absent	3.9	0.17	3	34
College	Control	Present	0.1	0.01	1	1
College	Control	Absent	0	0	0	0
Reinhart	Exclosure	Present	0.2	0.02	2	3
Reinhart	Exclosure	Absent	0.5	0.04	5	7
Reinhart	Control	Present	0	0.01	2	1
Reinhart	Control	Absent	11.3	0.01	1	1
Western	Exclosure	Present	0.3	0.02	2	3
Western	Exclosure	Absent	0.1	0.02	2	3
Western	Control	Present	1.9	0.08	3	16
Western	Control	Absent	0.7	0.05	2	10
Kramer	Exclosure	Present	0.2	0.01	1	2
Kramer	Exclosure	Absent	4.9	0.14	2	27
Kramer	Control	Present	0.	0.01	3	2
Kramer	Control	Absent	0	0	0	0

Table A12: Non-native vine response variables across all sites and deer treatments (exclosure or control) and *L. maackii* treatments (present or absent) in the Miami University Natural Areas. Includes basal area (cm^2) (BA), density (vines/m^2), species richness, and abundance. All vines measured in the 20 x 20 m plots were taller than 0.3 m.

Site	Deer	Lonicera	BA	Density	Richness	Abundance
Bachelor	Exclosure	Present	0.3	0.02	1	4
Bachelor	Exclosure	Absent	3	0.22	2	43
Bachelor	Control	Present	0.1	0.02	1	4
Bachelor	Control	Absent	2	0.11	1	22
College	Exclosure	Present	0.1	0.02	1	3
College	Exclosure	Absent	1.4	0.30	2	59
College	Control	Present	0	0	0	0
College	Control	Absent	0	0	0	0
Reinhart	Exclosure	Present	0	0.01	1	1
Reinhart	Exclosure	Absent	0.3	0.03	1	6
Reinhart	Control	Present	0.3	0.01	1	2
Reinhart	Control	Absent	0.2	0.02	1	3
Western	Exclosure	Present	0.1	0.01	2	2
Western	Exclosure	Absent	2.8	0.09	5	18
Western	Control	Present	6.9	0.28	2	55
Western	Control	Absent	5.0	0.18	1	36
Kramer	Exclosure	Present	0	0	0	0
Kramer	Exclosure	Absent	0	0	0	0
Kramer	Control	Present	0	0	0	0
Kramer	Control	Absent	0	0	0	0

Table A13: Changes from 2015 to 2021 in understory tree response variables across all sites and deer treatments (exclosure or control) and *L. maackii* treatments (present or absent) in the Miami University Natural Areas. Includes basal area (cm^2) (BA), density ($trees/m^2$), species richness, and abundance. All understory trees measured in the 20 x 20 m plots were taller than 2 m with DBH<10 cm. Also includes trees that passed the 10 cm DBH threshold from 2015 to 2021.

Site	**Deer**	**Lonicera**	**BA**	**Density**	**Richness**	**Abundance**
Bachelor	Exclosure	Present	43	0.01	1	1
Bachelor	Exclosure	Absent	27	0.03	4	6
Bachelor	Control	Present	283	0.06	-3	11
Bachelor	Control	Absent	181	0.09	0	18
College	Exclosure	Present	-18	-0.01	0	-1
College	Exclosure	Absent	14	0.01	1	1
College	Control	Present	6	0	-1	0
College	Control	Absent	39	0.02	0	3
Reinhart	Exclosure	Present	2	0.04	-1	7
Reinhart	Exclosure	Absent	39	0.06	3	12
Reinhart	Control	Present	-20	-0.05	-3	-9
Reinhart	Control	Absent	-10	-0.05	-2	-9
Western	Exclosure	Present	36	-0.02	0	-3
Western	Exclosure	Absent	12	0	0	0
Western	Control	Present	114	-0.02	0	-3
Western	Control	Absent	32	-0.01	0	-1
Kramer	Exclosure	Present	18	-0.01	0	-2
Kramer	Exclosure	Absent	-2	-0.02	0	-4
Kramer	Control	Present	83	0.01	0	1
Kramer	Control	Absent	-14	-0.02	0	-4

Table A14: Average seedling abundance in half-plots subjected to a combination of deer treatments (access, exclosure) and *L. maackii* treatments and grouped using palatability classes. Seedlings were grouped using palatability classes compiled by Koon (2022).

Deer Palatability	Deer excluded, *L. maackii* absent	Deer excluded, *L. maackii* present	Deer access, *L. maackii* absent	Deer access, *L. maackii* present
High	5.6	0.6	1.0	0.4
Moderate	158.1	23.2	55.6	29.4
Low	104.4	13.8	5.8	6.2
No preference	9.8	10.8	1.8	1.0

Table A15: Average seedling abundance in half-plots subjected to a combination of deer treatments (access, exclosure) and *L. maackii* treatments, grouped shade by shade tolerance categories. Seedlings were grouped using shade tolerance values according to Niinemets and Valladares (2006). Shade tolerance values below 2.75 were considered low; values above 2.75 but below 3.75 were considered medium; values above 3.75 were considered high.

Shade Tolerance	Deer excluded, *L. maackii* absent	Deer excluded, *L. maackii* present	Deer access, *L. maackii* absent	Deer access, *L. maackii* present
High	26.8	14.4	3.6	15.4
Medium	19.4	11.0	2.4	3.6
Low	231.6	23.0	58.2	18.0

Table A16: Understory tree species (see Table A13) that were lost (-) or gained (+) that influenced species richness from 2015 to 2021 in each site in deer (exclosure or control) and *L. maackii* (present or absent) treatments in the Miami University Natural Areas. Diameter (cm) values of trees that were lost were from 2015 and diameter of trees that were gained were from 2021 and correspond to individual understory trees that were responsible for loss (-) or gain (+) in richness from 2015 to 2021.

Site	Deer	Lonicera	*Acer negundo*	*Aesculus glabra*	*Asimina triloba*	*Carpinus caroliniana*	*Celtis occidentalis*	*Prunus serotina*	*Quercus rubra*	*Ulmus rubra*	Diameter of tree gained (cm)	Diameter of tree lost (cm)
Bachelor	Control	Absent										
College	Control	Absent										
Reinhart	Control	Absent								-		3.1
Western	Control	Absent										
Kramer	Control	Absent										
Bachelor	Control	Present					-		-			3.0, 9.6
College	Control	Present						-				6.3
Reinhart	Control	Present	-									4.4
Western	Control	Present										
Kramer	Control	Present										
Bachelor	Exclosure	Absent						+			1.2	
College	Exclosure	Absent			+						2.3	
Reinhart	Exclosure	Absent		+	+	+				+	2.7, 2.3, 1.7, 1.1	
Western	Exclosure	Absent										
Kramer	Exclosure	Absent										
Bachelor	Exclosure	Present		+							3.8	
College	Exclosure	Present										
Reinhart	Exclosure	Present								-		0.6
Western	Exclosure	Present										
Kramer	Exclosure	Present										

Table A17: Understory tree species across all sites and deer treatments (exclosure or control) and *L. maackii* treatments (present or absent) in the Miami University Natural Areas. Includes all understory trees measured in the 20 x 20 m plots taller than 2 m with DBH<10 cm.

Site	Deer	Lonicera	*Acer saccabrum*	*Aesculus glabra*	*Asimina triloba*	*Carpinus caroliniana*	*Fraxinus quadrangulata*	*Fraxinus americana*	*Ulmus rubra*	*Prunus serotina*	*Cornus florida*	*Fagus grandifolia*
Bachelor	Control	Absent	6	31	-	-	-	-	-	1	-	-
College	Control	Absent	12	-	3	-	-	-	-	-	1	-
Reinhart	Control	Absent	8	-	-	3	-	1	-	-	-	-
Western	Control	Absent	2	-	-	-	-	-	-	-	-	-
Kramer	Control	Absent	8	-	-	-	-	-	-	-	-	-
Bachelor	Control	Present	7	21	-	-	-	-	-	-	-	-
College	Control	Present	7	-	1	-	2	-	-	-	-	-
Reinhart	Control	Present	18	1	-	2	-	1	1	-	-	-
Western	Control	Present	11	-	-	-	-	-	-	-	-	1
Kramer	Control	Present	15	-	-	-	-	-	-	-	-	-
Bachelor	Exclosure	Absent	5	-	-	-	-	-	-	-	-	-
College	Exclosure	Absent	1	-	1	-	-	-	-	-	-	-
Reinhart	Exclosure	Absent	4	1	4	8	-	-	1	-	-	-
Western	Exclosure	Absent	1	-	-	-	-	-	-	-	-	-
Kramer	Exclosure	Absent	3	-	-	-	-	-	-	-	-	-
Bachelor	Exclosure	Present	6	3	-	-	-	-	-	-	-	-
College	Exclosure	Present	4	-	-	-	-	-	-	-	-	-
Reinhart	Exclosure	Present	6	-	18	-	-	-	-	-	-	-
Western	Exclosure	Present	8	-	-	-	-	-	-	-	-	-
Kramer	Exclosure	Present	6	-	-	-	-	-	-	-	-	-

Table A18: Density (shrubs/m^2) of all *L. maackii* shrubs >1 m in height and basal area (cm^2) of small (basal diameter of largest stem between 3-29 mm), large (basal diameter of the largest stem ≥ 30 mm), and total *L. maackii* shrubs across all deer treatment (exclosure or control) and *L. maackii* presence plots in the Miami University Natural Areas. Table also includes proportion of basal area of small and large shrubs that comprise total shrub basal area. Includes all small and large *L. maackii* shrubs in the 20 x 20 m plots. *L. maackii* recruit BA was excluded as contribution to total shrub BA was miniscule. Stems of species within 10 cm of each other were counted as being from the same individual shrub.

Site	**Deer**	**Lonicera**	**Density**	**Small BA**	**Large BA**	**Total BA**	**Prop. Small**	**Prop. Large**
Bachelor	Control	Present	0.33	271	245	516	0.53	0.47
Bachelor	Exclosure	Present	0.52	564	239	803	0.70	0.30
College	Control	Present	0.26	226	319	545	0.41	0.59
College	Exclosure	Present	0.28	237	149	386	0.61	0.39
Kramer	Control	Present	0.23	224	249	473	0.47	0.53
Kramer	Exclosure	Present	0.52	519	146	665	0.78	0.22
Reinhart	Control	Present	0.15	137	102	239	0.57	0.43
Reinhart	Exclosure	Present	0.51	422	427	849	0.50	0.50
Western	Control	Present	0.09	131	0	131	1.00	0.00
Western	Exclosure	Present	0.49	460	62.5	522	0.88	0.12

Table A19: Number of stems of native and non-native vine species across all sites and deer treatments (exclosure or control) and *L. maackii* treatments (present or absent) in the Miami University Natural Areas. Includes all vines measured in the 20 x 20 m plots taller than 0.3 m.

			Native					Non-native		
Site	Deer	Lonicera	*Smilax tamnoides*	*Vitis* spp.	*Parthenocissus quinquefolia*	*Dioscorea villosa*	*Menispermum canadense*	*Celastrus orbiculatus*	*Lonicera japonica*	*Euonymus fortunei*
Bachelor	Control	Absent	3	1	-	-	-	22	-	-
College	Control	Absent	-	-	-	-	-	-	-	-
Reinhart	Control	Absent	-	-	-	-	-	3	-	-
Western	Control	Absent	-	9	1	-	-	36	-	-
Kramer	Control	Absent	-	-	-	-	-	-	-	-
Bachelor	Control	Present	1	-	-	1	-	-	-	-
College	Control	Present	1	14	1	-	-	53	2	-
Reinhart	Control	Present	-	-	-	-	1	2	-	-
Western	Control	Present	1	-	-	-	-	-	-	-
Kramer	Control	Present	4	1	-	-	-	4	-	-
Bachelor	Exclosure	Absent	-	-	1	4	-	27	16	-
College	Exclosure	Absent	24	6	4	-	-	3	56	-
Reinhart	Exclosure	Absent	4	1	1	-	1	6	-	-
Western	Exclosure	Absent	1	-	2	-	-	17	-	3
Kramer	Exclosure	Absent	24	-	3	-	-	-	-	-
Bachelor	Exclosure	Present	2	-	-	-	-	-	-	-
College	Exclosure	Present	1	-	2	-	-	2	-	-
Reinhart	Exclosure	Present	3	-	-	-	-	1	-	-
Western	Exclosure	Present	2	-	1	-	-	-	3	-
Kramer	Exclosure	Present	2	-	-	-	-	4	-	-