Forest Ecology and Management 402 (2017) 204–212

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Effects of an invasive shrub, *Lonicera maackii*, and a generalist herbivore, white-tailed deer, on forest floor plant community composition

Jessica R. Peebles-Spencer [1], David L. Gorchov *, Thomas O. Crist

Department of Biology, Miami University, Oxford, OH 45056, USA

ARTICLE INFO

Article history:
Received 24 March 2017
Received in revised form 24 May 2017
Accepted 29 May 2017

Keywords:
Non-additive interactions
Distance-based multivariate analysis
Indicator species
Herb layer species richness
Plant functional types
Odocoileus virginianus

ABSTRACT

Both overabundant ungulates and invasive shrubs negatively impact forest floor plants, but few studies have investigated their interaction. We tested for direct effects and interactions of white-tailed deer, *Odocoileus virginianus*, and the invasive shrub, *Lonicera maackii*, on forest floor plant richness and composition in five sites in southwest Ohio. In each site a deer exclosure and an unfenced plot (each 20 × 20 m) were established in 2010; in half of each plot all *L. maackii* was removed. Each spring and summer, 2011–2014, percent cover of each plant species in 50 × 20 cm subplots was recorded.

Herb layer species richness was greater where *L. maackii* was removed, and this effect tended to be stronger where deer were excluded. Species composition in the spring was not affected by treatments, whereas summer species composition (in one year) was affected by *L. maackii* treatment. Cover of graminoids, spring herbs, and vines were lower where *L. maackii* was intact, whereas cover of shrubs and tree seedlings were lower, and cover of bare ground higher, where deer had access.

Our findings reveal that deer and *L. maackii* negatively impact different components of the forest herb layer. However, the combined effects on species richness tended to be antagonistic (less than additive), possibly due to deer browse reducing the cover of this invasive shrub. This suggests that the diversity of the herb layer will be enhanced more by both removal of invasive shrubs and reduction of the deer population than by either management action alone.

1. Introduction

Studies of plant-animal interactions have typically focused on direct effects (Krivtsov, 2004; Strauss and Irwin, 2004) rather than indirect effects, as indirect effects are more difficult to observe, predict, and quantify (Krivtsov, 2004; White et al., 2006). Indirect effects between plant and animal species are fundamental to understanding the workings of complex ecosystems (Wootton, 2002) and may be important for understanding invasions (White et al., 2006). While plant communities are often negatively impacted by invasive plants (Mack et al., 2000; Vilà et al., 2011; Jauni and Ramula, 2015) and overabundant generalist herbivores such as ungulates (Vavra et al., 2007), the interactive effects of these two drivers have not been well studied.

In many parts of the United States densities of white-tailed deer, *Odocoileus virginianus* (hereafter 'deer') are well above historical levels (McShea, 2012), after rebounding from widespread population declines and extirpations in the early-to-mid 1800s (Côté et al., 2004; Sotala and Kirkpatrick, 1973). This overabundance of deer has negatively impacted tree survival, recruitment, growth, and regeneration (Bradshaw and Waller, 2016; Côté et al., 2004; Csigi and Holzmueller, 2015; Horsley et al., 2003; Meiners and Martinkovic, 2002; Russell et al., 2001, 2017). At even moderate densities, deer greatly alter structure and composition of forests (Rooney, 2009). At densities as low as 3–10 deer/km^2, deer negatively impact preferred browse species (Côté et al., 2004; Horsley et al., 2003). These preferences for forage can influence the winners and losers of competition over time, acting as a driver of change (Wiegmann and Waller, 2006), and increasing the prevalence of grasses, ferns and other species deer find unpalatable (Horsley et al., 2003; Rooney, 2009). Deer have also been shown to negatively impact plant species richness (Habeck and Schultz, 2015; Rooney, 2009; Relva et al., 2010; Wiegmann and Waller, 2006). Additionally, areas with abundant deer show increased decomposition rates and decreased litter mass when compared to areas of deer exclosure (Bressette et al., 2012).

While the individual direct effects of deer and invasive shrubs on forest communities are well studied, only a modest number of studies have investigated indirect effects of deer on invasive plants,

* Corresponding author.
E-mail address: GorchoDL@miamioh.edu (D.L. Gorchov).
[1] Current address: Department of Biology, Ball State University, Muncie, IN 47306, USA.

http://dx.doi.org/10.1016/j.foreco.2017.05.053
0378-1127/

or interactive effects of deer and invasive plants on plant communities. Studies of indirect effects of deer on invasive plants suggest that some invasive plants are facilitated, even obligatorily so, by overabundant deer in forest settings (Dávalos et al., 2015a; Knight et al., 2009; Kalisz et al., 2014; Shen et al., 2016).

Studies of simultaneous and interactive effects of deer and invasive plants are rare. Aronson and Handel (2011) investigated the interactive effects of deer exclosure and removal of the invasive grass, *Microstegium vimineum*, finding a positive effect of *M. vimineum* removal, but not deer or their interaction, on plant species richness, and positive effects of removal of each stressor on survival and growth of tree seedlings. Waller and Maas (2013) found that *Alliaria petiolata* and deer negatively affected growth of four herb species and survival of one of those, and a significant interaction on growth of a tree species, with greater negative effects of *A. petiolata* in the absence of deer (Waller and Maas, 2013). Dávalos et al. (2015b) investigated the effects of deer and three invasive plants on recruitment of three rare plants, and found that one of these was negatively impacted by deer but positively impacted by *M. vimineum*.

We investigated the interaction of deer and *Lonicera maackii* (Rupr.) Herder (Caprifoliaceae), Amur Honeysuckle, a large shrub from northeast Asia (Luken and Thieret, 1996) that is one of several bush honeysuckle species that are invasive in the eastern United States. The current distribution of *L. maackii* spans the eastern half of the United States; *L. maackii* is considered invasive and is regulated in eight of those states (EDDMapS, 2016). Negative effects of *L. maackii* on forest composition have been documented in comparative and experimental studies. Compared to uninvaded stands, stands invaded by *L. maackii* had lower densities and species richness of tree seedlings and saplings and herbs (Hartman and McCarthy, 2008). Within stands, areas under *L. maackii* shrubs have lower species richness and cover of all species and of tree species with canopy potential (Collier et al., 2002) and lower tree seedling survival (Loomis et al., 2015). Experimental removal of *L. maackii* increased native and exotic plant species richness (Orrock et al., 2015), tree seedling survival and growth (Gorchov and Trisel, 2003), and herb growth and reproduction (Gould and Gorchov, 2000; Miller and Gorchov, 2004). Additionally, leaves of *L. maackii* decompose more rapidly than native tree species (Poulette and Arthur, 2012), leading to decreased litter mass and increased bare ground, factors often required for the establishment of other non-native species (Bartuszevige et al., 2007; Kuhman et al., 2013; Oswalt and Oswalt, 2007).

Christopher et al. (2014) found interactive effects of deer and *L. maackii* on the abundance of annuals and spring perennials: where *L. maackii* was present there was no effect of deer, but where *L. maackii* was removed or absent deer decreased the abundance of both. There was also an interactive effect of *L. maackii* and deer on *Maianthemum racemosum*; leaf count was reduced by *L. maackii* only where deer were excluded. Conversely, Orrock et al. (2015) found no significant interactions of mammalian consumers (including deer) and *L. maackii* on native species abundance and richness or exotic species abundance or richness. However, Gorchov and Trisel (2003) found that biomass of *Acer saccharum* seedlings planted where they were accessible to deer had greater biomass where *L. maackii* shoots were present than where they had been removed, but biomass of seedlings protected from deer was slightly lower where *L. maackii* shoots were present. That suggests *L. maackii* protects plants from deer damage, as does Cipollini et al.'s (2009) finding that herbaceous plants had higher reproduction and greater size beneath both standing dead and living shrubs of *L. maackii*. Conversely, Hartman and McCarthy (2004) and Loomis et al. (2015) found no significant effects of protection from deer browse on tree seedling growth and survival.

We investigated whether the effects of deer and invasive shrubs are additive, or whether they interact synergistically or antagonistically. If deer and *L. maackii* individually negatively affect forest floor plants without interactive effects of these two drivers, these effects are 'additive' (Fig. 1A). We predict that compositional changes should follow this trend, as deer and *L. maackii* affect

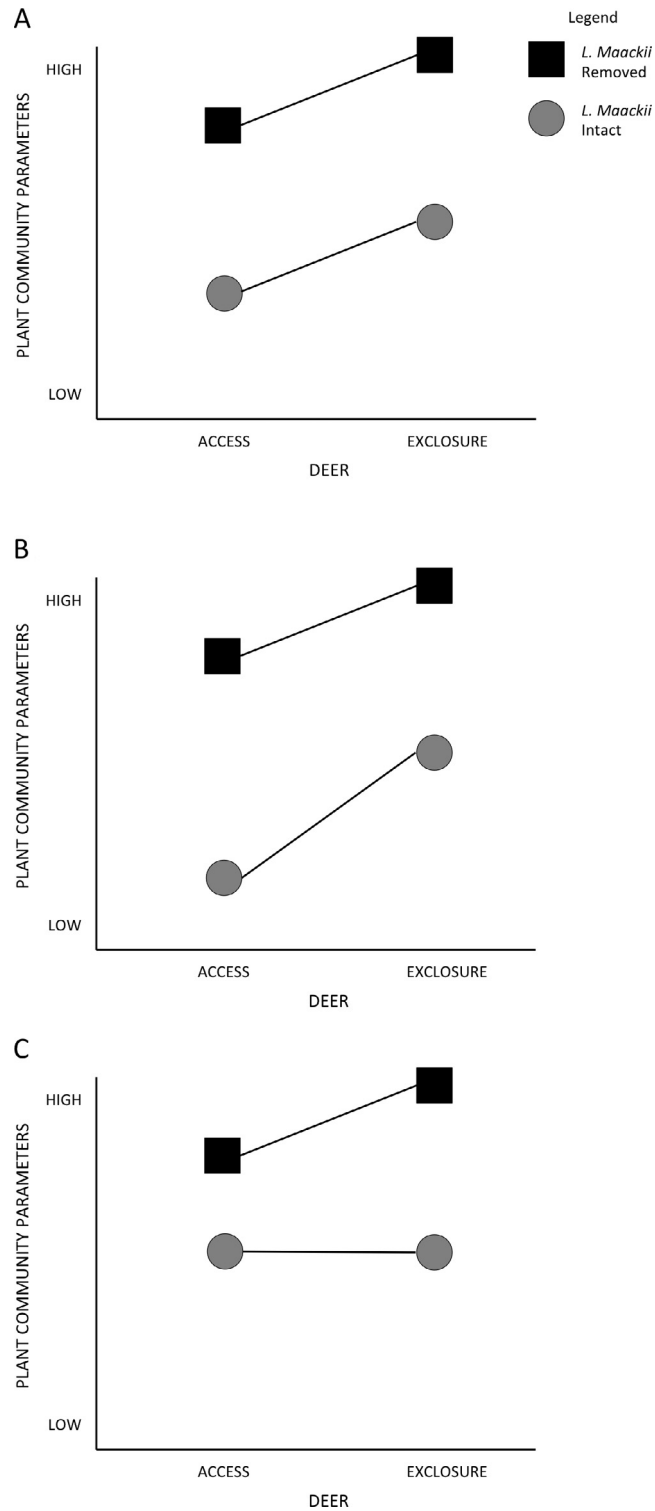

Fig. 1. Predictions of plant community responses (e.g. species richness, cover) A. based on the null hypothesis that effects of deer and *Lonicera maackii* are additive, B. based on the alternative hypothesis that effects of deer and *L. maackii* are non-additive and synergistic in nature, and C. based on the alternative hypothesis that effects of deer and *L. maackii* are non-additive and antagonistic in nature.

composition in different ways. Specifically, we predict species palatable to deer will be less abundant, and unpalatable species more abundant, in areas with deer (Horsley et al., 2003). In areas with *L. maackii* shrub cover, we predict a large negative impact on tree seedlings and a smaller effect on forbs (Collier et al., 2002; Hartman and McCarthy, 2008). As shading by the early leaf flush of *L. maackii* hinders spring perennials' access to sunlight (Miller and Gorchov, 2004), we also predict spring perennials will be more impacted by *L. maackii* than summer perennials.

Alternatively, deer and *L. maackii* may impact forest plants in a synergistic manner, where their joint effects are more negative than the sum of the two individual effects (Fig. 1B). This could be caused by certain indirect effects; e.g. if deer are attracted to areas with *L. maackii* (refuge-mediated apparent competition, *sensu* Orrock et al. (2010)), plant responses to shading by *L. maackii* makes them more susceptible to deer browse, or plant responses to deer browse makes them less tolerant to shading.

Antagonistic interactions occur if the joint negative effects of deer and *L. maackii* are less negative than the sum of the two individual effects (Fig. 1C). This would result if deer avoid browsing in areas with *L. maackii*, e.g., due to the physical barrier, so that *L. maackii* decreases the negative effect of deer (Gorchov and Trisel, 2003; Cipollini et al., 2009), or if deer browse on *L. maackii*, reducing its cover and therefore reducing its shading of other plant species. We predict that deer and *L. maackii* will show antagonistic interactions on tree seedlings and forest floor plant species richness, with deer avoiding areas of *L. maackii*, allowing for increased survival and growth of tree seedlings and other preferred species.

2. Materials and methods

2.1. Field methods

This study utilized deer exclosures and paired deer access plots arranged in a split-plot design in five sites in the Miami University Natural Areas, Butler County, Ohio (39°29′–39°31′N, 84°42′–84°43′W; Peebles-Spencer, 2016). Sites were separated by ≥1 km and chosen to have (1) closed-canopy mature deciduous forest, (2) level topography, and (3) a similar, moderate level of invasion by *L. maackii* (stem basal area 0.58–1.57 m^2 ha^{-1}, Peebles-Spencer, 2016). Within each site, two similar 20 m-by-20 m plots were selected; one each randomly assigned to deer exclosure and deer access treatments. Fencing 3 m high was placed around the deer exclosure plots in summer 2010. In fall of 2010, basal diameter of each *L. maackii* stem was measured in each half (10 × 20 m) of each plot. *Lonicera maackii* basal area did not differ between treatment types (P = 0.9305, linear mixed effects model, with site included as a random factor, Peebles-Spencer, 2016). Half-plots were randomly assigned to be *L. maackii* removed or intact (Supplementary material, Fig. A.1). Stems of *L. maackii* > 1 mm in diameter were clipped at the base, removed from the plots, and stumps treated with Tordon RTU, a herbicide composed of a combination of 5.4% Picloram (4-amino-3, 5,6-trichloropicolinic acid) and 20.9% 2,4-Dichlorophenoxyacetic acid (Dow AgroSciences, 2011). By late summer 2011, some of the treated shrubs had resprouted; these new stems were cut and treated again with Tordon RTU.

We sampled the forest floor vegetation in plots twice per growing season, in late spring and mid-summer, in 2011–2014 (Peebles-Spencer, 2016) using a modified version of Daubenmire plots (Abrahamson et al., 2011). Each half-plot included two, 20 m transects along which we placed nine 0.1 m^2 (20 cm-by-50 cm) subplots, centered every 2 m. Within each subplot, all species <1 m tall were identified and the area of each was estimated. Data were pooled for each 10 × 20 m half-plot and used to calculate species richness and cover of each species under 1 m, for spring and summer of each year (Peebles-Spencer, 2016). In every year and season after spring 2012 we also determined the area of bare ground (visible soil) for each sub-plot. In addition, in summer 2014, the number of reproductive plants of *Alliaria petiolata*, an invasive biennial, and the number of inflorescences or infructescences of *Sanicula odorata*, a native perennial, were censused to assess effects of deer and *L. maackii* on reproduction of these species. These species were the most prevalent invasive (*A. petiolata*) and native (*S. odorata*) species in the plots in spring of 2014.

2.2. Data analysis

Most analyses were completed using R version 3.1.1 (R Core Team, 2014) utilizing the nlme (linear mixed effects models, Pinheiro et al., 2014), indicspecies (indicator species analysis, Cáceres and Legendre, 2009), ggplot2 and sciplot packages (Morales et al., 2012; Wickham, 2009). Significance was determined at the $\alpha = 0.05$ level.

The effects of deer exclusion and *L. maackii* removal on species richness were assessed via split-plot, repeated measures analysis of variance (ANOVA) utilizing linear, mixed effects models. After testing for normality and skewness, richness was modeled individually by season as spring or summer richness = deer ∗ *L. maackii* ∗ year + error, with deer and *L. maackii* treatments, as well as year, as fixed effects, and site as a random effect. If the 3-way interaction was non-significant, that term was then dropped from the model, leaving spring or summer richness = deer ∗ *L. maackii* + deer ∗ year + *L. maackii* ∗ year + error.

To assess the effects of treatments on bare ground coverage in each year and season, we carried out split-plot ANOVAs, utilizing a linear, mixed effect model, bare ground = deer ∗ *L. maackii* + error, with deer and *L. maackii* treatments as fixed effects, and site as a random effect. If the 2-way interaction was non-significant (all years and seasons except spring 2012), it was dropped from the model, leaving bare ground = deer + *L. maackii* + error.

To assess the effects of treatment on plant community composition in each year and season we carried out distance-based multivariate analysis using DISTLM version 5 (Anderson, 2004). DISTLM is similar to permutational MANOVA except that it permits partitions of the variation in species dissimilarity among treatments involving blocked, split-plot, or unbalanced designs. We calculated Bray-Curtis dissimilarity using square-root transformed cover data from the 20 half-plots. The significance of treatment effects were evaluated with a split-plot model, with deer as the whole-plot factor, *L. maackii* as the nested factor, and site as a random effect. Hypothesis tests of treatment effects on species dissimilarity were conducted using 9999 permutations of the data, where the permuted sample units are represented by the denominator term of the F-ratio (sites for deer effects, and subplots for *L. maackii* effects). A design matrix is required to specify the appropriate randomization and hypothesis test for a split-plot design (Anderson, 2004).

For each year and season combination that had a significant treatment effect on composition, we carried out an indicator species analysis. Indicator species analysis uses data on species presence or absence as well as cover to assess strength and statistical significance of the relationship between species occurrence/abundance and groups of sites receiving different treatments (Bakker, 2008; Cáceres and Legendre, 2009; Cáceres et al., 2010; Hill et al., 1975). Indicator values (IV) are calculated with higher values indicating species that only occur in that group and lower values indicating species that occur across all groups (Bakker, 2008). Tests were run with 999 permutations.

We further investigated treatment effects on community composition by analyzing the cover of plant functional types in spring and summer of 2014, the last year of the study. Species were assigned to the functional types used by Christopher et al. (2014), according to Gleason and Cronquist (1991) and Hochstedler et al. (2007). These groups were vines, shrubs, trees, graminoids, ferns, spring perennials, summer perennials, annuals, and biennials. Percent cover of each functional type was tested with split-plot ANOVA, using a linear mixed-effects model: cover = deer ∗ *L. maackii* + error. Deer and *L. maackii* treatments were included as fixed effects, with site included as a random effect. Functional types that were not present in ≥5 half-plots were excluded from analyses. In each case the 2-way interaction was not significant and was dropped from the model.

Similarly, we analyzed cover of invasive plant species in spring and summer 2014 with split-plot ANOVAs, using the same linear mixed effects model as for functional types (above). Species were classified 'invasive' if listed as 'Introduced' in the lower 48 states in USDA NRCS (2015), as most of these were invasive in our area. Cover of *L. maackii* was excluded from the sum of the cover of all invasive species. If the 2-way interaction was not significant, it was dropped from the model.

Initial (2011) cover of *A. petiolata* and *S. odorata* were assessed via split-plot ANOVA, modeled with a linear mixed effects model, including deer and *L. maackii* as fixed effects, and site as a random effect. Because the 2-way interaction was non-significant, it was dropped from the model, leaving cover = deer + *L. maackii* + error. Reproductive data for these two herbs, number of individuals with flowers or fruits, did not meet assumptions for parametric analysis, so were instead analyzed with Mann-Whitney tests.

3. Results

3.1. Species richness

Removing *Lonicera maackii* had a positive effect on spring ($F_{1,59} = 17.26$, $P = 0.0001$, Fig. 2A) and summer ($F_{1,59} = 20.24$, $P < 0.0001$, Fig. 2B) species richness over the course of the study (Table A.1). Spring species richness differed among years ($F_{3,59} = 7.19$, $P = 0.0003$), though summer species richness did not. There was no direct effect of deer on spring or summer plant species richness. However, there was a marginally significant interaction between deer exclosure and *L. maackii* removal on summer plant species richness ($F_{1,59} = 3.76$, $P = 0.0573$); in areas where deer had access the negative effect of *L. maackii* presence on plant species richness was smaller than in it was areas where deer were excluded (Fig. 2B).

3.2. Species composition

Species composition differed significantly among sites each season and year ($P = 0.0001$, Table A.2), making it difficult to detect

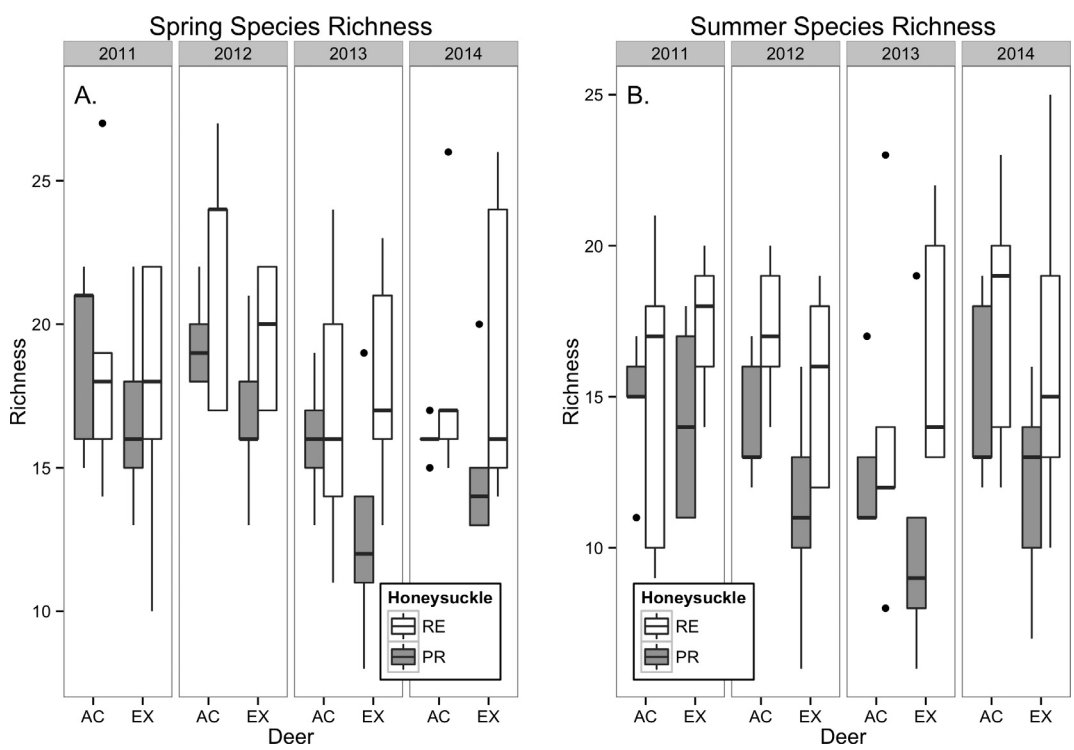

Fig. 2. Box plots of A. spring and B. summer plant species richness across the 4 years of the study. Gray boxes represent areas with *Lonicera maackii* intact (PR), white boxes represent areas with *L. maackii* removed (RE). Deer treatment is indicated on the x-axis, AC for areas with deer access and EX for deer exclosures. Repeated measures ANOVA statistics in online supplementary material, Table A.1.

Table 1
Indicator species of significant compositional treatment effects.

Indicator of	Indicator value	P	Common name	Scientific name
Honeysuckle intact	0.876	0.003	Amur Honeysuckle	*Lonicera maackii*
Honeysuckle removed	0.878	0.007	Virginia Creeper	*Parthenocissus quinquefolia*
Honeysuckle removed	0.707	0.035	Solomon's Seal	*Polygonatum biflorum*
Honeysuckle removed	0.691	0.047	Wild Licorice	*Galium circaezans*

treatment effects. *Lonicera maackii* removal affected summer species composition in 2013 (Pseudo $F_1 = 2.1842$, $P = 0.0055$), but not in any other season or year. Deer exclosure and the interaction between *L. maackii* and deer did not affect spring or summer species composition in any year.

3.3. Indicator species

Because summer 2013 was the only season where composition was affected by one of the treatments, we carried out indicator species analysis only for this season (Table 1). Removal of *L. maackii* was indicated by the presence of the vine *Parthenocissus quinquefolia* L. and the perennial herbs *Polygonatum biflorum* (Walter) Elliott and *Galium circaezans* Michx. The *L. maackii*-present treatment was indicated by the presence of *L. maackii* in the herb layer.

3.4. Cover of functional types

The *L. maackii* ∗ deer interaction was not significant for any functional group in either spring or summer 2014, so analyses were repeated with this term dropped from the ANOVA model. Deer exclusion increased the cover of tree seedlings and shrubs in the herb layer in summer 2014, with tree seedlings showing a trend in the same direction in spring 2014 (Table 2, Fig. 3). Tree seedlings also had greater cover in the *L. maackii* removal treatment in spring 2014. Shrub cover was lower where *L. maackii* was removed, but this difference was due more to cover of *Ligustrum* sp. than to *L. maackii*.

Lonicera maackii removal increased the cover of graminoids (significantly in spring, non-significant trend in summer), spring perennials, and vines (for the latter two groups, significantly in summer, but only a trend in spring) (Table 2, Fig. 3).

Deer exclusion tended to reduce the cover of biennials (chiefly *A. petiolata*), in summer (Table 2, Fig. 3).

3.5. Bare ground

There was greater area of bare ground (no leaf litter) in areas of deer access in spring 2014 and summer 2012, 2013, and 2014 (Fig. 4; Table A.3). In spring 2013, bare ground area was affected both by *L. maackii* removal and the interaction of deer and *L. maackii*: percent bare ground was greatest in areas where *L. maackii* was intact and deer had access, and the other treatment combinations had similar, low levels of bare ground.

Table 2
Significance of treatment effects on cover of plant functional types in spring and summer 2014, the last year of the study. Values determined using split-plot analysis of variance. Significant terms ($P < 0.05$) indicated in **bold font**. In each case the interaction term was not significant and was dropped from the model.

Season	Functional type		numDF	denDF	F-value	p-value
Spring	Biennials					
		Deer	1	4	2.678860	0.1770
		Honeysuckle	1	9	1.340441	0.2768
	Graminoids					
		Deer	1	4	2.511832	0.1882
		Honeysuckle	**1**	**9**	**10.457304**	**0.0103**
	Spring perennial forbs					
		Deer	1	4	1.934583	0.2366
		Honeysuckle	1	9	4.644981	0.0595
	Summer perennial forbs					
		Deer	1	4	0.808971	0.4193
		Honeysuckle	1	9	0.720032	0.4181
	Vines					
		Deer	1	4	0.042014	0.8476
		Honeysuckle	1	9	4.336452	0.0670
	Shrubs					
		Deer	1	4	0.377925	0.5720
		Honeysuckle	1	9	4.494003	0.0630
	Trees					
		Deer	1	4	6.980870	0.0575
		Honeysuckle	**1**	**9**	**5.569606**	**0.0426**
Summer	Biennials					
		Deer	1	4	7.273418	0.0543
		Honeysuckle	1	9	0.478555	0.5065
	Graminoids					
		Deer	1	4	3.706170	0.1265
		Honeysuckle	1	9	4.592648	0.0607
	Spring perennial forbs					
		Deer	1	4	4.191315	0.1100
		Honeysuckle	**1**	**9**	**22.599129**	**0.0010**
	Summer perennial forbs					
		Deer	1	4	0.866571	0.4046
		Honeysuckle	1	9	0.893694	0.3692
	Vines					
		Deer	1	4	0.688176	0.4534
		Honeysuckle	**1**	**9**	**6.069718**	**0.0359**
	Shrubs					
		Deer	**1**	**4**	**9.424057**	**0.0373**
		Honeysuckle	1	9	5.100910	0.0503
	Trees					
		Deer	**1**	**4**	**8.843975**	**0.0410**
		Honeysuckle	1	9	1.433882	0.2617

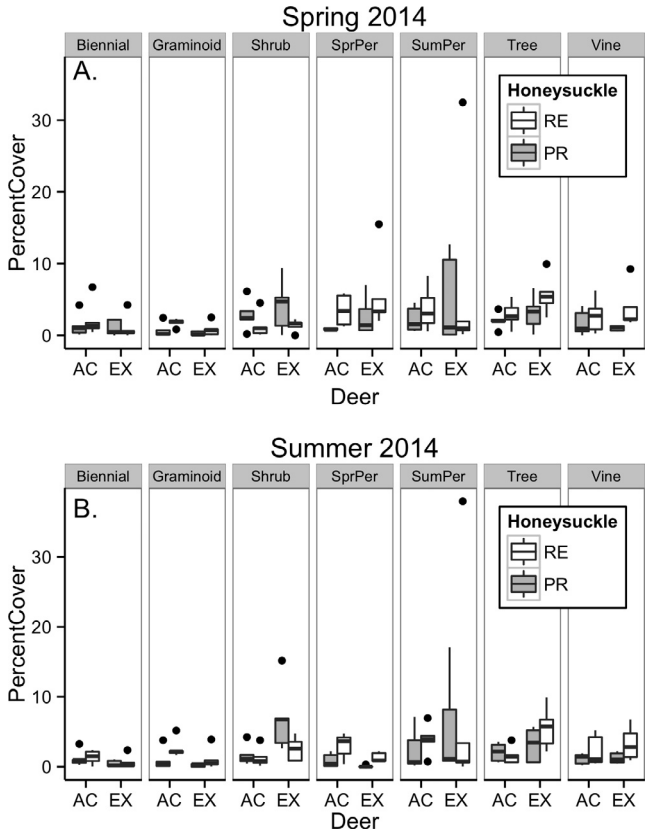

Fig. 3. Box plots of cover of plant functional types by treatment in A. spring and **B**. summer, 2014. Gray boxes represent areas with *Lonicera maackii* intact (PR), white boxes represent areas with *L. maackii* removed (RE). Black circles are outliers. Deer treatment is indicated on the x-axis: AC, deer access and EX, deer exclosures. Functional types 'SprPer' and 'SumPer' refer to spring and summer perennial forbs.

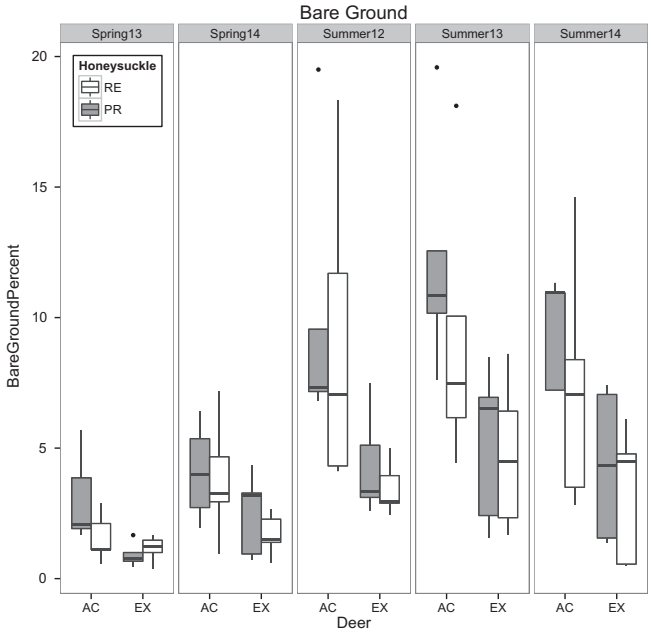

Fig. 4. Box plots of percent bare ground in spring 2013 and 2014 and summer 2012, 2013, and 2014. White boxes represent areas with *L. maackii* removed; gray boxes *L. maackii* present. Deer treatment is indicated on the x-axis: AC, deer access and EX, deer exclosures. ANOVA statistics reported in online supplementary material Table A.3.

3.6. Invasive species

The total cover of non-*L. maackii* invasive plant species was not affected by *L. maackii*, deer, or their interaction in spring or summer of 2014 (Peebles-Spencer, 2016).

3.7. Herb reproduction

All reproduction of *S. odorata* in summer 2014 (44 of 44 reproducing individuals) occurred in areas of deer exclosure; the number of reproducing individuals differed between deer treatments (Mann-Whitney Test, $W = 25$, $p = 0.015$) with no influence of *L. maackii* treatment (Peebles-Spencer, 2016). Almost all reproduction of *A. petiolata* in summer 2014 (7 of 8 reproducing individuals) occurred in areas of deer access (Mann-Whitney Test, $W = 71.5$, $p = 0.049$). There were no effects of *L. maackii*, deer, or their interaction on *S. odorata* cover in summer of 2011 or *A. petiolata* cover in spring 2011, suggesting initial equivalence of *S. odorata* and *A. petiolata* cover across treatment types (Peebles-Spencer, 2016).

4. Discussion

This study found many negative direct effects of *L. maackii* and of deer on plant communities. The only significant interaction between *L. maackii* and deer treatments was on percent cover of bare ground, where the effect was synergistic. There was also a marginally significant effect on species richness, in which the interaction was antagonistic.

4.1. Lonicera maackii direct effects

Removal of *L. maackii* had a positive effect on plant species richness during the course of the study, consistent with the findings of comparable studies of Collier et al. (2002) and Hartman and McCarthy (2008). Most functional groups (trees, spring perennial forbs, vines, and graminoids) had greater cover in areas of *L. maackii* removal, likely due to increased light availability (Chen and Matter, 2017). The effects of *L. maackii* that we observed on tree cover were both as predicted and consistent with the findings of others (Collier et al., 2002; Gorchov and Trisel, 2003; Hartman and McCarthy, 2008). Our finding that spring, but not summer, perennials increased where *L. maackii* was removed matched our prediction based on the greater sensitivity of spring perennials to shading. Miller and Gorchov (2004) found greater growth and reproduction of spring perennials where *L. maackii* was removed, while Collier et al. (2002) and Christopher et al. (2014) found *L. maackii* effects on abundance of both spring and summer perennials. While the significant effect of *L. maackii* on the cover of graminoids was not predicted, it matches Christopher et al.'s (2014) findings.

Shrubs were the one functional type to have lower cover in the *L. maackii* removal treatment. This was not simply an artefact of the removal treatment, since we only measured cover below 1 m, and recruits of *L. maackii* were present in this stratum in all treatments. In fact, lower cover of another invasive shrub, *Ligustrum* sp., contributed more to this treatment difference than lower *L. maackii* cover.

The effect of *L. maackii* on the area of bare ground was only significant in the spring of 2013, even though *L. maackii* leaves decompose at an accelerated rate compared to other native species (Poulette and Arthur, 2012).

4.2. Deer direct effects

Area of bare ground was greater in areas of deer access in nearly every year and season it was measured. While this bare ground

was not quantified until summer 2012, the effect size was larger in 2014 than 2012 (Fig. 4), suggesting an increase over time. Similar effects of deer on bare ground (Knight et al., 2009) and leaf litter depth (Heckel et al., 2010) have been reported, and are likely caused by increased leaf fragmentation by deer trampling.

The predicted effect of deer on plant species composition was not observed in this study, but treatment differences were difficult to detect due to compositional differences among sites and years. Deer exclusion significantly increased the cover of shrubs and trees, but not other functional types in the herb layer, consistent with a recent meta-analysis (Habeck and Schultz, 2015) that found that deer exclusion generally enhances metrics of woody plants, but not herbaceous plants.

Our finding that all reproduction of *S. odorata* occurred in areas of deer exclosure is likely due to deer grazing on *S. odorata* inflorescences, as stems in areas of deer access often had just the tips with inflorescences removed, and cover of this species was not an indicator of deer exclosure. Deer florivory can be extensive - up to 88–90% of all floral structures in one species of *Iris* experienced florivory (Wang and Mopper, 2008) - and can negatively affect seed production and resource allocation in flowering plants. Knight et al. (2009) found that much smaller proportion of native plants flower in areas of deer access compared to areas of deer exclusion.

The opposite pattern was detected for *A. petiolata*, where all but one of the reproducing individuals occurred in areas of deer access, in congruence with Kalisz et al.'s (2014) finding that deer facilitate growth and reproductive success of this invasive biennial, and that *A. petiolata* populations declined towards local extinction over six years of deer exclosure. *Alliaria petiolata* is not eaten by deer (Averill et al., 2016), and release from competition with plants that deer do browse likely accounts for its flowering in deer access plots, and perhaps the trend for greater cover of biennials in these plots. Greater cover of biennials in deer access plots may also be due to the greater cover of bare ground in this treatment, since establishment of *A. petiolata* is higher in areas of less litter (Bartuszevige et al., 2007). Although leaf litter disturbance promotes the establishment of some other non-native species (Kuhman et al., 2013; Oswalt and Oswalt, 2007), total cover of invasive species other than *L. maackii* was not affected by deer in this study.

Our finding that deer exclosure did not affect species richness contrasts with those of Wiegmann and Waller (2006) and Rooney (2009), who found lower richness in areas of deer access. Habeck and Schultz's (2015) meta-analysis found deer exclosure increased woody, but not total, plant species richness.

4.3. Interactions

While we predicted that deer and *L. maackii* would have additive effects (Fig. 1A) on plant composition, due to each driver affecting different species, this prediction was not realized. There was some evidence for additive effects on tree seedling cover; in spring 2014 this was negatively affected by *L. maackii*, and marginally negatively affected by deer, without a significant interaction. However, one year earlier (in both spring and summer 2013), tree cover showed a significant interaction between deer and *L. maackii* effects: only where *L. maackii* was removed was there greater cover of tree seedlings in areas of deer exclosure than deer access (Peebles-Spencer, 2016). This effect is likely due to *L. maackii* branches conferring protection from browse to tree seedlings, as indicated by Gorchov and Trisel (2003) and Cipollini et al. (2009). Because this pattern was not significant in 2014, it may be ephemeral, or too weak to be statistically significant with our level of replication.

We found only one significant interaction, a synergy (Fig. 1B) between deer access and *L. maackii* cover on bare ground cover in spring 2013, where the combined effects were greater than would be predicted from the sum of the two effects. However, in later years this interaction receded, leaving only a consistent effect of deer.

There was also a trend ($P = 0.0573$) for an interaction between deer and *L. maackii* on plant species richness in summer: where deer were excluded, species richness was much lower in areas with *L. maackii* than in areas of *L. maackii* removal, but in areas of deer access, species richness was similar between *L. maackii* treatments. This pattern is antagonistic (Fig. 1C), with areas of both deer and *L. maackii* presence having a less negative overall effect on richness than predicted from the additive response of the two treatments by themselves. This trend is consistent with our prediction of an antagonistic interaction on species richness, based on deer browse on *L. maackii* sufficient to reduce its cover and mitigate its negative effect on forest floor plants. Martinod and Gorchov (2017) found that >20% of first-year twigs of *L. maackii* in this study area showed signs of deer browse over a 12 month period. We found that where deer were excluded, there was higher *L. maackii* cover at heights of 0.5–1.5 m (Peebles-Spencer, 2016), within the 0.3–2 m height range in which deer typically browse (Rooney and Waller, 2003). Additionally, the basal area of *L. maackii* shrubs that were small enough to have extensive twigs within the deer browse range (largest stem 3–29 mm in basal diameter) was significantly greater in deer exclosures (Peebles-Spencer, Haffey, and Gorchov, unpubl.), suggesting that deer reduce *L. maackii* growth as well as cover.

5. Conclusions and management recommendations

Our results suggest that considering indirect effects, such as deer browse on *L. maackii* mitigating this shrub's negative effect on tree seedlings, contributes to understanding the roles of invasive plants and overabundant herbivores in complex natural systems. While we found negative impacts of both deer and *L. maackii* on native plant community parameters, over the course of this study some parameters were not as negatively affected as would be predicted if the impacts were additive. These findings have implications for management of stands impacted by both abundant deer and invasive shrubs. Management of either factor without also managing the other factor is likely to result in no appreciable improvement in parameters such as plant species richness. We argue it is necessary to reduce both deer and invasive shrub abundance in order to improve native plant communities

Acknowledgments

This work was supported by a grant from Miami University (Academic Challenge program, Botany Department). We thank Miami University Natural Areas Committee for permission to carry out the field work, Jim Reid for supervising the construction of the deer exclosures, R. Spencer, B. Hoven, M. Hassett, A. Bowen, A. Wagner, S. Pfeiffer, C. Freeman, H. Andrews, S. Rumschlag, G. Simson, J. Samu, J. Credico, E. Stempinski, S. Cramer, S. Khanal and C. Brakers for assistance in the field, and B. Hoven, A. Bowen and S. Castellano for help with plant identification. We thank Hank Stevens and Mike Hughes for assistance with statistical analyses, and H. Stevens, Melany Fisk, Jim Hickey, and anonymous reviewers for valuable input on earlier drafts of this manuscript.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2017.05.053.

References

Abrahamson, I.L., Nelson, C.R., Affleck, D.L.R., 2011. Assessing the performance of sampling designs for measuring the abundance of understory plants. Ecol. Appl. 21, 452–464.

Anderson, 2004. DISTLM V.5: A FORTRAN Computer Program to Calculate a Distance-Based Multivariate Analysis for a Linear Model. Department of Statistics, University of Auckland, New Zealand.

Aronson, M.F.J., Handel, S.N., 2011. Deer and invasive plant species suppress forest herbaceous communities and canopy tree regeneration. Nat. Areas J. 31, 400–407.

Averill, K.M., Mortensen, D.A., Smithwick, E.A., Post, E., 2016. Deer feeding selectivity for invasive plants. Biol. Invasions 18, 1247–1263.

Bakker, J.D., 2008. Increasing the utility of indicator species analysis. J. Appl. Ecol. 45, 1829–1835. http://dx.doi.org/10.1111/j.1365-2664.2008.01571.x.

Bartuszevige, A.M., Hrenko, R.L., Gorchov, D.L., 2007. Effects of leaf litter on establishment, growth, and survival of invasive plant seedlings in a deciduous forest. Am. Midl. Nat. 158, 472–477.

Bradshaw, L., Waller, D.M., 2016. Impacts of white-tailed deer on regional patterns of forest tree recruitment. For. Ecol. Manage. 375, 1–11.

Bressette, J.W., Beck, H., Beauchamp, V.B., 2012. Beyond the browse line: complex cascade effects mediated by white-tailed deer. Oikos 121, 1749–1760. http://dx.doi.org/10.1111/j.1600-0706.2011.20305.x.

Cáceres, M.D., Legendre, P., 2009. Associations between species and groups of sites: indices and statistical inference. Ecology 90, 3566–3574. http://dx.doi.org/10.1890/08-1823.1.

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

Chen, H., Matter, S.F., 2017. Quantification of changes in light and temperature associated with invasive Amur Honeysuckle (*Lonicera maackii*). Am. Midl. Nat. 177, 143–152.

Christopher, C.C., Matter, S.F., Cameron, G.N., 2014. Individual and interactive effects of Amur honeysuckle (*Lonicera maackii*) and white-tailed deer (*Odocoileus virginianus*) on herbs in a deciduous forest in the eastern United States. Biol. Invasions 16, 2247–2261. http://dx.doi.org/10.1007/s10530-014-0661-x.

Cipollini, K., Ames, E., Cipollini, D., 2009. Amur honeysuckle (*Lonicera maackii*) management method impacts restoration of understory plants in the presence of white-tailed deer (*Odocoileus virginiana*). Invasive Plant Sci. Manage. 2, 45–54. http://dx.doi.org/10.1614/IPSM-08-108.1.

Collier, M.H., Vankat, J.L., Hughes, M.R., 2002. Diminished plant richness and abundance below *Lonicera maackii*, an invasive shrub. Am. Midl. Nat. 147, 60–71.

Côté, S.D., Rooney, T.P., Tremblay, J.-P., et al., 2004. Ecological impacts of deer overabundance. Annu. Rev. Ecol. Evol. Syst. 35, 113–147.

Csigi (XIV), K.K., Holzmueller, E.J., 2015. Reduced seedling height of hard mast species in areas with low deer densities in an oak-dominated forest. Ecol Restor 33, 19–21.

Dávalos, A., Nuzzo, V., Blossey, B., 2015a. Single and interactive effects of deer and earthworms on non-native plants. For. Ecol. Manage. 351, 28–35. http://dx.doi.org/10.1016/j.foreco.2015.04.026.

Dávalos, A., Nuzzo, V., Blossey, B., 2015b. Interactive effects of deer, earthworms and non-native plants on rare forest plant recruitment. Biol. Cons. 187, 173–181. http://dx.doi.org/10.1016/j.biocon.2015.04.025.

Dow AgroSciences, 2011. Specimen label, Tordon® RTU <http://ws.greenbook.net/Docs/Label/L8081.pdf> (accessed 27 Jun 2016).

Eddmaps, 2016. Amur Honeysuckle (*Lonicera maackii*). Early Detection & Distribution Mapping System. The University of Georgia - Center for Invasive Species and Ecosystem Health <http://www.eddmaps.org/distribution/usstate.cfm?sub=3040> (accessed 27 Jun 2016).

Gleason, H.A., Cronquist, A., 1991. Manual of Vascular Plants of Northeastern United States and Adjacent Canada. New York Botanical Garden, Bronx, N.Y., USA.

Gorchov, D.L., Trisel, D.E., 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. http://dx.doi.org/10.1023/A:1023208215796.

Gould, A.M.A., Gorchov, D.L., 2000. Effects of the exotic invasive shrub *Lonicera maackii* on the survival and fecundity of three species of native annuals. Am. Midl. Nat. 144, 36–50. http://dx.doi.org/10.1674/0003-0031(2000)144[0036:EOTEIS]2.0.CO;2.

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, plv119. http://dx.doi.org/10.1093/aobpla/plv119.

Hartman, K.M., McCarthy, B.C., 2004. Restoration of a forest understory after the removal of an invasive shrub, Amur honeysuckle (*Lonicera maackii*). Restor. Ecol. 12, 154–165.

Hartman, K.M., McCarthy, B.C., 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. http://dx.doi.org/10.3159/07-RA-036.1.

Heckel, C.D., Bourg, N.A., McShea, W.J., Kalisz, S., 2010. Nonconsumptive effects of a generalist ungulate herbivore drive decline of unpalatable forest herbs. Ecology 91, 319–326. http://dx.doi.org/10.1890/09-0628.1.

Hill, M.O., Bunce, R.G.H., Shaw, M.W., 1975. Indicator species analysis, a divisive polythetic method of classification, and its application to a survey of native pinewoods in Scotland. J. Ecol. 63, 597–613. http://dx.doi.org/10.2307/2258738.

Hochstedler, W.W., Slaughter, B.S., Gorchov, D.L., et al., 2007. Forest floor plant community response to experimental control of the invasive biennial, *Alliaria petiolata* (garlic mustard). J. Torrey Bot. Soc. 134, 155–165. http://dx.doi.org/10.3159/1095-5674(2007)134[155:FFPCRT]2.0.CO;2.

Horsley, S.B., Stout, S.L., deCalesta, D.S., 2003. White-tailed deer impact on the vegetation dynamics of a northern hardwood forest. Ecol. Appl. 13, 98–118. http://dx.doi.org/10.1890/1051-0761(2003)013[0098:WTDIOT]2.0.CO;2.

Jauni, M., Ramula, S., 2015. Meta-analysis on the effects of exotic plants on the fitness of native plants. Perspect. Plant Ecol. Evol. Syst. 17, 412–420.

Kalisz, S., Spigler, R.B., Horvitz, C.C., 2014. In a long-term experimental demography study, excluding ungulates reversed invader's explosive population growth rate and restored natives. Proc. Natl. Acad. Sci. 111, 4501–4506.

Knight, T.M., Dunn, J.L., Smith, L.A., et al., 2009. Deer facilitate invasive plant success in a Pennsylvania forest understory. Nat. Areas J. 29, 110–116. http://dx.doi.org/10.3375/043.029.0202.

Krivtsov, V., 2004. Investigations of indirect relationships in ecology and environmental sciences: a review and the implications for comparative theoretical ecosystem analysis. In: Lugano Aftermath Contemp Adv Ecol Model Sel Mater IEMSS 2002 Conf 174, pp. 37–54. http://dx.doi.org/10.1016/j.ecolmodel.2003.12.042.

Kuhman, T.R., Pearson, S.M., Turner, M.G., 2013. Why does land-use history facilitate non-native plant invasion? A field experiment with *Celastrus orbiculatus* in the southern Appalachians. Biol. Invasions 15, 613–626.

Loomis, J.D., Matter, S.F., Cameron, G.N., 2015. Effects of invasive Amur honeysuckle (*Lonicera maackii*) and white-tailed deer (*Odocoileus virginianus*) on survival of sugar maple seedlings in a southwestern Ohio forest. Am. Midl. Nat. 174, 65–73. http://dx.doi.org/10.1674/0003-0031-174.1.65.

Luken, J.O., Thieret, J.W., 1996. Amur honeysuckle, its fall from grace. Bioscience 46, 18–24.

Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M., Bazzaz, F.A., 2000. Biotic invasions: causes, epidemiology, global consequences, and control. Ecol. Appl. 10, 689–710. http://dx.doi.org/10.1890/1051-0761(2000)010[0689:BICEGC]2.0.CO;2.

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. http://dx.doi.org/10.1093/aobpla/plx006.

McShea, W.J., 2012. Ecology and management of white-tailed deer in a changing world. Ann. N. Y. Acad. Sci. 1249, 45–56. http://dx.doi.org/10.1111/j.1749-6632.2011.06376.x.

Meiners, S.J., Martinkovic, M.J., 2002. Survival of and herbivore damage to a cohort of *Quercus rubra* planted across a forest—old-field edge. Am. Midl. Nat. 147, 247–255. http://dx.doi.org/10.1674/0003-0031(2002)147[0247:SOAHDT]2.0.CO;2.

Miller, K.E., Gorchov, D.L., 2004. The invasive shrub, *Lonicera maackii*, reduces growth and fecundity of perennial forest herbs. Oecologia 139, 359–375.

Morales, M., with code developed by the R Development Core Team, with general advice from the R-help listserv community, especially Duncan Murdoch, 2012. 'sciplot: Scientific Graphing Functions for factorial designs'. R package version 1.1-0.

Orrock, J.L., Dutra, H.P., Marquis, R.J., Barber, N., 2015. Apparent competition and native consumers exacerbate the strong competitive effect of an exotic plant species. Ecology 96, 1052–1061. http://dx.doi.org/10.1890/14-0732.1.

Orrock, J.L., Holt, R.D., Baskett, M.L., 2010. Refuge-mediated apparent competition in plant–consumer interactions. Ecol. Lett. 13, 11–20. http://dx.doi.org/10.1111/j.1461-0248.2009.01412.x.

Oswalt, C.M., Oswalt, S.N., 2007. Winter litter disturbance facilitates the spread of the nonnative invasive grass *Microstegium vimineum* (Trin.) A. Camus. For. Ecol. Manage. 249, 199–203.

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

Pinheiro, J., Bates, D., DebRoy, S., et al., 2014. nlme: linear and nonlinear mixed effects models.

Poulette, M.M., Arthur, M.A., 2012. The impact of the invasive shrub *Lonicera maackii* on the decomposition dynamics of a native plant community. Ecol. Appl. 22, 412–424. http://dx.doi.org/10.1890/11-1105.1.

R Core Team, 2014. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Relva, M., Nuñez, M., Simberloff, D., 2010. Introduced deer reduce native plant cover and facilitate invasion of non-native tree species: evidence for invasional meltdown. Biol. Invasions 12, 303–311. http://dx.doi.org/10.1007/s10530-009-9623-0.

Rooney, T.P., 2009. High white-tailed deer densities benefit graminoids and contribute to biotic homogenization of forest ground-layer vegetation. Plant Ecol. 202, 103–111. http://dx.doi.org/10.1007/s11258-008-9489-8.

Rooney, T.P., Waller, D.M., 2003. Direct and indirect effects of white-tailed deer in forest ecosystems. For. Ecol. Manage. 181, 165–176. http://dx.doi.org/10.1016/S0378-1127(03)00130-0.

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

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. For. Ecol. Manage. 384, 26–33.

Shen, X., Bourg, N.A., McShea, W.J., Turner, B.L., 2016. Long-term effects of white-tailed deer exclusion on the invasion of exotic plants: a case study in a mid-Atlantic temperate forest. PLoS ONE 11, e0151825. http://dx.doi.org/10.1371/journal.pone.0151825.

Sotala, D.J., Kirkpatrick, C.M., 1973. Foods of white-tailed deer, *Odocoileus virginianus*, in Martin County, Indiana. Am. Midl. Nat. 89, 281–286. http://dx.doi.org/10.2307/2424033.

Strauss, S.Y., Irwin, R.E., 2004. Ecological and evolutionary consequences of multispecies plant-animal interactions. Annu. Rev. Ecol. Evol. Syst. 35, 435–466. doi: 0.2307/30034123.

USDA NRCS, 2015. The Plants Database. National Plant Data Team Greensboro. NC 27401-4901 USA. <http://plants.usda.gov/> (accessed 27 Jun 2015).

Vavra, M., Parks, C.G., Wisdom, M.J., 2007. Biodiversity, exotic plant species, and herbivory: the good, the bad, and the ungulate. For. Ecol. Manage. 246, 66–72. http://dx.doi.org/10.1016/j.foreco.2007.03.051.

Vilà, M., Espinar, J.L., Hejda, M., et al., 2011. Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. Ecol. Lett. 14, 702–708.

Waller, D.M., Maas, L.I., 2013. Do white-tailed deer and the exotic plant garlic mustard interact to affect the growth and persistence of native forest plants? For. Ecol. Manage. 304, 296–302. http://dx.doi.org/10.1016/j.foreco.2013.05.011.

Wang, H.G., Mopper, S., 2008. Separate and interacting effects of deer florivory and salinity stress on iris herbivores. Oikos 117, 564–570.

White, E.M., Wilson, J.C., Clarke, A.R., 2006. Biotic indirect effects: a neglected concept in invasion biology. Divers. Distrib. 12, 443–455. http://dx.doi.org/10.1111/j.1366-9516.2006.00265.x.

Wickham, H., 2009. Ggplot2: Elegant Graphics for Data Analysis. Springer, New York.

Wiegmann, S.M., Waller, D.M., 2006. Fifty years of change in northern upland forest understories: identity and traits of "winner" and "loser" plant species. Biol. Cons. 129, 109–123. http://dx.doi.org/10.1016/j.biocon.2005.10.027.

Wootton, J.T., 2002. Indirect effects in complex ecosystems: recent progress and future challenges. J. Sea Res. 48, 157–172. http://dx.doi.org/10.1016/S1385-1101(02)00149-1.