



Experimental effects of white-tailed deer and an invasive shrub on forest ant communities

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Abstract

Ungulate browse and invasive plants exert pressure on plant communities and alter the physical and chemical properties of soils, but little is known about their effects on litter-dwelling arthropods. In particular, ants (Formicidae) are ubiquitous in temperate forests and are sensitive to changes in habitat structure and resources. As ants play many functional roles, changes to ant communities may lead to changes in ecosystem processes. We conducted a long-term experiment that controlled white-tailed deer (*Odocoileus virginianus*) access and presence of an invasive understory shrub in deciduous forests located in southwestern Ohio, USA from 2011 to 2017. Several leaf-litter ant community responses and litter biomass were measured in five paired deer access and exclosure plots, each with a split-plot removal of Amur honeysuckle (*Lonicera maackii*). Ant abundance and species richness increased with time in deer exclosures, but not in deer access plots. Honeysuckle removal reduced abundance and richness of ants. There were additive effects of deer and honeysuckle on ant richness, and interactive effects of deer and honeysuckle on ant abundance. Deer exclusion reduced variation in ant composition relative to access plots. There was little evidence that treatments directly influenced species diversity of ants. However, all ant measures were positively related to litter biomass, which was greater in deer exclosures relative to access plots. Our results indicate strong indirect effects of herbivores and honeysuckle on litter-dwelling ants, mediated through changes in litter biomass and likely vegetation structure, which may alter ant-mediated ecosystem processes.

Keywords Formicidae · Leaf litter · Temperate deciduous forest · Above–belowground interactions

Introduction

Recent studies have shown complex, interlinked biota between the above- and below-ground portions of terrestrial ecosystems (Bardgett and Wardle 2003; Wardle et al.

2004; Van der Putten et al. 2013). Specifically, plants and aboveground herbivores have extensive influence on organisms that live in the soil (Bezemer and Van Dam 2005; Van der Putten et al. 2013). Continuing studies on the interplay between above- and below-ground components of terrestrial ecosystems are broadening our understanding of feedbacks between ecosystem processes and biodiversity (Wardle et al. 2004; Van der Putten et al. 2013). Organisms inhabiting the soil litter, in particular, may reflect changes in ecosystem dynamics due to herbivores or plant invasions, since litter-dwelling organisms are sensitive to changes in litter quantity, microclimate, and soil properties (Herrera 1997; Kaspari and Yanoviak 2009). Moreover, these organisms often have key roles in ecosystem processes (e.g., seed dispersal, decomposition, and nutrient cycling), so that changes in their abundance and diversity may have cascading impacts on terrestrial ecosystems (Kremen et al. 1993). Local perturbations in eastern deciduous forests of the United States include the overabundance of ungulate herbivores and the

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invasion of non-native organisms (Côté et al. 2004; Simberloff et al. 2013).

White-tailed deer (*Odocoileus virginianus*) exert pressure on plant communities in temperate forests, causing shifts in ecosystem processes and successional paths (Côté et al. 2004; Allombert et al. 2005). Preferential browse by deer alters diversity and recruitment of herbaceous and woody plants, thereby reducing native plant richness, while benefitting subsets of invasive plants (Rooney 2009; Shelton et al. 2014; Averill et al. 2018). These changes can result in reduced vegetation cover and a homogenized plant community, simplifying vegetation structure of the forest understory (Rooney and Waller 2003; Rooney 2009). Deer-mediated shifts in plant communities have cascading effects on the detrital food web and can alter soil carbon and nutrient dynamics (Harrison and Bardgett 2003; Wardle et al. 2004; Bressette et al. 2012). Through changes in vegetation and ecosystem processes, strong ungulate herbivory can reduce the abundance and diversity of animals (Foster et al. 2014). Yet, deer browse effects on soil and forest floor invertebrate communities are unclear, as results of studies have been equivocal. Studies have found little to no effect of deer on overall abundance and diversity of litter- and soil-dwelling invertebrates (Duguay and Farfaras 2011; Lessard et al. 2012; but see Bressette et al. 2012). Thus, the effects of deer may be dependent on functional role of the invertebrate group. Specifically, large soil-dwelling decomposers (i.e., exotic earthworms) benefit from deer presence (Dávalos et al. 2015b; Mahon and Crist 2019). Conversely, deer negatively affect abundant arthropod groups that are predators or scavengers (e.g., ants, spiders, millipedes, and centipedes; Bressette et al. 2012; Christopher and Cameron 2012; Lessard et al. 2012). Understanding long-term trends of invertebrate communities in response to ungulate herbivory is key, as short-term population fluctuations may not translate to major ecosystem shifts (Foster et al. 2014).

Invasive, nonnative plants often negatively affect native plant and animal communities; additionally, these invasions alter ecosystem function, by increasing nutrient availability and cycling, but decreasing litter decomposition (Vilà et al. 2011). In deciduous forests of eastern US, the invasive Amur honeysuckle (*Lonicera maackii*) outcompetes native herbaceous plants, shrubs, and tree seedlings (Gorchov and Trisel 2003; Miller and Gorchov 2004; Haffey and Gorchov 2019) and drastically changes vegetation structure of the forest understory (Hartman and McCarthy 2008). Due to increased shrub layer cover, honeysuckle invasion reduces soil temperature and increases soil moisture (Watling et al. 2011). Honeysuckle also alters microbial communities by sustaining unique microbial communities on honeysuckle leaf litter and reducing soil mycorrhizal fungi on native plant roots (Arthur et al. 2012; Shannon et al. 2014). Shifts in microclimate and soil microbial communities may alter

decomposition rates under honeysuckle shrubs (Arthur et al. 2012; Poulette and Arthur 2012). Together, these alterations to vegetation structure, soil microclimate, and decomposition are likely to affect soil invertebrate communities (McNeish and McEwan 2016). Studies have found differential effects of honeysuckle on invertebrate communities, with reduced ground-dwelling spider abundance (Buddle et al. 2004; Christopher and Cameron 2012), increased ground-dwelling arthropod abundance and taxon richness (Masters et al. 2017), and increased shrub-dwelling arthropod diversity (Loomis and Cameron 2014).

Interactions between deer and honeysuckle are expected, as their ranges broadly overlap across forests in the eastern US and evidence suggests honeysuckle supports higher deer densities in fragmented landscapes (Peterson 2018). Deer feed on honeysuckle (Martinod and Gorchov 2017), which reduces growth of honeysuckle shrubs (Peebles-Spencer et al. 2018). Yet, honeysuckle protects some native tree seedlings from deer browse (Gorchov and Trisel 2003; Peebles-Spencer et al. 2017). Separate effects of white-tailed deer and invasive plants on forest ecosystems are widely studied (Côté et al. 2004; Vilà et al. 2011), but recent studies have shown interactive effects of herbivores and invasive plants on native plants and ecosystem processes (Waller and Maas 2013; Dávalos et al. 2015a), including interactive effects of deer and honeysuckle on native plants (Peebles-Spencer et al. 2017; Haffey and Gorchov 2019). In contrast, studies of interactive effects of deer and invasive plants on invertebrate taxa are rare (Foster et al. 2014). Christopher and Cameron (2012) found some evidence for positive effects of deer exclosure and honeysuckle removal on the abundance of Acari and Araneae, but little evidence for interactive effects on other invertebrates. Dávalos et al. (2015b) found positive effects of deer and several species of non-native plants on invasive earthworms, with some evidence for interactions mediated through soil pH. Thus, interactions between deer and honeysuckle are likely to be mediated through changes to vegetation structure and soil properties, which may amplify or diminish invertebrate responses to each factor alone.

The objective of this study was to understand how biodiversity in the forest litter layer changes in response to experimental exclosure of deer and removal of an invasive shrub, Amur honeysuckle. We established five paired deer exclosure and control (deer access) plots, each with a split-plot design of honeysuckle presence or removal. This design enabled us to investigate main, additive, and interactive effects of ungulate herbivory and plant invasion on insect biodiversity. In particular, we tested the effects of these experimental treatments on the taxonomic diversity of forest floor ants (Formicidae). Ants are known to be effective indicator taxa, are ubiquitous in temperate forests, and are sensitive to changes in habitat complexity and microclimate

(Lassau and Hochuli 2004; Stuble et al. 2013). Moreover, ants are key players in various ecosystem processes, including seed dispersal, food web dynamics, and nutrient cycling (Del Toro et al. 2012). Therefore, changes in the abundance and diversity of ants may have broader effects on ecosystems (Crist 2009).

We hypothesized that deer would alter the ant community through increased decomposition and subsequent reductions in litter biomass. Specifically, we predicted that deer enclosure would increase abundance, richness, and diversity of ants. We also hypothesized that honeysuckle would alter the ant community through increased aboveground vegetation structure, indirect changes in litter biomass, and direct effects on herbaceous plants. We predicted that honeysuckle removal would result in lower ant abundance and species richness, since ants are known to respond to changes in vegetation structure (Herbers 1989). Alternatively, if herbaceous plants have a greater influence on ants, we predicted that honeysuckle removal would result in greater ant abundance and species richness. Deer and honeysuckle may affect the ant community additively, if the ant community responds separately to changes in litter biomass and vegetation structure. Alternatively, if the ant community responds similarly to changes in litter biomass and vegetation structure, deer and honeysuckle effects would be antagonistic. Finally, we predicted shifts in ant species composition following deer exclusion and honeysuckle removal; specifically, we expected greater variation in species composition among deer enclosure plots relative to deer access plots, due to higher habitat complexity without deer.

Methods

Study sites and experimental design

This study was conducted in paired deer enclosure and access plots at five sites located in the Miami University Natural Areas, Butler County of SW Ohio, USA. The five sites were chosen to be closed-canopy, mature deciduous forest; to have similar upland topographic position (253 ± 5 m.a.s.l.); and to have moderate levels of Amur honeysuckle invasion ($0.58\text{--}1.57$ BA $\text{m}^2 \text{ha}^{-1}$; Peebles-Spencer et al. 2017). Study sites were separated by ≥ 1 km, and average distance from each site to a forest edge was 152 ± 25 m. The climate of the study area is temperate continental with mean temperature of -1 °C in January and 23 °C in July and average annual rainfall of 110 cm. Dominant soil type is fine, mixed active Hapludalfs. Dominant hardwood species are sugar maple (*Acer saccharum*), oak (*Quercus* spp.), hickory (*Carya* spp.), and American beech (*Fagus grandifolia*). Information on the understory plant community can be found in Peebles-Spencer et al. (2017).

Details of the experimental design are in Mahon and Crist (2019) and Mahon et al. (2017). Briefly, paired 20×20 -m plots were randomly assigned to either deer enclosure or deer access, each with a randomly assigned split-plot treatment of honeysuckle removal (10×20 -m subplots, ESM 1). In August of 2010, 2.5-m-tall fencing was erected to exclude deer. Amur honeysuckle was removed in 2010 and again in late summer 2015 by cutting each shrub at the base and applying Tordon (Dow AgroSciences, Indianapolis, IN, USA) directly to the cut stem. We did not expect herbicide application to affect the ant community, as ants have shown little response to broad foliar herbicide application in forests (Scoriza et al. 2015), herbicide application events occurred twice, and herbicide was directly applied to cut stems. Summer deer density in our study area ranged from 4.2 to 9.5 deer km^{-2} in 2017 (Peterson 2018).

Ant and litter sampling

We quantified ant abundance and diversity using litter samples and Winkler extraction in late May to early June from 2011 to 2017. A high richness and abundance of ants was expected in late spring and early summer, as this period has high precipitation and moderate temperatures in our study region and corresponds to the seasonal peak in understory vegetation. We collected all leaf litter and woody detritus present within three 0.25-m^2 quadrats in each honeysuckle treatment subplot along a line through the center of each subplot at 5-m intervals beginning 5 m from the subplot edge to avoid potential edge effects (ESM 1). We collected 12 samples from each site during each sampling period, for 60 samples per year and 420 samples for the duration of the study. Samples from a given site were all collected on the same day. We placed collected leaf litter and detritus in mesh bags (5-mm openings) and hung them inside Winkler extractors for 5 days. This method employs the natural drying of the litter to move ants and other invertebrates into an ethanol collection jar at the bottom of the extractor (Agosti and Alonso 2000; Mahon et al. 2017). To increase extraction efficiency, leaf litter was not collected until at least 2 days following a major storm event. Following invertebrate extraction, we sorted leaf litter to remove woody detritus; we then sifted litter with a #4 sieve (4.75 mm) to remove soil and small pieces of organic matter; litter was oven dried at 60 °C to constant mass to obtain standing litter biomass (g).

Winkler litter extraction was used rather than pitfall traps, as Winkler extraction in eastern US temperate forests yields higher ant abundance and richness, and better represents the entire ant community than pitfalls (Ivanov and Keiper 2009; Mahon et al. 2017). Ant specimens were identified to species using Covert (2005); only workers were included in analyses.

Statistical analyses

We used the R programming language version 3.5 for most statistical analyses (R Core Team 2018). We generated sample-size-based rarefaction/extrapolation curves and estimated sample coverage for each of our study sites from 2011 to 2017 as a measure of sampling completeness (iNEXT function, iNEXT package, R; Hsieh et al. 2018).

In addition to ant abundance and species richness, we assessed ant species diversity using Hill number diversity of order 1 (Shannon diversity), which can be interpreted as the effective number of species (Jost 2006). We analyzed ant abundance, species richness, and Shannon diversity in response to deer and honeysuckle treatments through time. We used generalized linear mixed effects models (glmmTMB, R; Brooks et al. 2017) with a Negative Binomial error distribution to test models of ant abundance, Poisson error distribution for species richness, and Gaussian error distribution for Shannon diversity. Experimental treatments, standing litter biomass, and time since treatment were used as predictor variables. Model selection allowed for interactions of all predictors. Each model included a random intercept of site and plot nested within site (1 | Site/Plot) to account for the split-plot design of our study, which incorporates unstructured covariance in response variables for treatments, plots, and sites (Brooks et al. 2017). To account for the temporal autocorrelation present within our data, we included an autoregressive (ar1) correlation structure in each model, which assumes correlation of repeat observations from experimental units through time (Brooks et al. 2017). To find best and competing models, we used the lowest Akaike's Information Criterion with bias-correction (AICc). Competing models were those models differing from the lowest AICc by $\leq 2 \Delta AICc$. We used likelihood ratio tests against a null model containing only random and autocorrelative terms to determine p values for best models. For best and competing models, we calculated AICc weights (w), and marginal (fixed) and conditional (fixed and random effects) R^2 values from Nakagawa et al. (2017).

To examine species-specific responses to treatments through time, we used a multilevel model approach (Jackson et al. 2012) using mixed models with a Negative Binomial error distribution (glmmTMB, R; Brooks et al. 2017). Species included in the multilevel model were present in all experimental treatments in at least 3 of the 7 years of the study to provide enough temporal resolution for these analyses. The model included the abundance of species as the response variable, the main and interactive effects of time and experimental treatments as predictors, and a covariate of standing litter biomass. The model included a random intercept and slope term of a time by treatment interaction across species (time*treatment | species). Further, the model included a random intercept of site and plot nested within

site (1 | Site/Plot) to account for the split-plot design of our study. Fixed and random effects coefficients were summed to provide the average response of individual species to experimental treatments through time (Jackson et al. 2012).

To examine changes in ant species composition among deer and honeysuckle treatments, we conducted analyses for multivariate location and dispersion using PRIMER and PERMANOVA+ (version 6; Anderson 2001). We used split-plot permutational multivariate analysis of variance (PERMANOVA) to test for overlap in species composition (multivariate location; Anderson 2001). We also tested for differences in multivariate dispersion using a crossed design to determine whether our sites and treatments differed in the amount of variation in species composition (Anderson et al. 2006). We used non-metric multidimensional scaling (NMDS) to visualize patterns of species composition among treatments (metaMDS function, vegan, R; Oksanen et al. 2018). All community analyses were based on Bray–Curtis distances using square-root transformed abundance data. We pooled data from the three quadrat samples in each subplot for each site and year. A single constant individual was added to each pooled subplot, to include a subplot that had no ants collected; 140 samples were used in the community analyses. To reduce the effect of rare species on multivariate analyses, we removed singleton species (*Lasius nearcticus*, *Aphaenogaster tennesseensis*, *Temnothorax schaumii*, and *Tetramorium immigrans*) from these analyses.

Results

We collected 4665 individuals comprising 30 ant species with 4 singleton species (ESM 2). Dominant species based on frequencies in quadrats were *Aphaenogaster rudis* (54%), *Temnothorax curvispinosus* (40%), *Ponera pennsylvanica* (33%), *Myrmica punctiventris* (32%), and *Lasius americanus* (27%). Mean ant density (individuals 0.25 m^{-2}) ranged from 2.1 to 45.6 individuals and richness (species 0.25 m^{-2}) ranged from 1.2 to 6.4 species across sites and years. Rarefaction curves showed relatively complete sampling coverage of ant species across study sites (ESM 3). Although an asymptote was not reached for all rarefaction curves, confidence intervals were broadly overlapping among sites (ESM 3).

Abundance

Ant abundance was best explained by standing litter biomass and the interaction among deer, honeysuckle, and time ($X^2(8) = 40.62$, $p < 0.001$; $w = 0.41$; Table 1). There were no competing models. Deer enclosure had a negative effect on ant abundance near the beginning of the study, but this relationship became positive through time (Fig. 1a). There were

Table 1 Best and competing models for each response variable and predictor variables of deer (exclusion or access), HS (honeysuckle present or removed), time since experiment start, and litter (standing litter biomass)

	<i>df</i>	AICc	Δ AICc	<i>w</i>	Marg. R^2	Cond. R^2
Abundance						
Litter + HS*Deer*Time	14	2803.6	0	0.41	0.07	0.17
Richness						
Litter + HS + Deer*Time	10	1513.0	0	0.32	0.10	0.29
Litter + Deer*Time	9	1513.1	0.1	0.31	0.10	0.28
Shannon						
Litter + Time	8	1337.6	0	0.29	0.07	0.29
Litter + Deer*Time	10	1338.0	0.4	0.24	0.08	0.30

Predictors, degrees of freedom (*df*), AICc, Δ AICc, AICc weight (*w*), and marginal (Marg.) and conditional (Cond.) R^2 are given for each model

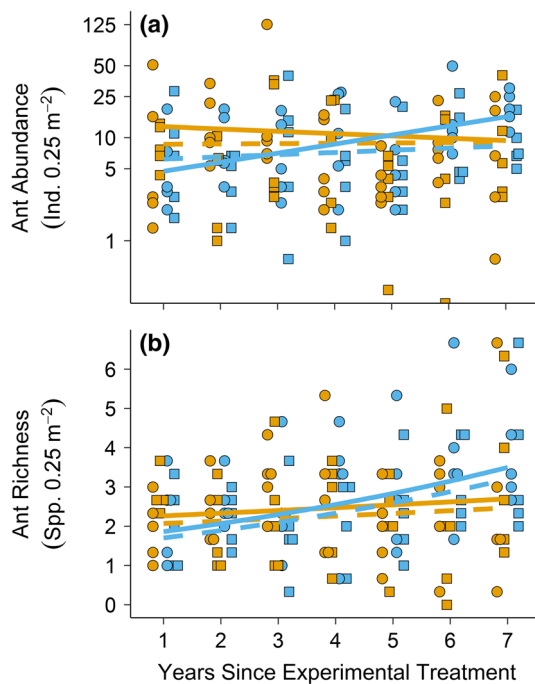


Fig. 1 Relationship between **a** ant abundance, **b** species richness, experimental treatments, and time. Each point is the mean ant abundance or species richness for each subplot in the corresponding year since experimental removal. Lines are the fixed effects from generalized linear mixed models while holding standing litter biomass constant at the median value. Deer access, honeysuckle present subplots are yellow circles and solid lines. Deer access, honeysuckle removal subplots are yellow squares and dashed lines. Deer exclusion, honeysuckle present subplots are blue circles and solid lines. Deer exclusion, honeysuckle removal subplots are blue squares and dashed lines. Note: y-axis of **(a)** is natural-log transformed

weak site-specific effects of deer exclusion treatment (ESM 4). Honeysuckle treatment effects were dependent on deer treatment and time, as there was an interaction among deer and honeysuckle treatments and time. Specifically, ant abundance in deer access, honeysuckle removal subplots was consistent through time, while in deer exclusion, honeysuckle removal subplots increased slightly over time. However,

abundance in these treatments was similar at the end of the study. Finally, there was a strong increase in abundance within deer exclusion, honeysuckle present subplots over time, while there was relative stability over time in all other subplots (Fig. 1a). There was a strong positive relationship between standing litter biomass and ant abundance; for every 50% increase in litter biomass, ant abundance increases by 28% (Fig. 2a). Accounting for differences in litter biomass between deer treatments, ant abundance was 25% higher in deer exclusions than deer access plots at the end of the study (Fig. 1a).

Species richness and diversity

Ant species richness was best explained by standing litter biomass, honeysuckle treatment, and the interaction between deer treatment and time ($X^2(5) = 32.43, p < 0.001; w = 0.32$; Table 1). There was a competing model of standing litter biomass and the interaction between deer and time ($w = 0.31$). Deer exclusion had a weak negative effect on richness at the beginning of the study, but a positive effect at the end of the study (Fig. 1b). There was little change in richness in deer access plots over the course of the study (Fig. 1b). Site-specific differences in ant richness between deer exclusion and deer access plots were stronger compared to ant abundance (ESM 5), but fixed effects patterns were consistent across sites. Honeysuckle removal had a negative effect on richness (Fig. 1b). There was a strong positive relationship between standing litter biomass and ant species richness; for every 50% increase in litter biomass, ant species richness increased by 12% (Fig. 2b). Accounting for differences in litter biomass, ant richness was 30% higher in deer exclusions than access plots (Fig. 1b).

Shannon diversity (1q) was strongly positively related to standing litter biomass and increased slightly over time ($X^2(2) = 18.40, p < 0.001; w = 0.29$; Table 1; Fig. 2c). There was a single competing model of standing litter biomass and an interaction between deer and time ($w = 0.24$).

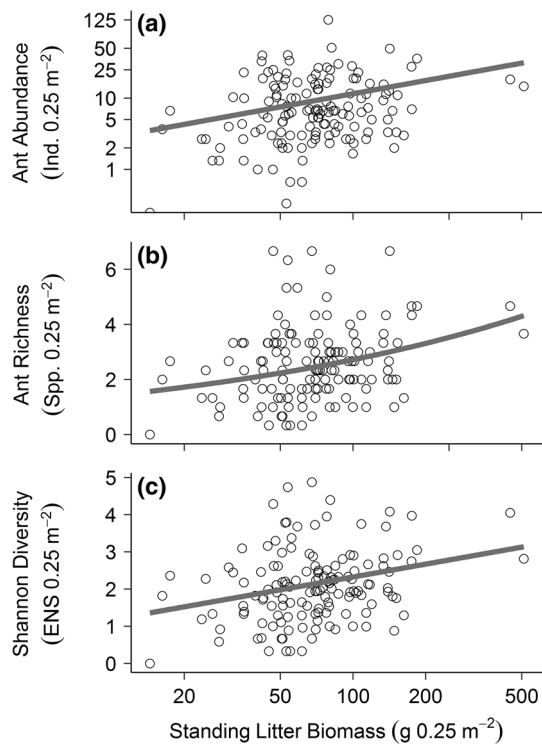


Fig. 2 Relationship between **a** ant abundance, **b** species richness, **c** Shannon diversity (effective number of species, ENS), and standing litter biomass. Each point is the mean ant abundance or diversity for each subplot and the corresponding mean litter biomass. Lines are the fixed effects from generalized linear mixed models while holding time constant at the median value and the treatment response at the mean value, when applicable (abundance and richness). Note: x -axis of all are natural-log transformed, y -axis of **(a)** is natural-log transformed

Shannon diversity increased more over time in deer exclosures relative to deer access plots; however, this was a weak trend.

Species-specific responses

Analyses of species-specific abundance response to treatments through time indicated that most species had relatively weak temporal trends across experimental treatments (Fig. 3). The number of workers of most species increased through time in deer exclosure subplots relative to deer access subplots (Fig. 3). Corresponding to the reduction in ant abundance through time in deer access, honeysuckle retention subplots (Fig. 1a), most of the common species decreased through time in this experimental treatment (Fig. 3). Similarly, the increase in ant abundance in deer exclosure, honeysuckle retention subplots (Fig. 1a) was likely driven by the strong increase in abundance of *Aphaenogaster rudis* and *Lasius americanus* (Fig. 3).

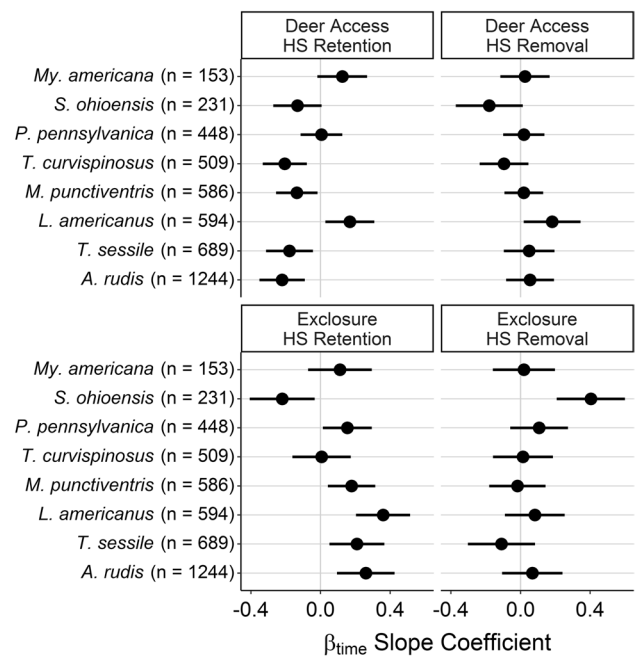


Fig. 3 Single-species responses to experimental treatments through time. Species were those that were present in all treatment combinations in at least 3 of 7 years of the study. Points are sums of fixed and species-specific random effects \pm standard error from multilevel model with litter biomass as a covariate. Positive β_{Time} coefficients indicate an increase in abundance through time in that experimental treatment. Species names are comprised of the first letter of the genus (capitalized) and the species name. The exception being *Myrmecina americana* abbreviated as “*My. americana*”

Community composition

Multivariate analyses indicated different ant communities among sites (NMDS, $k=4$, stress = 0.138, Fig. 4, ESM 6; PERMANOVA, Pseudo- $F=2.531$, $p=0.02$). There were no main or interactive effects of treatments on ant species composition (Table 2). Analysis of multivariate dispersion showed less dispersion in deer exclosures compared to access plots (Table 3). There were no differences in multivariate dispersion across sites, between honeysuckle treatments, or among deer–honeysuckle treatment subplots (Table 3).

Discussion

Following the long-term exclusion of deer and removal of honeysuckle, we found overall positive effects of deer exclusion on ant abundance and species richness, but negative effects of honeysuckle removal on these same endpoints. In contrast, there was weak evidence for the direct effects of deer exclusion or honeysuckle removal on Shannon diversity. Ant abundance, species richness, and Shannon diversity

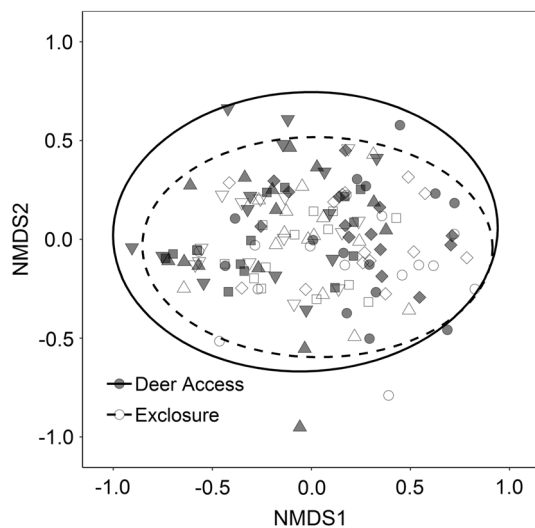


Fig. 4 Nonmetric Multidimensional Scaling (NMDS) ordination of the ant community composition ($n=140$). Site scores with 95% CIs of deer access (solid ellipses; gray symbols) and deer removal (dashed ellipses; open symbols) treatments. Sites are represented by symbol shape (circle—Bachelor; diamond—Kramer; triangle—Reinhart; square—College; inverted triangle—Western)

Table 2 Split-plot PERMANOVA results for the effect of site, deer exclosure, honeysuckle removal, and deer \times honeysuckle interaction on ant community composition across the entire study

Source	df	SS	MS	Pseudo- F	p
Site	4	2162	540.5	2.52	0.015
Deer	1	127	127.0	0.59	0.603
Whole-plot error	4	857	214.2		
Whole-plot total	9	3146			
Honeysuckle	1	179	179.5	0.67	0.650
Deer*Honeysuckle	1	248	248.3	0.92	0.474
Sub-plot error	8	2156	269.5		
Total	19	8874			

Table 3 Results for the effect of site, deer exclosure, honeysuckle removal, and deer \times honeysuckle treatment interaction on ant community dispersion over the entire study

Source	df1	df2	F	p
Site	4	135	1.80	0.183
Deer	1	138	5.98	0.025
Honeysuckle	1	138	0.93	0.362
Deer \times Honeysuckle	3	136	2.31	0.121

were positively associated with standing litter biomass, however. While we did not explicitly test for the effects of our treatments on litter biomass, previous studies have found

strong positive effects of deer exclosure on litter biomass (Bressette et al. 2012; Mahon and Crist 2019). These results indicate effects of deer exclosure on litter quantity, in turn, affect litter-dwelling ants (Bressette et al. 2012; Lessard et al. 2012). Similarly, invasive honeysuckle presence may alter litter-dwelling ants through related pathways (Arthur et al. 2012). As we found direct effects of our experimental treatments, effects of honeysuckle invasion and ungulate herbivory may also be mediated through other pathways, such as changes in habitat structure and microclimate, though we did not measure these responses (Rooney and Waller 2003; Loomis and Cameron 2014).

The effects of deer exclosure and honeysuckle removal on ants were dependent on the abundance of individual species. Specifically, in honeysuckle removal subplots, deer exclosure effects were positively related to overall abundance of each species, with strong positive effects of deer exclosure on *A. rudis* and neutral effects on *M. americana* (Fig. 3). Similarly, in deer access plots, honeysuckle removal effects were positively related to the overall abundance of each species, such that honeysuckle removal benefitted numerically dominant species, but with neutral effects on less common species (Fig. 3). These findings indicate drivers of ecosystem change may affect numerically dominant ant species more than less common ant species.

The variation in ant species composition was lower in deer exclosure plots relative to deer access plots (Fig. 4). Thus, deer exclosure resulted in increased alpha diversity (species richness), but reduced beta diversity (multivariate dispersion), indicating that a greater number of species were able to colonize conditions in the deer exclosure plots than in deer access plots, but these species were similar across sites. Moreover, as our multivariate analyses were conducted on subplots through time, these results suggest that community assemblages in the deer exclosure plots were less variable through time than in the deer access plots. Differences between deer exclosures and access plots are likely driven by changes in microhabitat (e.g., litter biomass), vegetation (Peebles-Spencer et al. 2017), and/or microclimate (Rooney and Waller 2003).

Litter biomass effects on ant communities

All univariate measures of the ant community were positively related to litter biomass, which is consistent with the findings of previous studies that have found positive relationships between litter quantity and ant abundance (Kaspari and Yanoviak 2009; McGlynn et al. 2009; Lessard et al. 2012). Overall, these findings support the hypothesis that ground-dwelling arthropods are altered by herbivore- and invasive plant-mediated changes in litter quantity, likely via changes in decomposition (Vilà et al. 2011; Lessard et al. 2012).

In these same experimental plots, a previous study found strong positive effects of deer enclosure on litter biomass (Mahon and Crist 2019). Deer accelerate decomposition directly through the consumption of leaf litter (Johnson et al. 1995) and trampling (Bressette et al. 2012) or indirectly through increased decomposer density (Dávalos et al. 2015b; Mahon and Crist 2019). At our study sites, the effects of deer on standing litter biomass are mediated through changes to earthworm abundance and decomposition rates (Mahon and Crist 2019; Mahon 2019). Exotic earthworms have drastic negative effects on litter-dwelling microorganisms (Ferlian et al. 2018) and may similarly affect litter-dwelling ants. There was little evidence to suggest honeysuckle treatment effects on litter biomass in our plots (Mahon and Crist 2019) and therefore, honeysuckle effects on ants likely occurred through other pathways.

By including litter biomass as a covariate in model selection, we were able to test for the direct effects of our experimental treatments on univariate ant response variables. Accounting for standing litter biomass, deer and honeysuckle treatments showed strong effects on ant abundance and richness, but weak effects on Shannon diversity. Consistent with our results, Lessard et al. (2012) found higher ant abundance in deer enclosures relative to deer access plots. However, these results contradict previous studies that have found no effects of deer (Bressette et al. 2012) or honeysuckle (Christopher and Cameron 2012) on ants. The direct effects of deer and honeysuckle treatments in our study were likely mediated through changes in vegetation structure, microclimate, or a combination of these factors.

Vegetation structure and ant communities

Several studies have shown that deer browse alters vegetation structure and reduces vegetation cover (Rooney 2009), while honeysuckle presence increases vegetation structural heterogeneity (Hartman and McCarthy 2008). Moreover, deer browse can reduce honeysuckle shrub cover (Peebles-Spencer et al. 2018), while honeysuckle shrubs protect some tree seedlings from deer browse (Gorchov and Trisel 2003; Peebles-Spencer et al. 2017). Studies of plant community responses to our treatments show non-honeysuckle plant cover increased following honeysuckle removal (Haffey and Gorchov 2019), as well as greater cover of honeysuckle and other shrubs in deer enclosure plots (Peebles-Spencer et al. 2017, 2018). However, as honeysuckle dominates the understory in our study sites, changes in non-honeysuckle plant cover are likely to be overshadowed by differences in honeysuckle cover between removal and retention subplots. Thus, the structural complexity of the understory vegetation was highest in the deer enclosure, honeysuckle present subplots, and lowest in the deer present, honeysuckle removal subplots.

Previous studies have indicated strong habitat structure controls on ant behavior, abundance, and diversity, due to differences in energetic costs and ability to detect chemical trails and resources across habitat structural complexity (Yanoviak and Kaspari 2000; Lassau and Hochuli 2004; Gibb and Parr 2010). Our results are consistent with these studies, as we found more individuals and species in more complex habitats, supporting the findings of previous studies showing similar ant–habitat complexity relationships (Retana and Cerdá 2000; Pacheco and Vasconcelos 2012). Similarly, Purdon et al. (2019) found vegetation structure simplification mediated by ungulate browse drove ant diversity and resource monopolization by dominant ant species. Additionally, Masters et al. (2017) found reductions in arthropod abundance and taxon richness in areas of honeysuckle removal, which was linked to simplification of vegetation structure. Increased availability of nesting sites (e.g., more plant cavities, less compact soil, more leaf litter) in complex habitats may explain this pattern, as microhabitat differences control nest site suitability in temperate forest ants where nesting availability is an important driver for these communities (Herbers 1989; Gotelli and Ellison 2002).

Microclimate effects on ant communities

Ant abundance and richness in our study may also have been influenced by changes in temperature and soil moisture as a consequence of our experimental manipulations. Although we did not measure these abiotic factors, deer and honeysuckle were shown to alter soil temperature and moisture in other studies (Rooney and Waller 2003; Watling et al. 2011). We would predict that the warmest, driest microclimate occurred in the deer present, honeysuckle removal subplots, while the coolest, wettest microclimate was expected in deer enclosure, honeysuckle present subplots. In temperate forests, ant abundance and diversity is higher in areas with higher temperatures (Diamond et al. 2012; Stuble et al. 2013; Pelini et al. 2014), due to temperature influences on ant trail following behavior (van Oudenhove et al. 2012), running speeds (Hurlbert et al. 2008), and daily foraging timing (Talbot 1946). In contrast to these expected patterns, more ant workers and species were found in areas of expected lower temperatures, but these results were consistent with soil moisture patterns. Ant richness often increases with soil moisture (Pelini et al. 2014), due to increased resource control (Baccaro et al. 2010), increased food availability (Levings 1983), and reduced desiccation risk (Kaspari and Weiser 2000). Yet, as leaf litter likely acts as insulation from changes in microclimate (Kaspari and Weiser 2000; Fekete et al. 2016), modest changes in temperature and soil moisture mediated by our treatments are likely buffered and may be less impactful than changes in habitat complexity (Gotelli and Ellison 2002; Purdon et al. 2019).

Temporal effects of treatments

Time since experimental manipulation was an important predictor in all univariate ant measurements, whether as a direct effect or interacting with treatments (Table 2). Ant abundance, ant richness, and individual ant species followed different temporal trajectories depending on the subplot treatment, which indicates delayed effects of deer exclosure and honeysuckle removal on ants and ecosystem processes. Due to the long-term nature of our study, we were more likely to detect changes in ant diversity that would have been missed during a short-term study (Foster et al. 2014). All of our ant abundance and diversity responses either increased or showed non-significant change through time. Thus, we found no indication of a loss of litter-dwelling ant abundance or diversity across our study sites, in contrast to other recent studies that show long-term loss of insect abundance and biomass (Gonzalez et al. 2016). Though our study encompassed several years, it still may be too short to detect long-term declines (Gonzalez et al. 2016). Nonetheless, the gradual loss of standing litter biomass in deer access plots across the study sites during our study (Mahon and Crist 2019), and the positive relationships of litter biomass and all univariate measures of the ant community, may portend a future decline in ant abundance and diversity in these forests. Alternatively, as the forest stands are 60–80-year-old post grazed pastures (Medley and Krisko 2007), we may be witnessing successional changes in the ant community (Palladini et al. 2007). This is supported by multivariate analyses that indicated clustering of older stands (Bachelor Preserve and Kramer Woods; ~70–80 years old) away from younger stands (College Woods, Reinhart Preserve, and Western Woods; ~50–60 years old).

Conclusions

White-tailed deer and invasive plants are key drivers of changes in ecosystem processes and native plant decline in temperate forests (Côté et al. 2004; Simberloff et al. 2013). Our study shows strong direct and indirect effects of white-tailed deer and Amur honeysuckle on forest floor ants mediated through changes in litter biomass and vegetation structure. Thus, our results support the hypotheses that ungulate herbivory and non-native plant invasion alter ground-dwelling arthropod communities through changes to leaf litter quantity (Vilà et al. 2011; Lessard et al. 2012). Our study is the first continuous long-term study of white-tailed deer exclosure or invasive plant removal effects on litter-dwelling organisms. We found delayed effects of deer exclosure and honeysuckle removal on ants, suggesting short-term manipulations may be insufficient to detect both direct and indirect effects mediated through changes in litter

quantity. Honeysuckle invasion may benefit litter-dwelling insects through increased vegetation structure and favorable microclimates. The direct and indirect effects of deer and honeysuckle on standing litter biomass and ant communities likely have cascading effects on other litter-dwelling invertebrates and ecosystem processes in forest ecosystems. Reduction of overabundant deer populations may increase the biodiversity of litter-dwelling insects.

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Author contribution statement MBM and TOC conceived and designed the experiment; MBM and KUC conducted fieldwork and specimen ID; MBM performed statistical analyses; MBM and TOC wrote the manuscript; comments from KUC improved the manuscript.

Compliance with ethical standards

Conflict of interest The authors declare they have no conflict of interest.

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