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Impact of the invasive shrub Lonicera maackii on shrub-dwelling arthropods in an eastern deciduous forest

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Impact of the invasive shrub *Lonicera maackii* on shrub-dwelling arthropods in an eastern deciduous forest

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Abstract

The exotic shrub *Lonicera maackii* is a problematic invader of southwestern Ohio forests. As *L. maackii* invades the forest interior, it negatively impacts native plant diversity and abundance and changes the structure of understory vegetation by replacing the native shrub layer, which has a patchy distribution of plant species, with a dense shrub layer. Changes in diversity or structure of native shrub layer vegetation caused by *L. maackii* invasion could, in turn, affect associated arthropod fauna. Our objective was to determine whether *L. maackii* invasion impacted arthropod community composition and structure in the forest shrub layer. We predicted that by negatively affecting the diversity of native plant species in the shrub layer, *L. maackii* invasion would decrease diversity and abundance of arthropod taxa, trophic groups, and feeding specialists. Alternatively, we predicted that invasion of forests by *L. maackii* could increase vertical cover of the shrub layer, which could increase diversity and abundance of arthropod taxa, trophic groups, and feeding specialists. We established paired plots in ten forested locations to compare both arthropod community characteristics and characteristics of the shrub layer vegetation between invaded and uninvaded areas. Within paired plots, we captured arthropods from shrub layer vegetation using fumigants and a beating stick and then identified or classified individuals to order and family, trophic group, and specialist/generalist feeder. Additionally, within paired plots, we measured percent vertical cover of shrub layer vegetation with a profile board and identified all individuals of woody shrub layer plants to species. In areas invaded by *L. maackii*, we found increased or unchanged values of richness and abundance of all arthropod taxa, trophic groups, and specialist feeders. We also observed increased or unchanged values of Shannon's diversity and evenness of all arthropod taxa and trophic groups and relative abundance of all trophic groups in invaded areas, with the exception of a decrease in evenness of detritivores. Shannon's species diversity, richness, and evenness of shrub layer vegetation did not differ between invaded and uninvaded forest; however, percent vertical cover was higher in areas invaded by *L. maackii*. In contrast to our first prediction, the diversity of shrub layer vegetation did not have a major impact on arthropods in our plots. Our alternative prediction was supported only in that abundance of spiders was affected by the increase in cover provided by *L. maackii*. Increases in diversity, richness, and abundance of several arthropod taxa and trophic groups in invaded areas were explained by the presence of *L. maackii* rather than by increases in vertical cover. It was likely that *L. maackii*, while minimally affecting the trophic structure of the arthropod community, directly and indirectly facilitated arthropods in the invaded shrub layer by providing additional architectural complexity, habitat space, or food resources compared to the uninvaded forest shrub layer. Management implications of this study suggest that measures to prevent further spread of this invasive shrub should be continued; however, total eradication of *L. maackii* in currently invaded areas may not be required.

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Introduction

Understanding the ecological consequences of biological invasions is of concern because exotic species can radically alter primary production, nutrient cycling, decomposition, disturbance regimes, and energy flow, as well as physical structure of invaded habitats, thereby threatening the health and biodiversity of native ecosystems (Vitousek, 1990; Vitousek *et al.*, 1997; Blossey *et al.*, 2001; Zavaleta *et al.*, 2001; Crooks, 2002; Gurevitch and Padilla, 2004; Campbell and Donlan, 2005; Lodge *et al.*, 2006). Similarly, exotic plants can change the structure and diversity of native vegetation in communities that they invade, and, in turn, they can negatively affect associated fauna (Bruce *et al.*, 1997; Blossey *et al.*, 2001; With, 2001; Huebner, 2003; Fagan and Peart, 2004; Rooney *et al.*, 2004). In particular, by affecting native plants, invasion by exotic plants can decrease abundance or diversity and alter species composition and trophic structure of arthropods that rely upon specific plants for food, refuge from predators, or reproduction (Zavaleta *et al.*, 2001; Herrera and Dudley, 2003; Hartley *et al.*, 2004; Gratton and Denno, 2005; Lindsay and French, 2006; Cameron and Spencer, 2010). Additionally, by negatively impacting native plant assemblages, exotic plant species pose a great risk to richness and abundance of arthropods that are dietary specialists that feed on only one or a few plant taxa (Strong *et al*., 1984; Blossey *et al*., 2001; Hartley *et al*., 2004; Gratton and Denno, 2005; Heleno *et al*., 2009; Carvalheiro *et al*., 2010).

Increased structural complexity and diversity of vegetation often is positively correlated with the diversity and abundance of arthropods and feeding guilds (Murdoch *et al*., 1972; Siemann *et al*., 1998; Koricheva *et al.*, 2000; Langellotto and Denno, 2004; Heleno *et al*., 2009). Although negative impacts of invasive plant species on arthropod communities have been emphasized, introduction of exotic plants instead may increase overall diversity and cover of native plants, resulting in increased abundance and diversity of arthropod taxa (Bolger *et al*., 2000; Crooks, 2002; Gilbert and Lechowicz, 2005). For example, riparian habitats invaded by exotic *Tamarix ramosissima* (saltcedar) supported larger and more heterogeneous communities of arthropods compared to uninvaded habitats (Ellis *et al*., 2000). Similarly, richness and abundance of some arthropod taxa increased when exotic herbs and grasses provided additional species and structural diversity in chaparral shrub and coastal sage-scrub habitats in California (Bolger *et al*., 2000).

Lonicera maackii (Amur honeysuckle) was introduced to eastern North America from northeastern Asia in 1896 (Luken and Thieret, 1995). This species, first detected in Ohio in 1961 (Braun 1961), now has invaded at least 24 eastern states (Trisel, 1997). *Lonicera maackii* has reduced recruitment and species diversity of native herbaceous plants and richness of native tree seedlings in southwestern Ohio (Collier *et al*., 2002; Hartman and McCarthy, 2004). These negative impacts resulted from competition between native flora and *L. maackii* for light, nutrients, and water (Deering and Vankat, 1999), and possibly also from allelopathic compounds secreted by the roots of *L. maackii* (Huebner, 2003; Hartman and McCarthy, 2004; Cipollini *et al*., 2008). In addition, in low-light environments, *L. maackii* out-competes *Lindera benzoin* (spicebush), the dominant native shrub in forests of southwestern Ohio, because of its greater rate of stem growth (Quigley and Platt, 1996; Luken *et al*., 1997). *Lonicera maackii* effectively changed the structure of understory vegetation in these forests by replacing *L. benzoin* and juvenile canopy and subcanopy trees, which have a patchy distribution (Quigley and Platt, 1996), with a dense shrub layer (Luken *et al*., 1997; Deering and Vankat, 1999; Collier *et al*., 2002; Meiners, 2007).

While effects of *L. maackii* on native vegetation have been well studied (Luken *et al.*, 1997; Deering and Vankat, 1999; Collier *et al.*, 2002; Hartman and McCarthy, 2004), it is not known whether *L. maackii* affects arthropod communities in the forest understory. Because their short generation time and high reproductive rate allows arthropods to react quickly to environmental disturbances (Rosenberg *et al.*, 1986; Williams, 1993; Pollet and Grootaert, 1996), changes to arthropod assemblages would be expected to occur rapidly after invasion by exotic plants. Understanding changes that occur within the arthropod community may not only help elucidate the reaction of the deciduous forest ecosystem to invasion by *L. maackii* but also may provide guidance for management of these invasions. Our objective in this study was to determine whether *L. maackii* impacted community composition and structure of arthropods in the shrub layer of deciduous forests in southwestern Ohio. We predicted that invasion of forest tracts by *L. maackii* would decrease the diversity and abundance of arthropod taxa, trophic groups, and dietary specialists, because growth and expansion of populations of *L. maackii* would negatively affect diversity of native species of plants in the shrub layer. Alternatively, invasion of forests by *L. maackii* could increase vertical structure and cover in the native shrub layer, which could increase diversity and abundance of arthropod taxa, trophic groups, and dietary specialists.

Methods

Site description and experimental design. Our general study area included approximately 1,029 km^2 of fragmented, urban and suburban forest in the Cincinnati metropolitan area of southwestern Ohio. Dominant canopy trees included *Acer saccharum* (sugar maple), *Acer rubrum* (red maple), *Carya cordiformis* (bitternut hickory), *Carya ovata* (shagbark hickory), *Fagus grandifolia* (American beech), *Fraxinus americana* (white ash), *Fraxinus pennsylvanica* (green ash), *Quercus alba* (white oak), *Quercus muehlenbergii* (chinkapin oak), and *Quercus rubra* (red oak). Native species dominant in the shrub layer of forests included *Lindera benzoin* (spicebush) and subcanopy and juvenile canopy tree species, particularly *Asimina triloba* (pawpaw) and *A. saccharum*.

Study sites were established in ten different metropolitan and state parks to encompass variation in vegetation, elevation, and slope in the study area (Table 1). Criteria used to select these study sites included: 1) contiguous forest $\geq$ 10-ha, 2) presence of an area $\geq$ 400-m^2 that contained portions of a native shrub layer with and without a dense shrub layer of *L. maackii*, 3) similarity between sites with respect to vegetation structure and environmental conditions, 4) no active management to remove *L. maackii*, and 5) remote area with infrequent visits from the general public. Distance between adjacent study sites ranged from approximately 1.3 km to 14 km. Within each study site, a single set of paired 3-m^2 plots separated by at least 30 m were established to sample arthropods and vegetation; one plot was in an area invaded by *L. maackii* (honeysuckle-present), while the other plot was in an area not yet invaded by *L. maackii* (honeysuckle-absent).

Arthropod sampling. Arthropods were sampled in the shrub layer (defined as all woody vegetation occurring from ground level to 2 m above ground) in each 3-m^2 plot on sunny days before 1400 h when foliage was dry. Because arthropods were most diverse and abundant and had a fully developed food web during summer months (Oliver and Beattie, 1996; Gratton and Denno, 2006), each plot was sampled once each in July and September 2008 to obtain all available adults. Fumigants followed by physical dislodging with a beating stick were used to sample arthropods (Hutchins, 1994; Janes, 1994; Kitching *et al.*, 2001). Prior to fumigation, collection cloths were placed beneath vegetation in each 3-m^2 plot, and all vegetation in the shrub layer, including foliage and stem/trunk bark, was fogged with insecticides (Pre-Strike^{TM} – active ingredients: piperonyl butoxide 1.0%, tetramethrin 0.2%, etofenprox 0.1%; Raid House & Garden^{TM} – active ingredients: d-cis trans allethrin 0.239%, 3-phenoxybenzyl d-cis and trans 2,2-dimethyl-3-(2-methylpropenyl) cyclopropanecarboxylate 0.096%) until the surface area was saturated. After fogging, plants were undisturbed for 20 minutes to allow arthropods to fall onto the collection cloth. Then vegetation in the shrub layer was lightly hit with a beating stick (61-cm long, 2.54-cm in diameter) or shaken by hand to dislodge any arthropods remaining on foliage and stems. Arthropods and small pieces of vegetation (e.g., leaves and small twigs) that had been collected on the ground cloths were placed into 1-gallon Ziploc® storage bags for transport to the lab. Any large pieces of vegetation that had fallen onto the ground cloths were visually inspected for arthropods and then removed from the sample in the field. Finally, individual plants in the shrub layer were visually inspected and any remaining arthropods were collected and placed in the sample bag.

Arthropods were separated by hand from any remaining vegetation in the lab and stored in 70% ethanol. Individual adults were counted, identified to family, and classified into trophic groups (carnivores, detritivores, herbivores, omnivores, parasites, and parasitoids) (Triplehorn and Johnson, 2005; Ubick *et al.*, 2005). Adult specimens also were designated as specialist or generalist feeders using information from Triplehorn and Johnson (2005) and an extensive review of the primary literature. Individuals in the suborder Prostigmata (order Acari) were classified into morphofamilies because identification to family was difficult.

Vegetation sampling. Vertical cover of vegetation in the shrub layer was measured with a profile board (Nudds, 1977; Skagen *et al.*, 1998). The profile board was a polyethylene tarpaulin

2-m high and 1-m wide and was attached to aluminum poles that held it upright. The profile board contained 800 5-cm^2 squares alternately painted blue and white.

Vertical cover in the shrub layer was measured in August 2008 while leaves of vegetation were fully expanded. The profile board was placed along the side of each 3-m^2 plot that visually contained the greatest amount of vegetative cover. The board was observed by standing at the opposite side of the plot**.** The number of white squares that were unobscured by vegetation was counted and then subtracted from 400, the total number of white squares, to determine the number of squares obscured by vegetation. Squares that were < 50% covered by vegetation were considered unobscured. Percent vertical cover was calculated by dividing the number of obscured squares by 4. Because the board was only 1-m wide, it was placed along the edge of the 3-m^2 plot 3 times to determine percent cover for the entire side of the plot. Percent cover was averaged among the readings for the three boards to obtain average cover of vegetation in the shrub layer for each plot. In August 2009, each 3-m^2 plot was expanded to 10-m^2, and all woody plants that occurred in the shrub layer were counted and identified to species.

Statistical analyses. Only those orders and trophic groups with total mean abundance >10 individuals/plot and > 1 family were included in the analyses of diversity, evenness, richness, and abundance in order to eliminate the least abundant taxa that were not represented among most paired study sites. Accordingly, Shannon diversity (H’), evenness, and richness were calculated for: (1) families included in All Arthropods, Hexapoda, Spiders (order Araneae), and Other Arthropods (orders Acari and Opiliones), (2) families included in the hexapod orders of Coleoptera, Diptera, Hemiptera, Hymenoptera, and Psocoptera, and (3) families included in each trophic group (carnivores, detritivores, herbivores, and parasitoids). Abundance was computed for: (1) All Arthropods, Hexapoda, Spiders, and Other Arthropods, (2) hexapod orders

Coleoptera, Diptera, Hemiptera, Hymenoptera, and Psocoptera, and (3) trophic groups (carnivores, detritivores, herbivores, and parasitoids). Orders Acari and Opiliones were lumped as Other Arthropods because total mean abundance for each order was <10 individuals/plot. Relative abundance of families in each trophic group also was calculated. Sørenson's similarity index (S_s) was calculated to compare families of All Arthropods and each trophic group between honeysuckle-present and honeysuckle-absent plots. Paired t-tests were used to analyze differences in diversity, richness, evenness, and abundance of arthropod taxa and trophic groups, and relative abundance of trophic groups between honeysuckle-present and honeysuckle-absent plots (JMP v. 7.0 software, SAS Institute Inc., Cary, NC, USA). Richness and abundance of specialist families were also analyzed with paired t-tests.

Shannon species diversity (H'), species richness, and evenness were calculated for plants in the shrub layer in each plot. Differences in species diversity, evenness, richness, and vertical cover of vegetation in the shrub layer between honeysuckle-present and honeysuckle-absent plots were tested with paired t-tests.

Percent vertical cover of vegetation and relative abundance of families in each trophic group were arcsine square-root transformed prior to analysis to achieve normality (Zar, 1999). Data for which means were not normally distributed were log transformed to meet the assumptions of the paired t-test (Zar, 1999). Non-transformed means were reported in tables and figures.

A general linear model was used to analyze the relationship between vertical cover of vegetation and those community characteristics of arthropods that differed significantly between honeysuckle-present and honeysuckle-absent plots (JMP v. 7.0 software, SAS Institute Inc., Cary, NC, USA). Because honeysuckle could have affected community characteristics of arthropods other than by increasing cover, a one-way analysis of covariance (ANCOVA), with honeysuckle as the main effect and vertical cover (arcsine square-root transformed) as the secondary response variable (covariate), was used to account for effects of each of these factors (Cochran, 1957; Maxwell *et al.*, 1993; Milliken and Johnson, 2002). ANCOVA was used to assess the effect of vegetation cover and presence of honeysuckle on: (1) richness of families of Coleoptera, Diptera, Hemiptera, Hymenoptera, and Psocoptera, (2) abundance of Diptera, Hymenoptera, Psocoptera, and Spiders (Araneae), (3) richness of families in trophic groups (carnivores, detritivores, herbivores, and parasitoids), (4) evenness of detritivores, and (5) relative abundance of detritivores. Orders and trophic groups of arthropods with significant differences in diversity between honeysuckle-present and honeysuckle-absent plots were not tested with ANCOVA, because these differences were largely explained by differences in richness of arthropods between treatments of honeysuckle. Trophic groups with significant differences in mean abundance were not analyzed with ANCOVA, because differences in relative abundance among most trophic groups were not significant between treatments of honeysuckle. Data that did not meet the assumption of normality were log transformed. All other assumptions of ANCOVA were met.

Results

Diversity of arthropods. We identified 18 orders and 126 families of arthropods, of which 37 families were unique to honeysuckle-present plots and 16 families were unique to honeysuckle-absent plots (Table 2; Appendix A). The mean similarity of families of All Arthropods between treatments of honeysuckle was $S_s = 0.59 \pm 0.04$. Richness ($t_{[9]}=-4.33$, $p=0.001$) of families of All Arthropods was significantly higher in honeysuckle-present plots than in honeysuckle-absent plots (Fig. 1b). However, neither diversity ($t_{[9]}$=-1.66, p=0.066) nor evenness ($t_{[9]}$=1.76, p=0.94) of families of All Arthropods differed between paired plots (Fig. 1a,c).

Hexapoda, representing 86.5% of all families identified, was the most diverse arthropod taxon (Fig. 1a). Hexapods included 109 families of which 35 were unique to honeysuckle plots and 15 were unique to plots where honeysuckle was absent (Table 2). Diversity ($t_{[9]}$=-2.49, p=0.017) and richness ($t_{[9]}$=-4.14, p=0.0013) of hexapod families were significantly higher in honeysuckle-present plots than in honeysuckle-absent plots (Fig. 1a,b). Evenness of hexapod families did not significantly differ between paired plots ($t_{[9]}$=1.23, p=0.88; Fig. 1c). Diversity of Coleoptera and Psocoptera was significantly higher in honeysuckle-present plots than in honeysuckle-absent plots (Table 3). Richnesses of Coleoptera, Diptera, Hemiptera, Hymenoptera, and Psocoptera also were significantly higher in plots where honeysuckle was present (Table 3). Evenness did not differ significantly between paired plots for any of the orders tested (Table 3).

Spiders (order Araneae) and Other Arthropods (orders Acari and Opiliones) represented 10.3% and 3.2% of all families, respectively. Only Spiders contained families unique to both plots with and without honeysuckle (Table 2; Appendix A). Diversity ($t_{[9]}$=-1.28, p=0.12; Fig. 1a), richness ($t_{[9]}$=-1.37, p=0.10; Fig. 1b), and evenness ($t_{[9]}$=0.76, p=0.77; Fig. 1c) of spider families did not differ significantly between paired plots. Richness of Other Arthropods was significantly higher in honeysuckle-present plots than in honeysuckle-absent plots ($t_{[9]}$=-2.86, p=0.0094; Fig. 1b), but neither diversity ($t_{[9]}$=-1.70, p=0.062; Fig. 1a) nor evenness ($t_{[4]}$=1.55, p=0.90; Fig. 1c) of families of Other Arthropods differed between paired plots.

Abundance of arthropods. We identified 3,164 individual arthropods with 108 individuals from families unique to honeysuckle-present plots and 22 individuals from families unique to honeysuckle-absent plots (Table 2). Mean abundance of All Arthropods was significantly higher in honeysuckle-present plots than in honeysuckle-absent plots ($t_{[9]}$=-3.59, p=0.0029; Fig. 2).

Hexapoda was the most abundant arthropod group with 2,314 individuals. The mean abundance of Hexapoda was significantly greater in honeysuckle-present plots than in honeysuckle-absent plots ($t_{[9]}$=-2.96, p=0.0080; Fig. 2). For the most abundant orders of Hexapoda, abundance of Diptera, Hymenoptera, and Psocoptera was higher in plots where honeysuckle was present (Table 3).

We identified 600 individual spiders (order Araneae) and 250 individuals in Other Arthropods (161 Acari; 89 Opiliones; Table 2). Abundance of both of these orders was significantly higher in honeysuckle-present than in honeysuckle-absent plots (Spiders: ($t_{[9]}$=-2.95, p=0.0081; Other Arthropods: $t_{[9]}$=-3.79, p=0.0022; Fig. 2).

Diversity and abundance of trophic groups. Mean (±SE) similarity in composition of trophic groups between honeysuckle-present and honeysuckle-absent plots was as follows: carnivores, $S_s = 0.62 \pm 0.06$; detritivores, $S_s = 0.57 \pm 0.06$; herbivores, $S_s = 0.55 \pm 0.05$; and parasitoids, $S_s = 0.54 \pm 0.06$. Herbivores contained the most arthropod families (43), 95% of which were from Hexapoda with the remaining families from Acari (Fig. 3a). Families of hexapods also comprised the majority of both detritivores (94%) and carnivores (55%) with orders Araneae and Opiliones, respectively, representing the remaining families in these trophic groups (Fig. 3b,c). Parasitoids were comprised primarily of Hymenoptera (85%), with fewer Diptera (10%) and Phthiraptera (5%) (Fig. 3d). All trophic groups had families unique to either honeysuckle-present or honeysuckle-absent plots (Fig. 3).

Diversity of parasitoids ($t_{[9]}$=-3.78, p=0.0022) was significantly greater in honeysuckle-present plots than in honeysuckle-absent plots, but diversity for other trophic groups did not differ between paired plots (carnivores, $t_{[9]}$=-1.35, p=0.10; detritivores, $t_{[9]}$=-0.99, p=0.17; herbivores, $t_{[9]}$=-1.22, p=0.13; Fig. 4a). Richness of all trophic groups was significantly higher in plots where honeysuckle was present (carnivores, $t_{[9]}$=-1.99, p=0.039; detritivores, $t_{[9]}$=-4.31, p=0.001; herbivores, $t_{[9]}$=-3.53, p=0.0032; parasitoids, $t_{[9]}$=-3.28, p=0.0047; Fig. 4b). Evenness of detritivores was significantly higher in honeysuckle-absent plots than in honeysuckle-present plots ($t_{[9]}$=3.92, p=0.0018; Fig. 4c), but evenness did not differ between paired plots for the other trophic groups (carnivores, $t_{[9]}$=0.65, p=0.73; herbivores, $t_{[9]}$=1.21, p=0.87; parasitoids, $t_{[9]}$=-0.08, p=0.47; Fig. 4c).

Herbivores (32%), carnivores (27%; primarily spiders), and detritivores (23%) contributed the highest proportion of individuals to total abundance, while parasitoids (9%) accounted for a smaller percentage of total abundance. Abundance of each trophic group was significantly higher in honeysuckle-present plots than in honeysuckle-absent plots (carnivores, $t_{[9]}$=-2.61, p=0.014; detritivores, $t_{[9]}$=-5.99, p<0.0001; herbivores, $t_{[9]}$=-2.67, p=0.013; parasitoids, $t_{[9]}$=-3.28, p=0.0047; Fig. 5a). However, only relative abundance of detritivores was significantly higher in plots where honeysuckle was present (detritivores, $t_{[9]}$=-2.07, p=0.034; carnivores, $t_{[9]}$=1.08, p=0.85; herbivores, $t_{[9]}$=-0.46, p=0.33; parasitoids, $t_{[9]}$=1.18, p=0.87; Fig. 5b).

Richness and abundance of specialist families. Of 126 families in our study, 23 (18.2%) were specialist feeders, 4 of which were unique to honeysuckle-present plots, and 3 of which were unique to honeysuckle-absent plots (Table 4). Mean richness of specialist families was significantly higher in honeysuckle-present plots (S = 10.1 ± 0.6) than in honeysuckle-absent plots ($S = 7.9 \pm 0.6$; $t_{[9]}=-4.71$, p=0.0005). Mean abundance of these families also was significantly higher in plots where honeysuckle was present ($t_{[9]}=-1.91$, p=0.044; Table 4).

Shrub layer diversity and cover. We identified 23 species of shrubs, tree saplings, and mature trees in the shrub layer in honeysuckle-present and honeysuckle-absent plots (Appendix B). Species diversity (H' = 0.9 ± 0.09; H' = 1.0 ± 0.09; $t_{[9]}=1.16$, p=0.86), richness ($S = 4.8 \pm 0.6$; $S = 5.5 \pm 0.6$; $t_{[9]}=0.92$, p=0.81), and evenness ($E = 0.6 \pm 0.05$; $E = 0.6 \pm 0.03$; $t_{[9]}=0.58$, p=0.71) of plants in the shrub layer did not differ significantly between honeysuckle-present and honeysuckle-absent plots, respectively. However, vertical cover of shrub layer plants was significantly higher in honeysuckle-present plots (mean proportion of vertical cover = 0.66 ± 0.06) than in honeysuckle-absent plots (mean proportion of vertical cover = 0.29 ±0.04; $t_{[9]}=-4.62$, p=0.0006).

Shrub layer effects on arthropod taxa and trophic groups. The presence of honeysuckle accounted for a significant proportion of the variation in the richness of families of Coleoptera, Hymenoptera, and Psocoptera, but not of Diptera or Hemiptera (Table 5). Vertical cover did not explain the variation in the richness of any of these orders (Table 5). However, vertical cover explained the variation in the abundance of Araneae, while presence of honeysuckle explained variation in abundance of Psocoptera (Table 5). Abundances of Diptera and Hymenoptera were not explained by either vertical cover or presence of honeysuckle (Table 5). The variation in the richness of families of detritivores and parasitoids, but not carnivores or herbivores, was explained by the presence of honeysuckle (Table 6). Vertical cover did not explain the variation in richness of any of the trophic groups. Evenness and relative abundance of detritivores was not explained by either presence of honeysuckle or vertical cover (Table 6).

Discussion

Diversity and abundance of arthropod taxa and trophic groups. We found a general trend of increased or unchanged diversity, richness, and abundance of All Arthropods and all trophic groups in the presence of the invasive shrub *L. maackii* compared to native vegetation in the forest understory. Richness was significantly higher in plots where honeysuckle was present for all arthropod groups, except spiders, and for all trophic categories (Table 3; Fig. 1; Fig. 3b). This pattern of richness explained the significant increases in diversity of Hexapoda and parasitoids in honeysuckle-present plots. Abundance of all arthropod taxa, except Coleoptera and Hemiptera, and all trophic groups also was significantly higher in plots where honeysuckle was present. These results contrasted with decreased diversity, richness, and abundance of arthropods in the presence of other invasive woody plants such as *Prosopis glandulosa* (honey mesquite) in southern Africa (Steenkamp and Chown, 1996) and *Chysanthemoides monilifera* (bitou bush) in Australia (Lindsay and French, 2006), and also contrasted with decreased richness and abundance of aerial and ground-dwelling arthropods in riparian habitats invaded by *Arundo donax* (giant reed) compared to uninvaded habitats (Herrera and Dudley, 2003). However, our results agreed with Harris *et al*. (2004) who found that species richness and abundance of most arthropod taxa was generally higher in the presence of the invasive shrub *Ulex europaeus* (European gorse) than in native scrub species in New Zealand. Such contrasting results among studies of invasive plants may reflect inherent structural differences between invasive woody plants and invasive herbaceous plants, or differences between conditions and resources in different geographical regions, which resulted in unique impacts on the native communities.

Evenness was high for all arthropod taxa (average E = 0.88) and all trophic groups (average E = 0.87), indicating a relatively equal apportionment of individuals among families.

Evenness, however, did not differ between treatments of honeysuckle except that evenness of detritivores was lower in honeysuckle-present plots (Table 3; Fig. 1c; Fig. 4c), indicating that *L. maackii* had little impact on the distribution of individuals among families. In contrast, Carvalheiro *et al*. (2010) reported significant increases in evenness of insect species and trophic groups in heath habitats invaded by the shrub *Gaultheria shallon* (salal) in the United Kingdom.

Similarity in the composition of arthropod families between plots with and without *L. maackii* in our study ($S_s = 0.59$) was comparable to results reported by Gratton and Denno (2005) who also found >50% similarity of arthropods between native *Spartina alterniflora* (smooth cordgrass) marshes and marshes containing both *S. alterniflora* and invasive *Phragmites australis* (common reed). However, 41% of the families we collected were unique to plots invaded by *L. maackii* compared to plots without *L. maackii*, resulting in an enhancement of richness and abundance of arthropod families in invaded areas. Approximately half of these families were typical of field habitats (e.g., Delphacidae, Gryllacrididae, Scarabaeidae) or edge habitats (e.g., Cantharidae, Cicadidae, Pipunculidae), while the rest were associated with vegetation in the forest canopy (e.g., Argidae and Heliozelidae), in herbaceous vegetation (e.g., Elateridae and Eucnemidae), in leaf litter (e.g., Hemipsocidae and Machilidae), or in the soil (e.g., Mycetophilidae and Nitidulidae). Invasion by *L. maackii* into the forest interior provided a dense, new habitat element within the shrub layer compared to the sparsely distributed and open structure of vegetation in the shrub layer of the native forest. As a consequence, these unique families likely entered this new habitat structure from either strata in the forest above or below the shrub layer or from edge habitats, thereby redistributing patterns of diversity, richness, and abundance of arthropods. Possible reasons for this movement into areas containing *L. maackii* could be related to changes in microclimate, increased food or space resources, or differences in predation pressure (Basset *et al*., 2003). This increase in unique families in honeysuckle-present plots led to our finding increased richness, diversity, and abundance of arthropods in this habitat.

Sax *et al*. (2005) and Rodriguez (2006) concluded that, for both plants and animals in general, increased or unaltered diversity, richness, and abundance of native species in habitats invaded by exotic species indicated that invasive species likely facilitated or had little effect on native species. Higher species richness and abundance, particularly for herbivorous and predatory taxa, in areas with invasive plants can be explained by increased physical space, habitat complexity, or food availability or by a close proximity of invasive plants to native plants (Sanchez and Parmenter, 2002; Herrera and Dudley, 2003; Hartley *et al*., 2004; Langellotto and Denno, 2004; Gratton and Denno 2005). Additionally, arthropods that became established on invasive plant species that were intermixed with native plant species better tolerated invasion and exploited resources or niches offered by invasive plants (Samways *et al*., 1996; Derraik *et al*., 2005; Gratton and Denno, 2005). Compared to species of native shrubs, *L. maackii* increased the complexity of the native vegetation in the shrub layer by providing more individual plants, more stems/plant, and more leaves/plant that were thicker, had a larger surface area, and were retained by the plant for a longer period of time during the year (Luken *et al*., 1997; Trisel, 1997; Deering and Vankat, 1999). These attributes of *L. maackii* could provide a longer-lasting and more diverse microhabitat than leaves of native vegetation for use by leaf-mining insects or arthropods that oviposit on the surfaces of leaves. Furthermore, close proximity of *L. maackii* to native vegetation in our plots may have promoted ephemeral use of resources contained on individual shrubs of *L. maackii* by highly vagile or transient arthropods. For instance, some arthropods may be attracted to this new vegetation layer because it could provide a refuge from predation, an alternative food resource, or a place for resting or sexual display (Moran and Southwood, 1982;

Langellotto and Denno, 2004). These characteristics of *L. maackii* could increase availability of food or habitat and thereby may explain the higher richness and abundance of herbivorous arthropods in areas with *L. maackii*. For example, many leaf-feeding and leaf-mining families identified in our study have been reported feeding on or using other species of *Lonicera* for refuge, reproduction, or habitat space, including Apidae (Hymenoptera), Pentatomidae (Hemiptera), and families of Lepidoptera and Thysanoptera (Johnson, 1984; Waipara *et al*., 2007; Nielsen and Hamilton, 2009). Others have reported that richness and abundance of predatory taxa increases as invasive plant species accumulate a more diverse and abundant assemblage of prey or host taxa (Crooks, 2002; Jukes and Peace, 2003; White *et al*., 2006). Thus, increased richness and abundance of carnivores and parasitoids in honeysuckle-present plots may be explained by higher richness and abundance of prey or host species in these plots. Hence, our results indicated the possibility that *L. maackii* facilitated richness and abundance of arthropods in invaded areas.

Relative abundance of arthropods may better portray changes in overall distribution of individuals among trophic groups caused by the presence of *L. maackii* (MacArthur, 1960; Williams, 1993). While herbivores and carnivores accounted for the largest proportion of individuals in both treatments of honeysuckle, relative abundance of all trophic groups increased equally in honeysuckle-present and honeysuckle-absent plots, except that the relative abundance of detritivores was higher in honeysuckle-present plots (Fig. 5b). In contrast to these results, the relative abundance of herbivores in coastal prairie habitat invaded by *Sapium sebiferum* (Chinese tallow tree) was lower compared to herbivores in native vegetation, while relative abundance of predators was higher (Hartley *et al*., 2004; Cameron and Spencer, 2010). Our finding that relative abundance of detritivores was higher in honeysuckle-present plots reflected 14 families of detritivores that were present in low abundance only in these plots in addition to an increase in abundance of the most abundant families of detritivores (Appendix A). These changes suggested that *L. maackii* provided additional resources for detritivores than were available in the vegetation of the native shrub layer, such as increased availability of food or habitat. Such changes in resource availability likely were caused by the rate of higher stem mortality of *L. maackii* compared to native vegetation (Luken, 1988) that increased the amount of dead wood in areas with *L. maackii*.

In our plots, 18% of All Arthropods were considered specialist feeders, with 18% and 21% in honeysuckle-present and honeysuckle-absent plots, respectively; this value was relatively low compared to studies from forest and agricultural habitats (5-61% specialist taxa; Futuyma and Gould, 1979; Andow and Imura, 1994). In many studies, invasion by exotic plants, with a concomitant loss of native species of host plants or host prey, resulted in loss of or reduction in richness, diversity, and abundance of specialist species of arthropods (Hartley *et al*., 2004; Gratton and Denno, 2005; Heleno *et al*., 2009; Carvalheiro *et al*., 2010). Alternatively, Memmott *et al*. (2000) suggested that abundance of specialist parasitoids increased as invasive plant species accumulated more individuals of herbivorous arthropod hosts. We also found that richness and abundance of families of arthropods which were dietary specialists, primarily including parasitoids and herbivores, were higher in honeysuckle-present plots than in honeysuckle-absent plots, and 4 of these families were unique to honeysuckle-present plots (Table 4). Because *L. maackii* produced more photosynthetic tissues than species of native shrubs (Luken *et al*., 1997), *L. maackii* may have provided increased architectural diversity that may explain the increased richness and abundance of specialist families of herbivores in plots where honeysuckle was present. Although it was unlikely that these specialist herbivores fed on alternative food resources provided by *L. maackii*, increases in arthropod host taxa in honeysuckle-present plots may have resulted in increased richness and abundance of specialist parasitoids.

Shrub layer diversity and cover. Some studies reported a reduction in diversity and richness of native shrubs and seedlings of canopy trees that comprised the shrub layers of forests after invasion by *L. maackii*, with further reduction with time since invasion (Collier *et al.*, 2002; Gorchov and Trisel, 2003). In our study, however, *L. maackii* did not affect diversity, richness, or evenness of woody vegetation in the shrub layer. Since *L. maackii* in our stands was older (>33 years; C. Christopher, *personal communication*) than in stands studied by Collier *et al.* (2002) (16 years), it was likely that any changes in richness and density affected by stand age had already occurred.

Vertical cover of vegetation in the shrub layer was higher in honeysuckle-present plots than in honeysuckle-absent plots. In contrast to the response by the native shrub *L. benzoin* in the low-light environment of the forest understory, *L. maackii* allocated more energy to stem and leaf growth than to root growth (Luken *et al*., 1997). This response resulted in a rapid increase in leaf area, leaf thickness, and growth of stems by *L. maackii*, which increased both biomass and cover in the invaded shrub layer (Luken, 1988; Luken *et al*., 1997; Deering and Vankat, 1999). Additionally, overall cover of the shrub layer increased as density of individual shrubs of *L. maackii* increased. In some forests invaded by *L. maackii*, density of the invaded shrub layer increased to more than 100 times the densities of native *L. benzoin* (Gorchov, 2005).

Shrub layer effects on arthropod taxa and trophic groups. In contrast to our prediction, diversity of shrub layer vegetation did not differ between treatments of honeysuckle and did not affect diversity or abundance of arthropods. This finding agreed with some studies (Koricheva *et* *al*., 2000; Longcore, 2003), but not others which found that diversity, richness, and abundance of arthropod taxa decreased with a decrease in diversity of native plants in areas invaded by exotic plant species (Siemann *et al*., 1999; Tilman, 1999).

Our alternative prediction that increased vertical cover afforded by *L. maackii* would increase abundance and diversity of arthropod taxa and trophic groups was supported only for the abundance of spiders (Table 5). *Lonicera mackkii* provided more vegetative substrate upon which individual spiders could build webs and hunt for prey (Fig. 2), as evidenced by increased abundance of both web-building (e.g., Araneidae, Linyphiidae, and Theridiidae), and hunting (e.g., Anyphaenidae, Clubionidae, Salticidae, and Thomisidae) families of spiders in honeysuckle-present plots (Appendix A). Other studies showed the importance of vegetative cover and habitat structure to diversity and abundance of spiders (Hatley and MacMahon, 1980; Uetz, 1991; Corcuera *et al*., 2008), and increased diversity and abundance of spiders in areas with exotic plant species that provided a structurally diverse habitat (Sanchez and Parmenter, 2002; Kjar and Barrows, 2004).

Independent of an increase in vegetative cover, the presence of *L. maackii* in native habitats explained increased richness of detritivores, Psocoptera, and Coleoptera, and abundance of Psocoptera in honeysuckle-present plots (Table 5; Table 6). Detritivores, particularly Psocoptera and Coleoptera, that fed on and lived on bark and dead foliage within the shrub layer (Mockford, 1930), may have responded to increased quantities of dead wood available as food or habitat (Jukes and Peace, 2003; Harris *et al*., 2004) afforded by *L. maackii*, which had a higher rate of stem mortality than native *L. benzoin* (Luken, 1998; Deering and Vankat, 1999). Furthermore, herbivorous Coleoptera may have used *L. maackii* as a food resource, while carnivorous Coleoptera may have responded to an increased availability of prey in honeysuckle-present plots. These responses also may explain the increased richness of predatory Coleoptera in the presence of *L. maackii*. Similarly, increased richness of predatory Coleoptera also was observed in habitats invaded by the exotic shrub *Ulex europaeus* in New Zealand (Harris *et al*., 2004). Detritivores and these other taxa also could have responded to increased humidity or less variation in humidity and air temperature in microhabitats where *L. maackii* was present (Hickman *et al*., 2009).

Variation in richness of parasitoids and Hymenoptera between paired plots also was explained by presence of honeysuckle (Table 5; Table 6). *L. maackii* may have benefited these groups by harboring higher abundance and richness of arthropod hosts. Other studies have established that such indirect facilitation of predators and parasitoids occurred when invasive plant species accumulated higher richness and abundance of herbivorous arthropod hosts (Memmott *et al*., 2000; Sax *et al*., 2005; Rodriguez, 2006 White *et al*. 2006). Families of Hymenoptera, such as Braconidae, Eulophidae, and Ichneumonidae, parasitize Psocoptera, Lepidoptera, Cecidomyidae (Diptera), and Curculionidae (Coleoptera) (Mockford, 1930; Askew and Shaw, 1974; Yefremova and Mistchenko, 2009), all taxa which were more abundant in honeysuckle-present plots (Appendix A). Additionally, many species of parasitoids fed on flowers and leaves of plants as adults (Triplehorn and Johnson, 2005), and some parasitoid families occupied cavities and galls abandoned by leaf-mining larvae, such as Cerambycidae (Coleoptera) (Georgiev *et al*., 2004). *Lonicera maackii* may have provided such food or habitat resources which also would explain increased richness of parasitoids and Hymenoptera in the presence of honeysuckle.

Increased richness of the orders Hemiptera and Diptera and the trophic groups herbivores and carnivores in addition to the abundance of the orders Diptera and Hymenoptera in honeysuckle-present plots was not explained by either vertical cover or presence of *L. maackii* (Table 5; Table 6). Lack of response by carnivores to either vertical cover or presence of honeysuckle further suggested that these families likely responded to increased prey abundance in honeysuckle-present plots. The lack of response to cover or presence of honeysuckle was unexpected for Hemiptera and other herbivores because larger, more structurally complex plants, evident in areas invaded by *L. maackii,* increased habitat heterogeneity and supported more herbivorous arthropods than smaller, less complex plants (Crooks, 2002; Rodriguez, 2006; Samways *et al*., 2006). Our measures of vertical cover may not have been adequate to detect responses of these arthropods to changes in architectural complexity or structural diversity, such as differences in quantity of individual leaves and stems or physical characteristics of the surface structure of vegetation (i.e., thickness of leaves and bark, diameter of stems, and roughness of bark). Alternatively, these taxa may have responded to changes in microclimate (e.g., changes in temperature, humidity, light availability, or wind speed) in dense stands of *L. maackii* rather than directly to increased vertical cover or presence of honeysuckle.

Conclusions. Management of invasive plant species is both time-consuming and expensive, and complete eradication of an invasive species is difficult to achieve and could have unexpected or harmful impacts on the native community (Samways *et al*., 1996; Zavaleta *et al*., 2001; Longcore, 2003; Sax *et al*., 2005). For these reasons, it is useful to consider the impacts, both negative and positive, of an invasive plant species on native plant and animal species at the ecosystem level to guide eradication strategies. Our results indicated that *L. maackii* provided additional habitat space or food resources for both generalist and specialist arthropods and that the positive response of most arthropods to presence of *L. maackii* suggested a direct or indirect facilitation of the arthropod community by this invasive shrub. While occurrence of *L. maackii* positively impacted the arthropod community, *L. maackii* negatively impacted richness and abundance of native forest vegetation at the ground level, primarily herbaceous plants and tree seedlings (Hutchinson and Vankat, 1997; Collier *et al*., 2002). Depression of native vegetation by the continued establishment of dense thickets of *L. maackii* into uninvaded forests could alter succession or nutrient cycling (Collier *et al*., 2002) or facilitate invasion by other exotic plants (Crooks, 2002), which could, over time, reverse the facilitative effects of *L. maackii* on arthropods that depend on the diversity and structure of the vegetation at the current level of invasion. Thus, negative impacts on native vegetation caused by *L. maackii* invasion may cascade throughout the local forest ecosystem if measures are not taken to prevent its further spread. Although the present level of invasion by *L. maackii* in the forest understory in southwestern Ohio is beneficial to the arthropod community, which could, in turn, benefit insectivorous organisms, management to prevent further spread of *L. maackii* into uninvaded areas is necessary to preserve native plant diversity and to maintain the ecological processes of local forests. However, complete eradication of this invasive shrub may not be required.

Table 1. Geographic description of paired plots at each study location. Sites are listed by name of metropolitan or state park from west to east across the Cincinnati metropolitan area. asl = above sea level.

	Honeysuckle-Present Plot			Honeysuckle-Absent Plot		
Study location	GPS coordinates	Elevation (m asl)	Aspect	GPS coordinates	Elevation (m asl)	Aspect
Miami Whitewater Forest	N39°15'47.7" W084°44'17.6"	228	South	N39°15'46.8" W084°44'17.5"	225	South
Mt. Airy Forest	N39°10'12.9" W084°33'44.5"	245	South	N39°10'14.7" W084°33'57.5"	255	North
Caldwell Preserve	N39°12'09.4" W084°29'25.4"	193	None	N39°12'08.1" W084°29"19.5"	193	None
Bradford-Felter/Tanglewood Preserve	N39°11'11.2" W084°33'25.0"	233	Southwest	N39°11'10.6" W084°33'24.2"	240	Southwest
Buttercup Valley Preserve	N39°10'22.7" W084°32'20.0"	222	Northeast	N39°10'26.6" W084°32'17.7"	190	Northeast
French Park	N39°11'59.3" W084°25'16.7	234	Northwest	N39°12'01.5" W084°25'06.1"	249	Northwest
Benedict Preserve	N39°15'42.3" W084°21'18.6"	254	None	N39°15'47.5" W084°21'17.9"	265	None
Ault Park	N39°08'11.3" W084°24'37.5"	198	Northeast	N39°08'07.9" W084°24'52.3"	208	Northeast
Cincinnati Nature Center	N39°07'40.0" W084°15'08.2"	219	Northwest	N39°07'36.3" W084°15'04.2"	230	Northwest
East Fork Lake State Park	N39°01'27.9" W084°05'04.0"	264	None	N39°01'18.9" W084°05'07.8"	262	None

Table 2. Number of arthropod families (mean abundance ± SE) captured in 3-m^2 plots common to both honeysuckle-present and honeysuckle-absent treatments (n = 20 plots) and unique to each treatment (n = 10 plots for each treatment). Total = overall mean abundance of arthropod families n = 20 plots). Mean abundance can be converted to total abundance by multiplying by sample size (n). Orders are arranged from most to least number of families within each arthropod category.

			Families unique to		
Category	Order	Common families	Honeysuckle-present	Honeysuckle-absent	Total
Hexapoda	Hymenoptera	15 (26.2 ± 3.9)	6 (1.2 ± 0.5)	5 (0.6 ± 0.3)	26 (27.1 ± 4.1)
	Coleoptera	11 (14.3 ± 3.1)	10 (4.7 ± 1.5)	3 (0.3 ± 0.2)	24 (16.8 ± 3.2)
	Hemiptera	12 (27.6 ± 5.7)	5 (2.3 ± 1.2)	2 (0.4 ± 0.3)	19 (28.9 ± 6.2)
	Diptera	12 (14.6 ± 3.0)	4 (0.6 ± 0.2)	3 (0.6 ± 0.3)	19 (15.2 ± 3.0)
	Psocoptera	3 (15.8 ± 4.6)	1 (0.2 ± 0.1)	0	4 (15.9 ± 4.6)
	Collembola	2 (3.2 ± 1.0)	1 (0.1 ± 0.1)	1 (0.1 ± 0.1)	4 (3.5 ± 1.0)
	Orthoptera	1 (3.2 ± 0.7)	2 (0.2 ± 0.1)	0	3 (3.3 ± 0.7)
	Thysanoptera	2 (4.4 ± 1.0)	0	0	2 (4.4 ± 1.0)
	Microcoryphia	0	2 (0.4 ± 0.2)	0	2 (0.2 ± 0.1)
	Phthiraptera	0	1 (0.4 ± 0.4)	0	1 (0.2 ± 0.2)
	Neuroptera	1 (0.15 ± 0.1)	0	0	1 (0.15 ± 0.1)
	Lepidoptera	0	1 (0.2 ± 0.1)	0	1 (0.1 ± 0.07)
	Phasmatodea	0	1 (0.1 ± 0.1)	0	1 (0.05 ± 0.05)
	Thysanura	0	0	1 (0.1 ± 0.1)	1 (0.05 ± 0.05)
	Trichoptera	0	1 (0.1 ± 0.1)	0	1 (0.05 ± 0.05)
Spiders	Araneae	10 (29.8 ± 4.1)	2 (0.3 ± 0.1)	1 (0.1 ± 0.1)	13 (30.0 ± 4.2)
Others	Acari	3 (8.1 ± 2.9)	0	0	3 (8.1 ± 2.9)
	Opiliones	1 (4.5 ± 1.7)	0	0	1 (4.5 ± 1.7)
Total	18	73 (151.6 ± 20.5)	37 (10.8 ± 2.7)	16 (2.2 ± 0.6)	126 (158.5 ± 21.8)

Table 3. Mean (± SE) values of community characteristics of orders of Hexapoda with abundance > 10 individuals/plot in 3-m^2 honeysuckle-present and honeysuckle-absent plots. t = value of t-test; df = degrees of freedom; * indicates p-values that were statistically significant.

Community Characteristic	Order	Honeysuckle Present	Honeysuckle Absent	t-value	df	p-value
Shannon Diversity (H')	Coleoptera	1.5 ± 0.1	0.80 ± 0.2	-5.92	9	0.0001*
	Diptera	1.2 ± 0.2	1.0 ± 0.2	-0.88	9	0.2
	Hemiptera	1.4 ± 0.1	1.3 ± 0.1	-0.8	9	0.22
	Hymenoptera	1.7 ± 0.2	1.6 ± 0.06	-1.12	9	0.15
	Psocoptera	0.98 ± 0.07	0.63 ± 0.1	-2.8	9	0.01*
Richness (S)	Coleoptera	6.9 ± 0.6	3.2 ± 0.5	-5.84	9	0.0001*
	Diptera	5.2 ± 0.7	3.8 ± 0.6	-1.87	9	0.047*
	Hemiptera	6.8 ± 1.0	5.2 ± 0.6	-1.78	9	0.05*
	Hymenoptera	9.5 ± 0.8	6.8 ± 0.7	-2.28	9	0.024*
	Psocoptera	3.1 ± 0.2	2.2 ± 0.3	-2.89	9	0.016*
Evenness (E)	Coleoptera	0.80 ± 0.05	0.78 ± 0.08	0.041	8	0.48
	Diptera	0.78 ± 0.08	0.88 ± 0.03	1.75	8	0.06
	Hemiptera	0.79 ± 0.03	0.83 ± 0.05	0.63	9	0.27
	Hymenoptera	0.76 ± 0.06	0.84 ± 0.03	1.38	9	0.1
	Psocoptera	0.87 ± 0.03	0.88 ± 0.07	0.14	7	0.45
Mean Abundance	Coleoptera	21.5 ± 4.5	12.0 ± 4.4	-1.64	9	0.068
	Diptera	20.0 ± 5.4	10.3 ± 2.2	-2.34	9	0.022*
	Hemiptera	37.5 ± 11.3	20.3 ± 4.3	-1.49	9	0.085
	Hymenoptera	36.3 ± 6.4	17.8 ± 3.3	-2.17	9	0.029*
	Psocoptera	26.1 ± 8.0	5.7 ± 1.4	-4.23	9	0.0011*

Table 4. Abundance (mean ± SE) of arthropod families that were dietary specialists sampled in 3-m^2 honeysuckle-present and honeysuckle-absent plots. Food habitats of arthropods were obtained from Triplehorn and Johnson (2005) and from review of the primary literature.

			Trophic	Honeysuckle	
Class	Order	Family	group	Present	Absent
Arachnida	Acari	Ixodidae	Parasite	1.2 ± 0.6	0.5 ± 0.2
Hexapoda	Coleoptera	Chrysomelidae	Herbivore	1.8 ± 0.6	0.5 ± 0.3
		Corylophidae	Detritivore	0.3 ± 0.2	0.3 ± 0.2
		Curculionidae	Herbivore	1.2 ± 0.3	0.8 ± 0.3
	Diptera	Corethrellidae	Parasitoid	0	0.2 ± 0.2
		Phoridae	Detritivore	8.3 ± 4.4	4.0 ± 0.9
		Pipunculidae	Parasitoid	0.2 ± 0.1	0
	Hemiptera	Aphididae	Herbivore	2.2 ± 1.6	4.2 ± 2.4
		Cicadellidae	Herbivore	8.5 ± 1.6	6.6 ± 1.8
		Psyllidae	Herbivore	0.9 ± 0.7	0.4 ± 0.2
	Hymenoptera	Aphelinidae	Parasitoid	0.4 ± 0.2	0.1 ± 0.1
		Braconidae	Parasitoid	1.6 ± 0.4	1.5 ± 0.5
		Chrysididae	Parasitoid	0	0.1 ± 0.1
		Cimbicidae	Herbivore	0.1 ± 0.1	0
		Diapriidae	Parasitoid	1.6 ± 0.6	1.2 ± 0.4
		Figitidae	Parasitoid	3.8 ± 0.6	2.3 ± 0.9
		Ichneumonidae	Parasitoid	1.8 ± 0.5	1.3 ± 0.4
		Orussidae	Parasitoid	0.1 ± 0.1	0
		Platygastridae	Parasitoid	0.5 ± 0.3	0.2 ± 0.1
		Pompilidae	Carnivore	0.1 ± 0.1	0.1 ± 0.1
		Scelionidae	Parasitoid	1.1 ± 0.4	0.2 ± 0.1
		Xyelidae	Herbivore	0	0.1 ± 0.1
	Phthiraptera	Linognathidae	Parasitoid	0.4 ± 0.4	0
			Total	36.1 ± 4.7	24.6 ± 4.3

Table 5. ANCOVA results for richness (S) and abundance of those orders of arthropods that significantly differed between honeysuckle-present and honeysuckle-absent plots when analyzed with paired t-tests. df = degrees of freedom, SS = sum of squares; F = value of F-test; * indicates p-values that were statistically significant.

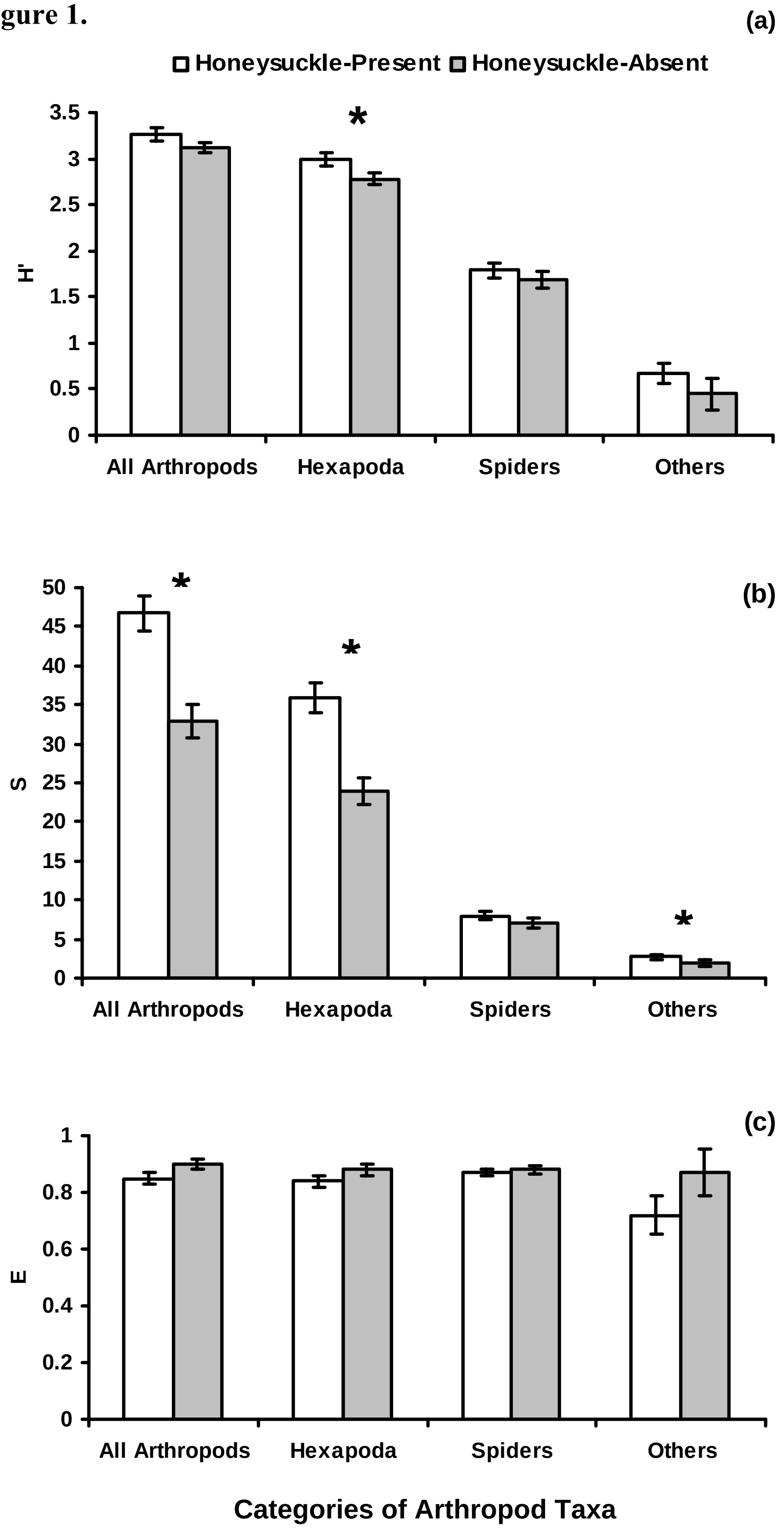
Response Variable	Source	df	Model SS	Mean Square	F	p-value
Coleoptera S	Cover	1	0.459	0.459	0.150	0.704
	Honeysuckle	1	23.879	23.879	7.800	0.013*
	Error	17	52.041	3.061		
	Total	19	120.950			
	R^2Adjusted = 0.519					
Diptera S	Cover	1	4.853	4.853	1.282	0.273
	Honeysuckle	1	0.140	0.140	0.037	0.850
	Error	17	64.347	3.785		
	Total	19	79.000			
	R^2 Adjusted = 0.090					
Hemiptera S	Cover	1	14.271	14.271	2.556	0.128
	Honeysuckle	1	0.278	0.278	0.050	0.826
	Error	17	94.929	5.584		
	Total	19	122.000			
	R^2 Adjusted = 0.130					
Hymenoptera S	Cover	1	10.442	10.442	1.895	0.187
	Honeysuckle	1	40.815	40.815	7.408	0.015*
	Error	17	93.658	5.509		
	Total	19	140.550			
	R^2 Adjusted = 0.255					
Psocoptera S	Cover	1	0.941	0.941	2.117	0.164
	Honeysuckle	1	4.200	4.200	9.439	0.007*
	Error	17	7.559	0.445		
	Total	19	12.550			
	R^2 Adjusted = 0.327					
Diptera Abundance	Cover	1	0.933	0.933	1.147	0.299
	Honeysuckle	1	0.066	0.066	0.081	0.780
	Error	17	13.840	0.814		
	Total	19	17.068			
	R^2 Adjusted = 0.094					
Hymenoptera Abundance	Cover	1	0.012	0.012	0.048	0.830
	Honeysuckle	1	0.986	0.986	4.028	0.061
	Error	17	4.163	0.245		
	Total	19	6.888			
	R^2 Adjusted = 0.325					

Psocoptera Abundance	Cover	1	0.575	0.575	1.016	0.328
	Honeysuckle	1	2.813	2.813	4.970	0.040*
	Error	17	9.621	0.566		
	Total	19	22.096			
	R^2 Adjusted = 0.513					
Araneae Abundance	Cover	1	1.552	1.552	6.648	0.020*
	Honeysuckle	1	0.000129	0.000129	0.001	0.982
	Error	17	3.968	0.233		
	Total	19	7.661			
	R^2 Adjusted = 0.421					

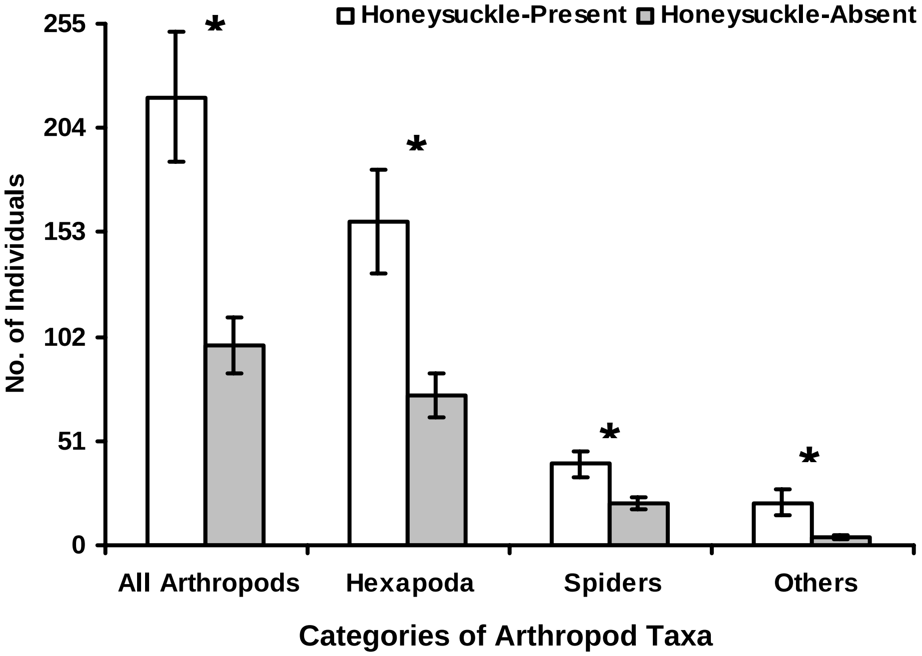
Table 6. ANCOVA results for richness (S), evenness (E), and relative abundance of those trophic groups that significantly differed between honeysuckle-present and honeysuckle-absent plots when analyzed with paired t-tests. df = degrees of freedom, SS = sum of squares; F = value of F-test; * indicates p-values that were statistically significant.

Response Variable	Source	df	Model SS	Mean Square	F	p-value
Carnivore S	Cover	1	6.192	6.192	0.844	0.371
	Honeysuckle	1	1.756	1.756	0.239	0.631
	Error	17	124.808	7.342		
	Total	19	155.200			
	R^2 Adjusted = 0.101					
Detritivore S	Cover	1	0.002	0.002	0.001	0.983
	Honeysuckle	1	22.118	22.118	5.530	0.031*
	Error	17	67.998	4.000		
	Total	19	119.200			
	R^2 Adjusted = 0.362					
Herbivore S	Cover	1	17.115	17.115	1.677	0.213
	Honeysuckle	1	28.409	28.409	2.784	0.114
	Error	17	173.485	10.205		
	Total	19	358.800			
	R^2 Adjusted = 0.460					
Parasitoid S	Cover	1	8.488	8.488	2.449	0.136
	Honeysuckle	1	36.021	36.021	10.394	0.005*
	Error	17	58.912	3.465		
	Total	19	101.200			
	R^2 Adjusted = 0.349					
Detritivore E	Cover	1	0.003	0.003	0.503	0.488
	Honeysuckle	1	0.018	0.018	3.162	0.093
	Error	17	0.095	0.006		
	Total	19	0.169			
	R^2 Adjusted = 0.369					
Relative Abundance of Detritivores	Cover	1	0.016	0.016	1.808	0.196
	Honeysuckle	1	0.038	0.038	4.331	0.053
	Error	17	0.149	0.009		
	Total	19				
	R^2 Adjusted = 0.115					

Figure 1.


(a)
□ Honeysuckle-Present ▨ Honeysuckle-Absent
H'
3.5
3
2.5
2
1.5
1
0.5
0
*
All Arthropods
Hexapoda
Spiders
Others
(b)
S
50
45
40
35
30
25
20
15
10
5
0
*
*
*
All Arthropods
Hexapoda
Spiders
Others
(c)
E
1
0.8
0.6
0.4
0.2
0
All Arthropods
Hexapoda
Spiders
Others
Categories of Arthropod Taxa

566 **Figure 2.**



567

Figure 3.

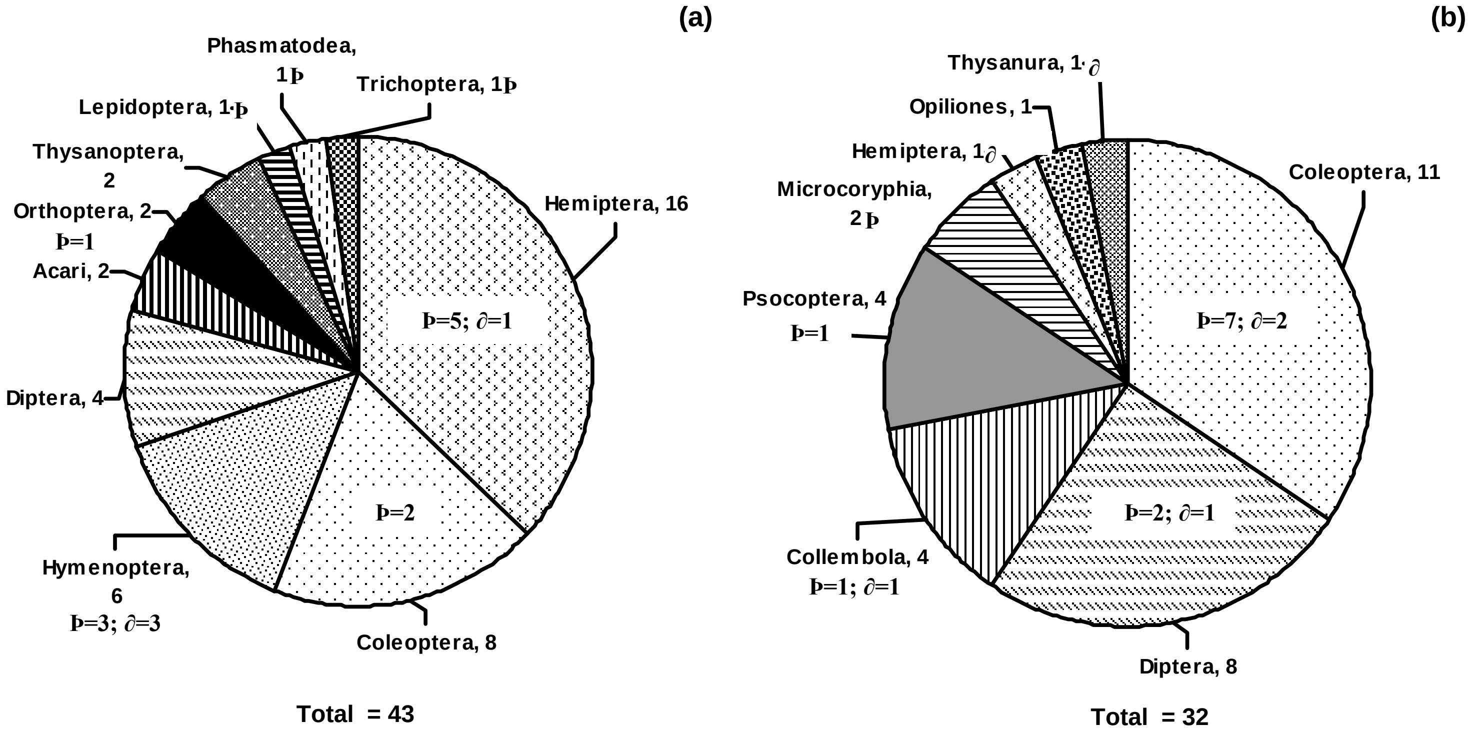

(a)
Phasmatodea, 1Þ
Trichoptera, 1Þ
Lepidoptera, 1Þ
Thysanoptera, 2
Orthoptera, 2 Þ=1
Acari, 2
Hemiptera, 16
Þ=5; ∂=1
Diptera, 4
Þ=2
Hymenoptera, 6 Þ=3; ∂=3
Coleoptera, 8
Total = 43
(b)
Thysanura, 1 ∂
Opiliones, 1
Hemiptera, 1∂
Microcoryphia, 2 Þ
Coleoptera, 11
Psocoptera, 4 Þ=1
Þ=7; ∂=2
Þ=2; ∂=1
Collembola, 4 Þ=1; ∂=1
Diptera, 8
Total = 32

Figure 3. (cont'd)

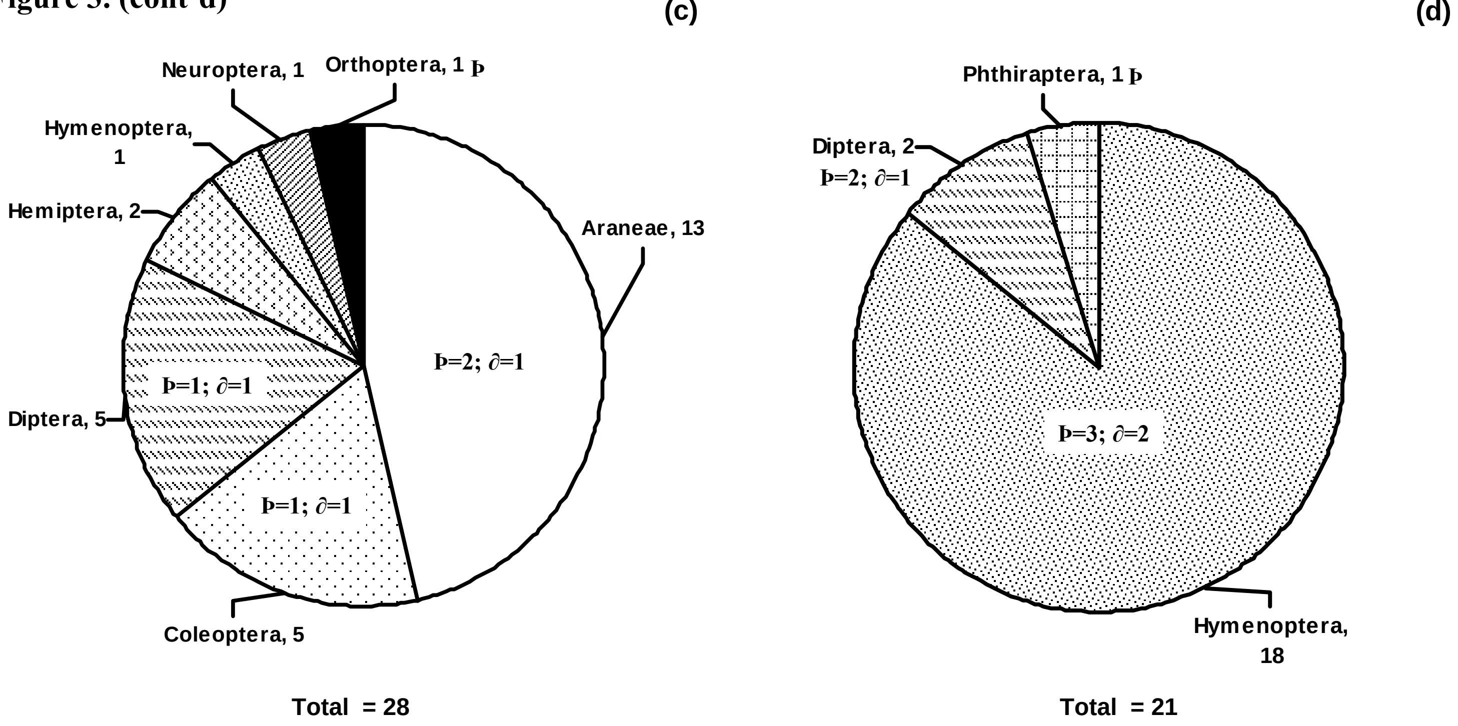


Figure 4.

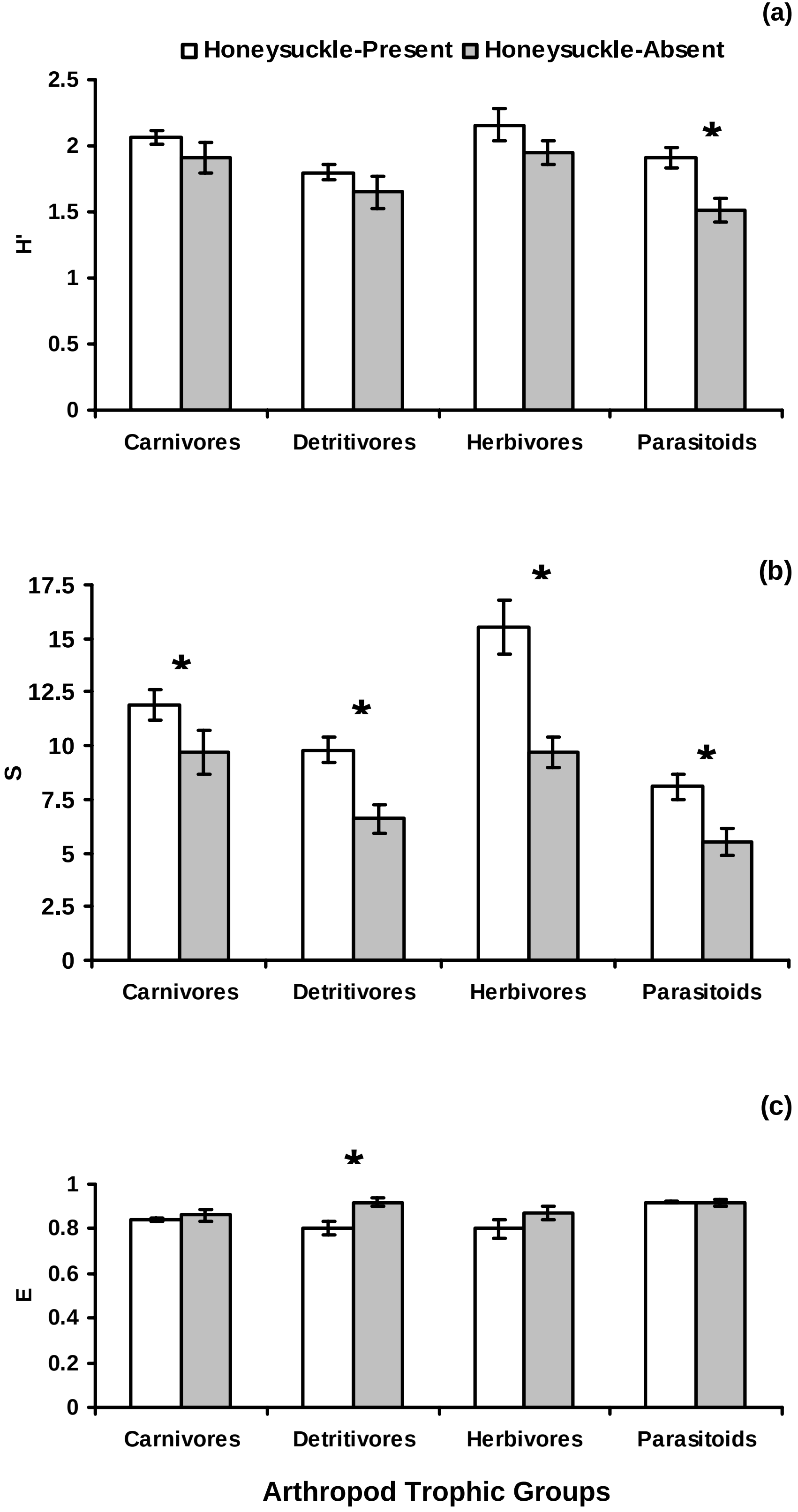
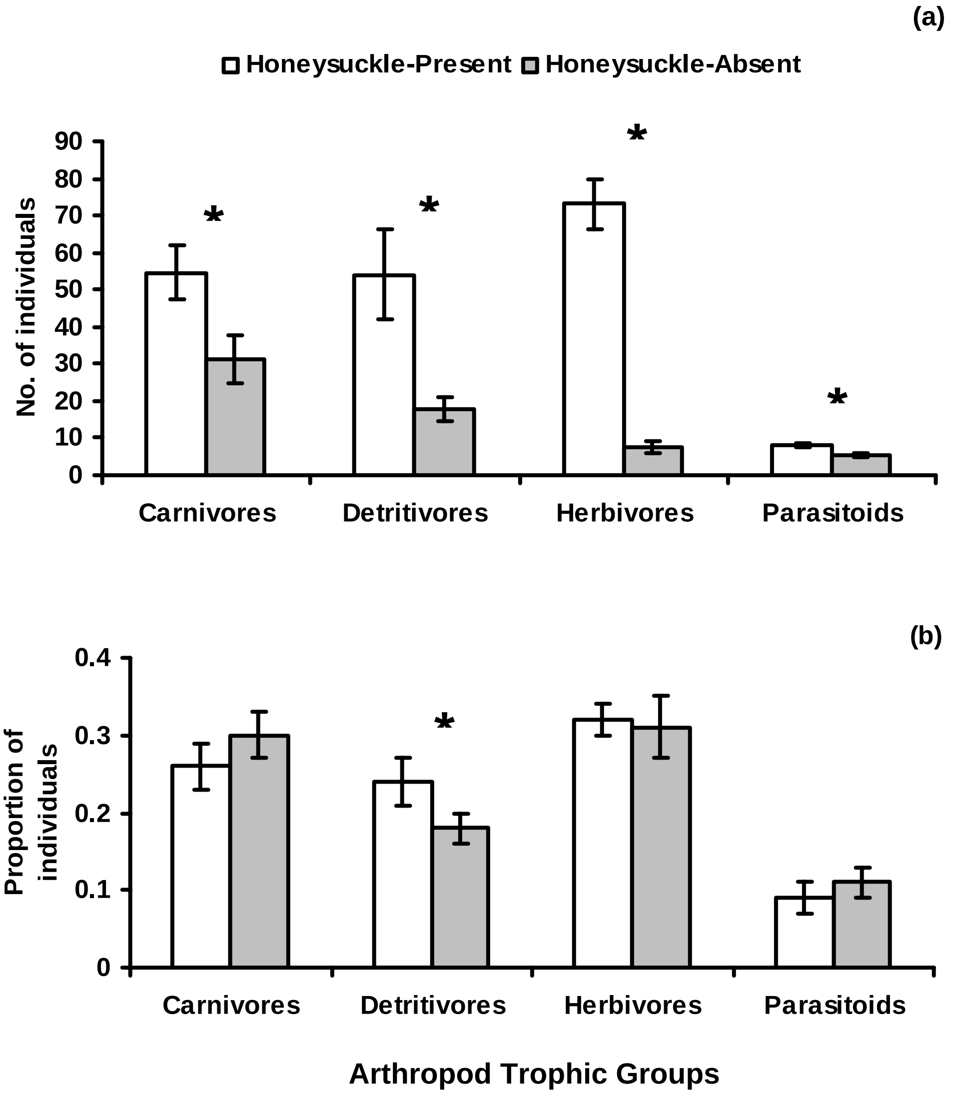

(a)
☐ Honeysuckle-Present ▨ Honeysuckle-Absent
H'
2.5
2
1.5
1
0.5
0
*
Carnivores
Detritivores
Herbivores
Parasitoids
(b)
S
17.5
15
12.5
10
7.5
5
2.5
0
*
*
*
*
Carnivores
Detritivores
Herbivores
Parasitoids
(c)
E
1
0.8
0.6
0.4
0.2
0
*
Carnivores
Detritivores
Herbivores
Parasitoids
Arthropod Trophic Groups

Figure 5.


(a)
□ Honeysuckle-Present ▨ Honeysuckle-Absent
No. of individuals
90
80
70
60
50
40
30
20
10
0
*
*
*
*
Carnivores
Detritivores
Herbivores
Parasitoids
(b)
Proportion of individuals
0.4
0.3
0.2
0.1
0
*
Carnivores
Detritivores
Herbivores
Parasitoids
Arthropod Trophic Groups

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Appendix A. Trophic group, mean abundance (±SE) of families of arthropods collected in honeysuckle-present and honeysuckle-absent plots (n = 10, 3-m^2 plots), and mean total abundance (n = 20, 3-m^2 plots). Absolute abundance can be computed by multiplying mean abundances by sample size (n = 10 or 20 plots). Suborder Prostigmata (order Acari) were identified to morphofamily. Taxonomy and trophic classifications follow Triplehorn and Johnson (2005) and Ubick *et al*. (2005). Taxa which are dietary specialists are listed in Table 4

Class	*Order*	*Family*	*Trophic group*	*Honeysuckle*		*Total*
				Present	*Absent*	
Arachnida	Acari	Ixodidae	Parasite	1.2 ± 0.6	0.5 ± 0.2	0.9 ± 0.3
		Prostigmata 1	Herbivore	10.5 ± 5.2	2.0 ± 0.6	6.3 ± 2.7
		Prostigmata 2	Herbivore	1.7 ± 0.7	0.2 ± 0.1	1.0 ± 0.4
	Araneae	Anyphaenidae	Carnivore	7.9 ± 1.7	4.0 ± 1.2	6.0 ± 1.1
		Araneidae	Carnivore	9.2 ± 2.6	3.8 ± 0.9	6.5 ± 1.5
		Clubionidae	Carnivore	4.9 ± 1.6	2.2 ± 0.9	3.6 ± 1.0
		Linyphiidae	Carnivore	1.7 ± 0.5	1.4 ± 0.4	1.6 ± 0.3
		Lycosidae	Carnivore	0	0.1 ± 0.1	0.05 ± 0.05
		Miturgidae	Carnivore	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.07
		Oxyopidae	Carnivore	0.1 ± 0.1	0	0.05 ± 0.05
		Philodromidae	Carnivore	1.7 ± 0.3	1.6 ± 0.5	1.7 ± 0.3
		Pisauridae	Carnivore	2.1 ± 0.6	1.6 ± 0.4	1.9 ± 0.4
		Salticidae	Carnivore	4.9 ± 1.5	0.9 ± 0.3	2.9 ± 0.9
		Tetragnathidae	Carnivore	0.2 ± 0.2	0	0.1 ± 0.1
		Theridiidae	Carnivore	1.8 ± 0.6	1.2 ± 0.6	1.5 ± 0.4
		Thomisidae	Carnivore	5.1 ± 0.6	3.4 ± 0.8	4.3 ± 0.5
	Opiliones	Phalangiidae	Detritivore	7.5 ± 3.1	1.4 ± 0.7	4.5 ± 1.7
Hexapoda	Coleoptera	Agyrtidae	Detritivore	0.1 ± 0.1	0	0.05 ± 0.05
		Anobiidae	Herbivore	0.5 ± 0.3	0.3 ± 0.2	0.4 ± 0.2
		Bostrichidae	Herbivore	0.2 ± 0.1	0.7 ± 0.6	0.5 ± 0.3
		Cantharidae	Carnivore	1.0 ± 0.4	0	0.5 ± 0.2
		Carabidae	Carnivore	0.6 ± 0.4	0.1 ± 0.1	0.4 ± 0.2
		Cerambycidae	Herbivore	0.6 ± 0.3	0.1 ± 0.1	0.4 ± 0.2
		Ceratocanthidae	Detritivore	0.3 ± 0.2	0	0.2 ± 0.1
		Chrysomelidae	Herbivore	1.8 ± 0.6	0.5 ± 0.3	1.2 ± 0.4
		Coccinellidae	Carnivore	0.3 ± 0.2	0.4 ± 0.2	0.4 ± 0.2
		Corylophidae	Detritivore	0.3 ± 0.2	0.3 ± 0.2	0.3 ± 0.1
		Cupedidae	Detritivore	0	0.1 ± 0.1	0.05 ± 0.05
		Curculionidae	Herbivore	1.2 ± 0.3	0.8 ± 0.3	1.0 ± 0.2
		Elateridae	Detritivore	0.6 ± 0.4	0	0.3 ± 0.2
		Eucnemidae	Detritivore	0.2 ± 0.1	0	0.1 ± 0.07
		Lampyridae	Carnivore	0	0.1 ± 0.1	0.05 ± 0.05
		Latridiidae	Detritivore	1.3 ± 0.7	0.1 ± 0.1	0.7 ± 0.4
		Mordellidae	Herbivore	0.9 ± 0.3	0.8 ± 0.5	0.9 ± 0.3
		Nitidulidae	Detritivore	0.7 ± 0.6	0	0.4 ± 0.3

	Phalacridae	Herbivore	1.1 ± 0.9	0	0.6 ± 0.5
	Pyrochroidae	Detritivore	0	0.1 ± 0.1	0.05 ± 0.05
	Scarabaeidae	Detritivore	0.5 ± 0.5	0	0.3 ± 0.3
	Scirtidae	Herbivore	0.1 ± 0.1	0	0.05 ± 0.05
	Staphylinidae	Carnivore	9.1 ± 4.0	7.6 ± 4.2	8.4 ± 2.8
	Tenebrionidae	Detritivore	0.1 ± 0.1	0	0.05 ± 0.05
Collembola	Entomobryidae	Detritivore	3.5 ± 1.8	2.6 ± 0.9	3.1 ± 1.0
	Hypogastruridae	Detritivore	0	0.1 ± 0.1	0.05 ± 0.05
	Isotomidae	Detritivore	0.4 ± 0.2	0.2 ± 0.1	0.3 ± 0.1
	Onychiuridae	Detritivore	0.1 ± 0.1	0	0.05 ± 0.05
Diptera	Asilidae	Carnivore	0.1 ± 0.1	0	0.05 ± 0.05
	Cecidomyiidae	Herbivore	0.4 ± 0.4	0.1 ± 0.1	0.3 ± 0.2
	Chironomidae	Herbivore	4.6 ± 1.9	1.9 ± 1.0	3.3 ± 1.1
	Corethrellidae	Parasitoid	0	0.2 ± 0.2	0.1 ± 0.1
	Culicidae	Herbivore	0.3 ± 0.2	0.1 ± 0.1	0.2 ± 0.1
	Dixidae	Detritivore	0.3 ± 0.3	0.1 ± 0.1	0.2 ± 0.2
	Dolichopodidae	Carnivore	0.8 ± 0.2	0.1 ± 0.1	0.5 ± 0.2
	Empididae	Carnivore	0.1 ± 0.1	0.5 ± 0.2	0.3 ± 0.1
	Heleomyzidae	Detritivore	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.07
	Lonchopteridae	Detritivore	0.1 ± 0.1	0.2 ± 0.2	0.2 ± 0.1
	Muscidae	Detritivore	0.2 ± 0.1	0	0.1 ± 0.07
	Mycetophilidae	Detritivore	0.1 ± 0.1	0	0.05 ± 0.05
	Phoridae	Detritivore	8.3 ± 4.4	4.0 ± 0.9	6.2 ± 2.3
	Pipunculidae	Parasitoid	0.2 ± 0.1	0	0.1 ± 0.07
	Rhagionidae	Carnivore	0.2 ± 0.2	0.3 ± 0.2	0.3 ± 0.1
	Sciaridae	Detritivore	2.8 ± 0.7	2.0 ± 0.6	2.4 ± 0.4
	Sciomyzidae	Carnivore	0	0.1 ± 0.1	0.05 ± 0.05
	Tephritidae	Herbivore	1.4 ± 0.5	0.3 ± 0.2	0.9 ± 0.3
	Tipulidae	Detritivore	0	0.3 ± 0.2	0.2 ± 0.1
Hemiptera	Acanaloniidae	Herbivore	0.3 ± 0.2	0.3 ± 0.2	0.3 ± 0.1
	Acanthosomatidae	Herbivore	0.3 ± 0.2	0.6 ± 0.3	0.5 ± 0.2
	Aphididae	Herbivore	2.2 ± 1.6	4.2 ± 2.4	3.2 ± 1.4
	Aradidae	Detritivore	0	0.3 ± 0.2	0.2 ± 0.1
	Berytidae	Herbivore	0.4 ± 0.3	0	0.2 ± 0.1
	Cicadellidae	Herbivore	8.5 ± 1.6	6.6 ± 1.8	7.6 ± 1.2
	Cicadidae	Herbivore	0.7 ± 0.3	0	0.4 ± 0.2
	Coreidae	Herbivore	0.1 ± 0.1	0	0.05 ± 0.05
	Delphacidae	Herbivore	1.0 ± 1.0	0	0.5 ± 0.5
	Dictyopharidae	Herbivore	0.1 ± 0.1	0	0.05 ± 0.05
	Flatidae	Herbivore	0.1 ± 0.1	0.2 ± 0.1	0.2 ± 0.08
	Issidae	Herbivore	13.5 ± 7.3	4.5 ± 2.0	9.0 ± 3.8
	Lygaeidae	Herbivore	0	0.1 ± 0.1	0.05 ± 0.05
	Miridae	Herbivore	4.4 ± 1.4	1.2 ± 0.6	2.8 ± 0.8
	Nabidae	Carnivore	1.3 ± 0.4	1.1 ± 0.5	1.2 ± 0.3
	Pentatomidae	Herbivore	2.4 ± 1.9	0.2 ± 0.1	1.3 ± 0.9
	Psyllidae	Herbivore	0.9 ± 0.7	0.4 ± 0.2	0.7 ± 0.4
	Reduviidae	Carnivore	1.0 ± 0.4	0.5 ± 0.3	0.8 ± 0.2
	Tingidae	Herbivore	0.3 ± 0.2	0.1 ± 0.1	0.2 ± 0.1
Hymenoptera	Aphelinidae	Parasitoid	0.4 ± 0.2	0.1 ± 0.1	0.3 ± 0.1

	Apidae	Herbivore	0	0.1 ± 0.1	0.05 ± 0.05
	Argidae	Herbivore	0.1 ± 0.1	0	0.05 ± 0.05
	Braconidae	Parasitoid	1.6 ± 0.4	1.5 ± 0.5	1.6 ± 0.3
	Chrysididae	Parasitoid	0	0.1 ± 0.1	0.05 ± 0.05
	Cimbicidae	Herbivore	0.1 ± 0.1	0	0.05 ± 0.05
	Diapriidae	Parasitoid	1.6 ± 0.6	1.2 ± 0.4	1.4 ± 0.3
	Encyrtidae	Parasitoid	0.9 ± 0.3	0.4 ± 0.2	0.7 ± 0.2
	Eulophidae	Parasitoid	1.0 ± 0.3	0.2 ± 0.1	0.6 ± 0.2
	Eupelmidae	Parasitoid	1.8 ± 0.5	0.8 ± 0.3	1.3 ± 0.3
	Figitidae	Parasitoid	3.8 ± 0.6	2.3 ± 0.9	3.1 ± 0.6
	Formicidae	Omnivore	18.8 ± 6.8	7.6 ± 1.6	13.2 ± 3.6
	Ichneumonidae	Parasitoid	1.8 ± 0.5	1.3 ± 0.4	1.6 ± 0.3
	Megaspilidae	Parasitoid	0.3 ± 0.2	0.1 ± 0.1	0.2 ± 0.09
	Mymaridae	Parasitoid	0.1 ± 0.1	0	0.05 ± 0.05
	Orussidae	Parasitoid	0.1 ± 0.1	0	0.05 ± 0.05
	Perilampidae	Parasitoid	1.0 ± 0.3	0.5 ± 0.3	0.8 ± 0.2
	Platygastridae	Parasitoid	0.5 ± 0.3	0.2 ± 0.1	0.4 ± 0.2
	Pompilidae	Carnivore	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.07
	Proctotrupidae	Parasitoid	0	0.1 ± 0.1	0.05 ± 0.05
	Pteromalidae	Parasitoid	0.4 ± 0.2	0.7 ± 0.3	0.6 ± 0.2
	Scelionidae	Parasitoid	1.1 ± 0.4	0.2 ± 0.1	0.7 ± 0.2
	Tenthredinidae	Herbivore	0	0.2 ± 0.2	0.1 ± 0.1
	Torymidae	Herbivore	0.7 ± 0.4	0	0.4 ± 0.2
	Trichogrammatidae	Parasitoid	0.1 ± 0.1	0	0.05 ± 0.05
	Xyelidae	Herbivore	0	0.1 ± 0.1	0.05 ± 0.05
Lepidoptera	Heliozelidae	Herbivore	0.2 ± 0.1	0	0.1 ± 0.07
Microcoryphia	Machilidae	Detritivore	0.1 ± 0.1	0	0.05 ± 0.05
	Meinertellidae	Detritivore	0.3 ± 0.2	0	0.2 ± 0.1
Neuroptera	Chrysopidae	Carnivore	0.2 ± 0.2	0.1 ± 0.1	0.2 ± 0.1
Orthoptera	Gryllacrididae	Carnivore	0.1 ± 0.1	0	0.05 ± 0.05
	Gryllidae	Herbivore	4.8 ± 1.1	1.6 ± 0.5	3.2 ± 0.7
	Tettigoniidae	Herbivore	0.1 ± 0.1	0	0.05 ± 0.05
Phasmatodea	Heteronemiidae	Herbivore	0.1 ± 0.1	0	0.05 ± 0.05
Phthiraptera	Linognathidae	Parasitoid	0.4 ± 0.4	0	0.2 ± 0.2
Psocoptera	Ectopsocidae	Detritivore	8.4 ± 2.1	1.1 ± 0.4	4.8 ± 1.3
	Hemipsocidae	Detritivore	0.2 ± 0.1	0	0.1 ± 0.07
	Liposcelididae	Detritivore	12.8 ± 4.4	3.3 ± 0.9	8.1 ± 2.4
	Psocidae	Detritivore	4.7 ± 2.2	1.3 ± 0.5	3.0 ± 1.2
Thysanoptera	Phlaeothripidae	Herbivore	5.7 ± 1.5	2.0 ± 0.7	3.9 ± 0.9
	Thripidae	Herbivore	0.8 ± 0.4	0.3 ± 0.2	0.6 ± 0.2
Thysanura	Lepismatidae	Detritivore	0	0.1 ± 0.1	0.05 ± 0.05
Trichoptera	Limnephilidae	Herbivore	0.1 ± 0.1	0	0.05 ± 0.05
		Total	218.9 ± 31.7	97.5 ± 13.4	158.2 ± 21.8

Appendix B. Mean abundance ± SE of shrub layer vegetation between honeysuckle-present and honeysuckle-absent plots (n = 10, 10-m^2 plots per plot type; n = 20, 10-m^2 plots for total). Absolute abundance can be computed by multiplying mean abundances by sample size (n = 10 or 20 plots).

	Honeysuckle		
Species	Present	Absent	Total
Acer negundo	0.5 ± 0.4	0.5 ± 0.3	0.5 ± 0.3
Acer saccharum	7.4 ± 1.7	10.4 ± 1.5	8.9 ± 1.2
Aesculus flava	0	0.1 ± 0.1	0.05 ± 0.05
Asimina triloba	0.6 ± 0.4	27.0 ± 10.2	13.8 ± 5.8
Carya cordiformis	1.5 ± 0.8	0	0.8 ± 0.4
Carya ovata	0	0.1 ± 0.1	0.05 ± 0.05
Celtis occidentalis	0.1 ± 0.1	0.5 ± 0.3	0.3 ± 0.1
Cercis canadensis	0.2 ± 0.1	0.1 ± 0.1	0.2 ± 0.08
Fagus grandifolia	0.3 ± 0.3	1.8 ± 0.8	1.1 ± 0.4
Fraxinus americana	1.9 ± 0.7	1.4 ± 0.6	1.7 ± 0.4
Juglans nigra	0	0.2 ± 0.2	0.1 ± 0.1
Lindera benzoin	0.4 ± 0.4	12.1 ± 5.8	6.3 ± 3.1
Liriodendron tulipifera	0.3 ± 0.3	0.2 ± 0.2	0.3 ± 0.2
Lonicera maackii	38.4 ± 6.0	0	19.2 ± 0.2
Ostrya virginiana	0	0.2 ± 0.2	0.1 ± 0.1
Populus deltoides	0.1 ± 0.1	0	0.05 ± 0.05
Prunus serotina	0.1 ± 0.1	0.8 ± 0.4	0.5 ± 0.3
Quercus alba	0.1 ± 0.1	0.2 ± 0.1	0.2 ± 0.08
Quercus muehlenbergii	0.8 ± 0.5	0.2 ± 0.2	0.5 ± 0.3
Quercus rubra	0	0.8 ± 0.4	0.4 ± 0.2
Robinia pseudoacacia	0	0.9 ± 0.9	0.5 ± 0.5
Sassafras albidum	0.1 ± 0.1	0	0.05 ± 0.05
Ulmus americana	0.5 ± 0.3	0.7 ± 0.5	0.6 ± 0.3
Total	53.3 ± 7.2	58.2 ± 10.5	55.8 ± 6.2