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forest management

Effects of Chinese Privet on Bees and Their Vertical Distribution in Riparian Forests

Michael D. Ulyshen, Scott Horn, and James L. Hanula

Chinese privet (*Ligustrum sinense* Lour.), is known to negatively affect biodiversity near the ground in invaded forests by forming thick layers of non-native vegetation in the midstory. Whether these effects extend above the shrub layer into the canopy remains unclear. We sought to test this question by using flight-intercept traps (clear plastic panels attached to a white bucket) to sample bees at three heights (0.5, 5, and 15 m) in plots in which *L. sinense* had or had not been experimentally eliminated. Privet removal (i.e., restoration) resulted in significantly higher bee abundance, richness, and diversity than in invaded sites, but this effect was only observed at 0.5 m. In restored plots, bee diversity was generally higher at 5 and 15 m than near the forest floor, but there were no differences between traps at 5 and 15 m. Our findings show that bees will benefit from the removal of invasive shrubs near the forest floor but not in the canopy. Why bee diversity is higher in the canopy than near the ground in temperate deciduous forests remains unknown.

Study Implications: Chinese privet is recognized as one of the most problematic plants invading southeastern US forests where it has strong negative effects on native plant and insect diversity near the forest floor. This study tested the impacts of privet removal on the diversity of bees at three heights to determine whether the effects of removing privet extend into the canopies of temperate deciduous forests. The findings indicate that management activities aimed at eliminating Chinese privet will greatly increase bee activity near the forest floor but will not immediately impact bee numbers in the canopy.

Keywords: biodiversity, invasive species, forest management, pollinators, vertical stratification

Given documented pollinator declines (Potts et al. 2010, Cameron et al. 2011, Burkle et al. 2013), there is an urgent need for studies aimed at improving conditions for bees and other flower-visiting insects. This is especially true in land-use categories that have historically received less attention from pollinator researchers (Tonietto and Larkin 2018). For example, surprisingly little is known about the diversity and distribution of pollinators in forests (Rivers et al. 2018) despite the fact that nearly one-third of global land area is forested (World Bank 2020). However, it is clear from a growing body of literature that forests can support diverse bee assemblages (Proesmans et al. 2019), especially under open forest conditions (Hanula et al. 2016), including a number of forest-dependent taxa (Winfree et al. 2007, Bogusch and Horák 2018). Moreover, bee diversity has been shown to be positively related to surrounding forest cover (Taki et al. 2007, Watson et al. 2011, Bailey et al. 2014), and there is an important spillover of forest bee diversity into neighboring agricultural lands (Blitzer et al. 2012, Marini et al. 2012, Monasterolo et al. 2015).

Forests are characterized by a complex vertical structure, with canopy height generally increasing toward the equator (Simard et al. 2011), and the relative inaccessiblity of this diffuse aerial zone remains one of the biggest challenges facing forest ecologists. The canopies of forests throughout the world support diverse invertebrate assemblages (Basset et al. 2003, Floren and Schmid 2008) which often differ greatly from those near the ground. Indeed, most taxa are unevenly distributed along the vertical gradient, resulting in complex patterns of vertical stratification that are driven by a wide variety of abiotic and biotic factors (Ulyshen 2011). This has been shown to be the case for bees in both tropical and temperate forests, with some species being more abundant in the canopy and others being more concentrated near the forest floor (Morato 2001, Ramalho 2004, Martins and Souza 2005, Ulyshen et al. 2010b, Smith-Ramírez et al. 2016).

Many insect taxa use resources in the canopy as well as near the forest floor and often move between these zones on a seasonal or even daily basis (Costa and Crossley 1991). Disturbances limited to a particular stratum therefore have the potential to influence

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insect assemblages throughout the canopy. By introducing thick layers of novel vegetation in the midstory, for example, certain invasive shrubs have the potential to indirectly alter insect assemblages high in the canopy by affecting habitat suitability near the forest floor. These non-native shrub layers are known to sometimes reduce plant and insect biodiversity near the ground, but few studies have investigated their effects on taxa active above their reach. In the southeastern United States, the removal of Chinese privet from the midstory resulted in significant increases in beetle diversity at ground level, but had no detectable effect on beetle assemblages in the canopy (Ulyshen et al. 2010a). Here, we test the same question on bees, a group that is present throughout the forest canopy but must largely return to the soil for nesting (Cane 1991).

Chinese privet was introduced into the United States as an ornamental shrub in the mid nineteenth century. It has since spread widely and is now considered one of the most problematic invasive plants in the southeastern United States (Merriam 2003, Webster et al. 2006). It forms a dense growth in the understories of many riparian forests and largely excludes native plants from the forest floor (Merriam and Feil 2003). Previous studies have documented the benefits of removing Chinese privet to pollinators near the ground (Hanula and Horn 2011, Hudson et al. 2013), but nothing is known about how privet affects bee assemblages in the canopy. We predicted that the negative effects of privet on bees near the forest floor would extend into the canopy above the privet layer, resulting in depressed bee numbers across the vertical gradient.

Methods

Study Area

This study made use of a Chinese privet eradication study initiated in 2005 (Hanula et al. 2009). The study was replicated at four locations in northeast Georgia, United States, all within the Oconee River watershed. Two locations (Sandy Creek Nature Center and the Georgia State Botanical Gardens) were established near the city of Athens in Clarke County, whereas the other two locations (Scull Shoals Experimental Forest and Watson Springs Forest) were situated in more rural areas in Oglethorpe and Greene counties (Figure 1). The forests at all four locations consisted primarily of hardwoods, being dominated by genera such as *Quercus*, *Acer*, *Fraxinus*, *Liquidambar*, *Populus*, etc. There was also a minor pine component at all sites, largely consisting of *Pinus taeda* L. Descriptions of the herbaceous plant communities and how they were affected by privet removal can be found in Hanula et al. (2009). All locations were near streams and experienced annual flooding during the winter or early spring months. Chinese privet

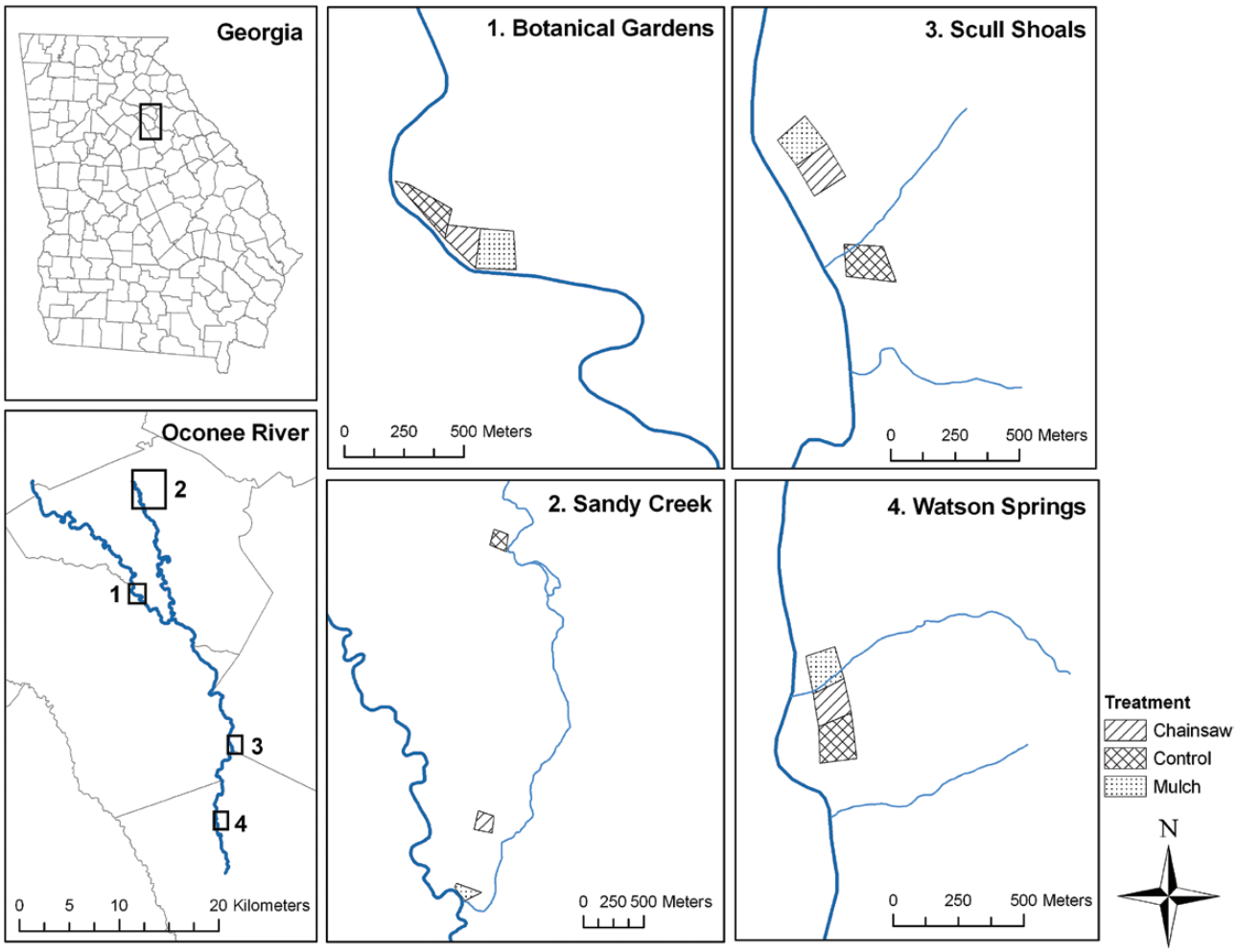

Figure 1. Map of locations in northeastern Georgia in which Chinese privet was either eradicated (Chainsaw and Mulch) or not (Control) beginning in 2005.

Table 1. List of species and their abundances in plots that had or had not (control) been restored by the eradication of Chinese privet.

Species	Treatment			Total
	Restored		Control	
	Chainsaw	Mulch		
Andrena atlantica Mitchell	0/0/0	0/0/1	0/0/0	1
A. cressonii Robertson	0/1/4	0/4/2	0/1/0	12
A. fragilis Smith	1/0/1	0/3/0	0/0/0	5
A. hilaris Smith	0/1/0	0/1/0	0/0/1	3
A. hippotes Robertson	0/2/0	0/0/0	0/1/1	4
A. ilicis Mitchell	0/2/0	0/0/1	0/0/0	3
A. imitatrix Cresson	2/6/5	3/3/1	0/1/2	23
A. mendica Mitchell	0/0/1	0/0/0	0/0/0	1
A. miserabilis Cresson	0/1/0	0/0/0	0/0/0	1
A. nasonii Robertson	1/1/2	1/1/0	0/0/2	8
Andrena obscuripennis Smith	0/1/0	0/0/1	0/0/0	2
A. perplexa Smith	0/4/3	1/0/0	0/3/5	16
A. personata Robertson	2/2/0	3/3/1	0/1/0	12
A. robertsonii Dalla Torre	0/0/1	0/0/2	0/0/5	8
A. salictaria Robertson	6/3/2	5/1/0	0/1/1	19
A. spiraeana Robertson	0/0/2	0/3/0	0/1/2	8
A. sp. 17	0/0/0	0/0/0	0/0/1	1
A. sp. 18	0/0/0	0/0/0	1/0/0	1
A. sp. 19	0/0/0	0/1/0	0/0/0	1
A. sp. 20	0/0/1	0/0/0	0/0/0	1
A. sp. 21	0/0/1	0/1/0	0/0/0	2
A. sp. 22	0/0/1	0/0/1	0/0/0	2
A. sp. 23	0/0/0	0/1/0	0/0/0	1
Apis mellifera Linnaeus	2/1/0	2/0/1	0/2/2	10
Augochlora pura (Say)	23/122/92	18/85/129	3/48/84	604
Augochlorella aurata (Smith)	3/5/2	7/5/4	0/1/1	28
Bombus bimaculatus Cresson	0/1/4	2/5/2	0/4/2	20
B. griseocollis (DeGeer)	0/0/0	3/1/0	0/0/0	4
B. impatiens Cresson	0/6/9	1/3/3	0/1/5	28
B. pensylvanicus (DeGeer)	0/0/1	0/1/0	0/0/0	2
B. vagans Smith	0/0/1	1/1/0	1/0/0	4
Ceratina calcarata Robertson	5/2/1	0/0/5	0/2/2	17
C. dupla Say	0/1/1	0/0/3	1/4/1	11
Colletes inaequalis Say	1/1/1	0/0/1	0/0/0	4
Eucera atriventris (Smith)	0/0/0	0/1/0	0/0/0	1
Halictus rubicundus (Christ)	0/0/1	0/1/1	0/1/0	4
Hoplitis micheneri Mitchell	0/0/0	0/1/0	0/0/0	1
H. producta (Cresson)	0/0/0	2/0/0	0/0/0	2
H. simplex (Cresson)	0/1/0	2/0/1	0/4/0	8
Hylaeus grossicornis (Swenk & Cockerell)	0/1/2	0/1/0	0/1/4	9
H. modestus Say	0/2/3	0/0/0	0/0/2	7
H. sparsus (Cresson)	0/0/1	0/0/0	0/0/2	3
H. teleporus (Lovell)	0/0/4	0/1/4	0/0/10	19
Lasioglossum bruneri (Crawford)	6/1/3	7/8/9	0/1/2	37
L. cattellae (Ellis)	0/2/0	0/0/0	0/0/1	3
L. coeruleum (Robertson)	1/0/1	0/1/1	0/0/0	4
L. coreopsis (Robertson)	0/0/1	0/0/0	0/0/0	1
L. fuscipenne (Smith)	0/1/0	0/0/0	0/0/0	1
L. hitchensi Gibbs	0/0/1	0/0/1	0/0/1	3
L. imitatum (Smith)	0/11/7	6/17/5	0/3/9	58
L. laevissimum (Smith)	0/1/0	0/1/1	0/0/2	5
L. macoupinense (Robertson)	2/0/0	2/1/0	2/0/0	7
L. oblongum (Lovell)	1/0/0	0/1/0	0/0/0	2
L. smilacinae (Robertson)	0/1/0	1/2/0	0/0/0	4
L. subviridatum (Cockerell)	0/0/0	0/1/0	0/0/0	1
L. truncatum (Robertson)	0/1/0	0/0/0	0/0/0	1
L. versatum (Robertson)	0/0/1	0/1/1	0/0/3	6
Megachile frigida Smith	0/0/0	2/0/0	0/0/0	2
M. xylocopoides Smith	0/0/0	0/0/2	0/0/0	2
Melissodes agilis Cresson	0/0/0	0/0/0	0/2/0	2
Nomada cressonii Robertson	0/0/0	0/1/0	0/0/0	1
N. denticulata Robertson	0/0/1	0/0/0	0/0/0	1
N. imbricata Smith	0/0/0	1/0/0	0/0/0	1
N. lepida Cresson	0/0/0	0/1/0	0/0/0	1
Osmia atriventris Cresson	0/0/0	0/0/0	0/2/0	2
O. conjuncta Cresson	0/0/0	2/0/0	0/0/0	2
O. proxima Cresson	0/1/1	0/1/1	0/1/0	5
O. pumila Cresson	0/2/0	1/0/1	0/0/1	5
Panurginus atramontensis Crawford	1/0/0	0/0/0	0/0/0	1
Total	57/188/163	73/164/186	8/86/154	1079

Note: Under each treatment, numbers correspond to the total number of specimens captured at the three trap heights (0.5/5/15 m). Note that the two privet-eradication treatments were both assigned to a single "restored" treatment in the analyses.

was well established at all four locations and had been for many years before the study was established.

Experimental Design

The privet eradication study was initiated in October/November 2005. At each of the four locations, three ~2-hectare plots were established in riparian forests dominated by privet in the understory. Two plots at each location were assigned to one of two privet-eradication treatments, whereas the third plot served as a control in which no privet was removed. Eradication treatments involved using either a machine to chop the stems into a fine mulch (Klepac et al. 2007) or chainsaws and other hand tools to create a layer of cut debris no more than 1 m high. These treatments were followed by chemical treatments in which all privet stumps were treated with 30 percent triclopyr (Garlon 4) or 30 percent glyphosate (Foresters') to prevent resprouting.

Sampling

Bees were sampled at 0.5, 5, and 15 m above the forest floor at two spots within each of the 12 plots using a total of 72 flight intercept traps. As described by Ulyshen and Hanula (2007), each trap consisted of two intersecting clear plastic panels measuring 20 × 30 cm attached to a white plastic bucket. Although somewhat unconventional, this trap design was found to be effective at capturing bees in a previous study (Ulyshen et al. 2010b). The traps at 5 and 15 m were suspended from ropes pulled over tree branches, whereas the traps at 0.5 m were suspended from metal poles driven into the ground at an angle. Privet averaged about 4–5 m in height at our sites, so all traps at 0.5 m were far beneath the privet layer, those at 5 m were just above it, and traps at 15 m were high above the privet layer. For simplicity, and because forest strata are difficult to define or separate (Parker and Brown 2000), we hereafter refer to traps at 5 and 15 m as being situated within the forest canopy. The traps were filled with a 1 percent formaldehyde solution containing salt and a small amount of dish soap to kill and preserve the catch. Sampling took place 1 week per month in April, May, and June in 2006 (the year after the plots were established).

Statistical Analysis

Because of repeated trap losses, we excluded data from two trapping locations (botanical garden control 5 m [both traps] and Sandy Creek control 0.5 m [both traps]) from all analyses. The three sampling periods were pooled, and the two traps at each height within each plot were combined prior to analysis. The mixed procedure of SAS 9.4 (SAS Institute 2013) was used to test how total bee abundance, richness, and Shannon's diversity were affected by treatment, trap height, and the interaction between treatment and height. Location was included as a random effect. Abundance was log(x + 1)-transformed to satisfy normality assumptions, but untransformed data are presented in the figures. Differences of least-square means were used to compare treatments at each trap height. Analyses indicated no significant differences of least-square means between the two eradication treatments for bee abundance ($t_{21.9}$ = –0.8, P = .5), richness ($t_{21.9}$ = 0.0, P = 1.0), and diversity ($t_{21.9}$ = –1.0, P = .3), so these were treated as a single "restored" treatment in all subsequent analyses.

Table 2. Results from the mixed model of total bee abundance, richness, and Shannon's diversity.

	Abundance	Richness	Diversity
Treatment	$F_{1,25.1}$ = 12.34**	$F_{1,25}$ = 6.14*	$F_{1,25}$ = 4.29*
Height	$F_{2,25.2}$ = 45.02***	$F_{2,25.1}$ = 14.65***	$F_{2,25.1}$ = 3.51*
Treatment × height	$F_{2,25.2}$ = 6.7**	$F_{2,25.1}$ = 1.9, P = .2	$F_{2,25.1}$ = 4.03*

Note: *P < .05, **P < .01, ***P < .001.

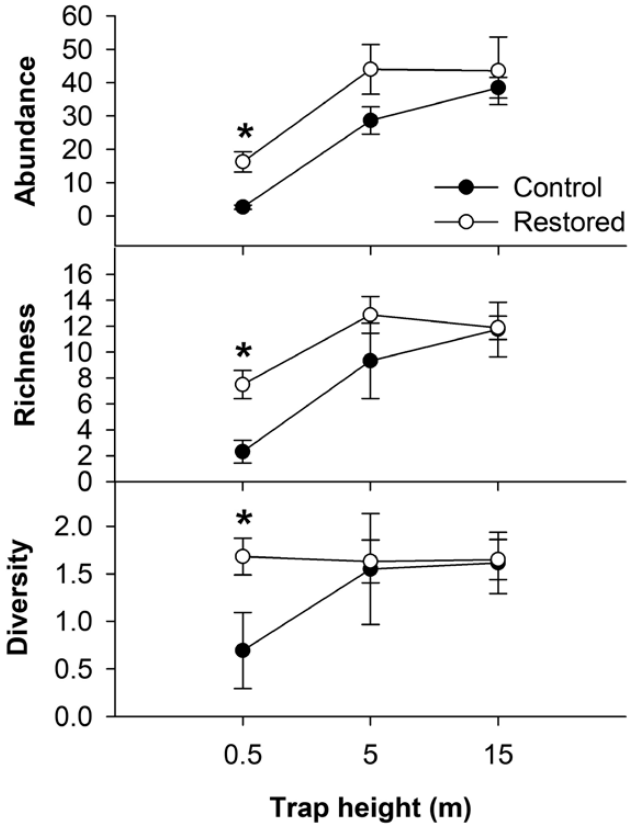

Figure 2. Mean ± SE total bee abundance, richness, and Shannon's diversity at three trap heights (0.5, 5, and 15 m) in plots that had or had not (control) been restored by the eradication of Chinese privet. Asterisks denote significant differences in least-square means between treatments at a given height at an alpha level of 0.05. The number of samples varied between treatments and heights: n = 8 at all heights in the restoration treatment, n = 4 at 15 m in the control treatment, and n = 3 at 0.5 m and 5 m in the control treatment.

We used iNEXT to compare bee diversity estimates between treatments and among trap heights based on the rarefaction and extrapolation sampling curves of Hill numbers, a mathematically unified family of diversity indices (Chao et al. 2014). The value of q determines how much weight is given to species based on their rarity, weighting rare and abundant species equally (q = 0, species richness), weighting species in proportion to their frequency in the sampled assemblage (q = 1, the exponential of Shannon entropy), or giving abundant species more weight relative to their frequency (q = 2, inverse Simpson concentration). Hill numbers thus provide a way to more fully interpret biodiversity data by incorporating information about relative abundance rather than focusing solely on species richness (Chao et al. 2014).

We analyzed sample-based (incidence) data and compared diversity at Chao's base sample size (Chao et al. 2014), defined as the greater value of the largest reference sample size or twice the minimal reference sample size. Differences are considered significant when 95 percent confidence intervals do not overlap at the base sample size. We compared treatments at each height separately to test if the documented negative effect of privet on bees near the forest floor also extended into the canopy. We limited our comparison of trap heights to only traps in the restoration treatments, as this condition provided the most reliable information on the vertical distribution of bees without the confounding effects of privet invasion.

To compare bee assemblages among the three trap heights, we performed nonmetric multidimensional scaling using PC-ORD (McCune and Mefford 2011). Because our focus here was on the vertical distribution patterns of bees under natural conditions, we limited this analysis to the two restored treatments, and the two sampling locations within each plot were not combined. The dataset used in this analysis was limited to species present in at least three of the 48 samples, resulting in a final matrix consisting of 34 species. Abundance values were relativized by species maxima, and the Bray–Curtis distance measure was used in the analysis. PERMANOVA was performed on the same reduced dataset to test whether bee assemblages differed significantly among the three heights.

Indicator species analysis was performed in R using the package "indicspecies." This approach differs from the traditional indicator species analysis (Dufrêne and Legendre 1997) in that it tests for associations with combinations of groups in addition to associations with specific groups (De Cáceres et al. 2010). In our analysis, for example, it allowed us to test whether species were associated with a single trap height or any combination of two trap heights. We used the function multipatt (multilevel pattern analysis) to conduct this analysis, using 9,999 permutations to calculate *P*-values for each combination. The resulting indicator values ranged from 0 to 1 (no association to complete association).

Results

The final dataset used in the analysis consisted of 1,079 specimens belonging to 69 species (Table 1). *Augochlora pura* (Say) was the most abundant species, accounting for about 56 percent of all bees captured, followed by *Lasioglossum imitatum* (Smith) (5 percent) and *L. bruneri* (Crawford) (3 percent) (Table 1).

Effects of Privet Removal

Our mixed model found bee abundance, richness, and diversity to vary significantly between treatments and among heights, and there was a significant treatment × height interaction for abundance and diversity (Table 2). Abundance, richness, and diversity were all significantly higher in the restored treatment than in the control treatment at 0.5 m, but there were no differences between treatments at 5 m or 15 m (Figure 2). All three metrics generally increased from 0.5 to 5 m, but they differed little between 5 and 15 m. Similar to the results from our mixed model, significantly more bee species were captured in the restored treatment than in the control treatment at 0.5 m, and this was true for all levels of *q* (Figure 3). There were no differences between these treatments at 5 and 15 m, however (Figure 3).

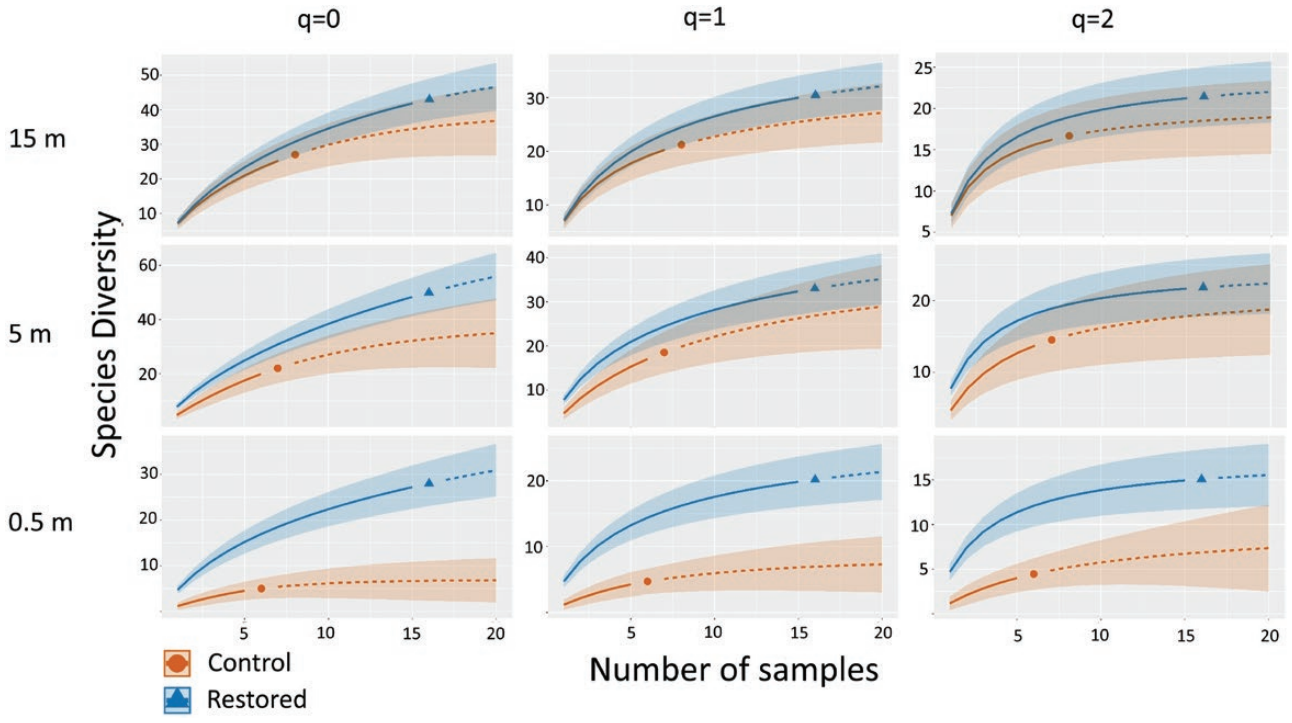

Figure 3. Rarefaction (solid lines) and extrapolation (dashed lines) of bee diversity at three trap heights (0.5, 5, and 15 m) in plots that had or had not (control) been restored by the eradication of Chinese privet. Separate results are given for Hill numbers 0, 1, and 2. The results for species richness (q = 0) are shown in the left-most panels, whereas those for q = 1 and 2 give increasing weight to abundant species. All curves include 95 percent confidence intervals, and comparisons are made at a base sample size of 16 (i.e., the largest reference sample size).

Vertical Distribution Patterns

Rarefaction, limited to the restoration treatments, showed more species at 5 m than at 0.5 m based on hill numbers 0 and 1 but not 2 (Figure 4). There were also more at 15 m than at 0.5 at q = 1. There was no difference between 5 and 15 m at any level of q, however. Nonmetric multidimensional scaling yielded a three-dimensional solution with a final stress of 19.6. The ordination indicated considerable overlap among the three trap heights but with the traps at 5 m and 15 m forming the tightest cluster (Figure 5). PERMANOVA indicated that assemblages differed significantly among trap heights ($F_{2,45}$ = 1.56, P = .03). There was a significant difference between traps at 0.5 and 15 m (t = 1.56, P = .001) but no significant differences between 0.5 and 5 m (t = 1.26, P = .08) or between 5 and 15 m (t = 0.77, P = .87). Based on indicator species analysis, three species were significantly associated with traps placed high above the ground. *Hylaeus teleporus* (IndVal = 0.577, P = .003) was significantly associated with traps at 15 m, whereas *Lasioglossum imitatum* (IndVal = 0.68, P = .038) and *Bombus impatiens* (IndVal = 0.598, P = .037) were both associated with the combination of 5 m and 15 m. No species was found to be significantly associated with traps placed at 0.5 m.

Discussion

Many studies indicate bees generally benefit from efforts aimed at creating more open forest conditions, including the elimination of invasive shrubs (McKinney and Goodell 2010, Hanula et al. 2016). Our results are consistent with this expectation, as we found overall bee richness, diversity, and abundance to be significantly higher in restored plots than in privet-invaded plots. However, this was only true near the forest floor, beneath the privet canopy. There were no significant differences between these treatments for traps placed at 5 or 15 m, similar to the results observed for beetles from the same study (Ulyshen et al. 2010a). In North Carolina, Campbell et al. (2018) also found bees and wasps to respond positively to mechanical felling and burning of shrubs and small trees near the forest floor but not in the lower canopy. Although the privet layer may reduce bee diversity near the forest floor by reducing the diversity and abundance of native plants (Hanula et al. 2009, Hudson et al. 2014), it may also reduce capture rates simply by reducing trap visibility or by impeding flight by bees. For example, Geroff et al. (2014) reported higher numbers of bees from pan traps elevated just 1 m above the ground than from those at ground level in a tallgrass prairie. By contrast, trap visibility and accessibility at 5 and 15 m would have been unaffected by the privet layer, and this could explain the lack of treatment differences at these heights.

Privet is also likely to reduce bee numbers near the forest floor by negatively affecting the abundance and diversity of herbaceous plants at ground level (Hanula et al. 2009, Hudson et al. 2014). It is also possible that privet affects soil conditions for ground nesting bees, but we suspect that our sites are all generally unfavorable for nesting because of the seasonal flooding they experience (Fellendorf et al. 2004, Cope et al. 2019). Regardless of why bees were less numerous beneath the privet than in restored areas, it is clear from our results that these negative effects did not extend into the canopy. Because trees in temperate deciduous forests flower only in spring, the bees present in the canopy throughout much of the year must be either using nonfloral resources or simply traveling through the canopy on their way to some distant floral resource.

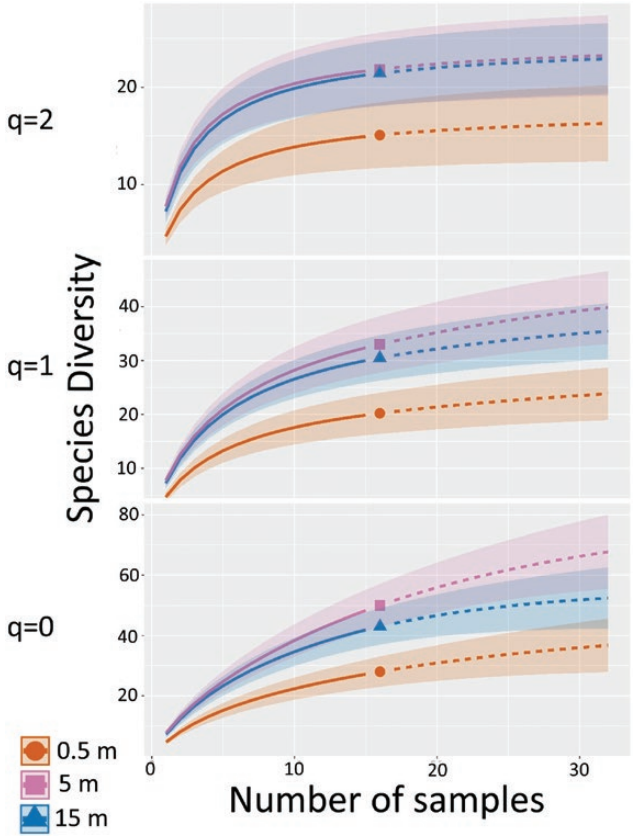

Figure 4. Rarefaction (solid lines) and extrapolation (dashed lines) of bee diversity at three trap heights (0.5, 5, and 15 m) following the eradication of Chinese privet based on Hill numbers 0, 1, and 2. The results for species richness (q = 0) are shown in the bottom panel, whereas those for q = 1 and 2 give increasing weight to abundant species. All curves include 95 percent confidence intervals, and comparisons are made at a base sample size of 32 (i.e., twice the minimum reference sample size).

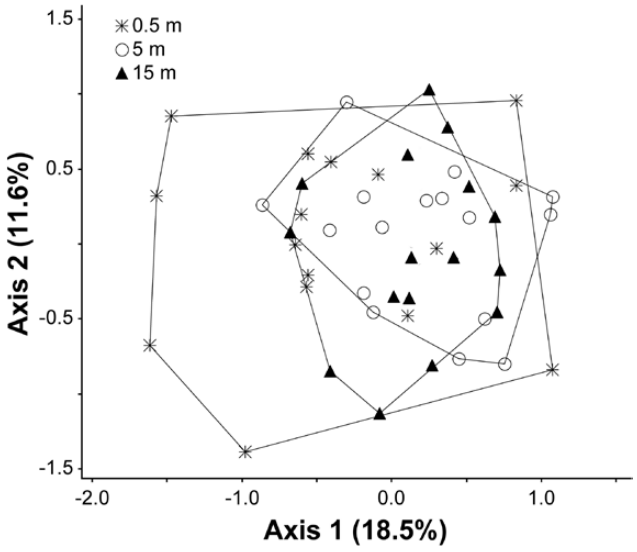

Figure 5. NMDS ordination of bee assemblages sampled at three trap heights (0.5, 5, and 15 m) following the eradication of Chinese privet.

Similar to previous studies (Ulyshen et al. 2010b), bee richness was significantly higher in the canopy than near the ground. The addition of an intermediate trap height (5 m) in the current study

Table 3. Reported height associations of forest bees in the eastern United States.

Species	Forest floor	Forest canopy
Andrena personata Robertson	Ulyshen et al. (2010b)	
Augochlora pura (Say)		>15 m: Ulyshen et al. (2010b); ~9 m: Campbell et al. (2018)
B. impatiens Cresson		5 and 15 m: current study
Hylaeus teleporus (Lovell)		15 m: current study
Lasioglossum imitatum (Smith)		>15 m: Ulyshen et al. (2010b); 5 and 15 m: current study
Lasioglossum macoupinense (Robertson)	Ulyshen et al. (2010b)	
Lasioglossum versatum sensu Mitch		>15 m: Ulyshen et al. (2010b)
Lasioglossum zephyrum (Smith)		>15 m: Ulyshen et al. (2010b)

Note: Forest canopy refers to any height at least several meters above the forest floor (heights are specified within the table).

provides further insight into these patterns. We detected higher bee richness at both 5 and 15 m than at 0.5 m, but there were no significant differences between the two trap heights in the canopy. Bee assemblages at 5 and 15 m appear to be quite similar, with only one species (*H. teleporus*) being significantly associated with one of these two heights. The association of *H. teleporus* with traps at 15 m may reflect the fact that members of this genus nest in twigs. In Germany, Sobek et al. (2009) captured two species of *Hylaeus* in trap nests suspended either in the canopy or in the understory. They reported 90 percent of the more common species, *Hylaeus communis*, from the canopy, although all nine specimens of the less common species, *H. confusus*, were captured in the understory. The other two species found to be significantly associated with particular trap heights in this study, *Bombus impatiens* and *Lasioglossum imitatum*, were associated with both 5 and 15 m, indicating they are widely and more evenly distributed within the forest canopy. Although many bees prefer to forage high above the ground (Frankie and Coville 1979, and references therein), the concentration of bees in the canopies of temperate deciduous forests is somewhat surprising, considering that floral resources are absent there throughout much of the year and that the majority of bee species nest in the soil. Possible explanations for this pattern include bees preferring to disperse high above the forest floor where conditions are sunnier, the presence of arboreal nest sites (for wood-nesting species), and use of nonfloral resources such as honeydew (as speculated by Ulyshen et al. 2010b). Because no bee species are known to be restricted to the canopies of temperate deciduous forests, however, the abundance of bees high above the ground suggests this group is characterized by regular movements between the forest floor and canopy.

Of the significant indicator taxa detected in this study, only the results for *L. imitatum* are consistent with previous studies, with Ulyshen et al. (2010b) also reporting a higher abundance in the canopy (Table 3). The most striking pattern reported by Ulyshen et al. (2010b) concerned an extremely high concentration of *Augochlora pura* in the canopy. Although this finding was supported by Campbell et al. (2018), no significant height associations for *A. pura* were detected in this study. However, it should be noted that more *A. pura* were captured overall at 5 and 15 m than at 0.5 m. Based on work conducted in Panama, Roubik (1993) concluded that because bees are opportunistic foragers, their vertical distribution patterns are quite unpredictable and thus likely to vary in time and space. Bees clearly move readily within the vertical space occupied by temperate deciduous forests as well but appear to commonly concentrate in the canopy. Whether these patterns reflect preferred dispersal heights or resource availability remains unknown.

Conclusions

Our results show that eliminating Chinese privet from invaded forests will increase the diversity of native bees near the forest floor, but these benefits do not appear to extend into the canopy above the privet layer. Because privet prevents the regeneration of native trees, however, even the canopy will be affected by the invasion in the long term. We found bee diversity to be higher at 15 and 5 m than at 0.5 m in restored plots, raising questions about the activities of bees in temperate deciduous canopies. Although these patterns may relate to preferred flight heights of bees, it is also possible that canopies provide important resources to bees throughout the season. More research into this question is needed to better understand the importance of forests to bees and to best protect this fauna in managed landscapes. Finally, we acknowledge that the conclusions from this study are based on just a single year of sampling and recognize that interannual variations in bee populations could result in different patterns, especially at the species level.

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