Removing an invasive shrub (Chinese privet) increases native bee diversity and abundance in riparian forests of the southeastern United States

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Abstract. 1. Chinese privet (*Ligustrum sinense* Lour.) was removed from riparian forests in the Piedmont of Georgia in November 2005 by mulching with a track-mounted mulching machine or by chainsaw felling. The remaining privet in the herbaceous layer was killed with herbicide in December 2006.

2. Bee (Hymentoptera: Apoidea) abundance, diversity and community similarity in the forests were measured for 2 years after shrub removal and compared with heavily invaded controls and with non-invaded forests (desired future condition) using pan traps.

3. In 2006, control plots averaged 8.8 species and 34.8 bees per plot. Privet mulching resulted in 32.5 bee species and 418.3 bees per plot, and privet felling plots had 29 species and 259 bees per plot. In 2007, control plots averaged only 10 species per plot and 32.8 bees per plot, while mulched and felled plots had 48 and 38 species per plot and 658.2 and 382.5 bees per plot, respectively.

4. The bee community on untreated control plots was dissimilar from the communities on privet felling, mulched and desired future condition plots during both years; however, by 2007, desired future condition, felling and mulched plots had similar bee communities.

5. Removal of an invasive shrub provided immediate benefits for native pollinators and resulted in bee communities similar to non-invaded forests even without further restoration of native plant communities.

Key words. Apoidea, diversity, forest, invasive plant, pollination services, pollinator.

Introduction

The diversity of invasive plant species and the variety of growth forms invading the world's forest is impressive (Kohli *et al.*, 2009). Forests of the eastern United States are no exception where plant invaders include a variety of ferns, forbs, grasses, vines, shrubs and trees, all probably having an impact on native flora (Luken, 2003; Miller, 2003; Kohli *et al.*, 2009). The presence of exotic plants and the degree of their invasion in forests is often related to human disturbance (Stapanian *et al.*, 1998; Gavier-Pizarro *et al.*, 2010). Once established, they compete with native plants for light, nutrients, water, space and pollina-

tors. Among the types of invasive plants, shrubs are some of the most common. The negative effects of invasive shrubs on pollinators include less sunlight and lower temperatures beneath them, which reduce native plant growth and possibly flower visitation, but they may benefit pollinators by increasing availability of pollen and nectar when they flower (McKinney & Goodell, 2010).

Like many invasive shrubs Chinese privet, *Ligustrum sinense* Lour., was introduced as an ornamental. Widely used in hedges and other plantings around buildings, it escaped cultivation and was established in forests of the southeastern United States by the 1930s (Small, 1933). Since then, it has continued to spread and currently occupies over one million hectares in 12 southern states based on USDA Forest Service Forest Inventory and Analysis data (Miller *et al.*, 2008). However, these data are collected from forest interior plots and do not include forest edges, or urban forests and parks and hence they underestimate the full magnitude of the problem. Although Chinese privet is found

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throughout the southeastern USA, it is not limited to this region of North America and it is a widespread, naturalised exotic in at least 12 other countries (Invasive Species Specialist Group 2005).

Chinese privet is a very shade-tolerant evergreen shrub that grows well in forests, particularly riparian forests dominated by deciduous hardwood trees. It remains unclear why privet does so well in these forests, but they appear to be prone to invasion (Stroh & Struckhoff, 2009) possibly as a result of the same factors that contribute to their overall high diversity, such as frequent disturbance from flooding. Once established, Chinese privet grows relentlessly and given enough time, it produces a thick shrub layer beneath the forest canopy that shades out most other plant species. Forests heavily infested for a long time have fewer trees, less native shrub cover, and low herbaceous plant richness and cover. Removing privet greatly alters the plant community, initially resulting in a more diverse collection of primarily ruderal species. These plant communities have little in common with communities on similar mature bottomland hardwood forests that have never been invaded by privet (Hanula *et al.*, 2009).

Although Chinese privet is widely used by honeybees, *Apis mellifera* L., (Butz Huryn & Moller, 1995; S. H. pers. obs.), its impact on the overall bee community remains unknown. Studies of the interactions of pollinators with other invasive species have produced varying results. For example, Tepedino *et al.* (2008) found that invasive species were visited by twice as many bee species as native plants, but that the bees were primarily generalists. They argued that the invasive plants were not interfering with native species pollination and over time, the invasive plants will increase the carrying capacity of the ecosystem for generalist pollinators. Bartomeus *et al.* (2008) suggested that invasive plants act as pollinator super generalists, but warned that they may alter the structure of the plant–pollinator network. Conversely, others have found that the presence of invasive plants can affect the reproductive success of natives (e.g. Grabas & Laverty, 1999; Brown & Mitchell, 2001; Brown *et al.*, 2002; Ghazoul, 2004; Traveset & Richardson, 2006; Aizen *et al.*, 2008; Muñoz & Cavieres, 2008; Vanparys *et al.*, 2008; McKinney & Goodell, 2010). However, these studies investigated disruption of pollinator services and not general degradation of the study area, and the pollinator communities within, due to plant invasion.

We investigated how removing Chinese privet from riparian forests affects bee abundance, diversity and community similarity in these forests for 2 years following removal and compared them with non-invaded forests. Plant community attributes (Hanula *et al.*, 2009) were included in the analysis to determine what characteristics of the treatments and recovering forest plant community most influenced the bee communities.

Materials and methods

Study area

Four study sites within the Oconee River watershed in northeast Georgia were selected based on their extensive privet infesta-

tions, access for machinery, and potential for public visitation and use in education and outreach programmes (see Hanula *et al.*, 2009 for map). The sites were the Sandy Creek Nature Center (N33° 59.167′, W083° 22.865′) on the North Oconee River north of Athens; the Georgia State Botanical Gardens (N33° 54.046′, W083° 23.435′) on the Middle Oconee River south of Athens; the Scull Shoals Experimental Forest (N33° 46.132′, W083° 16.897′) on the Oconee River in the Oconee National Forest; and the University of Georgia's, Warnell School of Forest Resources' Watson Springs Forest (N33° 41.908′, W083° 17.695′) that is also along the Oconee River. Common overstory tree species in the treatment areas were ash (*Fraxinus* spp.), willow oak (*Quercus phellos* L.), sugarberry (*Celtis laevigata* Willd.), sycamore (*Plantanus occidentalis* L.) and loblolly pine (*Pinus taeda* L.). Within each site, three homogeneous plots were located in areas with the heaviest privet infestation. Plots were approximately 2 ha in size and contained similar levels of privet in the shrub and herbaceous plant layers prior to treatment. All plots were located to provide at least a 10-m buffer of untreated area between the plot boundary and the stream bank to reduce stream edge effects and to minimise potential soil movement into the streams resulting from soil disturbance by heavy machinery.

We also selected three *desired future condition* plots on the Oconee National Forest near the Scull Shoals and Watson Springs treatment sites. Desired future condition plots were areas of mature riparian hardwood forest with little or no privet. They had similar overstory tree species, but the shrub layer and herbaceous plant community were distinctly different (Hanula *et al.*, 2009). Desired future condition plots were used for comparison and as representatives of the forest type in the absence of privet. All plots were located at least 10 m from rivers or streams. One plot was located along Harris Creek (N33° 41.503′, W083° 16.714′) in Greene County, a second was adjacent to the Apalachee River (N33° 39.463′, W083° 22.363′) in Greene County and the third was next to Falling Creek (N33° 46.977′, W083° 14.668′) in Oglethorpe County, Georgia. Only the Falling Creek plot had detectable levels of privet with 1.4% privet shrub cover and 0.35% privet cover in the herbaceous layer (Hanula *et al.*, 2009).

Privet removal

Initial treatments were applied in October and November, 2005 and consisted of mechanical removal of privet, hand-felling of privet, or no treatment. Specifics of the mechanical removal can be found in Klepac *et al.* (2007). Briefly, mechanical removal was done with a Gyrotrac® mulching machine (Gyrotrac, Summerville, SC, USA) mounted on rubber tracks (4.2 psi ground pressure) to minimise soil compaction. The contractor was asked to remove all privet possible, but to avoid removing non-privet trees 10 cm or larger and all large logs lying on the ground because of the ecological importance of coarse woody debris. We treated stumps on three of the sites with 30% triclopyr (Garlon® 4, Dow AgroSciences LLC, Indianapolis, IN, USA) herbicide to prevent sprouting. On the fourth, the Oconee National Forest, stumps were treated with 30% glyphosate

(Foresters'®, Riverdale Chemical Co., Burr Ridge, IL, USA) herbicide at the request of the forest manager.

Hand-felling was accomplished using chainsaws, brush saws or machetes depending on the size of the stem. All stems 1.5 cm diameter or larger near ground level were cut and left in place. Large shrubs were cut up further so that the total height of the remaining brush was 1 m or less. The surfaces of cut stumps were treated with 30% triclopyr (three sites) or 30% glyphosate (Oconee National Forest site) herbicide immediately after cutting to reduce stump sprouting.

Following the initial treatments newly sprouted seedlings, root and stump sprouts, or seedlings and saplings left because they were smaller than specified in the hand-felling contract, were abundant throughout the plots. In December 2006, both the mechanical and hand-fell plots were treated with a foliar spray of 2% glyphosate with backpack sprayers or Solo® backpack mistblowers (Solo, Newport News, VA, USA) to rid the plots of this low growing privet layer.

Bee sampling

Bees were sampled using pan traps during the growing seasons of 2006 and 2007. The traps consisted of blue and yellow Solo® bowls (530 ml capacity) supported approximately 30 cm above the ground by a wire loop (Campbell & Hanula, 2007). Bowls were filled with water containing Ajax® dishwashing detergent (Colgate-Palmolive Co., Morristown, NJ, USA) to reduce surface tension to facilitate bee capture. We used a total of 10 traps per plot. Two traps (one of each colour) were placed at each of five subplots, which were located at the centre and half the distance from the centre to each plot corner. Pan traps were operated for 7-day periods seven times (March, April, May, June, July, August and October) each year. Treatment and control plots were sampled in 2006 and all plots, including desired future condition plots, were sampled in 2007. Trap samples for each plot were combined into one sample per plot and stored in 70% alcohol until they were sorted, pinned and identified. Bees were identified using published keys and the bee collections at the Florida State Collection of Arthropods Museum of Entomology (Gainesville, FL, USA) and the Georgia Museum of Natural History (University of Georgia, Athens, GA, USA). *Lasioglossum* spp. were identified by Jason Gibbs (York University, Toronto, Ontario, Canada).

Plant sampling

The understory herbaceous plant community and shrub layer was surveyed on all plots in late June 2006 and 2007. Herbaceous plant and shrub community surveys were completed at the same time using the line-point intercept method (Godinez-Alvarez *et al.*, 2009; see Hanula *et al.* 2009 for details of plant survey techniques and results). Trees were surveyed in September 2007 on five permanent, fixed-size (0.04 ha) subplots on each plot that were located at the same positions within plots as the bee traps. We recorded tree species, diameter 1.4 m above ground (dbh) and calculated tree basal area from diameters.

Basal area is the cross-sectional area of the stems of all trees expressed as square units per unit area of forest. Plants on desired future condition plots were only sampled once in June 2006 since they were used as an example of what the composition of these forests should be and therefore we were not interested in how they changed.

Statistical analyses

Data on the effects of the three treatments on bee abundance, species richness and diversity were subjected to analysis of variance using the general linear models procedure of SAS (SAS Institute, 2000). We analysed the data as a randomised complete block experiment with sites as blocks although plots were not randomised within sites because not all plots were accessible to the mulching machinery. However, plots within sites were selected to be homogeneous in terms of forest condition and the amount of privet invasion and therefore randomisation was not deemed essential. The Shapiro–Wilk test for normality was conducted on ANOVA residuals (PROC UNIVARIATE; SAS 2000) to determine if they were normally distributed. Bee abundance data were not normally distributed and hence they were transformed using the square root transformation. Residuals of square root transformed data were then tested to ensure normality. Bartlett's test (PROC GLM) was used to ensure that variances were homogeneous. Means separation was achieved using the REGWQ multiple comparison procedure (SAS 1982; Day & Quinn, 1989). In addition to comparing the effects of treatments on bee abundance and species richness, we examined their effects on several other measures of the bee community including Shannon diversity (H′) and evenness (J). Shannon diversity quantifies species richness and the distribution of individuals among species. It is commonly used, and meets all of the criteria established by Elliott (1990) for an effective diversity index. Evenness is a measure of the distribution of individuals among species.

Simple linear regression analysis (PROC GLM; SAS 2000) was used to examine the relationships of bee abundance, richness, diversity and evenness with plot characteristics that included basal area of trees per ha, number of trees per ha, percentage of non-privet shrub cover, percentage of herbaceous plant cover, herbaceous plant diversity (H′), herbaceous plant richness and evenness (J). Measures of shrub cover and of the herbaceous plant community did not include privet.

Analyses of similarity (ANOSIM) of the bee communities among treatments and desired future condition plots were conducted with the PAST program (Hammer *et al.*, 2001) to perform ANOSIM using the Morista distance measure with 10 000 permutations. ANOSIM provides a method for determining if communities among the various treatments are significantly dissimilar. We included desired future condition plots in both the 2006 and 2007 analyses as these plots were meant to give an indication of the potential community composition in the absence of privet. Data were log transformed for analysis.

Non-metric multidimensional scaling (NMS) analysis of trends in bee abundance in the plots was used to analyse community responses further (PC-ORD; McCune & Mefford, 1999). Analyses were conducted for each year of sampling using

the *slow and steady* autopilot feature. Bee species that had less than three individuals per plot in a given year were excluded from analysis. A total of 53 species were included in 2006 and 57 species in 2007. Joint plots were used to examine relationships between bee community ordination scores and plant community variables (McCune & Grace, 2002). We included basal area of trees per ha, number of trees per ha, percentage of non-privet shrub cover, percentage of herbaceous plant cover, herbaceous plant diversity (H′), herbaceous plant richness and plant evenness (J). An R^2 of 0.3 was used as the cut-off for vector scaling of joint plots.

Results

We caught 119 species of bees during the study. A total of 2510 bees were caught in 2006 and 4585 in 2007 (Table 1). More bees were caught in 2007 because the desired future condition plots were sampled that year in addition to the other plots, and bee abundance on privet removal plots was higher in 2007 than in 2006. *Augochlora pura* (Say), *Augochlorella aurata* (Smith), *Ceratina calcarata* Robertson, *Lasioglossum* (*Dialictus*) *bruneri* Crawford and *Andrena violae* Robertson were some of the most common species captured (Table 1).

Privet shrub removal, regardless of method, resulted in three times as many bee species on removal plots compared with untreated control plots the first summer following removal (Fig. 1, 2006). Removal plots had approximately 30 bee species per plot while untreated controls had approximately nine species per plot. Pan traps on plots in which the privet was mulched captured an average of 418 bees, which was more than 10 times as many bees as untreated plots (35 bees per plot). Traps on mulched plots also caught more bees than traps on plots where the privet was felled (Fig. 1). Privet shrub removal resulted in higher bee diversity, but lower evenness than control plots (Fig. 1).

In winter 2006, privet in the herbaceous layer was killed with herbicide so that by June 2007 it covered <1% of the mulched or felled plots, whereas control plots had approximately 23% herbaceous privet plus the extensive privet shrub cover (Hanula *et al.*, 2009). This nearly complete removal of privet resulted in 20 times more bees captured on mulched plots compared with untreated ones in 2007 (Fig. 1). Likewise, plots where privet was felled had significantly more bees than control plots, but they were not significantly different from mulched plots (Fig. 1). Desired future condition plots were also surveyed in 2007. Although not compared statistically with treated plots, they provided a reference forest condition. These forests had similar numbers of bee species and diversity, and somewhat higher evenness than privet removal plots, but they had lower overall bee abundance (Fig. 1).

In 2006, the bee community on control plots was significantly dissimilar from the communities on privet felling, mulched and desired future condition plots (Table 2). Although desired future condition plots were measured in 2007, we included them in the 2006 analysis as they represent the community likely to occur on non-invaded riparian forests. Desired future condition bee communities were also dissimilar from both privet felling and

Table 1. Total number of bees of each species captured on all plots during 2006 and 2007 in riparian forests.

Family	Genus	Species	2006	2007
Andrenidae	*Andrena*	H2113	3	0
		H2116	3	0
		H2127	5	1
		H2225	0	2
		arabis	1	0
		confederata	0	4
		crataegi	0	2
		cressonii	4	16
		forbesii	4	0
		hippotes	1	1
		ilicis	3	6
		imitatrix	10	130
		mendica	1	2
		miserabilis	1	2
		morrisonella	1	2
		nasonii	2	30
		nida	0	5
		obscuripennis	0	1
		perplexa	5	62
		personata	9	198
		rubi	5	33
		salictaria	1	0
		sayi	0	3
		simplex	0	1
		spiraeana	2	1
		violae	107	227
	Panurginus	*polytrichus*	0	11
		potentillae	3	4
Apidae	*Anthophora*	*abrupta*	1	4
	Melissodes	*agilis*	0	1
		bimaculata	17	63
		comptoides	3	16
		denticulata	30	29
		dentiventris	3	41
		druriella	1	0
	Melitoma	*taurea*	6	7
	Nomada	H2102	3	0
		H2211	0	1
		H2233A	0	1
		autumnalis	1	0
		cressonii	12	10
		dentariae	0	1
		denticulata	2	15
		depressa	10	9
		illinoensis	3	3
		imbricata	7	15
		integerrima	0	1
		lepida	2	2
		luteola	1	22
		media	4	0
		ovata	2	2
		parva	1	20
		perplexa	1	2
		pygmaea	1	14
		sayi	0	11
		sulphurata	1	0
	Ptilothrix	*bombiformis*	3	6

Table 1. (*Continued*).

Family	Genus	Species	2006	2007
	Eucera	*atriventris*	7	11
		dubitata	5	32
	Apis	*mellifera*	35	5
	Bombus	*bimaculatus*	10	13
		griseocollis	4	0
		impatiens	23	32
		pensylvanicus	0	1
		vagans	15	2
		citrinus	3	7
	Ceratina	*calcarata*	382	653
		dupla	10	39
		strenua	0	3
	Xylocopa	*virginica*	2	20
Colletidae	*Colletes*	*inaequalis*	0	10
	Hylaeus	*H2266*	0	1
		fedorica	0	7
		illinoisensis	11	12
		modestus	4	16
		sparsus	2	21
		mesillae	0	3
Halictidae	*Augochlora*	*pura*	580	952
	Augochlorella	*aurata*	727	954
	Augochloropsis	*metallica*	1	1
	Dieunomia	*heteropoda*	0	1
	Halictus	*confusus*	0	1
		ligatus	6	7
		parallelus	0	1
		rubicundus	4	0
	Lasioglossum	*JG-04*	3	1
		apopkense	38	40
		atlanticum	61	118
		bruneri	123	225
		callidum	1	0
		coeruleum	5	9
		cressonii	1	2
		fuscipenne	0	5
		illinoense	0	1
		imitatum	29	22
		lustrans	0	2
		macoupinense	49	84
		oblongum	26	45
		puteulanum	0	2
		sopinci	0	6
		subviridatum	1	2
		tegulare	5	14
		versatum	13	19
		zophops	2	0
	Sphecodes	*carolinus*	2	6
		illinoensis	0	1
Megachilidae	*Heriades*	*H2230*	0	2
	Hoplitis	*producta*	4	2
		simplex	2	8
	Megachile	*campanulae*	2	2
		frigida	2	5
		petulans	2	0
	Osmia	*atriventris*	2	9
		collinsiae	0	4
		conjuncta	0	2

Table 1. (*Continued*).

Family	Genus	Species	2006	2007
		georgica	9	32
		lignaria	4	23
		michiganensis	1	11
		proxima	0	5
		pumila	5	17
		sandhouseae	1	12
	Paranthidium	*jugatorium*	0	2

Numbers in the species column represent unidentified morphospecies.
JG-04 was determined by Jason Gibbs. All other provisional identifications were by JLH.

mulched plots. Only privet mulched and felled plots had similar bee communities. In 2007, control plots were again dissimilar from the removal treatments and the desired future condition plots, but the latter had a similar bee community to both the felling and mulched treatments, which were also similar to each other.

Non-metric multidimensional scaling ordinations (Fig. 2) showed that a two-dimensional solution was optimal for the 2006 (final stress = 7.7) and 2007 (final stress = 4.5) bee community data when we included bee species that were caught at least three times on a given sampling plot. In 2006 and 2007, untreated controls were distinctly separated from treatment and desired future condition plots, but in 2006, none of the plot attributes was correlated with either axis. However, in 2007, percentage of non-privet herbaceous plant cover ($R^2 = 0.62$), herbaceous plant diversity (H′, $R^2 = 0.40$) and evenness (J, $R^2 = 0.39$) were correlated with axis 1 and percentage of herbaceous plant cover was also correlated ($R^2 = 0.34$) with axis 2. Other plant community or overstory tree characteristics were not correlated at $R^2 = 0.3$ or higher.

Consistent with the NMS results, no significant linear or nonlinear relationships between bee community characteristics and plant community attributes were found in 2006. In 2007, bee diversity, number of bee species and the log of total bee abundance exhibited significant linear relationships with percentage plant cover (Table 3). Conversely, bee community evenness was negatively correlated with plant community evenness. However, when the untreated control plots were removed from the analyses, these trends disappeared. Instead, bee diversity was found to be negatively correlated with plant diversity.

Discussion

Removing Chinese privet from 2 ha plots resulted in large increases in bee abundance and diversity. Initially, during the first year of sampling in 2006, after just the privet shrub layer was removed the previous fall, mulched plots had 12 times more bee captures and privet felling plots had seven times more than control plots. Likewise, both treatments resulted in four times more bee species than controls. This increase in bee abundance and richness occurred even though mulched and felled plots had
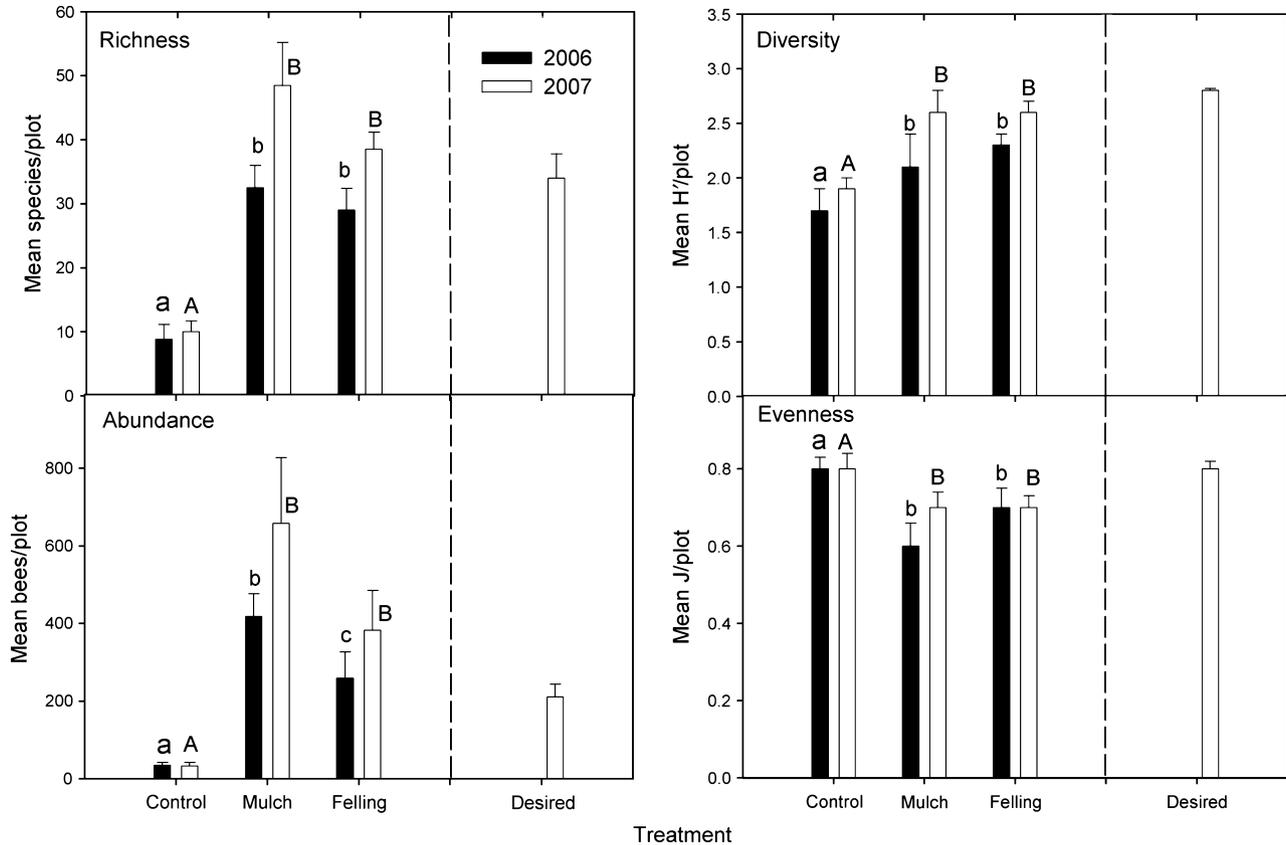
Fig. 1. Mean species richness, total abundance, Shannon diversity and evenness of bees on 2 ha plots of mature riparian forest where Chinese privet was removed by hand-felling or mulching in October 2005 followed by a ground level foliar herbicide application in November 2006. Bars of the same colour with the same letter are not significantly different (REGWQ, $P < 0.05$).

Table 2. Results of analysis of similarity of bee communities in privet removal treatment plots. Desired future condition plots were sampled in 2007, but compared with both years.

	ANOSIM pairwise comparison P-values†		
	Control	Felling	Mulch
2006			
Hand-felling	0.030	–	–
Mulch	0.027	0.426	–
Desired	0.029	0.025	0.026
2007			
Hand-felling	0.030	–	–
Mulch	0.027	0.66	–
Desired	0.031	0.63	0.91

†ANOSIM were conducted using Palaeontological Statistics (PAST), Version 1.89 (Hammer *et al.*, 2001). Numbers <0.05 indicate that bee communities are significantly dissimilar.

the same levels of privet in the herbaceous understory as the control plots in summer 2006 (Hanula *et al.*, 2009). Despite the similar levels of herbaceous privet cover among the plots, mulched plots had a greater cover of non-privet herbaceous plants than control plots (39% vs. 18% cover), probably due to the higher levels of soil disturbance caused by the mulching machine, while privet felling plots (21% cover) were similar to controls in 2006 (Hanula *et al.*, 2009). Consequently, the difference in bee abundance on mulched plots versus felling plots was likely due to the greater non-privet plant cover in 2006 on mulched plots. However, the more open forest and increased amount of sunlight reaching the forest floor may have also contributed to greater bee activity in removal plots. For example, McKinney and Goodell (2010) found that shade from the invasive shrub *Lonicera maackii* (Rupr.) Herder reduced flower visitation by pollinators to potted *Geranium maculatum* L. in a deciduous forest, although not all bees favour flowers in open sunlight (Herrera, 1997). Privet felling plots also had large amounts of cut privet covering the ground up to 1 m deep. What effect this had on bee visitation and captures remains unknown, but felling plots had similar numbers of bees to mulched plots in 2007. Since the wood had not decomposed much in that amount of time, it is unlikely that the dead privet was affecting bee visitation to the plots.

The effect of change in the herbaceous plant communities on bee communities was further demonstrated by the NMS joint plots for 2007 where percentage of plant cover, plant diversity and plant community evenness were all identified as factors shaping the bee communities on the study plots. Exploring these
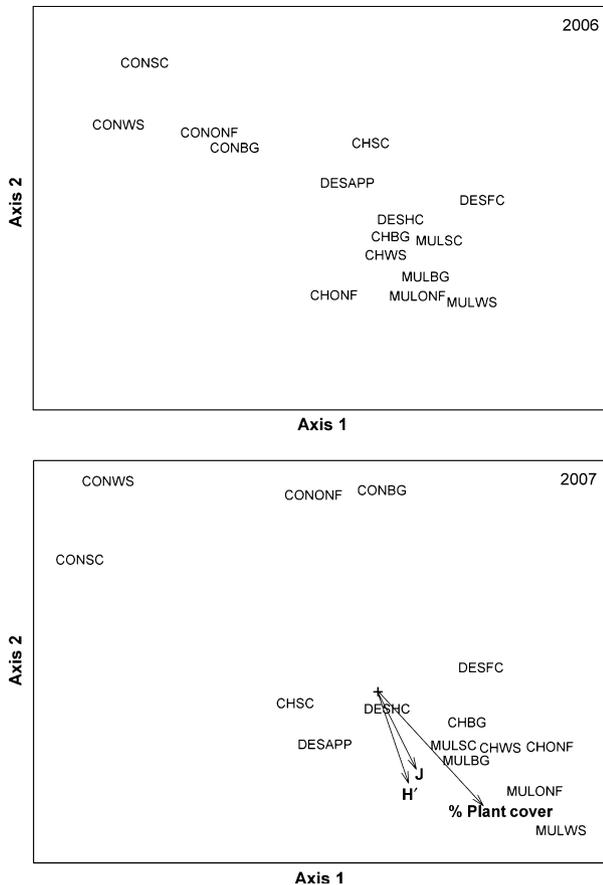
Fig. 2. NMS ordination graphs of the bee communities in 2006 and 2007 on plots receiving privet removal (October 2005) by hand-felling or mulching and subsequent herbicide treatment of privet in the herbaceous layer (November 2006). Plot abbreviations for treatments are DES, desired future condition; CON, control; MUL, mulched and CH, chainsaw or hand-felling. ONF, SC, WS, BG, FC, HC and APP refer to plot locations.

Table 3 Linear regression results of bee community and plant community characteristics on plots in which Chinese privet was either removed or not, or where there was no prior history of privet invasion. Only significant regressions are shown. Untreated control plots were included or removed to determine their overall contribution to the analysis.

Variables		Linear regression results			
Dependent (X)	Independent (Y)	P $(b > 0)$	R^2	Y^0	b
With control plots included					
% Plant cover	Number of bee species	0.0012	0.56	5.46	0.59
% Plant cover	Log (Number of bees)	0.0018	0.54	1.37	0.02
% Plant cover	Bee H′	0.0008	0.59	1.76	0.015
Plant J	Bee J	0.032	0.31	1.09	−0.49
Without control plots					
Plant H′	Bee H′	0.041	0.39	4.08	−0.28

were undisturbed with very different plant communities from the treated and control plots. For example, the highest plant community similarity between desired plots and treated plots was 0.18 (Morista's index, 1 = completely similar) between the desired and mulched plots in 2007, while the similarity between mulched and felled plots was 0.73 (Hanula *et al.*, 2009). Despite the very dissimilar plant communities and lack of disturbance on the desired future condition plots, by 2007, bee communities on privet mulched and felled plots were similar to the desired future condition plots. These results demonstrate that mature, closed canopy riparian forests have diverse and abundant bee fauna that are almost completely excluded when the understory is dominated by Chinese privet. Interestingly, beetles exhibited a similar trend to bees at 0.5 m above ground, but at greater heights, privet removal had no effect on the beetle community (Ulyshen *et al.*, 2010).

Little is known about the bee communities in temperate forests and how forest conditions and management affect them. Winfree *et al.* (2007) found that bee abundance and species richness were negatively associated with extensive forest cover in New Jersey. Although this is likely to be true for most forests in the Eastern United States when compared with fragmented forest, agricultural or suburban/urban areas, within forests there is likely to be wide variation in the quality of bee habitat. Understanding what factors favour diverse and abundant bee communities will help forest managers interested in improving pollinator habitat. For example, our results are similar to those of Campbell *et al.* (2007) who examined the effects of prescribed fire, shrub removal and the two combined on pollinators in the Southern Appalachian Mountains of North Carolina. They found that shrub removal alone and fire alone had no effect on pollinator communities, but the two combined increased pollinator abundance and richness. This occurred because the two treatments combined resulted in some overstory tree mortality and a reduction in live tree basal area or density. This reduced basal area was correlated with increased herbaceous plant cover and increasing numbers of pollinators. Likewise, increasing herbaceous plant cover was also correlated with increasing

relationships further showed that percentage of plant cover was positively correlated with the log of total bees captured, with bee species richness, and with bee diversity (H′). However, plant evenness was negatively correlated with bee evenness. When regression analyses were conducted after removing the control plots the above relationships disappeared. Thus, the control plots, which had distinct and degraded plant (Hanula *et al.*, 2009) and bee communities due to the extensive privet shrub cover on them, were strongly influencing the regressions. No relationships existed within the remaining plots because treated plots had similar plant communities after privet removal. The bee communities reflected that, even though different treatments were used. Desired future condition plots were included in these analyses but, as the NMS ordination and ANOSIM demonstrated, by 2007, bee communities on privet removal and desired future condition plots were similar.

The treatments disturbed the forest and hence it is possible that the bees were responding to the disturbances and the resulting plant communities. However, desired future condition plots

numbers of pollinators, as in this study. Despite very different approaches, the experiments resulted in similar forest conditions. Campbell *et al.* (2007) reduced overstory tree density via hot fires. Hanula *et al.* (2009) found that areas with the highest privet density had the lowest tree densities. Thus, tree thinning occurred as a result of Chinese privet preventing tree seedling establishment and growth over an extended period of time. Once the privet shrubs were removed, more light reached the forest floor promoting greater flowering plant establishment and growth. For example, early colonising species such as burnweed [*Erechtites hieraciifolia* (L.) Raf. ex DC], wingstem [*Verbesina alternifolia* (L.) Britton ex Kearney] and pokeweed (*Phytolacca americana* L.) were very common on our plots where privet was removed and bees were commonly observed on each of these plants during flowering. Others, such as violets (*Viola* spp.), lizard's tail (*Saururus cernuus* L.), and smartweed (*Polygonum pensylvanicum* L.) were not found in great numbers, but were still more prevalent on privet removal plots. Our results are also consistent with Romey *et al.* (2007) who found that some tree removal (60%) was beneficial to bees while complete removal was not. They too found that the increase in bee abundance and diversity was linked to increased abundance of flowering plants.

Chinese privet occupies over one million hectares of forest land in the southeastern USA (Miller *et al.*, 2008). However, these data are based on forest interior plots and hence it underestimates the privet-infested area by excluding forest, roadside, or other edges where privet probably has a serious impact on pollinators. Also, this estimate does not include forested urban areas where infestations are often the most severe. Clearly, bees caught in this study were not exclusively forest species restricted to our plots, but they probably came from surrounding areas. Therefore, it is impossible to know how much bees would benefit from large-scale privet removal based on this study. However, our data suggest that it is likely to be substantial as traps in undisturbed forest interior plots (desired future condition), with no history of privet invasion, caught an average of 210 bees from 34 species. In comparison, trap in privet-infested control plots, which were also undisturbed by privet removal, caught approximately 35 bees from nine species. Therefore, when disturbance is eliminated as a factor, traps in forests without privet captured 175 more bees per plot and 25 more species than traps in undisturbed, privet-invaded forest. If similar increases in bee abundance and diversity could be achieved across all one million hectares of privet-infested forest, southeastern US forests could contain substantially more bees if privet were removed from them. Furthermore, our results demonstrate that removal of this invasive shrub benefits forest pollinators even without further restoration of native plant communities.

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