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Removing Chinese privet from riparian forests still benefits pollinators five years later

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ABSTRACT

Chinese privet (*Ligustrum sinense*) is an invasive shrub of the Southeastern U.S. that forms dense stands and limits biodiversity. It was removed from heavily infested riparian forests of the Georgia Piedmont in 2005 by mulching machine or chainsaw felling and subsequent herbicide application. Abundance and species richness of bees and butterflies were sampled using pan traps on removal plots, heavily invaded control plots, and reference plots in 2012, approximately five years after complete removal of privet. Removal plots had nearly three times as many species as control plots and were similar to reference plots in numbers of species. Traps on removal plots captured four times more individuals than those on control plots and similar numbers to reference plots. Bee and butterfly abundance and richness were positively correlated with non-privet plant cover, diversity, and evenness and negatively correlated with privet shrub cover. Removing Chinese privet from riparian forests had a beneficial effect on insect pollinator communities five years after removal and is a relatively simple method of improving pollinator habitat. These findings provide justification for allocating resources for invasive shrub species removal to support long term conservation of these important insect groups and the ecological services they provide.

1. Introduction

Invasive plants are a severe threat to the biodiversity of forests worldwide. While directly competing with native plants for light, water, and nutrients (Morris et al., 2002), invaders also compete with native plants for floral visits from pollinators which can further limit propagation and biodiversity (McKinney and Goodell, 2010). Chinese privet, *Ligustrum sinense* Lour. (Oleaceae), is an invasive shrub widely distributed in the Southeastern U.S. In 2008, it was estimated to inhabit over 1 million ha of forest land with an unknown amount of infested land around cities, towns, and roadside or field edges (Miller et al., 2008).

Invasive shrubs like Chinese privet have the potential to affect invertebrate communities by reducing plant abundance, diversity, and host plants of specialized herbivores (Crisp et al., 1998; Siemann, 1998; Haddad et al., 2001, 2009; Biesmeijer et al., 2006). Bees (Hymenoptera: Apoidea) may be especially affected by the extensive shade privet produces and resulting reduction in herbaceous plant cover beneath it (Ghazoul, 2004; Hanula and Horn, 2011b; Ebeling et al., 2012). These insects help maintain plant communities in natural areas, which in turn impacts many ecosystem functions including water filtration and carbon sequestration (NAS, 2007). Pollinators also provide an estimated 2–3 billion dollars in pollination services each year to agricultural systems and high levels of infestation by invasive plants in forested areas near agricultural fields have the potential to decrease floral visitation rates to nearby crops (Ricketts, 2004; Losey and Vaughan, 2006; Garibaldi et al., 2013).

Previous studies examined invasive plant and native bee interactions and have reported conflicting results. Invasive plants like Chinese privet may attract more generalist bees with copious amounts of pollen and increase their abundance during their short flowering period, yet may reduce the presence of specialist bees and the rare or threatened plant species that they visit (Tepedino et al., 2008; Baskett et al., 2011). Williams et al. (2011) suggest that although bees use invasive plants in highly disturbed areas, they rarely prefer them. Still numerous other studies show that non-native invasive plants can reduce bee pollination of native plants (Grabas and Laverty, 1999; Brown et al., 2002; Ghazoul, 2004; Traveset and Richardson, 2006; Aizen et al., 2008; Vanparys et al., 2008; Muñoz and Cavieres, 2008; McKinney and Goodell, 2010; King and Sargent, 2012; Gibson et al. 2013).

Butterflies (Lepidoptera: Rhopalocera) may also be negatively affected by Chinese privet. Butterflies are one of the most recognizable insect groups to the public and they have been proposed as an umbrella taxon to detect changes in other natural communities (New, 1997). Although pesticide use and loss of habitat are factors

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that can contribute to reduced butterfly abundance and diversity, Wagner and Van Driesche (2010) regard invasive plants as the greatest threat to them in eastern North America. Unlike bees, butterfly larvae feed directly on specific host plants or groups and exotic plants only support a fraction of the species that native plants do (Tallamy and Shropshire, 2009).

Past studies have explored the role of native pollinators in the propagation of invasive plants (Bartomeus et al., 2008; Tepedino et al., 2008; Williams et al., 2011). While these interactions may be important to understand the mechanism of invasion, few studies have looked at degradation of an area due to invasion and its effect on native pollinators. Valtonen et al. (2006) found a decreased abundance and diversity of Lepidoptera in road verges inhabited by an invasive plant while shade produced by invasive shrubs has been shown to reduce presence of bees (McKinney and Goodell, 2010; Hanula and Horn, 2011b; Fiedler et al., 2012) and butterflies (Hanula and Horn, 2011a; Fiedler et al., 2012). Therefore, removing an invasive plant species may act to increase abundance and richness of native pollinator communities in the short term but little is known about long term effects. Still initial studies have produced encouraging results. Removing Chinese privet from riparian forests increased richness and abundance of both bees and butterflies for two years following treatment (Hanula and Horn, 2011a,b). Removing *Frangula alnus* from prairie fens (Fiedler et al., 2012) or invasive plants from forests on a tropical island (Florens et al., 2010) had the same short term effect.

We examined the effects of two methods for eliminating Chinese privet from riparian forests on bee and butterfly communities five years after removal. The communities on plots where privet was removed were compared to those on heavily invaded control plots and to plots with historically little or no privet invasion. We also examined how the communities changed from 2007 to 2012.

2. Material and methods

2.1. Study areas

The study sites are described in detail by Hanula et al. (2009). Briefly, four study areas were chosen within the Oconee River watershed in Northeast Georgia that were heavily infested with Chinese privet. Two of these areas, the Botanical Gardens of Georgia and Sandy Creek Nature Center, are located around Athens, Georgia in Clarke County. The other two areas, Watson Springs Forest and Oconee National Forest Scull Shoals Experimental Area, are located in Greene County. The overstory canopy of our study areas are dominated by green ash (*Fraxinus pennsylvanica*), sweet-gum (*Liquidambar styraciflua*) water oak (*Quercus nigra*), willow oak (*Quercus phellos*), box elder (*Acer negundo*), and loblolly pine (*Pinus taeda*). Also included in this study were three areas of the Oconee National Forest that had little or no privet invasion. These areas were deemed "desired future condition" plots and were included as a reference to what treatment areas might look like without privet. All three were mature riparian forests located at least 10 m from a river or stream. Two were located in Greene County along the Apalachee River and Harris Creek and the third was along Falling Creek in Oglethorpe County.

2.2. Privet removal

Chinese privet was removed by either mechanical mulching or hand-felling it on 2 ha plots in October 2005. Specifics of privet removal were reported in Hanula et al. (2009). Briefly, a GyroTrac® mulching machine was used to grind up privet on plots hereafter referred to as "mulched". After mulching, the residue was left in the plot. At the same time in nearby plots, crews with chainsaws and machetes cut privet and left the debris where it fell. The plots created in this way are referred to as "hand-felling". The stumps in both treatment plots were sprayed with either 30% triclopyr (Garlon 4®) or 30% glyphosate (Foresters®) herbicide to prevent resprouting. The herbicide used at each location was selected by the location's manager. One year later, in December 2006, sprouts and seedlings were sprayed with 2% glyphosate using back pack sprayers or mist blowers. By the next summer (2007), less than 1% of privet remained in the shrub and herbaceous layers in both treatment plots (Hanula et al., 2009).

Plant communities five years after removal were reported in Hudson (2013). Chinese privet re-infested approximately 7% of mulched plots and 3% of hand-felling plots. Non-privet herbaceous plants covered 70% of mulched plots and 60% of hand-felling plots which was higher than the 20% in control plots. Herbaceous plant cover on removal plots was similar to desired plots (70%). Species richness of herbaceous plants was also higher in removal and desired plots than control plots.

2.3. Pollinator sampling

Bees and butterflies were sampled for one week out of each month from March to October 2012 on mulched, hand-felling, control, and desired future condition plots. Blue and yellow pan traps (Solo® plastic bowls) were used to capture both groups (Campbell and Hanula, 2007). Pan traps were filled with soapy water and suspended above the ground ca. 30 cm using heavy gauge metal wire. Ten pan traps (five of each color) were placed in each 2 ha plot at five, 0.04 ha sub-plots (one blue and one yellow at each subplot). The subplots were located at the center and half the distance from the center to each corner.

Differences in the vegetation structure of removal and control plots were not expected to impact the effectiveness of pan traps. Traps were most visible below the privet canopy in control plots and were often the only source of "floral" color there. Plant cover in removal plots included tall (up to 2 m) herbaceous species as well as similar sized or taller tree saplings that reduced visibility of the bowls. Despite this, pan traps were effective for pollinators.

After each sampling period, insects were collected and stored in 70% ethyl alcohol until they could be sorted, pinned, and identified. Bees were identified using published keys (Mitchell, 1960; Gibbs, 2010) and a reference collection, and butterflies were identified using field guides (Opler and Malikul, 1992; Daniels, 2004). To account for disturbances to pan traps (by animals, weather, etc.), the numbers of bees and butterflies collected were divided by the number of bowls collected and then multiplied by 10 (the total number of bowls originally set out in each treatment at each location).

2.4. Experimental design and statistical analyses

This study was designed as a complete block experiment with locations as blocks. Treatments could not be randomly assigned due to limited access for the mulching machine, but plots were selected to be homogenous at each location so random allocation of treatments was not deemed essential. The effects of the three treatments on bee and butterfly abundance and species richness were subjected to analysis of variance (ANOVA) using the general linear model (GLM) of SAS (SAS, 2000). Means separation was achieved using the Ryan-Einot-Gabriel-Welch Quotient (REGWQ) multiple comparison procedure. Desired future condition plots were not included in any analysis due to their lack of association with a block but results are presented for comparison. Prior to analysis of variance, data were tested to insure they were normally distributed using the Shapiro–Wilks test. Only butterfly abundance

Table 1
Bees captured in 2012.

Family	Genus	Species	
Andrenidae			
	Andrena	*atlantica*	12
	Andrena	*imitatrix*	38
	Andrena	*mendica*	28
	Andrena	*miserabilis*	2
	Andrena	*morrisonella*	1
	Andrena	*nasonii*	15
	Andrena	*perplexa*	16
	Andrena	*personata*	56
	Andrena	*rubi*	16
	Andrena	*violae*	236
	Panurginus	*polytrichus*	4
Apidae			
	Anthophora	*abrupta*	1
	Apis	*mellifera*	1
	Bombus	*bimaculatus*	8
	Bombus	*impatiens*	4
	Bombus	*pennsylvanicus*	3
	Ceratina	*calcarata*	215
	Ceratina	*dupla*	51
	Ceratina	*strenua*	24
	Eucera	*atriventris*	32
	Eucera	*dubitata*	50
	Eucera	*fulvohirta*	1
	Melissodes	*bimaculatus*	10
	Melissodes	*comptoides*	1
	Melissodes	*denticulata*	12
	Melissodes	*dentriventris*	12
	Melitoma	*taurea*	1
	Nomada	*bishoppi*	4
	Nomada	*cressoni*	27
	Nomada	*dentariae*	1
	Nomada	*denticulata*	10
	Nomada	*depressa*	2
	Nomada	*illinoensis*	17
	Nomada	*luteola*	3
	Nomada	*media*	2
	Nomada	*ovata*	1
	Nomada	*perplexa*	5
	Nomada	*pygmaea*	17
	Nomada	*sayi*	28
	Nomada	*sulphurata*	3
	Ptilothrix	*bombiformis*	1
	Xylocopa	*virginica*	1
Colletidae			
	Colletes	*americanus*	1
	Hylaeus	*affinis*	1
	Hylaeus	*modestus*	2
Halictidae			
	Augochlora	*pura*	293
	Augochlorella	*aurata*	332
	Halictus	*ligatus*	8
	Halictus	*parallelus*	1
	Lasioglossum	*tegularis*	3
	Lasioglossum	*macoupinensis*	41
	Lasioglossum	*(E.)* sp.	1
	Lasioglossum	*bruneri*	138
	Lasioglossum	*coeruleus*	2
	Lasioglossum	*(D.)* sp.	1
	Lasioglossum	*imitatum*	4
	Lasioglossum	*mitchelli*	137
	Lasioglossum	*nelumbonis*	1
	Lasioglossum	*oblongum*	334
	Lasioglossum	*subviridatum*	5
	Lasioglossum	*versans*	35
	Sphecodes	*carolinus*	10
Megachilidae			
	Hoplitis	*producta*	1
	Megachile	*campanulae*	2
	Megachile	sp.	2
	Osmia	*atriventris*	1
	Osmia	*georgica*	22
	Osmia	*inspergens*	1
	Osmia	*lignaria*	3
	Osmia	*proxima*	1
	Osmia	*pumila*	58

was not normally distributed so the data were transformed using the $\log_{10}(x + 1)$ transformation.

Simple linear regression in SigmaPlot (Systat Software, 2006) was used to determine what attributes of the plant community measured in 2012 (Hudson, 2013) were correlated with bee and butterfly communities of the plots. Abundance and species richness of the bee and butterfly communities were compared to Shannon diversity and evenness of herbaceous plants and shrubs, non-privet herbaceous plant cover, non-privet shrub cover, and privet shrub cover. Abundance of bees and butterflies were log transformed for regressions.

Analysis of similarity (ANOSIM) was used to detect if bee and butterfly communities associated with control, hand-felling, mulched, and desired future condition plots were significantly dissimilar. The PAST program (Hammer et al., 2001) was used to perform the ANOSIM using the Bray–Curtis distance measure. In addition, PC-ORD was used to conduct non-metric multidimensional scaling (NMS) ordination of pollinator communities with joint plots (McCune and Mefford, 1999) using plant community characteristics measured in 2012 (Hudson 2013). We included Shannon diversity and evenness of the non-privet herbaceous plant and shrub layers, non-privet herbaceous plant cover, non-privet shrub cover, and privet shrub cover of each plot as the plant community attributes in the analyses. Two additional ordinations were used to compare bee and butterfly communities measured on these plots in 2007 (Hanula and Horn, 2011a,b) with those measured in 2012.

3. Results

We captured 2413 bees and 1616 butterflies in 2012. Collectively, 69 species of bees representing five families were captured. Some of the most common species captured were *Andrena violae* (Robertson), *Augochlora pura* (Say), *Augochlorella aurata* (Smith), *Ceratina calcarata* (Robertson), *Lasioglossum (Dialictus) bruneri* (Crawford), and *Lasioglossum (Dialictus) oblongum* (Lovell) (Table 1). Thirty-two species of butterflies were captured from six families including *Hermeuptychia sosybius* (Fabricius), *Poanes zebulon* (Boisduval and Leconte), *Larema accuis* (J.E. Smith), and *Chlosyne nycteis* (Doubleday) which were some of the most commonly captured (Table 2).

Abundance ($F_{2,6} = 23.33$ $P = 0.0015$ for bees, $F_{2,6} = 23.41$ $P = 0.0015$ for butterflies) and species richness ($F_{2,6} = 31.34$ $P = 0.0007$ for bees, $F_{2,6} = 25.16$ $P = 0.0012$ for butterflies) of pollinators were higher on plots where privet was removed than on control plots. The number of insects collected in removal plots was approximately five times higher than control plots for both groups (Fig. 1). Traps in removal plots captured more than twice as many species of bees and butterflies as those in untreated control plots regardless of method of privet removal (Fig. 1). On average, 30 species of bees and 10 species of butterflies were captured in privet removal plots while traps in control plots captured approximately 12 species of bees and 5 species of butterflies.

The number of bees captured in desired plots was lower than in removal plots, but higher than the control plots (Fig. 1). The number of bee species captured in desired future condition plots was comparable to both removal plots and twice as high as the control

Table 2
Butterflies captured in 2012.

Family	Genus	Species	
Hesperiidae			
	Achalarus	*lyciades*	2
	Ambylscirtes	*aesculapius*	10
	Amblyscirtes	*belli*	8
	Amblyscirtes	*hegon*	2
	Ancyloxypha	*numitor*	12
	Epargyreus	*clarus*	2
	Erynnis	*horatius*	3
	Erynnis	*juvenalis*	2
	Euphyes	*vestris*	2
	Lerema	*accius*	728
	Oligoria	*maculata*	2
	Poanes	*yehl*	1
	Poanes	*zabulon*	355
	Pompeius	*verna*	31
	Thorybes	*bathyllus*	1
	Wallengrenia	*egeremet*	3
Lycaenidae			
	Calycopis	*cecrops*	17
Nymphalidae			
	Chlosyne	*nycteis*	45
	Enodia	*portlandia*	3
	Euptoieta	*claudia*	1
	Hermeuptychia	*sosybius*	272
	Libytheana	*carinenta*	1
	Megisto	*viola*	1
	Phyciodes	*tharos*	9
	Polygonia	*comma*	7
	Vanessa	*atalanta*	1
Papilionidae			
	Eurytides	*marcellus*	2
	Papilio	*glaucus*	26
Pieridae			
	Anthocharis	*midea*	61
	Appias	*drusilla*	1
	Ascia	*monuste*	2
	Eurema	*nicippe*	3

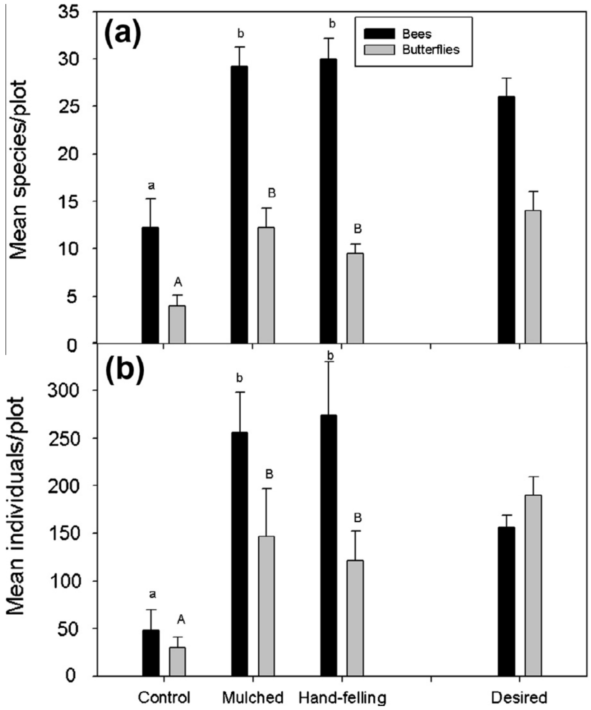

Fig. 1. Mean species richness (a) and abundance (b) of bees and butterflies in 2012 on control plots with no privet removed, privet mulched or hand-felled, and desired future condition plots (with no history of privet invasion).

plots. The number of butterflies and butterfly species captured on desired plots were similar to removal plots and higher than controls.

Bee and butterfly abundance (expressed as $\log_{10}$ of captures) and species richness increased with increasing plant cover, diversity and evenness and bee and butterfly species richness and butterfly abundance decreased with increasing privet cover (Table 3). Butterfly species richness was also positively correlated with non-privet shrub cover.

Hand-felling, mulched, and desired plots had similar bee and butterfly communities based on ANOSIM and hand-felling and mulched plots were dissimilar from control plots. Communities found in desired future condition plots were not significantly dissimilar from control plots at $\alpha = 0.05$ (Table 4). The NMS ordination of bee communities in 2012 produced a one dimensional solution with a final stress of 8.56. Chinese privet cover and herbaceous plant cover had the highest R^2 values in joint plot analyses (Table 5). The NMS ordination of butterflies in 2012 resulted in a two dimensional solution (final stress = 3.7). In joint plot analyses, privet shrub cover and herbaceous plant cover had the highest correlation with axis 1 while Shannon diversity of herbaceous plants had the highest for axis 2 (Table 4). On the NMS graph, removal plots were grouped with the desired plots (Fig. 2). One control plot was also grouped with removal plots while the remaining control plots were separated from removal and desired plots.

We included 120 species in the NMS ordination of bee communities of 2007 and 2012 which resulted in a two dimensional solution with a final stress of 8.13. Bee communities of privet removal and desired future condition plots were grouped together within years but separated by sampling year (Fig. 3). Control plots were also separate from the removal and desired future condition plots and by year of sampling. The NMS ordination of butterfly communities of 2007 and 2012 resulted in a two dimensional solution with 45 species and a final stress of 6.35. Removal plots from both sampling years were grouped together and exhibited little separation from desired future condition plots (Fig. 3). Butterfly communities on control plots were grouped separately from removal and desired plots except for one 2007 control plot.

4. Discussion

Bee and butterfly communities continued to be much more abundant and diverse on removal plots when compared to control plots five years after the invasive shrub, Chinese privet, was removed. Previous studies measured the immediate effects of removing an invasive plant from heavily infested areas on pollinator communities (Fiedler et al., 2012; Hanula and Horn, 2011a,b). The rapid positive responses they reported may have resulted from the initial forest disturbance and the early successional plant community associated with it or increased light penetration to which pollinators generally respond well (Waltz and Wallace, 2004; Campbell et al., 2007; Romey et al., 2007; Winfree et al., 2007; Proctor et al., 2012). This is the first study showing that these immediate responses of the pollinator communities to disturbance continue for at least five years despite secondary plant succession.

Searching for long-term effects of removing Chinese privet on pollinator communities based solely on abundance and species richness provides little insight into possible changes occurring in community composition. Ordination offers a means to compare community changes over time. In our study, bee communities of 2007 were distinctly different from those in 2012 even on control plots and desired future condition plots which have experienced

Table 3
Results of significant linear regressions of plant community characteristics and bee and butterfly community attributes measured in 2012.

Linear Regression Results					
Dependent (X) Plant	Independent (Y) Pollinator	*P*	R^2	Y_0	*b*
	Bees				
Plant H’	Richness	0.0043	0.4783	−0.7886	11.3819
Plant J	Richness	0.0108	0.4042	−10.5852	51.9571
Plant cover	Richness	0.0004	0.6305	9.489	0.2660
Privet cover	Richness	<0.0001	0.7055	28.4030	−0.2460
Plant H’	Log(bees)	0.0078	0.4320	0.9695	0.5285
Plant J	Log(bees)	0.0110	0.4033	0.4320	2.5355
Plant cover	Log(bees)	0.0020	0.5319	1.4697	0.0119
	Butterflies				
Plant H’	Richness	0.0008	0.5896	−5.4452	6.8649
Plant J	Richness	0.0027	0.5130	−11.6636	31.7991
Plant cover	Richness	0.0103	0.4083	3.2063	0.1163
Shrub cover	Richness	0.0101	0.4103	2.6768	0.2343
Privet cover	Richness	0.0019	0.5365	11.6262	−0.1165
Plant H’	Log(butterflies)	0.0137	0.3843	0.8540	0.4882
Plant J	Log(butterflies)	0.0312	0.3096	0.4693	2.1757
Plant cover	Log(butterflies)	0.0007	0.5974	1.2404	0.0124
Privet cover	Log(butterflies)	<0.0001	0.7185	2.21285	−0.0119

Table 4
Analysis of similarity (ANOSIM) of bee and butterfly communities in desired future condition, hand-felling, control, and mulched plots in 2012.

ANOSIM *p* values			
	Felling	Control	Mulched
Bees			
Desired	0.351	0.0551	0.1706
Felling		0.0268[*]	0.9738
Mulched		0.0299[*]	
Butterflies			
Desired	0.2861	0.0576	0.346
Felling		0.0293[*]	1
Mulched		0.0232[*]	

[*] Significant dissimilarities; $p < 0.05$.

little change in plant community characteristics (Hudson, 2013). Bee communities exhibit spatial as well as temporal variation (Williams et al., 2001). In addition, relatively little work has been done on bees in temperate forests and less on the effects of secondary and woody plant succession on them. Consequently, it is unknown whether the differences in the bee community in our study over this five year period are due to the changes in plant communities (Hudson, 2013), variation in the bee communities over time, or a combination of these.

Conversely, butterfly communities have experienced little change in the past five years. Past studies have documented a rapid response of butterflies after disturbance or invasive plant removal (Waltz and Wallace, 2004; Fiedler et al., 2012; Hanula and Horn, 2011a) yet few have documented this long term (Nelson and Wydoski, 2008; Florens et al., 2010). Our results demonstrate that this response continued for five years and that communities on privet removal plots have reached a desired condition.

At initial removal of privet, it was thought that the method of removal would have a significant impact on resulting plant and pollinator communities. Hanula and Horn (2011b) reported that piles of privet remained in hand-felling plots two years after felling and that the mulching machine used to create the mulched plot increased disturbance of the soil. Despite these two differences, hand-felling and mulched plots had similar bee communities in 2007 (Hanula and Horn, 2011b) while mulched plots had more butterflies than hand-felling plots (Hanula and Horn, 2011a). By 2012, the residual privet debris was gone and the plant communities of hand-felling and mulched plots were similar (Hudson, 2013). Consequently, there appears to be no difference in the effect of the method of removal on resulting pollinator communities after five years.

Floral abundance has been shown to be a main factor influencing abundance and diversity of pollinators (Potts et al., 2003; Hegland and Boeke, 2006; Grundel et al., 2010) yet floral abundance is relatively low in temperate forests. Hanula and Horn (2011a,b) found total plant cover was the best predictor of initial bee and butterfly diversity and abundance following privet removal. Likewise, we found that herbaceous plant cover was the best predictor of positive responses in the bee and butterfly communities five years after privet removal while both communities responded negatively to privet shrub cover. Privet removal resulted in greater non-privet herbaceous plant cover and much lower privet shrub and seedling cover than control plots (Hudson, 2013). Although privet may be an abundant floral resource in late spring, heavy infestations with dense shrub canopies severely limit abundance and richness of pollinators by decreasing availability of sunlight. Shade has been shown to have an inverse relationship with bees (Winfree et al., 2007; McKinney and Goodell, 2010) and butterflies (Sparks et al., 1996; Waltz and Wallace, 2004; Wagner and Van Driesche, 2010) probably due to a decreased richness of plants

Table 5
R^2 values for NMS ordination of bee and butterfly communities in 2012 with joint plots of plant community attributes.

	Plant Community Attributes						
	Plant H’	Plant J	Plant cover	Shrub cover	Privet cover	Shrub H’	Shrub J
Bees	0.400	0.362	0.593	0.106	0.703	0.038	0.127
Butterflies							
Axis 1	0.339	0.285	0.594	0.162	0.730	0.091	0.178
Axis 2	0.436	0.283	0.336	0.109	0.253	0.228	0.265

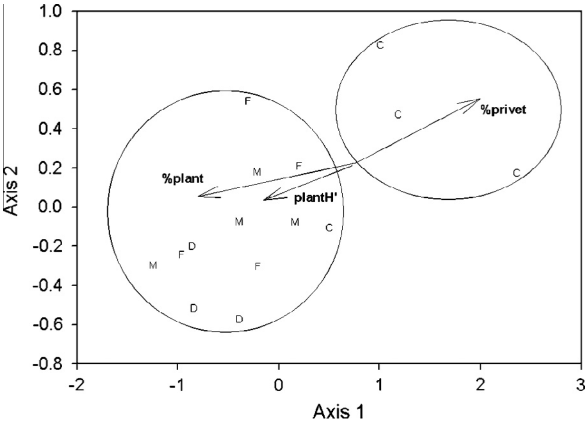

Fig. 2. NMS ordination of butterfly communities found on control plots with no privet removed, privet mulched or hand-felled, and desired future condition plots (with no history of privet invasion) in 2012 (final stress = 3.7): D = Desired future condition, F = Hand-felling, M = Mulched, C = Control.

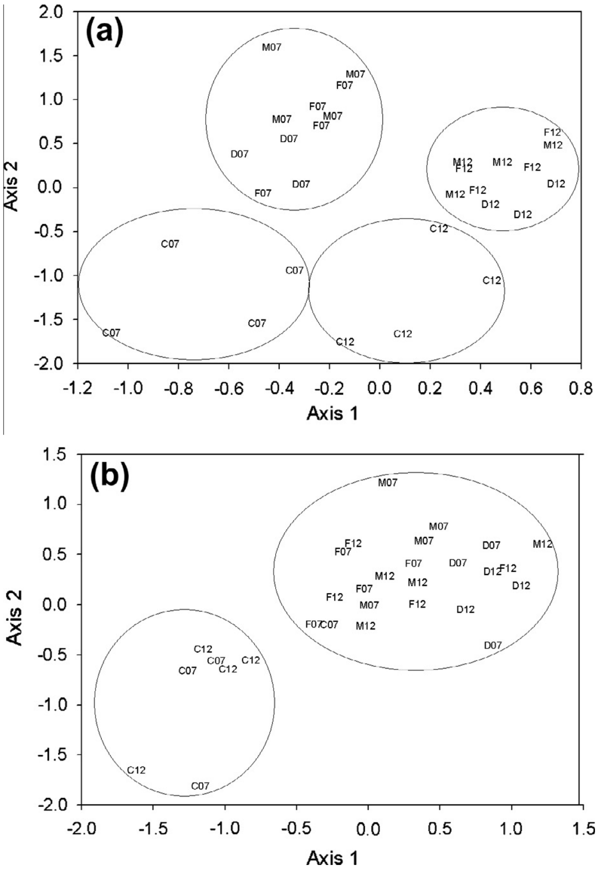

Fig. 3. NMS ordination of the bee (a, final stress = 8.17) and butterfly (b, final stress = 6.35) communities found on control plots with no privet removed, privet mulched or hand-felled, and desired future condition plots (with no history of privet invasion) in 2007 and 2012: D = Desired future condition, F = Hand-felling, M = Mulched, C = Control.

and less flowering with increased shade (Sparks et al., 1996; Grundel et al., 2010). Shade also lowers temperature which acts to decrease movement of insects by lowering their metabolism (McKinney and Goodell, 2010).

For these same reasons, we expected pollinator communities to be negatively affected by five years of woody succession on plots where privet was removed. Shrub cover on privet removal plots is currently 30–40% (Hudson, 2013), nearly double the 20% measured on these plots in 2007 (Hanula et al., 2009). The presence of woody saplings in the herbaceous layer has also increased from 2007 (Hanula et al., 2009; Hudson, 2013) and may produce additional shade for herbaceous plants and decrease the presence of bare ground which is important for many wild bees that nest there (Potts et al., 2005). However, overall abundance and species richness of bees and butterflies were similar to what was found in 2007 (Hanula and Horn, 2011a,b) and butterfly communities have experienced little change.

It is also evident that differences in the plant communities found on privet removal plots and desired future condition plots (Hudson, 2013) had little effect on the pollinator communities found here. Desired plots contained more grass species, mainly river oats *(Chasmanthium latifolium),* wild rye grass *(Elymus virginicus),* and panic grasses *(Dichanthelium* spp.). Privet removal plots contained more sedges (mostly *Carex* spp.), pokeweed (*Phytolacca americana*), and woody saplings (Hudson, 2013). It is possible that pollinators are fairly insensitive to differences in the herbaceous plant community and are mostly impacted by availability of sunlight, as mentioned above. However, it is unknown if continued succession with increased tree and shrub regeneration will be detrimental to these insects. Taki et al. (2012) found fewer bees in secondary forest when compared to primary forests in Japan so the presence of pollinators on our sites could decrease in the future if the forest becomes very dense.

Conversely, forests with dense privet infestations are not completely void of pollinators. On average, we caught ca. 100 individuals in control plots each year indicating that a privet thicket may limit passage of pollinators but does not prevent it. For example, dense edges effect movement of these insects into forests (Haddad, 1999; Ricketts, 2001; Dover and Settele, 2009), but some pollinators were able to penetrate into a dense privet thicket. Whether they find suitable habitat in these areas is unknown.

Additionally, individual control plots with less privet or storm created gaps had greater light penetrating to the forest floor and tended to be more associated with removal plots in ordinations. For example, the butterfly communities found on one control plot were more closely associated with removal plots (Fig. 2). Storms in 2012 felled some canopy trees at this site which created areas of increased sun adjacent to shady areas. Butterflies are known to be more abundant and species rich in canopy gaps of the rainforest (Spitzer et al., 1997; Hill et al., 2001) and some attribute this to variable conditions which allow for multiple behaviors of butterflies (Pryke et al., 2012). This increase may be short lived, however, as once the privet canopy closes conditions will return to pre-storm conditions.

Previous studies of pollinators in forests have surmised that increased plant cover associated with a decrease in canopy cover is associated with abundance and diversity of pollinators in these areas (Ghazoul, 2004; Campbell et al., 2007; Romey et al., 2007; Winfree et al., 2007; Florens et al., 2010; Hanula and Horn, 2011a,b; Proctor et al., 2012). Indeed, herbaceous plant cover was a primary factor correlated with pollinator communities in our study which increased dramatically following a reduction in the dense shrub layer of Chinese privet. The initial removal event benefited pollinators and the effects of that disturbance are currently sustained even after five years of secondary succession of the plant and tree communities. Chinese privet and possibly other shrub species that form dense stands beneath forest canopies may be more detrimental to native communities than herbaceous invasive plants and concentrating removal efforts on these species may be more beneficial to pollinators and the plant communities associated with them. Future work on these plots will determine at what level secondary succession and reinvasion of Chinese privet would be detrimental, and thus the frequency at which managers wishing to improve pollinator habitat would need to implement privet control.

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