

forest management

The Effects of Repeated Prescribed Fire and Thinning on Bees, Wasps, and Other Flower Visitors in the Understory and Midstory of a Temperate Forest in North Carolina

Joshua W. Campbell¹, Patrick A. Vigueira², Cynthia C. Viguiera², and Cathryn H. Greenberg³

We investigated the effects of repeated prescribed fire, mechanical thinning, and combinations of fire and mechanical thinning on pollinators and flower visitors within the herbaceous understory and midstory of a temperate forest in North Carolina. Using colored pan traps, we sampled flower visitors during the plant growing season between 2014 and 2016. We captured 5,520 flower visitors that were dominated by halictid bees and vespidae wasps. Twenty genera of bees representing at least 30 species were captured within our experimental plots. Within the forest understory, we found higher abundances and diversities of bees and other flower visitors within plots that had been treated with prescribed fire or a combination of mechanical thinning and prescribed fire compared to control plots. Within our midstory samples, we found that forest management practices did not affect the abundance of any common flower visitor species/family. However, *Augochlora pura* and *Vespula* spp. were more abundant in the midstory compared to the forest understory. Overall, our study demonstrates that repeated applications of prescribed fire maintained elevated abundances and diversity of bees and other flower-visiting insects compared to untreated plots, likely due to increased herbaceous plant diversity and enhanced quality of nesting habitat within the understory. Our results also indicate that many flower visitors utilize the midstory of a temperate forest potentially for foraging habitat.

Keywords: pollinators, forest midstory, canopy, understory, prescribed burn, *Augochlora pura*, *Vespula*

Healthy populations of native insects provide essential ecosystem functions, for example, pollination services provided by some species promote plant diversity and abundance. Bees provide the majority of pollination needs for flowering plants, including many economically important crop plants (Klein et al. 2007). Thus, the sharp decline in global pollinator abundance and diversity over the last century is cause for both environmental and economic concern (Buchmann and Nabhan 1996, Potts et al. 2010). Climate change, invasive species/diseases, habitat loss, and pesticide use have all been identified as contributing factors to declining populations (Potts et al. 2010, Burkle et al. 2013). The multifactorial nature of the decline increases the complexity of pollinating insect management, thus data-informed policy decisions are necessary to minimize the disruption of human activities on the forest ecosystem.

Anthropogenic fire has long shaped the landscape of the southeastern Appalachian Mountains. Native Americans used fire to aid in travel, hunting, defense, and agriculture (Williams 1989), and early European settlers burned forests to create grazing areas for livestock (Brose et al. 2001). However, the use of fire as a forest management tool began to fall out of favor in the 1930s, as it was viewed to be an artificial and destructive practice (Lorimer 1993). This reduced frequency in human-ignited fire has allowed a shrub cover to increase in some areas, and it may be a factor in increased red maple (*Acer rubrum* L.) and other shade-tolerant taxa in Appalachian forests (Brose et al. 2001). Modern forest management recognizes the value of frequent low-intensity fire, and managers throughout the southeastern United States regularly deploy prescribed fire and other treatments to limit fuel buildup in an effort to reduce the risk of large wildfires (McIver et al. 2013). Despite its recognized

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Affiliation: ¹University of Florida, Dept. of Entomology and Nematology, 1881 Natural Area Dr., Gainesville, FL 32611 Email: joshu.campbell@gmail.com Phone: 1-352-273-3958 ²High Point University, Biology Dept., One University Parkway, High Point, NC 27268 ³USDA Forest Service, Southern Research Station, 1577 Brevard Road, Asheville, NC 28806

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value, prescribed burning on public lands has become increasingly complex due to expanding human populations within the southern Appalachians; public concerns over cost, smoke, and the potential for fire escape can have significant influence on forest management decisions (Winter et al. 2002). Therefore, the development and investigation of surrogate fire management techniques to reduce fuel loads has become an important focus of forest ecology research (McIver et al. 2013).

Numerous arthropod groups have been used as bioindicators of ecosystem health within forest management schemes, including ground beetles (Pearce and Venier 2006, Werner and Raffa 2000), spiders (Vickers and Culin 2014), the general arthropod community (Greenberg et al. 2010), and pollinators (Campbell et al. 2007, Campbell et al. 2016). More specifically, the short-term impact of fire on bee populations has been explored in a number of geographically diverse regions: chaparral ecosystem of Greece (Lazarina et al. 2016), European temperate forests (Moretti et al. 2004), and temperate forests of Indiana (Grundel et al. 2010) and North Carolina (Campbell et al. 2007). While the ecological impacts of forest management practices have not been completely overlooked, most studies have examined arthropods immediately or shortly after treatments were applied, and thus the longer-term effects of repeated prescribed burns or fire surrogates on ecological communities remain somewhat poorly understood (Freckleton 2004).

The complex layered ecosystem of tropical forests is well documented, and thus most studies of tropical arthropod communities have appropriate sampling methods to effectively explore this stratified habitat. Thus, several studies have been conducted in tropical forests examining bees and other Hymenoptera within different strata (Bawa et al. 1985, Roubik 1993, Ramalho 2004, Nuttman et al. 2011). In contrast, the vast majority of pollinating insect research conducted within temperate forests consists exclusively of intensive ground-level sampling within the herbaceous understory. To date, only a few studies have examined the community composition of bees, wasps, and other flower visitors at different strata in temperate forests (Pucci 2008, Sobek et al. 2009, Ulyshen et al. 2010, Ulyshen et al. 2011). The impacts of temperate forest management practices on arthropod communities above the herbaceous understory have yet to be thoroughly investigated. The resulting dearth of ecologically relevant data is problematic, as forest managers make important decisions relating to pollinating insect populations with incomplete information.

We assessed how bee and other flower visitor abundance and diversity changed in response to four repeated prescribed burns (B), two mechanical thinnings (M), and a combination of one mechanical thinning followed by four repeated prescribed burns (MB) over a 15-year period, within forested plots in North Carolina. After implementing the first round of treatments (2001–2003), MB treatments were found to harbor higher abundances of bees compared to the other treatments and controls (C) (Campbell et al. 2007). We hypothesized that continued use of fuel reduction techniques would maintain greater abundances of flower-visiting insects within the MB treatments compared to C plots. In addition, we expected that B and M treatments would harbor an increased abundance of bees compared to C plots after multiple rounds of applied treatment over 15 years. We also evaluated the impact of forest fuel management, which primarily manipulates understory vegetation,

on midstory utilization by bees, wasps, and other flower-visiting insects.

Methodology

Study Site and Design

Our study was part of the USDA National Fire and Fire Surrogate Study (NFFS, McIver et al. 2013) and was conducted within the Green River Game Land (Polk County, NC, blocks 1 and 2, 35°17'9"N, 82°19'42"W, block 3, 35°15'42"N, 82°17'27"W with elevation ranging from 366–793 m [Greenberg et al. 2010]). The study area was located in three blocks (each block was a minimum of 56 ha) and is managed by the NC Wildlife Resources Commission (Figure 1). The Green River Game Land comprises 5841 ha and is situated within the Blue Ridge Physiographic Province. Our study area was dominated by oaks (*Quercus* spp.) and hickory (*Carya* spp.). Mountain laurel (*Kalmia latifolia* L.) and rhododendron (*Rhododendron maximum* L.) were common understory plants.

We used a randomized complete block design. Each of the three blocks was broken into four plots (minimum 14 ha each): one for each forest management treatment and an untreated control. The forest management treatments used in this study were (1) fuel reduction via mechanical felling (M), (2) fuel reduction via prescribed fire (B), fuel reduction via combination of mechanical felling and prescribed fire (MB), and an untreated control (C). Mechanical treatment (M and MB) cut all mountain laurel, rhododendron, and trees (>1.8 m tall and <10 cm dbh) with chainsaws, and debris was left onsite. Prescribed burns (B and MB) were conducted by various means (hand ignition using spot fire and strip-headfire techniques and spot fire via helicopter), and burns conducted in MB were completed one year after the mechanical thinning to allow for decomposition and curing in an effort to lessen fire intensity (Greenberg et al. 2010). Despite this waiting period, fire temperatures of the initial burns (measured 30 cm above ground) were hotter in the MB ($\bar{x} = 517^{\circ}\text{C}$) compared to B ($\bar{x} = 321^{\circ}\text{C}$) sites (Waldrop et al. 2010, Waldrop et al. 2016). The high intensity of the initial burn killed numerous trees and dramatically altered forest structure in MB sites. Subsequent prescribed fire applications to the MB plots were less intense compared to the

Management and Policy Implications

This research details how fuel reduction techniques in forests can affect pollinating bee and other flower visitor abundance and diversity. In this study, fuel reduction techniques that utilized fire created openings in the canopy that helped augment flower visitor abundance. In order to achieve these outcomes, repeated fire application may be necessary to create canopy gaps over time, which results in increased floral and nesting resources. Despite mechanical forest thinning not increasing bee and other flower visitor abundance, this technique did not negatively affect bee or flower visitor abundance. Although it is doubtful that a forest land-manager would make decisions or policies solely on bee and flower visitor abundance, our results suggest that managers should not be concerned that small-scale prescribed winter burns and understory thinning would negatively affect pollinators or flower visitors in North Carolina temperate forests. Conversely, it appears that intensive forest management practices are beneficial for many pollinators and other flower visitors.

initial burn (Waldrop et al. 2010). The timeline of treatment applications is described in Table 1.

Sampling Procedure

Colored pan traps filled with soapy water were used to sample pollinating insects. Colored pan traps have been shown to be a successful method for sampling bees and other flower visitors within forested habitats (Campbell and Hanula 2007, Campbell et al. 2016). Red, blue, white, and yellow bowls were placed at each corner of a 66 cm square of metal remesh (Nucoar), as illustrated in Figure 2. A bowl set (one square wire remesh with four bowls) was placed on the forest floor, and another set was hoisted into the midstory (Figure 2). Bowl sets deployed into the midstory were placed at a mean height of 29.9 ± 1.0 ft (9.1 ± 0.3 m), and height

did not differ significantly among treatments ($df=3, 20$; $F= 1.28$, $P < 0.308$). Within each treatment plot, two forest floor and two midstory bowl sets were deployed during each trapping period. At a given trapping site, a forest floor and midstory bowl set were placed within <10 meters of each other (horizontal distance). Each plot was sampled at two trapping sites that were a minimum of 50 meters apart. Bowl sets were deployed for 72 hours at monthly intervals (May/June–September/October) from 2014 to 2016. A total of 11 trapping periods were accomplished during the three-year study (three in 2014 and four in both 2015 and 2016).

Statistical Analysis

A square root or logarithmic transformation was applied to data that lacked normality (Shapiro-Wilk normality test) in order

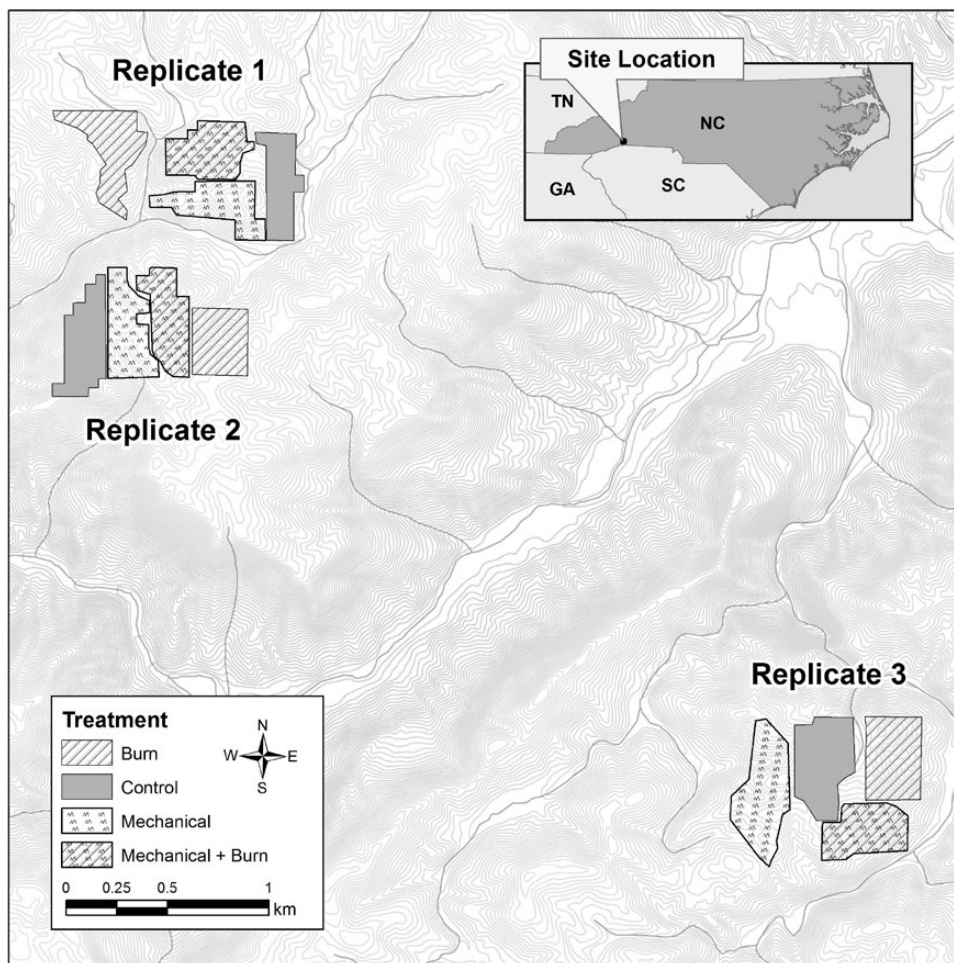


Figure 1. Map of Green River Game Land (Polk County, NC) in which experimental plots of three forest management treatments and controls were applied to three replicates or blocks.

Table 1. Dates of all applications of forest management treatments applied to experimental plots within the Green River Game Land (Polk County, NC) between 2001 and 2016. M = mechanical thinning, B = prescribed burn, MB = mechanical thinning and prescribed burn. Insect sampling was accomplished May/June–September/October from 2014 to 2016.

	Winter 2001/2002	Winter 2002/2003	Winter 2005/2006	Winter 2011/2012	Winter 2014/2015
M	x			x	
B		x	x	x	x
MB	x*	x**	x**	x**	x**

*Mechanical understory reduction only.

**Prescribed burn only.

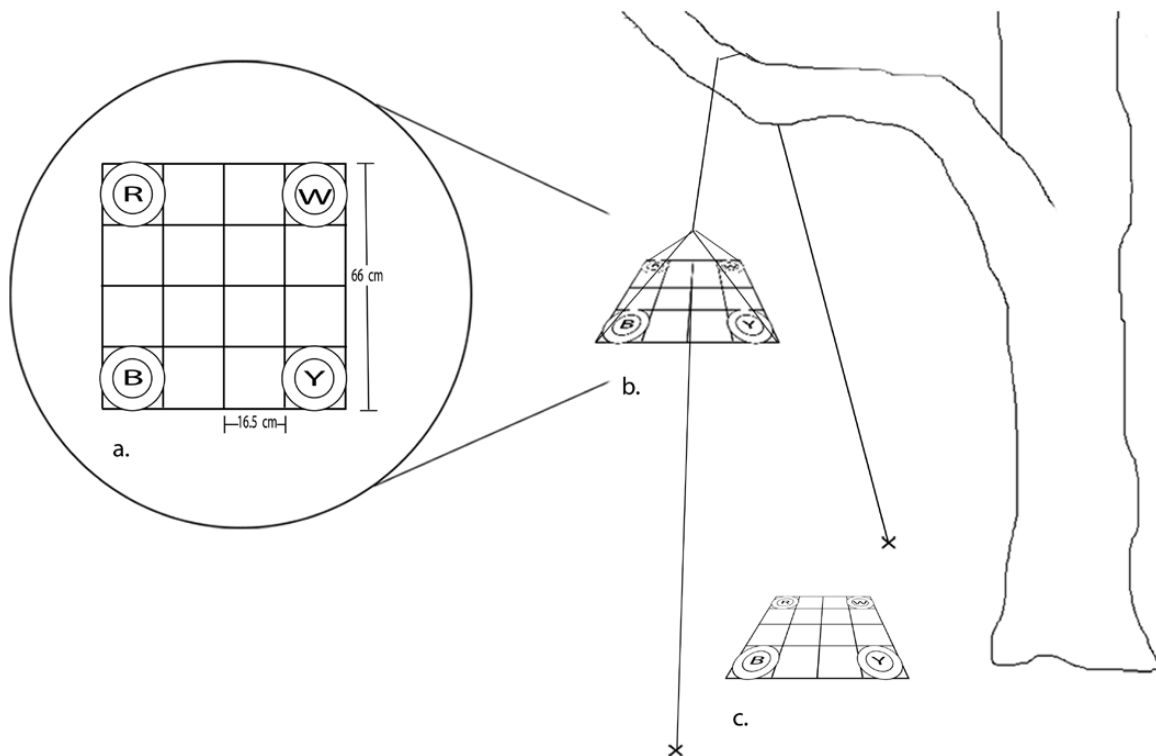


Figure 2. Schematic figure illustrating the colored pan trap setup within the midstory and on the forest floor. (a) wire remesh with 4 colored pans at each corner, R = red, B = blue, W = white, Y = yellow, (b) colored pan setup within the midstory, (c) colored pan trap setup on the forest floor.

to assure homogeneity of variance. If data could not be normalized, a Kruskal-Wallis one-way nonparametric analysis of variance test was used to test for differences between forest management treatments and the various insect abundances. For data that could be normalized, we tested our hypotheses using a general linear model to conduct one-way ANOVAs with forest management treatments as independent variables and insect abundances as dependent variables and used Tukey's multiple range test to determine differences in relative abundances and diversity of bee genera among treatments. We averaged abundances across all sampling occasions (months/years) and subsamples (trap sites) for each plot ($n = 36$). We did this because no differences were observed among the sampling years for bee abundances ($df = 2, 3$; $F = 0.70$, $P < 0.655$) or species richness ($df = 2, 3$; $F = 1.38$, $P = 0.241$) among the treatments using a split-plot analyses. We analyzed forest floor and midstory abundance data separately to examine spatial differences within treatments. Bee or wasp genera/species with fewer than 50 specimens collected were not included in abundance analyses. Two-sample t -tests or Wilcoxon rank sum tests were used to test for differences in abundance of insects between forest floor and midstory collections. All statistical tests were accomplished using Statistix 9 (Analytical Software, Tallahassee, FL, USA).

We used the Shannon-Wiener index (H') to compare diversity of bee genera among treatments and an ANOVA to compare Shannon-Weiner indices among the forest management practices. A t -test was used to determine differences between bee diversity on the forest floor compared to the midstory. We examined diversity from a genus level because some bee genera (e.g., *Lasioglossum*) were difficult to identify to species. An alpha level of 0.05 was used for all tests.

Results

We captured 5,520 flower visitors from our study sites over three years of sampling (Table 2). Bees were most commonly captured (53.9% of total captures), with 20 genera represented, followed by flower-visiting wasps (38.7%), syrphid flies (5.5%), and butterflies (1.9%). *Lasioglossum* spp. and *Augochlora pura* Say were the most common genera/species of bees captured, with *Lasioglossum* spp. and *Augochlora pura* comprising 40.3% and 51.6% of the total bee captures, respectively. Among the wasps, *Vespula* spp. (39.1% of total wasps collected), Pompilidae (31.3%), and Tiphiidae (17.4%) were the most commonly collected.

Forest Management Treatments

On the forest floor, bees were found in significantly higher abundances within MB plots compared to M and C plots ($\chi^2 = 16.17$, $df = 3$, $P < 0.0001$) (Table 3). The B plots were also significantly higher in bee abundances compared to the C plots but were not different compared to MB and M plots. However, the bulk of this trend was driven by *Lasioglossum*, one of the most common genera captured in this study. Compared to C plots, MB treatments had higher abundances of both *Lasioglossum* ($\chi^2 = 16.01$, $df = 3$, $P = 0.0002$) and *Bombus* ($\chi^2 = 10.77$, $df = 3$, $P = 0.007$) bees. The forest floor of MB plots also harbored greater bee diversity than M and C plots, as demonstrated by elevated Shannon-Weiner bee genera diversity indices ($df = 3, 34$; $F = 11.41$, $P < 0.0001$) and genera richness ($df = 3, 34$; $F = 9.63$, $P < 0.0001$) (Table 4). The abundance of common wasp families did not differ among the treatments. Within forest floor samples, syrphid flies were found in significantly lower abundances in C plots compared to all other

Table 2. List of all species captured with colored pan traps within the forest management treatments and controls. These numbers reflect both forest floor and midstory captures. M = mechanical thinning, B = prescribed burn, MB = mechanical thinning and prescribed burn, C = control.

Order	Family	Genus/species	Total captured	B	C	M	MB	
Hymenoptera (Bees)	Halictidae	<i>Agapostemon virescens</i>	4	3	0	0	1	
		<i>Augochlorella aurata</i>	16	4	0	3	9	
		<i>Augochlora pura</i>	1532	433	489	234	376	
		<i>Augochloropsis metallica</i>	1	1	0	0	0	
		<i>Halictus confusus</i>	1	0	1	0	0	
		<i>Halictus poeyillignatus</i>	7	3	0	0	4	
		<i>Lasioglossum</i> spp.	1198	368	113	201	516	
		<i>Sphecodes</i> sp.	1	1	0	0	0	
		Apidae	<i>Anthophora abrupta</i>	2	0	1	0	1
			<i>Apis mellifera</i>	7	3	1	0	3
	<i>Bombus</i> spp. (<i>B. bimaculatus</i> , <i>griseocollis</i> , <i>impatiens</i> , <i>perplexus</i>)		133	47	8	20	58	
	<i>Ceratina</i> spp. (<i>C. calcarata</i> , <i>dupla</i> , <i>strenua</i>)		44	13	2	12	17	
	<i>Holcopasites calliopsidis</i>		1	0	0	0	1	
	<i>Melissodes bimaculata</i>		2	0	0	0	2	
	<i>Melissodes denticulata</i>		1	0	0	0	1	
	<i>Svastra atripes</i>		1	0	0	0	1	
	Megachilidae		<i>Xylocopa virginica</i>	2	1	0	0	1
			<i>Hoplitis simplex</i>	1	0	0	0	1
		<i>Megachile mendica</i>	2	1	0	0	1	
		<i>Megachile mucida</i>	1	1	0	0	0	
		<i>Megachile parallella</i>	1	0	0	0	1	
		<i>Megachile relativa</i>	1	0	0	0	1	
	Andrenidae	<i>Andrena cressonii/macoupinensis</i>	2	0	0	1	1	
		<i>Andrena</i> sp.	2	1	0	0	1	
		<i>Calliopsis andreniformis</i>	4	1	0	0	3	
	Colletidae	<i>Hylaeus affinis/modestus</i>	1	1	0	0	0	
		<i>Hylaeus annulatus</i>	3	0	0	0	3	
	Hymenoptera (Wasps)	Chrysididae		46	9	16	13	8
		Crabronidae		30	8	8	8	6
		Mutillidae		79	9	34	24	12
		Pelicinidae	<i>Pelicanus polyturator</i>	2	1	0	0	1
		Pompilidae		666	169	181	189	127
		Sphecidae		40	8	4	4	24
Tiphidae			370	131	56	77	106	
Vespidae		<i>Dolichovespula maculata</i>	54	20	6	18	10	
		Eumeninae	5	1	1	0	3	
		<i>Polistes</i> spp.	4	2	0	0	2	
	<i>Vespula squamosa</i> & <i>flavopilosa</i>	833	190	192	209	242		
Diptera	Bombyliidae		1	0	0	0	1	
	Conopidae		3	1	1	0	1	
	Syrphidae		301	80	42	73	106	
Lepidoptera	Hesperiidae		103	22	9	26	46	
	Lycaenidae		7	1	0	1	5	
	Papilionidae		5	2	0	1	2	

treatments ($\chi^2 = 14.52$, $df = 3$, $P = 0.0006$). Midstory collections did not exhibit treatment effects for any of the commonly captured insects ($P > 0.05$).

Forest Floor vs. Midstory

While we did not detect any treatment effects in our midstory collections, we did observe numerous differences between the forest floor and midstory strata. Total bees were found in significantly higher abundances within the midstory compared to the forest floor ($z = 2.55$, $P = 0.01$), but this trend was largely driven by *Augochlora pura* ($z = 5.09$, $P < 0.0001$), the most common bee species captured in this study (Table 3). Among the commonly captured wasp families, Pompilidae ($z = 6.60$, $P < 0.0001$) were more abundant on the forest floor, while *Vespula* and *Dolichovespula maculata* L. were more abundant within the midstory ($df = 69$, $t = 6.65$, $P < 0.0001$; $z = 2.56$, $P = 0.05$, respectively) (Table 3). Hesperiidae, the most common butterfly family captured, was significantly more abundant within the forest floor compared to the midstory ($df = 69$, $t = 1.66$, $P = 0.01$).

Discussion

Previous studies of forests in the southeastern United States have found pollinators and flower visitors to be more abundant in fire-managed forests with a diverse understory of herbaceous and woody plants (Campbell et al. 2007, Hanula et al. 2015). Overall, bees and other flower visitors prefer forests that are open and lack dense shrub layers irrespective of geographic region (Hanula 2016). Management practices that employ prescribed fire maintain forests that are typically characterized by an understory habitat that contains a lower density of shrub cover and a greater diversity of herbaceous plant species compared to unmanaged forests (Campbell et al. 2007). This is consistent with our observation of greater bee abundance in B and MB treatment plots compared to C plots. However, we did not find an increase in flower visitor abundance in M treatments compared to C plots, possibly due to the inability of mechanical thinning to reduce the coverage of the overstory canopy, and thus the resulting lackluster recruitment of diverse vegetation on the forest floor (Waldrop et al. 2016). Unlike the M treatment plots, the B and MB treatments reduced the overstory

Table 3. Mean number (\pm SE) of common genera/species or families of flower visitors captured with colored pan traps from experimental plots from the forest floor and midstory within different forest management treatments and controls. The last two rows are the mean numbers (\pm SE) of common genera/species or families of flower visitors captured from all forest management plots combined. Columns with different letters indicate significant difference at $P = 0.05$. M = mechanical thinning, B = prescribed burn, MB = mechanical thinning and prescribed burn, C = control.

	TB	Lg	Ap	Bb	Pp	Vs	Dm	Sy	Hp
Forest floor									
C	0.8 (0.2) ^c	0.4 (0.2) ^b	0.4 (0.1)	0.02 (0.02) ^b	2.7 (0.3)	1.2 (0.4)	0.04 (0.02)	0.1 (0.06) ^b	0.1 (0.03)
M	2.8 (1.0) ^{bc}	2.1 (0.8) ^{ab}	0.4 (0.1)	0.1 (0.05) ^{ab}	2.9 (0.5)	1.4 (0.8)	0.2 (0.09)	1.0 (0.3) ^a	0.3 (0.1)
B	5.1 (2.0) ^{ab}	3.5 (1.3) ^a	0.9 (0.5)	0.3 (0.2) ^{ab}	2.5 (0.3)	1.0 (0.4)	0.05 (0.02)	0.9 (0.3) ^a	0.3 (0.09)
MB	7.6 (1.9) ^a	5.4 (1.5) ^a	1.1 (0.4)	0.4 (0.1) ^a	1.9 (0.7)	1.4 (0.7)	0.07 (0.07)	1.4 (0.4) ^a	0.6 (0.2)
Midstory									
C	8.0 (2.5)	1.2 (0.3)	6.6 (2.2)	0.1 (0.05)	0.3 (0.08)	2.1 (0.4)	0.09 (0.06)	0.5 (0.1)	0.04 (0.02)
M	4.4 (0.9)	1.1 (0.3)	3.0 (0.8)	0.2 (0.08)	0.4 (0.08)	2.3 (0.2)	0.2 (0.1)	0.3 (0.07)	0.1 (0.06)
B	10.0 (3.3)	3.4 (2.1)	5.7 (1.7)	0.8 (0.7)	0.4 (0.09)	2.8 (0.6)	0.3 (0.1)	0.6 (0.2)	0.2 (0.09)
MB	8.4 (1.6)	3.0 (1.0)	4.4 (1.4)	0.8 (0.3)	0.3 (0.04)	3.0 (0.8)	0.1 (0.05)	0.5 (0.2)	0.2 (0.1)
Forest Floor									
Midstory	4.1 (0.8) ^b	2.9 (0.6)	0.7 (0.2) ^b	0.2 (0.06)	2.5 (0.2) ^a	1.2 (0.3) ^b	0.08 (0.03) ^b	0.8 (0.2)	0.3 (0.07) ^b
	7.7 (1.1) ^a	2.2 (0.6)	4.9 (0.8) ^a	0.5 (0.2)	0.4 (0.04) ^b	2.5 (0.3) ^a	0.2 (0.05) ^a	0.5 (0.07)	0.1 (0.04) ^a

TB = total bees, Lg = *Lasioglossum* spp., Ap = *Augochlora pura*, Bb = *Bombus* spp., Pp = Pompilidae, Vs = *Vespula* spp., Dm = *Dolichovespula maculata*, Sy = Syrphidae, Hp = Hesperidiidae.

Table 4. Mean Shannon-Weiner Indices and genera richness (\pm SE) of bees captured with colored pan traps from experimental plots from the forest floor and midstory within different forest management practices and controls. The last two rows are the mean numbers (\pm SE) of bees captured from all forest management plots combined. Columns with different letters indicate significant difference at $P = 0.05$. M = mechanical thinning, B = prescribed burn, MB = mechanical thinning and prescribed burn, C = control.

	Shannon-Weiner Indices	Genera richness
Forest floor		
C	0.0259 (0.02) ^c	0.4 (0.2) ^c
M	0.1772 (0.02) ^{bc}	0.9 (0.2) ^{bc}
B	0.3139 (0.09) ^{ab}	1.3 (0.5) ^{ab}
MB	0.4751 (0.09) ^a	1.7 (0.4) ^a
Midstory		
C	0.2134 (0.04)	1.3 (0.4)
M	0.2335 (0.05)	1.7 (0.3)
B	0.2791 (0.07)	2.2 (0.4)
MB	0.3662 (0.05)	1.8 (0.3)
Forest floor		
Midstory	0.2731 (0.03)	1.1 (0.2)
	0.2501 (0.04)	1.7 (0.2)

cover, as some mature trees were killed during prescribed fires, thus improving plant diversity in the understory (Waldrop et al. 2016). It is also likely that many of the herbaceous plants that were established after prescribed burns regenerated from seed banks that can be found in forest soils (Roberts 1981). Prescribed fire can expose seed banks and, in some plants, stimulate germination with heat or smoke (Morgan and Neuenschwander 1988, Read et al. 2000). Additionally, unlike mechanical thinning, prescribed fire treatment in B and MB plots burned off the accumulated duff (leaf litter layer), leaving areas of exposed soil and effectively creating suitable nesting habitat for many insects (Waldrop et al. 2016). The removal of duff likely had profound effects on *Lasioglossum* abundance. *Lasioglossum*, the most commonly collected bee genera within our understory samples, are ground-nesters and usually need exposed soil for nest construction.

Our current study builds on previous work that characterized the short-term impact of forest management practices immediately following the establishment of the NFFS plots within the Green River Game Land (Campbell et al. 2007). Within one year of the initial fire or fire surrogate treatments, MB plots harbored a greater abundance and species richness of bees and other flower visitors compared to all other treatment and control plots (Campbell et al. 2007). Here we demonstrate that additional applications of treatments (four prescribed burns and two mechanical treatments in 15 years; see Table 1) resulted in increases in bee abundance and bee genera within MB and B plots compared to controls. Thus, many of the longer-term effects of forest management may not be immediately apparent, and multiple applications of a particular treatment over an extended period may be necessary for them to manifest. This may be especially important in forested areas that are near agricultural land. Watson et al. (2011) found that crops situated adjacent to forested habitats contained more diverse and abundant bees compared to the same crops that did not have adjacent forested habitats. Forested habitats that are near human developments and urban areas may not be eligible for prescribed burns and typically utilize other options such as mechanical thinning or herbicide use. However, frequently repeated applications, such as mechanical thinning, did not contribute to a marked increase in abundances of flower-visiting insects in our study. Despite its inability to augment flower visitor abundance, our data suggest that mechanical thinning accomplished the forest management goal of reducing fuel load without negatively impacting bee and wasp abundances (Waldrop et al. 2016). Forest thinning has been shown to increase abundance and richness of pollinators, but this included some overstory reduction (Taki et al. 2010). The mechanical thinning also had no impact on the basal area of standing trees, unlike the B and MB sites, which showed declines in basal area (Waldrop et al. 2016). Therefore, for mechanical thinning to have impacts on flower-visiting insects, a reduction in overstory canopy may be necessary.

Common wasp genera/families showed no responses to the treatments in the understory. Although *Vespula* and other wasps can occasionally be contributors to pollination of some forest

plants (Smith-Ramirez et al. 2005, Cheng et al. 2009), they are primarily predators. The lack of treatment effects on wasps in our study is likely driven by the availability of suitable nesting and nutrient resources within plots. The majority of wasps in our collections construct nests in the ground; however, many do not require bare soil in order to do so (e.g., *Vespula*). Moreover, it is likely that the availability of floral resources had a less profound effect on the abundances of wasps compared to that of bees; while adult wasps are known to utilize nectar and pollen resources, larvae primarily feed on other invertebrates collected by the adults. Despite the creation of diverse microhabitats by each management treatment, all of our plots probably had a multitude of prey items that supplied wasps with sufficient prey regardless of forest management treatment.

No differences in abundance of common bees, wasps, or other flower visitors were observed among treatments within the midstory. While some of the fire or fire surrogate treatments increased the diversity of plants in the understory and reduced canopy cover (e.g., MB and B), overall plant diversity within the midstory was largely unaffected by the treatments (Waldrop et al. 2016). Tree diversity was similar across plots, and thus we posit that the availability of nectar/pollen resources and wasp prey items would have been roughly equivalent among our treatment groups.

Although flower visitors showed no differences among forest management treatments within the midstory and variable differences within the forest floor, several genera and families exhibited clear preferences for particular vertical strata within the forest. Pompilidae nest in the ground and primarily hunt ground spiders to feed their young (Borror et al. 2005), explaining their higher abundances within the forest understory. Hesperidae primarily utilize grasses and other herbaceous vegetation for larval food, and adults visit flowering herbaceous plants for nectar (Opler and Malikul 1998). Therefore, their higher abundance within the forest floor compared to the midstory region is not unexpected.

Augochlora pura, *Vespula* spp., and *D. maculata* were found in higher abundances within the midstory collections. Over 90% of *A. pura* were collected within the midstory in this study; this observation is consistent with Ulyshen et al. (2010), who also found *A. pura* to dominate bee canopy captures in a deciduous forest in Georgia (USA). *Augochlora pura* typically nests in rotting logs and stumps of trees (Stockhammer 1966), and therefore are probably not utilizing the canopy for nesting structure. Although the majority of deciduous trees in our study area are wind pollinated, some nectar/pollen-abundant trees are partially insect pollinated (e.g., *Acer*) (Gabriel and Garrett 1984). Therefore, *A. pura* may be attracted to the midstory by the floral resources of flowering trees during parts of the spring and summer as well as by sap and honeydew (Ulyshen et al. 2010), both of which have been shown to be more abundant within forest canopies (Moran and Southwood 1982). Taken together, these data suggest that *A. pura* may be a canopy forager, allowing it to take advantage of a food niche that is underutilized by other bees. Its propensity for nesting in dead wood on the ground, a rare behavior among halictids, may allow this species to become especially prolific within forested habitats. Unlike Sobek et al.'s (2009) finding that the canopy of a temperate forest in Germany did not serve as important bee habitat, our results suggest that some bee species, like *A. pura*, potentially utilize the canopy for foraging habitat.

Vespula spp., a genus of ground-nesting wasps, was captured over 70% of the time in the midstory compared to the forest floor, which was consistent with Ulyshen et al. (2011), who also found that *Vespula* preferentially utilized the canopy compared to the forest floor of a deciduous forest in Georgia. We also found *Dolichovespula maculata*, a canopy/tree nesting species, to be more abundant in our midstory samples compared to the forest floor, likely due to the relative abundance of their preferred prey items within the canopy (Sobek et al. 2009). However, we cannot rule out the possibility that *D. maculata* were browsing the midstory for sap or honeydew.

Conclusion

Prescribed burns, thinnings, and other forest management strategies are important to maintain forest health and limit fuel build-ups that can lead to dangerous wildfires. Additionally, our results indicate that these management practices should also contribute to the maintenance of pollinator and other flower visitor populations, and therefore it is important to understand the long-term impacts of forest management practices on insect communities. Historically and in recent times, southeastern forests have been manipulated with fire and other techniques to accomplish a management goal. A more complete picture of forest flower visitor movement and response to these interventions is vitally important and would allow administrators to make pollinator-conservation-oriented management decisions in the future.

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