Old Dominion University

ODU Digital Commons

Biological Sciences Faculty Publications

Biological Sciences

2020

Apparent Resilience to Fire of Native Bee (Hymenoptera: Apoidea) Communities From Upland Longleaf Pine Forests in Louisiana and Mississippi

Sara A. Simmons Old Dominion University

Janice L. Bossart

Follow this and additional works at: https://digitalcommons.odu.edu/biology_fac_pubs



Commons

Part of the Biology Commons, Ecology and Evolutionary Biology Commons, and the Forest Biology

Original Publication Citation

Simmons, S. A., & Bossart, J. L. (2020). Apparent resilience to fire of native bee (Hymenoptera: Apoidea) communities from upland longleaf pine forests in Louisiana and Mississippi. Southeastern Naturalist, 19(3), 567-581. https://doi.org/10.1656/058.019.0316

This Article is brought to you for free and open access by the Biological Sciences at ODU Digital Commons. It has been accepted for inclusion in Biological Sciences Faculty Publications by an authorized administrator of ODU Digital Commons. For more information, please contact digitalcommons@odu.edu.



Apparent Resilience to Fire of Native Bee (Hymenoptera: Apoidea) Communities from Upland Longleaf Pine Forests in Louisiana and Mississippi

Authors: Simmons, Sara A., and Bossart, Janice L.

Source: Southeastern Naturalist, 19(3): 567-581

Published By: Eagle Hill Institute

URL: https://doi.org/10.1656/058.019.0316

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Apparent Resilience to Fire of Native Bee (Hymenoptera: Apoidea) Communities from Upland Longleaf Pine Forests in Louisiana and Mississippi

Sara A. Simmons^{1,2} and Janice L. Bossart^{1,*}

Abstract - Controlled burning is an essential tool for restoration and management of *Pinus palustris* (Longleaf Pine) habitats, yet effects of controlled burning on insect species, including pollinators, are rarely considered in conservation planning. We used blue vane traps to sample native bees (Hymenoptera: Apoidea) at recently burned and unburned sites in 2 Longleaf Pine upland forests in Mississippi and Louisiana. Our objective was to quantify short-term effects of controlled burns given fire-return intervals of 1–2 years are now regularly employed to manage Longleaf Pine woodlands. We sampled during 2016 and 2017 and collected 1777 native bees, representing 43 species. Recent fire was found to have no clear effect on species composition, richness, or community structure. Overall, bee communities from burned and unburned sites were similar. Even the community collected from a site that had remained unburned for 8 years was only marginally different from the others. These results suggest that native bee communities may be resilient to low intensity burns.

Introduction

Determining how insect communities respond to fire is critical for a comprehensive understanding of fire as a management tool in southern forests (Greene et al. 2016). Anthropogenic pressures, including certain management practices, are linked to worldwide insect declines (Sánchez-Bayo and Wyckhuys 2019). Factors triggering pollinator declines have attracted particular attention due to the essential role of pollinators in both natural and managed systems (Burkle et al. 2019, Potts et al. 2010, Winfree et al. 2009). Although prescription fires are widely viewed as beneficial by managers and policy makers, their effects can be context specific, and idiosyncratic across taxa, guilds, and trophic levels (Freeman et al. 2017). Additionally, fire-management programs generally focus on a few target taxa. Effects on insects, including the functionally important pollinators, are rarely considered.

Pinus palustris Mill. (Longleaf Pine) forests are a major conservation priority in the southeastern United States due to their dramatic decrease in extent and the many rare and declining species they harbor (Noss and Scott 1995). Recurrent fires are necessary for their long-term persistence (Andrews 1917). Historically, fires occurred at an estimated frequency of 3–10 years (Christensen 1981), and probably as frequently as every 2–4 years in some stands (Stambaugh et al. 2011). Regularly prescribed, low-intensity ground fires are now widely used to restore

Manuscript Editor: David Krementz

¹Department of Biological Sciences, Southeastern Louisiana University, Hammond, LA 70403. ²Current address - Department of Biological Sciences, Old Dominion University, Norfolk, VA 23529. *Corresponding author - jbossart@selu.edu.

and manage Longleaf Pine ecosystems (Mitchell et al. 2006). Priority taxa include game animals like the *Colinus virginianus* (L.) (Northern Bobwhite), and species of conservation concern, such as the *Picoides borealis* (Vieillot) (Red-cockaded Woodpecker), *Gopherus polyphemus* (Daudin) (Gopher Tortoise), and several other fire-associated endemics (Menges et al. 2017). Conservation management plans focused on Longleaf Pine forests often cite these high-priority species to justify burn schedules that mimic historical fire frequencies, which can be as frequent as every year (Little et al. 2014, McGrath et al. 2017). However, Longleaf Pine habitats also support diverse floral and arthropod understory communities, and these are generally overlooked when devising management strategies (Hanula et al. 2016, Noss et al. 2015). Broader understanding of how fire management affects pollinators is essential for long-term conservation of this threatened ecosystem's unique biota (Hanula et al. 2016).

In terms of richness and abundance, bees are by far the most dominant insect pollinators (Winfree 2010). How bees are impacted by fire varies depending on their foraging and nesting behaviors, and their ability to disperse (e.g., Carbone et al. 2019, Kral et al. 2017; Lazarina et al. 2016, 2017; Love and Cane 2016; Moretti et al. 2009; Ponisio et al. 2016; Simanonok and Burkle 2019). Adults and larvae of some species may be killed outright, but others, such as ground-nesting or highly mobile species, may be generally protected or able to escape from low-intensity fires (Cane and Neff 2011, Love and Cane 2016). Fire and post-fire succession can also indirectly affect bee communities by changing habitat structure and resources available. Fires likely reduce nesting sites for twig- and cavity-nesting bees by consuming coarse woody debris and forest duff (Aponte et al. 2014, Prichard et al. 2017), but tend to increase floral diversity and abundance as well as the number of nesting sites for ground-nesting species (Burkle et al. 2019, Ponisio et al. 2016). Prescription burning may thus either increase or decrease local bee community diversity, depending on the ratio of positive versus negative effects that result from the specific fire-management practices employed.

Here we report a comparative analysis of native bee communities in burned and unburned sites, replicated within and across 2 Longleaf Pine upland forests in southeast Louisiana and southwest Mississippi. Our primary objective was to examine the immediate, short-term effects of prescribed fire on bee community structure given fire frequencies of 1–2 years are now regularly employed to manage Longleaf Pine habitat. We quantify species composition, community diversity, and community similarity/dissimilarity to assess effects on communities present at each site. Only a few studies have investigated how prescribed burning impacts the local bee community in Longleaf Pine forests, and this is the first such study within Louisiana and Mississippi.

Field-Site Description

We surveyed sites in 2 forests: Sandy Hollow Wildlife Management Area (hereafter, Sandy Hollow) and Camp Shelby Joint Forces Training Center (hereafter, Camp Shelby). Both are naturally regenerating Longleaf Pine woodlands and

remnants of a system that historically occupied extensive swaths of the southeastern coastal plains. Sandy Hollow is a 1422-ha, state-managed conservation area located in Kentwood, LA. Camp Shelby, ~176 km (~110 mi) to the east in Mississippi, is a 55,559-ha section of the larger De Soto National Forest (154,589 ha). Both Sandy Hollow and Camp Shelby are open-canopy, predominantly Longleaf Pine-wiregrass communities managed with prescription burns in late winter and late spring. These upland forests are characterized by rolling hills, with generally sandy or sandy/silt soils overlying clay subsoils at depths typically greater than 2 m. Both sites are within the Southern Pine Plains and Hills (65f) Level IV ecoregion (US Environmental Protection Agency 2013). The climate is humid subtropical (Peel et al. 2007). Although Sandy Hollow is a relatively small tract of forest compared to Camp Shelby, it is the largest remaining upland Longleaf Pine forest within Louisiana's Southern Pine Hills and Plains ecoregion.

Materials and Methods

Site surveys

We selected 2 treatment and 2 unburned sites within each forest tract. Treatment sites were burned between late February and mid-March of the current fire-management season. Fire cleared most standing vegetation, other than Longleaf Pine, from burned locations, leaving varying amounts of charred woody debris on the soil surface. We observed extensive soil exposure on all recently burned patches. Unburned locations had regrowth that varied from a short, grassy understory, to brambles, taller shrubs, and small saplings. Management burns occur at regular frequencies at Sandy Hollow, generally every 13-18 months, whereas the burn schedule is less structured and less predictable at Camp Shelby. All unburned sites were 13-16 months post burn, except for 1 of the Camp Shelby sites (CU2), which hadn't been burned for 8 years. This site was initially thought to share a similar burn history as the others, but information uncovered well after sampling had ended indicated it had remained unburned due to recurring military training activities. We include collection data from this site as they provide a valuable comparison. Sites were sampled 6 times from June through November during the 2016 fire-management season at both Sandy Hollow and Camp Shelby. Two additional treatment and unburned sites were sampled in June of the 2017 burn season, but only at Sandy Hollow, where burns were more consistently and predictably applied. Replicated treatment and unburned sites within each forest were spaced a minimum of ~2 km apart. Most burn units at Sandy Hollow vary in size from 14 to 24 ha, and yearly burns are staggered across units, generating a heterogeneous habitat patchwork of unburned, and dormant/growing season burns. We determined burn histories at Sandy Hollow using site management records. Burn blocks at Camp Shelby are significantly larger, varying from 40 to >400 ha. Yearly burns are similarly staggered but create a much less heterogeneous landscape because of the much larger size of the blocks. We determined burn histories at Camp Shelby using MODIS burn maps (USDA, Forest Service, Geospatial Technology and Application Center. Salt Lake City, UT).

Trapping methods

We surveyed sites using only SpringStar® blue vane traps (Seattle, WA), which consist of a blue cross-vane top attached to a yellow bottom container. Our results are therefore conditional on those bees sampled by these traps. We established a single linear transect consisting of 4 traps at each site at least 300 m from the edge of each burn unit. In 2016, we increased the initial 4 traps to 5 and then 6 traps as the season progressed to increase numbers of bees collected. The 2017, June sampling consisted of 6 traps at each site. Individual traps were separated by 30 m. We hung traps from Shepherd's hook garden stakes at a height of ~1 m in open habitat with a sparse Longleaf Pine canopy; the traps were visible in all directions. We added a mixture of water, non-toxic antifreeze (propylene glycol), and a few drops of scentless dish soap to the collection container of each trap to capture, kill, and preserve bees. Traps remained in the field for 1 week at a time, followed by intervals of 3 weeks between sampling periods. Historic, catastrophic flooding throughout much of southeastern Louisiana prevented sampling in August 2016.

After collection, we sorted and pinned native bee specimens and then identified them to species or morphospecies based on standard dichotomous keys (e.g., Michener et al. 1994; Mitchell 1960, 1962), online identification guides (e.g., BugGuide.net, DiscoverLife.org), and comparison to museum specimens in the Louisiana State Arthropod Museum (LSAM; New Orleans, LA). Individuals of difficult groups were identified to genus and then classified based on morphospecies, e.g., *Lasioglossum* sp. 1–17, with identifying numbers unique to this study. Species and morpho species identifications were verified by personnel in the LSAM. We excluded *Apis mellifera* L. (European Honeybee) from the analysis.

Statistical analyses

We combined survey data from individual sites across sampling periods to generate a species (rows) by site (columns) abundance matrix. We analyzed data with and without the Sandy Hollow June 2017 sample. We generated rarefied species richness and diversity estimates using iNEXT (Chao et al. 2016, Hsieh et al. 2016) to standardize for comparison across samples of different sizes (Chao et al. 2014, Colwell et al. 2012). iNEXT calculates the effective number of species (Hill numbers) at q = 0 (species richness), q = 1 (Shannon diversity), and q = 2 (Simpson diversity). Extrapolated and interpolated values allow for comparison with larger and smaller overall samples, respectively. Extrapolation assumes community closure, with the number of species and their abundances remaining constant over time (Gotelli and Colwell 2011). Because few communities in nature are completely closed, extrapolated estimates may be an inflated prediction of the diversity at a larger sample size (Iknayan et al. 2014).

We used Primer 6 software to run various multivariate analyses (Clarke and Gorley 2006). Raw data were square-root transformed prior to analysis to give less weight to species that dominated the community data (Jongman et al. 1995, McCune and Grace 2002). We visualized Bray-Curtis similarities with non-metric

multidimensional scaling (NMDS), which uses an iterative process to position community samples in multidimensional space based on their similarity/dissimilarity. We tested significance of clustering in the NMDS with SIMPROF, a permutation-based test, and analyzed the contribution of different species to the overall similarity and dissimilarity between groups with SIMPER.

Results

We collected a total of 1021 individual bees representing 35 species from blue vane traps during 2016 (Table 1) and trapped an additional 756 individuals and 8 species from the single June 2017 sampling bout at Sandy Hollow. Most of the individuals collected were larger-bodied, eusocial or communal bees from the genera *Bombus* and *Melissodes*, respectively. More species of Halictidae were collected than species of the other 2 families, although these accounted for only 6% of the total abundance. Not surprisingly, given most bee species nest in the ground, ground-nesting species were dominant in the data in terms of both species and numbers collected. Very few of the species trapped nest exclusively above ground, in stems, twigs, or other cavities.

Overall diversity patterns were the same regardless of whether comparisons were only among the 2016 trap data or the Camp Shelby versus combined Sandy Hollow data. Richness-based rarefaction curves were still rising at all burn and unburned locations, indicating new species were still being trapped (Fig. 1A). Rarefied diversity estimates leveled off in all cases (Fig. 1B, C). Most had approached or were approaching an asymptote by 292, the size of the largest 2016 sample, including the SU ext and SB ext estimates. Although slightly more species were collected at CU 16, species accumulation curves for all locations had overlapping confidence intervals when extrapolated to the size of SU ext, the largest overall sample. Estimated diversity, however, was significantly higher at CU 16 than at every other site and driven by the greater rate of species collected per specimens trapped at CU2 (21 species per 103 individuals; Table 1). Notably, the CU2 community was otherwise remarkably similar to the other trap collections despite this site having remained unburned for 8 years. Nearly every species in this trap collection was additionally trapped at 1 or more of the other sites, regardless of recent burn history, and no species stood out as having benefited or suffered by being more or less abundant at this site.

Although several species were unique to burned or unburned sites, these were all collected at very low numbers (<6; Table 1). Bray–Curtis pairwise similarities among sites within forests were similar, regardless of their burn history. Similarities varied from 50% to 76% at Sandy Hollow and from 57% to 73% at Camp Shelby. Burned sites (Sandy Hollow mean = 59%, Camp Shelby mean = 61%) and unburned sites (Sandy Hollow mean = 64%, Camp Shelby mean = 58%) were no more similar to each other than were burned–unburned site pairwise similarities (mean = 64% at both Sandy Hollow and Camp Shelby). In fact, the highest community similarities were mostly burned–unburned site pairwise comparisons.

Table 1. Native bee species and their abundances collected from burned (B) and unburned (U) sites at 2 upland *Pinus palustris* (Longleaf Pine) forests, Sandy Hollow (S) and Camp Shelby (C). 1 and 2 = 2016 sampling; 3 and 4 = 2017 sampling. Data are listed by site, as totals for burned and unburned sites within forests, and as grand totals. [Table continued on following page.]

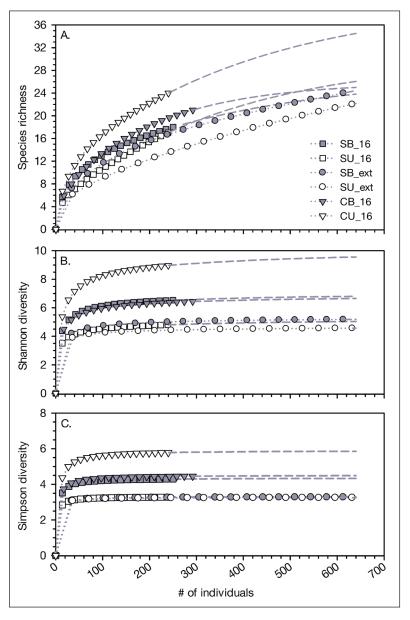
Species	Sandy Hollow									Camp S	Shelby		Sandy Hollow		mp elby		
	Burned				Unburned				Burned		Unburned			totals		tals	Grand
	SB1	SB2	SB3	SB4	SU1	SU2	SU3	SU4	CB1	CB2	CU1	CU2	В	U	В	U	totals
Apidae																	
Anthophorula micheneri Timberlake	;	6											6				6
Bombus bimaculatus Cresson	2	1								3	1		3		3	1	7
B. grisecollis (De Geer)					1									1			1
B. impatiens Cresson	11	3	32	7	4	8	20	51	18	59	6	24	53	83	77	30	243
B. pensylvanicus (De Geer)	16	33			13	32	3	3	1	12	11	10	49	51	13	21	134
Ceratina dupla Say												1				1	1
C. strenua Smith									2			9			2	9	11
Melissodes bimaculata (Lepeltier)	15	26	36	69	15	29	37	77		11	2	2	146	158	11	4	319
M. communis Cresson	58	42	72	124	52	63	44	138	48	46	60	13	296	297	94	73	760
M. denticulata Smith	3												3				3
Melitoma taurea (Say)	1	6		2	4	4	1	3	1		1	1	9	12	1	2	24
Ptilothrix bombiformis (Cresson)	2	9			1	1			36	27	37	17	11	2	63	54	130
Svastra aegis (LaBerge)									3	2	5	1			5	6	11
S. atripes (Cresson)					1					2	1			1	2	1	4
Xenoglossa strenua (Cresson)										2					2		2
Xylocopa virginica (Linnaeus)												1				1	1
Halictidae																	
Agapostemon splendens (Lepeltier)			1										1				1
Augochlora pura (Say)		1				1		3	1				1	4	1		6
Augochloropsis metallica (Fabricius	s)	1	4	1				1					6	1			7
Halictus ligatus Say	4	2	3	2	1								11	1			12
H. parallelus Say	1	1	2		1							6	4	1		6	11

2020

Table 1, continued. Sandy Camp																	
		Sandy Hollow									Camp Shelby					amp elby	
Species		Burned				Unburned				Burned Unburne			Hollow totals		totals		Grand
	SB1	SB2	SB3	SB4	SU1	SU2	SU3	SU4	CB1	CB2	CU1	CU2	В	U	В	U	totals
Lasioglossum sp. 1	1					1			3	2	9	3	1	1	5	12	19
L. sp. 2						1					2	2		1		4	5
L. sp. 3												1				1	1
L. sp. 4	2									1			2		1		3
L. sp. 5												1				1	1
L. sp. 6									1						1		1
L. sp. 7										1					1		1
L. sp. 8									1	1	1	4			2	5	7
L. sp. 9					1							2		1		2	3
L. sp. 10	1					1				4		1	1	1	4	1	7
L. sp. 11	1					2				2		1	1	2	2	1	6
L. sp. 13				1									1				1
L. sp. 14			1				1						1	1			2
L. sp. 15			4				2	6					4	8			12
L. sp. 16							2							2			2
L. sp. 17								1						1			1
Megachilidae																	
Heriades sp. 1										1					1		1
Megachile mendica (Cresson)	1				1	1				1		2	1	2	1	2	6
<i>M.</i> sp. 1												1				1	1
M. sp. 2			1										1				1
<i>M.</i> sp. 3			1										1				1
Osmia sp. 1											1					1	1
Total species	15	12	11	7	12	12	8	9	11	17	13	21	24	22	21	24	43
Total abundances	119	131	157	206	95	144	110	283	115	177	137	103	613	632	292	240	1777

Communities clustered by forest tract, and by sampling year at Sandy Hollow, but not by burn group (Fig. 2). All sites shared the same abundant species, which contributed to high global similarity within forests. Dissimilarities observed between forests (and also between 2016 and 2017 Sandy Hollow samples) were largely driven by the different relative abundances of 5 commonly trapped species (their combined contribution accounted for 45% and 50% of the dissimilarity between forests and sample years, respectively). For example, *Bombus impatiens* (Common Eastern Bumblebee) and *Ptilothrix bombiformis* (Hibiscus Bee) were relatively more abundant at Camp Shelby, whereas *Melissodes bimaculata* (Two-

Figure 1. Rarefied Hill numbers at q= 0 (Species richness; A), q = 1(Shannon diversity; B), and q = 2(Simpson diversity; C) for bees collected from burned (SB) and unburned (SU) sites at Sandy Hollow and burned (CB) and unburned (CU) sites at Camp Shelby. Data are from 2016 collections (16) or 2016 and 2017 collections combined (ext). Dashed lines indicate extrapolations.



spotted Longhorn), *M. communis* (Common Long-horned Bee), and *B. pensylvanicus* (American Bumblebee) were more abundant at Sandy Hollow (Table 1). However, 5 species trapped at generally low numbers—*Lasioglossum* sp. 1, *L.* sp. 8, *Svastra aegis*, *Ceratina strenua* (Nimble Ceratina), and *Halictus ligatus*—contributed an additional 20% to the dissimilarity between forests. These species were all either exclusively or nearly exclusively collected at one forest or the other (Table 1). Similarly, *L.* sp. 15, another species collected at low numbers, contributed an additional 6% to dissimilarity between sampling years at Sandy Hollow, where it was only collected from the 2017 trap sampling.

Discussion

Recent fire had no clear effect on species richness, composition, or community structure. Overall, bee communities from burned and unburned sites were similar. Although fire can produce distinct biotic communities, such distinctions may not be apparent in native bee communities, at least at the frequency and scale investigated here. Geographic location, rather than recent fire, produced the strongest differences in terms of unique species and relative dissimilarity between survey sites.

Studies of the effects of controlled burns on arthropod taxa have classified unburned groups as those as many as 30–75 years post burn (Andersen et al. 2014, Atchinson et al. 2018, Hanula and Wade 2003, Moretti et al. 2009, Moylett 2014).

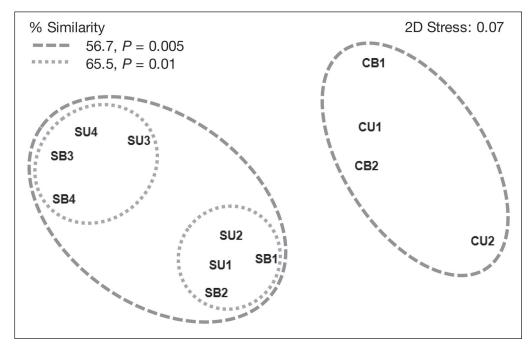


Figure 2. NMDS ordination with SIMPROF overlay showing significant clustering by forest tract and collection year (Sandy Hollow only) at 56.7% and 65.5% within-group similarity, but no clustering by burn history. Label codes are as described in Table 1.

However, in fire-dependent, Longleaf Pine ecosystems, longer burn intervals facilitate rapid succession, such that open-canopy pine woodlands become replaced by closed-canopy, broadleaf forests dominated by fire-intolerant species (Glitzenstein et al. 2012, Hanberry et al. 2018). Hence, changes in invertebrate community composition associated with extended post-burn periods develop due to fundamental changes in vegetation structure and ecosystem shifts rather than recovery after prescribed burns per se. While comparison of burned and long-unburned sites provides valuable information on community diversity associated with different ecosystems, this timescale falls far outside the fire frequencies necessary to manage for persistence of Longleaf Pine woodlands.

We focused on immediate, short-term effects of controlled burns because burn intervals of 1-2 years are now promoted and commonly employed to manage the rapid vegetative changes that occur in Longleaf Pine woodlands (e.g., Glitzenstein et al. 2012). At Sandy Hollow, for example, managed burns have occurred at an average frequency of 18 months for at least the past decade, and fire-return intervals as short as 13 or 16 months are common across individual burn units. We found no evidence that bee communities collected at recently burned sites differed from those at sites not burned for more than a year. Collections from all sites showed considerable overlap of species and also contained similar representations of both frequently and infrequently trapped species (versus, for example, one treatment or the other being dominated by only frequently trapped species). Even the community collected at the site unburned for 8 years was only marginally different from the others, and still lacked obvious evidence of any indicator species that had clearly benefitted or suffered from the extended absence of fire. Our results are generally consistent with those reported earlier by Breland (2015) and Moylett (2014), where bee communities in Longleaf Pine savannas showed either modest positive or no increase in diversity, depending on the measure used, in sites recently burned versus those either 1 or 2 years post burn. In fact, bee diversity in recently burned sites was only significantly higher when compared against control sites that were 50 years post burn (Moylett 2014).

This apparent resistance of native bee communities to low-intensity fires could be due to any number of species-specific traits and behaviors that facilitate rapid community recovery or community resilience. Ground-nesting bees, which were predominant in our trap collections, likely avoid many negative effects of disturbances occurring above the soil line. Even depths as shallow as 5–10 cm may protect ground nesters from damaging heat caused by surface fires (Cane and Neff 2011). Populations of some species, such as eusocial bees, which are active across seasons and have several generations per year, may simply be better able to quickly rebound following a fire during either the dormant or early growing season. Also, some bee species appear to have the physical capacity to move significant distances (Zurbuchen et al. 2010:table 1). Potentially, such species can change their foraging and homing behaviors and make longer trips after a fire if food is temporarily scarce. In general, high mobility fosters not only escape from fire, but also rapid recolonization of a burned site after fire, which can aid in rapid community recovery

(Moretti et al. 2006) and help mask any effects of low-intensity fire. Typical fire studies have focused on ground-dwelling insects, such as ants and beetles, caught in pitfall traps (Andersen et al. 2014, Hanula and Wade 2003). Observed responses have been mixed and complicated by differences in relative mobility. In contrast to pitfall trapping, the assemblage of species caught by blue vane traps necessarily includes those that are mobile and likely capable of moving away from low-intensity, localized fires.

At both Sandy Hollow and Camp Shelby, and probably most fire-managed woodlands, controlled burns also often leave behind unburned patches and strips of vegetation, especially along drainage channels. These residual, unburned areas potentially served as refugia, where even fire-susceptible, aboveground or shallowground nesters might survive the direct effects of fire. More generally, these are spaces to which individuals can temporarily flee to and then readily disperse back out of once conditions become favorable. Most of the species we trapped from burned sites were not yet active when the late February-March burns occurred and would have been unable to flee a fire. Some of the large-bodied, highly mobile bees, like Bombus and Melissodes, potentially recolonized these sites from undisturbed areas. However, Halictids and other small or philopatric bees, tend to have more limited dispersal capacity (Greenleaf et al. 2007; López-Uribe et al. 2015, 2019) and are less likely to have arrived from outside the burned area, especially by the time our earliest samples post fire were collected. As such, their presence within these recently burned sites could indicate survival in situ, either above ground in unburned vegetation, twigs, and forest duff, or as overwintering females and immatures nesting in soil. Bee communities appear to be astonishingly resistant to the impact of burns, with individuals actively foraging and provisioning nests immediately after even extreme fires, far inside massively burned landscapes (Love and Cane 2016).

Use of frequent fire for restoration and management of Longleaf Pine forests is widespread, well established, and necessary for the persistence of these conservation priority woodlands. But the health of any natural ecosystem is also dependent upon wild bee pollination, and even low-intensity burns have significant potential to impact the pollinator community. Consequently, understanding how fire-management practices affect wild bees in fire-dependent ecosystems is critical to achieve balance between conservation and management of the habitat with conservation and protection of the associated native bee community. Our finding that prescribed burning had no clear short-term negative effect on wild bee community diversity, a result consistent with earlier studies, suggests that current fire-management practices may be generally compatible with stability of extant native bee communities in Longleaf Pine forests. However, more expansive investigations based on multiple collection methods and multiple years of sampling over a wider seasonal range will be needed to provide a definitive picture of bee community response to fire-management regimes.

Acknowledgments

We thank personnel at the US Forest Service, Louisiana Department of Wildlife and Fisheries, The Nature Conservancy, and the Camp Shelby Environmental Office for permit assistance. Special thanks go to B. Owens and C. Carlton at the Louisiana State Arthropod Museum for assisting with specimen identification and confirmation. This study was funded in part by the Louisiana Department of Wildlife and Fisheries.

Literature Cited

- Andersen, A.N., R.R. Ribbons, M. Pettit, and C.L. Parr. 2014. Burning for biodiversity: Highly resilient ant communities respond only to strongly contrasting fire regimes in Australia's seasonal tropics. Journal of Applied Ecology 51:1406–1413.
- Andrews, E. 1917. Agency of fire in propagation of Longleaf Pines. Botanical Gazette 64:497–508.
- Aponte, C., K.G. Tolhurst, and L.T. Bennett. 2014. Repeated prescribed fires decrease stocks and change attributes of coarse woody debris in a temperate eucalypt forest. Ecological Applications 24:976–989.
- Atchinson, R.A., J. Hulcr, and A. Lucky. 2018. Managed-fire frequency significantly influences the litter arthropod community in Longleaf Pine flatwoods. Environmental Entomology 47:575–585.
- Breland, S.J.R. 2015. Bee assemblages and vegetation across a suite of restoration conditions in a fire-maintained Longleaf Pine savanna. M.Sc. Thesis. University of Georgia, Athens, GA. 103 pp.
- Burkle, L.A., M.P. Simanonok, J.S. Durney, J.A. Myers and R.T. Belote. 2019. Wildfires influence abundance, diversity, and intraspecific and interspecific trait variation of native bees and flowering plants across burned and unburned landscapes. Frontiers in Ecology and Evolution 7:252. DOI:10.3389/fevo.2019.00252.
- Cane, J.H., and J.L. Neff. 2011. Predicted fates of ground-nesting bees in soil heated by wildfire: Thermal tolerances of life stages and a survey of nesting depths. Biological Conservation 144:2631–2636.
- Carbone, L.M., J. Tavella, J.G. Pausas, and R. Aguilar. 2019. A global synthesis of fire effects on pollinators. Global Ecology and Biogeography 10:1487–1498.
- Chao, A., N.J. Gotelli, T.C. Hsieh, E.L. Sander, K.H. Ma, R.K. Colwell, and A.M. Ellison. 2014. Rarefaction and extrapolation with Hill numbers: A framework for sampling and estimation in species diversity studies. Ecological Monographs 84:45–67.
- Chao, A., K.H. Ma, and T.C. Hsieh. 2016. iNEXT (iNterpolation and EXTrapolation) online: software for interpolation and extrapolation of species diversity. Program and User's Guide. Available online at http://chao.stat.nthu.edu.tw/wordpress/software_download/. Accessed 11 October 2019.
- Christensen, N.L. 1981. Fire regimes in southeastern ecosystems. Pp. 112–136, *In* H.A. Mooney, T.M. Bonnicksen, N.L. Christensen, J.E. Lotan, and W.A. Reiners (Eds.). Proceedings of the conference: Fire regimes and ecosystem properties, December 1978, Honolulu, Hawaii. General Technical Report WO-26. US Department of Agriculture, Forest Service, Washington, DC. 594 pp.
- Clarke, K., and R. Gorley. 2006. PRIMER v6: User manual/tutorial. PRIMER-e. https://www.primer-e.com.
- Colwell, R.K., A. Chao, N.J. Gotelli, S. Lin, C.X. Mao, R.L. Chazdon, and J.T. Longino. 2012. Models and estimators linking individual-based and sample-based rarefaction, extrapolation and comparison of assemblages. Journal of Plant Ecology. 5:3–21.

- Freeman, J., L. Kobziar, E.W. Rose, and W. Cropper. 2017. A critique of the historical-fire-regime concept in conservation. Conservation Biology 31:976–985.
- Glitzenstein, J.S., D.R. Streng, R.E. Masters, K.M. Robertson, S.M. Hermann. 2012. Fire-frequency effects on vegetation in north Florida pinelands: Another look at the long-term Stoddard Fire Research Plots at Tall Timbers Research Station. Forest Ecology and Management 264:197–209.
- Gotelli, N.J., and R.K. Colwell. 2011. Estimating species richness. Pp. 39–54, *In A.E.* Magurran and B.J. McGill (Eds.). Biological Diversity: Frontiers in Measurement and Assessment. Oxford University Press, Oxford, UK. 345 pp.
- Greene R.E., R.B. Iglay, K.O. Evans, D.A. Miller, T.B. Wigley, and S.K. Riffell. 2016. A meta-analysis of biodiversity responses to management of southeastern pine forests: Opportunities for open pine conservation. Forest Ecology and Management 360:30–39.
- Greenleaf, S.S., N.M. Williams, R. Winfree, and C. Kremen. 2007. Bee foraging ranges and their relationship to body size. Oecologia 153:589–596.
- Hanberry, B.B., K. Coursey, and J.S. Kush. 2018. Structure and composition of historical Longleaf Pine ecosystems in Mississippi, USA. Human Ecology 46:241–248.
- Hanula, J.L., and D.D. Wade. 2003. Influence of long-term, dormant-season burning and fire exclusion on ground-dwelling arthropod populations in Longleaf Pine flatwoods ecosystems. Forest Ecology and Management 175:163–184.
- Hanula, J.L., M.D. Ulyshen, and S. Horn. 2016. Conserving pollinators in North American forests: A review. Natural Areas Journal 36:427–439.
- Hsieh, T., K. Ma, and A. Chao. 2016. iNEXT: An R package for rarefaction and extrapolation of species diversity (Hill numbers). Methods in Ecology and Evolution 7:1451–1456.
- Iknayan, K.J., M.W. Tingley, B.J. Furnas, and S.R. Beissinger. 2014. Detecting diversity: Emerging methods to estimate species diversity. Trends in Ecology and Evolution 29:97–106.
- Jongman, R.H., C.J. Ter Braak and O.F. Van Tongeren. 1995. Data Analysis in Community and Landscape Ecology, Vol. 2. Cambridge University Press, Cambridge, UK. 299 pp.
- Kral, K.C., R.F. Limb, J.P. Harmon, R.J. Hovick. 2017. Arthropods and fire: Previous research shaping future conservation. Rangeland Ecology and Management 70:589–598.
- Lazarina, M., S.P. Sgardelis, T. Tscheulin, A.S. Kallimanis, J. Devalez, and T. Petanidou. 2016. Bee response to fire regimes in Mediterranean pine forests: The role of nesting preference, trophic specialization, and body size. Basic and Applied Ecology 17:308–320.
- Lazarina, M., S.P. Sgardelis, T. Tscheulin, J. Devalez, V. Mizerakis, A.S. Kallimanis, S. Papakonstantinou, T. Kyriazis, and T. Petanidou. 2017. The effect of fire history in shaping diversity patterns of flower-visiting insects in post-fire Mediterranean pine forests. Biodiversity and Conservation 26:115–131.
- Little, A.R., M.M. Streich, M.J. Chamberlain, L.M. Conner and R.J. Warren. 2014. Eastern Wild Turkey reproductive ecology in frequently burned Longleaf Pine savannas. Forest Ecology and Management 331:180–187.
- López-Uribe, M.M., S.J. Morreale, C.K. Santiago, and B.N. Danforth. 2015. Nest suitability, fine-scale population structure, and male-mediated dispersal of a solitary groundnesting bee in an urban landscape. PLoS one 10:e0125719.
- López-Uribe, M.M., S. Jha, and A. Soro. 2019. A trait-based approach to predict population genetic structure in bees. Molecular Ecology 28:1919–1929.
- Love, B.G., and J.H. Cane. 2016. Limited direct effects of a massive wildfire on its sagebrush-steppe bee community. Ecological Entomology 41:317–326.
- McCune, B., and J.B. Grace. 2002. Analysis of Ecological Communities. MJM Software Design. Gleneden Beach, OR. 304 pp.

- McGrath, D.J., T.M. Terhune, II, and J.A. Martin. 2017. Northern Bobwhite habitat use in a food subsidized pyric landscape. Journal of Wildlife Management 81:919–927.
- Menges, E.S., K.N. Main, R.L. Pickert, and K. Ewing. 2017. Evaluating a fire management plan for fire regime goals in a Florida landscape. Natural Areas Journal 37:212–227.
- Michener, C.D., R.J. McGinley, and B.N. Danforth. 1994. The Bee Genera of North and Central America. Smithsonian Institution Press, Washington, DC. 209 pp.
- Mitchell, R.J., J.K. Hiers, J.J. O'Brien, S.B. Jack, and R.T. Engstrom. 2006. Silviculture that sustains: The nexus between silviculture, frequent prescribed fire, and conservation of biodiversity in Longleaf Pine forests of the southeastern United States. Canadian Journal of Forest Research 36:2724–2736.
- Mitchell, T.B. 1960. Bees of the eastern United States, Vol. I. North Carolina Agricultural Experiment Station, Technical Bulletin 141:1–538.
- Mitchell, T.B. 1962. Bees of the eastern United States, Vol. II. North Carolina Agricultural Experiment Station, Technical Bulletin 152:1–557.
- Moretti, M., P. Duelli, and M.K. Obrist. 2006. Biodiversity and resilience of arthropod communities after fire disturbance in temperate forests. Oecologia 149:312–327.
- Moretti, M., F. De Bello, S.P. Roberts, and S.G. Potts. 2009. Taxonomical vs. functional responses of bee communities to fire in two contrasting climatic regions. Journal of Animal Ecology 78:98–108.
- Moylett, H.M.C. 2014. The impact of prescribed burning on native bee communities (Hymenoptera: Apoidea: Anthophila) in Longleaf Pine (*Pinus palustris* Mill.) savannas in the North Carolina Sandhills. M.Sc. Thesis. North Carolina State University, Raleigh, NC. 96 pp.
- Noss, R.F., E.T. LaRoe, and J.M. Scott. 1995. Endangered ecosystems of the United States: A preliminary assessment of loss and degradation. Vol. 28. US Department of the Interior, National Biological Service, Washington, DC. 95 pp.
- Noss, R.F., W.J. Platt, B.A. Sorrie, A.S. Weakley, D.B. Means, J. Costanza, and R.K. Peet. 2015. How global biodiversity hotspots may go unrecognized: Lessons from the North American Coastal Plain. Diversity and Distributions 21:236–244.
- Peel, M.C., B.L. Finlayson, and T.A. McMahon. 2007. Updated world map of the Köppen-Geiger climate classification. Hydrology and Earth System Sciences Discussions 4:439–473.
- Ponisio, L.C., K. Wilkin, L.K. M'Gonigle, K. Kulhanek, L. Cook, R. Thorp, T. Griswold, and C. Kremen. 2016. Pyrodiversity begets plant-pollinator community diversity. Global Change Biology 22:1794–1808.
- Potts, S.G., J.C. Biesmeijer, C. Kremen, P. Neumann, O. Schweiger, and W.E. Kunin. 2010. Global pollinator declines: Trends, impacts, and drivers. Trends in Ecology and Evolution 25:345–353.
- Prichard, S.J. C.S. Stevens-Rumann, and P.F. Hessburg. 2017. Tamm Review: Shifting global fire regimes—Lessons from reburns and research needs. Forest Ecology and Management. 396:217–233.
- Sánchez-Bayo, F., and K.A.G Wyckhuys. 2019. Worldwide decline of the entomofauna: A review of its drivers. Biological Conservation 232:8–27.
- Simanonok, M.P., and L.A. Burkle. 2019. Nesting success of wood-cavity-nesting bees declines with increasing time since wildfire. Ecology and Evolution 9:12436–12445.
- Stambaugh, M.C., R.P. Guyette, and J.M. Marschall. 2011. Longleaf Pine (*Pinus palustris* Mill.) fire scars reveal new details of a frequent fire regime. Journal of Vegetation Science 22:1094–1104.

- US Environmental Protection Agency. 2013. Level IV Ecoregions of the Conterminous United States. Available online at https://www.epa.gov/eco-research/level-iii-and-iv-ecoregions-continental-united-states. Accessed 15 January 2020.
- Winfree, R. 2010. The conservation and restoration of wild bees. Annals of the New York Academy of Sciences 1195:169–197.
- Winfree, R., R. Aguilar, D.P. Vázquez, G. LeBuhn, M.A. Aizen. 2009. A meta-analysis of bees' responses to anthropogenic disturbance. Ecology 90:2068–2076.
- Zurbuchen, A., L. Landert, J. Klaiber, A. Müller, S. Hein, and S. Dorn. 2010. Maximum foraging ranges in solitary bees: Only few individuals have the capability to cover long foraging distances. Biological Conservation 143:669–676.