Frequent prescribed fires favour ground-nesting bees in southeastern U.S. forests

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Abstract. 1. Although most efforts to improve habitat for bees and other pollinators focus on floral resources, it is also important to consider the availability and suitability of nesting habitats in relation to various management activities.

2. We used soil emergence traps to compare the number of ground-nesting bees among treatments in a long-term fire frequency study in Florida. We regularly moved the traps, a strategy that appears to greatly improve the efficacy of this sampling approach. The experiment consisted of forested plots that have been burned annually, biennially or triennially for the past six decades as well as unburned reference plots.

3. Bee abundance was significantly lower in the unburned plots than in any of the burn treatments and was higher in annual plots than triennial plots. Bee richness was significantly higher in plots burned annually than in unburned plots. Bee Shannon’s diversity was significantly higher in plots burned biennially or triennially than in unburned plots. Evenness was significantly lower in annually burned plots than in any of the other treatments.

4. Indicator species analysis found six bee species to be significantly associated with one or more burn treatments. Four of them were strongly associated with plots burned annually or biennially while two species were significantly associated with plots burned biennially or triennially. None was significantly associated with unburned plots.

5. Our findings suggest that frequent fires generally improve habitat for ground-nesting bees in southeastern U.S. forests and that tolerances for particular burn frequencies vary by species.

Key words. Forest management, fuel reduction, nest site, pine forests, Pinus taeda.

Introduction

Given documented declines in bees and other pollinators there is much interest in understanding how various management decisions affect these insects (National Research Council, 2007; Goulson et al., 2015). Although most studies addressing these questions are focused on agricultural systems, there is strong evidence that natural habitats play an important role in sustaining healthy pollinator populations (Kim et al., 2006) as well as enhancing crop yields (Ricketts, 2004; Kremen et al., 2004). Defined broadly as ecosystems dominated by trees, forests comprise over 30% of global land cover (World Bank, 2021) and often support diverse pollinator communities (Hanula et al., 2016). Open forest conditions maintained by fire or created through management activities such as thinning have been shown to boost the availability of floral resources (Moylett et al., 2019) and increase populations of bees, butterflies, and other flower-visiting insects (Hanula et al., 2016; Galbraith et al., 2019). Forests are also likely to provide an abundance of nesting resources that may be unavailable or scarce in other land use types (Kim et al., 2006). This includes dead twigs, standing dead trees, and downed logs for species that nest in wood (Grundel et al., 2010) as well as relatively undisturbed soil for ground-nesting species. The local availability of nesting resources has been shown to strongly influence bee communities (Potts et al., 2005; Grundel et al., 2010; Carrié et al., 2018) and is thus an important consideration for improving pollinator habitat.

Many experimental studies of bee diversity involve either sampling directly from flowers using nets or passively sampling the community using coloured pan traps (Prendergast et al., 2020). These efforts provide many important insights...
into the ecology and habitat associations of bees and other flower-visiting insects but leave the question of nesting resources unresolved. While bees may prefer to nest near floral resources, many other factors are known to influence nest-site selection. Most bees are ground-nesting (Cane & Neff, 2011; Danforth et al., 2019) and, although specific requirements differ among species, they generally prefer sites with bare soil that is sloping, sun exposed, and relatively soft (Potts et al., 2005; Sardinas & Kremen, 2014). Shortages of suitable nesting sites can result in a highly clumped distribution of nests and may in part explain the gregarious nesting behaviours of some species (Wuellner, 1999). Thus, within the context of optimising pollinator habitat, efforts to provide suitable nesting habitat are needed in addition to those aimed at enhancing floral resource availability. Despite the recognised need for such efforts, there have been relatively few studies aimed at understanding the distribution of bee nests (Table 1) and particularly few involving experimental manipulations that can be used to guide management decisions (Buckles & Harmon-Threatt, 2019).

The purpose of this study was to compare the abundance and diversity of ground-nesting bees emerging from the soil in forest plots burned at different frequencies in the southeastern United States. This region historically experienced some of the highest natural fire frequencies in North America, with average return intervals of less than 2 years in some areas (Guyette et al., 2012). Prescribed fire is an important management tool throughout this region and many forests are burned regularly to control woody vegetation (Glitzenstein et al., 2012) and to decrease pest risk (Nowak et al., 2015). Although bees are generally thought to benefit from prescribed fire, due to increases in floral resource availability, it remains unknown how fire return intervals affect nest site selection. Because most species nest at sufficient depths to be protected from fire (Cane & Neff, 2011), and because fire creates patches of bare soil (Potts et al., 2005), we predicted that ground-nesting bee abundance, richness, and diversity would increase with increasing fire frequency.

We also provide a review of past studies employing soil emergence traps to sample ground-nesting bees. In addition to assessing the general utility of this approach, we were specifically interested in exploring the benefits of regularly moving the traps as opposed to leaving them in a fixed position.

Materials and methods

Study area

This study took place on Tall Timbers Research Station (TTRS), an ~1100 ha property in Leon County, Florida (30.66, −84.23). After a period of intensive agriculture, secondary forests have been regenerating on the site since the 1890s. Open stands dominated by loblolly pine (Pinus taeda L.) and shortleaf pine (Pinus echinata Mill.) dominate much of the property. These forests are maintained by prescribed fire on an approximately biennial schedule, resulting in open-canopy forest conditions and bee communities similar to those of the mature longleaf pine ecosystem endemic to the region (Ulyshen et al., 2018; Ulyshen et al., 2020). Forests burned less frequently are characterised by higher stem density as well as more shrub cover in the understory and midstory (Brockway & Lewis, 1997). Stands from which fire has been excluded are largely closed-canopy and hardwood-dominated. Although the average fire return interval on TTRS is about 2 years (Ulyshen et al. in press), some areas never or rarely experience fire. These include forests from which fire has been intentionally excluded for research purposes as well as forests growing near streams and other wet areas. We utilised plots from the Stoddard long-term fire frequency study established in 1959 (Glitzenstein et al., 2012). The plots are square-shaped and measure approximately 0.2 ha in size (Fig. 1). We sampled in plots that have been burned annually, biennially or triennially over the past 60 years as well as unburned reference plots (Fig. 1). We sampled in three plots of each treatment for a total of 12 plots. Because only one unburned plot from the original study remains, we established two additional unburned locations within a > 10-ha tract of forest that had not been burned since 1966 (Fig. 1). These plots were established in northern and southern portions of the forest and were separated by >400 m.

Bee sampling

Ground-nesting bees were sampled using soil emergence traps (bugdorm.com) as used in many previous studies (Table 1). The traps consist of small tents made of fine white polyester netting (Fig. 1). They are open on the bottom so that insects emerging from the enclosed patch (0.36 m²) of soil are directed upward and ultimately into a collection bottle situated at the top. The bottle was filled with propylene glycol to preserve the catch. The traps were pinned to the ground using tent stakes to prevent the escape or entrance of bees beneath the traps. We set up six traps within each of the 12 plots under overcast conditions on 20–21 February 2020. The traps were arranged in a linear transect within each plot with a 5 m separation between traps. Because a previously unsuccessful effort to sample the same plots yielded few bees when the traps were left in place for an entire season (i.e. 48 traps yielded just 21 bees over a six-month period, MDU, unpublished data), we chose to regularly (approximately biweekly) move the traps in the current study. This approach takes advantage of the fact that adult female bees return to their nest at night and during rainy or cloudy conditions (Danforth et al., 2019). We were thus careful to only move the traps early in the morning, in the evening, or during unfavourable weather when the bees would not be out foraging. Each move of the traps consisted of repositioning them 2 m further into the plot and perpendicular to the transect so that the entire transect moved across the plot as the season progressed. The traps were moved about every 2 weeks on the following dates in 2020: 4 March, 25–27 March, 8–10 April, 23 April, 6 May, 20–21 May, 8 June, 24–25 June and 8 July. The traps were left in place between moves and samples were collected approximately every 2 weeks and transferred into ethanol for storage. Sampling continued for 5 months, ending on 21 July 2020. The plots burned annually were either burned on 29 April or on 15 June, requiring the traps to be briefly removed on the day each plot was burned. They were returned to their original positions immediately (within a
Table 1. Chronology of studies using emergence traps to sample ground-nesting bees. Except for Kim et al. (2006), all studies used the same trap design as used in the current study.

<table>
<thead>
<tr>
<th>Study location</th>
<th>Habitat(s)</th>
<th>Trapping intensity</th>
<th>Traps moved?</th>
<th>No. bees (Individuals per trap-day)</th>
<th>Species</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>USA, California</td>
<td>Sunflower fields</td>
<td>98 pieces of rowcover fabric for one night</td>
<td>No</td>
<td>252 (2.57)</td>
<td>6</td>
<td>Kim et al. (2006)</td>
</tr>
<tr>
<td>USA, California</td>
<td>Mixed chaparral grey pine habitat</td>
<td>40 traps deployed continuously from May to Oct</td>
<td>No</td>
<td>252 (0.04)</td>
<td>15</td>
<td>Sardiñas and Kremen (2014)</td>
</tr>
<tr>
<td>USA, California</td>
<td>Hedgerows and field edges</td>
<td>480 traps deployed 1 day per period for three periods</td>
<td>Not clear</td>
<td>893 (0.62)</td>
<td>10</td>
<td>Sardiñas et al. (2016a)</td>
</tr>
<tr>
<td>USA, California</td>
<td>Hedgrows and sunflower fields</td>
<td>360 traps deployed for 1 day</td>
<td>NA</td>
<td>95 (0.26) (females, males not included)</td>
<td>10 (females, males not included)</td>
<td>Sardiñas et al. (2016b)</td>
</tr>
<tr>
<td>USA, Illinois</td>
<td>Restored prairies</td>
<td>12 traps 1 week per month for 3 months</td>
<td>Yes, moved each month</td>
<td>27 (0.11)</td>
<td>9</td>
<td>Pane and Harmon-Threatt (2017)</td>
</tr>
<tr>
<td>USA, Oregon</td>
<td>Recently harvested forest plots</td>
<td>20 traps ran continuously for 95 days</td>
<td>No</td>
<td>15 (0.01)</td>
<td>7</td>
<td>Rivers et al. (2018)</td>
</tr>
<tr>
<td>USA, Florida</td>
<td>Wildflower enhancement plots vs. fallow fields</td>
<td>160 traps, 1 day per month for 2 years (15 sample periods)</td>
<td>Yes</td>
<td>110 (0.05)</td>
<td>8 (Lasioglossum identified to genus only)</td>
<td>Cope et al. (2019)</td>
</tr>
<tr>
<td>USA, Florida</td>
<td>Upland pine vs. hammock forests</td>
<td>40 traps, 1 day per week for 21 weeks</td>
<td>Yes</td>
<td>31 (0.04)</td>
<td>7 (Lasioglossum identified to genus only)</td>
<td>Cope et al. (2019)</td>
</tr>
<tr>
<td>USA, Missouri</td>
<td>Tallgrass prairies</td>
<td>300 traps, 1 day</td>
<td>NA</td>
<td>36 (0.12)</td>
<td>7</td>
<td>Buckles and Harmon-Threatt (2019); Harmon-Threatt, personal communication</td>
</tr>
<tr>
<td>USA, Florida</td>
<td>Forests burned at different frequencies</td>
<td>72 traps, continuous sampling for 5 months</td>
<td>Yes, moved approximately every 2 wks (nine times)</td>
<td>505 (0.05)</td>
<td>30</td>
<td>Current study</td>
</tr>
</tbody>
</table>

The number of individuals per trap-day for each study was calculated by dividing the total number of individuals by the product of trap number and trapping duration.
few hours) after the fire. All collected bees were then pinned and identified to species by MDU using a combination of printed (Gibbs, 2011; Gibbs et al., 2013; Mitchell, 1960, 1962) and online keys (discoverlife.org). We followed the current nomenclature provided by discoverlife.org. Voucher specimens are deposited at the Georgia Museum of Natural History, Athens, Georgia as well as in the personal research collection of MDU.

**Analysis**

We pooled data from the six traps in each plot and across all sampling periods to calculate the total number of individuals, total number of species, Shannon’s diversity and species evenness (hereafter ‘abundance’, ‘richness’, ‘diversity’, and ‘evenness’, respectively) in each plot. We then tested how these four response variables varied among treatments using R (R Core Team, 2019). We first tested each variable for spatial autocorrelation by calculating Moran’s I in the package ape (Paradis and Schliep, 2019). Because the traps were moved regularly, we used coordinates for the centre of each plot in this analysis. To account for significant spatial autocorrelation detected for richness (see results), this variable was analysed using a generalised least square model using the Gaussian correlation function (Dormann et al., 2007) followed by multiple comparisons using the Tukey method. For abundance data, a preliminary model using the Poisson distribution was found to be overdispersed so we subsequently used negative binomial models for this response variable. This was done using the glm.nb function in the MASS package (Ripley et al., 2013). General linear models were used to model bee diversity and evenness and no transformations were necessary to satisfy assumptions. For abundance, diversity and evenness, pairwise comparisons between treatments were made using the emmeans package in R with P-values adjusted using the Tukey method (Lenth et al., 2018). Finally, to test for species associations with burn treatments, we performed indicator species analysis using the function multipatt (multilevel pattern analysis) in the package indicspecies (De Cáceres et al., 2010). We selected this approach over traditional indicator species analysis as it tests for indicator species of individual treatments as well as combinations of treatments. After an initial analysis of plot-level data found no significant indicator species, we repeated the analysis on trap-level data (pooled across sample periods) to increase sensitivity.

**Results**

Bees were captured in 54 (75%) of the 72 emergence traps used in this study. The proportion of traps yielding bees decreased as time between burns increased. While all traps placed in the annually burned plots caught bees, the percentages of traps yielding bees in the biennial, triennial, and unburned plots were 89%, 78% and 33%, respectively. In total, we collected 505 bees.
representing 30 species (Supporting Information Table S1). The three most abundant species, Lasioglossum imitatum (Smith), L. illinoense (Robertson) and L. apopkense (Robertson) accounted for over half the bees collected (Supporting Information Table S1). We detected significant spatial autocorrelation for bee richness (I = 0.27, P = 0.01) but not for abundance (I = −0.07, P = 0.89), diversity (I = 0.08, P = 0.27) or evenness (I = −0.27, P = 0.19). We captured significantly fewer bee individuals in the unburned plots (95% CI: 2.3–10.7) than in the annual (95% CI: 55.1–175.3, P < 0.0001), biennial (95% CI: 22.4–73.7, P = 0.0001) or triennial (95% CI: 13.2–44.9, P = 0.008) plots (Fig. 2). Bee abundance was highest in the annually burned plots where over 19 times more individuals were collected than in the unburned plots. Among the burn treatments, bee abundance was more than four times higher in the annual plots than in the triennial plots, a significant difference (P = 0.006) (Fig. 2). Similarly, over three times as many bee species were collected in plots burned annually than in unburned plots, a significant difference (estimate = −2.8, 95% CI: −5.6 to −0.07) (Fig. 2). Bee diversity was significantly lower in unburned plots (95% CI: 0.5–1.1) than in those burned biennially (95% CI: 1.6–2.2, P < 0.0001) or triennially (95% CI: 1.2–1.8, P = 0.01), but there was no difference in diversity between annually burned (95% CI: 1.0–1.7) and unburned plots (P = 0.11) (Fig. 2). Finally, evenness was significantly lower in annually burned plots (95% CI: 0.5–0.7) than in biennial (95% CI: 0.8–0.9, P = 0.002), triennial (95% CI: 0.7–0.9, P = 0.007) or unburned plots (95% CI: 0.7–0.9, P = 0.003) (Fig. 2). Indicator species analysis based on trap-level data found six bee species to be significantly associated with one or more burn treatments (Table 2). Four species [Andrena neonana Viereck, L. illinoense, L. imitatum, and L. pectorale (Smith)] were strongly associated with plots burned annually or biennially while two species (L. apopkense and Sphecodes heraclei Robertson) were significantly associated with plots burned biennially or triennially. We found no significant associations with unburned plots, however.

Discussion

The objective of this study was to determine how differences in fire frequency affect communities of ground-nesting bees. We captured significantly more bee individuals and species in
emergence traps placed in plots burned annually or biennially than in unburned reference plots. Bee abundance, but not richness, was also significantly higher in plots burned every 3 years than in unburned plots. Although more bees overall were captured in annual than in biennial plots, this difference was non-significant and was largely driven by large numbers of *L. imitatum* in two of the traps from the annual plots. This species is known to form eusocial colonies (Gibbs, 2011) and this likely explains the large numbers captured. The abundance of *L. imitatum* also largely explains the somewhat depressed diversity and evenness values observed from annually burned plots (Fig. 2). We acknowledge that the burns applied to the annually burned plots during this study may have affected our results through direct impacts on bees within their nests. However, we suspect that any such effect would have been minimal given the insulating properties of soil (Cane and Neff, 2011). Even if we disregard the results from this treatment, the main conclusion from this study, i.e., that frequent prescribed fire generally benefits ground-nesting bees, remains unchanged based on comparisons between the remaining three treatments.

There are several possible explanations for the positive effects of prescribed fire on ground-nesting bees observed in this study. First, frequent burns are known to result in more open conditions and was largely driven by large numbers of *L. imitatum* in two of the traps from the annual plots. This species is known to form eusocial colonies (Gibbs, 2011) and this likely explains the large numbers captured. The abundance of *L. imitatum* also largely explains the somewhat depressed diversity and evenness values observed from annually burned plots (Fig. 2). We acknowledge that the burns applied to the annually burned plots during this study may have affected our results through direct impacts on bees within their nests. However, we suspect that any such effect would have been minimal given the insulating properties of soil (Cane and Neff, 2011). Even if we disregard the results from this treatment, the main conclusion from this study, i.e., that frequent prescribed fire generally benefits ground-nesting bees, remains unchanged based on comparisons between the remaining three treatments.

This contribution adds to the number of studies using soil-emergence traps to sample ground-nesting bees (Table 1). The numbers of individuals captured per trap-day in these studies range from 0.01 to 0.62 with an average of 0.14 (Table 1). Given such low capture rates across studies, this approach requires either numerous traps or many days of sampling to yield adequate data. Capture rates appear to vary regionally and among ecosystems, with the highest reported rates (0.62 and 0.27) coming from agricultural areas in California (Sardiñas et al., 2016a; Sardiñas et al., 2016b) and the lowest published rates (0.01) coming from harvested forests in Oregon (Rivers et al., 2018). The rate of capture in this study (0.05) is quite similar to rates (0.04 and 0.05) previously reported from Florida (Cope et al., 2019). As in the current study, Cope et al. (2019) regularly moved their traps rather than leaving them in place for the entire sampling period. Because our previous attempt to use these traps without moving them resulted in a per trap day capture rate of 0.002 (MDU, unpublished data), this strategy appears to greatly increase the number of bees captured. Pane and Harmon-Threatt (2017) found the capture rate to peak during the first 24 h of trap placement, reflecting the rapid capture of adult females leaving their nests to forage. Thus, regular trap movements may represent a simple way to greatly increase the efficacy of this method. Despite biases arising from the workers of eusocial species (as we observed for *L. imitatum* in this study), soil emergence traps provide a standardised and simple way to investigate nest-site selection by ground-nesting bees.

While our results indicate that frequent fires may benefit ground-nesting bees in southeastern U.S. pine forests, this should not be taken to mean that burning frequently over large areas will optimise conditions for bees. Indeed, more research on the importance of landscape heterogeneity to pollinator populations will be needed before adequately nuanced management recommendations can be developed. A recent study reported a positive relationship between pyrodiversity and bee diversity in southeastern U.S. forests, with some species responding negatively to high burn frequency (Ulyshen et al., in press). Similar patterns were detected for butterflies in the same study. These findings suggest that while fire may locally improve conditions for ground-nesting bees, this fauna will also benefit from efforts to increase burn heterogeneity across the landscape.

**Conclusions**

Our results show frequent fire regimes improve nesting habitat for ground-nesting bees in southeastern U.S. forests. These findings nicely complement the results from past studies demonstrating the benefits of fire to floral resources and foraging bee numbers (Moylett et al., 2019). Although there were no major differences in bee communities between annually and biennially burned plots, significantly more individuals were captured in plots burned annually than in those burned biennially. Burning every 1 or 2 years may thus be the optimal burn schedule for many ground-nesting bees within our study area. Future work aimed at determining why frequent burns favour ground-nesting bees (e.g. floral resources, bare soil, etc.) would be of interest.
Acknowledgements

The authors thank Maren Johnson, Omie Coyne, Carl Blackmore and Adam Womble for help with the field work. The authors are also grateful to Jim Rivers and Alex Harmon-Threatt for sharing information about previous emergence trap studies. Finally, we thank the associate editor and five anonymous reviewers for comments which greatly improved the manuscript. This research was funded by the USDA Forest Service, Southern Research Station.

Data availability statement

The data that supports the findings of this study are available in the supplementary material of this article.

Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1: Supporting information.

References


Published 2021. This article is a U.S. Government work and is in the public domain in the USA. Insect Conservation and Diversity, 14, 527–534


Accepted 19 February 2021

Editor/associate editor: Laurence Packer