

# Pyrodiversity promotes pollinator diversity in a fire-adapted landscape

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Fire is a key determinant of vegetation structure and composition in ecosystems worldwide and is therefore an important management tool. The “pyrodiversity hypothesis”, which postulates that biodiversity will increase as fire diversity increases, remains largely untested for pollinators, a group of high conservation concern. We tested the relationship between pollinator diversity and pyrodiversity based on a decade of burn history in Florida, as well as testing other parameters, including burn frequency, the percentage of area burned during the year of sampling, canopy openness, and various plant metrics. Both bees and butterflies responded positively to pyrodiversity and to the percentage of area burned during the year of sampling. In addition, our results indicate that pollinators, especially butterflies, may be sensitive to high burn frequency. Our findings reveal the important role fire history plays in shaping pollinator communities and demonstrate that increasing burn heterogeneity can benefit this fauna in fire-managed landscapes.

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One of the most influential concepts in conservation biology is the “habitat heterogeneity hypothesis”, which predicts that greater heterogeneity will benefit biodiversity by increasing available niche space, providing refugia, and increasing the probability of speciation events (Tews *et al.* 2004; Stein *et al.* 2014). Although habitat heterogeneity has been shown to enhance the biodiversity of many taxa, some species exhibit the opposite response, possibly because they experience heterogeneity as fragmentation (Tews *et al.* 2004). Most research on this question has focused primarily on plants and vertebrates, while studies that concentrate on invertebrates remain comparatively infrequent (Tews *et al.* 2004).

Fire is a key source of habitat heterogeneity in many parts of the world, where it strongly influences both vegetation structure and composition (He *et al.* 2019). Fire-prone landscapes consist of a patchwork of unique burn histories, differing in burn frequency, severity, seasonality, and time since fire. As a special subset of the “habitat heterogeneity hypothesis”, the “pyrodiversity hypothesis” posits that high fire diversity will promote high biodiversity (Martin and Sapsis 1992). Fire alters vegetation structure and acts as an ecological filter on plant communities (Cavender-Bares and Reich 2012), and there is strong empirical evidence that landscapes with high pyrodiversity support high plant diversity (He *et al.* 2019). In contrast, few tests of the pyrodiversity hypothesis involving insects – and especially pollinators – have been conducted (Ponisio *et al.* 2016). Indeed, a recent global synthesis of fire effects on pollinators recognized the lack of information on how spatial heterogeneity of fire history affects pollinator populations as a major knowledge gap (Carbone *et al.* 2019).

The Coastal Plain of the southeastern US is characterized by a highly productive subtropical climate and experiences one of the highest fire frequencies in North America. Fire frequency is among the primary determinants of forest structure (Heyward 1939) and plant community composition (Brockway and Lewis 1997) throughout the region. Short fire return intervals (~2 years) are required to maintain the open conditions and high herbaceous plant diversity characteristic of the once-dominant longleaf pine (*Pinus palustris*) ecosystem, with plant species richness increasing with decreasing return interval (Glitzenstein *et al.* 2003). Less-frequent fires result in the displacement of herbaceous plants by shrubs and an absence of fire results in closed hardwood-dominated forests. Although previous studies reported positive responses of bees to prescribed fire in the region, presumably due to increases in floral resource availability following burns (Moylett *et al.* 2019), as in most regions, the importance of burn heterogeneity to pollinators remains largely unexamined in the southeastern US.

Here, we explore how fire diversity and frequency over the past decade affect bee and butterfly communities in a fire-managed open pine forest in Florida. We also consider the influence of local factors, such as canopy openness and vegetation metrics, on this fauna. We hypothesized that, at the community level, bees and butterflies would both respond positively to burn diversity and negatively to burn frequency. We further predicted that butterflies, which are generally confined to their host plants while in immature stages, and aboveground nesting bee species would be more sensitive to fire than would ground-nesting bees.

## Methods

### Study area and design

This work took place on Tall Timbers Research Station (TTRS), an ~1100-ha property in Leon County, Florida

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(WebFigure 1). This region, the “Red Hills”, is characterized by clayey ultisols and experiences a subtropical climate with a mean annual temperature of 19.6°C and a mean annual rainfall of 134.9 cm (www.usclimatedata.com). Forests have been regenerating on TTRS since the 1890s after a long history of intensive agriculture and are subjected to periodic light thinning operations using individual tree harvest methods (Neel *et al.* 2011). The property consists of numerous burn units of varying size that are burned in the late winter to early summer months on a schedule determined by various management or research objectives. While some units are burned every year, most are burned approximately biennially, resulting in open loblolly pine (*Pinus taeda*) stands similar in structure to the longleaf pine ecosystem that historically dominated the region. Less frequent burns result in dense understory vegetation dominated by woody shrubs and a gradual displacement of open pine-dominated forests by more closed-canopy hardwood-dominated stands (WebFigure 1). Due to the high burn frequency, fires throughout the region are typically low-severity ground fires.

We established 26 sampling locations within the boundaries of TTRS, all within the open pine-dominated forests described above (WebFigure 1). To ensure that a wide range of fire histories was represented among these locations, we prepared a preliminary map of burn frequency over the previous decade to visually identify areas with low, medium, and high variability of fire history. We then used a stratified random sampling approach in ArcGIS (www.esri.com) to select plots within these areas. The random selection process was limited to areas at least 250 m away from the property boundaries and major waterbodies.

### Fire history and land-use metrics

We used ArcGIS to calculate four fire-history metrics (described below) within a 250-m radius (ie 19.63-ha circular areas) of each of our sampling locations. We used annual burn layers for TTRS from 2007 to 2017 (including the decade before our sampling took place) for these calculations. These 11 layers were combined using the union tool in ArcGIS, with non-overlapping burn boundaries resulting in an output layer consisting of multiple polygons. Each resulting polygon was assigned a fire history based on whether it was burned (1) or not burned (0) for each year over this period of time, identified by a sequence of 1s and 0s (Figure 1); therefore, each unique sequence represents a unique burn history over the 11-year period assessed in this study (113 sequences were identified in total). The first pyrodiversity metric, “burn richness”, was calculated as the number of unique burn histories within the 250-m radius of each sampling location (burn richness ranged from 4 to 26, with an average of ~11). The second pyrodiversity metric, “burn diversity”, was based on the equation for Shannon’s diversity index  $H$ :

$$H = - \sum_{i=1}^S (p_i \ln p_i) \quad \text{Equation 1,}$$

where  $S$  is the number of unique burn histories and  $p_i$  is the proportion of the total area represented by burn history  $i$ . Burn diversity therefore takes into account both the number of unique burn histories and the relative size of each within the 250-m radius surrounding our sampling locations. We also calculated average “burn frequency” around our sampling locations. After first calculating the number of years each polygon had been burned over the past 11 years, we then calculated the average burn frequency within 250 m by multiplying each polygon’s burn frequency by its area, summing these products across all polygons, and then dividing this sum by the total area within the 250-m radius (burn frequency ranged from 3.4 to 6.8, with an average of ~5). Finally, we calculated the “percentage of area burned in 2017”, which reflects how much of the area surrounding each sampling location was burned the year sampling took place. All roads and waterbodies were excluded from these calculations. In addition, to eliminate potentially spurious polygons resulting from negligible deviations in burn boundaries over time, all calculations were made after excluding polygons <0.0025 ha.

### Pollinator sampling

To sample pollinators, a row of three bowls was established (yellow, white, and blue) at each location with 5 m between bowls. The bowls were filled with soapy water and were supported ~30 cm above the ground on wire stands. Although more effective for some groups of bees than others, pan traps provide a highly standardized and productive method for broadly sampling the pollinator fauna, and are a reliable method for sampling pollinators in the open pine forests of the southeastern US (Ulyshen *et al.* 2020). Traps were operated continuously at each location during the following 3-day periods in 2017: 14–17 February, 7–10 March, 4–7 April, 2–5 May, 30 May–2 June, 28 June–1 July, 25–28 July, and 12–15 September. All captured bees and butterflies were mounted and identified to species (WebTable 1).

### Plant data and canopy openness

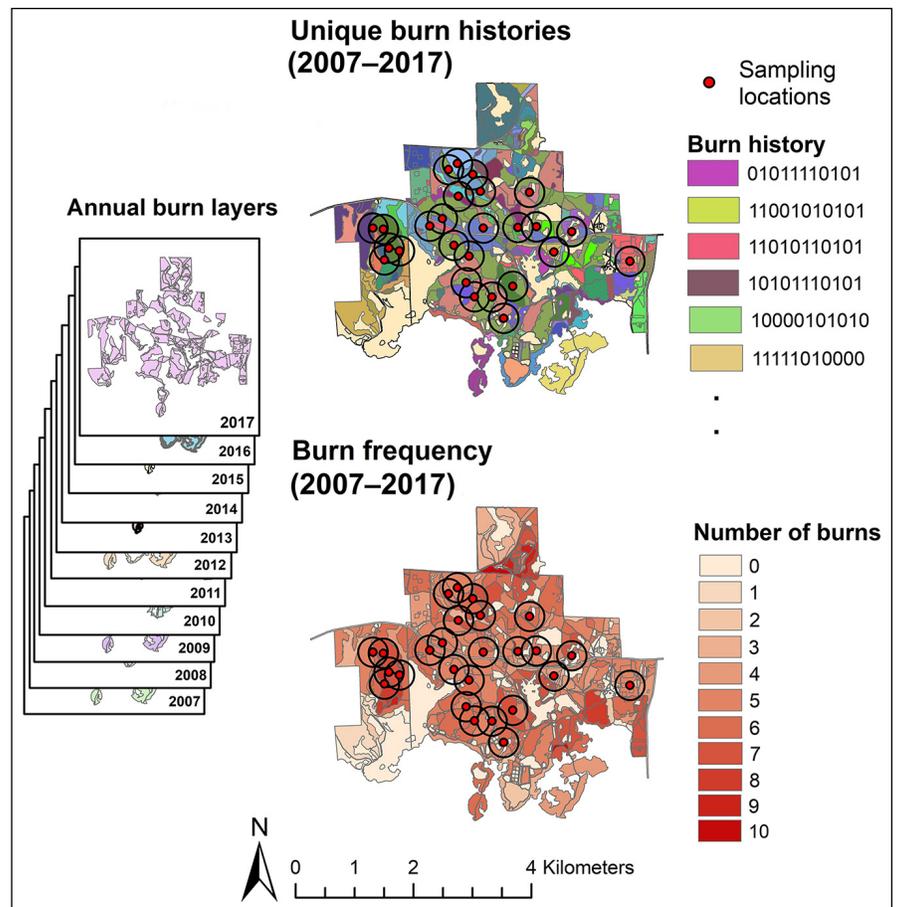
Data on plant cover and richness were collected from 10-m × 10-m square plots centered on each bee sampling location (WebPanel 1). Average maximum plant height was calculated from measurements made at the centers of the four sides of the square plots. Percent bare ground was based on observations made every 0.5 m around the perimeter of each plot (WebPanel 1). To estimate the number of plant species present, a 1-m<sup>2</sup> quadrat was haphazardly placed at two locations within each plot and, following Dell *et al.* (2017), the cumulative number of species (identified on site) was tallied for five categories: grasses, legumes, asters, other forbs (ie not legumes or asters), and shrubs. To collect data on canopy openness, hemispherical images of the canopy were taken with a camera outfitted with a fisheye lens mounted on a tripod at 1 m above ground level after leaf

expansion. One image was taken at each of the three bowl positions within each sampling location and canopy openness was calculated using WinSCANOPY software ([www.regeninstruments.com](http://www.regeninstruments.com)). We calculated average canopy openness from the three images taken at each sampling location.

### Data analysis

We calculated total bee and butterfly abundance (number of individuals), richness (number of species), and Shannon's diversity (see equation above) for each sampling location after pooling across sample periods. After testing each of these metrics for spatial autocorrelation by calculating Moran's  $I$  using the R package *ape* (Paradis and Schliep 2018), we developed a set of a priori candidate models to test which fire, canopy openness, and plant parameters most strongly influence pollinator communities, with bees and butterflies analyzed separately. To simplify model selection, the seven plant metrics (see above) were reduced to two with principal component analysis (PCA) using PC-ORD (McCune and Mefford 2011). The first axis was positively correlated with plant height ( $r = 0.65$ ) and negatively correlated with the richness of legumes ( $r = -0.83$ ), asters ( $r = -0.74$ ), and grasses ( $r = -0.72$ ). The second axis was positively correlated with bare ground ( $r = 0.81$ ) and the richness of "other forbs" ( $r = 0.71$ ).

Candidate models included one of the four fire metrics (burn richness, diversity, and frequency over the past 11 years, and percent burned in 2017) and all possible combinations of canopy openness and plant PCA axes 1 and 2. We also included models consisting of each fire parameter in isolation and all of the other parameter combinations without fire parameters included, for a total of 39 candidate models (WebTable 2). For bee abundance, initial general linear models (GLM) based on the Poisson distribution found the data (overall and for individual taxa) to be overdispersed, and therefore the negative binomial distribution was used instead. We used the Poisson distribution for bee richness and the normal distribution for models of bee diversity. The Box-Cox transformation ( $\lambda = 4$ ) was used on bee diversity data to normalize residuals. To account for significant spatial autocorrelation detected for butterfly richness, diversity, and abundance (see results), these metrics were analyzed with generalized least square models using the Gaussian correlation function (Dormann *et al.* 2007). After confirming there was no multicollinearity among predictors (variance inflation factor [VIF] < 2 in all cases), the models were ranked by explanatory power using Akaike's information criterion adjusted for small sample sizes (AICc), using the



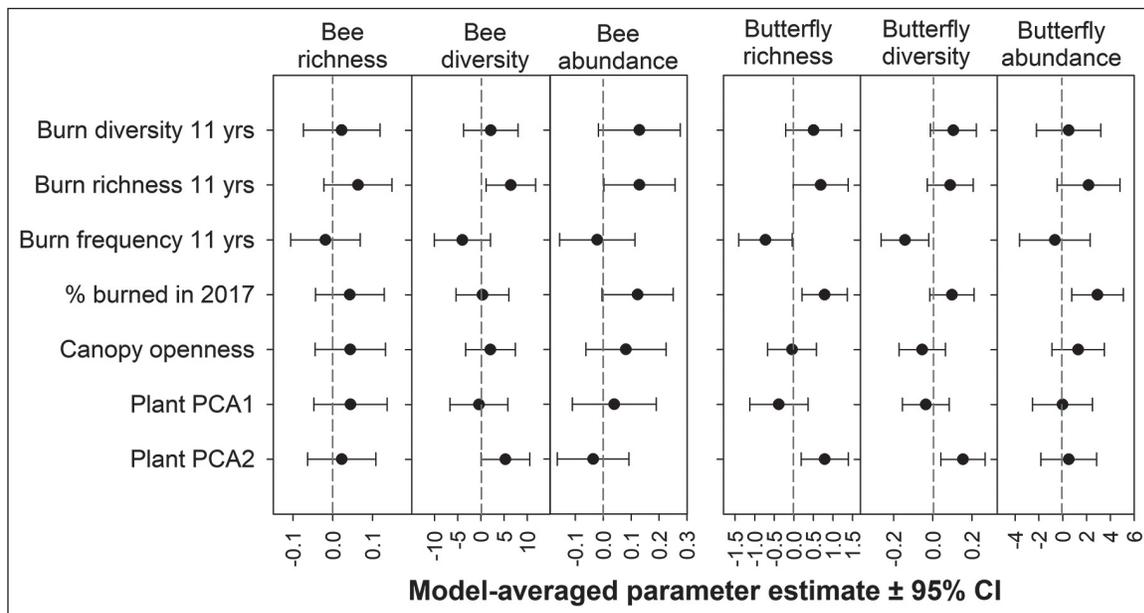
**Figure 1.** Annual burn records from the decade before bees were sampled were used to identify unique burn histories (sequences of 1s and 0s representing burned and unburned years, respectively). These were then used to calculate burn richness, burn diversity, and average burn frequency within 250 m of each sampling location.

*MuMIn* package (Barton 2019). To directly compare parameter estimates for each response variable, we standardized all parameters by calculating  $z$ -scores (ie subtracting the mean from each data point and dividing by the standard deviation). We then calculated model-averaged estimates and 95% confidence intervals (CIs) from all parameters within the 95% confidence set of best models (ie that excluded all models appearing after the cumulative Akaike weight exceeded 0.95; WebTable 3; Symonds and Moussalli 2011). The same analyses were carried out for the 11 individual bee species that were represented by at least 100 individuals. No single butterfly species was abundant enough to analyze individually. Finally, to determine how thoroughly the bee and butterfly communities in our study area were sampled, we calculated Chao1 richness estimators using the *rareNMtests* package in R (Cayuela and Gotelli 2014).

## Results

### Pollinator data

Our sampling yielded 3735 bees belonging to 70 species and 371 butterflies from 30 species (WebTable 1). The Chao1



**Figure 2.** Standardized model-averaged parameter estimates  $\pm$  95% confidence intervals (CIs) for total bee (left) and butterfly (right) richness, diversity, and abundance. The two pyrodiversity metrics were burn diversity and burn richness, with the latter being the number of unique burn histories surrounding the sampling locations (see main text).

richness estimates (and 95% CIs) were 78.3 (70.5–86.0) for bees and 54.9 (34.9–156.0) for butterflies, indicating that bees were more completely sampled than butterflies. We found no evidence of spatial autocorrelation for total bee abundance ( $I = 0.002$ ,  $P = 0.3$ ), richness ( $I = -0.01$ ,  $P = 0.5$ ), or diversity ( $I = -0.02$ ,  $P = 0.6$ ). However, we detected significant spatial autocorrelation for total butterfly abundance ( $I = 0.15$ ,  $P < 0.01$ ), richness ( $I = 0.12$ ,  $P < 0.01$ ), and diversity ( $I = 0.07$ ,  $P = 0.01$ ).

### Bee model selection

Depending on the response variable and which fire parameter was included in the model, the fullest models tested explained, on average, about 25% of the observed variation in bee data based on  $R^2$  values (WebTable 4). There were positive relationships between all three main response variables (overall bee richness, diversity, and abundance) and pyrodiversity (Figure 2; WebTable 3). Results were more mixed at the species level. While many species exhibited positive relationships with pyrodiversity, neutral or even negative relationships were detected for specific taxa (Figure 3). The percentage of area burned in 2017, the year in which pollinators were sampled, had positive effects on the total number of bees collected: an effect that was particularly strong for bee abundance (Figure 2) and for the numbers of *Augochlorella aurata* and *Melissodes communis*. This metric, however, had neutral or weak effects on many other species, and one species (*Lasioglossum illinoense*) responded negatively to it. Burn frequency had weak negative effects on the overall richness, diversity, and abundance of bees. At the species level, we detected both strongly negative

(*Augochloropsis sumptuosa* and *Lasioglossum pectorale*) and positive (*Lasioglossum apokense*) effects of burn frequency. Bee numbers overall were positively related to canopy openness, and species such as *L. apokense* and *L. illinoense* were positively associated with more open canopy conditions (Figure 3). The two plant PCA axes had mixed effects on bee numbers, with axis 2 being positively related to bee diversity (Figure 2). At the species level, two species (*A. aurata* and *Ceratina floridana*) responded positively to axis 1, whereas three others (*A. sumptuosa*, *L. apokense*, and *Lasioglossum reticulatum*) were negatively associated with it; species-level responses to axis 2 were similarly mixed, with *A. sumptuosa* showing a negative relationship and *C. floridana* and *Lasioglossum puteulanum* being positively associated.

### Butterfly model selection

As with that for bees, butterfly richness, diversity, and abundance were positively related to pyrodiversity (Figure 2; WebTable 3). Although all three metrics were positively related to the percentage of surrounding area that was burned in 2017, butterfly richness and diversity responded negatively to burn frequency over the past 11 years. Overall, there were weak negative or neutral relationships between butterfly metrics and PCA axis 1, whereas butterfly richness and diversity were positively related to PCA axis 2 (Figure 2).

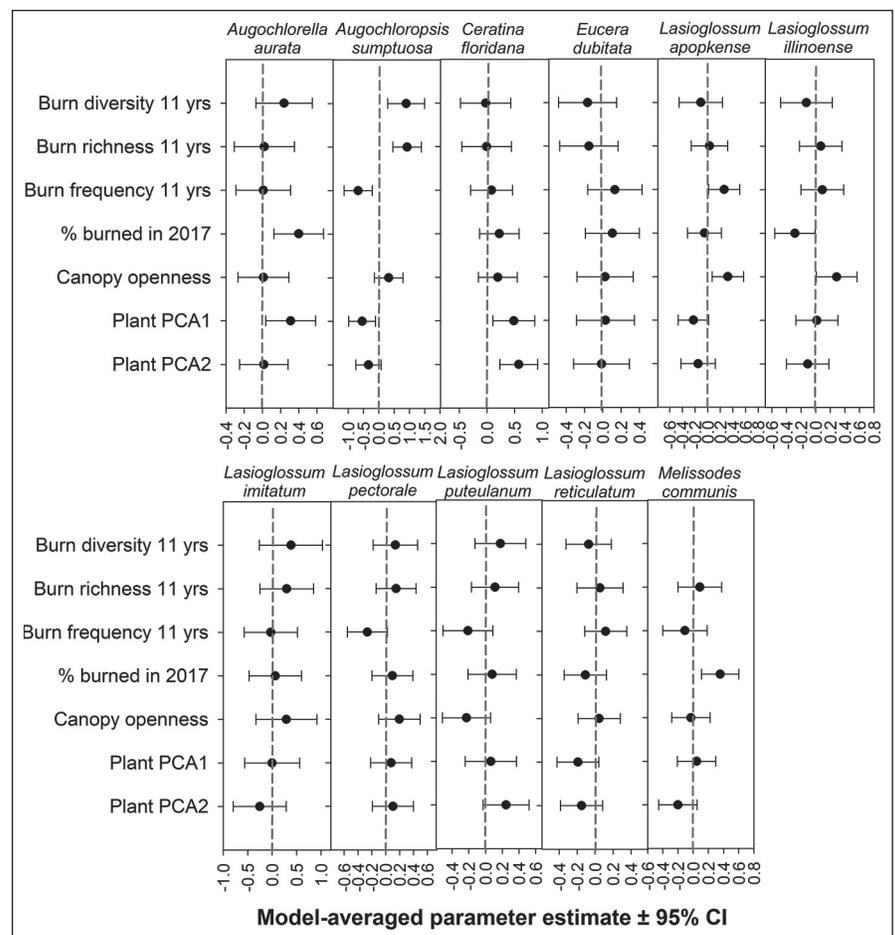
### Discussion

Our findings provide strong support for the pyrodiversity hypothesis, with the number of unique burn histories within

a 250-m radius being a positive predictor of overall bee and butterfly richness, diversity, and abundance. The foraging ranges, adult lifespans, and nesting habits of bees and butterflies may help explain these patterns. First, the foraging ranges of many small solitary bee species are limited to within a few hundred meters of the nest (Zurbuchen *et al.* 2010b), and adult females often have relatively short lifespans (~2 weeks for some species; see Danforth *et al.* 2019) during which to provision their brood cells. Large homogeneous burns may therefore limit many bees to resources within the burned area, which could reduce the reproductive success of some species (Zurbuchen *et al.* 2010a), especially during the recovery period following a fire. In contrast, a variety of smaller burns on different burn schedules may increase resource availability within the foraging ranges of nesting females. Regarding nesting habits, most native bee species are ground nesters and are thought to be largely protected from fire (Ulyshen *et al.* 2021). Species that create shallow nests are more vulnerable (Cane and Neff 2011), however, and aboveground nesting species (eg those that nest in the stems of plants) are often completely exposed (Williams *et al.* 2010). Similarly, the immature stages of many butterfly species are confined to their host plants and are at great risk from fire (Carbone *et al.* 2019).

High burn frequency has been shown to increase plant diversity in longleaf pine forests and some researchers recommend burning as frequently as fuels will allow (Glitzenstein *et al.* 2003). However, we detected negative relationships between burn frequency and pollinator numbers, particularly for butterflies, suggesting high burn frequency may be detrimental to portions of this fauna. Dell *et al.* (2019) recently compared caterpillar richness across a range of fire frequencies in longleaf pine forests and also reported a negative relationship, attributing the observed pattern to the presence of rare species and greater abundance of fire-sensitive plant species in infrequently burned stands. Despite the negative effects of burn frequency detected in the present study, it should be noted that the areas surrounding all of our sampling locations had experienced high burn frequency relative to many parts of the world, with the average fire return interval ranging from 3.3 to 1.6 years. Given the generally positive effects of fire on pollinators reported in the literature (Hanula *et al.* 2016), studies in less-frequently burned systems may find more positive relationships with burn frequency than we detected here.

Fire can be expected to act as an ecological filter on bees as it does on plants, ultimately resulting in a fire-adapted



**Figure 3.** Standardized model-averaged parameter estimates  $\pm$  95% CIs for all parameters appearing in the 95% confidence set of models for the 11 most common (>100 individuals) bee species collected. The two pyrodiversity metrics were burn diversity and burn richness, with the latter being the number of unique burn histories surrounding the sampling locations (see main text).

community. Nevertheless, our results clearly demonstrate that, even among the most common species, some taxa are negatively affected by high burn frequency while others respond positively. Similarly contrasting patterns were observed for the percentage of surrounding area burned during the year of sampling, canopy openness, and plant metrics. Contrary to expectations, we found no evidence that aboveground nesting species respond more strongly to pyrodiversity than ground-nesting species. The one stem-nesting species abundant enough to analyze individually (*C. floridana*) was largely unaffected by both burn diversity and frequency. Moreover, the species that responded most positively to high burn diversity and was most sensitive to high burn frequency (*A. sumptuosa*) is a ground-nester. Although aboveground nesting species were more sensitive to fire than ground-nesting species in previous studies (Williams *et al.* 2010), the frequent low-intensity prescribed fires typical of the southeastern US may pose less of a threat to this fauna (Moylett *et al.* 2019).

The idiosyncratic responses of individual species indicate there can be no “one-size-fits-all” management strategy for

bees with respect to prescribed fire. Nevertheless, our results provide some of the strongest evidence yet that pyrodiversity enhances pollinator diversity and indicate that pollinators will benefit overall from efforts to increase burn heterogeneity and vary burn frequency in southeastern US forests.

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## Supporting Information

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