Forest pollinator richness declines with distance into burned areas

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ABSTRACT

The effects of prescribed fire on forest pollinator communities are complex and incompletely understood. One of the least-studied questions concerns how these organisms are affected by the size, or spatial scale, of fire. We sought to address this by sampling bees (Hymenoptera: Apoidea), butterflies (Lepidoptera), and hover flies (Diptera: Syrphidae) at different distances along 500 m transects into forests burned every three years in the southeastern United States. We found combined pollinator richness to decline significantly with distance, being about 23.9 % lower near the centers of burn units than near the edges, and this did not change with time since fire. These patterns held true when small and large pollinators were analyzed separately, as well as for the richness of bees and butterflies (but not hover flies), and regardless of bee nesting guild. We found no relationship between the abundance of all pollinators and distance. However, the abundance of small pollinators decreased with distance whereas that of large pollinators increased. A competing model provided no support for the alternative hypothesis that the observed effects of distance can be explained by the length of road edges nearby as opposed to distance from unburned habitat. The richness and abundance of all pollinators combined and most taxonomic groups and species analyzed separately increased with increasing canopy openness as well as with increasing plant richness. Although pollinator richness declined with distance into large burns and small species appear to be particularly sensitive, we also found the richness and abundance of pollinators to decrease with time since fire. Our results show that fire can improve local conditions for pollinators but that unburned habitats serve as important refugia or sources of flowers following fire, underscoring the importance of pyrodiversity in managed landscapes.

1. Introduction

The value of semi-natural habitats to biodiversity, including pollinators, is well-established (Cusser et al., 2019; Maurer et al., 2022; Ulyshen et al., 2023a). However, these areas continue to be lost or degraded in many parts of the world to meet the demands of an increasing human population. It is therefore becoming increasingly important to understand how best to manage these habitats to protect as many endemic species, and their services, as possible. Forests support a large fraction of global pollinator diversity but the value of any particular forest to these organisms depends on a variety of interrelated factors including tree composition, forest structure, invasions of non-native species, forest age, and management history (Ulyshen et al., in press). Management practices such as thinning, removal of invasive shrubs, and

prescribed fire have all been shown to generally benefit pollinators (Hanula et al., 2016). However, decisions about how to implement these practices can affect outcomes. For example, the effects of prescribed fire on forest pollinators can vary depending on its frequency (Ulyshen et al., 2021), severity (Galbraith et al., 2019), patchiness (Love and Cane, 2016), and seasonality (Adedoja et al., 2022; Ulyshen et al., 2023b). One aspect of fire that has received particularly little attention from researchers is the size, or spatial scale, of burns. This is increasingly recognized as a major knowledge gap among fire ecologists (Mason and Lashley, 2021). To address this need, we investigated how forest pollinator diversity and abundance change with distance into burned areas in the southeastern United States.

Fire has both direct and indirect effects on pollinating insects. Whereas direct effects involve mortality caused by fire itself, indirect

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effects involve changes in the availability and suitability of foraging and nesting resources following a fire. Some pollinator taxa are more vulnerable to the direct effects of fire than others. Most soil-nesting bees nest deep enough below ground to be unaffected by even intense fires (Cane and Neff, 2011). However, species with shallow nests, as well as those that nest or otherwise develop (e.g., butterfly caterpillars) above ground, are likely to experience much higher rates of mortality (Williams et al., 2010). Fire can have a wide variety of indirect effects on pollinators. These include temporarily eliminating flowers and other vegetation (Love and Cane, 2016), creating more open conditions which stimulate flower production in the understory (Moylett et al., 2020), exposing soil for ground-nesting bees (Ulyshen et al., 2021), and altering the quality and quantity of dead wood used by many species (e.g., many bees, wasps, beetles, and flies) for breeding (Galbraith et al., 2019). Thus, the effects of any particular fire will differ among pollinator species depending on the requirements and vulnerabilities of each.

There are several reasons to expect fire size to be an important factor for pollinating insects. First, the recolonization of burned areas by species directly killed by fire should happen more readily near refugia than near the centers of burns. Second, the short adult life spans and limited foraging distances of many bees may mean reduced reproductive success for species emerging far within recently burned areas. The elimination of floral resources by recent fires may pose serious challenges to bees that forage within just a few hundred meters of their nest and live as adults for only a few weeks (Gathmann and Tscharntke, 2002; Zurbuchen et al., 2010; Danforth et al., 2019). Because dispersal ability correlates positively with body size (Sekar, 2012), smaller species may be particularly sensitive to burn size. Bees may be more sensitive than other pollinator taxa because they must provision their nests with pollen and therefore forage within a limited distance from their nest site. Other taxa, like butterflies and hover flies, simply lay their eggs on or in suitable substrates and thus have more freedom to roam widely in search of floral patches.

Forests of the southeastern U.S. historically experienced some of the highest fire frequencies on the continent, with most of the region burning every 2–6 years (Guyette et al., 2012). Prescribed fire remains one of the most important tools for controlling woody plants in the understory and midstory, reducing bark beetle outbreaks, improving conditions for endangered birds such as the red-cockaded woodpecker, and benefiting game species such as deer and quail (Glitzenstein et al., 2012; Nowak et al., 2015; Weiss et al., 2019). While these fires tend to be low intensity and rarely extend into the overstory, they can kill fire-sensitive tree taxa, and generally favor pines over time (Keeley et al., 2009; Dey and Schweitzer, 2018; Brown and Smith, 2000). Frequently-burned forests in the region are characterized by open canopy conditions and rich communities of flowering herbaceous plants in the understory (Keeley et al., 2009; Peet et al., 2018; Brown and Smith, 2000). In this study, we sampled pollinators at different distances along transects extending 500 m into burn units (burned every three years) on the Piedmont National Wildlife Refuge in central Georgia, U.S. Our objectives were to 1) investigate how the richness and abundance of pollinators change with distance into burn units; 2) compare these patterns among bees, butterflies, and hover flies; 3) determine whether responses to distance vary with body size or between below- and above-ground nesting bees; and 4) test whether the effect of distance changes with time since fire.
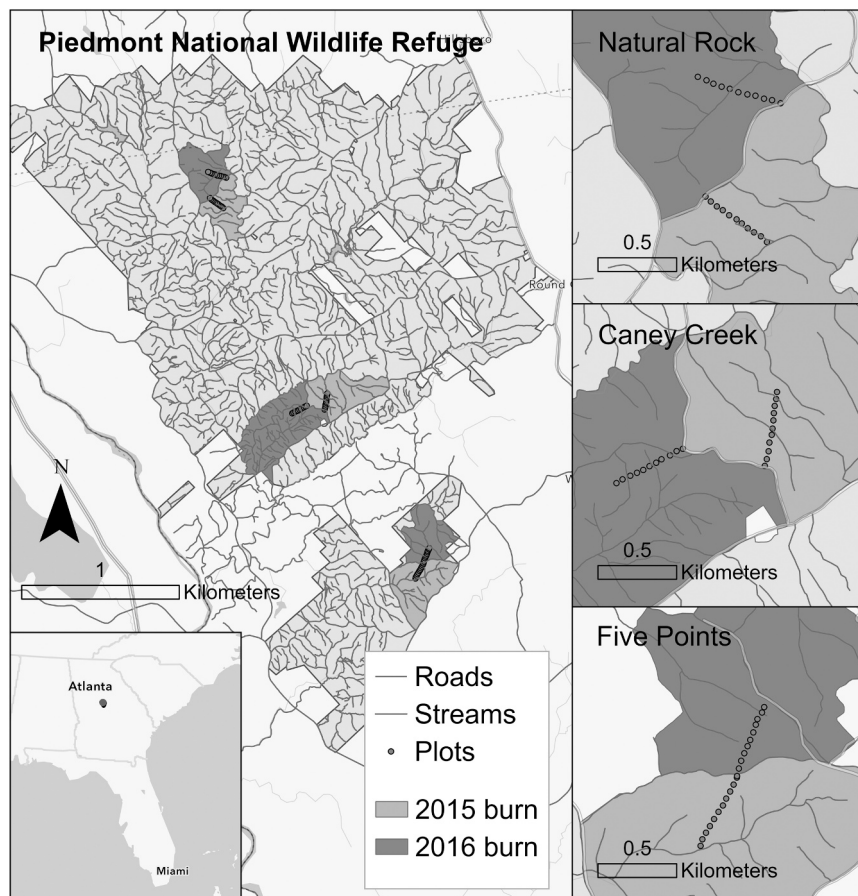

Fig. 1. Map of sampling transects in units that were burned either in 2015 or 2016.

2. Methods

2.1. Study location and design

This work took place on the 141.6 km^2 Piedmont National Wildlife Refuge in central Georgia, USA (Fig. 1). The refuge was established in 1939 by the US Fish & Wildlife Service on land degraded from intensive cotton farming (USFWS, 2010). At the time of our study, the gently rolling topography was almost completely (97 %) forested, with about three quarters consisting of pine (mostly *Pinus taeda* L.) and the rest consisting of mixed broadleaf taxa (*Quercus, Carya, Acer, Liquidambar, Liriodendron*) typical of the region. The understory consisted of a wide variety of forbs, grasses, ferns, woody shrubs, and regenerating hard-wood saplings (see Table S2 for complete list of species and their relative abundances). The refuge is largely focused on restoring and enhancing habitat for endangered or threatened birds. These include the red cockaded woodpecker (*Leuconotopicus borealis* (Vieillot)), Bachman's sparrow (*Peucaea aestivalis* (Lichtenstein)), and northern bobwhite (*Colinus virginianus* (L.)) (USFWS, 2010). Management activities largely consist of prescribed fire on a 2–3 year cycle as well as timber harvests to maintain a balanced age class distribution. Vegetation recovers quickly following fire on the refuge, with the greatest herbaceous response within the first year, woody plant regrowth after two years, and woody plants dominating forbs and grasses three years post-burn (CS, personal observation).

We selected a pair of adjacent burn units at three locations on the refuge, referred to as Natural Rock (NR), Caney Creek (CC), and Five Points (FP) (Fig. 1). In every case, the units comprising each pair were separated by a gravel road. The units, ranging from 222 to 382 ha, were all on a three-year burn cycle and had been burned this way for over a decade prior to this study. However, they were scheduled to be burned in different years, with one burn unit in each pair scheduled to burn in 2015 and the other in 2016 (Fig. 1). This design was key to testing the idea that neighboring unburned areas (defined here as units that were not burned in a particular year) benefit pollinator assemblages following a burn. Sampling transects were established in each burn unit, beginning at the edge adjacent to the other burn unit and extending 500 m toward the unit center (Fig. 1). Sampling plots were placed in a line at 50 m increments, resulting in 11 distances per transect and 66 plots in total. Each transect was planned to ensure that plots did not get closer to other burn units than the unit they were paired with (Fig. 1). The burns took place between January and March both years (Table 1) and pollinator sampling did not begin in either year until these burns were complete. Although we did not collect information on fire severity, observations made along the transects suggest burns were homogenous in both years with patches of unburned leaf litter and vegetation being largely confined to low areas adjacent to small streams. Because we sampled at all locations in both years, this design yielded pollinator data from 0, 1, and 2 years post-fire, which allowed us to test for an interaction between distance and time since fire.

2.2. Data collection

We used colored pan traps to collect bees, butterflies, and hover flies in each plot. The traps were commercially available (Solo®) white,

yellow, and blue plastic food bowls with a 15.5 cm opening and a capacity of ∼ 400 ml. One trap of each color (as manufactured, not painted) was installed in each plot; one placed at the center and the others 5 m away on both sides and perpendicular to the transect. The traps were suspended ∼ 30 cm off the ground on wire stands. During operation, they were filled with water and a few drops of soap to reduce surface tension. They were operated for four-day periods six times throughout the season in 2015 (27 April–1 May, 7–11 May, 4–8 June, 6–10 July, 31 July–4 Aug, 14–18 September) and seven times in 2016 (21–25 March, 18–22 April, 9–13 May, 13–17 June, 21–25 July, 29 August–2 September, and 15–19 September) during periods of clear weather. At the time of collection, the samples from the three pan traps in each plot were combined into a single container. All bees, butterflies, and hover flies were pinned, labeled, and identified to species with a combination of printed (Gibbs, 2011; Gibbs et al., 2013; Glassberg et al., 2000; Mitchell, 1960, 1962; Skevington et al., 2019) and online (discoverlife.org) resources as well as an established reference collection.

For each group of pollinators, we distinguished between small- and large-bodied species. This was done by measuring inter-tegular distances for bees (using only female specimens and only worker bumble bees), and forewing lengths for butterflies and hover flies. We ranked each group by size and separated them into approximate thirds, resulting in small and large bees with inter-tegular distances ranging from 0.71 to 1.36 mm and 2.20 to 5.23 mm, respectively; small and large butterflies with forewing lengths ranging from 1.1 to 1.6 cm and 2.0 to 5.4 cm; and small and large hover flies with wing lengths ranging from 0.46 to 0.67 and 0.81 to 1.42 cm. We also classified bees according to nesting habits with the major categories being below-ground nesters and above-ground nesters. Species with variable (e.g., bumble bees) or unknown nesting habits were not included in this portion of the analysis.

To better isolate the effect of distance into burned units, we also collected data on understory plant diversity and canopy openness, which have both been shown to be important predictors of pollinator diversity in previous studies (Rhoades et al., 2018; Urban-Mead et al., 2021). First, we measured the richness of the understory plant community in all plots in both 2015 and 2016 (Fig. S1B). In both years, these measurements were made in July, after at least 4–5 months of plant community recovery since the most recent fires. To do this, a 10-m transect was established in each cardinal direction from plot center and plant data were recorded every meter along these transects. For the plots situated at the edges of burn units (0 m), we established just two transects and these were oriented 45 degrees into the forest from the edge on both sides. Plant species richness was calculated as the total number of distinct taxa (typically species) encountered in each plot. We also measured canopy openness above each trap position once per year after leaf expansion. This was done using a fisheye lens facing upward on a self-leveling tripod about 0.9 m off the ground. We then used WinScanopy v. 2006 (Regent Instruments Inc. Quebec City, CA) to calculate canopy openness from each photograph. The average openness was calculated from the three photos taken at each plot to obtain a single composite value for each plot and year.

2.3. Statistical analysis

Unless otherwise indicated, all analyses were performed in R. As response variables, we calculated the richness and abundance of the following after pooling data by plot and year: all pollinators, all small pollinators, all large pollinators, bees, below-ground nesting bees, above-ground nesting bees, butterflies, and hover flies. We also calculated the abundance of the 21 most common (i.e., represented by at least 100 individuals, which together accounted for over 87 % of all pollinators collected) species by plot and year. After ensuring there was no multicollinearity among predictors (variance inflation factor (VIF) < 2 in all cases), we then ranked six candidate generalized linear mixed-effects models for each response variable (Table 2) based on Akaike's information criterion (AICc) (Barton, 2019). Except for the null model,

Table 1
Burn unit sizes and burn dates for 2015 and 2016.

Location	Hectares	Burn dates
Five points	222.58	10 March 2015
Natural rock	347.63	7 February 2015
Caney creek	341.96	30 January 2015
Five points	250.50	14 March 2016
Natural rock	231.08	1 March 2016
Caney creek	382.43	13 February 2016

Table 2

Fixed effects included in the candidate models.

Fixed effects
~ 1 (null)
~ distance + year + canopy_openness + plant_richness
~ time_since_fire + year + canopy_openness + plant_richness
~ distance + time_since_fire + year + canopy_openness + plant_richness
~ distance + time_since_fire + distance*time_since_fire + year + plant_richness
~ length_of_roads + time_since_fire + year + canopy_openness + plant_richness

all models included terms for year, canopy openness, and plant richness (Table 2). To these terms we added 1) distance, 2) time since fire (TSF), 3) distance + TSF, 4) distance + TSF + distance * TSF, and 5) length of road + TSF. For the last model, the total length of all roads within 500 m of each plot was calculated (summary analysis) in ArcGIS pro. That model was included to test the possibility that any observed effect of distance is driven by proximity to roads rather than by effects of fire. In all models we used (1|location/unit/plot) as an error term, reflecting that plot was nested within unit which was nested within location. This term also accounts for the fact that plot was sampled repeatedly. Initial models assumed a Poisson distribution but, when overdispersion was detected (based on c_hat of the AICcmodavg package, Mazerolle and Mazerolle, 2017), a negative binomial model (glmer.nb) was used instead. Models that failed to converge were dropped from the analysis. For each response variable, we report the results from all models with a delta AICc < 2.

3. Results

We collected over thirteen thousand pollinator specimens representing 195 species of bees (120), butterflies (43), and hover flies (32) (Table S1). We also recorded a total of 107 plant taxa across all plots and both years, with a range of 4–28 per plot (Table S2). The richness of all pollinators, large pollinators, small pollinators, bees, above-ground nesting bees, and below-ground nesting bees declined significantly with distance into the burn units (Table S3). The predicted richness of all pollinators was about 23.9 % lower 500 m into burn units than at 0 m, representing a loss of about 1.4 species for every 100 m of distance

(Fig. 2). Predicted bee richness was about 30.8 % lower at 500 m than at 0 m, representing a loss of about 1.2 species per 100 m (Fig. 2). Butterfly richness dropped by 20.4 % over the same distance (Fig. 2). However, no such pattern was detected for hover fly richness for which the null model ranked highest (Table S3). The richness of all pollinators, small pollinators, bees, and below-ground nesting bees declined significantly with time since fire. The predicted richness of all pollinators decreased by about 13.8 % from the year of the fire to two years post fire (Fig. 3). Finally, the richness of all pollinators and most smaller groups declined significantly from 2015 and 2016, and was positively correlated with both canopy openness and plant richness (Table S3).

By contrast to richness, the abundance of all pollinators, as well as for bees, butterflies and hover flies, was largely unaffected by distance (Table S3). However, we did detect significant and contrasting patterns based on body size, with the abundance of small pollinators decreasing with distance and that of large pollinators increasing (Table S3, Fig. 4). Individual species also exhibited idiosyncratic relationships with distance. While the abundance of many declined with distance (*Lasioglossum apopkense* (Robertson), *L. hitchensi* Gibbs, *L. illinoense* (Robertson), *L. raleighense* (Crawford), *L. tegulare/puteulanum, Nastra iherminer* (Latreille), *Oligoria maculata* (Edwards)), the abundance of others increased (*Augochlorella aurata* (Smith), *L. subviridatum* (Cockerell), *Toxomerus geminatus* (Say)) (Table S3). However, like richness, the abundance of most groups and species declined with time since fire. The predicted abundance of all pollinators decreased by about 22.2 % from the year of the fire to two years post fire (Fig. 3). Also like the patterns observed for richness, the abundance of most groups and individual species also declined from 2015 to 2016, and correlated positively with both canopy openness and plant richness.

Very few of the highest-ranking models for richness or abundance included the interaction term between distance and time since fire
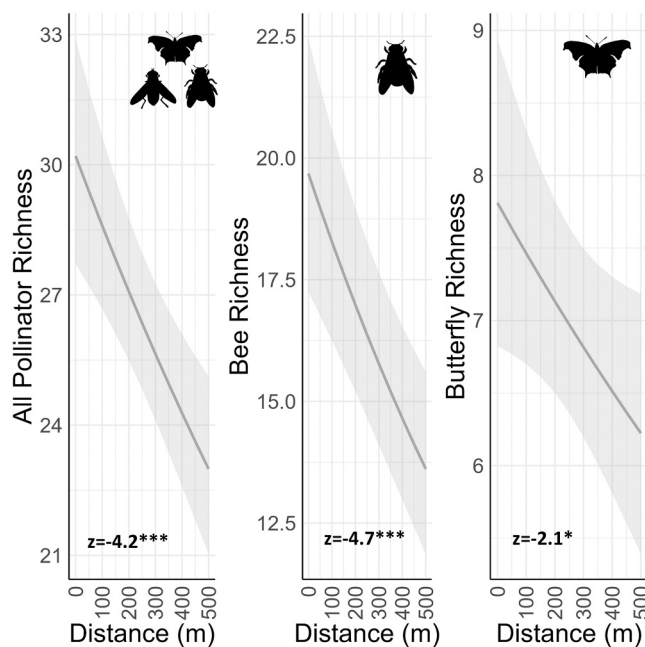
Fig. 2. Predicted relationship between the richness of all pollinators, bees, and butterflies with distance into burn units. Predictions come from the highest-ranking model for each response variable, see Table S3 for details.
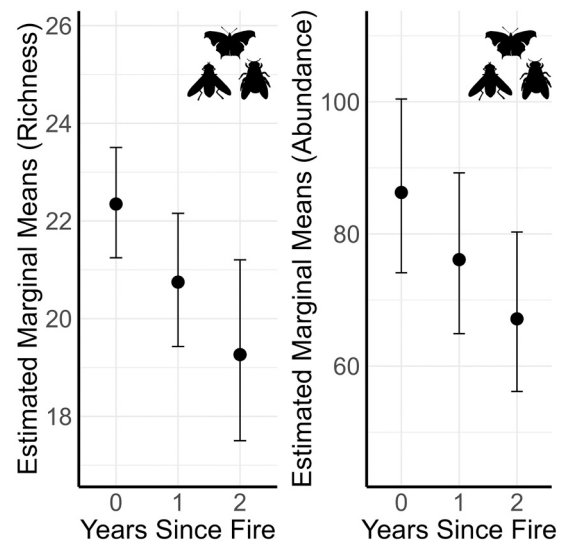
Fig. 3. Estimated marginal mean (± 95 % CI) richness and abundance of all pollinators with time since the last prescribed fire. These estimates come from the highest-ranking model for each response variable, see Table S3 for details.
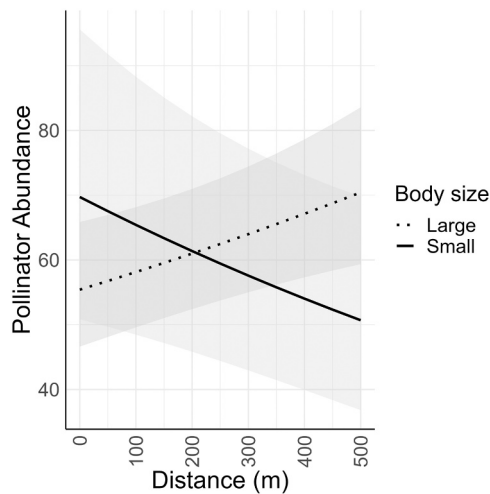
Fig. 4. Relationship between abundance and distance for large and small pollinators. Predictions come from the highest-ranking model for each response variable, see Table S3 for details.

(Table S3). Only for two species (*L. apopkense* and *L. hitchensi*) was this interaction significant. Similarly, in only two cases, for the abundance of *L. tegulare/puteulanum* and *Xylota ejuncida* Say, was length of roads a significant predictor and the relationship was negative for both.

4. Discussion

This study represents the first effort to determine how pollinator richness and abundance change with distance into burned areas. We found total pollinator richness to decline by nearly a quarter from the edges of burn units (i.e., next to areas that are burned on a different cycle) to 500 m into the units. These results suggest that adjacent unburned areas provide important sources of floral resources to pollinators following a fire or act as refugia from which pollinators recolonize recently burned areas. We found no support for the alternative hypothesis that the observed negative relationship with distance was driven by some beneficial effect of road edges. In fact, length of roads was a significant predictor in only two of our highest-ranking candidate models across all response variables and had a negative effect in both cases. One possible explanation for the observed declines in pollinator richness with distance into burned areas concerns direct mortality of pollinators caused by fire. However, we found little support for this as ground-nesting bees, which are largely protected from fire by the insulating properties of soil (Cane and Neff, 2011), responded just as negatively to distance as above-ground nesting bees and butterflies. A second potential explanation for our findings concerns reductions in floral resource availability caused by fire. Because most solitary bees are short-lived and forage within a limited distance of their nest, they are inherently sensitive to the local availability of floral resources. Even temporary fire-driven reductions in flower availability might be enough to reduce the reproductive success of such species. This may be particularly true for small-bodied species which tend to have weaker dispersal abilities than large species. Our results support this expectation, at least in part. Although pollinator richness declined significantly with distance into burn units for both small and large pollinators, the abundance of small pollinators declined with distance while that of large pollinators increased. These patterns suggest that smaller pollinator taxa may be more negatively affected by large burns, but it is unclear why large pollinators responded positively to distance. Our findings also indicate that the loss of pollinators from the centers of large burned areas can be long-lasting as we found no evidence for an interactive effect between distance into burn units and time since fire on total pollinator richness or abundance. This suggests that there is no substantial recovery of

pollinator diversity in the centers of burn units within the three-year fire return interval at our study site.

Despite the observed declines in pollinator richness and abundance with distance into burned areas, our results also hint at beneficial effects of fire on these organisms. The richness and abundance of all pollinators and many of the groups and species analyzed separately declined with time since the last burn. This is consistent with previous work and may reflect increased flower availability in recently burned areas. Fires are known to promote plant diversity in the understory and, although we did not specifically record the amount and variety of flowers in this study, we did detect a positive relationship between pollinator numbers and the richness of understory plants. However, it is also likely that colored pan traps attract more pollinators in recently burned areas simply because they are more visible against a charred background devoid of vegetation. Indeed, this probably explains why some previous studies have reported boosts in pollinator numbers following fire despite no changes in floral resource availability (Ulyshen et al., 2022a). Similarly, studies on the effects of invasive shrubs on pollinators in forests report strong effects beneath the shrub layer (Ulyshen et al., 2022c) but no effects above it (Traylor et al., 2022). Such patterns strongly suggest that trap visibility may confound efforts to isolate effects of interest in such studies. Thus, we encourage future researchers to either collect directly from flowers (especially if plots are small) or suspend traps above the shrub layer to avoid this complication. Suspended traps have the additional advantage of better sampling bees active within the canopy (Ulyshen et al., 2010, 2020; Urban-Mead et al., 2021, 2023; Cunningham-Minnick et al., 2024).

One factor likely to influence pollinator community response to burn size concerns burn heterogeneity. Pollinators are likely to decline more strongly with distance into burn units following homogenous burns that leave few unburned patches, as in this study, compared to more heterogenous burns that leave patches of unburned plants across the landscape. For example, Love and Cane (2016) reported limited effects of wildfire on bees even > 7 km within an area of burned sagebrush steppe. Bees were persisting on the only surviving flowering plant, wild sunflowers, which remained in unburned drainage ditches. Such patches are likely critical to the reproductive success of many pollinators, especially small species, active immediately following a fire. Thus, the effect of burn size on bees will likely depend on the number of unburned patches remaining within the burned areas. Another important consideration in forests concerns flowering trees in the overstory which may provide another important resource to bees within recently burned areas. Even wind-pollinated taxa such as oaks can provide an important source of pollen to many bees (Urban-Mead et al., 2021, 2023) and bee diversity correlates positively with flowering tree diversity (Traylor et al., in press). Flowering trees may be particularly important sources of flowers to bees in our study region as they typically bloom in early spring when or soon after most prescribed burning takes place.

Although fire is likely to locally benefit many pollinators in southeastern forests by maintaining more open canopy conditions (Keeley et al., 2009), enhancing flower availability in the understory (Moylett et al., 2020), and improving conditions for ground-nesting bees (Ulyshen et al., 2021), the results from the current study highlight the importance of maintaining a patchwork of different burn histories on the landscape. This is consistent with studies reporting positive correlations between pyrodiversity (i.e., the number of unique burn histories) and pollinator diversity (Ponisio et al., 2016), including work from the southeastern U.S. (Ulyshen et al., 2022b). Similarly, previous work from other regions has shown that setting aside unburned refugia in otherwise fire-managed landscapes can benefit butterflies (Swengel and Swengel, 2007) and help maintain pollinator-plant interaction networks (Adedoja et al., 2019). While pollinators can be expected to benefit from efforts to increase fire heterogeneity on the landscape, specific recommendations will depend on local management goals, fire characteristics, resource availability and logistical challenges inherent to a particular location. At locations where maximizing pollinator diversity is the priority, and

where prescribed fire typically leaves few unburned patches within burn units, our findings suggest efforts to burn adjacent units in different years or even reduce burn unit size may be beneficial. Studies from other locations and forest types are needed to develop more refined recommendations.

CRediT authorship contribution statement

Emily J. Forrester: Writing – review & editing, Investigation. **Conor Fair:** Writing – review & editing, Investigation. **Scott Horn:** Writing – review & editing, Validation, Methodology, Investigation. **Michael Ulyshen:** Writing – original draft, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Carl Schmidt:** Writing – review & editing, Methodology. **Andrew Young:** Writing – review & editing, Investigation. **Samm K. Reynolds:** Writing – review & editing, Investigation.

Declaration of Competing Interest

The corresponding author confirms, on behalf of all co-authors, that there are no known conflicts of interest associated with this publication and no financial support that could influence its outcome. All authors declare that they have no competing financial interests or personal relationships that could have influenced the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2024.122049.

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