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Fire effects on floral abundance of bumble bee host plants in mixed-oak forests

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Abstract

Background Pollinators are declining due to habitat loss, pesticides, and climate change. Fire may be an effective management tool for enhancing pollinator habitat in fire-maintained ecosystems. Many studies have demonstrated that fire can promote understory plant biodiversity and cover, but considerably less is known about the effects of fire on floral abundance and pollinators, particularly in mixed-oak forests of the eastern USA. Our goal was to assess the long-term effects of repeated prescribed fire on floral abundance and the abundance of bumble bees, a globally important group of pollinators, in mixed-oak forests. We hypothesized that repeated prescribed fire would increase floral abundance, particularly the abundance of bumble bee host plants.

Results We sampled 22 vegetation plots in the Wayne National Forest, Ohio, USA, that were part of a fire experiment initiated in 1995 with three treatments: frequent fire, periodic fire, and no fire. To determine if fire treatment, plant cover, and environmental variables were related to floral abundance, we fitted generalized linear models with a negative binomial distribution, and then used model selection using AICc. Total floral abundance and floral abundance of bumble bee host plants were significantly higher in plots with repeated fire relative to unburned plots. Plant cover and soil texture were also significant predictors of floral abundance: plots with higher herbaceous plant cover and fine-textured soils generally had higher floral abundance. We detected a relatively small number of bumble bees, had low power to detect differences in bumble bee abundance, and this may be why bumble bee abundance was similar between the repeated fire and no fire plots.

Conclusions These results suggest that prescribed fire enhanced floral abundance for bumble bees and potentially other pollinator groups in our mixed-oak forest plots and may be an effective tool for enhancing pollinator habitat. Additional studies are needed to characterize the effects of different fire regimes on bumble bees and pollinators more broadly in mixed-oak forests of the eastern USA.

Keywords *Bombus*, Bumble bees, Fire frequency, Floral abundance, Mixed-oak forests, Prescribed fire, *Quercus*

Resumen

Antecedentes Los polinizadores están declinando debido a la pérdida de hábitat, a los pesticidas, y al cambio climático. El fuego puede ser una herramienta de manejo efectiva para mejorar el hábitat de polinizadores en ecosistemas mantenidos por el fuego. Muchos estudios han demostrado que el fuego puede promover la biodiversidad y cobertura del sotobosque, aunque son considerablemente menos conocidos los efectos del fuego sobre la abundancia floral y en los polinizadores, particularmente en bosques mixtos de roble del este de los EEUU. Nuestro objetivo fue determinar los efectos a largo plazo de quemas prescriptas repetidas en la abundancia floral y la abundancia

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de abejorros, un grupo importante de polinizadores a nivel global en bosques mixtos de roble. Hipotetizamos que las quemas prescriptas repetidas incrementan la abundancia floral, particularmente de las plantas que sirven como huéspedes del abejorro.

Resultados Muestreamos 22 parcelas de vegetación en el *Wayne National Forest*, de Ohio, EEUU., que fueron parte de un experimento de quemas prescriptas iniciado en 1995 con tres tratamientos: quemas frecuentes, fuegos periódicos, y no fuegos (control). Para determinar si el tratamiento de fuego, la cobertura de plantas y otras variables ambientales estaban relacionados con la abundancia floral, ajustamos modelos lineales generalizados con una distribución binomial negativa, y luego usamos un modelo de selección usando AICc. La abundancia floral total y la abundancia de plantas huéspedes de abejorros fueron significativamente mayores en los tratamientos con fuegos repetidos en relación con el no fuego o control. La cobertura de plantas y la textura del suelo fueron también predictores significativos de la abundancia floral: parcelas con mayor cobertura de herbáceas y suelos finamente texturados generalmente tuvieron una mayor abundancia floral. Detectamos un número relativamente pequeño de abejorros, lo que tuvo un bajo poder para detectar diferencias en abundancia de abejorros, y puede explicar el por qué la abundancia de abejorros fue similar entre los fuegos repetidos y el control.

Conclusiones Estos resultados sugieren que las quemas prescriptas aumentan la abundancia floral para los abejorros, y potencialmente para otros grupos de polinizadores en nuestros bosques mixtos de roble, y pueden ser una herramienta efectiva para mejorar el hábitat de los polinizadores. Estudios adicionales son necesarios para caracterizar los efectos de diferentes regímenes de fuegos en abejorros y otros polinizadores de manera más amplia en los bosques mixtos de roble del este de los EEUU.

Background

Globally, insect diversity and abundance have been declining drastically in the last century (Dirzo et al. 2014; Leather 2018; Kehoe et al. 2021; Sánchez-Bayo and Wyckhuys 2021). In some regions, insect abundance has decreased by ~78% since the 1990s (Hallmann et al. 2017) mainly due to the combined impacts of habitat degradation and fragmentation, agricultural intensification, increased pesticide use, parasites, and climate change (Hallmann et al. 2017; Dicks et al. 2021; Brown and Caruso 2023). These declines are ecologically significant as insects are estimated to pollinate 75% of crops, globally, providing critical ecosystem services (Klein et al. 2007; Potts et al. 2010; Dirzo et al. 2014; Requier et al. 2023).

Wild bees are the most abundant insect pollinators (Potts et al. 2010; Calderone 2012) and have been declining due to the loss of host plants and habitat, pesticides, and invasion of non-native species (Dirzo et al. 2014; Cameron and Sadd 2020; Dicks et al. 2021). Among bees, bumble bees (*Bombus* spp.) are ecologically important as they have unique life history traits that allow them to forage in poor weather conditions over longer periods of the day. This is possible because they are able to regulate their internal temperature (i.e., their bodies need to be at 30 °C in order to fly), which in temperate regions can be above ambient temperatures, especially in spring and fall (Goulson 2010; Colla et al. 2011; Mola and Williams 2018). Bumble bees rely completely on floral resources for food; adults feed on nectar and pollen and use pollen to feed their larvae (Colla et al. 2011). Bumble bees are mostly regarded as generalists, visiting different flowering species, although studies suggest different bumble bee species partition resources by foraging flowers with a similar depth to their tongue length to optimize nectar foraging (Goulson 2010). Also, because of the length of their reproductive cycle (most queens are active from May to October), bumble bees need to feed from a variety of plant species, both during early and late flowering seasons (Goulson 2010; Colla et al. 2011; Mola and Williams 2018). For some plant taxa, bumble bees are critical for pollination as stamens must be shaken to release pollen, a process known as buzz pollination, where bumble bees collect pollen by vibrating their wing muscles to release pollen grains from the anthers (De Luca et al. 2013). Many nectar-producing and non-nectar-producing plants rely on buzz pollination by bumble bees, including economically important species in the heath, nightshade, legume, and cucurbit families (Ericaceae, Solanaceae, Fabaceae, and Cucurbitaceae) (Vallejo-Marín 2019). Because of this, bumble bees effectively pollinate many plant species that generalists such as honey bees (*Apis mellifera* L.) cannot (Goulson 2010).

Bumble bees are entirely dependent on floral resources and studies have shown that loss of floral diversity and abundance is directly related to a decrease in bee diversity (Goulson 2010; Cameron and Sadd 2020). In fire-adapted mixed-oak forests of the eastern USA, fire maintains or enhances herbaceous layer biodiversity and productivity as fire can reduce the abundance of dominant woody species, remove leaf litter, and increase canopy openness (Burton et al. 2011; Saladyga et al. 2022;

Hutchinson et al. 2024). These changes result in reduced competition in the mid-story and understory layers and increased light and nutrient availability (Boerner and Brinkman 2003; Lettow et al. 2014; Black et al. 2018), which collectively promote plant species coexistence and enhance plant establishment via seed germination (Glasgow and Matlock 2007; Lamont et al. 2019). Herbaceous layer productivity also can respond positively to fire (Vander Yacht et al. 2017; Hutchinson et al. 2024) as many herbaceous species (i.e., graminoids and forbs) increase their abundance post-fire due to several life-history traits such as perennating meristems at or below the soil surface and promote higher relative growth rates (Raunkier 1934; Whigham 2004). These fire-mediated effects on the herbaceous layer are likely to have important implications for floral abundance, in turn benefiting bumble bee communities. In the absence of fire, the dominant, competitively superior woody species increase in abundance, resulting in more closed conditions and reduced opportunities for establishment, which can lead to declines in biodiversity and herbaceous plant cover via competitive exclusion (Nowacki and Abrams 2008; Alexander et al. 2021).

Identification of land management strategies that specifically enhance bumble bee habitat may be useful in slowing ongoing bumble bee decline. Prescribed fire may be one potential management tool. In fire-adapted mixed-oak forests of the eastern USA, prescribed fire is primarily implemented to reverse the effects of mesophication resulting from long-term fire exclusion (Abrams 1992; Shumway et al. 2001; Nowacki and Abrams 2008). Mesophication is the process in which fire-tolerant oaks and hickories are replaced by mesophytic, less fire-tolerant species such as maples and beech, which over time results in heavily shaded understories, as well as increased fuel moisture and decreased flammability (Nowacki and Abrams 2008; Alexander et al. 2021). In this context, prescribed fire management goals in mixed-oak forests include the following: reduce the abundance of mesophytic tree species, increase canopy openness, and enhance oak regeneration and herbaceous layer biodiversity and cover (Brose et al. 2001; Nowacki and Abrams 2008; Arthur et al. 2012; Hutchinson et al. 2024).

Despite a long history of research on the effects of fire on plant biodiversity and abundance, considerably less is known about the effects of fire on bumble bee abundance and the floral resources they depend on. Some studies have examined the effects of fire frequency, time since fire, and fire severity on bumble bee communities, the majority of which have been conducted in grassland, savanna, and open woodland ecosystems (Grundel et al. 2010; Mola and Williams 2018; Simanonok and Burkle 2020; Tai et al. 2022). In these settings, fire can increase bumble bee richness and abundance by facilitating greater floral abundance near nesting sites and increased nesting success relative to unburned areas through a reduction in leaf litter, as many bumble bee species prefer to nest in bare ground (Potts et al. 2003; Campbell et al. 2007; Burkle et al. 2019). In evergreen forests of the western USA, areas that were unburned, had not burned recently or experienced low severity fire, wood-cavity nesting bumble bees had decreased nesting success due to reduced floral resources near nest sites (Simanonok and Burkle 2019). Another study in mixed-conifer forest in California found that pyrodiversity, or diversity of fire history, positively affected richness of flowering plants and pollinators, and in the case of bumble bees, pyrodiversity created a greater diversity of nesting resources thus benefitting species with diverse nesting habits (Ponisio et al. 2016). Conversely, fire can also have adverse effects on bumble bees depending on the habitat type, and timing and severity of fire. High severity burns, relative to mixed and low severity burns, can decrease pollen quality for foraging bumble bees (Tarbill et al. 2023) via a reduction in available nitrogen in pollen (Simanonok and Burkle 2020), and can destroy colonies of species nesting on the ground surface or in hollow logs (Potts et al. 2003).

Far fewer studies have examined the effects fire frequency has on bumble bees and on their host plants in eastern US mixed-oak forests (Campbell et al. 2007; Simanonok and Burkle 2019). This is despite the fact that prescribed fire is expected to increase as a practice and these ecosystems provide critical nesting habitat and resources for several endangered bumble bee species: the rusty-patched bumble bee (*Bombus affinis* Cresson), the yellow-banded bumble bee (*B. terricola* Kirby), the yellow bumble bee (*B. fervidus* Fabricius), and the critically endangered variable cuckoo bumble bee (*B. variabilis* Cresson) (Potts et al. 2003; Grundel et al. 2010; Simanonok and Burkle 2019; Mola et al. 2021; Hepner et al. 2024; IUCN 2024).

The goal of our study was to understand how prescribed fire influences bumble bees by sampling plant and bumble bee communities in mixed-oak forests that have different recent fire histories. Our specific questions were as follows: (1) How does fire frequency influence floral abundance? (2) How does fire frequency influence floral abundance of species specifically utilized by bumble bees? and (3) How does fire frequency influence bumble bee abundance? We hypothesized that repeated fire would positively affect bumble bees by increasing floral abundance and the diversity of bumble bee foraging resources. To our knowledge, this work is one of the few studies that quantified floral abundance in mixed-oak forests of the eastern US in response to prescribed fire and thus may provide perspective on whether fire can be

used as a tool to enhance pollinator habitat and benefit bumble bees and other declining pollinators in oak-dominated ecosystems.

Methods

Study area

This study was conducted at Bluegrass Ridge on the Ironton Ranger District of the Wayne National Forest in southern Ohio, which lies within the Southern Unglaciated Allegheny Plateau region (Fig. 1). The Allegheny Plateau has a dissected topography consisting of narrow ridges, steep slopes, and attenuated valleys (McNab 1996). Prior to the fire suppression era (ca. 1875–1930), the fire return interval for this area is estimated to be 6 to 12 years based on fire scar data and fires were typically low-intensity and occurred in the dormant season (McEwan et al. 2007; Hutchinson et al. 2008, 2019). However, the pre-European fire regime is not well understood. Bluegrass Ridge has an elevation ranging from 192 to 296 m and is characterized by well-drained, acidic soils derived from sandstone and shale bedrocks (Hutchinson et al. 2008). The mean annual temperature is 12.2 °C and the mean annual precipitation is 124 cm (Thornton et al. 2022). Bluegrass Ridge consists of secondary mature mixed-oak forests (Hutchinson et al. 2005) dominated by oaks (*Quercus* spp. L.) and hickories (*Carya* spp. Nutt.) in the overstory, while maples (*Acer* spp. L.), American beech (*Fagus grandifolia* Ehrh.), and other shade-tolerant species comprise the majority of the midstory. The most common and diverse group of understory non-tree plants are perennial native herbaceous forbs, in addition to shrubs, vines, and graminoids (Table S1). We sampled 22 vegetation plots that were part of a prescribed fire experiment initiated in 1995 (Hutchinson et al. 2005) (Fig. 1). There was no evidence of recent fire or other major disturbances in the decades preceding the initiation of the study in 1995.

The study was implemented from 1995 to 1999 in three 25-ha fire treatment areas: no fire (nine plots), periodic fire (nine plots), and frequent fire (nine plots), to examine how prescribed fire could mitigate or reverse the effects of mesophication (Hutchinson et al. 2005; Fig. 1).

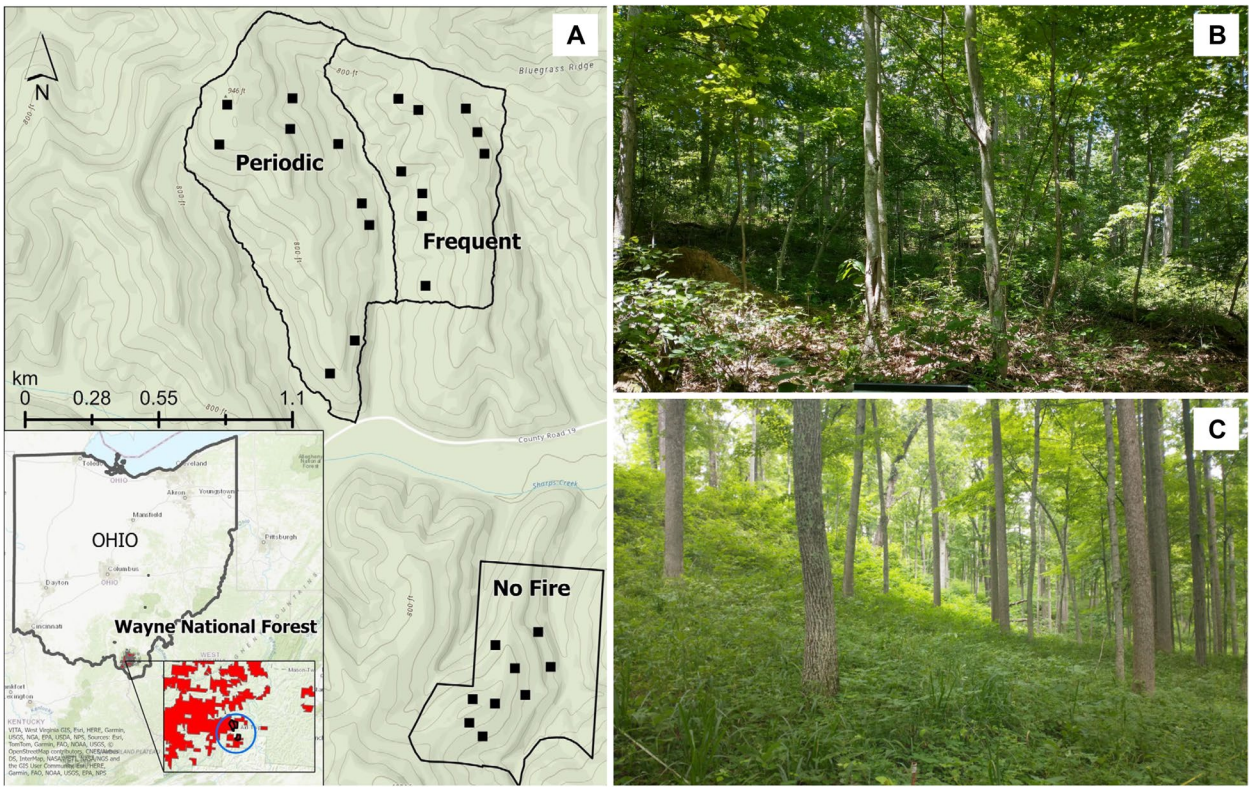

Fig. 1 Map of study plots within the Ironton District, Wayne National Forest, Ohio (**A**). The three fire treatment areas (no fire, periodic fire, frequent fire) are shown as polygons. From 1995 to 1999, the no fire plots were unburned, periodic fire plots experienced fire every other year, and frequent fire plots experienced annual burning. Since the end of the original fire experiment in 1999, subsequent prescribed fires have been conducted in the periodic and frequent areas. Periodic plots had five fires from 1995 to 2019, and frequent plots had seven fires from 1995 to 2019. Originally there were 27 plots; however, only 22 plots could be relocated and resampled: no fire = 9, periodic = 7, and frequent = 6. Photos show an example of a no fire plot (**B**) and frequent fire plot (**C**). The base layer shown is the Topographic (with Contours and Hillshade) basemap from Esri (Esri 2020)

Periodic plots were burned in 1996 and 1999 and frequent plots were burned annually from 1996 to 1999 (four fires). After 1999, subsequent operational prescribed fires were implemented on both burn treatment units, with the most recent occurring in 2019 (Table 1). In total, the no fire, periodic, and frequent treatment areas received zero, five, and seven fires, respectively. Due to the similarity of fire regimes in periodic and frequent treatment areas, in this study, we present results for the no fire treatment area and the other treatment areas which experienced repeated fire (i.e., no fire vs. fire). We provide additional results in some cases differentiating periodic vs. frequent fire treatment areas. Fires were low-intensity surface fires (Iverson and Prasad 2003; Sutherland and Hutchinson 2003) that occurred during the spring dormant season (March and April). Plots within each treatment area were chosen to represent the moisture gradient driven by the complex topography of the region and hence span xeric to mesic conditions (Hutchinson et al. 2008). While there was compositional variation among plots within treatment areas at the start of the fire experiment, driven by differences in soil moisture and topographic position, treatment areas were floristically comparable to one another (Hutchinson et al. 2005, 2008). Several existing manuscripts have been published or are in preparation that resulted from data collected as a part of this fire experiment: short-term fire effects on stand structure and oak regeneration (Hutchinson et al. 2008), short-term fire effects on the herbaceous layer (Hutchinson et al. 2005), long-term fire effects on stand structure and oak regeneration (Shupe 2021), and long-term fire effects on the herbaceous layer (Shupe 2021). Thus, this manuscript focuses on the effects of fire on floral abundance and bumble bee abundance; effects of fire on other aspects of the plant community are described elsewhere (Hutchinson et al. 2005, 2008; Shupe 2021).

Table 1 Prescribed fire history of Bluegrass Ridge, Wayne National Forest, Ohio, USA, since 1995. Years in bold denote the fires that occurred during the fire experiment (Hutchinson et al. 2005). Subsequent fires were implemented by the Wayne National Forest, Ironton Ranger District to increase canopy openness and enhance oak regeneration and herbaceous layer biodiversity. No fires have occurred in the control plots for at least 30 years

Control	Periodic	Frequent
-	**1996**	**1996**
-	**1999**	**1997**
-	2004	**1998**
-	2015	**1999**
-	2019	2004
-	-	2015
-	-	2019

Vegetation surveys

In the summer of 2022, we sampled 22 vegetation plots twice: once from May to June (time one) and a second time from July to September (time two) to capture both early-season and late-season plant species. Plots were permanently marked using steel rebar in 1995 and were relocated using a Global Positioning System (GPS) and a metal detector. We relocated and resampled all nine no-fire plots, seven periodic fire plots, and six frequent fire plots. Vegetation plots were 1250 m^2 and broken into two sections, the herbaceous and regeneration subplots (625 m^2). Within the herbaceous subplot, we sampled four 2-m^2 quadrats along four 25-m transects (for a total of 16 2-m^2 quadrats per plot). In each quadrat, we recorded all vascular plant species present, excluding trees. During time one, we visually estimated the cover of each species rooted in the quadrat using cover classes: 0–1% = 2; 1–2% = 3; 2–5% = 4; 5–10% = 5; 10–25% = 6; 25–50% = 7; 50–75% = 8; 75–90% = 9; 90–100% = 10 (Peet et al. 1998). Species that could not be identified in the field were collected, identified in the lab using Weakley and Southeastern Flora Team (2022), and deposited in the Marshall University Herbarium.

To quantify floral abundance, we counted the number of buds, flowers, inflorescences, and fruits individually for each species present in each quadrat. For species with inflorescences, we counted each individual inflorescence. Similar to species presence, we estimated floral abundance twice during the field season (May–June, July–September) to capture early and late blooming species. The floral abundance of graminoids (grasses, sedges, rushes) was not characterized as these species are primarily wind-pollinated.

In addition to the floral abundance counts, we also determined which of the species present at our plots were considered bumble bee host plants for the 16 bumble bee species extant in southeastern Ohio: rusty patched bumble bee, Ashton cuckoo bumble bee (*B. ashtoni* Cresson), black and yellow bumble bee (*B. auricomus* Robertson), two-spotted bumble bee (*B. bimaculatus* Cresson), lemon cuckoo bumble bee (*B. citrinus* Smith), yellow bumble bee, southern plains bumble bee (*B. fraternus* Smith), brown belted bumble bee (*B. griseocollis* De Geer), common eastern bumble bee (*B. impatiens* Cresson), indiscriminate cuckoo bumble bee (*B. insularis* Smith), American bumble bee (*B. pensylvanicus* De Geer), confusing bumble bee (*B. perplexus* Cresson), tricolored bumble bee (*B. ternarius* Say), yellow banded bumble bee, half black bumble bee (*B. vagans* Smith), and variable cuckoo bumble bee (Ascher and Pickering

2020). We determined which plant species were known to be used by bumble bees using the Discover Life database (Ascher and Pickering 2020), which contains a list of plant hosts for each bumble bee species. We supplemented this initial list with our observations of bumble bee visitations on plants during fieldwork in 2022.

Bumble bee surveys

Bumble bee surveys were conducted on the vegetation plots during the day, generally between the late morning to early afternoon (1000 to 1400) on days where there was no precipitation and light winds (Tai et al. 2022). Most surveys were conducted from 1200 to 1230. Like floral surveys, bumble bee surveys took place twice during the summer, once from May to July (time one) and once from July to September (time two). We used a fine mesh insect net and a sweeping technique to survey both the regeneration and herbaceous subplots for a total of 60 person minutes (two people would sample 30 min each) per survey. We walked in transects to locate and capture bees within the plot. If bumble bees were caught, the timer would be stopped, and we would resume sweeping after the bumble bee was processed. We also identified some bumble bees visually during floral visitation; these were not captured. For identification, we transferred captured bumble bees to an observation jar with small holes for ventilation and released them thereafter. Each bumble bee was identified to species using Holm (2022), and the number of individuals for each bumble bee species was recorded.

Plot characteristics

To investigate whether floral abundance varied depending on environmental conditions, we characterized several environmental variables in each plot. Soil samples were collected in each of the 22 plots in 2019 as part of another study (Shupe 2021), and soil physical and chemical properties were characterized by Brookside Laboratories Inc. (Bremen, OH). Here, we focus on pH and soil texture (clay, silt, sand), which collectively reflect soil nutrient and water-holding capacity. In addition, the integrated moisture index (IMI), which is a long-term estimate of soil moisture based on topography (hill shade, flow accumulation, and curvature of the landscape) (Iverson and Prasad 2003) was determined for each plot.

We also characterized canopy openness in each plot to investigate the mechanism through which fire frequency influences floral abundance. Specifically, periodic fire may have reduced canopy cover by reducing seedling recruitment and preventing seedlings from advancing into the sapling layer, thus increasing light availability in the understory. To estimate canopy openness, we took one hemispheric photo in the center of each plot using a fisheye lens attached to a Nikon CoolPik camera (Nikon Inc., Melville, NY). We then determined the canopy openness of each plot using Gap Light Analyzer 2.0 (Frazer et al. 1999).

Data analysis

Data were analyzed using R v.4.3.0 (R Core Team 2023). We calculated floral abundance separately for time one and time two for each plot by summing all buds, flowers/inflorescences, and fruits within each quadrat for all species. We then calculated a mean floral abundance for each plot by averaging the quadrat values. We repeated this process for plants we identified as bumble bee host plants.

We identified a priori several predictor variables that were likely to be related to floral abundance patterns: fire treatment, total percent cover for all vascular plants, forb percent cover, woody percent cover (shrubs and vines), canopy openness (%), pH, IMI, and soil texture (clay, silt, sand %). For fire treatment, we primarily summarize results for plots without fire (no fire) vs. plots with repeated fire (fire), but also provide perspective on differences between periodic and frequent fire treatments in Supplementary Materials 4, 5, and 10. We total cover and forb cover in relation to floral abundance as plots with higher cover could inherently lead to higher floral abundance. We also examined non-tree woody plant cover to explore if competition with woody plants reduced floral abundance of herbaceous plants via a reduction in light availability in the understory layer. Cover values were calculated as midpoints of each cover class and then summed cover of all species present to evaluate the total cover in each respective quadrat. We then calculated the mean cover for each plot by averaging the summed cover across all quadrats in each plot. We also examined the relationship between canopy openness and floral abundance to understand if light availability was related to floral abundance. In addition to light availability, pH and water availability are two other limiting factors for plants. Therefore, we examined the relationship between pH, IMI, soil texture (clay, silt, and sand %), and floral abundance.

To fit models with the predictors described above and to identify parsimonious models that explained the most variation in floral abundance, we used generalized linear models and model selection using the corrected Akaike Information Criteria (AICc) (Akaike 1974; Burnham and Anderson 2002) due to our relatively small sample size ($N = 22$). We fit generalized linear models (glms) since our estimates of floral abundance are count data. Initially, we explored whether the error structure would be better represented by a Poisson distribution or a negative binomial distribution. To achieve this, we evaluated the

residuals of each model and then calculated a likelihood ratio to compare the fit of the Poisson and negative binomial regressions. The likelihood ratio suggested that the negative binomial was a better fit to the data ($P < 0.001$), and we used a negative binomial distribution within all models described below.

Before fitting models, we constructed a Pearson correlation matrix for the continuous predictor variables to identify which were correlated (defined as at least 0.6 or −0.6) to avoid collinearity (Table S2). We also performed a variance inflation factor analysis using function "vifstep" in R package "usdm" (Naimi et al. 2014) and excluded any predictors from models with VIF > 10, which indicated significant multicollinearity. We then fit a global model separately for total floral abundance and for the floral abundance of bumble bee host plants and used the "dredge" function in R package MuMIn (Bartoń 2023) to run GLMs with all possible combinations of uncorrelated predictors and predictors with VIF > 10. These analyses focus on data collected during time one and not the combined data for time one and time two because several predictor variables (total percent cover, forb cover, woody cover, and canopy openness) were not estimated during time two. During model fitting, we explored linear and non-linear relationships (i.e., quadratic, power function) through data visualization and fit non-linear relationships where appropriate. We determined the relationship between woody plant cover and total floral abundance was best fit as a quadratic. All other models were fit linearly. We fit models with fire treatment alone for time one and time two data to understand the effects of repeated prescribed fire in different parts of the growing season. We then performed Holm Bonferroni corrections on those models. Models were ranked by AICc using function "model.sel" in R package MuMIn (Bartoń 2023) and top models were identified within ΔAICc < 2. Models are presented in Table 2 and Fig. S1.

To quantify bumble bee abundance, we calculated the number of observed bumble bees for each plot individually for time one and time two. Due to low detection of bumble bees in 2022 (see "Discussion" for further details), we pooled bumble bee abundance data across time one and time two. Specifically, we calculated the total number of observed bumble bees across time one and two by summing time one and time two abundance values for each plot. Since we did not detect bumble bees in many plots (nine plots had zero detections), we fit a zero inflated negative binomial model to explore the relationship between mean bumble bee abundance and fire treatment using function "zeroinfl" in R package pscl (Zeileis et al. 2008). Finally, we performed a power analysis on the bumble bee glm with fire treatment as the single predictor using function "pwr.f2.test" in R package pwr (Champely 2020). We evaluated power at the 0.05 significance level and assumed a medium effect size of 0.15 as recommended by Cohen (1988).

Results

We identified 222 non-tree plant species across all plots. The most common understory species were bearded shorthusk (*Brachyelytrum erectum* (Schreb. ex Spreng.) P. Beauv.), licorice bedstraw (*Galium circaezans* Michx.), Virginia creeper (*Parthenocissus quinquefolia* (L.)

Table 2 Top models for total floral abundance. Models are ordered by the lowest corrected Akaike Information Criteria (AICc). Significant predictor variables include fire treatment (fire vs. no fire), total cover (%), forb cover (%), clay (%), sand (%), silt (%), and woody cover (%) fit as a quadratic. IMI, pH and canopy cover were not significant predictors

Predictor	Intercept	Slope	*P*	Deviance	AICc	logLik
Fire treatment (no fire/fire)	2.54	0.82	< 0.01	24	159.1	− 75.9
Total cover + woody cover + woody cover ^2	2.13	0.04	< 0.02	23.14	160.1	− 73.2
	–	0.12	0.29	–	–	–
	–	− 0.02	0.04	–	–	–
Total cover	2.44	0.03	< 0.01	23	163.4	− 78.0
Forb cover	2.6	0.08	< 0.01	23	165.8	− 79.2
Clay	2.06	0.04	< 0.01	22.8	167.3	− 80.0
Sand	3.59	− 0.02	< 0.01	23	168.4	− 80.5
Silt	1.95	0.03	0.04	23.2	171.7	− 82.2
Woody cover + woody cover ^2	2.57	0.32	0.05	23.3	174.1	− 81.9
	–	− 0.03	0.08	–	–	–
IMI	2.57	0.01	0.39	23.2	174.2	− 83.4
pH	2.09	0.2	0.39	23.2	174.3	− 83.5
Canopy cover	3.17	− 0.009	0.88	23.2	174.9	− 83.8

Planch.), roundleaf greenbrier (*Smilax rotundifolia* L.), three-lobe violet (*Viola palmata* var. *triloba* (Schwein.) Gingins ex DC.), grapevine (*Vitis* sp. L.), slender woodland sedge (*Carex digitalis* Willd.), nakedflower ticktrefoil (*Hylodesmum nudiflorum* (L.) H.Ohashi & R.R.Mill), fragrant bedstraw (*Galium triflorum* Michx.), cat greenbrier (*Smilax glauca* Walter), and perfoliate bellwort (*Uvularia perfoliata* L.), all of which occurred in > 90% of plots (Table S1). We documented eight non-native species across the 22 plots, which generally were infrequent and had low cover (< 3%) with the exception of Japanese stiltgrass (*Microstegium vimineum* (Trin.) A. Camus), which occurred in 12 plots and had a mean cover of 5.5%. Of the non-graminoid species (N= 192), 124 species had reproductive structures during sample periods (Table S1). The mean total cover across all plots was 23.4% (range = 3.3 to 56.7%). Mean total cover increased with fire: 11.7% in no-fire plots versus 31.9% in fire plots. Frequent fire plots had slightly higher cover (36.8%) than periodic fire plots (27%).

Floral abundance

Total floral abundance (number of reproductive structures per m^2) was significantly lower in no-fire plots than in plots with fire (P< 0.01 for time one and time two) (Fig. 2). No fire plots had a mean total floral abundance of 12.6 (SE = 2.3) and 4.3 (SE = 1.1) for time one and time two, respectively. Plots with fire had a mean total floral abundance of 28.6 (SE = 2.5) and 20.3 (SE = 2.6). There was no difference in total floral abundance between periodic and frequent plots, which was consistent for time one and time two (Fig. S2).

One hundred and twenty-seven species were identified as plants used by bumble bees (57% of the species in our plots, Table S1). Common bumble bee host plants included nakedflower ticktrefoil, perfoliate bellwort, white snakeroot (*Ageratina altissima* (L.) R.M. King & H. Rob.), American hogpeanut (*Amphicarpaea bracteata* L. Fernald var. *bracteata*), Allegheny blackberry (*Rubus allegheniensis* Porter), smooth Solomon's seal (*Polygonatum biflorum* (Walter) Elliott var. *biflorum*), wreath goldenrod (*Solidago caesia* L.), and dwarf cinquefoil (*Potentilla canadensis* L.) (see Table S1 for full list). The mean floral abundance (number of reproductive structures/m^2) of bumble bee host plants was higher in plots with fire for both periods, relative to plots with no fire (P< 0.01, Fig. 3). The mean floral abundance of bumble bee host plants was 0.9 (SE = 0.3) and 1.3 (SE = 0.6) for no fire plots during time one and time two, compared to 6.4 (SE = 1.4) and 11 (SE = 2.9) for plots that experienced

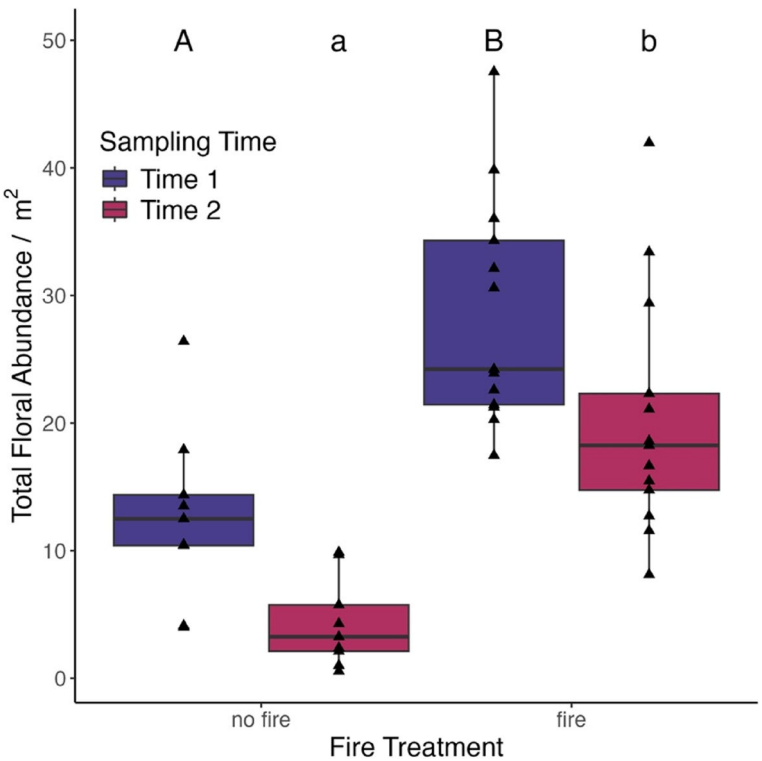

Fig. 2 Total floral abundance (buds, flowers, inflorescences, and fruits) for all plant species per m^2 for time one and time two for each fire treatment (no fire, fire). Boxplots show the median, interquartile range, and range. Letters indicate significant differences in floral abundance

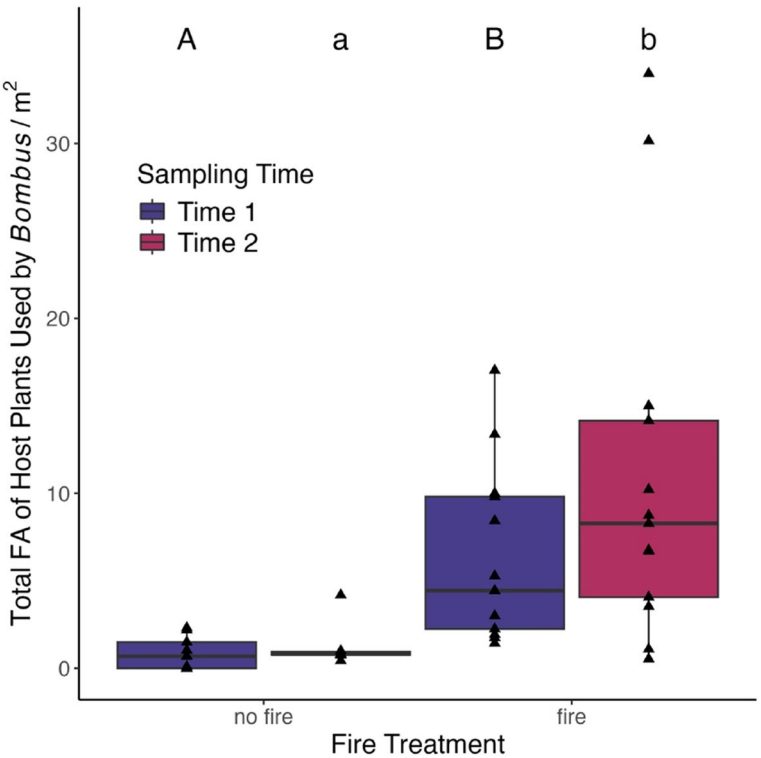

Fig. 3 Total floral abundance (buds, flowers, inflorescences, and fruits) of bumble bee host plants per m^2 for time one and time two for each fire treatment (no fire, fire). Bumble bee host plants were identified using the Discover Life database (Ascher and Pickering 2020) and observations in the field. Boxplots show the median, interquartile range, and range. Letters indicate significant differences in floral abundance with capital letters (A, B) indicating time one results and lower-case letters (a, b) indicating time two results

fire. Burned plots exhibited considerable variation and floral abundance of bumble bee host plants was highest in burned plots in time two (Fig. 3). Floral abundance of bumble bee host plants between the periodic and frequent burn plots was not significantly different for time one ($P = 0.5$), but was marginally significant for time two ($P = 0.06$) (Fig. S3). Late-season asters were primarily responsible for higher late summer floral abundance counts for bumble bee host plants at frequent fire plots relative to periodic and no fire plots.

Variance inflation analysis indicated that two variables (percent clay and percent sand) were collinear, and these variables were excluded from all models. Predictor variables that were significantly correlated ($r > +0.6$, $r < -0.6$) are shown in Table S2. The top model for total floral abundance contained fire treatment as the sole predictor: repeatedly burned plots had higher total floral abundance ($P < 0.01$, Table 2). Other top models that contained significant predictors with AICc < 2 included total percent cover and quadratically transformed woody cover. Other supported models that contained significant predictors (but with AICc > 2) included total percent cover, percent forb cover, percent clay, percent sand, and percent silt (Table 2, Figs. 4 and 5). Total cover and forb cover had significant positive relationships with total floral abundance (Table 2, Fig. 4). Percent woody cover was marginally significantly related to total floral abundance (Table 2). The relationship between total floral abundance and woody cover was non-linear: total floral abundance was initially positively related to woody cover, but then declined at higher woody cover values (Fig. 4C). Percent clay and silt were positively related to floral abundance while percent sand was negatively related to floral abundance (Table 2, Fig. 5). IMI, pH, and canopy openness were not significantly related to total floral abundance (Table 2, Fig. S1).

We repeated the same model selection process with floral abundance of bumble bee host plants. Results were similar; the top model contained fire treatment ($P < 0.01$), followed by the model with total cover ($P < 0.01$, AICc < 2) (Table S3). Other supported models included woody cover, percentage clay, percentage sand, forb cover, percentage silt, and canopy openness, which were significantly positively related to floral abundance of the bumble bee host plants with the exception of percentage sand, which was negatively related (Table S3, Figs. S4 and S5). The floral abundance of bumble bee host plants was not related to pH or IMI (Table S3, Fig. S6).

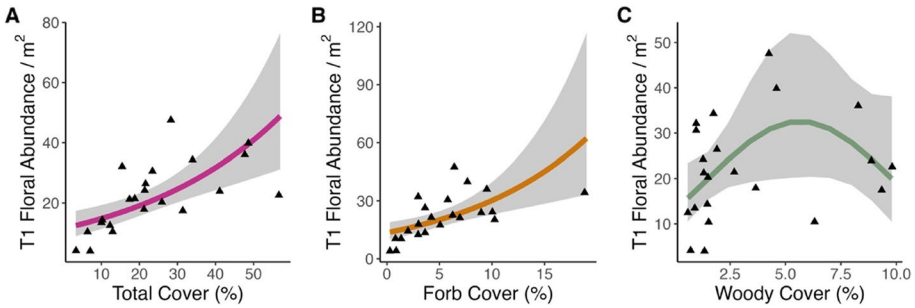

Fig. 4 Total floral abundance (buds, flowers, inflorescences, and fruits) per m^2 for time one versus mean percent cover for all plant species (**A**), mean percent cover of forbs (**B**), and mean percent cover of woody plants (**C**). Colored lines represent the fitted negative binomial models, with 95% confidence limits in gray

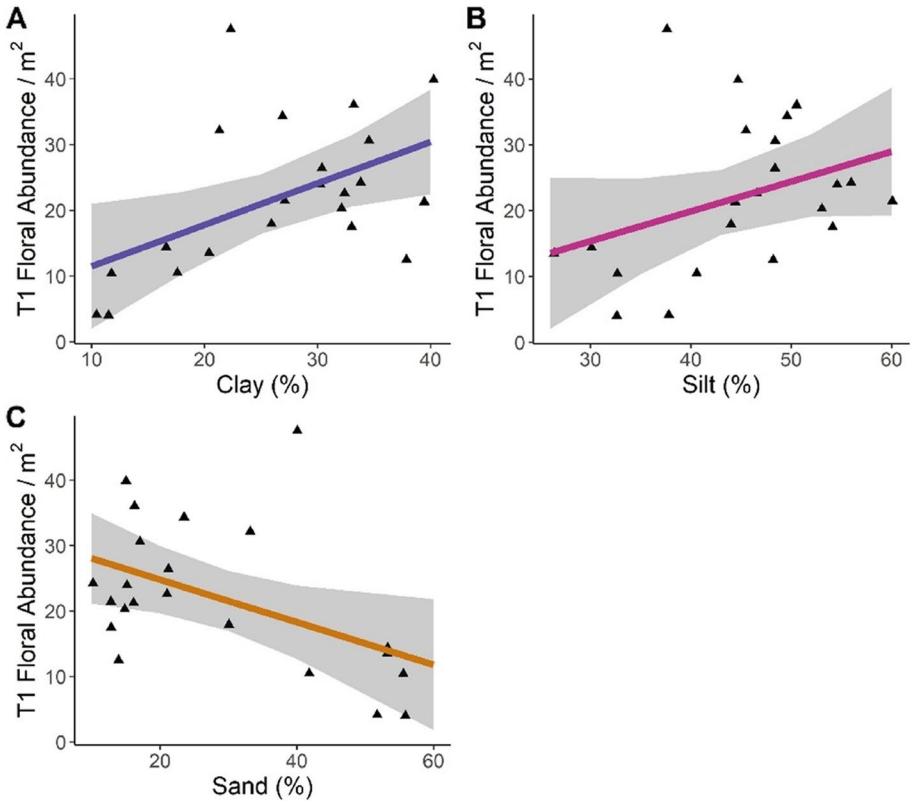

Fig. 5 Total floral abundance (buds, flowers, inflorescences, and fruits) per m^2 for time one versus percent clay in the A horizon (**A**), percent silt in the A horizon (**B**), and percent sand in the A horizon (**C**). Colored lines represent the fitted negative binomial models, with the 95% confidence interval in gray

Bumble bee abundance

Only two bumble bee species were found during surveys (two-spotted bumble bee and common eastern bumble bee). Over both surveys and across all 22 plots, we detected a total of 75 bumble bee individuals (range per plot over both surveys = 0 to 30). Of the 75 bumble bee individuals, 51 (68%) were the common eastern bumble bee. Notably, there was one observation of 30 common eastern bumble bees foraging on a large patch of shrubby St. Johnswort (*Hypericum prolificum.* L.) in a periodically burned plot. The mean observed bumble bee abundance for no fire and fire plots for time one and time two combined was 1.4 (SE = 0.9) and 4.8 (SE = 2.3), respectively. We did not find a significant relationship between fire treatment and bumble bee abundance (count model $P = 0.95$, logit model $P = 0.2$) (Figs. 6 and S7). The lack

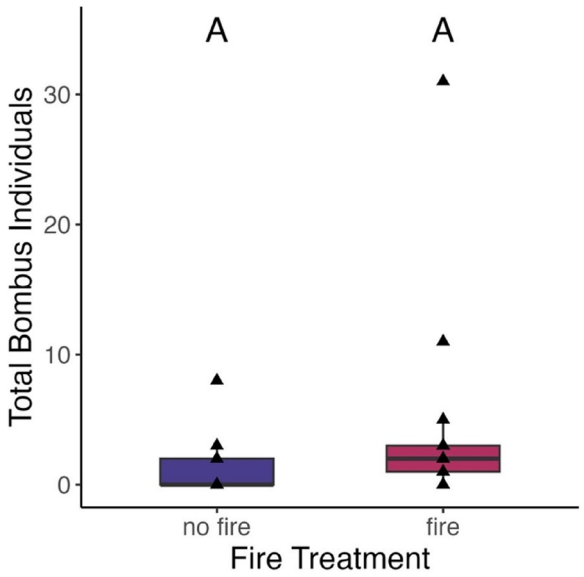

Fig. 6 Total bumble bee individuals observed in each plot for each fire treatment (no fire, fire). Data shown were pooled across the time one and time two surveys. Boxplots show the median, interquartile range, and range. Letters indicate significant differences in floral abundance

of significant differences was likely due to our low power (0.41) to detect significant differences in bumble bee abundance between fire treatments.

Discussion

We sampled plant and bumble bee communities in mixed-oak forests with different prescribed fire frequencies to quantify the effects on bumble bee floral resources and bumble bee abundance. Areas that experienced repeated fire had considerably higher total floral abundance relative to areas that were unburned. Fire enhanced the floral abundance of bumble bee host plants, especially in frequently burned plots sampled during late summer. Model selection using AICc revealed fire treatment and total plant cover were the best predictors of floral abundance. These results indicate that repeated prescribed fires promoted floral resources with potential direct benefits to bumble bee communities.

Many fire-adapted plants have fire-dependent cues, such as post-fire flowering and seed germination, and floral and seed production often increases post-fire due to enhanced resource availability (Gowe and Brewer 2005; Fill et al. 2012; Beck et al. 2023). Fire often increases light and nutrient availability, decreases the dominance of woody species and hence competition in the understory, and stimulates flower production (Hutchinson et al. 2005; Burton et al. 2011; Zirondi et al. 2021), which is likely why we detected higher floral abundance in areas that experienced fire.

In addition to fire treatment, total cover and forb cover were positively related to floral abundance. Higher cover may have enhanced floral abundance in our plots due to higher numbers of plant individuals and therefore potentially greater flower production. Collectively, our results suggest that higher plant cover in burned plots may be fire-mediated effects, as fire often increases herbaceous abundance via increases in resource availability (Vander Yacht et al. 2017; Shupe 2021; Hutchinson et al. 2024), and enhancing fire-stimulated germination (Glasgow and Matlock 2007; Lamont et al. 2019). The higher germination rates of some species coupled with the stimulation of flower stalk production on burned plots may be acting concurrently, leading to higher plant cover and thus higher floral abundance. Our finding is consistent with other fire effects studies that document higher floral abundance in burned sites (Greenberg et al. 2007; Zirondi et al. 2021; Gelles et al. 2023); however, positive effects of fire on floral abundance are often short-lived and occur within 1 year post-fire (Gelles et al. 2023). In our study, those effects had persisted 4 years after the last fire, possibly due to high light availability in the understory resulting from repeated fire in burned sites.

Total floral abundance did not differ significantly between periodic and frequently burned plots. This likely occurred because those treatment areas ultimately had similar fire frequencies (five vs. seven fires over a 24-year period), despite initial differences in fire frequency during the fire experiment from 1995 to 1999. In addition, mean cover in 2022 was similar between the burn treatments; therefore, it is not surprising that floral abundance was also similar. However, mean floral abundance of bumble bee host plants was somewhat higher in frequently burned plots relative to periodically burned plots. Differences in bumble bee host plant floral abundance may have resulted from increased establishment of fire-stimulated plants, such as species from the daisy family in frequent fire plots in the early stages of the fire experiment. We are unable to evaluate differences in floral abundance and percent cover through time, as neither was collected during the original fire experiment, which is a limitation of our study. However, given species richness and species composition did not differ between the three treatments at the initiation of the study (Hutchinson et al. 2005), it is likely that floral abundance was also similar.

One mechanism through which fire can promote floral abundance is by increasing canopy openness and light availability to the forest understory (Vander Yacht et al. 2020; Saladyga et al. 2022). As such, we hypothesized that plots with more frequent fire would have greater canopy openness and higher floral abundance. We found

a positive relationship between canopy openness and floral abundance of bumble bee host plants, which provides some support for this hypothesis. However, we did not find a significant positive relationship between canopy openness and total floral abundance. This could have occurred because many of the bumble bee host plants in our sites are heliophytic species in the daisy and legume families, which are likely to be more responsive to enhanced light availability relative to sciophytic herbs and shrubs common in mixed-oak forest understories. Although there was variation in canopy openness among our sites, we did not find that canopy openness was higher in burned sites relative to unburned sites ($P=0.6$). Overstory canopy openness may have been similar among treatment areas because prescribed fires were generally low-intensity with minimal overstory mortality (Hutchinson et al. 2005) or resulted in somewhat temporary reductions in canopy openness that are infilled by tree canopy growth in subsequent years. In addition, ice storm events impacted our study area in 2020 and 2021 and resulted in tree falls and increases in canopy openness throughout the three treatment areas. Another factor that could explain why canopy openness was similar is tree mortality from emerald ash borer (*Agrilus planipennis* Fairmaire), which occurred in all treatment areas. The emerald ash borer was first observed in Lawrence County, Ohio in 2010 (USDA 2024) and resulted in almost complete mortality of all overstory ash trees and consistent increases in canopy openness. Although mortality occurred in the overstory in plots without fire, total floral abundance may have remained unchanged because of the lack of fire and its impacts on litter depth and midstory shade.

However, we did find that woody plant cover in the understory layer (excluding trees) was related to total floral abundance. Specifically, there was a non-linear relationship between woody plant cover and total floral abundance: plots with higher woody plant cover had lower total floral abundance than plots with intermediate woody cover, suggesting decreased light availability and/or increased competition with woody plants may have had negative effects on total floral abundance. The most abundant non-tree woody species that contributed to this relationship were Virginia creeper, grapevines, Allegheny blackberry, cat greenbrier, and roundleaf greenbrier (Table S1).

Floral abundance had a positive relationship to percent silt, likely due to soil texture effects on nutrient- and water-holding capacity (Owens and Rutledge 2005). Soils with more silt and clay have a greater ability to hold moisture and nutrients due to their smaller particle size and high surface area, resulting in higher resource availability that can be allocated towards growth and reproduction (i.e., floral abundance). Conversely, sandy soils have a lower capacity to hold water and nutrients, thus resource availability and reproduction are likely to be lower. In contrast to soil texture, IMI was not related to floral abundance patterns, indicating that floral resources may be responding to plot-level soil moisture and drainage differences driven by soil texture that are not captured by topographically predicted soil moisture.

While total floral abundance and bumble bee host plant floral abundance changed with fire treatment, we did not detect significant differences in bumble bee abundance among treatments. This was likely due to the low number of bumble bee individuals we captured in our plots: most individuals were common eastern bumble bees and on average we only found 3 individuals per plot. We had low power (0.41) to detect a true difference in bumble bee abundance among no fire and fire plots because our sample size was too low. Therefore, our bumble bee results need to be interpreted with caution and additional studies with a larger sample size are needed. There are several possible explanations for the low detection of bumble bees in our plots. Reports from several researchers in different parts of the USA through the beemonitoring listserv (e.g., D. Larson, R. Barsh, pers. comm.; Beemonitoring 2022) documented a low observation rate of bumble bees in 2022, the year we surveyed, although no clear explanations have yet emerged for lower bumble bee abundance. Factors affecting bumble bee populations could be explained by yearly weather patterns, including a cooler or warmer than normal spring which could alter bee and plant phenology (Anderson 2022). The duration of our surveys may also have been inadequate to fully capture the bumble bee community. We opted not to use bowl or vane traps because we did not want to cause direct mortality of bumble bees. However, the use of multiple collection techniques, such as bowl or vane traps and net surveys, could have resulted in increased detection of bumble bees in our plots.

Other than impacting floral resources, fire can also affect nesting of bumble bees. Ground-nesting bumble bees (i.e., common eastern bumble bee, two-spotted bumble bee, rusty-patched bumble bee, black and yellow bumble bee, tricolored bumble bee, and yellow-banded bumble), construct their nests under the ground at depths varying from 15 to 120 cm, and would not be affected by low-severity fires, as low-severity surface fires cause small fluctuations (< 20 ℃) in soil temperature within the top 2.0 cm and do not reach lethal temperatures (40 ℃) (Plath 1934; Iverson and Hutchinson 2002). Conversely, bumble bee species nesting mostly on the surface of the ground (i.e., yellow bumble bee, brown belted bumble bee, American bumble bee, confusing bumble bee, and half black bumble bee) might be affected

by these fires, as well as the cuckoo bumble bee species that parasitize them (lemon cuckoo bumble bee, variable cuckoo bumble bee, and indiscriminate cuckoo bumble bee) (Plath 1934). Other pollinators might respond differently to fire. For example, most bee species seem to become more abundant after fire (Potts et al. 2003; Burkle et al. 2019; Mason et al. 2021); ground beetles seem to have a positive response to fire as well (Mason et al. 2021); whereas fire effects on butterflies can be positive or negative depending on the species and life stage (Swengel 2001; Mason et al. 2021). Many aspects and impacts of prescribed fire will thus be important to forest management goals for enhancing pollinator habitat, such as fire frequency (as demonstrated by our study), but also the timing of fire (i.e., dormant or growing season), and fire severity (Swengel 2001; Campbell et al. 2007).

Our results indicate that a regime of periodic prescribed fire enhanced floral resources for bumble bees and likely other pollinator groups, which suggests prescribed fire may be a useful management strategy to enhance pollinator food resources and habitat. However, the effects of other widely used management strategies on floral and pollinator abundance have yet to be evaluated. In mixed-oak forests of the eastern USA, many studies have demonstrated positive effects of prescribed fire coupled with other treatments such as mechanical thinning on oak regeneration and herbaceous layer biodiversity and cover (Brose and Van Lear 1998; Hutchinson et al. 2024) and in some cases, prescribed fire alone can be insufficient to enhance herbaceous layer cover and biodiversity and presumably floral abundance. Thus, the combination of prescribed fire and forest thinning via mechanical removal in some areas may be the most beneficial option for increasing pollinator food resources and habitat as it can increase herbaceous cover and provide a greater variety of niches to be occupied by different insects (Campbell et al. 2007). However, very few studies have evaluated the joint impact of prescribed fire and strategic forest thinning on floral resources for bumble bees in particular and pollinators in general. Therefore, an outstanding knowledge gap is the potential benefits of prescribed fire and mechanical thinning for pollinator communities.

Conclusions

Overall, our results indicate that repeated prescribed fires enhanced floral abundance for bumble bees in mixed-oak forests. Increased fire frequency often increases plant species richness and cover in the herbaceous layer of mixed-oak forests. Fire stimulates flowering and enhances seed germination, which are additional mechanisms in which fire can increase total floral abundance. Fire could stimulate flowering beyond increased richness and cover, via greater establishment from seed. Fire may also increase nesting habitat for ground nesting bumble bees that prefer more bare ground, as well as wood cavity nesting bumble bees. With ongoing declines of pollinator populations, additional research is needed on the use of prescribed fire as a management tool in mixed-oak forests, which will increase our understanding of fire effects on pollinator habitat and bumble bee abundance.

Abbreviations

AICc	Corrected Akaike Information Criteria
IMI	Integrated Moisture Index
GPS	Global Positioning System
GLM	Generalized linear model
VIF	Variance inflation factor

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s42408-025-00367-2.

Supplementary Material 1: Table S1. Frequency and mean percent cover of all plant species found. All unique plant species found in time one and time two, the plant functional type they belong to (pgrass = perennial graminoid, pforb = perennial forb, aforb = annual forb), the mean cover (%) of each plant species across all plots sampled in time one, and the total number of plots that each species occurred in across the time one and two sampling ($N = 22$). Species that were reproductive in at least one plot are denoted in the R (reproductive) column with a 1. Bumble bee host plants are colored in gray. Species are ordered from most to least frequent. Species with a NA in Cover (%) were only found during time two and cover was not estimated.

Supplementary Material 2: Table S2. Correlation matrix for a priori predictor variables used in model selection using AICc. Correlation matrix of a priori predictor variables used in model selection using the Akaike Information Criteria (AICc). Variables with a Pearson correlation coefficient of > 0.6 and < -0.6 were determined to be correlated. A priori continuous variables included total cover (%), woody cover (%), forb cover (%), percentage clay, percentage silt, percentage sand, soil pH, canopy openness, and IMI (integrated moisture index).

Supplementary Material 3: Figure S1. Scatterplot of total floral abundance (buds, flowers, inflorescences, and fruits) per m^2 for time one in relation to percent canopy openness, soil pH, and IMI. Total floral abundance (buds, flowers, inflorescences, and fruits) per m^2 for time one in relation to percent canopy openness (A), soil pH (B), and Integrated Moisture Index (IMI) (C). No significant relationship was found between these variables and floral abundance. Each plot is colored by fire treatment (no fire, fire).

Supplementary Material 4: Figure S2. Total floral abundance (buds, flowers, inflorescences, and fruits) for all plant species per m^2 for time one and time two for no fire, periodic fire, and frequent fire. Boxplots show the median, interquartile range, and range. Letters indicate significant differences in floral abundance between fire frequencies.

Supplementary Material 5: Figure S3. Total floral abundance (buds, flowers, inflorescences, and fruits) of bumble bee host plants per m^2 for time one and time two for no fire, periodic fire, and frequent fire. Bumble bee host plants were identified using the Discover Life database (Ascher and Pickering 2020) and observations in the field. Boxplots show the median, interquartile range, and range. Letters indicate significant differences in floral abundance between fire frequencies with capital letters (A, B) indicating time one results and lower-case letters (a, b) indicating time two results.

Supplementary Material 6: Table S3. Top models for floral abundance of bumble bee host plants. Top models for the total floral abundance of bumble bee host plants that emerged from model selection using AICc. Models are ordered by the lowest AICc. Significant predictor variables include fire treatment (fire, no fire), total cover (%), woody cover (%), forb

cover (%), canopy openness (%), clay (%), sand (%), and silt (%). pH and integrated moisture index (IMI) were not significant predictors.

Supplementary Material 7: Figure S4. Scatterplots for total floral abundance for bumble bee host plants in relation to total cover, forb cover, and woody cover. Bumble bee host plant floral abundance (buds, flowers, inflorescences, and fruits) per m^2 for time one in relation to mean percent cover for all plant species (A), mean percent cover of forbs (B), and mean percent cover of woody plants (C). Colored lines represent the fitted negative binomial models in A, B, and C, with 95% confidence limits in gray. Confidence limits end before the x-axis as they extend beyond the limit of the y-axis.

Supplementary Material 8: Figure S5. Scatterplots of total floral abundance in relation to percent clay, percent silt, percent sand, and canopy openness. Total bumble bee host plant floral abundance (buds, flowers, inflorescences, and fruits) per m^2 for time one in relation to percent clay in the A horizon (A), percent silt in the A horizon (B), percent sand in the A horizon (C), and percent canopy openness (D). Colored lines represent the fitted negative binomial models, with the 95% confidence interval in gray. Confidence limits end before the x-axis as they extend beyond the limit of the y-axis.

Supplementary Material 9: Figure S6. Scatterplot of bumble bee host plant floral abundance (buds, flowers, inflorescences, and fruits) per m^2 for time one in relation to soil pH and IMI. Total floral abundance (buds, flowers, inflorescences, and fruits) per m^2 for time one in relation to soil pH (A), and Integrated Moisture Index (IMI) (B). No significant relationship was found between these variables and floral abundance. Each plot is colored by fire treatment (no fire, fire).

Supplementary Material 10: Figure S7. Total bumble bee individuals observed in each plot for no fire, periodic fire, and frequent fire. Data shown were pooled across the time one and time two surveys. Boxplots show the median, interquartile range, and range. Letters indicate significant differences in floral abundance between fire frequencies.

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Authors' contributions
MRS, PP, KAP, and TFH identified the questions and designed the study. TF established the original study in 1995. MRS led field data collection in 2022. MRS, PP, and KAP analyzed the data. MRS led writing of the manuscript, and all authors contributed to editing and revising the manuscript.

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Marshall University

Data availability
The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Competing interests
The authors declare that they have no competing interests.

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