RESTORATION ECOLOGY
The Journal of the Society for Ecological Restoration
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RESEARCH ARTICLE

Fire frequency and timing influence bee–flower interactions: a case study from an oak-pine savanna restoration on the Cumberland Plateau

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Abstract

Introduction: Native plant communities have declined in the southeastern United States over the past century because of habitat loss and fire suppression. While restoration of these communities often requires prescribed fire, the effects of fire on endemic insects remain unclear. Pollinators of savanna plants, including bees, are an important group to study in restoration contexts. Fire timing and frequency may impact both plant composition and plant-bee interactions.

Objectives: We studied the influence of fire timing (early and late growing-season) and frequency (1-, 2-, and 3-year fire-return interval) on plant-bee interactions.

Methods: As a case study, we surveyed plants, plant flowering, and plant-bee interactions across different long-term vegetation management fire treatments in an oak-pine savanna on the Cumberland Plateau, Tennessee in 2023.

Results: Fire frequency influenced greater forb coverage in the 1- and 2-year fire-return interval treatments and greater woody coverage in the 3-year fire-return interval treatments. Continual burning during the early growing-season (EGS) on a 2-year interval over 15 years led to greater grass coverage and reduced floral resources except when compared to the EGS 3-year unit. Increased grass coverage led to decreased floral resources in the EGS 2-year treatment compared to the late growing-season (LGS) 1-year treatment. Similarly, we observed an increased number of plant-bee interactions in the 1-year LGS treatment relative to the 2- and 3-year EGS treatments.

Conclusions: A 1- or 2-year fire-return interval was required to maximize floral abundances, and burning during the late growing season is preferable to maximize floral resource availability.

Conceptual Implications: The bee community at the Bridgestone-Firestone Fire Demonstration Area was diverse and included species not previously documented in Tennessee, indicating fire-restored savannas can provide habitat for rare species. Our results indicate frequent fire regimes promote the greatest floral resources for bees in this region. Season of burning influenced plant community composition, and we recommend restoration practitioners vary fire timing to include burning during the latter portion of the growing season to prevent excessive grass coverage and encourage increased forb coverage. Practitioners should also consider working with the naturally occurring seedbank response, especially when restoring areas where a diverse native seedbank likely still exists.

Key words: Cumberland Plateau, early succession, plant-bee interactions, pollinators, prescribed fire, restoration

Introduction

Oak-pine savannas are early successional vegetation types threatened globally by anthropogenic change (Van Lear et al. 2005; Hanberry et al. 2014). Fire suppression, agriculture, and increased wood fiber production are principal threats that have led to a reduction in the extent and distribution of these plant communities (Van Lear et al. 2005; Jose et al. 2006; Vander Yacht et al. 2017). In the eastern United States, oak-pine savannas and open woodlands historically covered 36 million hectares (Earley 2005; Oswalt et al. 2012) but declined by more than 50% between 1980 and 2018 (Guldin & Black 2018). The reduction of these systems has resulted in precipitous declines in various vertebrate species that require oak or pine savanna, such as *Dryobates borealis* Vieillot (red-cockaded woodpecker), *Gopherus polyphemus* Daudin (gopher tortoise), and *Melanerpes erythrocephalus* Linnaeus (red-headed woodpecker) (McCoy et al. 2006; Vander Yacht et al. 2016; Koenig

Author contributions: SRW, LR, CAH identified the questions and designed the study; SRW, LR, MML collected and analyzed the data; CAH organized the treatments; SRW led the writing of the manuscript with all authors contributing to its editing and revision.

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doi: 10.1111/rec.70533
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et al. 2017). Declines in invertebrate species also may be occurring, but they are more difficult to track. Insects such as bees can be surveyed via their association with flowering plants, but more information is needed on the distribution of flowering plant communities and their insect pollinators (Smith DiCarlo et al. 2020; Ulyshen et al. 2024). Moreover, investigating how underlying ecological associations between the native flora and fauna change under different fire regimes may have important implications when restoring oak-pine savannas.

Restoration and persistence of open oak-pine woodlands and savannas in the southeastern United States requires frequent fire. Dendrochronological evidence dating from the seventeenth century indicates relatively low-intensity fire occurred, on average, every 2–3 years on the Tennessee barrens and the Cumberland Plateau until fire suppression in the twentieth century (Stambaugh et al. 2016; Stambaugh et al. 2020). Relatively low-intensity surface fire every 1–3 years discourages mesophyte encroachment and maintains a diverse assemblage of forbs, graminoids, and their insect associates (DeSelm 1994; Barrioz et al. 2013; Turner et al. 2025). Frequent fire consumes aboveground plant matter, encourages germination of the seedbank, and promotes fire-adapted plant species (Pausas et al. 2004; Snyman & Van Wyk 2005; Pausas & Schwilk 2012). The timing of fire can influence vegetation composition and structure (Howe 2011; Harper et al. 2016; Bones et al. 2026). Most of the historic fire on the Cumberland Plateau occurred during the dormant season (Stambaugh et al. 2020), but recent efforts to restore savannas and open woodlands have incorporated fire during the growing season, which more accurately reflects the timing of lightning-caused fire in some regions, especially along the Coastal Plain of the southeastern United States. In general, frequent fire occurring earlier in the year tends to promote warm-season grasses, whereas late growing-season fire may promote more forbs (Howe 2000; Gruchy et al. 2009; Bones et al. 2026). Thus, fire timing may have important implications for pollinator communities, and seasonal fire events over multiple years are likely necessary to detect significant differences in plant community composition (Drewa et al. 2002; Robertson & Hmielowski 2014).

Understanding the diversity and ecology of bees native to the Cumberland Plateau and broader Central Hardwoods ecoregion is essential to long-term restoration of the diverse plant communities common to open woodlands and savannas (Folkerts et al. 1993). However, it is still unclear how bee communities and their plant associations in this region respond to different burn regimes. Fire can have positive effects on savanna and grassland bee communities. For example, in tallgrass prairies, more nests of ground-nesting bees were found in recently burned patches than adjacent unburned patches, perhaps owing to increased bare ground and reduced litter (Brokaw et al. 2023). In other fire-prone grassland systems, plant–pollinator interaction networks were resilient to the effects of fire, with both bees and plants switching partners multiple times as time-since-fire increased (da Silva Goldas et al. 2022). Grassland restoration via burning benefits flower-visiting insects by promoting increased floral resources (Shafer et al. 2025) and thus can alter the subsequent foraging patterns of some bee species (Mola & Williams 2018). The composition of bee communities is both a driver and a result of the restoration process, further exemplifying how restoration of open woodlands and savannas on the Cumberland Plateau would benefit from a community approach to maintain critical ecological interactions.

The direct effects of fire timing and frequency vary across different groups of bees. For example, in a Florida longleaf pine (*Pinus palustris* Mill.) ecosystem, pollen specialists dependent upon fall-flowering species were negatively affected by fire occurring during the fall flowering period (Ulyshen et al. 2023). Growing-season burns have been associated with greater bee abundance than dormant-season burns in tallgrass prairies, likely because of increased bare ground (Decker & Harmon-Threatt 2019). Ulyshen et al. (2023) reported bee abundance and richness did not vary between winter, spring, summer, or fall burns, and the richness of bee–flower interactions was greater in spring- and summer-burned plots than fall-burned plots. Moylett et al. (2020) reported ground-nesting bees in the North Carolina Sandhills were more abundant in plots burned within 1, 2, or 3 years previously compared to unburned control plots, but they did not differ between burn treatments. Although it is important to assess how differences in timing and frequency of burning affect flowering dynamics of plants used by bees, multiple fire events may be required to realize an effect on plant composition and the bee community. Additionally, the effectiveness of such restoration protocols should be assessed on a regional basis to determine which burn regimes best promote occupancy by the native plant–bee interaction communities distinctive to the focal area.

Our objectives were to (1) evaluate the influence of fire frequency and timing on interactions between flowering plants and bees and (2) document the bee taxa and their plant hosts in the restoration of an oak-pine savanna on the Cumberland Plateau in Tennessee. We hypothesized fire timing and frequency would impact the plant-bee community by influencing the diversity and abundance of flowering forbs, thereby altering the diversity of bees via changes in bee–plant interactions. We predicted areas with more frequent fire during the latter portion of the growing-season would have a greater abundance and diversity of flowering forbs. We further predicted that more-frequent late growing-season fire would lead to increased plant–bee interactions.

Methods

Field-Site Description

We conducted our surveys at the Bridgestone-Firestone Prescribed Fire Demonstration Area (Fig. 1), which is located at the Bridgestone-Firestone Wildlife Management Area, owned and managed by the Tennessee Wildlife Resources Agency (TWRA), in White County, TN. The Fire Demonstration Area is a 54-ha area on the Cumberland Plateau in the greater Central Hardwoods region. The area where the Fire Demonstration Area now exists was managed as a loblolly pine plantation by prior ownership until TWRA bought the property in 1997. The area was allowed to revegetate naturally from 2000 to 2010, and the only disturbance during that period included two dormant-season prescribed fires. By 2011, the dominant vegetation included *Piptochaetium avenaceum* (L.) Parodi (black needleseed grass), *Coreopsis verticillata* L. (greater

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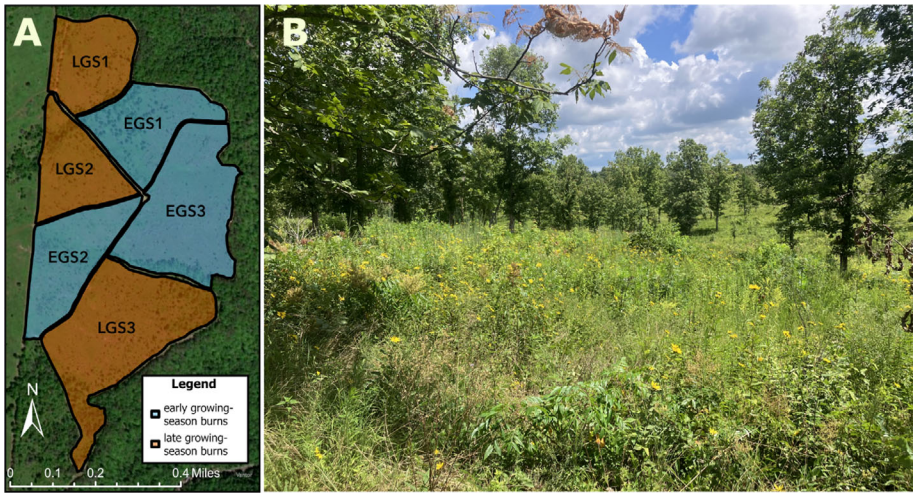

Figure 1. (A) Map of the six surveyed units. Darker orange polygons are late growing-season burns (denoted LGS), lighter blue polygons are early growing-season burns (denoted EGS), and the numbers refer to the frequency of treatment: 1 refers to annual burns, 2 refers to biennial burns, and 3 refers to triennial burns. (B) Photo of the field site taken in July.

coreopsis), *Solidago* spp. L. (goldenrod species), *Symphyotrichum ericoides* Willd. (white heath aster), *Lespedeza repens* (L.) W.P.C. Barton (creeping lespedeza), *Schizachyrium scoparium* Michx. (little bluestem), *Rhus copallinum* L. (winged sumac), and *Quercus* spp. L. (oak species).

In 2011, the Fire Demonstration Area was created through a collaborative effort between University of Tennessee (UT) Extension and TWRA. Six fire treatment units were created that ranged from 7 to 14 ha. Each unit was randomly assigned a fire frequency and timing (or season). Two units were burned annually, one in the early portion of the growing-season (April/May) and the other in the latter portion of the growing-season (September/October); these are hence referred to throughout as "EGS 1-year" (early growing-season) and "LGS 1-year" (late growing-season). These units only missed one burn year since 2011: the LGS burn in 2013 and the EGS burn in 2014. Two units were burned on a 2-year interval, one in April/May (EGS 2-year) and the other in Sept/Oct (LGS 2-year), and two units were burned on a 3-year interval, one in April/May (EGS 3-year) and the other in Sept/Oct (LGS 3-year) (Fig. 1, Table S1). As such, all treatments were represented in only one treatment unit each, without replication, thereby providing opportunity for a case study. Since the onset of restoration, annual treatment units had been burned 11 times, biennial units 6 times, and triennial units 4 times (Table S1). All data collection occurred in the summer (2023) at the end of a fire-free interval for five of the six units (i.e., these five units were scheduled to be burned in September/October or April/May following data collection). The EGS 1-year treatment occurred earlier in the year.

Fire Treatments

UT staff and students and TWRA employees implemented all the prescribed fire treatments. We used a combination of low-intensity backing, strip-heading, and flanking fires based on weather and fuel conditions to maintain average flame lengths <1.5 m. Weather conditions during burns included average temperatures between 12°C and 27°C, relative humidity between 25% and 50%, and wind speed at ground level between 4 and 13 km/hour.

Vegetation Data Collection

We conducted line-point intercept transects to quantify vegetation coverage and composition during August 2023. We placed five random points in each unit and placed a transect tape at each point that stretched from the eastern edge of the treatment unit to the western edge of the treatment unit. The length of each transect differed based on the location of each random point, and average transect length was approximately 250 m (range: 60–480 m). We documented all plant species less than 1.37 m tall at each 10 m mark along each transect.

Flowering Plant Surveys

In each unit, we selected an area with representative levels of considerable flowering plant abundance. Floral abundance, defined here as the total number of inflorescences, is a background predictor of flower-visitor abundance and diversity (Kwaiser & Hendrix 2008; Fowler et al. 2016). We chose to conduct flowering plant surveys in an area of each unit that offered a large amount of floral resources for two reasons. First, because plant flowering is patchy across space, it is difficult to select an area that represents the "average" amount of floral abundance, whereas areas of considerable bloom abundance are more discernable. Secondly, high-density floral areas may act as the primary attraction for the foraging bee community. We placed a 50-m transect in each of these high floral density areas and recorded floral abundance within 5 m on both sides of the transect along 10-m sections, totaling five 100 m^2 sections per

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transect. We counted flowers from every forb or shrub within each section, and we recorded all plants to species or to genus when we were unable to identify plants to species.

Bee Surveys

We surveyed the bee fauna in each of the fire treatment units four times (May 4th, May 25th, June 15th, and August 5th) during the spring and summer flowering season of 2023. Our primary goal was to document bees native to the area, so we did not collect the introduced honeybee (*Apis mellifera* L.), which was the only nonnative bee species that we encountered. On each sampling date, we conducted one survey in each treatment unit, with two treatment units randomly assigned to each of three researchers. Each survey entailed actively exploring each treatment unit in search of flower-visiting bees for 30 minutes; we only collected bees that were in contact with flowers. This "variable transect walk" methodology (Westphal et al. 2008) ensured the richness of plants and floral hosts at each unit was adequately represented, especially if they were sparse or unevenly distributed. Additionally, we report some bee records of interest that were collected in the firebreaks between treatment units. These collections were not part of the bee surveys and not included in the statistical analysis, but they helped to document the bee fauna of the restoration area.

We collected bees that contacted plants' flowering organs with a hand net and placed each insect in a centrifuge tube labeled with the plant species on which it was collected. We paused the timer while transferring bees from the net to a tube. Specimens were placed on ice in the field and later euthanized by freezing, then washed, pinned, and identified to species. Specimens were identified by a professional bee taxonomist (Sam Droege, United States Geological Survey) except for bumblebees (*Bombus* spp.), which we identified using Williams et al. (2014). Vouchered specimens are housed at the Department of Ecology and Evolutionary Biology at UT.

Data Analysis

We used R for all statistical analyses and conducted all linear modeling using the *stats* and *lme4* packages (Bates et al. 2015; R Core Team 2026). We aggregated data by transect and used transect as the random effect to account for within-plot variance. Our transects were placed a minimum of 40 m apart within a given plot, limiting spatial correlation between transects. This approach used repeated measurements in the context of the case study to assess plot-level differences in the plant and bee communities occurring at Bridgestone WMA.

We used the data from our line-point intercept transects (see *Vegetation Data Collection*) to calculate the percent coverage of four vegetation classes—forbs, grasses, semi-woody (brambles and vines), and woody (shrubs and tree saplings), by dividing the number of points on the transect with at least one plant from the given vegetation class by the total number of points on the transect. By aggregating the data by transect, we obtained five estimates of percent cover for each unit ($n = 5$). To compare how coverage of each vegetation class varied across treatments, we used generalized linear models with a logit link function for proportional data. Given our transects were different lengths, we weighted the model using the number of points per transect. We used the percent coverage of each vegetation class as the response variable and fire treatment (the cross between fire frequency and fire timing) as the predictor variable. We used a Tukey's post hoc test to compare marginal means of percent coverage using the *emmeans* (Lenth 2025) and *multcomp* packages (Hothorn et al. 2008).

To compare how floral abundance (see *Flowering Plant Surveys*) varied across treatments, we built a generalized linear mixed effects model. We used the treatment (cross between fire frequency and fire timing) as the fixed effect with survey date as the random effect. This model addressed the fact that each unit received a combination of fire frequency and timing. We fitted models using a Poisson distribution for count data. We used a log-transformed response (floral abundance summed across each transect) and the treatment as a fixed effect with survey date as the random effect. We used the 1-year late growing-season treatment as our baseline, based on previous research indicating that frequent fire best reduces invasion of woody plant species in a savanna (Knapp et al. 2009). To test how floral richness varied across different treatments, we used a generalized linear mixed-effects model with the log-transformed floral richness of each floral survey as a response variable and the same predictor variables from the floral abundance model. After the residuals failed a Shapiro–Wilk test for normality, we log-transformed the response variable.

To compare the effects of fire management on the abundance of plant–bee interactions, we used generalized linear mixed effect models with a Poisson distribution. As a response variable, we used the number of times each unique pairwise interaction occurred between a bee and plant species per each individual survey (from *Bee Surveys*). We used survey date as the random effect to account for within-plot variance. We used fire treatment (the cross between fire frequency and fire timing) as the fixed effect. We compared bee diversity across the six units, using Hill numbers and computed sample coverage rarefaction with functions from the *iNEXT* package in R (Chao et al. 2014; Hsieh et al. 2016). Hill numbers are diversity indices that give weight to different aspects of a community by adjusting the parameter q. When $q = 0$, the index gives raw species richness; when $q = 1$ it returns the exponential of Shannon entropy and considers the abundance of species; and when $q = 2$, it returns the inverse Simpson index and gives weight to common species. The outputs for Shannon entropy and the inverse Simpson index show how numbers of effective species change in a linear fashion. Together, these metrics provide a quantitative description of how the bee communities documented in our samples differ from one another.

We used nonmetric multidimensional scaling (NMDS) with Bray–Curtis dissimilarity to compare community composition across treatments and time, using the metaMDS function from the *vegan* package in R (Oksanen et al. 2025). This analysis compresses high-dimensional data from a dissimilarity matrix to produce plots that show the relative dissimilarity of composition among x number of discrete communities; these graphs plot

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samples (here, the bee species collected on a given survey) as points and similar samples cluster together more closely than dissimilar samples. We ran a PERMANOVA using the adonis2 function in *vegan* to test for differences in community composition between treatments; fire treatment and survey date were the environmental variables we used to parameterize the analysis.

Results

We identified 87 species or morphotypes of plants across treatment units along our line-point intercepts (see *Vegetation Data Collection*) (Table S2). The most common forbs recorded during our August vegetation transects included *Helianthus hirsutus* (Raf.) (rough-haired sunflower), *Symphyotrichum dumosum* (L.) G.L.Nesom (bushy aster), *Coreopsis major* Walter (greater coreopsis), *Lespedeza hirta* (L.) Hornem. (hairy lespedeza), and *Solidago odora* (Aiton) Kuntze (fragrant goldenrod). Nonnative plant species accounted for <0.5% of the species we recorded on our transects.

Forb coverage averaged 81.5% in the LGS 1-year unit, which was 50–53% more forb coverage than the 3-year units (z-ratio = 4.5, $p < 0.001$). Forb coverage in the LGS 2-year was 37–40% greater than that in the 3-year units (z-ratio = 3.1, $p < 0.03$; Fig. 2). Woody understory plant coverage in the LGS 3-year unit was 128% greater than that in the EGS 2-year unit (z-ratio = 5.7, $p < 0.001$), 76% greater than in the EGS 1-year unit (z-ratio = 4.6, $p < 0.001$), and 54% greater than in the LGS 1-year unit (z-ratio = 3.7, $p < 0.003$; Fig. 2). Similarly, woody understory plant coverage in the EGS 3-year unit was 104% greater than in the EGS 2-year unit (z-ratio = 4.4, $p < 0.001$) and 57% greater than in the EGS 1-year unit (z-ratio = 3.3, $p < 0.02$; Fig. 2). Grass coverage in the EGS 2-year unit was 11–47% greater than in all other units except the EGS 3-year unit (z-ratio = 3.0–4.6, $p < 0.04$; Fig. 2). Semi-woody understory plant coverage in the EGS 1-year unit was 219% greater than in the EGS 2-year unit (z-ratio = 3.1, $p < 0.03$; Fig. 2).

We encountered 49 flowering species or morphotypes in our plant surveys (see *Flowering Plant Surveys*). Overall floral abundance was 56% less in the EGS 2-year unit compared to the LGS 1-year unit (est = −0.82, $p = 0.03$) (Table 1). We did not detect any other significant differences in floral abundance between units with our flowering plant surveys. Floral richness did not vary among the 6 treatments (Table S3).

We netted bees from 41 plant species or morphotypes. *Packera anonyma* (Wood) W.A. Weber & Á. Löve (Small's ragwort) had the greatest abundance of visitors of all plants ($n = 76$), followed by winged sumac ($n = 60$) and *Orbexilum pedunculatum* (P. Miller) Rydberg (Sampson's snakeroot) ($n = 50$). The EGS 2-year treatment (est = −0.34, $p = 0.02$) and EGS 3-year treatment (est = −0.39, $p = 0.01$) had significantly fewer interactions than the LGS 1-year treatment (approximately 29% and 32%, respectively) (Fig. 3, Table 2). Although the vast majority of bee visits were associated with forbs, 14% of the interactions were with flowering shrubs. Among the interactions with shrubs, 82% were between winged sumac and 18 bee species.

We collected 514 bee specimens representing 64 species or morphotypes (Table S4). The most abundant species we collected was *Augochlorella persimilis* (Viereck), which we collected 46 times across the 6 units on 16 different floral hosts.

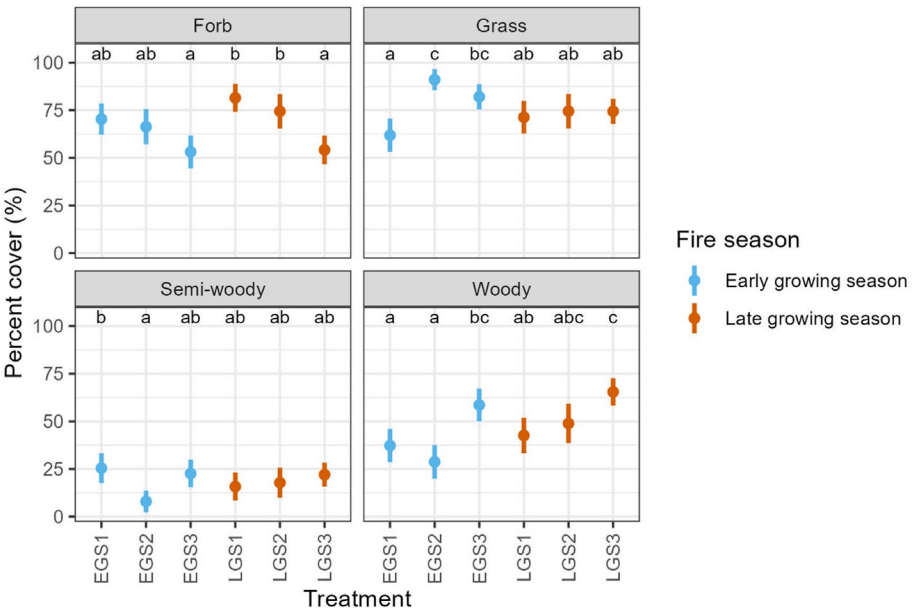

Figure 2. Percent coverage of the four vegetation classes (forb, grass, semi-woody, and woody) in each treatment. Late growing-season treatments are indicated on the graph in blue and early growing-season treatments are indicated on the graph in orange. The treatment acronyms on the x-axis refer to the timing and frequency of treatment: "LGS" refers to the "late growing-season," and "EGS" refers to the "early growing-season," while the terms "1-Year," "2-Year," and "3-Year" refer to the frequency at which these treatments are applied. Points represent the estimated percent coverage and lines indicate the 95% CI. Letters indicate significant differences ($p < 0.05$) between treatments.

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Table 1. Output of the generalized linear mixed effects model examining the relationship between floral abundance and type of burn treatment, including the estimate, standard error, *t*-value, and *p*-value. This model used a Gaussian distribution and a log-transformed response variable. The treatment acronyms refer to the timing and frequency of treatment: "LGS" refers to the "late growing-season," and "EGS" refers to the "early growing-season," while the terms "1-Year," "2-Year," and "3-Year" refer to the frequency at which these treatments are applied. All contrasts are relative to the LGS 1-Year treatment. Significant contrasts are indicated in bold.

Response Variable: Log Floral Abundance

Model: Log(Floral Abundance +1) ~ Factor(Unit) + (1 | Survey Date)

	Estimate	*SE*	t	p
Intercept	3.10	0.27	11.66	<2e-16
LGS 2-Year	−0.45	0.37	−1.23	0.22
LGS 3-Year	−0.39	0.38	−1.02	0.31
EGS 1-Year	−0.04	0.38	−0.09	0.92
EGS 2-Year	−0.82	0.37	−2.23	**0.03**
EGS 3-Year	−0.32	0.37	−0.88	0.38

Lasioglossum imitatum (Smith) (bristle sweat bee) and *Bombus impatiens* Cresson (common eastern bumblebee) were second-most abundant with each collected 41 times. We collected five rare bee species that were state records for Tennessee (S. Droege, personal communication), three of which were collected during surveys: *Nomia maneei* Cockerell ($n = 1$) was collected on *Lespedeza repens*, *Colletes solidaginis* Swenk (goldenrod cellophane bee; $n = 3$) was collected on *Eupatorium rotundifolium* L. (roundleaf thoroughwort) and *Senega curtissii* (A.Gray) J. F. B. Pastore & J. R. Abbott (Curtiss' milkwort), and *Anthidium psoraleae* Robertson ($n = 1$) was collected on *Orbexilum pedunculatum*. In between bee surveys, we discovered a large nesting aggregation of *Panurginus polytrichus* Cockerell in a sandy embankment along the firebreak between the EGS 2-year unit and the LGS 3-year unit. Although the natural history of this species has been documented (Neff 2003), this aggregation was only the second recorded occurrence of this species in Tennessee. Notably, none of the panurgines collected at the aggregation were *Panurginus potentillae* Crawford, which was collected during our bee surveys. It is unclear whether these congeners share the same nesting area. Finally, we collected *Melecta pacifica* ssp. *atlantica* Linsley ($n = 1$) off-transect in the same area as the *P. polytrichus* aggregation. This species is a brood parasite of bees in the genus *Anthophora* (Michener et al. 1994). Although we collected *Anthophora abrupta* Say (abrupt digger bee) during a bee survey in LGS 2-year unit ($n = 1$), we did not find any *Anthophora* nests in or nearby the *P. polytrichus* nesting aggregation.

Sampling coverage scores ranged from 0.75 (EGS 3-Year treatment) to 0.87 (1-year, LGS treatment) (Fig. S1, Table S5). Thus, our surveys captured approximately 75–87% of the estimated species richness of the flower-visiting bee community at each unit. According to our extrapolation, we would have needed to collect roughly 225 specimens per unit to increase sample coverage to approximately 90% (Fig. S1). Furthermore, based on the overlapping confidence intervals, treatments were

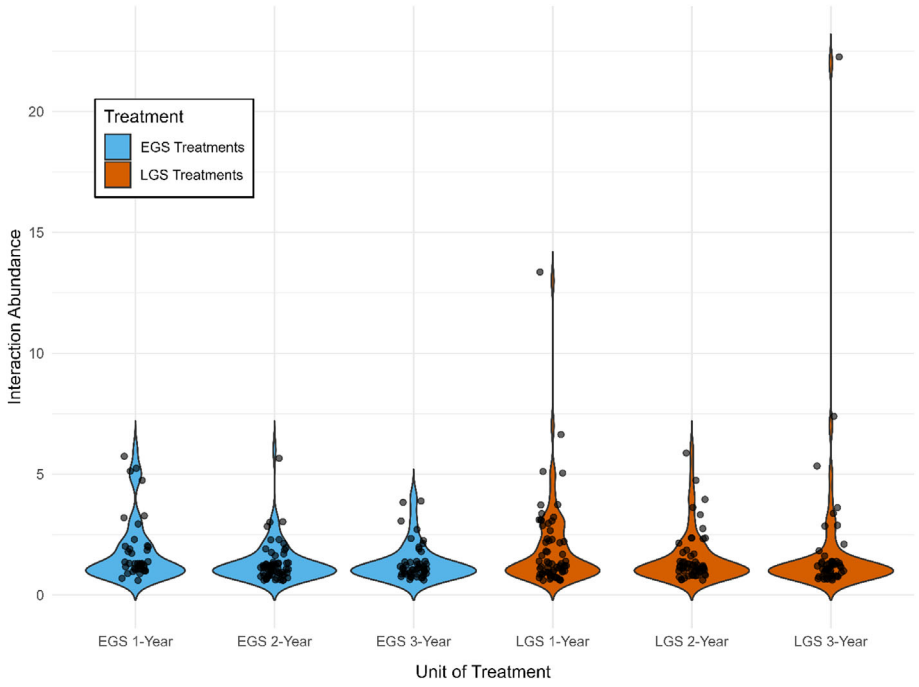

Figure 3. Violin plots showing the distribution of interaction abundance (the sums of the occurrences of each pairwise interaction) data for each of the six units across the four sampling events. The treatment acronyms refer to the timing and frequency of treatment: "LGS" refers to the "late growing-season," and "EGS" refers to the "early growing-season," whereas the terms "1-Year," "2-Year," and "3-Year" refer to the frequency the treatments were applied. LGS treatments are denoted in orange and EGS treatments are denoted in blue.

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Table 2. Output of the linear model examining the effects of treatment (full cross between timing and frequency) on the abundance of interactions. This model used a Poisson distribution. Included are the effect sizes, standard errors, *z*-values, and *p*-values. The treatment acronyms refer to the timing and frequency of treatment: "LGS" refers to the "late growing-season," and "EGS" refers to the "early growing-season," while the terms "1-Year," "2-Year," and "3-Year" refer to the frequency at which these treatments are applied. All contrasts are relative to the LGS 1-Year treatment. Significant contrasts are in bold.

Response Variable: Interaction Abundance

Model: Interaction Abundance ~ Factor(Unit) + (1 | Survey Date), Family = Poisson

	Estimate	*SE*	z	p
Intercept	0.75	0.17	4.35	<2e-16
LGS 2-Year	−0.22	0.15	−1.46	0.14
LGS 3-Year	−0.1	0.14	−0.74	0.46
EGS 1-Year	−0.02	0.16	−0.11	0.92
EGS 2-Year	−0.34	0.15	−2.36	**0.02**
EGS 3-Year	−0.39	0.15	−2.53	**0.01**

similar across the three orders of q when diversity was compared to the number of individuals caught (Fig. S2).

Our PERMANOVAS showed that the compositions of the bee communities in the six treatments were similar ($R^2 = 0.04$, $F = 0.92$, $p = 0.56$; Figure 4). However, the bee communities were significantly dissimilar across the four survey dates ($R^2 = 0.15$, $F = 3.82$, $p < 0.001$; Figure 4). Thus, the bee communities differed more over time than space in our study.

Discussion

The results of our case study indicate that, independent of floral phenologies, a longer fire-return interval resulted in declining forb coverage because of woody plant encroachment. However, patches of high floral density continued to persist within the 3-year interval treatments and the bee community was mostly similar across all treatments. Seasonal effects were present in the EGS 2-year treatment which promoted more grass than any other treatment and had reduced floral abundance and bee interactions. Frequent fire during the latter portion of the growing season promoted greater forb coverage and floral abundance. Overall, the effects of fire frequency and timing on the bee community were subtle, but our data illustrate how frequent fire in our region is requisite to maintain an early seral stage dominated by forbs and how fire timing influences plant composition.

Fire frequency had a large effect on forb and woody plant coverage, and the relative amounts of each varied significantly by treatment. Units burned on an annual or biennial fire-return interval supported significantly greater forb coverage than those burned every 3 years, consistent with previous research reporting forb coverage is promoted by frequent fire (Peterson & Reich 2007; Powell et al. 2022; Turner et al. 2024). Meanwhile, units burned on a three-year return interval had greater coverage of woody plants, which suppress growth of forbs because of shading (Peltzer & Köchy 2001; Nowacki & Abrams 2008). Thus, our vegetation surveys demonstrated that forb communities were most robust with more frequent fire because woody vegetation was suppressed (Lettow et al. 2014). Although woody species, such as winged sumac, may provide floral resources for bees, the positive effects are ephemeral in comparison to the greater problem that woody encroachment poses to the forb community throughout the growing-season (Nowacki & Abrams 2008; Wieczorkowski & Lehman 2022). Additionally, the majority of bee interactions occurred with forbs rather than woody plants in our study. Frequent fire regimes are thus necessary to maintain maximum floral resources for bees in savanna systems.

Specific plant-bee assemblages may benefit from annual fire, especially if plants exhibit fire-stimulated flowering. For

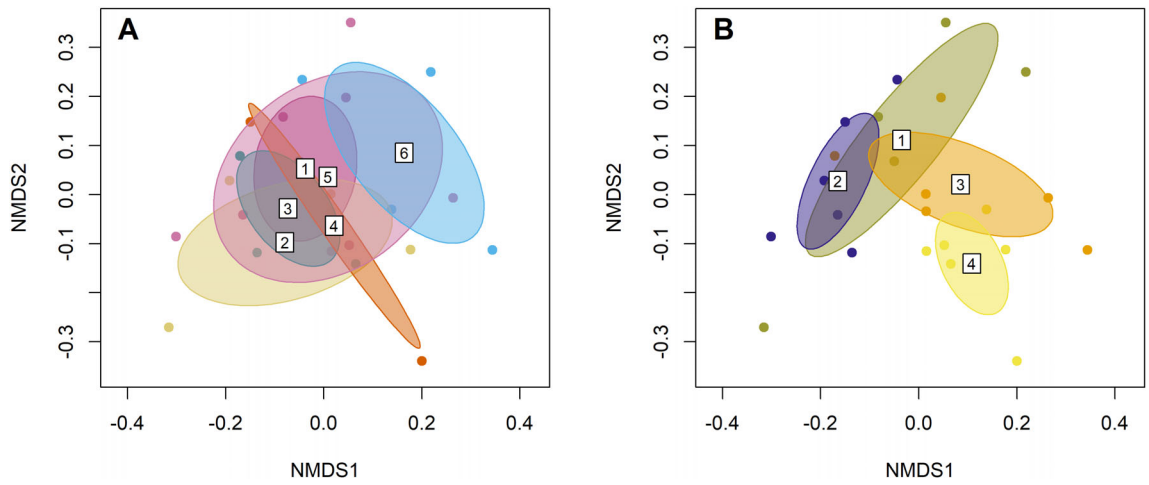

Figure 4. Ordination plots showing the bee community composition across (A) the six treatment types and (B) the four individual surveys. In panel (A), the numbers and colored ovals each correspond to a treatment unit; 1 = LGS 1-Year; 2 = LGS 2-Year; 3 = LGS 3-Year; 4 = EGS 1-Year; 5 = EGS 2-Year; 6 = EGS 3-Year. Numbers in panel (B) correspond to each survey. 1 = Survey 1 (May 4th); 2 = Survey 2 (May 25th); 3 = Survey 3 (June 15th); 4 = Survey 4 (August 5th).

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example, 34 of the 35 recorded interactions for *Tephrosia virginiana* (L.) Pers. (goat's rue) were from the EGS 1-year unit—the only unit burned in the early growing-season preceding data collection—and 18 of these interactions were with Megachilidae species. *Tephrosia virginiana* is known to flower following early growing-season fire in oak-pine savannas, though previous studies have shown no effect of burn timing on its pollination success (Hiers et al. 2000; Hiers et al. 2003). Fire-stimulated flowering may be driven by factors indirectly related to pollination, such as plant competition, soil nutrient availability, or the age of the plant (Pyke 2017), and species that benefit from frequent fire may increase in abundance and competitive ability (Suding 2001). Therefore, future work on plant–bee interactions in burned savannas could consider the effects of fire frequency on fire-stimulated flowering and determine whether fire frequency is the proximal driver for species' mass-flowering events.

Flowers are the stationary anchor of plant–bee interactions, and the floral community is a major determinant of the associated bee community (Platt et al. 1988; Hegland & Boeke 2006; Hyjazie & Sargent 2022). Grassland plants differing in phenology exhibit a variety of functional responses to the timing of fire in terms of their reproduction (Wrobleski & Kauffman 2003; Pavlovic et al. 2011; Liu et al. 2022). Among our treatments, the EGS 2-year unit showed the greatest differences in plant, flower, and bee interactions because perennial warm-season grasses are promoted by early growing-season fire (Howe 1994, 2000; Holcomb et al. 2014), and the spread of these grasses may suppress the persistence or spread of forbs through competitive exclusion (Freeman & Trotta 2024). Encouraging additional forb coverage in areas with extensive grass coverage may be achieved by avoiding chronic biennial burning during the early growing-season.

Our data collection methodology may explain some of the differences in vegetation composition we documented between our vegetation transect sampling and our flowering plant surveys. We collected floral data in areas of each unit with the greatest abundance or richness of flowering plants available to foraging insects, as these features are known to be important for bee visitation (Hegland & Boeke 2006; Vrdoljak et al. 2016). We collected vegetation data along fixed transects and accounted for species coverage and richness (Godínez-Alvarez et al. 2009), but not the phenological stage of each species. Forb coverage decreased with time since fire, whereas woody plant coverage increased, but it is important to note that the species surveyed were not necessarily in flower when surveyed along transects, and our transect data do not necessarily reflect floral resources available to bees at the time of our bee surveys. A previous study reported the composition of co-flowering associations does not differ with seasonality of treatment within 1 year post-fire (Dixon & Robertson 2025). However, our flowering plant surveys were necessary to include as a predictor of bee–plant interaction assembly, as the flowering community may vary according to fire frequency (Teixido et al. 2024).

Given that spatial features of a landscape, such as patch size and isolation, may affect plant and animal community composition (Bell et al. 1997), the proximity of our treatment units and their relative similarity in plant composition likely explains why there was not a clearer partition of bee–plant interaction communities between treatments. We expect such a partition could only be detected with spatial replication at the landscape scale. Bees were not restricted to treatment unit boundaries and were able to actively move around the landscape and find patches of floral resources (Fragoso et al. 2021). It is therefore difficult to determine the extent to which our results would scale up to the flowering and interaction dynamics that would have accompanied the region's historical fire regime. Pyrodiversity in fire-adapted systems has been documented to promote diverse communities of pollinating insects and plants (Ponisio et al. 2016; Ulyshen et al. 2022; Waters et al. 2024), but the scale at which this diversity was realized historically would have covered a much larger area and included fires that were much larger than our treatments. Regardless, our data illustrate how both plant and bee species richness and diversity can be improved and maintained in a relatively small area and are representative of what many private and public land managers could implement.

The Fire Demonstration Area provided habitat for several uncommon native bee species. The most abundant of these was *Andrena gardineri* Cockerell, a specialist on the tribe Senecionae in the spring (LaBerge 1967; Larkin et al. 2008), which exclusively visited Small's ragwort. This bee species is considered rare in some areas of its distribution (Fowler 2016), so the apparent robustness of the population at Bridgestone is encouraging. Our singleton collections of *Anthidium psoraleae* and *Nomia maneei*, two rare specialists on plants in Fabaceae, represent significant distribution expansions of these species in the Southeast (S. Droege, personal communication). The occurrence of these species at a site outside the geographic core of their distributions indicates the value of a restored oak/pine savanna for a diverse bee community. Further evaluation of the population demographics and phenologies of rare species such as these will expand our knowledge of how burn regimes may fit into their niche dynamics and promote their ecological success.

Our results indicate restored oak-pine savannas on the Cumberland Plateau can support a diverse community of native plants and bees and foster their interactions. Although prescribed fire can maintain habitat for pollinating insects, optimal floral diversity and abundance are not guaranteed with any one fire regime. However, our results exemplify how a more frequent fire regime (i.e., <3 years) is necessary in our region to limit woody encroachment and maintain a plant community dominated by flowering forbs. This result is similar to the "canopy saturation" that occurs in longleaf pine savannas, wherein plant species richness ceases to increase in areas where the fire interval exceeds 3 years (Glitzenstein et al. 2012). Additional research investigating the effect of timing of burning on the plant and bee community across multiple sites in the Central Hardwood region would help further identify differential effects on both plant and pollinator diversity in the region.

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Acknowledgments

We would like to thank S. Baldwin, M. Clarke, and K. McKim for their assistance with fieldwork, B. Oye for his feedback on early versions of the analysis, and S. Droege for his assistance in identifying bee specimens. We thank J. Hill and the Mississippi Entomological Museum for their willingness to house the bee specimens we collected in this project.

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Supporting Information

The following information may be found in the online version of this article:

Table S1. Summary of fire-return interval, seasonality, unit size, dates of fire events, and total number of fires applied to units in the Bridgestone-Firestone Fire Demonstration Area, 2011–2023.

Table S2. List of species, scientific names, and growth form class of species detected along line-intercept transects at the Bridgestone Firestone Fire Demonstration Area, August 2023.

Table S3. Output from the linear model that examined whether treatment influenced differences in floral richness across each treatment unit and the four sampling events.

Table S4. List of all bee species collected across the 6 units, sorted by family.

Table S5. Rarefaction analysis output listing (1) the number of individual insects we caught across the four sampling events per unit (abundance), (2) observed species richness per sample, (3) the total sampling coverage achieved per unit.

Figure S1. Sample coverage curves for each bee survey.

Figure S2. Graphs of the three Hill numbers (species richness left, Shannon diversity center, and Simpson's diversity right) for the treatment units.

Coordinating Editor: Alison Ritchie

Received: 16 March, 2026; First decision: 11 May, 2026; Revised: 28 July, 2026; Accepted: 12 August, 2026

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