

# Within-Year Effects of Prescribed Fire on Bumble Bees (Hymenoptera: Apidae) and Floral Resources

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## Abstract

Despite the importance of bumble bees (genus *Bombus* Latreille) for their services to natural and agricultural environments, we know little about the relationship between grassland management practices and bumble bee conservation. Prescribed fire is a common grassland maintenance tool, including in areas where endangered and threatened bumble bees are present. Thus, knowledge of the effects of prescribed fire on bumble bees is essential for designing management schemes that protect and bolster their populations. Using nonlethal surveys to record bumble bee species richness, abundance, and community composition, we evaluated the effects of spring controlled burns on summer bumble bee gynes and workers across five sites in southern Wisconsin. In addition, we explored the effects of fire on floral resources by measuring floral genus richness, abundance, ground cover, and proportion of transects containing blooming flowers in adjacent burned and unburned parcels. Prescribed fire had no measurable effects on bumble bee gyne or worker community composition, species richness, or abundance. However, consistent with previous studies prescribed fire increased floral genus richness and ground cover. The disconnect between bumble bee and floral responses to fire highlights some opportunities for improving our understanding of fire's effects on bumble bee diapause, nest site choice, and foraging.

**Key words:** restoration, prairie, fire, bees

Bumble bees (genus *Bombus* Latreille) are the second most economically productive pollinators in global agriculture and can be more efficient than honey bees due to the ‘buzz pollination’ they provide (Goulson 2010, Moissett and Buchmann 2011, Morgan et al. 2016). In addition, the ecosystem services of bumble bees extend beyond agriculture as they pollinate a variety of plants that provide food and shelter for wildlife (Hatfield et al. 2012). Bumble bees also foster a vital human connection with nature, as they are familiar and cherished characters on the landscape (Edwards and Williams 2004). Due to the tremendous value of these pollinators, it is harrowing that at least 7 of the 40 native U.S. species have experienced declines or range contractions in recent years (Goulson et al. 2008).

Thus, in devising conservation strategies for this genus, it is essential to identify land management practices that bolster habitat for bumble bees at all life stages. In particular, prescribed fire is a common tool for maintaining bumble bees’ prairie habitat in the United States. A survey of tallgrass prairie managers in the Midwestern United States reported that over 90% employed burns to keep woody plants at bay, prevent ground litter buildup, and make space for forbs to grow (Harmon-Threatt and Chin 2016). However, despite its popularity as a management tool, its influence on plants that could be beneficial to bees, and recent meta-analyses

suggesting that bees may benefit from prescribed fires (Carbone et al. 2019, Mason et al. 2021), little is known about the direct and indirect effects of prescribed fire on bumble bees.

Burning may affect bumble bees early in their life cycle by altering environmental features that are important during diapause and nest establishment. The heat from prescribed fire administered in autumn, winter, or spring could warm bumble bee gynes overwintering in the soil or duff. Prescribed fire tends not to burn intensely in grasslands due to the low level of fuel available for fire (DeBano et al. 1998), and soils below five centimeters of depth do not exceed 50°C (DeBano et al. 1979). However, given our lack of knowledge on bumble bee hibernation location, depth in the substrate, and thermal tolerance during diapause, it is difficult to predict whether fire may directly impact bumble bee survivorship or reproductive fitness. Prescribed fire can also alter the ground surface by reducing leaf litter depth, increasing soil temperature by altering surface insulation, and decreasing soil moisture (Henry et al. 2006, Greenberg et al. 2010), which may make conditions more or less favorable to nest-searching gynes after diapause. As the dynamics of bumble bee nesting occur largely underground or in hidden cavities and are poorly understood (Harmon-Threatt 2020), it is again difficult to predict how fire might influence the process of nest burrow selection.

Prescribed fire may affect bumble bees later in their life cycle by shaping the flowering plant communities available as forage during colony establishment and buildup. Since bumble bees rely on nectar- and pollen-rich flowers to sustain adults and feed their young (Goulson 2010, Moisset and Buchmann 2011), the composition of the floral community is important for colony survival. Some research has shown that prescribed fire promotes wild bee abundance by allowing forage plants to flourish (Campbell et al. 2007, Van Nuland et al. 2013). In studies of wildfire, forb abundance is higher in burned sites than unburned sites postfire (DiCarlo et al. 2019) and burned patches boast higher floral density than unburned patches (Mola and Williams 2018). These results may be explained in part by fire's ability to promote forbs by suppressing competitive plants like grasses, promoting certain fungi and bacteria, increasing soil mineral content, and improving nutrient availability through ash deposition and catalysis (Christensen and Muller 1975, Henry et al. 2006, DiCarlo et al. 2019). Whatever the mechanism, there is a potential indirect effect of fire on bumble bees through the improvement of floral availability.

Given the importance of fire for maintaining prairie and its effects on habitat structure and plant community, our knowledge of its impact on bumble bees is surprisingly scant and is only recently beginning to be explored (Bruninga-Socolar et al. 2021, Griffin et al. 2021). The literature that does exist on this topic typically focuses on wildfire, as natural fire creates a mosaic of burned and unburned patches which allow for comparison studies. For example, a California grassland study showed that in the summer directly following a fall wildfire, *B. vosnesenskii* Radoszkowski workers were more abundant in patches affected by the fire than in adjacent unburned areas (Mola and Williams 2018). Similarly, in an Oregon forest system where wildfire left a gradient of minimally to intensely burned land, higher wildfire intensity was associated with higher *Bombus* abundance (Galbraith et al. 2019). These findings suggest a beneficial effect of fire on bumble bees but are not readily extrapolated to grasslands maintained with prescribed fire. This is because the timing, regularity, intensity, geographic extent, and impacted habitat of wildfires vary more widely than for prescribed fire on grasslands.

While the relationship between fire and bumble bees is understudied, research on other wild bee communities can provide insight into the potential effects of prescribed fire on *Bombus*. In forest systems, higher wildfire intensity has been associated with higher abundance and richness of non-*Bombus* wild bees (Galbraith et al. 2019) and a combination of shrub removal and prescribed fire has resulted in higher Hymenoptera abundance in the 2 yr following burn (Campbell et al. 2007). Studies in grassland systems generally confirm the positive impact of fire on wild bees, with higher abundance, diversity, and richness found immediately and up to 3 yr after wildfire (DiCarlo et al. 2019) or prescribed fire (Moylett et al. 2020) compared with unburned controls. However, most wild bee taxa examined are composed of small solitary species with different nesting, mating, and foraging life histories from bumble bees. Although these results suggest that fire may be beneficial to bumble bees as well, more work must be done to elucidate the unique effects of fire on social bumble bees compared to relatively small solitary bees.

To address the knowledge gap of prescribed fire's effect on bumble bees, we assessed the impact of spring burning on *Bombus* communities during both the nest initiation and colony buildup stages of the life cycle in southern Wisconsin grasslands managed regularly with prescribed fire. In burned and unburned parcels at five different sites, we surveyed bumble bee gynes in the early summer

and workers in the late summer to determine whether the use of fire in the spring of that same year corresponded to changes in bumble bee species composition, richness, or abundance. In addition, we documented the floral communities of burned and unburned parcels in order to understand whether bumble bee responses could be related to the effects of fire on flower availability. We hypothesized that gyne community composition, abundance, and richness would differ between burned and unburned parcels, as recently cleared ground could be either more or less attractive to particular species of gynes searching for nesting cavities or foraging. We also hypothesized that a higher variety and abundance of flowers on burned land would be associated with greater abundance and richness of bumble bee workers later in the summer.

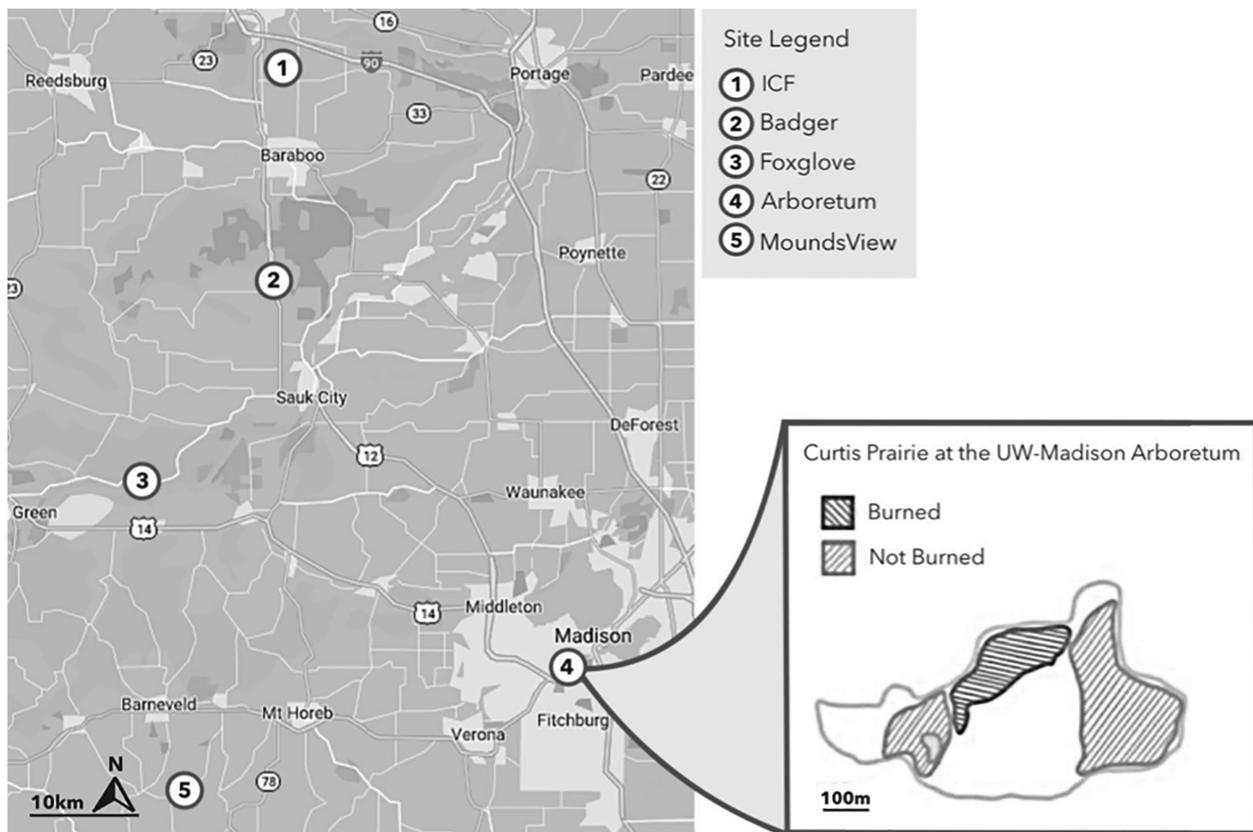
## Materials and Methods

### Site Selection

In 2019, we established study sites in five grasslands in southern Wisconsin that are managed regularly with prescribed fire as well as mechanical removal of woody plants, seeding for native plants, and herbicide application depending on land manager preferences. These sites included grasslands at the UW–Madison Arboretum (Arboretum), the International Crane Foundation (ICF), the former Badger Army Ammunitions Plant (Badger), Mounds View Grassland (Mounds View), and Foxglove Savanna (Foxglove; Fig. 1). At each study site, we identified one to four parcels that had not been burned in 2019 and one to four parcels that had been burned in either March, April, or May 2019 (Fig. 1; Supp Table 1 [online only]). Collectively, the five study sites contained a total of 10 burned and 10 unburned parcels, with the same number of burned and unburned parcels at sites when possible (Supp Table 1 [online only]). Land managers reported that all parcels were burned every two to six years depending on woody plant growth and availability of equipment and labor. Parcels ranged in size from 6.47 to 124.24 ha in size (median 11.03 ha) with parcels within a given site located between 0 m (i.e., immediately adjacent) and 3,000 m (median 950 m) from each other. This setup allowed for comparisons of the *Bombus* and floral communities in burned versus unburned parcels while controlling for variation among sites.

### Bee Survey Protocol

Bee surveys were conducted during summer 2019 on days with ambient temperatures between 10 and 33°C. No sampling occurred on days with fog, mist, rain, or strong winds. Temperature (°C) was recorded at the start of each survey using a handheld weather meter (Kestrel Instruments, Boothwyn, PA). To reduce the strength of edge effects, surveys began at least 10 m away from the edge of each parcel. Surveys were standardized by distance and time. During each survey, a timer was set for 30 min and the surveyor walked at a slow pace in a meandering path across the parcel. When a bumble bee was encountered within 1.5 m of the surveyor, the timer was paused as the bee was netted, transferred to a vial, identified to species and caste, and released. Once captured, any bee that could not be identified within 2 min was photographed for later identification. This continued until the timer ran out, covering a distance of roughly 400 m. Preliminary surveys following these methods in 2018 were tracked using a handheld GPS to verify that the path distance was consistent across surveys and parcels. Care was taken not to retrace any paths already covered during a survey walk, but bees were free to move across the parcel after being released and could have been resampled during the same or subsequent surveys. At each parcel, three gyne surveys were conducted



**Fig. 1.** Study sites. The following grassland sites in southern Wisconsin were included in this study: The University of Wisconsin–Madison Arboretum ('Arboretum'), the former Badger Army Ammunitions Plant ('Badger'), Foxglove Savanna ('Foxglove'), the International Crane Foundation ('ICF'), and Mounds View Grassland ('MoundsView'). Pop-out (lower right) shows an example of adjacent burned and unburned parcels at the Arboretum site. Maps data ©2020 Google.

between May 15 and June 20, with a minimum of 10 d between the first and last survey (maximum 26 d, median 14 d; [Supp Table 1 \[online only\]](#)). Four worker surveys were conducted at each parcel, which occurred in both the morning and afternoon between July 8 and 17 ('early July') and between July 23 and 31 ('late July'; [Supp Table 1 \[online only\]](#)).

### Gyne Data Analysis

All three 30-min gyne surveys were pooled to the parcel level to yield one total bumble bee species richness and one abundance measure per parcel. Of the 20 total parcels, two parcels from each burn treatment at the Badger site were not surveyed for gynes and one unburned parcel at the International Crane Foundation had incomplete data ( $n = 15$ , [Supp Table 1 \[online only\]](#)). Abundance and species richness were then analyzed using separate linear mixed effects models (LMM) using the 'lme4' package in R ([Bates et al. 2015](#)), with burn treatment (burn, no burn) as a fixed effect and grassland site as a random effect. The data were not transformed, as assumptions of homoscedasticity and normality of residuals were met. Gyne communities in burned and unburned parcels were also compared using a nonparametric PERMANOVA test with 999 permutations constrained by site using the 'vegan' package in R ([Oksanen 2019](#)). For all models, a  $P \leq 0.05$  was considered statistically significant and a  $P \leq 0.10$  was considered marginally significant. Mean abundance and richness values are reported with an error margin of one standard deviation. A principal components analysis (PCA) was generated from the gyne species by parcel matrix using the `rda()` function in the 'vegan' package, which scales species proportional

to eigenvalues and leaves parcels unscaled. Bi-plots of PC1 and PC2 were used to visualize the community data in 2D space.

### Worker Data Analysis

The 30-min worker surveys conducted in the morning and afternoon of the same week were pooled together for each parcel, yielding one species richness and one abundance measure per parcel for early July and late July. At the Mounds View site, one parcel from each burn treatment was not surveyed in early July ( $n = 18$  early July,  $n = 20$  late July, [Supp Table 1 \[online only\]](#)). Abundance and species richness were then analyzed using separate linear mixed effects models with burn treatment (burn, no burn) and season (early or late July) as fixed effects and grassland site and parcel as random effects to account for repeated measurements. Temperature (morning and afternoon survey average) was also included as a fixed effect, as temperature is known to affect bumble bee foraging activity ([Kwon and Saeed 2003](#)). The data were not transformed, as assumptions of homoscedasticity and normality of residuals were met. Worker communities in burned and unburned parcels were compared using a nonparametric PERMANOVA test and visualized using a PCA as described above for gyne analysis.

### Floral Survey Protocol

Floral surveys were conducted at each parcel of land between July 8 and 17 and again between July 23 and 31 on the same day as worker surveys took place. For each survey, a single 100-m linear transect was marked using pin flags across the parcel in the same area where worker surveys took place. Transects were positioned with the

intention of representing the variation in floral cover and species variety present in each parcel. Every 10 m along this transect, surveyors dropped a 1 × 1 m quadrat, identified all blooming plants within the quadrat to genus, and recorded the number of flower heads in bloom for each genus present. Overall floral abundance and genus richness for each survey in a parcel were calculated by summing the values of the 10 survey quadrats. In addition, the proportion of the quadrats that contained at least one blooming flower ('proportion of quadrats with flowers') was calculated as an index of flower cover in a parcel. Finally, surveyors recorded a visual estimate of the percent of the ground covered with blooming flowers across the entirety of the visual range of the surveyor across the parcel ('percent floral ground cover'). This metric is subjective compared with the other indices used but was intended to provide a rapid assessment of the parcel-wide flower cover compared with the fine-scale quadrat data.

### Floral Data Analysis

Floral abundance, genus richness, proportion of quadrats containing flowers, and percent floral ground cover were analyzed using separate linear mixed effects models with burn treatment (burn, no burn) and season (early or late July) as fixed effects and grassland site and parcel as random effects. The data were not transformed, as assumptions of homoscedasticity and normality of residuals were met. Floral communities in burned and unburned parcels were compared using a nonparametric PERMANOVA test and PCA as described above.

## Results

### Gyne Communities

In total, we found 42 gynes from six species across all of the parcels, with *B. impatiens*, *B. griseocollis*, and *B. auricomus* comprising 81% of all gynes encountered (Table 1A). The gyne data set was sparse and highly variable, with zero to nine individuals surveyed per burn treatment at a given site (Supp Fig. 1 [online only]). Prescribed fire

had no detectable effect on bumble bee gyne abundance, with an average of  $5.0 \pm 4.6$  gynes found on burned parcels and  $5.7 \pm 4.2$  gynes found on unburned parcels (burn treatment,  $P = 0.76$ ; Fig. 2A, Table 2A). Likewise, fire had no measurable effect on gyne species richness, with an average of  $1.8 \pm 1.3$  species detected on burned parcels and  $1.4 \pm 1.7$  species detected on unburned parcels (burn treatment,  $P = 0.40$ ; Fig. 2B, Table 2A). The multivariate community analysis found that burn treatment had a marginally significant effect on bumble bee gyne species composition (PERMANOVA,  $R^2 = 0.19$ ,  $P = 0.08$ ; Table 2A). The ordination of gyne communities using PCA found that PC1 and PC2 accounted for 79.86% of variation in the gyne data, with unburned parcels clustering loosely with each other and somewhat separately from burned parcels (Fig. 3). Examination of individual species trends reveals that *B. impatiens* was more than twice as common in burned parcels (41.7%) compared with unburned parcels (16.7%; Table 1A, Supp Fig. 2 [online only]). The opposite pattern was true for *B. auricomus*, which was more than three times as common at unburned parcels (50.0%) compared with burn parcels (16.7%; Table 1A, Supp Fig. 2 [online only]).

### Worker Communities

In total, we found 672 workers from nine species across all of the parcels, with *B. impatiens*, *B. griseocollis*, and *B. vagans* comprising 80% of all workers encountered (Table 1B). There was no significant effect of prescribed fire on worker abundance, with an average of  $26.8 \pm 26.1$  workers found per survey on burned parcels and  $23.4 \pm 23.8$  workers per survey on unburned parcels (burn treatment,  $P = 0.73$ ; Fig. 4A and B, Table 2B). There was also no significant effect of prescribed fire on worker species richness, with an average of  $3.8 \pm 1.7$  species detected per survey on burned parcels and  $3.5 \pm 1.7$  detected on unburned parcels (burn treatment,  $P = 0.64$ ; Fig. 4C and D, Table 2B). The effect of temperature was not significant in explaining worker abundance ( $P = 0.15$ ) or richness ( $P = 0.92$ ; Table 2B). Overall abundance and species richness increased over the course of the colony buildup phase from early

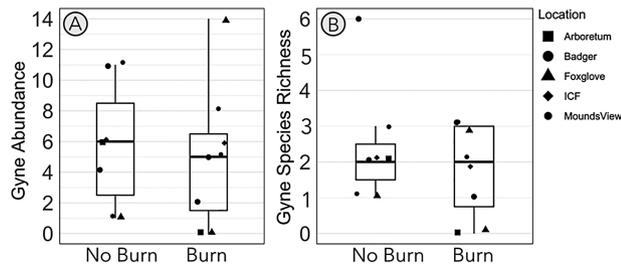
**Table 1.** Gyne and worker survey summaries. Species are listed in order of highest proportional abundance within the burned treatment.

(A) Gyne Survey Summary	Burned Parcels ( $n = 8$ )		Unburned Parcels ( $n = 7$ )	
	No. individuals	% of total	No. individuals	% of total
<i>Bombus impatiens</i> Cresson	10	41.7	3	16.7
<i>Bombus vagans</i> Smith	6	25.0	2	11.1
<i>Bombus auricomus</i> Robertson	4	17.6	9	50.0
<i>Bombus griseocollis</i> De Geer	2	8.3	1	5.6
<i>Bombus rufocinctus</i> Cresson	2	8.3	1	5.6
<i>Bombus bimaculatus</i> Cresson	0	0.0	2	11.1
Total	24	100.0	18	100.0
(B) Worker Survey Summary	Burned parcels ( $n = 10$ )		Unburned parcels ( $n = 10$ )	
	No. individuals	% of total	No. individuals	% of total
<i>Bombus impatiens</i>	110	32.0	129	39.3
<i>Bombus griseocollis</i>	98	28.5	64	19.5
<i>Bombus vagans</i>	68	19.8	70	21.3
<i>Bombus bimaculatus</i>	28	8.1	23	7.0
<i>Bombus borealis</i> Kirby	18	5.2	11	3.4
<i>Bombus auricomus</i>	12	3.5	19	5.8
<i>Bombus fervidus</i> Fabricius	4	1.2	6	1.8
<i>Bombus rufocinctus</i>	4	1.2	6	1.8
<i>Bombus affinis</i> Cresson	2	0.6	0	0.0
Total	344	100.0	328	100.0

to late July (season effect: abundance,  $P < 0.001$ , Fig. 4A vs. Fig. 4B; richness,  $P = 0.02$ , Fig. 4C vs. Fig. 4D, Table 2B). There were no apparent differences in the relative abundance of species of workers across the burn treatments (Supp Fig. 2 [online only]), and the community analysis found no significant effect of burn treatment on species composition (PERMANOVA,  $P = 0.46$ , Fig. 5, Table 2B).

### Floral Communities

Overall, we found 8,155 inflorescences from across 18 families of flowering plants (Supp Table 2 [online only]). Floral abundance (i.e., number of inflorescences per transect) was not different between burned and unburned parcels (mean abundance  $291.0 \pm 272.1$



**Fig. 2.** Bumble bee gyne abundance and richness in burned and unburned parcels. (A) Gyne abundance (total number of individuals observed during three 30-min surveys) in the early spring (points) in burned and unburned parcels. (B) Gyne richness per parcel in the early spring in burned and unburned parcels. Boxplot rectangles for each treatment show the lower 25% quartile, median (horizontal line), and upper 75% quartile of data, while the lower and upper whiskers show the 5 and 95% values, respectively, of the data.

burned,  $168.0 \pm 156.0$  unburned, burn treatment,  $P = 0.15$ , Fig. 6A and B, Table 2C). Prescribed fire also did not have a significant influence on the proportion of quadrats containing flowers (burned  $0.8 \pm 0.2$ , unburned  $0.7 \pm 0.2$ , burn treatment,  $P = 0.11$ , Fig. 7C and D, Table 2C). However, prescribed fire was associated with a significantly higher percent floral ground cover (burned  $48.1 \pm 24.0\%$ , unburned  $29.2 \pm 23.9\%$ , burn treatment,  $P = 0.026$ , Fig. 7A and B, Table 2C).

Prescribed fire resulted in higher floral genus richness per survey (mean  $6.9 \pm 1.7$  genera) than in parcels that were not burned ( $5.3 \pm 2.3$  genera, burn treatment,  $P = 0.01$ , Fig. 6C and D, Table 2C). Both Fabaceae and Asteraceae were the dominant families across burned and unburned parcels, but they differed in their relative abundance. Flowers in the Fabaceae family were twice as common in burned (67.8%) compared to unburned parcels (36.3%; Supp Table 2 [online only], Supp Fig. 3 [online only]). Within Fabaceae, flowers in burned parcels were dominated by the genus *Lotus* (28.7%), *Medicago* (22.7%), and *Trifolium* (16.4%), whereas in unburned parcels, flowers were mostly *Trifolium* (50.5%) and *Melilotus* (33.9%; Supp Table 3 [online only]). Flowers in the Asteraceae family were three times as common in unburned parcels than in burned parcels (10.0% burned, 33.7% unburned). Within Asteraceae, flowers in burned parcels were dominated by the genus *Rudbeckia* (33.4%), *Centaurea* (25.6%), and *Erigeron* (21.7%; Supp Table 3 [online only]). In unburned parcels, *Erigeron* (49.4%), *Centaurea* (29.0%), and *Heliopsis* (16.0%) were the most common genera (Supp Table 3 [online only]).

The next most abundant families were shared by both burn treatments. These included Apiaceae (8.9% burned, 5.1% unburned) and Lamiaceae (7.0% burned, 12.0% unburned). Notably abundant genera from these families included *Monarda* and *Daucus* on

**Table 2.** Results of statistical analyses. (A) Gyne results for abundance, richness, and community composition. (B) Worker results for abundance, richness, and community composition. For analyses with two  $n$  values listed, the first represents early July and the second represents late July. (C) Floral results for abundance, richness, percent cover, proportion of quadrats with flowers, and community composition. Independent variables (variable column) were modeled using either linear mixed-effects models (LMM) or permutation-based multivariate analysis of variables for community data (PERMANOVA). Random effects of site and date not shown.

(A) Gyne results	Method	Variable	n	df	F	p
Gyne abundance	LMM	Burn treatment	15	1, 10	0.10	0.76
Gyne species richness	LMM	Burn treatment	15	1, 10	0.77	0.40
Gyne community	PERMANOVA	Burn treatment	15	1, 12	2.53	0.08
(B) Worker results	Method	Variable	n	ndf, ddf	F	p
Worker abundance	LMM	Burn	18; 20	1, 30.04	0.12	0.73
		Temperature	18; 20	1, 30.79	2.18	0.15
		Season	18; 20	1, 29.98	26.06	<0.001*
Worker species richness	LMM	Burn treatment	18; 20	1, 17.08	0.22	0.64
		Temperature	18; 20	1, 34.00	0.01	0.92
		Season	18; 20	1, 23.72	5.88	0.02*
Worker community Composition	PERMANOVA	Burn treatment	20	1, 18	0.62	0.45
(C) Floral results	Method	Variable	n	ndf, ddf	F	p
Floral abundance	LMM	Burn	20	1, 15.94	2.33	0.15
		Season	20	1, 18.37	1.33	0.26
Floral genus richness	LMM	Burn treatment	20	1, 32.90	7.79	0.01*
		Season	20	1, 32.51	0.35	0.35
Floral percent cover	LMM	Burn	20	1, 12.01	6.41	0.03*
		Season	20	1, 19.00	11.91	0.003*
Floral quadrat proportion	LMM	Burn treatment	20	1, 14.39	2.95	0.11
		Season	20	1, 18.44	1.86	0.19
Floral community composition	PERMANOVA	Burn treatment	20	1, 18	1.16	0.08

Values in bold indicate  $P$ -values  $< 0.05$ .

parcels of both burn treatments (Supp Table 3 [online only]). The community response of plants, which combines information of both relative abundance and genus richness at each parcel, showed a marginally significant effect of burning relative to unburned areas (PERMANOVA,  $P = 0.08$ , Table 2C). Because axes one and two of a PCA accounted for only 0.68% of variation in the floral data, PCA was not useful as a visual estimate of community difference.

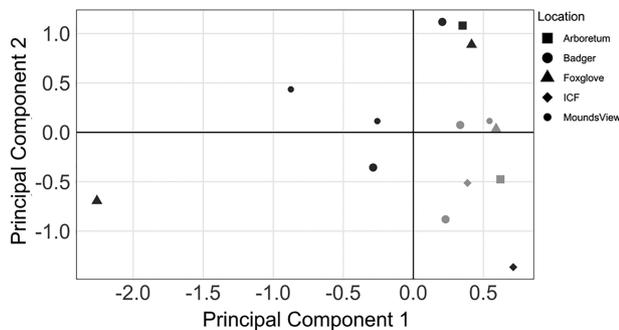
## Discussion

Given the importance of prescribed fire in maintaining open grasslands and flower availability, it is important to know how this management approach affects bumble bees in prairie habitats. This study found that spring burning positively influenced grassland plant communities compared with unburned parcels, consistent with prior literature that has established the positive effects of fire on floral abundance and diversity in grassland contexts (DiCarlo et al. 2019). However, bumble bee richness, abundance, and community composition showed limited differences between parcels that were either burned or unburned in the spring, in line with recent findings that prescribed fire had no impact on the abundance or proportion of

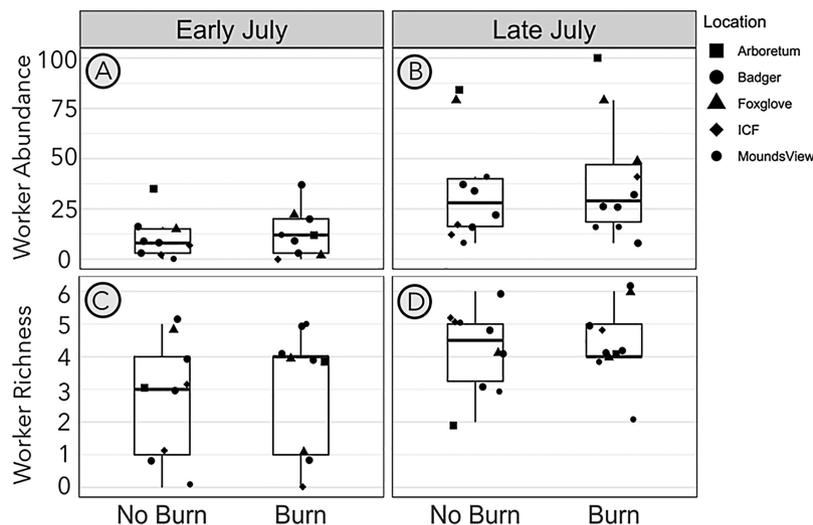
bumble bees within the larger bee communities of Illinois tallgrass prairies (Bruninga-Socolar et al. 2021). This pattern was true for gynes during nest establishment and workers during colony buildup. Overall, there was no evidence that conducting controlled burns as performed in this study resulted in measurable differences in bumble bee communities within the same year.

As expected, the use of prescribed fire in the spring had a positive effect on summer flowering plant communities in this study. Genus richness and the percent of ground covered by blooming flowers were significantly greater in burned than unburned parcels, while both the number of inflorescences and the proportion of quadrats containing flowers per transect trended in this direction as well. This aligns with previous studies that have found fire promotes forb growth and can extend flowering times for some flowers (Wroblewski and Kaufman 2003, Van Nuland et al. 2013). In particular, fire was associated with higher abundances of nitrogen-fixing legumes, which are known to flourish as a result of fire in grasslands (e.g., Kucera and Koelling 1964, Carter et al. 2000). On the other hand, asters were relatively less common in burned parcels, also consistent with prior studies which have posited that species of the family Asteraceae are not directly harmed by fire but diminish in fire-treated prairie due to the competitive advantage of more fire-adapted forbs and grasses (Kucera and Koelling 1964, Hartnett 1991). The floral results of this study underscore the benefit of prescribed fire in maintaining abundant and varied floral resources for potential bumble bee forage.

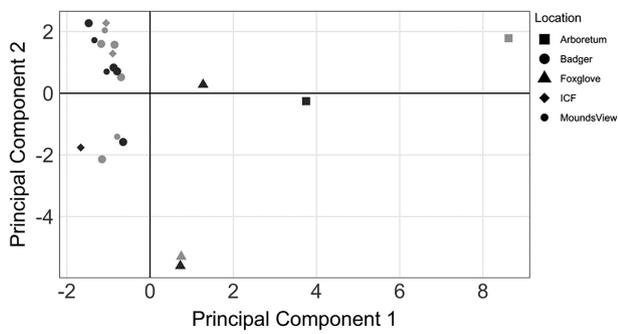
Given the impact of prescribed fire on the floral resources at each parcel, it was unexpected that there were no clear effects on the *Bombus* communities. The similarity of gyne abundance and richness across burned and unburned parcels was contrary to our expectation that burning would impact gynes by altering the quality of forage, attractiveness of potential nest burrows, or successful emergence of gynes from diapause. The gyne community composition of burned and unburned parcels were marginally different from one another, suggesting burns may have influenced gynes differently depending on species. For example, while *B. impatiens* gynes were relatively more abundant in burned parcels, gynes of the larger, longer-tongued, and later-emerging *B. auricomus* species may have been more abundant in unburned parcels due to differences in life-history or behavioral



**Fig. 3.** Principal component analysis for bumble bee gynes surveyed on burned versus unburned parcels. Gray symbols represent unburned parcels; black symbols represent burned parcels. Principal components 1 and 2 accounted for 79.86% of variation in gyne data.



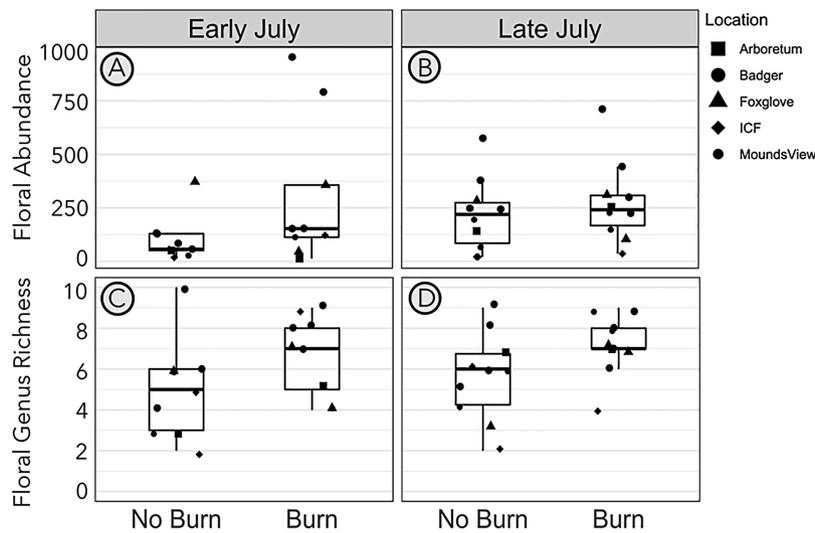
**Fig. 4.** Bumble bee worker abundance and richness in burned and unburned parcels. Summer worker abundance (total number of individuals observed during two 30-minute surveys) in burned and unburned parcels in (A) early July and (B) late July. Summer worker richness in burned and unburned parcels in (C) early July and (D) late July. Boxplot rectangles show the lower 25% quartile, median (horizontal line), and upper 75% quartile of data, while the lower and upper lines show the 5% and 95% values, respectively, of the data (excluding outliers).



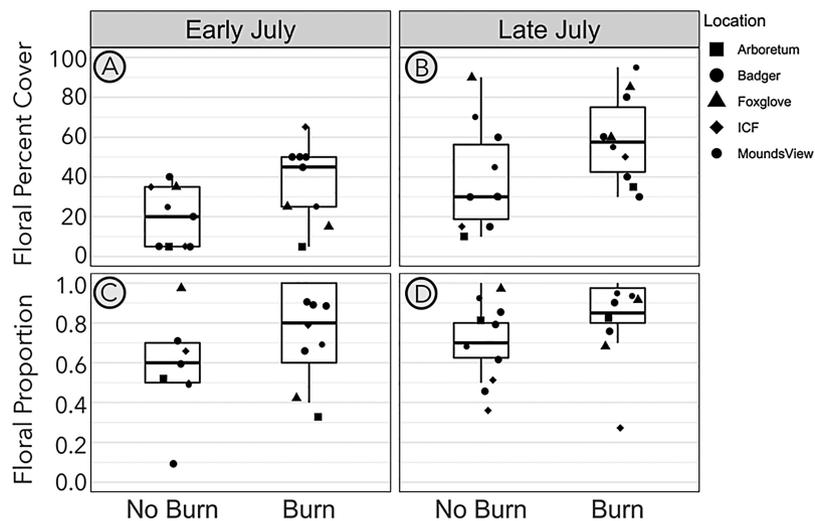
**Fig. 5.** Principal component analysis for bumble bee workers surveyed on burned versus unburned parcels. Gray shapes represent unburned parcels; black shapes represent burned parcels. Principal components 1 and 2 accounted for 93.95% of variation in gyne data.

traits (Williams et al. 2014). Pindar (2014) examined bumble bee community composition changes in response to prescribed fire, and while no differences in burned versus unburned plots were identified, their study did not explore gynes separately from workers or record bee responses within the same year as fire. It is possible that small (or no) differences in gynes in the first year of the study could be amplified in subsequent years if colony growth or survivorship is lower within the first summer after a burn. Because the present study surveyed a small number of gynes and their communities varied widely between parcels, it would be valuable to verify if community differences between burned and unburned parcels persist with increased sampling within the window of gyne activity in the spring or across seasons.

The specific mechanisms through which fire could influence gyne presence at a parcel are not well understood. While prescribed fire as administered in this study did not appear to influence gyne activity



**Fig. 6.** Floral abundance and genus richness in burned and unburned parcels. Summer floral abundance (total number of inflorescences observed across 10 quadrats) in burned and unburned parcels in (A) early July and (B) late July. Summer floral genus richness in burned and unburned parcels in (C) early July and (D) late July. Boxplot rectangles show the lower 25% quartile, median (horizontal line), and upper 75% quartile of data, while the lower and upper lines show the 5 and 95% values, respectively, of the data (excluding outliers).



**Fig. 7.** Floral percent ground cover and proportion of quadrats with flowers in burned parcels than in unburned parcels. Summer floral percent ground cover in burned and unburned parcels in early (A) and late (B) July. Proportion of quadrats with flowers in burned and unburned parcels in early (C) and late (D) July. Boxplot rectangles show the lower 25% quartile, median (horizontal line), and upper 75% quartile of data, while the lower and upper lines show the 5 and 95% values, respectively, of the data.

during the nest establishment stage, it is not clear whether this means that there are no differences in postfire survivorship or nesting that could occur if gynes were killed by fires or strongly influenced in their nest choices by fire's impact on the ground surface. Because gynes can forage as far as 1.5 km from their nests—and presumably from their original hibernacula locations—new gyne immigration into burned parcels could make patterns between burn treatments look similar even if fire had impacted local gynes (Mola et al. 2020). The direct effects on gyne diapause emergence and nest choice could be examined in more detail to identify the ways fire may impact each of these time points in the colony cycle.

As with bumble bee gynes in early summer, prescribed fire was not associated with measurable differences in worker abundance, richness, or community composition during colony build up mid-summer. In July, the same eight species were observed across burned and unburned parcels, representing nearly all of the common species expected in Southern Wisconsin (Williams et al. 2014). The only exception to this pattern was *B. affinis*, the U.S. Federally endangered rusty patched bumble bee, which was sighted twice in burned parcels. While two sightings of a rare species is not sufficient information to make inferences about the impact of burning, it is notable that *B. affinis* was found on recently burned parcels. From the gyne and worker results combined, we conclude that burning grasslands in patches every few years does not seem to meaningfully alter bumble bee abundance at the site level. It is worth noting that control plots varied in the time since they were last burned (~2–6 yr). As bee species may recover over time since a disturbance like fire, parcels that had only been burned with 2 yr may be similar to parcels that were burned within the same year, and thus differences between control and burned parcels may thus grow over time (Vogel et al. 2010). However, it remains unclear why differences in floral composition at burned versus unburned parcels do not result in differences in worker communities, as previous work has shown that fire can alter floral visitation networks in prairie settings (Welti and Joern 2018).

A reason for the similarities in bee communities of burned and unburned parcels could be that the flowers influenced by fire are not relevant to *Bombus*. If postfire shifts occur in floral taxa that are not valuable food sources, these changes would not be reflected in the worker communities. For example, in the Fabaceae, black medic (genus *Medicago*) accounted for roughly 15% of the floral community in burned parcels and only 0.5% in unburned parcels, but workers were never seen foraging on medic flowers (first author, personal observation) and the scientific literature does not contain information on their attractiveness to *Bombus*. Alternatively, relative increases of desirable flowers in the burn treatment may have been balanced by increases of other desirable flowers in the unburned treatment. For example, while Fabaceae was relatively more abundant in burned parcels and offers useful forage such as white clover for *Bombus* (Hülsmann et al. 2015), nectar-rich bee balm (genus *Monarda*) and knapweed (genus *Centaurea*) were more abundant in unburned parcels. Finally, plant surveys only captured information about flowers in July and did not provide a picture of the floral landscape earlier in the summer or spring. Plant communities at these study sites could have been more similar across burned and unburned parcels during the critical time when gynes first emerged to establish colonies. Studies exploring floral visitation networks earlier in the spring and later in the summer could examine these potential explanations.

Because these study sites were all stewarded by land managers who sought to maintain native prairie plants and exclude woody species encroachment, bumble bees may have been less sensitive to variability in flowers induced by fire at the parcel level in one

particular year. Prescribed fire was applied at these sites following a patch mosaic burning scheme (Parr and Andersen 2006) which creates pockets of burned and unburned land, allowing bees to use resources in both burned land and unburned refugia (Sugihara et al. 2006). If these sites were already saturated with bee-attractive plants and had similar habitat between them regardless of which parcel was burned in 2019, small fire-induced shifts in forage quality or other parcel characteristics would not have greatly influenced the total pool of individuals moving across the sites. For example, a 2021 study in high-quality tallgrass prairie recently established that landscape composition was more impactful on wild bee communities than patch-scale floral resources (Griffin et al. 2021). This could explain the contrast between the present study and those demonstrating benefits of wildfire to bumble bees in areas that are dominated by woody nonflowering plants or otherwise unmanaged for bee habitat (Mola and Williams 2018, Galbraith et al. 2019).

This study supports the use of fire for enriching floral resources and suggests that spring burning has a net neutral effect on bumble bees in prairies at both the nest establishment and colony buildup phases in the following summer. However, this conclusion requires further investigation. We know that the season of controlled burning (e.g., in the dormant winter versus early spring) can alter its effect on bee habitat (Decker and Harmon-Threatt 2019), and this study exclusively investigated spring burns. Thus, this work should be replicated following burns during other seasons. Additionally, research monitoring grasslands over multiple years following fire could investigate whether the results found here are stable across time, as the impacts of controlled burns and wildfire on wild bees are known to fluctuate over time (Pindar 2014, Mola et al. 2020). Finally, this study took place at just five sites and did not account for surrounding landscape or the quality of bee habitat at parcels prior to the use of fire. The proximity of burned and unburned parcels to one another could also have made it difficult to detect direct and indirect effects of fire on bumble bees. Studies of larger burn units or parcels spaced further apart could address questions of recolonization after potential negative local effects of burns on bumble bees. In addition, the overall high quality of sites used in this study raises the question of how these results translate to sites with lower-quality bee habitat or different landscape contexts.

Because bumble bees are of great significance to our food systems and wildlife, it is imperative that the maintenance practices employed on prairies are sensitive to their needs. Prescribed fire has been an important tool in providing resource-rich habitat to bumble bees and is currently a common practice among grassland managers. Research exploring bumble bee responses to burning in a diversity of regimens (e.g., modulating burn season, time since last burn, spatial extent, and surrounding habitat) will allow grassland managers to fine-tune their decisions so that grassland conservation can be achieved in tandem with *Bombus* conservation.

## Supplementary Data

Supplementary data are available at *Journal of Insect Science* online.

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## Author Contributions

TMT and CG conceived of the study. TMT, AK and DU performed field sampling. TMT performed the initial analyses and wrote the initial draft of the manuscript. TMT and CG edited and modified subsequent drafts. Authors report no conflicts of interest.

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