

## A Survey of the Bees of the Six Mile Marsh Prairie Restoration in Minnesota Suggests Benefits from Haying

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**Abstract** - Prairie restorations are increasingly being used to benefit bees and other pollinators. However, the management practices that best benefit bees remain poorly understood. We surveyed the bees of the Six Mile Marsh Prairie Restoration in Minnetrista, Minnesota, and compared the effects of different management practices on the relative abundance and diversity of bees. The restoration was divided into three sections: haying, burning, and control. Bees were surveyed from 2018–2020 on four transects per section. In total, we collected or observed 2,404 bees from 60 species or morphospecies in 20 genera. Comparing the different management techniques, we found that the haying treatment had significantly higher bee diversity in the final year of sampling. Although the small scale of this study limits the conclusions we can draw, our results suggest that managing prairie restorations by haying could benefit bees.

### Introduction

Supporting native bee communities is often a primary goal of restoring prairie ecosystems because bees are important pollinators of a majority of flowering herbaceous plant species (Ollerton et al. 2011). In general, prairies are managed with the goal of maintaining plant diversity, which has the indirect effect of helping bees (Griffin et al. 2017, 2021; Tonietto et al. 2017). Common methods for managing prairie restorations include burning, grazing, mowing, and haying, but the relative effects of different management methods on bees are relatively poorly understood (Buckles and Harmon-Threatt 2019, Hanberry et al. 2021, Harmon-Threatt and Chin 2016, Tonietto and Larkin 2018). In addition, there can be interactive effects, where multiple management techniques can have combined effects on bees, or there can be contrasting effects on different bee guilds (Bruninga-Socolar et al. 2021).

Burning is one of the most common techniques for managing prairie restorations and is generally thought to have beneficial long-term effects on bees (Decker and Harmon-Threatt 2019, Hanberry et al. 2021, Harmon-Threatt and Chin 2016, Tonietto et al. 2017). Burning has also been found to benefit other pollinators, such as butterflies (Bohls et al. 2016). In contrast to burning, studies have suggested that haying has a negative effect on bee diversity (Buckles and Harmon-Threatt 2019, Tonietto and Larkin 2018). However, haying has been found to benefit plant diversity and forb richness, which can help bees (Collins et al. 1998, Foster and Jeannine 2003, Spiesman et al. 2019). Finally, haying can also have complex effects that depend on the bees' nesting guild. For example, Spiesman et al. (2019) found that harvesting vegetation for bioenergy positively affected richness of below-ground nesting bees but negatively affected above-ground nesting bees. Teasing apart the relative effects of these different management practices is important, especially since these are methods that are widely used by land managers.

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The goal of this study was to examine effects of common methods of prairie restoration management on bees at the Six Mile Marsh Prairie Restoration in Minnesota. Our specific goals were to (1) document the bee fauna of the restoration and (2) compare the bee response (relative abundance and diversity) to different management treatments (burning, haying, and untreated control areas).

### Methods

#### Site Overview

The Six Mile Marsh Prairie Restoration is a 110-acre restoration in Minnetrista, Minnesota (44.911, -93.724), along Six Mile Creek (Fig. 1). The land was used for row crop agriculture (corn and soy) before being purchased in 2011 and 2012 by the Minnehaha Creek Watershed District (MCWD). The MCWD acquired the property to improve water quality, improve habitat, and increase the biodiversity of Six Mile Marsh and Lake Minnetonka. In 2013, MCWD removed drain tiles and planted Minnesota State Seed Mix 35-241 (MN-BWSR 2019) by seed drilling. Prairie vegetation was well-established at the time of our study in 2018. In addition, from 2014–2017, invasive species were controlled with targeted herbicide application 4–5 times a year.

In 2018, the MCWD, in collaboration with the non-profit habitat restoration organization Great River Greening, divided the Six Mile Marsh Prairie Restoration into three primary treatment areas: haying, burning, and control. Each treatment contained four 100-m fixed transects, which were each located a minimum of 30 m from treatment edges or other transects. Haying occurred in August 2018 and 2019. Burning occurred in April 2019. Supplemental seeding occurred in half of the treatment units in April 2019, but there was not enough time to allow sufficient establishment from that seeding to examine its effects on bees during this study.

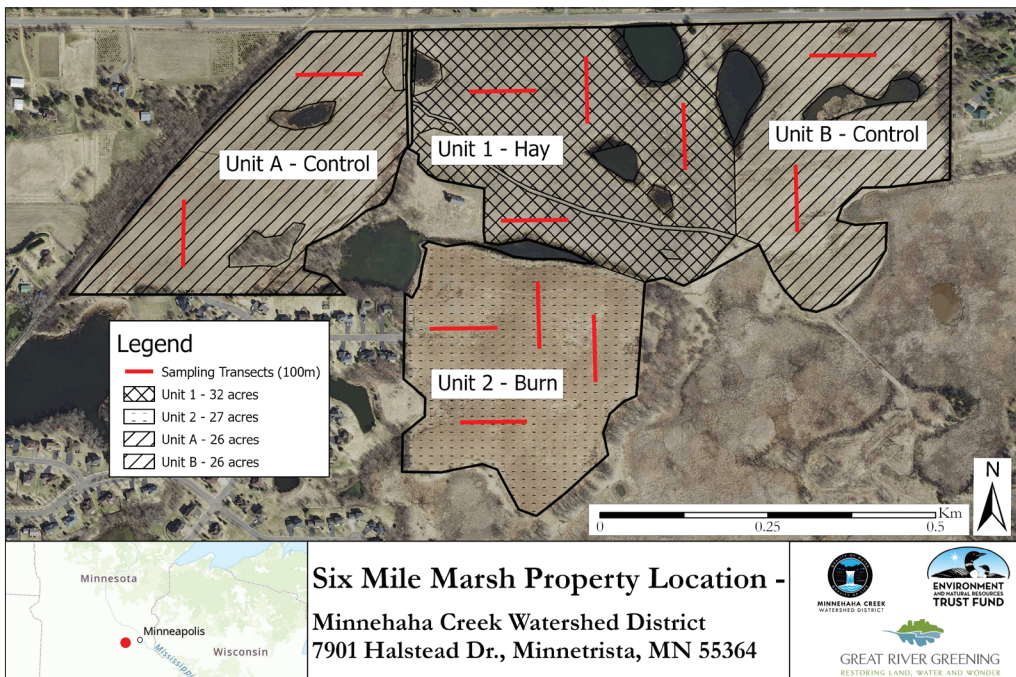


Figure 1. Map of the Six Mile Marsh Prairie Restoration.

### Bee Sampling

Sampling took place over the course of three years, with two sampling periods in 2018 and four each in 2019 and 2020. In 2018, we sampled on 27–28 July and 12–13 August. In 2019, we sampled on 30–31 May, 25–26 June, 30–31 July, and 30 August and 2 September. In 2020, sampling was delayed compared to other years because of limitations imposed by the COVID-19 pandemic. Sampling occurred on 5–6 June, 4–5 July, 3–4 August, and 2 and 4 September. Insects were sampled along 12 fixed 100-m transects over two days, with six of the transects sampled each day. All sampling and observations were performed by ZP using a hand net and targeting pollinators on flowers along a 3-m transect corridor (1.5 m to each side). Sampling and observations focused on bees, Diptera, Lepidoptera, and other flower-visiting Hymenoptera; only the bee data are reported here.

In 2019 and 2020, each transect was sampled for 24 standardized minutes, with the clock paused while specimens were extracted from the net and/or data recorded. The 24 minutes of sampling were divided into two 12-minute blocks, with one block in the AM and the other in the PM. This approach represents a shorter sampling period than in 2018, when there were 30 minutes of sampling divided into two 15-minute blocks. The sampling time was shortened in 2019 because the 30 standardized minutes took too long in 2018, with some of the AM sampling periods extending into the afternoon. Floral associations were recorded for all observed and sampled insects. At the start of each transect survey period, the temperature and wind speed were recorded using a Kestrel 2000 Weather Meter (Kestrel Instruments, Boothwyn, PA).

### Bee Identification

We followed the methods of Evans (1986) to limit the number of collected specimens by relying on field identifications. In short, we avoided collecting easily-identifiable bees, such as honey bees and bumble bees. For other bees, all specimens were collected initially, but after familiarity with the bee fauna increased, a portion of them were subsequently field-identified. For example, for the bee *Augochlorella aurata*, specimens were collected initially, but then once it was found that the closely related *Augochlorella persimilis* did not occur in the area, most specimens were thereafter identified in the field, with a limited number of voucher specimens collected to ensure accuracy. For taxa that are especially difficult to identify (e.g., *Lasioglossum*), specimens were always collected. To help prevent double-counting field-identified bees, they were shooed away with the net after being recorded. Shooing away generally appeared to be effective with bumble bees, but honey bees often flew right back to the same spot after being shooed away. As a result, plants or flower patches with large numbers of honey bees (10+) were only counted once, with numbers updated only if a greater number of bees were counted subsequently. All collected pollinator samples are stored in the collection of the Cariveau Native Bee Lab and the University of Minnesota Insect Collection, St. Paul, MN.

All bees were identified by ZP (both field and lab identifications) with reference to the following taxonomic resources: Andrenidae: *Andrena* (Bouseman and LaBerge 1978; Donovan 1977; LaBerge 1969, 1985, 1989; LaBerge and Bouseman 1970; Portman et al. 2020b), *Pseudopanurgus* (Mitchell 1960); Apidae: *Bombus* (Lavery and Harder 1988, Williams et al. 2014), *Ceratina* (Rehan and Sheffield 2011), *Nomada* (Mitchell 1962), *Melissodes* (LaBerge 1956, 1961); Colletidae: *Hylaeus* (Oram 2018); Halictidae: *Agapostemon* (Roberts, 1972), *Augochlorella* (Coelho 2004), *Augochloropsis* and *Dufourea* (Mitchell 1960), *Halictus* (Roberts 1973), *Lasioglossum* (Gibbs 2011, Gibbs et al. 2013), *Sphecodes* (Mitchell 1960); Megachilidae: *Coelioxys* (Baker 1975), *Heriades*, *Hoplitis*, *Megachile*, and *Stelis* (Mitchell 1962).

## Statistics

We assessed the completeness of our sampling by using a species accumulation curve and extrapolated species richness using a Chao estimator with EstimateS software (version 9.1.0) (Colwell 2009). We used 2-way analysis of variance (ANOVA), followed by Tukey's honestly significant difference (HSD) test, to examine trends in bee abundance and species richness. We combined observations in seeded and unseeded transects within each treatment for the statistical analyses. Further, because of the small distances separating the transects within each treatment, our analyses focused on the summed richness (or abundance) of bees on all four transects within each treatment. We excluded *Apis mellifera* from statistical analyses. We built four additive models each for both abundance and species richness: one model to test effects of treatment and year on abundance and species richness across all years, and three models to test effects of treatment and sampling period within each year of the study (2018, 2019, and 2020). Abundance was square-root transformed to meet the assumptions of normality and heteroscedasticity. These analyses were conducted using the package 'stats' in R version 3.6.3 (R Core Team, Vienna, Austria).

## Results

### Summary

In total, we recorded 2,404 bees consisting of 60 species in 20 genera (Table 1). Of these records, 571 were collected and 1,833 were observed. The species accumulation curve for all records shows that sampling is likely to sufficiently characterize the bee community (Fig. 2). Our recorded total of 60 species is close to the range of the extrapolated species richness,  $71.2 \pm 5.26$  (SD), calculated using the Chao equation (Chao 1987). Broken down by family, there were 10 species in Andrenidae, 17 in Apidae, 3 in Colletidae, 24 in Halictidae, and 6 in Megachilidae. The most species-rich genus was *Lasioglossum* (14 species), followed by *Andrena* (9), *Bombus* (7), and *Melissodes* (5). All but two species were native, with *A. mellifera* and *Andrena wilkella* being the only non-native species. By far the most abundant bee species was the Western Honey Bee, *A. mellifera*, with a total of 982 records. *Apis mellifera* was the most abundant bee recorded across all years, making up 28% of records in 2018, 51% in 2019, and 36% in 2020. Bees were recorded from a total of 34 plant species (Supplemental Table 1, available online at <https://eaglehill.us/prnaonline/suppl-files/prna-010c-portman-s1.pdf>). Five plants hosted at least 15 bee species: *Zizia aurea* (22 species), *Monarda fistulosa* (19 species), *Solidago canadensis* (16 species), *Dalea candida* (15 species), and *Dalea purpurea* (15 species).

Table 1. Total bee numbers by species across all three years of sampling at the Six Mile Marsh Prairie Restoration, Minnetrista, Minnesota.

#	Family	Species	2018	2019	2020
1	Andrenidae	<i>Andrena carlini</i> Cockerell, 1901			4
2	Andrenidae	<i>Andrena crataegi</i> Robertson, 1893			2
3	Andrenidae	<i>Andrena cressonii</i> Robertson, 1891		3	20
4	Andrenidae	<i>Andrena hirticincta</i> Provancher, 1888	1		
5	Andrenidae	<i>Andrena nubecula</i> Smith, 1853	4	2	
6	Andrenidae	<i>Andrena wheeleri</i> Graenicher, 1904			5
7	Andrenidae	<i>Andrena wilkella</i> (Kirby, 1802)			1

Table 1. Continued.

#	Family	Species	2018	2019	2020
8	Andrenidae	<i>Andrena wilmattae</i> Cockerell, 1906			1
9	Andrenidae	<i>Andrena ziziae</i> Robertson, 1891		59	186
10	Andrenidae	<i>Pseudopanurgus andrenoides</i> (Smith, 1853)			1
11	Apidae	<i>Apis mellifera</i> Linnaeus, 1758	138	531	313
12	Apidae	<i>Bombus auricomus</i> (Robertson, 1903)	10	12	9
13	Apidae	<i>Bombus bimaculatus</i> Cresson, 1863	21	12	9
14	Apidae	<i>Bombus borealis</i> Kirby, 1837	1	1	1
15	Apidae	<i>Bombus fervidus</i> (Fabricius, 1798)	1		3
16	Apidae	<i>Bombus griseocollis</i> (De Geer, 1773)	126	146	34
17	Apidae	<i>Bombus impatiens</i> Cresson, 1863	53	66	11
18	Apidae	<i>Bombus vagans</i> Smith, 1854	8	6	4
19	Apidae	<i>Ceratina dupla</i> Say, 1837	4	4	2
20	Apidae	<i>Ceratina mikmaqi</i> Rehan and Sheffield, 2011	1	1	
21	Apidae	<i>Melissodes bimaculatus</i> (Lepeletier, 1825)	1		
22	Apidae	<i>Melissodes druriellus</i> (Kirby, 1802)		4	1
23	Apidae	<i>Melissodes rivalis/desponsus</i> morphospecies	1		1
24	Apidae	<i>Melissodes subillatus</i> LaBerge, 1961		1	1
25	Apidae	<i>Melissodes trinodis</i> Robertson, 1901	23		1
26	Apidae	<i>Nomada aff. cuneata</i> morphospecies		1	
27	Apidae	<i>Nomada denticulata</i> Robertson, 1902		2	5
28	Colletidae	<i>Hylaeus affinis</i> (Smith, 1853)	16	19	9
29	Colletidae	<i>Hylaeus mesillae</i> (Cockerell, 1896)	8	4	3
30	Colletidae	<i>Hylaeus</i> “ <i>modestus</i> group” morphospecies	1		
31	Halictidae	<i>Agapostemon virescens</i> (Fabricius, 1775)		5	8
32	Halictidae	<i>Augochlorella aurata</i> (Smith, 1853)	41	114	123
33	Halictidae	<i>Augochloropsis metallica fulgida</i> (Smith, 1853)	1		1
34	Halictidae	<i>Dufourea monardae</i> (Viereck, 1924)			3
35	Halictidae	<i>Halictus confusus</i> Smith, 1853	3	6	23
36	Halictidae	<i>Halictus ligatus</i> Say, 1837	3	2	6
37	Halictidae	<i>Halictus rubicundus</i> (Christ, 1791)	5	1	1
38	Halictidae	<i>Lasioglossum admirandum</i> (Sandhouse, 1924)	1		3
39	Halictidae	<i>Lasioglossum albipenne</i> (Robertson, 1890)	2	14	11

Table 1. Continued.

#	Family	Species	2018	2019	2020
40	Halictidae	<i>Lasioglossum anomalum</i> (Robertson, 1892)		5	18
41	Halictidae	<i>Lasioglossum cinctipes</i> (Provancher, 1888)	1		
42	Halictidae	<i>Lasioglossum coriaceum</i> (Smith, 1853)			1
43	Halictidae	<i>Lasioglossum hitchensi</i> Gibbs, 2012		2	1
44	Halictidae	<i>Lasioglossum imitatum</i> (Smith, 1853)			1
45	Halictidae	<i>Lasioglossum lineatulum</i> (Crawford, 1906)	2		8
46	Halictidae	<i>Lasioglossum paradmirandum</i> (Knerer and Atwood, 1966)	4	9	18
47	Halictidae	<i>Lasioglossum pruinosum</i> (Robertson, 1892)		5	4
48	Halictidae	<i>Lasioglossum</i> “ <i>tegulare</i> group” morphospecies		1	1
49	Halictidae	<i>Lasioglossum versatum</i> (Robertson, 1902)	1		1
50	Halictidae	<i>Lasioglossum weemsi</i> (Mitchell, 1960)			1
51	Halictidae	<i>Lasioglossum zephyrus</i> (Smith, 1853)	1		3
52	Halictidae	<i>Sphecodes pimpinellae</i> Robertson, 1900	2		
53	Halictidae	<i>Sphecodes ranunculi</i> Robertson, 1897			1
54	Halictidae	<i>Sphecodes</i> sp. 1 morphospecies		2	
55	Megachilidae	<i>Coelioxys rufitarsis</i> Smith, 1854	1		
56	Megachilidae	<i>Heriades carinata</i> Cresson, 1864			3
57	Megachilidae	<i>Hoplitis pilosifrons</i> (Cresson, 1864)	1		1
58	Megachilidae	<i>Megachile latimanus</i> Say, 1823	5	1	2
59	Megachilidae	<i>Megachile mendica</i> Cresson, 1878		1	
60	Megachilidae	<i>Stelis lateralis</i> Cresson, 1864			1

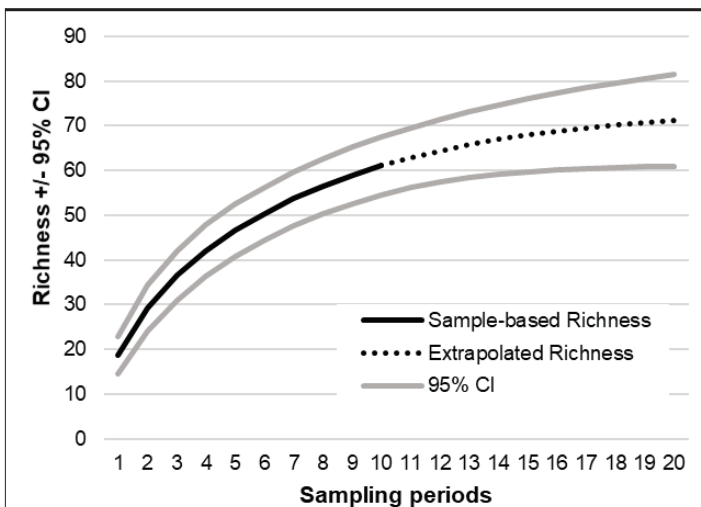


Figure 2. Species accumulation curve for bee sampling at Six Mile marsh prairie restoration. Estimated species richness with 95% C.I. was determined using Chao estimation with 100 permutations. The observed species richness over 10 sampling periods was 61 and the extrapolated richness at 20 sampling periods was 71. We found that sampling across years and treatments sufficiently characterized the bee community.

## Treatments

We compared the three different management treatments (hay, burning, and control) used in the Six Mile Marsh Prairie Restoration. Qualitatively, the hay treatment had the highest raw abundance of bees (both including and excluding honey bees), though this difference was not significant (Table 2). With all three years combined, the hay treatment also had slightly higher raw species richness (47 species) than the burning (35 species) and control (37 species) treatments (Table 2).

Across all three years, treatment had no significant effect on bee abundance or species richness (Fig. 3). However, when each year was modeled separately, the hay treatment had significantly higher richness in 2020 compared to the other treatments in the same year (Fig. 4C, ANOVA result:  $F = 6.55$ ,  $df = 2$ ,  $P = 0.02$ ; compared to burn treatment: Tukey's HSD test  $P = 0.046$ ; compared to control treatment: Tukey's HSD test  $P = 0.026$ ), but there was no effect of treatment on abundance in 2020. In the third sampling period of 2018 and the third and fourth sampling periods of 2019, there was a non-significant trend toward higher species richness and abundance in the hay treatment (Fig. 4B). The effect of sampling period on species richness and abundance varied among years, with lower bee abundance during mid to late summer in 2020 ( $F = 26.81$ ,  $df = 1$ ,  $P < 0.001$ ) and a non-significant trend toward higher bee abundance during mid to late summer in 2019. There were no significant differences in richness as a function of treatment or sampling period in 2018 (Fig. 4A).

## Discussion

Across the different treatments—burning, hay, and control—we found that the hayed plots contained the highest species richness of bees. This effect was only significant in 2020, the third and final year of sampling. However, the treatments were ongoing throughout the sampling period, with hay occurring in late summer in 2018 and 2019 and burning occurring in spring 2019. The marked increase in bee richness in the hay treatment in 2020 suggests that hay was beneficial and, at the very least, did not result in a reduction of bee diversity.

The underlying mechanism for the increased richness in the hay treatment is unclear, but anecdotally, the areas in the hay treatment appeared more visually similar to remnant prairies because of the shorter height of the vegetation and low levels of litter (ZP, pers. obs.). In contrast, the burning treatment was characterized by higher vegetation height and a general dominance of grasses, and the control treatment was characterized by higher vegetation height as well as large patches of litter that suppressed plant growth. The shorter and sparser vegetation in the hay plots could potentially be due to the reduction in total

Table 2: Raw abundance and species richness of bees in the different management treatments (combining all four transects per treatment) at the Six Mile Marsh Prairie Restoration, Minnetrista, Minnesota. Abundance does not include honey bees (*Apis mellifera*). The final row shows the combined values over all three years of sampling.

Year	Control		Hay		Burn	
	Richness	Abundance	Richness	Abundance	Richness	Abundance
2018	22	79	21	183	19	92
2019	21	127	20	217	21	167
2020	23	141	39	217	23	199
All years	37	347	47	617	35	458

biomass of the plants because of haying, and removal of excess nutrients could also potentially play a role in limiting plant growth. Haying has been proposed as a way to remove excess nutrients in restorations (Brye and Moreno 2006, Perry et al. 2010, Vasquez et al. 2008), but determining whether nutrient removal is driving the patterns observed in the bee community of Six Mile Marsh Prairie Restoration was outside the scope of this study. While our results tentatively suggest that haying can support bees in prairie restorations, it is less clear whether haying should be used as a long-term management strategy.

Previous studies on the effects of prairie management on pollinator communities have found mixed effects of haying (Buckles and Harmon-Threatt 2019). Haying has immediate and negative effects on pollinators because it removes actively flowering plants and can reduce flowers available for pollinators (Hudewenz et al. 2012, Weiner et al. 2011). We saw this pattern in our study, with hayed plots typically having lower pollinator diversity and abundance immediately after mowing because few flowers remained. However, in the long term, haying can help establish or maintain plant diversity, which would ultimately benefit pollinators (Collins et al. 1998, Foster and Jeannine 2003). Haying can also have differing effects based on the life history of different bee species, primarily benefitting species that nest below-ground rather than above-ground (Spiesman et al. 2019). The vast majority of bee species we saw in Six Mile Marsh Prairie Restoration were underground nesters, so this differential effect of haying according to bee life history could explain the positive association between haying and richness.

The timing of haying may impact its effects on plants and bees. At the Six Mile Marsh Prairie Restoration, haying occurred in August between the third and fourth sampling periods in 2018 and 2019. This late-summer timing is often done in prairies to avoid negative effects on nesting birds (Luscier and Thompson 2009, Winter 1998). August mowing (but not May mowing) has been found to increase the abundance of *Z. aurea* the following year (Howe 1999). As a result, the timing of haying in our study likely benefitted bee diversity in the hayed treatments, since *Z. aurea* was one of the most important forage plants for bees,

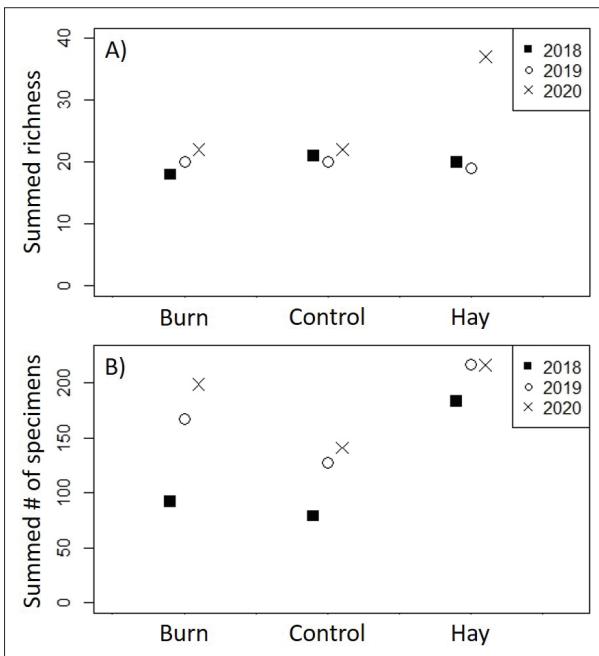


Figure 3. Species richness (A) and abundance (B) of bees summed across transects within each year of the study, grouped by treatment. There were no significant effects of treatment or year. However, the species richness in the haying treatment in 2020 was significantly higher than the other treatments, and abundance was higher (but not significantly so) in the haying treatment than other treatments within each year.



a finding consistent with other studies on prairie bees (Harmon-Threatt and Hendrix 2015, Lane et al. 2021). While this timing may have benefited bees in our study, other plant species and the bees that depend on them may react differently to mowing, and the relative effects of the timing of haying on plants and bees should be further investigated.

Our study has many limitations that warrant caution when interpreting the results. In particular, the study took place on a small scale at a single site. The Six Mile Marsh Prairie Restoration is ~1.2 km wide and 0.75 km long, meaning that each of the treatments is well within the foraging range of most bees, and it is quite possible bees were foraging across multiple treatments or foraging in the haying area but nesting in the other treatments. In addition, we surveyed along fixed transects, which did not always intersect the areas of highest floral diversity and abundance within the treatments. Further, our practice of performing non-lethal observations whenever possible could have led to double-counting of bees. Like many other bee studies, we only looked at bees foraging at flowers, which

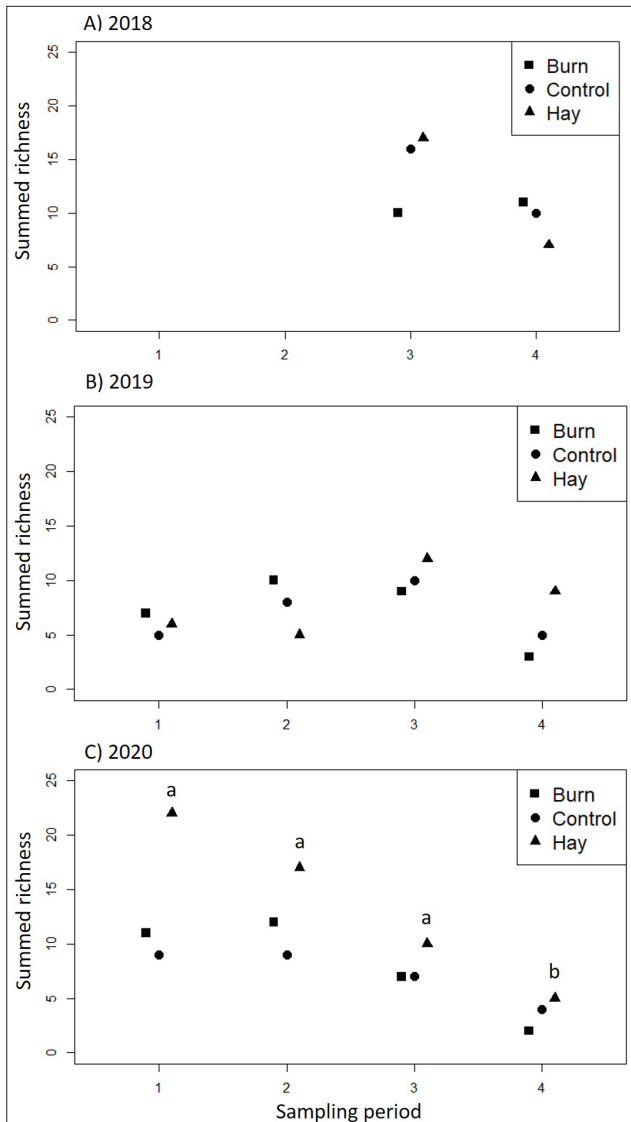


Figure 4. Species richness on each sampling date within each year of the study (A = 2018, B = 2019, C = 2020), summed across the transects within each treatment. In 2020, there was a significant effect of sampling date (panel C, coefficient = -3.57,  $P < 0.001$ ) and treatment ( $P < 0.03$ ). The haying treatment had significantly greater species richness than the burn treatment ( $P < 0.05$ ) and the control treatment ( $P < 0.03$ ) across sampling date (indicated by the asterisk in the legend). There were no significant effects of treatment or sampling date in 2018 or 2019. Letters indicate significance according to a Tukey HSD test, where sampling dates sharing a letter are not significantly different from each other.

provides limited insight into other important aspects of bee biology, such as nesting. In addition, treatments that boost the overall diversity of bees may still be detrimental for groups of bees with certain traits (Tonietto et al. 2017). For example, both mowing and burning can have negative effects on stem-nesting bees by reducing availability of nest sites (Bruninga-Socolar et al. 2021, Spiesman et al. 2019). Lastly, we note that, while there was a difference in richness, there was no significant difference in bee abundance among treatments. However, abundance is generally a poor way to assess bee communities (Portman et al. 2020a). Despite the limitations of this study, we believe that it still provides valuable data that can contribute to the conversation on how to best restore and manage prairies to support bees.

Overall, we found that the Six Mile Marsh Prairie Restoration project hosted a moderately diverse array of bees. We performed a baseline survey of bees at this site, documenting a total of 60 bee species or morphospecies across the 3 years of sampling. The increased species richness in the final year of sampling and the fact that new specialist species (e.g., *Dufourea monardae*, *Pseudopanurgus andrenoides*) were found only in the last year of sampling suggest that the site continues to be colonized by new species. This finding is in line with previous research on prairie restorations that has found that bee communities in newer restorations increase in diversity over time (Griffin et al. 2017). However, a few key bee groups were conspicuously absent or species-poor, particularly the genus *Colletes* and the fall-flying *Andrena*. More of these taxa would be expected to occur based on the findings of studies in similar environments (Evans 1986, Lane et al. 2020). It would be good to revisit this site in the future to determine if those species eventually colonize the site.

### Management Implications

Our results suggest that managing prairie restorations with late-season haying supported a higher diversity of bees than did burning or no management, but further investigation is needed to determine the effectiveness of haying as a method to restore and maintain prairies for bees. In addition, though our results supported haying as a management option, it is also important to maintain a heterogeneous landscape that can provide a mix of nesting and floral resources for different bee guilds.

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