

Seed Mix and Prescribed Fire Impact Soil Conditions: Implications for Below-Ground Bee Nesting

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ABSTRACT


Ground nesting bees comprise the majority of native bee species in the United States, yet their nesting ecology is poorly understood. Habitat restoration for native bees typically employs diverse wildflower seed mixes to provide floral resources without consideration of how these seed mixes might affect nest site availability. Ground nesting bees nest in a variety of microhabitats beneath or at the soil surface. We examined the effects of variation in seed mix type and prescribed fire on two variables generally considered to be important in nest site selection by ground nesting bees: soil temperature and moisture, both at the soil surface and at 11.5 cm depth. We collected data on soil temperature and moisture across 42 plots of a common garden experiment. We hypothesized that soil temperature and moisture are affected by seed mix density and amount of bare ground. We also hypothesized that fire affects microhabitat by making soil warmer and drier. Overall, we found no significant effect of seeding density on our dependent variables. Plots with more bare ground were drier at the surface than those with less bare ground. Burned plots were warmer and drier at the surface, but wetter and warmer at depth than unburned plots. Our results suggest that prescribed burns may play a large role in creating suitable nesting habitat for below-ground nesting bees. Our results highlight the need for greater understanding of the effects of plant communities and management on abiotic soil conditions that influence bee nesting conditions in prairie restorations.

Keywords: native bees, pollination, seed mix, soils, tallgrass prairie restoration

Restoration Recap

- Habitat restoration for native bees provides flowering plants without explicit consideration of nest sites within pollinator plantings. Many ground nesting bee species prefer warmer and drier soils, but it is unknown how plant communities influence those soil conditions.
- We measured soil temperature and moisture at the surface and at 11.5 cm as a function of pollinator seed mix design to explore variation in soil conditions in different pollinator planting communities.
- We found that pollinator seed mix design did not impact soil conditions.
- Management affected soil conditions. A prescribed burn made soils warmer and wetter at depth compared to control plots but made surface soil warmer and drier.
- While additional research is needed to understand bee nesting habits and management techniques, land managers should consider that prescribed burns may create warmer and drier soil conditions at the surface, which may be conducive to bee nesting.

Many bee species are experiencing widespread declines from habitat destruction, pesticide use, and disease (Potts et al. 2010, Lever et al. 2014, Burkle et al. 2017).

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Ecological restoration is important for bee populations and the plant populations that rely on them for pollination services (Klein et al. 2007, Garibaldi et al. 2013, Burkle et al. 2017). Bees require appropriate nesting sites in addition to floral (food) resources, an aspect of their ecology that is frequently overlooked in the restoration of pollinator habitat and may be a limiting factor for the growth of wild bee populations (Buckles and Harmon-Threatt 2019).

Most bee species are solitary and construct nests below ground or at the interface between litter and soil (Antoine

and Forrest 2021). Harmon-Threatt (2020) notes that abiotic soil conditions influence the survival and community composition of ground nesting bees, with loosely textured soil (sand or sandy loam) and exposed soil making nesting sites preferable to some wild bees. Through a variety of multivariate approaches, Cane (1991) demonstrated a weak positive association between bee nesting and soil sand content. He also found broad variation in other microhabitat variables at bee nesting sites, including soil texture and moisture. The differences in nesting conditions were not associated with the taxonomic distance between species. Bees may, in general, prefer drier, warmer soils, but these variables are less conclusively researched (Wuellner 1999, Weissel et al. 2006, Harmon-Threatt 2020, Antoine and Forrest 2021). The litter layer also may affect bee nest site choice by regulating soil moisture or providing concealment of nest entrances (Antoine and Forrest 2021). While there is variation in preferences among species, it is clear that variation in these abiotic variables is an important yet under-researched driver of bee nesting.

Habitat restoration for native bee conservation is partially accomplished by planting diverse wildflower seed mixes (Tonietto and Larkin 2018, Hanberry et al. 2020). Commercially available seed mixes vary in plant diversity, the density at which seeds are planted, and the ratio of forb seed to grass seed (Harmon-Threatt and Hendrix 2015, Havens and Vitt 2016, Müller et al. 2024a). These mixes provide food resources for bees and have been shown to support bee abundance and diversity (Williams et al. 2015, Griffin et al. 2017). However, the use of restorations by bees as nesting habitat remains poorly understood. A good first step in closing this knowledge gap is to understand the impact of seed mix design on the abiotic conditions which are thought to be important to nesting bees.

Soil conditions affect the establishment and persistence of plant communities, and plant communities can, in turn, alter soil conditions. Previous work in restored meadows documented that surface soil moisture (0–10 cm depth) is positively correlated with plant community height, coverage, and root-shoot ratio, and negatively correlated with plant density (An et al. 2019). Plant functional groups play different roles in water retention throughout the year (Zou et al. 2015). Plant species with tap roots or extensive root systems reduce soil compaction and increase permeability (Chen et al. 2014, Colombi and Keller 2019). Because of the complex relationship between plant communities and soil conditions, we expect that plant establishment in restored landscapes plays a role in creating nesting sites for wild bees.

Restored tallgrass prairie plant communities are frequently managed by prescribed fire. Prescribed fire impacts abiotic soil conditions and therefore may affect nest site availability for ground nesting bees. Nests in the soil are deep enough to avoid direct mortality effects of prescribed fire (Cane and Neff 2011), but prescribed fire exposes bare

ground, increases surface temperature, and decreases soil moisture content (Hulbert 1969, Wagle and Gowda 2018, but see O’Keefe and Nippert 2017). The number of ground nesting bee nests increases in recently burned tallgrass prairie (Brokaw et al. 2023), but a better understanding of the relationships between native bees, restored plant communities, prescribed fire, and soil conditions is needed.

Because the plant community can have dramatic effects on the abiotic soil conditions tied to bee nesting success, research investigating differences in soil conditions across a wide range of seed mixes is needed to determine whether seed mixes may be affecting the quality of bee nesting habitat. To explore this issue, we used an existing seed mix experiment in which wildflower seed mixes vary in their planting density and ratio of forb seed to grass seed. We hypothesize that seed mix design will have a significant effect on abiotic soil conditions, specifically soil temperature and soil moisture. We hypothesize that plots with more bare ground will have higher surface temperatures and lower moisture than those with less. If supported, this would suggest that sites with more bare ground are potentially high-quality bee nesting habitat. Lastly, we hypothesize that fire will have a significant effect on soil conditions and predict that recently burned plots will have more bare ground than unburned plots, a state seemingly preferred by many nesting bees. The results gained from this study will help restoration practitioners design seed mixes that provide nesting resources to bees in addition to floral resources.

Methods

Our study was conducted within a larger experiment testing the effects of variation in seed mix design on the floral resources provided for wild bees in restored tallgrass prairie (Müller et al. 2024b). In 2018, we established a seed mix experiment at the Rosemount Research and Outreach Center in Rosemount, MN, USA (44.71505, -93.09726). The seed mixes varied across three values of flowering plant diversity, three values of seeding density, and three ratios of forb to grass seed nested within seeding density. We investigated soil conditions in high-diversity plots (30 forb species and five native grass species) because land managers commonly plant high-diversity seed mixes to support wild bees. We selected three forb:grass treatments representing the lowest density of forb seeds (226 forb:1280 grass seeds/m² [21 forb:119 grass seeds/ft²]), the highest density of forb seeds at the highest total seeded density (904 forb:602 grass seeds/m² [84 forb:56 grass seeds/ft²]), and the highest density of forb seeds at the lowest total seeded density (226 forb:150 grass seeds/m² [21 forb:14 grass seeds/ft²]; Table 1). These treatments represent a potential trade-off between the total amount of floral resources provided for bees versus the cost of high densities of forb seed. Plots were 3 m × 3 m in size, and were selected from a larger pool of plots arranged in a 15 × 28 grid, separated

Table 1: The experimental design of our seed mix experiment showing variation in the total seeding density and forb:grass seed ratio applied at the time of planting. All plots were planted with seed mixes containing 30 forb species.

Total seeding density	Forb:grass seed ratio	Number of forb seeds to number of grass seeds per ft ²	# of plots 2021	# of plots 2022
Low	1.5	21:14	14	13
Low	0.18	21:119	14	14
High	1.5	84:56	14	13

by 3 m mowed pathways. The additional plots consisted of additional treatments that we did not examine in the soil sampling study presented here. Treatments were randomly assigned across plots. Half of the plots were burned on May 28, 2022, which enabled us to evaluate differences in soil conditions between burned and unburned plots in 2022. In total, we sampled around 40 plots in each of two years; however not all measurements were collected in every plot in the second year due to equipment failures.

To measure variation in soil nesting resources for bees as a function of the forb:grass ratio of seed mixes, we collected data on the soil temperature, soil moisture, and the amount of bare ground observed across a gradient of forb:grass ratios. We collected data early in the morning (7:00–10:00 AM) on sunny days and collected data in each plot once per year. Sampling took place on June 27, 30, and July 2 in 2021 and on June 18 and 19 in 2022. In each plot, the soil conditions were determined both at the soil surface and at approximately 11.5 cm below the surface. We measured soil temperature and moisture levels at the soil surface and at 11.5 cm by inserting a digital thermometer (Cooper-Atkins®, Middlefield, CT, USA) and a soil moisture meter (Tech Instrumentation®, Nashua, NH, USA) directly into the soil at three randomly selected sets of coordinates in the plot (i.e., 56 cm north by 30 cm east). While many bees nest deeper than 11.5 cm, Cane and Neff (2011) report that in a survey of 449 ground nesting bee species, most were found to nest at depths of ≤ 10 cm. In each plot, we quantified the amount of bare ground by reconciling two researchers' independent rankings on a scale from 0 to 4 (0: 0% bare ground, 1: 1–25%, 2: 26–50%, 3: 51–75%, and 4: >75%) following Buckles and Harmon-Threatt (2019). During the 2022 sampling, we recorded whether each plot had been burned that spring.

We aimed to quantify the effects of forb:grass ratio, amount of bare ground, and sampling year on our four dependent variables: surface temperature, temperature at depth, surface soil moisture, and soil moisture at depth. Because we collected three measurements per plot on the same date each year, we used the average value of each measurement per plot per year in our models. We first attempted four three-way ANOVAs; however, there were not enough residual degrees of freedom to conduct Tukey's HSD tests on ANOVA models with interaction terms. Therefore, for each dependent variable, we conducted three one-way ANOVAs to quantify the effect of each independent variable. Because the burn treatment only affects measurements taken in 2022, we conducted four one-way ANOVAs on the 2022 data to test the effect of the prescribed burn on each of our dependent variables. We visually checked histograms of all model residuals for normality. We conducted Tukey's HSD test on all ANOVAs. All analyses were conducted in R version 4.2.1 (R Core Team 2022).

Results

We hypothesized that seed mix design would affect soil temperature and soil moisture. We found a marginally significant effect of forb:grass ratio on surface temperature (Table 2A, Figure 1A) where surface temperature in the lower seeding density treatment, 226f:150g seeds/m² (21f:14g seeds/ft²), was higher than in one of the higher seeding density treatments, 226f:1280g seeds/m² (21f:119g seeds/ft²; [Supplementary Material Table S1A](#)). However, seed mix design had no effect on soil temperature at depth (Table 3A), or on soil moisture at the surface or at depth (Tables 4A and 5A respectively).

Table 2. Results of the three one-way ANOVAs testing the effects of a) forb: grass ratio, b) bare ground score, and c) year on average surface temperature per plot. (* indicates significance at the 0.05 level.)

	Df	Sum Sq	Mean Sq	F value	p value
a) Forb:grass ratio	2	137	68.50	2.45	0.09
Residuals	79	2212	28.0		
b) Bare ground score	3	76.2	25.40	0.87	0.46
Residuals	78	2272.7	29.14		
c) Year	1	740.3	740.3	36.82	< 0.0001*
Residuals	80	1608.5	20.1		

Table 3. Results of the three one-way ANOVAs testing the effects of a) forb: grass ratio, b) bare ground score, and c) year on average soil temperature at depth per plot. (* indicates significance at the 0.05 level.)

	Df	Sum Sq	Mean Sq	F value	p value
a) Forb:grass ratio	2	50.3	25.16	2.29	0.11
Residuals	49	539.3	11.01		
b) Bare ground score	3	76.7	25.56	2.39	0.08
Residuals	48	512.9	10.69		
c) Year	1	360.3	360.3	78.56	< 0.0001*
Residuals	50	229.3	4.6		

Table 4. Results of the three one-way ANOVAs testing the effects of a) forb: grass ratio, b) bare ground score, and c) year on average surface soil moisture per plot. (* indicates significance at the 0.05 level.)

	Df	Sum Sq	Mean Sq	F value	p value
a) Forb:grass ratio	2	1.5	0.77	0.08	0.92
Residuals	79	721.1	9.13		
b) Bare ground score	3	218.5	72.83	11.27	< 0.0001*
Residuals	78	504.1	6.46		
c) Year	1	413.3	413.3	106.9	< 0.0001*
Residuals	80	309.3	3.9		

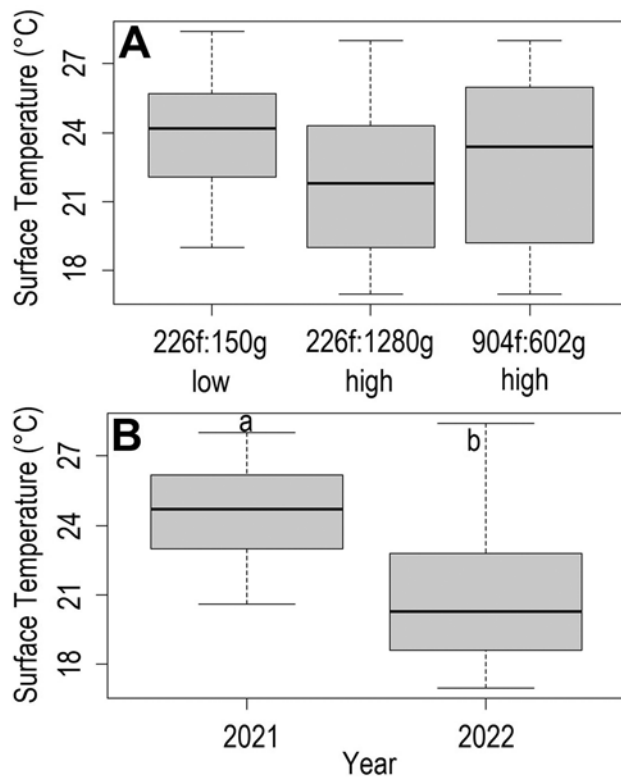


Figure 1. Average soil surface temperature per plot as a function of (A) seeding density (low versus high) and forb:grass ratio and (B) sampling year. The figure shows all data from both years and includes burned plots (N = 82). Letters in (B) indicate significant comparisons according to the Tukey's HSD test (Supplementary Material Table S1). The difference between the 226f:150g seeds/m² (21f:14g seeds/ft²), low seeding density and 226f:1280g seeds/m² (21f:119g seeds/ft²), high seeding density treatments is marginally significant (Supplementary Material Table S1).

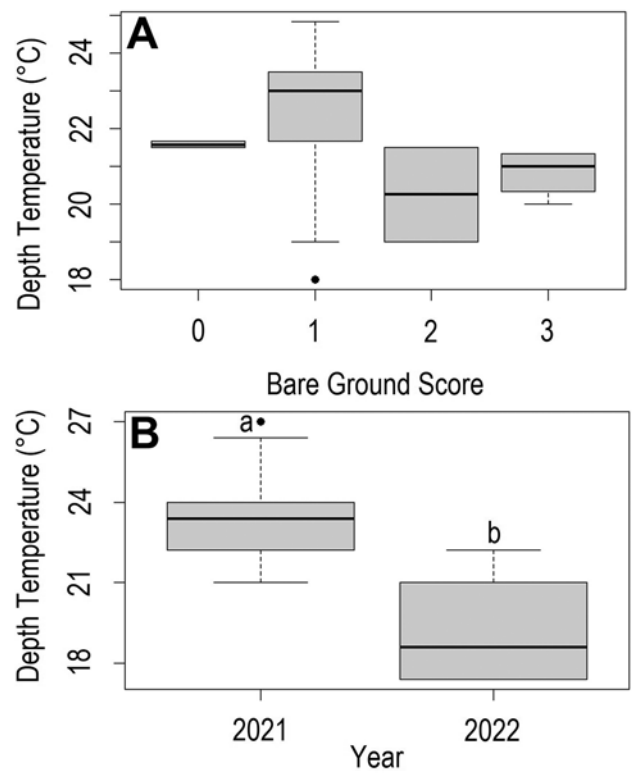


Figure 2. Average soil temperature at depth per plot as a function of (A) bare ground score and (B) sampling year. Because only a few measurements were taken in the 4+ category, it was not included in the analysis. The figure shows all data from both years and includes burned plots (N = 82). Letters in (B) indicate significant comparisons according to the Tukey's HSD test (Supplementary Material Table S2). Bare ground score has a marginally significant effect on depth temperature (Table 3).

Table 5. Results of the three one-way ANOVAs testing the effects of a) forb: grass ratio, b) bare ground score, and c) year on average soil moisture at depth per plot. (* indicates significance at the 0.05 level.)

	Df	Sum Sq	Mean Sq	F value	p value
a) Forb:grass ratio	2	1.5	0.77	0.08	0.92
Residuals	79	721.1	9.13		
b) Bare ground score	3	218.5	72.83	11.27	< 0.0001*
Residuals	78	504.1	6.46		
c) Year	1	413.3	413.3	106.9	< 0.0001*
Residuals	80	309.3	3.9		

We hypothesized that the amount of bare ground would impact soil temperature and soil moisture. Bare ground score had a marginally significant effect on temperature at depth (Table 3B, Figure 2A); however, the Tukey’s HSD post hoc test did not indicate significance between any factor levels (Supplementary Material Table S2B). Surface soil moisture generally decreased with increasing bare ground score (Figure 3A, Supplementary Material Table S3B). Overall, we found that the amount of bare ground significantly impacted soil surface moisture (Table 4B). Since we did not experimentally manipulate the amount of bare ground in plots, these results do not show any causal relationship between the variables.

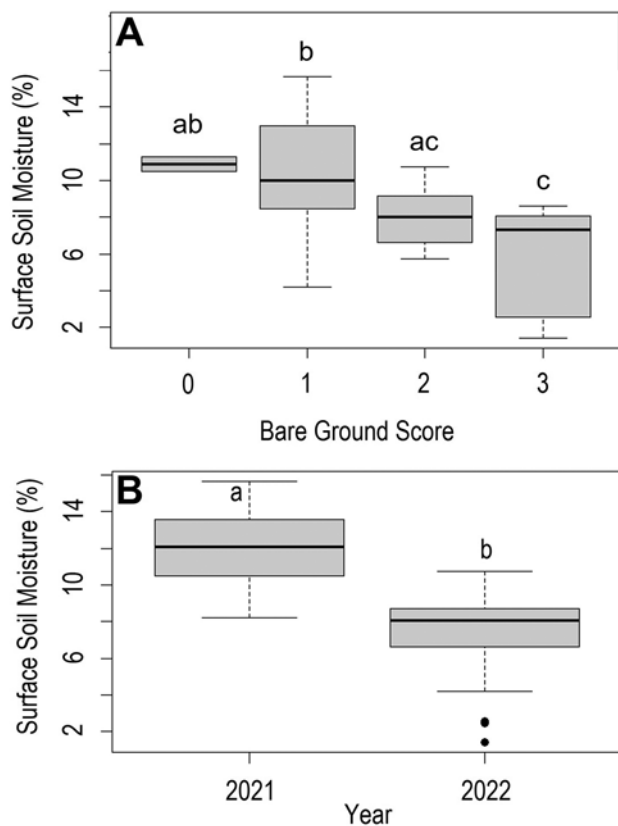


Figure 3. Average surface soil moisture per plot as a function of (A) bare ground score and (B) sampling year. The figure shows all data from both years and includes burned plots (N = 82). Letters in both plots indicate significant comparisons according to the Tukey’s HSD test (Supplementary Material Table S3).

All of the dependent variables were significantly affected by sampling year (Tables 2–5), with values of all four dependent variables decreasing in 2022 compared to 2021 (Figures 1B, 2B, 3B, 4, Supplementary Material Tables S1c, S2c, S3C, S4C).

Lastly, we hypothesized that fire would significantly affect soil variables. Plots burned in 2022 had increased surface temperature, depth temperature, and depth moisture compared to controls, but decreased surface moisture (Figure 5, Table 6, Supplementary Material Table S5).

Discussion

Overall, we found that fire had significant effects on soil microhabitat variables: recent burning was associated with warmer, drier soil at the surface and warmer, wetter soil at depth. Higher temperatures may be induced by the removal of shading provided by thatch, as well as the deposition of darker charred material which absorbs energy from sunlight. These changes in microhabitat could result in higher evaporation and lower soil moisture, though we were not able to test this hypothesis here. The trend we observed at the soil surface is consistent with previous research and model predictions, which showed soil drying as it warmed (Iverson and Hutchinson 2002, Lakshmi et al. 2003, Craine and Nippert 2014, Robichaud et al. 2025). The higher moisture observed at depth ran contrary to our predictions, but

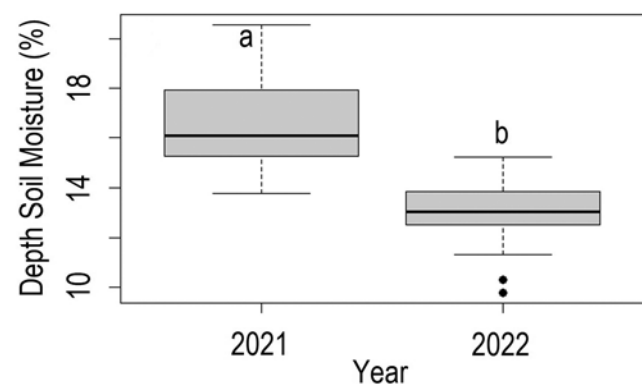


Figure 4. Average soil moisture at depth per plot as a function of sampling year. The figure shows all data from both years and includes burned plots (N = 82). Letters indicate significant comparisons according to the Tukey’s HSD test (Supplementary Material Table S4).

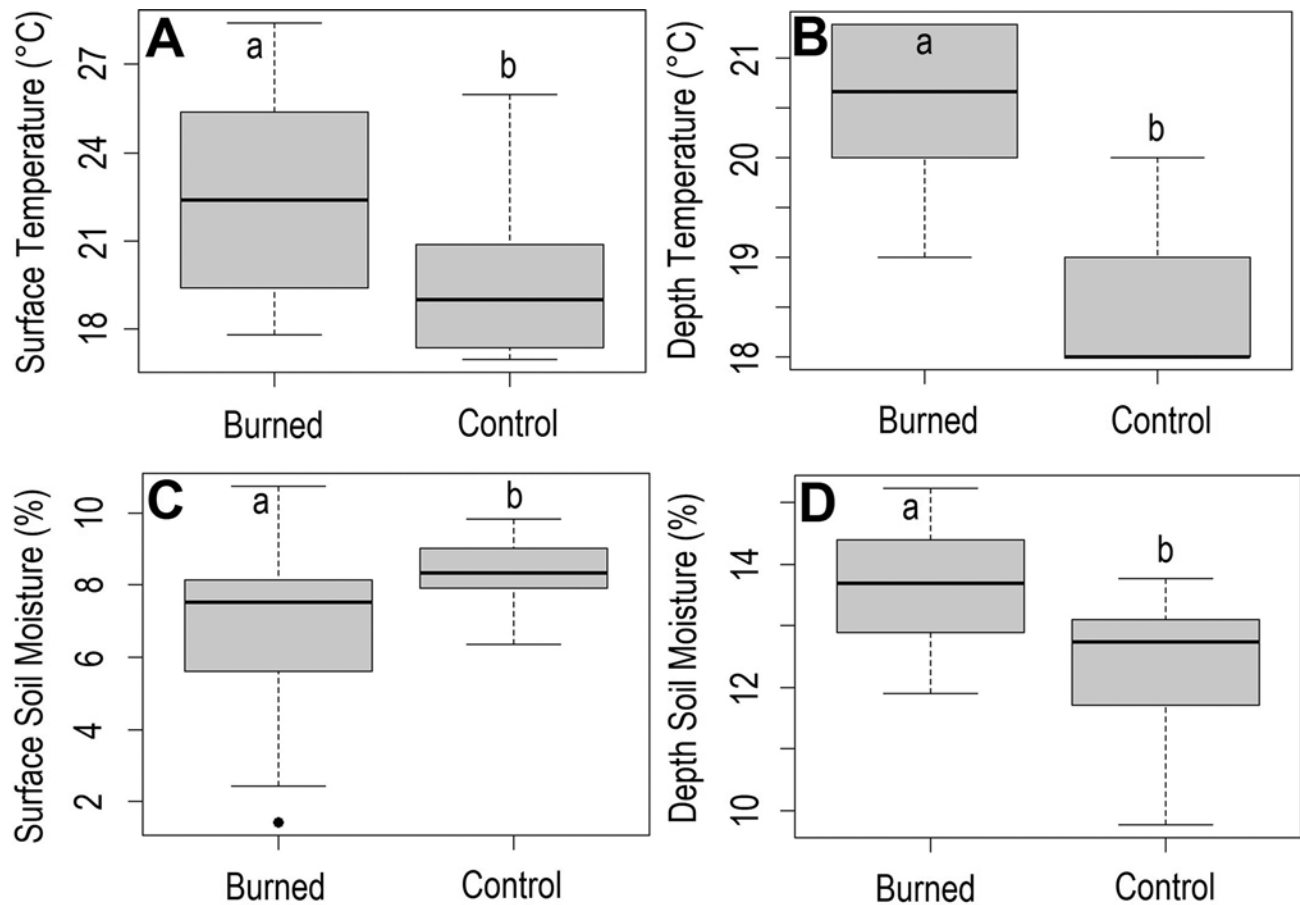


Figure 5. Average soil variables per plot (A) surface temperature, (B) depth temperature, (C) surface soil moisture, and (D) depth soil moisture plotted by burned versus unburned (control) treatments. Letters indicate significant comparisons according to the Tukey's HSD test (Supplementary Material Table S5).

models predict that soil moisture at depth should be less affected by prescribed fire than soil moisture at the surface (Robichaud et al. 2025). The relationship between burning and soil moisture content is complex and time-dependent (Mullen et al. 2006) and effects of fire on soil conditions vary by fire severity, vegetation type, soil texture, starting soil moisture, and time since fire (Huffman et al. 2001).

Impacts of prescribed fire on soil conditions may change over time; for example, soil moisture may decrease immediately after a fire but increase compared to control areas in the long term (Craine and Nippert 2014). Previous work found a positive relationship between prescribed fire and the abundance of ground nesting bee nests (Brokaw et al. 2023), but untangling the mechanisms driving this effect,

Table 6. Results of the four one-way ANOVAs testing the effects of the burn treatment on a) surface temperature, b) temperature at depth, c) surface moisture, and d) moisture at depth. (* indicates significance at the 0.05 level.)

	Df	Sum Sq	Mean Sq	F value	p value
a) Surface temperature					
Burn treatment	1	259.7	259.7	10.78	0.002*
Residuals	38	915.8	24.1		
b) Depth temperature					
Burn treatment	1	34.86	34.86	9.80	0.01*
Residuals	8	28.46	3.56		
c) Surface moisture					
Burn treatment	1	25.21	25.21	6.86	0.01*
Residuals	38	139.72	3.68		
d) Depth moisture					
Burn treatment	1	16.87	16.87	16.58	< 0.001*
Residuals	38	38.68	1.02		

and describing any variation in the effects of prescribed fire on ground nesting bee nests requires further research. Our results suggest that prescribed fire has positive impacts on soil characteristics that favor bee nesting, while variation in seed mix design has little to no impact.

Contrary to our hypothesis, we found no significant effects of seed mix design on the microhabitat conditions of potential bee nesting habitat in experimental restored prairie plots. It is important to note that we only considered forb:grass seed ratios and seeding densities at the time of planting and did not assess the forb:grass ratio of the established plant community; planting ratios may not predict soil conditions as well as using established ratios. Because plant communities alter soil conditions and vice versa (Chen et al. 2014, Zou et al. 2015, An et al. 2019, Colombi and Keller 2019, Shovon et al. 2020), the established forb:grass seed ratios may be more predictive of bee nesting conditions than seeded forb:grass seed ratios. Previous work has shown that the forb establishment rates can be impacted by grass seeding density in prairie restorations (Dickson and Busby 2009), making forb:grass ratios and overall seeding densities potentially important when predicting plant establishment for both floral and nesting resources. Future studies examining the plant community's effect on soil conditions should consider a real-time assessment of which plants are present in a plot, in addition to which seed mix was applied.

Understanding the nesting preferences of ground nesting bees is essential to their conservation, especially in applied habitat restoration projects where nesting resources should be provided in addition to floral resources. Bee nesting preferences are diverse and under-researched, but in general, many ground nesting bee species exhibit preferences for relatively dry and warm soils (Antoine and Forrest 2021). However, the prevalence of these conditions will depend on the plant communities in question, as well as their management. It is possible that trade-offs exist between high planting densities, which maximize food resources for native bees, and lower density options, which better promote their nesting. Our results suggest that prescribed fire is an important tool to expose bare ground and produce warmer, drier microhabitats at the surface, which may be important for nesting bees. Earlier work found more active nests of ground nesting bees in recently burned prairies compared to unburned prairie (Brokaw et al. 2023) and our results suggest a possible mechanism by documenting warmer and drier soils in burned plots.

Our study is the first to consider the effect of seed mix design parameters on bee nesting conditions. To provide valuable habitat for native bees, it is vital to understand how best to supply them with both food and nesting resources, and to understand the impacts of management actions on those resources. Practitioners who are interested in creating ground nesting bee nesting habitats should consider employing frequent prescribed fire to improve nesting

conditions for bees. Future research work should explore the trade-offs between seed density, forb:grass ratio, and resource provisioning for bees, considering both foraging and nesting resources.

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