

FLORAL ABUNDANCE AND SOIL CHARACTERISTICS AFFECT WILD BEE
COMMUNITY STRUCTURES AND NESTING DYNAMICS IN TALLGRASS PRAIRIES

BY

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THESIS

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ABSTRACT

Tallgrass prairies have been reduced to less than 5% of their former range, yet provide essential habitats for many native plants and animals such as pollinators. Land managers work to preserve the biodiversity within these tallgrass prairies by implementing management techniques such as burning, haying, and patch-burn-grazing (PBG). All treatments utilize burning, but haying removes aboveground biomass and PBG includes grazing by cattle. The impacts of these management practices on important ecological factors for bee species, such as floral community structure and nesting resources are examined in this study.

Floral resources and bee communities are usually positively correlated within ecosystems due to their mutualistic interactions. The interactions between flowers and bees are important in maintaining the sustainability of many ecosystems including managed prairies. In Chapter 1, I investigate how management alters the abundance, richness, diversity, and composition of both plant and bee communities and whether there are differences in the interactions between bee species and the plants they forage on within 20 different prairie sites in Missouri. Analyses were conducted for the four treatments and by collapsing the treatments into two groups, grazed and ungrazed.

I discovered that floral abundance in ungrazed sites is higher than on sites that support cattle. However, the bee communities that utilize prairie ecosystems do not change based on management techniques. This may be due to the resilience of the bee species that occur in Missouri compared to the species that occurred in Missouri before the landscape was fragmented. Species remaining in the highly disturbed prairie fragments may be less specialized and better adapted at persisting despite the difference in management. Despite there being no difference in bee communities in grazed and ungrazed patches, the interaction networks between bee species and their host plants are more complex in the prairies without cattle and more

competitive in the prairies with cattle. Additionally, out of the 1769 bees included in my study, only two were honey bees. Therefore, I found no evidence that honey bees are displacing native bees in prairie ecosystems.

Soil characteristics could also affect bee community structure and nesting rates on prairies because most bees nest underground for the majority of their lives. In Chapter 2, I investigate the soil characteristics within the four management treatments including temperature, moisture, pH, bulk density, composition, and bare ground ranks and compare the measurements to ground-nesting bee nesting rates. I used emergence tents to collect ground-nesting bees and associated soil cores. The soil composition was not different based on management techniques, but sites without grazers supported a higher nesting rate compared to PBG sites. This difference may be attributed to lower soil moisture and bulk density, and higher pH and bare ground in ungrazed sites compared to sites that included cattle all of which have been previously associated with increased bee nesting.

In Chapter 3, I discuss collecting the rare *Macropis steironematis* Robertson 1891. She was collected at Stony Point Prairie Conservation Area (37° 31.640', -94° 01.688') on June 19, 2014 while foraging on *Rosa carolina*, the prairie rose. Only a few ambiguous records of this species have been recorded in the United States and, to the best of my knowledge, no extant specimens are available from the state of Missouri. My study provides evidence that the oil-collecting bee, *M. steironematis* is still present in Missouri.

Overall, this study assesses differences in prairie management such as burning, haying, and the time of burning in PBG. I found that PBG, regardless of the time of the last burning, reduces floral abundance and nesting rates of ground-nesting bees compared to sites that are burned and hayed. Additionally, PBG sites had higher soil moisture and bulk density, and lower

pH and bare ground compared to sites that were burned or hayed, which could negatively affect nesting rates on prairies. However, PBG does not reduce the tallgrass prairie bee communities, but it does interfere with important bee-plant interactions by increasing competition between bees and decreasing the complexity of the interactions when compared to sites that are managed with burning or haying.

TABLE OF CONTENTS

CHAPTER 1: EFFECTS OF LAND MANAGEMENT TECHNIQUES USED IN TALLGRASS PRAIRIES ON FLORAL AND BEE ABUNDANCE, RICHNESS, DIVERSITY, AND COMPOSITION	1
CHAPTER 2: EFFECTS OF LAND MANAGEMENT ON SOIL CHARACTERISTICS AND NESTING DYNAMICS OF WILD BEES	31
CHAPTER 3: NEW RECORDS FOR THE BEE SPECIES <i>MACROPIS STEIRONEMATIS</i> IN MISSOURI	56

CHAPTER 1: EFFECTS OF LAND MANAGEMENT TECHNIQUES USED IN TALLGRASS PRAIRIES ON FLORAL AND BEE ABUNDANCE, RICHNESS, DIVERSITY, AND COMPOSITION

Abstract

Tallgrass prairies provide essential habitat for many species of plants and animals and are managed with a wide variety of techniques to restore and preserve their biodiversity. I sampled 20 prairie sites in Missouri to investigate how three management techniques (burning, haying, and patch-burn-grazing) influence floral and bee abundance, richness, diversity, and composition. I also examined whether there were differences in the interactions between plants and bees across management as changes in plant or bee communities can tell us more about stability of the communities. Patch-burn-grazing sites had lower abundance of flowering plants, but bee communities did not differ between treatments. This could be due to a loss of species that are not adapted to the significant disturbance and habitat loss that was experienced in prairies considering that less than 5% of prairie ecosystems remain intact compared to before European settlement in the United States. It is possible that the communities of bees are a subset of what used to be. However, I also found evidence that the bee-plant interactions on PBG sites were less complex and show more competition compared to sites managed by burning and haying. Notably, of nearly 1,800 bees sampled, I only detected two honey bees in my surveys. My results have important implications for how prairies are managed, particularly to preserve diversity of native plants and their pollinators.

Introduction

There is an increased public concern regarding the loss of native, wild pollinators (Buchmann and Nebhan 1996) because bees are the primary pollinators in most regions (Michener 2000), with an estimated 87.5% of flowering plant species depending on insects for pollination (Ollerton *et al.* 2011). In fact, President Barack Obama (2014) recently issued a Presidential Memorandum to promote the health of pollinators and to help combat the current pollination crisis. Bee abundance and diversity have positive correlations with plants (Tadey 2015; Potts *et al.* 2003b) that thus, have extensive ramifications for world food supply, security, and trade (Kevan and Philips 2001). The loss of pollinators could have widespread consequences for ecosystem stability (Potts *et al.* 2003b) as many plants are dependent on pollinators for successful seed set (Ollerton *et al.* 2011). Bee communities, however, are also affected by the availability of floral resources within their flight range (Winfree *et al.* 2009). A better understanding of effective pollinator conservation techniques could help reduce bee declines. Thus, it is imperative to understand whether ecosystems are able to maintain plant and bee communities and whether habitat management efforts to help maintain plant communities are effective. Nonetheless, few studies have examined whether different habitat management techniques change plant or bee communities or their interactions.

Bees provide essential ecosystem services and their community structure is influenced by floral diversity (Tepedino and Stanton 1981; Gathmann *et al.* 1994) and abundance (Banaszak 1996), and pollen and nectar availability (Petanidou and Vokou 1990). Flower abundance and diversity can then have a direct effect on bee community structure because the availability of floral resources is crucial to the survival and reproduction of bees. Moreover, changes in plant community diversity and abundance can have significant effects on bee communities and vice versa, particularly if they alter mutualistic interactions that stabilize ecosystems (Potts *et al.*

2003b). Habitat changes that affect the composition of flowering plants could have strong consequences on bee communities (Winfree *et al.* 2009).

Tallgrass prairies are disturbance dependent ecosystems that require management to prevent encroachment of woody plants and invasive species (Anderson 1990). In particular, seasonal burnings, which are a common method for managing tallgrass prairies, can have a positive effect on floral resources (Hitchmough and De la Fleur 2006) and are critical to maintaining ecosystem diversity and preserving the health of native prairies. Fire influences vegetation and ecosystem dynamics in tallgrass prairies by removing detritus and initiating a cascade of soil changes that many plants depend on (Collins and Wallace 1990). These changes in vegetation can affect many forms of wildlife including monarch butterflies, grasshoppers, and beetles that respond positively to disturbance (Moranz *et al.* 2012, Swengel 2001) and springtails, parasitoid wasps, and spiders that respond negatively to disturbance such as fire (Harper *et al.* 2000).

Under many management plans, burning is accompanied by additional treatments such as haying and grazing but to date little work has examined whether there are differences in response across different management techniques. Haying, the rolling of aboveground biomass into bales which is then sold as cattle or horse feed, is often used in addition to burning because it provides an additional revenue source and is assumed to be similar to natural grazing. While small prairie mammals are known to respond negatively to haying (Kaufman and Kaufman 2008), bee richness was not different on sites that were only managed with burning (Andres 2007). The removal of biomass can increase the cover and diversity of native floral resources and reduces alien species (Brudvig *et al.* 2007) which suggests haying may be a favorable alternative to burning alone.

Grazing, another common prairie management method (Bond 2008) used in addition to burning, can have the opposite effect of haying by reducing plant density (Tadey 2015) and bee abundance (Potts et. al 2003a; Andres 2007). Specifically, patch-burn grazing (PBG) refers to the process of burning approximately equal patches of a prairie each year in rotations and allowing cattle to preferentially graze on the fresh plant growth in burned patches. This produces a heterogeneous landscape with patches of different ages since last burn and different amounts of current grazing intensity. Knapp *et al.* (1999) suggested that patch burning could prevent loss of local disturbance-sensitive plant species and grazing may select for increased species richness, however, many prairie flowers cannot tolerate grazing (Madson 1993) and defoliation can reduce growth and reproduction in prairie plants (Damhoureyeh and Hartnett 2002). How grazing affects insect communities, however, is still largely unknown with both positive and negative effects observed for different groups (Leahy and Underwood 2010; Moranz *et al.* 2012). Thus, while grazing is often used as a management technique to maintain prairies, there is some evidence that it could negatively affect floral abundance and density (Tadey 2015).

In this chapter, I investigate if floral and bee communities change under different prairie management techniques. Native species cover can be reduced in grazed sites compared to burned and hayed sites (Damhoureyeh and Hartnett 2002; Brudvig *et al.* 2007; Moranz *et al.* 2012) and reduction in floral resources also decreases pollinator richness compared to sites without cattle (Westphal *et al.* 2008). Therefore, I first predict that ungrazed sites (managed with burning and haying) will display increased floral and bee abundance, richness, diversity, and composition compared to sites managed by PBG. PBG-new sites are especially attractive to grazing cattle, which seek out forbs (Kurz 2010) and additionally, I predict that PBG-new sites will have lower floral and bee richness compared to PBG-old sites due to preferential visits by grazers. Finally, I

predict that bee and floral community interaction networks will be more complex and show less competition in sites managed by burning and haying compared to PBG because grazing impacts bee communities (Potts *et al.* 2003a) by decreasing flower abundance, thereby increasing pollinator visitation rate per flower and competition for pollinators among flowering plant species (Tadey 2015).

Methods

I sampled 20 1 ha prairie sites under three different management techniques--burned, hayed, and PBG--in southeast Missouri (Table 1). The PBG sites were divided into two categories (PBG-new: <1 year post fire, and PBG-old: >2 years post fire) to further investigate the effect of time since burning for a total of 4 treatments. The sites were sampled in June, 2014. The 20 sites were located within 12 different prairies and separated by a minimum of 300 m to maintain independence between samples. The 20 sites were subdivided into 5 groups that included one of each of the four treatments. The groups were chosen based on management type, geographic location, and size to control for differences among sites due to climate and soil conditions.

Floral Survey Records

At each site, an area of 1 ha of relatively uniform vegetation was chosen for sampling. The center hectare was sampled at each site to avoid possible edge effects. Floral diversity was estimated via transects 100 m long x 2 meters wide, covering approximately 10% of the total site area. All flowers of blooming species encountered within 1 m on either side of the transect was counted. Flowering plant species that were observed off transects but inside the center hectare were recorded as present (Table 2a) but abundance was not measured.

Bee Survey Records

Bee emergence tents (BugDorm Model No BT2006), hand netting, and bee bowls were used to collect bees at each of the sites. Fifteen bee emergence tents were randomly installed at dusk in the center hectare of each site to capture female bees as they attempted to forage the next morning. These tents were recently used in a similar fashion to estimate nesting density in fossorial communities (Sardinas and Kremen 2014). Forty-seven bee bowls were set up (Droege *et al.* 2010) in the morning after the tents were collected and left until 1:00 pm consistently

within each site. They were set up in alternating colors of yellow, blue and white, three meters apart in a diagonal line throughout the center hectare of each site and filled with soapy water according to the protocol by Droege *et al.* (2010). Bees were hand-netted with an insect net for one hour from flowers during peak flight time. A stop-watch was used to stop time measurement during handling for each bee and resume time measurement while searching for the next specimen. I maintained floral associations for each bee by collecting bees into individual jars for each plant species. Wind speed and temperature were recorded at each site to ensure they were within optimal flight conditions for bees (above 15.5 °C with wind speeds below 32 km/hr respectively) (Kwaiser and Hendrix 2007). All bees were identified to species by the author (Arduser 2014) and specimens were verified by Michael Arduser, local bee expert from the Missouri Department of Conservation.

Data Analysis

One-way analysis of variance was used to determine if abundance, richness, and diversity measures were different in plant and bee communities between treatments. The Shannon-Wiener index was used to calculate bee and plant species diversity using cumulative abundances across the treatment groups. The Simpson diversity index was applied to estimate diversity rates with an emphasis on common species. Multi-response permutation procedures (MRPP) (McCune *et al.* 2002) were performed to test the null hypothesis that floral composition was not significantly different among the four prairie management types. MRPP was performed using the vegan package in R version 3.0.3. The MRPP analysis does not require assumptions such as normality and equal variance and can be used to calculate the average distance within each treatment group, delta - the weighted mean within group distance, and provides a graphical representation of the relationships among groups through an overlay of communities. Additionally, a non-metric

multidimensional scaling (NMDS) was run using grid, ggplot2, lme4, lmerTest, bbmle, vegan, and gridExtra packages in R version 3.0.3. The scaling attempts to minimize stress, which is related to dissimilarities that are represented as plotted distances. It maximizes the rank correlation between the distances to create plotted distances and sequential ranks to create a visual estimate of the positions of communities. The model is considered good when the level of stress is low. An NMDS analysis was also conducted to visualize the difference in bee communities between treatments.

Interaction networks were used to visualize associations between bee species and the plant species on which they were collected foraging on at each site. The analysis conducted provides values for many variables within networks including connectance, web asymmetry, links per species, mean number of shared partners HL, mean number of shared partners LL, C score HL, C score LL, V ratio HL, V ratio LL, nestedness, nich overlap HL, niche overlap LL, generality HL, vulnerability LL, interaction evenness, Shannon diversity, and H2 (bipartite package in R version 3.0.3). These metrics explain how the interaction between the bees and plant species are assembled within each site and could be used to compare interactions between sites. Multivariate analysis of variance (MANOVA using packages plyr, ggplot, ggplot2, scales, and grid in R version 3.0.3) was performed on the reported values to assess differences among grazed (burn and hay) and ungrazed (PBG-new and PBG-old) treatments.

Results

Prairie Flowers

I identified over 45,600 flowers to sixty-three species within the prairies (Table 1). The most common species were *Erigeron strigosus* (false daisy), followed by *Rudbeckia hirta* (black eyed Susan) (Table 2b). The surveys that I conducted determined that the prairie with the highest number of flowers was Mon-Shon, a hayed prairie with more than 8,000 flowers per hectare. Overall, floral abundance differed among the four management techniques (ANOVA, $F=4.49$, $DF=3$, $p>0.02$) and this difference was largely driven by PBG new and haying treatments. Prairie flower abundance was lower in prairies that were grazed (ANOVA, $F=13.87$, $DF=1$, $p>0.002$) compared to prairies that were not grazed (Figure 1).

The site with the greatest number of flowering plant species was a burned prairie, Twenty-five Mile, which supported 24 species of flowering plants during the time of sampling. However, flower species richness among the management types were not difference (ANOVA, $F=1.36$, $DF=3$, $p>0.29$). Simpson index values, which incorporate dominance, were greatest at Wah'Kon-Tah (PBG-old) and Dorris Creek (hay), but were not different among treatments (ANOVA, $F=1.35$, $DF=3$, $p>0.24$). Shannon's species diversity index estimates were also not different among management types (ANOVA, $F=1.58$, $DF=3$, $p>0.23$). The relative abundance of the 10 most common species can be seen in Figure 2.

Non-metric multidimensional scaling (NMDS), revealed some clustering of floral communities by management type (Figure 3). The clusters separate into two distinctive categories of grazed and ungrazed prairies. A multi-response permutation procedure (MRPP) suggests that the management treatments do support significantly different floral communities within the sampled prairies (MRPP, $A=0.10$, $p>0.02$).

Tallgrass Prairie Bees

I identified nearly 1,700 bees, 21 genera, and 57 species across all sites. Seventeen species were only detected once (singletons) and only two honey bees (*Apis mellifera*) were collected in the bee surveys. The dominate genus was *Lasioglossum* at 68% and the dominant species was *Lasioglossum coreopsis* which made up 25% of the entire collection of bees. There was no difference among management types in bee species measures of abundance between the management (ANOVA, $F=0.71$, $DF=3$, $p>0.56$), species richness (ANOVA, $F=1.18$, $DF=3$, $p>0.35$), diversity using Shannon's index: (ANOVA, $F=1.08$, $DF=3$, $p>0.34$), or Simpson's index: (ANOVA, $F=1.11$, $DF=3$, $p>0.37$). The NMDS supported that the bee communities overlap considerably across management types suggesting similarity among communities (Figure 4).

Interactions between bee species and the plant species on which they forage (Table 3) suggest that the interactions were very similar among treatments with the exception of two variables: the C score HL (higher level) and links per species. The C scores in the grazed sites were higher, suggesting higher aggregation or competition (MANOVA, $F=4.45$, $DF=17$, $p>0.05$). Links per species were higher in ungrazed sites, suggesting that the interactions are more complex compared to grazed sites (MANOVA, $F=4.33$, $DF=17$, $p>0.05$). The treatment techniques did not affect the interaction network connectance (MANOVA, $F=0.02$, $DF=17$, $p>0.90$), web asymmetry (MANOVA, $F=0.28$, $DF=17$, $p>0.6$), mean number of shared partners HL (MANOVA, $F=1.84$, $DF=17$, $p>0.20$), mean number of shared partners LL (MANOVA, $F=1.55$, $DF=17$, $p>0.20$), C score LL (MANOVA, $F=1.10$, $DF=17$, $p>0.30$), V ratio HL (MANOVA, $F=1.43$, $DF=17$, $p>0.20$), V ratio LL (MANOVA, $F=1.64$, $DF=17$, $p>0.22$), nestedness (MANOVA, $F=0.70$, $DF=17$, $p>0.41$), niche overlap HL (MANOVA, $F=1.29$,

DF=17, $p > 0.27$), niche overlap LL (MANOVA, $F=0.24$, DF=17, $p > 0.63$), generality HL (MANOVA, $F=0.41$, DF=17, $p > 0.53$), vulnerability LL (MANOVA, $F=1.49$, DF=17, $p > 0.24$), interaction evenness (MANOVA, $F=0.15$, DF=17, $p > 0.70$), Shannon diversity of the networks (MANOVA, $F=2.57$, DF=17, $p > 0.13$), and H2 (MANOVA, $F=0.31$, DF=17, $p > 0.59$).

Discussion

Grazing affected some aspects of the floral community such as abundance and composition, but the bee communities did not differ between management techniques, including PBG-new and PBG-old. Despite the relative uniformity of the bee communities among sites, some components of pollinator interaction networks did vary among sites. Fragmentation might have caused these bee communities to become resilient to the observed environmental differences caused by cattle. For example, bee species could have lost their trait of specialization.

Grazed sites (PBG-new and PBG-old combined) supported fewer flowers compared to the ungrazed sites and the composition of the floral communities was very different between grazed and ungrazed sites as predicted. The comparison of interaction networks between management techniques suggest that bee species in PBG sites experience more competition than bees in ungrazed sites where the interaction networks are more complex. This indicates that my third hypothesis was supported. These results are similar to those in Tadey (2015), which suggested that increased competition might be due to the overall reduction of floral resources at PBG sites compared to ungrazed sites. However, it should be noted that the site interaction networks in this study were small, and may lack the power to identify C score HL (competition), and links per species (complexity) as significantly different between grazed and ungrazed sites.

Many of the characteristics measured in this study were not found to be different between management techniques including floral richness and diversity. Surprisingly, bee abundance, diversity, richness, and community composition were not different under the four management techniques. For example, I collected 33 species of wild bees in burned sites, 36 species in hayed sites, 34 species in PBG-new, and 37 species in PBG-old. These results are not in accordance with other studies, such as Andres (2007), in which 71 species of bees were collected in burned

sites, 53 species in hayed sites, and only 27 species in grazed prairies. The difference could be due to increased sampling or grazing intensity. Additionally, time since the last burn under the PBG management technique did not affect floral and bee richness as predicted. Therefore, my second hypothesis was not supported. Surprisingly, only two collections of the honey bee were made, the rest of the samples consisted of native, primarily ground-nesting bees, stressing the conservation value of native bees to prairie plant communities. Some research (see Paine 2004) suggests that honey bees are outcompeting native bees in conservation areas, but this study suggests that feral honey bee colonies do not prosper in tallgrass prairies, or compete with native bees. Furthermore, the interaction network analysis suggested that 15 of the 17 metrics analyzed were not different between grazed and ungrazed sites. I could not detect an effect of treatment techniques on the number of species combinations, balance between the two trophic levels (bees and flowers), variance ratio of species, nestedness within the matrices, similarity in the interaction pattern, effective number of flowers per bee, effective number of bee per flower, Shannon's evenness, Shannon's diversity of interactions, and the network-level measure of specialization.

Land managers should consider the effect of PBG on floral communities when considering conservation efforts. For example, burning without grazing allows the development of denser, taller vegetation (Moranz *et al.* 2012) and PBG can have devastating effects on plant species, because the practice focuses on vegetative structure over species richness and floral abundance (Kurz 2010). Grazing by wild bison in combination with natural fires benefited prairie systems prior to habitat fragmentation by promoting a diverse prairie landscape (Underwood 2010). The difference in floral abundance in cattle-grazed sites may be attributed to cattle exhibiting different foraging behaviors than bison (Plumb and Dodd 1993). Unfortunately,

it is difficult to replicate pre-settlement conditions because prairies have been reduced from their former state and few sites use bison or for grazing. As a result, it is difficult to know if cattle-grazing changes the bee community compared to natural bison-grazing. However, the similarity of bee communities between treatment techniques could be interpreted positively for land managers that employ PBG techniques, because PBG provides a revenue source that could also incentivize bee conservation efforts (Curtin and Western 2008). Although, cattle did greatly reduce the abundance of flowering prairie species, and alter two key metrics for the interactions between plants and pollinators.

Experiencing habitat fragmentation could have stressed some species of bees beyond recovery (Rathcke 1986) and it is possible that the unknown initial bee communities of Missouri could have been filtered to the extant communities documented in this study. For example, species-specific specialization was rare within the interaction networks, suggesting that some bees may have lost the trait of specialization due to habitat fragmentation and only the bee species that are able to survive in prairie systems remain, regardless of the management technique employed. Tallgrass prairie bees might be resilient to differences in floral abundance and community structure, and are strong enough to survive under the management techniques investigated in this study.

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Tables and Figures

Table 1. Locations included in this study. Management techniques for the prairies include burning, haying, patch-burn-grazing (PBG). PBG prairies are separated into units based on the time of burning, PBG-new (burned within the year of sampling) and PBG-old (burned more than two years prior to sampling). GPS coordinates were taken from the center hectare at each of the twenty sites. Some prairies were used more than once, but units are considered independent due to a distance greater than 300m. Bee and floral richness (Rich.) and abundance (Ab.) are recorded for each site.

Prairie Conservation Area	Type	County	GPS Coordinates	Bee Rich.	Bee Ab.	Floral Rich.	Floral Ab.
Mon-Shon	burn	Barton	37° 22.033', -94° 37.007'	3	27	10	3891
Niawathe A	burn	Dade	37° 31.008', -93° 58.163'	7	142	19	7430
Niawathe B	burn	Dade	37° 30.790', -93° 58.136'	12	214	22	1164
La Petite Gemme	burn	Polk	37° 33.811', -93° 24.581'	5	40	12	1726
Twenty-Five Mile	burn	Polk	37° 46.922', -93° 31.785'	8	142	24	3089
Buffalo Wallow	hay	Barton	37° 38.131', -94° 16.523'	4	41	7	2658
Dorris Creek	hay	Barton	37° 23.014', -94° 13.707'	4	44	6	2306
Mon-Shon	hay	Barton	37° 22.174', -94° 36.987'	4	115	15	8102
Sky	hay	Cedar	37° 41.628', -93° 56.925'	9	137	19	1526
Horse Creek	hay	Dade	37° 24.358', -93° 59.413'	8	46	19	7017
Wah'Kon-Tah	PBG- new	Cedar	37° 53.674', -93° 59.222'	6	74	17	446
Stony Point A	PBG- new	Dade	37° 31.453', -94° 01.301'	4	34	17	992
Stony Point B	PBG- new	Dade	37° 32.161', -94° 01.430'	4	64	13	365
Wade and June Shelton Memorial	PBG- new	Dade	37° 27.614', -93° 59.146'	2	142	7	66

Table 1 (cont.)

Taberville	PBG-new	St. Clair	38° 03.447', -93° 58.519'	7	96	12	122
Wah'Kon-Tah	PBG-old	Cedar	37° 53.541', -93° 59.172'	6	28	17	426
Stony Point A	PBG-old	Dade	37° 31.746', -94° 00.374'	8	132	9	76
Stony Point B	PBG-old	Dade	37° 31.640', -94° 01.688'	4	9	9	309
Wade and June Shelton Memorial	PBG-old	Dade	37° 27.632', -93° 58.219'	4	131	7	1745
Taberville	PBG-old	St. Clair	38° 03.137', -93° 58.651'	5	111	12	2168

Table 2a. Blooming plant species. The plant species code is used in Table 2b. Here the plant species code is arranged with its scientific and common names.

Plant Species Code	Species Name	Common Name
ACMI	<i>Achillea millefolium</i>	yarrow
AMCA	<i>Amorpha canescens</i>	lead plant
ARPL	<i>Arnoglossum plantagineum</i>	Indian plantain
ASVE	<i>Asclepius verticillata</i>	whorled milkweed
ASVI	<i>Asclepius viridiflora</i>	green milkweed
BAAL	<i>Baptisia alba</i>	white wild indigo
BUAM	<i>Buchnera americana</i>	American bluehearts
CACO	<i>Castilleja coccinea</i>	Indian paint brush
CADI	<i>Callirhoe digitata</i>	fringed poppy mallow
CEAM	<i>Ceanothus americanus</i>	New Jersey tea
COLA	<i>Coreopsis lanceolata</i>	tickseed coreopsis
COPA	<i>Coreopsis palmata</i>	prairie coreopsis
COTR	<i>Coreopsis tripteris</i>	tall coreopsis
DACA	<i>Dalea candida</i>	white prairie clover
DAPU	<i>Dalea purpurea</i>	purple prairie clover
DAUCAR	<i>Daucus carota</i>	wild carrot
DIAR	<i>Dianthus armeria</i>	18septford pink
ECPA	<i>Echinacea pallida</i>	pale purple coneflower
ERST	<i>Erigeron strigosus</i>	daisy fleabane, false daisy
ERYU	<i>Eryngium yuccifolium</i>	rattlesnake master
EUCO	<i>Euphorbia corollata</i>	flowering spurge
HEFL	<i>Helenium flexuosum</i>	purple headed sneezeweed
HYPE	<i>Hypericum perforatum</i>	common St. John's wort
HYSP	Unknown <i>Hypericum</i>	St. John's Wort – unknown
LEVU	<i>Leucanthemum vulgare</i>	ox-eye daisy
LISU	<i>Linum sulcatum</i>	grooved yellow flax
LOSP	<i>Lobelia spicata</i>	pale spiked lobelia
LUAL	<i>Ludwigia alternifolia</i>	seedbox
LYAL	<i>Lythrum alatum</i>	winged loosestrife
MELU	<i>Medicago lupulina</i>	black medick
MINU	<i>Mimosa nuttallii</i>	sensitive briar
MOFI	<i>Monarda fistulosa</i>	wild bergamot
ORPE	<i>Orbexilum pedunculatum</i>	Sampson's snakeroot
OXDI	<i>Oxalis dillenii</i>	gray-green wood sorrel
OXST	<i>Oxalis stricta</i>	yellow wood sorrel
PAIN	<i>Parthenium integrifolium</i>	wild quinine
PEDI	<i>Penstemon digitalis</i>	foxglove beardtongue
PETU	<i>Penstemon tubiflorus</i>	white wand beardtongue
PHAN	<i>Physostegia angustifolia</i>	obedient plant

Table 2a (cont.)

PHPI	<i>Phlox pilosa</i>	pink phlox
POIN	<i>Polygala incarnata</i>	pink milkwort
PORE	<i>Potentilla Recta</i>	rough-fruited cinquefoil
POSA	<i>Polygala sanguinea</i>	field milkwort
PSTE	<i>Psoraleidium tenuiflorum</i>	scurfy pea
PTNU	<i>Ptilimnium nuttallii</i>	lace flower
PYTE	<i>Pycnanthemum tenuifolium</i>	slender mountain mint
PYVI	<i>Pycnanthemum virginianum</i>	common mountain mint
ROCA	<i>Rosa carolina</i>	prairie rose
RUBI	<i>Rubus spp.</i>	rubus variety
RUHI	<i>Rudbeckia hirta</i>	black eyed Susan
RUHU	<i>Ruellia humilis</i>	hairy wild petunia
SACA	<i>Sanguisorba canadensis</i>	American burnet
SILA	<i>Silene latifolia</i>	bladder campion
SIOF	<i>Sisymbrium officinale</i>	hedge mustard
SOCA	<i>Solanum carolinense</i>	horse nettle
STBI	<i>Stylosanthes biflora</i>	pencil flower
TEVI	<i>Tephrosia virginiana</i>	goat's rue
TOAR	<i>Torilis arvensis</i>	hedge parsley
TROH	<i>Tradescantia ohiensis</i>	common spiderwort
VEHE	<i>Verbena helianthoides</i>	wingstem

Table 2b. Blooming plant species by management technique. The plant species code represents the species described in Table 2a. The prairie management techniques include haying, burning, and patch-burn-grazing (PBG). PBG is separated into two independent units based on the time of burning. PBG-Old was burned more than two years before sampling and PBG-New was burned within the year of sampling. The values show how many flowers of each plant species were in bloom at each site during the time of sampling.

Plant Species Code	Hay	Burn	PBG-Old	PBG-New	Total
ACMI	105	137	64	72	378
AMCA	24	2104	0	0	2128
ARPL	12	0	0	0	12
ASVE	3	0	0	5	8
ASVI	0	10	0	0	10
BAAL	0	0	17	52	69
BUAM	9	4	0	4	17
CACO	7	0	1	2	10
CADI	0	4	0	0	4
CEAM	14	1773	60	7	1854
COLA	0	0	0	2	2
COPA	29	17	14	21	81
CORA	0	21	0	0	21
COTR	70	13	11	204	298
DACA	5	10	0	2	17
DALCAN	0	12	0	0	12
DAPU	26	11	0	0	37
DAUCAR	0	0	2	19	21
DIAR	0	0	3	3	6
ECPA	130	687	23	3	843
ERST	8841	3457	1777	391	14466
ERYU	0	6	0	0	6
EUCO	38	7	6	0	51
HEFL	236	32	0	3	271
HYPE	19	0	9	0	28
HYSP	0	5	0	0	5
LEVU	0	10	0	0	10
LISU	0	185	0	13	198
LOSP	0	0	0	13	13
LUAL	1	0	0	0	1
LYAL	0	0	9	0	9

Table 2b (cont.)

MELU	9	0	8	0	17
MINU	147	29	131	89	396
MOFI	0	10	0	0	10
ORPE	0	16	0	0	16
OXDI	0	0	0	6	6
OXST	0	0	0	9	9
PAIN	6	2198	0	0	2204
PEDI	3	670	18	0	691
PETU	14	15	0	25	54
PHAN	2981	3587	73	7	6648
PHPI	0	0	0	21	21
POIN	0	1	0	0	1
PORE	0	0	2	0	2
POSA	280	49	165	273	767
PSTE	0	60	0	0	60
PTNU	24	0	0	0	24
PYTE	2170	186	0	0	2356
PYUI	163	0	0	0	163
PYVI	0	9	0	0	9
ROCA	0	12	193	31	236
RUBI	12	0	40	4	56
RUHI	5577	1564	1882	19	9042
RUHU	268	76	41	66	451
RUMI	371	0	0	0	371
SACA	0	4	0	0	4
SILA	0	0	0	7	7
SIOF	0	0	0	123	123
SOCA	0	13	47	140	200
STBI	3	225	12	240	480
TEVI	0	0	0	87	87
TOAR	3	0	9	0	12
TROH	9	66	0	8	83
VEHE	0	5	107	20	132

Table 3. Bee species according to their foraging resource. The bee species were collected while foraging on the associated plant species in tallgrass prairies.

Plant species	Bee visitor(s)
<i>Amorpha canescens</i>	<i>Andrena quintilus</i> , <i>Andrena vestal</i> , <i>Bombus griscocollis</i> , <i>Halictus parallelus</i> , <i>Lasioglossum callidum</i> , <i>Lasioglossum coreopsis</i> , <i>Lasioglossum hitchense</i> , <i>Lasioglossum tegulare</i> , <i>Lasioglossum versatum</i>
<i>Anthemis cotula</i>	<i>Ceratina strenua</i> , <i>Lasioglossum coreopsis</i>
<i>Asclepias verticillata</i>	<i>Protandrena cockerelli</i>
<i>Asclepias viridiflora</i>	<i>Bombus bimaculatus</i>
<i>Baptisia alba</i>	<i>Lasioglossum pruinum</i>
<i>Ceanothus americanus</i>	<i>Lasioglossum versatum</i>
<i>Cicuta maculata</i>	<i>Augochlorella aurata</i> , <i>Ceratina strenua</i>
<i>Coreopsis palmata</i>	<i>Andrena beameri</i> , <i>Andrena helianthiformis</i> , <i>Augochlorella aurata</i> , <i>Lasioglossum coreopsis</i> , <i>Lasioglossum disparile</i>
<i>Coreopsis tripteris</i>	<i>Lasioglossum coreopsis</i>
<i>Dalea candida</i>	<i>Augochlorella aurata</i> , <i>Lasioglossum callidum</i>
<i>Dalea purpurea</i>	<i>Augochlorella aurata</i> , <i>Lasioglossum callidum</i> , <i>Lasioglossum coreopsis</i> , <i>Lasioglossum illinoense</i> , <i>Lasioglossum nymphaearum</i> , <i>Lasioglossum tegulare</i> , <i>Lasioglossum versatum</i>
<i>Echinacea pallida</i>	<i>Agapostemon virescens</i> , <i>Andrena helianthiformis</i> , <i>Andrena rudbeckiae</i> , <i>Augochlorella aurata</i> , <i>Augochloropsis metallica</i> , <i>Bombus griscocollis</i> , <i>Ceratina strenua</i> , <i>Halictus ligatus</i> , <i>Lasioglossum coreopsis</i> , <i>Lasioglossum lustrans</i> , <i>Lasioglossum versatum</i>
<i>Erigeron strigosus</i>	<i>Ceratina strenua</i> , <i>Lasioglossum coreopsis</i>
<i>Helenium flexuosum</i>	<i>Augochlorella aurata</i> , <i>Lasioglossum coreopsis</i>
<i>Linum sulcatum</i>	<i>Lasioglossum coreopsis</i> , <i>Lasioglossum hitchense</i>
<i>Lythrum alatum</i>	<i>Ceratina strenua</i>
<i>Mimosa nuttallii</i>	<i>Agapostemon virescens</i> , <i>Augochlorella aurata</i> , <i>Augochloropsis metallica</i> , <i>Bombus griscocollis</i> , <i>Halictus parallelus</i> , <i>Lasioglossum callidum</i> , <i>Lasioglossum coreopsis</i> , <i>Lasioglossum disparile</i> , <i>Lasioglossum hitchense</i> , <i>Lasioglossum pruinum</i> , <i>Lasioglossum versatum</i> , <i>Megachile brevis</i> , <i>Xylocopa virginica</i>
<i>Monarda fistulosa</i>	<i>Augochlorella aurata</i> , <i>Augochloropsis metallica</i> , <i>Bombus pensylvanicus</i> , <i>Dialictus sp. B</i> , <i>Lasioglossum lustrans</i> , <i>Lasioglossum subviridatum</i>
<i>Parthenium integrifolium</i>	<i>Andrena helianthiformis</i> , <i>Lasioglossum callidum</i> , <i>Lasioglossum coreopsis</i> , <i>Lasioglossum smilacinae/laevissimum/gotham</i>

Table 3 (cont.)

<i>Penstemon digitalis</i>	<i>Ceratina calcarata/dupla/mikmaqi</i> , <i>Physostegia angustifolia</i> , <i>Andrena rudbeckiae</i> , <i>Apis mellifera</i> , <i>Augochlorella aurata</i> , <i>Augochloropsis metallica</i> , <i>Bombus bimaculatus</i> , <i>Bombus pensylvanicus</i> , <i>Ceratina calcarata/dupla/mikmaqi</i> , <i>Eucera hamata</i> , <i>Eucera rosae</i> , <i>Lasioglossum callidum</i> , <i>Lasioglossum coreopsis</i> , <i>Lasioglossum hitchense</i> , <i>Lasioglossum nymphaearum</i> , <i>Lasioglossum pruinsum</i> , <i>Lasioglossum versatum</i> , <i>Xylocopa virginica</i>
<i>Physostegia angustifolia</i>	<i>Megachile exilis</i>
<i>Pycnanthemum tenuifolium</i>	<i>Bombus griscocollis</i> , <i>Lasioglossum versatum</i>
<i>Rosa carolina</i>	<i>Andrena helianthiformis</i> , <i>Augochlorella aurata</i> , <i>Bombus griscocollis</i> , <i>Ceratina strenua</i> , <i>Eucera rosae</i> , <i>Lasioglossum callidum</i> , <i>Lasioglossum coreopsis</i> , <i>Lasioglossum hitchense</i> , <i>Lasioglossum lineatulum</i> , <i>Lasioglossum pruinsum</i> , <i>Lasioglossum versatum</i> , <i>Macropis steironematis</i> , <i>Megachile brevis</i> , <i>Megachile petulans</i>
<i>Rubus spp.</i>	<i>Augochlorella aurata</i> , <i>Lasioglossum versatum</i>
<i>Rudbeckia hirta</i>	<i>Agapostemon texanus</i> , <i>Andrena beameri</i> , <i>Andrena cressonii</i> , <i>Andrena helianthiformis</i> , <i>Andrena rudbeckiae</i> , <i>Augochlorella aurata</i> , <i>Augochloropsis metallica</i> , <i>Halictus ligatus</i> , <i>Hylaeus mesillae</i> , <i>Lasioglossum callidum</i> , <i>Lasioglossum coreopsis</i> , <i>Lasioglossum disparile</i> , <i>Lasioglossum hitchense</i> , <i>Lasioglossum lustrans</i> , <i>Lasioglossum nymphaearum</i> , <i>Lasioglossum pruinsum</i> , <i>Lasioglossum quebecense</i> , <i>Lasioglossum subviridatum</i> , <i>Lasioglossum versatum</i> , <i>Megachile inimical</i> , <i>Melissodes coreopsis</i>
<i>Ruellia humilis</i>	<i>Agapostemon virescens</i> , <i>Augochlorella aurata</i> , <i>Halictus ligatus</i> , <i>Lasioglossum callidum</i> , <i>Lasioglossum coreopsis</i> , <i>Lasioglossum disparile</i> , <i>Lasioglossum lustrans</i> , <i>Lasioglossum nymphaearum</i> , <i>Lasioglossum tegulare</i> , <i>Lasioglossum truncatum</i> , <i>Lasioglossum versatum</i> , <i>Pseudopanurgus albitarsis</i>
<i>Solanum carolinense</i>	<i>Bombus bimaculatus</i>
<i>Stylosanthes biflora</i>	<i>Augochlorella aurata</i> , <i>Lasioglossum coreopsis</i>
<i>Tephrosia virginiana</i>	<i>Lasioglossum callidum</i> , <i>Megachile addenda</i>
<i>Verbesina helianthoides</i>	<i>Augochlorella aurata</i>

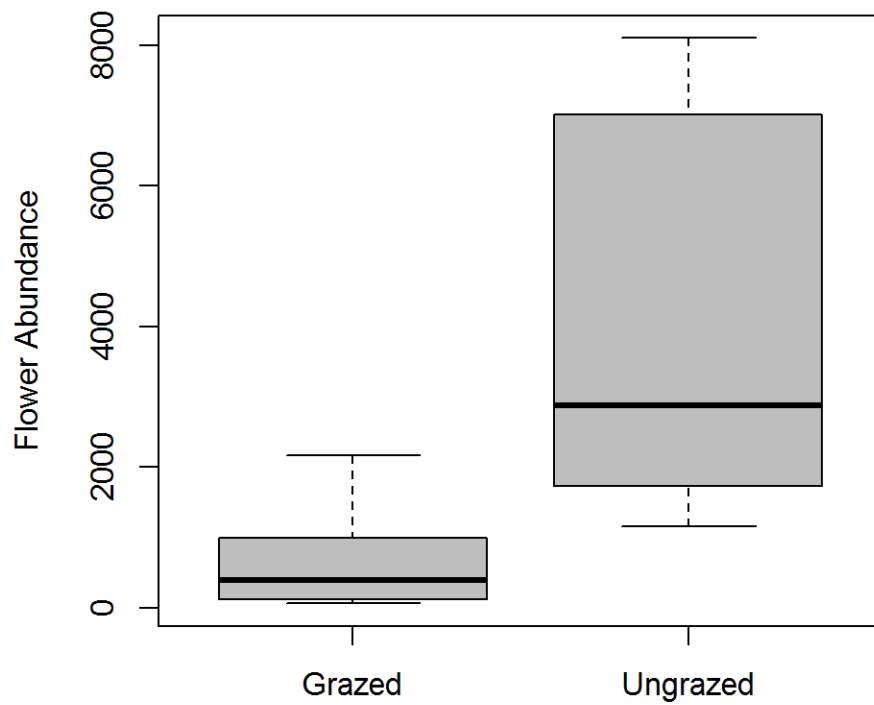


Figure 1. Flower abundance. (Mean $\pm$ standard error) in grazed sites compared with flower abundance in ungrazed sites. Mean flower abundance is lower in prairies with grazing management techniques compared to prairies that were ungrazed (ANOVA, $F=4.49$, $DF=3$, $p>0.02$).

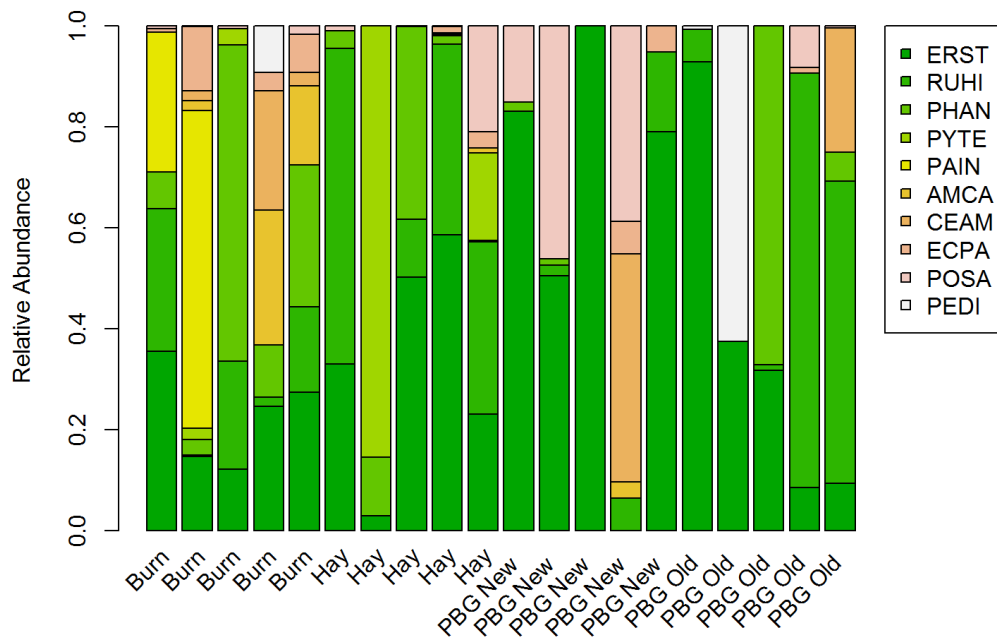


Figure 2. Flower survey results. The center hectare of prairies from each management technique was surveyed. The techniques include burn, hay, and patch-burn-graze (PBG). PBG is divided into units that were burned more than two years before sampling (PBG Old) and units that were burned within the year of sampling (PBG New). The floral code abbreviates the species name from top to bottom as follows: daisy fleabane or false daisy (*Erigeron strigosus*), black eyed Susan (*Rudbeckia hirta*), obedient plant (*Physostegia angustifolia*), slender mountain mint (*Pycnanthemum tenuifolium*), wild quinine (*Parthenium integrifolium*), lead plant (*Amorpha canescens*), New Jersey tea (*Ceanothus americanus*), pale purple coneflower (*Echinacea pallida*), field milkwort (*Polygala sanguinea*), and foxglove beardtongue (*Penstemon digitalis*).

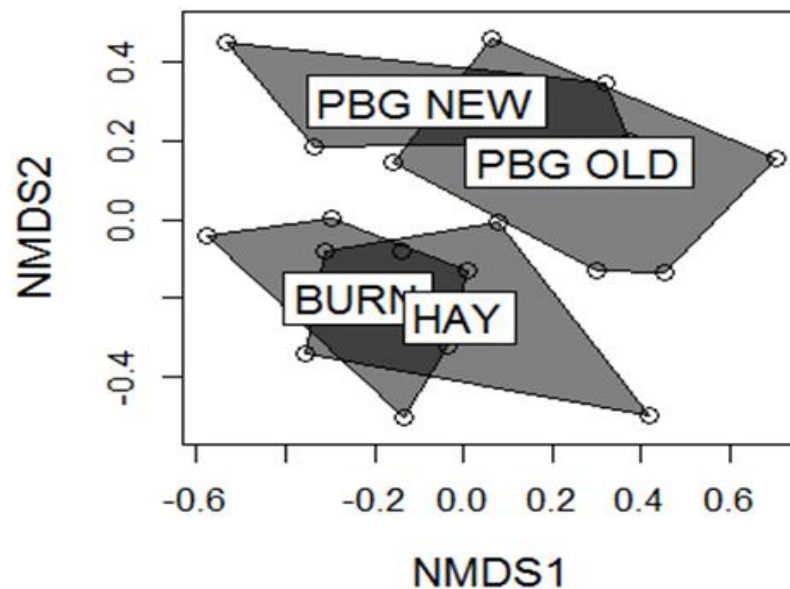


Figure 3. Non-metric multidimensional scaling (NMDS) of the floral communities in prairie ecosystems based on management type. An NMDS is a graphical representation of the relationships among management techniques through an overlay of plant species. NMDS views the communities in a high-dimensional space by displaying the strongest structure based on an $n \times n$ distance matrix that eliminates stress, or the measure of departure from monotonicity in the relationship between dissimilarity, which is represented by distance within and between the clusters. The prairie management types are burn, hay, and patch-burn-graze (PBG). PBG new was burned within the year of sampling and PBG old was burned more than two years before sampling. PBG supports cattle. The sites are clustered by management technique, and are associated closely as two distinctive groups which include sites that were grazed and sites that were ungrazed, suggesting that the floral communities structure are different.

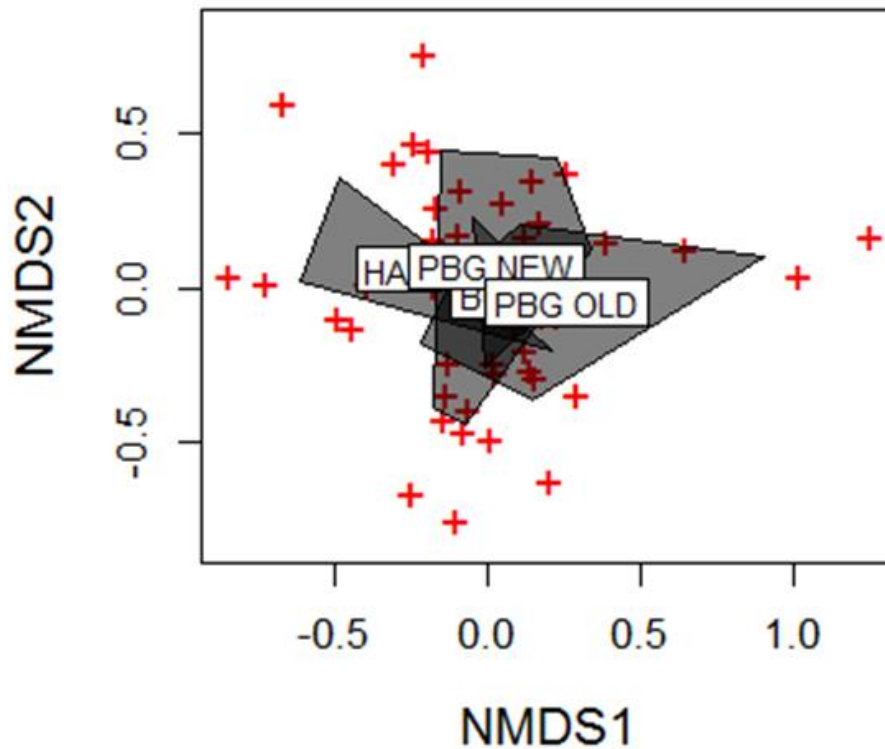


Figure 4. Non-metric multidimensional scaling (NMDS) of the bee communities in prairie ecosystems based on management type. An NMDS is a graphical representation of the relationships among management techniques through an overlay of bee species. The communities are viewed in a high-dimensional space by displaying the structure with the smallest departure from monotonicity in the relationship between dissimilarity. NMDS represents distance within and between the clusters. The prairie management types are burn, hay, and patch-burn-graze (PBG). PBG new was burned within the year of sampling and PBG old was burned more than two years before sampling. PBG supports cattle. The sites are clustered by management technique and overlaying, suggesting that the floral communities structure are very similar.

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CHAPTER 2: EFFECTS OF LAND MANAGEMENT ON SOIL CHARACTERISTICS AND NESTING DYNAMICS OF WILD BEES

Abstract

Most wild bee research has been conducted on the relationship between bee community structure and their floral resources, however, most bee species only live as adults for four to six weeks and much of their lives are spent as immatures in underground nests. Therefore, soil characteristics likely play an important role in nesting rates in prairie ecosystems. Moreover, management techniques that affect important soil habitat characteristics such as temperature, moisture, pH level, bulk density, bare ground, and soil types, could have a large effect on bee community structure. In this study, I measured soil characteristics of prairies with four management types (hay, burning, PBG-new, and PBG-old) and related them to ground-nesting bee nesting rates as measured with emergence tents. Sites without cattle supported higher nesting rates compared to sites with grazers. This difference could be due to lower soil moisture, lower top bulk density, higher pH, and more bare ground in the ungrazed sites compared to soil on sites that supported cattle.

Introduction

Unmanaged native pollinators are effective contributors to pollination services in managed systems (Klein *et al.* 2007) and interest in wild bee conservation has increased with the decline of managed honey bees (Winfree 2010). While much work on bees focuses on their floral associations, nesting availability is considered more important for determining bee diversity, and bee guilds are based primarily on nesting characteristics (Potts *et al.* 2005). This is particularly true for the 80% of bee species that belong to the mining guilds that excavate cavities into bare ground and line the cavities with glandular secretions for water resistance (O'Toole and Raw 1991; Cane 1991). Despite the dominance of miner bee species, comparatively little is known about their requirements for nesting in the ground. They spend the majority of their life underground (Michener 1974), compared to the four to six weeks of the year when they are active as adults (Cane and Neff 2011). With such a large proportion of wild bees nesting in soils, soil characteristics have the potential to influence bee community structure (Potts *et al.* 2003) and miner abundance within the community (Cane 1991).

The structure of floral communities and their associated foraging rewards are generally accepted as the primary drivers for local bee community structure, and nesting resources are not equally recognized as important (Petanidou and Ellis, 1996; Potts *et al.* 2003), and while it is known that bee nesting rates can be affected by certain soil characteristics (e.g., Cane 1991), there are few studies investigating the role of nesting resources in determining nesting rates, resulting in a paucity of knowledge regarding the nature of nesting preferences (but see Cane 1991; Willmer, 1997; Wuellner 1999; Potts *et al.* 2005 Potts; and Sardinas and Kremen 2014). More than 20 years ago, Cane (1991) suggested that future direction for understanding bee nest site selection should include investigation of surface temperature and soil texture. For example, Cane (1991) discovered that bees did not nest in clay or silt soils and bees in the genera *Colletes*,

Halictus, *Andrena*, *Perdita*, *Hesperapis*, and *Habropoda* primarily nested in sandy soils. Other potential important soil characteristics for ground-nesting bee nesting rates include soil hardness, or bulk density (Potts and Willmer, 1997; Wuellner 1999; and Sardinas and Kremen 2014), soil moisture (Wuellner 1999), the availability of bare ground (Potts *et al.* 2005), and possibly pH (Potts and Willmer 1997). For example, grazing can increase soil bulk density through compaction (Van Haveren 1983) and indirectly deter ground nesters.

Tallgrass prairies are highly endangered representations of the native landscape that has been lost due to habitat fragmentation, which is the leading cause of global pollinator decline (Thomas *et al.* 2004). Burning is a common management technique, however, most ground-nesting bees survive these fires because they place their offspring 10 cm or more underground, where they are safe from the heat of the fires (Cane and Neff 2011). Active management is essential for restoring and maintaining prairies, but the changes to soil characteristics are relatively unknown. Changes in the soil due to management techniques may affect bee community nesting and persistence in sites.

I investigated the effects of management techniques on certain soil characteristics and the relationships between management techniques and ground-nesting bee nesting rates. I predicted that nesting rates will be lower on sites with cattle due to higher bulk density and lower pH compared to similar sites without cattle. Bee emergence tents will collect ground-nesting bees and allow me to identify nesting rates and collect soil cores from under the emergence tents to identify optimal soil characteristics for ground-nesting bees. Additionally, I predict the length of time since last burning should affect bee nesting rates through changes in the plant communities in locations that practice patch-burn-grazing (PBG). The time of burning was investigated within independent units of PBG. PBG-new was burned within the year of sampling and PBG-old was

burned over two years prior to sampling. Sections of those prairies may show different soil characteristics between units based on the duration of time since the last burning treatment.

Methods

I sampled 20 1 ha prairie sites under three different management techniques--burned, hayed, and PBG--in southeast Missouri (Table 1). The PBG sites were divided into two-categories (PBG-new: <1 year post fire, and PBG -old: >2 years post fire) to further investigate the effect of time since burning for a total of four treatments. The sites were sampled in June, 2014. The 20 sites were located within twelve different prairies and separated by a minimum of 300 m to maintain independence between samples. The 20 sites were subdivided into five groups that included one of each of the four treatments. The groups were chosen based on management type, geographic location, and size to control for differences among sites due to climate and soil conditions. Nesting rates from one site was excluded from this study because the emergence tents blew over during a storm.

Bee nests were sampled using bee emergence tent traps (BugDorm Model No BT2006) (Figure 5). Fifteen ground emergence tents were installed in a randomly chosen area within each site at or after 7 pm when bee activity decreased significantly. Each tent was staked down and covered with soil to prevent overturning and limit insects crawling out of the tent, as was done by Sardinas and Kremen (2014). A kill jar filled with soapy water was attached to the top of each tent (Figure 5). Bee specimens were collected the following afternoon and the tents were dismantled. To limit cattle damage to tents in PBG sites, two Gallagher Smart Fences (Model No 2) and Gallagher Portable Fence Energizers (Model No s17) were erected around a randomly chosen area within each unit of the site (Figure 6). I identified the bees to species (Arduser 2014) and local bee expert, Micheal Arduser of the Missouri Department of Conservation verified the identifications.

Soil Sampling

As tents were removed, soil cores which were two cm in diameter and 30 cm deep were taken from the center of the ground under each tent using a backsaver (JMC dry PN007). This depth was chosen because the average minimum cell depth for bee nests is 17 ± 26 cm (Cane and Neff 2011). The soil core was divided evenly and labeled as top soil and bottom soil for laboratory analyses, including pH, bulk density, and soil type; this division was made because the top soil layer is more vulnerable to environmental degradation. Temperature and moisture levels were recorded for the top three cm of the soil and at the bottom of the soil core using a Cooper ATKINS® digital thermometer (Model No DPP800W) and an EXTECH® Soil Moisture Meter (Model No MO750). Ambient air temperature was also recorded using a Kestrel® Pocket Weather® Meter (Model No 3000) to determine temperature differences between air, surface soil and bottom soil. In some cases, soil sampling was incomplete due to an inability to collect a full 30 cm soil core preventing analyses of bottom soil characteristics, with soil being too dry and crumbling, preventing bulk density, pH, or soil type measures. Additionally, bare ground ranks were taken from under each emergence tent. The scale ranged from 0 to 4, with 0 as no bare ground, 1 as less than 25%, 2 as more than 25% but less than 50%, 3 as more than 50% but less than 75%, and 4 as more than 75% bare ground.

Laboratory Soil Tests

The soil cores were placed in bags and brought into the laboratory. The bags remained open for the first month (20°C, about 45% humidity) to reduce the moisture content within the soil cores. After this period, three tests were conducted on each top and bottom section of every core to determine soil composition, pH, and bulk density. To determine soil composition, 15 g of soil was added to 15 mL of distilled water and shaken vigorously. The soil slurry sat overnight

and developed well-defined layers of clay, silt, and sand in that order. After 24 hours, a soil triangle, as used in Cane (1991), was utilized to determine the soil type of each soil core half. Ten grams of the top and bottom soil cores were placed in 10 mL of distilled water, shaken, and allowed to sit for 15 minutes before testing the soil slurry's pH using a pH meter (Mettler Toledo Model No S220). Finally, exactly 2 cm of the full core was cut and weighed before drying in a laboratory oven (Heratherm IMH 180) for 24 hours at 105°C to remove moisture. After 24 hours, the 2-cm core was weighed again (Soil and Plant Analysis Council 1992; Carter 1993). Bulk density values were recorded as g/cm³. All soil variables and methods are shown in Table 4.

Statistical methods

One-way analysis of variance was used to test for differences among the four management treatments in soil characteristics, including differences specifically between the PBG-new and PBG-old techniques. Comparisons of means were conducted on collapsed site types, with two categories, grazed (burned and hayed sites) and ungrazed (PBG-new and PBG-old). The comparisons were employed to determine if the soil characteristics changed significantly if cattle were supported by the prairie, or if the prairie was just burned or hayed.

A graphical representation of the relationships among groups through an overlay of characteristics called a non-metric multidimensional scaling (NMDS) was used to visualize the soil types of the top soil cores in the four management types included in this study: hay, burn, PBG-new, and PBG-old. NMDS views the characteristic in a non-multidimensional space by displaying the strongest structure based on an $n \times n$ distance matrix that eliminates stress, or the measure of departure from monotonicity in the relationship between dissimilarity, which is represented by distance (McCune *et al.* 2002).

Results

Age of burning affected the soil temperature, moisture, and bare ground ranking. The soil temperature highly varied among treatments (top soil: ANOVA, $F=39.03$, $DF=3$, $p>0.001$, $N=300$; bottom soil: ANOVA, $F=15.14$, $DF=3$, $p>0.001$, $N=289$) for both top and bottom soil (Figure 7). The soil moisture was also different between treatments (top soil: ANOVA, $F=13.8$, $DF=3$, $p>0.001$, $N=300$; bottom soil: ANOVA, $F=3.78$, $DF=3$, $p>0.001$, $N=288$). There was more bare ground in PBG-new compared to PBG-old (ANOVA, $F=33.30$, $DF=3$, $p>0.001$, $N=300$). However, soil pH and bottom bulk density were similar among treatments.

The presence of cattle influenced top soil moisture (t-test, $t=2.89$, $DF=298$, $p>0.004$, $N=300$) and top soil bulk density (t-test, $t=2.22$, $DF=240$, $p>0.03$, $N=242$), both were higher in sites that supported cattle. In contrast, top soil pH (t-test, $t=5.36$, $DF=296$, $p>0.001$, $N=298$) and bare ground ranks (t-test, $t=2.77$, $DF=298$, $p>0.006$, $N=300$) were both lower in sites that supported cattle (Table 5). The means and standard deviations for the soil characteristics are shown in Table 5 for the different site types.

Sandy loam was the most frequent soil type for the top 15 cm across management types (Figure 8). Burned and PBG-new sites had sandy loam as the most dominant soil type on the bottom soil cores as well, however, the remaining two management treatments had mostly silt loam soil type (Figure 8). Other top soil types identified were loam, silt loam, and loamy sand. The distribution of top soil types is similar to the types in the bottom soil core samples except loamy sand is replaced with sandy clay loam. The overlap in the NMDS plot visually confirms the similarity of the top soil types between management methods (Figure 9).

As similarly reported by Sardinas and Kremen (2014), most bees collected using the emergence tents were in the genus *Lassioglossum* including *L. coreopsis*, *L. hitchense*, *L. tegulare*, *L. disparile*, and *L. lustrans* (Table 6). The range of soil characteristics recorded for the

soil cores collected from under the emergence tents that captured bees is reported in Table 7. The percentage of emergence tents with bees at each site across the treatment techniques ranged from 0% to 33% (Figure 10) and one-way analysis of variance suggests that the grazed locations had a lower capture rate than ungrazed sites (ANOVA, $F=2.514$, $DF=18$, $p>0.02$, $N=19$) (Figure 11), however the age of burning within the PBG treatments did not affect nesting rate.

Discussion

Most bees nest in the ground for the majority of their lives (O'Toole and Raw 1991; Cane 1991). Therefore, certain soil characteristics such as temperature, moisture, bulk density, pH, soil composition, and bare ground ranking could impact the nesting rates of ground-nesting bees. Prairie management techniques, such as, burning, haying, and PBG, have the potential to alter important soil characteristics and nesting rates for ground-nesting bees. I found that the ground-nesting bee nesting rates were lower in PBG sites compared to ungrazed sites and nesting rates on PBG sites did not differ depending on the time of burning as predicted.

The greater nesting rate observed in ungrazed sites suggest that the soil characteristics in these prairies are more attractive to ground-nesting bees compared to the soil characteristic found in grazed sites. Cattle could impact bee communities by altering their nesting resources. The soil collected from grazed sites was characterized by higher soil moisture, higher top soil bulk density, more acidic top soil, and decreased bare ground ranking. Therefore, my first hypothesis was supported. A study conducted by Sardinas and Kremen (2014) suggests that bees prefer soft soils for nesting, which is also supported in this study. My study also supports the observation that nesting rates increase with bare ground ranking, as was shown by Potts *et al.* (2005).

PBG-new and PBG-old sites had different temperatures of soil and moisture percentages of soil. The newly burned PBG sites had higher top and bottom temperatures compared to sites that were burned over two years before sampling and showed lower moisture percentages. These differences did not seem to affect nesting rates. Therefore, the hypothesis that nesting rates would be higher in newly burned patches compared to patches burned over two years before sampling was not supported. The overall low nesting rate in PBG sites suggests that grazing may negatively affect bee nesting and thus limit the response to temperature and moisture.

Although grazing is considered a suitable method for maintaining prairies, it could destabilize bee communities by reducing nesting and overall fecundity of species nesting in grazed sites. Cattle could increase soil bulk density by compacting the soil over time under their weight, lower pH with their waste, and even trample suitable nesting sites and destroy nests that have already been excavated into the ground (Potts *et al.* 2005; Tadey 2015). This makes solitary bee nests especially vulnerable to habitat degradation caused by cattle (Potts *et al.* 2005). In order to support diverse bee communities and the pollination services they provide, successful management techniques should aim to provide both foraging resources and nest site availability (Potts *et al.* 2005).

Acknowledgments

I would like to thank the invaluable field researchers Nicholas Anderson and Nicole Wonderlin, the soil analyzers, Christina Vercillo and Jonathan Balthazar, and the bee species identifiers, Keelan Lang and local bee expert, Michael Arduser. Special thanks to Cem Kuru for his positive energy and encouraging me throughout this project and Dr. Brenda Molano-Flores for helping me think-through each step of this project. I also thank the Missouri Department of Conservation for the protection of nature and sampling permission. The University of Illinois at Urbana-Champaign funded this project.

Tables and Figures

Table 4. Definition and methods for measuring nesting resources in Missouri Department of Conservation Prairies. Top refers to the top 15 cm of the soil core and bottom refers to the bottom 15 cm of the soil core that was removed from under the emergence tents in the field.

Resource	Method	Field/Lab
temperature top	thermometer	field
temperature bottom	thermometer	field
moisture top	moisture meter	field
moisture bottom	moisture meter	field
bare ground rank	0-4 rank, with 0 being no bare ground	field
pH top	pH meter	lab
pH bottom	pH meter	lab
bulk density top	heated soil 105°C overnight, weighed in grams	lab
bulk density bottom	heated soil 105°C overnight, weighed in grams	lab
soil type top	added distilled water, let sit 24 hrs, soil triangle	lab
soil type bottom	added distilled water, let sit 24 hrs, soil triangle	lab

Table 5. Summary table for soil characteristic at each management type (values are mean $\pm$ standard deviation). Prairie management types include burn, hay, and patch-burn-graze (PBG). PBG prairies were separated into independent units based on the time of burning, PBG-new (burned within the year of sampling) and PBG-old (burned more than two years before sampling). The subscripted letters signify differences between treatments for each soil characteristic. The soil characteristics were not different between management techniques if they share a subscripted letter. If the letters are different, the analysis of variance detected significant differences.

	Top Soil Temp (°C)	Top Soil Moisture %	Top pH	Top Bulk Density g/(cm ³)	Bare Ground Rank
Burn	25.87 $\pm$ 2.22 ^a	8.89 $\pm$ 4.3 ^a	5.73 $\pm$ 0.52 ^a	1.35 $\pm$ 0.21 ^a	1.67 $\pm$ 1.14 ^{a,b}
Hay	24.54 $\pm$ 0.01 ^b	10.91 $\pm$ 0.03 ^b	5.56 $\pm$ 0.01 ^{a,b}	1.48 $\pm$ 0.01 ^{a,b}	1.27 $\pm$ 0.01 ^a
PBG-new	27.02 $\pm$ 1.77 ^c	9.97 $\pm$ 2.09 ^{a,b}	5.36 $\pm$ 0.34 ^c	1.53 $\pm$ 0.24 ^b	1.85 $\pm$ 1.11 ^b
PBG-old	24.19 $\pm$ 1.99 ^{b,d}	11.97 $\pm$ 3.14 ^c	5.38 $\pm$ 0.36 ^{b,c}	1.48 $\pm$ 0.26 ^{a,b}	0.35 $\pm$ 0.6 ^c

	Bottom of Soil Core Temp (°C)	Bottom of Soil Core Moisture %	Bottom pH	Bottom Bulk Density g/(cm ³)
Burn	24.24 $\pm$ 1.55 ^a	9.46 $\pm$ 4.09 ^{a,b}	5.52 $\pm$ 0.48 ^a	1.58 $\pm$ 0.29 ^a
Hay	23.95 $\pm$ 0.02 ^a	9.82 $\pm$ 0.04 ^{a,b}	5.22 $\pm$ 0.01 ^b	1.65 $\pm$ 0.01 ^a
PBG-new	24.84 $\pm$ 1.14 ^b	8.89 $\pm$ 3.3 ^a	5.36 $\pm$ 0.26 ^c	1.72 $\pm$ 0.34 ^a
PBG-old	23.38 $\pm$ 1.49 ^c	10.75 $\pm$ 3.67 ^b	5.33 $\pm$ 0.2 ^{b,c}	1.56 $\pm$ 0.43 ^a

Table 6. Bee species collected using emergence tents (BugDorm Model No BT2006) on prairies.

The prairie management consists of burn, hay, and patch-burn-graze (PBG). The PBG support cattle and are separated into two groups depending on the time of burning, PBG-new (burned within the year of sampling) and PBG-old (burned more than two years before sampling).

Site	Management	Bee Species	Abundance
Twenty-Five Mile	burn	<i>Lasioglossum coreopsis</i>	5
		<i>Lasioglossum hitchense</i>	2
		<i>Lasioglossum tegulare</i>	1
Mon-Shon	burn	<i>Lasioglossum disparile</i>	1
Niawathe A	burn	<i>Lasioglossum coreopsis</i>	6
		<i>Lasioglossum disparile</i>	1
Niawathe B	burn	<i>Lasioglossum coreopsis</i>	3
Buffalo Hay	hay	<i>Lasioglossum coreopsis</i>	6
		<i>Lasioglossum disparile</i>	2
Mon-Shon	hay	<i>Lasioglossum disparile</i>	4
Wah'Kon-Tah	PBG-new	<i>Augochlorella aurata</i>	1
Taberville	PBG-old	<i>Lasioglossum coreopsis</i>	1
		<i>Lasioglossum lustrans</i>	1
		<i>Lasioglossum lustrans</i>	1
Wah'Kon-Tah	PBG-old	<i>Andrena rudbeckiae</i>	1

Table 7. Range of soil characteristics. Soil cores and bare ground ranks were taken from under emergence traps that collected ground-nesting bees in prairies. Top refers to the top 15 cm of the soil core and bottom refers to the lower 15 cm. Bulk density is similar to compaction and bare ground rank ranged from 0-4, with 4 being all bare ground, and 0 being no bare ground or covered entirely by vegetation.

Top Soil Temp (°C)	Top Soil Moisture (%)	Top pH	Top Dry Weight (g)	Top Bulk Density g/(cm ³)	Bare Ground Rank
21.2-33.9	0.1-19	4.76-6.18	5.04-11.4	1.11-2.51	0-3
Bottom Temp (°C)	Bottom Moisture (%)	Bottom pH	Bottom Dry Weight (g)	Bottom Bulk Density g/(cm ³)	
21-28.8	0.2-15.4	4.62-5.99	5.36-9.59	1.18-2.11	



Figure 5. Emergence tent. Ground-nesting bees are collected using emergence tents (BugDorm Model No BT2006). Each tent includes a kill jar filled with soapy water. The tents were securely staked down with metal flags and weighed down by soil on the edge flaps at dusk, when the foragers had returned to their nests. The ground-nesting bees were preserved in ethanol and the emergence tents were disassembled at 1:00 pm the following day.



Figure 6. Cattle and electric fences. Gallagher Smart Fences (Model No 2) and Gallagher Portable Fence Energizers (Model No S17) were used in patch-burn-graze (PBG) sites. The cattle in PBG sites were very interested in the emergence tent traps. I used portable electric fences and solar powered batteries to dissuade the cattle from trampling the emergence tents while they were left out overnight.

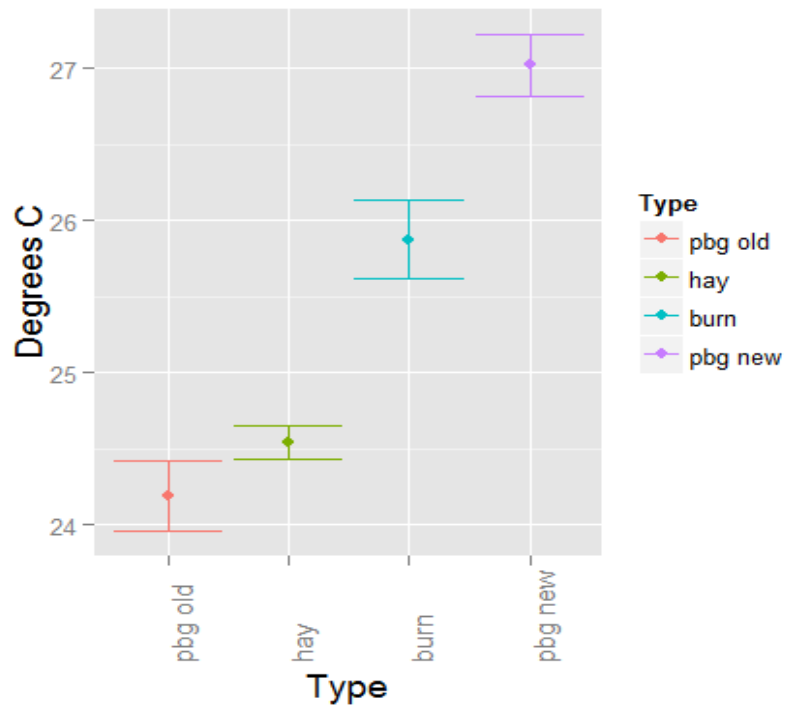
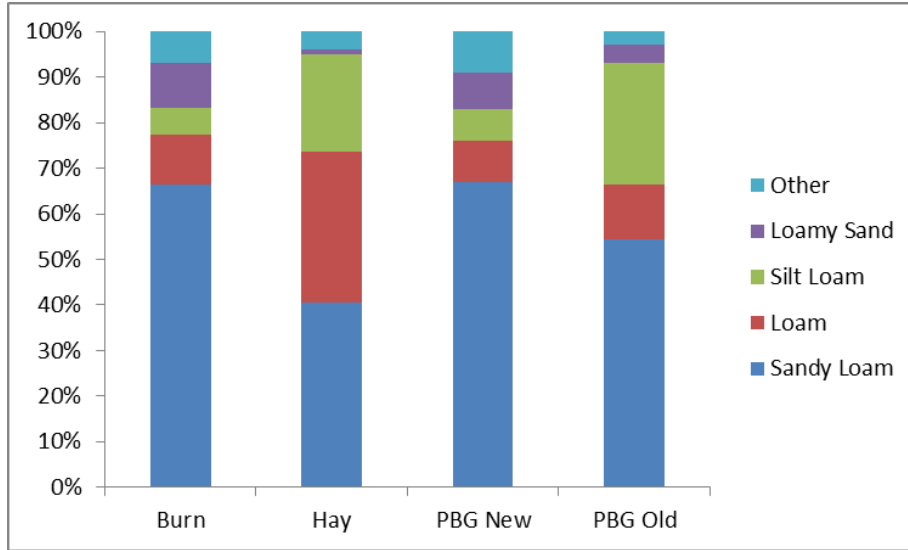
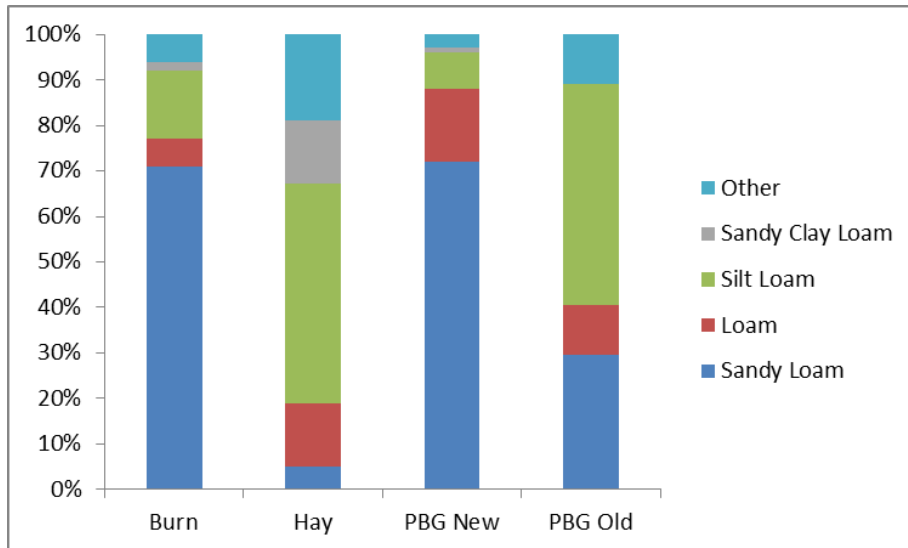


Figure 7. Top soil temperature in °C. Mean temperatures were different between prairie management techniques (ANOVA, $F=39.03$, $DF=3$, $p>0.001$, $N=300$). Management techniques include hay, burn, and patch-burn-graze (PBG). PBG was separated into independent units based on time of last burning, PBG new was burned within the year of sampling, and PBG old was burned more than two years before sampling.



(A)



(B)

Figure 8. Soil types based on the soil triangle technique used by Cane (1991). Figure A is top soil and B is bottom soil types. Management techniques include hay, burn, and patch-burn-graze (PBG). PBG was separated into independent units based on time of last burning, PBG New was burned within the year of sampling, and PBG Old was burned more than two years before sampling.

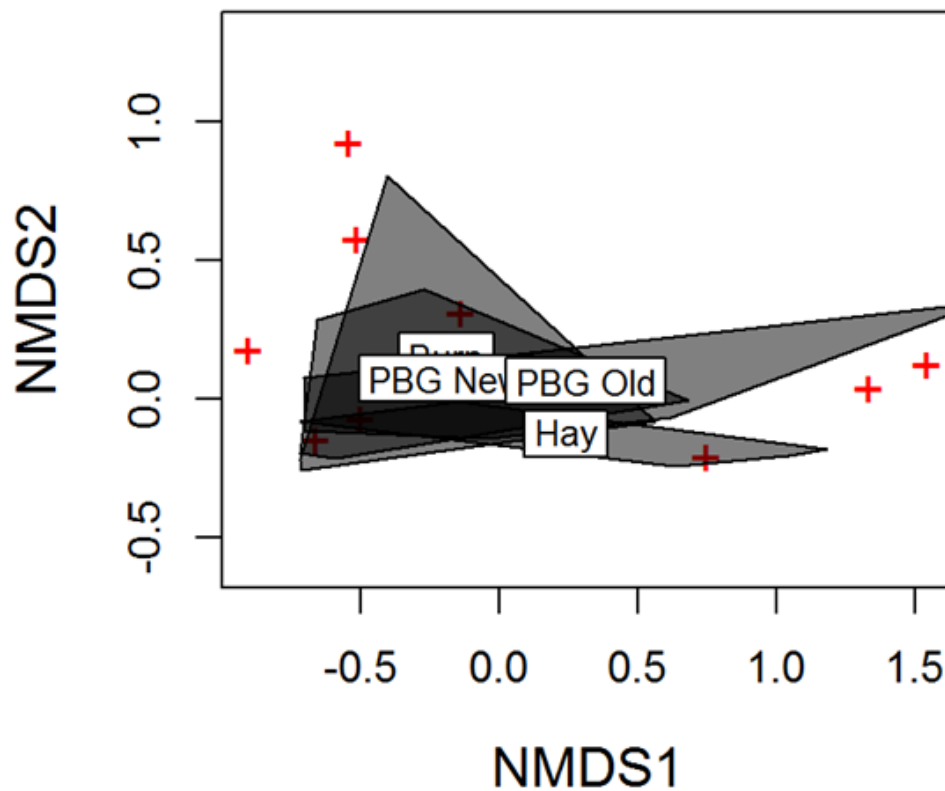


Figure 9. Non-metric multidimensional scaling (NMDS) of the soil types for the top 15 cm of the soil cores taken from prairies. NMDS is a graphical representation of the relationships among management techniques through an overlay of soil types (see Cane 1991). The communities are viewed in a high-dimensional space by displaying the structure with the smallest departure from monotonicity in the relationship between dissimilarity. The management techniques form clusters around the associated soil types. The prairie management types are burn, hay, and patch-burn-graze (PBG). PBG new was burned within the year of sampling and PBG old was burned more than two years before sampling. The clusters overlap, suggesting similarity between the top soil types of each management treatment.

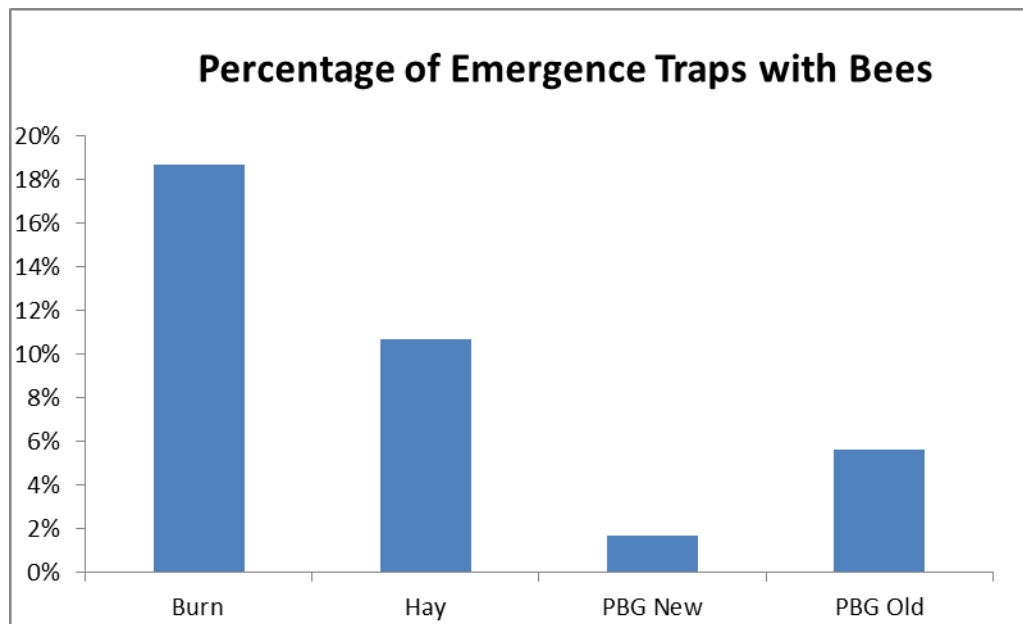


Figure 10. Percentage of emergence traps (BugDorm Model No BT 2006) that collected ground-nesting bees at each site type. The prairie management types are burn, hay, and patch-burn-graze (PBG). PBG supports cattle. PBG new was burned within the year of sampling and PBG old was burned more than two years before sampling.

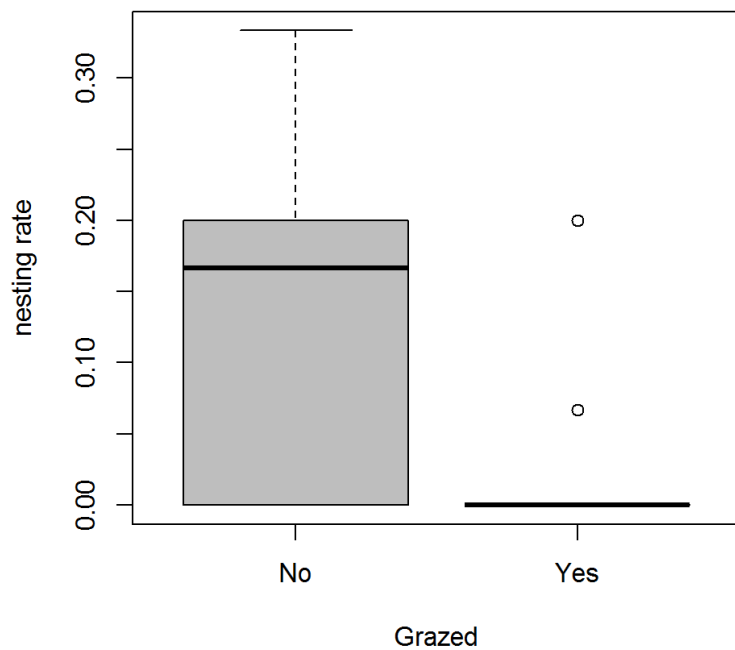


Figure 11. Comparison of nesting rates in grazed and ungrazed sites. Analysis of variance detects that the nesting rates on prairies that were grazed are significantly different compared to prairies that were not grazed. Sites without cattle showed a higher ground-nesting bee nesting rate compared to the sites with grazers (ANOVA, $F=2.514$, $DF=18$, $p>0.02$, $N=19$).

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CHAPTER 3: NEW RECORDS FOR THE BEE SPECIES *MACROPIS STEIRONEMATIS* IN MISSOURI

The *Melittidae* comprises a relatively small family of ground-nesting, oil-collecting bees, with 200 described species worldwide (Michez and Patiny 2005; Michez and Eardley 2007; and Ascher *et al.* 2008). Only a few records of these bees are from the United States. *Macropis* Panzar 1809 is one of 14 genera in *Melittidae* (Michener 2000). *Macropis* includes 16 species (Michener 1981). Specifically, Snelling and Stage (1995) reported *Macropis steironematis* Robertson 1891, in North America. Although Mitchell (1960) recorded the distribution of *M. steironematis* to be from Iowa and Missouri, east to Virginia, North Carolina and Georgia, few specimen records exist for this species, including none from Missouri. Robertson (1981) recorded finding the species in Missouri, but did not voucher a specimen. Marlin and LaBerge (2001) resampled Robertson's sites in Carlinville, Illinois and did not find *M. steironematis*.

On June 19, 2014, a female *M. steironematis* (Figure 12) was collected while it was foraging on *Rosa carolin.*(*Rosaceae*). Previously, this species had been recorded foraging only on *Apocynum cannabinum* (*Apocynaceae*), *Ceanothus americanus* (*Rhamnaceae*), *Lysimachia* (= *Steironema*) sp. (*Primulaceae*), *Melilotus alba* (*Fabaceae*), and *Seriocarpus lineifolius* (*Asteraceae*) (Mitchell 1960). I collected a specimen of this species from Stony Point Prairie Conservation Area (37° 31.640', -94° 01.688'), which is managed by the Missouri Department of Conservation (MDC) using a technique called patch-burn grazing (PBG). This technique requires dividing the division of the prairie into patches, then rotationally burning one patch each year. The patch of prairie where *M. steironematis* was collected was burned more than two years before the collection date. Stony Point Prairie supports cattle that are stocked at a rate on the lower end of moderate, according to the MDC (Kurz 2010). I found PBG sites to have low flower abundance and low nesting frequency for mining bees (Chapter 1 of this thesis),

suggesting that this species may be robust to disturbance in view of the fact that it was not captured in any nearby ungrazed sites. Collection of this individual indicates that *M. steironematis*, a Great Plains species, is still present in Missouri.

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Figure



Figure 12. *Macropis steironematis* Robertson 1891 was collected from Stony Point Prairie Conservation Area (37° 31.640', -94° 01.688') on June 19.VI.14 (photo by Horace Zeng).

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