

Providing for pollinators: conserving and integrating natural habitats to support pollinator
conservation efforts

by

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Abstract

Pollinators have been in decline for at least the past four decades due to habitat loss from agricultural intensification. Natural pollinator habitat, such as tallgrass prairies, have shrunk to less than 10% of their original extent. Because over one-third of food crops are completely pollinator-dependent, we are under the threat of food instability if pollinator decline is not stabilized and improved. Additionally, little work has been done in terms of understanding how different land management strategies, such as fire rotations or native flower plantings, impact different groups of pollinators, such as bees and butterflies. In an effort to address these issues, I implemented a two-year study on the impact of conservation and ecological intensification strategies on pollinators. My objectives were to 1) understand how fire and grazing management on a prairie reserve impacts the pollinator community and 2) examine how land managers can attract and provide for pollinators in an agricultural setting through the implementation of perennial border crops.

For my first objective, I found that bison grazing had positive effects on nearly all pollinators, from lepidopterans to ground-nesting bees, while different fire rotations had both positive and negative effects on pollinators through different pathways. I also found that both fire and grazing had significant impacts on pollinator habitat, such as soil characteristics and forb species richness. In an agricultural setting, I found that pollinators in general were most attracted to diverse, flowering border crops such as prairie mixes, as well as native sunflower species planted in a monoculture. Besides crop treatment, we also found that “year” had a significant impact on pollinators, indicating that establishment periods of crops need to be taken into consideration. These findings offer valuable insight into the impacts of different land

management strategies on different pollinator groups, and provide landowners such as farmers and restoration biologists, more information about how their management practices may affect specific pollinator groups.

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Dedication

I dedicate this thesis to my aunt, Karen Jean Thompson, or as we like to call her, Aunt Bean. Keep fighting the good fight. You have supported my education and career choices in every way possible, from taking me to science museums in the summer as a kid, to studying abroad in college, to my time here in Kansas. You've sent me pamphlets on job descriptions for everything from geologists to park rangers. You were the first to take me camping. You are an incredible woman. We always hope to have more time together. Whatever comes to be, know that you have made a difference in the time you were here, and helped guide me in the direction of where I belong. As always, "Love you bunches!".

Introduction

Pollinators have become a focus for conservation efforts due to their recent declines and the loss of their natural habitat, mainly due to agricultural intensification (Kremen et al. 2002, and as reviewed by Bommarco et al. 2013). Thirty-five percent of the world's food crops rely upon pollinator services, and their decline consequently imperils the stability of our global food systems (Klein et al. 2007). It is estimated that pollinators alone provide billions of dollars' worth of services per year, such as increased yields and seedset (Calderone 2012). However, current agricultural practices are impeding this service and the benefits it provides to crop yields (Kremen et al. 2002, Klein et al. 2003, Calderone 2012). In order to address the connected issues of pollinator conservation and food security, it is imperative to 1) implement sustainable land management strategies that conserve natural land and 2) integrate natural habitat into agricultural systems to support pollinators and pollination services. To address these needs, my objectives were to 1) understand which fire and grazing strategies best support the pollinator community in a natural setting and 2) examine how land managers can attract pollinators from natural areas to their fields through the implementation of perennial border crops.

To address the first objective, I implemented a two-year study examining the direct and indirect effects of fire and grazing (common land management practices for natural grasslands) on pollinator foraging and nesting habitat, and the impact the habitats had on separate pollinator taxonomic groups. While many studies have measured the impacts of fire and grazing on the floral resources of pollinators, few studies have focused on the impacts of fire and grazing on the nesting-resources of pollinators, especially below-ground nesting bees (Harmon-Threatt 2020). This is a major oversight in efforts to understand how to aid declining pollinator populations,

especially when considering that most bees (above 70%) nest below-ground (Vaughan and Black 2007). The specific responses of different pollinator groups, such as butterflies and bees, to habitat changes is also unclear. Some studies have found that bees and lepidopterans respond similarly to management, such as grazing, while other studies have found pollinator groups respond in opposing ways (Sjödín et al. 2008, Davis et al. 2008, Kimoto et al. 2012). The first objective attempts to untangle these responses to understand how management practices affect different pollinator groups, and how they support wild pollinators and the services they provide.

My second objective was addressed by a two-year study in partnership with The Land Institute, a non-profit research organization with a mission to develop perennial crop systems. Perennial flowering plants provide excellent resources for pollinators, as they provide foraging resources and require less management, consequently providing undisturbed habitat. Growing natural habitats such as this near agricultural fields may mitigate the harmful effects of intense agricultural practices on beneficial insects by providing foraging and nesting resources to pollinators. One way of including these natural habitats in an agricultural setting is through the implementation of border crops, also known as hedgerows, on nonarable land such as grass waterways and field buffers. Providing natural habitat adjacent to agricultural fields facilitates pollinator spillover, allowing wild pollinators to provide up to 100% of crop pollination needs (Kremen et al. 2002, Winfree et al. 2008, Blaauw and Isaacs 2014).

In order to stabilize our global food security, we need to develop land management practices at the intersection of conservation and agriculture. Finding practices that benefit both the natural landscape and agricultural production will be the most sustainable and desirable practices, as they will be more readily adopted by growers and will benefit the natural areas that provide the pollination services. I believe my objectives have satisfied these requirements, and

offer valuable insight into beneficial land management strategies, and their specific effects on pollinator habitat and different pollinator groups.

Literature Cited

- Blaauw, B. R., and R. Isaacs. 2014. Flower plantings increase wild bee abundance and the pollination services provided to a pollination-dependent crop. *Journal of Applied Ecology* 51:890–898.
- Bommarco, R., D. Kleijn, and S. G. Potts. 2013. Ecological intensification: harnessing ecosystem services for food security. *Trends in Ecology & Evolution* 28:230–238.
- Calderone, N. W. 2012. Insect Pollinated Crops, Insect Pollinators and US Agriculture: Trend Analysis of Aggregate Data for the Period 1992–2009. *PLoS ONE* 7:e37235.
- Davis, J. D., S. D. Hendrix, D. M. Debinski, and C. J. Hemsley. 2008. Butterfly, bee and forb community composition and cross-taxon incongruence in tallgrass prairie fragments. *Journal of Insect Conservation* 12:69–79.
- Harmon-Threatt, A. 2020. Influence of Nesting Characteristics on Health of Wild Bee Communities. *Annual Review of Entomology* 65:39–56.
- Kimoto, C., S. J. DeBano, R. W. Thorp, R. V. Taylor, H. Schmalz, T. DelCurto, T. Johnson, P. L. Kennedy, and S. Rao. 2012. Short-term responses of native bees to livestock and implications for managing ecosystem services in grasslands. *Ecosphere* 3:art88.
- Klein, A.-M., I. Steffan-Dewenter, and T. Tscharntke. 2003. Fruit Set of Highland Coffee Increases with the Diversity of Pollinating Bees. *Proceedings: Biological Sciences* 270:955–961.
- Klein, A.-M., B. E. Vaissière, J. H. Cane, I. Steffan-Dewenter, S. A. Cunningham, C. Kremen, and T. Tscharntke. 2007. Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B: Biological Sciences* 274:303–313.
- Kremen, C., N. M. Williams, and R. W. Thorp. 2002. Crop pollination from native bees at risk from agricultural intensification. *Proceedings of the National Academy of Sciences* 99:16812–16816.
- Sjödin, N. E. 2007. Pollinator behavioural responses to grazing intensity. *Biodiversity and Conservation* 16:2103–2121.
- Vaughan, M., and S. H. Black. 2007. Enhancing Nest Sites For Native Bee Crop Pollinators:4.

Winfree, R., N. M. Williams, H. Gaines, J. S. Ascher, and C. Kremen. 2008. Wild bee pollinators provide the majority of crop visitation across land-use gradients in New Jersey and Pennsylvania, USA. *Journal of Applied Ecology* 45:793–802.

Chapter 1 - Fire rotation and bison presence have indirect below- and above-ground effects on pollinator communities

Introduction

Insect pollinator biodiversity is currently under threat due to habitat loss and fragmentation (Williams et al. 2010, Calderone 2012, Powney et al. 2019). Native tallgrass prairies are ideal pollinator habitats due to the high abundance and diversity of floral resources. However, over 90% of the tallgrass prairie land cover has been lost since the arrival of Europeans to North America, with Homestead Act of 1862 setting off a chain of events leading to land use change from natural prairie habitat to agricultural fields (Kremen et al. 2002, Samson et al. 2004). Because pollinators are vitally important to our world food system (one-third of world crops require pollination), prairies have been the target of conservation efforts in the Midwest for the last 20 years (Samson and Knopf 1994, Klein et al. 2007). However, not all land management practices yield similar beneficial results for pollinators and plant species. For instance, past studies have shown that plant, bee, and butterfly communities respond differently to habitat shape, their response to overall landscape resources versus management strategies, and respond differently to different grazing intensities, (Kruess and Tscharntke 2002, Davis et al. 2008, Griffin et al. 2021). Therefore, as we continue to protect and restore grasslands, it is imperative that we understand how the management of these protected areas support wild pollinators and plant communities.

Tallgrass prairies are dependent upon disturbance, and are generally maintained through a combination of fire and grazing to impede woody encroachment and maintain a high floral

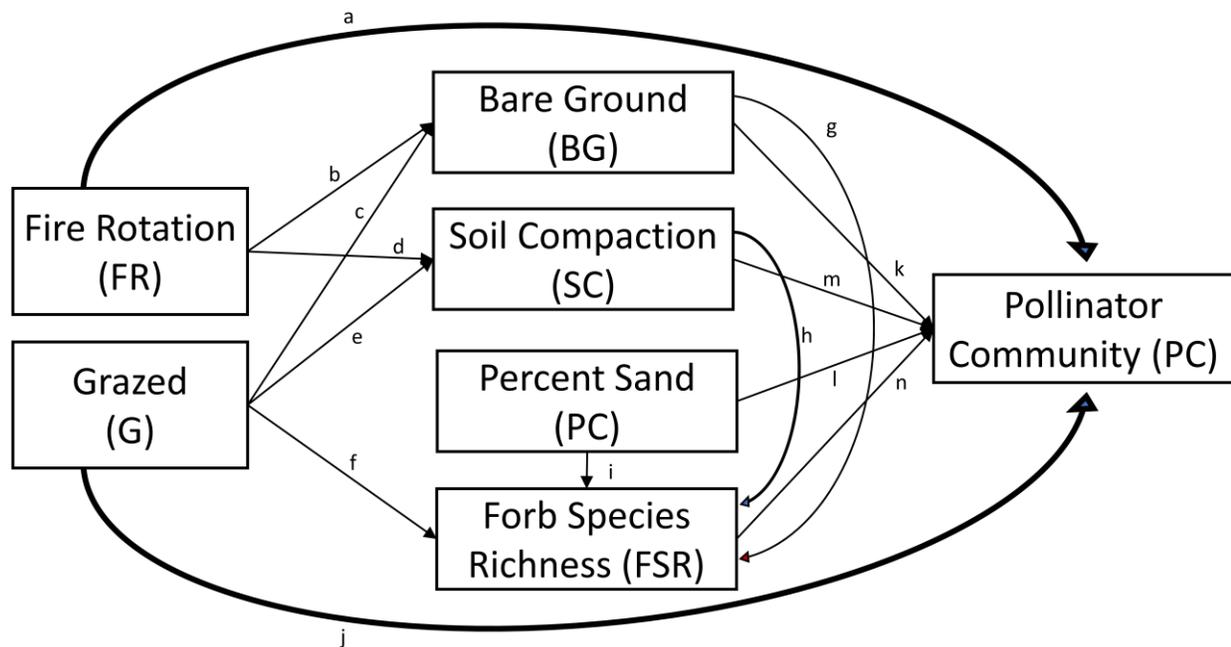
diversity (Knapp et al. 1999). However, it is unclear how often and to what intensity these two practices should be executed, and how they differentially affect different pollinator groups such as bees and butterflies. Some studies determined that frequent fires increase plant heterogeneity and diversity, and therefore benefit pollinator richness and abundance (Simanonok and Burkle 2019, Burkle et al. 2019, Carbone et al. 2019, Moylett et al. 2020). Other studies show that different fire rotations have no effect at all (Moranz et al. 2012, Carbone et al. 2019), or that infrequent burns have positive impacts on pollinators and floral resources (Collins and Calabrese 2012, Welti and Joern 2018), suggesting that fire should not be a tool used to benefit pollinators but simply a way to maintain prairies by discouraging woody encroachment. These different findings indicate that there must be a multitude of indirect effects that fire can have on pollinator communities, such as the plant community, the amount of vegetative cover, and its influence on grazing behavior (Vinton et al. 1993, Archibald et al. 2005, Collins and Calabrese 2012, Russell and Bisinger 2015, Buckles and Harmon-Threatt 2019, Burkle et al. 2019, Moylett et al. 2020). It also suggests that management strategies that benefit the native plant community may not necessarily benefit pollinators.

The impact of grazing is also unclear, with many studies claiming it a useful practice in maintaining plant and landscape diversity (Collins and Calabrese 2012, van Klink et al. 2015, Welti and Joern 2018). Grazing has consistently been associated with an increased amount of bare soil (Kimoto et al. 2012, van Klink et al. 2015, Elwell et al. 2016), which is known to be positively associated with successful bee nesting (Potts et al. 2005, Buckles and Harmon-Threatt 2019). However, some studies have still found grazing to have either negative effects or neutral effects on pollinator communities, and many found that grazing affected pollinator species differently (Kimoto et al. 2012, Minckley 2014, van Klink et al. 2015, Elwell et al. 2016,

Buckles and Harmon-Threatt 2019). It is clear that the combination of fire and grazing, along with their direct and indirect effects, is a complex management system needing more research.

Previous studies have focused on the impacts on floral resources or floral visitation networks, but few studies have compared and contrasted overall pollinator resource needs, especially for ground-nesting bees, which make up 70-80% of all bees (Vaughan and Black 2007, Harmon-Threatt 2020). For instance, bees may respond differently to an area’s soil characteristics and vegetation height than lepidopterans (Kruess and Tschardtke 2002). Our study attempts to add to the understanding of the nesting and foraging requirements of both lepidopterans and bees in reference to different combinations of common land management practices. We hypothesized the direct and indirect effects of fire and grazing through the following path analysis:

Figure 1.1. Hypotheses of the effects of fire rotation and bison presence on forb community, soil characteristics, and pollinator communities.



We hypothesize that fire directly affects bees through mortality (path “a”, Figure 1.1), and will increase the amount of bare ground within the burned area (path “b”). Consequently, fire effects will impact the plant community by removing established plant species and allowing less dominant plant species to grow (path “g”) and create nesting opportunities for ground-nesting bees, as seen in path “k” (Potts et al. 2005), ultimately impacting the pollinator community (path “n”). Areas utilizing different fire regimes may differ in soil composition as well, due to the differences in the amount and frequency of plant material decomposition (Turner et al. 2007). Soil composition, especially the presence of sand, has been shown to play an important role in the nesting requirements of ground-nesting bees, as they require soil types that can hold the integrity of the nest, yet be soft enough to excavate, which is indicated by path “l” (Potts and Willmer 1997, Sardiñas and Kremen 2014, Harmon-Threatt 2020). We also expect soil composition to affect the plant community (measured as forb species richness, path “i”, Fig. 1).

We also hypothesized that grazing would have direct and indirect impacts on pollinator communities (Figure 1.1). We hypothesize that grazing will increase soil compaction (path “e”) and the amount of bare ground (path “c”) (Vinton et al. 1993, Collins and Calabrese 2012, O’Keefe and Nippert 2017). These soil characteristics will similarly affect bee nesting densities, as previously mentioned, through paths “k” and “m”; soil compaction may help with nest integrity for gregarious nesting bees (Potts et al. 2005, Sardiñas and Kremen 2014). Because bison prefer to graze on grasses over forbs, we expect that this will release forbs from competition with grasses and allow more forb species to persist (path “f”), ultimately increasing pollinator floral resources (path “n”, Figure 1.1).

Few studies have teased apart the direct and indirect relationships between different members of the pollinator community in response to multiple land management strategies (Harmon-Threatt and Chin 2016). Understanding mechanisms by which fire and grazing practices affect pollinators will allow land managers to better target conservation and restoration efforts to support both natural areas and the pollinator community.

Methods

Location

We conducted our experiment at the Konza Prairie Biological Station (hereafter “Konza”), located in the Flint Hills of northeastern Kansas, near Manhattan (39°05'N, 96°35'W). Konza is a long-term ecological research site owned and operated jointly by Kansas State University and The Nature Conservancy since its inception in 1977, and consists of natural tallgrass prairie, mixed wood lots, and sections of riparian forest along with several small agricultural fields. The research sites are divided into 50 separate watersheds, each receiving a fire regime treatment (from 1-, 4-, or 20-year fire rotations) and grazing treatment (bison-grazed, cattle grazed, and ungrazed control).

During a two-year study, we conducted pollinator observations, soil collections, and soil compaction measurements from a total of 12 watersheds. In the summers of 2019 and 2020 we sampled 12 watersheds, consisting of six ungrazed and six bison-grazed watersheds. Within these two groups of watersheds, we utilized a fully factorial design with each grazing treatment crossed with three fire rotation treatments (burned once every: one year, four years, or twenty years). Sampling was conducted at two permanent sampling transects located in each watershed, providing a total of 24 sampling sites.

Pollinator Collection

During the summers of 2019 and 2020, we collected moths, butterflies, skippers, bees, syrphid flies, and bee flies along sampling transects using both hand collecting and pan-trapping. Hand-collected specimens were captured during two replications of 10 minutes at each transect (totaling 20 minutes/transect) using aerial nets (38 cm in diameter) and hand-held insect vacuums (Heavy Duty 18-volt Hand-Held DC Vac/Aspirator built on Skil® hand-held vac platform from BioQuip®, Catalogue number: 2820GA). Pollinators were collected if they landed on vegetation or ground located within the 50 m long, 5 m wide transect area. If a specimen escaped capture, it was counted in abundance data. If the species identity of the specimen was apparent, it was also included in species richness data. Monarch and regal fritillary butterflies were not collected due to their conservation status, but were identified on-the-wing and included in the data as if they were captured. The rest of the captured specimens were placed in 100 mL plastic twist-cap sample vials and placed on ice in the field, then stored in a 0°C freezer until they were processed.

Two arrays of pan traps were set up at the ends of each sampling transect, totaling 48 trap arrays. Each pan trap array consisted of one blue, one yellow, and one white 18 oz. Solo™ cup, cable-tied into a triad around a stake and placed at the height of the surrounding vegetation. Pan traps were set with soapy water during the time of hand-collections and were collected 48 hours later. Collected specimens were drained and then stored in 75% ethanol until they were washed, dried, and pinned for identification.

Specimens were identified to the species level, including the vast majority of the subgenus *Lasioglossum* (*Dialictus*) (Hymenoptera: Halictidae). Only a few specimens were identified down to subgenus rather than species. Additionally, females of the species *Heriades*

leavitti and *Heriades variolosa* (Hymenoptera: Megachilidae) cannot be reliably distinguished, and therefore specimens of these two species were identified down to the two possible species names. For species richness calculations, it was assumed that only one of these two species was present so that an underestimation of species richness was provided rather than an overestimation. The species *Hylaeus modestus* (Hymenoptera: Colletidae) was identified to species and not subspecies. Hover and bee flies were only identified down to family (Diptera: Syrphidae and Bombyliidae, respectively).

The keys utilized to identify bee species were: *Bees of the tallgrass prairie region and greater Midwest* (unpublished, Mike Arduser 2019), *Key to the Agapostemon of eastern North America*, by Zach Portman and Mike Arduser (Portman and Arduser 2019), and *Bumble bees of North America: An Identification Guide* (Williams et al. 2014). Species identification was confirmed by Dr. Michael Arduser at Saint Louis University, St. Louis, MO., and *Agapostemon* (Hymenoptera: Halictidae) specimens were verified using specimens from the Museum of Entomological and Prairie Arthropod Research, at Kansas State in Manhattan, KS.

Soil sampling and measurements

At the end of the 2019 and 2020 growing seasons, we evaluated characteristics of bee nesting habitat by measuring the percentage of bare ground, soil compaction, and calculating soil composition within each transect. Soil samples for composition analysis were only collected in 2019, as soil properties are not likely to change between the two experimental years. Soil compaction and bare ground were measured in both 2019 and 2020. Bare ground was estimated by randomly placing a 1 m² quadrat within our pollinator collecting transects and visually estimating the percentage of bare ground within the quadrat (estimations to the nearest 5%). After the amount of bare ground was estimated, soil compaction was measured in three readings

within the quadrat using a penetrometer, in pounds per square inch (PSI). In 2019, we utilized the FieldScout SC 900 Soil Compaction Meter, Item 6110FS, from Spectrum Technologies, Inc.; and in 2020 we used the SpotOn® Digital Soil Compaction Meter, Item# 29360. Soil samples were then collected within the quadrat using a soil corer inserted 15-20 cm into the ground, and composition was measured in the lab using the hydrometer method to calculate the percentage of sand, silt, and clay within each soil sample. However, percent sand was used in the statistical analyses, as this soil property is most likely to influence bee nesting (Potts and Willmer 1997) and as reviewed by (Harmon-Threatt 2020). All soil measurements and collections were replicated three times within each transect.

Plant Community Data

Our plant community data is based on plant species composition data collected in 2019 by Konza staff within the same sampling transects we utilized for our experiment (Hartnett et al. 2021). Plant species richness data was collected within 20 sampling plots established along the sampling transects. Each sampling plot was 10 m², and the percent cover of each species within each plot was recorded. We extracted forb data from this dataset and simplified the cover measurements into presence/absence data. We then calculated the forb species richness data for each of our sampling transects and used forb species richness as a measurement of foraging habitat within our path analysis.

Statistical analysis

We utilized a piecewise structural equation model (SEM) to understand the causal effects of fire and bison grazing on soil/plant community factors, and how these factors ultimately influence the pollinator community. To do this, we divided the captured pollinator specimens into three main groups (all pollinators (including lepidopterans, hymenopterans, and dipterans);

only hymenopterans, and only lepidopterans) and measured abundance and species richness within each, averaged across years for each transect. We also further divided the bee species into above- and below-ground nesters using the nesting traits assigned to each species by Spiesman et al (Spiesman et al 2019) and ran separate SEMs for each nesting type. For each pollinator group tested, we constructed a separate SEM and input all measured predictors (soil measurements, forb species richness data, fire rotation, and presence or absence of bison grazing) along with the pollinator abundance and richness data. This resulted in 10 separate SEMs. Each response and predictor variable relationship was tested for and showed no evidence of nonlinearity. We then utilized a backwards stepwise model selection approach to find the best fit model by removing non-significant relationships until the lowest Akaike's information criterion (AIC) and a p-value > 0.05 for each linear model was achieved. All SEMs were conducted in R v4.0.0, utilizing the *piecewiseSEM* package (Lefcheck 2016).

Results

Over the course of our two-year experiment, we observed a total of 3,617 individual pollinators, captured 3,305 specimens, and identified 112 different subgenera and species, of which 54 species were lepidopteran species, 57 were species of bees, and 1 subgenus of bees (*Lasioglossum*, subgenus *Dialictus*). Among these captured specimens, 171 bee specimens belonging to species with above-ground nesting behavior were captured, and 1,944 below-ground nesting bee specimens were captured. Lastly, we observed a total of 108 individuals belonging to the families of Bombyliidae and Syrphidae.

We found significant relationships ($p \leq 0.05$) between fire, grazing, and habitat characteristics. Frequent fire rotation negatively influenced the amount of bare ground (Figure 1.3, (β_b = standard path coefficient) $\beta = -0.470$, $df = 21$, $p = 0.007$) and soil compaction ($\beta_c = -$

0.434, $df = 21$, $p = 0.009$), while grazing had the opposite relationship with these soil characteristics (see Table 1, Figure 1.3). A higher amount of bare ground negatively impacted forb species richness (Figure 1.3, $\beta_g = -0.399$, $df = 19$, $p < 0.001$), while forb richness was positively affected by soil compaction ($\beta_h = 0.242$, $df = 19$, $p = 0.045$) and percent of sand ($\beta_i = -0.290$, $df = 19$, $p = 0.007$).

Table 1.1. Standardized path coefficients of correlations between fire, grazing, and habitat characteristics. Blank cells indicate that relationship was removed from analysis during the backward stepwise model approach (* $p \leq 0.05$, ** $p \leq 0.001$).

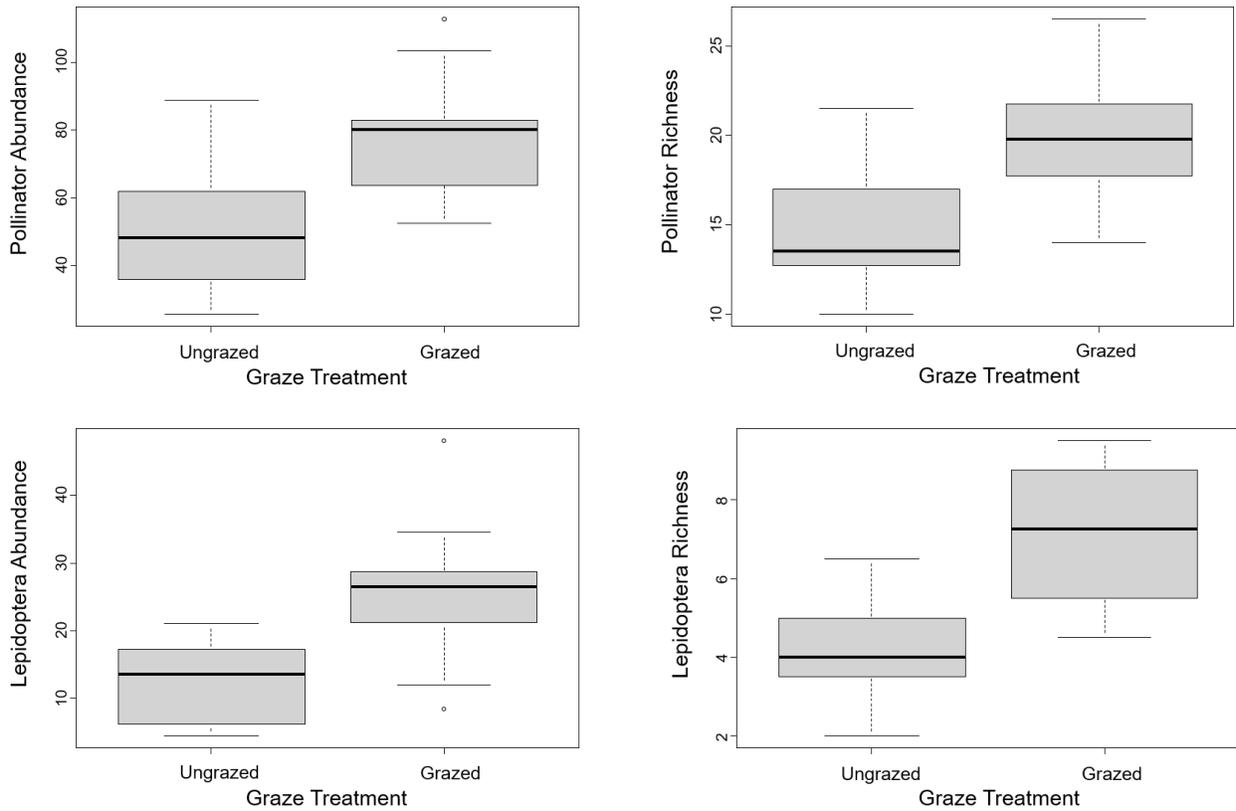
Variables	Bare Ground	Soil Compaction	Percent Sand	Forb Species Richness
Fire Rotation	-0.470*	-0.434*	0.310	
Grazing	0.504*	0.580**	-0.280	
Bare Ground				-0.399**
Soil Compaction				0.242*
Percent Sand				0.290*
Forb Species Richness				

Table 1.2. Standardized coefficients of correlations tested between habitat characteristics and pollinator groups. Grazing had the most impact on pollinators out of any other variable. Blank cells indicate that relationship was removed from analysis during the backward stepwise model approach. (* $p \leq 0.05$, ** $p \leq 0.001$).

Variables	Pollinator Abundance	Pollinator Species Richness	Bee Abundance	Bee Species Richness	Above-ground Nesters	Below-ground Nesters	Lepidopteran Abundance	Lepidopteran Species Richness
Fire								
Grazing	0.90*	1.07**		0.97*			0.62**	0.53**
Bare Ground	0.38		0.67*			0.61*		
Soil Compaction					0.76*			
Soil Composition								
Forb Species Richness	-0.56			-0.89*				

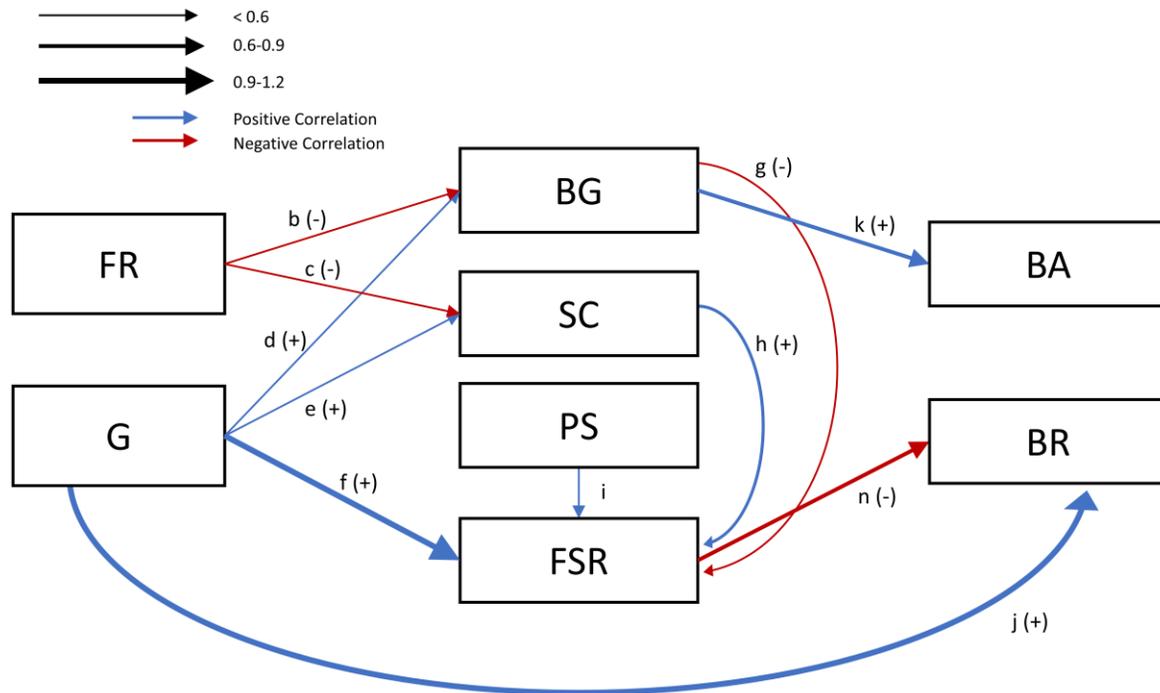
We found grazing had a direct, positive impact on overall pollinator abundance ($\beta = -0.470$, $df = 21$, $p = 0.007$) pollinator species richness ($\beta = -0.470$, $df = 21$, $p = 0.007$), and lepidopteran abundance ($\beta = -0.470$, $df = 21$, $p = 0.007$) and richness ($\beta = -0.470$, $df = 21$, $p = 0.007$, Figure 1.2). Fire had no direct impact on any pollinator group.

Figure 1.2. Grazing had a strong direct, positive effect on overall pollinators and lepidopterans.



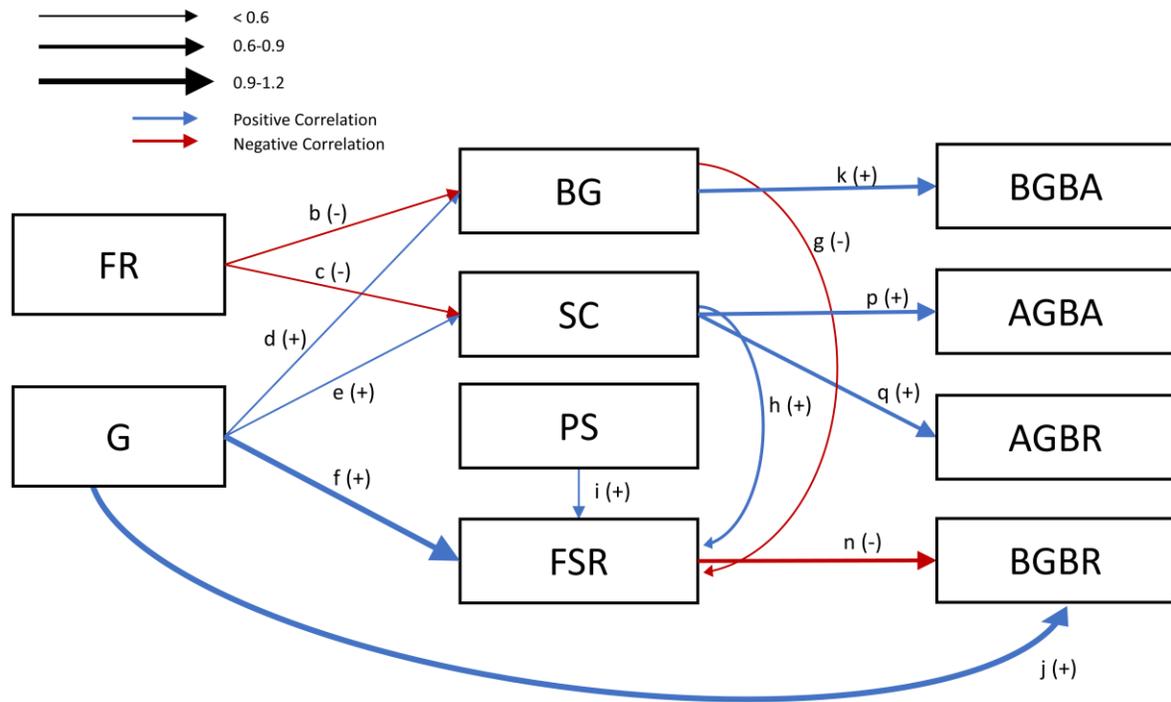
Grazing and fire had cascading effects on bee species richness and abundance. Besides directly affecting bee species richness (BR), grazing positively impacted forb species richness (path “f”, Figure 1.3), which in turn negatively impacted bee species richness (path “n”). Grazing and fire had opposite effects on the amount of bare ground, with grazing positively associated with bare ground (path “d”) and fire negatively associated (path “b”). Bee abundance (BA) was positively impacted by bare ground (path “k”, Figure 1.3).

Figure 1.3. Grazing directly and indirectly affected the bee species richness and abundance, while fire only indirectly affected bees through its impact on bare ground. Fire and grazing directly impacted soil and forb variables. Abbreviations are listed in Figure 1.1 and previous text.



Longer fire rotations, or less frequent fires, negatively impacted bare ground and soil compaction while bison grazing positively impacted bare ground, soil compaction, and forb species richness. Consequently, more bare ground reduced forb species richness, while greater soil compaction and the percentage of sand positively impacted forb species richness (Figure 1.3). Forb richness went on to negatively impact the species richness of below-ground nesting bees (Figure 1.4, path “n”). Alternatively, increased levels of bare ground positively affected the abundance of below ground nesting bees (Figure 1.4, path “k”), while more compact soils increased the abundance (path “p”) and richness (path “q”) of above-ground nesting bees (Figure 1.4). Although we saw no direct impact of fire on any pollinator group, we did see the effects of fire and grazing on the soil and plant community, through which different groups of bees were significantly impacted.

Figure 1.4. The direct and indirect effects of fire and grazing on above- and below-ground nesting bees. BGBA = Below-ground nesting bee abundance, AGBA = above-ground nesting bee abundance, AGBR = above-ground nesting bee richness, BGBR = below-ground nesting bee richness.



Discussion

I hypothesized that besides the direct effects fire and grazing may have on the pollinator community, there would be indirect effects through their impact on pollinator nesting and foraging habitat (soil and plant community characteristics). I hypothesized that longer fire rotations (infrequently burned) would decrease the amount of bare ground and impact the soil composition in burned areas, ultimately impacting the plant species richness. I also hypothesized that grazing would increase the amount of bare ground, soil compaction, and forb richness. These results instead indicate that long fire rotations and the presence of bison have nearly

opposing effects on overall pollinator habitat, and that my hypothesized effects on habitat characteristics were largely supported.

Effects of fire and grazing on plants and soil

As the length of the fire rotation increased, the amount of bare ground and soil compaction also decreased, while grazing positively impacted bare ground, soil compaction, and forb richness. Fire has been shown to increase vegetative growth during post-fire succession by opening up ground cover and eliminating leaf litter and other material, encouraging plant growth (especially the growth of fast-growing plants) and over time lowers the amount of bare ground (Turner et al. 2007). The watersheds included in my experiment were burned in the spring, while all model variables (soil characteristics, forb richness, and pollinator observations) were measured in the summer. The fast-growing plants encouraged by any spring burns would have been established by summer, and the increase in plant cover may have consequently increased the amount of roots in the soil, ultimately breaking up the soil structure and therefore lowering the amount of soil compaction (Phillips et al. 2000).

Alternately, large ungulate grazing has been repeatedly associated with increased levels of bare ground, soil compaction, and forb richness (Vinton et al. 1993, Collins and Calabrese 2012, O’Keefe and Nippert 2017). Many areas in which bison graze have higher amounts of bare ground due to wallowing, a behavior in which bison scrape the ground bare of vegetation and roll in the dust or mud. Bison also revisit and graze specific areas throughout the year, creating plots with lower vegetative cover and higher amounts of visible bare ground (Trager et al. 2004). Bison are heavy ungulates weighing upwards of 800 kg, and sites that are frequently visited and trampled underfoot will experience higher levels of soil compaction or hardening (Knapp et al. 1999). Lastly, bison preferentially graze on C₄ grasses over forbs, which consequently reduces

the amount of the more dominant grass species in the grazed area and allows room for less dominant forbs to grow, resulting in higher forb species richness in bison-grazed sites (Collins and Calabrese 2012, O’Keefe and Nippert 2017).

Soil and forb effects on bee communities

Bare ground positively impacted overall bee abundance and below-ground nesting bees, which aligns with the findings of previous studies that bare ground is highly associated with the presence of below-ground nesting bees (Potts et al. 2005, Sardiñas and Kremen 2014, Harmon-Threatt 2020). The presence of bare ground allows for warmer nest temps (through access to direct sunlight) and makes nest entrances easier for bees to locate (Potts et al. 2005, Sardiñas and Kremen 2014). Interestingly, soil compaction was positively associated with above-ground nesting bees (in abundance and species richness) rather than on below-ground nesting bees (on which compaction had no significant effect). This was unexpected, as I expected soil characteristics to impact below-ground nesting bees to a higher degree than above-ground nesting bees. However, moderately compact soils that can hold the nest shape with integrity and reduce nest “cave-ins” can attract more eusocial bee species, as it will allow more nests in a smaller area to be successfully constructed (Potts and Willmer 1997, Wuellner 1999, Sardiñas and Kremen 2014). It may be that the harder, more “compactable” soils made it easier for other animals, besides below-ground nesting bees, to burrow and excavate nests, in turn allowing above-ground species of bees (such as *Bombus pensylvanicus*) to utilize abandoned burrows as their own nests, and therefore flourish under higher levels of soil compaction (Thoenes 1993, Lanterman et al. 2019). It also could mean that the hardest of soils were too compact for below-ground nesting species to burrow, and this allowed for lower competition for above-ground nesting bees when it came to foraging in those highly-compact areas (Wignall et al. 2020).

Forb species richness had a negative impact on bee species richness and below-ground nesting bee richness. When taking a closer look at the forb data, we saw that some of the most commonly-occurring forbs in my sampling sites were those that are wind-pollinated, such as *Ambrosia psilotachya* and *Artemisia ludoviciana* (Asterales: Asteraceae). This may mean that although some sites have a high forb species richness, the species present, or the most prominent forb species, may not be one that is attractive pollinators. Therefore, plant species identity may be more important for pollinators rather than the number of plant species per se.

Soil effects on forb species richness

In my study, I found that bare ground negatively impacted forb species richness, while soil compaction and composition had positive effects. While bare ground may allow room for forbs to grow in the absence of more dominant grass species, it also may indicate a poor microhabitat. For instance, while bison wallowing may open up the amount of available ground in which to grow, if it is repeatedly disturbed throughout the year it is nearly impossible for plants to grow within the wallow until the disturbance stops. While there were no wallows located directly within our sampling transects, many transects had bison wallows at least within approximately 50 feet of them. Wallowing can also increase the amount of exotic species in the area, and lower the overall forb species richness due to these species ability to dominate native forbs (Trager et al. 2004). Compaction and the percentage of sand in soil composition had significant but weak, positive effects on forb richness. Different plant species respond to different levels of soil compaction, and it could be that native tallgrass prairie plants, which evolved under the disturbance of bison-grazing, prefer more compact soils (Ludvíková et al. 2014). Forbs have also been shown to increase with sand content in soil (Leach and Givnish

1999). I expect forb richness to affect soil characteristics over time; however, this effect would not be observed over the timescale of my study and therefore was not included in the analysis.

Direct effects of grazing on pollinators

Fire had no direct effects on any pollinator group, while grazing had direct and positive effects on overall pollinator abundance and species richness, overall bee richness and below-ground bee richness, and lepidopteran abundance and richness. Grazing affects not only the plant community, but can also decrease the vegetation structure, making it difficult for above-ground bees to nest (Kimoto et al. 2012). Because most bees caught in our experiment were ground-nesters, it could be that the lack of vegetative structure had a positive effect for most bees by lowering competition between bee species. Because more than 75% of bees are ground-nesters (Vaughan and Black 2007, Harmon-Threatt 2020), a lack of vegetative structure may impeded above-ground nesters from foraging in an area, consequently boosting overall bee richness and below-ground nesting bee richness (Wignall et al. 2020). However, the presence of direct effects of bison grazing indicate that there may be factors affecting our variables that were not included in our model.

A significant direct effect would also mean that a variable we did not account for was impacting pollinators directly, such as soil hydrology. Grazing can impact the soil hydrology of an area through defoliation and compaction, the first of which opens up more bare ground to directly receive precipitation, and lowers the amount of evaporation from plant foliage (Harrison et al. 2010). Soil moisture is important for below-ground nesting bees, as it can make nest excavation easier by softening soil crusts and reducing the chance of cave-ins (because certain levels of moisture make soil easier to shape and mold) (Wuellner 1999). Soil moisture content is also utilized by bees as an important factor in egg and larval development, as moist soils reduce

the risk of desiccation and therefore increase the chances of brood survival (Potts and Willmer 1997). Grazing also significantly increased forb species richness and native plant cover, which is related to higher abundances of lepidopterans (Moranz et al. 2012), although in our study that specific relationship was not significant.

Overall, we found that besides direct effects, fire and grazing have significant indirect effects on the pollinator community through their impact on nesting and foraging resources. Soil compaction and bare ground had significant effects on above-ground and below-ground nesting bees, respectfully. The impact of fire and grazing on soil ultimately affects different bee groups and may ultimately affect the ability of certain bee species to nest in these managed habitats. The nesting traits of bees were particularly impacted by habitat, rather than directly by grazing, in contrast to lepidopteran individuals. These findings indicate that more studies need to examine the impact of fire and grazing on soil properties, and not just floral resources.

Conclusion

We found that different pollinator groups respond differently to a variety of management strategies and habitat characteristics, consistent with a previous study finding that bee and lepidopteran diversity were negatively associated (Davis et al. 2008). Because pollinator groups respond differently, it is important for land managers to understand which pollinator group they want to be the focus of management strategies. Plant community also responded differently to soil characteristics than pollinators, indicating that management in support for native plants may not mean support for native pollinators, which was found to be true in a previous study (Griffin et al. 2021). Landowners who want to benefit most pollinator groups should implement bison grazing, while other landowners may look for ways to increase bare ground to benefit below-ground nesting bees. While we were able to measure the effects of different habitat

characteristics on bees with different nesting traits, it would be useful to conduct a similar study utilizing emergence traps to have a better understanding of which combination of land characteristics bees are choosing to nest in. Many native bees with small body sizes can forage within a radius of 59-121 m (Hofmann et al. 2020) from their nests, so habitats in which bees choose to forage may not be the same habitats they choose to nest in.

Our study offers valuable insight into the cause-and-effect relationships between land management strategies, the resulting land characteristics, and the ultimate effect on pollinator populations. The pathways tested in this study show that bison grazing has a direct, positive impact on most pollinator groups and forb richness, while showing no negative effects on pollinators. Fire was shown to have no direct effects on pollinators, but it did affect soil characteristics. Our results indicate that bison grazing is an effective management strategy in supporting a diverse set of pollinators, and can possibly mitigate their decline.

Literature Cited

- Archibald, S., W. J. Bond, W. D. Stock, and D. H. K. Fairbanks. 2005. Shaping the Landscape: Fire–Grazer Interactions in an African Savanna. *Ecological Applications* 15:96–109.
- Buckles, B. J., and A. N. Harmon-Threatt. 2019. Bee diversity in tallgrass prairies affected by management and its effects on above- and below-ground resources. *Journal of Applied Ecology* 0.
- Burkle, L. A., M. P. Simanonok, J. S. Durney, J. A. Myers, and R. T. Belote. 2019. Wildfires Influence Abundance, Diversity, and Intraspecific and Interspecific Trait Variation of Native Bees and Flowering Plants Across Burned and Unburned Landscapes. *Frontiers in Ecology and Evolution* 7:252.
- Calderone, N. W. 2012. Insect Pollinated Crops, Insect Pollinators and US Agriculture: Trend Analysis of Aggregate Data for the Period 1992–2009. *PLoS ONE* 7:e37235.
- Carbone, L. M., J. Tavella, J. G. Pausas, and R. Aguilar. 2019. A global synthesis of fire effects on pollinators. *Global Ecology and Biogeography* 28:1487–1498.
- Collins, S. L., and L. B. Calabrese. 2012. Effects of fire, grazing and topographic variation on vegetation structure in tallgrass prairie. *Journal of Vegetation Science* 23:563–575.
- Davis, J. D., S. D. Hendrix, D. M. Debinski, and C. J. Hemsley. 2008. Butterfly, bee and forb community composition and cross-taxon incongruence in tallgrass prairie fragments. *Journal of Insect Conservation* 12:69–79.
- Elwell, S. L., T. Griswold, and E. Elle. 2016. Habitat type plays a greater role than livestock grazing in structuring shrubsteppe plant–pollinator communities. *Journal of Insect Conservation* 20:515–525.
- Griffin, S. R., B. Bruninga-Socolar, and J. Gibbs. 2021. Bee communities in restored prairies are structured by landscape and management, not local floral resources. *Basic and Applied Ecology* 50:144–154.
- Harmon-Threatt, A. 2020. Influence of Nesting Characteristics on Health of Wild Bee Communities. *Annual Review of Entomology* 65:39–56.
- Harmon-Threatt, A., and K. Chin. 2016. Common Methods for Tallgrass Prairie Restoration and Their Potential Effects on Bee Diversity. *Natural Areas Journal* 36:400–411.

- Harrison, M. T., W. M. Kelman, A. D. Moore, and J. R. Evans. 2010. Grazing winter wheat relieves plant water stress and transiently enhances photosynthesis. *Functional Plant Biology* 37:726.
- Hofmann, M. M., A. Fleischmann, and S. S. Renner. 2020. Foraging distances in six species of solitary bees with body lengths of 6 to 15 mm, inferred from individual tagging, suggest 150 m-rule-of-thumb for flower strip distances. *Journal of Hymenoptera Research* 77:105–117.
- Kimoto, C., S. J. DeBano, R. W. Thorp, R. V. Taylor, H. Schmalz, T. DelCurto, T. Johnson, P. L. Kennedy, and S. Rao. 2012. Short-term responses of native bees to livestock and implications for managing ecosystem services in grasslands. *Ecosphere* 3:art88.
- van Klink, R., F. van der Plas, C. G. E. T. van Noordwijk, M. F. WallisDeVries, and H. Olf. 2015. Effects of large herbivores on grassland arthropod diversity: Large herbivores and arthropods. *Biological Reviews* 90:347–366.
- Knapp, A. K., J. M. Blair, J. M. Briggs, S. L. Collins, D. C. Hartnett, L. C. Johnson, and E. G. Towne. 1999, January 1. The keystone role of bison in North American tallgrass prairie. <https://link-galegroup-com.er.lib.k-state.edu/apps/doc/A53535756/AONE?sid=lms>.
- Kremen, C., N. M. Williams, and R. W. Thorp. 2002. Crop pollination from native bees at risk from agricultural intensification. *Proceedings of the National Academy of Sciences* 99:16812–16816.
- Kruess, A., and T. Tscharrntke. 2002. Grazing Intensity and the Diversity of Grasshoppers, Butterflies, and Trap-Nesting Bees and Wasps. *Conservation Biology* 16:1570–1580.
- Lanterman, J., P. Reeher, R. J. Mitchell, and K. Goodell. 2019. Habitat Preference and Phenology of Nest Seeking and Foraging Spring Bumble Bee Queens in Northeastern North America (Hymenoptera: Apidae: *Bombus*). *The American Midland Naturalist* 182:131.
- Leach, M. K., and T. J. Givnish. 1999. Gradients in the Composition, Structure, and Diversity of Remnant Oak Savannas in Southern Wisconsin. *Ecological Monographs* 69:353–374.
- Ludvíková, V., V. V. Pavlů, J. Gaisler, M. Hejman, and L. Pavlů. 2014. Long term defoliation by cattle grazing with and without trampling differently affects soil penetration resistance and plant species composition in *Agrostis capillaris* grassland. *Agriculture, Ecosystems & Environment* 197:204–211.

- Minckley, R. L. 2014. Maintenance of richness despite reduced abundance of desert bees (Hymenoptera: Apiformes) to persistent grazing. *Insect Conservation and Diversity* 7:263–273.
- Moranz, R. A., D. M. Debinski, D. A. McGranahan, D. M. Engle, and J. R. Miller. 2012. Untangling the effects of fire, grazing, and land-use legacies on grassland butterfly communities. *Biodiversity and Conservation* 21:2719–2746.
- Moylett, H., E. Youngsteadt, and C. Sorenson. 2020. The Impact of Prescribed Burning on Native Bee Communities (Hymenoptera: Apoidea: Anthophila) in Longleaf Pine Savannas in the North Carolina Sandhills. *Environmental Entomology* 49:211–219.
- O’Keefe, K., and J. B. Nippert. 2017. Grazing by bison is a stronger driver of plant ecohydrology in tallgrass prairie than fire history. *Plant and Soil* 411:423–436.
- Phillips, D. H., J. E. Foss, E. R. Buckner, R. M. Evans, and E. A. FitzPatrick. 2000. Response of Surface Horizons in an Oak Forest to Prescribed Burning. *Soil Science Society of America Journal* 64:754–760.
- Portman, Z. M. and Arduser, M. 2019. Key to the *Agapostemon* of eastern North America. Accessed 9 March 2020.
- Potts, S. G., B. Vulliamy, S. Roberts, C. O’Toole, A. Dafni, G. Ne’eman, and P. Willmer. 2005. Role of nesting resources in organising diverse bee communities in a Mediterranean landscape. *Ecological Entomology* 30:78–85.
- Potts, S., and P. Willmer. 1997. Abiotic and biotic factors influencing nest-site selection by *Halictus rubicundus*, a ground-nesting halictine bee. *Ecological Entomology* 22:319–328.
- Powney, G. D., C. Carvell, M. Edwards, R. K. A. Morris, H. E. Roy, B. A. Woodcock, and N. J. B. Isaac. 2019. Widespread losses of pollinating insects in Britain. *Nature Communications* 10:1018.
- Russell, J. R., and J. J. Bisinger. 2015. FORAGES AND PASTURES SYMPOSIUM: Improving soil health and productivity on grasslands using managed grazing of livestock1. *Journal of Animal Science* 93:2626–2640.
- Samson, F. B., F. L. Knopf, and W. R. Ostlie. 2004. Great Plains ecosystems: past, present, and future. *Wildlife Society Bulletin* 32:6–15.
- Samson, F., and F. Knopf. 1994. Prairie Conservation in North America. *BioScience* 44:418–421.

- Sardiñas, H. S., and C. Kremen. 2014. Evaluating nesting microhabitat for ground-nesting bees using emergence traps. *Basic and Applied Ecology* 15:161–168.
- Simanonok, M. P., and L. A. Burkle. 2019. Nesting success of wood-cavity-nesting bees declines with increasing time since wildfire. *Ecology and Evolution* 9:12436–12445.
- Thoenes, S. C. 1993. Fatal Attraction of Certain Large-Bodied Native Bees to Honey Bee Colonies. *Journal of the Kansas Entomological Society* 66:210–213.
- Trager, M. D., G. W. T. Wilson, and D. C. Hartnett. 2004. Concurrent Effects of Fire Regime, Grazing and Bison Wallowing on Tallgrass Prairie Vegetation. *The American Midland Naturalist* 152:237–247.
- Turner, M. G., E. A. H. Smithwick, K. L. Metzger, D. B. Tinker, and W. H. Romme. 2007. Inorganic nitrogen availability after severe stand-replacing fire in the Greater Yellowstone ecosystem. *Proceedings of the National Academy of Sciences* 104:4782–4789.
- Vaughan, M., and S. H. Black. 2007. Enhancing Nest Sites For Native Bee Crop Pollinators:4.
- Vinton, M. A., D. C. Hartnett, E. J. Finck, and J. M. Briggs. 1993. Interactive Effects of Fire, Bison (*Bison bison*) Grazing and Plant Community Composition in Tallgrass Prairie. *The American Midland Naturalist* 129:10–18.
- Welti, E. A. R., and A. Joern. 2018. Fire and grazing modulate the structure and resistance of plant–floral visitor networks in a tallgrass prairie. *Oecologia* 186:517–528.
- Wignall, V. R., B. Matthew, U. Cassandra, K. E. Norton, H. M. Chipperfield, N. J. Balfour, and R. F. L. W. 2020. Exploitative competition and displacement mediated by eusocial bees: experimental evidence in a wild pollinator community. *Behavioral Ecology and Sociobiology* 74.
- Williams, N. M., E. E. Crone, T. H. Roulston, R. L. Minckley, L. Packer, and S. G. Potts. 2010. Ecological and life-history traits predict bee species responses to environmental disturbances. *Biological Conservation* 143:2280–2291.
- Williams, P., Thorp, R., Richardson, L., and Colla, S. 2014. *Bumble bees of North America: An Identification Guide*. Princeton University Press, Princeton, NJ.
- Wuellner, C. T. 1999. Nest site preference and success in a gregarious, ground-nesting bee *Dieunomia triangulifera*. *Ecological Entomology* 24:471–479.

Chapter 2 - Candidate border crops attract different pollinator abundances and species richness

Introduction

Current land management practices are eliminating natural habitat critical to wildlife, imperiling native insects and their ecosystem services (Cardoso et al. 2020). Agricultural expansion is currently the main component of land use change, increasing the amount of homogenized land and arthropod habitat loss (Kremen et al. 2002, Williams et al. 2010, Calderone 2012). Greater chemical input, physical disturbances, and loss in plant biodiversity have all contributed to biodiversity declines, particularly of beneficial insects such as wild pollinators (Cardoso et al. 2020). With thirty percent of the world's food supply relying on pollination services (Klein et al. 2007), it is clear that new and sustainable agricultural practices need to be implemented to support beneficial insects, and maintain important ecosystem services such as pest control, pollination, and decomposition.

The introduction of non-crop perennial plant species in heavily farmed areas can mitigate landscape homogenization resulting from agricultural practices, providing an environment in which landowners can benefit from ecosystem services (Bianchi et al. 2006). One of the emergent ways to integrate these plant species more seamlessly into current land use is through their implementation on marginal cropland, such as grass waterways and buffer regions that are unfit for cultivation. These non-crop plantings, also called border crops, hedgerows, buffer strips, or crop strips, diversify landscapes and provide natural and undisturbed habitat in heavily farmed landscapes. Border crops have the potential to provide a plethora of benefits, such as increasing

soil health, reducing erosion and runoff, and providing a secondary crop with minimal cost to yields (Pywell et al. 2015, NRCS 2020).

The addition of perennial border crops can offer the added benefit of providing additional food and nesting resources year-round for beneficial insects such as pollinators and natural enemies (Winfree et al. 2007), while decreasing the amount of pest damage and improving yields in adjacent crop fields (Bianchi et al. 2006, Kim et al. 2006, Wratten et al. 2012). When given ample natural habitat near farming operations, native pollinators have the ability to provide up to all pollination services for crop fields (Kremen et al. 2002, Winfree et al. 2008, Blaauw and Isaacs 2014), and can even improve the fruit set of crops that are able to self-pollinate (Klein et al. 2003). Providing highly diverse flowering strips can further increase pollination and biocontrol services, indicating that the efficacy of border crops is dependent upon the type and quality of the border planting (as reviewed by (Albrecht et al. 2020). Flowering border strips also have the ability to provide floral resources when native floral resources are scarce, or even when the primary crop is not in bloom (Winfree et al. 2007).

Despite the possibility of receiving a multitude of benefits, many farmers are reluctant to plant border crops from fears of economic loss and a general lack of knowledge (Morandin and Kremen 2013). Not only do natural border crops require upfront costs from the landowner, but the landowner must wait until the border crops establish to begin receiving benefits that “pay back” the cost of implementation (Morandin et al. 2016) (Morandin et al. 2016). Also, if the border crop is planted in a polyculture, such as the standard prairie mix offered by the Natural Resources and Conservation services (NRCS), the crops themselves can be difficult to harvest and ineffective as livestock forage (Jefferson et al. 2004). Therefore, selecting border crops that provide direct benefits to farmers, such as foraging and grain crops, or low-maintenance

plantings such as perennial mixes, may encourage the adoption of this conservation practice. Perennial border crops that establish quickly, and are effective in pollinator attraction as a single species, rather than in a polyculture planting, would be highly desirable as well, as they would better fit traditional farming equipment and management practices and may therefore encourage implementation.

My objective was to measure the ability of flowering, perennial, border crops to attract and support a high species richness and abundance of pollinators. I investigated six candidate border crops (a diverse prairie mix, and monocultures of alfalfa, sainfoin, cup plant, silflower, and Kernza™) to determine which crop is most likely to attract the highest abundance and diversity of pollinators. I hypothesized that border crops containing the most diverse and long-lasting floral resources would attract the most abundance and diverse set of pollinator species (Potts et al. 2003). Therefore, I predicted that the native prairie seed mix will perform the best overall, as this mix contains nine different native prairie species with an array of bloom times, providing this crop with a long bloom period.

I also examined bee and lepidopteran individuals separately. I hypothesized that besides the prairie crop treatment, the two sunflower treatments (cup plant and silflower) would attract the highest amount of bees, as there are several bee species in Kansas that are sunflower obligates and bees have been previously observed in larger abundances than other pollinators in sunflower plantings (Parker 1981, Mallinger et al. 2018). I expected Kernza™, a wind-pollinated wheat variety, to perform the worst in pollinator attraction. Determining the ability of border crops to attract pollinators is imperative to taking the next step towards a more healthy and diverse agricultural landscape, as this equips growers and conservationists with information on possible practices that can serve both farming and conservation interests. Implementing crops

that can utilize marginal land, provide a secondary harvest, and support native insect biodiversity will offset the negative effects of intensified agriculture, leading to more effective and sustainable agricultural practices.

Methods

I executed the experiment at the Land Institute located in Salina, KS (38°46'6.3"N 97°33'58.9"W). The Land Institute (TLI) is a non-profit research organization with the mission of advancing perennial and polyculture cropping systems. Most of the surrounding landscape is typical of central Kansas, and consists of alfalfa, wheat, and pasture fields, with natural surrounding areas consisting of woodlands and native prairie, making it an ideal research area for testing new crops in an agricultural landscape.

During a two-year study, I conducted pollinator observations and measured flowering phenology among six different border crop candidate species: alfalfa (*Medicago sativa*), sainfoin (*Onobrychis viciifolia*), cup plant (*Silphium perfoliatum*), silflower (*Silphium integrifolium*), Kernza™ (*Thinopyrum intermedium*), and the NRCS pollinator mix. Information regarding their functional groups and target benefits for growers is outlined in Table 2.1, with species included in the diverse prairie mix (NRCS Pollinator Mix) listed in Table 2.2.

Table 2.1. The six candidate border crops and their benefits. *Species included in the NRCS Pollinator Mix are outlined in Table 2.2.

Border Crop	Scientific Name	Functional Group	Benefits	Planting Practice
Alfalfa	<i>Medicago sativa</i>	Legume	<ul style="list-style-type: none"> • Nitrogen-fixing¹ • Fodder¹ 	Monoculture
Sainfoin	<i>Onobrychis viciifolia</i>	Legume	<ul style="list-style-type: none"> • Nitrogen-fixing • Anti-bloat fodder² • Harvested after flowering³ 	Monoculture
Cup Plant	<i>Silphium perfoliatum</i>	Native aster	<ul style="list-style-type: none"> • Flood and freeze resistant⁴ • Fodder⁴ • Biofuel⁵ • Oilseed 	Monoculture
Silflower	<i>Silphium integrifolium</i>	Native aster	<ul style="list-style-type: none"> • Drought tolerant⁶ • Fodder • Biofuel • Oilseed Crop⁷ 	Monoculture
Kernza™	<i>Thinopyrum intermedium</i>	Grain	<ul style="list-style-type: none"> • Perennial grain crop 	Monoculture
NRCS Pollinator Mix*	See Table 2.2	Native grasses, legumes, asters, mints	<ul style="list-style-type: none"> • Grain crop⁸ • Perennial Fodder 	Polyculture

1. (Carlsson and Huss-Danell 2003), 2. Howarth et al. 1978), 3. (Borreani et al. 2003), 4. (Weaver et al. 1935), 5. Vilela et al. 2018), 6. (Schramm 1990), 7. (Gansberger et al. 2015), 8. (Schlautman et al. 2018).

Table 2.2. Plant species list for the NRCS Pollinator Mix.

Common Name	Scientific Name	Description	Bloom period
Big bluestem	<i>Andropogon gerardi</i>	Grass	July-September
Little bluestem	<i>Schizachyrium scoparium</i>	Grass	August-September
Tall dropseed	<i>Sporobolus aspera</i>	Grass	August-October
Purple prairie clover	<i>Dalea purpurea</i>	Legume	June-August
Maryland senna	<i>Senna marliandica</i>	Legume	July-September
Pitcher sage	<i>Salvia azurea</i>	Mint	July-October
Maximilian sunflower	<i>Helianthus maximiliani</i>	Aster	August-September
Cudweed sagewort	<i>Artemisia ludoviciana</i>	Aster	August-September
Dotted gayfeather	<i>Liatris punctata</i>	Aster	August-September

I established four study sites at TLI in 2018, with each site 1-2 km apart. Each site contained six plots (each plot 5.5 m x 5.5 m in size); each representing one of the six different crop treatments. This design resulted in a total of 24 sampling plots (four sites x six treatments). Plot placement was randomized to ensure early-blooming and late-blooming treatments would not be planted adjacent to one another. Plots within a site were separated by about a 10 m wide border of tall fescue grass (*Festuca arundinacea*), which was mowed on a bi-weekly basis.

Each crop species was started from seed in peat pellets within a greenhouse for several weeks, then established the plants within the designated plots. Individual plants of silflower, cup plant, prairie plants, and Kernza™ were planted 1 m apart from each other within their respective plot. Alfalfa and sainfoin were planted as normal row crops, with a distance of 1 m between each row within a plot. No herbicides or pesticides of any kind were used on the plots. Weeds were managed by mowing plot perimeters and hand-weeding within the plots. Nitrogen fertilizer was applied as necessary to aid in the establishment of research plots.

Pollinator collection

One year after establishment, I conducted pollinator observations for two growing seasons (2019-2020). During the blooming period of each crop treatment, I conducted time-observations for 10 minutes in each plot (two observations for each plot). I sampled each crop treatment about once a month during its bloom period, which resulted in sampling about 2-3 times per year per crop, giving me a total of 32-48 observation hours over the course of two years. The treatments received varying sampling efforts due to differences in the length of their bloom periods throughout the year. Kernza™ was observed for a total of 4 hours throughout the study period, alfalfa was observed for a total of 5.3 hours, sainfoin for a total of 4 hours, cup plant for 4 hours, silflower for 5.3, and prairie had a total of 8 hours.

Pollinators (bees, syrphids, bee flies, moths, skippers, and butterflies) that landed on inflorescences within the plot were hand-collected using aerial nets (38 cm in diameter) or hand-held insect vacuums (Heavy Duty 18-volt Hand-Held DC Vac/Aspirator built on Skil® hand-held vac platform from BioQuip®, catalogue number: 2820GA). Specimens were placed in twist-cap sample vials on ice until they were transported to a 0°C freezer. They were then pinned and identified to the species level, with the exception of hover and bee flies, which were identified to the family level. The keys utilized to identify bee species were: *Bees of the tallgrass prairie region and greater Midwest* (unpublished, Mike Arduser 2019), *Key to the Agapostemon of eastern North America*, by Zach Portman and Mike Arduser (Portman and Arduser 2019), and *Bumble bees of North America: An Identification Guide* (Williams et al. 2014). Species identification was confirmed by Dr. Michael Arduser at Saint Louis University, St. Louis, MO., and *Agapostemon* (Hymenoptera: Halictidae) specimens were verified using specimens from the Museum of Entomological and Prairie Arthropod Research, at Kansas State in Manhattan, KS.

Floral resources

I measured flower abundances in each plot during the bloom period. Flower abundance was measured by counting the number of inflorescences within a 0.25m² quadrat randomly placed within each treatment plot for three replications. In 2019, flower abundance was measured twice in each plot during the crop's bloom period. In 2020, flower abundance was measured more frequently (biweekly from May-September) rather than just during specific treatment bloom periods. Flower counts of each crop treatment were then multiplied by the average inflorescence size of each crop to estimate the average floral area provided by each crop treatment (League 2004, Michigan State 2021, Native Plant Trust 2021, NC State 2021). To meet model assumptions, floral area was transformed in each regression by a logarithmic transformation, pollinator abundance by a square root transformation, bee abundance by a logarithmic transformation, and lepidopteran abundance by a square root transformation.

Statistical analyses

For each sampling year, pollinator abundance and species richness were recorded per treatment and was standardized by sampling effort, as each crop received a different sampling effort. We standardized by totaling the pollinator abundance of each treatment and then dividing by the number of times that treatment was sampled, giving us a standardized measurement across treatments. This was done separately for the two different years, as sampling efforts differed between years. Species richness counts were standardized by totaling the species richness per treatment observed in each sampling round, and then averaging this total richness across the number of sampling rounds each treatment received per year.

To test the effect of crop treatment on overall pollinator abundance and species richness, we conducted a two-way ANOVA with crop treatment and year as the predictor variables and

standardized pollinator abundance or species richness as the response variables. Preliminary results showed no difference in the response variables among sites (Supplemental Table 1), so we removed “site” from the statistical model. To determine relative treatment performance in attracting pollinator abundance or species richness, we ran a Tukey HSD (honest significant difference) multiple comparison test to test for significant differences between treatments, averaged across years. To determine how bee and lepidopteran abundance and richness were differentially affected by crop treatment, we conducted ANOVAs as mentioned above separately for bees and lepidopterans.

To measure treatment effect on overall pollinator community composition, I conducted a permutational MANOVA (PERMANOVA, Bray Curtis dissimilarity). To measure the effect of floral resource amount on different pollinator groups, I calculated floral area by multiplying the number of inflorescences per plot with the average inflorescent width of each species. I then utilized a one-way ANOVA to determine whether there were significant differences in floral area between crop treatments. A Tukey HSD comparison test was used to test for significant differences between treatments. I then ran a simple linear regression to test the relationship between floral area and each pollinator group. All analyses were conducted in R v4.0.0, utilizing the *vegan* and *packages* (v2.5-6, Oksanen et al. 2019).

Results

All Pollinators

During this experiment, I observed a total of 596 individual arthropods, and captured 377 pollinators consisting of 74 different species of bees and lepidopterans, and 36 total individuals belonging to Syrphidae. Of this total, 293 bees were captured, with 50 species identified; and 84

lepidopterans were captured, out of which 23 species were identified. A complete species list for each crop treatment is listed in Table 2.3.

Table 2.3. List of bee and lepidopteran species caught in each crop treatment in summers of 2019 and 2020.

Crop Treatment	Bee Species	Lepidopteran Species
Alfalfa	<i>Halictus ligatus</i> <i>Lasioglossum tegulare</i>	<i>Atalopedes campestris</i> <i>Colias eurytheme</i> <i>Cupido comyntas</i> <i>Epargyreus clarus</i> <i>Erynnis baptisiae</i> <i>Euptoita claudia</i> <i>Haematopis grataria</i> <i>Hylephila phyleus</i> <i>Junonia coenia</i> <i>Nomophila nearctica</i> <i>Pholisora catullus</i> <i>Phyciodes tharos</i> <i>Pieris rapae</i> <i>Pontia protodice</i> <i>Epargyreus clarus</i> <i>Strymon melinus</i>
Cup Plant	<i>Agapostemon texanus</i> <i>Agapostemon virescens</i> <i>Apis mellifera</i> <i>Bombus impatiens</i> <i>Halictus ligatus</i> <i>Lasioglossum imitatum</i> <i>Lasioglossum trigeminum</i> <i>Megachile brevis</i> <i>Megachile inimica</i> <i>Megachile mendica</i> <i>Melissodes agilis</i> <i>Melissodes comptoides</i> <i>Melissodes coreopsis</i> <i>Melissodes desponsus</i> <i>Nomada texana</i> <i>Svastra obliqua</i> <i>Tetraloniella spissa</i>	<i>Atalopedes campestris</i> <i>Poanes zabulon</i> <i>Epargyreus clarus</i>

Crop Treatment	Bee Species	Lepidopteran Species
Kernza	<i>Bombus bimaculatus</i> <i>Hoplitis pilosifrons</i>	
Prairie	<i>Agapostemon texanus</i> <i>Agapostemon virescens</i> <i>Andrena accepta</i> <i>Anthophora walshii</i> <i>Apis mellifera</i> <i>Augochlora pura</i> <i>Augochlorella aurata</i> <i>Augochlorella karankawa</i> <i>Augochlorella persimilis</i> <i>Augochloropsis metallica</i> <i>Bombus bimaculatus</i> <i>Bombus griseocollis</i> <i>Bombus impatiens</i> <i>Bombus pensylvanicus</i> <i>Halictus ligatus</i> <i>Halictus parallelus</i> <i>Halictus tripartitus</i> <i>Hoplitis pilosifrons</i> <i>Lasioglossum callidum</i> <i>Lasioglossum hudsoniellum</i> <i>Lasioglossum imitatum</i> <i>Lasioglossum pectorale</i> <i>Lasioglossum pruinatum</i> <i>Lasioglossum tegulare</i> <i>Lasioglossum trigeminum</i> <i>Megachile brevis</i> <i>Melissodes communis</i> <i>Melissodes coreopsis</i> <i>Pseudopanurgus albitarsis</i> <i>Pterosarus albitarsis</i> <i>Svastra obliqua</i> <i>Tetraloniella cressoniana</i> <i>Triepeolus lunatus</i> <i>Xylocopa virginica</i>	<i>Anagrapha falcifera</i> <i>Anatrytone logan</i> <i>Atalopedes campestris</i> <i>Colias eurytheme</i> <i>Colias philodice</i> <i>Epargyreus clarus</i> <i>Erynnis baptisiae</i> <i>Helicoverpa zea</i> <i>Hylephila phyleus</i> <i>Nomophila nearctica</i> <i>Poanes zabulon</i> <i>Pontia protodice</i> <i>Epargyreus clarus</i> <i>Strymon melinus</i>
Sainfoin	<i>Agapostemon texanus</i> <i>Apis mellifera</i> <i>Augochlorella aurata</i> <i>Bombus pensylvanicus</i> <i>Halictus ligatus</i> <i>Hoplitis pilosifrons</i>	<i>Echinargus isola</i> <i>Epargyreus clarus</i>

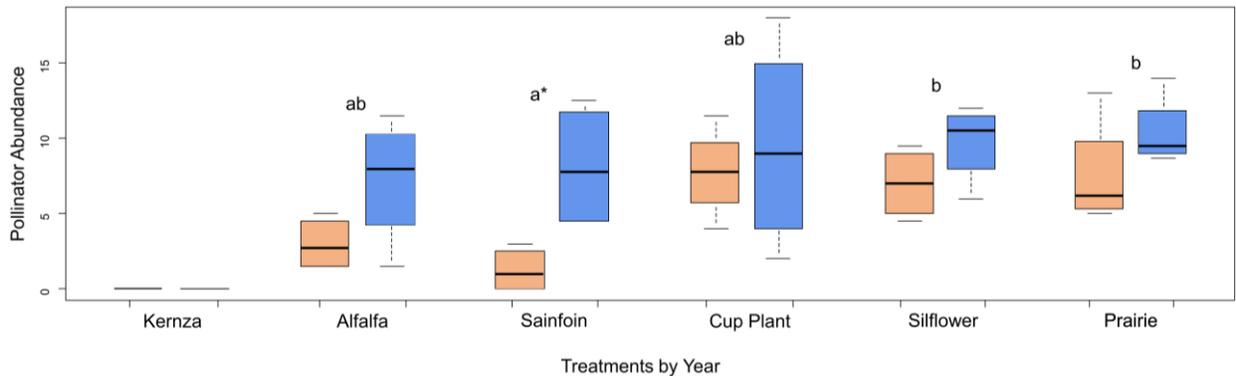
Crop Treatment	Bee Species	Lepidopteran Species
Sainfoin	<i>Lasioglossum disparile</i> <i>Lasioglossum pruinosum</i> <i>Lasioglossum tegulare</i> <i>Lasioglossum trigeminum</i> <i>Megachile addenda</i> <i>Megachile brevis</i> <i>Megachile exilis</i>	
Silflower	<i>Agapostemon texanus</i> <i>Agapostemon virescens</i> <i>Augochlorella aurata</i> <i>Augochlorella persimilis</i> <i>Bombus fraternus</i> <i>Bombus griseocollis</i> <i>Bombus pensylvanicus</i> <i>Dieunomia heteropoda</i> <i>Halictus ligatus</i> <i>Lasioglossum disparile</i> <i>Lasioglossum imitatum</i> <i>Lasioglossum zephyrum</i> <i>Megachile brevis</i> <i>Megachile inimica</i> <i>Megachile mendica</i> <i>Megachile petulans</i> <i>Melissodes agilis</i> <i>Melissodes communis</i> <i>Melissodes coreopsis</i> <i>Melissodes desponsus</i> <i>Melissodes trinodis</i> <i>Perdita albipennis</i> <i>Svastra obliqua</i> <i>Xylocopa virginica</i>	<i>Anatrytone logan</i> <i>Atalopedes campestris</i> <i>Caenurgina erechtea</i> <i>Colias philodice</i> <i>Hylephila phyleus</i> <i>Lerodea eufala</i> <i>Danaus plexippus</i> <i>Poanes zabulon</i>

To calculate crop treatment effects on the overall pollinator abundance, species richness, and community composition, Kernza™ was removed from these analyses due only five specimens being caught in its plots after standardization. For all pollinators (bees, lepidopterans, and syrphids), their combined abundances varied with treatment ($F_{4,39} = 4.12$, $p = 0.01$) and year ($F_{1,39} = 12.14$, $p = 0.002$) The interaction between treatment and year was not significant

($F_{4,39} = 1.89$, $p = 0.14$). Prairie and silflower attracted significantly higher overall pollinator abundance than sainfoin (see Table 4, Figure 2.1). Pollinator species richness was also affected by treatment ($F_{4,39} = 3.89$, $p = 0.01$) but was not affected by year ($F_{4,39} = 0.30$, $p = 0.87$).

Pollinator species richness followed the same trend as pollinator abundance, with prairie and silflower attracting significantly greater number of species compared to sainfoin (See Table 2.4).

Figure 2.1. Crop treatment effects on pollinator abundances, standardized by sampling effort. Pollinators were sampled from each of the six crop treatments in 2019 (represented in orange) and 2020 (in blue). Lowercase letters denote significant differences between crop treatments, while the asterisk represents a significant difference between years within one crop treatment. Kernza was not included in this statistical analysis.



Community composition was significantly impacted by crop treatment (Permutational MANOVA $F_{4,36} = 2.11$, $p < 0.01$), year ($F_{1,36} = 2.788$, $p < 0.01$), and the interaction of treatment and year ($F_{4,36} = 1.30$, $p = 0.03$; see Figure 2.2). Alfalfa treatments were dominated by species belonging to *Lasioglossum* (Hymenoptera: Halictidae) (see Table 2.3), while sainfoin was dominated by *Apis mellifera* (Hymenoptera: Apidae) and *Megachile brevis* (Hymenoptera: Megachilidae). Cup plant had a majority of *Agapostemon texanus* and *A. virescens* (Hymenoptera: Halictidae) and species belonging to *Melissodes* (Hymenoptera: Apidae), which was similar to silflower, which attracted mostly *A. virescens* and *Halictus ligatus* (Hymenoptera:

Halictus). Prairie was dominated by *A. virescens* (and other members of the Augochlorini tribe) and *Melissodes communis*.

Figure 2.2. Overall pollinator community composition between crop treatments was insignificant. Kernza™ was excluded from analysis.

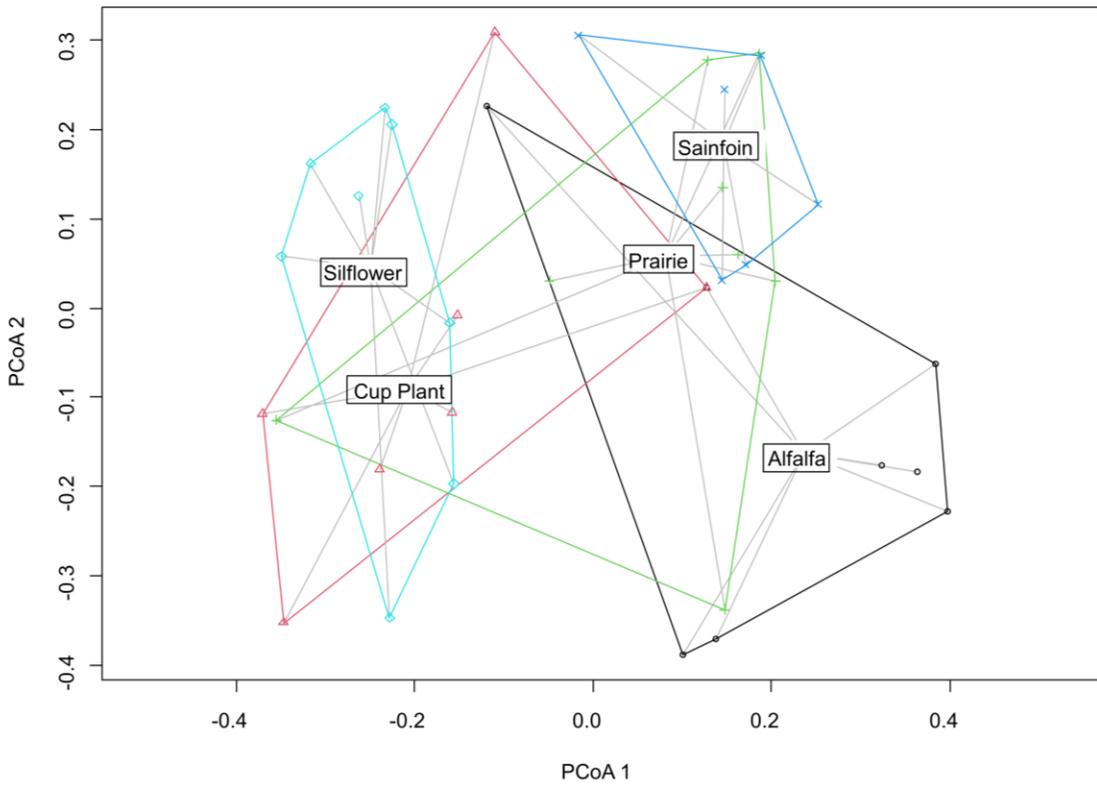


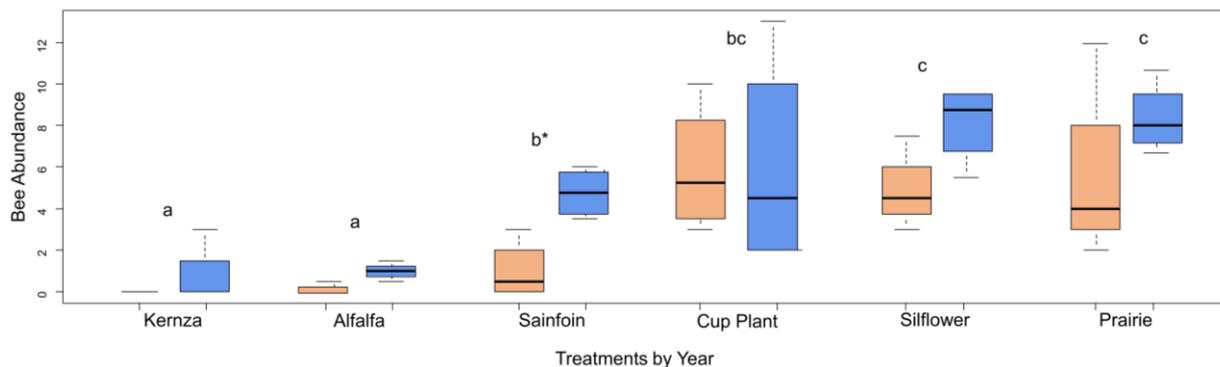
Table 2.4. Adjusted p-values from Tukey HSD multiple comparison test to test for significant differences between crop treatments, averaged across years, in their ability to attract different taxonomic groups of pollinators in terms of abundance and species richness. The * indicates significance, while “N/A” indicates that one or both of the treatments being compared were excluded from analysis due to lack of data.

Treatment Comparisons	Pollinator Abundance	Pollinator Richness	Bee Abundance	Bee Richness	Lepidoptera Abundance	Lepidopteran Richness
Cup plant-Alfalfa	0.335	0.789	< 0.001*	< 0.001*	N/A	0.365
Kernza-Alfalfa	N/A	N/A	0.898	N/A	N/A	N/A
Prairie-Alfalfa	0.175	0.287	< 0.001*	< 0.001*	N/A	0.292
Sainfoin-Alfalfa	0.885	0.801	0.003*	0.010*	N/A	0.022*
Silflower-Alfalfa	0.281	0.209	0	< 0.001*	N/A	0.292
Kernza-Cup plant	N/A	N/A	< 0.001*	N/A	N/A	N/A
Prairie-Cup plant	0.995	0.904	0.940	1.00	N/A	1.00
Sainfoin-Cup plant	0.058	0.193	0.104	0.594	N/A	0.353
Silflower-Cup plant	0.100	0.823	0.935	1.00	N/A	1.00
Prairie-Kernza	N/A	N/A	< 0.001*	N/A	N/A	N/A
Sainfoin-Kernza	N/A	N/A	0.041	N/A	N/A	N/A
Silflower-Kernza	N/A	N/A	< 0.001*	N/A	N/A	N/A
Sainfoin-Prairie	0.024*	0.030	0.011*	0.592	N/A	0.406
Silflower-Prairie	0.999	1.00	1.00	1.00	N/A	1.00
Silflower-Sainfoin	0.045*	0.019	0.011*	0.522	N/A	0.406

Bees

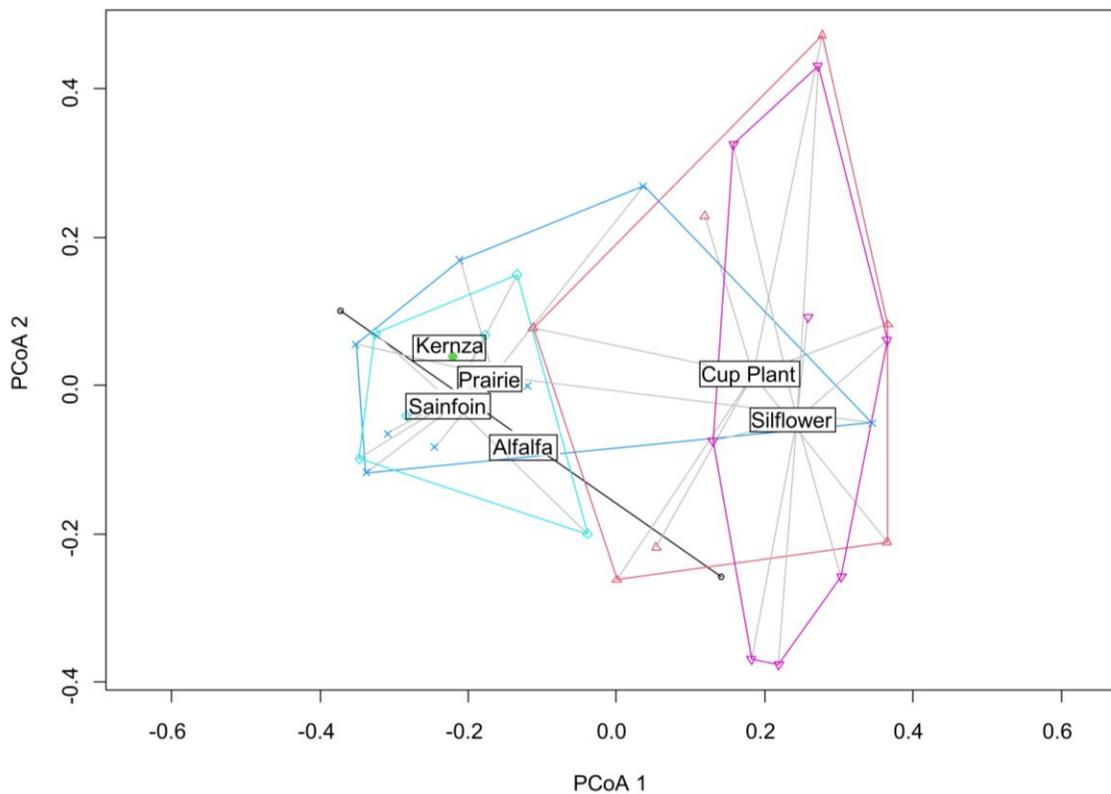
Bee abundance and richness were significantly impacted by crop treatment ($F_{5,47} = 23.50$, $p < 0.01$ and $F_{4,39} = 9.68$, $p < 0.01$). Bee abundance and richness were significantly higher in sainfoin, cup plant, prairie, and silflower compared to alfalfa and Kernza™ (Table 2.4, Figure 2.3). Prairie and silflower also attracted significantly higher bee abundance and richness than sainfoin and Kernza™ (see Table 2.4). Bee abundance increased with year ($F_{4,30} = 9.05$, $p < 0.01$), while there was significant interaction with year and treatment for bee richness ($F_{1,47} = 9.19$, $p < 0.01$). Sainfoin attracted higher bee abundance in 2020 compared to its bee abundance in 2019 (Tukey HSD $p = 0.04$), although it did not impact the overall interaction between year and treatment. This treatment did not perform significantly better than alfalfa and Kernza™, in terms of pollinator abundance, in 2019, but did so in 2020 (Tukey HSD $p < 0.01$ and $p = 0.04$, respectively).

Figure 2.3. Average bee abundance in each crop treatment, standardized by sampling effort. Abundance values from 2019 are represented in orange, and 2020 counts are represented in blue. Lowercase letters denote differences between crop treatments, while the asterisk represents a significant difference between years within one crop treatment.



Bee community composition was affected by the interaction between treatment and year ($F_{3,31} = 1.39$, $p = 0.04$), crop treatment ($F_{5,31} = 1.78$, $p < 0.01$), and year ($F_{1,31} = 2.67$, $p < 0.002$; see Figure 2.4). Alfalfa treatments were dominated by species belonging to *Lasioglossum* (see Table 2.3), sainfoin was dominated by *Apis mellifera* and *Megachile brevis*. Cup plant attracted *Agapostemon texanus* and *A. virescens* and species belonging to the genus *Melissodes*, which overlaps with the species attracted by silflower (*A. virescens* and *Halictus ligatus*) and prairie (*A. virescens* and other members of the Augochlorini tribe and *Melissodes communis*; see Table 2.3).

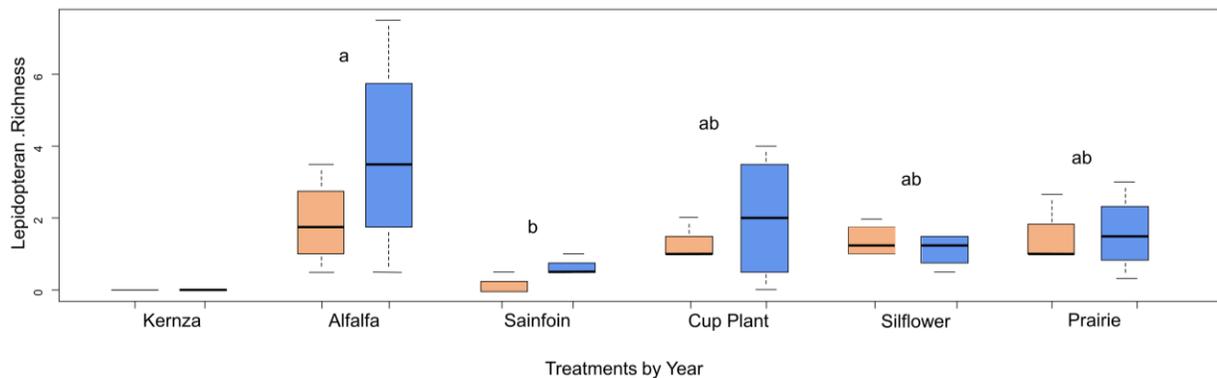
Figure 2.4. Crop treatments showed significant differences in bee community composition.



Lepidopterans

Because no lepidopteran specimens were caught in the Kernza™ treatments, they were removed from all lepidopteran data analysis. Treatment did not have an overall significant effect on lepidopteran abundance ($F_{4,30} = 2.26$, $p = 0.09$), nor did year or the interaction between year and treatment ($F_{1,30} = 0.61$, $p = 0.44$ and $F_{4,30} = 1.42$, $p = 0.25$, respectively). However, a Tukey HSD multiple comparison test showed that alfalfa attracted a higher lepidopteran abundance than sainfoin (Table 2.4 and Figure 2.5). Lepidopteran species richness followed a similar trend, with alfalfa attracting significantly higher species richness than sainfoin (see Table 2.4).

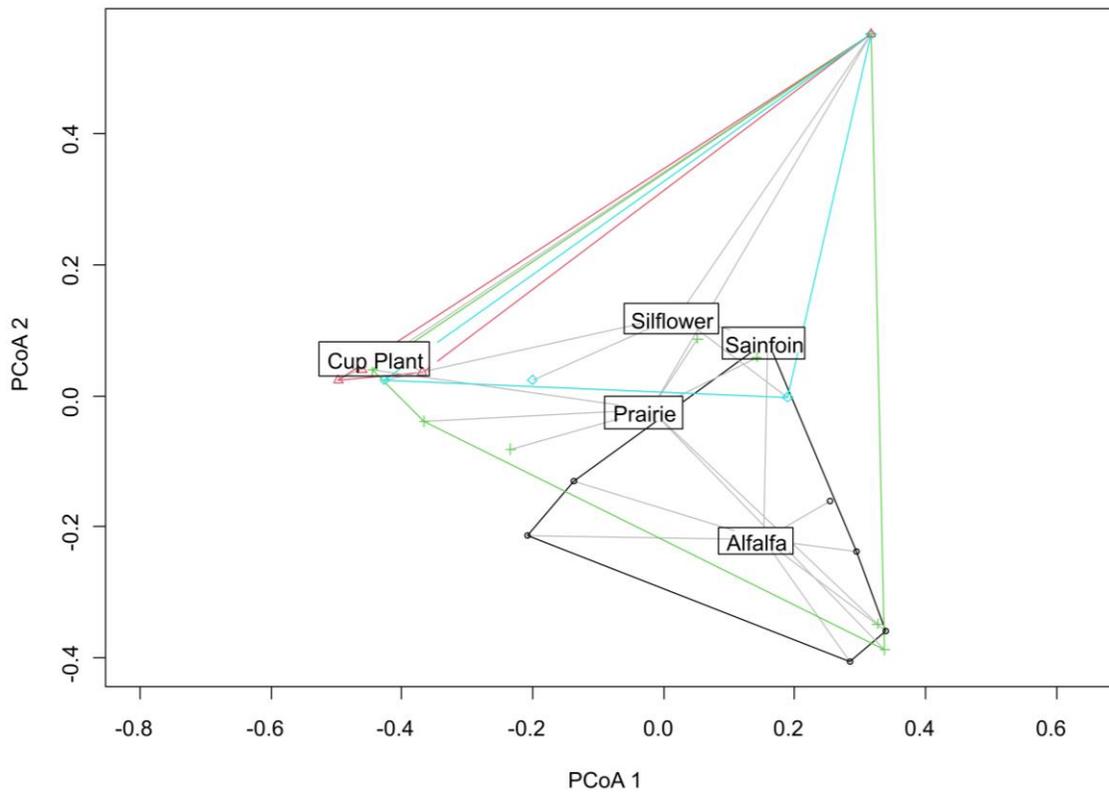
Figure 2.5. Alfalfa had significantly higher lepidopteran species richness than sainfoin. There were no other differences between treatments. Data collected in 2019 is represented in orange, and 2020 data is represented in blue. Lowercase letters denote differences between crop treatments.



Significant overall differences in community composition between crop treatments and year were found for the lepidopterans ($F_{4,26} = 1.43$, $p = 0.04$ and $F_{1,26} = 1.90$, $p = 0.04$, see Figure 2.6). The interaction between treatment and year was insignificant ($F_{3,26} = 0.65$, $p = 0.95$). Alfalfa was defined by *Cupido comyntas* (Lepidoptera: Lycaenidae) and *Epargyreus clarus* (Lepidoptera: Hesperiiidae), while sainfoin was only observed attracting two total lepidopteran individuals: *Echinargus isola* (Lepidoptera: Lycaenidae) and *Epargyreus clarus* (see Table 2.3).

The cup plant lepidopteran community was separate from other treatments, as it only attracted four total species over the two-year study: *Atalopedes campestris*, *Poanes zabulon*, *Epargyreus clarus* (Lepidoptera: Hesperiiidae), and *Vanessa cardui* or *V. virginiensis* (Lepidoptera: Nymphalidae). Silflower attracted a similar set of species, attracting mostly *Atalopedes campestris* and *V. cardui* or *V. virginiensis*, overlapping some with the cup plant community. Prairie attracted a high diversity of lepidopterans and overlapped with most other crop treatment communities, and attracted mostly *Epargyreus clarus*, *Helicoverpa zea* (Lepidoptera: Noctuidae), and *Atalopedes campestris*.

Figure 2.6. Lepidopteran community composition between the six difference crop treatments was significant.



Floral Resources

Crop treatments had significantly different floral resource areas ($F_{5,42} = 21.43$, $p < 0.01$) with prairie having the highest average floral area. Prairie and silflower had significantly more floral area than Kernza™ and sainfoin. Alfalfa, cup plant, and sainfoin had significantly higher floral area than Kernza™ but not sainfoin (see Figure 2.7, Table 2.5). All pollinator groups, whether considering abundance or species richness, increased significantly with floral area (see Table 2.6, Figures 2.8 a, b, and c). Overall pollinator abundance was the most strongly related pollinator group tied to floral abundance with an R^2 value (coefficient of determination) of 0.51 ($p < 0.01$, $F_{1,46} = 49.86$, while bee richness had the weakest relationship with floral area ($R^2 = 0.10$, $p = 0.02$, $F_{1,46} = 6.29$; Table 2.6). Abundance and richness results were very similar within each pollinator group (Table 2.6).

Figure 2.7. Floral area was significantly different between crop treatments.

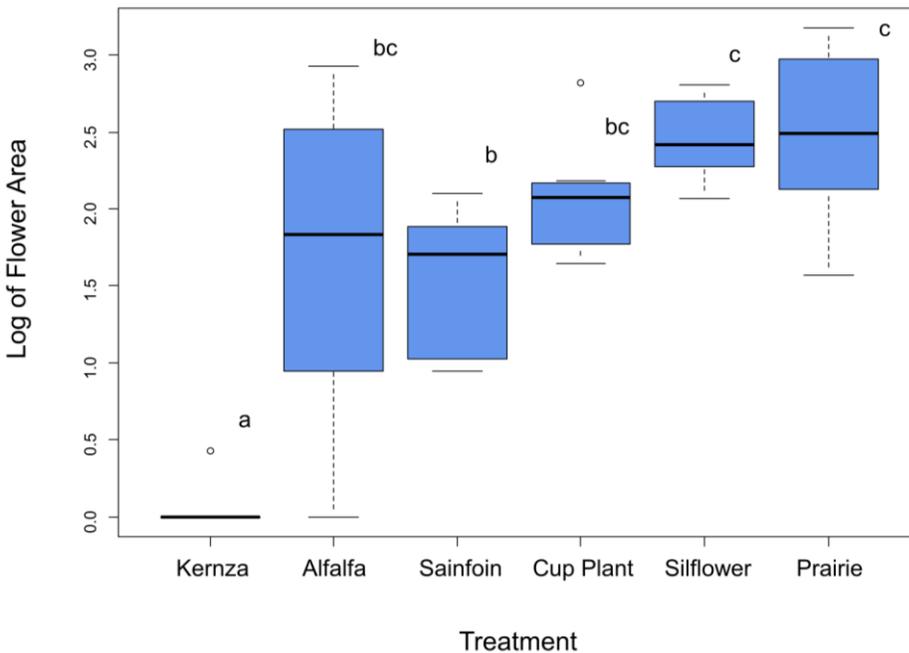
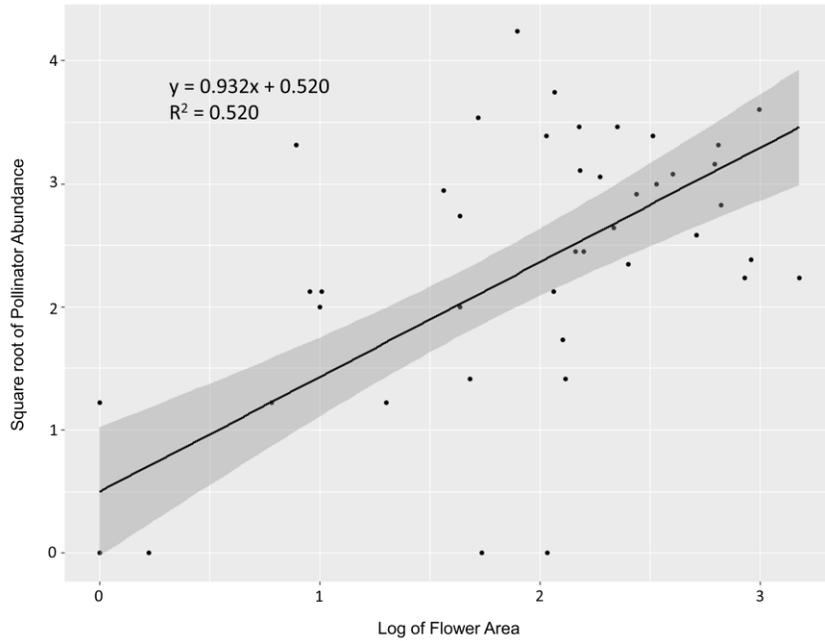
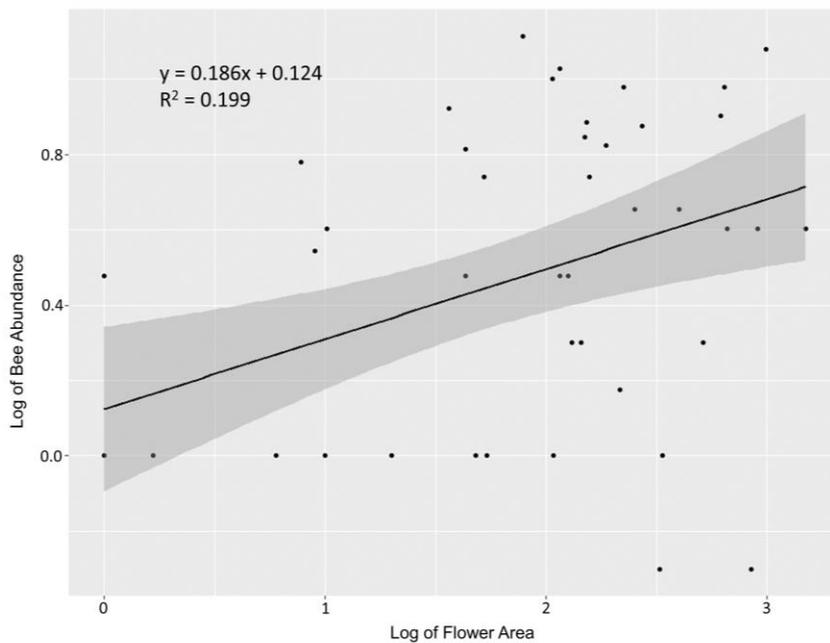


Figure 2.8. Three separate, simple linear regressions were ran for each pollinator group, with floral area as the predictor variable and the pollinator group as the response. Plot (A): Pollinator abundance increased significantly as floral area increased. (B): The relationship between bee abundance and floral area was weak but statistically significant. (C): Lepidopteran richness significantly increased with floral area.

A) Pollinator abundance



B) Bee abundance



C) Lepidopteran richness

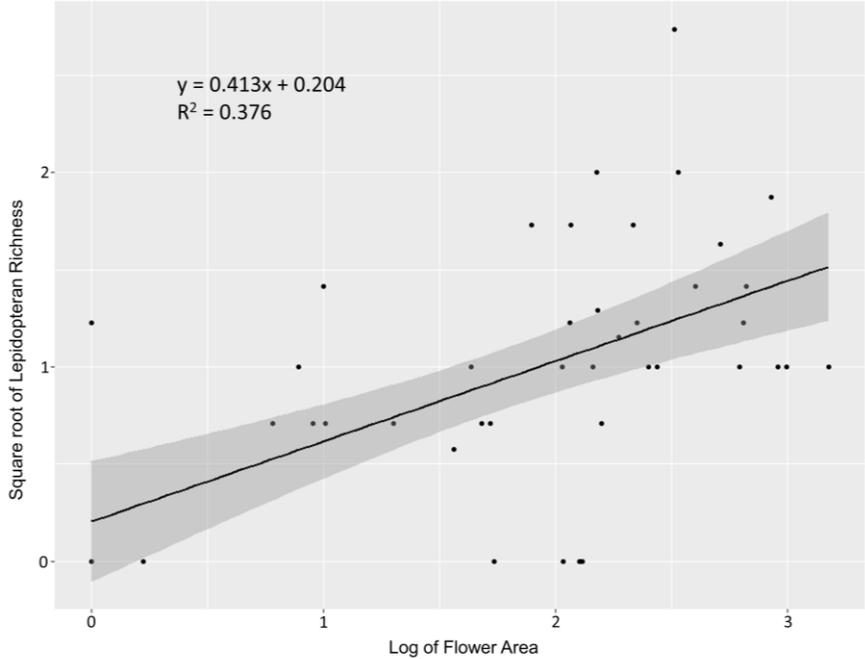


Table 2.5. Tukey HSD adjusted p-values comparing floral area between crop treatments. All treatments had higher floral area than Kernza™. Prairie had the highest floral area.

Treatment Comparisons	Adjusted P value
Cup plant-Alfalfa	0.7354958
Kernza-Alfalfa	0.0000078
Prairie-Alfalfa	0.0567182
Sainfoin-Alfalfa	0.992692
Silflower-Alfalfa	0.0749725
Kernza-Cup plant	0.0000001
Prairie-Cup plant	0.6364141
Sainfoin-Cup plant	0.3866676
Silflower-Cup plant	0.7103051
Prairie-Kernza	0
Sainfoin-Kernza	0.0000493
Silflower-Kernza	0
Sainfoin-Prairie	0.0133424
Silflower-Prairie	0.9999963
Silflower-Sainfoin	0.0184074

Table 2.6. Simple linear regression output for each pollinator group as a response to floral area.

Variable	Estimate	Standard Error	t-Value	p -value	R ²
Pollinator Abundance	0.932	0.132	7.061	< 0.0001	0.520
Pollinator Richness	1.074	0.221	4.862	< 0.0001	0.340
Bee Abundance	0.186	0.055	3.385	0.001	0.199
Bee Richness	0.105	0.042	2.508	0.016	0.120
Lepidoptera Abundance	0.145	0.049	2.989	0.004	0.163
Lepidoptera Richness	0.413	0.078	5.263	< 0.0001	0.376

Discussion

Overall, we found that cup plant, silflower, and prairie border crops, which are native to Kansas and are perennial flowering plants; attracted the highest overall pollinator abundance and species richness. Alfalfa attracted the highest abundance and richness of lepidopteran species only; it performed poorly for all other pollinator groups. Although our plot sizes were smaller than border strips that would be implemented into normal farming operations, we were able to compare the relative attractiveness of crop treatments to pollinators. We also found that the differences in pollinator attraction between years was significant, suggesting that as border crops establish, their attractiveness may vary with time. Different crops also had significantly different floral areas, or the number and size of inflorescences, giving us insight into why certain border crops may attract more pollinators than others. Studying the ability of crops to attract pollinators during their establishment year may provide valuable insight into the costs and benefits growers may experience during years of establishment for their border crops.

In terms of lepidopterans, alfalfa had significantly higher lepidopteran abundance and species richness compared to sainfoin. Kernza™ was left out of pollinator abundance and richness, bee richness, and lepidopteran abundance and richness analyses because it did not attract visitors. Alfalfa may have attracted a high amount of lepidopterans due to its flower morphology, as lepidopterans are attracted to red-pink flowers that grow in clusters in short, tube-like shapes; all of which are characteristic of alfalfa (Bancroft 2020).

Community composition was significantly different between treatments and year in regard to the overall pollinator community. The interaction between treatment and year was also significant. This reiterates that establishment periods for border crops can not only impact the ability of the crop to attract an abundance of pollinators, but also impact the community the crop

attracts between years. Cup plant and silflower pollinator communities usually had few overlapping species with sainfoin and alfalfa, as they attracted far more bee species. Prairie treatments overlapped with both the sunflower and legume groups, showing that prairies as border crops can attract a broader pollinator community. Kernza™ attracted a very low amount of pollinators, as expected considering it is an intermediate wheatgrass that is wind-pollinated. Alfalfa attracted a low amount of bee richness as well. While alfalfa attracted a high amount of lepidopterans, its pollinator community overlapped with other treatments and was not statistically different from prairie, silflower, or cup plant. When Kernza™ (and sometimes alfalfa and sainfoin, for bees and lepidopterans, respectively) were left out of community spread analysis, no significant differences in the variability within pollinator communities was observed. So while the different crop treatments had significantly different community composition, the variability within treatment communities did not differ greatly between treatments.

Specialty crop cultivation in the United States has been an area of focus and a place of financial incentives, such as the Specialty Crop Block Grant Program (SCBGP) (Gude et al. 2018, Walker 2021). Besides this, many crops grown throughout the US such as apples, almonds, blueberries, and squash are dependent upon insect pollination, and would benefit greatly from pollinator spillover from natural habitat facilitated by flowering border crops (Kremen et al. 2004). While row crops such as corn and wheat do not specifically rely on invertebrate pollination, soybeans, the crop with the second largest land area in the United States, may benefit significantly from insect pollination (USDA 2020, Garibaldi et al. 2021). Soybeans are flowering legumes, and yields were found to increase by an average of 21% if access to insect pollination was provided. The study also found that utilizing benefits from pollination

could offset millions of hectares being restored to natural habitat with no production losses (Garibaldi et al. 2021).

The implementation of specific border crops is dependent upon the needs of the grower, and the grower's main crop of concern. If the grower's main goal is to attract the most diverse set of pollinators over the course of the growing season, we suggest the implementation of a prairie mix such as the Pollinator Mix offered by the NRCS, as this crop treatment attracted the highest pollinator abundance and richness overall. Its long bloom period, high diversity of native prairie plants, and high floral area enable it to attract a wide variety and an abundance of both bees and lepidopterans throughout the growing season (Kremen and Miles 2012). If the grower is interested in having a high visitation rate of pollinators, but does not need a lengthy pollination period for their main crop, then silflower or cup plant could be implemented interchangeably. The sunflower crop treatments are also statistically comparable to prairie mixes in terms of the floral area they provide. This would be especially beneficial if the grower was interested in harvesting the border crop for one of the benefits previously mentioned in Table 1, such as fodder or biofuel, as cup plant and silflower have a similar pollinator visitation rate to prairie, but can be grown in monocultures and therefore will align more with traditional farming practices.

Year, as a predictor variable, significantly impacted overall pollinator abundance and bee abundance, while the interaction between treatment and year also significantly impacted bee species richness. This is mainly due to sainfoin attracting significantly higher pollinator and bee abundance in its second year of establishment (2020) compared to its first (2019). No other differences within crop treatments between years were significant. This improvement may be due to sainfoin being much more susceptible to weed invasion in its first year of establishment compared to its second year (Hybner 2013). This indicates that border crops are not equal in the

amount of time it takes for them to “pay back” any input costs in terms of pollinator attraction. Growers who need their border crops to establish within the first year of planting should choose a prairie mix or one of the sunflower border crops to attract a high amount of pollinators to their fields immediately. Growers who do not require an immediate pollination service payoff, or want to prioritize growing a perennial, anti-bloat forage for cattle, could implement sainfoin as a border crop, and can expect to see significant improvements in pollinator attraction in its second year of establishment.

When it comes to border crop implementation, growers may perceive a potential economic loss due to concerns of pest control, as the ability of border crops to attract or actually aid in controlling crop pests is still debated (Bianchi et al. 2006, Morandin and Kremen 2013). Our results indicate that border crops pose a small risk in attracting adult, lepidopteran agricultural pests, with only one major and one minor adult pest species caught throughout the two-year study (*Helicoverpa zea*, or “corn earworm” and *Colias eurytheme*, or “alfalfa caterpillar butterfly”), of which there were five and seven specimens caught in total, respectively, throughout the entire experiment. However, pest attraction was not a central goal to our experiment, and collecting sweep-net samples in our crop treatments will provide more conclusive results in terms of pest attraction.

Conclusion

We have found that border crops have the ability to increase the ecological intensification of agricultural landscapes by attracting high levels of pollinator abundance and species richness, especially if the border crops are native, flowering perennials. Depending on the main crop’s pollination needs and specific landowner goals, different border crops can be implemented to either attract high numbers of pollinators to crops through the implementation of native prairie

mixes, or planted to attract fairly high rates of pollinators through a monoculture of perennial border crops, such as silflower and cup plant, and harvested as a secondary crop. The different crop treatments tested offer flexibility to farmers and their goals, and therefore may be more readily implemented by growers that will benefit from attracting abundant and diverse sets of pollinators to their land.

Literature Cited

- Albrecht, M., D. Kleijn, N. M. Williams, M. Tschumi, B. R. Blaauw, R. Bommarco, A. J. Campbell, M. Dainese, F. A. Drummond, M. H. Entling, D. Ganser, G. A. de Groot, D. Goulson, H. Grab, H. Hamilton, F. Herzog, R. Isaacs, K. Jacot, P. Jeanneret, M. Jonsson, E. Knop, C. Kremen, D. A. Landis, G. M. Loeb, L. Marini, M. McKerchar, L. Morandin, S. C. Pfister, S. G. Potts, M. Rundlöf, H. Sardiñas, A. Sciligo, C. Thies, T. Tschardtke, E. Venturini, E. Veromann, I. M. G. Vollhardt, F. Wäckers, K. Ward, A. Wilby, M. Woltz, S. Wratten, and L. Sutter. 2020. The effectiveness of flower strips and hedgerows on pest control, pollination services and crop yield: a quantitative synthesis. *Ecology Letters* 23:1488–1498.
- Bancroft, K. 2020. Butterfly Pollination. United States Department of Agriculture. <https://www.fs.fed.us/wildflowers/pollinators/animals/butterflies.shtml>.
- Bianchi, F. J. J. A., C. J. H. Booij, and T. Tschardtke. 2006. Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. *Proceedings of the Royal Society B: Biological Sciences* 273:1715–1727.
- Blaauw, B. R., and R. Isaacs. 2014. Flower plantings increase wild bee abundance and the pollination services provided to a pollination-dependent crop. *Journal of Applied Ecology* 51:890–898.
- Borreani, E., P. Peiretti, E. Tabacco. 2003. Evolution of yield and quality of sainfoin (*Onobrychis viciifolia* Scop.) in the spring growth cycle. *Agronomie, EDP Sciences*, 23, 3, 193–201
- NRCS. Buffer Strips: Common Sense Conservation | Natural Resources Conservation Service. 2020. Date accessed: 3 March, 2020. https://www.nrcs.usda.gov/wps/portal/nrcs/detail/national/home/?cid=nrcs143_023568.
- Calderone, N. W. 2012. Insect Pollinated Crops, Insect Pollinators and US Agriculture: Trend Analysis of Aggregate Data for the Period 1992–2009. *PLoS ONE* 7:e37235.
- Cardoso, P., P. S. Barton, K. Birkhofer, F. Chichorro, C. Deacon, T. Fartmann, C. S. Fukushima, R. Gaigher, J. C. Habel, C. A. Hallmann, M. J. Hill, A. Hochkirch, M. L. Kwak, S. Mammola, J. Ari Noriega, A. B. Orfinger, F. Pedraza, J. S. Pryke, F. O. Roque, J. Settele, J. P. Simaika, N. E. Stork, F. Suhling, C. Vorster, and M. J. Samways. 2020. Scientists’ warning to humanity on insect extinctions. *Biological Conservation* 242:108426.
- Carlsson, G., K. Huss-Danell. 2003. Nitrogen fixation in perennial forage legumes in the field. *Plant Soil*. 253, 353–372.

- Gansberger, M., L. F. R. Montgomery, P. Liebhard. 2015. Botanical characteristics, crop management and potential of *Silphium perfoliatum* L. as a renewable resource for biogas production: A review. *Ind. Crops Prod.* 63, 362–372.
- Garibaldi, L. A., L. A. Schulte, D. N. Nabaes Jodar, D. S. Gomez Carella, and C. Kremen. 2021. Time to Integrate Pollinator Science into Soybean Production. *Trends in Ecology & Evolution* 36:573–575.
- Gude, K., C. L. Rivard, S. E. Gragg, K. Oxley, P. Xanthopoulos, and E. D. Pliakoni. 2018. Day-neutral Strawberries for High Tunnel Production in the Central United States. *HortTechnology* 28:154–165.
- Howarth, R. E., B. P. Goplen, A. C. Fesser, S. A. Brandt. 1978. A Possible Role for Leaf Cell Rupture in Legume Pasture Bloat. *Crop Sci.* 18, 129–133.
- Hybner, R. M. 2013. SAINFOIN *Onobrychis viciifolia* Scop. Natural Resources Conservation Service MT-91:6.
- Jefferson, P. G., W. P. McCaughey, K. May, J. Woosaree, and Li. McFarlane. 2004. Forage quality of seeded native grasses in the fall season on the Canadian Prairie Provinces. *Canadian Journal of Plant Science* 84:503–509.
- Kim, J., N. Williams, and C. Kremen. 2006. Effects of Cultivation and Proximity to Natural Habitat on Ground-nesting Native Bees in California Sunflower Fields. *Journal of the Kansas Entomological Society* 79:309–320.
- Klein, A.-M., I. Steffan-Dewenter, and T. Tscharntke. 2003. Fruit Set of Highland Coffee Increases with the Diversity of Pollinating Bees. *Proceedings: Biological Sciences* 270:955–961.
- Klein, A.-M., B. E. Vaissière, J. H. Cane, I. Steffan-Dewenter, S. A. Cunningham, C. Kremen, and T. Tscharntke. 2007. Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B: Biological Sciences* 274:303–313.
- Kremen, C., and A. Miles. 2012. Ecosystem Services in Biologically Diversified versus Conventional Farming Systems: Benefits, Externalities, and Trade-Offs. *Ecology and Society* 17.
- Kremen, C., N. M. Williams, R. L. Bugg, J. P. Fay, and R. W. Thorp. 2004. The area requirements of an ecosystem service: crop pollination by native bee communities in California: Area requirements for pollination services to crops. *Ecology Letters* 7:1109–1119.

- Kremen, C., N. M. Williams, and R. W. Thorp. 2002. Crop pollination from native bees at risk from agricultural intensification. *Proceedings of the National Academy of Sciences* 99:16812–16816.
- League, K. R. 2004. *Dalea purpurea*. USDA, Forest Service. <https://www.fs.fed.us/database/feis/plants/forb/dalpur/all.html>.
- Mallinger, R. E., J. Bradshaw, A. J. Varenhorst, and J. R. Prasifka. 2018. Native Solitary Bees Provide Economically Significant Pollination Services to Confection Sunflowers (*Helianthus annuus* L.) (Asterales: Asteraceae) Grown Across the Northern Great Plains. *Journal of Economic Entomology* 112:40–48.
- Michigan State, E. 2021. *Liatris punctata* (Dotted blazing star) - Michigan Natural Features Inventory. University. <https://mnfi.anr.msu.edu/species/description/13584/Liatris-punctata>.
- Morandin, L. A., and C. Kremen. 2013. Hedgerow restoration promotes pollinator populations and exports native bees to adjacent fields. *Ecological Applications* 23:829–839.
- Morandin, L. A., R. F. Long, and C. Kremen. 2016. Pest Control and Pollination Cost–Benefit Analysis of Hedgerow Restoration in a Simplified Agricultural Landscape. *Journal of Economic Entomology* 109:1020–1027.
- Native Plant Trust. 2021. *Helianthus maximiliani* (Maximilian’s sunflower): Go Botany. <https://gobotany.nativeplanttrust.org/species/helianthus/maximiliani/>.
- NC State, E. 2021. *Salvia* (Sage) | North Carolina Extension Gardener Plant Toolbox. University. <https://plants.ces.ncsu.edu/plants/salvia/>.
- Oksanen, F., G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P. Minchin, R. B. O’Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, E. Szoecs, H. Wagner. 2019. *Vegan: Community Ecology Package*. R package version 2.5-6. <https://CRAN.R-project.org/package=vegan>.
- Parker, F. D. 1981. How Efficient Are Bees in Pollinating Sunflowers? *Journal of the Kansas Entomological Society* 54:61–67.
- Portman, Z. M. and Arduser, M. 2019. Key to the *Agapostemon* of eastern North America. Accessed 9 March 2020.
- Potts, S. G., B. Vulliamy, A. Dafni, G. Ne’eman, and P. Willmer. 2003. Linking bees and flowers: how do floral communities structure pollinator communities? *Ecology* 84:2628–2642.

- Pywell, R. F., M. S. Heard, B. A. Woodcock, S. Hinsley, L. Ridding, M. Nowakowski, and J. M. Bullock. 2015. Wildlife-friendly farming increases crop yield: evidence for ecological intensification. *Proceedings of the Royal Society B: Biological Sciences* 282:20151740.
- Schlautman, B., S. Barriball, C. Ciotir, S. Herron, A. Miller. 2018. Perennial Grain Legume Domestication Phase I: Criteria for Candidate Species Selection. *Sustainability*. 10, 730.
- Schramm, P. 1990. Proceedings of the 12th North American Prairie Conference: recapturing a vanishing heritage 169–177.
- USDA, N. A. S. S. 2020. Crop Production 2020 Summary 01/12/2021. *Crop Production*:125.
- Vilela, A., L. González-Paleo, K. Turner, K. Peterson, D. Ravetta, T. E. Crews, D. Van Tassel. 2018. Progress and Bottlenecks in the Early Domestication of the Perennial Oilseed *Silphium integrifolium*, a Sunflower Substitute. *Sustainability*. 10, 638.
- Walker, J. 2021, April 26. Specialty Crop Grant Opportunity. <https://agriculture.ks.gov/news-events/news-releases/2021/04/26/kansas-department-of-agriculture-announces-specialty-crop-grant-opportunity>.
- Weaver, J. E., L. A. Stoddart, W. Noll. 1935. Response of the Prairie to the Great Drought of 1934. *Ecology*. 16, 612.
- Williams, N. M., E. E. Crone, T. H. Roulston, R. L. Minckley, L. Packer, and S. G. Potts. 2010. Ecological and life-history traits predict bee species responses to environmental disturbances. *Biological Conservation* 143:2280–2291.
- Williams, P., Thorp, R., Richardson, L., and Colla, S. 2014. *Bumble bees of North America: An Identification Guide*. Princeton University Press, Princeton, NJ.
- Winfree, R., N. M. Williams, J. Dushoff, and C. Kremen. 2007. Native bees provide insurance against ongoing honey bee losses. *Ecology Letters* 10:1105–1113.
- Winfree, R., N. M. Williams, H. Gaines, J. S. Ascher, and C. Kremen. 2008. Wild bee pollinators provide the majority of crop visitation across land-use gradients in New Jersey and Pennsylvania, USA. *Journal of Applied Ecology* 45:793–802.
- Wratten, S. D., M. Gillespie, A. Decourtye, E. Mader, and N. Desneux. 2012. Pollinator habitat enhancement: Benefits to other ecosystem services. *Agriculture, Ecosystems & Environment* 159:112–122.

Conclusion

Overall, we found that management strategies that benefit one group of pollinators does not necessarily benefit other pollinator groups, although in general there are two main management strategies that seem to have clear, positive impacts on pollinator communities: bison grazing, and the implementation of native flowering plants within the agricultural landscape.

For our first objective, we utilized a piecewise structural equation model to measure the causal effects of fire and grazing on pollinators and their habitat, and to measure how fire and grazing impact pollinators through cascading effects through their impact on nesting and foraging habitats (forb richness). We found that bison grazing had a direct, positive effect on most pollinator groups, and also indirectly impacted pollinators through its effects on the amount of bare ground, soil compaction, and forb species richness. Fire had no direct impacts on pollinators, but had cascading effects through its impact on the amount of bare ground and soil compaction. Our findings indicate that the effects of fire and grazing on habitat characteristics affect different groups of pollinators, and that landowners may have to choose a focal group of pollinators to support when deciding between management strategies.

For our second objective, we tested six candidate border crops and found that native, flowering border crops such as prairie mixes, silflower, and cup plant attracted the highest abundance and species richness of overall pollinator groups and bees. Nonnative crops such as alfalfa and sainfoin were poor at attracting bees and most pollinators overall. Year also significantly impacted pollinator attraction, indicating that the establishment period of border crops must be taken into consideration when choosing which crop to implement. Depending

upon grower goals, different border crops can be utilized to obtain different pollination and ecosystem services.

Our overall findings indicate that landowners have a plethora of options when it comes to implementing management strategies that benefit both their land and wild pollinator communities. However, not all management strategies are equal in terms of which pollinator group is supported, and the overall goals can be complicated by the many indirect effects management can have on pollinator habitat. Our findings present options for management practices at the intersection of conservation and agriculture, and provide insight for sustainable strategies that support pollinator communities and the beneficial services they provide.