The Revery Alone Won't Do: Fire, Grazing, and Other Drivers of Bee Communities in Remnant Tallgrass Prairie

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Nora Pennarola

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Acknowledgement:

This research was conducted on the colonized homelands of the Anishinaabe, Dakota, and Lakota peoples, who are still here.

Dedication

To Anya, for who you are

To my child, for whoever you become

To Nora, for the courage to see it through

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Bees and their decline:

Bees (Hymenoptera: Anthophila) consist of some 20,000 species within 7 families (Bartomeus et al. 2013). They arose approximately 130 MYA from within the wasp family Crabronidae (Debevec et al. 2012). The evolution of bees, which rely upon floral resources throughout their lifecycles, is associated with the radiation of Angiosperms (Grimaldi 1999). These two groups have evolved in tandem, with bees serving as highly efficient vectors for pollen transfer. While many other insect (and non-insect) taxa visit flowers and transfer pollen between individuals, bees are considered the most important pollinators given their frequency of floral visitation and the diversity of flowers visited (Grimaldi 1999).

There are currently 418 species of bees known to occur in Minnesota (Minnesota DNR 2016). These include social and solitary bees, ground-nesting and aboveground-nesting bees, pollen collecting and kleptoparasitic bees, large and small bees. These bees provide pollination services in all ecosystems within the state, from the boreal forests to the oak savannahs and prairies. Without their facilitation of pollen transfer, many flowering plants would either be unable to produce seeds or be set on a path to lose genetic diversity through selfing. Many crops are also reliant upon or benefitted by bee pollination (Klein et al. 2007). In 2017, the United States Department of Agriculture estimated the cost to pollinate 34 crops in the US at $319,604,000 (USDA 2017). The cost of pollinating almonds alone was over $253,000,000. These figures were based only upon honey bee (*Apis mellifera*) pollination and thus did not include any contribution by bumble bees or other native bees. However, non-*Apis* bee pollination was associated with higher fruit set, regardless of honey bee pollination (Garibaldi et al. 2014). The contributions of wild bee pollinators should not be discounted.

Lately, there have been worries about bee decline. Honey bees, which in North America are a non-native domesticated animal, have seen significant attention. In the winters of 2006/2007 and 2007/2008, bee keepers saw unusually high mortality in their hives (vanEngelsdorp et al. 2009). A number of causes were speculated to be the culprit of the phenomenon, dubbed "colony collapse disorder"; viruses, bacteria, protozoa, fungi, mites, pesticides, genetically modified crops, stress from excess transport, and cool nest temperatures were all proposed as possible explanations (Cox-Foster et al. 2007, Oldroyd 2007). Leading experts, including Dennis vanEngelsdorp, no longer consider colony collapse disorder a major threat to commercial honey bees in the USA (Milius 2018), though it persists in the cultural zeitgeist (Romo 2018).

The picture for non-*Apis* bees is a bit murkier. Among these, bumble bees (genus *Bombus*) have seen the most intensive study. In Europe, declines of bumble bees have been well-documented (Goulson et al. 2008), as have taxa-wide declines in bee species richness. Solitary, oligolectic species have suffered the most in Britain, whereas long-tongued species have been in decline in The Netherlands (Biesmeijer et al. 2006). In the northeastern US, records show declines in some bumble bee species compared to historic samples (Bartomeus et al. 2013). Certain species, particularly *Bombus affinis, B. pensylvanicus,* and *B. ashtoni* have declined dramatically (Colla and Packer 2008). It was also shown that bees with a narrow diet breadth and short flight period are declining in relative abundance. Bumble bee species richness in Illinois has declined over the course of the 20th century, even without accounting for the dramatically increased survey efforts in recent decades (Grixti et al. 2009). Several pathogens, including fungi such as *Nosema bombi*, are believed to be partially responsible for bumble bee declines (Cameron et al. 2011). Much attention has been given to pesticides as well (USFWS 2016). Bees can encounter pesticides in the environment while foraging for food, including systemic pesticides that are incorporated into nectar or pollen. As bee larvae are all provisioned with floral resources, bees may be exposed to these compounds across all stages of development. These chemicals can be lethal or produce sublethal effects, including reduced male production, egg hatch, queen production, queen lifespan, brood production, feeding, ovary development, and worker size; and increased risky behaviors (USFWS 2016). Particularly of interest are neonicotinoid pesticides. These compounds, which work as insect neurotoxins, have seen greatly increased usage since the turn of the century. They can be applied to crop seeds and become incorporated into plant tissues. Neonicotinoids also accumulate in soils. Many bumble bees nest underground, possibly increasing their exposure to these chemicals even further. The increased adoption of neonicotinoid pesticides is strongly correlated with the decrease in at least one bumble bee species – the rusty-patched bumble bee (*Bombus affinis*) (USFWS 2016).

In January 2017, the United States Fish & Wildlife Service (USFWS) placed the rusty-patched bumble bee under the protection of the Endangered Species Act. Having been one of the bumble bees with the highest relative abundance some twenty years ago, *B. affinis* is now rarely found across most of its historic range. It is believed that a number of factors is responsible for this decline: extensive loss of grassland habitats, agricultural intensification, changes in pesticide practices, and the deleterious effects of small population sizes. In the FWS's species assessment (2016), it was reported that *B. affinis* has declined from representing 8% of total *Bombus* observations to approximately 1%. Looking spatially, the number of counties occupied had decreased by 89%. This recent listing should serve as a wake-up call; common species do not always stay common.

One major issue with assessing declines in native bees is a lack of longitudinal studies that look at the entire suite of bees in a given area. There do exist some data sets, however, that can be plumbed for insights. In the late 19th century, Charles Robertson collected extensive information on insect-plant interactions, including bee visitation, in Carlinville, Illinois (Burkle et al. 2013). This same area was sampled in the 1970's and again in 2009-2010. During this period, the historic forests and prairie were mostly converted to agriculture. A 2013 follow up to Roberston's collections documented which of the bee-forb interactions persisted from the initial study, which were lost, and any novel plant-bee interactions that were not originally observed (Burkle et al. 2013). Of the original 532, only 125 persisted. There were an additional 121 novel interactions, meaning that "the absolute difference of interactions lost was 46% (246 of 532)" (Burkle et al. 2013, page 1612). Nearly half of the lost interactions were due to the extirpation of the bee involved in the interaction. They found that specialists, cavity-nesters (including bees within the family Megachilidae), and parasites (including bees in the genus *Nomada*), were more likely to have disappeared. The persisting bees have greater phenological overlap with their associated forbs. This in part echoes the models of Bartomeus et al. (2013) which showed "species with a small dietary breadth [and] narrow phenological breadth" were more likely to be in decline (Bartomeus et al. 2013, page 4658).

In order to combat these trends, conservation efforts are underway. For bees, these generally take the form of habitat protection and enhancement. Unlike most mammalian megafauna, which produce few offspring, each requiring high energetic investment, bees generally produce many offspring, each at a low energetic cost. Therefore, while it may be worthwhile to protect individual elephants from poaching or disease, bee conservation usually cannot be so targeted. Rather, efforts are focused on habitats; if the right (and uncontaminated) food sources and nesting sites are available at the right times of the year, bees of concern should be able to make use of a habitat.

Tallgrass prairie in Minnesota:

Tallgrass prairie once covered some 170 million acres in central North America, stretching from the Gulf Coast well into modern-day Manitoba (Samson and Knopf 1994). It was akin then to a vast sea of grass with scattered stands of trees, particularly along the riparian corridors that meandered through it, and the numerous prairie-pothole lakes. Receiving more precipitation than the grasslands further west, tallgrass prairie is characterized by vegetation that can reach over 2 meters in height (Anderson 2006). While dominated by graminoids such as big bluestem (*Andropogon gerardii*), Indian grass (*Sorghastrum nutans*), and switch grass (*Panicum virgatum*), tallgrass prairie supports an extensive forb community (Damhoureyeh and Hartnett 1997, Moranz et al. 2014). In turn, this supports an array of insect pollinators, including bees, butterflies, moths, beetles, and flies. This is a landscape reliant on disturbance; left uninhibited, woody plant growth quickly converts prairie into savannah and forest. Historically, this disturbance was supplied by fire, bison (*Bison bison*), and drought (Anderson 2006, Allred et al. 2011, Middleton 2013). In the 10,000 years between the last glacial maximum and the 19th century, this balance persisted.

Prior to European settlement, fires, set either by lightning or native peoples, would have periodically burned through great swathes of prairie, removing woody material and accumulated fuel (Anderson 2006, Middleton 2013, Moranz et al. 2014). Prairies with exposed soil heat up faster than those with layers of decaying grass, meaning that many plants start growing earlier in the spring following burns (Vogel et al. 2010). Layers of dead biomass can also prevent atmospheric nitrogen from making its way into the soil, making unburned prairies more nitrogen limited (Anderson 2006). Grasses can tolerate most prairie fires, as their meristems are located below ground, where temperatures do not rise to a lethal level. Shrubs and trees, in contrast, have meristems that are exposed to fire (Anderson 2006). Fire can be fatal to these plants and those that do survive will have suffered energetically from the loss of tissue. By returning nutrients to the soil, exposing soil to nitrogen deposition and light, fires spur new growth. Native Americans used this to their advantage to keep prairies open, promoting grazer populations and easing hunting (Anderson 2006). Grazers, predominantly bison, roamed the landscape, foraging and providing additional disturbance and seed dispersal (Kohl et al. 2013). Bison preferentially feed on young plants, leaving less nutritious, older vegetation alone. They also tend to ignore forbs, leading to more diverse floral communities (Collins et al. 1998). In their yearly migrations, bison return to most favored patches, continually disturbing these areas. By creating a patchwork of grazed and ungrazed prairie, they fostered further diversity (Knapp et al. 1999, Harmon-Threatt and

Chin 2016). Every year, some patches would be abandoned and others adopted, meaning areas would not become irreparably over-grazed (Knapp et al. 1999). Bison also return nitrogen to the environment through their urine (Day and Detling 1998).

Drought is driven primarily by climatic factors rather than factors impacted by European settlers. Therefore, while the climate has changed and continues to change, the mechanisms by which drought impacts prairie remnants would have occurred as it does today. Lakebed soil samples show that over the 4500 years before the present, droughts are associated with decreased deposition of charcoal and grass pollen as compared to wetter years (Clark et al. 2002, Brown et al. 2005). This suggests that droughts decrease the frequency of grassland burns, possibly due to a decrease in grass growth resulting in a diminished fuel load. Droughts can be important in weakening or killing trees (Anderson 2006). Grasses, which have relatively shallow roots as compared to trees, can be more quickly replenished by rains that occur during droughts. Trees must wait for deep soil moisture to be recharged. The interplay of drought effects on grasslands have been important in shaping this ecosystem.

Today, approximately 200 years since first European settlement of Minnesota, less than 1% of native tallgrass prairie remains (Samson and Knopf 1994). While once compared to a sea, it now resembles an archipelago, fragmented by agriculture, development, and highways. The processes that had kept woody growth in check can no longer function in such a landscape (Samson et al. 2004). Bison have been extirpated from most of their native range and fires are not left to sweep across the acres of crops, homes, and highways that may separate prairie fragments. Therefore, if this imperiled habitat is to persist going forward, disturbance must occur on a fragment by fragment basis, and be provided by humans.

Prescribed burns are one method of providing disturbance. Like natural fires, these burns remove woody plant growth and accumulated fuel. Many weedy plant species have not evolved in ecosystems so shaped by fire, making burns an effective tool at fighting back this growth (Harmon-Threatt and Chin 2016). Additionally, when resources for habitat improvement are scarce, land managers can burn a prairie once every few years to keep succession at bay without additional effort (S. Vacek 2016, pers. comm). This also induces recruitment from the soil seed bank, which may hold natural diversity that has been crowded out at a site (Davies et al. 2013). There is uncertainty in the landscape level effects of current fire management given the high levels of fragmentation (Driscoll et al. 2010). In a vast connected prairie system, it would be possible for species to disperse into burned patches from surrounding, unburned areas. Now, with many prairie fragments seemingly isolated from one another, those dispersal corridors may not function.

Another means by which land managers replicate historic disturbance is domestic cattle grazing. While taxonomically close relatives (both fall within the subtribe Bovina), cows (*Bos taurus*) graze differently than bison (Anderson 2006, Allred et al. 2011, Kohl et al. 2013). Whereas bison avoid woody areas, cows preferentially spend time in these areas, either grazing or resting (Allred et al. 2011). Cows will also graze near water sources such as ponds and streams, while bison will travel to water sources specifically to drink (Kohl et al. 2013). If stocked at too-high rates, this can lead to the degradation of riparian areas and increased vulnerability to invasive plant species (Bear et al. 2012).

However, cows are plentiful in the American landscape. Dairy and beef cows are an important part of the agricultural economy, and a great deal of plant biomass is necessary to support these herds. Increasingly, cattle are employed by land managers as a means of grassland conservation, with reduced stocking rates and the intention of preventing overgrazing (Moranz et al. 2012). This has the double benefit of providing both land managers with the disturbance needed to prevent succession and cattle-owners with forage for their herds. However, the effects of cattle grazing on prairie remnants are not as well documented as those of prescribed burns. Given the massive decline in prairie cover and its highly fragmented distribution, mismanagement can have serious consequences.

Bees' responses to management:

Grasslands burns can have differing effects on bees. Those that nest underground can tolerate most burns, provided fires don't burn too hotly or move too slowly; as long as bees nest 10cm or more below the ground, most grassland fires should not be lethal (Cane and Neff 2011). Given that 75% of mining bees place at least some of their young deeper than this threshold (Cane and Neff 2011), it can be assumed that ground-nesting species are at least partially tolerant of fire. In removing vegetation and exposing more bare ground, fires also serve to create more ground-nesting bee habitat (Potts et al. 2005). Burns can also increase the length of the flowering season (Wrobleski and Kaufman 2003) which in turn has beneficial impacts on bumble bees which have relatively long flight periods (Mola and Williams 2018). The increased flowering season length documented by Mola and Williams (2018) was not explained by a shifting floral community; rather the same plant species seen unburned sites flowered longer at burned sites. This benefit may be passed to other generalist bees, which rely upon different flowers throughout their flight periods.

Species nesting aboveground are more negatively impacted by recent burns than ground-nesters (Williams et al. 2010). Mortality doesn't just come from the combustion of nests – while not looking at bees, Tooker and Hanks (2004) found that very few endophytic wasps emerged from nests that were left intact during burns, as compared to nests collected from non-burned prairies. In the years following burns, populations of the study organisms did return, though at significantly lower densities. Within sites, distance from unburned edges had no impact on occurrence in years following burns. Stem nesters generally fare better when fire is infrequent (Davis et al. 2008). Interestingly, there is evidence that ground-nesting bees are more negatively impacted when burns are infrequent, possibly due to dense vegetation growth following burns (Williams et al. 2010). In Mediterranean landscapes, stem-nesting bees are most abundant 10 years after fires, when pithy-stemmed shrubs dominate the plant community (Potts et al. 2005). Bees nesting in cavities in wood, such as a repurposed beetle gallery, respond in more complex ways as the conditions of the fire can have different effects on wood. If the cambium layer beneath the bark is extensively damaged, beetles may not bore into trees, meaning that fewer nesting sites may be available (Cane and Neff 2011). However, burns that damage living woody plants may increase their susceptibility to beetle infestation and eventual bee residence.

Grazing has been less well studied than burning. Kimoto et al. (2012) found no significant difference in overall bee abundance with regard to grazing intensity in central Oregon prairies. There were differences between some taxonomic groups though, with grazing intensity more negatively impacting *Bombus* abundance than *Lasioglossum* abundance. Kimoto et al. speculate that this may be due to differences in foraging behaviors; large-bodied bumble bees can travel greater distances than small-bodied sweat bees, meaning bumble bees may be better equipped to seek out higher quality floral resources occurring in non-grazed areas in the surrounding environment, leading to decreased bumble bee abundance. Smaller-bodied bees, such as *Lasioglossum*, may be unable to forage much beyond the confines of these grazed prairies, or they may in fact be seeing positive effects on nesting habitats due to grazing. The increased occurrence of bare soil and increased soil compaction may provide better nesting sites. In Kimoto et al. study (2012) total species richness did not significantly differ. However, increased grazing intensity was associated with lower Shannon diversity of bees in the early season. This seemed to be related to declines in floral resources, though changes in soil characters are also a possible additional explanatory factor. Likewise, Sjödin (2007), observed that flower visitor (which included bees along with beetles, flies, true bugs, wasps, ants, moths, butterflies, and scorpionflies) abundance was positively correlated with taller vegetation and increased floral abundance, meaning that under grazing's shortened vegetation and decreased floral abundance, bee abundance was suppressed. These findings are not universal however. Carvell (2002) found that bumble bees were found in higher abundances in pastures grazed by cattle within the past year as compared to pastures that had gone at least one year without cattle grazing, pastures that were sheep-grazed, disturbed edges, unmanaged edges, and reverting arable land.

Conclusion

The bee community in Minnesota's tallgrass prairie is doubly threatened. The conversion of prairie to agriculture and development has fragmented the landscape nearly beyond recognition. Over vast swathes of the state, single species exist in monocultures where once highly diverse grasslands grew. On top of this, bees across the continent face pressures from parasites, pathogens, and pesticides.

The pockets of remnant prairie that persist are dependent on human-mediated disturbance. Grazing and burning, which can be seen as analogues to historic disturbance patterns, are effective and important tools in maintaining prairie health. Through this thesis, I seek to parse out the differing impacts of these two management techniques on bee communities and to explore how environmental characteristics impact the suite of traits bees display in remnant prairies.

Note on format: As the following two chapters have been written with the intent of publication, there is some necessary overlap between this introduction and the introductions of the chapters. The two chapters also overlap in their methods.

Chapter 1: The role of fire and grazing in driving patterns of bee abundance, species richness, and diversity

Synopsis:

Bee communities globally face a litany of threats, including pesticides, pathogens, and habitat loss. One North American habitat that has seen extensive conversion in the time since European settlement is the tallgrass prairie. Wildfires and bison grazing, which historically prevented succession from grassland into savannah or forest, have been functionally removed from this landscape and prescribed fire and cattle grazing are now employed by land managers to mimic the historic patterns of disturbance in prairie remnants. Using directed netting and pan traps, I surveyed the bee community of 20 tallgrass prairie remnants in Minnesota. Sites were visited three times in the summers of 2016 and 2017. The plant community was surveyed using nested frequency plots and soil texture was assessed at each study site in 2016 and 2017. Analyses show that management type is not a significant predictor of bee abundance, species richness, or diversity. The frequency of forbs and the proportion of sand in soils have significant positive correlations with bee abundance, richness, and diversity. The bee communities of tallgrass prairie remnants with a ten year history of grazing or burning do not significantly differ, giving land managers flexibility in their habitat management decisions.

Introduction

Bees globally face growing threats (Colla et al. 2006, Colla and Packer 2008, Cameron et al. 2011, Goulson et al. 2008, Grixti et al. 2009, Potts et al. 2010, Oldroyd 2007, vanEngelsdorp et al. 2009). Declines in abundance and species richness have been tied to various causes, including pesticides, pathogens, parasites, and poor nutrition (Brown and Paxton 2009, Cameron et al. 2011, Colla and Packer 2008, Goulson et al. 2008, Goulson et al. 2015, Potts et al. 2010, vanEngelsdorp et al. 2009). As with many insects, declines are also tied to habitat loss and conversion (Brown and Paxton 2009, Colla and Packer 2010, Goulson et al. 2008, Potts et al. 2010). In central North America and in Minnesota in particular, one ecosystem that has declined precipitously is the tallgrass prairie (Samson and Knopf 1994, Samson et al. 2004, Anderson 2006).

At the time of European settlement (~1775-1800 CE), tallgrass prairie covered approximately a third of Minnesota, representing the edge of a vast grassland in the heart of North America. Tallgrass prairie, while dominated by graminoids such as big bluestem (*Andropogon gerardii*), Indian grass (*Sorghastrum nutans*), and switch grass (*Panicum virgatum*), supports an extensive forb community and its associated insect pollinators (Damhoureyeh and Hartnett 1997, Moranz et al. 2014). In the intervening centuries, native tallgrass prairie in the state has nearly completely disappeared; less than 1% remains, and that which persists is fragmented by agriculture, development, and highways (Samson and Knopf 1994). This is a landscape shaped by and reliant upon disturbance; left uninhibited, woody plant growth can convert prairie into savannah and forest in a matter of decades. Disturbance can also increase the density and abundance of floral resources (Mola and Williams 2018). Historically, this disturbance was supplied by fire, bison (*Bison bison*), and drought (Anderson 2006, Allred et al. 2011). Bison have been extirpated from most of their native range and fire suppression practices prevent natural fires from spreading between fragments that may be separated by miles by cropland, homes, and roads (Samson et al. 2004). Land managers now supply disturbance on a fragment by fragment basis, typically through prescribed fire and conservation grazing.

Fire can affect tallgrass prairie vegetation and bee communities through various means. Fires remove accumulated fuel and expose soil to radiation and to atmospheric nitrogen deposition (Allred et al. 2011). Grasses, with their meristems below ground, can tolerate most prairie fires as their regions of growth are protected from the majority of the heat (Anderson 2006). Shrubs and trees, in contrast, have terminal meristems that are exposed to fire. Fires are more likely to be fatal to these plants, and any that survive will require significant energy to replace lost tissue. This keeps woody growth in check. This can also be used to control invasive gramminoids, like Kentucky bluegrass (*Poa pratensis*) and smooth brome (*Bromus inermis*). These plants have come to dominate many prairie fragments, forming dense mats of vegetation that may inhibit bees' access to the soil. By burning in the late spring, after these plants have invested much energy into growing, managers can set them back, requiring them to draw upon reserves to regrow (Salesman and Thomsen 2011). This can allow less dominant, native graminoids a chance to take back a prairie fragment. Many forbs within the seedbank will also emerge following fires (Davies et al. 2013), though overly frequent fires may suppress forb diversity (Damhoureyeh and Hartnett 1997). Depending on where they build their nests, grassland fire can have differing effects on bees. Those that nest 10cm or deeper underground (which accounts for 75% of ground-nesting taxa) can tolerate most fires, provided they don't burn too hotly or move too slowly (Cane and Neff 2011). For aboveground nesters, which can nest in a variety of substrates such as cavities in rocks, repurposed beetle galleries in dead trees, and dead hollow or pithy stems, fire mortality arises from both the combustion of nests and from lethal temperatures (Tooker and Hanks 2004). Fire frequency can also be important. In a review of bees' responses to environmental disturbances, Williams et al. (2010) documented lower ground-nesting bee abundance in burned sites than unburned controls, but ground-nesting bee abundance was significantly lower in sites that had been burned >20 years prior to their study as compared to sites burned within the past five years. Conversely, species nesting aboveground were relatively more abundant in sites with older burns than in those with burns within the past five years following burns (Williams et al. 2010).

While tallgrass prairie was historically shaped by bison grazing, that has been largely replaced by domestic cows (*Bos taurus*), which graze differently than bison (Anderson 2006, Allred et al. 2011, Kohl et al. 2013). Cows will graze nearer to water sources such as ponds and streams than do bison which can lead to the degradation of riparian areas and increased vulnerability to invasive plants (Bear et al. 2012). Forbs make up a greater portion of the diet of cows than bison (Damhoureyeh and Hartnett 1997, Collins et al. 1998). Whereas bison avoid woody areas, cows preferentially spend time in these areas, either grazing or resting (Allred et al. 2011). Cows, however, are plentiful in the American landscape, unlike bison. Like fire, grazing can be used to control for *B. inermis* (Salesman and Thomsen 2011). Similarly, intense, early grazing can disrupt these invasive graminoids and promote the recovery of native grasses. Kimoto et al. (2012) found that grazing intensity had no significant effect on total bee abundance or species richness in central Oregon prairies. There were differences in response between genera, with higher grazing more negatively impacting *Bombus* (bumble bee) than *Lasioglossum* (sweat bee) abundance. Increased grazing intensity was also associated with a lower Shannon diversity in bees in the early season, potentially due to declines in floral resources. These findings are not universal: Carvell (2001) found higher abundance of bumble bees in pastures grazed by cattle within the past year.

Bees respond to abiotic factors as well as the vegetative community. Therefore, these factors, such as soil texture, are another means by which management may impact bees. Fires increase bare soil exposure, which some ground-nesting bees will excavate, depending on the species and the texture of the soil; in particular, many ground-nesters prefer sandy-loams, rather than silt or clay-rich soils (Cane 1991, Potts and Willmer 1997, Potts et al. 2005). Grazing generally does not expose soil completely, though cattle may create bare ground through compaction (Kimoto et al. 2012). Compaction can influence soil's permeability, making heavily compacted sites more prone to flooding and erosion (Batey 2009). The impacts of burning and grazing on grassland soils may be important in shaping bee communities, in addition to impacts via the vegetation.

Increasingly, land managers are using conservation grazing to provide disturbance to tallgrass prairies. This can offer several advantages over prescribed fire. Fires are expensive, with personnel requiring training and maintenance of skills prior to burns, and with many professionals present on the day of the burn. There are often narrow windows for management when conditions are prime and the potential impact on desired organisms is low. Burns can impact nearby landowners negatively, particularly if winds shift unexpectedly and inundate houses with smoke. Cattle grazing can mitigate (or eliminate in the case of smoke) some of these concerns. Conservation grazing is a profit generating process; cattle owners benefit from converting forage into animal-mass, and public lands benefit from fees that owners pay for the ability to graze their herds.

Objectives:

Here, I seek to elucidate the on-the-ground differences these management techniques, as practiced today, promote in Minnesota's tallgrass bee communities. I offer the following hypotheses:

H_0 = Management type is not a significant predictor of bee abundance, species richness, or diversity.

H_a = Management type is a significant predictor of bee abundance, species richness, or diversity.

Methods

Site selection –

Because the effects of land management on perennial vegetation can take years to become evident and are in part dependent on variation in abiotic factors, I used a retrospective approach to assess the relative effects of management by grazing versus fire on native tallgrass prairie vegetation, prairie dependent bees, and invasive grasses. The Minnesota DNR, The Nature Conservancy (TNC), and the U.S. Fish & Wildlife Service all include conservation grazing and fire in their prairie management strategies and all expressed a willingness to allow me to study these prairies. In 2015 and 2016, I compiled a list of prairie remnants under federal, state, TNC, and private management, and identified 10 prairies with graze-only management and 10 prairies with burn-only management strategies. Grazed prairies had and average intensity of 0.92 AUM (animal unit months)/year between 2005 and 2015 or 2016, with a range of 0.17 – 2.91. At burned prairies, an average of 5.6 years had passed since the previous burn, (range: 2 - 9). I obtained soils data from Natural Resources Conservation Service for available sites, and used drainage class as a proxy for dry, mesic, and wet prairie types. I also collected information on year of management action and stocking rates for all sites. Due to access limitations, I dropped one grazed site from my study in 2016 and replaced it in 2017.

Bee survey methods –

Bees were surveyed in two ways, passively via pan traps ("bee bowls"), and actively, via netting. I conducted these surveys three times each summer at each of the 20 sites (2016: June 15 – August 31; 2017: May 14 – August 18). When possible, visits were confined to days that were at least 70^{o} F with low wind speeds and no precipitation.

Pan traps –

I used 3.25 oz. plastic bowls in three colors (white, yellow, and blue) placed at 20-m intervals along the same transects as used for the vegetation surveys; at each 20-m interval, a bowl was placed on the transect, and 2 additional bowls were placed perpendicular to the transect, 5-m from the center bowl. This adaptation of the standardized pan trap transect was made to create gaps in the transect through which cattle could potentially pass without disturbing traps. Thirty bowls in total were placed in each site. Pan traps were divided between prairie types, such that the number of sets of traps on transects in a given prairie type was proportional to that prairie type's contribution to the site, rounded up to the nearest ten percent. The bowls were filled with soapy water (mixture of water and Dawn dish soap), placed on bamboo poles of approximately 60 cm (2ft) in length, and left in place for approximately 24 hours. All insects captured on a transect were placed in a single Whirl-Pak bag, placed in a freezer, then processed and pinned. Pan traps were not placed at Glynn Prairie during the second two visits in 2016 because I did not want to disrupt ongoing surveys by Minnesota DNR. Through a data-sharing agreement, I have obtained bee collection data from two DNR visits that occurred at similar times during that summer.

Pan traps have both benefits and pitfalls. Pan traps consistently collect bee species that are missed by other collection techniques, such as aerial netting (Cane et al. 2000, Roulston et al. 2007, Grundel et al. 2011, Rhoades et al. 2017). They are efficient and limit user bias extensively (Droege et al. 2010). However, pan traps can be greatly impacted by nearby floral abundance, with more bees collected in florally depauperate sites (Cane et al. 2000, Baum and Wallen 2011). Pan traps are in effect competing with flowers: if pan traps are among the few perceived resources for bees, they will get visited more frequently than if they are perceived as one option of many (Cane et al. 2000).

Netting –

To mitigate these concerns and as pan traps do not attract all bee taxa, all site visits also included a meandering walk in which bees were netted when observed on flowers. The length of the meandering walk scaled with site size, lasting between 30 minutes and 2 hours. Netted bees were placed individually in a glassine envelope, which was then put into an ethyl acetate-charged kill jar. Envelopes were labelled with the date, time, and site name. These envelopes and their contents were then frozen until specimens were pinned.

Identification –

Bumble bee (*Bombus*) specimens were identified to species using *Bumble Bees of North America* (Williams et al. 2014). All non-*Bombus* specimens were brought to Sam

Droege of the U.S. Geological Survey who aided in specific identification during the spring and summer of 2018. A table of all species identified is included in Appendix A.

Vegetation survey methods –

Geographic Information System (GIS) maps were created using ArcGIS (version 10.3.1 for Desktop) for each site prior to the field season. In addition, random transects were delineated on these maps, running parallel to any elevation gradient; if none existed, a random number was used to select a compass bearing through which the transect passed. The prairies ranged widely in size, from 1 to 145 hectares. Vegetation surveys were conducted between June 1 – August 31, 2016 and May 30 – September 5, 2017 using nested frequency plots along the random transects (DeBacker et al. 2011).

Soil evaluation –

Within each drainage class polygon at each site 5 soil samples along one of the random transects were collected and combined. These were analyzed by the Research Analytical Laboratory at the University of Minnesota for soil texture using the hydrometer method. The percent of sand, silt, and clay in soil samples were reported. A site-wide proportion of sand in soils was calculated as follows:

$$\frac{Area_{wet}}{Area_{total}} * percent\ sand_{wet} + \frac{Area_{mesic}}{Area_{total}} * percent\ sand_{mesic} + \frac{Area_{dry}}{Area_{total}} * percent\ sand_{dry}$$

Bee analyses –

Bee abundance and species richness were the principal response variables. Bee abundance was adjusted to account for the fact that at grazed sites when cattle were present, many pan traps were lost. The adjusted bee abundance was calculated as:

$$\left(\frac{Total\ number\ of\ bees\ collected}{Total\ number\ of\ bowls\ retrieved} * 30\right) rounded\ to\ the\ nearest\ integer$$

As thirty bowls were placed at each site, multiplying the ratio of bee collected: number of bowls retrieved by thirty provides an approximation for the number of bees that would have been collected had an entire set of traps been recovered. Rounding to the nearest integer allows for the use of the Poisson distribution, which is appropriate for count data. For most site visits, where all thirty pan traps were recovered without issue, the adjusted bee abundance and raw bee abundance were identical. Hereafter, “bee abundance” will refer to adjusted bee abundance.

The suite of species observed at a site can be very sensitive to bias. The size of the site, the conditions during site visits, and the effort used during surveys can all bias species lists (Chao et al. 2014). Observed species richness can thus be an unreliable measure of the full bee community at a site, especially considering that some species may be very rare and therefore unlikely to be detected. To address this issue of bias, I used the Chao 2 estimator for species richness (Chao 1984, Colwell and Coddington 1994). This is calculated as:

$$S_{Y,T} + \frac{{L_{Y,T}}^2}{2M_{Y,T}}$$

The term $S_{Y,T}$ represents the number of species observed in all samples at site T during year Y, $L_{Y,T}$ is the number of species that occur in only one sample from site T during year Y, and $M_{Y,T}$ is the number of species that occur in exactly two samples site T during year Y. The estimated richness and the observed richness become more similar as the ratio of unique species to doubly observed species gets smaller. This is based upon the assumption that in the true community, many fewer species should occur in a single sample than in two samples. Thus, as the ratio of L to M gets smaller, the Chao 2 estimator approaches S. As species richness is a count of discrete species, a Poisson distribution is appropriate for models. I therefore rounded the Chao 2 estimator to the nearest integer for subsequent analyses. I used the fossil package in R to calculate this for each site in 2016 and 2017 (Vavrek 2011). Hereafter, "bee species richness" will refer to the Chao 2 estimated value.

Shannon's H was calculated for each site as a measure of diversity using the vegan package in R (Oksanen et al. 2018). Data from the three site visits in each year were compiled, reducing the sample size from 117 to 40. This diversity index takes into account the abundance and evenness of species present. As it relies upon the identity of species in samples, I cannot use the Chao 2 estimator. Shannon's H for each sample is calculated as:

$$-\sum_{i=1}^{R} p_i \ln p_i$$

in which R is the number of species within a site and p_i is the proportion of individuals of the *i*th species within R.

Prairie buffer -

For each site, I determined the percent of prairie in the surrounding landscape by first creating a 1.5 km buffer around each site using ArcMap (v 10.5.1) and overlaying this buffer onto landscape data obtained from the US Department of Agriculture, Minnesota Department of Natural Resources, and South Dakota State University. I then calculated the percentage of the land within the buffer that was classified as prairie. This served as a measure of fragmentation and isolation of prairie fragments. Fragmentation is generally associated with decreased bee species richness and abundance in various habitats (Cane 2001, Shuey 2013, Smith and Mayfield 2017).

Data Analysis –

Three generalized linear mixed-effects models (GLMM's) were constructed to predict of bee abundance (Table 1). The first, including data from all 20 sites, included management type as a categorical variable, the total proportion of sand in soils, the proportion of prairie within 1.5km, and from vegetation surveys, forb frequency, the frequency of *Poa pratensis*, the frequency of *Bromus inermis*. To account for effort and experimental design, the total time during which pan traps were deployed at each sampling event, the ordinal day of the sampling event (lubridate package in R, Grolemund and Wickham 2011), and site area were included. The random effect term chosen was site nested within year. Early data visualization showed that 2016 and 2017 differed significantly in the number of bees collected. As each site was visited in both 2016 and 2017, it was appropriate to set an intercept for each site in each year.

The second model of abundance included data from the 10 burned sites. Rather than include management type, the number of years since the last burn was included. All other terms were the same. The third model included data from the 10 grazed sites. The average grazing intensity between 2005 and 2015 was included instead of management type. All other terms were the same as the previous two models.

Three GLMMs were built to model species richness (Table 1). As with bee abundance, the first model included data from all 20 sites with management type as a categorical variable. The total proportion of sand in soils, the proportion of prairie within 1.5km, and from vegetation surveys, forb frequency, the frequency of *Poa pratensis,* the frequency of *Bromus inermis*, the ordinal day of the sampling event, and site area were also included. The random effect term chosen was site nested within year. As with models of abundance, the second and third models are for burned sites only and grazed sites only, respectively. Due to decreased sample sizes, not all terms could be included in these models. Apart from the management specific terms (years since last burn and average stocking rate since 2005) these two models have the same terms: the proportion of sand in soil, the frequency of smooth brome, the proportion of prairie in the 1.5km surrounding sites, and the year. Site was a random effect. These Poisson-distributed GLMMs were built in R 3.2.4 (package lme4 in R, Bates et al. 2015) and tested for significance using the Anova function (package car in R, Fox and Sanford 2011).

Simple linear models (base R) were built for Shannon's H and forb frequency. As with bee abundance and species richness, models for bee diversity were constructed for all sites, only burned sites, and only grazed sites. In the first, management type was included as a categorical variable, in the next, years since last burn, and in the third, average grazing intensity between 2005 and 2015. The total proportion of sand in soils, the proportion of prairie within 1.5km, and from vegetation surveys, forb frequency, the frequency of *Poa pratensis*, the frequency of *Bromus inermis*, and site area were also included.

Forb frequency was included as a predictor in several bee community models. To aid in interpretation of those models, a linear model of the response of forb frequency to management type, site area, the proportion of sand in soils, the proportion of prairie in a 1.5km buffer was built, and the year of sample was built (Table 1).

Results

Bee abundance – bee bowl data:

Bowl traps collected 11,969 bees in the summers of 2016 and 2017. Three samples out of 117 were unusable – two were lost and one was unlabeled. The time over which bowls were deployed varied from 1190 minutes (19.83 hours) to 1670 minutes (27.83 hours), with a median of 1415 minutes (23.58 hours).

At all sites, bee abundance was greater the longer bowls were deployed and at sites with sandier soils (Table 2). Fewer bees were collected later in the season. The area of the site, the frequency of forbs, the frequencies of *P. pratensis* and *B. inermis*, the proportion of prairie in a 1.5 km buffer, and management type did not significantly explain differences in bee abundance.

At burned sites, the years since the last burn was not a significant predictor of adjusted bee abundance, nor were the site area, the frequency of *B. inermis*, the frequency of *P. pratensis*, the proportion of prairie in a 1.5 km buffer, or forb frequency (Table 2). As seen across all sites, bee abundance was greater at sandier sites and the longer bowls were deployed, and lower later in the summer.

At grazed sites, the average stocking rate since 2005 was not a significant predictor of adjusted bee abundance, nor was the site area, the proportion of prairie in a 1.5 km buffer, the proportion of sand in soils, the frequency of forbs, the frequencies of

P. pratensis and *B. inermis*, or the time over which bowls were deployed (Table 2). Significantly fewer bees were collected later in the season.

Bee species richness – pooled (bee bowl and meandering walk) data:

One-hundred twenty-one species, representing 30 genera, were identified from pooled samples collected in 2016 and 2017. Fifty-nine specimens were not identified to species or species complex and were discounted from richness analyses. Ninety-eight species were seen at burned sites, 27 of which were exclusive to burned prairies (Table 5). Ninety-four species of bees were collected at grazed sites, 23 species exclusively (Table 5). Twenty-eight species were only represented by a single specimen ("singletons") (Table 5).

Management type was not a significant predictor of species richness across all sites. Fewer species of bees were collected as the frequency of smooth brome rose (Table 3). Sites that were larger in area also saw depressed species richness. The frequency of forbs, the proportion of sand in soils, the frequency of Kentucky bluegrass, and the proportion of prairie in the 1.5km surrounding sites were not significant predictors.

At burned sites, bee species richness decreased as more time passed since the previous burn (Table 3). Fewer species were seen as the frequency of smooth brome increased and as the proportion of prairie surrounding sites increased. More bee species were collected at sites with higher proportions of sand in soil. Bee species richness at burned sites was significantly lower in 2017 than in 2016.

At grazed sites, more bee species were present as the average stocking rate since 2005 increased. Significantly more bee species were collected in 2017 than in 2016. The proportion of sand in soil, the frequency of *B. inermis*, and the proportion of prairie in a 1.5km buffer were not significant predictor of estimated species richness (Table 3).

Shannon diversity:

No predictors significantly explained site-wide Shannon diversity (Table 4); site area, the proportion of sand in soils, forb frequency, the frequencies of *P. pratensis* and *B. inermis*, proportion of prairie in a 1.5km buffer, year, and management type were all nonsignificant.

This held true when looking at surveys that took place at burned sites and grazed sites (Table 4); at burned sites, the time since the last burn was also nonsignificant and at grazed sites the average stocking rate since 2005 was also nonsignificant.

Vegetation analyses:

Across all sites, forb frequency increased with a greater proportion of prairie in the 1.5km buffer surrounding sites (Table 6). Management type, the proportion of sand in soils, and site area were all nonsignificant.

Discussion

Management type was not a significant predictor of bee abundance, species richness, or diversity at my study sites in Minnesota's tallgrass prairie (Figure 2) though, bee species richness responded significantly to the time since last burn at burned sites and average stocking rate at grazed sites (Figure 3). Fewer species were detected in prairie remnants that had not been recently burned (Table 3). A meta-analysis by Williams et al. (2010) offers some insight on this finding. As time passes after a burn, bare soil that was exposed by fire is covered by vegetation (Potts et al. 2005) and shrubs and trees that may have been knocked back return or spread at sites (Collins and Calabrese 2012). With this change, there is a corresponding shift in the bee community supported by these habitats. While the presence of pithy-stemmed shrubs is a boon to stem-nesters (Potts et al. 2005), most bee species that I collected are ground-nesters (Appendix B). The relative decline in soil access can hamper the ability of ground-nesting bee species to make use of sites (Tonietto et al. 2017), resulting in the observed decrease in species richness. At grazed sites, the average grazing intensity between 2005 and 2015 was a significant negative predictor of bee species richness. This is in contrast to previous findings by Kimoto et al. (2012), which documented no significant effect of grazing intensity on bee species richness. In this study, sites with the lowest stocking rates are publicly owned prairie remnants, in which cattle are set to graze in relatively low numbers for relatively short periods of time in nonconsecutive years. The goal of these practices is to promote heterogeneity in prairie; by moving cattle frequently, refugia of undisturbed grassland are maintained while creating space for forbs and other plants that may have been crowded out by dominant graminoids (Undersander et al. 2002). This heterogeneity and increased vegetative diversity compared to heavier grazing can in turn support more species rich bee communities (Roultson and Goodell 2011). While management type itself is not predictive of bee communities, within sites with a single management type, the timing or intensity of disturbance plays a significant role.

Beyond management, vegetation or soil predictors were significant terms in the majority of models, though for any given response variable, these responses often differed between models of burned and grazed prairie (Tables 2 – 3). Other studies have shown that fire and grazing can influence these measures, perhaps providing a path by which management can indirectly affect prairie bee communities.

Despite support in the literature (Roulston and Goodell 2011, Inari et al. 2012, Ogilvie et al. 2017), I find no evidence that bee abundance is limited by floral resource availability, as measured by forb frequency. This lack of response suggests that bees may not be in competition for food in the prairies sampled. Alternatively, bees may still compete for resources, though the effects of floral resource availability may be desynchronized from bee abundance; as many adult bees in a given year were provisioned with resources abundant in the previous year, the past shapes populations in the present (Inari et al. 2012, Crone 2013). Forb frequency may be a poor proxy for pollen and nectar availability. Not all forbs are available to bees during any given day, either due to the forb's unsuitability as a food-source (such as yarrow, which is seemingly exclusively fly-pollinated) or because a given forb may not be in bloom. If the species-makeup of the forb community at a prairie varies greatly throughout the season, there may be periods when relatively more floral resources are available per plant. As forb frequency does not account for plants' specific identity, this variability in resource availability is obscured. Finally, the use of pan traps may influence the response of bee abundance to forb frequency. Pan traps attract fewer bees when nearby floral resources are abundant. (Cane et al. 2000, Baum and Wallen 2011). Even if bee abundances are in actuality greater when forb frequency is greater, the fact that bee bowls in effect compete with flowers for visitors may hide this relationship completely. While floral resources have previously been shown to be predictive of bee abundance, I found no support for this relationship.

The plant community of prairies can also shape bees via its effect on nesting opportunities. Many bee species nest in hollow and pithy forb stems, such as bergamot, Joe Pye weed, and various sunflowers (Goulson et al. 2015). While deemed "plausible" by Roulston and Goodell (2011), little evidence exists for nest-limitation of bees (Coudrain et al. 2016, Westerfelt et al. 2018). Additionally, stem-nesting taxa make up a relatively small proportion of the kinds of bees collected (15% of species), meaning that even if their responses were significantly predicted by forb frequency, the entire bee community might not reflect this relationship. Graminiods also shaped the bee community, though of the two of interest, *Poa pratensis* had no significant effect in any models. *Bromus inermis* frequency was associated with depressed species richness in pooled data across all sites and burned sites, though this was not seen at grazed sites (Table 3). This trend could be due to nesting preferences. As most bees in my study were ground-nesters (Appendix B), some of these species may have been excluded from sites where dense mats of thatch inhibited access to nesting sites. While plants are necessary food-sources for bees, they can also impact bees' ability to nest in prairie remnants.

In addition to the plant community, the soil of prairie remnants can play an important role in bee nesting. Different bee species prefer to nest in soils of different texture, though relatively few bees are associated with clay-rich soils; most prefer sandy loams (Cane 1991). This matches what I found regarding bee abundance across all sites and burned sites alone as well as species richness at burned sites (Figure 4). Of the 121 species of bees I collected, 85% are ground-nesters (Appendix B). It is these bees that likely respond most directly to soil composition and drive the relationship between the proportion of sand in soils and the bee community (Sardiñas and Kremen 2014). Approximately 88% of individuals collected (11,004 of 12,540) were sweat bees in the family Halictidae, bees that are mostly small ground-nesters (Appendix A). These bees generally prefer sandier soils (Cane 1991, Potts and Willmer 1997), perhaps because these soils are easier to excavate, or perhaps because they are less susceptible to flooding than silt- or clay-heavy soils (Skiba and Ball 2002). While soil-nesting bees often have both structural and chemical means by which to mitigate the risk of inundation, flooded soils have decreased oxygen compared to dry soils (Fellendorf et al. 2004) and over extended periods, immature bees, particularly eggs and larvae, may succumb to hypoxia. This may also explain why soil is not a significant predictor of bee abundance or richness at grazed sites; cows compact soil and compaction can make soils less permeable to water (Batey 2009, Alaoui et al. 2018). If the benefits to ground-nesting bees of well-drained sandy soils are counteracted by compaction, the net effect may not be significant. Soil's characteristics have important implications for ground-nesting bees, and those relationships are reflected in my models.

Site area was not a significant predictor of bee abundance but was predictive of bee richness. Across all sites, fewer bee species were collected as prairie size increased. This is somewhat counter-intuitive. Larger, contiguous habitats seemingly offer certain advantages over smaller sites. Bees with low dispersal capability may be better able to survive in larger sites if they have sufficient floral resources without needing to venture outside of prairie fragments (Jauker et al. 2009). A larger site might support a wider diversity of nesting habitats for bee species to exploit or might contain more species of flowers used by specialist bees. However, I have found the opposite effect. This may be a result of differences in the meandering walk. As described above, the length of the meandering walk scaled with site size. While larger sites were surveyed for a greater period of time, the ratio of time spent meandering versus site area is lower at larger sites.

This ratio can be taken as a measure of sampling effort, which is known to be strongly linked to observed species richness. While large sites may in fact support diverse plant and bees with limited dispersal capabilities, I have not detected this, likely due to a bias in sampling effort.

As prairie remnants have shrunk in size, so too have they grown more isolated. Though habitat isolation is generally associated with decreased species richness and diversity (Cane 2001, Shuey 2013, Smith and Mayfield 2017), I did not observe this effect. In fact, at burned sites, I collected fewer species of bees at sites with more prairie nearby. A prairie fragment in Minnesota, surrounded by a typical monocrop planting, such as corn or soy, exists as a rich pocket of floral resources. Bees drawn to this concentration of resources may be more likely to encounter a pan trap or be netted than if floral resources were more distributed in the landscape. Effectively, the attractiveness of pan traps, which is known to vary in response to nearby floral resources (Baum and Wallen 2011), may vary at a landscape level as well. If bees are choosing between nearby fragments and the fragment being sampled, traps may attract fewer bees, and thus a less species-rich sample of bees. The effect of isolation, despite evidence in the literature of its importance, may be confounded by bees' response to traps and floral resource availability.

Floral resource availability may also have contributed to the seasonal variance in bee abundance in which more bees were collected earlier in the season. Pan traps have been shown to be relatively less attractive to bees when more abundant floral resources are available nearby (Baum and Wallen 2011). Thus, when floral resources are scarce, pan traps may be very attractive to bees. Anecdotally, I observed that the early in the surveying period, from mid-May through the middle of June, it could be difficult to find flowers on which to net bees during the meander walk. This could in part explain the relatively higher bee abundance detected in pan traps during that time (Figure 5). If more flowers became available as the summer progressed as I anecdotally observed, bee abundance in bowls may have tapered off.

I have sought to address the limitations of my study design, though we learned some important lessons. If pan traps are to be used, they must be deployed being fully aware of their pitfalls. Pan traps are a cost effective, efficient means of collecting large numbers of bees (Baum and Wallen 2011). Many other studies have relied upon them and my data can be compared with other data sets in the literature, perhaps making meta-analyses simpler for some future researcher (Wilson et al. 2008). However, I would highly recommend assessing floral resource availability at the time when traps are in place, such that, even if traps in florally abundant sites are relatively less attractive, floral abundance can be used as a covariate. Additionally, bee bowls should not be deployed unprotected into pastures with cows. Cows may have been curious about bowls, or their weight may have simply disturbed bowls enough to topple them. The loss of data caused by destroyed bowls may in part explain the wide variance in models of grazed sites. Additionally, while abundance could be adjusted to extrapolate from the bees retrieved, species richness could not be reconstructed in this way. In future studies, if bowls and cows must overlap, I would highly recommend a protective structure around each bowl.

Some limitations are also imposed due to the retrospective nature of this study. Without experimental manipulation, I could not test the extent to which burning and grazing lead directly to bee mortality. This makes parsing out the direct and indirect effects of management difficult. I was limited in my ability to control the extent of variation between sites for factors unrelated to the direct and indirect effects of management, such as site area or latitude. Controls for variation in sites had to be made at the time of site selection, but perhaps variables outside of my consideration, such as site history before 2005, are obscuring signals. However, a retrospective study offered a duration of a single management type that would have been impossible to achieve through manipulation in the time-frame of this project. Additionally, tallgrass prairie is a precious resource. The land managers I worked with are tasked with protecting and promoting that resource, either for the public or for their herds. It was only through an observational study like this that we could work together without compromising their missions.

Through this retrospective lens, I have found that a ten-year history of burning and grazing, in isolation, do not significantly predict bee abundance, species richness or diversity; the null hypothesis cannot be rejected. Though I do not show a significant difference in bee abundance, species richness, or diversity, there are differences in the suite of species collected between management techniques. However, only 16% of those species found in a single management type were represented by more than two specimens out of the 12,500 thousand collected (Table 5). Whether they are truly limited to one management type or are just rarely encountered is difficult to ascertain. This equivalency between burned and grazed prairies may be the result of dispersal from other remnant prairies, indicating there is resilience in isolated fragments, even with remnants separated by seemingly unsuitable habitat. This could support findings by Jauker et al. (2009) that the quality of the dominantly agricultural matrix in which semi-natural grassland habitats existed had no significant effect on bee abundance. The majority of individuals collected do not rely solely upon prairie fragments; the four most abundant bee species in my study, *Lasioglossum pruinosum, Lasioglossum albipenne*, *Lasioglossum versatum*, and *Augochlorella aurata*, which account for 54% of all bees collected, are widely distributed across North America in various habitats (Coelho 2004, Gibbs 2011). Management's effects, while potentially destructive to the individuals in its path, may have minimal impacts on these species at a landscape scale, leading to seeming equivalency between management regimes for bee abundance, species richness, and diversity.

Fire and grazing, while both can supply necessary disturbance to tallgrass prairie (Damhoureyeh and Hartnett 1997, Carvell 2002, Anderson 2006, Allred et al. 2011, Harmon-Threatt and Chin 2016), are not inherently exclusive processes. Historically, they would have co-occurred across North America's grasslands and many land management agencies have begun recoupling these processes. Patch-burn grazing, in which cattle are set to graze on recently burned vegetation, is an increasingly implemented management practice that creates a patchwork of heavily and lightly disturbed areas (Helzer and Steuter 2005, Fuhlendorf et al. 2009). This holds promise for promoting diverse and heterogeneous plant communities. Subsequent research should investigate how the bee community responds to this management regime as compared to the unimodal techniques studied here. By building that knowledge, I can hope to better understand how historic processes shaped pollinator communities, how to best manage populations presently, and how to safeguard their futures.

Table 1: Parameters for all linear models and generalized linear mixed-effects models built. Check marks (✓) indicate that a term is included in the model for the given response and scope. Cross marks (**X**) indicate that a given term, while available, was not included in the model for the given response and scope. If a term was not applicable, either by the scope of the model (e.g. Stocking rate for a model of burned sites), or the nature of the data collected (e.g. Date for a site-wide statistic), it was noted as such (N/A).

RESPONSE	**Scope**	**Management Type (burned or grazed)**	**Years since last burn**	**Stocking rate (amu)**	**Forb frequency (proportion of plots in which forbs occur)**	***Poa pratensis* frequency (proportion of plots in which *P. pratensis* occurs)**	***Bromus inermis* frequency (proportion of plots in which *B. inermis* occurs)**	**Proportion of sand in soils**	**Proportion of prairie within 1.5km buffer**	**Site area (hectares)**	**Date (Julian day)**	**Total time (min)**	**Year (2016 or 2017)**	**Random effect**
Adjusted bee abundance	All sites	✓	N/A	N/A	✓	✓	✓	✓	✓	✓	✓	✓	**X**	Site/year
	Burned sites	N/A	✓	N/A	✓	✓	✓	✓	✓	✓	✓	✓	**X**	Site/year
	Grazed sites	N/A	N/A	✓	✓	✓	✓	✓	✓	✓	✓	✓	**X**	Site/year
Chao2 species richness estimation	All sites	✓	N/A	N/A	✓	✓	✓	✓	✓	✓	N/A	N/A	**X**	Site/year
	Burned sites	N/A	✓	N/A	X	X	✓	✓	✓	X	N/A	N/A	✓	Site
	Grazed sites	N/A	N/A	✓	X	X	✓	✓	✓	X	N/A	N/A	✓	Site
Shannon's H	All sites	✓	N/A	N/A	✓	✓	✓	✓	✓	✓	N/A	N/A	**X**	N/A
	Burned sites	N/A	✓	N/A	✓	✓	✓	✓	✓	✓	N/A	N/A	**X**	N/A
	Grazed sites	N/A	N/A	✓	✓	✓	✓	✓	✓	✓	N/A	N/A	**X**	N/A
Forb frequency	All sites	✓	N/A	N/A	N/A	**X**	**X**	✓	✓	✓	N/A	N/A	✓	N/A

Table 2. Wald's Test χ^2 values for terms in generalized linear model of adjusted bee abundance. The χ^2 value of each term in models for adjusted bee abundance is reported. Significant terms are bolded; (+) or (-) indicate the direction of the slope estimate for significant terms. If a term was not included within a model, it is marked as not applicable. Column **B** refers to the model for burned sites. Column **G** refers to the model for grazed sites.

Predictor variable	*All sites (B + G)*	*B*	*G*
Management type	0.462	*N/A*	*N/A*
Years since last burn	*N/A*	0.331	*N/A*
Stocking rate	*N/A*	*N/A*	0.0336
Forb frequency	0.180	2.40	0.267
***Poa pratensis* frequency**	0.344	3.80	2.29
***Bromus inermis* frequency**	0.161	0.837	0.268
Proportion of sand in soils	**4.50 (+)**	**5.46 (+)**	2.21
Proportion of prairie within 1.5km buffer	0.0528	0.0546	0.421
Site area	0.0021	1.02	0.582
Date	**5481.48 (-)**	**2497.83 (-)**	**2982.97 (-)**
Total time	**136.94 (+)**	**191.45 (+)**	3.42

Table 3. Wald's Test χ^2 values for terms in generalized linear model of Chao 2 estimated species richness. This model is based upon bowl and meandering walk data. The χ^2 value of each term in models for estimated species richness is reported. Significant terms are bolded; (+) or (-) indicate the direction of the slope estimate for significant terms. If a term was not included within a model, it is marked as not applicable. Column **B** refers to the model for burned sites. Column **G** refers to the model for grazed sites.

Predictor variable	*All sites (B + G)*	*B*	*G*
Management type	17.23	*N/A*	*N/A*
Years since last burn	*N/A*	**25.2 (-)**	*N/A*
Stocking rate	*N/A*	*N/A*	**4.51 (-)**
Forb frequency	0.248	*N/A*	*N/A*
***Poa pratensis* frequency**	3.27	*N/A*	*N/A*
***Bromus inermis* frequency**	**15.82 (-)**	**16.32 (-)**	0.589
Proportion of sand in soils	2.45	**46.25 (+)**	1.68
Proportion of prairie within 1.5km buffer	2.54	**14.58(-)**	0.708
Site area	**7.00 (-)**	*N/A*	N/A
Year	*N/A*	**4.53 (2016 >2017**	**25.11 (2016 < 2017)**

Table 4. *F*-test values for terms in linear model of Shannon's H diversity index. The *F* value of each term in the models for Shannon's H is reported. As no terms were significant, no values are bolded. If a term was not included within a model, it is marked as not applicable. Column **B** refers to the model for burned sites. Column **G** refers to the model for grazed sites.

Predictor variable	*All sites (B + G)* *F (8,30)*	*B* *F (8,11)*	*G* *F(8,10)*
Management type	1.59	*N/A*	*N/A*
Years since last burn	*N/A*	3.94	*N/A*
Stocking rate	*N/A*	*N/A*	0.334
Forb frequency	0.581	0.671	0.101
***Poa pratensis* frequency**	0.193	0.0001	0.0501
***Bromus inermis* frequency**	0.190	0.207	0.125
Proportion of sand in soils	0.0080	0.0028	0.136
Proportion of prairie within 1.5km buffer	0.508	1.69	0.632
Site area	0.450	2.34	0.0675
Year	0.0005	1.12	0.0795

Table 5. Species seen in a single management. Listed are species/species complexes observed in only burned or grazed sites. Singletons are defined as species/species complexes represented in the dataset by a single specimen and are marked by a single check (✔). Doubletons are represented by two individuals and marked with two checks (✔✔).

Species	*Management*	*Singleton/Doubleton*
Andrena erythrogaster	Grazed	✔
Andrena milwaukeensis	Grazed	✔✔
Andrena rudbeckiae	Grazed	✔
Andrena simplex	Grazed	✔
Calliopsis nebraskensis	Grazed	✔
Coelioxys octodentata	Grazed	✔
Colletes solidaginis	Grazed	✔✔
Colletes susannae	Grazed	✔
Heriades carinata	Grazed	✔✔
Lasioglossum michiganense	Grazed	
Lasioglossum paradmirandum	Grazed	
Lasioglossum subviridatum	Grazed	✔
Lasioglossum vierecki	Grazed	
Lasioglossum zephyrum	Grazed	
Nomada articulata	Grazed	✔
Nomia universitatis	Grazed	✔✔
Perdita perpallida	Grazed	✔✔
Perdita swenki	Grazed	✔
Protandrena bancrofti	Grazed	
Sphecodes atlantis/cressonii	Grazed	✔
Sphecodes davisii	Grazed	✔✔

Svastra obliqua	Grazed	✔	
Xenoglossa kansensis	Grazed		
Andrena bisalicis	Burned	✔	
Andrena chromotricha	Burned	✔	✔
Andrena cressonii	Burned	✔	
Andrena hirticincta	Burned	✔	
Andrena nivalis	Burned	✔	
Andrena placata	Burned	✔	
Andrena thaspii	Burned	✔	✔
Andrena ziziae	Burned	✔	
Bombus perplexus	Burned	✔	
Bombus rufocinctus	Burned	✔	
Bombus terricola	Burned	✔	
Coelioxys rufitarsis	Burned	✔	
Colletes robertsonii	Burned	✔	
Colletes simulans	Burned	✔	✔
Hylaeus nelumbonis	Burned	✔	✔
Lasioglossum cinctipes	Burned	✔	
Lasioglossum foxii	Burned	✔	
Lasioglossum imitatum	Burned	✔	
Lasioglossum tincatulum	Burned	✔	
Megachile mendica	Burned	✔	✔
Megachile relativa	Burned	✔	✔
Melissodes communis	Burned	✔	

Melissodes denticulatus	Burned		
Nomada near_MR_2	Burned	✔	
Osmia near_collinsiae	Burned		
Sphecodes mandibubris	Burned	✔	
Stelis lateralis	Burned	✔	✔

Table 6. *F*-test values for terms in linear model of forb frequency. The *F* value of each term in the model for forb frequency. Significant terms are bolded; (+) or (-) indicate the direction of the slope estimate for significant terms.

Predictor variable	*All sites (B + G)* *F (4, 15)*
Management type	0.556
Proportion of sand in soils	1.26
Proportion of prairie in 1.5km buffer	**4.88 (+)**
Site area	0.108

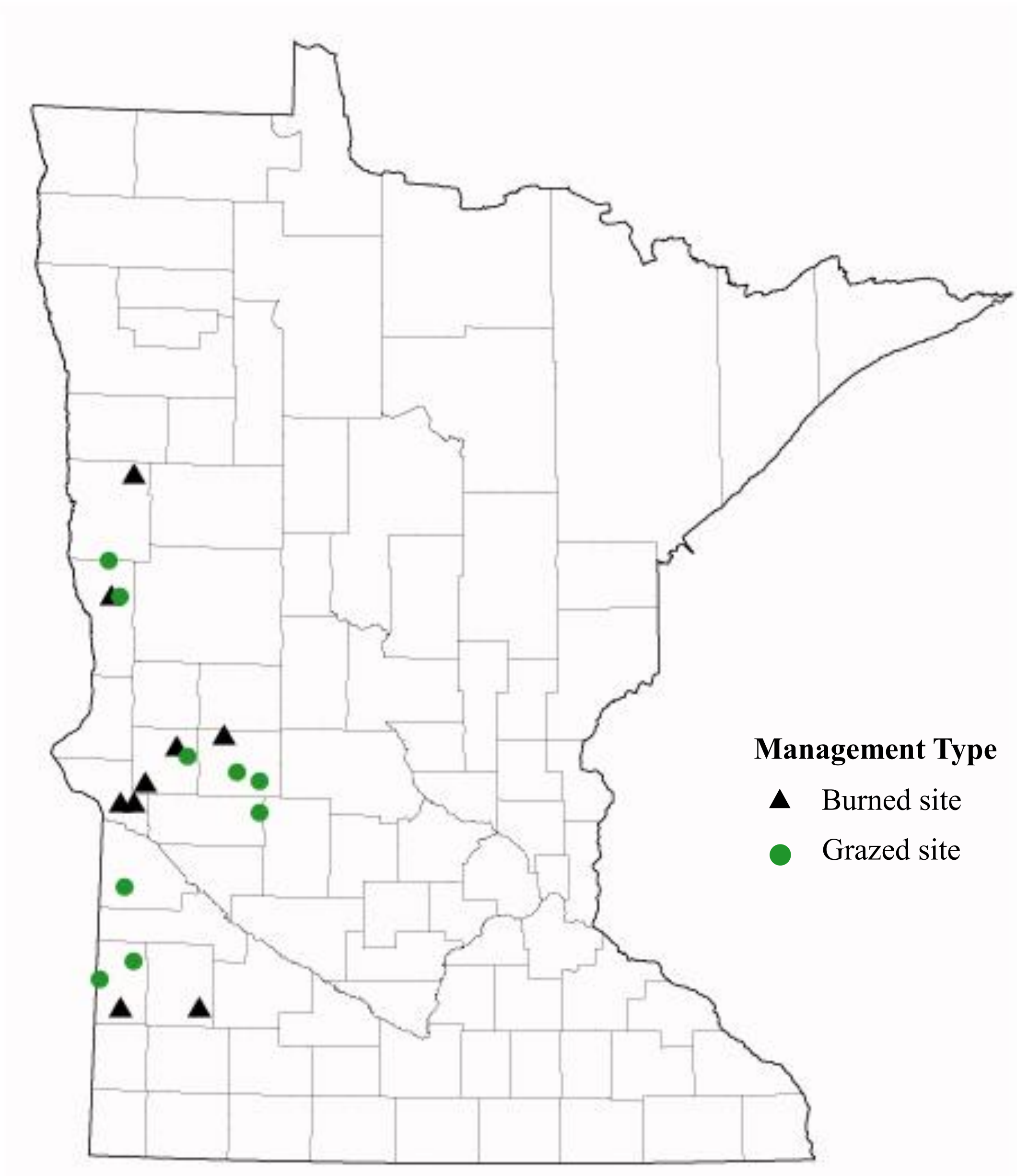

Figure 1 – Map of study sites in western Minnesota – Twenty study sites were included in bee and vegetation surveys, ten of which were burned (indicated by triangles) and ten of which were grazed (indicated by the circles).

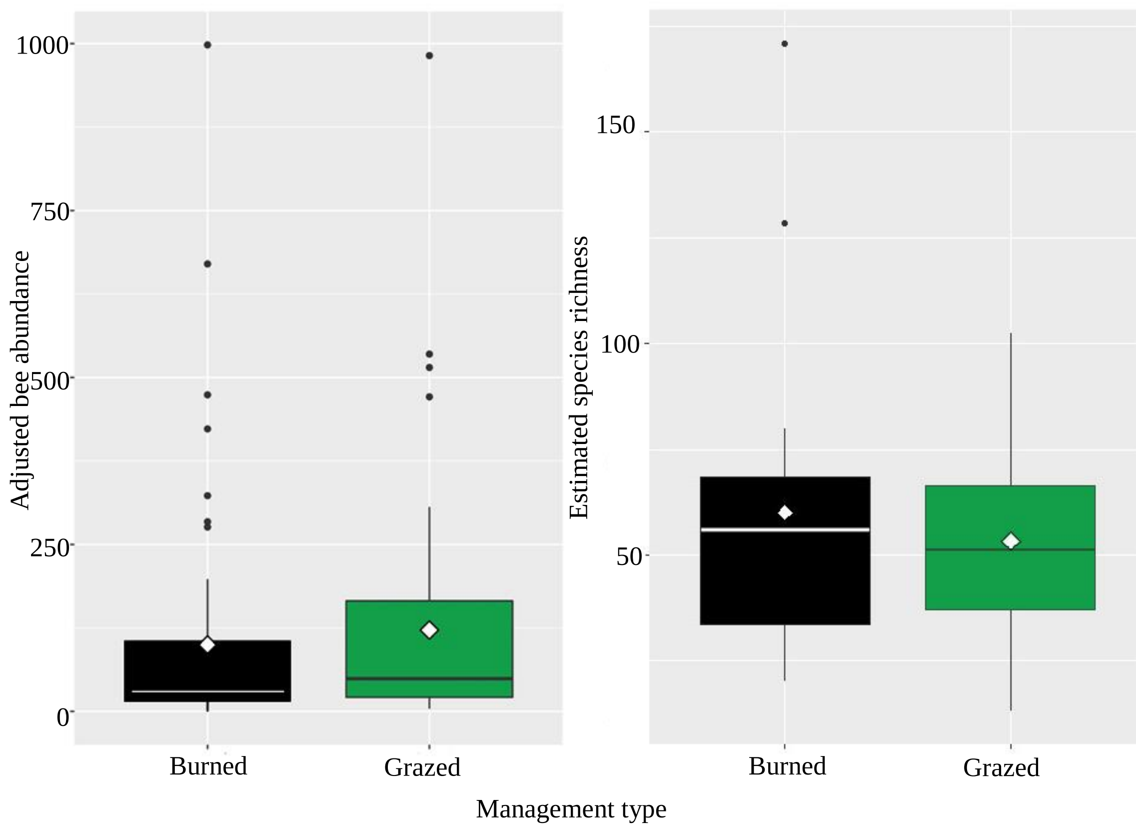

Figure 2: The response of bee abundance and species richness to management type. There were no significant differences between treatments for either bee abundance (p = 0.50) or species richness (p = 0.21).

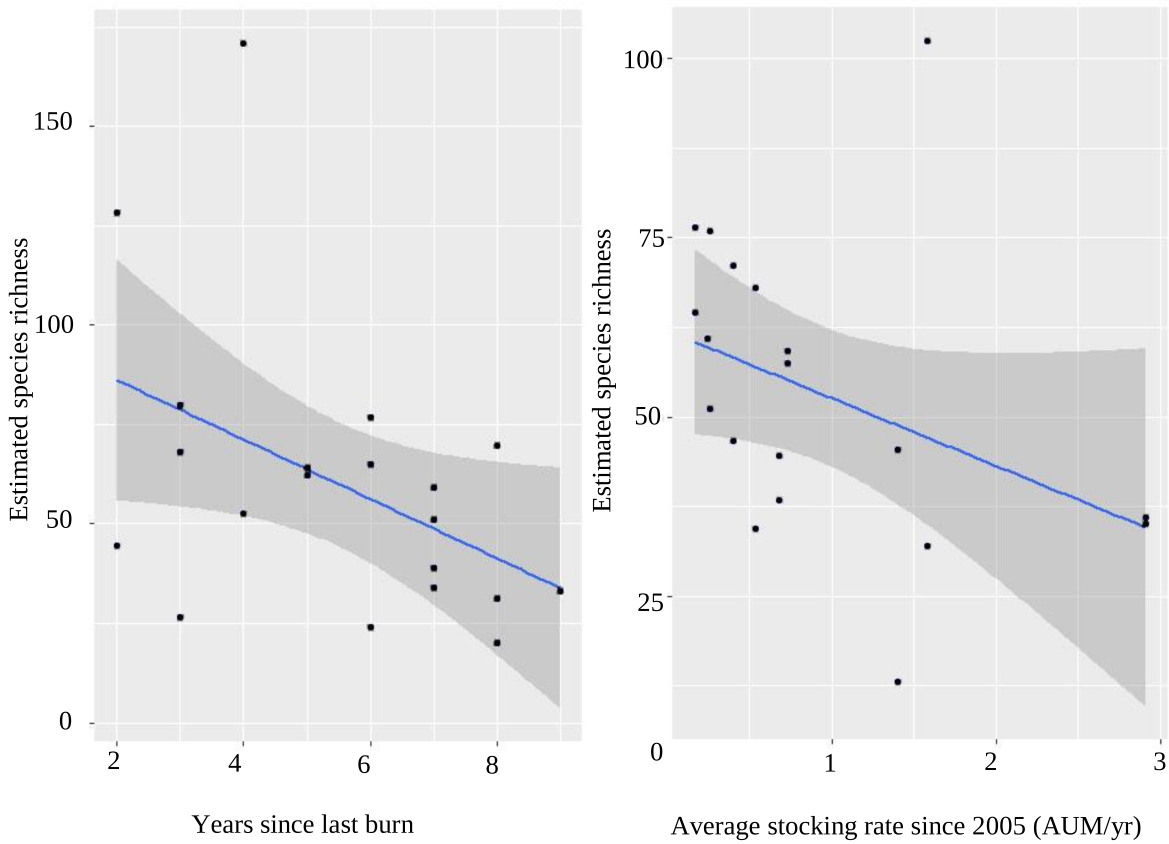

Figure 3: The response of bee species richness to management factors (Years since last burn and Average stocking rate since 2005). Both measures were significantly negative predictors of bee species richness ($p < 0.001$, $p = 0.034$ for burned and grazed, respectively).

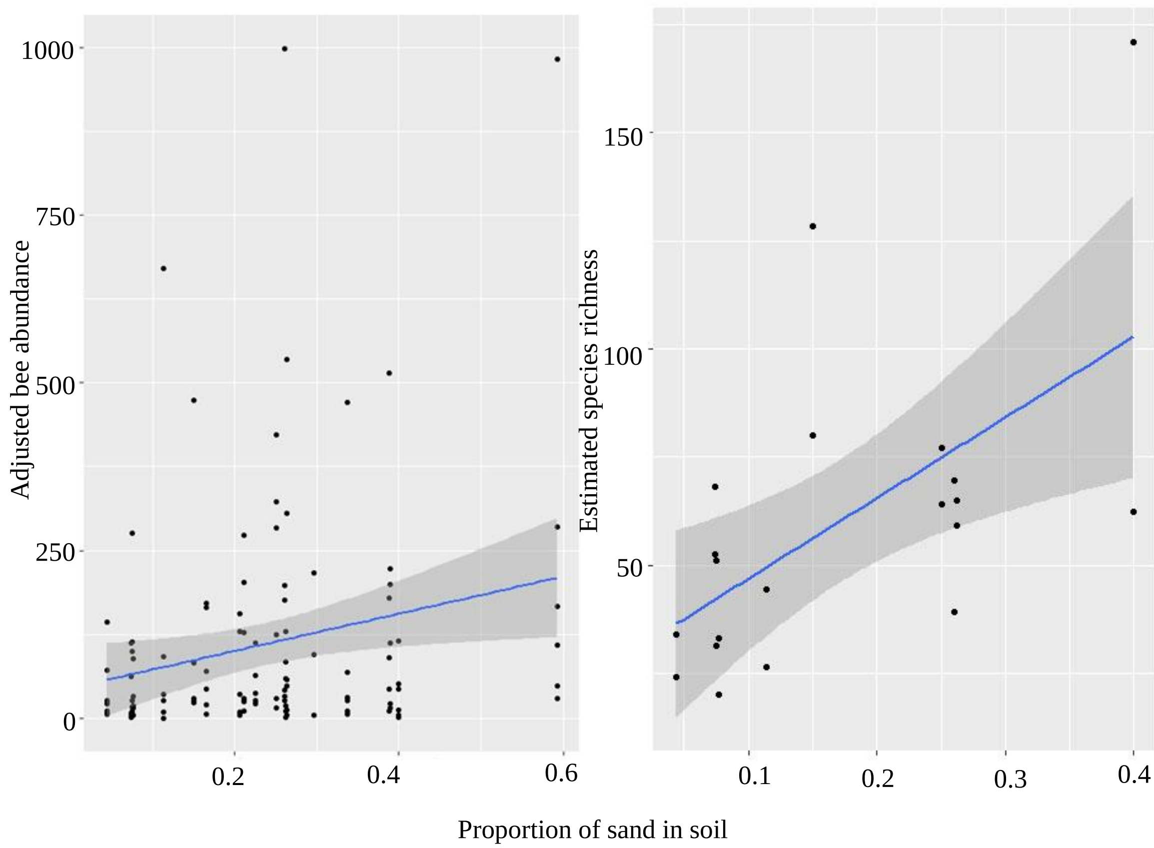

Figure 4: The response of bee abundance across all sites and species richness at burned sites to the proportion of sand in soil. This was a significant positive relationship for bee abundance ($p = 0.034$) and species richness at burned sites ($p < 0.001$).

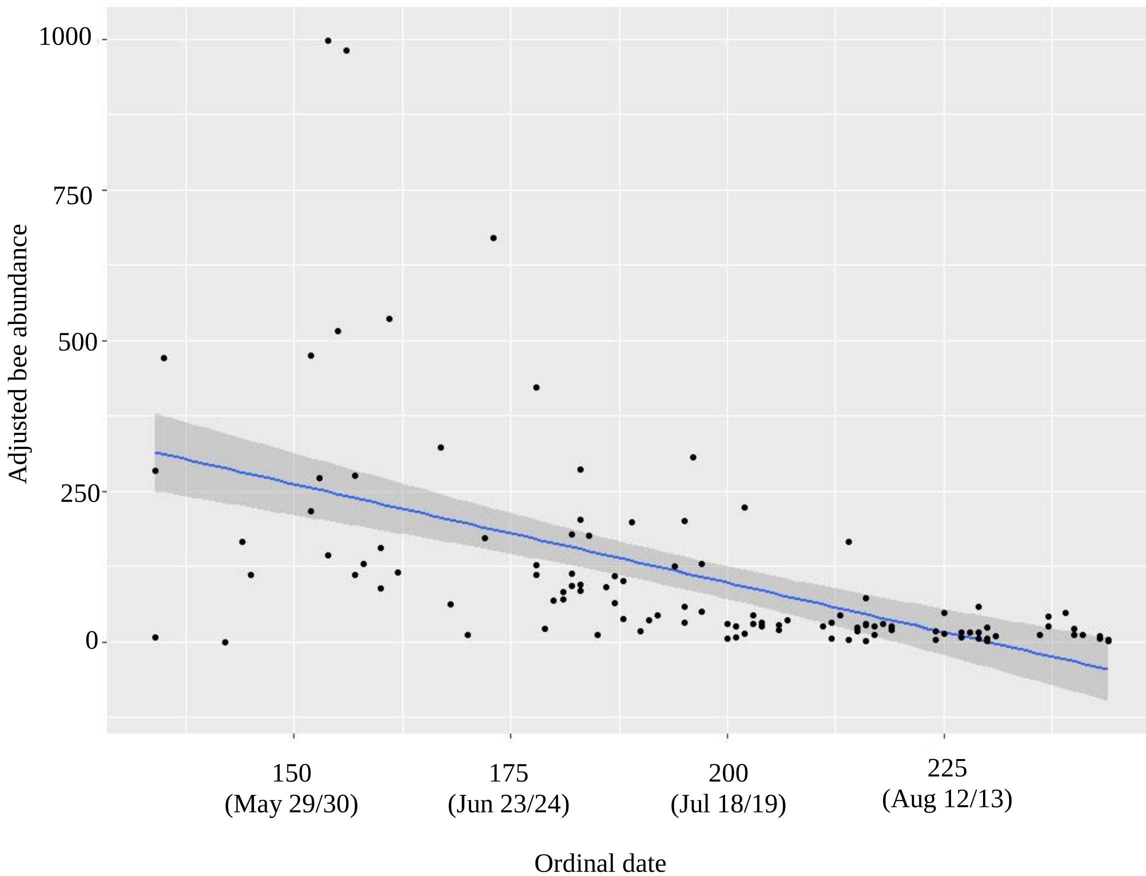

Figure 5: The response of bee abundance to the date of surveys. This was significant negative relationship ($p < 0.0001$).

Chapter 2: The trait-based responses of bee communities to environmental drivers of tallgrass prairie

Synopsis

Trait-based analyses provide the ability to examine how the environmental characteristics of habitats of concern shape the phenotypic makeup of bee communities. North American tallgrass prairie is one such habitat, having seen extensive declines and fragmentation in the time since European settlement. Prairie remnants may differ in their forb communities, in the extent of invasive graminoids present, soil texture, area, and isolation from other natural grasslands. Remnants also may differ in the nature and intensity of managed disturbance, usually provided by prescribed fire or cattle grazing. Using directed netting and pan traps, I surveyed the bee community of 20 tallgrass prairie remnants in Minnesota. Sites were visited three times in the summers of 2016 and 2017. The plant community was surveyed using nested frequency plots in 2016 and 2017; soil texture was assessed once at each study site in 2016 or 2017. Via fourth-corner analyses, I have modelled how these environmental characteristics are correlated with bees' nesting habits, social structure, size, prairie specialization, and kleptoparasitism. Among netted bees only, nesting habit was significantly associated with several environmental traits; aboveground-nesting was negatively correlated with the proportion of sand in soils and the percent of prairie in the surrounding landscape. Soil-excavating ground-nesting was significantly positively correlated with the sandiness of soil. Non-excavating ground-nesting was significantly negatively correlated with the frequency of the invasive graminoid *Bromus inermis*. Finally, solitary nesting was positively correlated with forb

frequency. Though management type is not significantly correlated with any bee traits, vegetation and soil traits do shape bee communities via nesting habit and sociality.

Introduction

Tallgrass prairie is a highly fragmented, disappearing resource. Prior to European settlement in the 18th and 19th centuries it covered some 170 million acres in central North America, stretching from the Gulf Coast well into modern-day Manitoba (Samson and Knopf 1994). It was akin then to a vast sea of grass with scattered stands of trees, particularly along the riparian corridors that meandered through it, and the numerous prairie-pothole lakes. Today some two centuries later, less than 1% of native tallgrass prairie remains (Samson and Knopf 1994). While once compared to a sea, it now resembles an archipelago, fragmented by agriculture, development, and highways. Invasive graminoids, such as Kentucky bluegrass (*Poa pratensis*) and smooth brome (*Bromus inermis*), form dense mats of vegetation and crowd out native vegetation (Printz and Hendrickson 2015). The processes that had kept woody growth in check can no longer function in such a landscape (Samson et al. 2004). Bison have been extirpated from most of their native range and fires are not left to sweep across the acres of crops, homes, and highways that may separate prairie fragments.

As prairie becomes rarer and more fragmented, the characteristics of given remnants take on increased significance. In a more connected landscape, individuals may experience a gradient of various conditions within their preferred habitat and be able to disperse to areas that are more favorable. However, fragmentation and isolation hamper individuals' dispersal beyond their current surroundings. Thus, the suite of environmental traits within and between fragments is important in determining the community of species that persist. Within tallgrass prairie today, one major source of variation between fragments is the form of managed disturbance.

Prescribed burns are one method of providing disturbance. Like natural fires, these burns remove encroaching woody plants and accumulated fuel. As grasses have their meristems below ground, they can tolerate most prairie fire while woody plants have terminal meristems exposed to fire (Anderson 2006). Burns also can be used to fight back graminoids like smooth brome and Kentucky bluegrass if properly timed, such as in the late spring after these plants have invested energy into growth (Salesman and Thomsen 2011). By making conditions less favorable for these invasive plants and requiring them to draw upon underground reserves to compensate for tissue losses, managers can allow native plant diversity to maintain a hold, even in degraded prairies (Salesman and Thomsen 2011). Fire also induces recruitment from the soil seed bank, which may hold native diversity that has been crowded out at a site (Davies et al. 2013) though overly frequent fires may suppress forb diversity (Damhoureyeh and Hartnett 1997). Fire, once an important natural process in maintaining tallgrass prairie, is now employed by land managers to promote plant diversity and heterogeneity.

Another means by which land managers provide disturbance to prairies is through cattle grazing. Like fire, grazing removes plant tissue, promoting subsequent growth (McNaughton 1979). While fire converts “consumed” materials to smoke and ash, grazing sees this material converted into animal tissue, while some is returned to soils as urine and feces. Compared to bison, the historic grazers of tallgrass prairie, domestic cows have a relatively broader diet breadth, consuming graminoids as well as forbs that bison tend to ignore (Coppedge et al 1998, Allred et al. 2011). The majority of their diet is graminoids, though they will preferentially feed on some forbs (Damhoureyeh and Hartnett 1997). They are not uniform in their disturbance, though, leaving chemically or structurally unpalatable forbs, such as curlycup gumweed (*Grindelia squarrosa*) and nodding thistle (*Carduus nutans*), and concentrating their grazing in low-lying areas near water-sources (Allred et al. 2011, Kohl et al. 2013). Cattle grazing can also change prairies through compaction. This can lead to soils becoming more prone to flooding and erosion (Alaoui et al. 2018). Cattle grazing differs from burning in its place on the wider landscape as well. Cows are plentiful in North America, giving land managers ample opportunities to employ either their own herds or those of local partners.

Through the plant community, management can also shape the communities of organisms that rely upon prairie vegetation, including bees. One defining trait of bees is their reliance on floral products throughout their lives; adults feed on pollen and nectar and collect these same resources to provision their young. By changing the phenology, abundance, or specific identity of prairie forbs, management can indirectly drive the prairie bee community (Roulston and Goodell 2011). Wrobleski and Kaufman (2003) documented a longer growing season following burns, which in turn can benefit bumble bees (genus *Bombus*), which have relatively long flight periods (Mola and Williams 2018). Kimoto et al. (2012) found that abundance of both bumble bees and bees in the genus *Lasioglossum* decreased with increased grazing intensity, though the magnitude of the effect was significantly greater for bumble bees. This supports findings by Sjödin (2007) that flower visitor abundance was positively correlated with taller vegetation and increased floral abundance, meaning that under grazing's shortened vegetation and decreased floral abundance, it may follow that the abundances of these two bee genera were suppressed.

Management may also affect bees' nesting opportunities. Many bees nest in the ground. By clearing away vegetation and exposing more bare ground, fires can create ground-nesting bee habitat (Potts et al. 2005, Spiesman et al. 2019) and, provided nests are located deeper than 10cm below the soil surface, most ground-nesting bees can tolerate prairie fires (Cane and Neff 2011). The greatest benefits of fire to ground-nesters are conferred soon after burns, with ground-nesters negatively correlated with the years since fire (Lazarina et al. 2016). However, stem-nesting bees may find fires to be lethal to immobile life-stages, like eggs, larvae, and pupae (Tooker and Hanks 2004, Spiesman et al. 2019). Fire does not pose the only risk; a foraging cow would certainly be capable of consuming or trampling a bee nest within a stem. Cows can also impact site conditions for ground-nesters, as their weight compacts soil, increasing erosion potential and increasing bare soil access which ground-nesters can exploit (Potts et al. 2005, Cane and Neff 2011).

There are environmental factors beyond management that may shape bee communities as well. Soil texture can strongly influence bees in tallgrass prairie, promoting greater species richness and overall bee abundance (Chapter 1, this thesis). This may be the result of a disproportionate benefit to small-bodied ground-nesters belonging species-rich taxa, like the sweat bees in the genus *Lasioglossum*. While vegetation is shaped by management, it may function independently of the form of disturbance as well. As bees feed exclusively on pollen and nectar as both larvae and adults, the abundance of floral resources can greatly impact bees (Roulston and Goodell

2011). Bees may also respond to the structural makeup of prairie plant communities, such as those fostered by invasive graminoids which form mats of thatch that inhibit soil access, disrupt nitrogen deposition, and crowd out some growing forbs (Printz and Hendrickson 2015). As discussed above, remnant tallgrass prairie is highly fragmented. The degree of isolation from other fragments is negatively correlated with bee species richness and abundance in various habitats (Cane 2001, Shuey 2013, Smith and Mayfield 2017), though prior work with this data indicated that bee species richness may be elevated in isolated prairie fragments (Chapter 1, this thesis). Carrié et al. (2019) showed that a greater amount of semi-natural habitat surrounding study sites was negatively correlated with bee size, suggesting that smaller-bodied bees are better able to disperse between sites when suitable habitat is nearby. Prairie bee communities are shaped by the environmental conditions and pressures they encounter.

Species' traits can also be vital to understanding how management or other environmental processes impact bees' responses (Williams et al. 2010, Bartomeus et al. 2013, Hopfenmüller et al. 2014, Tonietto et al. 2017, Carrié et al. 2019, Spiesman et al. 2019). Taxonomic approaches shed light on how metrics like species richness or relative abundance are influenced, but the pressures that determine the community of bees that persist in a site do not act upon a species concept. They act upon bees' phenotypes. The traits of individuals determine whether a given location is suitable or unsuitable. Therefore, a trait-based approach may offer a more direct interpretation of how bee communities are shaped by their environments. Via this trait-based lens, we may uncover trends in bees that might be masked by taxonomic approaches alone. In a habitat such as the tallgrass prairie, where isolated populations may be at risk of blinking out, identifying the traits which are either beneficial or detrimental to bees in relation to environmental characteristics could help predict the fates of various species going forward.

Here, I seek to predict the response of five bee traits (nesting location, body size, sociality, tallgrass prairie specialization, and kleptoparasitism) to eight environmental characteristics (management technique, site area, frequency of forbs, frequencies of the invasive graminoids *Bromus inermis* and *Poa pratensis,* the proportion of sand in soil, the proportion of prairie in the area around sites, and management intensity in management-specific models).

Methods

Site selection –

I used a retrospective approach to assess the relative effects of management by grazing versus fire on bees in tallgrass prairie. The Minnesota DNR, The Nature Conservancy (TNC), and the U.S. Fish & Wildlife Service all include conservation grazing and fire in their prairie management strategies and all expressed a willingness to allow me to study the prairies they manage. In 2015 and 2016, I compiled a list of prairie remnants under federal, state, TNC, and private management, and identified 10 prairies with graze-only management and 10 prairies with burn-only management strategies that were surveyed in 2016 and 2017. I obtained soils data from Natural Resources Conservation Service for available sites, and used drainage class as a proxy for dry, mesic, and wet prairie types. I selected burned and grazed sites such that each treatment had a similar variety of sites with different proportions of these three prairie types. I also collected information on year of management action and stocking rates for all sites. Due to access limitations, I dropped one grazed site from my study in 2016 and replaced it in 2017. For each site, I determined the percent of prairie in the surrounding landscape by first creating a 1.5 km buffer around each site using ArcMap (v 10.5.1) and overlaying this buffer onto landscape data obtained from the US Department of Agriculture, Minnesota Department of Natural Resources, and South Dakota State University. I then calculated the percentage of the land within the buffer that was classified as prairie. This served as a measure of fragmentation and isolation of prairie fragments. Fragmentation is generally associated with decreased bee species richness and abundance in various habitats (Cane 2001, Shuey 2013, Smith and Mayfield 2017).

Bee survey methods –

Bees were surveyed in two ways, passively via pan traps ("bee bowls"), and actively, via netting. I conducted these surveys three times each summer at each of the 20 sites (2016: June 15 – August 31; 2017: May 14 – August 18). When possible, visits were confined to days that were at least 70^{o} F with low wind speeds and no precipitation. Air temperature, wind-speed, and cloud-cover data were collected during each visit.

Pan traps –

I used 3.25 oz. (96.1 mL) plastic bowls in three colors (white, yellow, and blue) placed at 20-m intervals along the same transects as used for the vegetation surveys (see below); at each 20-m interval, a bowl was placed on the transect, and 2 additional bowls were placed perpendicular to the transect, 5-m from the center bowl. This adaptation of the standardized pan trap transect was made to create gaps in the transect through which cattle could potentially pass without disturbing traps. Pan traps were divided between prairie types, such that the number of sets of traps on transects in a given prairie type was proportional to that prairie type's contribution to the site, rounded up to the nearest ten percent. The bowls were filled with soapy water (mixture of water and Dawn dish soap), placed on bamboo poles of approximately 60 cm (2ft) in length, and left in place for approximately 24 hours. All insects captured on a transect were placed in a single Whirl-Pak bag, and kept frozen until processed and pinned. Pan traps were not placed at Glynn Prairie during the second two visits in 2016 because I did not want to disrupt ongoing surveys by Minnesota DNR. Through a data-sharing agreement, I have obtained bee collection data from two DNR visits that occurred at similar times during that summer.

Pan traps have both benefits and pitfalls. Pan traps consistently collect bee species that are missed by other collection techniques, such as aerial netting (Cane et al. 2000, Roulston et al. 2007, Grundel et al. 2011, Rhoades et al. 2017). They are efficient and limit user bias (Droege et al. 2010). However, pan traps can be greatly impacted by nearby floral abundance, with more bees collected in florally depauperate sites (Cane et al. 2000, Baum and Wallen 2011). Pan traps are in effect competing with flowers: if pan traps are among the few perceived resources for bees, they will get visited more frequently than if they are perceived as one option of many (Cane et al. 2000).

Netting –

To mitigate these concerns and as pan traps do not attract all bee taxa, all site visits also included a meandering walk in which bees were netted. To account for detectability biases, bees were only collected on flowers. The length of the meandering walk scaled with site size, lasting between 30 minutes and 2 hours. These surveys averaged 57.3 minutes with a standard deviation of 23.7 minutes. The average for surveys at burned sites averaged 54.3 minutes (σ = 21.7 mins). Surveys at grazed sites averaged 60.6 minutes (σ = 25.4 mins). Netted bees were placed individually in a glassine envelope, which was then put into an ethyl acetate-charged kill jar. Envelopes were labelled with the date, time, and site name. These envelopes and their contents were then frozen until specimens were pinned.

Identification –

Bumble bee (*Bombus*) specimens were identified to species using Bumble Bees of North America (Williams et al. 2014). All non-*Bombus* specimens were brought to Sam Droege of the U.S. Geological Survey who aided in specific identification during the spring and summer of 2018. A list of all species identified is included in Appendix A.

Species trait data –

Bee species trait data come from an in-progress database from Bartomeus et al. (2013). This included nesting location, body size, and sociality for most bee species identified in this study (Appendix B). Supplemental searches of literature were used to fill gaps when possible and to determine if bees were kleptoparasitic. Species were marked as potential tallgrass prairie specialists following a 1996 report to the U.S. Fish & Wildlife Service (Reed 1996).

Nesting location is defined as a trichotomous factor, with aboveground-nesting, soil-excavating ground-nesting, and non-excavating ground-nesting as the three possible levels. As outlined above, nesting habit has seen extensive attention in the literature regarding burning and grazing. I have split ground-nesters into two categories as I hypothesize that soil-excavating bees will respond differently to soil texture than non-excavators, who make use of existing cavities underground (McFrederick and LeBuhn 2007).

Body size is a continuous variable, representing average body length for female bees in millimeters. Size has been used as a proxy for bee dispersal capability in previous studies (Greenleaf et al. 2007). As prairie remnants in Minnesota are embedded within and separated by a matrix of agriculture and development (Minnesota Prairie Plan Working Group 2011), dispersal ability is likely important in determining the bee communities that inhabit sites following disturbance.

Sociality is a trichotomous factor as well, with eusocial, facultatively social, and solitary life-histories as the three possible values. Different social structures allow bees to differentially divide reproduction and foraging (Gullan and Cranston 2010). This may influence their abilities to exploit resources when they are available. If environmental traits have different significant relationships with individual life-histories, it may inform management decisions for future conservation efforts.

Tallgrass prairie specialization is a dichotomous factor, with either a value of "tallgrass prairie specialist" or "non tallgrass prairie specialist". This division is based upon a single publication (Reed 1996). Many of the species collected during this study belong to species that exist well beyond the confines of prairie (Chapter 1, this thesis). As they do not depend solely upon prairie, they may not be tied directly to the conditions within prairie. Habitat specialists, in contrast, may respond differently or more strongly to those conditions.

Finally, kleptoparasitism is a dichotomous factor, with bees either coded as kleptoparasites or non-kleptoparasites. Kleptoparasites are bees that do not provision their own larvae with pollen and nectar, instead infiltrating the nests of other bees and surreptitiously laying their own eggs in their hosts' brood cells. Once the cell is fully provisioned and sealed off by the host, the kleptoparasite's offspring will destroy the host's offspring and feed on the food it provided. While breaking human social mores, these "cuckoo bees" are considered indicators of healthy habitat (Sheffield et al. 2013); if bee communities can support detectable populations of "free-loaders", populations may be more robust than if no kleptoparasites were detected. Knowing whether and how management technique or other environmental traits influence this measure of health could be useful to conservation efforts going forward.

Vegetation survey methods-

Geographic Information System (GIS) maps were created using ArcGIS (version 10.3.1 for Desktop) for each site prior to the field season. Random transects were delineated on these maps, running parallel to any elevation gradient; if none existed, a random number was used to select a compass bearing through which the transect passed. The prairies ranged widely in size, from 1 to 145 hectares. A two-tiered approach to vegetation surveys was used, enabling comparisons of species richness among this wide range of site sizes, and minimizing exclusion of rarer species. Two botanists conducted vegetation surveys between June 1 – August 31, 2016 and May 30 – September 5, 2017 using a combination of nested frequency plots along the random transects, as well as a time-constrained, botanist-directed walk to add to site species lists.

Soil evaluation –

As soils can be important in shaping prairie plant communities, at each site 5 soil samples within each drainage class polygon were collected and combined. These were analyzed by the Research Analytical Laboratory at the University of Minnesota for soil texture using the hydrometer method. The percent of sand, silt, and clay in soil samples were reported. Soil texture shapes and is shaped by water drainage. While clay or silt could have been used as the texture measure of choice, I have used the proportion of sand in soils as it has been demonstrated that bees prefer to nest in sandy loams (Cane 1991, Chapter 1, this thesis). I averaged this sandiness of soils across sites, as sites varied in their relative composition of drainage-based prairie types. This site-wide proportion of sand in soils was calculated as follows:

$$\frac{Area_{wet}}{Area_{total}} * percent\ sand_{wet} + \frac{Area_{mesic}}{Area_{total}} * percent\ sand_{mesic} + \frac{Area_{dry}}{Area_{total}} * percent\ sand_{dry}$$

Analyses:

The fourth corner problem and solution –

Using species abundance measures, one cannot directly associate species traits with environmental characteristics. This has been given the moniker, "the fourth corner problem," following Legendre et al (1997). One imagines four lists of variables: a list of species, a list of those species' traits, a list of study sites, and a list of those sites' traits. With these, one can construct four matrices:

1.) *Species* x *Site*

2.) *Species* x *Species traits*

3.) *Site* x *Site traits*

4.) *Species traits* x *Site traits*

The first three matrices can be constructed directly – by collection, observation, or through the literature. The fourth is not directly observable, hence the "fourth corner problem."

Fourth-corner analysis, pioneered by Legendre and further developed by Dray (Legendre et al. 1997, Dray and Legendre 2008), can shed light on trait-trait relationships. In these analyses, **R** is defined as the matrix of sites by environmental traits, **Q** as the matrix of species by species traits, and **L** as the matrix of species by sites. **D** is the matrix of species traits by environmental traits that is predicted by this method (number 4 above). The fourth-corner analysis calculates a Pearson correlation coefficient (r^2) for quantitative-quantitative trait relationships, chi-squared statistic (χ^2) for qualitative-qualitative trait relationships, and an eta-squared statistic (η^2) for qualitative-quantitative trait relationships. These calculated statistics are compared to values generated by permuting data from matrix **L** and/or **Q.** Thus, matrix **D** is reported as the sign and significance of all pairwise relationships between species traits and environmental traits.

As originally conceived, one can choose between four models of permutation. The first permutes presence-absence data of species by site. The second permutes the entire community of species across sites, maintaining species assemblages. The third permutes the presence-absence data of sites by species. The fourth permutes the values of species traits by species. Subsequently, the ability to combine the second and fourth models has been developed, providing the most conservative estimates of significance for trait-trait relationships. I have chosen to use this conservative approach ("model 6" within the fourthcorner function of the ade4 package in R, Dray and Dufour 2007). Though Dray and Legendre (2008) originally suggested $\alpha = \sqrt{0.05}$, I have followed the example of ter Braak et al. (2012), keeping a standard α of 0.05 to limit type I error. To test the within-treatment effect of management intensity, I performed this analysis two more times, including the number of years since the last burn at burned sites and the ten-year average grazing intensity at grazed sites.

Species traits –

The five species traits included in matrices **Q** and **D** are nesting location, body size, sociality, tallgrass prairie specialization, and kleptoparasitism (Appendix B). The motivations for including these variables are described above under heading **Species trait data**.

Environmental traits –

I have selected nine environmental traits to include in matrices **R** and **D:** management type, forb frequency, site area, the frequency of *Bromus inermis*, the frequency of *Poa pratensis*, the proportion of sand in soils, the proportion of prairie within 1.5-km surrounding the remnants, the number of years since the previous burn (burned sites only), and the average grazing intensity between 2005 and 2015 (grazed sites only). Traits varied in their pairwise covariance (Table 7).

Management type is included as a dichotomous factor (Burned or Grazed). This is the primary environmental trait of interest, for reasons explained above.

Forb frequency is a continuous variable obtained from vegetation surveys. It is meant primarily as a proxy for floral resource availability, though it does not account for phenology of flowering or the identity of forbs, meaning that some plants unused by bees for food, such as yarrow (*Achillea millefolium*), are included. Some aboveground-nesting bees will also make use of forb stems as nesting sites.

Site area is a continuous variable. This data was obtained from GIS data layers from landowners or from layers created with input from landowners. Sites varied in area from 1.13 hectares to 144.70 hectares, with a median of 9.06 hectares. At burned sites, the average site was 27.28 hectares in area, with a standard deviation of 41.76 ha. At grazed sites, the average site was 43.26 hectares, with a standard deviation of 56.623 hectares. Larger sites may include a more diverse patchwork of microhabitats, promoting greater functional trait diversity in bees.

The frequencies of *Bromus inermis* and *Poa pratensis* are continuous variables obtained from vegetation surveys. These invasive graminoids are nearly ubiquitous in tallgrass prairie remnants. They form mats of thatch that inhibit soil access, disrupt nitrogen deposition, and crowd out some growing forbs (Printz and Hendrickson 2015).

The total proportion of sand in soils is a continuous variable, collected and calculated as described above. Soil texture can be an important factor in shaping the bee community of prairie (Chapter 1, this thesis). Many bees nest in soil, and soil is an avenue by which grazing and burning differentially impact prairies (Potts et al. 2005, Allred et al. 2011, Alaoui et al. 2018).

The proportion of prairie within the 1.5-km buffer surrounding remnants is a continuous variable, calculated as described above. This serves as a measure of fragmentation and isolation of prairie fragments. Fragmentation is generally associated with decreased bee species richness and abundance in various habitats (Cane 2001, Shuey 2013, Smith and Mayfield 2017).

In analyses restricted to burned sites, the number of years since the last burn is included as a continuous variable obtained from landowners. The vegetation community of burned grasslands change over time, leading to changes in bee communities as well (Potts et al. 2005). Testing how specific bee traits respond over time could provide insights on how frequently to burn for the bee community.

In analyses restricted to grazed sites, the average grazing intensity between 2005 and 2015 (AUM/year) is included as a continuous variable obtained from landowners and cattle owners. One "animal unit month" measures the amount of forage consumed by a 1000-pound cow over the course of one month. Some grazed prairies in this study were only grazed twice within the ten years prior to data collection, other were grazed every year.

Pooled data vs. netted data –

Analyses were run for pooled data (combined data from pan traps and netted specimens) and for netted data alone. While the pooled analyses were based upon the 12,160 specimens not eliminated by the above described-methods, netted analyses were made using the 461 specimens collected from flowers during the meandering walk component of sites visits. A number of bee bowls were lost at grazed sites, due to interference by cattle (Chapter 1, this thesis), skewing the sampling effort between management types. The netted data represent another measure of the bee community that is not skewed in this way.

Note on honey bees:

Honey bees (*Apis mellifera*) are likely not responding to their environment in the same way that other, non-managed bees, are. Honey bees do not rely upon prairie for nesting sites. Colonies are provisioned for the winter and treated to prevent disease. The environmental pressures that shape wild bee populations are not in effect. As the trait-specific response of bees to these pressures is sought, I have chosen to exclude honey bees from fourth-corner analyses.

Results

Bees–

Between the summers of 2016 and 2017, I collected 12,541 bees. Of these, 11,969 were from pan traps and the remaining 572 from directed netting. Three pan trap samples out of 117 were unusable – two were lost and one was unlabeled. One site visit of netted bees was lost in the field. Efforts to recover the lost kill jar were unsuccessful.

Sixty-two specimens could not be identified beyond genus and were removed from analyses. Of the remaining 12,479, 664 specimens within the genus *Lasioglossum* and one member of the genus *Sphecodes* could only be identified as belonging to a species complex of two species (e.g. *Lasioglossum admirandum/versatum*). These bees were included in analyses, as all traits barring body size were the same between the possible species. For body size, the average of the two possible species identifications, rounded to the nearest 0.5mm was used. As outlined in the methods, honey bees were excluded from subsequent analyses, reducing the number of specimens by 314 to 12,167. Of the individuals remaining, five additional individuals, representing two species, *Andrena cressonii* and *Nomia universitatis*, were dropped from analyses due to lack of of trait data, for a final sample size of 12, frequency 162 individuals.

Vegetation and soil -

Forb frequency –

Forb frequency, measured as the proportion of nested plots in which forbs were detected, varied between 0.40 and 0.69 at study sites, with an average forb frequency of 0.59 (σ = 0.0077).

***Bromus inermis* frequency –**

Bromus inermis frequency, measured as the proportion of nested plots in which *B. inermis* was detected, varied between 0.00 and 1.00, with an average of 0.66 (σ = 0.34)

***Poa pratensis* frequency –**

Poa pratensis frequency, measured as the proportion of nested plots in which *P. pratensis* was detected, varied between 0.125 and 1.00, with an average frequency of 0.78 (σ = 0.26)

Proportion sand in soil –

The site-wide proportion of sand in soil samples varied between 0.04 and 0.59, with an average proportion of 0.24 (σ = 0.14).

Fourth corner analysis -

Pooled -

Using pooled data, the fourth-corner analysis identified no significant relationships between species traits and environmental traits (Figure 6A). This was true within burned sites (n = 5,870 bees), within grazed sites (n = 6,290 bees), and across all sites (n = 12,160 bees).

Netted -

There were several significant relationships when pan trap data were not included in analyses. Within burned sites (n_{bees} = 247, $n_{species}$ = 48), there was a significant negative relationship between aboveground-nesting bees and the proportion of sand in soils (Table 8, Figure 6B). Within grazed sites (n_{bees} = 215, $n_{species}$ = 44) , solitary bees were significantly positively correlated with forb frequency, and soil-excavating ground-nesting bees were positively correlated with the proportion of sand in soils (Table 8, Figure 6B).

Across all sites (n_{bees} = 461, $n_{species}$ = 65), the sign and significance of these relationships persisted (Table 8, Figure 4B). Additionally, aboveground-nesters were negatively correlated with the percentage of prairie in the surrounding landscape and non-soil-excavating ground-nesters had a significant negative relationship with the frequency of *Bromus inermis*.

Discussion

The form of management does not significantly predict the suite of species traits in bees collected in Minnesota's tallgrass prairie. Rather, several significant correlations arise between bees' traits and the vegetation and soil characteristics of prairie remnants. Importantly, these significant relationships are observed only in specimens collected by aerial netting; when pan trap data were included in analyses, no trait-trait relationships were significant.

In contrast to this study, prior research has shown that fire (Wroblseki and Kaufman 2003, Potts et al. 2005, Mola and Williams 2018) and grazing (Carvell 2002, Kimoto et al. 2012) as habitat managements can influence the communities of bees found at sites. Generally, ground-nesters are tolerant of burns that do not move too slowly or burn too hotly (Cane and Neff 2011). Infrequent fire can allow dense vegetation to grow up, possibly inhibiting access by ground-nesters (Williams et al. 2010) and promoting aboveground-nesters (Potts et al. 2005, Davis et al. 2008), though the initial burn can be lethal to insects nesting within plants (Tooker and Hanks 2004). Grazing has been associated with a decrease in large bees, like bumble bees, and a corresponding increase in small bees, like sweat bees in the genus *Lasioglossum* (Kimoto et al. 2012) However, I saw no such effects of fire or grazing. There were no significant relationships between nesting location and management type. Body size was not correlated with any environmental predictors, including grazing. This lack in response may be due to the structure of data. There are no control groups in this study; burning and grazing are compared to one-another, whereas in the studies cited, bee communities following individual management techniques have been compared to communities receiving no management. It is also simply possible that for tallgrass prairie remnants, burning and grazing in isolation are equivalent for bee communities. This is in-line with previous analyses via generalized linear mixed effects models (GLMMs) on the same data (Chapter 1, this thesis), which found no significant effect of management type on bee abundance or diversity, though species richness was greater in netted samples at burned sites than at grazed sites. While there is evidence in the literature for a differing response of the trait-makeup of bee communities due to management, no significant relationships were uncovered by fourth-corner analysis of the current data set.

Though management was not significantly correlated with any species traits, vegetation traits were. Forb frequency was positively associated with solitary bees. While in a different agricultural landscape (coffee in Southern Mexico), this supports Fisher et al. (2017), who showed that solitary bee abundance increased with increased floral resources from herbaceous ground cover. Solitary bees may have to travel less distance if floral resources are concentrated, allowing them to provision more offspring than if they had to travel farther (Zurbuchen et al. 2010). Looking to the choices of semi-social bees may offer some insight. Within the facultatively social carpenter bee *Xylocopa pubescens*, individuals may exhibit solitary or social behaviors (Dunn and Richards 1999). These bees prefer to live solitarily until environmental constraints, including food availability, are severe, at which point some adult females may switch to nesting with another female. When resources are more plentiful, such as when the concentration of flowers is high, solitary bees may benefit. The positive significant correlation between solitary bees and forb frequency indicates that floral resource availability is an important component to healthy bee communities.

Ground-nesting bees that do not excavate their own nests were significantly negatively associated with the frequency of the invasive graminoid *Bromus inermis*. In this data set, all bees with this nesting habit were members of the genus *Bombus* (bumble bees). In its guidance on the conservation of the rusty patched bumble bee (*B. affinis*), the U.S. Fish & Wildlife Service (2016) indicates that the timing of burns to control for smooth brome could have detrimental impacts on bumble bees. Burns later in the spring are ideal for controlling brome (Wilson and Stubbendireck 2000), but many bumble bee workers and queens are actively foraging at this time (Williams et al. 2014). This could hamper their ability to collect enough resources to provision larvae and result in the negative correlation seen.

The composition of prairie soils also influences the traits of bee communities. At grazed sites, soil-excavating ground-nesting bees were positively correlated with sand in soil. This indicates that at grazed sites, aboveground-nesters are relatively consistent regardless of soil, and that soil-excavators are driven in part by the sandiness of soil. This effect could be due to compaction; as cattle compact soils, the baseline risk of erosion to sandy soils (Middleton 1930) is compounded (Alaoui et al. 2018). Erosion can create more bare ground which in turn promotes ground-nesters (Potts et al. 2005, Cane and Neff 2011). At burned sites, aboveground-nesters were significantly negatively correlated with the proportion of sand in soil. This could indicate that fire makes sandy sites less suitable to aboveground nesters, but it also might mean that fire makes less-sandy sites relatively *more* suitable to these bees. More hollow and pithy-stemmed plants may arise, particularly in the years following fires (Potts et al. 2005). Anecdotally, the forb community at several of the least sandy sites were dominated by goldenrod (*Solidago spp.*) and Maximilian sunflower (*Helianthus maximiliani)*, plants that can offer nesting opportunities to bees. If these are the communities that burns promote in less-sandy sites, aboveground nesters may fare relatively better in those sites than in sandier prairie remnants. Both the positive correlation of soil excavators and the negative correlation of aboveground-nesters to the proportion of sand in soils were significant when all sites where included in analyses. The management-specific effects on soil could be strong enough to drive the same relationship when surveys from both sites are included, or it could indicate a more general pattern regarding nesting behavior and soil. Soil excavators, regardless of management, benefit from sandier soils.

Nesting behavior is also implicated in bees' response to the amount of prairie near remnants. Aboveground-nesters in remnants were negatively correlated with the amount of prairie in the surrounding 1.5-km buffer, meaning that as prairie fragments become more isolated, these bees are more represented in the community. Prairie in Minnesota is generally found within a matrix of agriculture and development (Minnesota Prairie Plan Working Group 2011). Bees within that matrix may be drawn to the relatively abundant floral resources that prairie offers. Isolated prairie remnants might concentrate the local bee community into a single area. However, if there were additional florally rich grasslands nearby, such as other tallgrass prairie, that same bee community might be distributed between those patches. Each prairie may be relatively less attractive when there are more options nearby. As for nesting behavior's role in the interaction, while ground-nesters can find accessible soil outside of prairie, aboveground-nesters in particular may be drawn to isolated prairie remnants as they rely upon those vegetative communities for nesting locations as well as food. This negative relationship between prairie isolation and aboveground-nesting deserves further attention in subsequent studies of tallgrass prairie bees.

While various methods of modeling trait-based biodiversity, such as the fourth-corner method, have flourished in the last two decades (CATS, Traitspace, RLQ analyses, Trait Driver Theory), there is reason to be cautious (Laughlin et al. 2018). These models rely upon several key assumptions. Namely, they assume that trait-frequency is tied to trait-fitness; the more adaptive a trait is to its environment, the more frequently that trait should be observed. Secondarily, they assume that for any given trait, there is an optimal value that confers the greatest fitness (Muscarella and Uriarte 2016). It is difficult to demonstrate that these assumptions have been met, and I cannot claim that I have in this instance. However, in their critique of these methods, Laughlin et al. (2018), acknowledged that trait-based models of biodiversity are still useful in certain instances. They highlight their use in generating predictions about species and community distributions in an era of global change, and in accounting for ecosystem processes. I believe this study is using the fourth-corner approach to these ends. By incorporating the bee communities of 20 tallgrass prairie remnants, I have generated predictions for how communities may be distributed in relation to environmental traits in other remnants, and in response to the ecosystem processes of burning and grazing. There are limitations in applying these methods, but I have tried in good faith to stay within those guidelines.

Some limitations are also imposed due to the retrospective nature of this study. Without experimental manipulation, I could not test the extent to which burning and grazing lead directly to bee mortality. This makes parsing out the direct and indirect effects of management difficult. However, a retrospective study offered a duration of a single management type that would have been impossible to achieve through manipulation in the time-frame of this project. Additionally, tallgrass prairie is a precious resource. The land managers I worked with are tasked with protecting and promoting that resource, either for the public or for their livelihood. It was only through an observational study like this that we could work together without compromising their missions.

A ten-year history of burning or grazing, in isolation, does not predict significant differences in the trait-makeup of bee communities in remnant tallgrass prairie. Perhaps bees are more readily able to recolonize remnants after they have been excluded by management. Perhaps bees with traits that might be negatively impacted by fire or grazing in the near-term, like being a stem-nester in a prairie that is burning, can return and obscure those negative impacts. Even in its fragmented, diminished state, the network of tallgrass prairie may be resilient enough that bees are able to disperse between pockets of suitable habitat. It is also possible that the current community of bees that persists in prairie remnants consists of a subset of the historic community, and that the species that would have been most threatened by methods of disturbance have either been extirpated or make up such a small segment of the community as to not drive models. This may be why models that included pan traps had no significant correlations between environments and traits; the majority of bees collected, belonging to a handful of widely distributed species, may have so dominated the community as to obscure all other signals. Burning and grazing, as exclusive managements, have seemingly equivalent effects on bee communities and their component functional traits.

Fire and grazing were not historically mutually exclusive processes in tallgrass prairie. Today, many land-managers have begun recoupling these forces through practices like patch-burn grazing, in which cattle are set to graze on recently burned vegetation (Helzer and Steuter 2005, Fuhlendorf et al. 2009). This leverages the interactions of fire and herbivory to create patchworks of heavily and lightly disturbed grassland. Subsequent research should investigate how prairie bee communities respond to this form of management as compared to the unimodal techniques analyzed here.

Additionally, there may be other important life history traits that drive bees' responses to their environments, such as diet breadth or phenology. Understanding if and how these traits explain how bees are distributed in relation to their environments could help inform decisions regarding management type and timing. By continually building our base of knowledge, we can hope to better understand how historic processes have shaped pollinator communities, how to best management populations presently, and how to safeguard their futures.

Table 7 – Covariance of continuous environmental traits – The covariance of all pairwise relationships between continuous environmental variables. Numbers reported are for the analysis across all sites, except for the rows for treatment-specific intensity measures, which are based upon the treatment-specific analyses.

Site traits	Forb frequency	Site area	Frequency of *B. inermis*	Frequency of *P. pratensis*	Proportion of sand in soil	Percent prairie in surrounding buffer
Years since last burn*	0.0144	32.48	0.160	-0.0131	-0.0146	-11.8
Average grazing intensity*	-0.0446	33.7	-0.0355	0.0348	0.0104	4.30
Forb frequency		-0.895	-0.00263	-0.0104	-0.00110	-0.881
Site area			-7.34	-0.213	-0.208	480
Frequency of *B. inermis*				0.0342	0.00812	-2.82
Frequency of *P. pratensis*					0.0122	1.34
Proportion of sand in soil						1.66

Table 8 – **Pearson coefficients for significant trait-trait relationships** – Pearson coefficients generated by the fourth-corner analysis. All relationships reported here are significant (Figure 6).

Trait-trait relationship	Scope	Pearson coefficient
Aboveground-nesting vs. proportion sand in soil	All sites	-2.67
Aboveground-nesting vs. percent prairie in buffer	All sites	-1.96
Soil-excavating ground-nesting vs. proportion sand in soil	All sites	2.42
Non soil-excavating ground-nesting vs. frequency of *B. inermis*	All sites	-2.13
Solitary nesting vs. forb frequency	All sites	1.96
Aboveground-nesting vs. proportion sand in soil	Burned sites	-2.34
Soil-excavating ground-nesting vs. proportion sand in soil	Grazed sites	2.07
Solitary nesting vs. forb frequency	Grazed sites	2.20

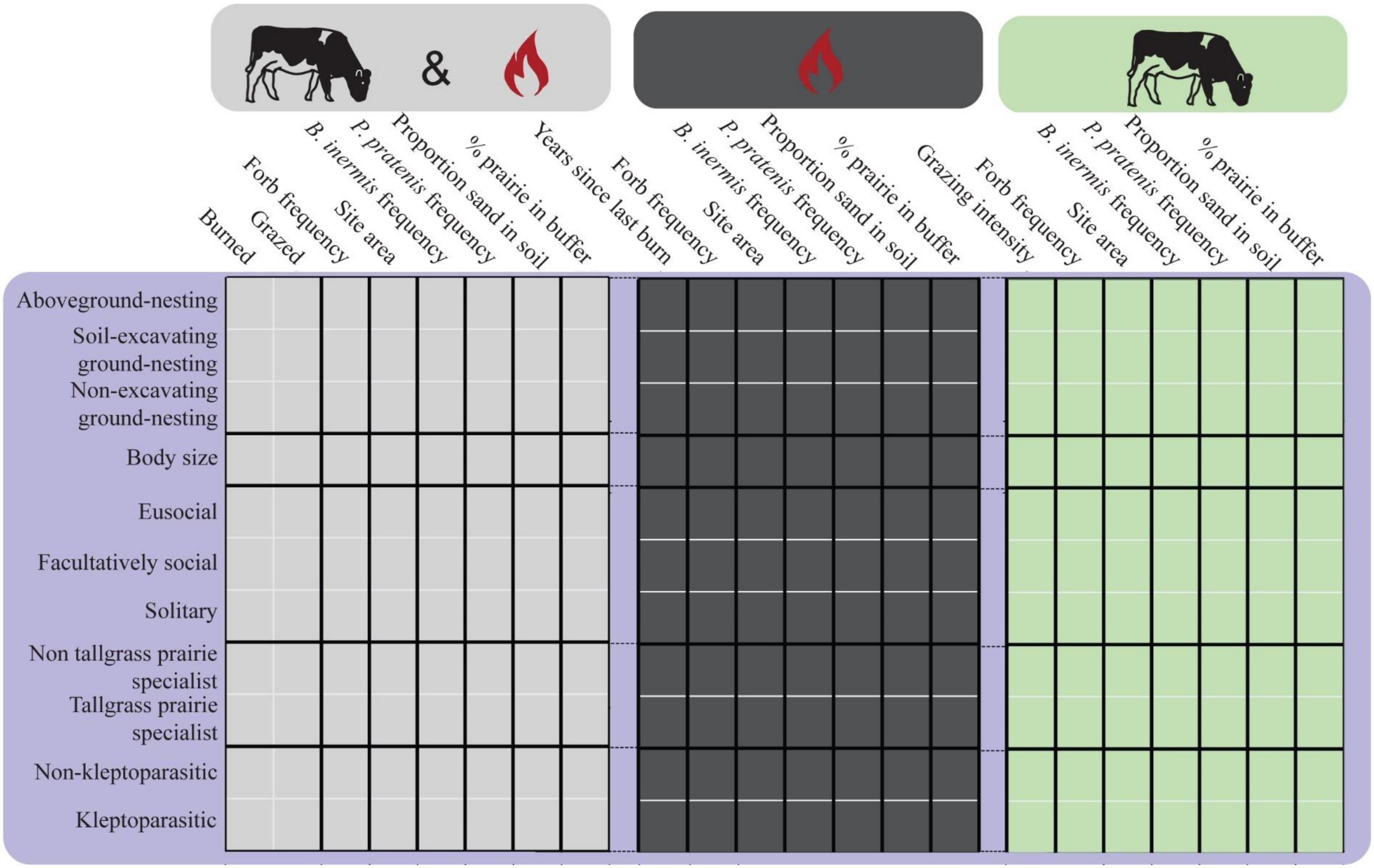

Figure 6a. Fourth corner analyses of bee traits vs. prairie traits, pooled data. *p* = 0.05. The rightmost matrix represents analysis across all sites, while the middle matrix and leftmost matrix represent analyses of burned and grazed sites, respectively. Squares with a plus (+) sign would indicate a positive significant correlation and significant negative correlations would be indicted with a minus (-) sign, but none were detected.

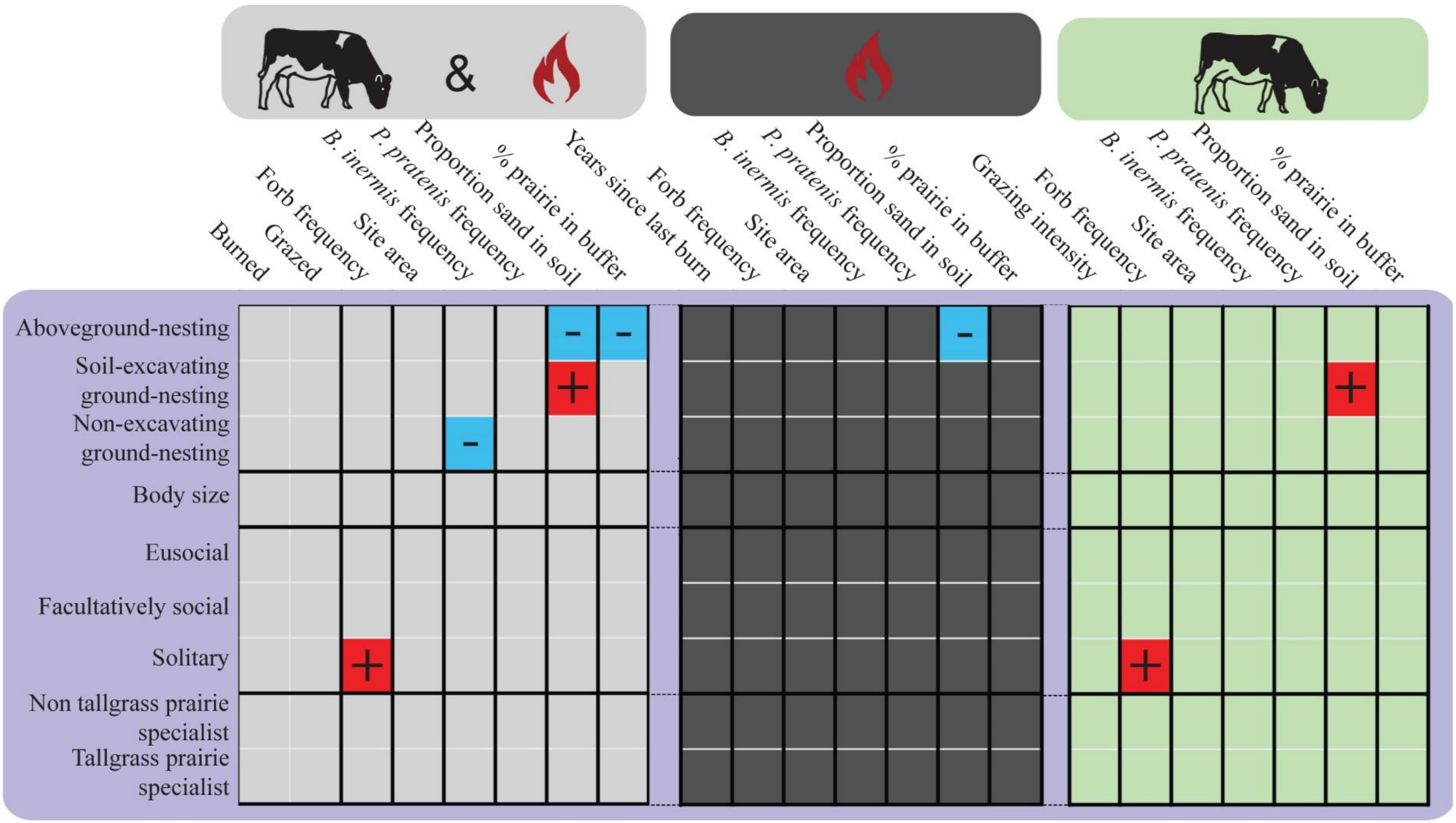

Figure 6b. Fourth corner analyses of bee traits vs. prairie traits, netted data. p = 0.05. The rightmost matrix represents analysis across all sites, while the middle matrix and leftmost matrix represent analyses of burned and grazed sites, respectively. Squares with a plus (+) sign indicate a positive significant correlation. Significant negative correlations are indicted with a minus (-) sign.

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Appendix A – Table of species collected.

Family	Binomial	Author	Determined by	Number collected
Andrenidae	*Andrena bisalicis*	Viereck, 1908	Sam Droege	1
	Andrena carlini	Cockerell, 1901	Sam Droege	10
	Andrena ceanothi	Viereck, 1917	Sam Droege	5
	Andrena chromotricha	Cockerell, 1899	Sam Droege	2
	Andrena commoda	Smith, 1879	Sam Droege	62
	Andrena cressonii	Robertson, 1891	Sam Droege	1
	Andrena erythrogaster	Ashmead, 1890	Sam Droege	1
	Andrena forbesii	Robertson, 1891	Sam Droege	2
	Andrena helianthi	Robertson, 1891	Sam Droege	2
	Andrena hirticincta	Warncke, 1975	Sam Droege	1
	Andrena milwaukeensis	Graenicher, 1903	Sam Droege	2
	Andrena nasonii	Robertson, 1895	Sam Droege	8
	Andrena nivalis	Smith, 1853	Sam Droege	1
	Andrena perplexa	Smith, 1853	Sam Droege	15
	Andrena placata	Mitchell, 1960	Sam Droege	1
	Andrena rudbeckiae	Robertson, 1891	Sam Droege	1
	Andrena simplex	Smith, 1853	Sam Droege	1
	Andrena sp.	N/A	Sam Droege	1
	Andrena thaspii	Graenicher, 1903	Sam Droege	2
	Andrena wilkella	(Kirby, 1802)	Sam Droege	14
	Andrena ziziae	Robertson, 1891	Sam Droege	1
	Calliopsis nebraskensis	Crawford, 1902	Sam Droege	1
	Perdita perpallida	Cockerell, 1901	Sam Droege	2
	Perdita swenki	Crawford, 1915	Sam Droege	11
	Protandrena bancrofti	Dunning, 1897	Sam Droege	4
Apidae	*Anthophora terminalis*	Cresson, 1869	Sam Droege	3
	Anthophora walshii	Cresson, 1869	Sam Droege	2
	Apis mellifera	Linnaeus, 1758	Nora Pennarola	309
	Bombus auricomus	Linnaeus, 1758	Nora Pennarola	16
	Bombus bimaculatus	Cresson, 1863	Nora Pennarola	9
	Bombus borealis	Kirby, 1837	Nora Pennarola	18
	Bombus fervidus	(Fabricius, 1798)	Nora Pennarola	38
	Bombus griseocollis	(DeGeer, 1773)	Nora Pennarola	48
	Bombus impatiens	Cresson, 1863	Nora Pennarola	19
	Bombus pensylvanicus	(DeGeer, 1773)	Nora Pennarola	10
	Bombus perplexus	Cresson, 1863	Nora Pennarola	1
	Bombus rufocinctus	Cresson, 1863	Nora Pennarola	1
	Bombus sp.	N/A	Nora Pennarola	4
	Bombus ternarius	Say, 1837	Nora Pennarola	4
	Bombus terricola	Kirby, 1837	Nora Pennarola	1
	Bombus vagans	Smith, 1854	Nora Pennarola	21

	Ceratina mikmaqi	Rehan&Sheffield, 2011	Sam Droege	141
	Eucera hamata	(Bradley, 1942)	Sam Droege	17
	Melissodes agilis	Cresson, 1878	Sam Droege	20
	Melissodes bimaculatus	(Lepeletier, 1825)	Sam Droege	20
	Melissodes communis	Cresson, 1878	Sam Droege	1
	Melissodes denticulatus	Smith, 1854	Sam Droege	3
	Melissodes desponsus	Smith, 1854	Sam Droege	25
	Melissodes druriellus	(Kirby, 1802)	Sam Droege	3
	Melissodes sp.	N/A	Sam Droege	5
	Melissodes trinodis	Robertson, 1901	Sam Droege	396
	Nomada articulata	Smith, 1854	Sam Droege	1
	Nomada near_MR_2	N/A	Sam Droege	1
	Svastra obliqua	(Say, 1837)	Sam Droege	1
	Triepeolus donatus	(Smith, 1854)	Sam Droege	2
	Xenoglossa kansensis	Cockerell, 1905	Sam Droege	6
Colletidae	*Colletes kincaidii*	Cockerell, 1898	Sam Droege	6
	Colletes robertsonii	DallaTorre, 1896	Sam Droege	1
	Colletes simulans	Cresson, 1868	Sam Droege	2
	Colletes solidaginis	Swenk, 1906	Sam Droege	2
	Colletes susannae	Swenk, 1925	Sam Droege	1
	Hylaeus affinis	(Smith, 1853)	Sam Droege	63
	Hylaeus mesillae	(Cockerell, 1896)	Sam Droege	9
	Hylaeus nelumbonis	(Robertson, 1890)	Sam Droege	2
Halictidae	*Agapostemon sericeus*	(Furster, 1771)	Sam Droege	4
	Agapostemon sp	N/A	Sam Droege	1
	Agapostemon texanus	Cresson, 1872	Sam Droege	310
	Agapostemon virescens	(Fabricius, 1775)	Sam Droege	996
	Augochlorella aurata	(Smith, 1853)	Sam Droege	1299
	Augochloropsis metallica	(Fabricius, 1793)	Sam Droege	4
	Halictus confusus	Smith, 1853	Sam Droege	316
	Halictus ligatus	Say, 1837	Sam Droege	104
	Halictus parallelus	Say, 1837	Sam Droege	37
	Halictus rubicundus	(Christ, 1791)	Sam Droege	21
	Lasioglossum admirandum	(Sandhouse, 1924)	Sam Droege	83
	Lasioglossum admirandum/versatum	(Sandhouse, 1924) / (Robertson, 1902)	Sam Droege	601
	Lasioglossum albipenne	(Robertson, 1890)	Sam Droege	1570
	Lasioglossum cinctipes	(Provancher, 1888)	Sam Droege	1
	Lasioglossum coriaceum	(Smith, 1853)	Sam Droege	379

Lasioglossum cressonii	(Robertson, 1890)	Sam Droege	58
Lasioglossum ephialtum	Gibbs, 2010	Sam Droege	115
Lasioglossum foxii	(Robertson, 1895)	Sam Droege	1
Lasioglossum hitchensi	(Mitchell, 1960)	Sam Droege	13
Lasioglossum imitatum	(Smith, 1853)	Sam Droege	1
Lasioglossum laevissimum	(Smith, 1853)	Sam Droege	12
Lasioglossum leucocomum	(Lovell, 1908)	Sam Droege	79
Lasioglossum leucozonium	(Schrank, 1781)	Sam Droege	20
Lasioglossum lineatulum	(Crawford, 1906)	Sam Droege	30
Lasioglossum michiganense	(Mitchell, 1960)	Sam Droege	3
Lasioglossum novascotiae	(Mitchell, 1960)	Sam Droege	405
Lasioglossum paradmirandum	(Knerer&Atwood, 1966)	Sam Droege	3
Lasioglossum paraforbesii	McGinley, 1986	Sam Droege	181
Lasioglossum pectorale	(Smith, 1853)	Sam Droege	9
Lasioglossum perpunctatum	(Knerer&Atwood, 1966)	Sam Droege	3
Lasioglossum pilosum	(Smith, 1853)	Sam Droege	55
Lasioglossum planatum	(Lovell, 1905)	Sam Droege	6
Lasioglossum pruinosum	(Robertson, 1892)	Sam Droege	2419
Lasioglossum semicaeruleum	(Cockerell, 1895)	Sam Droege	244
Lasioglossum sp.	N/A	Sam Droege	47
Lasioglossum subviridatum	(Cockerell, 1938)	Sam Droege	1
Lasioglossum tegulare	(Robertson, 1890)	Sam Droege	62
Lasioglossum tegulare/ellisiae	(Robertson, 1890) / (Sandhouse 1924)	Sam Droege	62
Lasioglossum versans	(Lovell, 1905)	Sam Droege	18
Lasioglossum versatum	(Robertson, 1902)	Sam Droege	1396
Lasioglossum vierecki	(Crawford, 1904)	Sam Droege	3
Lasioglossum weemsi	(Mitchell, 1960)	Sam Droege	4

	Lasioglossum zephyrum	(Smith, 1853)	Sam Droege	7
	Lasioglossum zonulum	(Smith, 1848)	Sam Droege	16
	Nomia universitatis	Cockerell, 1908	Sam Droege	2
	Sphecodes atlantis/cressonii	Mitchell, 1956 / Robertson, 1903	Sam Droege	1
	Sphecodes davisii	Robertson, 1897	Sam Droege	2
	Sphecodes mandibularis	Cresson, 1872	Sam Droege	1
	Sphecodes sp.	N/A	Sam Droege	1
Megachilidae	*Coelioxys octodentata*	Say, 1824	Sam Droege	1
	Coelioxys rufitarsis	Smith, 1854	Sam Droege	1
	Dianthidium simile	(Cresson, 1864)	Sam Droege	2
	Heriades carinata	Cresson, 1864	Sam Droege	2
	Heriades leavitti	Crawford, 1913	Sam Droege	3
	Hoplitis pilosifrons	(Cresson, 1864)	Sam Droege	84
	Megachile brevis	Say, 1837	Sam Droege	2
	Megachile latimanus	Say, 1823	Sam Droege	31
	Megachile mendica	Cresson, 1878	Sam Droege	2
	Megachile montivaga	Cresson, 1878	Sam Droege	4
	Megachile relativa	Cresson, 1878	Sam Droege	2
	Osmia near_collinsiae	N/A	Sam Droege	3
	Stelis lateralis	Cresson, 1864	Sam Droege	2

Appendix B – Table of species by traits.

Trait	Designation	Species
Nesting habit		
	Aboveground	*Anthophora terminalis*
		Ceratina mikmaqi
		Coelioxys octodentata
		Coelioxys rufitarsis
		Heriades carinata
		Heriades leavitti
		Hoplitis pilosifrons
		Hylaeus affinis
		Hylaeus mesillae
		Hylaeus nelumbonis
		Lasioglossum cressonii
		Lasioglossum subviridatum
		Megachile brevis
		Megachile mendica
		Megachile montivaga
		Megachile relativa
		Stelis lateralis
	Soil excavating ground-nester	*Agapostemon sericeus*
		Agapostemon texanus
		Agapostemon virescens
		Andrena bisalicis
		Andrena carlini
		Andrena ceanothi
		Andrena chromotricha
		Andrena commoda
		Andrena cressonii
		Andrena erythrogaster
		Andrena forbesii
		Andrena helianthi
		Andrena hirticincta
		Andrena milwaukeensis
		Andrena nasonii
		Andrena nivalis
		Andrena perplexa
		Andrena placata
		Andrena rudbeckiae
		Andrena simplex

		Andrena thaspii
		Andrena wilkella
		Andrena ziziae
		Anthophora walshii
		Augochlorella aurata
		Augochloropsis metallica
		Calliopsis nebraskensis
		Colletes kincaidii
		Colletes robertsonii
		Colletes simulans
		Colletes solidaginis
		Colletes susannae
		Dianthidium simile
		Eucera hamata
		Halictus confusus
		Halictus ligatus
		Halictus parallelus
		Halictus rubicundus
		Lasioglossum admirandum
		Lasioglossum admirandum/versatum
		Lasioglossum albipenne
		Lasioglossum cinctipes
		Lasioglossum coriaceum
		Lasioglossum ephialtum
		Lasioglossum foxii
		Lasioglossum hitchensi
		Lasioglossum imitatum
		Lasioglossum laevissimum
		Lasioglossum leucocomum
		Lasioglossum leucozonium
		Lasioglossum lineatulum
		Lasioglossum michiganense
		Lasioglossum novascotiae
		Lasioglossum paradmirandum
		Lasioglossum paraforbesii
		Lasioglossum pectorale
		Lasioglossum perpunctatum
		Lasioglossum pilosum
		Lasioglossum planatum
		Lasioglossum pruinosum
		Lasioglossum semicaeruleum

		Lasioglossum tegulare
		Lasioglossum tegulare/ellisiae
		Lasioglossum versans
		Lasioglossum versatum
		Lasioglossum vierecki
		Lasioglossum weemsi
		Lasioglossum zephyrum
		Lasioglossum zonulum
		Megachile latimanus
		Melissodes agilis
		Melissodes bimaculatus
		Melissodes communis
		Melissodes denticulatus
		Melissodes desponsus
		Melissodes druriellus
		Melissodes trinodis
		Nomada articulata
		Nomia universitatis
		Perdita perpallida
		Perdita swenki
		Protandrena bancrofti
		Sphecodes atlantis/cressonii
		Sphecodes davisii
		Sphecodes mandibubris
		Svastra obliqua
		Triepeolus donatus
		Xenoglossa kansensis
	Non-excavating ground-nester	*Bombus auricomus*
		Bombus bimaculatus
		Bombus borealis
		Bombus fervidus
		Bombus griseocollis
		Bombus impatiens
		Bombus pensylvanicus
		Bombus perplexus
		Bombus rufocinctus
		Bombus ternarius
		Bombus terricola
		Bombus vagans
Body size (mm)		
	12	*Agapostemon sericeus*

	11	*Agapostemon texanus*
	11	*Agapostemon virescens*
	9	*Andrena bisalicis*
	14	*Andrena carlini*
	10	*Andrena ceanothi*
	9	*Andrena chromotricha*
	11	*Andrena commoda*
	10	*Andrena erythrogaster*
	10	*Andrena forbesii*
	12	*Andrena helianthi*
	11	*Andrena hirticincta*
	11	*Andrena milwaukeensis*
	8	*Andrena nasonii*
	13	*Andrena nivalis*
	13	*Andrena perplexa*
	9	*Andrena placata*
	13	*Andrena rudbeckiae*
	9	*Andrena simplex*
	10	*Andrena thaspii*
	11	*Andrena wilkella*
	7	*Andrena ziziae*
	12.25	*Anthophora terminalis*
	14	*Anthophora walshii*
	5.5	*Augochlorella aurata*
	9	*Augochloropsis metallica*
	20	*Bombus auricomus*
	11	*Bombus bimaculatus*
	13	*Bombus borealis*
	10.55	*Bombus fervidus*
	13.75	*Bombus griseocollis*
	12.25	*Bombus impatiens*
	16	*Bombus pensylvanicus*
	13	*Bombus perplexus*
	11.75	*Bombus rufocinctus*
	10.5	*Bombus ternarius*
	11.5	*Bombus terricola*
	6	*Bombus vagans*
	8	*Calliopsis nebraskensis*
	7	*Ceratina mikmaqi*
	10	*Coelioxys octodentata*
	15	*Coelioxys rufitarsis*

	10	*Colletes kincaidii*
	12	*Colletes robertsonii*
	10.5	*Colletes simulans*
	8.5	*Colletes solidaginis*
	10	*Colletes susannae*
	8	*Dianthidium simile*
	16.5	*Eucera hamata*
	7	*Halictus confusus*
	9	*Halictus ligatus*
	12	*Halictus parallelus*
	10.5	*Halictus rubicundus*
	7	*Heriades carinata*
	7	*Heriades leavitti*
	7.5	*Hoplitis pilosifrons*
	5.5	*Hylaeus affinis*
	4	*Hylaeus mesillae*
	7.5	*Hylaeus nelumbonis*
	5.25	*Lasioglossum admirandum*
	5.5	*Lasioglossum admirandum/versatum*
	6	*Lasioglossum albipenne*
	8	*Lasioglossum cinctipes*
	9	*Lasioglossum coriaceum*
	6.5	*Lasioglossum cressonii*
	5.5	*Lasioglossum ephialtum*
	6.5	*Lasioglossum foxii*
	5	*Lasioglossum hitchensi*
	4	*Lasioglossum imitatum*
	6	*Lasioglossum laevissimum*
	5	*Lasioglossum leucocomum*
	8	*Lasioglossum leucozonium*
	6	*Lasioglossum lineatulum*
	5.5	*Lasioglossum michiganense*
	7	*Lasioglossum novascotiae*
	5.5	*Lasioglossum paradmirandum*
	6	*Lasioglossum paraforbesii*
	6	*Lasioglossum pectorale*
	6	*Lasioglossum perpunctatum*
	6	*Lasioglossum pilosum*
	5.5	*Lasioglossum planatum*
	6	*Lasioglossum pruinosum*
	8	*Lasioglossum semicaeruleum*

		5	*Lasioglossum subviridatum*
		5	*Lasioglossum tegulare*
		5	*Lasioglossum tegulare/ellisiae*
		6	*Lasioglossum versans*
		6	*Lasioglossum versatum*
		4	*Lasioglossum vierecki*
		4.5	*Lasioglossum weemsi*
		6	*Lasioglossum zephyrum*
		9	*Lasioglossum zonulum*
		10.5	*Megachile brevis*
		13	*Megachile latimanus*
		11	*Megachile mendica*
		12	*Megachile montivaga*
		10.5	*Megachile relativa*
		12.75	*Melissodes agilis*
		14	*Melissodes bimaculatus*
		13	*Melissodes communis*
		10.25	*Melissodes denticulatus*
		12.75	*Melissodes desponsus*
		10.5	*Melissodes druriellus*
		11.5	*Melissodes trinodis*
		8.5	*Nomada articulata*
		6	*Perdita perpallida*
		6	*Perdita swenki*
		10	*Protandrena bancrofti*
		8	*Sphecodes atlantis/cressonii*
		8	*Sphecodes davisii*
		8	*Sphecodes mandibubris*
		5.5	*Stelis lateralis*
		15	*Svastra obliqua*
		11	*Triepeolus donatus*
		15	*Xenoglossa kansensis*
Sociality			
	Eusocial		*Augochlorella aurata*
			Bombus auricomus
			Bombus bimaculatus
			Bombus borealis
			Bombus fervidus
			Bombus griseocollis
			Bombus impatiens
			Bombus pensylvanicus

		Bombus perplexus
		Bombus rufocinctus
		Bombus ternarius
		Bombus terricola
		Bombus vagans
		Halictus ligatus
		Halictus parallelus
		Lasioglossum admirandum
		Lasioglossum admirandum/versatum
		Lasioglossum albipenne
		Lasioglossum cinctipes
		Lasioglossum cressonii
		Lasioglossum ephialtum
		Lasioglossum hitchensi
		Lasioglossum imitatum
		Lasioglossum laevissimum
		Lasioglossum leucocomum
		Lasioglossum lineatulum
		Lasioglossum novascotiae
		Lasioglossum paradmirandum
		Lasioglossum perpunctatum
		Lasioglossum pilosum
		Lasioglossum planatum
		Lasioglossum pruinosum
		Lasioglossum semicaeruleum
		Lasioglossum subviridatum
		Lasioglossum tegulare
		Lasioglossum tegulare/ellisiae
		Lasioglossum versans
		Lasioglossum versatum
		Lasioglossum weemsi
		Lasioglossum zephyrum
	Facultatively social/semisocial	*Agapostemon sericeus*
		Agapostemon texanus
		Agapostemon virescens
		Ceratina mikmaqi
		Halictus confusus
		Halictus rubicundus
		Lasioglossum coriaceum
		Lasioglossum leucozonium
		Lasioglossum paraforbesii

		Lasioglossum zonulum
	Solitary	*Andrena bisalicis*
		Andrena carlini
		Andrena ceanothi
		Andrena chromotricha
		Andrena commoda
		Andrena cressonii
		Andrena erythrogaster
		Andrena forbesii
		Andrena helianthi
		Andrena hirticincta
		Andrena milwaukeensis
		Andrena nasonii
		Andrena nivalis
		Andrena perplexa
		Andrena placata
		Andrena rudbeckiae
		Andrena simplex
		Andrena thaspii
		Andrena wilkella
		Andrena ziziae
		Anthophora terminalis
		Anthophora walshii
		Augochloropsis metallica
		Calliopsis nebraskensis
		Coelioxys octodentata
		Coelioxys rufitarsis
		Colletes kincaidii
		Colletes robertsonii
		Colletes simulans
		Colletes solidaginis
		Colletes susannae
		Dianthidium simile
		Eucera hamata
		Heriades carinata
		Heriades leavitti
		Hoplitis pilosifrons
		Hylaeus affinis
		Hylaeus mesillae
		Hylaeus nelumbonis
		Lasioglossum foxii

		Lasioglossum michiganense
		Lasioglossum pectorale
		Lasioglossum vierecki
		Megachile brevis
		Megachile latimanus
		Megachile mendica
		Megachile montivaga
		Megachile relativa
		Melissodes agilis
		Melissodes bimaculatus
		Melissodes communis
		Melissodes denticulatus
		Melissodes desponsus
		Melissodes druriellus
		Melissodes trinodis
		Nomada articulata
		Perdita perpallida
		Perdita swenki
		Protandrena bancrofti
		Sphecodes atlantis/cressonii
		Sphecodes davisii
		Sphecodes mandibubris
		Stelis lateralis
		Svastra obliqua
		Triepeolus donatus
		Xenoglossa kansensis
Tallgrass prairie specialization		
	"No"	*Agapostemon sericeus*
		Agapostemon texanus
		Agapostemon virescens
		Andrena bisalicis
		Andrena carlini
		Andrena ceanothi
		Andrena chromotricha
		Andrena commoda
		Andrena cressonii
		Andrena erythrogaster
		Andrena forbesii
		Andrena hirticincta
		Andrena milwaukeensis
		Andrena nasonii

		Andrena nivalis
		Andrena perplexa
		Andrena placata
		Andrena thaspii
		Andrena wilkella
		Anthophora terminalis
		Anthophora walshii
		Augochlorella aurata
		Augochloropsis metallica
		Bombus auricomus
		Bombus bimaculatus
		Bombus borealis
		Bombus griseocollis
		Bombus impatiens
		Bombus pensylvanicus
		Bombus perplexus
		Bombus rufocinctus
		Bombus ternarius
		Bombus terricola
		Bombus vagans
		Ceratina mikmaqi
		Coelioxys octodentata
		Coelioxys rufitarsis
		Colletes kincaidii
		Colletes solidaginis
		Dianthidium simile
		Eucera hamata
		Halictus confusus
		Halictus ligatus
		Halictus parallelus
		Halictus rubicundus
		Heriades carinata
		Heriades leavitti
		Hoplitis pilosifrons
		Hylaeus affinis
		Hylaeus mesillae
		Hylaeus nelumbonis
		Lasioglossum admirandum
		Lasioglossum admirandum/versatum
		Lasioglossum albipenne
		Lasioglossum cinctipes

		Lasioglossum coriaceum
		Lasioglossum cressonii
		Lasioglossum ephialtum
		Lasioglossum foxii
		Lasioglossum hitchensi
		Lasioglossum imitatum
		Lasioglossum laevissimum
		Lasioglossum leucocomum
		Lasioglossum leucozonium
		Lasioglossum lineatulum
		Lasioglossum michiganense
		Lasioglossum novascotiae
		Lasioglossum paradmirandum
		Lasioglossum paraforbesii
		Lasioglossum pectorale
		Lasioglossum perpunctatum
		Lasioglossum pilosum
		Lasioglossum planatum
		Lasioglossum pruinosum
		Lasioglossum semicaeruleum
		Lasioglossum subviridatum
		Lasioglossum tegulare
		Lasioglossum tegulare/ellisiae
		Lasioglossum versans
		Lasioglossum versatum
		Lasioglossum vierecki
		Lasioglossum weemsi
		Lasioglossum zephyrum
		Lasioglossum zonulum
		Megachile brevis
		Megachile latimanus
		Megachile montivaga
		Megachile relativa
		Melissodes bimaculatus
		Melissodes communis
		Melissodes druriellus
		Nomada articulata
		Nomia universitatis
		Sphecodes atlantis/cressonii
		Sphecodes davisii
		Sphecodes mandibubris

		Stelis lateralis
		Svastra obliqua
		Triepeolus donatus
		Xenoglossa kansensis
	"Yes"	*Andrena helianthi*
		Andrena rudbeckiae
		Andrena simplex
		Andrena ziziae
		Bombus fervidus
		Calliopsis nebraskensis
		Colletes robertsonii
		Colletes simulans
		Colletes susannae
		Megachile mendica
		Melissodes agilis
		Melissodes denticulatus
		Melissodes desponsus
		Melissodes trinodis
		Perdita perpallida
		Perdita swenki
		Protandrena bancrofti
Kleptoparasitism		
	"No"	*Agapostemon sericeus*
		Agapostemon texanus
		Agapostemon virescens
		Andrena bisalicis
		Andrena carlini
		Andrena ceanothi
		Andrena chromotricha
		Andrena commoda
		Andrena cressonii
		Andrena erythrogaster
		Andrena forbesii
		Andrena helianthi
		Andrena hirticincta
		Andrena milwaukeensis
		Andrena nasonii
		Andrena nivalis
		Andrena perplexa
		Andrena placata
		Andrena rudbeckiae

		Andrena simplex
		Andrena thaspii
		Andrena wilkella
		Andrena ziziae
		Anthophora terminalis
		Anthophora walshii
		Augochlorella aurata
		Augochloropsis metallica
		Bombus auricomus
		Bombus bimaculatus
		Bombus borealis
		Bombus fervidus
		Bombus griseocollis
		Bombus impatiens
		Bombus pensylvanicus
		Bombus perplexus
		Bombus rufocinctus
		Bombus ternarius
		Bombus terricola
		Bombus vagans
		Calliopsis nebraskensis
		Ceratina mikmaqi
		Colletes kincaidii
		Colletes robertsonii
		Colletes simulans
		Colletes solidaginis
		Colletes susannae
		Dianthidium simile
		Eucera hamata
		Halictus confusus
		Halictus ligatus
		Halictus parallelus
		Halictus rubicundus
		Heriades carinata
		Heriades leavitti
		Hoplitis pilosifrons
		Hylaeus affinis
		Hylaeus mesillae
		Hylaeus nelumbonis
		Lasioglossum admirandum
		Lasioglossum admirandum/versatum

		Lasioglossum albipenne
		Lasioglossum cinctipes
		Lasioglossum coriaceum
		Lasioglossum cressonii
		Lasioglossum ephialtum
		Lasioglossum foxii
		Lasioglossum hitchensi
		Lasioglossum imitatum
		Lasioglossum laevissimum
		Lasioglossum leucocomum
		Lasioglossum leucozonium
		Lasioglossum lineatulum
		Lasioglossum michiganense
		Lasioglossum novascotiae
		Lasioglossum paradmirandum
		Lasioglossum paraforbesii
		Lasioglossum pectorale
		Lasioglossum perpunctatum
		Lasioglossum pilosum
		Lasioglossum planatum
		Lasioglossum pruinosum
		Lasioglossum semicaeruleum
		Lasioglossum subviridatum
		Lasioglossum tegulare
		Lasioglossum tegulare/ellisiae
		Lasioglossum versans
		Lasioglossum versatum
		Lasioglossum vierecki
		Lasioglossum weemsi
		Lasioglossum zephyrum
		Lasioglossum zonulum
		Megachile brevis
		Megachile latimanus
		Megachile mendica
		Megachile montivaga
		Megachile relativa
		Melissodes agilis
		Melissodes bimaculatus
		Melissodes communis
		Melissodes denticulatus
		Melissodes desponsus

		Melissodes druriellus
		Melissodes trinodis
		Nomia universitatis
		Perdita perpallida
		Perdita swenki
		Protandrena bancrofti
		Svastra obliqua
		Xenoglossa kansensis
	"Yes"	*Coelioxys octodentata*
		Coelioxys rufitarsis
		Nomada articulata
		Sphecodes atlantis/cressonii
		Sphecodes davisii
		Sphecodes mandibubris
		Stelis lateralis
		Triepeolus donatus