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A Descriptive Study of Wild Bees (Hymenoptera: Apoidea: Apiformes) and Angiosperms in a Tallgrass Prairie Corridor of Southeastern Nebraska

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A DESCRIPTIVE STUDY OF WILD BEES (HYMENOPTERA: APOIDEA: APIFORMES) AND ANGIOSPERMS IN A TALLGRASS PRAIRIE CORRIDOR OF SOUTHEASTERN NEBRASKA

by

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The presence of diverse bee communities in an ecosystem is vital for maintaining healthy plant communities, promoting habitat resilience, and supporting sustainable agricultural production and urbanization. Approximately 20,000 known species of bees exist worldwide and assist with the successful reproduction of nearly 80% of Earth's flowering plants by providing pollination services. In the US, wild bee declines have led to increased monitoring efforts for bees but there remain critical data gaps in prairies of the Great Plains ecoregion. Specific to the Tallgrass prairie where only 1-3% remains in native vegetation, the Nebraska Wildlife Action Plan has identified the loss of pollinators as a key stressor as well as a lack of sufficient data from which to monitor this stressor. This thesis seeks to 1) review current literature on the status of prairie ecosystems and the interdependency of wild bees, 2) establish and describe baseline data on wild bees and flowering forb communities, and examine their existing interactions in southeastern Nebraska Tallgrass prairies, 3) assess how the variation in vegetation cover influences the richness and abundance of wild bees, and 4) provide an extension guide highlighting a bee's role in conserving the biological diversity of prairies. Over a period of 2 years, 85 species of wild bees and 114 species of flowering forbs were identified, and a preference index was calculated (based off of the abundance of bee visits to observed flowering forbs) to improve pollinator seed mixtures and inform future restoration efforts. Additionally, this thesis presents evidence that newly-restored prairies seeded with high diversity mixes support higher richness and abundance of wild bees compared to remnant prairies, however remnant prairies provide consistent support to wild bees on a temporal scale. Collectively, the resulting information of this thesis will aid in the design, management and reconstruction of the Prairie Corridor on Haines Branch (Lincoln, Nebraska) by providing recommendations tailored to enhance and sustain diverse bee communities.

Table of Contents

Acknowledgments

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List of Figures

Figure 3.4. Results for all 5 measures when modeled against Treatment (left column) and modeled against Season (right column). Letters denote significant difference (a =0.05), and the breakdown of N (total=429) is represented inside each bar.

Figure 3.5. Results for all 5 measures when modeled against the interaction between Treatment and Season. Letters denote significant difference (a=0.05), and the breakdown of N (total=429) is represented inside each bar.

List of Tables

Table 2.5. Comparison of Top 10 bee-visited forbs and available forbs by color, displaying difference in species composition. Bee-visited forbs are in order from most to least supportive of bee richness per color, and available forbs are in order of cumulative abundance on the landscape. * denotes forbs that bees were not observed visiting throughout this study.

Table 3.1. Summary of ANOVA results for all 5 measures. Significance was observed for all measures when tested against Treatment (High Diversity, Low Diversity, Remnant), Season (Early: Apr-mid Jun, Mid: late Jun-mid Aug, Late: late Aug-Oct), and the interaction of Treatment*Season meaning the effect of treatment cannot be understood without considering season or the reverse.

Table 3.2. Top 5 most abundant mid-season forbs observed on the landscape compared to Top 5 most-visited mid-season forbs. Mid-season forb richness and forb abundance values were not significantly different between the Remnant and High Diversity treatments, however the High Diversity treatment had significantly higher mid-season bee richness and abundance values. This suggests the composition of the forb community is driving the bee community. * denotes non-native forbs relative to Nebraska as classified by The PLANTS Database (USDA).

Chapter 1: Literature Review of Grasslands and Wild Bees

1.1. Introduction to the Great Plains

Existing in temperate North America is a vast mosaic of grassland ecosystems collectively referred to as the North American Great Plains. As classified by the Environmental Protection Agency (EPA) Level 1 North American Ecoregions, the Great Plains ecoregion extends from Canada to Texas including 3 provinces (AB, MB, SK) and 13 states (CO, IA, KS, MN, MO, MT, ND, NE, NM, OK, SD, TX, WY) (Commission for Environmental Cooperation, 1997) (Figure 1.1). This ecoregion naturally exhibits high levels of biological diversity in flora and fauna, and is known worldwide for its immense plant diversity, countless endemic birds, and populations of large herbivores (Henwood, 2010). Prairies are a particular type of grassland within the Great Plains, characterized by their dominant vegetation cover of grasses, shrubs and herbaceous broadleaf plants (forbs). Three types of prairie exist in the Great Plains and from east to west are classified as Tallgrass, Mixed-grass and Shortgrass Prairie (Figure 1.2). These three systems are differentiated by a north-south cold to hot temperature gradient and an east-west wet to dry precipitation gradient (USGCRP, 2014). In the east, the Tallgrass Prairie is characterized by fertile, deep soils (mollisols), average annual precipitation of >750 mm, and tall grasses exceeding a height of 1.5m at maturity. Shortgrass Prairie in the west is characterized by mostly coarse mollisols with the dominant texture being a fine sandy loam, average annual precipitation of ~375 mm, and grasses reaching heights of 0.6m (WRANLGE, 2019). In between Tallgrass and Shortgrass Prairie resides Mixed-grass Prairie which is characterized by low and irregular precipitation averaging ~500 mm annually, and the soils are deep, fertile loess deposits that range in texture from loamy sands to clay (WRANGLE, 2019). Historically, these three types of prairie occupied 2,626,600 km^2 of undisturbed and contiguous land that was home to some of the Earth's largest wildlife assemblages; however, it is estimated that only 859,562km^2, or 32%, remains in original vegetation in the form of highly fragmented and degraded remnants (Hendwood, 2010).

Factors contributing to such mass destruction are largely related to agricultural intensification and urban expansion, consequently resulting in the classification of North American prairies as critically endangered landscapes (Noss et al., 1995; Anderson et al., 2006). For example, between 2008-2012 the United States experienced a net cropland increase of nearly 1.2 million hectares, 77% of which converted grassland into crop production (Lark et al., 2015). Due to these dramatic land use changes, the Great Plains has been identified as an area of high priority for conservation actions in order to protect the nation's Areas of Biodiversity Significance (Martinuzzi et al., 2013). Areas of Biodiversity Significance are classified as having high diversity of native species, natural communities, and complex networks. Model predictions indicate losses of these areas potentially up to 30% by 2050 due to further agricultural and urban expansion (Martinuzzi et al., 2013). The negative effects of this habitat loss and fragmentation have been extensively documented using grassland birds, a group whose highest diversity exists in the North American Great Plains. Grassland birds are highly sensitive to environmental changes and populations may respond quickly which has allowed researchers to record the declination of species occurrence as a result of climatic (precipitation and temperature) and land use changes (Niemuth et al., 2017). While these findings are specific to birds, many other vertebrates, such as mammals, and invertebrates occupy these same areas and therefore may be similarly affected.

A well-known group of animals experiencing repercussions of environmental and land use change are pollinators, consisting of bats, beetles, bees, birds, butterflies, and flies, the presence of which provide vital ecosystem services (Ghanem and Voigt, 2012; Bartomeus et al., 2013; Kennedy et al., 2013; Vanbergen et al., 2013). A global assessment in pollinator trends revealed that since 1988, an average of 2.5 species per year of pollinating mammals and birds have been moving towards extinction in accord to the International Union for Conservation of Nature (IUCN) Red List of Threatened Species criteria (Regan et al., 2015). However, IUCN lacks information on many invertebrates from which to assess the trends of the most dominant and highest-valued pollinators because sufficient baseline is not available (Ollerton 2017; Knight et al., 2018).

Pollinators and prairies are two fragile systems so strongly interrelated that it is difficult to discuss their declines independently. Many of the factors contributing to pollinator decline also degrade, diminish, or threaten the prairie, indirectly if not directly, creating an increasingly important need to conserve and enhance biological diversity in the Great Plains (Ordonez et al., 2014; Becerra et al., 2017). For example, the decline of grassland-dominated landscapes and their forb communities have been correlated with the decline of bee species richness (Biesmeijer et al., 2006). However, the strong mutualistic relationship also allows for targeted pollinator restoration efforts to equally benefit prairie ecosystems, where the increase of plant and pollinator functional diversity has been demonstrated to recruit diverse plant communities (Fontaine et al., 2005). Promoting pollinator diversity and their associated plants will help maintain the stability and resilience of prairie ecosystems, which are increasingly important to conserve and restore.

1.2. Importance of Bees

Bees are recognized worldwide for being the most effective and efficient pollinator. Setting them apart from other pollinators, such as bats, beetles, butterflies and flies, bees have adapted specialized morphological structures that allow them to collect and distribute pollen. The purpose of collecting pollen and nectar is to secure nutritious protein and carbohydrates, and in doing so the bee transfers pollen grains from the male anther of a flower to the female stigma of another, thus providing pollination or fertilization allowing for the production of seeds for many forbs. In fact, of all the known Angiosperms (flowering plants) on Earth, 87.5% of them require cross-pollination services in order to successfully reproduce (Ollerton et al., 2011). The relationship existing between bees and flowering plants is of high mutual benefit, and collectively helps sustain biological diversity across landscapes.

Biological diversity (biodiversity) refers to the variability among living organisms from all sources, including within species, between species and of ecosystems (Speight et al., 2008). Biodiversity can be explored at different hierarchical levels, namely genetic diversity, species diversity and ecosystem diversity. When bees provide pollination services, the benefits can be observed across all levels in the plants and wildlife that depend on them (Kremen et al., 2007). For example, bees, other beneficial insects, and products of pollinated flowers provide food and shelter allowing birds, mice, deer and other wildlife to sustain healthy populations, which are necessary to support species of higher trophic levels such as foxes, snakes and raptors. Diverse plant communities also help maintain ecosystem resilience, where mature root systems help cycle nutrients within the soil, prevent erosion and enhance water quality (Vinton and Burke, 1995; Diaz and Cabido, 2001; Cardinale, 2011). Thus it is apparent that ecosystem services provided by bee and plant communities collectively sustain biodiversity, wherein increased levels of biodiversity lead to a more stable and resilient ecosystem (Naeem et al., 1995, Steffan-Dewenter and Tscharntke, 1999).

In addition to sustaining biodiversity, the pollination services that bees provide have an immense impact on the global economy and human health. Approximately 35% of global food production relies on insect pollination, and in the United States alone the economic value of pollinators is estimated at $15 billion annually (Klein et al., 2006; Calderone, 2012). The agricultural industry is continuously increasing the amount of land used for crop production in order to meet growing demand for food and energy resources. For example, in Nebraska the high profitability of corn has led to crop coverage increasing from 3.1 to 3.8 million hectares in the last 20 years (USDA NASS). This expansion of cropland reduces critical pollinator forage and habitat, especially in areas producing high volumes of wind-pollinated crops (corns, soy beans, wheat), while simultaneously increases the demand for pollinators in insect-dependent crops (fruits, nuts, vegetables) (Aizen and Harder, 2009; Kennedy et al., 2013; Otto et al., 2016).

Therefore, the presence of healthy bee communities in an ecosystem is vital for maintaining diverse plant communities, promoting habitat resilience, and supporting sustainable agricultural production and urbanization. Though conserving and restoring to support and promote bee diversity is a difficult task because such vast morphological and behavioral variation exists, in turn producing many different nesting and foraging requirements.

1.3. Natural History of Bees

1.3.1. Phylogeny

Bees belong to a monophyletic group called the Apiformes (Order Hymenoptera) which is comprised of 7 families, 25 subfamilies and ~20,000 species globally (Michener, 2007; Danforth et al., 2013). The diversification of bees occurred in the mid-Cretaceous era (140-110 million years ago), almost in tandem with the Angiosperm radiation (Danforth et al., 2013). The 7 recognized bee families (Andrenidae, Apidae, Colletidae, Halictidae, Megachilidae, Melittidae, and Stenotritidae) display worldwide distributions, with the exception of Stenotritidae which are only found in Australia (Michener, 2007). Morphological characteristics and molecular data support the monophyletic classification of these families, however the phylogenetic placement of species within Melittidae remain unresolved (Danforth et al., 2006; Michener, 2007; Danforth et al., 2013).

In North America alone it is estimated there are ~4,000 species of wild bees. Of those, approximately 300-400 reside in Nebraska, although this estimate is uncertain due to lack of sufficient data. Immense morphological and behavioral diversity exists in wild bees, including but not limited to color, size, nesting habits, sociality, and foraging preferences.

1.3.2. Nesting

Bees display a wide variety of nesting strategies and are categorized according to their nesting habits as above-ground or below-ground nesters. Above-ground nesting bees utilize stems, tree cavities, vegetation thickets and even human-made structures as nesting substrates. These bees can be further divided in "renters" or "excavators". A renter builds its nest by utilizing pre-existing cavities on the landscape such as beetle-bored tunnels in logs, old mice burrows in dense vegetation, underneath rocks or in snail shells (Cane et al., 2007). When constructing brood cells in a pre-existing cavity, many above-ground renters rely on materials from the environment or their own secretions to reinforce brood chambers. For example, members in Megachilidae may partition, construct or cap brood cells using leaf pieces, flower petals, plant trichomes, masticated leaf matter, mud, resin, and even pebbles (Cane et al., 2007). Inversely, an above-ground excavator constructs its nest by boring into pithy stems, hard or soft wood, or builds a free-standing nest. Substrate preference is partial to the bee species. For example, the Large Carpenter bee (*Xylocopa spp.* Latreille) may bore into coniferous wood, canes, bamboo or yucca, while the Small Carpenter bee (*Ceratina* Latreille) bores into pithy stems of broken, dead and erect twigs (Balduf, 1962; Michener, 1962; Vicidomini, 1996; Rehan and Richards, 2010).

In contrast to above-ground nesters, bees that nest below ground generally excavate tunnels into soil, sand, muddy banks, or dry cliffs. Nest architecture may be simple, consisting of a single vertical or horizontal tunnel, or be a complex network of tunnels. Many below-ground nesters produce glandular secretions to line their nest and seal brood cells, in order to protect the developing brood and prevent desiccation. For example, members in Colletidae produce a highly-resistant, hydrophobic polyester compound that creates a controlled environment protecting the developing brood from water, fungi, bacteria and other soil-welling organisms (Hefetz et al., 1979). Often, below-ground nesters will excavate nests in close proximity to one another, or "aggregate", suggesting favorable conditions such as soil composition or moisture. However, assessing these favorable nesting conditions has proven difficult for a myriad of reasons. Few strong correlations have been found regarding preference for soil composition, moisture, compaction, temperature, percent bare ground, or slope (Cane, 1991; Sardinas and Kremen, 2014). Though, Cane (1991) concluded bees are more commonly found nesting in loam or sandy soils where the ratio of sand particles is higher than silt or clay particles.

In addition to the former nesting guilds, a small portion of bees do not build or provision their own nest but rather parasitize the nest of another bee and are referred to as cleptoparasites. Cleptoparasites may specialize on a particular host or prey upon numerous bee taxa, and when laying her egg on the existing food provision the host's offspring are killed by the adult or later by the cleptoparasitic larvae (Bogusch et al., 2006). Cleptoparasitic bees are considered the apex of bee communities, and as members of a higher trophic level they may serve as indicators of the bee community itself given that diversity decreases in a bottom-up fashion in many natural systems (Duffy, 2003; Sheffield et al., 2013).

1.3.3. Foraging

Nearly all bees are reliant on floral resources for survival, with the exception of a few necrophagous species in the genus *Trigona* (Mateus and Noll, 2004). The contents of nectar, namely sugar and water, provide energy to adult bees during their active season, while pollen serves as a protein-rich food source containing essential amino acids for developing larvae (Goulson, 1999). Given that pollen is used for rearing brood, the task of collecting it is only done by females because most males do not take part in brood care, although they may still be observed foraging for nectar. In 1884 it was discovered that some bees possess dietary restrictions, and later in 1925 Charles Robertson discovered those restrictions only pertain to pollen foraging (Robertson, 1925; Müller, 1996). Similar to nesting categories, Roberston introduced the terms "oligolectic" and "polylectic" to classify wild bees according to their dietary habits. An oligolectic, or specialist, bee exhibits plant-host specialization meaning they rely heavily on one or a few closely-related plants when foraging for pollen. In contrast, a polylectic, or generalist, bee will forage on a wide variety of plants. The most recent phylogenetic studies suggest oligolecty is the primitive state from which polylectic bees evolved (Danforth et al., 2013). Depending on geographic location and climate, the number of oligolectic species in a community will vary. For example, the desert and Mediterranean climates of California are rich with oligoleges, reaching between 40-60% of observed species, while in temperate regions their presence is a moderate ~25%, and the lowest observations of oligolectic species occur in the tropics (Müller, 1996). Oligoleges express lower genetic variation and are presumed to exist in small, isolated populations relative to polyeges and as such display a higher sensitivity to land use change making them a high priority for conservation (Packer et al., 2005; De Palma et al., 2015). Cleptoparasites are not classified as oligolectic or polylectic because they do not forage for pollen.

1.3.4. Sociality

In the broadest sense, bees are classified as solitary or social based on their life history strategies. Solitary bees are those that construct, provision and tend to their own nest without the help of others. In contrast, social bees are those with a caste system and division of labor in place between the queen and non-reproductive females ("workers"). The queen is responsible for egg laying, and the workers maintain the colony by filling roles related to brood care, hygiene and foraging. Though in reality, social and solitary behaviors in bees represent the two extremes that encompass a variety of in-between sociality traits. For example, solitary bees may nest communally, in which multiple females share a single nest entrance but there is no cooperative brood care or food sharing. Communal nesting is considered advantageous because females rotationally guard the entrance, which decreases the chance of parasitism or predation (Abrams and Eickwort, 1981). Additionally, bees may display socially polymorphic behavior, such as *Lasioglossum* Curtis, in which case species may function as solitary in some populations and social in others, or facultatively social behavior, like *Xylocopa* Latreille, where solitary and social behavior is present in the same population at the same time (S. Rehan, per. comm.) The expression of social or solitary behavior in those cases is generally correlated with an environmental gradient, for example *Halictus rubicundis* Christ may function socially at lower altitudes where long growing seasons occur but solitary at high altitudes where short growing seasons occur (Eickwort et al., 1996; Davison and Field, 2016). While these degrees of social behavior exist, the majority of bees are in line with the phylogeny's primitive state of being solitary (Danforth et al., 2013). Truly social bees, such as honey bee, bumble bees, and sweat bees, are only found in Apidae and Halictidae, and interestingly, some of the social lineages within Halictidae have given rise to now secondarily solitary descendants (Danforth 2003).

1.4. Bee Decline

In the early 2000's pollinator decline became a widespread topic of concern as honey bees suffered dramatic losses from a myriad of factors including habitat loss, agrochemicals, pathogens and parasites, climate change, and the interactions of the like (Potts et al., 2010; Goulson et al., 2015). While much of the concern was focused on the globally-domesticated honey bee, *Apis mellifera* L., observations regarding wild bees experiencing similar declines were soon to follow. As demonstrated by Koh et al. (2016), a 23% decrease in mean abundance of wild bee populations was depicted across the United States between 2008-2013, and 60% of that decrease occurred in 11 Great Plains states where an increase of corn and grain cropland replaced grassland and pasture. Due to its rich soils and limited topographic relief, the Great Plains has allowed the agricultural industry to flourish which has simultaneously led to a decrease in the availability of suitable pollinator habitat, and an increase in potential agrochemical exposure to declining pollinator populations (Peterjohn and Sauer 1999; Steffan-Dewenter and Tscharntke 1999; NRCC, 2007; Hendrickx et al., 2007; LeFeon et al., 2010; Mineau and Whiteside, 2013; Thogmartin et al., 2017). This is not only troublesome for wild bee populations, but the agricultural industry as well when it has been shown the yield of most crop plants increase with sufficient pollination (Klein et al., 2006). Thus arises the juxtaposition to meet growing anthropogenic needs for food and energy while conserving suitable habitat intended to support much-needed pollinators.

In addition to agricultural intensification, urbanization has further contributed to the current fragmented-state of the Great Plains. Not only is habitat lost, but the connectivity of habitat allowing for species dispersal and thus the sustainability of genetic diversity is greatly diminished by the increase of impervious surfaces on the landscape (Packer et al., 2005; Zayed, 2009). Although some bee taxa have been shown to persist in conditionally-based urban settings, the result of urbanization places limitations on numerous species in relation to nesting and floral resources (Cane et al., 2005; McKinney, 2008; Zanette et al., 2009; Martins et al., 2013).

Moreover, unpredictable and often extreme fluctuations in temperature and precipitation caused by changing climate patterns may drive further bee decline. Adult bees are carefully timed to emerge in the spring or summer as to align with the bloom period of flowering plants. However, with the early onset of spring, phenological mismatch, or the misalignment of floral bloom period and bee emergence time, is an issue of concern but has proven difficult to form predictions around as species will react to changing environmental conditions differently. Fortunately, phenologies of co-occurring plants and pollinators are likely to respond to changes in the environment in similar manners (Bartomeus et al., 2011; Forrest, 2015). However, phenological mismatch is of higher concern for oligolectic bees, where perfectly-timed emergence is key to these bees' survival as their floral host may only bloom for 2 weeks. Additionally, phenological mismatch is predicted to limit reproductive success of spring ephemeral plants, reduce species richness of plants and bees and ultimately affect population dynamics (Kudo and Ida, 2013; Petanidou et al., 2014).

Further resulting from climate change is the likelihood of species being forced to shift their range in order to adapt with shifting temperature and precipitation gradients. It is important for ecosystems to maintain high levels of biodiversity so they remain stable and resilient when faced with this shift in species composition. In highly fragmented landscapes, such as the Great Plains, bees serve as dispersal agents for many plants that maintain genetic diversity by transferring pollen across fragments. However, some of the smaller bees become may isolated as well, because they are not equipped with the endurance to fly from one fragment to another. Therein, promoting connectivity in fragmented landscapes will help maintain dispersal, genetic variation and thus conservation of biodiversity.

As we have seen, wild bees are vital organisms that help maintain the function of natural and agricultural systems by providing pollination services. Additionally, wild bees help to recruit and sustain diverse plant communities which together help stabilize the ecosystem (Garibaldi et al., 2011). Striving to conserve, connect, and restore the fragmented remains of prairies is an essential step in slowing the rate of wild bee decline because it will improve the availability of nesting and foraging resources. Prairie restoration efforts focused on increasing the species composition and functional diversity of plant communities have proven successful in increasing pollinator diversity, though sufficient baseline data from which to properly deisgn, reconstruct and measure the progress of the restorations is still largely lacking (M'Gonigle et al., 2015; Griffin et al., 2017; Tonietto et al., 2017). Therefore, this thesis and the subsequent chapters seek to establish and describe baseline data on wild bees and flowering forb communities, and examine their existing interactions in southeastern Nebraska Tallgrass Prairies (chapter 2), assess how the variation in vegetation cover influences the richness and abundance of wild bees (chapter 3), and provide an extension guide highlighting a bee's role in conserving the biological diversity of Tallgrass Prairies (chapter 4).

1.5. Figures

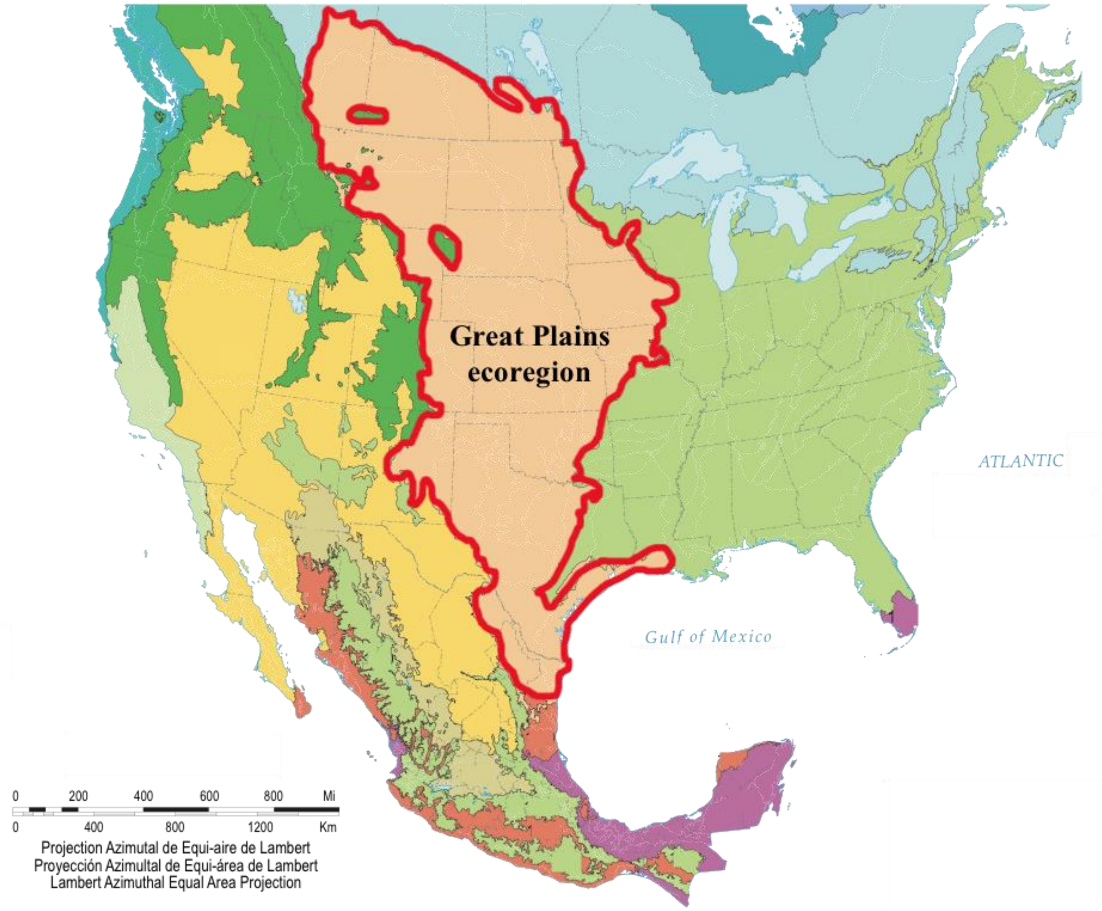

Figure 1.1 North American Great Plains ecoregion (outlined in red) as defined by the Environmental Protection Agency Level I North American Ecoregions, which includes 3 Canadian provinces and 13 US states. (map from EPA).

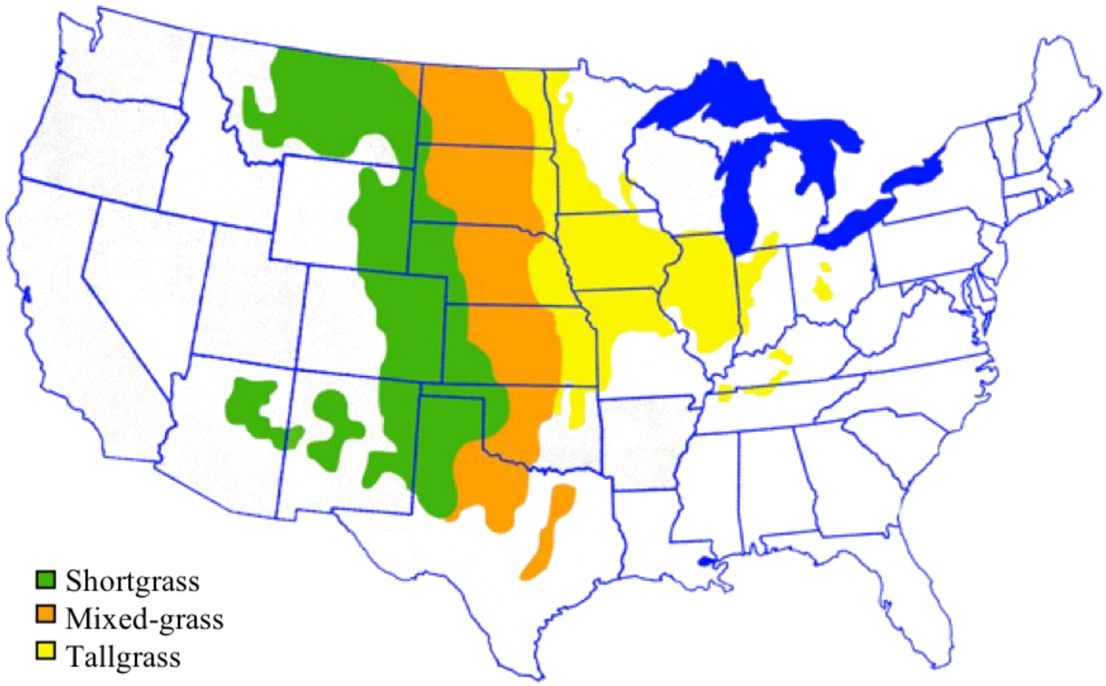

Figure 1.2. Shortgrass, Mixed-grass and Tallgrass prairie ecosystems within the North American Great Plains (map from Illinois Natural History Survey).

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Chapter 2: Inventory of Wild Bees and Forbs in Prairie Corridor

2.1. Introduction

In the field of pollination ecology, the traditional approach focused on researching the reproductive success of a specific plant and its floral visitors but has since shifted to a community approach (Knight et al., 2018). Usually involving plant-pollinator interaction surveys, this community approach allows for a broader ecological understanding of plant-pollinator networks; for instance, which bees are interacting with which plants, how life history strategies and nutritional requirements of different bee species may be driving the structure of plant communities, and how land use change may be playing a role in the diversity of plant and pollinator communities. While sufficient baseline data is still lacking for this type of information, plant-pollinator interaction studies have become foundational in understanding bee communities, and how to best support and promote their diversity (Sheffield et al., 2013; Knight et al., 2018). However with such vast variation present in bee behavior and morphology, restoring to promote their diversity is a difficult task because species exhibit a wide range of habitat requirements and respond to disturbance in different ways. For example, oligolectic bees require a specific plant to be present on the landscape, whereas smaller bees require sufficient resources to be within close proximity to their nest in order to accommodate their smaller flight radius (Greenleaf et al., 2007). In relation to disturbance, above-ground nesting bees may be affected differently than below-ground nesting bees when faced with a prescribed burning or grazing management regime.

Despite this challenge of accounting for the needs of all bees, research has identified a few factors that are key in supporting pollinator diversity. Particularly in landscapes where high levels of agricultural intensification exist, such as the Great Plains, maintaining areas of natural or semi-natural habitat has been closely linked to supporting bee diversity (Kremen et al., 2002; Klein et al., 2012; Grover et al., 2017). These natural or semi-natural habitats, such as prairie remnants, woodland edges or seeded restorations, are critical in driving bee richness and abundance because they provide diverse foraging and nesting resources throughout the season by maintaining high diversity amongst the plant community (Hines and Hendrix, 2005; Kwaiser and Hendrix, 2008; Mallinger et al., 2016; Neoskosmidis et al., 2016; Delaney et al., 2017). Increasing the amount of heterogeneous habitat at the landscape level allows for the preservation of biodiversity, which is a conservation priority in the Great Plains (Goulson et al., 2015).

In the state of Nebraska, a nationally recognized greenway system exists in the City of Lincoln whose purpose is to preserve biodiversity and connect remaining fragments of high-quality habitat (Figure 2.1). The greenways and connected corridors serve to protect freshwater and saline wetlands, riparian corridors, place buffers around lakes and encourage public access with an extensive trail system. Lincoln is located within the Tallgrass Prairie region of the Great Plains, of which 1-3% remains in its native vegetation cover as a result of conversion to agriculture (Henwood, 2010) (Figure 2.2). Specific to Nebraska's Tallgrass prairie, the loss of pollinators has been identified as a key stressor because the services they provide are essential for promoting biologically diverse and healthy plant communities which are critical for sustaining ecosystem function (Henwood, 2010; Schneider et al., 2011). In response to this, the City of Lincoln Parks & Recreation Department initiated an effort in 2012 to build upon the existing greenway system to create the Prairie Corridor on Haines Branch. This effort was split into two phases wherein Phase 1 was to form the actual corridor by acquiring recommended land based off a habitat assessment focused on maximizing connectivity of high-quality habitat (City of Lincoln, 2012). Following the effort of Phase 1 which has currently protected ~3,157 hectares, the mission of Phase 2 is to examine how to increase pollinator species in the design and management of prairie reconstruction, and monitor plant and pollinator communities to identify areas in the corridor that are most supportive of high pollinator diversity (Prairie Corridor, prairiecorridor.org). In line with the Prairie Corridor's mission, the objective of this research is to assess the richness and abundance of wild bees throughout the Corridor, and survey the diversity of foraging resources available to them. The collected data will produce descriptive inventories for bee species, forb species (herbaceous flowering plants), and forb species that were visited by bees (from here on bee-visited forbs). Collectively these will serve as a baseline inventory of wild bees from which the Prairie Corridor may use to monitor the progress of future restorations, and will build upon the limited knowledge regarding the distribution and phenology of species and plant-pollinator networks that exist within the Tallgrass Prairie.

2.2. Methods

2.2.1. Survey Location

The Prairie Corridor is located in southwest Lincoln, Nebraska (Lancaster County). This newly-protected greenway forms a 17.7-kilometer nearly-contiguous passage between Pioneers Park Nature Center and Spring Creek Prairie Audubon Center, which are two of Lincoln's valuable nature preserves (Figure 2.3). The fragments that compose the Corridor vary in size and consist of Tallgrass Prairie remnants, established restorations, 1-5 year-old seeded restorations, pastureland and hay meadows. The management of parcels vary in type and intensity, but include combinations of burning, grazing and haying (Appendix A). Throughout the length of the corridor 20 plots were defined in a non-random fashion to coincide with a vegetation survey being run by the University of Nebraska's School of Natural Resources (Figure 2.4). The plots were chosen to represent the variety of management and land use present in the Corridor, and each plot was ~1.2 hectares in size.

2.2.2. Survey Methods

All 20 plots were assigned an individual number and were surveyed every other week between May-October 2017 and April-October 2018. Sampling was only conducted when the temperature was 15.5-35˚C, average wind speeds ≤24km/hr, and it was not raining. Each sampling week was considered a round, in which all 20 plots were surveyed. A sampling round consisted of surveying two randomly-selected transects that spanned 2 x 20m, and ran south to north, within each 1.2ha plot. Two surveys were run on each transect, and consisted of a blooming-forb survey and a bee survey (described below). Temperature, average wind speed, relative humidity and cloud cover were recorded during each sampling round.

In 2018, the study was adjusted to incorporate running two biased transects per plot, in addition to the random transects, as an attempt to capture a more accurate account of the composition of bees present in the Corridor. Biased transects were completed in the same 1.2ha plots as random transects, and were chosen based off of their likelihood of attracting a higher number of bees due to a higher abundance or richness of blooms relative to the given plot. One plot from 2017 was removed from the study due to accessibility issues that led to inconsistent sampling and one plot was added in 2018.

2.2.2.1. Forb Survey

Forb surveys were always conducted before bee surveys on each transect. Only blooming forbs within transects (2 x 20 m) were recorded. Each species was quantified by counting the number of stems bearing open flowers at the time of surveying, and was identified to its lowest taxonomic rank when possible. Photographs were taken of unknown forbs and later identified.

2.2.2.2. Bee Survey

The bee survey began immediately upon completion of the forb survey. The surveyor collected bees on the transect by walking a steady unidirectional-pace from south to north over a period of 5 minutes. Bees were only collected when observed visiting a blooming forb within the transect by use of aerial nets and visual observations. Visual observations were used when species could be identified on the wing, or to note the genus when a specimen was missed during netting. Each time a bee was netted, the surveyor paused the 5-minute timer to transfer the specimen into a kill jar and assign a label with associated plant information. For each transect, bees caught on different plants were placed in separate vials, which meant many kill jars had to be carried to often remote locations during sampling. In an effort to reduce size, weight and cost, kill jars were constructed by wrapping solid ammonium carbonate in empty tea bags and securely placing it at the bottom of 50ml polypropylene falcon tubes. At the end of each sampling day, collected bees were curated within 2 days and labeled with a unique identifier allowing the specimen to be traced back to the specific transect and plant it was caught on, along with any associated metadata, such as geographic coordinates, elevation, temperature, wind speed and cloud cover.

2.2.3. Analysis

In creating an inventory of flowering forbs present in the Prairie Corridor, raw cumulative totals of bloom abundance and richness were calculated for

114 observed species across both years. The PLANTS Database (USDA, 2018) was consulted to standardize scientific names, authorities, common names, and indigenous status to Nebraska. The proportion of forbs were examined in terms of richness and abundance based on indigenous status, as well as color. Four human-color categories were selected based on bee-vision, or the UV spectrum, that would display the highest contrast of a flower in a grassland setting, and included: Blue-Violet, Yellow-Orange, White-Green and Red-Pink (Backhaus, 1993; Droege, 2006; Arnold et al., 2009). Assessing the status and color of forbs in the Corridor may allude to possible preference of floral traits being sought out by visiting bees which will improve our ability to design effective pollinator seed mixes.

An inventory of bee species was also produced by calculating richness and abundance values for 85 species based on raw cumulative observations of both years. The majority of bees were identified to the species level using three main sources, including *Bees of the Tallgrass Prairie Region and Greater Midwest* (Arduser, 2018), *Discover Life Species Guide and World Checklist (Hymenoptera: Apoidea: Anthophila)* (Ascher and Pickering, 2016), and *Bumble Bees of North America: An Identification Guide* (Williams et al., 2014), although numerous genera-specific keys were consulted (see Appendix B). Identification of specimens were confirmed by Mike Arduser (Missouri Dept. of Conservation (*retired*)), though a few remaining specimens collected in 2018 still await verification. Taxonomic groups difficult to identify to species-level included *Lasioglossum*

(*Dialictus*) Curtis (n=49) and *Ceratina* Latreille (n=5) and were thus resolved to the generic level. In addition, 19 females identified as members of the *Ceratina dupla* complex were classified as *Ceratina spp.* and may represent *C. calcarata, C. dupla* or *C. mikmaqi* which are near impossible to distinguish without male specimens or use of DNA barcoding (Rehan and Sheffield, 2011). Following identification, species were categorized by lecty, sociality, and nesting habits in order to examine the proportion and diversity of life history strategies present in the Corridor. For lecty, each unique species was classified as polylectic, oligolectic, or cleptoparasitic. For sociality, species were classified as social (includes facultatively social), solitary (includes communal), or cleptoparasitic. Lastly for nesting habits, each species was classified as an above-ground or below-ground nester or cleptoparasitic. Sources used to categorize each species to its appropriate class may be found in Appendix B.

The third and final inventory created was for bee-visited forbs, in which plant data was extracted from the plant-pollinator interaction survey to produce a list of blooming forbs that bees were specifically observed visiting in the Corridor. Similar to the total observed forb inventory, these plants were classified by taxonomic rank, status and color. Only richness totals were calculated for this inventory, because abundance would have been a replicate of the observed bee abundance given that the data came from an interaction survey. However, when examining the proportion of status and color of bee-visited forbs in relation to total available forbs, the number of individual bee-visits to each forb was used to calculate an abundance value.

Using all three inventories, a floral preference index was created that ranks all 114 observed forb species from most to least “preferred” by bees following the simple rank method used in Williams et al. (2011). First, a rank system was formed by splitting observed abundance values for bee visits and total blooms into 8 sections based on the maximum and average abundance values for each (Table 2.1). Then, each forb species was assigned a rank based on its individual number of bee visits from 1-8 (most to least visits) to serve as Rank Use. Next, each forb species was assigned an additional rank based on its total bloom abundance from 1-8 (most to least abundant) to serve as Rank Availability. Then to calculate Bee Preference, Rank Use was subtracted from Rank Availability, wherein negative values signify higher preference. While there remain many limitations when calculating a Floral Preference Index for bees, such as disregarding whether the foraging visits were for nectar or pollen, or the lecty and sociality of the observed bees, the index is a step forward in better describing and addressing floral-foraging needs of wild bees.

All curated specimens are currently stored in the University of Nebraska-Lincoln Bee Lab collection, and voucher specimens will be sent to the University of Nebraska State Museum. For collection details regarding specific bees contact the author. Additionally, the plant-pollinator interaction data will be added to the US Geological Survey’s Pollinator Library (USGS

Pollinator Library; http://www.npwrc.usgs.gov/pollinator/). The Pollinator Library is a website populated by a large and growing national database of plant-pollinator interactions. Having this data readily available allows researchers to better understand and assess plant-pollinator networks over large spatial and temporal scales, identify trends and help land managers improve habitat to suit the floral-foraging needs of pollinators.

2.3. Results

The following results are expressed as raw cumulative totals, in which years and transect type are pooled; and whether forbs or bees, abundance values are the number of individuals observed, and richness values are the number of unique species observed. The addition of biased transects in 2018 nearly doubled the richness and abundance observations for flowering plants and wild bees, thus greatly enhancing the value and ability of this survey to describe the species composition of Prairie Corridor (Table 2.2). Statistical analyses and comparisons of flowering forb and wild bee richness and abundance values will be presented in Chapter 3.

2.3.1. Forb Survey

A total of 25 sampling rounds were completed over the two-year study. An abundance of ~42,866 forbs were observed blooming on the landscape, representing 35 families, 87 genera, and 114 species (presented as part of Table 2.3). At the plot level, cumulative forb abundance of blooming stems ranged from 269-5,468 ($\bar{x}$ = 2,256.11) and species-level forb richness ranged from 5-43 ($\bar{x}$ = 23.84). The most abundant plant families were Asteraceae (n=17,578), with 27 genera and 34 species, and Fabaceae (n=10,486) with 13 genera and 20 species. The top 5 most abundant species on the landscape were *Melilotus officinalis* (L.) Lam. (n=6,259), *Erigeron strigosus* Muhl. Ex. Willd. (n=4,444), *Dianthus armeria* L. (n=2,832), *Solidago canadensis* L. (n=2,816), and *Convolvulus arvensis* L. (n=2,442), which collectively accounted for 44% of total abundance. Of the 114 forb species observed, 25 were detected with an abundance of ≤ 10, and 28 species were detected only once throughout both years, such as *Spiranthes vernalis* Engelm. & A. Gray which is listed as threatened or rare in Indiana, Illinois and Iowa. Forb abundance had a strong peak in June, likely due to a mass bloom of *Melilotus officinalis* (L.) Lam. (n=4,361), while richness peaked in July (Figure 2.5a). In terms of indigenous status, 73% of observed forb species held native status, which dropped to 50% when looking at forb abundance (Figure 2.5a).

2.3.2. Bee Survey

An abundance of 1,013 bees were collected or observed, representing 5 families, 27 genera and 85 species (see Table 2.4, Figure 2.6). At the plot level, cumulative bee abundance ranged from 1-143 ($\bar{x}$ = 50.65) and bee richness ranged from 1-33 ($\bar{x}$ = 15.2). The most abundant genera were *Bombus* Latreille (n=433 individuals), *Lasioglossum* Curtis (n=142) and *Augochlorella* Sandhouse (n=104), which collectively account for 67% of total abundance. The most speciose genera were *Lasioglossum* Curtis (n=15 unique species), *Melissodes* Latreille (n=11) and *Andrena* Fabricius (n=7), collectively accounting for 39% of total richness. It is worth noting 49 individuals within *Lasioglossum* have only been resolved to the generic level and thus n=15 unique species may be very conservative as this genus is one of the largest in terms of richness. As for singletons, 29 species were observed only once, and 44 species were represented by an abundance ≤3 observations. Bee abundance and richness gradually increased from May to a peak in August, and both exhibited a steep decline from August to September (Figure 2.5b). In relation to sociality and nesting habits, social below-ground nesters represented 42% of the total species and 43% of individuals collected while social above-ground nesters represented 21% of species and 36% of individuals. Similarly, solitary species were comprised of more below-ground nesters (21% of species and 13% of individuals) than above-ground nesters (13% of species and 7% of individuals) while only 3% of species and 1% of individuals were cleptoparasites (Figure 2.7c). Pertaining to foraging habits, polylectic bees were dominant, accounting for 73% of species and 91% of individuals, whereas oligolectic bees accounted for 19% of species and 8% of individuals, and the remaining 8% of species and 1% of individuals were cleptoparasitic bees (Figure 2.7b).

Bees were observed visiting 20 plant families consisting of 51 genera and 70 species, or 57%, 59%, and 61% of the total families, genera, and species surveyed. At the plot level, richness of bee-visited forbs ranged from 1-18 ($\bar{x}$ = 9.8), and raw abundance for bee-visited forbs was not calculated given the data were collected as a bee-forb interaction and would therefore be a replicate of bee abundance. The most-visited plant families were Asteraceae (n=497 bee visits) with 19 genera and 25 species, and Fabaceae (n=109) with 11 genera and 14 species. The top 5 most-visited species on the landscape were *Silphium integrifolium* Michx. (n=108 bee visits), *Monarda fistulosa* L. (n=81), *Solidago canadensis* L. (n=68), *Carduus nutans* L. (n=67), and *Melilotus officinalis* (L.) Lam. (n=64), which collectively account for 34% of all observed plant-pollinator interactions. The top 5 forbs that supported the highest richness of bee-visitors were *Melilotus officinalis* (L.) Lam. (n=20 unique bee species), *Carduus nutans* L. (n=19), *Solidago canadensis* L. (n=19), *Vernonia baldwinii* Torr. (n=19) and *Convolvulus arvensis* L. (n=18).

When examining the proportion of indigenous status of all observed forbs compared to bee-visited forbs, 70% of bee visits were made to native forbs despite the near-equal proportion of native to non-native forbs (50% to 46%) available on the landscape (Figure 2.6a). In terms of flower color, available forbs and bee-visited forbs exhibited similar proportions, the most abundant for both being in the yellow-orange category (42% of all forbs, 44% of total bee-visits) followed closely by blue-violet (30%, 33%), and white-green (21%, 20%) (Figure 2.6b). However, the species composition of forbs within the latter percentages varied when looking at available forbs versus those visited by bees (Table 2.5).

In relation to the produced Floral Preference Index, 4 plants came out equally as most-preferred by bees including *Carduus nutans*, *Cirsium* *altissimum* (L.) Hill, *Silphium perfoliatum* L., and *Symphyotrichum ericoides* (L.) G.L. Nesom (Table 2.3). Interestingly, all four of those plants exhibited relatively low abundance of availability on the landscape. Again, this index is specific to Tallgrass prairie systems in southeastern Nebraska and should be used with caution as there remain many limitations that prevent accuracy in calculating floral preference for bees.

2.4. Discussion

Drawn from these results, the three inventories allowed for a description of the species composition of available forbs, wild bees, and bee-visited forbs within Nebraska's southeastern Tallgrass Prairies, and serve as a baseline pollinator dataset from which future restorations of the Prairie Corridor may be monitored. Additionally, the inventories highlighted areas in the Corridor that may function as a model from which to model restorations after due to the presence of oligolectic or cleptoparasitic bees. Oligolectic bees have been shown to express reduced levels of genetic variation and are presumed to exist in smaller, more isolated populations than their polylectic counterparts making them more prone to extinction (Packer et al., 2005). Therefore, plots within the Corridor that are currently supporting oligoleges indicate that the given land management regime, whether type or intensity, is helping to sustain these tight plant-pollinator mutualisms. Similar to oligoleges, the presence of cleptoparasitic bees also serve as an indicator of rich habitat supporting a diverse community because they exist in a higher trophic level, and as such their presence relies on the presence of their host and host's resources (Sheffield et al., 2013). For example, a cleptoparasite in the genus *Nomada* Scopoli was collected in one particular plot, and although none of its host species (largely *Andrena*) were collected we may infer *Andrena* are present if their cleptoparasite is present. Overall, cleptoparasitic bees were collected in 7 of the 20 surveyed plots, including 3 hay meadows, 2 remnant prairies, and 2 seeded restorations (in year 2 and year 5). Unlike the hay meadows and restorations where only a single cleptoparasite observation occurred in each, one of the remnant prairies accounted for 3 unique species from 3 unique genera including *Coelioxys* Latreille, *Nomada*, and *Stelis* Panzer. Areas in the Corridor, such as the latter remnant prairie, that exhibit relatively high richness and abundance across trophic levels will be important to further dissect in terms of habitat composition when designing restorations.

In addition to indicating areas within the Corridor that support diverse bee communities, the results of this survey highlight the importance of plant-pollinator interaction studies. While many research projects aimed at understanding the composition of bees present in a system collect bees using blue-vane traps or long-term bee bowls, the amount of information one may extract is significantly lower relative to the mass number of bees killed in the process. Through use of targeted aerial-netting and blooming-forb surveys, this study was able to examine differences between the composition of available forbs and those visited by bees in terms of richness, abundance, indigenous status, as well as floral color. One such difference arose when examining the flower color of forbs available on the landscape versus those visited by bees.

While percentages of the 4 color groups were similar in terms of richness and abundance for both available forbs and bee-visited forbs, the composition of forb species varied between the two. For example, in the Blue-Violet category, the top 3 most abundant forbs on the landscape were *Psoralidium tenuiflorum* (Pursh) Rydb., *Glechoma hederacea* L., and *Monarda fistulosa*, whereas the top 3 forbs most-visited by bees were *Monarda fistulosa*, *Carduus nutans*, and *Cirsium altissimum*, suggesting that abundance does not necessarily translate to bee visits (Table 2.5). Building upon this, when looking at the Yellow-Orange category, not only does the composition of species vary between available forbs and bee-visited forbs, but so does the indigenous status. For example, *Melilotus officinalis* and *Hypericum perforatum* L. are non-native forbs that appeared as two of the Top 5 most-abundant yellow forbs on the landscape and as two of the Top 5 forbs most-visited by bees; in contrast *Medicago lupulina* L., also a non-native appearing in the Top 5 most-abundant yellow forbs on the landscape, was not visited by a single bee throughout this entire study (Table 2.5). What shows from this information is that some non-native plants clearly support pollinators, whether as a nectar resource or filling a gap where sufficient floral resources fail to exist, while others despite high abundance contribute no support to pollinators. Using these inferences from plant-pollinator interaction surveys aids in our ability to address highly-debated and unclear issues like the one at hand of whether or not to include non-native plants in pollinator seed mixes (Palladini and Maron, 2014). For example, some research has demonstrated bee richness and abundance to be lower in areas dominated by non-native or noxious plants, and that their presence may greatly reduce the fitness of oligolectic bees who possess dietary restrictions (Memmott and Waser, 2002; Hopwood, 2008; Stout and Morales, 2009). In contrast, others have shown bumble bees to readily incorporate non-native plants into their diet if sufficient amounts of protein are gained, and that pollinators may benefit from intentionally-planted non-natives that extend the growing season (Harmon-Threatt and Kremen, 2015; Salisbury et al., 2015). The only way to continue addressing issues like this, teasing out preference in relation floral traits, and improving floral preference indices is to carry out plant-pollinator interaction surveys. As this type of data builds up, trends and patterns will naturally arise and aid in our ability to produce effective pollinator seed mixes that are cognizant of incorporating floral diversity at both ecological and functional levels, and account for widest possible breadth of life history strategies displayed by wild bees.

2.5. Figures

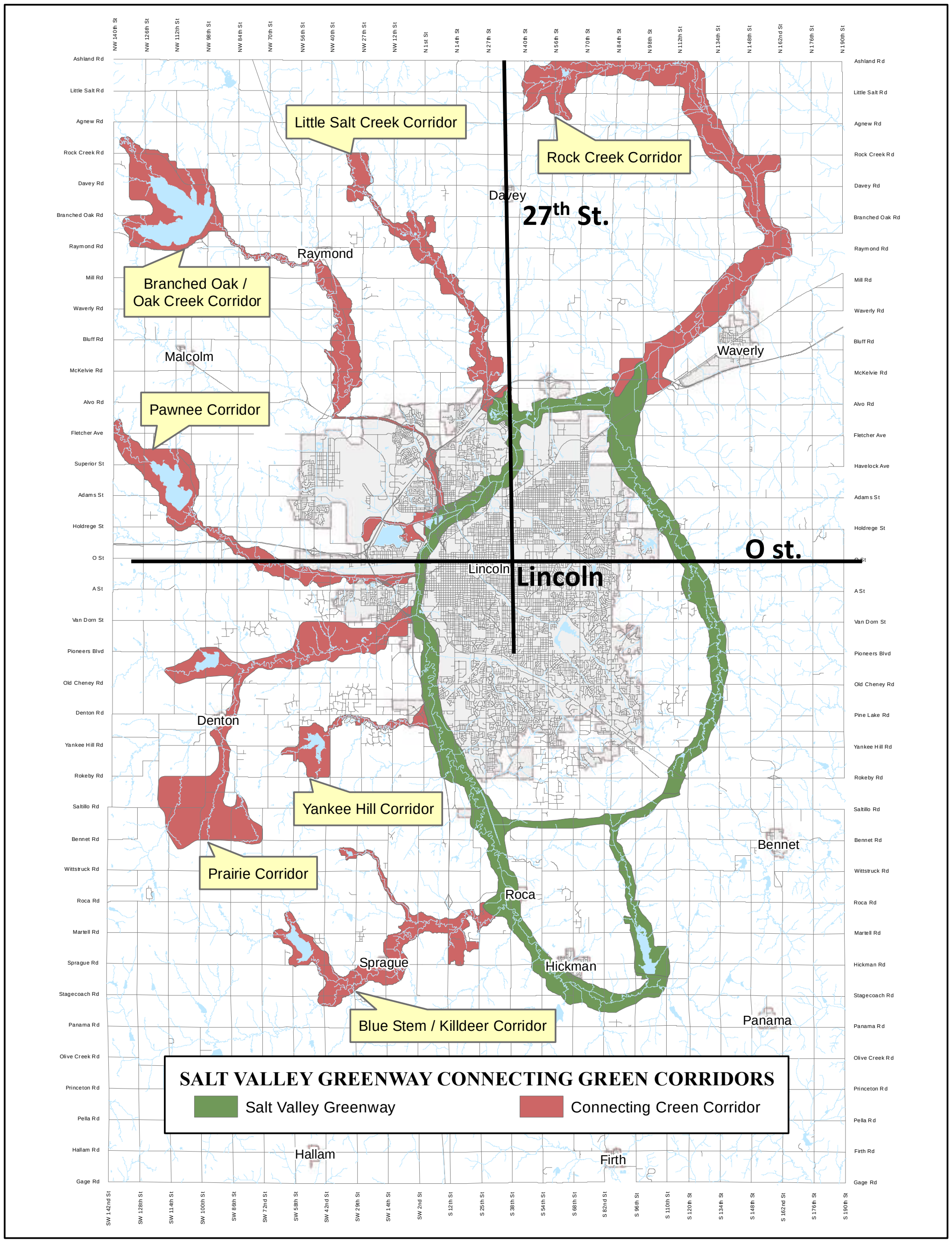


Figure 2.1. Lincoln, Nebraska's nationally recognized greenway system encompassing the City. The main Salt Valley Greenway is displayed in green, and connecting corridors are in red. The newest addition to this greenway system is the Prairie Corridor, located at the top of the lower left quadrat. Map from City of Lincoln (2012).

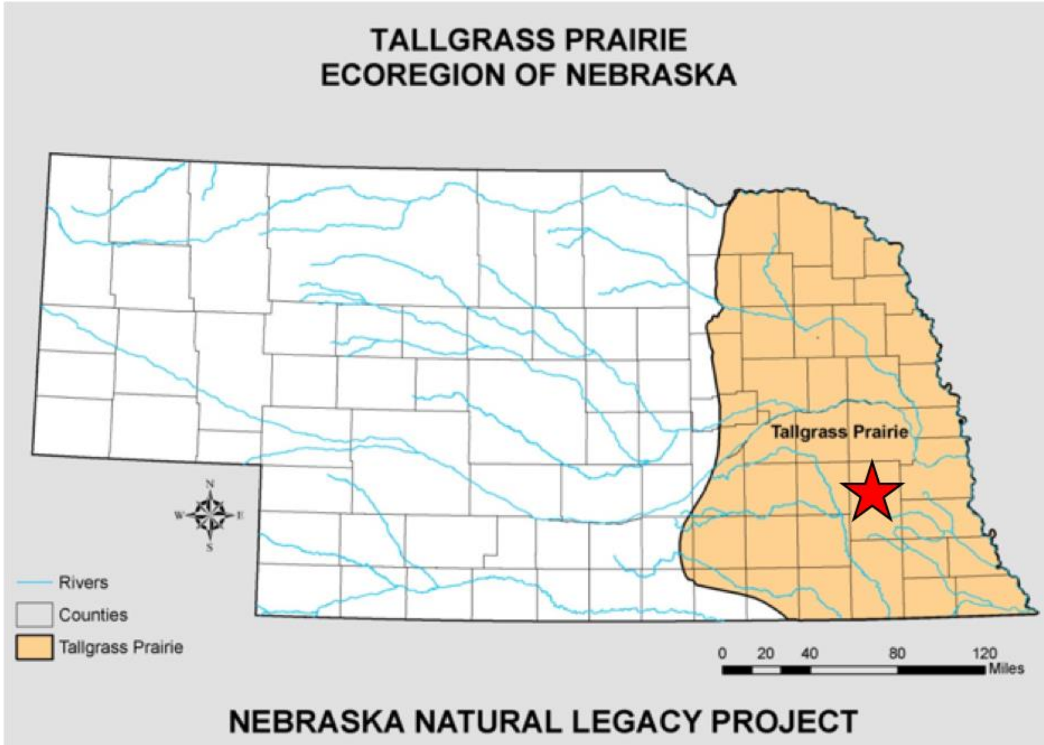


Figure 2.2. Tallgrass prairie ecoregion of Nebraska, star denotes location of Lincoln, Ne. Map from City of Lincoln (2012).

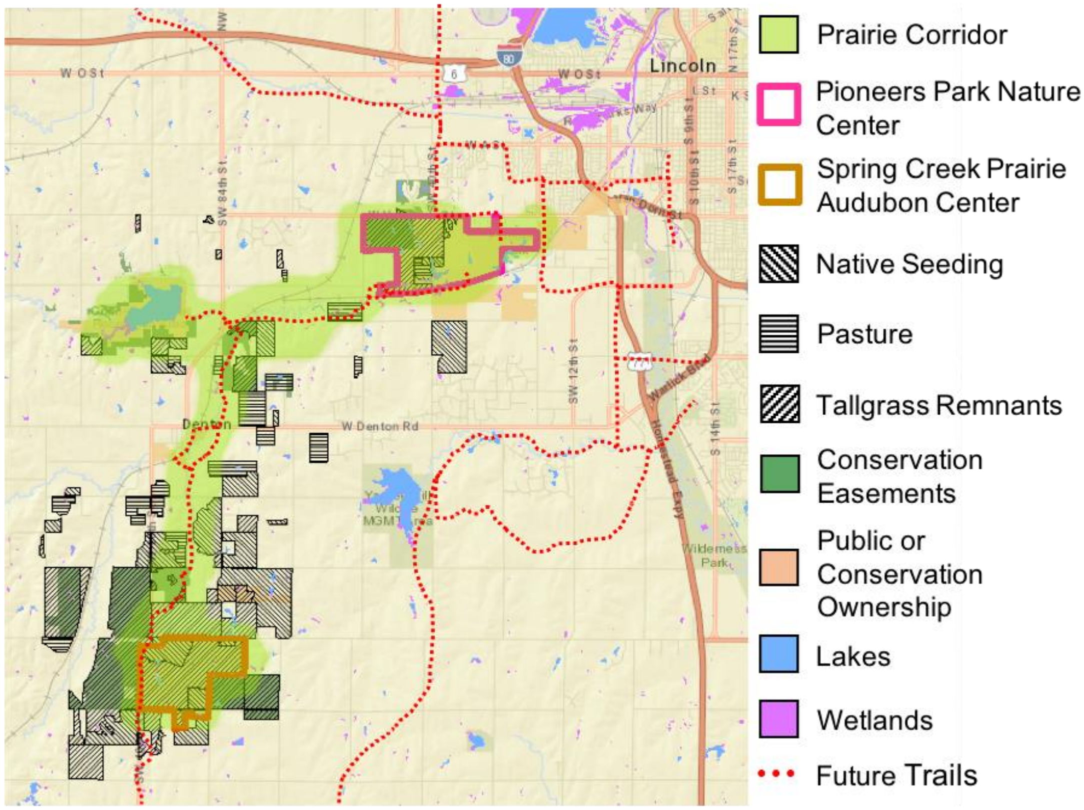


Figure 2.3. Prairie Corridor on Haines Branch (green) in Lincoln, NE, encompassing ~7,800 acres and stretching 11 miles from Pioneers Park Nature Center down to Spring Creek Prairie Audubon Center. Map from City of Lincoln (2012).

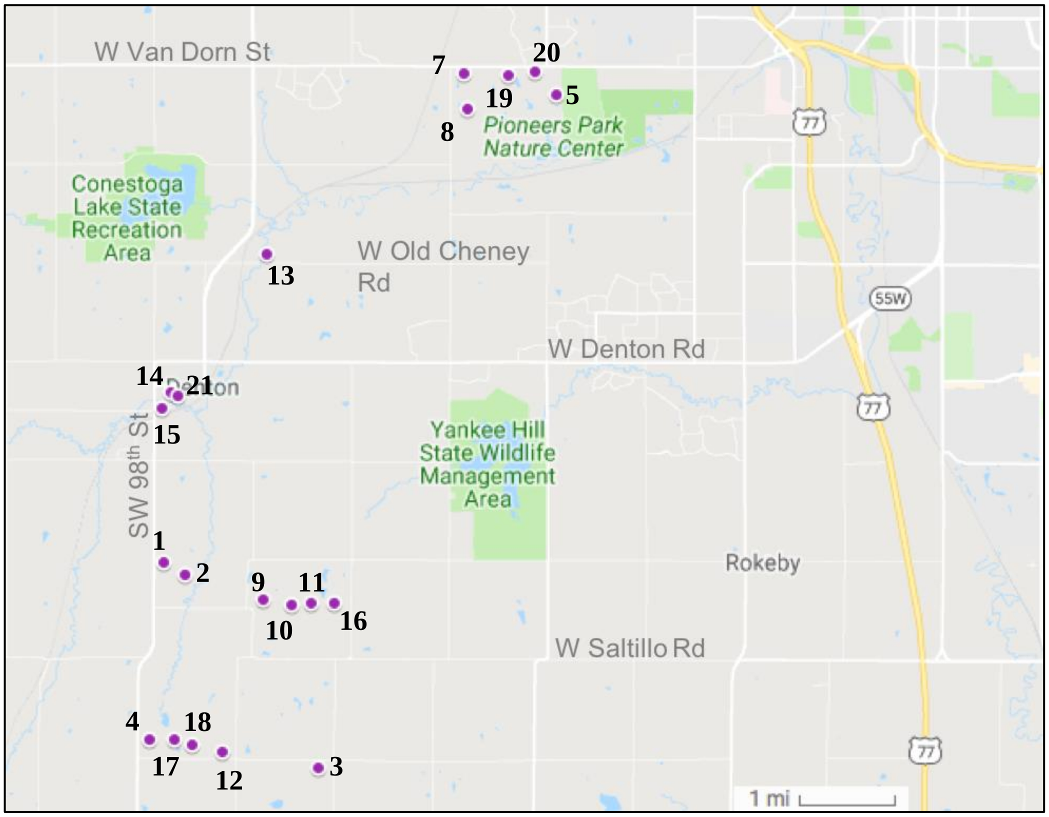
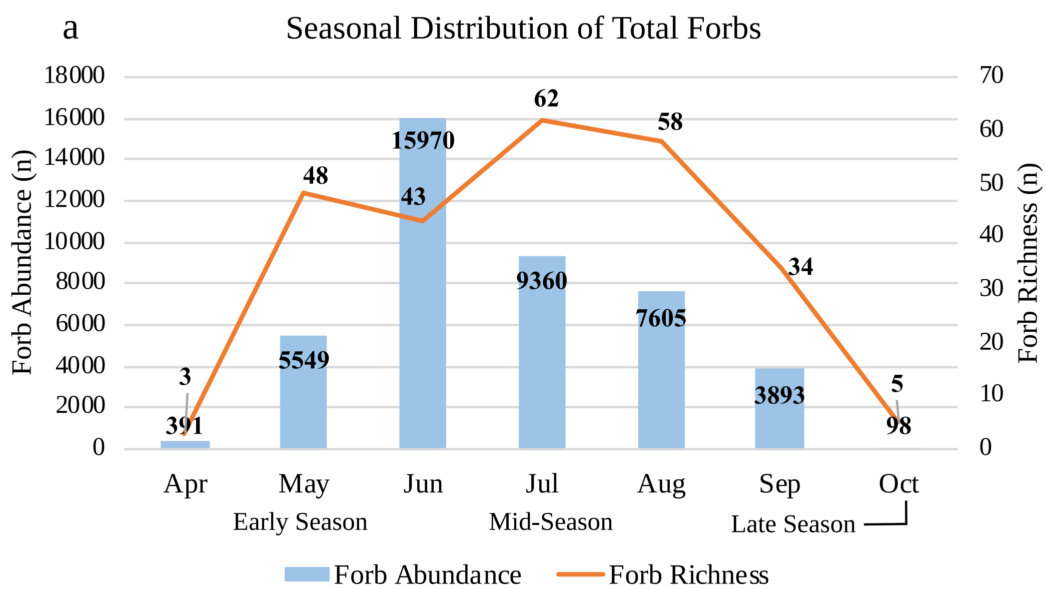


Figure 2.4. Locations and numbers of plots sampled throughout the Prairie Corridor, for detailed plot descriptions see Appendix A.



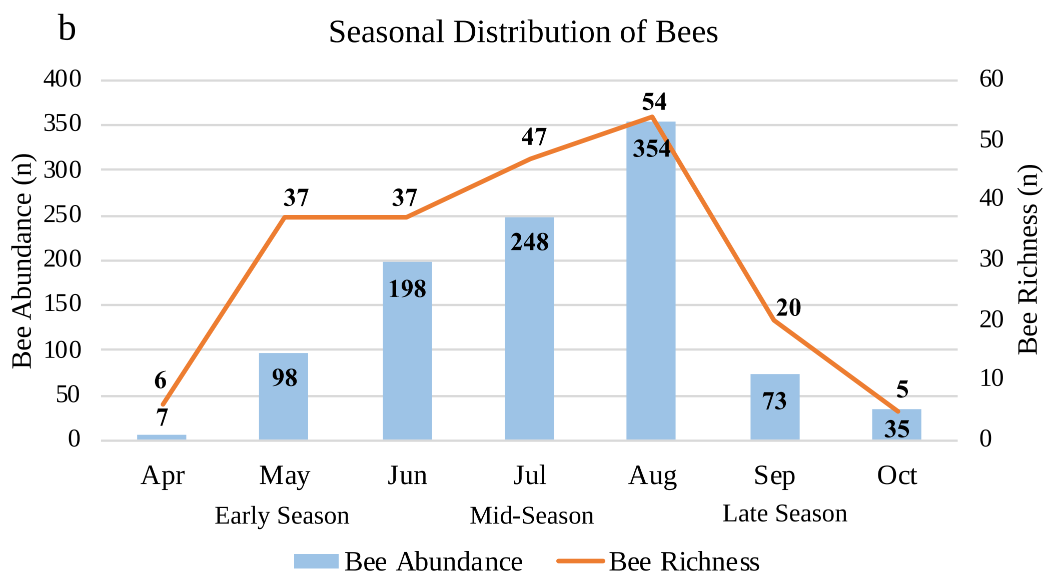


Figure 2.5. Seasonal distributions using cumulative sampling totals for (a) total flowering forbs and (b) wild bees pooled by year (2017 & 2018) and plot (n=20). Numbers inside the bar correspond to n individuals observed (forb abundance: n=42,866; bee abundance: n=1,013). Numbers above the orange line correspond to n unique species observed in each month, and the same species may be present across multiple months. Early, Mid- and Late Season shading corresponds with Chapter 3.

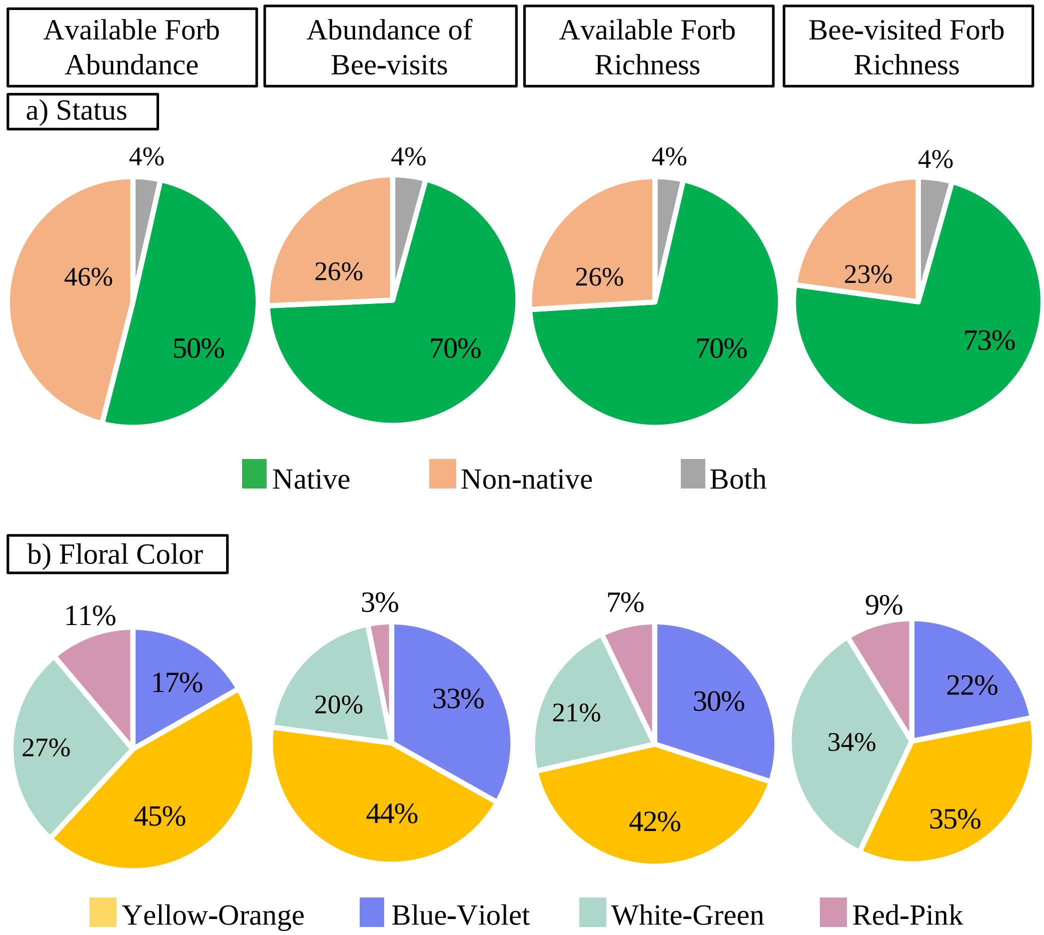


Figure 2.6. Visualization of both forb inventories for (a) status and (b) floral color. Available Forb Abundance is the individual number of blooming forbs observed on the landscape (n=42,866), Abundance of Bee-visits is the number of individual bees observed on forbs (n=1,013), Available Forb Richness is the number of unique forb species observed on the landscape (n=114), and Bee-visited Forb Richness is the number of unique forb species bees were observed visiting (n=70). The classification of indigenous status pertains to Nebraska and was lifted from The PLANTS Database (USDA).

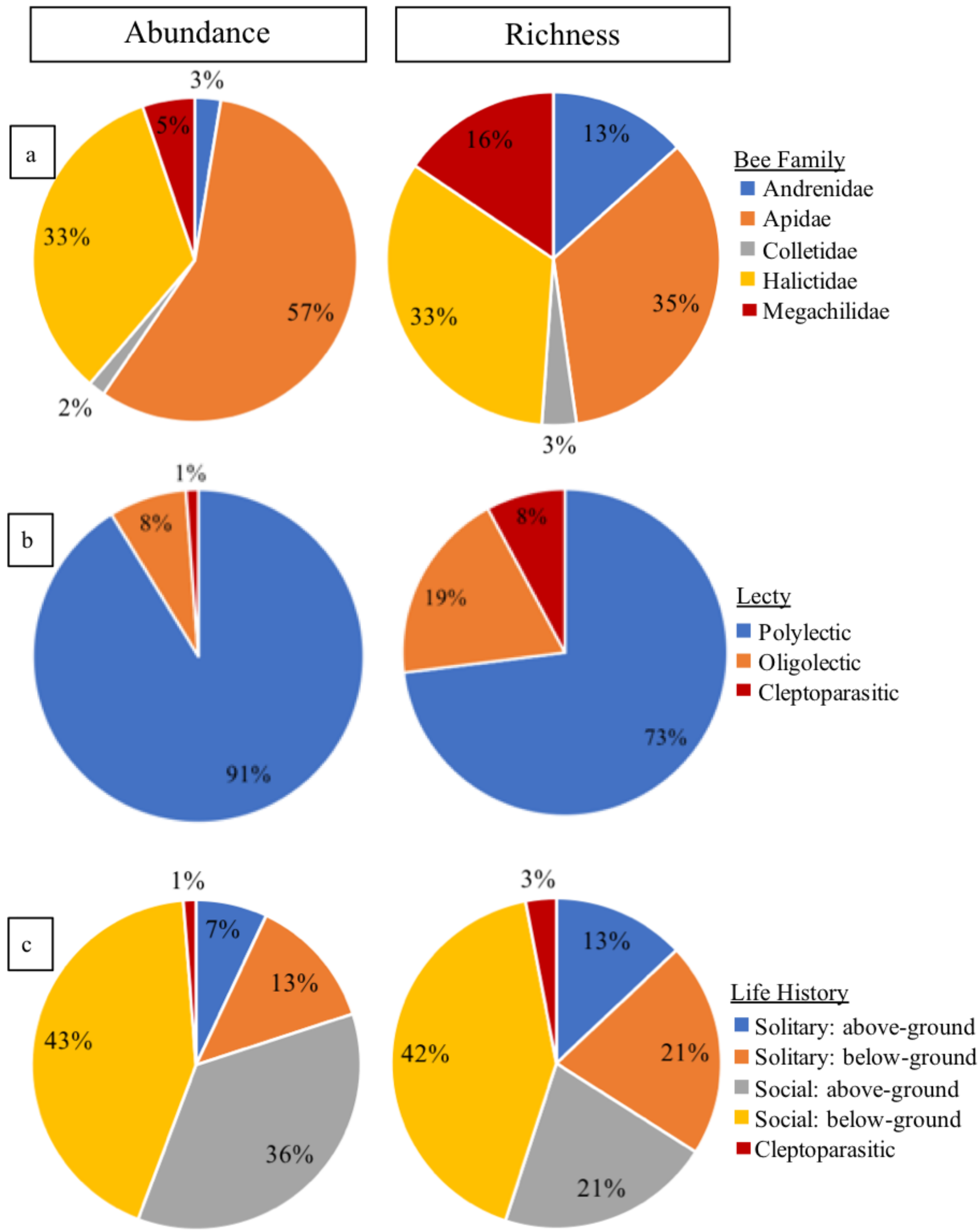


Figure 2.7. Cumulative abundance (n=1,013) and richness (n=85) of collected wild bees broken down by (a) Family, (b) Lecty (pollen-foraging behavior) and (c) Life History. For Lecty, 12 individuals were not included because they were only resolved to the genus level. Species that display communal nesting behavior were classified as solitary, and facultatively social bees were classified as social.

2.6. Tables

Table 2.1. Metrics used for assigning a rank to all forb species based on Abundance of Bee Visits and Abundance of Blooms. The 8 rankings were formed using the maximum and average abundance values, and go from 1-8 or highest to lowest abundance. These rankings were used to create Rank Use and Rank Abundance, from which Bee Preference was calculated Preference in the Floral Preference Index (Table 2.3).

Rank	Abundance of Bee Visits (Rank Use)	Abundance of Blooms (Rank Availability)
1	108-74	6259-4412
2	73-50	4411-2942
3	49-25	2941-1470
4	24-9	1469-376
5	8-7	375-282
6	6-5	281-188
7	4-2	187-94
8	1-0	93-0

Table 2.2. Cumulative totals for species richness and abundance of bees and forbs according to year (2017 or 2018) and transect type (Random or Biased). *Values in richness columns contain overlap and therefore do not sum to the "Total" row, which *does* exclude species overlap.

	Bee Richness	Bee Abundance	Bee-visited Forb Richness	Forb Richness	Forb Abundance
2017 Random Transects	42	255	33	75	12,227
2018 Random Transects	40	163	29	64	10,586
2018 Biased Transects	72	595	54	95	20,053
Total*	**85**	**1,013**	**70**	**114**	**42,866**

Table 2.3. Floral Preference Index ranking observed forb species in order from most to least preferred by bees. This index is specific to Tallgrass Prairie systems in southeastern Nebraska and should be used with caution as there remain many limitations that prevent accuracy in calculating floral preference for bees. Bee Preference was calculated by first ranking total abundance of bee visits to observed forb species from 1-8 (most to least visits) for Rank Use, then ranking abundance of total availability of forb species from 1-8 (most to least abundant) for Rank Availability, and finally subtracting Rank Use from Rank Availability, wherein negative values signify highest preference. Relative Forb Abundance (%) is the bloom abundance per forb species relative to total blooming forbs (n=42,866). Status refers to the Native, Non-native (NonNat.) or "Both" indigenous status of the forb in relation to Nebraska as classified by The PLANTS Database (USDA). Color refers to flower color: B-V (Blue-Violet), Y-O (Yellow-Orange), W-G (White-Green), and R-P (Red-Pink). * denotes forbs that were not visited by bees during this study.

Forb Species	Common Name	Bee Preference	Relative Forb Abun.	Status	Color
Carduus nutans	Nodding Plumeless Thistle	-4	0.621%	NonNat.	B-V
Cirsium altissimum	Tall Thistle	-4	0.567%	Native	B-V
Silphium perfoliatum	Cup Plant	-4	0.201%	Native	Y-O
Symphyotrichum ericoides	White Heath Aster	-4	0.373%	Native	W-G
Asclepias syriaca	Common Milkweed	-3	0.352%	Native	R-P
Grindelia squarrosa	Curlycup Gumweed	-3	0.355%	Native	Y-O
Monarda fistulosa	Wild Bergamot	-3	2.428%	Native	B-V
Nepeta cataria	Catnip	-3	0.322%	NonNat.	B-V
Silphium integrifolium	Wholeleaf Rosinweed	-3	1.617%	Native	Y-O
Solidago missouriensis	Missouri Goldenrod	-3	0.215%	Native	Y-O
Asclepias verticillata	Whorled Milkweed	-2	1.568%	Native	W-G
Baptisia australis	Wild Blue Indigo	-2	0.016%	Native	B-V
Erechtites hieraciifolius	American Burnweed	-2	0.100%	Native	W-G
Lactuca serriola	Pricly Lettuce	-2	0.208%	NonNat.	Y-O
Salvia azurea	Azure Blue Sage	-2	0.742%	Native	B-V
Tragopogon dubius	Yellow Salsify	-2	0.084%	NonNat.	Y-O
Verbena hastata	Hoary Verbena	-2	0.023%	Native	B-V
Amorpha canescens	Leadplant	-1	0.096%	Native	B-V
Astragalus canadensis	Canadian Milkvetch	-1	0.413%	Native	W-G
Cirsium vulgare	Bull Thistle	-1	0.007%	NonNat.	B-V
Convolvulus arvensis	Field Bindweed	-1	5.697%	NonNat.	W-G
Desmodium	Hoary Ticktrefoil	-1	1.122%	Native	B-V

canescens					
Heliopsis helianthoides	Smooth Oxeye	-1	1.311%	Native	Y-O

Forb Species	Common Name	Bee Preference	Relative Forb Abun.	Status	Color
Lespedeza capitata	Roundhead Lespedeza	-1	0.173%	Native	W-G
Medicago sativa	Alfalfa	-1	0.198%	NonNat.	B-V
Oxalis stricta	Yellow Wood Sorrel	-1	0.282%	Native	Y-O
Packera plattensis	Prairie Groundsel	-1	0.033%	Native	Y-O
Potentilla recta	Sulphur Cinquefoil	-1	0.084%	NonNat.	Y-O
Sisyrinchium campestre	Prairie Blue-eyed Grass	-1	0.352%	Native	B-V
Solidago canadensis	Canada Goldenrod	-1	6.569%	Native	Y-O
Tradescantia ohiensis	Bluejacket	-1	0.009%	Native	B-V
Vernonia baldwinii	Baldwin's Ironweed	-1	1.304%	Native	B-V
Zizia aurea	Golden Zizia	-1	0.005%	Native	Y-O
*Allium canadense**	Meadow Garlic	0	0.005%	Native	R-P
*Amaranthus palmeri**	Carelessweed	0	0.208%	Native	W-G
*Apocynum cannabinum**	Indianhemp	0	0.005%	Native	W-G
*Asclepias stenophylla**	Slimleaf Milkweed	0	0.002%	Native	W-G
Asclepias tuberosa	Butterfly Milkweed	0	0.033%	Native	Y-O
*Astragalus crassicarpus**	Groundplum Milkvetch	0	0.077%	Native	B-V
Brassica napus	Yellow Mustard	0	2.104%	NonNat.	Y-O
Brassica sp.	Mustard	0	0.002%	NonNat.	Y-O
*Calylophus serrulatus**	Yellow Sundrops	0	0.002%	Native	Y-O
*Cannabis sativa**	Ditchweed	0	0.033%	NonNat.	W-G
*Catalpa speciosa**	Northern Catalpa	0	0.047%	Native	W-G
*Chamaesyce nutans**	Small Eyebane	0	0.061%	Native	W-G
*Conium maculatum**	Poison Hemlock	0	0.177%	NonNat.	W-G
*Coreopsis tinctoria**	Golden Tickseed	0	0.091%	Native	Y-O
Dalea candida	White Prairie Clover	0	0.334%	Native	W-G
*Delphinium carolinianum**	Carolina Larkspur	0	0.002%	Native	B-V
*Descurainia pinnata**	Western Tansymustard	0	0.028%	Native	Y-O
*Desmanthus illinoensis**	Illinois Bundleflower	0	0.070%	Native	W-G
*Elaeagnus umbellata**	Autumn Olive	0	0.037%	NonNat.	W-G

*Eupatorium serotinum**	Lateflowering Thoroughwort	0	0.063%	Native	W-G
Euphorbia marginata	Snow on the Mountain	0	0.947%	NonNat.	W-G
*Euphorbia sp.**	Spurge	0	0.002%	NonNat.	W-G
Forb Species	**Common Name**	**Bee Preference**	**Relative Forb Abun.**	**Status**	**Color**
*Galium boreale**	Northern Bedstraw	0	0.009%	Native	W-G
*Gentiana puberulenta**	Downy Gentian	0	0.012%	Native	B-V
*Hedeoma drummondii**	Drummond's False Pennyroyal	0	0.002%	Native	B-V
Helianthus annuus	Common Sunflower	0	2.137%	Native	Y-O
Helianthus maximiliani	Maximillian Sunflower	0	1.215%	Native	Y-O
*Hieracium longipilum**	Hairy Hawkweed	0	0.040%	Native	Y-O
Hypericum perforatum	Common St. Johnswort	0	4.064%	NonNat.	Y-O
*Lespedeza cuneata**	Sericea Lespedeza	0	0.198%	NonNat.	W-G
*Lithospermum incisum**	Narrowleaf stoneseed	0	0.026%	Native	Y-O
*Oenothera villosa**	Hairy Evening Primrose	0	0.012%	Native	Y-O
Oxalis dillenii	Slender Yellow Wood Sorrel	0	0.107%	Native	Y-O
Penstemon digitalis	Foxglove Beardtongue	0	0.049%	Native	W-G
Physalis longifolia	Common Ground Cherry	0	0.012%	Native	Y-O
*Polygonum sp.**	Knotweed	0	0.040%	Both	R-P
*Potentilla arguta**	Tall Cinquefoil	0	0.014%	Native	W-G
*Potentilla simplex**	Common Cinquefoil	0	0.021%	Native	Y-O
*Pseudognaphalium obtusifolium**	Rabbit-tobacco	0	0.023%	Native	W-G
*Pycnanthemum tenuifolium**	Narrowleaf Mountainmint	0	0.033%	Native	W-G
*Pycnanthemum virginianum**	Virginia Mountainmint	0	0.028%	Native	W-G
*Ratibida columnifera**	Upright Prairie Coneflower	0	0.072%	Native	Y-O
*Rosa arkansana**	Prairie Rose	0	0.191%	Native	R-P
Rudbeckia hirta	Blackeyed Susan	0	1.148%	Native	Y-O
Ruellia humulis	Fringeleaf Wild Petunia	0	0.140%	Native	B-V
*Sambucus nigra**	American Black Elderberry	0	0.184%	Both	W-G
Scrophularia lanceolata	Lanceleaf Figwort	0	0.049%	Native	W-G
Silphium laciniatum	Compassplant	0	0.093%	Native	Y-O
*Solanum carolinense**	Carolina Horsenettle	0	0.068%	Native	W-G

*Solanum rostratum**	Buffalobur Nightshade	0	0.016%	Native	Y-O
*Spiranthes vernalis**	Spring Lady's Tresses	0	0.005%	Native	W-G
Taraxacum officinale	Common Dandelion	0	1.047%	Both	Y-O

Forb Species	Common Name	Bee Preference	Relative Forb Abun.	Status	Color
*Teucrium canadense**	Canada Germander	0	0.026%	Native	R-P
*Trifolium repens**	White Clover	0	0.107%	NonNat.	W-G
*Triodanis leptocarpa**	Slimpod Venus' Looking-glass	0	0.093%	Native	W-G
*Triodanis perfoliata**	Clasping Venus' Looking-glass	0	0.005%	Native	W-G
*Verbascum thapsus**	Common Mullein	0	0.002%	NonNat.	Y-O
Verbena stricta	Swamp Verbena	0	0.816%	Native	B-V
Viola pedatifida	Prairie Violet	0	0.404%	Native	B-V
*Ageratina altissima**	White Snakeroot	1	0.350%	Native	W-G
*Brickellia eupatorioides**	False Boneset	1	0.296%	Native	W-G
Euphorbia esula	Leafy Spurge	1	0.646%	NonNat.	W-G
*Lotus unifoliolatus**	American Bird's-foot Trefoil	1	0.387%	Native	Y-O
Melilotus alba	White Sweet Clover	1	0.551%	NonNat.	W-G
Melilotus officinalis	Yellow Sweet Clover	1	14.601%	NonNat.	Y-O
Psoralidium tenuiflorum	Slimleaf Scurfpea	1	3.845%	Native	B-V
Trifolium pratense	Red Clover	1	2.438%	NonNat.	R-P
Centaurea sp.	Knapweed	2	0.443%	Both	B-V
Chamaecrista fasciculata	Partidge Pea	2	0.462%	Native	Y-O
Desmodium illinoense	Illinois Ticktrefoil	2	0.009%	Native	B-V
*Helianthus pauciflorus**	Stiff Sunflower	2	0.457%	Native	Y-O
Linum sulcatum	Grooved Flax	2	0.684%	Native	Y-O
Oenothera suffrutescens	Scarlet Beeblossom	2	0.467%	Native	R-P
Oligoneuron rigidum	Stiff Goldenrod	2	2.123%	Native	Y-O
Achillea millefolium	Common Yarrow	3	1.836%	Both	W-G
Conyza canadensis	Canadian Horseweed	3	1.820%	Native	W-G
Erigeron strigosus	Prairie Fleabane	3	10.367%	Native	W-G
Glechoma hederacea	Ground Ivy	3	3.128%	NonNat.	B-V
Oenothera filiformis	Longflower Beeblossom	3	1.012%	Native	R-P

Dianthus armeria	Deptford Pink	4	6.607%	NonNat.	R-P
*Medicago lupulina**	Black Medic	4	3.187%	NonNat.	Y-O

Table 2.4. Inventory of bee species collected in the Prairie Corridor (USA: NE: Lancaster Co., Denton). * denotes Oligolectic bee

Bee Family	Bee Species	Sociality	Nest Location	Host Plant
Andrenidae	*Andrena carlini*	Solitary	Below ground	
	*Andrena erythrogaster**	Solitary	Below ground	*Salix*
	Andrena heraclei	Solitary	Below ground	
	Andrena hippotes	Solitary	Below ground	
	Andrena miserabilis	Solitary	Below ground	
	Andrena rugosa	Solitary	Below ground	
	*Andrena ziziae**	Solitary	Below ground	*Zizia*
	*Calliopsis coloradensis**	Solitary	Below ground	*Grindelia*
	*Calliopsis nebraskensis**	Solitary	Below ground	*Verbena*
	Protandrena bancrofti	Solitary	Below ground	
	*Pseudopanurgus albitarsis**	Solitary	Below ground	Heliantheae
	*Pseudopanurgus labrosiformis**	Solitary	Below ground	Heliantheae
Apidae	*Anthophora walshii*	Solitary	Below ground	
	Bombus auricomis	Social	Above ground	
	Bombus bimaculatus	Social	Above ground	
	Bombus fraternus	Social	Above ground	
	Bombus griseocollis	Social	Above ground	
	Bombus impatiens	Social	Above ground	
	Bombus pensylvanicus	Social	Above ground	
	*Melissodes agilis**	Solitary	Below ground	*Helianthus*
	Melissodes bimaculatus	Solitary	Below ground	
	Melissodes communis	Solitary	Below ground	
	Melissodes comptoides	Solitary	Below ground	
	*Melissodes denticulata**	Solitary	Below ground	*Vernonia*
	*Melissodes desponsa**	Solitary	Below ground	*Cirsium*
	*Melissodes nivea**	Solitary	Below ground	Asteraceae
	*Melissodes rivalis**	Solitary	Below ground	Asteraceae
	*Melissodes trinodis**	Solitary	Below ground	*Helianthus*
	*Melissodes vernoniae**	Solitary	Below ground	*Vernonia*
	Melissodes sp.	Solitary	Below ground	
	*Svastra obliqua**	Solitary	Below ground	Asteraceae
	*Tetraloniella cressoniana**	Solitary	Below ground	*Salvia*
	Epeolus sp.	Cleptoparasite	Cleptoparasite	
	Nomada sp.	Cleptoparasite	Cleptoparasite	

Bee Family	Bee Species	Sociality	Nest Location	Host Plant
	Ceratina calcarata	Fac. Social	Above ground	
Apidae	*Ceratina floridiana*	Fac. Social	Above ground	
	Ceratina spp.	Fac. Social	Above ground	
	Ceratina strenua	Fac. Social	Above ground	
	Ceratina sp.	Fac. Social	Above ground	
	Xylocopa virginica	Fac. Social	Above ground	
Colletidae	*Colletes latitarsis**	Solitary	Below ground	*Physalis*
	Hylaeus affinis	Solitary	Above ground	
	Hylaeus mesillae	Solitary	Above ground	
Halictidae	*Agapostemon angelicus/texanus*	Solitary	Below ground	
	Agapostemon sericeus	Solitary	Below ground	
	Agapostemon virescens	Solitary	Below ground	
	Augochlora pura	Solitary	Above ground	
	Augochlorella aurata	Social	Below ground	
	Augochlorella persimilis	Social	Below ground	
	Augochloropsis metallica	Social	Below ground	
	Halictus confusus	Social	Below ground	
	Halictus ligatus	Social	Below ground	
	Halictus parallelus	Social	Below ground	
	Halictus sp.	Social	Below ground	
	Lasioglossum albipenne	Social	Below ground	
	Lasioglossum callidum	Social	Below ground	
	Lasioglossum coreopsis	Social	Below ground	
	Lasioglossum disparile	Social	Below ground	
	Lasioglossum hitchensi	Social	Below ground	
	Lasioglossum illinoense	Social	Below ground	
	Lasioglossum imitatum	Social	Below ground	
	Lasioglossum oceanicum	Social	Below ground	
	Lasioglossum pectorale	Solitary	Below ground	
	Lasioglossum pruinosum	Social	Below ground	
	Lasioglossum semicaeruleum	Social	Below ground	
	Lasioglossum sp.	Social	Below ground	
	Lasioglossum tegulare	Social	Below ground	
	Lasioglossum versatum	Social	Below ground	

Bee Family	Bee Species	Sociality	Nest Location	Host Plant
Halictidae	*Lasioglossum zephyrum*	Social	Below ground	
	Sphecodes sp. A	Cleptoparasite	Cleptoparasite	
	Sphecodes sp. B	Cleptoparasite	Cleptoparasite	
Megachilidae	*Coelioxys octodentata*	Cleptoparasite	Cleptoparasite	
	Coelioxys rufitarsis	Cleptoparasite	Cleptoparasite	
	Heriades carinata	Solitary	Above ground	
	Heriades variolosa	Solitary	Above ground	
	Hoplitis pilosifrons	Solitary	Above ground	
	Hoplitis producta	Solitary	Above ground	
	Megachile brevis	Solitary	Above ground	
	*Megachile inimica**	Solitary	Above ground	Asteraceae
	Megachile mendica	Solitary	Above ground	
	Megachile montivaga	Solitary	Below Ground	
	Megachile policaris	Solitary	Above ground	
	Megachile rugifrons	Solitary	Above ground	
	Megachile sp.	Solitary	Above ground	
	Stelis sp.	Cleptoparasite	Cleptoparasite	

Table 2.5. Comparison of Top 10 bee-visited forbs and available forbs by color, displaying difference in species composition. Bee-visited forbs are in order from most to least supportive of bee richness per color, and available forbs are in order of cumulative abundance on the landscape. * denotes forbs that bees did not visit

	Bee-visited Forb Species	Bee Rich.	Bee Abun.	Available Forb Species	Forb Abun.
Yellow-Orange	*Melilotus officinalis*	20	64	*Melilotus officinalis*	6259
	Solidago canadensis	19	68	*Solidago canadensis*	2816
	Hypericum perfoliatum	14	23	*Hypericum perfoliatum*	1742
	Silphium integrifolium	13	108	*Medicago lupulina**	1366
	Heliopsis helianthoides	13	28	*Helianthus annuus*	916
	Helianthus annuus	11	14	*Oligoneuron rigidum*	910
	Brassica napus	9	21	*Brassica napus*	902
	Rudebckia hirta	9	20	*Silphium integrifolium*	693
	Taraxacum officinale	7	12	*Heliopsis helianthoides*	562
	Helianthus maximiliani	4	11	*Helianthus maximiliani*	521
Blue-Violet	*Carduus nutans*	19	67	*Psoralidium tenuiflorum*	1648
	Salvia azurea	19	29	*Glechoma hederacea*	1341
	Cirsium altissimum	15	53	*Monarda fistulosa*	1041
	Vernonia baldwinii	15	40	*Vernonia baldwinii*	559
	Monarda fistulosa	14	81	*Desmodium illinoense*	481
	Nepeta cataria	10	12	*Verbena stricta*	350
	Psoralidium tenuiflorum	8	9	*Salvia azurea*	318
	Verbena stricta	5	5	*Carduus nutans*	266
	Sisyrinchium campestre	4	6	*Cirsium altissimum*	243
	Baptisia australis	4	6	*Centaurea sp.**	190
White-Green	*Convolvulus arvensis*	18	50	*Erigeron strigosus*	4444
	Erigeron strigosus	16	19	*Convolvulus arvensis*	2442
	Asclepias verticillata	15	51	*Achillea millefolium*	787
	Euphorbia marginata	9	20	*Conyza canadensis*	780
	Symphyotrichum ericoides	4	32	*Asclepias verticillata*	672
	Erechtites hieraciifolius	3	5	*Euphorbia marginata*	406
	Euphorbia esula	3	4	*Euphorbia esula*	277
	Astragalus canadensis	2	6	*Melilotus alba*	236
	Conyza canadensis	2	3	*Astragalus canadensis*	177
	Melilotus alba	2	2	*Symphyotrichum ericoides*	160
Red-Pink	*Trifolum pratense*	7	8	*Dianthus armeria*	2832
	Oenothera filiformis	3	3	*Trifolium pratense*	1045
	Asclepias syriaca	2	18	*Oenothera filiformis*	434
	Dianthus armeria	2	2	*Oenothera suffrutescens*	200
	Oenothera suffrutescens	1	1	*Asclepias syriaca*	151
	-	-	-	*Rosa arkansana**	82
	-	-	-	*Polygonum sp.**	17
	-	-	-	*Teucrium canadense**	11
	-	-	-	*Allium canadense**	2

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Chapter 3: Influence of Vegetation Cover on Wild Bees

3.1. Introduction

Wild bee and plant communities within prairies are two largely interdependent systems, and collectively maintain the high level of biodiversity expressed in the ecosystem. Wild bees rely on flowering plants for nutritious food and nesting resources, and as such provide vital pollination services and function as dispersal agents for the flowering plants they visit. In turn, plants are able to successfully reproduce and provide food and shelter for wildlife across various size and trophic levels, as well maintain soil health and stability, and assist with water filtration and carbon sequestration. Together, the diversity of bee and plant communities provide ecosystems that allow the prairie to function at a high level and absorb disturbance. However, wild bee and plant communities residing in the Great Plains are threatened by many of the same factors leading to decline, such as agricultural intensification and urbanization contributing to severe habitat loss, as well as increased agrochemical exposure and susceptibility to pathogens and parasites lowering the ecosystem's health (Winfree et al., 2009; Potts et al., 2010; Giannini et al., 2012; Koh et al., 2016). Further, the severe habitat loss Great Plains prairies have experienced has led to a highly fragmented landscape where native vegetation exists as small, patchy or linear remnants which decreases species dispersal and increases isolation (Zayed, 2009; Schüepp et al., 2011; Lark et al., 2015). This is of high concern because many species are threatened with forceful range shifts due to climate change and must be able to disperse, while the ecosystem itself must be resilient enough to absorb and adapt this shift in species composition. Therein, it is apparent that minimization of further habitat loss must be made a priority while agriculturally intensified landscapes must be made more bee-friendly in order to conserve the vital ecosystem services bees and plants provide (Brown and Paxton, 2009; Potts et al., 2010).

In minimizing habitat loss, protecting and restoring areas with high habitat heterogeneity at the landscape level has been identified as a key driver of bee richness, because these areas support diverse plant communities both ecologically and functionally speaking. This diversity accommodates a wider breadth of bee niches and offer foraging and nesting resources throughout all growing seasons (Fontaine et al., 2005; Mallinger et al., 2016; Neokosmidis et al. 2016). Additionally, floral diversity allows bees to forage on a higher diversity of pollen, leading to an improved diet which has been shown to improve their health, reproduction and resilience to stress (Vaudo et al., 2015). Particularly in agriculturally intensified landscapes, areas of heterogeneous habitat that maintain such diverse plant communities are typically remnant prairies and semi-natural habitats (Hines and Hendrix, 2005; Kwaiser and Hendrix, 2008; Delaney et al., 2017).

As stated in Chapter 2, Nebraska's City of Lincoln Parks and Recreation Department initiated the Prairie Corridor on Haines Branch project in 2012 as an effort to conserve, connect and restore Tallgrass prairie fragments. This effort was split into two phases wherein Phase 1 was to form the actual corridor by acquiring recommended land based off a habitat assessment focused on maximizing connectivity of high-quality habitat (City of Lincoln, 2012). Following the effort of Phase 1 which has currently protected ~3,157 hectares, the mission of Phase 2 is to examine how to increase pollinator species in the design and management of prairie reconstruction, and monitor plant and pollinator communities to identify areas in the corridor that are most supportive of high pollinator diversity (Prairie Corridor, prairiecorridor.org). In line with the Prairie Corridor's mission, the objective of this research is to assess how vegetation cover influences the richness and abundance of wild bees by combining the baseline wild bee data described in Chapter 2 with baseline vegetation data collected by the University of Nebraska-Lincoln's School of Natural Resources. While the descriptive inventory produced in Chapter 2 is important for understanding the composition of the bee community, it is not sufficient on its own to examine the suitability of habitat present in the Corridor because such vast diversity exists. For example, numerous studies have attempted to correlate or predict bee response in terms of abundance, richness, or fitness when looking at land use change, disturbance gradients, habitat variables, or sensitivity to management regimes through use of functional traits and have only found weak or contrasting patterns (Steffan-Dewenter and Tscharntke, 2002; Williams et al., 2010; Rader et al., 2014; De Palma et al., 2015; Forrest et al., 2015; Bartomeus et al., 2018). Therefore, combining the parallel baseline datasets will provide the Prairie Corridor with more constructive and generalized recommendations on how to best design and manage restorations because it will represent the landscape as a whole, and allow for better detection of patterns.

3.1.1. School of Natural Resources Vegetation Survey

Throughout the length of the Corridor, the same twenty 1.2ha plots surveyed for bees in Chapter 2 were surveyed for vegetation cover. Vegetation surveys occurred twice each year, in which 30 random $1m^2$ quadrats were sampled per plot. For each quadrat, all vegetation was identified and quantified and then used to calculate frequency of occurrence per species per plot. Using these values, a mean species composition per plot was calculated. Resulting from the vegetation survey, 236 plant species were identified, and based on a multivariate cluster analysis the plots naturally sorted into three groups based on mean species composition (Figure 3.1). The group with the highest mean species composition is classified as Remnant ($\bar{x}$ = 13 species/m^2), followed by High Diversity ($\bar{x}$ = 7.5) and then Low Diversity ($\bar{x}$ = 5). Plots that grouped into Remnant included true remnants, 28 year-old established restorations, hay meadows and rotational pastureland. Plots that grouped into High Diversity included 4-5 year-old restorations seeded with high-diversity local-ecotye mixes, and a 10 year-old restoration enrolled in USDA's Conservation Reserve Program. Plots that grouped into Low Diversity included 28 year-old restorations seeded with low diversity mixes, a new restoration in year 1-2, and many plots that are intensely managed or overrun by non-native plants (see Appendix A for detailed plot descriptions).

These three natural groupings will serve as treatment groups from which to assess the influence of vegetation cover on the richness and abundance of wild bees and their foraging resources. Given our knowledge on the importance of heterogenous habitat in supporting diverse bee and plant communities, and the relatively high presence of nesting and foraging resources throughout all seasons in established restorations or remnant prairies I expect to find (1) Highest Forb Richness in the Remnant treatment, (2) Highest Bee Richness in the Remnant treatment and (3) Highest Bee Abundance in the Remnant treatment. Lastly, I expect to find (4) Highest Forb Abundance in the High Diversity treatment because these plots may exhibit a higher ratio of flowering forbs to grasses given that they were seeded.

3.2. Methods

3.2.1. Survey Location

The Prairie Corridor is located in southwest Lincoln, Nebraska (Lancaster County). This newly-protected greenway forms a 17.7-kilometer nearly-contiguous passage between Pioneers Park Nature Center and Spring Creek Prairie Audubon Center, which are two of Lincoln's valuable nature preserves (Figure 3.2). The fragments that compose the Corridor vary in size and consist of Tallgrass Prairie remnants, established restorations, 1-5 year-old seeded restorations, pastureland and hay meadows. The management of parcels vary in type and intensity, but include combinations of burning, grazing and haying (Appendix A). Throughout the length of the corridor 19 plots were defined in a non-random fashion to the University of Nebraska-Lincoln's School of Natural Resources vegetation survey (Figure 3.3). The plots were chosen to represent the variety of management and land use present in the Corridor, and each plot was ~1.2 hectares in size. For two consecutive years, 2017 and 2018, each plot was surveyed for vegetation cover by UNL's School of Natural Resources, and for wild bees by UNL's Department of Entomology.

3.2.2. Survey Methods

All 19 plots were assigned an individual number and were surveyed every other week between May-October 2017 and April-October 2018. Sampling was only conducted when the temperature was 15.5-35˚C, average wind speeds ≤24km/hr, and it was not raining. Each sampling week was considered a round, in which all 19 plots were surveyed. A sampling round consisted of surveying two randomly-selected transects that spanned 2 x 20m, and ran south to north, within each 1.2ha plot. Two surveys were run on each transect, and consisted of a blooming-forb survey and a bee survey (described below). Temperature, average wind speed, relative humidity and cloud cover were recorded during each sampling round.

3.2.2.1. Forb Survey

Forb surveys were always conducted before bee surveys on each transect. Only blooming forbs within transects (2 x 20 m) were recorded. Each species was quantified by counting the number of stems bearing open flowers at the time of surveying, and was identified to its lowest taxonomic rank when possible. Photographs were taken of unknown forbs and later identified. Once identified, The PLANTS

Database (USDA, 2018) was consulted to standardize scientific names, authorities, and common names.

3.2.2.2. Bee Survey

The bee survey began immediately upon completion of the forb survey. The surveyor collected bees on the transect by walking a steady unidirectional-pace from south to north over a period of 5 minutes. Bees were only collected when observed visiting a blooming forb within the transect by use of aerial nets and visual observations. Visual observations were used when species could be identified on the wing, or to note the genus when a specimen was missed during netting. Each time a bee was netted, the surveyor paused the 5-minute timer to transfer the specimen into a kill jar and assign a label with associated plant information. For each transect, bees caught on different plants were placed in separate vials, which meant many kill jars had to be carried to often remote locations during sampling. In an effort to reduce size, weight and cost, kill jars were constructed by wrapping solid ammonium carbonate in empty tea bags and securely placing it at the bottom of 50ml polypropylene falcon tubes. At the end of each sampling day, collected bees were curated within 2 days and labeled with a unique identifier allowing the specimen to be traced back to the specific transect and plant it was caught on, along with any associated metadata, such as geographic coordinates, elevation, temperature, wind speed and cloud cover. Once curated, bees were identified to the species level using three main sources, including *Bees of the Tallgrass Prairie Region and Greater Midwest* (Arduser, 2018), *Discover Life Species Guide and World Checklist (Hymenoptera: Apoidea: Anthophila)* (Ascher and Pickering, 2016), and *Bumble Bees of North America: An Identification Guide* (Williams et al., 2014), although numerous genera-specific keys were consulted (see Appendix B). Identification of specimens were confirmed by Mike Arduser (Missouri Dept. of Conservation (*retired*)), though a few remaining specimens collected in 2018 still await verification. Taxonomic groups difficult to identify to species-level included *Lasioglossum* (*Dialictus*) Curtis (n=49) and *Ceratina* Latreille (n=5) and were thus resolved to the generic level. In addition, 19 females identified as members of the *Ceratina dupla* complex were classified as *Ceratina spp.* and may represent *C. calcarata*, *C. dupla* or *C. mikmaqi* which are near impossible to distinguish without male specimens or use of DNA barcoding (Rehan and Sheffield, 2011).

Additionally, forbs specifically observed visited by bees (or bee-visited forbs) was extracted from the plant-pollinator interaction survey. Similar to the forb inventory, these plants were identified to lowest taxonomic rank and the taxonomic names, authorities and common names were standardized according to The PLANTS Database (USDA).

3.2.3. Measures

Richness and abundance values were calculated for flowering forbs observed and bees captured at each plot. Forb richness pertains to the number of unique flowering plants observed blooming on the landscape, and forb abundance is the count of individual stems yielding blooms. Likewise, bee richness pertains to the number of unique bee species while bee abundance is the number of individuals observed. Bee-visited forb richness, or the number of unique flowering plants bees were observed visiting, was also measured. Bee-visited forb abundance was not calculated because the values would have been a replication of bee abundance given the data was extracted from plant-pollinator interaction surveys. All response measures were tested against treatment (High Diversity, Low Diversity and Remnant) and season as independent variables. Season consists of Early (April-mid June), Mid (late June-mid August) and Late (late August-October).

3.2.4. Analysis

Each of the 5 response measures described above (Forb Richness, Bee Richness, Bee-visited Forb Richness, Forb Abundance and Bee Abundance) were compared across treatment (High Diversity, Low Diversity and Remnant), season (Early: Apr-mid Jun, Mid: late Jun-mid Aug, Late: late Aug-Oct), year (2017-18), and the interactions among the factors using Analysis of Variance (ANOVA) statistical models followed by post-hoc Tukey's Honest Significant Difference (HSD) tests to determine treatment means that were significantly different from each other. Forb richness and abundance measures were normally distributed as determined by Shapiro–

Wilk tests (W=0.946, p=0.342; and W=0.952, p=0.432, respectively); however, bee richness, bee-visited forb richness and bee abundance measures were log-transformed to normalize the data (W=0.943, p=0.079; W=0.936, p=0.079; W=0.942, p=0.0688, respectively). No significant differences were found in all measured responses (forb richness ($F_{1,427}$=3.7, p>0.05), forb abundance ($F_{1,427}$=0.013, ns), bee richness ($F_{1,427}$=0.96, ns), bee abundance ($F_{1,427}$=0.33, ns), and bee-visited forb richness ($F_{1,427}$=0.006, ns)) between random transects completed in 2017 and 2018, therefore transects were pooled across years. To account for the uneven distribution of plots per treatment (High Diversity n=4; Low Diversity n=9; Remnant n=7), mean values were calculated for response measures by summing the two transects per sampling round per plot per year which yielded 429 sample data points per measure. Statistical analyses were conducted in R version 3.5.2 using the *agricolae* package (R Core Team, 2018; de Mendiburu, 2019).

3.3. Results

Significant differences were observed in main effects treatment (High Diversity, Low Diversity and Remnant) (Figure 3.4), season (Early: Apr-mid Jun, Mid: late Jun-mid Aug, Late: late Aug-Oct) (Figure 3.4), and the interaction between treatment*season (Figure 3.5) for all 5 response measures. A summary of results is displayed in Table 3.1. Where there were significant interactions between treatment*season, the interaction effects were reported rather than main effects.

3.3.1. Forb Measures

Significant interaction effects were observed between treatment and season on forb richness ($F_{4, 420}$=9.175, p= 4.09e-07) and on forb abundance ($F_{4, 420}$=4.285, p=0.002). Forb richness, as measured by the number of distinct species, was significantly higher in mid-season High Diversity (avg ± SD: 4.8 ± 2.4 species) and Remnant (avg ± SD: 4.5 ± 3.7 species) plots compared to other plots with the exception of late-season High Diversity plots (avg ± SD: 3.0 ± 3.0 species). The lowest richness was observed in all Low Diversity plots (early: avg ± SD: 0.23 ± 0.8 species; mid: avg ± SD: 1.1 ± 1.5 species; late: avg ± SD: 0.6 0± 1.1 species) and early-season High Diversity (avg ± SD: 0.52 ± 0.8 species) plots ($F_{4, 420}$=9.2, p=<4.1e-7). Interestingly, Remnant (avg ± SD: 2.5 ± 2.6 species) plots were significantly higher in forb richness than both High Diversity (avg ± SD: 0.52 ± 0.8 species) and Low Diversity (avg ± SD: 0.23 ± 0.8 species) plots but only in the early-season (Figure 3.5). Similarly, forb abundance was significantly higher ($F_{4, 420}$=9.548, p=8.78e-05) in early and late season Remnant plots (early: avg ± SD: 104.5 ± 208 flowers; mid: avg ± SD: 122.9 ± 166 flowers) compared to all Low Diversity plots, late season Remnant, and early season High Diversity plots. However, High Diversity plots in mid (avg ± SD: 87.5 ± 68 flowers) and late (avg ± SD: 70 ± 77 flowers) plots were not statistically different from all other treatment groups (Figure 3.5).

3.3.2. Bee Measures

Significant interaction effects were observed between treatment and season on bee richness ($F_{4, 420}$=8.093, p= 2.71e-06) and on bee abundance ($F_{4, 420}$=8.787, p=8.05e-07). High Diversity plots in mid-season had significantly more bee species (avg 9.550, 95% *C.I.*: 1.698-53.703) than all other plots, whereas all Low Diversity (early: avg 1.221, 95% *C.I.*: 0.475-3.140; mid: avg 1.479, 95% *C.I.*: 0.589-3.715; late: avg 1.318, 95% *C.I.*: 0.490-3.548) and early-season High Diversity (no flowers observed) had the least rich bee communities (Figure 3.5). Additionally, mid-season High Diversity plots also exhibited significantly higher bee abundance (avg 17.378, 95% *C.I.*: 1.749-204.174) in comparison to all other plots (Figure 3.5).

Significant interactions were observed between treatment and season on bee-visited forb richness ($F_{4, 420}$=7.65, p= 5.89e-06). The most extreme mean differences segregated into three groups setting mid-season High Diversity (avg 5.129 species, 95% *C.I.*: 1.622-12.218) plots apart from mid-season Remnant (avg 2.399 species, 95% *C.I.*: 0.741-7.762) further apart from all season Low Diversity (early: avg 1.122 species, 95% *C.I.*: 0.724-1.738; mid: avg 1.380 species, 95% *C.I.*: 0.661-2.884; late: avg 1.175 species, 95% *C.I.*: 0.661-2.455) and early season High Diversity plots which had no observed bee-visited forbs.

3.4. Discussion

In relation to our initial hypotheses, the results yielded unanticipated findings. As predicted, the Remnant treatment did support the highest richness and abundance of flowering forbs, although they were not significantly different from the richness and abundance observed in the High Diversity treatment. Both forb abundance and richness peaked in the mid-season for Remnant and High Diversity treatments which aligns with flowering-forb phenology of the Midwest (Kirt et al., 1995). However, the Remnant treatment supported significantly more Early season forbs in terms of richness and abundance compared to the High and Low Diversity treatments, while High Diversity treatment support significantly more Late season forbs. This suggests Remnant and High Diversity plots are critical for sustaining diverse communities to accommodate early-emerging bees and those who are active late in the season.

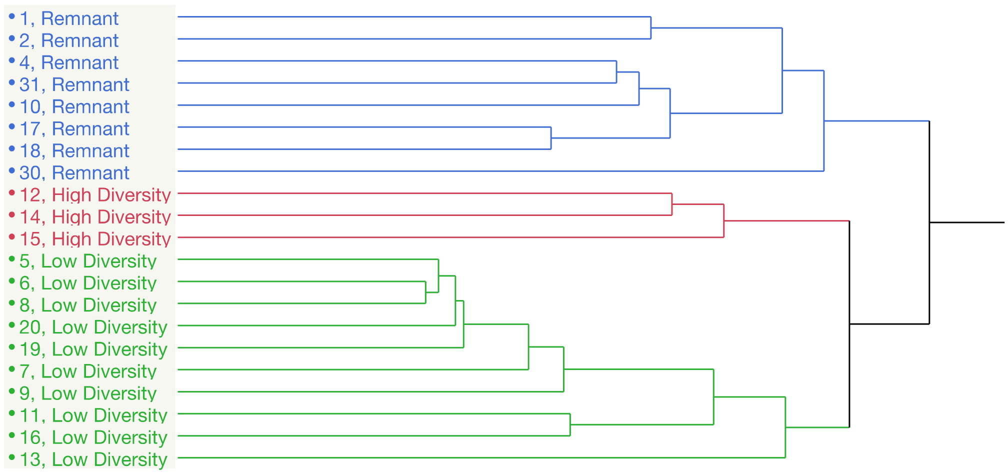
When examining bee richness and abundance, peaks were again seen in the mid-season for all treatments, and despite the similarity in available forbs during this season in Remnant and High Diversity treatments, High Diversity supported a significantly higher bee abundance and richness. This observation aligns with recent research demonstrating restoration efforts have the ability support the needs of bees comparable to, if not better than, remnant prairies (Griffin et al., 2017; Breland et al., 2018; Denning and Foster, 2018). Though it is worth noting that while the highest bee measures were not found in the Remnant treatment, it did support bees consistently throughout all seasons unlike the High Diversity treatment. This consistency is likely due to the habitat composition of the Remnant treatment providing a variety of floral and nesting resources throughout all growing seasons (Klein et al., 2012; Mallinger et al., 2016). Similarly, the significantly high bee measures observed in the High

Diversity treatment may correspond to the presence of a dense riparian corridor, formed by the Haines Branch of Salt Creek that directly splits two of the three plots within this treatment. Riparian corridors have been correlated with high floral diversity and offer a wide variety of nesting resources from which pollinators benefit (Naiman et al., 1993; Cole et al., 2017). Additionally, those same two plots in the High Diversity treatment are in close proximity of a cemetery which are known to support a high richness of bees (Tonietto et al., 2011; Normandin et al., 2017). While this study does not account for the surrounding landscape context, it may be of interest for future pursuit.

When looking at the final measure, bee-visited forb richness, peak is again observed in the mid-season and is significantly higher in the High Diversity treatment than Remnant. Similar to forb richness, the Remnant treatment displays consistency across all season unlike the High Diversity treatment which is significantly low in the early season. Inferred from all measures is that a pattern exists across vegetation type and season; Mid-season supports peak richness and abundance values, though depending on treatment type these values are more heavily weighted in the early-mid seasons as see in Remnant, the mid-late season as seen in High Diversity, or consistently low as seen Low Diversity. This suggests that the Remnant treatment may benefit from added late-blooming forbs, while the High Diversity treatment may benefit from added early-blooming forbs. The significantly low means observed for all measures in the Low Diversity treatment may be a result of the abundance of non-native forbs on the landscape, the management strategies used to remove the non-natives, or the lack of management that allow cedars to encroach; all of which may impact the diversity of bee and forb communities present in these areas. Additionally, something about the mid-season forbs present in the High Diversity treatment prove to be more attractive to bees than those in the Remnant treatment given that the similar values observed for forb richness and abundance did not equally translate to the observed bee richness and abundance values. To further dissect this, the Top 5 most abundant mid-season forbs of each treatment were pulled out to compare against the Top 5 most-visited mid-season forbs in each treatment (Table 3.2). Three of the five most abundant mid-season forbs in the High Diversity treatment are also three of the most-visited mid-season forbs, including *Monarda fistulosa* L., *Silphium integrifolium* Michx., and *Solidago canadensis* L.. Additionally, both Top 5 lists for mid-season High Diversity are composed of forbs indigenous to Nebraska as classified by The PLANTS Database (USDA). In the Remnant treatment however, only two of the five most abundant forbs appear in the most-visited Top 5 list, both of which are non-native plants (*Melilotus officinalis* (L.) Lam. and *Hypericum perforatum* L.). Further, 4/5 of the Top 5 most abundant mid-season forbs in the Remnant treatment are non-native, one of which no bees were observed on (*Medicago lupulina* L.), while 3/5 of the Top 5 most-visited mid-season forbs held indigenous status. This suggests that floral traits present in each vegetation cover type, such as indigenous status, or possibly other functional traits like floral color or corolla shape, are driving the structure of bee communities present in these treatments.

The best way to increase our understanding of the floral-foraging needs and preferences of wild bees is to carry out plant-pollinator interaction surveys rather than using passive sampling techniques like blue vane or bowl traps. With an improved understanding of floral-preferences exhibited by wild bees, our ability produce effective pollinator seed mixes will be enhanced (Havens and Vitt, 2016). This research has shown that prairies seeded with high-diversity mixes have the ability to support wild bees in terms of richness and abundance similar to, if not better than remnant prairies, although both are critical for sustaining bee communities throughout all growing seasons. Future research aimed at assessing the floral trait diversity between restorations varying in age, seeding, size or quality of surrounding habitat may allude to key components of a successful pollinator restoration and a new understanding of plant-pollinator networks.

3.5. Figures



	Remnant	High Diversity	Low Diversity
Mean Species/m^2	13	7.5	5

Figure 3.1. Vegetation survey results from the School of Natural Resources. The dendrogram was produced from a multivariate cluster analysis based off of the species composition of each plot. Numbers on the dendrogram correlate to plot numbers. Plots naturally sorted into 3 groups, which were classified as Remnant (highest species richness), High Diversity and Low Diversity (lowest species richness). These 3 groups then served as treatments from which to assess the abundance and richness of bees and blooming forbs observed in the corridor.

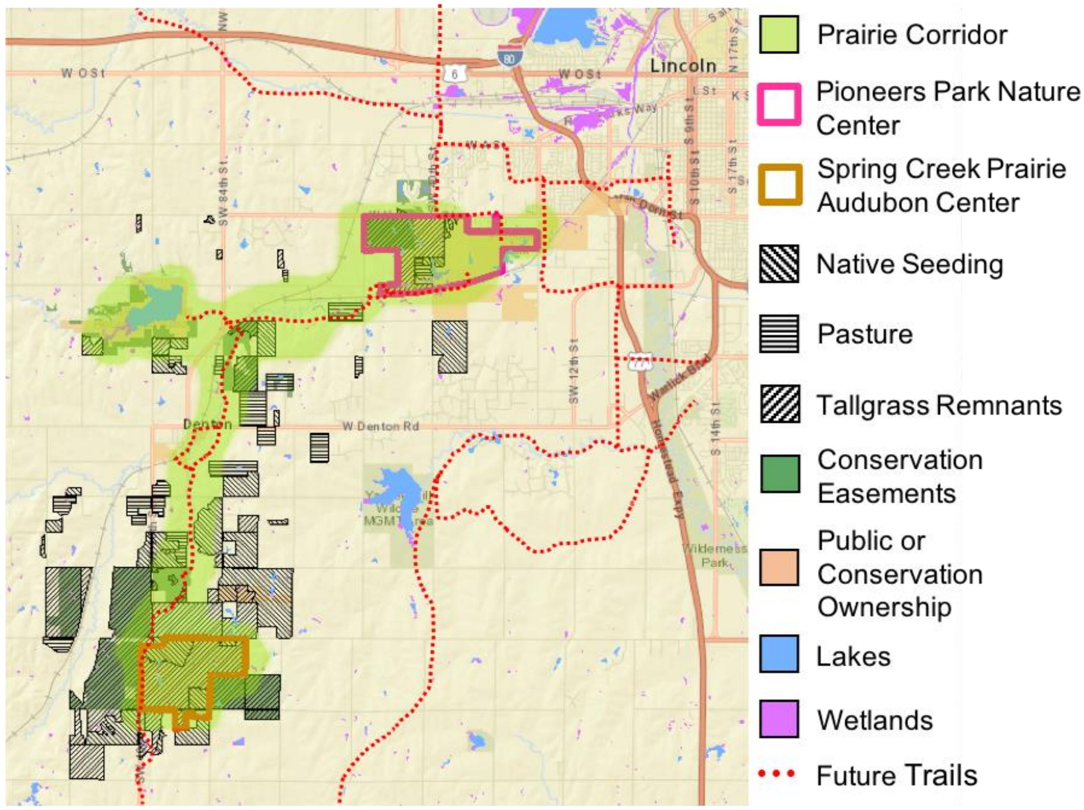


Figure 3.2. Prairie Corridor on Haines Branch (green) in Lincoln, NE, encompassing ~7,800 acres and stretching 11 miles from Pioneers Park Nature Center down to Spring Creek Prairie Audubon Center. Map from City of Lincoln (2012).

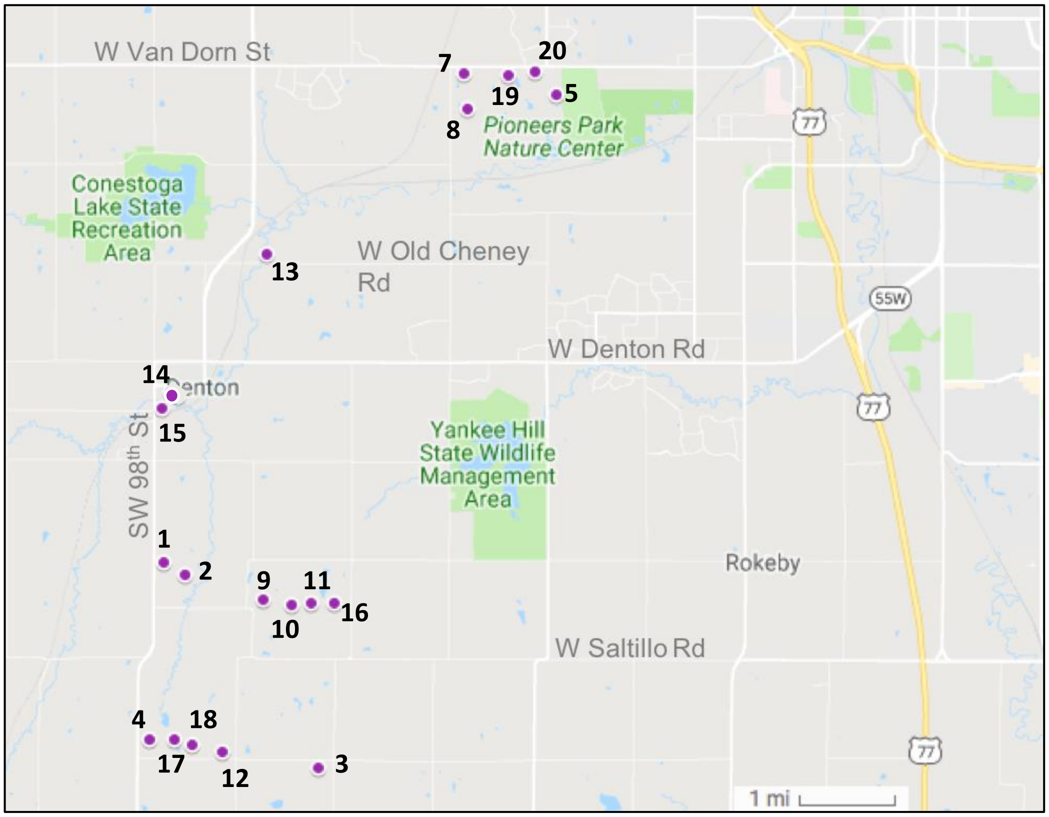


Figure 3.3. Locations and numbers of plots sampled throughout the Prairie Corridor, for detailed plot descriptions see Appendix A.

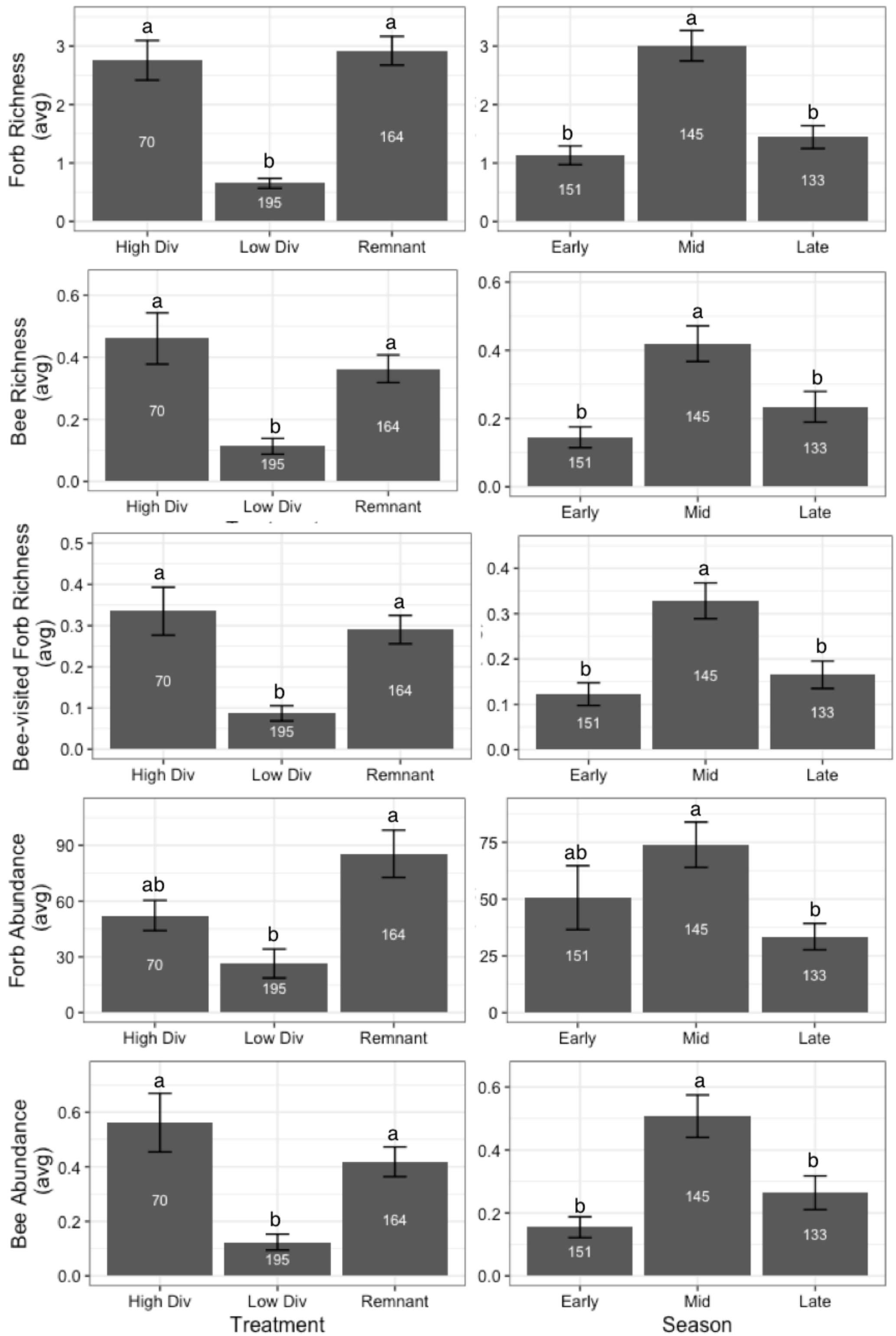


Figure 3.4. Results for all 5 measures when modeled against Treatment (left column) (High Diversity, Low Diversity and Remnant) and modeled against Season (right column) (Early: Apr-mid Jun, Mid: late Jun-mid Aug, Late: late Aug-Oct). Letters denote significant difference (alpha=0.05), and the breakdown of N (total=429) is represented inside each bar.

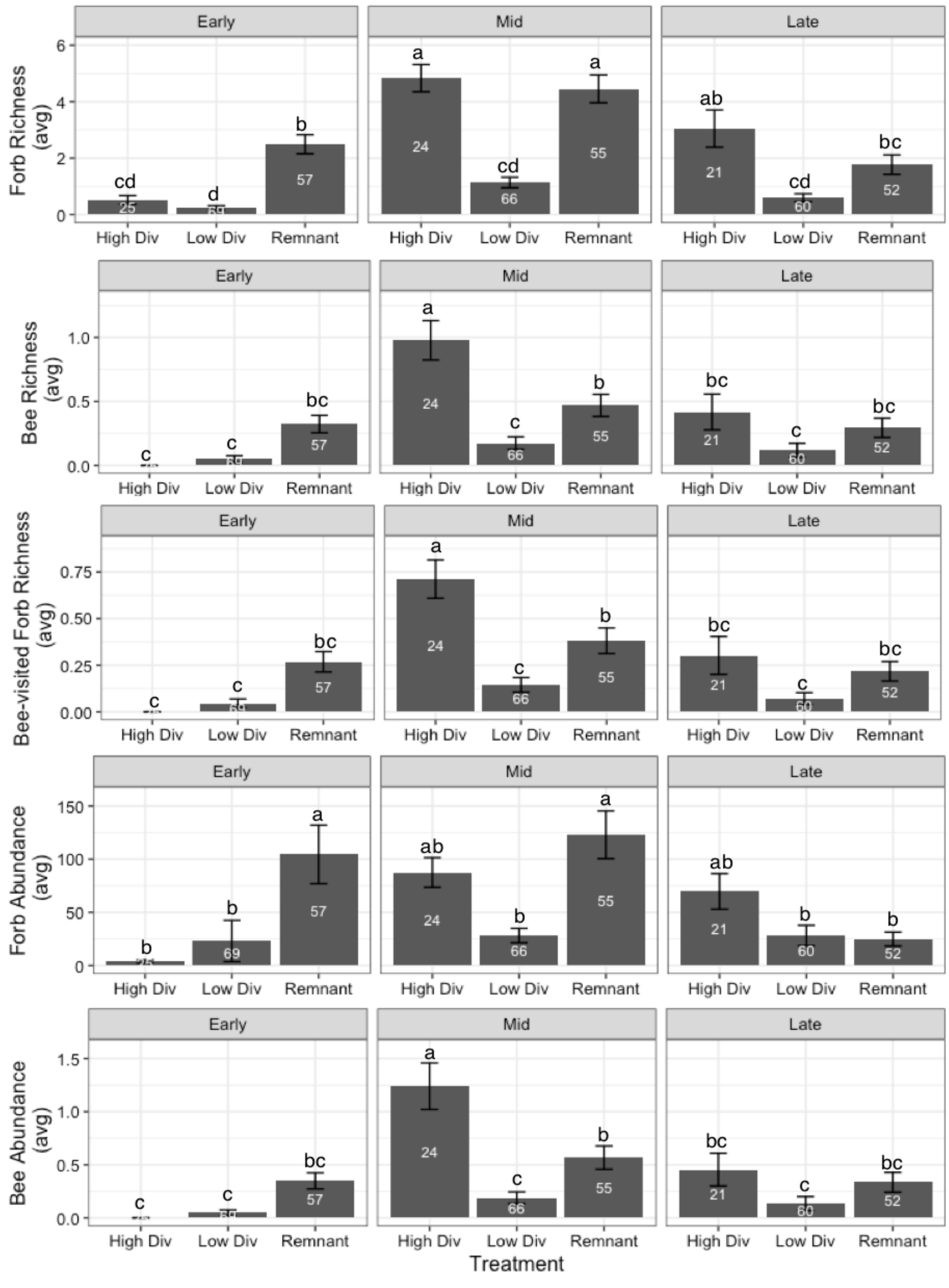


Figure 3.5. Results for all 5 measures when modeled against the interaction between Treatment (High Diversity, Low Diversity and Remnant) and Season (Early: Apr-mid Jun, Mid: late Jun-mid Aug, Late: late Aug-Oct). Letters denote significant difference (alpha=0.05), and the breakdown of N (total=429) is represented inside each bar.

3.6. Tables

Table 3.1. Summary of ANOVA results for all 5 measures. Significance was observed for all measures when tested against Treatment (High Diversity, Low Diversity, Remnant), Season (Early: Apr-mid Jun, Mid: late Jun-mid Aug, Late: late Aug-Oct), and the interaction of Treatment*Season meaning the effect of treatment cannot be understood without considering season or the reverse.

Variable	df	F (residuals)	P value
Treatment			
Forb Richness	2	45.76 (426)	<2e-16***
Bee Richness	2	13.19 (426)	2.77e-06***
Bee-visited Forb Richness	2	16.81 (426)	9.42e-08***
Forb Abundance	2	9.548 (426)	8.78e-05***
Bee Abundance	2	8.506 (426)	0.00024***
Season			
Forb Richness	2	23.35 (426)	2.38e-10***
Bee Richness	2	8.922 (426)	0.00016***
Bee-visited Forb Richness	2	11.88 (426)	9.5e-06***
Forb Abundance	2	3.437 (426)	0.0331*
Bee Abundance	2	6.346 (426)	0.0192**
Treatment*Season			
Forb Richness	4	9.175 (420)	4.09e-07***
Bee Richness	4	7.735 (420)	5.07e-06***
Bee-visited Forb Richness	4	7.408 (420)	8.98e-06***
Forb Abundance	4	4.285 (420)	0.00208**
Bee Abundance	4	6.980 (420)	1.9e-05***

Table 3.2. Top 5 most abundant mid-season forbs observed on the landscape compared to Top 5 most-visited mid-season forbs. Mid-season forb richness and forb abundance values were not significantly different between the Remnant and High Diversity treatments, however the High Diversity treatment had significantly higher mid-season bee richness and abundance values. This suggests the composition of the forb community is driving the bee community. * denotes non-native forbs relative to Nebraska as classified by The PLANTS Database (USDA).

	Remnant	**High Diversity**	**Low Diversity**
Top 5 Most Abundant Forbs	*Melilotus officinalis**	*Monarda fistulosa*	*Conyza canadensis*
	Erigeron strigosus	*Silphium integrifolium*	*Convolvulus arvensis**
	*Dianthus armeria**	*Desmodium illinoense*	*Melilotus officinalis**
	*Hypericum perforatum**	*Solidago candensis*	*Lotus unifoliatus*
	*Medicago lupulina**	*Rudbeckia hirta*	*Euphorbia esula**
Top 5 Most-visited Forbs	*Vernonia baldwinii*	*Monarda fistulosa*	*Rudbeckia hirta*
	*Melilotus officinalis**	*Solidago canadensis*	*Cirsium altissimum*
	Asclepias verticillata	*Silphium integrifolium*	*Melilotus officinalis**
	Asclepias syriaca	*Solidago missouriensis*	*Convolvulus arvensis**
	*Hypericum perforatum**	*Vernonia baldwinii*	*Solidago canadensis*

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Chapter 4: Extension Circular Deliverable

4.1. Conserving Biodiversity: A Bee's Role in Tallgrass Prairies

The following document represents a synthesis of the previous chapters designed to serve as a resource for land managers, conservation agencies or the general public interested in learning more about wild bees. The 19-page extension circular covers the topic and importance of biodiversity, factors leading to decline of wild bees and prairies, descriptions of wild bee life history strategies, brief descriptions of management and restoration efforts aimed at promoting pollinator diversity, as well as a basic guide of bee families residing in Nebraska.

Conserving Biodiversity:
A Bee's Role in Tallgrass Prairies

  

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This publication highlights the importance of wild, native bees and how their interaction with flowering plants supports the overall function of prairie ecosystems. The topic of biodiversity is explained, and the benefits of and threats to wild, native bees and prairie ecosystems are introduced. Considerations for restoration and management practices in relation to pollinator conservation are presented, along with a brief inventory of wild, native bees that occur in Nebraska's Tallgrass Prairies.

What is biological diversity?

In the simplest form, biological diversity, or **biodiversity,** refers to all variation of life present in an ecosystem, including the interactions that occur within and between the biotic (birds, mammals, insects, fungi, plants, etc.) and the abiotic factors (soil quality, water accessibility, temperature, etc.) that drive ecological functions. Maintaining biodiversity is important because it allows for ecosystems to be stable and healthy, meaning when faced with disturbance the ecosystem is able to absorb any change and adapt if needed.

Residing in many healthy ecosystems are what scientists have termed **keystone species**, an organism whose presence is vital as they provide valuable services that allow the ecosystem to properly function. These species typically affect the ecosystem as a whole, and their absence would drastically alter the landscape leading to negative impacts like the loss of biodiversity. Here in Nebraska, bees are considered to be a keystone species of the prairie, and their decline is one of many factors threatening what remains of these grassland ecosystems.

Why are bees important?

Bees are a remarkable group of animals, along with bats, birds, beetles, butterflies and flies, that we collectively call **pollinators**. These animals rely on pollen and nectar as their nutritional food source, and when visiting flowers to collect these substances, pollinators simultaneously transfer pollen from one flower to another which allows the plant to reproduce. Of all the known flowering plants on Earth, 87.5% of them require a pollinator to successfully reproduce.[1] Once pollinated, plants grow to produce seeds and fruits (e.g., nuts and berries) which serve as food for birds, mice, deer, and other wildlife. When the herbivores are healthy and fed, they maintain steady population sizes, which are necessary to support higher predators like foxes, snakes, and raptors. In addition to serving as the foundation of terrestrial food webs, plants cycle nutrients within the soil, aid in water filtration, sequester carbon, and provide shelter for organisms of all sizes. Therein the connection between plants and pollinators becomes apparent, in that their support for one another allows the ecosystem to function smoothly. John Muir pleasantly summarized this process in saying "When one tugs on a single thing in nature, he finds it attached to the rest of the world."

The act of pollination has countless direct and indirect effects on an ecosystem, and through time bees have adapted a suite of special characteristics that have allowed them to perform as the most effective and efficient pollinator.

What are "wild bees"?

Initially, when thinking of "bees" many of us produce the image of honey bees; organisms that live in large colony consisting of a queen bee and thousands of worker bees, living in a hive that is typically managed by a beekeeper wearing a funky suit. While this image is true, it is not representative of the bees found in most natural landscapes. Honey bees are an agricultural commodity, and livestock, that have an immense impact on the economy estimated at $12 billion annually in the United States.[2] They are able to be manipulated and transported all across the US to supply invaluable pollination services for some of the country's leading crops, such as almonds, apples, and cherries. As such, honey bees have been tightly woven into society, gaining much recognition over the past decade while they suffered great loss from various compounding stressors like disease, parasites, pesticide exposure, and habitat loss. However, the honey bee only represents 1 out of 4,000 known bee species found in the US, while the rest are deemed "wild bees." When referring to a group or number of organisms, scientists will often use the word *known,* to imply the high likelihood that many species are still waiting to be discovered, as is the case with bees. Worldwide there are approximately 20,000 different species, and it is estimated that ~300-400 of these reside in Nebraska.

Similar to other animals, different types of bees are found in different types of habitats. For example, just as there are certain birds associated with wetlands and grasslands, there are certain bees associated with wetlands and grasslands. Some bees are found all across the United States, while others have a restricted geographic distribution. Additionally, great variation exists when looking at nesting behaviors, social behaviors, and morphological features like color or size. For example, the largest bee may reach 1.5 inches (39mm) in length while the smallest bee measures in at a mere 0.08 inches (2mm). Likewise, bees range in color range from bright metallic blues and greens to displaying vibrant hair patterns of reds, oranges, and yellows--some even display a mother-of-pearl sheen. Due to such vast diversity, the habitat requirements necessary for each species' survival also varies, and in a more biodiverse ecosystem there will likely be more species present because a higher variety of nesting and foraging resources are available.

What do wild bees need to survive?

In order to survive and reproduce, bees need suitable nesting locations, nesting materials and sufficient floral resources.

Beginning with nesting location, wild bees tend to be divided into a couple categories: renter or excavator, and above ground or below ground. A **renter** is a bee that utilizes existing cavities on the landscape, such as old mice burrows or beetle-bored tunnels, or even snail shells. An **excavator** is a bee that digs, carves, or bores into the earth, wood, or pithy stems, or constructs its own free-standing nest using various materials from the environment. Those who nest **above ground** are typically found in hollow plant stems, old logs or snags, or beneath a layer of dead vegetation. In contrast, those who nest **below ground** may be found tunneling in soil, sand, muddy banks, or dry cliffs.

While 70% of bees nest below ground, the remaining above-ground nesters generally require materials from the environment to build or partition their nest. For example, leafcutting bees, as the name suggests, cut numerous symmetrical pieces of leaf to construct an intricate nest (Figure 2). Other nest materials bees use to build nests include flower petals, chewed leaf matter, resin, mud, clay, pebbles, and wooly plant fibers.

In locating a proper nest site, a key consideration is its proximity to flowers. If nesting locations and materials are not within range of a bee's preferred flowers or enough flowers, additional stress is placed upon the bee. The bee will have to spend more time and energy traveling between resources, which will likely decrease the number of eggs she can lay. In general, small bees have a small foraging radius, sometimes traveling only ~200 yards from their nest, while large bees can endure flight distances of ~2 miles to gather what they need.

When a bee visits a flower, its intention is not to provide pollination services but to harvest nectar and pollen from the flower. These rewards are referred to as **floral resources**, and function as a bee's main source of food. Nectar is a sugary substance, or carbohydrate, that provides bees with quick energy, while pollen serves as a nutritious protein source containing essential amino acids. Different types of flowers offer different qualities and quantities of nectar and pollen, and similar to humans, bees typically need a variety of resources to form a nutritiously complete and healthy diet.

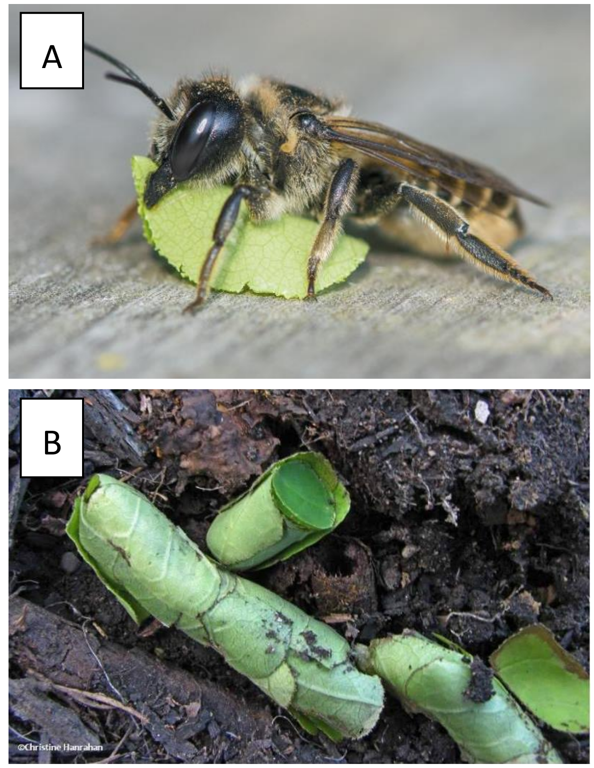


Figure 2: (A) Leafcutting bee (genus *Megachile)* using mandibles to transport leaf material back to her nest (Image: Rodger Evans);(B) Leafcutting bee nest found underneath a rock, made of numerous leaf pieces (Image: Christine Hanarahan)

As with nest categorizations, wild bees are also classified by their dietary needs as specialists or generalists, specifically when foraging for pollen. A **specialist**, or oligolectic, bee is largely dependent on one type of plant or a select few that are closely related. Inversely, a **generalist**, or polylectic, bee will utilize many different plant species on the landscape to obtain what it needs. However, these categories only apply to female bees because the main purpose of pollen collection is to feed the developing young, and since male bees do not partake in caring for the young they do not collect pollen. Specialists often exist in lower numbers on the landscape and are more sensitive to change, relative to generalists, and as such are a conservation priority in fragmented areas like the Tallgrass Prairie region. In many cases, a bee's foraging behavior is generally related to their seasonality and degree of sociality.

Seasonality

Similar to other insects, bees go through metamorphosis, which is a four-stage process where the egg transforms into a larva, a pupa, and lastly an adult. During the first three stages, the bee is changing from an egg to a pupa all within the nest, a majority of which occurs during the winter season. It is only during the fourth and final stage when bees emerge as adults that we see them buzzing around. This period when adults are foraging on flowers and constructing nests is called the **active season**. In Nebraska, the active season typically runs late April through October, peaking in July and August.

The active season varies greatly between bee species and is partly related to the speed and timing of which they carry out metamorphosis. Highly seasonal bees are only active for a couple weeks and tend to be specialists, timing their emergence with the bloom period of their preferred plant. In contrast, other bees may be active for many months across multiple growing seasons. These are typically generalist foragers, utilizing whatever plants happen to be flowering on the landscape.

A bee's active season coupled with its nesting and foraging behavior typically lends insight to its degree of sociality, which is the final way wild bees are categorized.

Degrees of Sociality

A characteristic representing the majority of wild bees is their solitary lifestyle – in which there is no a colony, no division of labor, and no mass honey production. This bit of information generally gets largely overlooked, because the highly-social honey bee is our object of familiarity. Of the ~4,000 bees in the United States, the only truly social species are ~45 bumble bees, a few members of the sweat bees, and the non-native European honey bee; all others are solitary.

Social bees are those with a queen and division of labor in place, where the queen is responsible for egg laying while worker bees tend the eggs, nest hygiene, and foraging. Social bees will usually produce multiple generations within a single year, have a long active season, and are generalist foragers. For most social wild bees, like bumble bees, new queens will be reared in fall towards the end of the colony's active season, following which the original queen and all her workers die off. The new queens will overwinter as adults, in most cases, and begin a new colony the following spring.

Solitary bees on the other hand are those where a single female bee locates and tends to her own nest, collects her own nectar and pollen, and lays and tends to her own eggs without the help of other bees. Male bees are typically only seen early spring and late fall, where their sole purpose is to mate with females. Due to the amount of time and energy it takes to carry out all the latter tasks alone, solitary bees do not produce high numbers of offspring like other insects. Solitary bees will typically produce one generation in a single year, consisting of about 6 to 30 eggs. Due to this reproductive strategy, the adult female targets all of her active season efforts towards creating a protective environment for her eggs. This includes finding a safe and sturdy nest location that will be less apt to predatory attack, using proper materials to create a waterproof and antifungal protective layer, and providing the perfect combination, consistency, and amount of nutritious food. That whole process is carried out for each individual egg (Figure 3), after which the adult female dies; only rarely does the adult female live to see her offspring.

As is the case with most things in nature, there are the extremes, here social and solitary bees, and then everything in between. Some bees are classified as semi-social, where there may be one or a few adult females who focus on egg laying while others help forage and construct tunnels beneath the soil surface. Other bees may nest communally, meaning there is a single nest entrance shared by multiple females, but each constructs their own tunnels and lays their own eggs. An additional behavior is aggregate nesting, in which thousands of bees may construct individual nests in the same general location but maintain separate entrances (see Figure 4). Further, some bees are known as socially polymorphic, where the species may function socially at low altitudes where the growing season is long, but function as solitary in high altitudes where the growing season is relatively short. While there are many variations and degrees of sociality, the majority of wild bees display solitary behavior.

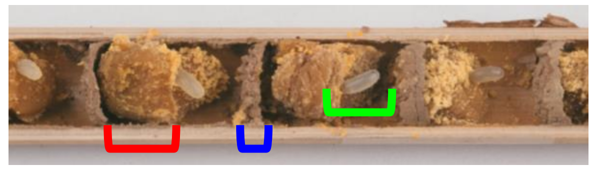


Figure 3: Bee nest inside a hollow plant stem that has been cut in half for observation. Three complete nest "cells" are seen in the frame. The adult bee creates a food mass of pollen and nectar (red), lays one egg on it (green), and then seals that section off with a substance from the environment before starting on the next provision. Here, the Blue Orchard Bee (*Osmia lignaria*) divided her sections using mud (blue). (Image: USDA-ARS)

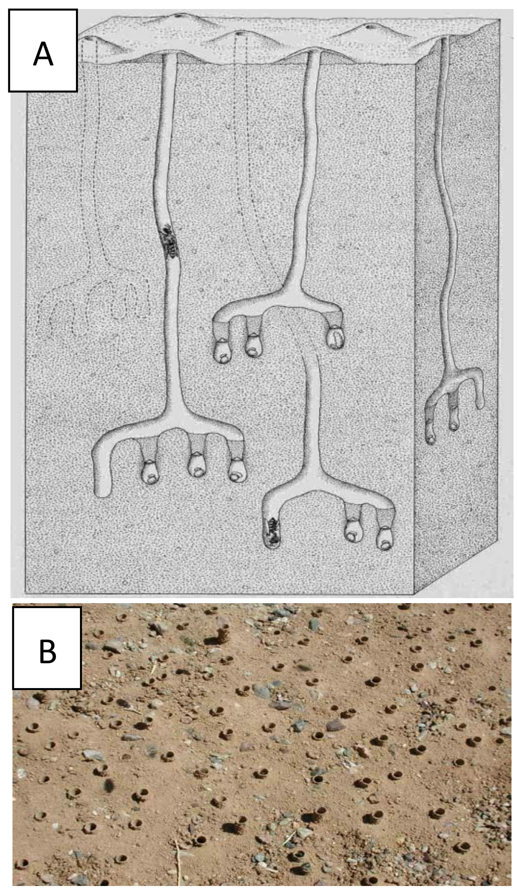


Figure 4: Ground-nesting bees exhibiting aggregate behavior. (A) Diagram illustrating tunnel architecture beneath the soil surface, and (B) soil surface peppered with nest entrances.

Introduction to Tallgrass Prairies

Tallgrass Prairie is one of three broad types of prairie found in the temperate Great Plains, along with Shortgrass and Mixed-grass Prairie (Figure 5). Tallgrass Prairie is dominated by grasses and herbaceous broadleaf flowering plants that may exceed heights of 5ft (1.5m) at maturity. Separating Tallgrass from Shortgrass and Mixed-grass prairie is its high average of annual precipitation (>750mm), and deep, fertile soils. Tallgrass Prairie once spanned from Canada to Oklahoma, comprising an area of ~600,000km^2, though over the past ~150 years this region has been severely fragmented and destroyed to a point where it is estimated that only 18,000km^2, or 1-3%, still remains in native vegetation.

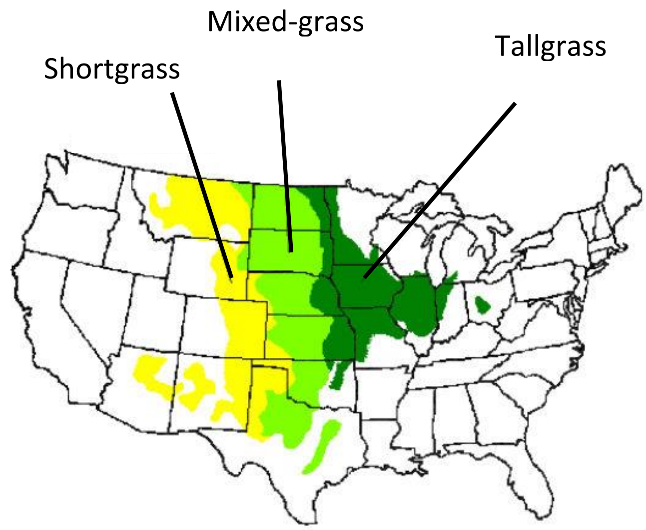


Figure 5: Map of the United States highlighting the three broad types of prairie found in North America's Great Plains. In the east, Tallgrass Prairie is characterized by average annual precipitation of >750mm, where plants exceed heights of 5ft (1.5m). In the west, Shortgrass Prairie is characterized by average annual precipitation of ~375mm, and plants reach heights of 2-3ft (0.6m). In between these two type of prairie is Mixed-grass prairie, which exhibits a transitional gradient between Tallgrass and Shortgrass averaging ~500mm of annual precipitation. (Image: USFS)

What is threatening the Prairie?

In North America, prairie ecosystems have been classified as critically endangered landscapes for the past 30 years, meaning they are at a high risk of becoming extinct.[3,4] The major factors and threats contributing to the degradation of Tallgrass Prairie are agricultural intensification, urbanization, and climate change. Collectively these factors have caused severe habitat loss, created a highly fragmented landscape, and have decreased the overall amount biodiversity present in the ecosystem.

Agriculture

Due to its rich soils and limited topographic relief, the Tallgrass Prairie region has allowed the agricultural industry to flourish and as such much of the native grassland has been, and continues to be, converted for crop production. While this intensive land use change has helped meet the growing anthropogenic need for food and energy, it has simultaneously decreased the amount of habitat available to pollinators. Additionally, the increased use and dependency of agrochemicals in these highly-cultivable landscapes, from issues like rising pest outbreaks resulting from climate change, has been identified as a factor contributing to bee decline.[5,6] The presence of these chemicals in the environment poses risk to bee health because the bees are essentially consuming toxicants or feeding them to their developing offspring. Similar to humans, a bee's level of functioning and rate of productivity tends to be lower when unhealthy. This is problematic because 35% of global food production, or 1 of every 3 bites of food, relies on pollination services (Table 1)[7]. Therefore, it is important to find a balance between habitat conservation and agriculture in order to sustain pollinators and anthropogenic needs as we move into the future.

List of Pollinated Foods		
Alfalfa	Coffee	Pear
Almond	Cranberry	Peppermint
Apple	Grape	Pumpkin
Apricot	Grapefruit	Raspberry
Blueberry	Kiwi	Sesame
Cashew	Mango	Strawberry
Cherry	Melon	Tomato
Chocolate	Papaya	Vanilla

Table 1: The listed foods are reliant upon or enhanced by pollination, although this list is by no means exhaustive.

Urbanization

Apart from agricultural intensification, urbanization is also leading to the degradation and fragmentation of prairie. Not only is habitat being lost to impervious surfaces, such as housing developments or expanding cities, but it also is being replaced by weed-free and herbicide-ridden lawn, which from a bee's perspective is no better than a slab of concrete. Managers of numerous public parks, golf courses, and schools have made an effort to supply bees with nesting or foraging resources by creating bee hotels or planting pollinator gardens. Private residents can plant their own pollinator garden and become certified in the University of Nebraska-Lincoln's Nebraska Pollinator Habitat program. This simple yet beneficial program provides a list of flowers to choose from and requires a minimum of 5 different types of flowering plants to bloom during spring, summer and fall. For more information on this program and building bee hotels, refer to *Further Resources* at the end of this article. While these efforts are beneficial for some bees, the urban expansion still decreases the amount of natural habitat and further leads to the fragmentation of prairie.

Climate Change

The last major threat to cover regarding the degradation of prairies is climate change. Prairie ecosystems reside in temperate regions, where the physical environment is characterized by its moderate amount of precipitation, hot summers, and cold winters. Though, as global temperatures are expected to continue rising, and the frequency of heat waves, drought, freeze events, and flooding are expected to increase, it is highly likely that the biodiversity of prairie ecosystems will shift. Each species, whether plant, insect, bird or mammal, will be affected differently; Some may be able to react to the changing environment and adapt to new conditions, while others may not, in which case they are at risk of becoming isolated or extinct. For example, a decline in the abundance and composition of grassland birds has already been detected in certain regions of the Great Plains, likely due to their high sensitivity of a changing environment. While these findings are specific to birds, the many other vertebrates and invertebrates that occupy these areas may be similarly affected. Species that have historically been found in Nebraska, whether birds, insects, mammals or plants, may begin to shift northwards to follow the temperature gradient they require. Likewise, species from southern states, such as Kansas or Oklahoma, may become common in Nebraska. Maintaining high levels of biodiversity in the Tallgrass Prairie will help the ecosystem absorb this potential shift in species composition, and allow the prairie to continue functioning in a healthy manner.

In addition to altering the composition of the ecosystem, the early arrival of spring is also resulting from climate change which is creating a key issue for pollinators: **phenological mismatch**. This occurs when the timing of life cycles between interacting species are no longer in sync. Here, the interacting species being flowers and bees are at risk when bloom periods and bee emergence times do not occur together. Depending on a species' ability to adapt, a flower may bloom before its pollinator has emerged, or a bee may emerge before the flower has bloomed. A generalist bee will likely forage on other available flowers, but early-spring specialist bees who rely on a single type of flower will be placed in a state of peril if they emerge before their particular flower has bloomed. Consequently, this mismatch may lead to local extinctions and further effect the level of biodiversity present in the prairie.

As one can see, prairie ecosystems and the species that reside within them continue to be diminished, degraded and destroyed from factors such as agricultural intensification, urban expansion and the effects of climate change. Together, these factors have led to a severely fragmented landscape in which remaining habitat pieces are largely separated by barriers like cities, highways or expansive crop fields, making it harder for species to adapt and find refuge in new locations as our changing climate forces them to shift. Anticipating this changing environment will be key in designing, managing and restoring Tallgrass Prairie remnants that are aimed at sustaining the biodiversity present in the ecosystem.

Restoring Habitat for Pollinators

Ecological restoration is the practice of helping an ecosystem return to a former state, especially in landscapes that have been diminished or degraded. Such efforts help protect historical landscapes, the many plants and animals that reside in them, and provide resources and experiences of value to the public.

Restoring land for a seemingly small group of animals, like pollinators, provides benefits to the entire prairie ecosystem that is rather fragile itself. This is because our wild bees, with the well-earned title of keystone species, supply pollination services that have many direct and indirect effects helping to maintain the health of the ecosystem. In return, bees are rewarded with nutritious food sources, as well as materials and locations to nest, all of which are necessary for their survival. For flowering plants, the pollination services sustain their diversity, prevent inbreeding, and allow for reproduction.

Restoring for pollinators is largely focused on diversifying the quantity and quality of flowering plants available on the landscape. This is because a more complex plant community supports a more complex bee community, and other animals can utilize plants for food and shelter. Additionally, the root systems of an established plant community help to cycle nutrients within the soil, prevent erosion, and improve the water quality of creeks and streams. The challenge then comes in deciding which combination of flowering plants will establish a community that is most supportive of bees.

Flowers have evolved many characteristics that make themselves attractive to bees. This includes variation in color, shape, scent, quality, and quantity of nectar and pollen, as well as bloom period.

The visible spectrum of a bee is in the ultraviolet wavelength, meaning blues and violets really stand out on the grass-dominated prairie; whereas reds and oranges do not. Research has demonstrated bees are highly likely to visit blue, violet, white, and yellow flowers. And while red flowers are not particularly attractive to bees, they are tailored to suit other pollinators like hummingbirds.

The sizes and shapes of flowers also play a role in attracting bees. Generally, the more complex a flower's structure is, the more time and energy a bee will need to spend foraging for its reward. For example, a sunflower with openly exposed nectar and pollen may attract more pollinators than an iris. However, the physical structures a bee is equipped with will determine which flowers it is most efficient in pollinating. Some bees transport pollen on their hind legs while others use the underside of their abdomen; some have stiff hairs on their face that help dislodge pollen and others do not. The size of a bee also determines which flowers it can forage on. For example, smaller bees are better equipped to crawl inside small tube-shaped flowers while larger bees are better equipped to maneuver heavy floral structures when foraging. Therefore, to support a high diversity of bees on the prairie, it is important to establish a plant community that has flowers of varying shapes and sizes.

Along with color, shape, and size, flowers also exhibit diversity in their production of nectar and pollen, wherein some may produce higher or lower quantities or qualities of either. Intuitively, one might think bees would forage for high quality pollen whenever possible, however this is not always the case. For example, in areas where many parasites coexist, researchers have observed bees preferring to supply their offspring with low quality pollen. These parasites grow and develop on the same food mass intended for developing bee, but the low-quality pollen is not nutritious enough to support the parasite, thus aiding in the survival of the bee. Therein, establishing a diverse plant community that ranges in quantity and quality of pollen and nectar production will further support the diverse foraging needs of bees.

The last major consideration, and one of the most important, when restoring for pollinators is to diversify flowering plants by their bloom period. To support bee communities, it is necessary to have flowers blooming on the landscape during all three growing seasons, namely spring, summer and fall. As of recently, researchers have become aware that many natural landscapes are lacking sufficient blooms in the spring, meaning early season bees are limited in their available resources. In addition to covering all growing seasons, it is important that each season has similar amounts of floral resources. This ensures enough food and nesting resources are available to bees throughout their various active seasons.

To summarize, restoration efforts aimed at pollinator conservation will need to consider floral diversity. This includes having flowers on the landscape that vary in color, size, shape, and quantity and quality of nectar and pollen, as well as equal dispersion across growing seasons (Figure 6). When a diverse floral community is established, it will support a diverse bee community, where the mutualistic trade-off of pollination services for nutritious food and nesting resources collectively sustain the health of the ecosystem.

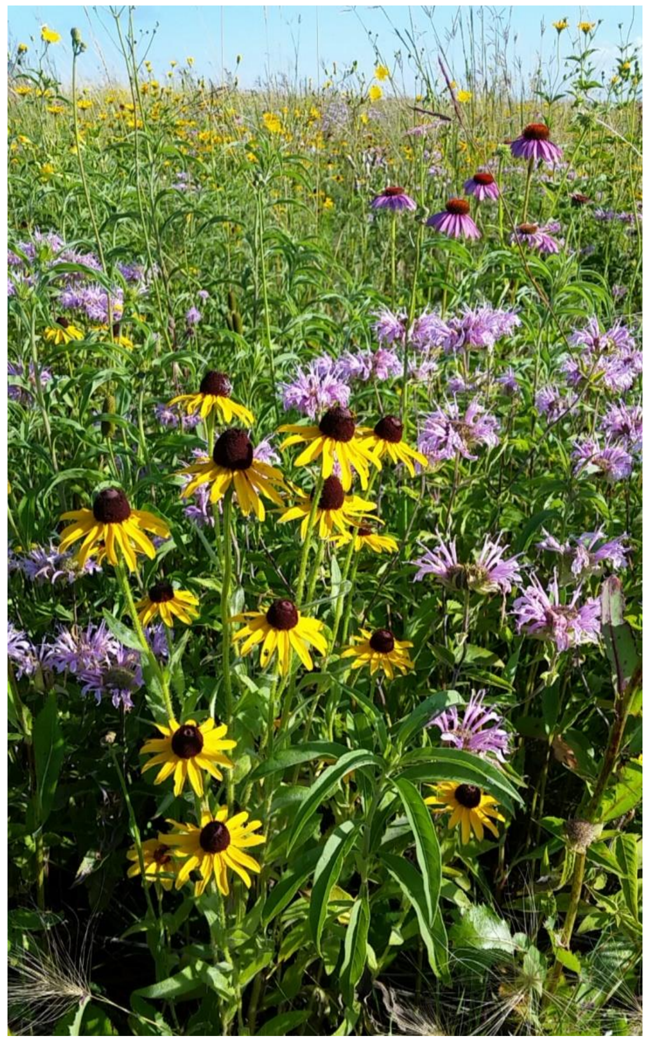


Figure 6: Diverse floral resources on a prairie that is in its 5th year of being restored and managed to promote pollinator communities. (Image: Katie Lamke)

Managing for Pollinators

Along with restoration efforts, management regimes also effect the presence and diversity of bee communities on a given prairie. However Periodic disturbance is foundational in maintaining a prairie's high level of biodiversity, as it how they were naturally maintained long before humans intervened. Whether the disturbance is achieved through prescribed burning, haying, or grazing, these techniques help suppress non-native plant species (including herbaceous and woody plants) while encouraging the growth of native grasses and wildflowers. Management regimes also effect the presence and diversity of bee communities on a given prairie. However, due to the vast variation in bees, not all species are affected in the same way. For example, above-ground nesting bees may be harmed more than below-ground nesting bees when a faced with a prescribed burn. In addition to contrasting bee responses, the actual response for many bees in regards to management practices are still largely unknown making it difficult to design generalized best management practices. However, there are some key factors to incorporate into a management plan aimed at supporting pollinators.

The formation of any successful management plan begins with setting measurable, long-term goals that take into account the intensity and timing of practices best fit for pollinators. In selecting management techniques, along with appropriate timing and intensity of implementation, local extension offices should be consulted to discuss available options and to design ways from which to measure progress. Again, while there is no single management practice suited to promote all pollinators, there are techniques that align best with the various land types and long-term goals. Current practices for pollinator conservation generally set up a 3- to 5-year rotational management regime, where the land is divided and managed in zones. The particular zone being managed should not be more than ⅓ of the total area, as to allow pollinators a constant refuge with food and nesting resources. These refugia zones also allow pollinators the ability to recolonize the disturbed zones throughout the rotation cycle.

Prescribed Burning

Fire is an important factor in maintaining a prairie because it helps to clear accumulated dead vegetation, suppress invasive plant species, and create a spatially variable distribution of bare ground and plant cover. Many plants that are native to the prairie have evolved to be fire-tolerant, meaning they are positively affected by fire while weedy non-natives and encroaching young trees are controlled.

For pollinator conservation, cool-season burns are generally recommended, such as those in early spring or late fall during the pre- and post-growing seasons. This strategy invites more wildflowers to grow than if covered in a dense layer of dead vegetation, and avoids removing a bee's necessary resources during peak foraging times. Additionally, cool-season burns tend to unevenly disturb the landscape, in turn leaving behind heavy fuels and unburned patches that act as important refuge areas for bees and other prairie inhabitants. If heavier fuels such as stumps or snags can exist on the landscape without being hazardous, they will serve as a high-quality resource for above-ground nesting bees.

Haying

Haying is another common approach that can help maintain levels of biodiversity in prairies by cutting back non-native plants that may compete with native warm-season plants. Similar to burning, it is best to hay during the pre- or post-growing seasons when managing for pollinators. This ensures that floral resources are available during the various active seasons of bees. An additional consideration is to cut as high as possible in order to maximize the number of hollow stems available to above-ground nesters. When the option is available, not mowing ditches or edges can also be beneficial for above-ground nesting bees that have either created a nest within the present stems or may utilize the stems in the following season.

Grazing

Grazing as a management practice can be both harmful and helpful in terms of pollinator conservation. The outcome depends upon the particular bee species, coupled with the intensity and timing of grazing. The most favorable strategy to date is to design a rotational grazing plan. Rotational grazing forms a compromise between bees that will be positively affected by grazed areas, while leaving refugia for those subject to a negative effect.

In summary, the key to managing for pollinators are to (1) establish zones to be rotationally managed in a 3-5 year cycle and (2) manage pre- and post-growing season to allow for maximal floral and nesting resources during a bee's active season. For more detailed pollinator conservation guidelines regarding Nebraska management practices and programs see *Further Resources*.

Bees of Nebraska Prairies

Throughout the world there are 7 groups of bees, which are referred to as "families." One family is restricted to Australia while the remaining 6 all occur in North America, only 5 are common in our area: Mining bees (Family Andrenidae), the Bumble, Carpenter and Long-horned bees (Family Apidae), the Cellophane and Yellow-faced bees (Family Colletidae), the Green Metallic and Sweat bees (Family Halictidae), and the Leafcutter, Mason and Wool Carder bees (Family Megachilidae). The following pages provide additional detail on each family's diversity, degree of sociality, nesting habits, and diet preferences. All photos were taken by Sam Droege out of the US Geological Survey Bee Inventory and Monitoring Lab.

Mining Bees

Family: Andrenidae

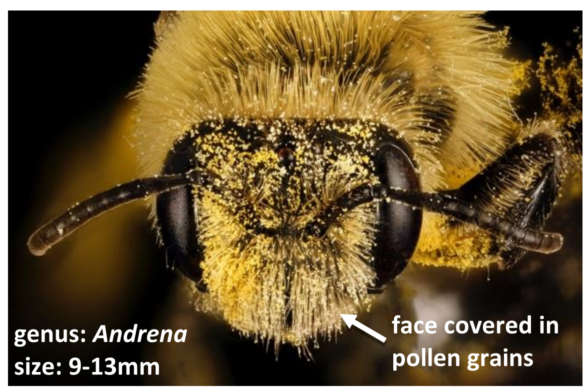
Diversity: Mining bees are a very diverse family, accounting for nearly one third of all bee species found in the United States.

Sociality: All members of this family are solitary, though occasionally will display communal behavior in which multiple females share a nest entrance but tend to their own tunnels beneath the soil surface.

Nesting: Mining bees are ground-nesters, most often found excavating tunnels within the first 2 feet of the soil surface.

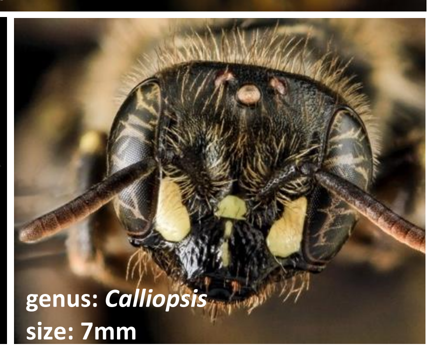
Pollen Foraging: Many specialist bees occur in this family, displaying preference for one or a select few type of floral resources.


genus: ***Andrena***
size: 9-13mm



genus: ***Andrena***
size: 9-13mm


genus: ***Perdita***
size: 5mm


genus: ***Calliopsis***
size: 7mm

Bumble, Carpenter, and Long-horned Bees

Family: Apidae

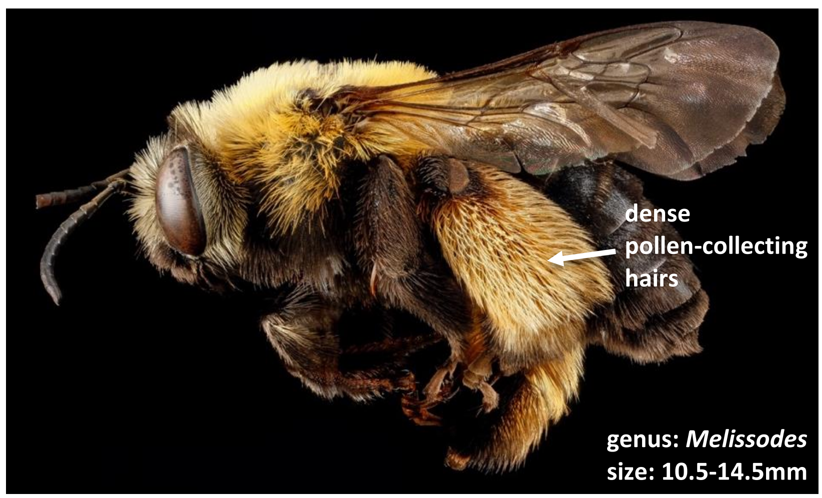
Diversity: This family expresses great diversity both morphologically and behaviorally. There is no dominant character linking the members of this family, they are vastly different in size, color, degree of sociality, nesting habits and foraging preferences.

Nesting: Nesting habits occur above and below ground, and include both excavators, utilizing substrates such as soil, wood or stems, as well as renters, who locate pre-existing cavities like old mouse burrows or empty beetle-bored tunnels.

Sociality: Levels of sociality in this family range from highly social, such as bumble and honey bees, to completely solitary species, with many others existing somewhere in between the two extremes.

Pollen Foraging: This family is comprised of a good mix of specialist and generalist foragers. Many solitary species are specialists, exhibiting preferences for plants such as the aster (Asteraceae) and squash (Cucurbitaceae) families. Inversely, social species exhibit generalist behavior utilizing any floral resource to help sustain their colony's active season.

genus: ***Bombus***
size: 9.5-25mm



genus: ***Melissodes***
size: 10.5-14.5mm

genus: ***Ceratina***
size: 6-8mm

genus: ***Melissodes***
size: 11.5-14.5mm

Cellophane and Yellow-faced Bees

Family: Colletidae

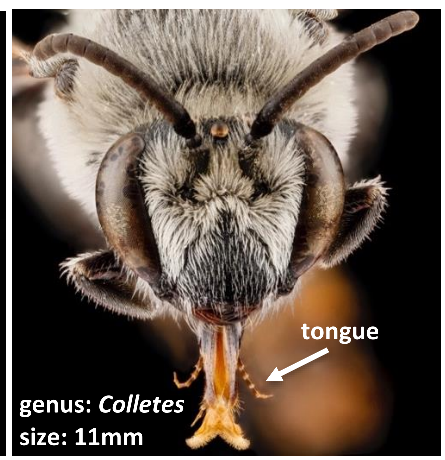
Diversity: Within this family two types of commonly found bees are the Cellophane bees (genus *Colletes*) and the Yellow-faced bees (genus *Hylaeus*) that are strikingly different in appearance and behavior.

Nesting: Nesting habits occur above and below ground, including both soil excavators as well as those utilizing small pithy stems or pre-existing cavities. Some soil-dwelling species (genus *Colletes*) are known to line their nest with a cellophane-like secretion which creates a waterproof, antifungal and antibacterial environment for their egg to safely develop in.

Sociality: All members in this family are solitary.

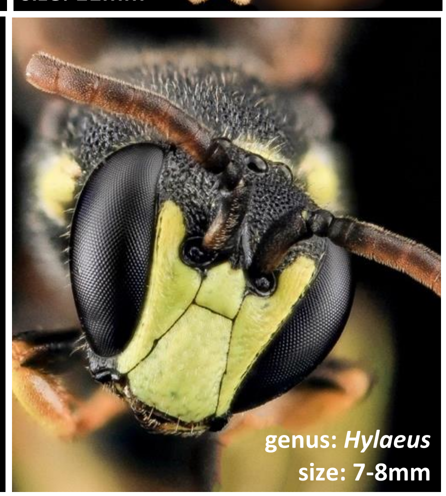
Pollen Foraging: While there are generalist species within this family, a large number also exhibit specialist behaviors. Unlike most bees who transport pollen externally, the Yellow-faced bees transport pollen internally. The female essentially consumes pollen and nectar, holds the mixture in her crop, and later regurgitates the liquid mixture in her nest, and lays her buoyant egg on top of it.

genus: *Colletes*
size: 11mm



genus: *Colletes*
size: 11mm

genus: *Hylaeus*
size: 7-8mm



genus: *Hylaeus*
size: 7-8mm

Green Metallic and Sweat Bees

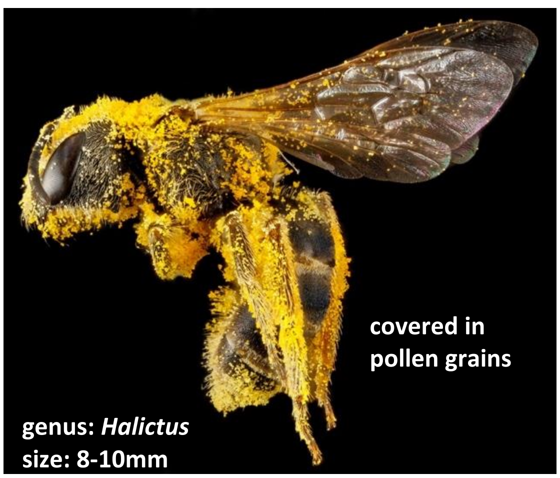
Family: Halictidae

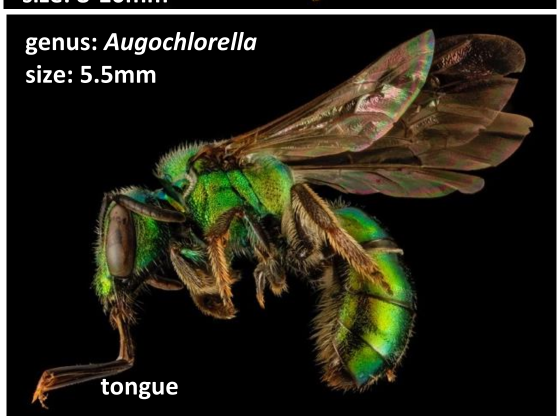
Diversity: While this family does not maintain high species diversity, relative to the other families, they generally dominate in number of individuals existing on the landscape.

Nesting: Green metallic and sweat bees all nest in the ground. In a social or communal setting, a female may often be seen protruding her head out of the nest entrance, acting as a guard.

Sociality: Members of this family display a wide range of social behavior including solitary, communal, semi-social and social.

Pollen Foraging: Many species within this family are generalist foragers and will utilize a wide variety of available blooms. This aligns with their sociality, in that many social species produce multiple generations in a single season and need continuous floral resources to sustain the health of the colony.





Leafcutter, Mason, and Wool Carder Bees

Family: Megachilidae

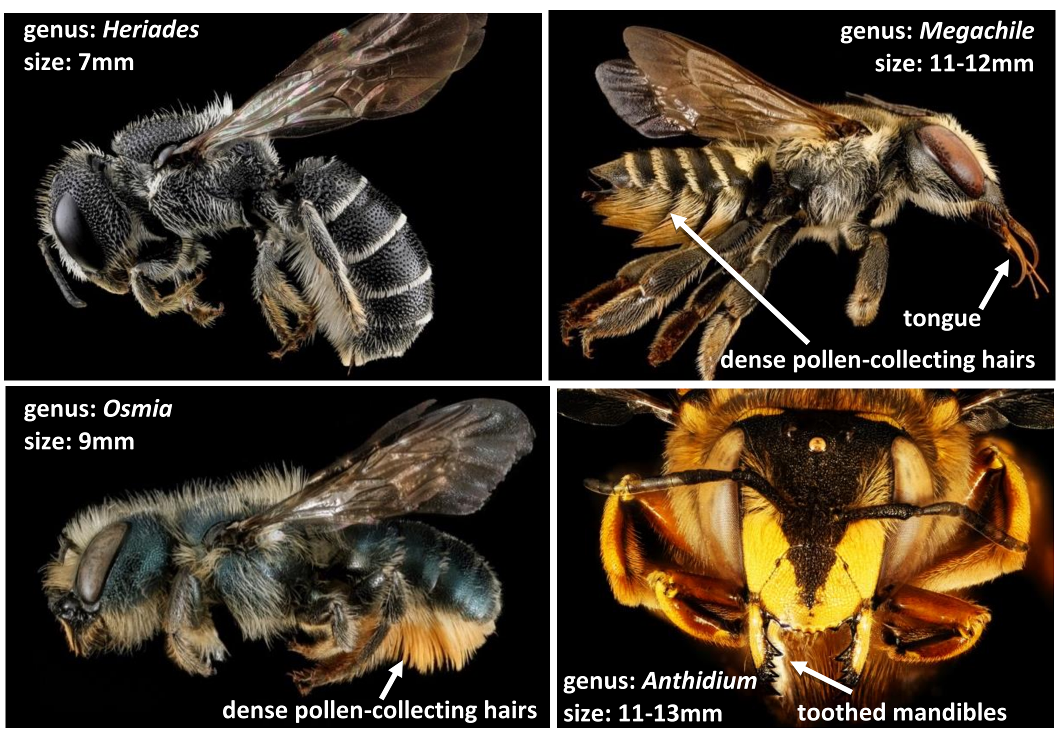
Diversity: Much diversity exists within this family, in terms of appearance, and the variety of unique nesting habits.

Nesting: With the exception of a few species, the vast majority of bees in this family will nest above ground. Nests may be constructed in stems, galls, existing holes in fence posts or cement cracks, be a free-standing nest, or they will occupy a hole in a man-made “bee hotel” (see *Further Resources* for instruction).

Leafcutter bees (genus *Megachile*) prefer to collect leaf pieces or flower petals, mason bees (genera *Osmia*, *Heriades*) may use resin, clay, mud or pebbles, and wool carder bees (genus *Anthidium*) will generally scrape plant fibers to construct their nest. Many bees in this family are equipped with robust mandibles that are outfitted with teeth, which together allow for higher efficiency when collecting nesting material.

Sociality: All species within this family are solitary.

Foraging: Many members of this family are specialist foragers, and unlike most bees who transport pollen on their hind legs, Megachilids carry pollen on the underside of their abdomen.



Further Resources

Building Wild Bee Hotels
http://extensionpublications.unl.edu/assets/pdf/g2256.pdf

Nebraska Pollinator Habitat Certification
https://entomology.unl.edu/pollinator-habitat-certification

Pollinator Habitat Programs for Public Land Managers in Nebraska
(Kayla's NebGuide Link)

US Geological Survey Pollinator Library
https://www.npwrc.usgs.gov/pollinator/home

Xerces Society: Managing Habitat for Pollinators
https://xerces.org/pollinator-conservation-managing-habitat/

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Appendix A. Prairie Corridor on Haines Branch Plot Descriptions

Plot Number	Location	Parcel Size (ha)	Ch. 3 Treatment Group	Description	Management
1	40.71197, -96.85285	1.48	Remnant	Hay meadow connected to alafalfa field	Hayed: Jun 2017, Sep 2017, Apr 2018, Jul 2018
2	40.71008, -96.84806	1.67	Remnant	Hay meadow connected to alafalfa field	Hayed: Jun 2017, Sep 2017, Apr 2018, Jul 2018
3	40.68189, -96.8213	5.44	Remnant	Hay meadow, rotational burn/ graze	Hayed: Sep 2017, Apr 2018, Aug 2018
4	40.68487, -96.85586	9.73	Remnant	Remnant prairie, rotational pastureland	Burned: Oct 2018; Grazed: May 2017
5	40.78093, -96.776	6.48	Low Diversity	Remnant prairie, rotational pastureland	Burned: 2012; Grazed: 2013, 2016; Sprayed: Fall 2017 (2, 4D amine)
6	40.77675, -96.78162	5.5	NA	Pastureland	Not Surveyed in 2018; Burned: 2009, Apr 2010, 2013; Grazed: 2013, 2016; Sprayed: Fall 2015 (Plataeu)
7	40.78368, -96.79383	31	Low Diversity	Pastureland, dominated by leafy spurge	Burned: Jan 2009, Apr 2011, Apr 2018; Grazed: 2014, 2015, Jun 2017, May-Sep 2018; Sprayed: Fall 2014 (Plataeu)
8	40.77834, -96.79394	31	Low Diversity	Pastureland, dominated by leafy spurge	Burned: Apr 2010, Apr 2011, Apr 2018; Grazed: 2014, 2015, Jun-Jul 2017, May-Sep 2018; Sprayed: Fall 2014 (Plataeu)
9	40.7059, -96.83163	8.16	Low Diversity	Established prairie, dominated by cedar; east edge bordered by Spring Creek Tributary Riparian area	Seeded: 1989, Low Diversity CRP (5 warm season grasses)

10	40.70567, -96.82721	9.2	Remnant	Virgin prairie, Spring Creek tributary runs through middle	Heavily hayed until 2014; Tree removal in 2014/15
11	40.70607, -96.82411	13	Low Diversity	Established prairie	Seeded: 1989, Low Diversity CRP (5 warm season grasses)
12	40.68391, -96.84137	16.3	High Diversity	CRP	Seeded: 2009
13	40.75727, -96.83243	6.81	Low Diversity	New restoration	Seeded: 2017
14	40.73669, -96.85077	9.88	High Diversity	Young restoartion; south edge bordered by riparian corridor, east edge bordered by cemetery	East half burned in 2018 converted into Plot 21, unburned west half surveyed as Plot 14 in 2018; Seeded: 2014, High Divesity Local Ecotype
15	40.73448, -96.85307	3.4	High Diversity	Young restoartion of old soybean field; north edge bordered by riparian corridor	Seeded: 2015, High Diversity Local Ecotype
16	40.70593, -96.81895	6.74	Low Diversity	Primarily cool-season non-native grasses	Burned: Spring 2017; Hayed: Apr 2018; Seeded: 2017, broadcast dormant overseeding of burned area Woody debris removal 2016/17 Low maintenance prior to City acquisition
17	40.68622, -96.85029	23	Remnant	Remnant prairie, rotational pastureland	Grazed: May 2017, May 2018
18	40.68527, -96.84662	23	Remnant	Remnant prairie	
19	40.78359, -96.78585	10.6	Low Diversity	Pastureland, dominated by annual ragweed	Burned: Winter 2016; Grazed: 2014, 2015; Sprayed: Fall 2014 (Plataeu)
20	40.78375, -96.78046	7.91	Low Diversity	Remnant prairie	Burned: Winter 2016; Grazed: 2013, 2016, May 2017; Sprayed: Fall 2014 (Plataeu), Fall 2015 (Plataeu)

21	40.73596, -96.84941	4	NA	Young restoration of old soybean field; south edge bordered by riparian corridor, east edge bordered by cemetery	Not Surveyed in 2017 (east half of Plot 14); Burned: 2018 Seeded: 2014, High Diversity Local Ecotype

Appendix B. Bee Identification and Life History Sources

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