Are managed honey bees (*Apis mellifera*) altering native pollinator diversity, or their interactions with plants in Western Canadian grasslands?

by

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Abstract

The grasslands region of southern Alberta, Canada, is dominated by agricultural activity, and approximately 75% of native grasslands have been lost to development. Honey bees (*Apis mellifera*) were introduced about a century ago, and today they are used to facilitate the pollination of crops; in one season, the region supports approximately 3.15 billion individuals. These super-generalists have been known in other places to compete with native pollinators, and may contribute to the decline of wild pollinator diversity and richness. Mounting evidence has also suggested that honey bees may alter the structure and function of plant-pollinator network interactions in a wild pollinator community, which may affect its resilience to perturbations and persistence into the future. This study examined the effects of honey bee abundance on native grassland pollinator communities by experimentally introducing honey bee hives to grasslands at the U. of A. Rangeland Research Institute's Mattheis Research Ranch in southern Alberta, where pollinator abundance and diversity and plant-pollinator interactions over two summer seasons were sampled. Eighteen transects, at distances of 100 m, 500 m, and 5000 m from three clusters of honey bee hives, were established and floral insect visitors at each transect were sampled almost weekly. Flower species and flower visitors were then identified, and their interactions were compiled into plant-pollinator networks, from which species abundance, diversity, species composition, and network metrics related to network stability, structure, and resource use overlap, were analyzed. My findings indicate that honey bees did not affect wild pollinator abundance, richness, diversity, or species composition. Instead, flower species richness generally explained the variation in pollinator abundance, richness, and diversity. Additionally, honey bees impacted network structure by decreasing interaction evenness, and affected resource use overlap by increasing plant and pollinator functional complementarity. However, these network structural changes were due mostly to the added honey bee-plant interactions, and not to honey bees causing changes in how native pollinators interacted with plants. This study demonstrates that honey bees may not negatively impact native plant-pollinator communities in all contexts, and that, despite influencing interaction network structure and floral resource use, they may not affect the diversity of wild insect pollinators or their interactions with plants. Although caution should be used in generalizing these results in other regions, evidence suggests that honey bees are not a major threat to the wild pollinators in this area, at least in regard to changes to their diversity or interactions.

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The Grassland Natural Region of southern Alberta rests within the prairies of Canada, and includes both Mixedgrass and Dry Mixedgrass Subregions, further divided into grasslands, wetlands, badlands, sand dunes, agricultural cropland and semi-natural rangeland. This region is not known to be especially speciose in terms of vertebrate wildlife (Alberta Environmental Protection, 1997), but it supports a notable diversity of insect pollinators. Wild bees in the prairie ecozone represent 48% of Canada's total bee fauna, and 23% of the grassland species are not found elsewhere in Canada (Sheffield et al., 2014). There is a diversity of other pollinators as well, such as butterflies and moths, flies, and pollinating beetles (Giberson & Cárcamo, 2014a, 2014b). Unfortunately, this region is under intense strain: approximately 50% of the land is used for crop production alone (Alberta Parks, 2015), and approximately 75% of the native grassland has been lost to development (CPAWS, 2020). This poses a risk to the diversity of wild pollinators, which contribute to the fitness of native flowering plants (Biesmeijer et al., 2006; Ollerton et al., 2011; Ssymank et al., 2008), as well as providing pollination services to flowering crops.

Pollination is an essential ecosystem service for agricultural crops provided by wild and managed pollinators, where pollination can increase crop production up to 90%, depending on the crop (Klein et al., 2007). In Alberta, pollination services provided by managed pollinators can increase canola production by up to 30% (Morandin & Winston, 2005), which is significant for a region that supplies a quarter of Canada's total canola production (CCC, 2020). This desire for pollination services has increased the demand for managed pollinators over time, producing the now 314,800 managed honey bee colonies in Alberta (Emunu, 2020). Commercial beekeepers in Alberta, which produce 80% of Canada's honey and 70% of Canada's honey bees, can have greater than 1000 colonies (Melhim et al., 2010). It is conceivable that beekeepers add a minimum of 3.15 billion honey bees to the Alberta grasslands per season, excluding any feral populations that exist. However, a diversity of pollinators improves crop pollination, and honey bees are not the most efficient pollinators (Albrecht et al., 2012; Woodcock et al., 2013). Furthermore, with plans to double 2012 canola production by 2025 (CCC, 2020), the demand for honey bees will only intensify their presence on the landscape. This is a potential concern for wild pollinator conservation, as honey bees have been found to negatively impact wild pollinators.

Some studies have suggested potential negative effects of honey bees on wild pollinators, as well as effects on native plants (Geslin et al., 2017; Ropars et al., 2019). Honey bees are thought to impact specialized native pollinator species with a narrow niche range by increasing exploitative competition; alternatively, they may impact native generalist species with high shared resource overlap through competition (Waser & Ollerton, 2006). Studies have found effects of honey bees on wild bee fitness (Walther-Hellwig et al., 2006), diversity and abundance (Forup & Memmott, 2005; Nielsen et al., 2017), foraging behavior and niche breadth (Goulson & Sparrow, 2009; Lindström et al., 2016). Furthermore, honey bees have been found to decrease the densities and visitation rates of non-bee insect pollinators (Lindström et al., 2016; Ropars et al., 2019).

Currently, pollinator conservation efforts often prioritize honey bees over wild pollinators, in response to recent honey bee declines and their value to agriculture (Geldmann & González-Varo, 2018). In some major Alberta cities, policy has shifted to allow urban beekeeping to promote pollinator conservation (Colla & MacIvor, 2017). However, honey bees may outcompete native pollinators for limited resources in urban areas, where mass-flowering crops are not available (Geldmann & González-Varo, 2018). This, then, may be an example of confused conservation messaging: if honey bees impact native pollinators, then their promotion in urban centres will be harmful.

Interactions between pollinators and the plants they visit can be thought of as a network that can be examined for structural changes due to honey bees (Delmas et al., 2019). The structure of a plant-pollinator network is thought to relate to the community's resilience, the rate at which a community returns to a steady state following perturbations, and the likelihood of secondary extinctions after initial species loss (Bastolla et al., 2009; Peterson et al., 1998). Recently, studies have found that honey bees, being widely polylectic, change the stability and functionality of a native plant-pollinator network by altering existing interactions and acting as new, central nodes (Mallinger et al., 2017; Valido et al., 2019). They may increase the "cohesiveness", the level of connectedness within a network, or the stability of the mutualistic network by modifying network properties such as nestedness (the tendency for a core of generalist species to interact among themselves, and for specialists to interact with only the most generalist species) and modularity (the extent to which interactions are clumped into modules with many interactions within them and few interactions between them) (Bascompte et al., 2003; Bastolla et al., 2009). For mutualistic networks, high nestedness and low modularity have been theoretically demonstrated to increase stability (Thébault & Fontaine, 2010). Whether or not increases in network stability conferred by incorporation of "exotic" or non-native species, like the honey bee, are desirable from a conservation perspective is an open question; an increase in stability metrics, like nestedness and connectance, may mean that the exotic species is then hard to remove, or its removal causes species loss that has a cascading effect (Campbell et al., 2012; Heleno et al., 2012). So far, the few studies on honey bee effects on network structure have not all found that honey bees change modularity and nestedness in a consistent direction (Campbell et al., 2012; Santos et al., 2012; Valido et al., 2019) and all these studies have been correlative rather than experimental, so it is hard to know whether honey bees are in fact causing these changes.

Changes to network metrics relating to resource use overlap can also indicate whether honey bees are creating competitive pressure on native species. Finding direct evidence of competition between honey bees and any other single pollinator species is difficult, and so far has only been done for bumble bee species that nest in nest boxes, and so can be moved around (Elbgami et al., 2014; Thomson, 2004), or in cage experiments (Hudewenz & Klein, 2015). Because pollinators tend to have large foraging ranges, confounding variables are difficult to control, and survival and reproductive success is difficult to observe for most pollinator species. Assessing competitive effects of honey bees on all pollinators in a community by assessing changes to their fitness is simply not tractable. However, assessing changes to network metrics related to number and frequency of interaction partners (resource use) can give insight into immediate effects of honey bees on species interactions across the community, before these competitive effects translate into changes in diversity through native species loss. Functional changes to the network, like those that indicate resource overlap between pollinators and plants, are immediately observable (Magrach et al., 2017). If changes are observed, then competition is likely occurring. In a region already at risk from habitat loss and agricultural activity, the addition of more honey bees may pose concern for native pollinators. In comparison to habitat loss and agricultural activity, honey bee keeping on native grasslands would be an easier potential threat to native pollinators to address, so it is worth determining whether it is indeed a threat in this region.

In this thesis, I will examine whether honey bee abundance has any effect on wild pollinator abundance, diversity, or the diversity of their interactions; and, similarly, if honey bee abundance has any effects on the stability and function of the native plant-pollinator network. In Chapter 2, I assess this by examining differences in richness, diversity, abundance, species composition, and the diversity of plant-pollinator interactions between sites 100 m, 500 m, and 5000 m away from honey bee hives. In Chapter 3, I assess this by examining differences in network metrics related to network structure and stability, and resource overlap between pollinators, and pollinator overlap between plants, from the networks constructed from interaction data from sites at these different distances from honey bee hives.

Chapter Two: Diversity, abundance, species composition and interaction diversity of a native Canadian grassland pollinator community are resilient to the introduction of honey bees

Introduction

With the widespread use of managed honey bees for honey production and crop pollination in parts of the world where they are not native, many studies have suggested that high honey bee densities may have negative effects on wild pollinator diversity through competition for floral resources such as nectar and pollen (Badano & Vergara, 2011; Mallinger et al., 2017). A high diversity of wild pollinator species within an ecosystem can promote the resilience (or capacity to absorb disturbance and remain the same; Walker et al., 2004) of the community against major changes, including extirpations (Peterson et al., 1998) and can provide greater and more stable crop pollination ecosystem services than can any single pollinator species (Albrecht et al., 2012; Garibaldi et al., 2013; Rader et al., 2016). Additionally, plant-pollinator interaction webs with high pollinator functional diversity can protect ecosystem function, promote plant diversity, and support an ecosystem's persistence into the future (Fontaine et al., 2006). Regarding diversity loss through competition, it may be that specialized species, with a narrow niche range, are less flexible in shifting their resource use, and are therefore at risk from exploitative competition with introduced super-generalist pollinators, like honey bees, which interact with many species and take on a central role in the community interactions (Waser & Ollerton, 2006). Additionally, native generalist species are thought to be at risk from greater shared resource overlap, and therefore more direct competition with introduced super-generalists (Waser & Ollerton, 2006).

Together, this suggests that honey bees may negatively affect both generalists and specialists in wild pollinator populations.

Bumble bees, with similar body sizes and foraging habits to honey bees, may be especially subject to honey bee competition (Wojcik et al., 2018). While bumble bee and honey bee resource overlap appears to be low outside periods of resource scarcity (Thomson, 2006), honey bee abundance has been shown to negatively affect bumble bee fitness (Elbgami et al., 2014; Thomson, 2006) and to be negatively correlated with bumble bee abundance (Forup & Memmott, 2005; Nielsen et al., 2017) and foraging behaviour (Walther-Hellwig et al., 2006). Honey bees may also impact solitary wild bees and non-bee insect pollinators. Honey bees outperform solitary bees, bees that do not live in social caste systems with labour division, in pollen collection (Cane & Tepedino, 2017).They can also affect flower visitation, niche breadth, and reproductive output of solitary bees (Hudewenz & Klein, 2015). Lindström et al. (2016) found that honey bees depressed the densities of a variety of fly groups in oilseed rape, despite a high density of floral resources. Ropars et al. (2019) also noted a negative correlation between honey bee abundance and flower visitation rates for large-bodied bees and beetles, but not other groups, such as hover flies or butterflies.

However, despite the potential for negative effects of honey bee abundance on wild solitary bee and non-bee insect pollinators, not all studies concur. In their review, Mallinger et al. (2017) found that, in studies regarding competition, 53% reported negative effects of honey bees, while 28% reported no effect and 19% had mixed effects. Competitive effects on wild pollinators were lower in studies where honey bees were within their native range (Mallinger et al., 2017).

Herbertsson et al. (2016) found that honey bee abundance was associated with the suppression of bumble bee density in homogenous landscapes, but not in heterogenous landscapes, though Zink (2013) found the opposite. Tscharntke & Steffan-Dewenter (2000) also found no effect of honey bees on richness or abundance of wild bees. Overall, the effect of honey bees seems to vary temporally, regionally, and by landscape, and therefore appears to be context-dependent.

Honey bees may also affect plant-pollinator interaction richness (the number of unique plant-pollinator species pair interactions) and interaction diversity (the number and relative frequency of individual plant-pollinator interactions), calculated using Simpson's diversity index, which may have implications for not only native pollinators, but their native plant mutualists. Interaction diversity can be compared across communities to interpret of patterns of unique interaction loss, helping to gauge the state of the system and its relationships (Dyer et al., 2010). In an experiment performed within a national park on Tenerife, Valido et al. (2019) determined that honey bees had a negative effect on interaction richness in their plant-pollinator network but did not impact interaction diversity.

Honey bee effects may also vary temporally, as populations fluctuate. As pollen and nectar resources become increasingly available, the population of a honey bee colony in Canada grows to a peak in summer, reaching between 50,000-80,000 individuals per hive (Canadian Honey Council, 2018). At its peak, a strong honey bee colony can procure the amount of pollen needed to produce 100,000 progeny of an "average-sized solitary bee", *Megachile rotundata* (Cane & Tepedino, 2017). Little work has been done on seasonal or temporal effects of honey bee colony size on wild pollinators, with some exceptions. Walther-Hellwig et al. (2006) looked at the effect of honey bee density throughout the day, when a higher density of honey bees was associated with the depression of bumble bee density. Additionally, during the summer months of July and August, Wignall et al. (2020) found that exploitative competition increased between bumble bees and honey bees. Honey bees may have strong competitive effects on wild pollinator species that have a short emergence window that coincides with peak honey bee colony size. Furthermore, because non-bee pollinator groups, such as flies, beetles, and butterflies, are valuable pollinators alongside bees (Rader et al., 2016, 2020; Ssymank et al., 2008; Valido et al., 2019), it remains important to investigate whether honey bees are also affecting these groups during the summer season when the potential for competitive pressure is highest.

Alberta's grasslands, predominantly mixedgrass and dry mixedgrass, are an agricultural and livestock grazing region where approximately 50% of the land is used for crop production alone (Alberta Parks, 2015), and where approximately 75% of the native grassland has been lost to development (CPAWS, 2020). Consequently, this area has a high apiary density for crop pollination and honey production (Melhim et al., 2010), and honey bees have already been present in the region for at least a century (Philpott's Honey Producers, 2016). Honey bee colonies comprise between 10,000 to 50,000 individuals. By comparison, wild bumble bee colonies comprise between 70-1800 individuals, and most other wild bees in the region are solitary, without colonies (Cueva del Castillo et al., 2015; Sheffield et al., 2014). There were approximately 314,800 managed honey bee colonies in Alberta in 2019 (Emunu, 2020) suggesting that a minimum of 3.15 billion honey bees are added to the region annually, with substantial increases in mid-summer. Additionally, the greatest diversity of wild bees in Alberta is found within the prairie ecozone (Sheffield et al., 2014), and with the current intensity of agricultural activity and increasing use of honey bees, the need for investigation of any potential effect of honey bees is imperative.

In this study, my objectives were to 1) determine whether honey bee abundance impacts the species richness, diversity, abundance, or species composition of other pollinators; 2) determine whether honey bee abundance impacts the richness and diversity of plant-pollinator interactions; 3) determine whether honey bee abundance affects the richness, diversity or abundance of certain higher taxa more than others; and 4) determine whether effects of honey bees are greater when honey bee colony size is largest, and whether this differs for different higher taxa.

Methods

Field site selection

This study took place in the grassland region of Alberta, on the University of Alberta's Mattheis Research Ranch. This region is characterized by dry mixedgrass rangeland, agricultural cropland, salt flats, sand hills, riparian areas, badlands, and wetlands. Low annual rainfall (approximately 300 mm annually) in this area may limit floral resources for pollinators in some years. Here, it was expected that the effects of honey bees, if any exist, would be apparent.

I established eighteen 30 x 2 m transects at distances of 100 m, 500 m, and 5000 m from three clusters of honey bee hives (48 hives, 32 hives, and 16 hives, respectively) (Figure 1), attempting to create honey bee densities similar to those near commercial apiaries. Eastern Irrigation District information indicated no known apiaries within 19 km of the Mattheis Ranch (although feral hives may exist in abandoned burrows or riverine trees, presumably at low densities). Another managed pollinator, the alfalfa leafcutter bee (*Megachile rotundata*), was present approximately 1500 m from the southern transects. Transect locations (Appendix I) were selected based on similar microtopography and non-graminoid plant species composition. When flowers were not present, and sampling could not be completed, I moved the transect up to 10 m from the original transect location to reach any flowers. Without flowers, the pollinator diversity visiting flowers could not be measured, so in moving the transect and keeping the same distance to the hives, this did not affect measurements of honey bee density on the community, only created an opportunity to measure the community.

I placed the hive clusters ≥3000 m apart, and expected the transects ≥5000 m from hives not to have honey bees, because this distance is larger than the typical foraging distance of honey bees; exceeding 5000 m, honey bees expend more energy than the energy gained, so very few move that far (Hagler et al., 2011). Bumble bees have a foraging distance of approximately 1000 m (Elliott, 2009), and foraging distance decreases with body size among bees in general (Greenleaf et al., 2007). Larger-bodied syrphids possess similar flight patterns to honey bees (Golding et al., 2001, 2005), while the mobility and distribution of butterfly species varies widely, with larger-winged species having greater vagility (Burke et al., 2011).

The study took place from May 28 to August 28, 2019. After July 9th, 2019, I abandoned the 5000 m transect “F5000” because I observed numerous honey bees around the transect even though it was meant to be without honey bees. I selected a new 5000 m transect, “G5000”, approximately 8000 m away from the northern 48 hive cluster (Figure 1, Appendix I). I needed six replicates of transects with few to no honey bees, so G5000 was established in place of F5000, though both were considered in analysis.

Sampling plant-pollinator interactions and flower abundance

An assistant and I observed each transect for 30 minutes for a total of 60 person-minutes per transect per collection round (4200 total collection minutes). We walked along opposite sides of the transect and collected all insects that visibly contacted the anthers/stigma of open flowers ("flower visitors") with a hand net and placed them in individual vials, along with a label including date, flower, and transect code. Vials were kept frozen until transportation back to the lab. I refer to this dataset hereinafter as the "hand-caught" dataset. After sampling flower visitation, we identified all flowering plants on the transect (using Bain et al. (2014); Moss & Packer (1994); Tannas (2003, 2004)) and counted their flowers.

Each transect was visited once per week, weather permitting, for a total of 10 collection rounds. However, some transects could not be sampled in some weeks due to lack of flowers or cattle disturbance, resulting in different numbers of sampling events for each transect (Appendix I). However, all transects had cattle disturbance at least once in the entire season. Transects were visited only on warm, sunny days with winds under 50 km/h, as insects avoid flight when wind speeds are higher than the insect's flight speed, as well as when it is raining (Pasek, 1988; Sanderson et al., 2015). I measured wind speed with a Brunton Sherpa, a handheld meteorological instrument, by holding it vertically above head level and noting wind speeds.

Because flower visits increase between the hours of 9:30am and 5:00pm (Lefebvre et al., 2014), all sampling occurred within this period.

Measuring flower visitor abundance and diversity with pan traps

I used pan traps to take a second set of measurements of flower visitor diversity, abundance, and species composition at each transect that were more independent of the local plant assemblage than the same measurements from the hand-caught dataset. Three pan traps were placed at 10 m intervals along each side of each transect. I used two each of blue, white and yellow bowls per transect with a few drops of Dawn dish detergent in water (Kearns & Inouye, 1993; Wilson et al., 2016). I set up pan traps in the morning before 9:30am and retrieved them no later than 55 hours after placement, depending on weather and collection round, recording the time exposed to the nearest quarter hour. Trap contents were sieved into a vial and preserved with 70% ethanol. During some collection rounds, some pan traps could not be collected due to cattle disturbance, weather, or road conditions; consequently, not all transects had complete collections (Appendix I). I refer to this dataset hereinafter as the “pan-trapped” dataset.

Insect Identification

In the lab, all flower visitors and pan trap samples of bees, butterflies, and beetles were mounted, and identified to species where possible, or to morphospecies (5% and 18% of species in hand-caught and pan-trapped datasets, respectively). A voucher of each species and morphospecies (Appendix II, Appendix III) will be deposited in the University of Alberta E. H. Strickland

Entomological Museum. All identifications were completed using a dissecting microscope, dichotomous keys, and comparison with reference specimens at the University of Alberta E. H. Strickland Entomological Museum and the University of Calgary Zoology Museum. Assistance with identification was provided by John Acorn for beetles and butterflies, Irene Jimenez Roncancio for wasps, Brittany Wingert for flies, James Glasier for ants, Greg Pohl for moths, and Lincoln Best for bees.

Flower visitor diversity metrics

I used both the hand-caught and pan-trapped datasets to examine the effects of honey bee abundance on native pollinator richness, diversity, abundance, and species composition, as well as interaction richness and interaction diversity, and if these effects change seasonally with honey bee density. To test this, I created several separate datasets from the hand-caught data: 1) the full season all taxa dataset, 2) two full season higher taxa datasets: native bees (plus *Megachile rotundata* and hereinafter referred to as "non-*Apis* bees"), and flies, 3) a mid-season all taxa dataset, which was a reduced dataset including only three collection rounds from July 8th to July 31st, and 4) a mid-season non-*Apis* bees dataset. Additionally, I created two groups of datasets from the pan-trapped data: 5) three full season datasets with the pan-trapped higher taxa considered separately (non-*Apis* bees, beetles, and butterflies) and 6) two mid-season pan-trapped higher taxa datasets (non-*Apis* bees and beetles), where butterflies were not abundant enough to do analysis.

For each dataset, I calculated flower visitor rarefied species richness, which is a measure of the expected species richness for a given sample size, with sample size held constant across all sites, and equal to the number of individuals collected at the site with the fewest individuals collected (vegan package, Oksanen et al., 2019; Gotelli & Colwell, 2001) As such, rarefaction is a method of removing the dependence of a richness estimate for a site on the number of individuals sampled at that site. When calculating rarefied species richness in the datasets 1, 2 and 5, I retained the transects "E100" and "G5000" in all calculations, despite lower values because of a lack of flowers and because of moving the transects mid-season. However, in the mid-season datasets 3, 4, and 6, where only three collection rounds were kept, I established a cut-off point that excluded transects, or higher taxa, with numbers of individuals below values of 15 (depending on the taxon) from rarefaction analysis, to increase the accuracy of richness estimates. Transects with low values were the result of low sampling effort (due to weather, cattle, lack of flowers, or other conditions), and assessing these small sample sizes could produce misleading results. To account for this, I chose 15 as an arbitrary cut off value, which was the minimum richness of the full season E100 transect. For some mid-season higher taxa groups, such as flies and butterflies, numbers of individuals sampled were too low to calculate a richness estimate and these groups were excluded from analysis. For the full season all taxa dataset I calculated rarefied interaction richness, or the expected number of unique interactions, holding the total number of interactions sampled constant. I refer to rarefied species richness hereinafter as "species richness", and to rarefied interaction richness as "interaction richness".

I used Simpson's Hill number (Goslee & Urban, 2007; Hill, 1973) to assess flower visitor species diversity (hereinafter referred to as "species diversity"). Simpson's index of diversity is a metric that takes into account both the number of species present and their relative abundances. The Hill number converts Simpson's index into the number of equally abundant species needed to produce the observed value of diversity (Hill, 1973). For the full season all taxa dataset, I also calculated Hill numbers for the pairwise interactions between pollinators and plants, referred to hereinafter as "interaction diversity". I measured abundance as the number of individual flower visitors of each species. I recorded flower visitor species composition (hereinafter "species composition") as a matrix of species abundances by transect (rows) and flower visitor species (columns).

Statistical analyses

Honey bee abundance as a predictor variable

In order to test the effect of honey bee abundance on species richness, species diversity, abundance, species composition, interaction richness and interaction diversity, I used linear regression, with the abundance of honey bees from each transect in the full season all taxa hand-caught dataset, divided by collection effort for that transect, as the predictor variable, rather than using transect distance to hives, or honey bee abundance from the pan-trapped dataset. The number of honey bees in the pan traps did not appear to reflect the number of honey bees that I observed in flight, or on flowers while sampling, as well as the number of honey bees caught by hand did. Furthermore, neither hand-caught (Figure 2) nor pan-trapped (Appendix IV) honey bee abundance strictly followed a pattern of decreasing abundance as hive distance increased, meaning that distance from bee hives probably did not reflect actual "effect" of honey bees as much as my measures of honey bee abundance. However, hand-caught honey bee abundance was still more abundant than pan-trapped honey bee abundance. Therefore, this was the predictor variable of interest in all statistical models, including those modeling pan-trapped abundance and diversity of all taxa.

Effect of honey bee abundance on species diversity metrics

I used general linear models (GLMs) or general linear mixed models (GLMMs) to test the effect of honey bee abundance on each response variable (species richness, species diversity, and abundance), for all datasets (1 through 6). I also tested the effect of honey bee abundance on interaction richness and interaction diversity in the full season all taxa dataset. First, for each response variable, I ran a GLMM with honey bee abundance as the only predictor variable. Because some of my transects were close together (e.g., the two 100 m transects on either side of the same group of hives were only 200 m apart), I visually inspected whether a special correlation structure was necessary to account for spatial autocorrelation of close together transects. I did this by plotting a map of the standardized residuals of each GLMM and visualizing the size and sign of each residual for each transect (Appendix V). I then ran generalized least squares (GLS) mixed models with different correlation structures (no correlation, corEcp, corGaus, corSpher, corLin, corRatio) for each response variable (nlme package, Jose et al., 2020). After each set of models was run, the AICc (Akaike's Information Criterion, corrected for small sample size) values were calculated, and the model with the lowest AICc value (or any simpler model within 2 AICc points of the model with the lowest AICc; Richards, 2007) was selected (MuMin package, Bartoń, 2020). The best models for each response variable did not include special correlation structures, so GLMs rather than GLMMs were run, with the exception of beetle abundance and non-*Apis* bee species richness in dataset 5 and 6, respectively (Appendix VI).

The response variables of interest (flower visitor species richness, species diversity, and abundance) may have been influenced by flower abundance, the number of available flower species, and sampling effort at each transect. When I found that honey bee abundance was significant in the first model, I ran an additional GLM (or GLMM) for each response variable, with these additional predictor variables as well as honey bee abundance, and used a model selection approach to select the predictor variable(s) that best explained that response variable. The predictor variables included in each full model were honey bee abundance, flower abundance, flower species richness, total number of collections, as well as the interaction between honey bee abundance and flower abundance, and the interaction between honey bee abundance and flower species richness. Each continuous predictor variable was standardized by subtracting the variable's mean from each observed value and dividing by the variable's standard deviation (Quinn & Keough, 2002). I ran the full model, and all possible simpler models, for a total of 21 linear models per response variable (nlme package, Jose et al., 2020). If honey bee abundance remained in the best model after model selection, and was significant, that would suggest that there was an effect of honey bees on that response variable that could be unambiguously attributed to honey bees, rather than to correlated effects of flower abundance, flower species richness or collection effort. If honey bee abundance was significant in the first model run for each response variable (where only honey bee abundance was the predictor variable) but was either not kept or not significant in the second GLMM model (with the additional flower and collection predictor variables), that would suggest that that response variable is related to honey bee abundance, but that any effects of honey bees cannot unambiguously be attributed to honey bees, and may be due to flower community variables or collection effort, which honey bees were responding to themselves.

I examined the assumptions of normality for each response variable by running a Shapiro-Wilk test on the residuals of the best models and visually examining Quantile-Quantile plots for the normal distribution. Homogeneity of variance was assessed for each response variable by examining plots of fitted values versus residuals to look at whether variance of the residuals was homogenous along the range of fitted values. If the assumptions were not met, that response variable was log transformed and model selection was repeated on the transformed response variable, after which if assumptions were still not met, I applied a Box-Cox transformation (MASS package, Venables & Ripley, 2002). In some cases, transformation did not improve normality or variances, in which case I interpreted the p-values cautiously.

To assess whether flower visitor species composition was affected by honey bee abundance, I used permutational multivariate analysis of variance (PERMANOVA). PERMANOVA calculates within- and among- group multivariate dissimilarity and reveals how variation is linked to experimental treatments (vegan package, Oksanen et al., 2019). I used both the Bray-Curtis (which incorporates species relative abundances) and Jaccard (which only considers species presence or absence) distance metrics. To visualize patterns in species composition, I used non-metric multidimensional scaling (NMDS). NMDS is a non-parametric ordination method that preserves rank-order dissimilarities and represents the original position of data in multidimensional space by reducing the number of dimensions (ecodist package, Goslee &

Urban, 2007). The NMDS was run with the function metaMDS which runs the function monoMDS until two similar configurations with minimized stress are found (Oksanen et al., 2019). All analyses were completed using R version 3.2.4. (R Core Team, 2020). For a list of datasets and the metrics calculated for each, see Table 1.

To assess whether the effects of honey bee abundance on pollinator species richness, species diversity, abundance, and species composition were more pronounced in the mid-season, when honey bee population size was highest, I plotted honey bee abundance across the season and divided the whole season into three roughly equal-length periods: “early”, “mid” and “late”, based on natural breaks in the abundances of honey bees (Appendix VII). The mid-season period was reduced to collection rounds 5 through 7, from July 8th to July 31st, 2019. Because honey bee abundance was highest in the mid-season window, when honey bee population size is typically largest (Canadian Honey Council, 2018), I tested the effects of honey bee abundance on all the same response variables as above, for only the mid-season datasets (datasets 3, 4, and 6). Next, I fitted the GLM (or GLMM) for each response variable with honey bee abundance and all additional predictor variables listed above, and used model selection as described above to arrive at the best model. I then ran a PERMANOVA for each dataset, testing for effects of honey bee abundance on species composition (abundance of all flower visitor species).

Lastly, this analysis involved interpreting 60 separate models, so to maintain Type I Error at 0.05, I used a Bonferroni-Holm correction. The Bonferroni-Holm correction is a less conservative form of adjusting for multiple comparisons, but I present all P-values, to allow consideration of uncorrected P-values.

Results

Richness of pollinators in the grassland plant-pollinator community

In the full season all taxa dataset, I recorded a total of 281 pollinator species and 36 plant species. Bees were identified to 73 species (half of the diversity of bees found in pan traps, and a quarter of the known bee diversity in the region (Sheffield et al., 2014)). Butterflies were identified to 15 species (approximately half of the diversity of butterfly pan traps, and 27% of the known diversity in the region, based on maps in Bird et al. (1995) excluding riparian species, but including occasional migrants). Beetles and ants were identified to 14 and 11 species, respectively (11.8% of ant diversity estimates in the region (Giberson & Cárcamo, 2014b). Detailed identifications, including other less abundant pollinator groups, are listed in Appendix II. Honey bees were the most common pollinator and western snowberry (*Symphoricarpos occidentalis)* was the most common flowering plant. These species were involved in 1,814 interactions, with 654 unique plant-visitor interactions (distinct interactions between one species of visitor and plant), 425 of those being one-time interactions (where the unique interaction was observed only was).

From pan traps, 11,437 specimens were identified to 245 species from three groups (bees, beetles, and butterflies). Flower-count data revealed a total of 46 species of flowering plants, approximately 33% of the diversity of flowering plants in the region (Schroeder, 2018). All plant species are listed in Appendix VIII. A total of 6,655 bees were identified to 149 species, approximately half of the known bee diversity of southern Alberta (Sheffield et al., 2014). A total of 2515 butterflies were identified to 28 species, representing half of the known butterfly diversity of the region (Bird et al., 1995). A total of 2,278 beetles were identified to 68 species. Total pan-trapped hours were 6032.25 pooled across the 2019 season.

Overall, bees were predominantly small-bodied sweat bees (Halictidae: *Lasioglossum spp.*). The most abundant butterfly was the plains skipper (Hesperiidae: *Hesperia assiniboia*), and the most abundant beetle was the rust-coloured blister beetle (Meloidae: *Epicauta ferruginea*). The most abundant wasp species were *Stenodynerus anormis* (Vespidae) and *Ectemnius rufifemur* (Crabronidae). The most abundant fly species was *Eristalis stipator* (Syrphidae) and the most abundant ant species was *Formica lasioides* (Formicidae). All pan trap identifications are listed in Appendix III.

Rarefaction curves were plotted for the full season all taxa dataset and mid-season all taxa datasets, which did not plateau; the pan-trapped higher taxa dataset and the mid-season pan-trapped higher taxa dataset began to flatten but did not fully plateau (Figure 4). This suggests that sampling was more complete for the pan-trapped datasets.

Effect of honey bees on flower visitor diversity metrics in all datasets (1-6)

Out of all the diversity metrics tested for all higher taxa, trapping methods, and even in the mid-season datasets, honey bee abundance did not significantly affect any metric after Bonferroni-Holm correction (Tables 2-5), except that there was a significant increase in beetle species diversity as honey bee abundance increased, after controlling for flower abundance, flower species diversity, collection effort, and the interactions between honey bee abundance and flower abundance, flower species diversity, and collection effort (Table 3c). In general, the lowest (though non-significant) P-values were associated with positive relationships between honey bee abundance and the diversity metrics, rather than the predicted negative associations (Table 3).

Species composition was not significantly related to honey bee abundance for any dataset, and the NMDS for the full season all taxa dataset showed no substantial separation of species composition by honey bee treatment (Figure 3). Stress levels for the NMDS plot were 0.20, indicating a good fit for the model. For the PERMANOVAs run with both Bray-Curtis and Jaccard dissimilarity, the lowest (though non-significant after Bonferroni-Holm correction) P-values were for effects of honey bee abundance on mid-season Non-*Apis* bee species composition (Tables 4-5).

Discussion

I found that the diverse insect pollinator community of the grassland region of Alberta appears to maintain or quickly recover ecosystem function, despite the addition of managed honey bees. There was no change to pollinator species richness, species diversity, abundance, or species composition observed visiting flowers, and no change to plant-pollinator interaction richness, or interaction diversity with the addition of honey bees, even at high densities. The pan traps caught higher beetle species diversity the higher the honey bee abundance, when differences in the flower community and collection effort between sites were accounted for, but all other diversity metrics for all other taxa caught in pan traps had no significant relationship to honey bee abundance. This suggests that honey bees have little to no impact on the native pollinator community or the number and frequency of their interactions with plants. Although many studies have indicated negative impacts of honey bees on native pollinators (Cane & Tepedino, 2017; Elbgami et al., 2014; Goulson & Sparrow, 2009; Hudewenz & Klein, 2015; Lindström et al., 2016; Ropars et al., 2019; Valido et al., 2019; Wignall et al., 2020), this study is in agreement with those that found either a neutral or positive effect on wild pollinators (Forup & Memmott, 2005; Herbertsson et al., 2016; Ropars et al., 2019; Roubik & Wolda, 2001; Tscharntke & Steffan-Dewenter, 2000).

I found only a positive relationship between honey bee abundance and the species diversity of native beetles. Though not significant, honey bee abundance also had a positive relationship to other variables related to richness and diversity (Table 2-3). One explanation may be that when honey bees are present, there may be other, unmeasured variables that also attract other wild pollinators. These variables may be aspects of floral quality, such as volatiles, flower density, stem height, corolla length, nectar quality, or pollen availability (Fenster et al., 2004; Mallinger & Prasifka, 2017). Interestingly, there was no effect of honey bee abundance on interaction richness or interaction diversity, despite Valido et al. (2019) finding a negative effect on interaction richness. However, the high number of one-time interactions may indicate a large number of potential interactions were undetected by sampling; caution should therefore be used when interpreting these interaction richness and interaction diversity results.

Unfortunately, due to low abundances of some taxa, only flies, butterflies, bees, and beetles could be examined separately for effects of honey bees on their diversity metrics. Still, this is one of the few studies to examine the effects of honey bees on non-bee taxa, which therefore considers the entire community as a whole, not just one or two groups. Lindström et al. (2016) found a negative relationship between honey bee densities and wild pollinator densities, however Ropars et al. (2019) found that visitation rates of wild solitary bees, flies, and butterflies were related to plant species richness rather than honey bee density. In this study, there did not appear to be a greater effect of honey bee abundance on one taxon over another, with the exception of the positive relationship with beetle species diversity. In analyzing the second GLMM model for each response variable in each dataset, which included all predictor variables (honey bee abundance, flower abundance, flower species richness, and collection effort), flower species richness appeared to have the strongest positive relationship with species richness, species diversity, and fly species diversity. This would indicate that flower species richness is more related to the pollinator richness and diversity in this area than is honey bee abundance. Overall, my results suggest that the presence of honey bees alone, even at varying densities and different temporal periods, does not negatively impact the diversity or abundance of native pollinators, or the diversity of their plant-pollinator interactions.

Because I worked in a landscape with a variety of flowering plants, it may be that the niches of honey bees and other pollinating insects did not totally overlap, as noted by (Herbertsson et al., 2016). Based on observations in the field, honey bees (and other large-bodied bees, such as *Bombus* spp.) did not appear to visit small-flowered and small-stemmed plants, such as *Campanula rotundifolia*, which many other flower visitors did visit. Honey bees also appeared to prefer introduced species, such as *Astragalus cicer* and *Melilotus* spp., which is supported by findings that honey bees prefer introduced plant species (Urbanowicz et al., 2020). Therefore, honey bees may have avoided a resource that small-bodied pollinators could utilize. It is also possible that honey bees, which were introduced over 100 years ago to Alberta's prairies, have already caused the competitive exclusion of some species, and the community may be adapting to its presence.

One major difference between this study and most others on this topic was the effort put into identification, and the incorporation of a broad range of pollinators in the analysis, not just wild bees. Wild bees often overshadow other taxa, which can also hold important pollinating roles (Albrecht et al., 2012; Garibaldi et al., 2013; Rader et al., 2016, 2020). Additionally, this study encompassed most of the flowering period for native plants in the region. This large-scale study also answered some uncertainties surrounding the effects of honey bees on wild pollinators in Alberta's grasslands, indicating that their presence is not as detrimental to native plant-pollinator communities as might have been predicted from the literature, and that reducing managed honey bee densities may not be an effective – or necessary – action for native pollinator conservation in this region.

Caveats to this study are that in sampling flower visitors, collector bias (and/or taxonomic bias) will mean that more large-bodied pollinators will be preferentially caught simply due to their visibility (Westphal et al., 2008), though there is evidence that this bias can be negligible (de Manincor et al., 2020), Similarly, pan traps can be useful for measuring richness of some taxa, such as bees and flies (O'Connor et al., 2019), but pan traps do not reveal which individuals or species are flower visitors or pollinators. Ultimately, these issues are well-known in studying plant-pollinator communities and are notoriously difficult to avoid completely (O'Connor et al., 2019; Westphal et al., 2008). A study of this nature is also reliant upon how completely the community was sampled. While I only sampled approximately 20-50% of the richness in the region (depending on the pollinator group), pan trap and sampling hours rivaled or surpassed that of other studies that found a negative association of honey bee abundance on native plant-pollinator networks (Magrach et al., 2017; Valido et al., 2019). This indicates that the sampling effort in this study should have been sufficient to detect any effects of honey bees, if they existed. Lastly, this study was only done over one summer, and sampling began immediately after hive placement. It was designed to detect the effect of honey bee abundance on behavioural responses of wild pollinators, rather than to effects on their population sizes, with the exception of colonial species that produce multiple generations of workers in one summer. Over a longer period of time, some effects of honey bee abundance may have become detectable, as other variables, such as rainfall or temperature, may have affected competition between honey bees and wild pollinators.

In addition to this study, I have also assessed the effect of honey bees on native plant-pollinator network interactions (Chapter 3). Though Chapter 2 shows no strong relationship between honey bee abundance and the richness, diversity, abundance, or species composition of native pollinators, or on the diversity or richness of their interactions, there may still be effects on the patterns of interactions in the plant-pollinator network that are not visible from diversity metrics alone.

Conclusions

Overall, these results show, for the first time in Alberta's grasslands, that the presence of managed honey bees has no detectable negative impacts on the richness, diversity, or abundance of pollinators, or on the diversity of their plant-pollinator interactions. The effects of honey bees on native pollinator communities has been contentious, and this study provides further evidence indicating that negative effects may be context-dependent. Future research is needed, however, to determine whether honey bees can coexist in the long run with wild pollinators in an agriculturally-dominant region where available land is becoming more scarce. While this study indicated no strong relationship between honey bee abundance and wild pollinator diversity, it did not address the potential negative effects of disease transmission from honey bees. Caution should be used in generalizing these results in other regions; even though evidence suggests that honey bees are not a major threat to the wild pollinators in the Canadian grasslands, effects in other environments may differ.

Tables

Table 1. List of datasets and metrics calculated for each dataset. Each metric was used as the response variable in a statistical test of the effect of honey bee abundance on that variable. Blocks of similarly shaded rows demarcate separate datasets. Analyses for some higher taxa from the mid-season all taxa dataset could not be completed when abundances were too low (flies, butterflies, ants, moths, true bugs). Interaction richness and interaction diversity were only analyzed for the pooled hand-caught dataset.

Dataset Group	Response Variables Tested
1) Full season all taxa dataset	Species richness
	Species diversity
	Abundance
	Species composition
	Interaction richness
	Interaction diversity
2) Full season higher taxa datasets	Non-*Apis* bee species richness
	Non-*Apis* bee diversity
	Non-*Apis* bee abundance
	Non-*Apis* bee species composition
	Fly species richness
	Fly species diversity
	Fly abundance
	Fly species composition
3) Mid-season all taxa dataset	Species richness
	Species diversity
	Abundance
	Species composition
4) Mid-season Non-*Apis* bee dataset	Non-*Apis* bee species richness
	Non-*Apis* bee species diversity
	Non-*Apis* bee abundance
	Non-*Apis* bee species composition
5) Pan-trapped higher taxa datasets	Non-*Apis* bee species richness
	Non-*Apis* bee species diversity
	Non-*Apis* bee abundance
	Non-*Apis* bee species composition
	Beetle species richness
	Beetle species diversity
	Beetle abundance
	Beetle species composition

	Butterfly species richness
	Butterfly species diversity
	Butterfly abundance
	Butterfly species composition
6) Mid-season pan-trapped higher taxa datasets	Non-*Apis* bee species richness
	Non-*Apis* bee species diversity
	Non-*Apis* bee abundance
	Non-*Apis* bee species composition
	Beetle species richness
	Beetle species diversity
	Beetle abundance
	Beetle species composition

Table 2. Selected model with the lowest AICc value for each response variable from each dataset, where honey bee abundance was the only predictor variable. No P-values were significant with Bonferroni-Holm correction. Bolded P-values denote P ≤ 0.05, which meant that the second GLMM model, with all predictor variables, was run (Table 3). Asterisk (*) denotes Box-Cox transformation, and other transformations are listed with the response variable. Blocks of similarly shaded rows demarcate separate datasets, while letters demarcate groups of datasets.

Response variable	**Partial regression coefficient**	**t-value**	**P-value**
a) Full season all taxa (Dataset 1)			
Species richness	0.9031	2.63	**0.0175**
log(Species diversity)	0.3180	2.42	**0.0272**
Abundance	0.1916	0.81	0.4320
Interaction richness	-0.4232	-0.76	0.4580
log(Interaction diversity)	-0.2386	-1.33	0.2020
b) Full season higher taxa (Dataset group 2)			
Non-*Apis* bee species richness	0.7680	1.60	0.1330
Non-*Apis* bee species diversity	1.3050	1.50	0.1520
Non-*Apis* bee abundance	0.1994	0.84	0.4130
Fly species richness*	0.3081	1.12	0.2910
Fly species diversity	1.9134	2.12	**0.0488**
log(Fly abundance)	0.1063	1.13	0.2750
c) Mid-season all taxa (Dataset 3)			
Species richness*	11.0520	0.75	0.4680
log(Species diversity)	0.2915	0.19	0.8490
Abundance	-3.0870	-0.81	0.4320
d) Mid-season Non-*Apis* bees (Dataset 4)			
log(Non-*Apis* bee species richness)	0.1555	1.23	0.2570
Non-*Apis* bee species diversity	-0.1812	-0.24	0.8110
Non-*Apis* bee abundance	-1.4310	-0.53	0.6010
e) Pan-trapped higher taxa (Dataset group 5)			
Non-*Apis* bee species richness*	0.7676	0.81	0.4280
Non-*Apis* bee species diversity	1.0920	0.96	0.3520
Non-*Apis* bee abundance	53.9500	1.65	0.1180
Beetle species richness	0.8696	3.06	**0.0075**
Beetle species diversity	1.0625	3.30	**0.0043**
Beetle abundance (*CorGaus*)	7.4453	0.56	0.5846
Butterfly species richness	1.0842	1.76	0.0982
Butterfly species diversity	0.5262	2.22	**0.0405**
Butterfly abundance	-20.1000	-1.52	0.1470
f) Mid-season pan-trapped higher taxa (Dataset group 6)			
Non-*Apis* bee species richness (*CorRatio*)	0.5922	2.55	**0.0212**
Non-*Apis* bee species diversity	-0.0288	-0.62	0.5470
Non-*Apis* bee abundance	-15.6300	-1.01	0.3280

Beetle species richness	0.6788	1.93	0.0723
Beetle species diversity	0.5039	1.91	0.0739
Beetle abundance*	-0.2950	-1.04	0.3145

Table 3. The second GLMM model with the lowest AICc value for each response variable, where the full model for each response variable contained honey bee abundance, flower abundance, flower species richness, collection rounds, the interactions between honey bee abundance and flower abundance, and between honey bee abundance and flower species richness, as predictor variables. Bolded P-values denote significance with Bonferroni-Holm correction. Transformations and generalized least squares correlation structures are listed with the response variable. Blocks of similarly shaded rows demarcate separate datasets.

Response variable	**Predictor variables retained in final model**	**Partial regression coefficient**	**t-value**	**P-value**
a) Full season all taxa (Dataset 1)				
Rarefied species richness	flower richness	1.3589	5.69	**2.66E-05**
log(Species diversity)	flower richness	0.5287	6.40	**6.61E-06**
b) Full season higher taxa (Dataset 2)				
Fly species diversity	flower richness	3.3275	5.42	**4.59E-05**
c) Pan-trapped higher taxa (Dataset group 5)				
Beetle species richness	honey bee abundance	0.8696	3.06	0.0075
Beetle species diversity	honey bee abundance	1.6862	4.68	**0.0003**
	flower richness	-0.9695	-2.69	0.0160
Butterfly species diversity	honey bee abundance	0.5262	2.22	0.0405
d) Mid-season pan-trapped higher taxa (Dataset 6)				
Non-*Apis* bee species richness (*CorRatio*)	collection effort	0.5872	2.64	0.0177

Table 4. Results for PERMANOVA models with Bray-Curtis dissimilarity, where honey bee abundance was the only predictor variable. Bolded P-values denote significance with Bonferroni-Holm correction. Blocks of similarly shaded rows demarcate separate datasets.

Response variable	**Sum of squares**	**F-model**	**R²**	**P-value**
a) Full season all taxa (Dataset 1)				
Species composition	0.0401	0.6463	0.0366	0.4690
b) Full season higher taxa (Dataset group 2)				
Non-*Apis* bee species composition	0.0628	0.7170	0.0405	0.4520
Fly species composition	0.1349	1.0950	0.0605	0.3470
c) Mid-season all taxa (Dataset 3)				
Species composition	0.0782	1.3707	0.0789	0.2650
d) Mid-season bees only (Dataset 4)				
Non-*Apis* bee species composition	0.2813	3.5867	0.1930	0.0380
e) Pan-trapped higher taxa (Dataset group 5)				
Non-*Apis* bee species composition	0.1612	3.0765	0.1532	0.0800
Beetle species composition	0.0794	0.6682	0.0378	0.4860
Butterfly species composition	0.1391	1.9684	0.1038	0.1240
f) Mid-season pan-trapped higher taxa (Dataset group 6)				
Non-*Apis* bee species composition	0.0611	0.9139	0.0540	0.3570
Beetle species composition	0.2049	1.7215	0.0971	0.1880

Table 5. Results for PERMANOVA models with Jaccard dissimilarity, where honey bee abundance was the only predictor variable. Bolded P-values denote significance with Bonferroni-Holm correction. Blocks of similarly shaded rows demarcate separate datasets.

Response variable	**Sum of squares**	**F-model**	**R²**	**P-value**
a) Full season all taxa (Dataset 1)				
Species composition	0.0561	0.5033	0.0288	0.6470
b) Full season higher taxa (Datset group 2)				
Non-*Apis* bee species composition	0.0899	0.6204	0.0352	0.5960
Fly species composition	0.1739	0.9161	0.0511	0.4300
c) Mid-season all taxa (Dataset 3)				
Species composition	0.1409	1.2865	0.0744	0.2660
d) Mid-season bees only (Dataset 4)				
Non-*Apis* bee species composition	0.3792	2.8226	0.1584	0.0450
e) Pan-trapped higher taxa (Dataset group 5)				
Non-*Apis* bee species composition	0.2522	2.5984	0.1326	0.0550
Beetle species composition	0.1555	0.8649	0.0484	0.4370
Butterfly species composition	0.2559	2.4356	0.1253	0.0990
f) Mid-season pan-trapped higher taxa (Dataset group 6)				
Non-*Apis* bee species composition	0.1655	1.4208	0.0816	0.2420
Beetle species composition	0.3095	1.7453	0.0984	0.1800

Figures

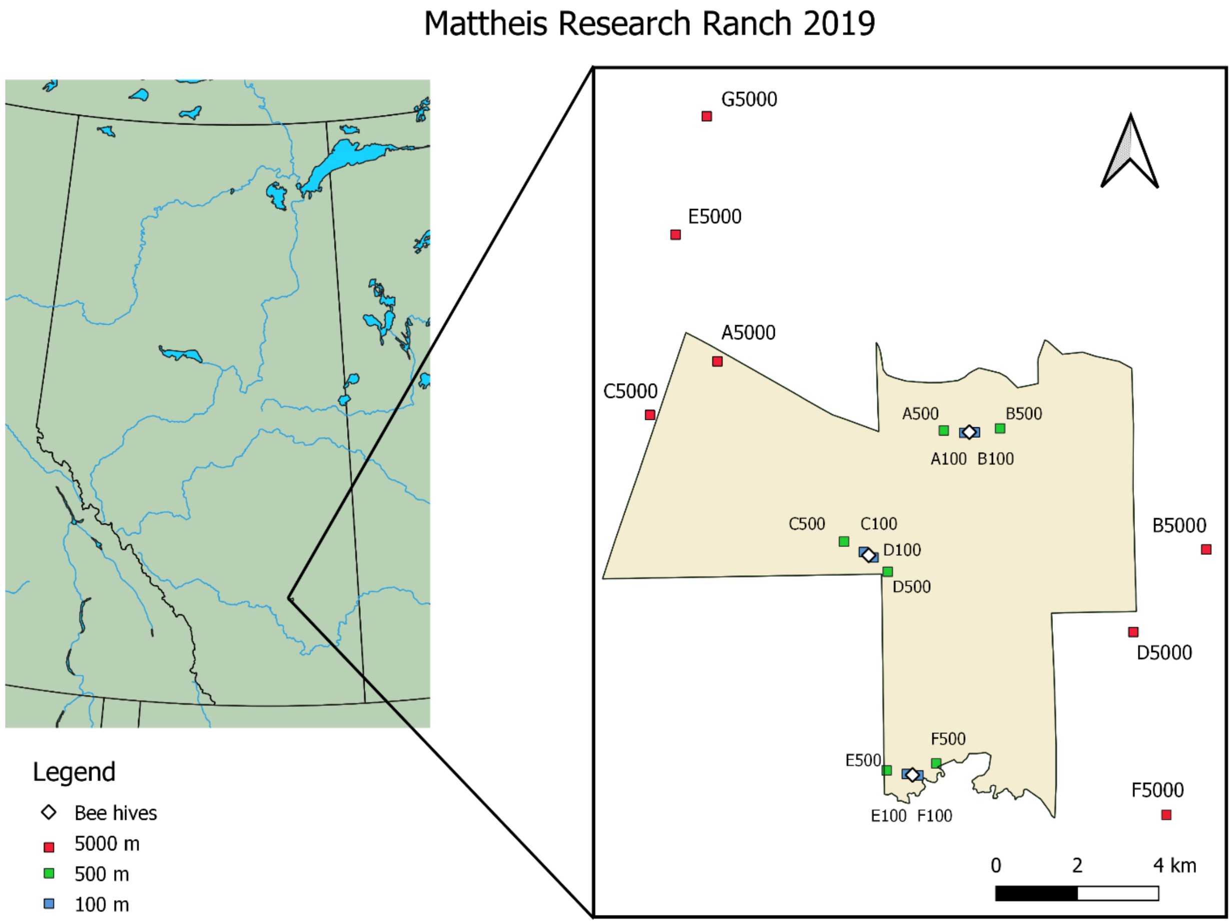

Figure 1. Locations of the transects and honey bee hives. Each hive location contained a cluster of hives, decreasing in hive number from north to south (northernmost: 48 hives, central: 32 hives, southernmost: 16 hives). The transect G5000 indicates the new location for F5000 after July 9th, 2019. Land outside the Mattheis Ranch border is managed by the Eastern Irrigation District.

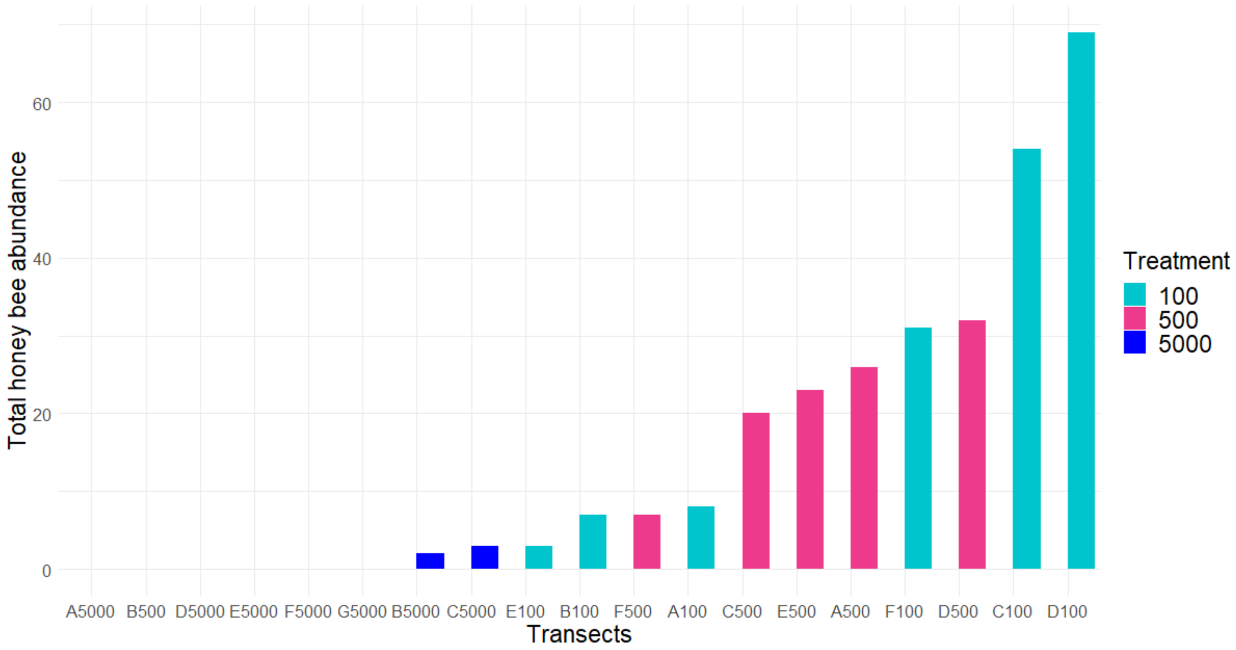

Figure 2. Abundance of honey bees caught visiting flowers (full season all taxa hand-caught dataset), pooled across the full season per transect, with transects ordered by increasing honey bee abundance, and coloured by distance from bee hives. In the transect names, 100 indicates 100 m, 500 indicates 500 m, and 5000 indicates 5000 m distances from hives.

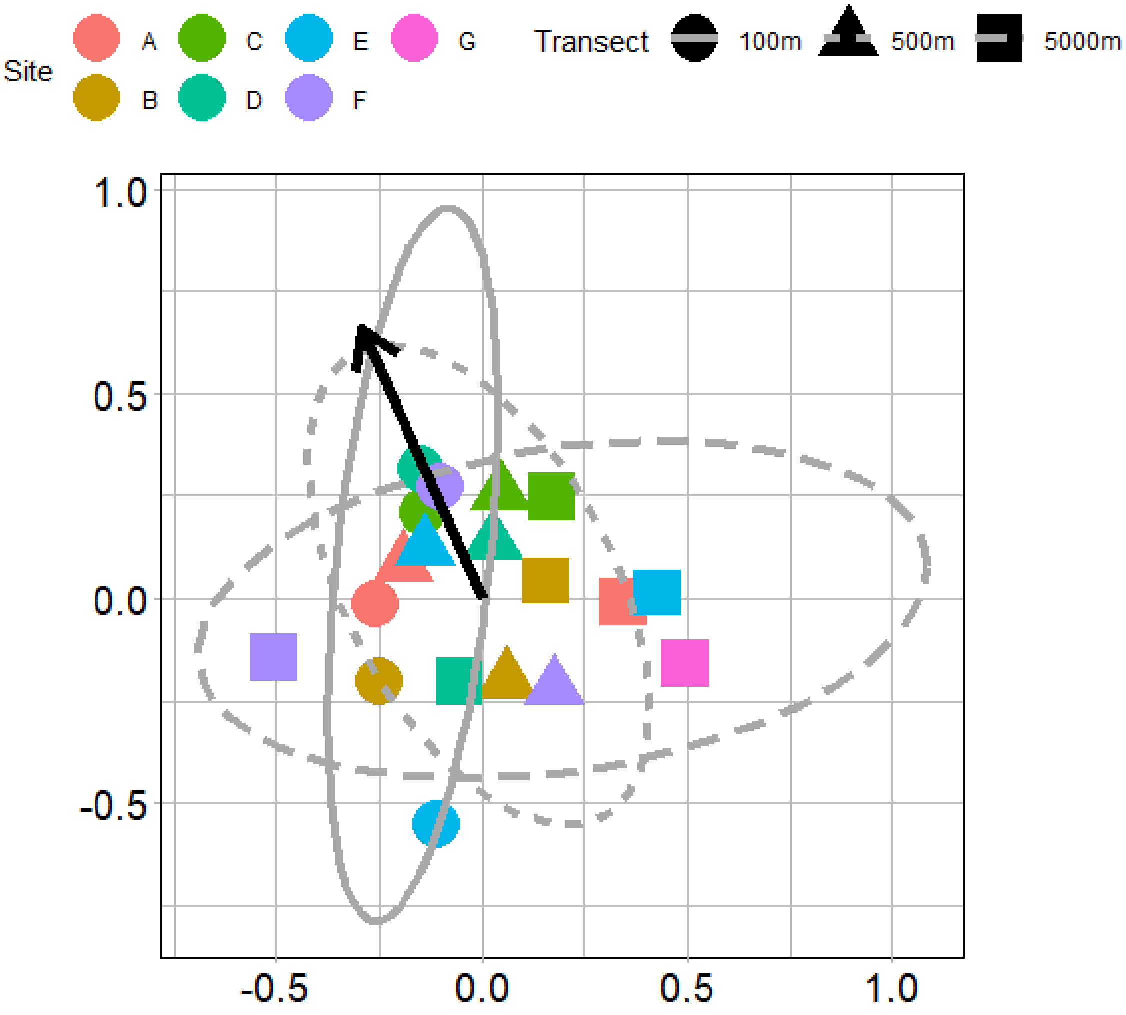

Figure 3. NMDS Plot of flower visitor species composition per transect. Each point represents a transect, with closer-together points on the plot having more similar flower visitor species composition. Ellipses and shapes indicate treatment (100 m, 500 m, or 5000 m distances from a hive). The stress score was 0.20. Bolded vector indicates Apis mellifera.

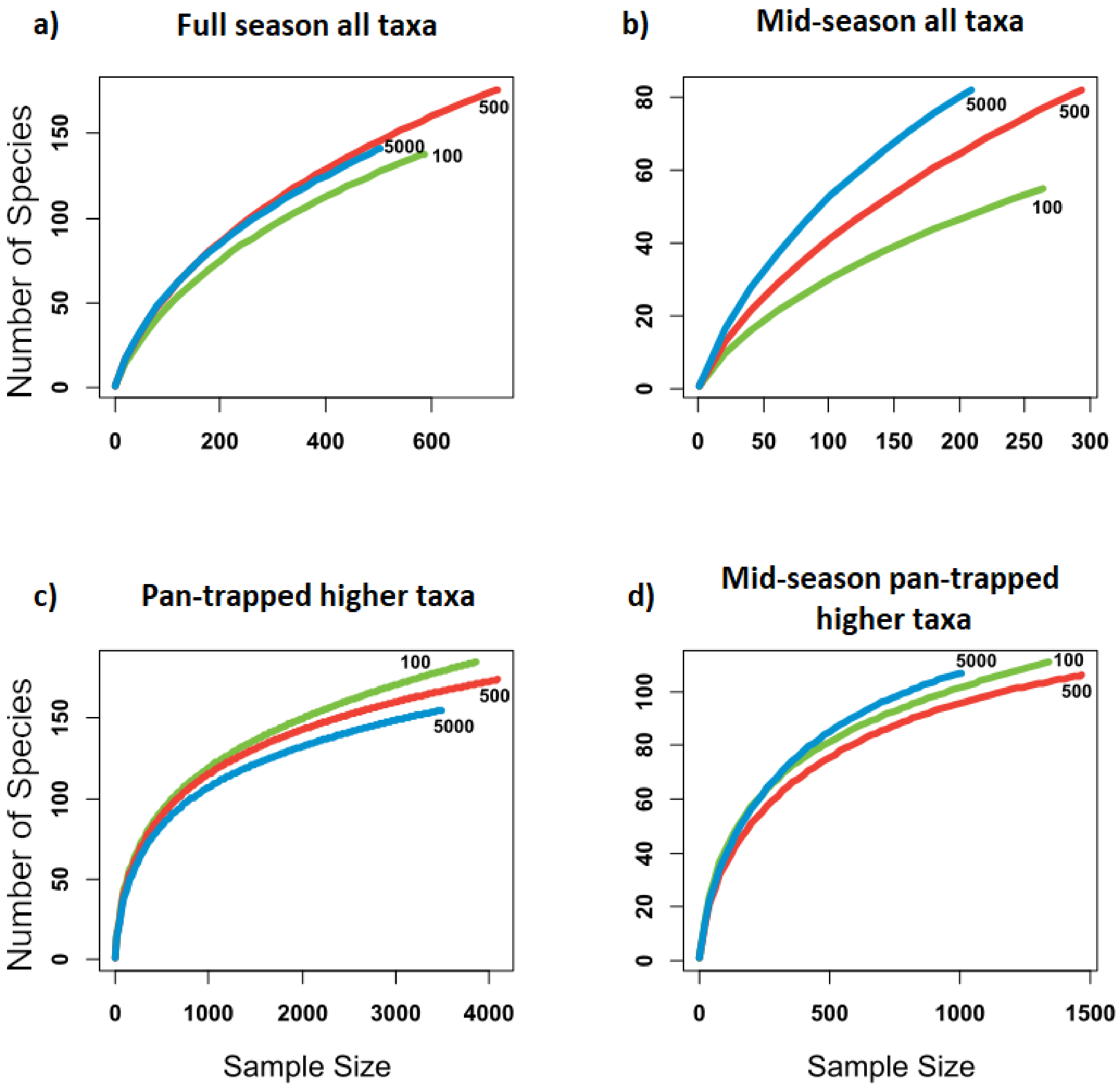

Figure 4. Rarefaction curves for the a) full season all taxa dataset (1), b) mid-season all taxa dataset (3), c) pan-trapped higher taxa dataset (5), and d) mid-season pan-trapped higher taxa dataset (6), where the richness of each higher taxon in pan-trapped data (bees, beetles, butterflies) were pooled together. These curves plot the average number of species obtained from repeated random re-sampling of the number of individuals given on the x-axis. Transects were pooled to 100 m, 500 m, and 5000 m groups, as indicated by green (100 m), red (500 m), and blue (5000 m).

Chapter Three: Native plant-pollinator interactions are resilient to the addition of honey bees in a Canadian grassland community

Introduction

The demand for pollination services has risen alongside agricultural growth (Aizen & Harder, 2009), increasing the density of honey bee apiaries in many agricultural landscapes (Aizen et al., 2009). This increased honey bee use has caused concerns over the potential negative effects of honey bees on wild pollinators and patterns of their interactions with plants. Honey bee density has been linked to declines in wild pollinator diversity (Badano & Vergara, 2011; Nielsen et al., 2017), abundance (Elbgami et al., 2014; Forup & Memmott, 2005; Herbertsson et al., 2016; Nielsen et al., 2017; Ropars et al., 2019), and fitness (Cane & Tepedino, 2017; Hudewenz & Klein, 2015; Walther-Hellwig et al., 2006). Many of these studies suggest that honey bees can outcompete native species and affect flower visitation (Lindström et al., 2016; Ropars et al., 2019). Honey bees can affect plant reproduction by carrying the pollen of many flowering species, reducing conspecific pollen deposition (Geslin et al., 2017; Valido et al., 2019). Honey bees may also alter wild pollinator interactions, modifying or reducing their resource use, which may eventually lead to species loss, either for plants or for pollinators or both (Geslin et al., 2017).

Species interactions can be considered at the community level by visualizing them as networks, which have origins in graph theory. These networks comprise the set of interactions (or "links") observed between species (or "nodes"), which can then be used to examine changes in the interactions between species within the community (Delmas et al., 2019). Honey bees may disrupt the structure and function of a native plant-pollinator network by altering these existing interactions (Geslin et al., 2017). To test this, a plant-pollinator community can be depicted as a bipartite network, with an upper trophic level of pollinator species and a bottom trophic level of plant species, connected by links representing flower visitation frequencies. A variety of metrics have been used to quantify plant-pollinator network structure. Some relate to resource use overlap, and some have been theoretically linked to network stability (Okuyama & Holland, 2008; Thébault & Fontaine, 2010). I calculated six metrics that are thought to relate to stability: nestedness, modularity, connectance, link density, interaction strength asymmetry, and interaction evenness. To assess resource overlap, I used seven metrics: vulnerability, generality, pollinator and plant niche overlap, pollinator and plant functional complementarity, and potential for competition. All these metrics (except the last) are commonly reported in ecological network studies, and all are defined in Appendix IX. Not all studies report on all metrics, and many of these metrics overlap in their usefulness. In selecting which of the many possible metrics to analyze, I chose those used in previous studies on how honey bees affect plant-pollinator network structure (Magrach et al., 2017; Valido et al., 2019).

Introducing honey bees is predicted to increase or decrease some plant-pollinator network metrics simply because the honey bee is a super-generalist species, such that adding its node and links to the network will have certain predictable effects on the network structure, just based on graph theory. For other metrics it is less obvious what to expect, though some empirical results have been reported. For most metrics, it is unclear what to expect when considering honey bee ecological effects on just the set of native plant-pollinator interactions, without the honey bee node and links included in the calculation of the metric. This ecological effect of honey bees on just the set of native plant-pollinator interactions is what of interest from a conservation perspective, though this is often not reported in the few existing studies that have investigated honey bee effects on plant-pollinator network structure (Magrach et al., 2017; Valido et al., 2019). These studies often include honey bee interactions in the networks that they analyze, which confounds predictable changes based on how generalist species contribute to network structure, with ecologically interesting changes to native plant-pollinator interactions that arise from ecological effects of honey bees. Here, I calculate network metrics both including and excluding honey bees in the networks, for maximal comparability to previous studies.

Of the network metrics related to plant-pollinator network stability, nestedness has been the most strongly associated with stability. A highly nested network is one in which interactions of specialists are subsets of the interactions of generalists. In this way, the interactions in the network become highly asymmetrical and organized around a few generalist species (Bascompte et al., 2003). Plant-pollinator networks are generally nested, and this structure is thought to minimize interspecific competition and enhance species coexistence, and to arise when new species enter the network where they have minimal competitive load (Bastolla et al., 2009). Nestedness increases plant-pollinator network stability (Thébault & Fontaine, 2010), and almost all studies that have examined honey bee effects on nestedness concur that honey bees increase network nestedness (Geslin et al., 2017; Giannini et al., 2015; Santos et al., 2012). Modularity (the extent to which interactions are clumped into semi-separate modules) is thought to decrease stability in plant-pollinator networks (Thébault & Fontaine, 2010) and to be decreased by honey bees, because they introduce new links that join previously separate modules (Geslin et al. 2017; Santos et al. 2012; but Valido et al. 2019 found the opposite). Other network metrics are more tenuously linked to stability, such as connectance (number of observed interactions over total possible interactions) and link density, which is similar (total number of interactions over the total number of nodes, or the mean number of interactions per species). Both are expected to increase stability (Thébault & Fontaine, 2010) and be decreased by honey bees (Aizen et al., 2008; Magrach et al., 2017; Valido et al., 2019). Network metrics of interaction strength asymmetry (the asymmetrical strength of one species interaction relative to the reciprocal interaction, averaged across all species pairs in the network) and interaction evenness (the uniformity of the interaction frequencies distributed through the network, calculated using Shannon's evenness index) may also be related to stability. Interaction strength asymmetry has been found to increase, as honey bees dominate interactions with wild plants (Aizen et al., 2008), but interaction evenness has been found to decrease, as the distribution of interactions was skewed toward honey bees (Magrach et al., 2017). While interaction strength asymmetry is thought to be stabilizing, interaction evenness may be destabilizing, though it has only been tested in antagonistic networks, not in mutualistic networks (Frost et al., 2019).

Despite the typical nested (competition-minimizing) structure of plant-pollinator networks, adding a generalist is predicted to cause competition between the new generalist and many other species, which may exclude these species from some of their floral resources and narrow their niches. This would be visible in network metrics related to resource use overlap, where we would see decreasing niche overlap, decreasing mean number of pollinators per plant and plants per pollinator (generality and vulnerability), and increasing functional complementarity (the dissimilarity of plants' and pollinators' set of species that they interact with) and potential for competition. If an added generalist species increases functional complementarity, the system becomes more specialized, and less likely to withstand species loss, where the role of the lost species cannot be fulfilled by another (Blüthgen & Klein, 2011). Additionally, another way to examine whether honey bees are excluding some pollinator species from flowers would be to compare the number of pollinator species present at a site that are observed interacting, and how this proportion changes with honey bee abundance. Likewise, to examine whether honey bees are pushing flower visitors to use less-preferred flower species, the proportion of available flowers that are visited over total flowers on the transect can be assessed to see if there is variation with honey bee abundance. Although these proportions are similar in concept to connectance (the number of observed interactions out of all possible interactions), connectance has as its denominator the number of plant species multiplied by the number of pollinator species observed in a flower visitation dataset, whereas these proportions have as their denominator the number of pollinator or plant species (respectively) from sampling at the site that is independent of the interaction dataset.

So far, the effect of honey bees on plant-pollinator networks where honey bees are experimentally introduced has not been studied; rather, several studies compare the structure of an empirical network that includes honey bees to the structure of the same network from which the honey bee node has been deleted (Geslin et al., 2017; Santos et al., 2012), and sometimes also relate variation in network structure between sites to honey bee abundance (Aizen et al., 2008; Ropars et al., 2019). Many of these node-deletion studies show a potential effect of honey bee abundance on nestedness, modularity, and interaction strength asymmetry (Geslin et al., 2017). These studies give an idea of how honey bees contribute to network structural properties in networks where they occur, but cannot show more than correlative relationships between honey bee density and the structure of wild plant-pollinator interactions.

More recently, two natural experiments have examined plant-pollinator interactions in locations with vs. without honey bees to test honey bee effects on wild plant-pollinator network interactions. Magrach et al. (2017) studied the effects of honey bee spillover from orange grove crops into surrounding native woodland. With increased honey bee abundance, there was an unsurprising increase in potential for competition with honey bees and, more interestingly, a resulting shift in wild pollinators' preferred plants, decreasing link density in the plant-pollinator network (Magrach et al., 2017). Additionally, Valido et al. (2019) examined the effects of honey bees on native plant-pollinator networks at a site before and after addition of honey bees, over several years. They compared honey bee-periods and "pre" honey bee-periods, and found that during honey bee-periods, honey bees decreased weighted nestedness and connectance, and increased modularity of the interaction network. Other metrics, such as interaction strength asymmetry and interaction diversity were unaltered, however (Valido et al., 2019).

Overall, these studies suggest an effect of honey bee abundance on native plant-pollinator interactions; however, these studies do not all report the same network metrics, and greatly differ in experimental design, and therefore it is not possible to know how general these reported effects of honey bees may be. Plant-pollinator network interaction studies are complicated by the fact that sampled network structure depends heavily on flower abundance and diversity, which vary temporally, and are not always controlled for. Honey bee density also varies temporally, so we might also expect the effect of honey bees on network metrics to change throughout a season. Network metrics also depend on sampling completeness, which varies with sampling methods. This makes comparability low for previous studies on how honey bees affect network structure.

However, though I have used similar sampling effort and honey bee densities, and have calculated the same network metrics as Valido et al. (2019) and Magrach et al. (2017), this study is the first to test experimentally whether changes to network structure are caused by honey bees, and to control for effects of flower diversity, abundance, and sampling effort. I also tested to what extent the honey bee node and links were responsible for any observed changes in network structure, or whether any changes were actually due to changes in native plant-pollinator interactions.

The grasslands of Western Canada is a region with a high diversity of wild bees (Sheffield et al., 2014) and other insect pollinators (Giberson & Cárcamo, 2014a, 2014b; Pohl et al., 2014), and with a high and increasing density of apiaries (Emunu, 2020; Melhim et al., 2010) and extensive crop production and associated habitat loss (Alberta Parks, 2015; CPAWS, 2020). As so little natural land remains, results of this study would be beneficial to inform conservation efforts; if honey bees are indeed detrimental to natural grassland systems, the of use apiaries in the region may need to be minimized, particularly in conservation areas. Alternatively, if honey bees have no apparent effect, conservation efforts can be focused elsewhere. In this same study system I found that wild pollinator diversity, richness, abundance, and species composition did not change with the addition of honey bees (Chapter 2). However, changes to species interactions may occur before changes to species diversity, so here, my analysis is instead focused on the effects of honey bees on plant-pollinator network interactions. By experimentally introducing honey bees, mimicking densities near commercial apiaries, and controlling for seasonal changes in flower abundance and diversity, I sampled plant-pollinator interactions throughout the season, and calculated a set of network metrics among replicated sites to test whether honey bees change native plant-pollinator interactions.

In this study my objectives were to 1) determine if honey bees affect network metrics related to stability, plant overlap between pollinators, and pollinator overlap between plants; 2) determine if honey bees affect the proportion of pollinator species present that are observed visiting flowers and the proportion of available flowers that are visited; 3) determine if the effect of honey bees on network metrics is higher in the part of the season with highest honey bee colony size; and 4) determine if any effect of honey bees on plant-pollinator network metrics is due to changes in native plant-pollinator interactions, or due to honey bee-plant interactions.

Methods

This study took place over two years, 2018 to 2019, in the summer months between May to September. The methods were modified in 2019 to address issues in the sampling design (cattle presence, flower abundance, etc.), to allow for more robust sampling. Here, I first compare network structure for "meta-networks" (networks pooled across sites) for 2018 and 2019, in a qualitative examination of the effects of honey bees on network structure across years and honey bee treatments. These meta-networks were constructed from interaction data from all sites at a given distance from honey bee hives, pooled over the whole season within each year. Second, I use the 2019 data alone to statistically analyze the effect of honey bee abundance on network metrics for networks constructed from each site sampled in 2019.

2018 field site selection and study design

In 2018, I observed insect flower visitation along twelve 30 x 2 m transects at different distances from honey bee hives at Mattheis Research Ranch, near Brooks, Alberta, Canada. This grasslands region is characterized dry mixedgrass rangeland, agricultural cropland, salt flats, sand hills, riparian areas, badlands, and wetlands. The average high and low temperatures are 18.3 °C in July and -12.9 °C in January, respectively, with 300 mm of rainfall annually.

To use honey bees as a treatment, I placed three honey bee hives ≥2500 m apart, and placed sampling transects at set distances from these hives. I located six transects 100 m from a hive (with two per hive), to examine network interactions with honey bees. To examine network interactions without honey bees, I placed six transects 2500 m from any hive (see site map in Appendix X). As honey bees tend to forage less than 1000 m from their hive (Hagler et al., 2011), this ensured high densities of honey bees around the 100 m transects and lower densities around the 2500 m transects. The hives were fenced to prevent cattle disturbance.

2019 field site selection and study design

Field site selection was altered in 2019 to mitigate complications experienced in 2018, including disturbance by cattle, and to increase replication. In 2019, I established eighteen 30 x 2 m transects at 100 m, 500 m, and 5000 m distances from three clusters of honey bee hives (Figure 1). I increased the hive number in 2019 compared to 2018 to create honey bee densities more similar to those around commercial apiaries, and to increase the likelihood of detecting an effect of honey bees if there was one. Selected transects had similar microtopography and vegetation.

GPS coordinates for all transects and hive locations are in Appendix I for 2019 and Appendix XI for 2018. In 2018, honey bees were detected at transects 2500 m from hives, so in 2019 the farthest transects were placed ≥5000 m from hives. Honey bees can, but do not often, travel farther than 1000 m from their hive; exceeding 5000 m they expend more energy than the energy gained (Hagler et al., 2011), and as anticipated, I found very few honey bees at the 5000 m transects. Foraging distance in bees increases with body size (Greenleaf et al., 2007), so I expected the foraging distance for small-bodied bees to be less than for large-bodied pollinators. I assumed that syrphids have a range similar to bees and wasps (Golding et al., 2001, 2005), and small-bodied butterflies and beetles are unlikely to go much further than 2500 m. As such, I expected pollinator communities to be less independent at my 100m and 500m transects than at my 5000 m transects. However, as interaction network structure is a result of pollinator choice of floral resources as well as of what individual pollinators are present, complete independence of pollinator communities likely would not have produced very different results from those I obtained, especially as plant species composition similarity was not related to spatial proximity of the sites (compare Figure 2 and Appendix XII).

After July 9th, 2019, I stopped sampling at the 5000 m transect “F5000” because I observed many honey bees when there should have been few. I selected a new 5000 m transect, “G5000”, approximately 8000 m away from the northern 48 hive cluster (Figure 1).

Sampling plant-pollinator interactions and flower abundance

Each transect was visited once per week from June 12 to September 6 in 2018 for a total of 11 collection rounds, and from May 28 to August 28, 2019 for a total of 10 collection rounds.

However, during some collection rounds, some transects could not be sampled due to cattle disturbances or weather, resulting in different amounts of sampling for each transect (Appendices I; XI). Transects were visited only on warm (at least 15°C), sunny conditions with winds under 50 km/h to improve the chance of pollinator activity (Pasek, 1988; Sanderson et al., 2015). I measured wind speed with a Brunton Sherpa. We sampled between the hours of 9:30am and 5:00pm, when flower visits are highest (Lefebvre et al., 2014).

Transects were observed for 30 minutes by two observers for a total of 60 person-minutes per transect per collection round (3060 total collection minutes in 2018 and 4200 total collection minutes in 2019, for a total of 7260 collection minutes over the whole study). All insects that visibly contacted the anthers/stigma of open flowers were collected with a hand net and placed in individual vials with a label including date, flower, and transect code. Vials were kept frozen and brought back to the lab. All flowering plants on the transect were identified (using Bain et al. (2014); Moss & Packer (1994); Tannas (2003), (2004)), and their flowers were counted after visitation sampling.

In 2018, there were often periods where flowers were not present on the transect, and sampling could not be completed as originally planned. In 2019, when this occurred, I opted to move the transects up to 10 m in order to reach any flowers near the original transect demarcation. Moving the transect did not change distance to the hives. I will refer to these 2018 and 2019 datasets hereinafter as the “hand-caught” datasets.

Measuring flower visitor abundance and diversity with pan traps

To determine the proportion of pollinator species present that were observed visiting flowers, I used pan traps to sample flower visitor abundance and diversity independently of what I caught visiting flowers. Three pan traps were placed at 10 m intervals along each side of each transect, using two each of blue, white and yellow bowls. Pan traps were set out in the morning and retrieved no later than 55 hours after placement, with time exposed recorded to the nearest quarter hour. Trap contents were preserved in vials with 70% ethanol. Not all transects had complete collections due to cattle disturbance, weather, or road conditions (Appendices I; XI)

Insect Identification

All flower visitors from both seasons were pinned and identified to species in the lab. Pan trap samples from 2019 of bees, butterflies, and beetles were also identified. Some specimens, for which keys do not exist, were identified to "morphospecies" for 5% and 18% of species in hand-caught and pan-trapped datasets, respectively (Appendices II; III). All identifications were completed using a dissecting microscope, dichotomous keys, and comparison with reference specimens at the University of Alberta E. H. Strickland Entomological Museum, Edmonton, Canada and the University of Calgary Zoology Museum, Calgary, Canada. Identification assistance was provided by John Acorn for beetles and butterflies, Irene Jimenez Roncancio for wasps, Brittany Wingert for flies, James Glasier for ants, Greg Pohl for moths, and Lincoln Best for certain bee taxa.

Statistical analyses

Calculating network metrics

I was interested in testing whether the structure of the plant-pollinator interaction networks changed with honey bee abundance. In 2018 there were not enough flower visitors collected at each transect to analyze plant-pollinator networks for each transect separately, due to uneven sampling (Appendix XI). Therefore, similar to Valido et al. (2019), I pooled the network interactions across the season for the 100 m transects and 2500 m transects into two separate meta-networks (Figure 5). To compare these to 2019, when there were more hives and higher densities of honey bees, I also created one meta-network each for the full season interactions from the 100 m, 500 m, and 5000 m transects from 2019 (Appendix XIII). I calculated each network metric for each meta-network and compared these qualitatively (Table 6). In 2019, transects were sampled more evenly and frequently (Appendix I), so I pooled the hand-caught dataset across the full season to create one bipartite network for each transect, for a total of 19 networks, each representing the full period of sampling for that transect.

To analyze the effects of honey bees on network stability for the 2018 and 2019 hand-caught data, I calculated six network metrics. The first network metric for stability, weighted nestedness based on overlap and decreasing fill (Weighted NODF, hereinafter referred to as "weighted nestedness") is a measurement of nestedness, where nestedness means that interactions of specialists are subsets of the interactions of generalists (Almeida-Neto & Ulrich, 2011). The network metric modularity has many methods of calculation. I adopted the methods used by Valido et al., 2019 and calculated modularity using DIRT_LBA_wb_plus which computes modules with Newman's modularity measure (bipartite package, Dormann et al., 2008; Newman & Girvan, 2004). With this function, I ran 50 trials for each transect's network matrix and retained the output to two decimals. Interaction strength asymmetry describes, on average, how asymmetric the interactions are between interacting species pairs from each trophic level, where strength is the frequency of visits (Bascompte et al., 2003). Similarly, interaction evenness measures the evenness of the frequency of unique interactions using Shannon's evenness (Bersier et al., 2002; Tylianakis et al., 2007). Weighted connectance is a calculation of the proportion of interactions relative to the number of possible interactions in a network, and is therefore calculated by dividing the number of links by the number of cells in the species interaction matrix (Dormann et al., 2008). Lastly, link density measures the mean number of interactions per pollinator species weighted by the average number of interactions of each species (Bersier et al., 2002; Tylianakis et al., 2007).

To analyze honey bee effects on range of resource use and resource use overlap, I calculated seven additional network metrics. Weighted vulnerability and weighted generality are measurements of the weighted (by interaction frequency) mean number of pollinators per plant (vulnerability) and the weighted mean number of plants per pollinator (generality) (Bersier et al., 2002). Niche overlap describes the mean similarity in interactions between species at the same trophic level in the network. Values at 0 indicate no shared use of species, while a value of 1 indicates perfect niche overlap (Hurlbert, 1978). Functional complementarity is a multivariate measure of the dissimilarity of resource use within a trophic level (where pollinators are considered "resources" for plants, and plants are resources for pollinators). Higher values of functional complementarity indicate more complementary (or distinct) resource use between species within a trophic level (see more detail in Appendix IX). I calculated potential for competition for flowers between honey bees and all other pollinators at a site using the PAC function in the bipartite package (Dormann et al., 2009; Magrach et al., 2017). This function was originally written to calculate potential for apparent competition, based on (Müller et al., 1999), but following Magrach et al. (2017), I ran it with a transposed plant-pollinator matrix, such that it calculates potential for competition for flowers between each pair of pollinators in a plant-pollinator network. I summed the potential competitive effect of honey bees on every other pollinator species within a site, to calculate a single value representing the total potential for honey bees to affect all other pollinators through competition for shared flower species. All network metric calculations and statistical analyses were completed using R version 3.2.4. (R Core Team, 2020).

Proportion of species present that were observed interacting

One potential effect of a high density of honey bees on wild plant-pollinator interactions could be competitive exclusion of some pollinators from flowers, such that the excluded pollinators may shift to using flowers that they would not normally prefer in areas where honey bee densities are low. To determine the proportion of pollinator species that were observed visiting flowers out of the total pollinator species visiting the transect, I divided the number of bee species, beetle species, and butterfly species observed in the hand-caught dataset by the number of species observed in the pan trap samples, for bees, beetles, and butterflies, respectively, at each transect for the 2019 dataset. I first removed beetle species that are not known to pollinate (for example, ground beetles) but which were present in the pan traps. Additionally, to determine the proportion of flower species visited during visitation sampling, out of the total flower species on the transect, I divided the number of flower species occurring in the hand caught dataset by the total number of available flower species on the transect from the flower count dataset.

Honey bee abundance as a predictor variable

To test the effect of honey bee abundance on all the above network metrics and proportions of interacting bee, beetle, butterfly, and flower species for the 2019 data, I used linear regression, with the abundance of honey bees from the hand-caught dataset as the predictor variable, instead of using transect distance to hives, or honey bee abundance from the pan trap dataset. Neither pan-trapped nor hand-caught honey bee abundance had strictly decreasing abundance as hive distance increased (Figure 2, Appendix IV), meaning that distance from bee hives probably did not reflect actual “effect” of honey bees as much as my measurement of honey bee abundance visiting flowers. Honey bee abundance from the 2019 hand-caught data was therefore pooled across the full season for each transect and divided by number of collection rounds, and was used as the predictor variable in all statistical models (Figure 2). However, the structure of a plant-pollinator network will also depend on what flower species are available to pollinators, their relative abundances, and sampling effort, and local honey bee abundance may also respond to these variables. Because of this, I tested whether flower community variables (flower abundance and flower species richness) and collection effort (number of collection rounds at that transect) were correlated with honey bee abundance by calculating Pearson correlation coefficients between all these variables (Appendix XIV).

Effect of honey bee abundance on full season network structure

I used general linear mixed models (GLMMs) to test the effect of honey bee abundance on each response variable (weighted nestedness, modularity, interaction strength asymmetry, interaction evenness, weighted connectance, link density, vulnerability, generality, pollinator and plant niche overlap, pollinator and plant functional complementarity, potential for competition, and proportion of interacting pollinator and plant species) for the 2019 data. I tested the effects of honey bee abundance on these response variables for several datasets: 1) each transect's network from the full season 2019 hand-caught dataset ("Full season all taxa"); 2) only bees, including honey bees, from these same networks ("Full season bees-only"; and 3) for each transect's network for the mid-season only ("Mid-season all taxa"; described below). Modularity was only calculated for the full season all taxa dataset; as it was not significant, I did not calculate it for other datasets. Using these methods I was able to test across higher taxa (bees) and different time periods whether honey bees affect network structure in this region.

First, for each response variable, I ran a GLMM with honey bee abundance as the only predictor variable. Some of the transects were close together, so I plotted a map of the standardized residuals of each GLMM and visualized whether similar residuals were close together in space, to examine whether a special correlation structure was necessary to account for any spatial autocorrelation (Appendix XV). I then ran generalized least squares (GLS) mixed models with different correlation structures (no correlation, corEcp, corGaus, corSpher, corLin, corRatio) for each response variable (nlme package, Jose et al., 2020). After all models with correlation structures (including no special correlation structure) were run, the AICc values were calculated, and the lowest AICc value model was selected (MuMin package, Bartoń, 2020). The best models for each predictor variable did not include special correlation structures, so GLMs rather than GLMMs were run.

After analyzing the effect of only honey bee abundance as a predictor variable, I ran an additional GLM for each response variable. Because I found that the variables flower abundance, number of available flower species, and collection effort were positively correlated with honey bee abundance (Appendix XIV), I included them as additional predictor variables in the second set of models. I used the same model selection approach as above to select the predictor variable(s) that best explained that response variable. The predictor variables included in each full model were honey bee abundance, flower abundance, flower species richness, total number of collections, as well as the interactions between honey bee abundance and flower abundance, and the interaction between honey bee abundance and flower species richness. All continuous predictor variables were standardized. I then ran the full model, and all possible simpler models, for a total of 21 linear models per response variable (nlme package, Jose et al., 2020), and selected the best model using AICc. If honey bee abundance was retained after model selection and was significant, it would suggest that there was an unambiguous effect of honey bees on that response variable that could not be attributed to other correlated predictor variables. If honey bee abundance was significant in the first model (where it was the only predictor variable), but was either not retained or not significant for the second model (with the additional predictor variables), it would suggest that that response variable is related to honey bee abundance, but any effects of honey bees cannot be unambiguously attributed to honey bees, as they may be due to flower variables or collection effort, which honey bees were responding to themselves.

The assumptions of normality for each response variable were examined by running a Shapiro-Wilk test and visually examining Quantile-Quantile plots. I examined the homogeneity of variances for each response variable by examining plots of fitted values versus residuals to look at whether variance of the residuals was homogenous along the range of fitted values. If any assumptions were not met, that response variable was log transformed and model selection was repeated, after which, if assumptions were still not met, I applied a Box-Cox transformation (MASS package, Venables & Ripley, 2002). Transformation did not improve normality or variance homogeneity for bees-only interaction strength asymmetry, so I interpreted the P-values cautiously, though they were not significant.

Effects of honey bee abundance on mid-season network structure

I was also interested in whether the effects of honey bee abundance on the network metrics differed mid-season, when honey bee population size was highest. I divided honey bee abundance across the season into three roughly equal-length periods: “early”, “mid” and “late”, based on natural breaks in the abundances of honey bees (Appendix VII). Because honey bee abundance was highest in the mid-season window, when honey bee population size is typically largest (Canadian Honey Council, 2018), I tested the effects of honey bee abundance on all the same response variables as above, for only the mid-season all taxa dataset. First, I fitted the GLM for each response variable, with honey bee abundance as a fixed predictor variable, and used model selection as described above to arrive at the best model. Because some transects’ networks were too small in the mid-season to obtain accurate values (A100, B100, B500, E100), they were removed from this analysis.

Effect of honey bees on structure of the full season without-honey bees network

After all model selection was completed for the above analyses, I created a reduced network from the full season all taxa dataset where all honey bees were removed from the network. In this without-honey bee dataset I tested all the same response variables for which honey bee abundance was a significant predictor in the second set of models described above. If honey bee abundance remained a significant predictor in these models, it would indicate that honey bees altered how wild pollinators interact. If honey bee abundance did not remain a significant predictor in these models, it would indicate that the changes caused by honey bee abundance were just due to the honey bee node and links contributing to the network structure.

This analysis involved interpreting 67 separate P-values, so to maintain Type I Error at 0.05, I used a Bonferroni-Holm correction. The Bonferroni-Holm correction is a less conservative form of adjusting for multiple comparisons, but I present all P-values, to allow consideration of uncorrected P-values.

Lastly, to estimate the interaction sampling completeness in both 2018 and 2019, I divided the raw interaction richness across all transects by the Chao1 estimated total interaction richness across all transects (SpadeR, Chao et al., 2016). This estimated the proportion of the estimated total number of unique interactions that my sampling detected (as in Chacoff et al., 2012).

Results

Diversity of interactions in the grassland plant-pollinator community

I recorded a total of 123 pollinator species and 27 plant species involved in 534 interactions from the 2018 full season all taxa dataset, with 236 unique plant-visitor interactions (distinct interactions between one species of visitor and plant). Of these interactions, 136 were one-time interactions (where an interaction between a given plant and pollinator species was observed only once). The Chao1 estimated true total number of unique interactions for this year was 540 interactions (95% confidence interval: 430-712 interactions), meaning that I observed 33 - 55% of the estimated interactions (Appendix XVI). Honey bees made up 108 (20%) of the interactions; at 100 m transects, honey bees made up 26.7% of the total interactions, and at 2500 m transects, 0.75% of the interactions. Of total full-season all-taxa interactions, bees (including honey bees) made up 236 (44.2%), flies made up 38 (7.1%), butterflies made up 50 (9.4%), ants made up 23 (4.3%), beetles made up 20 (3.7%), and wasps made up 11 (2.1%). Moths and true bugs were not included in identifications in 2018 but remained uncommon in 2019. Honey bees were the most common pollinator and hairy goldenaster (*Heterotheca villosa)* was the most common flower visited.

I recorded a total of 281 pollinator species and 37 plant species involved in 1,814 interactions from the 2019 full season all taxa dataset, with 654 unique plant-visitor interactions. Of these interactions, 425 were one-time interactions. The Chao1 estimated true total number of unique interactions for 2019 was 1,779 interactions (95% confidence interval: 1500-2148 interactions), meaning that I observed 31 – 44% of the estimated interactions (Appendix XVI). Honey bees made up 286 (16%) of the total full season all taxa interactions; at 100 m transects, honey bees made up 29.4% of the total interactions, at 500 m transects, 14.9% of the total interactions, and at 5000 m transects, 1% of the interactions. Of total full season all taxa interactions, bees (including honey bees) made up 872 (48.1%). Of remaining interactions, flies made up 494 (27.2%), butterflies made up 130 (7.2%), ants made up 104 (5.7%), beetles made up 100 (5.5%), wasps made up 62 (3.4%), true bugs made up 27 (1.5%), and day-flying moths made up 25 (1.4%). Honey bees were the most common pollinator in the full season all taxa dataset and western snowberry (*Symphoricarpos occidentalis)* was the most common flower visited. In the mid-season all taxa dataset, at 100 m transects, honey bees made up 49.6% of the interactions, at 500 m transects, 25.2% of the interactions, and at 5000 m transects, 2.4% of the interactions. All species identifications are listed in Appendices II, III, and VIII. The proportion of observed flower visiting pollinator species over number of pollinator species in pan traps, as well as the proportion of flowers visited over the number of total flowers on the transect, was tested against honey bee abundance, but there was no significant effect (Table 7d).

Network structure of full season meta-networks

The 2018 and 2019 full season meta-networks had a general increase in each network metric with distance to a hive, with the exception of plant niche overlap, plant and pollinator functional complementarity, and generality (Table 6). In 2019, some metrics, such as modularity, weighted connectance, and interaction strength asymmetry, decreased from 100 m distances to 500 m distances, before increasing at 5000 m transects. Conversely, generality increased from 100 m distances to 500 m distances, before decreasing at 5000 m transects (Table 6).

Effect of honey bees on network structure in full season dataset 2019

In the first set of models testing honey bee abundance as the only predictor against all network metrics, increasing honey bee abundance was associated with significant increases in network metrics related to resource use and niche overlap. Here, all reported P-values are significant after the Bonferroni-Holm correction. Plant functional complementarity (t = 6.39, P = 6.66E-06) and pollinator functional complementarity (t = 5.92, P = 1.67E-05) significantly increased with honey bee abundance, suggesting that for both plants and pollinators, resource use is more dissimilar between species the more abundant honey bees are. Potential for competition also had a significant positive relationship to honey bee abundance (t = 7.82, P = 4.99E-07), indicating that the potential for honey bees to compete for floral resources with other pollinator species increases as honey bee abundance increases (Table 7a). Increasing honey bee abundance was associated with significant decreases in network metrics related to stability: interaction evenness (t = -4.33, P = 0.0005) and weighted connectance (t = -4.07, P = 0. 0008) (Table 7a).

In the second set of models, including all predictor variables (honey bee abundance, flower abundance, flower species richness, total number of collections, as well as the interactions between honey bee abundance and flower abundance, and the interactions between honey bee abundance and flower species), if honey bee abundance was retained after model selection, and was significant, this indicated that honey bee abundance affected the response variable over and above any correlation between honey bee abundance and the other predictor variables. In running the second set of models, total flower species richness and collection effort best explained most response variables (Table 8a). However, increasing honey bee abundance was still associated with significant increases in pollinator functional complementarity (t = 5.51, P = 4.80E-05), plant functional complementarity (t = 5.75, P = 2.96-E-05, and potential for competition (t = 7.82, P = 4.99E-07), and a significant decrease in interaction evenness (t= -0.0475, P = 0.0005) (Table 8a).

In comparison to the full season all taxa dataset, the results for the full season bees-only dataset, with honey bee abundance as the only predictor variable, were very similar, though after the Bonferroni-Holm correction, weighted connectance was no longer significant. Increasing honey bee abundance was associated with significant increases in pollinator functional complementarity (t = 4.42, P = 0.0004), plant functional complementarity (t = 7.52, P = 8.39E-07), and potential for competition (t = 5.40, P = 4.81E-05) (Table 7b). Increasing honey bee abundance was also associated with a significant decrease in interaction evenness (t = -6.33, P = 7.53E-06) (Table 7b). After running the second set of models including all predictor variables, honey bee abundance was associated only with a significant increase in plant functional complementarity (t = 6.64, P = 5.65-E-06), and a significant decrease in interaction evenness (t = 4.56, P = 0.0003) (Table 8b).

Effect of honey bees on network structure in mid-season all taxa dataset 2019

The results for the mid-season all taxa dataset were similar to those for the full season all taxa dataset with honey bee abundance as the only predictor variable, after the Bonferroni-Holm correction, though weighted connectance and potential for competition were no longer significant. Increasing honey bee abundance was associated with significant increases in pollinator functional complementarity (t = 4.41, P = 0.0007) and plant functional complementarity (t = 10.11, P = 1.58E-07), which had high, positive slopes (Table 7c). Increasing honey bee abundance was also associated with significant decrease in interaction evenness (t = -7.94, P = 2.43E-06), which had a high, negative slope (Table 7c). After running the second set of models including all predictor variables, honey bee abundance was still associated with a significant increase in pollinator functional complementarity (t = 4.41, P = 0.0007) and plant functional complementarity (t = 10.11, P = 1.58E-07), and a significant decrease in interaction evenness (t = -7.94, P = 2.43E-06) (Table 8c).

Effect of honey bees on structure of the full season without-honey bees network

In comparison to the full season all taxa dataset, the full season without-honey bees dataset with only honey bee abundance as a predictor variable showed that honey bees no longer had a significant effect on pollinator functional complementarity, plant complementarity, or interaction evenness (Table 8d). The three main response variables that were significantly related to increasing honey bee abundance (pollinator functional complementarity, plant functional complementarity, and interaction evenness), across all three with-honey bee datasets above, are shown in Figure 6, and shown again in Figure 7, as calculated from without-honey bee networks.

Discussion

When considering all interactions (including honey bee interactions), network structure did change with increasing honey bee abundance, as has been reported in other studies. Change may not have been observed if honey bees replaced a role within the network. Across all three datasets (full season all taxa, full season bees-only, and mid-season all taxa), pollinator functional complementarity and plant functional complementarity significantly increased, and interaction evenness significantly decreased with increasing honey bee abundance, though pollinator functional complementarity did not change significantly when looking at the bees-only dataset (Table 8b). Additionally, in the full season all taxa dataset, potential for competition significantly increased with honey bee abundance (Table 8a). When looking at the meta-networks for 2018 and 2019, interaction evenness, pollinator functional complementarity and plant functional complementarity all qualitatively matched the statistical results from 2019, and all matched the slopes for each metric calculated in 2019 (Table 6). However, when considering only native plant-pollinator interactions (in the full season dataset from which honey bee interactions were removed), honey bee abundance did not affect any network metrics, even during the mid-season when honey bee density is highest (Table 8d). This suggests that all changes to network structure associated with honey bee abundance in this study were caused by the honey bees node and links contributing substantially to the network structure, rather than by honey bees altering the interactions of wild pollinators. As well, native bees, which are usually thought most likely to face competition from honey bees, made up approximately a third of the total interactions, but their resource use, niche overlap, and functional complementarity were not affected by honey bees. Additionally, honey bees did not affect the proportion of observed species interacting, or the proportion of flowers visited (Table 7d). These results, therefore, strongly suggest that adding honey bees had no effect on the network structure of the native plant-pollinator interactions in this region. This has not been assessed by other studies.

Magrach et al. (2017) found similar results to my with-honey bee networks: honey bees decreased interaction evenness and increased functional complementarity in their system. The increase in functional complementarity indicates increasing dissimilarity in the interaction composition of pollinators and plants in the network which can be thought of as a reduction of their resource use overlap (Devoto et al., 2012). However, Magrach et al. (2017) only tested with- versus without-honey bees networks for honey bee effects on link density (which were very small in without-honey bee networks), but not on interaction evenness or functional complementarity. So, although their with-honey bee network results are similar to mine, I found that when honey bees were removed from the network, the effect of honey bee abundance disappeared, suggesting no effect of honey bees on native plant-pollinator interactions. This suggests that the changes to interaction evenness and functional complementarity reported by Magrach et al. (2017) may have been entirely due to honey bee-plant interactions (i.e., the new honey bee node and all its links to plants added to the network), as opposed to due to competitive effects of honey bees causing changes to the existing structure of the native pollinator nodes and their links to plants. Just like in my study, it may well be that native plant-pollinator interactions were not affected by honey bees in their study either, but this was not tested.

Valido et al. (2019) did not assess interaction evenness or functional complementarity, but also did not remove honey bees from the network and re-test effects of honey bee abundance on the network metrics that they report. Additionally, they did not control for floral abundance or flower species richness as potentially correlated predictor variables. Thus, it is hard to be sure what the significant changes in network metrics associated with honey bees in their study (connectance, weighted nestedness, modularity) actually mean ecologically. Furthermore, in comparing my study to Magrach et al. (2017) and Valido et al. (2019), mine had similar sampling effort, range of honey bee abundances tested, and estimated sampling completeness. Magrach et al. (2019) had a total of 4080 collection minutes over two sampling years; comparatively, my study had 3060 collection minutes in 2018 and 4200 in 2019, for a total of

7260 collection minutes over two years. As well, in my study, honey bees made up 0.75%-26.7% of interactions in 2018 and 1%-29.4% of interactions in 2019, in comparison to Magrach et al. (2017) with 38.66 ± 15% to 72.93 ± 10%, and Valido et al. (2019) with 0.3-33.6% of interactions. Taken together, this suggests that if they had used more robust methods, these two studies may also have found a non-significant effect of honey bees on native plant-pollinator network structure. Although changes to the entire network structure when honey bees are present (that result just from the added honey bee node and its links) are interesting in terms of understanding the network role of a generalist species (Geslin et al., 2017), Magrach et al (2017) and Valido et al (2019) interpret their results from a conservation perspective, as though they have showed that honey bees cause changes to native plant-pollinator interactions, which in fact they have not. In short, I present a more robust analysis of the effect of honey bees on a native plant-pollinator community than has previously been reported, and I found that there was no significant effect. This is corroborated by observations in the field: there did not appear to be observable reductions in the preference or use of flowers by native pollinators, despite honey bee presence on the same flower or individual plant. These findings add support to my conclusion that the effect of honey bees on functional complementarity and interaction evenness is likely due to honey bee links in the network, and not from modifications to native plant and pollinator interactions. Native plant-pollinator interactions appear to be resilient to the addition of high abundances of honey bees in this dry grassland ecosystem.

There are some possible explanations for my results. In this community with diverse flora, it could be that honey bees do not have a competitive advantage over wild pollinators, due to abundant floral resources that are not limiting, a variety of generalist pollinators, and/or the competition-minimizing nested structure of most plant-pollinator networks. Generalists can have dispersed interactions with a variety of native plants, weakening their interactions and therefore weakening their impact on already existing mutualisms (Traveset & Richardson, 2006). As the proportion of plants available that were visited did not change with increasing honey bee abundance, it supports the idea that honey bees were not shifting the niches of other pollinators to use less-preferred plants, and that floral resources were not limiting for pollinators. Floral resource use did not change when honey bees were abundant, except that honey bees also visited them. This is also reflected in the vulnerability metric (the weighted average number of pollinator species visiting each plant species), which did not significantly change with honey bee abundance (Table 7).

Though the Alberta grasslands are diverse and dominated by native plant species, there are also many exotic plants in the region; sweet clover (*Melilotus* spp.), sow-thistle (*Sonchus* spp.), and cicer milk-vetch (*A. cicer*), in particular, are widespread. Some of these were historically introduced for cattle grazing and all occurred in numerous patches throughout the study site. These exotic species were also observed to be highly attractive to pollinators of all types. In their network study, Bendel et al. (2019) determined that honey bees preferred exotic plants over native plants, which also agrees with our observations in the field. Small-flowered and small-stemmed plants, such as *C. rotundifolia* or *Symphiotrichum falcatum,* appeared to be unappealing to large-bodied pollinators (honey bees and *Bombus* spp. alike). The preference for exotic plants may have helped prevent honey bees from outcompeting wild pollinators for resources, preserving native plant-pollinator interactions in the network.

It is also a possibility that the plants and pollinators in this region are undergoing a state of exaptation. Since honey bees have been present in the region for at least a century (though not present on Mattheis Ranch this long), they may have already replaced the role of a hypothetical wild generalist pollinator and assumed its central role. This may retain the network's structure and the functional diversity of interactions, but may impact specialists in the network into the future by competition for their specific resources (Aslan, 2019). Furthermore, a study by Vilà et al. (2009) determined that exotic generalist plants did not create substantial changes in bipartite plant-pollinator network connectance, link density, or nestedness, in sites where they were present versus absent, in six locations across Europe, and the same may hold true for some systems where generalist honey bees have been introduced. The plant-pollinator network may be resilient to the introduction of honey bees, integrating them into the system without major changes, despite their taking a central role (Vilà et al., 2009). This is also supported by ideas from complexity theory, which would predict that plant-pollinator networks with a few large central nodes, and many small less-central nodes, would exhibit resilience in the face of most perturbations (Gunderson, 2000).

A future study will measure morphological traits of the plants and pollinators from the 2019 hand-caught dataset, to test whether trait matching is important in determining which plants and pollinators interact. Additionally, pollen was removed from bees from three collection rounds in 2019, and analysis of the pollen may may reveal the most polylectic species, their preferences, and the proportions of conspecific pollen they carried, indicating honey bee preferences that are not visible through network data alone. It should also be mentioned that this study does not address concerns over pathogens or disease, and the possibility that they may be spreading from honey bees to wild pollinators. These data will be used in future work to attempt to predict pathways of disease transmission and the potential of disease spread through the network.

Conclusions

Mutualistic systems, such as plant-pollinator networks, are complex and dynamic and can change through time (Bendel et al., 2019) or through the introduction of new species (Magrach et al., 2017; Valido et al., 2019). In the grasslands region of southern Alberta, where honey bee abundance is high and increasing, I expected that abundant honey bees would alter, in some way, native plant-pollinator network interactions. However, upon inspection of network structure, results indicated that honey bees did not affect the native plant-pollinator interactions in this system. This implies that the system is resilient, at least in the short term, to honey bee addition, and that it can integrate the introduction of non-native species into its structure without major impact. While this study does not cover all the potential negative effects that honey bees can have on native plant-pollinator communities, it raises doubts about whether honey bees negatively impact native interaction networks in all contexts. These findings suggest that honey bees have no apparent effect on native grassland plant-pollinator communities in this region, and resources for conservation efforts can be focused elsewhere.

Tables

Table 6. Comparison of the full season meta-network metrics calculated for both the 2018 and 2019 hand caught datasets. There was a general increase in each network metric with distance to a hive, with the exception of plant niche overlap, functional complementarity, and generality. Bolded values indicate results that were unexpected based on the literature and/or expectations if competition between honey bees and wild pollinators is occurring. Positive (+) indicates a positive correlation between honey bee abundance and the metric, while negative (-) indicates a negative correlation.

	2018 Data			**2019 Data**			
	100 m	**2500 m**		**100 m**	**500 m**	**5000 m**	
Weighted nestedness	**6.60**	**9.66**	**-**	**4.21**	**4.15**	**5.97**	**-**
Modularity	0.47	0.51	-	0.59	0.58	0.63	-
Weighted connectance	**0.06**	**0.11**	**-**	**0.04**	**0.04**	**0.05**	**-**
Interaction strength asymmetry	**0.16**	**0.28**	**-**	**0.18**	**0.13**	**0.23**	**-**
Link density	6.63	7.72	-	6.11	7.69	8.25	-
Interaction evenness	0.60	0.64	-	0.54	0.60	0.61	-
Pollinator niche overlap	0.14	0.26	-	0.12	0.09	0.14	-
Plant niche overlap	**0.11**	**0.06**	**+**	**0.06**	**0.07**	**0.04**	**+**
Pollinator functional complementarity	255.97	63.99	+	476.78	427.39	339.66	+
Plant functional complementarity	171.05	64.82	+	411.43	355.71	255.55	+
Generality	**2.95**	**1.78**	**+**	**2.29**	**2.94**	**2.06**	**+**
Vulnerability	10.31	13.65	-	9.92	12.45	14.44	-

Table 7. Selected models with the lowest AICc values for each response variable, where the full model for each response variable contained honey bee abundance as the only predictor variable. Results are shown for the three 2019 datasets: a) the full season all taxa dataset, b) the full season bees-only dataset, c) the mid-season all taxa dataset, and d) the proportion of species present that were observed interacting. Bolded P-values denote significance with Bonferroni-Holm correction. Transformations are listed with the response variable.

Response variable with honey bee abundance	**Partial regression coefficient**	**t-value**	**P-value**
a) Full season all taxa			
Weighted nestedness	-0.3371	-0.58	0.5730
Modularity	0.0011	0.05	0.9650
Weighted connectance	-0.0262	-4.07	**0.0008**
Interaction strength asymmetry	-0.0879	-2.25	0.0381
log(Pollinator niche overlap)	-0.1398	-1.82	0.0910
Plant niche overlap	-0.0040	-0.55	0.5910
log(Generality)	0.0238	0.58	0.5720
Vulnerability	-0.8657	-1.44	0.1710
Interaction evenness	-0.0475	-4.33	**0.0005**
Link density	-0.3514	-1.02	0.3200
Pollinator functional complementarity	34.594	5.924	**1.67E-05**
Plant functional complementarity	32.421	6.394	**6.66E-06**
Potential for competition	2.9422	7.82	**4.99E-07**
b) Full season bees-only			
Weighted nestedness	-0.1993	-0.17	0.8700
Weighted connectance	-0.0361	-3.05	0.0073
Interaction strength asymmetry	-0.0376	-1.24	0.2333
Pollinator niche overlap	-0.0375	-1.28	0.2240
Plant niche overlap	-0.0031	-0.12	0.9058
Generality	0.0617	0.88	0.3960
log(Vulnerability)	-0.0927	-1.86	0.0851
Interaction evenness	-0.0777	-6.33	**7.53E-06**
Link density	-0.1088	-0.90	0.3820
log(Pollinator functional complementarity)	0.6516	4.42	**0.0004**
Plant functional complementarity	34.6900	7.52	**8.39E-07**
Potential for competition	1.3992	5.40	**4.81E-05**
c) Mid-season all taxa			
Weighted nestedness	1.2010	0.60	0.5679
Weighted connectance	-0.0360	-2.22	0.0450
Interaction strength asymmetry	-0.0880	-1.53	0.1500
Pollinator niche overlap	-0.0596	-0.93	0.3790
Plant niche overlap	-0.0154	-0.48	0.6474
Generality	0.0023	0.04	0.9660
Vulnerability	-2.2903	-2.18	0.0605
Interaction evenness	-0.1242	-7.94	**2.43E-06**
Link density	-0.8758	-2.58	0.0227

log(Pollinator functional complementarity)	0.6423	4.41	**0.0007**
Plant functional complementarity	31.8550	10.11	**1.58E-07**
Potential for competition	1.1894	3.62	0.0031
d) Proportion of species present that were observed interacting			
Bees	1.7780	1.00	0.3340
log(Beetles)	0.4361	1.79	0.0912
log(Butterflies)	-0.0225	-0.15	0.8810
Flower species richness	1.5790	0.44	0.6660

Table 8. Selected model with the lowest AICc value for each response variable, where the full model for each response variable contained honey bee abundance, flower abundance, flower species richness, the interactions between honey bee abundance and flower abundance, and between honey bee abundance and flower species richness, and collection effort as predictor variables. Results are shown for four 2019 datasets: a) the full season all taxa dataset, b) the full season bees-only dataset, c) the mid-season all taxa dataset, and d) the full season without-honey bees dataset. Bolded P-values denote significance with Bonferroni-Holm correction. Transformations are listed with the response variable.

Response variable	**Predictor variables retained in final model**	**Partial regression coefficient**	**t-value**	**P-value**
a) Full season all taxa				
Weighted connectance	flower species richness	-0.0212	-3.57	0.0025
	collection	-0.0143	-2.41	0.0285
Interaction strength asymmetry	flower species richness	-0.1136	-3.25	0.0047
Interaction evenness	honey bee	-0.0475	-4.33	**0.0005**
Pollinator functional complementarity	honey bee	26.2380	5.51	**4.80e-05**
	collection	18.8970	3.97	0.0011
Plant functional complementarity	honey bee	25.8630,	5.75	**2.96e-05**
	collection	14.8320	3.30	0.0045
Potential for competition	honey bee	2.9422	7.82	**4.99E-07**
b) Full season bees-only				
Weighted connectance	flower species richness	-0.0476	-5.20	**0.0001**
Interaction evenness	honey bee	-0.0887	-4.56	**0.0003**
log(Pollinator functional complementarity)	honey bee	0.4534	3.57	0.0026
	collection	0.4481	3.52	0.0028
Plant functional complementarity	honey bee	29.6150	6.64	**5.65e-06**
	collection	11.4760	2.57	0.0204
Potential for competition	honey bee	0.9331	3.13	0.0065
	flower species richness	0.7245	2.43	0.0273
c) Mid-season all taxa				
Weighted connectance	flower species richness	-0.0486	-2.93	0.0116
Interaction evenness	honey bee	-0.1242	-7.94	**2.43E-06**
Link density	honey bee	-0.8758	-2.58	0.0227
log(Pollinator functional complementarity)	honey bee	0.6423	4.41	**0.0007**
Plant functional complementarity	honey bee	31.8550	10.11	**1.58E-07**
Potential for competition	honey bee	1.1894	3.62	0.0031
d) Full season without-honey bees				

Interaction evenness (*CorGaus*)	honey bee	-0.0142	-1.85	0.0817
Pollinator functional complementarity	honey bee	0.9445	0.15	0.8810
Plant functional complementarity	honey bee	1.7320	0.32	0.7530

Figures

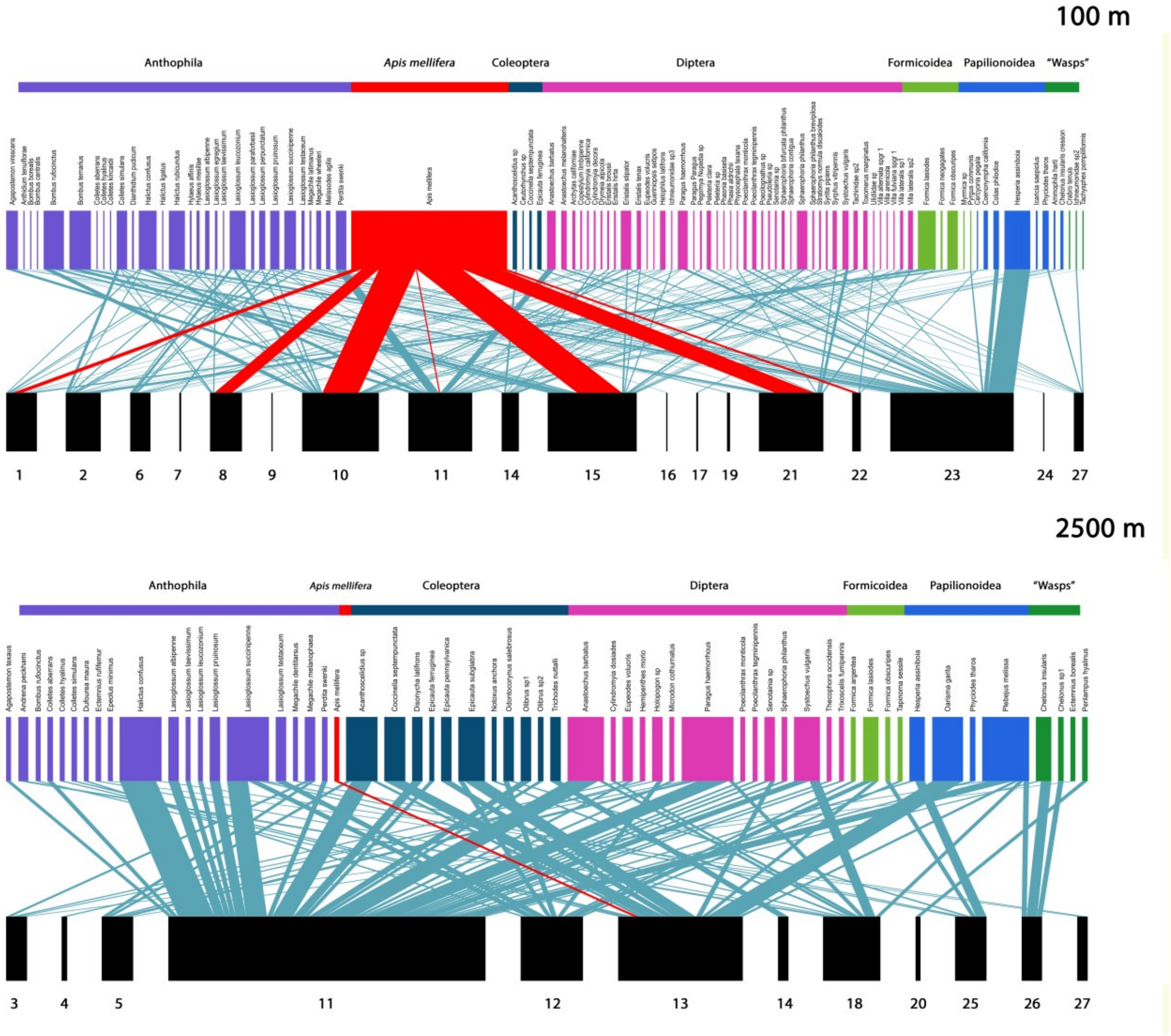

Figure 5. Plant-pollinator meta-networks from the 2018 full season all taxa hand-caught dataset. The data from transects 100 m (upper) and 2500 m (lower) from honey bee hives are pooled across the season. The bottom row (in black) depicts the plant species (see Appendix XVII) and the upper row depicts the pollinator species by their given taxonomic "group" or Order. For full species list, see Appendix II. "Wasps" are insects within Aculeata that excludes ants (Formicoidea) and bees (Anthophila). The width of each upper and lower bar represents the relative frequency of interactions observed for that species. The interactions between the plants

and pollinators are represented by blue lines, and width indicates the frequency of the interaction. Honey bees are indicated in red. The 100 m meta-network had 400 interactions between 94 pollinator species and 18 plant species; the 2500 m meta-network had 134 interactions between 57 pollinator species and 12 plant species.

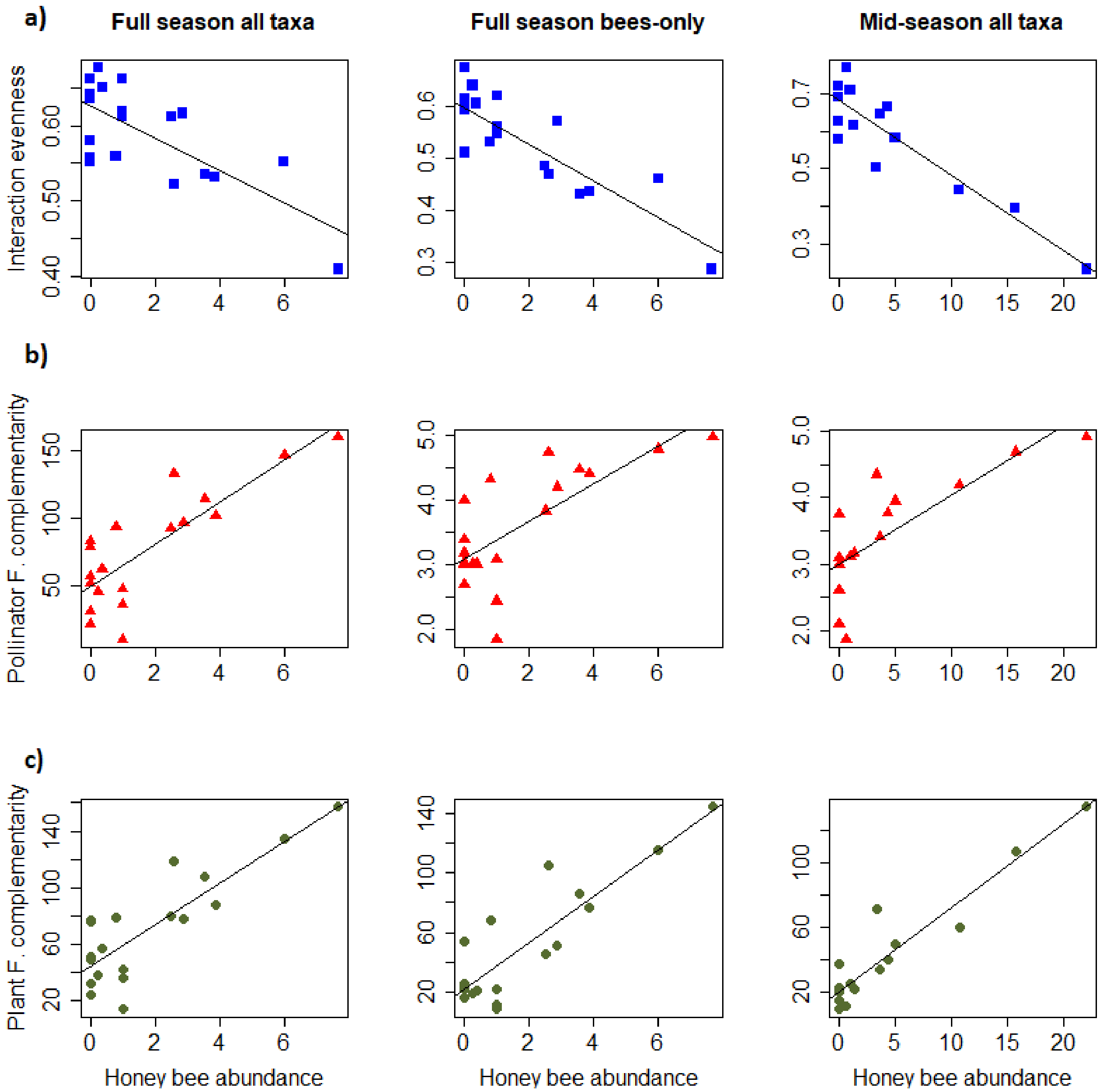

Figure 6. Relationships between honey bee abundance (divided by number of collection rounds) and the network metrics: (a) interaction evenness, (b) pollinator functional complementarity, and (c) plant functional complementarity that were significantly related to honey bee abundance across three datasets (full season all taxa, full season bees-only, and mid-season all taxa). Solid regression lines all indicate significant relationships with Bonferroni-Holm correction.

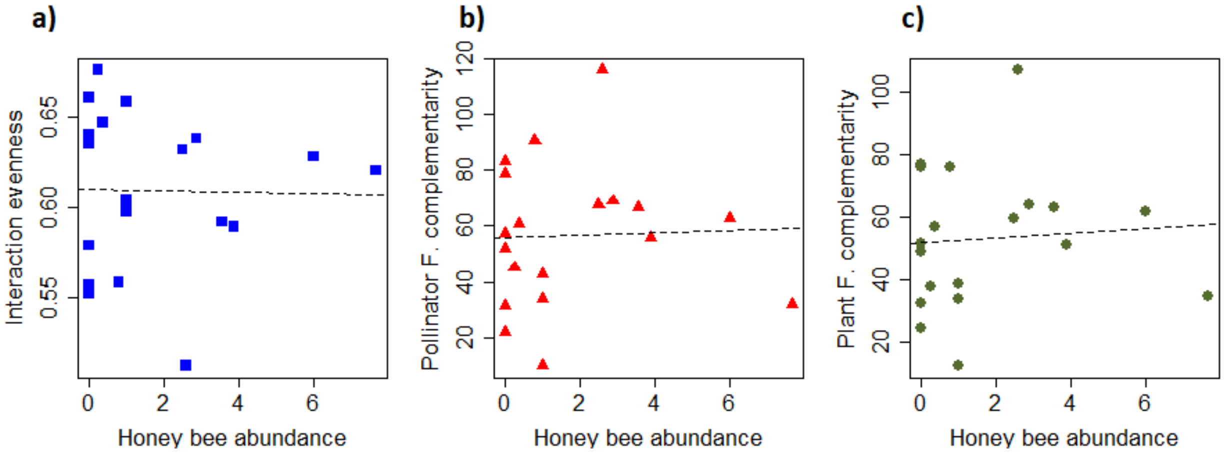

Figure 7. Relationships between honey bee abundance (divided by number of collection rounds) and the network metrics: (a) interaction evenness, (b) pollinator functional complementarity, and (c) plant functional complementarity in the without-honey bees dataset. Dashed regression lines all indicate non-significant relationships with Bonferroni-Holm correction.

Chapter four: Summary & Conclusion

In this study, my aim was to examine if honey bee abundance affected wild pollinator diversity, abundance, or the diversity of their interactions; and, similarly, if honey bee abundance affected the structure and function of the native plant-pollinator network.

In Chapter 2, I assessed this by examining differences in flower visitor richness, diversity, abundance, species composition, and the diversity of plant-pollinator interactions at sites 100 m, 500 m, and 5000 m away from honey bee hives. Across the full season dataset, as well as six subsets of this dataset focusing on single insect orders or the part of the season with highest honey bee abundance, I found a positive relationship between honey bee abundance and native beetle diversity, but other positive effects were attributed more strongly to the abundance and diversity of flower species. Honey bees, even at high densities in mid-season, did not negatively impact the diversity or abundance of native pollinators, or the diversity of their plant-pollinator interactions.

In Chapter 3, I assessed this same general question by examining differences in network structural metrics related to network stability, and resource overlap between pollinators and between plants. I looked at three datasets, a full season all taxa dataset, full season bees-only dataset, and mid-season all taxa dataset, in which honey bee abundance had a significant positive relationship to pollinator functional complementarity and plant functional complementarity, and a significant negative relationship to interaction evenness, over and above correlated effects of flower community variables and collection effort. However, after reassessing the same networks with honey bee interactions removed, these variables were no longer significantly affected by honey bee abundance. This suggested that honey bees themselves contributed to the network structure by their interactions with plants, rather than altering wild pollinators' interactions. As in Chapter 2, a diverse array of flower species, providing abundant nectar and pollen resources, may explain these results. Honey bees may not competitively exclude wild pollinators due to dispersed interactions with a variety of native plants, weakening the strength of their interactions with any one plant species, and as a result their impact on existing mutualisms.

This study provides, for the first time, a robust, experimental analysis of the effects of introduced honey bees on native plant-pollinator communities. The Alberta grassland communities where this study took place are at risk, but are resilient to the introduction of honey bees, maintaining their diversity, and integrating honey bees into the network structure without any detectable change to pre-existing plant-pollinator interactions. The negative effects of honey bee abundance reported in other studies may be context-dependent and may vary between regions and years, suggesting that there is yet no clear answer on the way they should be managed. However, maintaining the diversity and abundance of wild pollinators and plants should be prioritized, if we want them to remain resilient to disturbances and introduced species.

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Appendix

Appendix I. Longitude and latitude for each hive location and transect in 2019, and collection effort at each transect. The northernmost, central, and southernmost hive locations are listed as Bee48, Bee32, and Bee16 respectively, indicating their number of hives. Each transect is indicated by its treatment (100 m, 500 m, or 5000 m distance from a hive location). Letters indicate each replicate (See Figure 1). G5000 indicates the new position for F5000 that was moved mid-season.

Longitude	Latitude	Transect	Total hand-caught collections	Total pan trap collections
-111.91850	50.90210	Bee48		
-111.94658	50.88120	Bee32		
-111.93580	50.84320	Bee16		
-111.91992	50.90202	A100	10	10
-111.92545	50.90248	A500	10	10
-111.98687	50.91594	A5000	8	8
-111.91699	50.90205	B100	7	10
-111.91010	50.90265	B500	6	6
-111.85447	50.88185	B5000	8	8
-111.94792	50.88178	C100	9	9
-111.95325	50.88365	C500	8	8
-112.00554	50.90691	C5000	8	8
-111.94533	50.88081	D100	9	9
-111.94149	50.87831	D500	9	9
-111.87483	50.86788	D5000	8	6
-111.93735	50.84338	E100	3	10
e-111.94283	50.84407	E500	8	10
-111.99767	50.93795	E5000	7	6
-111.93415	50.84310	F100	8	10
-111.92928	50.84510	F500	7	8
-111.86687	50.83544	F5000	2	2
-111.98858	50.95827	G5000	5	3

Appendix II. Identifications of insect pollinators from the 2019 hand-caught dataset to species-level or morphospecies level. Morphospecies identifications are listed by "[Genus] spp. #". Some species could not be differentiated between genera, and so both genera are listed along with the epithet "sp". Specimens listed beside "cf" (confer, meaning compare with) are specimens that were damaged or for which taxonomic keys are insufficient, and were compared to other specimens to determine identification.

Group/ Order	Family	*Species*	100 m	500 m	5000 m	Total
Anthophila						
	Andrenidae	*Andrena amphibola*	1	0	0	1
	Andrenidae	*Andrena cyanophila*	0	2	0	2
	Andrenidae	*Andrena lupinorum*	0	1	1	2
	Andrenidae	*Andrena medionitens*	0	1	0	1
	Andrenidae	*Andrena peckhami*	0	3	6	9
	Andrenidae	*Andrena prunorum*	0	1	0	1
	Andrenidae	*Andrena* sp1	0	1	0	1
	Andrenidae	*Andrena* sp2	1	0	0	1
	Andrenidae	*Andrena thaspii*	4	1	2	7
	Andrenidae	*Panurginus beardsleyi*	0	2	0	2
	Andrenidae	*Perdita bruneri*	7	12	0	19
	Andrenidae	*Perdita swenki*	26	4	0	30
	Apidae	*Apis mellifera*	172	108	5	285
	Apidae	*Bombus borealis*	7	2	4	13
	Apidae	*Bombus fervidus*	1	0	0	1
	Apidae	*Bombus rufocinctus*	2	0	0	2
	Apidae	*Bombus ternarius*	0	1	1	2
	Apidae	*Epeolus compactus*	0	0	2	2
	Apidae	*Epeolus minimus*	0	5	4	9
	Apidae	*Holcopasites pulchellus*	0	1	0	1
	Apidae	*Melissodes* cf. *coreopsis*	3	2	4	9
	Apidae	*Melissodes rivalis*	1	0	0	1
	Apidae	*Neolarra pruinosa*	2	0	0	2
	Apidae	*Neolarra vigilans*	1	0	0	1
	Apidae	*Triepeolus helianthi*	0	1	1	2
	Colletidae	*Colletes brevicornis*	0	18	23	41
	Colletidae	*Colletes fulgidus*	3	0	1	4
	Colletidae	*Colletes hyalinus*	28	46	15	89
	Colletidae	*Colletes impunctatus*	6	11	6	23
	Colletidae	*Colletes kincaidii*	6	11	10	27
	Colletidae	*Colletes* cf. *petalostemonis*	2	0	0	2
	Colletidae	*Colletes* cf. *simulans*	3	3	1	7
	Colletidae	*Hylaeus annulatus*	2	0	0	2
	Colletidae	*Hylaeus mesillae*	1	3	0	4
	Halictidae	*Agapostemon femoratus*	1	0	0	1
	Halictidae	*Agapostemon texanus*	1	0	2	3

	Halictidae	*Agapostemon virescens*	1	1	0	2
	Halictidae	*Dufourea maura*	0	1	10	11
	Halictidae	*Halictus confusus*	5	7	4	16
	Halictidae	*Halictus ligatus*	0	2	0	2
	Halictidae	*Halictus rubicundus*	1	1	5	7
	Halictidae	*Lasioglossum* cf. *albohirtum*	2	4	5	11
	Halictidae	*Lasioglossum egregium*	0	1	0	1
	Halictidae	*Lasioglossum hudsoniellum*	2	2	1	5
	Halictidae	*Lasioglossum leucozonium*	0	2	1	3
	Halictidae	*Lasioglossum paraforbesii*	0	0	1	1
	Halictidae	*Lasioglossum pruinosum*	1	2	2	5
	Halictidae	*Lasioglossum sagax*	2	0	0	2
	Halictidae	*Lasioglossum* sp1	2	1	2	5
	Halictidae	*Lasioglossum* sp2	0	0	6	6
	Halictidae	*Lasioglossum* sp3	0	1	0	1
	Halictidae	*Lasioglossum succinipenne*	2	3	1	6
	Halictidae	*Lasiogossum* cf. *rufulipes*	6	12	18	36
	Megachilidae	*Anthidium clypeodentatum*	0	4	0	4
	Megachilidae	*Coelioxys rufitarsus*	0	1	0	1
	Megachilidae	*Hoplitis fulgida*	0	1	0	1
	Megachilidae	*Hoplitis pilosifrons*	3	4	1	8
	Megachilidae	*Hoplitis producta*	5	1	0	6
	Megachilidae	*Hoplitis spoliata*	0	1	1	2
	Megachilidae	*Megachile brevis*	2	1	2	5
	Megachilidae	*Megachile circumcincta*	0	1	0	1
	Megachilidae	*Megachile dentitarsus*	1	1	32	34
	Megachilidae	*Megachile frigida*	0	1	0	1
	Megachilidae	*Megachile inermis*	0	2	0	2
	Megachilidae	*Megachile latimanus*	5	9	3	17
	Megachilidae	*Megachile perihirta*	1	4	2	7
	Megachilidae	*Megachile rotundata*	11	4	0	15
	Megachilidae	*Megachile wheeleri*	0	1	0	1
	Megachilidae	*Osmia distincta*	5	2	3	10
	Megachilidae	*Osmia integra*	0	1	0	1
	Megachilidae	*Osmia simillima*	10	9	5	24
	Megachilidae	*Osmia* sp1	0	1	0	1
	Megachilidae	*Stelis lateralis*	0	2	0	2
Coleoptera						
	Anthicidae	*Notoxus* cf. *anchora*	10	2	10	22
	Chrysomelidae	*Acanthoscelides* sp	0	0	1	1
	Chrysomelidae	*Erynephala* cf. *puncticollis*	1	0	0	1
	Cleridae	*Phyllobaenus humeralis*	4	25	8	37
	Cleridae	*Trichodes nutalli*	1	0	2	3
	Coccinellidae	*Brachiacantha albifrons*	0	1	0	1

	Meloidae	*Epicauta ferruginea*	0	1	0	1
	Meloidae	*Epicauta pruinosa*	0	1	0	1
	Meloidae	*Epicauta puncticollis*	0	1	0	1
	Meloidae	*Epicauta subglabra*	0	1	5	6
	Melyridae	*Collops vittatus*	0	1	0	1
	Melyridae	*Listrus* sp	0	2	0	2
	Mordellidae	*Mordella atrata*	0	2	1	3
	Staphylinidae	*Philonthus caerulipennis*	1	7	10	18
Diptera						
	Acroceridae	*Ogcodes eugonatus*	2	0	0	2
	Anthomyiidae	*Adia* sp	0	0	1	1
	Anthomyiidae	*Adia* or *Paregle* sp	0	0	1	1
	Anthomyiidae	*Botanophila* sp	1	0	0	1
	Anthomyiidae	*Delia* sp	0	0	5	5
	Anthomyiidae	*Delia* or *Lasiomma* sp	0	0	1	1
	Anthomyiidae	*Fucellia* sp	0	2	0	2
	Anthomyiidae	*Fucellia* or *Delia* sp	0	1	0	1
	Anthomyiidae	*Hydrophoria* or *Delia* sp	0	1	0	1
	Anthomyiidae	*Pegohylemyia* or *Delia* or *Lasiomma* sp	0	1	1	2
	Anthomyiidae	*Pegohylemyia* or *Delia* sp	0	0	5	5
	Anthomyiidae	*Pegohylemyia* or *Lasiomma* sp	1	0	0	1
	Anthomyiidae	*Pegomya* sp	0	1	1	2
	Anthomyiidae	*Pegomya* or *Adia* sp	0	0	1	1
	Anthomyiidae	*Pegoplata* sp	1	1	1	3
	Anthomyiidae	*Phorbia* or *Hydrophoria* or *Pegohylemyia* sp	1	0	1	
	Asillidae	*Dicropaltum mesae*	0	1	0	1
	Asillidae	*Holopogon albopilosa*	1	0	1	2
	Bombyliidae	*Anastoechus barbatus*	12	18	4	34
	Bombyliidae	*Anastoechus melanohalteralis*	2	6	1	9
	Bombyliidae	*Anthrax picea*	1	0	0	1
	Bombyliidae	*Chrysanthrax costata*	0	0	1	1
	Bombyliidae	*Geron* sp	0	1	0	1
	Bombyliidae	*Hemipenthes morio*	4	2	0	6
	Bombyliidae	*Hemipenthes sinuosa*	0	0	1	1
	Bombyliidae	*Poecilanthrax alcyon*	0	1	1	2
	Bombyliidae	*Poecilanthrax monticola*	0	3	0	3
	Bombyliidae	*Poecilanthrax tegminipennis*	0	1	11	12
	Bombyliidae	*Poecilanthrax willistonii*	0	2	0	2
	Bombyliidae	*Poecilognathus* sp	0	0	1	1
	Bombyliidae	*Systoechus vulgaris*	4	10	2	16
	Bombyliidae	*Villa fulviana*	1	1	3	5
	Bombyliidae	*Villa lateralis*	2	2	1	5

Bombyliidae	*Villa lateralis* spgr.	0	2	0	2
Calliphoridae	*Phormia regina*	1	0	0	1
Calliphoridae	*Protophormia terraenovae*	0	0	1	1
Conopidae	*Thecophora occidensis*	0	1	0	1
Conopidae	*Zodion cinereiventre*	0	0	2	2
Conopidae	*Zodion fulvifrons*	0	1	1	2
Conopidae	*Zodion hitchensi*	0	1	0	1
Conopidae	*Zodion lisafyrea*	1	0	0	1
Conopidae	*Zodion* sp	0	1	1	2
Dolichopodidae	sp. indet.	1	0	0	1
Milichiidae	*Eusiphona mira*	0	1	1	2
Milichiidae	*Pholeomyia* sp	0	1	0	1
Muscidae	*Haematobia irritans*	0	1	0	1
Muscidae	*Hydrotaea meteorica*	1	1	0	2
Muscidae	*Neomyia cornicina*	0	2	2	4
Pipunculidae	sp. indet.	0	0	1	1
Sarcophagidae	*Ravinia* sp	2	1	6	9
Sarcophagidae	*Ravinia* or *Arachnidomyia* sp	0	0	1	1
Sarcophagidae	sp. indet.	2	2	3	7
Sarcophagidae	*Senotainia* sp	1	9	1	11
Sarcophagidae	*Senotainia* or *Macronychia* sp	0	2	0	2
Sarcophagidae	*Sphixapata trilineata*	0	1	0	1
Sarcophagidae	*Sphixapata triliniata*	0	3	0	3
Sarcophagidae	*Udamopyga niagarana*	0	1	0	1
Stratiomyidae	*Nemotelus* or *Camptopelta* sp	1	0	0	1
Syrphidae	*Cheilosia* sp	0	0	2	2
Syrphidae	*Copestylum marginatum*	1	0	0	1
Syrphidae	*Copestylum* sp	0	1	0	1
Syrphidae	*Eristalis dimidiata*	0	0	1	1
Syrphidae	*Eristalis hirta*	1	0	1	2
Syrphidae	*Eristalis stipator*	15	16	14	45
Syrphidae	*Eristalis tenax*	0	0	1	1
Syrphidae	*Eupeodes* sp	0	2	0	2
Syrphidae	*Eupeodes volucris*	2	1	1	4
Syrphidae	*Helophilus hybridus*	3	1	1	5
Syrphidae	*Helophilus latifrons*	3	7	4	14
Syrphidae	*Helophilus obscurus*	1	1	0	2
Syrphidae	*Lapposyrphus lapponicus*	0	0	1	1
Syrphidae	*Paragus haemorrhous*	6	10	9	25
Syrphidae	*Paragus* sp	4	13	2	19
Syrphidae	*Sphaerophoria bifurcata*	2	2	0	4
Syrphidae	*Sphaerophoria contigua*	1	3	2	6
Syrphidae	*Sphaerophoria philanthus*	8	13	4	25
Syrphidae	*Sphaerophoria* sp	1	0	0	1
Syrphidae	*Syritta pipiens*	1	0	0	1

	Syrphidae	*Syrphus vitripennis*	0	0	1	1
	Syrphidae	*Toxomerus marginatus*	6	7	16	29
	Syrphidae	*Trichopsomyia apisaon*	1	0	0	1
	Tachinidae	*Aphria ocypterata*	5	3	1	9
	Tachinidae	*Archytas californiae*	0	0	1	1
	Tachinidae	*Belvosia canadensis*	1	0	0	1
	Tachinidae	*Besseria brevipennis*	0	1	4	5
	Tachinidae	*Chaetocrania antennalis*	0	1	0	1
	Tachinidae	*Cylindromyia californica*	0	3	0	3
	Tachinidae	*Cylindromyia decora*	0	1	2	3
	Tachinidae	*Dinera grisescens*	1	1	0	2
	Tachinidae	*Estheria* sp	3	4	0	7
	Tachinidae	*Exorista* sp	1	0	0	1
	Tachinidae	*Gonia* sp	0	6	0	6
	Tachinidae	*Gymnoclytia immaculata*	0	1	0	1
	Tachinidae	*Lydina americana spcomplex*	1	0	1	2
	Tachinidae	*Panzeria fasciventris*	0	1	0	1
	Tachinidae	*Peleteria clara*	4	18	11	33
	Tachinidae	*Peleteria* sp	1	3	2	6
	Tachinidae	*Peleteria* or *Oxydosphyria* sp	0	3	0	3
	Tachinidae	*Peleteria* or *Sphyromyia* sp	0	0	1	1
	Tachinidae	*Ptilodexia rufipennis*	1	0	4	5
	Tachinidae	*Siphona medialis*	0	1	0	1
	Tachinidae	*Spallanzania hebes*	1	0	0	1
	Tachinidae	*Spallanzania hesperidarum*	0	2	1	3
	Tachinidae	*Tachina* sp	1	0	0	1
	Tachinidae	*Tachinidae* sp	1	0	0	1
	Tachinidae	*Tachinidae* sp2	0	1	0	1
	Tachinidae	*Tachinidae* sp3	2	0	0	2
	Tachinidae	*Tachinidae* sp4	1	0	0	1
	Tachinidae	*Tachinidae* sp6	1	0	0	1
	Tachinidae	*Tachinidae* sp8	0	0	1	1
	Tachinidae	*Tachinidae* sp9	0	1	0	1
	Therevidae	*Ozodiceromya platancala*	0	1	0	1
	Ulidiidae	sp. indet.	1	1	0	2
Papilionoidea						
	Hesperiidae	*Hesperia assiniboia*	2	19	55	76
	Hesperiidae	*Oarisma garita*	3	3	0	6
	Hesperiidae	*Pyrgus communis*	0	4	0	4
	Lycaenidae	*Glaucopsyche lygdamus*	1	0	0	1
	Lycaenidae	*Icaricia saepiolus*	3	4	0	7
	Lycaenidae	*Lycaena dione*	0	0	1	1
	Lycaenidae	*Plebejus melissa*	7	0	0	7
	Nymphalidae	*Cercyonis pegala*	2	4	3	9

	Nymphalidae	*Coenonympha california*	2	0	0	2
	Nymphalidae	*Phyciodes tharos*	0	2	1	3
	Nymphalidae	*Speyeria aphrodite*	0	0	1	1
	Nymphalidae	*Speyeria callippe*	1	0	0	1
	Pieridae	*Colias alexandra*	1	0	0	1
	Pieridae	*Colias philodice*	2	5	2	9
	Pieridae	*Pontia occidentalis*	1	0	1	2
Non-Papilionoidea Lepidoptera – "Moths"						
	Coleophoridae	*Coleophora trifolii*	1	0	0	1
	Crambidae	*Pediasia dorsipunctellus*	0	0	1	1
	Gelechiidae	sp. indet.	1	0	0	1
	Gelechiidae	*Gnorimoschema* sp	0	0	1	1
	Geometridae	sp. indet.	1	0	0	1
	Noctuidae	*Euxoa ochrogaster*	0	0	1	1
	Noctuidae	*Euxoa* sp	0	0	1	1
	Noctuidae	*Lacinipolia lorea*	1	2	0	3
	Noctuidae	Noctuinae sp. indet.	0	0	1	1
	Noctuidae	*Ponometia tortricina*	1	0	1	2
	Noctuidae	*Schinia villosa*	1	0	0	1
	Scythrididae	*Landryia scintillifera*	0	1	1	2
	Scythrididae	*Rhamphura ochristriata*	0	1	1	2
	Scythrididae	*Scythris eboracensis*	0	1	3	4
	Scythrididae	*Scythris inspersella*	0	0	2	2
	Tortricidae	*Hystrichophora ochreicostana*	1	0	0	1
Formicoidea						
	Formicidae	*Formica canadensis*	2	1	1	4
	Formicidae	*Formica lasioides*	18	9	4	31
	Formicidae	*Formica montana*	1	0	1	2
	Formicidae	*Formica neogagates*	0	5	0	5
	Formicidae	*Formica obscuripes*	13	5	0	18
	Formicidae	*Formica oreas*	1	26	0	27
	Formicidae	*Formica podzolica*	7	3	0	10
	Formicidae	*Formica ravida*	0	1	0	1
	Formicidae	*Myrmica fracticornis*	0	0	1	1
	Formicidae	*Myrmica* sp	1	0	0	1
	Formicidae	*Tapinoma sessile*	0	4	0	4
Hemiptera						
	Alydidae	*Alydus* sp	4	1	2	7
	Cicadellidae	*Cicadellidae* sp1	1	1	1	3
	Cicadellidae	*Cicadellidae* sp2	0	0	1	1
	Miridae	*Lopidea* sp	1	0	0	1
	Miridae	*Lygus* sp	0	0	2	2
	Reduviidae	*Phymata americana*	4	5	5	14
	Rhyparochromidae	sp. indet.	0	1	0	1

Aculeata (non-Anthophila & non-Formicoidea) – “Wasps”						
	Braconidae	*Braconidae* sp	1	1	0	2
	Braconidae	*Chelonus annulipes*	1	2	0	3
	Braconidae	*Chelonus* sp	0	1	0	1
	Crabronidae	*Belomicrus* sp	0	0	3	3
	Crabronidae	*Cerceris deserta*	0	1	0	1
	Crabronidae	*Cerceris nigrescens*	2	0	0	2
	Crabronidae	*Ectemnius arcuatus*	0	1	0	1
	Crabronidae	*Ectemnius rufifemur*	1	0	5	6
	Crabronidae	*Eucerceris tricolor*	1	0	0	1
	Crabronidae	*Gorytes simillimus*	0	4	0	4
	Crabronidae	*Nysson recticornis*	0	1	1	2
	Crabronidae	*Philanthus bilunatus*	0	2	0	2
	Crabronidae	*Tachysphex aequalis*	0	1	1	2
	Crabronidae	*Tachysphex pompilliformis*	0	1	1	2
	Cynipidae	*Diplolepsis rosae*	0	3	0	3
	Ichneumonidae	*Himerta* sp1	0	0	1	1
	Ichneumonidae	*Himerta* sp2	0	1	0	1
	Ichneumonidae	sp. indet.	1	0	0	1
	Ichneumonidae	*Ophion* sp	0	0	1	1
	Perilampidae	*Chrysolampus schwarzi*	0	1	0	1
	Perilampidae	*Perilampus hyalinus*	0	0	3	3
	Pompilidae	*Arachnospila michiganensis*	0	1	0	1
	Pompilidae	*Episyron oregon*	0	0	1	1
	Pompilidae	*Evagetes crassicornis*	1	0	0	1
	Sphecidae	*Ammophila harti*	0	2	2	4
	Sphecidae	*Prionyx atratus*	0	0	1	1
	Sphecidae	*Sphex ichneumoneus*	1	0	0	1
	Vespidae	*Ancistrocerus* sp	0	1	0	1
	Vespidae	*Euodynerus crypticus*	0	0	1	1
	Vespidae	*Euodynerus leucomelas*	1	0	0	1
	Vespidae	*Paranstrocerus* or *Stenodynerus* sp	0	0	1	1
	Vespidae	*Stenodynerus anormis*	2	2	2	6
			586	**726**	**502**	**1814**

Appendix III. Identifications of insect pollinators from the 2019 pan-trapped dataset to species-level or morpho-species level. Morpho-species identifications are listed by "[Genus] spp. #". Some species could not be differentiated between genera, and so both genera are listed along with the epithet "sp". Specimens listed beside "cf" (confer, meaning compare with) are specimens that were damaged or for which taxonomic keys are insufficient, and were compared to other specimens to determine identification.

Order/Group	Family	Species	100 m	500 m	5000 m	Total
Anthophila						
	Andrenidae	*Andrena amphibola*	12	15	9	36
	Andrenidae	*Andrena barbilabris*	7	14	9	30
	Andrenidae	*Andrena canadensis*	0	0	2	2
	Andrenidae	*Andrena chromotricha*	16	7	8	31
	Andrenidae	*Andrena lupinorum*	4	8	12	24
	Andrenidae	*Andrena* cf. *medionitens*	1	1	2	4
	Andrenidae	*Andrena* cf. *nigrihirta*	0	0	2	2
	Andrenidae	*Andrena peckhami*	10	9	10	29
	Andrenidae	*Andrena prunorum*	6	4	0	10
	Andrenidae	*Andrena* cf. *sigmundi*	2	1	0	3
	Andrenidae	*Andrena* sp	0	0	1	1
	Andrenidae	*Andrena* sp1	0	1	2	3
	Andrenidae	*Andrena* sp2	0	1	0	1
	Andrenidae	*Andrena* sp3	0	1	3	4
	Andrenidae	*Andrena* sp4	3	1	4	8
	Andrenidae	*Andrena* sp5	0	0	3	3
	Andrenidae	*Andrena* sp6	1	0	0	1
	Andrenidae	*Andrena* sp7	0	1	0	1
	Andrenidae	*Andrena* sp8	0	1	0	1
	Andrenidae	*Andrena* sp9	1	2	1	4
	Andrenidae	*Andrena thaspii*	7	5	8	20
	Andrenidae	*Andrena trevoris*	1	0	0	1
	Andrenidae	*Panurginus beardsleyi*	1	1	0	2
	Andrenidae	*Perdita bruneri*	22	35	9	66
	Andrenidae	*Perdita* sp1	1	0	0	1
	Andrenidae	*Perdita* sp2	38	44	15	97
	Andrenidae	*Perdita swenki*	3	2	1	6
	Apidae	*Anthophora bombiodes*	1	0	1	2
	Apidae	*Anthophora occidentalis*	3	7	0	10
	Apidae	*Anthophora porterae*	3	0	0	3
	Apidae	*Anthophora terminalis*	1	3	1	5
	Apidae	*Apis mellifera*	103	53	13	169
	Apidae	*Bombus borealis*	26	32	34	92
	Apidae	*Bombus fervidus*	4	7	14	25
	Apidae	*Bombus griseocollis*	0	0	2	2
	Apidae	*Bombus insularis*	1	0	0	1

Apidae	*Bombus rufocinctus*	18	7	8	33
Apidae	*Bombus suckleyi*	0	1	1	2
Apidae	*Bombus ternarius*	11	11	10	32
Apidae	*Bombus vagans*	1	0	0	1
Apidae	*Diadasia australis*	10	15	4	29
Apidae	*Diadasia diminuta*	14	8	4	26
Apidae	*Epeolus compactus*	0	0	1	1
Apidae	*Epeolus minimus*	79	40	21	140
Apidae	*Eucera fulvitarsis*	4	2	1	7
Apidae	*Eucera speciosa*	4	3	2	9
Apidae	*Melissodes agilis*	17	12	6	35
Apidae	*Melissodes confusus*	6	5	7	18
Apidae	*Melissodes* cf. *coreopsis*	172	270	135	577
Apidae	*Melissodes* cf. *druriella*	1	2	0	3
Apidae	*Melissodes microsticta*	1	1	0	2
Apidae	*Melissodes perlusa*	2	3	5	10
Apidae	*Melissodes rivalis*	28	24	36	88
Apidae	*Melissodes* cf. *semilupina*	1	0	0	1
Apidae	*Melissodes snowii*	9	3	0	12
Apidae	*Nomada articulata*	1	0	1	2
Apidae	*Nomada lehighensis*	1	0	0	1
Apidae	*Nomada* sp1	0	0	1	1
Apidae	*Nomada* sp2	2	3	1	6
Apidae	*Nomada* sp3	0	1	0	1
Apidae	*Nomada* sp4	0	1	0	1
Apidae	*Triepeolus balteatus*	0	0	1	1
Apidae	*Triepeolus helianthi*	0	0	1	1
Apidae	*Triepeolus micropygius*	0	1	0	1
Apidae	*Triepeolus* sp1	0	2	3	5
Colletidae	*Colletes* cf. *aberrans*	1	0	0	1
Colletidae	*Colletes brevicornis*	25	32	41	98
Colletidae	*Colletes hyalinus*	51	33	50	134
Colletidae	*Colletes impunctatus*	10	23	20	53
Colletidae	*Colletes kincaidii*	13	9	7	29
Colletidae	*Colletes nigrifrons*	0	1	6	7
Colletidae	*Colletes phaceliae*	1	2	2	5
Colletidae	*Colletes* cf. *simulans*	0	9	0	9
Colletidae	*Hylaeus affinis*	0	0	2	2
Colletidae	*Hylaeus annulatus*	1	4	0	5
Colletidae	*Hylaeus mesillae*	24	12	8	44
Colletidae	*Hylaeus modestus*	1	0	0	1
Halictidae	*Agapostemon femoratus*	2	1	0	3
Halictidae	*Agapostemon obliquus*	0	1	0	1
Halictidae	*Agapostemon splendens*	1	2	2	5
Halictidae	*Agapostemon texanus*	72	55	15	142

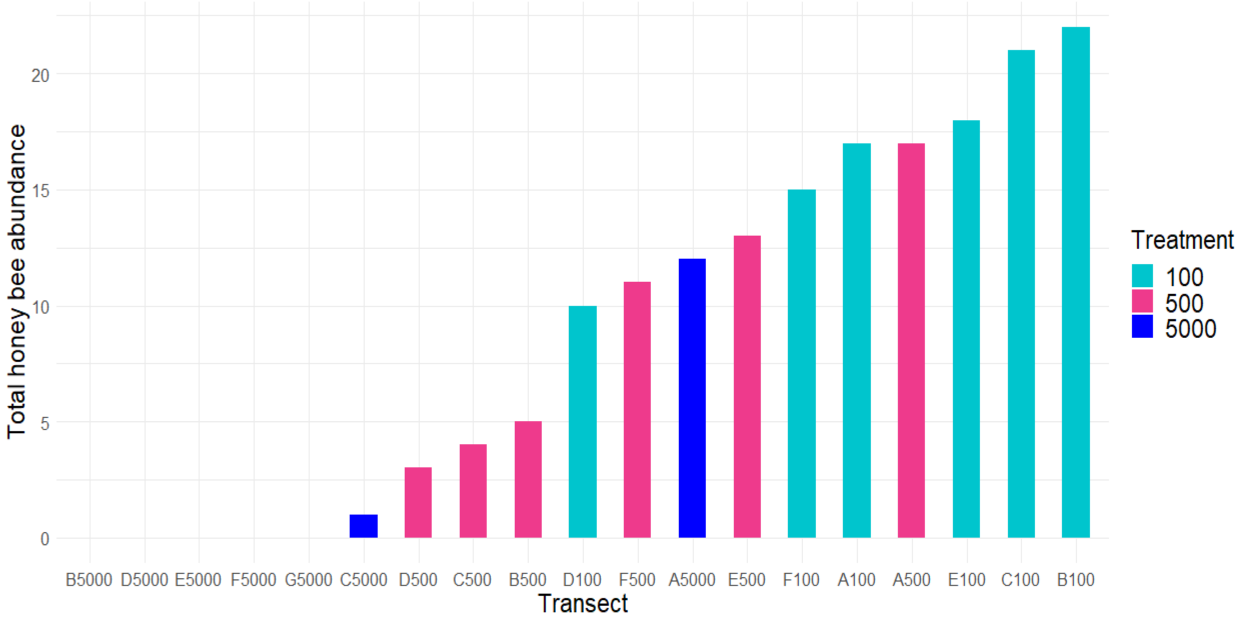
Halictidae	*Agapostemon virescens*	100	90	56	246
Halictidae	*Agapsotemon obliquus*	1	0	0	1
Halictidae	*Dufourea marginata*	7	4	11	22
Halictidae	*Dufourea maura*	20	20	59	99
Halictidae	*Halictus confusus*	100	87	33	220
Halictidae	*Halictus ligatus*	1	5	1	7
Halictidae	*Halictus rubicundus*	71	62	79	212
Halictidae	*Lasioglossum* cf. *albipenne*	6	1	2	9
Halictidae	*Lasioglossum anomalum*	9	23	7	39
Halictidae	*Lasioglossum egregium*	1	1	1	3
Halictidae	*Lasioglossum hudsoniellum*	60	84	13	157
Halictidae	*Lasioglossum* cf. *laevissimum*	23	17	12	52
Halictidae	*Lasioglossum leucozonium*	22	21	11	54
Halictidae	*Lasioglossum* cf. *nigroviride*	12	19	5	36
Halictidae	*Lasioglossum paraforbesii*	97	47	30	174
Halictidae	*Lasioglossum* cf. *pavoninum*	15	12	12	39
Halictidae	*Lasioglossum perpunctatum*	71	60	37	168
Halictidae	*Lasioglossum pruinosum*	133	139	102	374
Halictidae	*Lasioglossum* cf. *rufulipes*	2	7	1	10
Halictidae	*Lasioglossum sagax*	102	94	82	278
Halictidae	*Lasioglossum* sp1	0	1	0	1
Halictidae	*Lasioglossum* sp2	0	0	2	2
Halictidae	*Lasioglossum* sp3	0	2	0	2
Halictidae	*Lasioglossum succinipenne*	362	435	287	1084
Halictidae	*Lasioglossum testaceum*	3	11	2	16
Halictidae	*Lasioglossum zonulum*	1	2	0	3
Halictidae	*Sphecodes arroyanus*	2	0	0	2
Halictidae	*Sphecodes minor*	2	2	1	5
Megachilidae	*Anthidium clypeodentatum*	10	9	7	26
Megachilidae	*Anthidium tenuiflorae*	9	6	1	16
Megachilidae	*Coelioxys moestus*	0	0	1	1
Megachilidae	*Coelioxys rufitarsis*	10	7	27	34
Megachilidae	*Coelioxys sodalis*	1	3	2	6
Megachilidae	*Dianthidium pudicum*	3	2	0	5
Megachilidae	*Hoplitis pilosifrons*	52	31	25	108
Megachilidae	*Hoplitis producta*	38	27	6	71
Megachilidae	*Hoplitis robusta*	0	0	3	3
Megachilidae	*Hoplitis spoliata*	1	6	0	7
Megachilidae	*Megachile brevis*	4	8	19	31
Megachilidae	*Megachile centuncularis*	1	0	2	3
Megachilidae	*Megachile dentitarsus*	6	11	26	43

	Megachilidae	*Megachile fortis*	0	0	1	1
	Megachilidae	*Megachile frigida*	0	0	2	2
	Megachilidae	*Megachile inermis*	1	6	0	7
	Megachilidae	*Megachile latimanus*	11	15	12	38
	Megachilidae	*Megachile manifesta*	1	0	0	1
	Megachilidae	*Megachile melanophaea*	17	9	10	36
	Megachilidae	*Megachile montivaga*	3	3	1	7
	Megachilidae	*Megachile perihirta*	5	5	8	18
	Megachilidae	*Megachile rotundata*	39	31	4	74
	Megachilidae	*Megachile wheeleri*	1	3	0	4
	Megachilidae	*Osmia* cf. *distincta*	48	31	26	105
	Megachilidae	*Osmia integra*	17	13	6	36
	Megachilidae	*Osmia* cf. *longula*	2	2	1	5
	Megachilidae	*Osmia* cf. *proxima*	0	1	0	1
	Megachilidae	*Osmia* cf. *simillima*	7	19	8	34
	Megachilidae	*Osmia* sp1	0	1	2	3
	Megachilidae	*Osmia* sp2	19	13	3	35
	Megachilidae	*Osmia* sp3	1	0	2	3
	Megachilidae	*Osmia* sp4	6	2	0	8
	Megachilidae	*Osmia* sp5	112	83	56	251
	Megachilidae	*Osmia* cf. *tersula*	11	0	0	11
	Megachilidae	*Osmia texana*	0	3	1	4
	Megachilidae	*Stelis lateralis*	1	1	1	3
	Megachilidae	*Stelis nitida*	0	0	1	1
	Megachilidae	*Stelis* sp1	2	1	0	3
			2524	**2453**	**1678**	**6645**
Papilionoidea						
	Hesperiidae	*Anatrytone delaware*	0	1	1	2
	Hesperiidae	*Anatrytone logan*	10	7	0	17
	Hesperiidae	*Hesperia assiniboia*	462	483	796	1741
	Hesperiidae	*Hesperia nevada*	3	3	0	6
	Hesperiidae	*Oarisma garita*	25	26	30	81
	Hesperiidae	*Ochlodes sylvanoides*	7	10	7	24
	Hesperiidae	*Polites mystic*	4	2	0	6
	Hesperiidae	*Polites peckius*	2	6	5	13
	Hesperiidae	*Polites themistocles*	1	2	0	3
	Lycaenidae	*Glaucopsyche lygdamus*	0	4	0	4
	Lycaenidae	*Icaricia saepiolus*	3	4	3	10
	Lycaenidae	*Lycaena helloides*	0	0	1	1
	Lycaenidae	*Lycaena rubida*	2	4	1	7
	Lycaenidae	*Lycaena rubidus*	1	0	0	1
	Lycaenidae	*Plebejus melissa*	23	17	15	55
	Nymphalidae	*Boloria bellona*	1	0	0	1
	Nymphalidae	*Cercyonis pegala*	20	13	45	78
	Nymphalidae	*Coenonympha california*	32	48	42	122
	Nymphalidae	*Oeneis uhleri*	13	6	10	29
	Nymphalidae	*Phyciodes tharos*	1	1	0	2

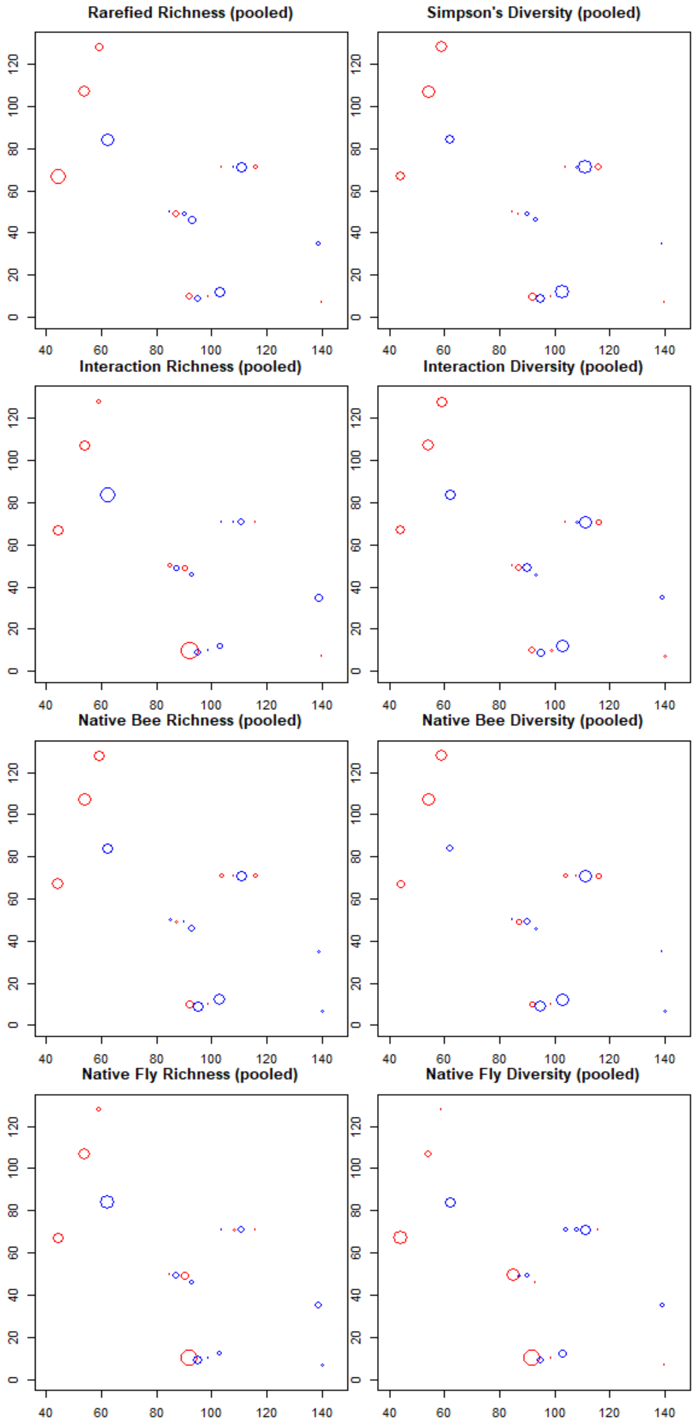
	Nymphalidae	*Speyeria aphrodite*	6	4	8	18
	Nymphalidae	*Speyeria callippe*	1	2	1	4
	Nymphalidae	*Vanessa cardui*	2	3	3	8
	Pieridae	*Colias alexandra*	22	4	0	26
	Pieridae	*Colias philodice*	78	60	48	186
	Pieridae	*Pieris rapae*	14	28	12	54
	Pieridae	*Pontia occidentalis*	2	8	3	13
	Pieridae	*Pontia protodice*	2	0	0	2
			737	**746**	**1031**	**2514**
Coleoptera						
	Anthicidae	*Anthicus* sp	1	0	0	1
	Anthicidae	*Notoxus* cf. *anchora*	100	171	127	398
	Cantharidae	*Cantharis* sp	2	0	0	2
	Carabidae	*Agonum ferruginosum*	0	1	0	1
	Carabidae	*Amara littoralis*	2	0	0	2
	Carabidae	*Amara sinuosa*	0	1	0	1
	Carabidae	*Calosoma calidum*	0	0	1	1
	Carabidae	*Cymindis cribricollis*	0	0	1	1
	Carabidae	*Amara* (Curtonotus) sp	0	1	0	1
	Chrysomelidae	*Distigmoptera borealis*	1	1	0	2
	Chrysomelidae	*Erynephala* cf. *puncticollis*	1	1	1	3
	Chrysomelidae	*Pachybrachis hepaticus*	4	0	0	4
	Chrysomelidae	*Phyllotreta* cf. sp	2	0	0	2
	Cleridae	*Phyllobaenus humeralis*	7	9	9	25
	Cleridae	*Trichodes nuttalli*	69	147	222	438
	Coccinellidae	*Brachiacantha albifrons*	1	1	1	3
	Coccinellidae	*Hippodamia parenthesis*	1	0	2	3
	Coccinellidae	*Hyperaspis inflexa*	0	1	0	1
	Coccinellidae	*Hyperaspis lugubris*	1	0	0	1
	Coccinellidae	*Hyperaspis undulata*	0	0	1	1
	Coccinellidae	*Hyperaspis undulata*	0	0	1	1
	Coccinellidae	*Scymnus* cf. *lacustris*	1	0	0	1
	Curculionidae	*Acanthoscelidius* sp	11	11	123	145
	Curculionidae	*Baris* sp	1	1	3	5
	Curculionidae	*Cosmobaris scolopacea*	1	0	0	1
	Curculionidae	*Glocianus punctiger*	9	0	0	9
	Curculionidae	*Listronotus* sp	1	0	0	1
	Curculionidae	*Odontocorynus* sp	1	1	0	2
	Curculionidae	*Otiorhynchus ovatus*	9	3	3	15
	Curculionidae	*Sciaphilus* cf. *asperatus*	0	2	1	3
	Curculionidae	*Sitona cylindricollis*	4	1	1	6
	Elateridae	*Aeolus mellillus*	0	5	0	5
	Elateridae	*Hypnoidus* sp	2	0	0	2
	Elateridae	*Selatosomus aeripennis*	2	0	0	2
	Histeridae	*Atholus falli*	0	1	0	1
	Hydrophilidae	*Hydrobius fuscipes*	1	0	0	1
	Meloidae	*Epicauta ferruginea*	192	338	85	615
	Meloidae	*Epicauta pennsylvanica*	1	2	2	5
	Meloidae	*Epicauta pruinosa*	88	109	115	312
	Meloidae	*Epicauta puncticollis*	10	7	5	22
	Meloidae	*Epicauta subglabra*	1	0	0	1

Meloidae	*Lytta nuttalli*	0	1	0	1
Meloidae	*Nemognatha lutea*	1	1	1	3
Melyridae	*Collops bipunctatus*	1	1	1	3
Melyridae	*Collops vittatus*	5	2	13	20
Melyridae	*Listrus* sp	2	0	0	2
Miridae	*Hadronema* cf. *pictum*	1	0	0	1
Mordellidae	*Mordella atrata*	10	20	10	40
Mordellidae	*Mordellistena* sp1	2	19	4	25
Mordellidae	*Mordellistena* sp2	7	2	15	24
Mordellidae	*Mordellistena* sp3	1	0	0	1
Mordellidae	*Mordellistena* sp4	5	10	2	17
Mordellidae	*Mordellistena* sp5	1	2	1	4
Nitidulidae	*Nitops pallipennis*	2	3	7	12
Phalacridae	*Olibrus* sp	0	1	0	1
Ptinidae	*Xyletinus* sp	1	0	0	1
Pyrochroidae	*Pedilus* sp	0	1	0	1
Scarabaeidae	*Cryptoscatomaseter* cf. *criddlei*	0	1	0	1
Scarabaeidae	*Dichelonyx truncata*	1	1	1	3
Scarabaeidae	*Diplotaxis obscura*	0	0	2	2
Scarabaeidae	*Flaviellus consentaneus*	2	0	2	4
Scarabaeidae	*Onthophagus nuchicornis*	0	1	0	1
Scarabaeidae	*Otophorus haemorrhoidalis*	2	0	0	2
Scarabaeidae	*Serica curvata*	23	19	19	61
Tenebrionidae	*Blapstinus metallicus*	2	0	0	2
		596	**900**	**782**	**2278**
		3857	**4099**	**3491**	**11437**

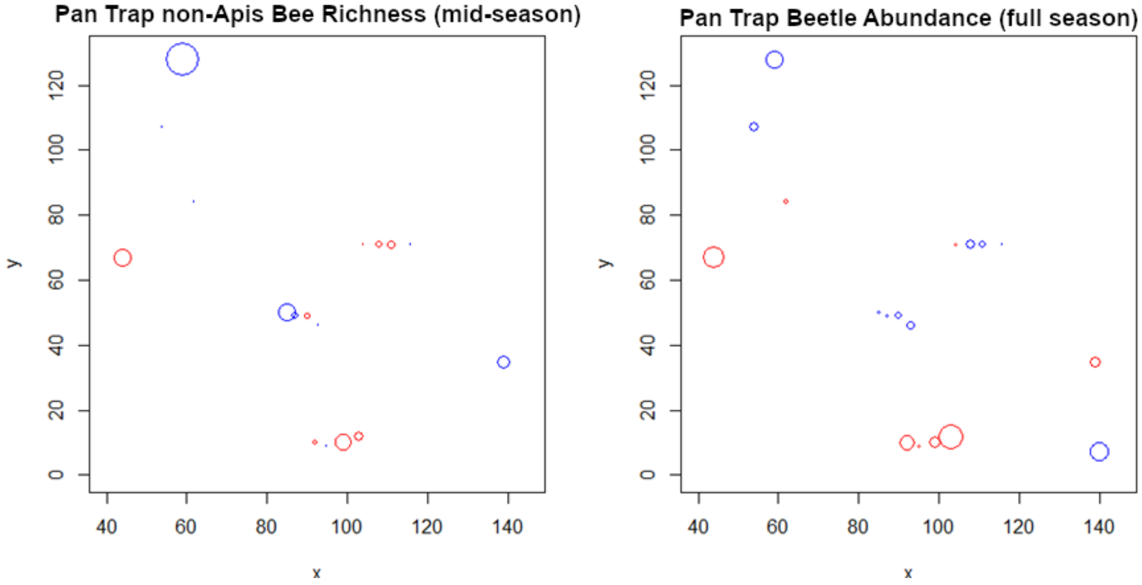
Appendix IV. Honey bee abundance in pan-trapped data, pooled across the full season per transect, with transects ordered by increasing honey bee abundance, and coloured by distance from bee hives. In the transect names, 100 indicates 100 m, 500 indicates 500 m, and 5000 indicates 5000 m distances from hives.



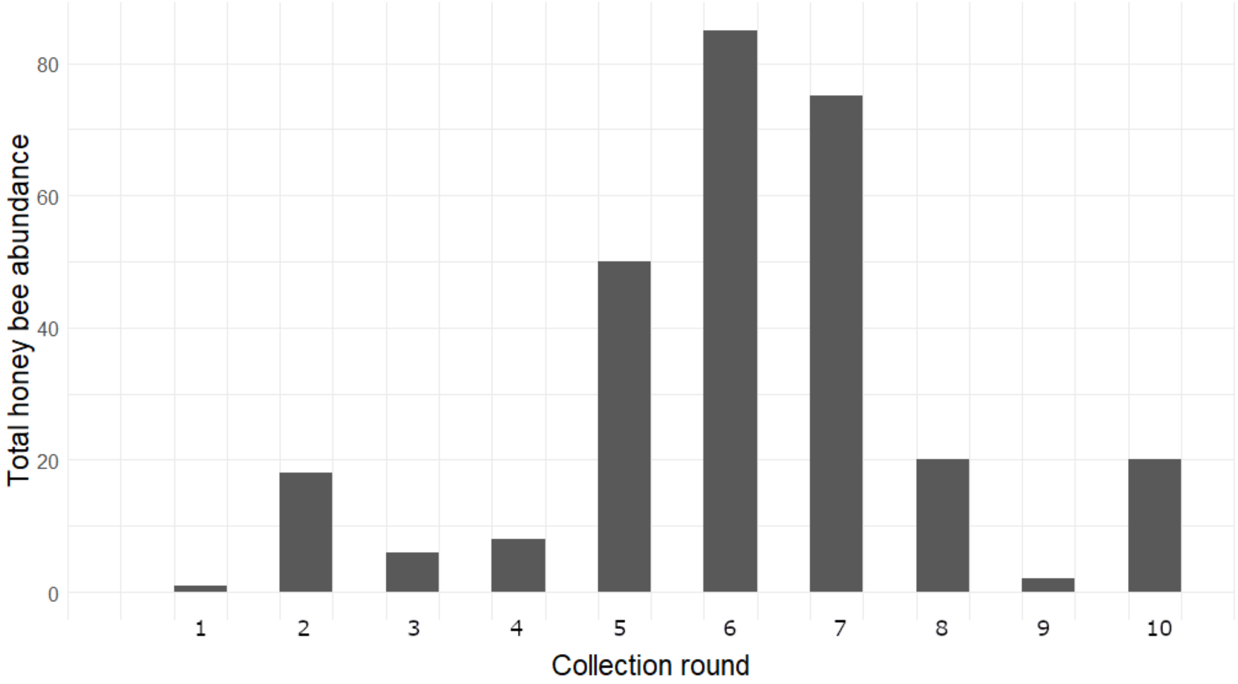
Appendix V. Visual representation of the spatial autocorrelation of each response variable against honey bee abundance for response variables that did not need a special correlation structure, as determined by model selection on different correlation structures. Circles indicate the size of the residual for each transect (smaller circles = better model fit). Colour indicates the sign of the residual; blue shows values lower than 0 and red values higher than 0. In this figure, if close together transects have similarly sized and coloured residuals, that suggests that there is spatial autocorrelation in that response variable.



Appendix VI. Visual representation of the spatial autocorrelation of the two response variables that did require special correlation structures, as determined by model selection on different correlation structures. Both models required rational quadratic special correlation structures. Circles indicate the size of the residual for each transect (smaller circles = better model fit). Colour indicates the sign of the residual; blue shows values lower than 0 and red values higher than 0. In this figure, if close together transects have similarly sized and coloured residuals, that suggests that there is spatial autocorrelation in that response variable.



Appendix VII. Total honey bee abundance (caught visiting flowers) across the 2019 season. The entire season was split into three; collection rounds 1-4 represented "early" season, 5-7 represented "mid" season, and 8-10 represented "late" season.



Appendix VIII. Identifications of flowering species from each transect in 2019 to species level.

Family	Species	100 m	500 m	5000 m	Total
Asteraceae	*Achillea millefolium*	68	183	115	366
Asteraceae	*Antennaria microphylla*	0	0	47	47
Asteraceae	*Cirsium arvense*	0	0	4	4
Asteraceae	*Cirsium undulatum*	18	21	2	41
Asteraceae	*Erigeron philadelphicus*	9	27	6	42
Asteraceae	*Erigeron speciosus*	0	0	2	2
Asteraceae	*Grindelia squarrosa*	15	346	178	539
Asteraceae	*Gutierrezia sarothrae*	0	7	0	7
Asteraceae	*Happlopappus spinulosus*	0	2	0	2
Asteraceae	*Heterotheca villosa*	117	281	47	445
Asteraceae	*Liatris punctata*	30	84	197	311
Asteraceae	*Lygodesmia juncea*	0	72	4	76
Asteraceae	*Mulgedium pulchellum*	0	1	0	1
Asteraceae	*Solidago canadensis*	96	91	47	234
Asteraceae	*Solidago missouriensis*	8	67	8	83
Asteraceae	*Sonchus arvensis*	33	34	3	70
Asteraceae	*Sonchus oleraceus*	0	0	1	1
Asteraceae	*Taraxacum officinale*	52	0	1	53
Asteraceae	*Trogopogon dubius*	1	0	4	5
Boraginaceae	*Lithospermum incisum*	28	61	0	89
Brassicaceae	*Descurainia sophia*	36	4	0	40
Brassicaceae	*Erysimum inconspicuum*	3	2	4	9
Cactaceae	*Escobaria vivipara*	1	3	4	8
Campanulaceae	*Campanula rotundifolia*	18	151	526	695
Caprifoliaceae	*Symphoricarpos occidentalis*	368	443	367	1178
Caprifoliaceae	*Symphyotrichum falcatum*	30	75	140	245
Caryophyllaceae	*Cerastium arvense*	0	9	7	16
Elaeagnaceae	*Elaeagnus commutata*	7	0	0	7
Fabaceae	*Astragalus adsurgens*	0	6	0	6
Fabaceae	*Astragalus cicer*	245	164	118	527
Fabaceae	*Astragalus flexuosus*	0	0	2	2
Fabaceae	*Astragalus striatus*	20	12	9	41
Fabaceae	*Dalea purpurea*	5	21	0	26
Fabaceae	*Glycyrrhiza lepidota*	67	497	413	977
Fabaceae	*Medicago sativa*	34	0	0	34
Fabaceae	*Melilotus albus*	66	21	0	87
Fabaceae	*Melilotus officinalis*	0	1	0	1
Fabaceae	*Thermopsis rhombifolia*	117	48	0	165
Fabaceae	*Vicia americana*	0	7	0	7
Liliaceae	*Allium textile*	68	2	0	70
Onagraceae	*Oenothera nuttallii*	0	5	1	6
Onagraceae	*Oenothera suffrutescens*	0	11	1	12

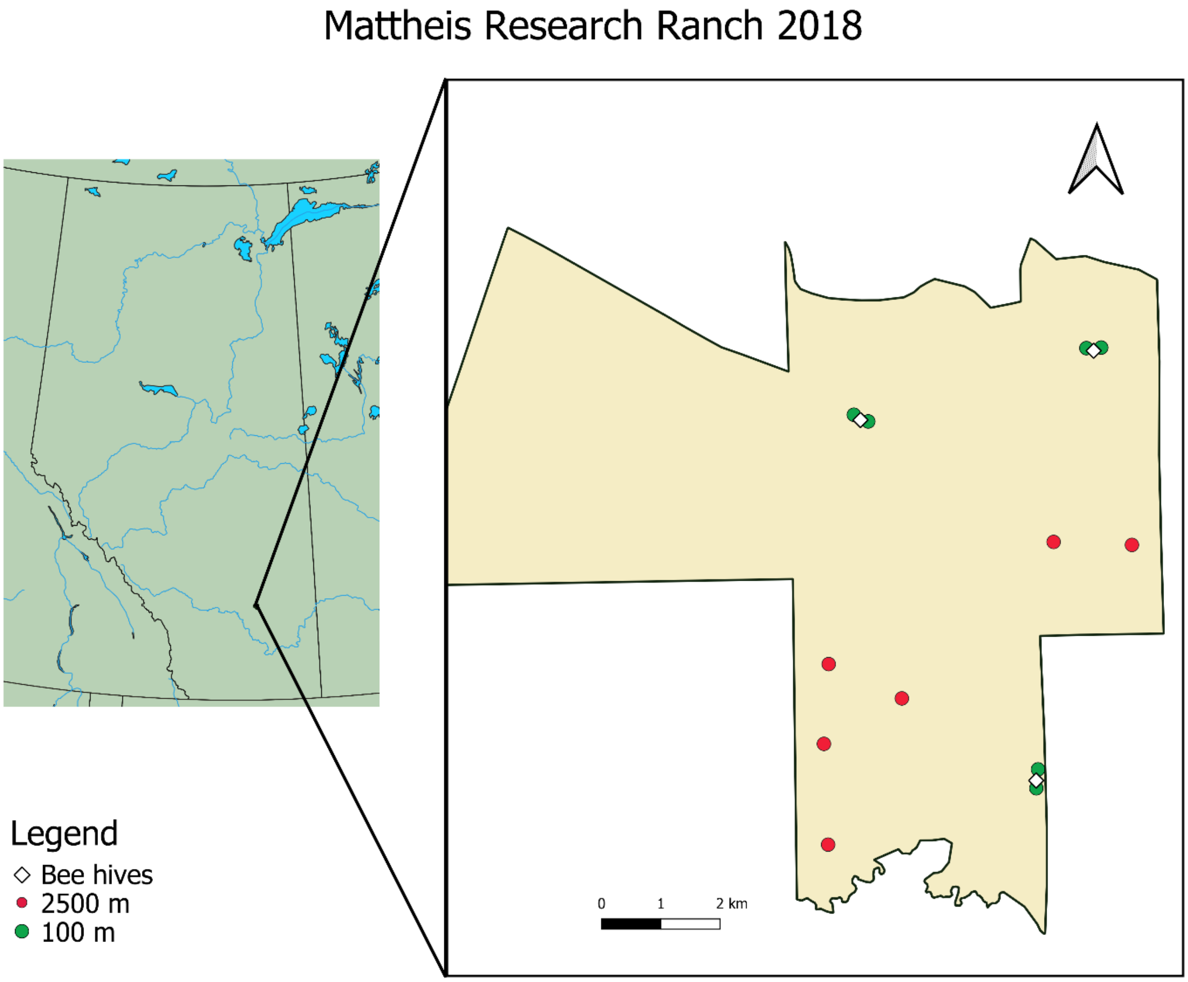
Rosaceae	*Potentilla arguta*	0	2	1	3
Rosaceae	*Potentilla concinna*	3	85	0	88
Rosaceae	*Potentilla pensylvanica*	0	1	0	1
Rosaceae	*Rosa arkansana*	14	14	10	38
Rosaceae	*Rosa woodsii*	16	8	5	29
Santalaceae	*Comandra umbellata*	81	62	0	143
		1674	**2931**	**2274**	**6879**

Appendix IX. Descriptions of network metrics calculated in chapter three. In all cases, these are the weighted versions of the metrics (calculated for “quantitative” interaction networks for which link strength is known), rather than the unweighted versions (calculated for “binary” networks for which link strength is not explicit.

Network metrics for structure and stability	
Modularity	Extent to which species interactions are organized into “modules”: species within a module interact more frequently with each other than with species in other modules (Olesen et al., 2007).
Nestedness	Describes how interactions of specialists are nested subsets of the larger sets of interactions of generalists. Calculated here as “weighted NODF”, as per Almeida-Neto & Ulrich, (2011), where presence-absence nestedness from the matrix is weighted by ranking of the interaction frequency (where generalists have high frequency and specialists have low frequency).
Interaction Strength Asymmetry	Measures the asymmetrical interaction effect of plant species (i) on animal species (j), where the effect does not match the reciprocal effect of species j on species i. Zero indicates a balanced network; values toward -1 or 1 indicate high asymmetry (Blüthgen et al., 2007; Vázquez et al., 2007).
Interaction Evenness	Measures the uniformity of the distribution of interactions, by calculating Shannon’s evenness for the cells of an interaction matrix (Dormann et al., 2009).
Connectance	The number of observed interactions (L) over total possible interactions in a network (m), calculated as $\frac{L}{m}$ (Delmas et al., 2019).
Link Density	The mean number of interactions per species (plant or pollinator), calculated as $\frac{L}{s}$, the total number of interactions (L) over the total number of species (s). This indicates how many interactions a randomly selected species would likely have (Delmas et al., 2019).
Network metrics for resource use overlap	
Vulnerability & Generality	A measure of the mean number of pollinators per plant (vulnerability) and plants per pollinator (generality), weighted to account for link strength, such that a higher link weight increases the value (Bersier et al., 2002).
Niche Overlap	Measures the similarity in interactions between species (pollinators or plants) at the same trophic level in the network, using Horn’s Index of overlap (Dormann et al., 2008).
Functional Complementarity	A multivariate measure of the dissimilarity of resource use within a trophic level. Calculates Euclidean distance between each species based on the identity and frequency of their interactions, then clusters the distance matrix to produce a dendrogram, and calculates the total branch length of the dendrogram, which expresses the difference between pollinators in the set of plants they interact with, for pollinator functional complementarity, and the difference between plants in the set

	of pollinators they interact with, for plant functional complementarity (Devoto et al., 2012).
Potential for Competition	Sum of the potential competitive influence of a species (in this case honey bees) on the interactions of all other species in the same trophic level that share some or all of the same resources (Magrach et al., 2017). Note that Magrach et al. 2017 erroneously term this “apparent competition”, so I use a different name.

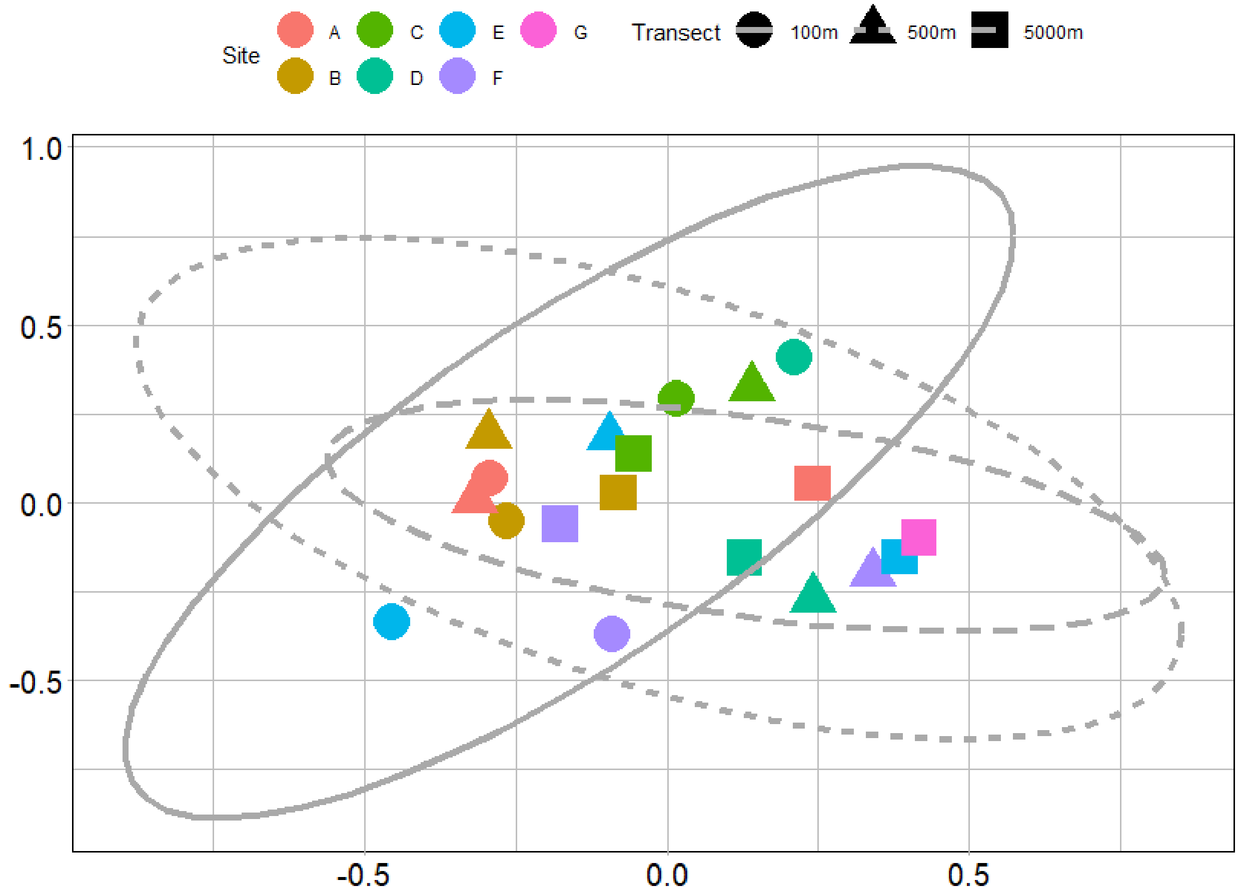
Appendix X. Locations of the 2018 transects and honey bee hives. Each 2500 m transect (in red) indicates distance of 2500 m, and was paired with a 100 m transect (in green) adjacent to a honey bee hive (in white).



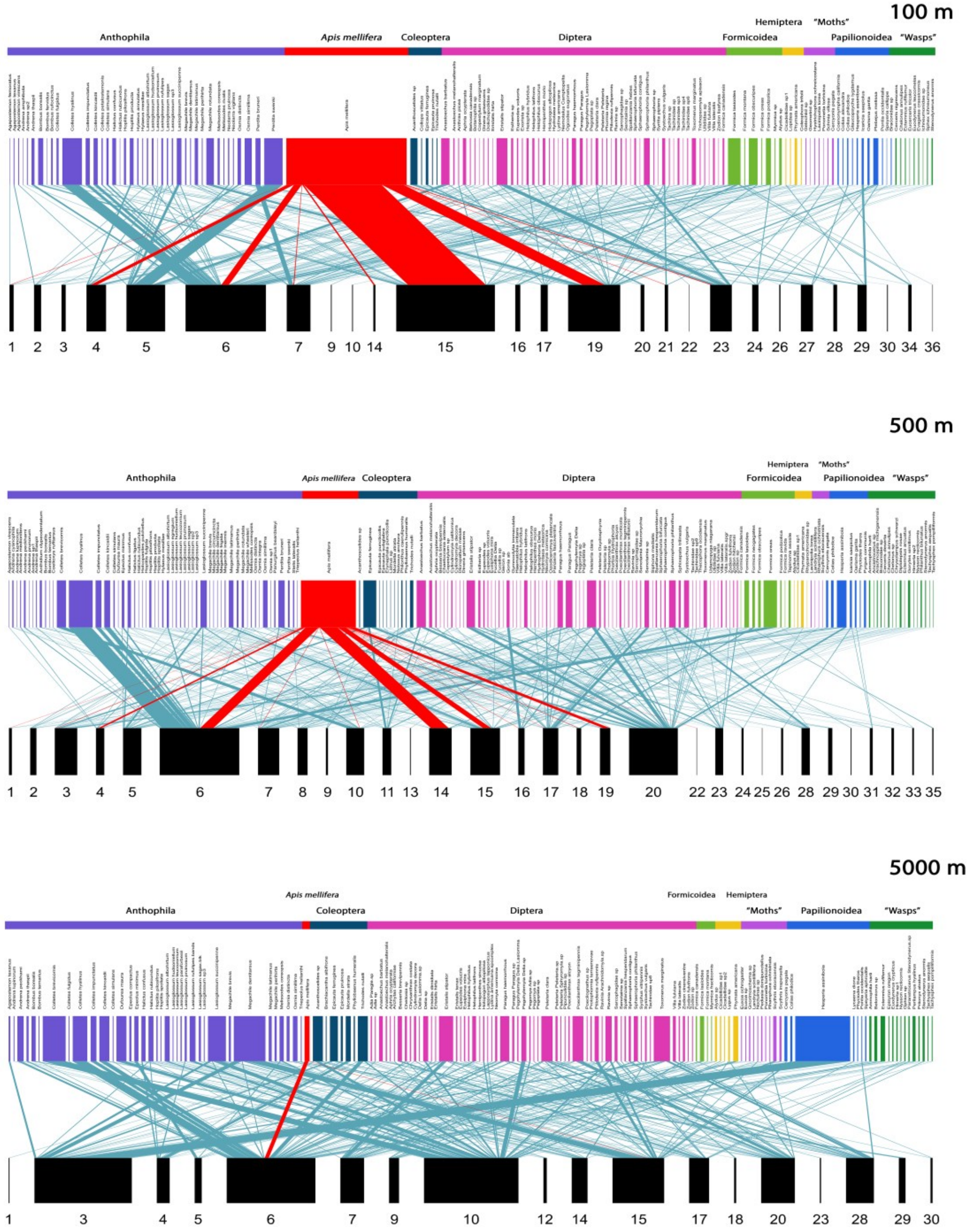
Appendix XI. Longitude and latitude for each hive location and transect in 2018, and collection effort at each transect. The northernmost, central, and southernmost hive locations are listed as Bee1, Bee2, and Bee3 respectively. Each transect is indicated by its treatment, 100 m or 2500 m, and by its location (N = north, C = central, S = south). A and B indicate different transects that shared a hive (see Appendix X).

Longitude	**Latitude**	**Transect**	**Total hand-caught collections**	**Total pan trap collections**
-111.88596	50.90427	Bee1		
-111.94731	50.88246	Bee2		
-111.93791	50.84357	Bee3		
-111.89419	50.88171	N_2500A	2	2
-111.87954	50.88117	N_2500B	0	1
-111.93677	50.86777	C_2500A	5	7
-111.92319	50.86354	C_2500B	3	4
-111.93794	50.85833	S_2500A	3	5
-111.93752	50.84639	S_2500B	8	8
-111.88732	50.90459	N_100A	10	10
-111.88454	50.90462	N_100B	1	2
-111.93114	50.89725	C_100A	7	8
-111.92848	50.89642	C_100B	10	10
-111.89797	50.85482	S_100A	0	3
-111.89836	50.85259	S_100B	2	3

Appendix XII. NMDS plot indicating the abundances of flowering plant species per transect in 2019. Each point represents a transect, with closer-together points on the plot having more similar plant species composition. Ellipses and shapes indicate treatment (100 m, 500 m, or 5000 m distances from a hive). The stress score was 0.18.



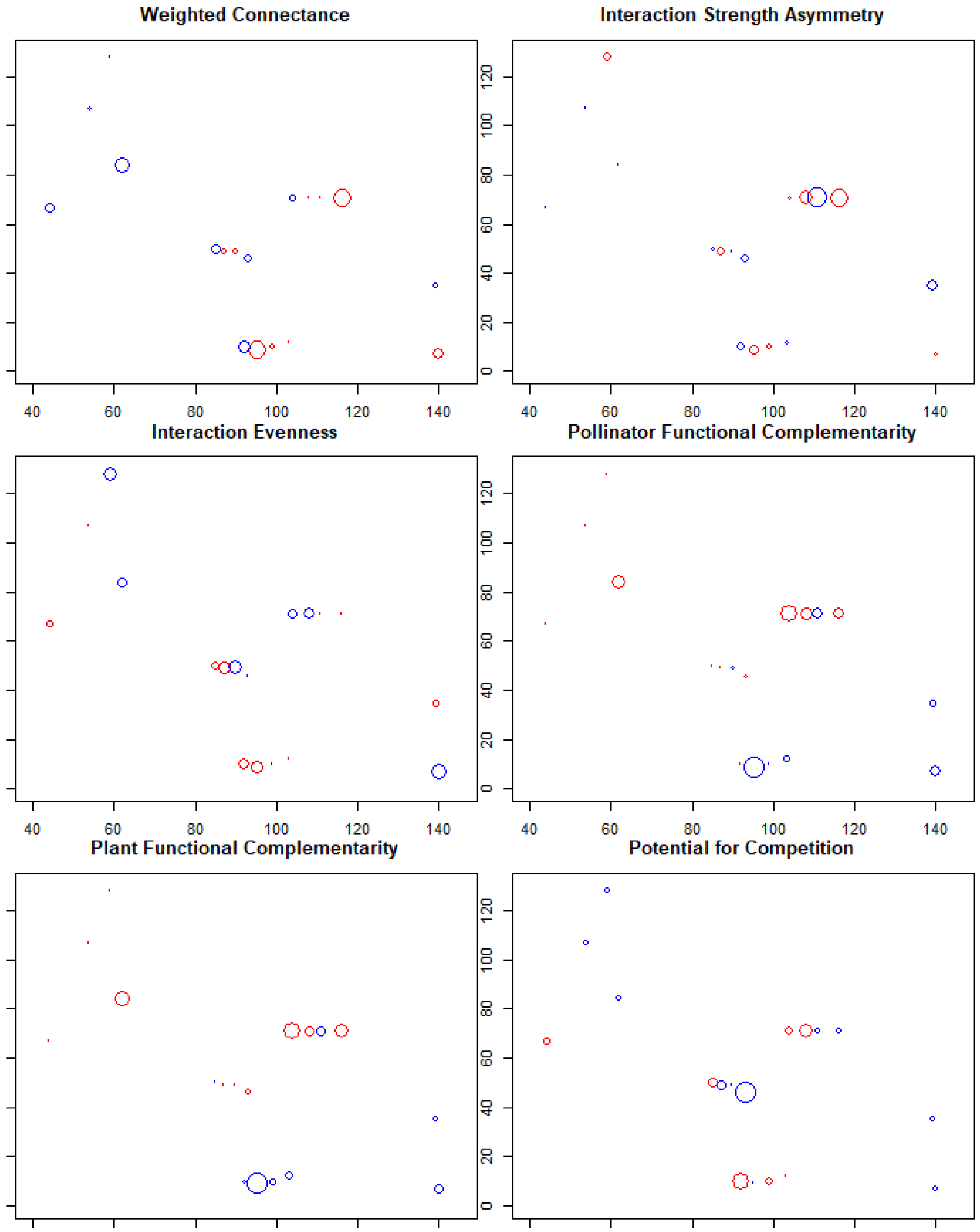
Appendix XIII. Plant-pollinator meta-networks from the 2019 full season all taxa hand-caught dataset. The data from transects 100 m (upper), 500 m (mid) and 5000 m (lower) from honey bee hives are pooled across the season. The bottom row (in black) depicts the plant species (see Appendix XVIII) and the upper row depicts the pollinator species by their given taxonomic "group" or Order. For full species list, see Appendix II. "Moths" are Lepidoptera excluding butterflies (Papilionoidea). "Wasps" are Aculeata excluding ants (Formicoidea) and bees (Anthophila). The width of each upper and lower bar represents the relative frequency of interactions observed for that species. The interactions between the plants and pollinators are represented by the blue lines; width indicates the abundance of the interaction. Honey bees are indicated in red.



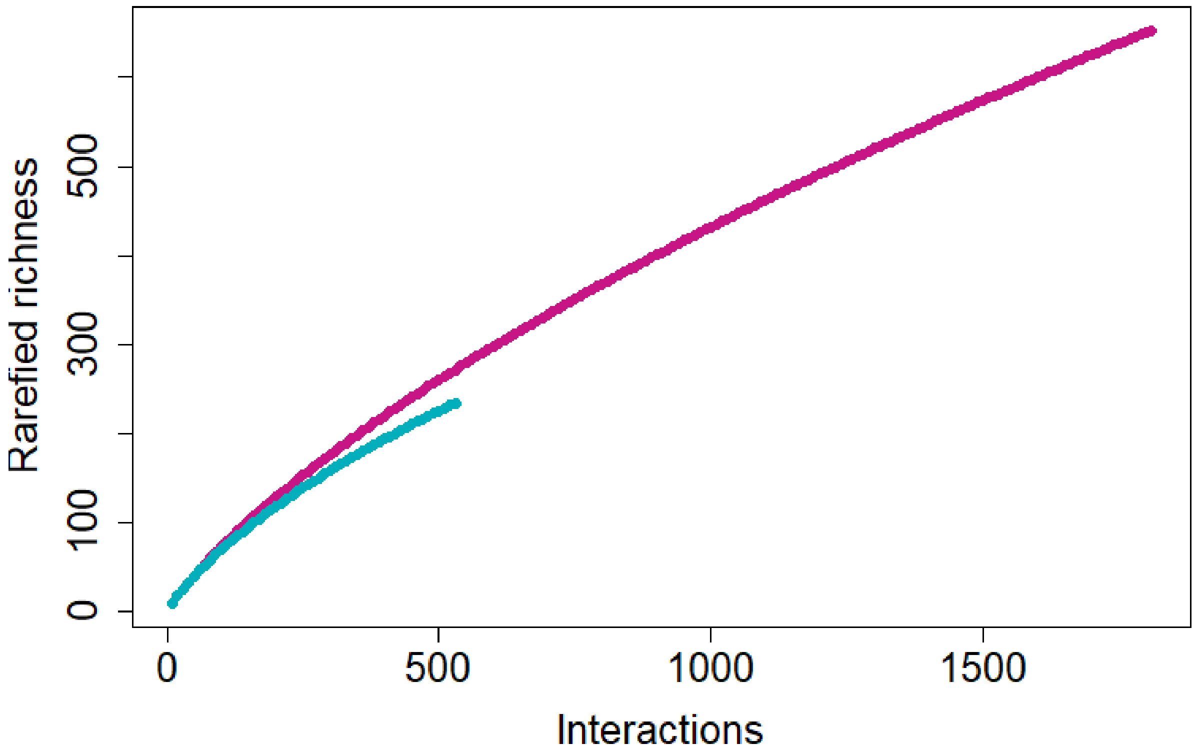
Appendix XIV. Correlation between predictor variables. “Collections” refers to the number of collection rounds at each transect, “Honey bee abundance” refers to hand-caught honey bee abundance at each transect, “Flower species” refers to the number of flowering species at each transect, and “Flowers” refers to the number of individual flowers at each transect.

	Honey bee abundance	Collections	Flower species	Flowers
Honey bee abundance		0.4454	0.6178	0.8517
Collections	0.4454		0.4343	0.3848
Flower species	0.6178	0.4343		0.5981
Flowers	0.8517	0.3848	0.5981	

Appendix XV. Visual representation of the spatial autocorrelation of residuals from the model for each response variable for the full season all taxa dataset, for which honey bee abundance was a significant predictor (before Bonferroni-Holm correction) when it was the only predictor in the model, for full season hand caught data from 2019. Each panel is a map of the transect locations in space (compare to Figure 1). Circles indicate the residual from each transect, with circle size proportional to residual size (smaller circle = better model fit for that transect). Colour indicates the sign of the residual; blue shows values lower than 0 and red values higher than 0. Circles close together in space having the same colour and size would indicate that spatial autocorrelation might be a problem, in which case a special correlation structure would be likely to be selected during model selection (see Chapter 3 Methods).



Appendix XVI. Rarefaction of interaction richness in 2018 (in blue) and 2019 (in pink). 2018 had a total interaction richness of 236, and Chao1 estimated 540 interactions (95% confidence interval: 430-712 interactions), meaning 33 - 55% of the estimated interactions were observed. In 2019, there was a total interaction richness of 654, and Chao1 estimated 1,779 interactions (95% confidence interval: 1500-2148 interactions), meaning 31 – 44% of the estimated interactions were observed.



Appendix XVII. Identifications of flowering species from 2018 meta-networks in Figure 5.

Plant number	Plant Species
1	*Rosa woodsii*
2	*Erysimum inconspicuum*
3	*Astragalus flexuosus*
4	*Vicia americana*
5	*Astragalus striatus*
6	*Taraxacum officinale*
7	*Sphaeralcea coccinea*
8	*Psoralea lanceolata*
9	*Astragalus missouriensis*
10	*Sonchus arvensis*
11	*Heterotheca villosa*
12	*Campanula rotundifolia*
13	*Glycyrrhiza lepidota*
14	*Achillea millefolium*
15	*Melilotus officinalis*
16	*Rosa arkansana*
17	*Descurainia sophia*
18	*Chondrilla juncea*
19	*Tragopogon dubius*
20	*Symphoricarpos occidentalis*
21	*Melilotus albus*
22	*Cirsium arvense*
23	*Grindelia squarrosa*
24	*Solidago canadensis*
25	*Liatris punctata*
26	*Artemesia frigida*
27	*Symphyotrichum ericoides*

Appendix XVIII. Identifications of flowering species from 2019 meta-networks in Appendix XIII. For family names, see Appendix VIII.

Plant number	Plant Species
1	*Rosa woodsii*
2	*Thermopsis rhombifolia*
3	*Liatris punctata*
4	*Rosa arkansana*
5	*Heterotheca villosa*
6	*Symphoricarpos occidentalis*
7	*Solidago canadensis*
8	*Potentilla concinna*
9	*Solidago missouriensis*
10	*Campanula rotundifolia*
11	*Lygodesmia juncea*
12	*Tragopogon dubius*
13	*Potentilla arguta*
14	*Glycyrrhiza lepidota*
15	*Astragalus cicer*
16	*Comandra umbellata*
17	*Achillea millefolium*
18	*Escobaria vivipara*
19	*Melilotus albus*
20	*Grindelia squarrosa*
21	*Medicago sativa*
22	*Erigeron philadelphicus*
23	*Sonchus arvensis*
24	*Cirsium undulatum*
25	*Oenothera nuttallii*
26	*Astragalus striatus*
27	*Taraxacum officinale*
28	*Symphyotrichum falcatum*
29	*Vicia americana*
30	*Erigeron speciosus*
31	*Astragalus adsurgens*
32	*Happlopappus spinulosus*
33	*Cirsium arvense*
34	*Allium textile*
35	*Lithospermum incisum*
36	*Erysmum inconspicuum*