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Are honey bees altering wild plant–bee interactions in reconstructed native habitats? An investigation of summer season effects in row-crop agroecosystems with prairie strips

Kate E. Borchardt[1] | **Morgan Moore**[1] | **Randall Cass**[1,2] | **Matthew O'Neal**[2] | **Amy L. Toth**[1,2]

[1]Department of Ecology, Evolution, and Organismal Biology, Iowa State University, Ames, Iowa, USA

[2]Department of Plant Pathology, Entomology, & Microbiology, Iowa State University, Ames, Iowa, USA

Correspondence
Kate E. Borchardt, Department of Ecology, Evolution, and Organismal Biology, Iowa State University, Ames, IA 50011, USA.
Email: dr.kateborchardt@gmail.com

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Abstract

1. Including native habitats in the margins of an intensifying agricultural environment may help conserve organisms such as bees, which can also utilise crop species for sustenance. Nearly 25% of wild bee species in the United States are in danger of extinction and finding floral resources for managed honey bees (*Apis mellifera* [L.], Apidae) is becoming increasingly difficult. Therefore, both beekeepers and wild bee populations are increasingly reliant on the shrinking native habitat in agroecosystems.
2. We investigated the compatibility of beekeeping with pollinator conservation in one conservation practice known as 'prairie strips' integrated into agricultural landscapes. Prairie strips are native plant communities planted within crop fields that provide agronomic benefits while conserving native organisms. We analysed plant–bee interactions and bumble bee body condition at row-crop fields integrated with prairie strips with and without the presence of a commercial-sized apiary of 20 honey bee colonies, during the summer season (June to August) in 2021.
3. We found no effect of apiaries on the abundance and richness of wild bees or bumble bees and no difference in plant–pollinator network structure. *Bombus bimaculatus* [Cresson, Apidae] had a lower dry mass at prairie strips with apiaries than at prairie strips without. However, there was no difference in dry mass in the other two bumble bee species and no difference in all three bumble bee species when we analysed body size and average wing area.
4. Our study suggests commercial-sized apiaries may have little effect on ecosystem function, wild bee communities and bumble bee body condition from June to August. However, this study did not address the effects of honey apiaries across seasons and years. More research is needed to determine if a commercial-sized

apiary would affect wild bee communities after August when honey bees begin visiting native prairie plants more frequently.

KEYWORDS
body condition, conservation, honey apiary, native bee, plant–bee interactions

INTRODUCTION

Increasing native plant communities within and around agricultural environments has immense potential to improve biodiversity conservation efforts globally (Garibaldi et al., 2021). Integrated native habitats have been shown to reduce sediment and fertiliser runoff (Schulte et al., 2017), increase populations of beneficial organisms from soil microbes to pest–predators (Landis et al., 2012; Philips et al., 2014), and in some cases even increase crop yield and quality (Brittain et al., 2013; Gómez et al., 2023; Wietzke et al., 2018). However, there are still debates about how to best balance environmental and agricultural goals within these landscapes (Hatfield et al., 2015; Kleijn et al., 2015; Kremen & Miles, 2012; Werling et al., 2014).

One such area of debate relates to the tension between balancing priorities for the conservation of wild bees and apiculture (i.e. honey production). Important agricultural crop systems in the United States are highly dependent on managed honey bees (*Apis mellifera* [Cresson, Apidae]) for crop pollination (DeGrandi–Hoffman, 2003) but many beekeepers have difficulty finding floral resources for their colonies outside of the pollination season (Aizen & Harder, 2009; Durant, 2019). One possible solution is to allow beekeepers to utilise native vegetative enhancements within working landscapes for honey bee forage; however, this has the potential to decrease insect pollinator conservation gains (Hatfield et al., 2015) in heavily farmed landscapes that often also exhibit regional native bee declines (Bartomeus et al., 2013; Grixti et al., 2009). Most studies show that managed honey bees outside of their native range can negatively affect wild bee foraging behaviour and species interactions (Mallinger et al., 2017); such effects are symptoms that can signal or precede biodiversity loss (Valiente–Banuet et al., 2015). This is not surprising given the highly efficient foraging behaviour and colony size of honey bees. For example, honey bees can impact plant fitness without affecting native pollinators foraging on that plant species (do Carmo et al., 2004). In addition, a 40-colony apiary placed in a natural environment may collect enough pollen to displace 4 million wild bees in 3 months (Cane & Tepedino, 2017). Honey bees as supergeneralists can especially impact wild generalist bees, which can in turn have detrimental community effects (Brosi et al., 2017; de Santos et al., 2012; Magrach et al., 2017; Wignall et al., 2020) including increased isolation of plant–bee interaction groups and less support for specialised species (Valido et al., 2019).

One federally subsidised U.S. conservation practice with the potential to balance both wild bee conservation and managed honey production is prairie strips (Conservation Reserve Program CP43). Prairie strips are linearly arranged areas within and at the edge of row-crop fields planted with native grasses and forb species to provide multiple environmental benefits including habitat for organisms such as native birds and beneficial insects (Schulte et al., 2017) within agricultural landscapes. Prairie strips have consistently shown benefits for wild plants and pollinators through increased species richness and abundance (English, 2020; Kordbacheh et al., 2020; Murray, 2021) and ecological functions (Borchardt et al., 2023; Borchardt et al., 2024). In addition, prairie strips also have positive effects on honey bee productivity and overwintering success (Zhang et al., 2023). The increasing popularity of prairie strips has immense potential for increasing native habitat for both wild pollinators (Luther et al., 2022) and managed honey bees (Durant, 2019; Zhang et al., 2023). However, there is still a lack of information on whether the small area of native vegetation provided by prairie strips (typically 10% of the total crop field area) is enough to simultaneously support wild bee populations and managed honey bee colonies.

We investigated the effect of a mid-size honey bee apiary of 20 colonies on wild bee communities in prairie strip habitat to address this knowledge gap of the effect of honey bees on wild bee communities within agricultural landscapes. Previous research suggests that in prairie strips the summer season (June to August) may be a ‘safe period’ with less floral resource usage overlap between honey bees and wild bees in native prairie plant communities, compared to late summer into fall (August to September). Honey bees forage for pollen from exotic plant species in June and July before foraging more equally on native and exotic plant species in August and September (Zhang et al., 2021). We note this trend can differ slightly between years (Zhang et al., 2022) and less is known about honey bee nectar foraging in this environment. Placing apiaries at prairie strip sites is also known to increase the abundance of free-flying honey bees in these environments (St. Clair, Dolezal, et al., 2020), which have fairly low honey bee density if apiaries are not present (Gill & O'Neal, 2015; Wheelock et al., 2016). Therefore, we focused on this time period (June to August) as a potential ‘safe period’ of overlap between honey bees and wild bees. We first confirmed that the addition of apiaries increased the presence of honey bee foragers on flowers at our experimental sites and that honey bees shifted from exotic to native plants throughout the season. Then, we compared prairie strip sites with and without the addition of apiaries to examine whether the addition of a honey bee apiary affected well-established metrics such as wild bee abundance and richness. However, most previous studies investigating the effect of managed honey bees on wild pollinator communities did not necessarily find changes in wild bee richness and abundance, but often found changes in plant–bee interaction networks and wild bee foraging behaviour (Giannini et al., 2015; Mallinger et al., 2017; Valido et al., 2019). Therefore, we also analysed two more sensitive measures – plant–bee interaction network structure and the body condition of individual wild bees collected at these sites. Loss of species interactions can be an indicator of impending local species extinctions (Valiente–Banuet et al., 2015) and community functions such as support for specialised species, pollinator foraging behaviour, isolation of groups in the community and chance for animal-mediated pollination. Additionally, we collected more in-depth body condition data on three native generalist bee species, which we suspected may be disproportionately affected by apiary presence due to their overlap in floral resource usage (Magrach et al., 2017; Valido et al., 2019; Wignall et al., 2020) – *Bombus bimaculatus* [Cresson], *Bombus griseocollis* [DeGeer] and *Bombus impatiens* [Cresson]. Body size and wing area metrics are correlated with many aspects of the fitness of an organism (CaraDonna et al., 2018): indirectly through activity (Foster & Cartar, 2011; St. Clair, Dolezal, et al., 2020) and total lifespan (Bosch & Kemp, 2004; Dukas & Dukas, 2011; Higginson et al., 2011; Kemp & Bosch, 2005) as well as reproductive fitness (Kingsolver & Huey, 2008).

Our general hypothesis was that honey bee apiaries would affect wild bee community composition, interactions with plants and bumble bee health metrics in prairie strips. Specifically, relative to farm fields integrated with prairie strips without the addition of apiaries, we predicted those with apiaries would show the following: lower wild bee richness and abundance, along with bumble bee richness and abundance, network traits indicating lower foraging efficiency of wild bees, lower support for specialised plant and bee species, greater isolation of groups in the network, lower chance for bee-mediated pollination, lower pollinator fidelity and higher pollinator foraging competition. We also predicted that bumble bees would be smaller, have lower dry mass and show more wing wear and foraging effort in prairie strips with apiaries compared to those without. Support, or lack thereof, for these hypotheses can help inform management decisions related to the placement of honey bee apiaries in reconstructed native habitats within working landscapes.

METHODS

Site selection

We monitored plant–bee interactions at privately-owned row-crop fields conventionally managed with CP43 prairie strip established (seeded more than 3 years before this study) in central Iowa, a Midwestern state in the U.S. Corn Belt that is highly agricultural (Smith, 1998; Figure 1). The climate of the state of Iowa is continental with cold winters (average January temperature of −4.7°C), warm summers (average July temperature of 25°C) and moderate annual

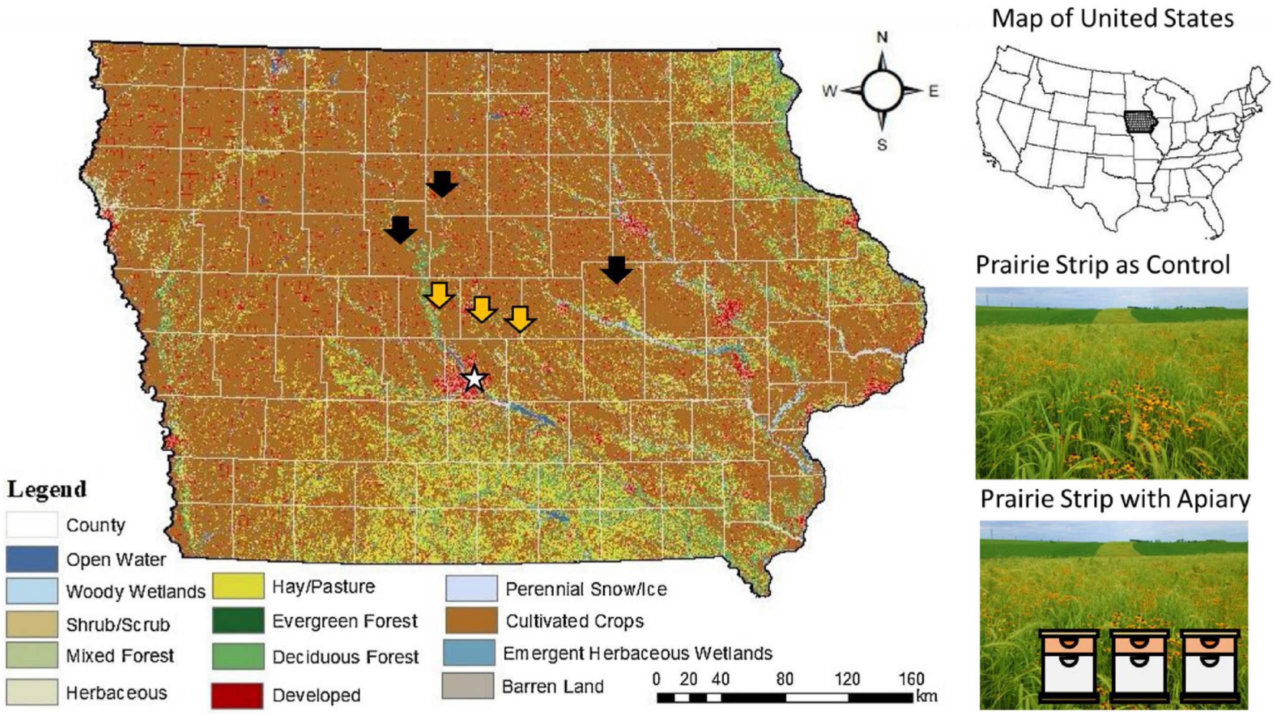

FIGURE 1 Our study sites consisted of six commercial farm fields participating in the prairie strip practice (CP43; USDA) in central Iowa, a state in the US Midwest (map, top right). The tip of each arrow indicates the location of a study site: Three sites were used as controls (black arrows, top) and three sites had a honey bee apiary of 20 colonies established at the site ('Honey Bee' sites, yellow arrows, bottom), with the star indicating the state capital of Des Moines. Site names are abbreviations of private farm names to ensure privacy and are indicated as arrows as follows from top to bottom: SMI (black, upper middle), SME (black, upper left), STO (black, middle right), WHO (yellow, middle left), GUT (yellow, bottom middle) and RHO (yellow, bottom right). Upadhaya et al. (2021) created the landscape map above using National Land Coverage Data (Dewitz, 2019) and this was modified from Borchardt et al. (2023).

precipitation (approximately 92.0 cm; U.S. National Weather Service, 2022). Farming in Iowa is primarily of corn (*Zea mays* [L.], Poales: Poaceae) grown in a rotation with soybean (*Glycine max* [(L.) Merr], Fabales: Fabaceae) both as monocultures with soil tillage, synthetic fertilisers and pesticides and winter fallow between crop seasons.

We surveyed wild bee communities at six prairie strips within row-crop field sites (Figure 1). Sites were given three letter abbreviations to maintain the privacy of the landowners (GUT, RHO, SME, SMI, STO, WHO). Three farms integrated with prairie strips had an apiary of 20 honey bee colonies ('Honey Bee Sites'; GUT, RHO, WHO; Hatfield et al., 2018) and three farms were without apiaries ('Control Sites'; SME, SMI, STO). The three closest sites were chosen as the Honey Bee sites to help facilitate equipment transportation and colony monitoring checks. A survey of the apiary registry in the four Iowa counties where these farms were located (Story, Tama, Webster and Wright) found self-reported 'commercial' beekeepers kept approximately 16 honey bee colonies at a single location (Borchardt, unpublished data; this did not include hobbyists and queen production apiaries), which makes our apiaries slightly larger than average-sized commercial apiaries in our study regions. It is voluntary to register honey bee hives with the Apiary Registry; therefore, it does not report all honey bee colonies in the environment. Sites were a minimum of 3.2 km apart to ensure bees were not foraging between sites based on previous estimates of honey bee foraging distance (Couvillon et al., 2014; Danner et al., 2014). Managed honey bee colonies are common in the region, and two of our honey bee sites (WHO, RHO) and one control site (SME) had self-reported honey bee colonies within 3.2 km from the site. All sites had a similar prairie strip size, were established between 5 and 7 years prior to our surveys, around 40 originally sown native plant species and have a history of research on both wild bee, honey bee and plant establishment (Borchardt et al., 2023; Borchardt et al., 2024; Kordbacheh et al., 2020; Zhang et al., 2022). Prairie strips typically consisted of one to five strips (typically six meters wide) within fields, occupying ~10% of the field area and seeded with a mix of native grasses and forbs (CP43; U.S. Department of Agriculture, 2019). At the time of the study, prairie strips were still relatively uncommon in the landscape. Forty-seven farmers had planted prairie strips by 2017 (Love, 2017; Schulte et al., 2017) establishing less than 2,000 acres based on the average farm size in 2017 (Perdue & Hamer, 2019) before increasing to more than 22,000 acres of prairie strips in December 2023 (Farm Service Agency, 2023).

Apiary management

Honey bee sites had 20 honey bee colonies started from packages purchased from Spring Valley Honey Farms in Perry, Iowa in late April 2021 and put into Langstroth deep colony boxes with some honey, pollen, drawn and empty comb frames. At the end of May 2021, colonies were inspected, weighed and assigned to sites to maintain roughly equal overall hive weight at each site. Colony weight was estimated by tipping colonies onto a postal scale and subtracting the average weight of comparable empty hive equipment. Colonies were then moved to the prairie strip sites and placed in a location that would be easy for a beekeeper to access while not disrupting farming operations (Figure S1). Our honey bee apiaries were monitored monthly for disease indicators, queen presence, adult bee population, honey sample collection for pollen analysis and the need for additional deeps or honey supers for the colony to expand into. Estimating the adult population of a honey bee colony can be accomplished by removing each frame and counting the number of frames covered by adults. This procedure requires disturbing each colony, which results in many adults dispersing from the colony. We reduced the impact of this measurement on both honey bees and wild bees by estimating adult populations of each colony by counting the presence of bees in the 'seams' between adjacent frames as observed from the top of each hive box, to use beekeeping terminology. We estimated whether a seam was completely full of adult bees, half full or nearly empty. Seam counts provided a good estimate of the bee population, showing a high correlation to the more disruptive adult honey bee population estimator, frame sides of bees (Frame Side $= 0.9288\ *$ Seams $+\ 0.8459$; $R^2 = 0.7298$). Ultimately, using seams provided a quick estimate of the adult honey bee population in the colonies kept at Honey Bee Sites without excessively disturbing each colony. After converting seams to frame sides, we estimated the adult bee population using Delaplane et al. (2013) method. Honey was harvested on 17 August 2021. One hive was found dead during the season at WHO on 8 July and was replaced with a healthy hive. The hives were removed from the site in late September and placed at a different location to overwinter.

A sample of honey was collected from five randomly selected colonies at each Honey Bee site once per month from June to September. These honey samples were combined for each site and month and were contracted out for pollen grain identification by Dr. Carol Fassbinder–Orth from Creighton University into five broad categories as follows: native forbs (Asteraceae; Fabaceae/ Scrophulariaceae spp.; *Monarda* spp.), exotic forbs (*Trifolium/Melilotus* spp.), soybean (*G. max*), tree species (*Betulaceae* spp., *Robinia pseudoacacia* [L.], *Tilia americana* [L.]) and grass (Poaceae spp.). We conducted a Fisher's exact test to conservatively test (due to our small sample size) if the overall composition of pollen changed over time.

Bee collections and surveys

Surveys were conducted at each site once a month from June 2021 to August 2021, a period of peak forb bloom that primarily covers the summer season (Murray, 2021). This period includes a time (June, July) when honey bees primarily forage on soybean and clover before honey bees begin foraging more frequently on native plants starting in August (Zhang et al., 2021; Zhang et al., 2022). We thus selected these dates as a putative 'safe period' for concurrent conservation and honey production benefits, as this is a time period during which honey bees utilise trees, exotic plant species and soybeans as food resources more than native prairie plant species. We intended to conduct bee surveys on days with ideal weather for pollinators to forage (i.e. temperature above 16°C; sky conditions of bright overcast, partly cloudy or sunny; and wind speeds below 3.5 m/s; Ward et al., 2014), but relaxed temperature and wind criteria due to too few ideal weather days in this region. Sites (one Honey Bee and one Control site) were paired by sampling date (i.e. both sites were sampled during the same week to account for weather and floral bloom period between the site treatments). These pairs were chosen to streamline the fieldwork schedule even though the pairs were not true-matched pairs due to different owners, countries and other site traits. Sites were sampled twice to capture species active at different times of the day (Baldock et al., 2011) – once in the AM sample (starting between 8 AM and 11 AM), and once in the PM (usually starting between 12 PM and 3 PM; at least 3 h after the start of the AM sample). In addition, three transects 100 m long and approximately six metres wide (depending on prairie strip width) were sampled at each site in relation to the best location for an apiary regardless of site treatment (Figure S1). The three transects consisted of the unmanaged field edge next to the apiary location ('Edge'; ~25 m from apiary centre), the nearest prairie strip to the apiary location ('Near'; ~59–92 m from apiary centre) and the second-nearest prairie strip to the apiary location ('Far'; ~120–184.9 m from apiary centre).

Many bee species adjust their foraging behaviour in the absence of competitors in a sub-daily time period (Brosi et al., 2017; Wignall et al., 2020), suggesting that plant–pollinator interactions may vary with the absence of honey bees within 24 h. We sampled each site on two separate days ('Day Treatment') to understand the influence of apiaries on wild plant–bee interactions when the colonies are open or temporarily closed. For the Honey Bee sites, the first survey was conducted with the honey bee colonies in their normal, open state ['Day 1 (Open)'] and the second-day survey was conducted while the honey bee colonies closed with metal mesh at the hive entrance since the night before at the Honey Bee sites ['Day 2 (Closed)']. The metal mesh was removed from all the hives following the Day 2 survey. The purpose of this was to examine the acute effects of honey bee removal on foraging and plant interactions of wild bees. For the control sites, we surveyed on two consecutive days (Day 1 and Day 2) – the purpose was to control for the effect of sampling depletion on wild bee communities from 1 day to the next.

During bee surveys, we collected all bees observed touching the reproductive region of a flower (indicating potential for pollination) for 10 observational minutes during each time period (AM and PM sample) and transect ('Edge', 'Near' and 'Far'; Figure S1) while walking through each transect at a constant pace (Williams et al., 2015). With the two sample days each month and three transects (Edge, Near and Far) per each time period (AM and PM), each site had a total of 120 min of active sample per site per month, which is comparable to other interaction network studies (80 total observation minutes per plot, Brosi et al., 2017; 70 total observations minutes per site, Borchardt et al., 2023; a minimum of 50 observation minutes per plant species, Valido et al., 2019). Specimen processing and data recording did not count towards observation time. We recorded captured bees with the plant they were observed visiting ('observed interaction') along with the relative abundance of plant groups observed in bloom. Honey bees and queen bumble bees were caught, identified to species and released. Collected specimens were stored in 1.5 mL centrifuge tubes and identified as species under dissection scopes using Ascher and Pickering (2020) except for *Lasioglossum* spp., which were identified as morpho-species according to St. Clair, Zhang, et al. (2020).

Wild bee abundance was calculated using both collected specimen counts and records of missed bees identified in the field; however, wild bee richness and network metrics only used collected specimen data due to the unreliability of field visual identification to species. Similar methods were used to analyse bumble bee abundance and richness, which included only observations of bees in the genus *Bombus* and associated specimens. We analysed bee abundance and richness trends across the entire season using a generalised linear model with Poisson error to investigate the effect of site treatment, day treatment and the interaction between site and day treatment. We included weather variables, such as average temperature, wind speeds and month, to account for non-ideal pollinator weather during sampling. Then, we created statistical contrasts of all pairwise combinations of site and day treatment alongside Cohen's D effect size to determine the significance and magnitude of differences between the means using pooled standard deviation. We only considered our results informative if they were both significant and had a large effect size (Cohen's D > 0.2) meaning the difference between the means was large enough to be meaningful. For wild bee abundance and richness, this was further separated by month (June, July and August) as well as overall contrasts; however, there was not enough data for the models to converge and test the effect during each month for bumble bee abundance and richness. We used the 'emmeans' package in R (Lenth et al., 2023; R Core Team, 2023) and used the Bonferroni method to adjust our interpretation of our *p*-values when testing multiple statistical contrasts in wild bee abundance and richness due to the large number of contrasts we tested (16 each for abundance and richness; adjusted alpha = 0.003125).

Network analysis

Networks were created using observed interactions in the field for each site (GUT, RHO, SME, SMI, STO and WHO) per month (June, July and August). All bee species had at least one interaction due to our collection methods; however, some plant species could be unvisited by a bee during our observation periods (Jordano, 2016) but were included in the network because they were observed in bloom at the site. Networks were analysed using the 'bipartite' package (Dormann et al., 2009) in R (R Core Team, 2023). Network metrics were calculated using the 'networklevel' or 'computeModules' functions. We chose five network metrics to measure which we describe in the following paragraph: links per plant species, weighted nestedness (NODF), niche overlap (bees and plants separately), network-level specialisation (H_2') and modularity.

Links per plant species is an indirect binary measure of pollination for plants, calculated as the average number of interacting partners or links for all plant species in the network and indicates the chance for bee-mediated pollination (Tur et al., 2013). NODF is a binary calculation of nestedness that shows the level of network structural support for more specialised plant and bee species (Bascompte et al., 2003; Bascompte & Jordano, 2014). NODF is calculated by sorting the columns representing bee species by the marginal total of interacting partners or 'links', and then by comparing each column to all other columns with fewer links to determine the per cent of links observed in both columns. Niche overlap is a weighted measure of similarity between species at the same trophic level, meaning it is calculated separately for bees and plants. A value of one indicates perfect niche overlap, where all species are filling similar roles and there is redundancy in the network that is robust to the effects of species loss (Hooper et al., 2005), and a value of 0 indicates that the network is made of strongly isolated islands of interacting species. Network-level specialisation (H_2') shows whether generalist bee species are optimising their foraging behaviour by specialising on a few plants to decrease the costs of switching between floral types when floral resource abundance is high (Goulson, 2000; Petanidou et al., 2008; Woodward & Laverty, 1992). Network-level specialisation (H_2') is a weighted calculation of the deviation of the observed interactions against what is expected from the total number of interactions for that species, then averaged across species in the network (Blüthgen et al., 2006). Modularity measures how isolated different subsets of the network or modules of interacting species are from each other. Networks often become isolated after the loss of highly connective generalist species (Aslan et al., 2018; Valido et al., 2019) which increases the risk of local extinction for these isolated subsets (Bascompte & Jordano, 2014).

We used multiple statistical methods to analyse the plant–bee interaction networks between Honey Bee sites and Control sites, drawing conclusions from consensus trends between the methods (Borchardt et al., 2023) and using metrics robust to confounding effects such as species richness differences (Blüthgen et al., 2006; Fründ et al., 2016). First, we analysed metrics from the observed networks without modification ('raw traits'). Second, we used null models to check the likelihood that the observed network structure was caused by random assortment (i.e. if raw traits are similar to null model traits the result is rejected as not biologically meaningful). Null models were calculated based on marginal totals of rows and columns (Pellissier et al., 2018) using the 'mgen' function in the 'bipartite' package (Dormann et al., 2009). Third, within a site pair and month, we rarefied networks ($n = 1000$) so that both networks had the same number of plant and bee species to investigate if the trend is observed without the influence of species richness (Table S1; Pellissier et al., 2018). Some network pairs were too small for rarefaction analysis, including GUT–SMI in July and WHO–SME in June. The rarefied network metrics were averaged and analysed using a non-parametric Mann–Whitney U test to calculate the significance of differences in the network traits between the site treatments.

Bumble bee body condition

We measured body condition metrics that can serve as health indicators in the worker caste of three bumble bee species with sufficient specimens (Table S2) – *B. bimaculatus*, *B. griseocollis* and *B. impatiens* – to determine if honey bees competed with these abundant, native generalist species. We investigated three health indicators – bee body size through intertegular distance, dry mass and wing area.

Intertegular distance was measured as the distance in mm between the two tegulae on the thorax of each collected bumble bee specimen using callipers. Intertegular distance was analysed using a linear model predicting intertegular distance from site treatment. The guts were dissected for pathogen analysis in a related research project, which found no presence of *Nosema* spp. Even though at least one honey bee colony was infected with the pathogen. Wings were removed from collected specimens, plated onto a microscope slide and imaged using a Leica dissection microscope. Wing area was measured using tpsDIG (Rohlf, 2018) and analysed in a linear model accounting for relative age and body size (intertegular distance). Relative age was measured as the number of days the specimen was collected after the first collection date of that species, within the same year. Wing wear increases with age and body size (Mueller & Wolf–Mueller, 1993) and we calculated relative age as the number of days since the first observation of that species for that season. The remaining wingless and gutless specimen was then dried in a Thelco Laboratory incubator for 24 h at 50°C. Each dried individual was weighed on a Mettler AE100 balance and dry mass was recorded in grams. Dry mass was analysed using a linear model accounting for body size (intertegular distance). Age decreased model fit by more than two units of the Akaike Information Criterion (AIC) and Bayesian Information Criterion (BIC) and was therefore excluded from the model. The metrics AIC and BIC estimate the amount of information lost in a model while accounting for the number of terms in the model, making them useful metrics for determining which models best balance the risks of overfitting and underfitting. Models within two units of either AIC or BIC of each other are considered to fit the data similarly, with a lower value of more than 2 units indicating a better fit of the data.

RESULTS

Honey bee population

The average adult honey bee population at each apiary site increased steadily throughout the season as follows: approximately 100,000 in June, 200,000 in July, 250,000 in August and 300,000 in September (Figure 2). In terms of floral visitation observed during our collection period, we observed 48 honey bee visits to flowering plants in total – 47 at Honey Bee sites and only one at a Control site (Figure 3). Although there are clear trends suggesting more honey bees are present at the Honey Bee sites compared to Control sites, the relatively small number of observations (27 out of the 36 total bee surveys observing no honey bee interactions at all) prevented a robust

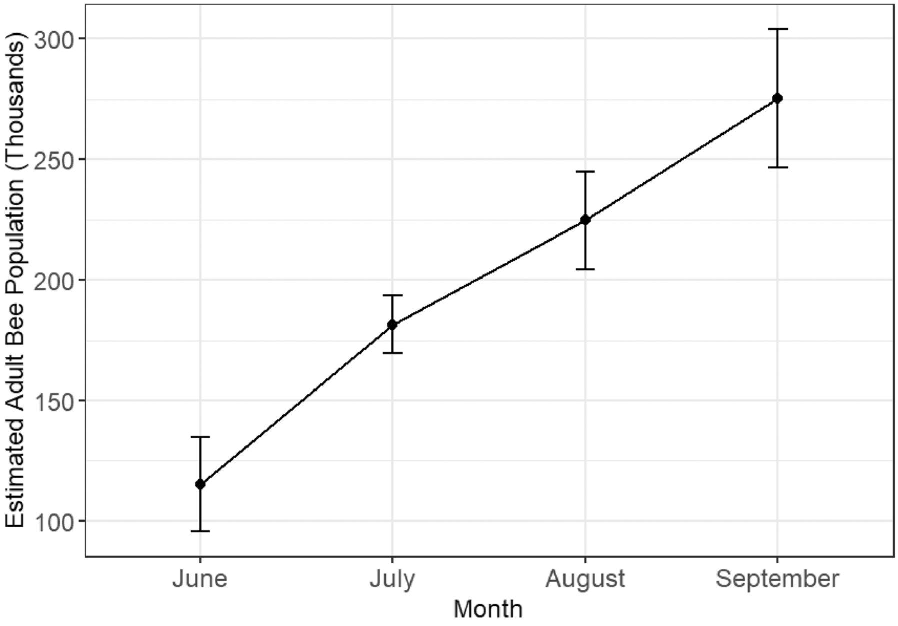

FIGURE 2 Estimates of the average and standard error of the adult honey bee population for our three sites across the season. Population was estimated by counting 'seams', looking in the spaces between hive frames from the top of each hive box, and was converted into frame sides of bees using data collected on the same colonies (Frame_Side = 0.7846 * Seams +1.7054; R^2 = 0.7045) and then was converted to approximate adult bee population using Delaplane et al. (2013).

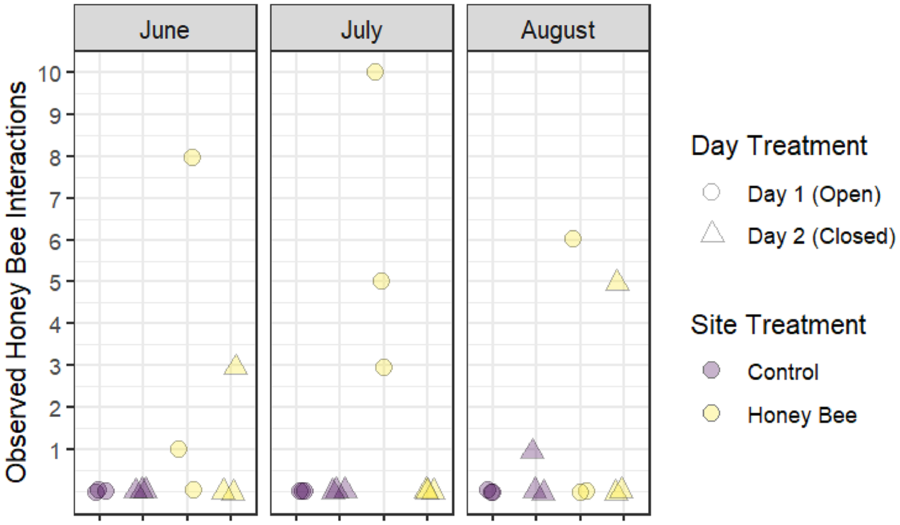

FIGURE 3 Observed interactions of honey bees with plants during field surveys, broken down by site treatment and day treatment. Of all observations made at Control sites, only a single honey bee was observed interacting with a plant (STO field site in August).

statistical analysis. Controlling for weather conditions and day treatment, we found no significant difference in honey bee observations between our Honey Bee sites and Control sites when apiaries were open (Day 1) (glm, Honey Bee sites, estimate = 20.503 ± 2934.25, z-value = 0.007, *p*-value = 0.994), despite the strong aforementioned numerical difference. Further supporting the notion that apiary placement increased honey bee foraging, a previous study using a similar experimental design (St. Clair, Dolezal, et al., 2020) found very few free-flying honey bees in this landscape when apiaries are not present in the immediate vicinity, and the placement of an apiary increased the activity-density of honey bees (assessed through pan traps).

Based on pollen grains found in freshly capped honey in our apiaries, native prairie plant use as nectar sources was as follows: 19.9% in June, 5.8% in July, 2.4% in August and 26.4% in September (Figure 4). The highest proportion of pollen grains in freshly capped honey was as follows: 54.4% tree pollen in June, 59.0% soybean pollen in July, 86.9% exotic plant pollen in August and 66.2% exotic plant pollen in September. We found a significant difference in honey

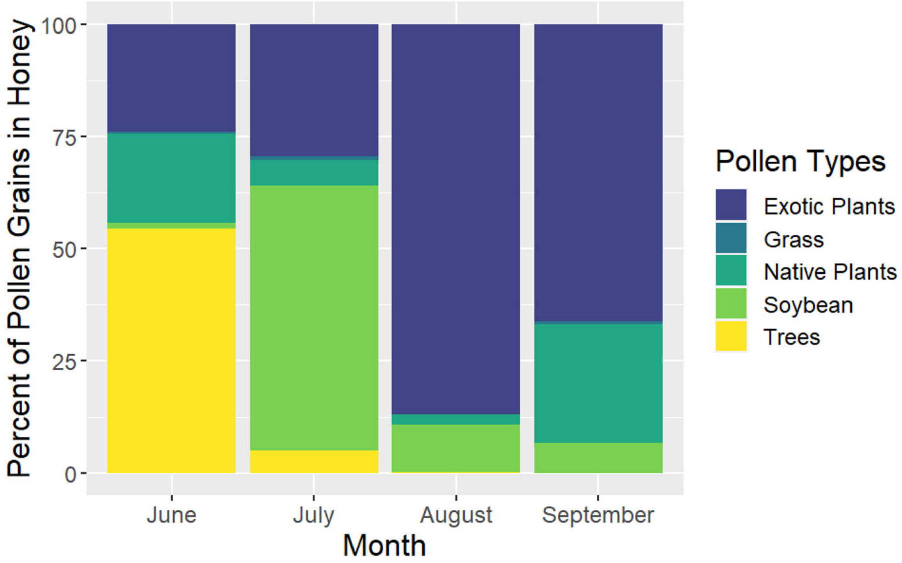

FIGURE 4 The occurrence of plant pollen types found in honey collected by hives in prairie strips. Honey was collected from five randomly selected colonies (pooled together for pollen analysis) at each Honey Bee site once per month from June to September. A Fisher's exact test showed a significant difference in honey pollen composition between the 4 months (p-value = 0.0005). Pollen grains were identified into five broad categories: Native plants (Asteraceae, Fabaceae/Scrophulariaceae spp., *Monarda* spp.), exotic plants (*Trifolium*/*Melilotus* spp.), soybean (*Glycine max*), tree species (*Beluaceae* spp., *Robinia pseudoacacia*, *Tilia americana*) and grass (Poaceae spp.).

pollen composition between the 4 months (two-sided Fisher's exact test, p-value = 0.0005).

Wild bee community

We observed 93 bee species or morphospecies and 43 plant groups in total: 75 bee groups and 34 plant groups at the control sites and 68 bee groups and 32 plant groups at the honey bee sites (Tables S3 and S4). We observed 1453 plant–bee interactions in total: 742 interactions at control sites and 711 interactions at honey bee sites (Figure S2).

Wild bee abundance showed some significant differences between treatments when controlling for weather variables (Figure 5 and Table S5), but these had very small effect sizes and were contrary to predictions; thus, the differences may not be biologically relevant (Cohen's $d < 0.2$; Table S6). Specifically, wild bee abundance was significantly higher in the presence of apiaries (generalised linear model; abundance, Site Treatment (Honey Bee), estimate = 0.172 ± 0.070, z-value = −2.47, p-value = 0.0135). Although wild bee abundance was higher on the first survey day overall (Day 1 (open); estimate = 0.321 ± 0.070, z-value = 4.61, p-value <0.001), the interaction indicates a greater decrease in wild bee abundance at Honey Bee sites between the first and second sampling days as compared to the Control sites between the first and second sampling days (Day Treatment (Day 1; Open) * Site Treatment (Honey Bee), estimate = −0.477 ± 0.096, z-value = −4.97, p-value <0.001). Month showed a significant effect on wild bee abundance (month; estimate = −0.017 ± 0.009, z-value = −2.00, p-value = 0.0453). Therefore we analysed the statistical contrasts for each month. The difference between the site treatments was driven by higher wild bee abundance at Control sites on the first survey day (Contrast: Control Day 1 – Honey Bee Day 1 (open), estimate = 0.305 ± 0.066, z-value = 4.655, p-value <0.0001) similarly found in the June and July sample, but was absent in August (Table S6). The difference between the day treatments was driven by higher wild bee abundance at Control sites on the first survey day compared to the second survey day 2 to 3 days later (Contrast: Control Day 1 – Control Day 2, estimate = 0.321 ± 0.070, z-value = 4.606, p-value <0.0001) but this did not appear in when contrasts were separated by month. However, there was a significant difference in August where there was higher wild bee abundance at Honey Bee sites when the colonies were closed (Day 2) compared to Control sites on the second survey day (Contrast: Control Day 2 – Honey Bee Day 2 (closed), estimate = −0.468 ± 0.127, z-value = −3.697, p-value = 0.0002). However, small effect sizes between the different site and day treatments (Cohen's $d < 0.2$; Table S6) indicate these significant differences represent only slight changes in actual wild bee abundance.

Wild bee richness was not significantly different in the presence of apiaries (Table S5: generalised linear model; Site Treatment (Honey Bee), estimate = 0.186 ± 0.135, z-value = −1.38, p-value = 0.169), day treatments (glm; Day Treatment (Day 1; Open), estimate = −0.031 ± 0.132, z-value = −0.24, p-value = 0.812) or the interaction between day and site treatments (glm; Day Treatment (Day 1; Open) * Site Treatment (Honey Bee), estimate = −0.100 ± 0.189, z-value = −0.53, p-value = 0.595). However, there were biologically meaningful (based on effect size analysis) differences in wild bee richness between sampling days. Specifically, we found lower richness at Honey Bee sites when colonies were open (Day 1) than when colonies were closed (Day 2) in July (Cohen's d = −0.656), and

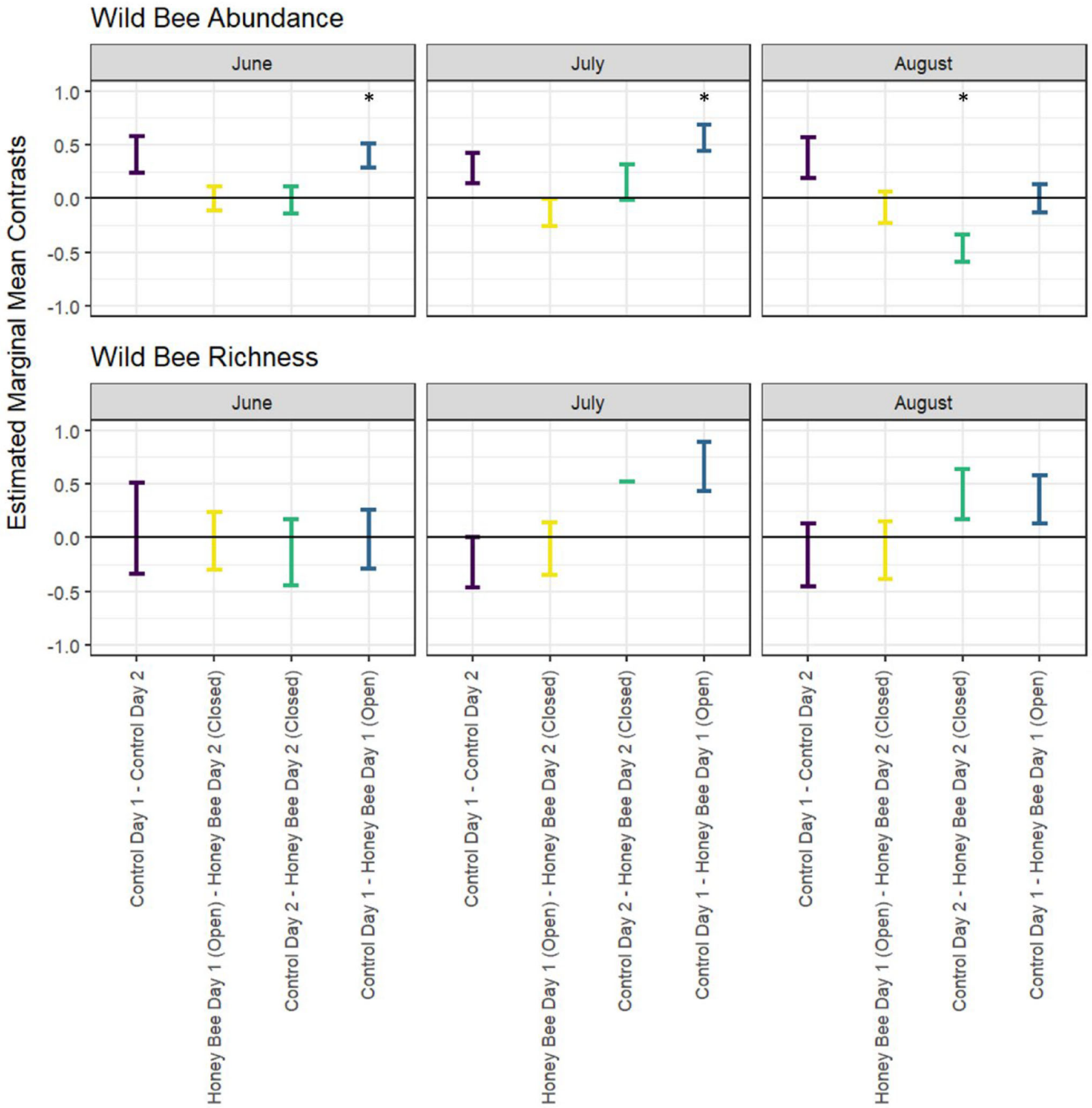

FIGURE 5 Statistical contrasts showing the difference in estimated marginal means for wild bee abundance (top row) and wild bee richness (bottom row) separately for each month (columns; June, July and August). We corrected for multiple testing using a Bonferroni method ($n = 16$, adjusted alpha = 0.003125) and indicated significant differences in the estimated marginal means contrast with a '*'. No contrasts with significant differences had a corresponding biological meaning effect size (Table S6). Bumble bee abundance and richness did not have sufficient data to separate estimated marginal mean contrasts by month, however, overall contrasts are reported in Table S8. Error bars are coloured by the contrast being tested to highlight similar contrasts across the 3 months and two population metrics (Control Day 1 – Control Day 2, purple line; Honey Bee Day 1 (colonies open) – Honey Bee Day 2 (colonies closed), yellow line; Control Day 1 – Honey Bee Day 2 (colonies closed), green line; Control Day 1 – Honey Bee Day 1 (colonies open), blue line).

higher richness on the second survey day when colonies were closed at Control sites compared to Honey Bee sites in August (Cohen's $d = 0.228$) (Table S6).

Overall, bumble bees responded similarly in terms of abundance and richness to the broader wild bee community when controlling for weather variables (Table S7). However, our post hoc statistical contrasts did not find significant differences with sufficient effect sizes, nor in predicted directions (Table S8). For completeness, we reported the direction of these differences. Bumble bee abundance was overall lower on the first survey day (Day 1) than the second survey day (Day

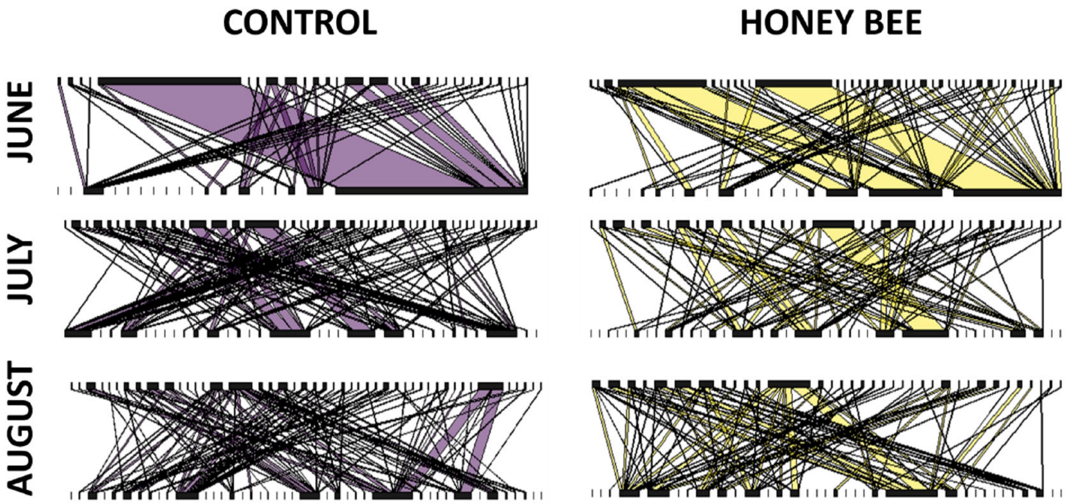

FIGURE 6 Interaction networks for the two site treatments (Control, Honey Bee) over time, showing differences between the first 3 months of the native prairie plant bloom period. Each network shows bee species (top black boxes) and plant species (bottom black boxes) and the interactions (connecting lines) are sized based on the number of times that interaction was observed relative to the rest of that network.

2) (generalised linear model: Day Treatment (Day 1; Open), estimate = −0.653 ± 0.310, z-value = −2.108, *p*-value = 0.035) and higher at Honey Bee sites than Control Sites (glm: Site Treatment (Honey Bee), estimate = 0.675 ± 0.241, z-value = 2.804, *p*-value = 0.005). However, the interaction between day and site treatment was not significant (glm: Day Treatment (Day 1; open) * Site Treatment (Honey Bee), estimate = 0.556 ± 0.331, z-value = 1.680, *p*-value = 0.093). The statistical contrasts show higher bumble bee abundance at Honey Bee sites when the colonies were open (Day 1) compared to Control sites on the first survey day (Contrast; Control Day 1 – Honey Bee Day 1 (open), estimate −1.231 ± 0.282, z-value = −4.370, *p*-value <0.0001).

Bumble bee richness was not significantly affected by the presence of apiaries (Table S7; glm, Site Treatment (Honey Bee), estimate = 0.014 ± 0.392, z-value = 0.036, *p*-value = 0.971), Day Treatment (glm, Day Treatment (Day 1; Open), estimate = −0.801 ± 0.451, z-value = −1.776, *p*-value = 0.076), or the interaction between day and site treatment (glm, Day Treatment (Day 1; Open) * Site Treatment (Honey Bee), estimate = 0.297 ± 0.563, z-value = 0.528, *p*-value = 0.598). The estimated marginal means contrast similarly showed no significant contrasts or biologically meaningful effect sizes (Cohen's *d* < 0.2; Table S7).

We returned to previously published data (Borchardt et al., 2023) collected at five of our six sites in 2019 (excluding the honey bee site RHO) to investigate whether there may be site differences in wild bee species composition that could contribute to the observed trends in this study. In that publication, an apiary of four colonies was present at each site. A post hoc analysis of those data indicates that the sites selected for the honey bee treatment in the current study (GUT, WHO) had lower wild bee abundance (generalised linear model; estimate = −0.300 ± 0.106, z-value = −2.846, *p*-value = 0.004) and richness (glm; estimate = −0.331 ± 0.155, z-value = −2.140, *p*-value = 0.032) than the three sites we selected for our control treatment (SME, SMI, STO) when controlling for weather effects of the month, average temperature and average wind speed). These site differences may have also been present in the current study (conducted in 2021) and suggest the trends we found may have been partially driven by site differences in wild bee community composition.

Plant–bee interaction networks

Visually, networks looked similar between sites; however, they appeared to gain complexity as the season progressed (Figure 6). There was also no indication that the presence of honey bees affected which plants wild bees foraged on. This is indicated by the lack of change in interaction network structure in the presence of honey bee apiaries. Specifically, we found no significant differences in raw network metrics between Control and Honey Bee sites (Table 1 and Figure S3; showing paired Wilcoxon rank exact tests: network-level specialisation (H2), v = 30, *p*-value = 0.426; weighted nestedness (NODF), v = 17, *p*-value = 0.570; modularity, v = 34, *p*-value = 0.203; links per plant species, v = 23, *p*-value = 1.000; niche overlap plants, v = 17, *p*-value = 0.570; niche overlap bees, v = 21, *p*-value = 0.910). In addition, rarefied network metrics that subsampled networks to the same species richness also showed no difference between the Control and Honey Bee sites (Table 1 and Figure S3; showing paired Wilcoxon rank exact tests: network-level specialisation (H2), v = 22, *p*-value = 0.219; weighted nestedness (NODF), v = 4, *p*-value = 0.109; modularity, v = 18, *p*-value = 0.578; links per plant species, v = 8, *p*-value = 0.375; niche overlap plants, v = 11, *p*-value = 0.688; niche overlap bees, v = 12, *p*-value = 0.813). However, all metrics showed some network structures may have been attributable to a random assortment of interactions (Table 1 and Table S9) indicating our networks may not have been sampled sufficiently to fully analyse them.

TABLE 1 Paired Wilcoxon signed-rank exact test comparing network metric values between raw and averaged rarefied network results.

Metric	Raw networks V	Raw networks p-value	Null models Similar of total	Rarefied networks V	Rarefied networks p-value
Network-level specialisation (H_2')	31	0.359	1 of 17	23	0.156
Weighted nestedness (NODF)	16	0.496	4 of 17	3	0.078
Modularity	33	0.250	6 of 17	18	0.578
Links per plant species	19	0.734	4 of 17	5	0.156
Niche overlap plants	17	0.570	5 of 17	10	0.578
Niche overlap bees	21	0.910	1 of 17	12	0.813

Note: The null model's column shows the number of raw networks similar to the null models, suggesting the metric was influenced by a random assortment of interactions rather than the underlying biological structure. Ecological meanings of network metrics are as follows: Network-level specialisation (H_2') describes the ability of generalist pollinators to forage efficiently, weighted nestedness (NODF) describes support in the network for specialised bee and plant species, modularity identifies the level of isolation of groups of interacting species in the network, links per plant species indicates the chance for bee-mediated pollination, niche overlap plants describes the level of pollinator fidelity in plant visitation and niche overlap bees describes the level of foraging competition between pollinator species. Rarefied networks were randomly selected subsets of equal size between the site pair networks ($N = 1000$), after which each site and month combination was averaged to a single value to compare to the raw network metrics.

Bumble bee body condition

For bee body condition metrics, we analysed 29 *B. griseocollis*, 32 *B. bimaculatus* and 30 *B. impatiens* workers across the two site treatments (Table S2). For all three bumble bee species, intertegular distance (proxy for body size) was not affected by the presence of apiaries (Figure 7 and Table S10; Results for Honey Bee sites; *B. bimaculatus*, estimate = 0.455 ± 0.245, *t*-value = 1.85, *p*-value = 0.084; *B. griseocollis*, estimate = −0.093 ± 0.130, *t*-value = −0.71, *p*-value = 0.484; *B. impatiens*, estimate = −0.206 ± 0.191, *t*-value = −1.08, *p*-value = 0.289). However, only one species, *B. bimaculatus*, had significantly lower dry mass at Honey Bee sites than at Control sites (estimate = −0.0170 ± 0.0066, *t*-value = −2.584, *p*-value = 0.0216); however, there was no difference in dry mass in the presence of an apiary in the other two bumble bee species (glm, *B. griseocollis*, estimate = 0.006 ± 0.010, *t*-value = 0.612, *p*-value = 0.549; *B. impatiens*, estimate = −0.0089 ± 0.0060, *t*-value = −1.483, *p*-value = 0.1501). All three species showed no difference in wing area based on apiary presence (glm: *B. bimaculatus*, estimate = −90.587 ± 70.358, *t*-value = −1.288, *p*-value = 0.2204; *B. griseocollis*, estimate = 61.366 ± 62.754, *t*-value = 0.978, *p*-value = 0.3427; *B. impatiens*, estimate = 0.4413 ± 40.6766, *t*-value = 0.011, *p*-value = 0.991).

DISCUSSION

Introducing exotic pollinators like managed honey bees into areas managed for conservation has the potential to affect wild bee populations and interactions. This result may be especially pronounced in small areas surrounded by a matrix of weed-controlled agricultural fields that are devoid of forage for bees, especially when cultivated plants senesce (Dolezal et al., 2019). We investigated the effect of a mid-sized honey bee apiary on wild bee communities in prairie strips (CP43) in the first half of the season before honey bees begin more heavily utilising native plants as forage (Figure 4; Zhang et al., 2022; St. Clair, Zhang, et al., 2020), using sensitive metrics such as interaction network metrics and bee body condition, as well as traditional community measures (Table 2).

Our experimental design of placing 20 colonies in prairie strips appeared to be successful in increasing the presence of honey bee foragers. Our colonies produced increasing adult bee populations from June to September (Figure 2), and all but one of our direct honey bee observations on flowers within our sites were at Honey Bee sites (Figure 3). However, the fact that relatively few honey bees were observed overall suggests our honey bees may have also been foraging on other resources such as trees and exotic plant species outside of prairie strips. This result supported our honey pollen analysis, which showed less than 20% native plant pollen from June to August (Figure 4).

While we found some significant effects of honey bee apiaries (day and site treatments) on wild bee abundance and richness, the differences had small effect sizes that may not be biologically relevant. The directionality of these effects was also not consistent with our hypothesis that honey bees negatively impact wild bees. We suggest these differences are likely to be driven by site differences in bee community composition. Likewise, network traits were not different between matched pairs of Honey Bee and Control sites for both raw network metrics and rarefied network metrics, in any month sampled (Table 1). Instead, most metrics showed networks were driven to some extent by a random assortment of interactions rather than underlying biological structures. It is possible some bee species benefit from apiary presence while other species are outcompeted, resulting in the network metrics remaining relatively similar overall between the site treatments. Since the networks showed no differences, this supports our finding of no difference in bee abundance and richness, which are often less sensitive than changes in interactions (Valido et al., 2019; Valiente–Banuet et al., 2015).

Prior studies have suggested honey bees disproportionately affect wild generalist native bee species (Magrach et al., 2017; Valido et al., 2019; Wignall et al., 2020) such as bumble bees. In our study,

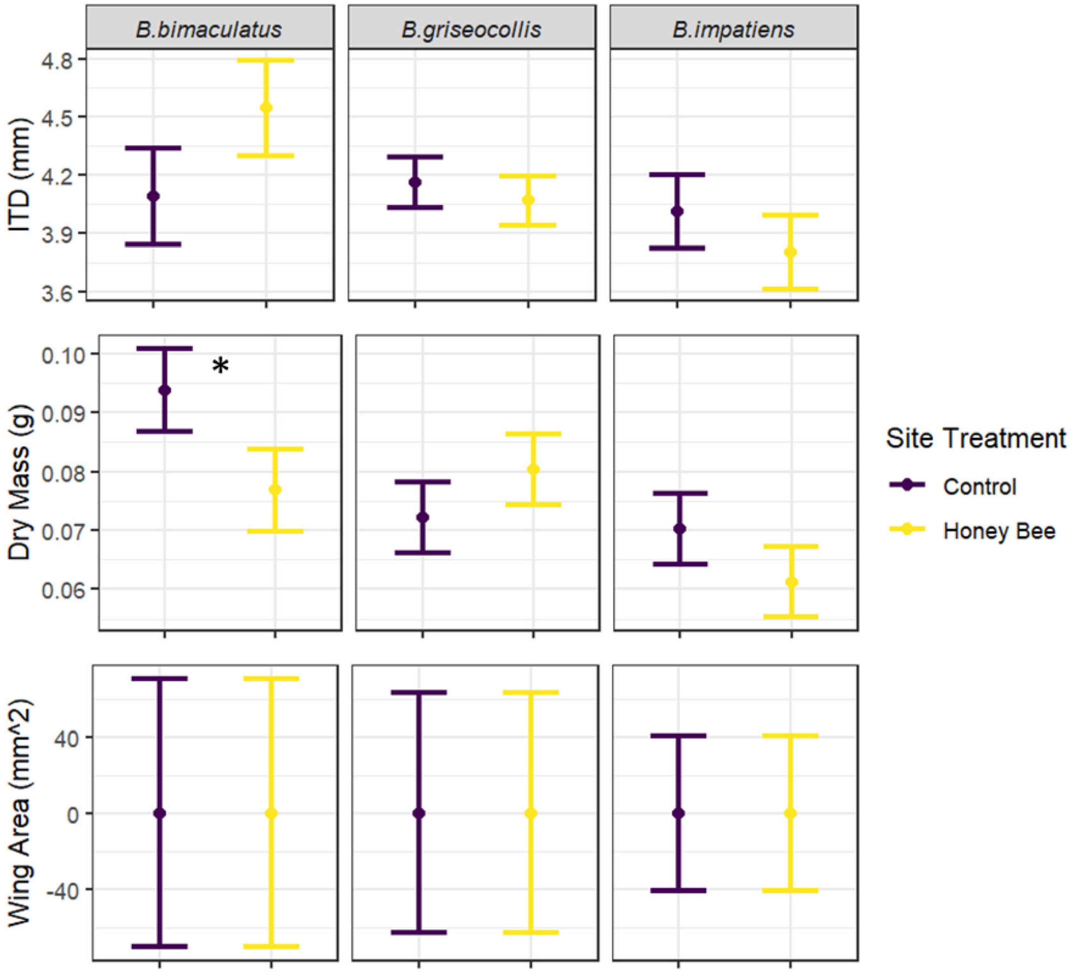

FIGURE 7 Boxplots showing the estimated mean and standard errors of intertegular distance (ITD; top), dry mass (middle) and wing area (bottom) of three bumble bee species (columns) at Honey Bee (yellow) and Control sites (purple) as predicted by generalised linear models. Intertegular distance was modelled with the equation ITD ~ Site_Treatment. The model for dry mass included intertegular distance as a proxy for body size: Dry_Mass ~ ITD + Site_Treatment. The model for wing area included intertegular distance as a proxy for body size as well as relative age (the number of days since the first observation of that species the particular specimen was collected): Wing_Area ~ ITD + Relative_Age + Site_Treatment. Asterisks indicate a significant effect of Site Treatment in the generalised linear model.

we only found a significantly lower dry mass at Honey Bee sites than at Control sites for one bumble bee species, *B. bimaculatus*. For the other two species, *B. griseocollis* and *B. impatiens*, there was no difference in any of the three traits (dry mass, intertegular distance, and average wing area). Taken together with our community and network results, we suggest that during the first half of the season (June to August) in this highly agricultural environment, honey apiaries do not appear to have detectable negative impacts on most wild bee species in prairie strips. This differs from many studies that found an effect of apiary or honey bee presence on native bee populations and plant–pollinator networks (Mallinger et al., 2017; Valido et al., 2019; Wignall et al., 2020). However, studies investigating the effect of honey bee apiaries tend to focus on natural environments instead of the highly agricultural landscape used in our study. Therefore, the bee communities we surveyed may be robust to the effect of honey bees because more sensitive bee species were excluded from the environment due to other agricultural stressors (chemical usage, lack of floral resources, tilling disturbance, etc). In addition, our study did not encompass the entire period bees are active. Prairie plants are a crucial late-season resource for honey bee colonies and can increase overwintering success (Dolezal et al., 2019), and our results (Figure 4) also indicated that honey bees are more likely to utilise native forb species later in the season (e.g. September). Therefore, more research is needed on the second half of the season (August to October) before we fully understand if honey production can be balanced with wild bee conservation in these small native plant communities.

Based on our study, we recommend future studies incorporate high-intensity effort to collect sufficient plant–bee interactions for robust network analyses. Our study consisted of 120 min of active sampling per network, which is comparable to other studies (80 total observation minutes per network, Brosi et al., 2017; 70 total observation minutes per site, Borchardt et al., 2023) but resulted in fewer interactions per network overall (1453 interactions across 18 networks for an average of 80 interactions each in our study; 7637 interactions

TABLE 2 Summary of metrics, hypothesised result and realised result separated by the community analysed (top, entire wild bee community; bottom, only bumble bees) and the metric group (Population measures = 'Pop.'; Interaction Networks = 'Int.'; Body Condition = 'Body').

Group	Metric	Description	Hypothesis	Result
(A) All wild bees				
Pop.	Wild bee richness	Number of species of wild bees	Lower with apiaries	No difference
Pop.	Wild bee abundance	Number of individual wild bees	Lower with apiaries	No difference
Int.	Network-level specialisation (H2)	Ability to forage efficiently	Lower with apiaries	No difference
Int.	Weighted nestedness (NODF)	Support for specialised species	Lower with apiaries	No difference
Int.	Modularity	Isolation of groups in the network	Higher with apiaries	No difference
Int.	Links per plant species	Chance for bee-mediated pollination	Lower with apiaries	No difference
Int.	Niche overlap plants	Level of pollinator fidelity	Lower with apiaries	No difference
Int.	Niche overlap bees	Level of foraging competition	Higher with apiaries	No difference
(B) Bumble bees				
Pop.	Bumble bee richness	Number of species of wild bumble bees	Lower with apiaries	No difference
Pop.	Bumble bee abundance	Number of individual wild bees	Lower with apiaries	No difference
Body	Intertegular distance	Size of bee body	Lower with apiaries	No difference
Body	Dry mass	Size of bee body mass	Lower with apiaries	Lower in apiaries for 1 of 3 species
Body	Wing area	Age and foraging effort	Lower with apiaries	No difference

across 30 networks for on average 255 interactions each, Brosi et al., 2017; 1666 interactions across 10 networks for on average 167 interactions each, Borchardt et al., 2023). Therefore, future studies investigating the influence of honey apiaries in prairie strips during the period from August to October should either increase observation minutes or estimate interactions using other methods (Jordano, 2016) such as estimating interactions through body pollen carriage (Borchardt et al., 2023; Fisogni et al., 2018).

These results preliminarily support that placing mid-sized honey apiaries in prairie strips from June to August does not have short-term, detectable effects on wild bee communities and wild plant–bee ecosystem functions. Previous studies have found that prairie strips increase insect pollinator abundance and richness (Schulte et al., 2017) as well as the chance for bee-mediated pollination of plants, support for specialised species and bee body condition, such as foraging effort and developmental stress in some bee genera (Borchardt et al., 2023). This study provided a thorough investigation of the possible effects of honey bees in the context of prairie strips, and our design allowed us sufficient power to detect differences. Although our site replication was relatively low, we supported our conclusions by conducting multiple statistical tests (generalised linear models, effect size analyses, raw networks, rarified networks and null models) and examining several different metrics (abundance and richness, network metrics and body condition). While we found some significant differences in wild bee abundance and bumble bee abundance across site treatments, these differences were not supported by a biologically meaningful difference in the means via effect size and therefore do not support the hypothesis that honey bees negatively impact wild bee communities. The one exception was smaller *B. bimaculatus* body size at Honey Bee sites compared to Control sites, suggesting some possible resource competition with a subset of large-bodied, generalist bees. This topic deserves further research attention.

We also note that our study is limited both in scope, timeframe studied and replication across multiple years. First, while we found no meaningful difference in bee abundance and richness, we also found fewer species (76 bee species when grouping the genus *Lasioglossum* together in our study) than previous studies comparatively (*Lasioglossum* grouped as genus; 88 bee species, Kordbacheh et al., 2020; 88 bee groups, Borchardt et al., 2023). This suggests our results might be due to the condition in the year we sampled. Second, our study only encapsulated the first half of the season before honey bees begin foraging on native prairie plants heavily (Figure 4; Zhang et al., 2022; St. Clair, Zhang, et al., 2020), and a gap in understanding the effect of honey apiaries in this habitat from August to October remains. We suggest an intensive study of the community of interactions during the second half of the season, alongside other traits like body condition focusing on solitary bee species, will be needed to inform future decisions about balancing bee conservation and honey production at prairie strips.

Given the decline of biodiversity globally, especially pollinators (Zattara & Aizen, 2021), it is crucial to fully understand how to balance conservation in working environments, especially with regard to practices like prairie strips that have immense adoption potential in agricultural landscapes that often have limited resources for many pollinator species (Dolezal et al., 2019; Luther et al., 2022). Part of that balancing act is incorporating economic values via agricultural production (in this case, honey production) into sustainable agricultural practices in ways that do not impede conservation goals. Our research shows that both honey beekeeping and wild bee communities can be supported in specific landscapes during long periods of the growing season, providing the opportunity for economic growth alongside wildlife conservation in agricultural landscapes.

AUTHOR CONTRIBUTIONS

Kate E. Borchardt: Conceptualization; methodology; investigation; data curation; formal analysis; writing – original draft. **Morgan Moore:** Investigation; writing – review and editing. **Randall Cass:** Investigation; writing – review and editing. **Matthew O'Neal:** Methodology; funding acquisition; resources; writing – review and editing. **Amy L. Toth:** Conceptualization; methodology; writing – original draft; funding acquisition; resources.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in github at: https://github.com/kateborc/Prairie-Strip-Beekeeping/tree/main.

ORCID

Kate E. Borchardt https://orcid.org/0000-0003-0687-0413
Matthew O'Neal https://orcid.org/0000-0002-1642-6941
Amy L. Toth https://orcid.org/0000-0003-0824-0933

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Layout of the Honey Bee sites, with circles indicating the Honey Bee apiary and rectangles indicating the three observation transects (field 'Edge', 'Near' prairie strip and 'Far' prairie strip).

Figure S2. A food web of links and interaction abundances between Control and Honey Bee sites. Plant species are on the y-axis and bee species on the x-axis in the exact same position and order in both graphs, with circles indicating a link between two species and the size of the circle indicating how many interactions occurred between those two species. Some species are highlighted that comprise many interactions with vertical blue lines indicating bee species or genera and horizontal purple lines indicating plant species or genera.

Figure S3. Raw (top six graphs) and average rarefied (bottom six graphs) plant–bee interaction network metrics in Control and Honey Bee sites shown both as a boxplot and as pairs of sites sampled during the same week. Colours indicate the site pairing and line type indicates the month the sample took place. The middle line inside the box shows the median value, the upper and lower limits of the box show the 75th and 25th quartiles, respectively, and each whisker from the 75th and 25th quartile up to the most extreme value within 1.5 * Interquartile Range from the box, respectively. Points outside of the box and whiskers are plotted individually as outliers.

Table S1. Size of smallest networks in a site pair for each month by bee and plant species. Two pairs were removed (GUT-SMI July, WHO-SME June) because they were too small for rarefaction analysis.

Table S2. Summary of specimens used to test bee body condition in three bumble bee species at the two site treatments.

Table S3. All bee species or groups found at the observed sites are separated by site abbreviation, site treatment (Control, Honey Bee) and day treatment (Day 1 (open), Day 2 (closed)). The bee genus *Lasioglossum* was identified as a morpho-species based on a key developed by St. Clair et al. (2020b).

Table S4. All plant species found at each Control site during each month and the number of bee interactions observed for that plant. Due to our sampling protocol, some plants were recorded as in bloom but had no observed bee interactions (Jordano, 2016).

Table S5. Wild bee abundance (top) and richness (bottom) results from a generalised linear model with Poisson error including weather variables average daily temperature (C) and average wind speed (mph). Asterisks indicate significance levels: < 0.05*, <0.01**, < 0.001***.

Table S6. Statistical contrasts and Cohen's D effect sizes for wild bee abundance and richness overall and for each month (June, July, August) showing the relationships between site treatments (Control, Honey Bees) and sampling day treatments (open, closed) using the generalised linear model from Table SB. Asterisks indicate if the *p*-value was below the Bonferroni-adjusted significance level adjusting for multiple testing ($n = 16$; alpha $= 0.003125$) or if the Cohen's D value was greater than 0.2 showing a meaningful difference between means.

Table S7. Results of a generalised linear model on bumble bee abundance (top) and richness (bottom) between site treatments and day treatments. Weather variables were included due to difficulty restricting sampling to ideal pollinator weather. Asterisks indicate levels of significance as follows: * < 0.05, ** < 0.01, *** < 0.001.

Table S8. Statistical contrasts and Cohen's D effect sizes for bumble bee abundance and richness showing the relationships between site treatments (Control, Honey Bees) and sampling day treatments (open, closed) using the generalised linear model from Table SB. Asterisks indicate if the *p*-value was below an alpha of 0.05. There was not enough data for the models to converge when analysing richness and abundance for each month separately, as we did for wild bees in Table S6.

Table S9. Null model results from the raw network metrics for the three Honey Bee (.hb) and Control (.con) sites for each month. Highlighted cells indicate *p*-values greater than 0.05, which means the metric values might be caused by an independent assortment of interactions rather than an underlying biological structure.

Table S10. Results of a generalised linear model analysing intertegular distance (ITD; top), dry mass (middle) and wing area (bottom) for our three bumble bee species. Wing area included dry mass as a measure of body size in order to scale the overall wing area. Significance levels are shown with asterisk: * < 0.05, ** < 0.01, *** < 0.001. Site Treatment results are shown for Honey Bee sites (HB). Intertegular distance was used to account for differences in body size when analysing dry mass and wing area. In addition, the number of days since the first observation of a bee species was used to account for relative specimen age when analysing the wing area.

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