Agroecosystem landscape diversity shapes wild bee communities independent of managed honey bee presence

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ABSTRACT

Large scale agricultural production can lead to a reduction in availability of habitat used by wild bees for nesting and forage and has been implicated in worldwide bee population declines. There is growing concern that further declines in wild bee populations will occur because of continued transformations of natural or seminatural landscapes into crop monocultures. Managed honey bees, often used for pollination services in agricultural systems, can compete with wild bees and are hypothesized to negatively affect their communities. Although the response of wild bees to both agriculture and honey bees (i.e., apiculture) has been studied, the relative importance of each and their potential interactions on wild bee communities are not well understood. To forecast the extent to which landscape simplification can affect wild bees and to better understand whether honey bee presence in an already disturbed landscape might further exacerbate declines, we conducted a replicated, longitudinal assessment of wild bee community richness and richness of functional guilds (e.g., floral specificity and nesting preference) in an intensively farmed region of the United States where much of the landscape is devoted to monoculture annual crop (maize and soybean) production and managed honey bee colonies co-occur. The presence of a small apiary (4 colonies) had no immediate effect on wild bee richness, suggesting honey beekeeping may not always negatively impact wild bees. Rather, landscape composition analysis showed strong responses of wild bees to land use, with communities being less speciose in landscapes with high proportions of crop production. The availability of woodland and grassland habitat, especially at the local scale (<800 m), was associated with the greatest increase in bee richness especially for rarer aboveground nesting and floral specialist species. These data suggest large scale monocultures have a greater impact on bee communities than the presence of small apiaries. The results of this research provide important information on possible solutions in agroecosystem management to support increased bee diversity where annual crop production and apiculture are practiced. Namely, mitigation of wild bee declines in such agroecosystems may benefit more from the reintegration of landscape biodiversity, with priority on the re-introduction of perennial vegetation, like that found in woodland and grassland habitats, than the restriction of honey bee apiculture.

Data Availability: Data will be archived through Iowa State Universities digital data repository.

1. Introduction

The ecosystem services provided by wild bees are essential to maintain natural communities (Winfree et al., 2009). However, wild bees are experiencing worldwide declines in population, diversity, and health (Cameron and Sadd, 2020; Potts et al., 2010; Zattara and Aizen, 2021), which are attributed to several threats including habitat loss and degradation which result in reduced nesting and forage quality and quantity, exposure to pesticides, pathogens, and climate change (Goulson et al., 2015). Agricultural regions with low landscape diversity (Brown and Schulte, 2011) are arguably the most detrimental to bee populations, with documented declines in pollinator abundance (Koh et al., 2016) and diversity (Kremen et al., 2002), likely as a results of the increased risk of habitat conversion and interactive effects of additional stressors such as pesticides. These landscapes feature inadequate nesting sites and insufficient floral resources to support healthy and robust wild

bee communities (Kline and Joshi, 2020). Although some agriculturally adapted bee species thrive in these systems (Kleijn et al., 2015; Clair et al., 2020b), they generally do not support rarer specialized species which rely on resources not found in crop fields (Harrison et al., 2019). Wild bee populations may be particularly at risk in landscapes where millions of hectares are committed to the production of annual crops that do not require insect pollination, including most annual row crops like maize, soybean, cotton, and cereal crops (Koh et al., 2016; Rollin et al., 2019). There has been a global increase in crop production in response to rising demand for food and biofuels to meet expanding human population needs (Popp et al., 2014; Searchinger et al., 2008). The widespread production of these crops, particularly in regions of the United States (U.S.), China, Brazil, and Argentina, reduces the presence of natural and semi-natural landscape features that lower the quantity, quality, and connectivity of habitat used for nesting and forage (Rollin et al., 2019). Additionally, the scale of agricultural production can have profound effects on bee diversity (Tylianakis et al., 2006), with increased landscape diversity surrounding agricultural fields mitigating losses of bee abundance and richness (Shackelford et al., 2013), especially when incorporated at a local scale (i.e., small spatial scale) (Scheper et al., 2015).

Furthermore, wild bees may experience increased stress from apiculture, a form of agriculture that involves keeping honey bee colonies in varying amounts, often adjacent to crop fields. Pressure from managed honey bees via floral resource competition (Mallinger et al., 2017) and transmission of disease (Tapia-González et al., 2019) may further exacerbate wild bee declines (Geslin et al., 2017). Although wild bees and honey bees are important pollinators of crops (Losey and Vaughan, 2006), there is debate over the importance of conserving wild bee biodiversity versus developing more sustainable apiculture, particularly in regions where honey bees are not native. Recommendations for safeguarding wild bees include practicing apiculture only in agricultural areas and not in natural or protected habitats (Geldmann and González-Varo, 2018; González-Varo and Geldmann, 2018), as additional competition with honey bees may increase the stresses wild bees already suffer in areas of extensive agricultural production (Le Feon et al., 2010). In maize and soybean production systems the impact of apiculture may be especially deleterious for wild bees for two reasons: (1) countries where maize and soybean are produced on a large scale are also countries which have some of the world's largest managed honey bee colony populations (e.g., China, Argentina, U.S., Brazil) and (2) these landscapes possess a lack of non-cultivated floral resources which may force wild and managed bees to share resources in crop fields (Evans et al., 2018), increasing the likelihood for potential interaction and competition. Understanding if these interactions occur is essential for effective management plans to conserve wild bees in agricultural systems.

The Midwestern state of Iowa, USA is one of the most extensively farmed landscapes in the world. Iowa has the highest percent of cropland per area of any state in the U.S. (NASS-USDA, 2019), resulting in a landscape where the remaining natural habitat is embedded within a heavily cropped agricultural matrix. As a result, Iowa is classified as a critical area for pollinator conservation (Grixti et al., 2009) with low overall wild bee abundance and declines expected to continue (Koh et al., 2016). Thus, Iowa is an ideal model region to study the interactions among wild and managed honey bees in an area of extreme extensive agricultural production. As such, studies here may help forecast the future of wild bee communities in regions currently undergoing similar landscape conversions (Decourtye et al., 2019; Otto et al., 2016). Here, we pose two questions related to wild bee communities in landscapes where annual crop production and apiculture are practiced. (1) Does the proportion of cultivated crops in the surrounding landscape affect wild bee communities? a) Specifically, does bee species richness vary with landscape based on floral specialization and nesting preference? b) Are effects stronger at smaller, more local spatial scales than wider spatial scales? (2) Does the presence of honey bees affect the wild

bee community in this landscape? To accomplish this, we identified 38 fields over two years that were planted with soybean and surrounded by either high- or low- amounts of annual row crop production, and then placed an apiary of four honey bee colonies at a subset of those sites. To address question 1(a), we sampled the wild bee community richness and classified bees by their degree of nesting and floral specialization. We predicted that fields in low-cultivation landscapes without an apiary would provide a best-case scenario (i.e., more diverse, and abundant resources with reduced competition), resulting in the highest wild bee richness. To address question 1(b), we used landscape analysis and model selection to identify landscape features at three spatial scales (800 m, 1600 m, and 2400 m) that contributed the most to wild bee richness. Lastly, for question 2, we predicted that the combination of crop cultivation and apiculture would increase the likelihood of resource competition as landscapes committed to intensive agricultural production result in reduced floral resources for wild and managed bees alike (Kovács-Hostyánszki et al., 2017; Kremen et al., 2018; Otto et al., 2016) and apiary presence creates competition for resources with honey bees (Angelella et al., 2021; Mallinger et al., 2017). Although we do not directly measure competition, we predict that high-cultivation landscapes with apiaries present create a worst-case scenario for wild bees resulting in the lowest wild bee richness.

2. Methods

2.1. Site selection

In 2015 and 2016 we identified soybean fields in Central Iowa that were greater than 20 ha (mean 39.71 ha $\pm$ 4.52SEM) and did not have an apiary of honey bees present within 1.6 km. We determined that no apiaries were present by checking Iowa's state-wide voluntary registry for beehives (DriftWatch Inc., West Lafayette, IN https://ia.driftwatch. org/map). Distinct high and low-cultivation landscapes were designated following the methods of Dolezal et al. (2019). Specifically, we used ArcMap 10.3.1 and the 2015 and 2016 USDA-NASS CropScape data layers at a 30 m $\times$ 30 m resolution to classify and measure the area of all land cover features within a 1.6 km radius of the field (https://na ssgeodata.gmu.edu/CropScape/). This resulted in sites that were separated by at least 3.2 km, except for two sites in 2015 in the high-cultivation category which overlapped by 160 m in the perimeter of the buffer. However, because those sites were in the same cultivation category and possible species crossover would likely not result in significant changes in the community composition, we elected to keep them in the study. To measure the proportion of the landscape committed to each feature, we used the 'isecpolyrst' function in Geospatial Modeling Environment (Version 0.7.4.0) to quantify pixels within the 1.6 km buffer associated with each land cover type and we categorized all land cover features within six groups (maize, soybean, other crops, developed, grassland, and woodland). For maize and soybean only those individual land cover types were included in each category. The category of 'other crops' included land types sorghum, sweet maize, rye, oats, alfalfa, other hay, and other crops. Grassland included clover and wildflowers, fallow crop, grass, and pasture. Developed land included open water, developed open space, low, medium, and high intensity developed land and barren land. Woodland included land cover types deciduous forest, evergreen forest, mixed forest, shrubland, woody wetlands, and herbaceous wetlands.

Fields were classified as surrounded by either "high" or "low" amount of maize and soybean based on the percentage of land in the 1.6 km radius dedicated to annual production of either crop. Statewide, Iowa dedicates approximately 85.5% of its land to farming with 65.5% planted with annual crops, and 91% of Story County dedicated to farming with 73% planted with annual crops (NASS-USDA, 2019) (Fig. 1 A). We defined a site as being in a landscape of "High-cultivation" if it was surrounded by > 73% maize or soybean production. Due to the dominance of crop production in this region, fields surrounded by
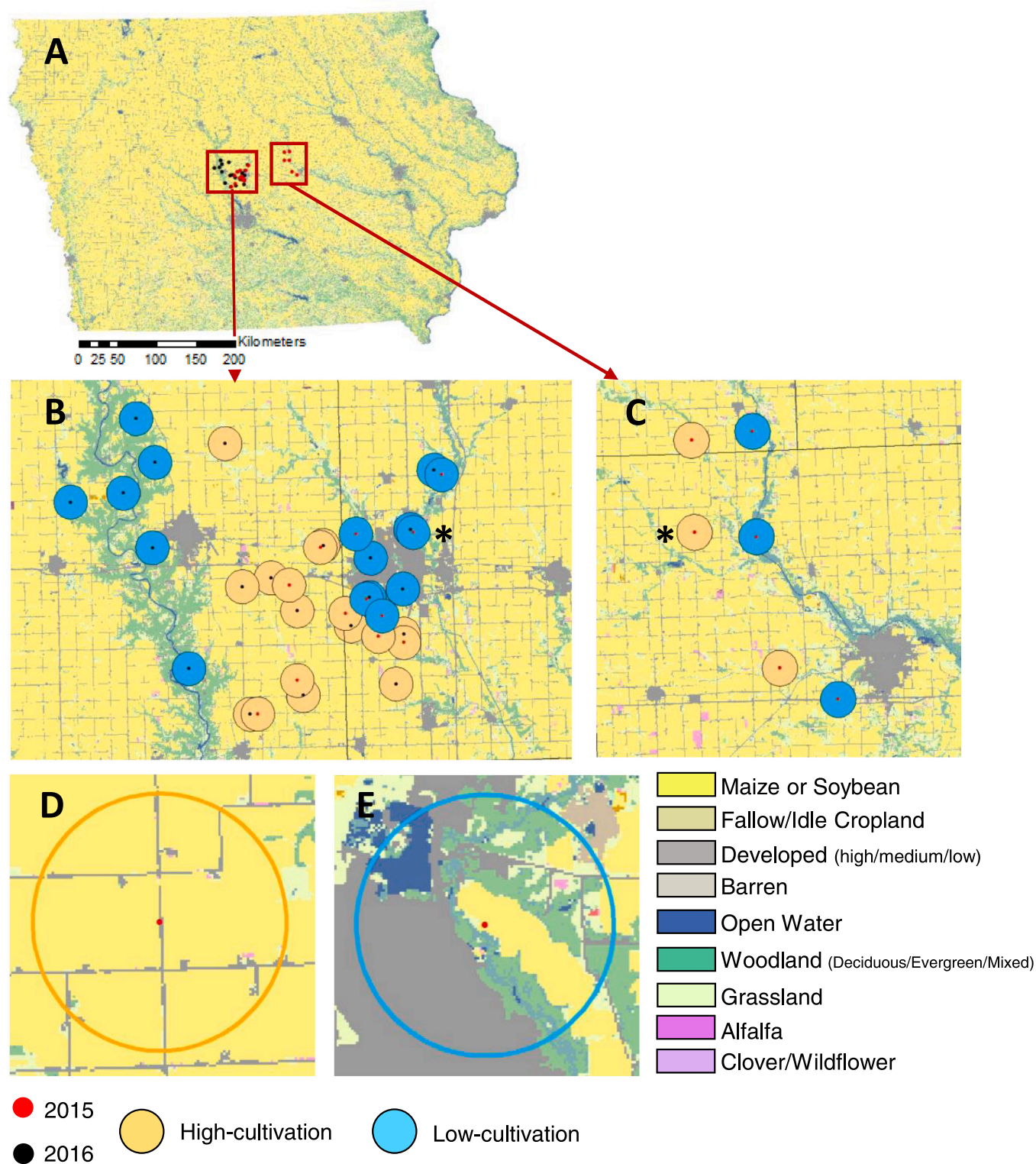
Fig. 1. (A) Map of Iowa, USA land use with the location of soybean sites in 2015 (red circles; 18 sites) and 2016 (black circles; 20 sites). Location of sites in Boone and Story county Iowa (B) and location of sites in Hardin and Marshall county Iowa (C) with a 1.6 km buffer indicating High-cultivation (orange circles) or Low-cultivation (blue circles) surrounding sites in 2015 and 2016. Up-close view of landuse variation surrounding a soybean site in a (D) High-cultivation landscape and (E) Low-cultivation landscape. Asterisks represent the sites that were used

"Low-cultivation" were difficult to find resulting in a wider range in the percentage of maize and soybean in the surrounding landscape (range of 1–64%). From this selection process, we identified 10 fields that were classified as High-cultivation in 2015 and 10 additional fields in 2016. Over the two years High-cultivation fields were surrounded by a mean of

82.9% ± 1.5% SEM maize and soybean production at the 1.6 km radius (Fig. 1B – E; Table S1). We identified 8 fields classified as Low-cultivation in 2015 and 10 additional fields in 2016. Over the two years Low-cultivation fields were surrounded by a mean of 33.6% ± 4.6% SEM maize and soybean production at the 1.6 km radius (Fig. 1B –

E; Table S1).

After fields were selected, we conducted an exploratory analysis using nonmetric multidimensional scaling (NMDS) and permutated analysis of variance (pMANOVA) to confirm that our two cultivation categories were in fact statistically different in their proportions of landscape cover (Fig. S1A; $F_{1, 35} = 50.41$; $P = 0.001$). A two-tailed *t*-test was used to compare the proportion of individual land cover types surrounding High- and Low-cultivation fields. High-cultivation sites were surrounded by more maize and soybean compared to Low-cultivation, and Low-cultivation sites were surrounded by higher proportions of other crops, grassland, developed land, and woodland (Fig. S1B). Because our sites were clustered into two spatial groups (Boone/Story Counties and Hardin/Marshall Counties; Fig. 1) we conducted an analysis of variance to verify that there was no spatial autocorrelation between the two areas ($F_{1, 33} = 1.85$, $p = 0.18$).

It is important to note that cultivation is frequently used to refer to land used for agriculture specifically in relation to productivity and management inputs, but it can also reference the way in which soil is prepared for growing crops (i.e., tillage). For this study, we use the former definition, electing not to consider variation in tillage practices or inputs, noting that majority of fields sown with soybean are tilled in Iowa (Horowitz et al., 2010). At all soybean fields, weeds were managed with glyphosate. Soybeans were planted with seed-applied treatments; ISU fields were planted with a fungicide only (Fluopyram, ILeVO, Bayer, Pittsburgh PA), while private fields were planted with an insecticide and fungicide (Imidacloprid and ILeVo, respectively; Acceleron seed treatment, Bayer, Pittsburgh PA) (Table S1). Wild bee sampling took place only after all fields were planted to reduce direct exposure risks due to planting (July 1 2015 and June 15,2016); no significant differences in bee abundance ($F_{1,36} = 0.47$, $P = 0.50$), richness ($F_{1,36} = 1.59$, $P = 0.22$), or diversity ($F_{1,36} = 3.42$, $P = 0.07$) were observed between fields planted with an insecticidal seed treatment compared to fungicide only. No insecticides were applied to soybean foliage or in fields directly surrounding soybeans during the study period. All fields were in a maize and soybean rotation with maize planted in the previous year. Field margins associated with soybean fields consisted of grassy habitats that were populated with several wild blooming forbs such as common milkweed, chicory, and wild asparagus. Field margins were sprayed with herbicide and/or mown back by the state once or twice a season.

Each year, we randomly selected five fields in both cultivation categories and placed a small apiary of four honey bee colonies 3 m from the field edge (i.e., Apiary(+) sites), while remaining sites had no colonies present (i.e., Apiary(-) sites). Colonies were sourced and managed as in Dolezal et al. (2019). This resulted in 10 High-cultivation/Apiary (+), 10 Low-cultivation/Apiary(+), 10 High-cultivation/Apiary(-), and 8 Low-cultivation/Apiary(-) soybean fields across the two years. Apiaries were transported to fields after 90% of the maize and soybean had been planted in Iowa (June 2015, May 2016) (USDA-NASS, 2016, 2015) and prior to our assessments of the wild bee community. The estimated adult worker bee population within each beehive varied throughout the season ranging in size from an average of 5–28 frame sides of adult bees, with peak colony populations in both 2015 and 2016 occurring during the first week of August. We confirmed that the presence of an apiary increased the activity-density of honey bees in soybean fields based on their presence in pan-traps (St. Clair et al., 2020a). The number of honey bees in pan traps at Apiary(-) fields was significantly lower than Apiary (+) (Fig. S2; $F_{1, 34} = 13.56$, $P = 0.0008$) based on ANOVA. There were no significant effects of cultivation category and no interaction with apiary presence (Fig. S2).

2.2. Sampling and identification of the bee community

We used pan-traps to quantify wild bee richness within soybean fields. Pan-traps have drawbacks when used to monitor bee communities as they may be biased towards certain families of bees (e.g., Halictidae), and measure activity-density, not absolute abundance of bees within the community (Portman et al., 2020). Despite these caveats, we chose to use pan-traps because they were the most consistent and highly standardized method for sampling bees at each location simultaneously (Roulston et al., 2007). There is a known inverse relationship between pan trap effectiveness and floral resource availability (Baum and Wallen, 2011; St. Clair et al., 2020a), therefore, in order to not misrepresent the community recorded at our sites, in this paper we only report richness of species estimated by traps.

Pan-traps were based on previously described design by St. Clair et al. (2020b), with three 3.2 oz. bowls deployed on a post and painted either fluorescent yellow, blue, or left an unpainted white. In 2015, each field had 3 posts (9 pan-traps) placed 10 m apart and 10 m into the soybean field. At Apiary(+) sites, traps were placed on the field edge where colonies were present. In 2016, we repeated trap placement as in 2015 and increased our sampling effort by adding an additional 3 posts placed 10 m outside the field edge and on the same side as when apiaries were present. We sampled bees every other week for 13 weeks from June through September. Pan-traps were adjusted so that their height was level with the soybean plant canopy (trap height varied between 0.3 and 1.5 m) and were deployed for 24 hr using a 0.2% soap-water solution. Trap collections within a date were combined and bee community was described at the field level.

Specimens were processed following Droege et al. (2010) and then identified following standardized methods for monitoring bee populations (LeBuhn et al., 2003), where bees were identified to species or the lowest taxonomic unit, with the exception of the genus *Lasioglossum*. Members of the genus *Lasioglossum* were identified to subgenus then morphotyped following methods from St. Clair et al. (2020b) where individuals were identified to genus using the dichotomous key 'The Bee Genera of North and Central America' (Michener, 1994) and to species using the online dichotomous key 'Discover Life' (Ascher and Pickering, 2015) and 'Key to Pollinators of the Midwest' (Arduser, 2016). Specimens were verified against a voucher collection deposited at ISU (Science II Hall, Ames, IA) which consisted of bee specimens collected and identified by Dr. Mary Harris. Due to difficulties in gaining reliable species level identifications of some species using these taxonomic keys, genera that were rare and only appeared once in our collection were only identified to the genus level.

For each of the bee species collected, we assigned their nesting preference (i.e., above or belowground) and floral specificity (i.e., oligolectic or polylectic) by referencing peer reviewed publications addressing the functional guilds of bees (Lerman and Milam, 2016; Normandin et al., 2017) both of these publications followed the formats of Giles and Ascher (2006) and Matteson et al. (2008). Due to their generally low abundance, stem, cavity, and burrow nesting bees were combined to create the aboveground nesting category. Cleptoparasitic bee nesting preference was assigned as being the same as the preference of the host species parasitized. Although there are a few specialist *Lasioglossum* species, we chose to consider all *Lasioglossum* morphospecies as belowground nesting and polylectic as that is the primary trait classification for most members of the genus (Table S2) (Michener, 2007). All bees that are considered to forage on a single genus or single family of plants were considered oligolectic.

2.3. Statistical analyses

To ensure we had sufficient and equal sampling effort of the wild bee community across our treatments, we constructed coverage, sample-size, and incidence-based rarefaction and extrapolation curves using the statistical software R version 3.6.2 (R Core Team 2019) and the Vegan package following St. Clair et al. (2020b). Our percent coverage for each treatment was above 98% (Fig. S3A – D), confirming we had equal and high sampling effort at all locations (Chao and Jost, 2012).

To visually represent the bee community, we used NMDS as described above to create a plot indicating the Bray-Curtis dissimilarity of the bee community for each site within treatments over 2015 and

2016. We conducted a pMANOVA in R using the packages lme4, lmertest, and multcomp to test for significant differences in bee communities in each treatment by creating a model with cultivation category, apiary presence, and their interaction as predictor variables.

To test whether or not wild bee richness at the community level and of bees based on functional guild varied across treatments we created a repeated-measures mixed effect model (PROC GLIMMIX) in SAS 9.4. Cultivation category, apiary presence, and their interactions were fixed effects and site:year was a random factor. If significant interactions between main effects were observed, we performed post hoc comparisons of all groups with a Tukey HSD adjustment. To ensure normality, we performed a logarithmic transformation on richness by nesting preference, all other metrics were normal.

To investigate which individual land cover types were correlated with the bee richness, we conducted multiple regressions with stepwise model selection (PROC REG) in SAS. The bee community captured in soybean fields represent a wide variation of foraging ranges (Greenleaf et al., 2007). Although some bee species have reduced foraging ranges (e.g., <300 m from nesting site; Zurbuchen et al., 2010) we chose a minimum distance that encompasses the reduced ranges of bees while also still capturing the variation in surrounding landscape of the soybean fields between the two cultivation categories. Thus, we explored if variation in bee richness could be explained across varying spatial scales by expanding our landscape analysis to include 800 m, 1600 m, and 2400 m scales. Because land use types are inherently related to each other, we first ran a Pearson's correlation (PROC COR) to ensure that there were no collinearities among variables. Due to the potential for multiple collinearity we removed maize from our model selections as it was the most related to other land use features (Table S3). The remaining land use types (soybean, other crops, developed land, grassland, and woodland) were included in our model selections and required a p-value < 0.15 for model inclusion (Littell, 2002). In addition to land cover types, we compared apiary presence within the model as a binary measure. We chose to analyze all the data (from both low and high cultivation sites) together, rather than performing model selection on each cultivation category individually. We chose this approach because this approach increased statistical power and allowed us to better understand how cropping intensity alters bee communities on a continuous scale ranging from 0% to 100% crop production.

3. Results

3.1. Wild bee community response to crop cultivation and honey bee presence

In total, we collected 6296 wild bees from 93 taxa (Table S2). *Lasioglossum* (Family Halictidae) accounted for 57% of the community, from which we identified 36 morphospecies. Twenty-seven species were present as singletons or doubletons within a cultivation/apiary treatment (Table S2). There were 45% more species collected exclusively in soybean fields surrounded by Low-cultivation compared to species collected exclusively in fields surrounded by High-cultivation (18 versus 10 species respectively: Table S2). The community composition includes both solitary and social bees (*Bombus*), however, honey bees captured in pan traps were not considered part of the community.

The composition of the wild bee communities varied significantly between cultivation categories ($F_{1, 34} = 6.04$, $P = 0.001$), but did not vary with the presence of an apiary ($F_{1, 34} = 0.47$, $P = 0.922$) and there was no significant interaction ($F_{1, 34} = 0.51$, $P = 0.91$) (Fig. 2). Bee richness (Fig. 3A; $F_{1, 34} = 5.30$, $P = 0.03$) was significantly lower in fields surrounded by High-cultivation compared to Low-cultivation. We did not observe a difference in the richness of the wild bee community based on apiary presence (Fig. 3A; $F_{1, 34} = 0.36$, $P = 0.55$) and there were no interactions of cultivation with apiary presence ($F_{1,34} = 0.13$, $p = 0.76$).

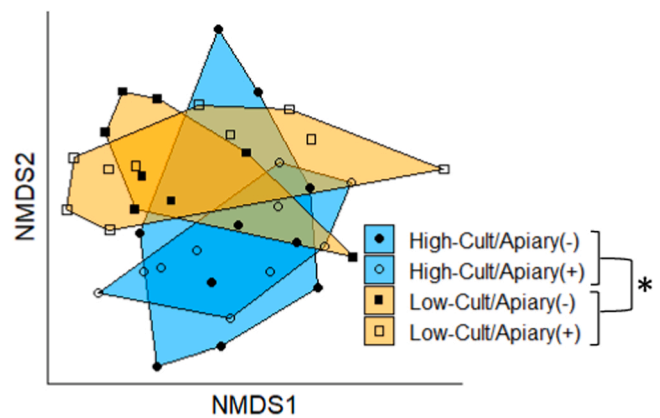Richness of belowground nesting bees was significantly higher than

Fig. 2. NMDS plot of the wild bee community found in soybean fields surrounded by High-and Low-cultivation and with and without an apiary present in central Iowa during 2015 and 2016. Statistical results based on pMANOVA ($F_{1, 34} = 6.04$, $P = 0.001$). Asterisks represent significance at ($p < 0.05$).

aboveground nesting bees ($F_{1, 34} = 908$, $p = <0.0001$); therefore, we graphed them separately to better show the magnitude of treatment effects (Fig. 3B). There was no observed difference in the richness of below or aboveground nesting bees at Apiary (+) vs Apiary (-) sites (Fig. 3B; Table S4). Richness of aboveground nesting bees was lower in fields surrounded by High-cultivation compared to Low-cultivation (Fig. 3B; $T_{60.86} = 3.02$, $p = 0.004$), while no differences were observed for belowground nesting bees (Fig. 3B; $T_{60.86} = 1.09$, $p = 0.28$). There were no interactions between any main effects based on nesting preference (Table S4). In total there were 24 taxa of above ground nesting bee species captured representing eight genera (Table S2). Burrow nesters consisted completely of the genus *Bombus* which were found evenly across cultivation categories. There were 14 stem/cavity nesting taxa belonging to the genera *Anthidium*, *Augochlora*, *Ceratina*, *Hyleaus*, *Megachile*, *Osmia*, and *Xylocopa*. Of the aboveground nesting bees collected 37.5% (9 taxa) were collected exclusively in Low-cultivation and primary consisted of stem/cavity nesting bees (6 taxa), while only 3 taxa were collected exclusively in High-cultivation.

Richness of polylectic bees was significantly higher than oligolectic bees ($F_{1, 34} = 321.12$, $p = <0.0001$). The presence of an apiary did not alter richness based on floral specificity (Fig. 3C; Table S5). Richness of oligolectic and polylectic bees varied by cultivation category (Fig. 3C; Table S5). Specifically, polylectic bee richness was significantly lower in fields surrounded by High-cultivation compared to Low-cultivation (Fig. 3C; $T_{66.84} = 2.95$, $p = 0.004$), while no difference was observed between oligolectic bees (Fig. 3C; $T_{66.84} = 0.58$, $p = 0.56$). There were no interactions of any main effects of bees for either floral specialization (Table S5). In our collections majority taxa were polylectic (85 taxa or 91.4% of specimens), while there were only 8 taxa classified as oligolectic of which 6 belonged to the Eucerini tribe (long horned bees) and were collected in all cultivation/apiary categories.

Due to the prevalence of *Lasioglossum* collected, likely because of the inherent bias of pan traps, we opted to also run our community analyses with all morphospecies of *Lasoglossum* removed. In this community, we observed similar trends as above, with a higher bee richness in sites surrounded by Low-cultivation ($F_{1, 34} = 5.36$, $p = 0.03$), and no main effect of apiary presence ($F_{1, 34} = 0.40$, $p = 0.53$) and no interaction ($F_{1, 34} = 0.08$, $p = 0.78$).

The richness of polylectic bees remained significantly higher than oligolectic bees when *Lasioglossum* were excepted ($F_{1, 34} = 236.98$, $p = <0.0001$). There were no main effects of apiary presence and no interactions with any other effects measured (Table S6). Richness remained lower in High-cultivation sites compared to Low-cultivation ($F_{1, 34} = 5.57$, $p = 0.02$), and there were no interactions between floral specialization and cultivation category ($F_{1, 34} = 3.05$, $p = 0.09$).
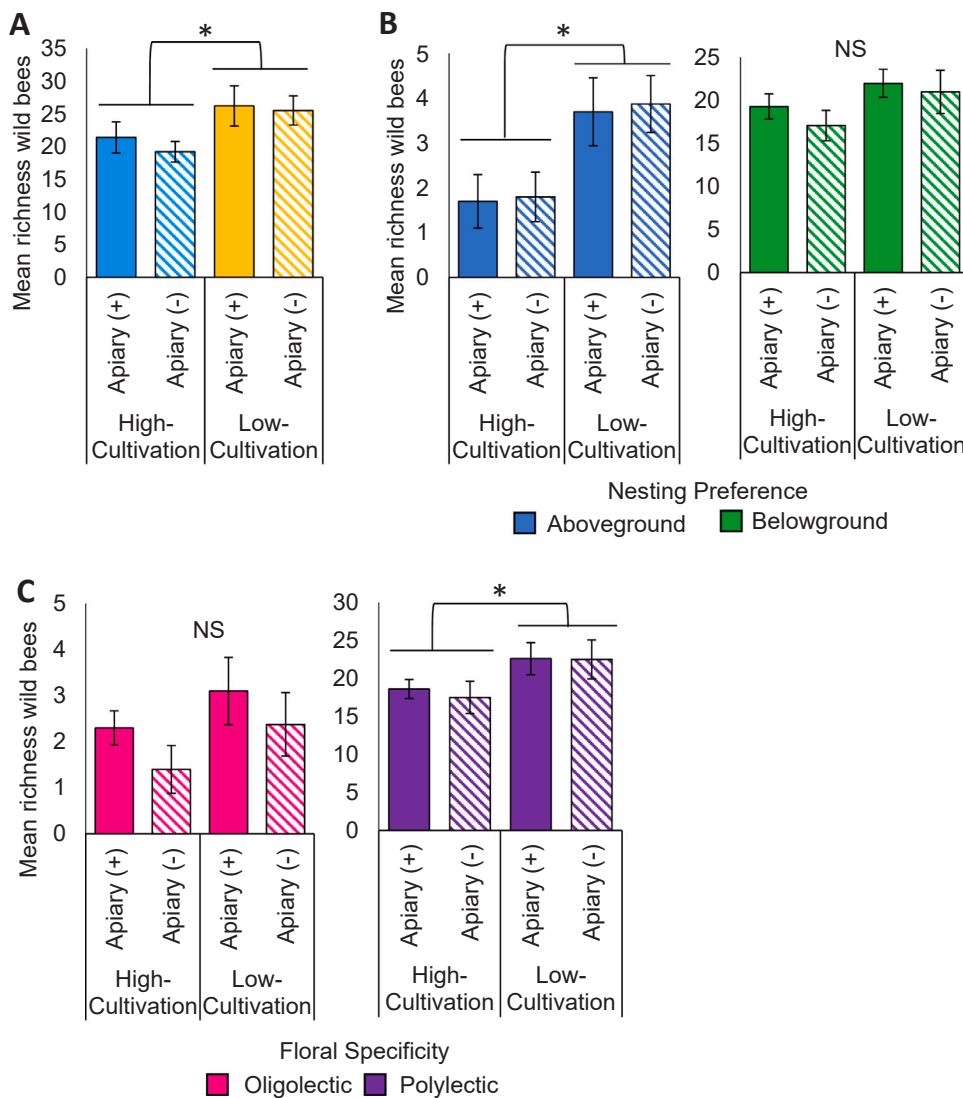
Fig. 3.. A) Richness (mean per site) of the wild bee community in soybean fields surrounded by High-and Low-cultivation of maize and soybean and with and without the presence of a honey bee apiary in 2015 and 2016. (B) Richness of wild bees by nesting type and (C) richness of wild bees by floral specificity in soybean fields surrounded by High-and Low-cultivation of maizeand soybean and with and without the presence of a honey bee apiary in 2015 and 2016. Error bars represent one standard error of the mean. Results based on mixed model ANOVA (Tables S5-6). Asterisks represent significance at ($p < 0.05$).

Richness of polylectic bees remained lower in High-cultivation compared to Low-cultivation when *Lasioglossum* were removed ($F_{1, 34} = 4.70$, $p = 0.04$).

The richness of belowground nesting bees remained significantly higher than aboveground nesting bees when *Lasioglossum* were excepted ($F_{1, 34} = 288.74$, $p = <0.0001$). There were no main effects of apiary presence and no interactions with any other effects measured (Table S7). Richness remained lower in High-cultivation sites compared to Low-cultivation ($F_{1, 34} = 5.57$, $p = 0.02$), and there were no interactions between floral specialization and cultivation category ($F_{1, 34} = 2.39$, $p = 0.13$). In addition to a lower richness of aboveground nesting bees in High-cultivation compared to Low-cultivation landscapes ($F_{1, 34} = 6.19$, $p = 0.02$), we also observed a lower richness of belowground nesting bees in High-cultivation when *Lasioglossum* were removed ($F_{1, 34} = 5.57$, $p = 0.02$).

3.2. Relationship between surrounding landscape and wild bee community

We quantified the responses of wild bee richness to landscape cover on a continuous landscape scale at an 800 m, 1600 m and 2400 m scale. Like the response of bees within cultivation category, we observed a significantly higher richness of bees when in fields surrounded by increasing proportions of non-cropped land (i.e., woodland, grassland, and developed land; Table 1).

Table 1

Linear regression comparing the richness of wild bees to the proportion of non-cropped land (woodland, grassland, and developed land) surrounding each soybean field at an 800 m, 1600 m, and 2400 m radius from field edge.

Spatial scale	DF	F Value	Pr > F	r_2
800 m	1, 36	7.57	**0.0092***	0.18
1600 m	1, 36	7.32	**0.0104***	0.18
2400 m	1, 36	6.84	**0.0129***	0.17

+ signifies marginal statistical significance at P < 0.1

* signifies statistical significance at P < 0.05

Overall, wild bee communities had the strongest response to landscape variation at 800 m and the weakest response at 2400 m (indicated by model R^2; Table 2). Regardless of scale, richness was always positively related to the proportion woodland in the surrounding landscape and richness of wild bees was lower when production of other crops was more prevalent (Table 2). There was a consistent response of richness of above and belowground nesting bees to the proportion of woodland in the surrounding landscape at all spatial scales (Table 2). There was a higher richness of polylectic generalist foragers when surrounded by increased proportions of woodland at all spatial scales, and the proportion of other crops was generally negatively associated with polylectic bee richness (Table 2). For specialist oligolectic bees, there was a

Table 2

Multiple regression for wild bee richness using landscape features soybean, other crops, woodland, grassland, and developed land, as well as honey bee apiary presence as possible parameters. Stepwise model selection was used to obtain the final variables in each model ($P < 0.15$ for inclusion in the model).

	Spatial scale	Parameters	Slope	SE	F	P	Model r^2
Overall Community	800 m	Woodland	26.83	6.51	14.22	**0.0006***	
		Other Crop	-74.92	32.96	5.17	**0.03***	0.38
	1600 m	Woodland	26.77	7.63	12.31	**0.001***	0.25
	2400 m	Woodland	23.44	8.02	8.54	**0.006***	0.19
Belowground	800 m	Woodland	18.49	5.26	9.95	**0.003***	
		Other Crop	-65.37	26.60	6.04	**0.02***	0.33
	1600 m	Woodland	19.36	6.15	8.14	**0.007***	
		Other Crop	-72.88	43.55	2.80	0.10	0.24
	2400 m	Woodland	14.62	6.52	5.02	**0.03***	0.12
Aboveground	800 m	Woodland	3.06	1.01	9.22	**0.004***	0.20
	1600 m	Woodland	3.21	1.11	8.35	**0.007***	0.19
	2400 m	Woodland	2.41	1.11	5.54	**0.02***	
		Developed	1.99	0.96	4.31	**0.05***	0.23
Polylectic	800 m	Woodland	23.50	5.44	15.44	**0.0004***	
		Other Crop	-64.80	27.50	5.72	**0.02***	0.40
	1600 m	Soybean	-21.95	10.64	2.35	0.13	
		Other Crop	-92.26	44.98	2.21	**0.05***	
		Woodland	13.01	8.29	12.60	**0.001***	0.38
	2400 m	Woodland	18.15	6.75	8.22	**0.007***	
		Developed	9.44	5.78	2.67	0.11	0.24
Oligolectic	800 m	Developed	-4.61	1.96	4.20	**0.05***	
		Grassland	5.54	2.50	4.92	**0.03***	0.21
	1600 m	Developed	-3.59	1.69	4.51	**0.04***	
		Grassland	9.32	4.26	3.46	0.07+	0.19
	2400 m	Developed	-3.09	1.71	3.28	0.07+	
		Grassland	10.07	5.01	3.02	0.09+	0.16

* signifies statistical significance at $P < 0.05$
+ signifies marginal statistical significance at $P < 0.1$

negative relationship between proportion developed land and wild bee richness at all spatial scales (Table 2). At the 800 m scale the proportion grassland was significantly positively related to oligolectic bee richness and marginally significant at the 1600 m and 2400 m spatial scales (Table 2).

4. Discussion

The causes and consequences of global biodiversity loss are of increasing concern as anthropogenic landscape changes threaten the health and existence of many species (Crist et al., 2017). Habitat loss resulting from increased conversion of natural and semi-natural landscapes into intensive agricultural systems has been argued to be the most important driver of biodiversity loss, particularly for pollinators and other insects (Sánchez-Bayo and Wyckhuys, 2019). In addition to

stressors associated with crop production, commercially managed honey bee colonies, often used in crop pollination services, may act as a catalyst for wild bee declines (Geslin et al., 2017; Russo, 2016). We provide one of the first assessments of the relative importance of agricultural intensification and managed honey bee presence on wild bee communities in one of the most intensively cropped agricultural regions of the world, Iowa, USA.

Our study suggests that wild bee communities in the examined agricultural system are more strongly affected by landscape composition than the presence of a small apiary. Wild bee communities in soybean fields were more speciose when the surrounding landscape was characterized by less cropping area and more non-crop features (Table 1). This response was strongest for aboveground nesting bees, more specifically for stem and cavity nesting bees belonging to the genera *Megachile*, *Anthidium*, *Ceratina*, and *Osmia* (Fig. 3). Contrary to our

predictions, we did not observe that the presence of a small apiary altered wild bee richness at the community level or within functional groups (Fig. 3). Together, these data support the hypothesis that the stresses of agricultural industrialization are more drastic than direct competition with managed honey bees (Hudewenz and Klein, 2013), at least at the scale of apiculture and time period we measured.

Studies have shown that the presence of honey bees can result in reduced wild bee abundance and richness (Angelella et al., 2021; Garibaldi et al., 2021), floral visitation rates (Wojcik et al., 2018) and nesting success (Hudewenz and Klein, 2013). In our study, we documented an increase in honey bee activity density within the immediate soybean field at sites where they were placed (Fig. S2), however, our data suggest the activity of those honey bees was insufficient to affect the wild bee community within those fields. Although we found no effect of the presence of a small apiary, these results are likely to be very region and context-specific, thus we urge caution in generalizing this finding for several reasons.

First, competition for resources within a year has the potential to restrict the ability of wild bees to produce healthy offspring (Goulson and Sparrow, 2009), however, to observe changes in the wild bee community would require measurements taken over multiple years because many offspring do not emerge until the following season. For example, two studies focused on honey bee competition with wild bees in Australia, one over a short term period (6 month; Paini et al., 2005), and another over a long term study period (>2 years chronic exposure; Paini and Roberts, 2005), observed that short term competition did not alter the reproductive success of a single bee species while the long term exposure resulted in reduced fecundity of a separate bee species. Because maize and soybean are rotated annually, our experimental design which focused on soybean fields did not permit monitoring the same location for multiple years, precluding an assessment of the long-term effects of apiary presence.

Second, wild bees are expected to respond more negatively with higher densities of honey bee foragers, which are a function of the number of colonies in an apiary (St. Clair et al., 2020a). This has been demonstrated with increased foraging competition for wild bees when there is high density honey beekeeping (Henry and Rodet, 2018). Here, the four colonies at each site may not have produced a large enough population of foraging workers to negatively affect the overall bee community. In Brazil, honey bees and other native species only had a negative influence on wild bees when they were the dominant species within the community, and even then it was only the African subspecies that influenced the wild bee community (Garibaldi et al., 2021). Assessing wild bee communities over multiple years and varying colony densities is needed to evaluate the long-term effects of honey bee presence on wild bee communities in agricultural systems.

Our results support the hypothesis that a limited amount of diverse natural habitat is a strong driver of wild bee community declines in agricultural landscapes. The community composition of wild bees collected in soybean varied with the proportion of cropland in the surrounding landscape (Fig. 2), with the lowest species richness observed in landscapes comprised of High-cultivation (Fig. 3). Similar to other studies, we found the highest number of unique and numerically rare species (eighteen species) associated with landscapes surrounded by Low-cultivation (Table S2) (Harrison et al., 2019). A subset of species were invariably abundant, a phenomenon that is common for bee community assemblages (Kleijn et al., 2015; St. Clair et al., 2020b), likely driving the lack of variation in overall bee abundance in High-versus Low-cultivation landscapes (Table S2). Regardless, communities had a significantly higher richness at the local and landscape scale when surrounded by more non-crop resources (Table 1), which could provide valuable forage and nesting habitat to wild bees (Mallinger et al., 2016; Smith et al., 2016).

The effect of land use and variation in features surrounding study sites had the greatest impact on aboveground nesting species. This is not surprising given the frequency of disturbances associated with annual crop production (e.g., tillage, planting, harvesting) that result in the removal of aboveground biomass. Not only does agricultural simplification increase disturbance associated with crop production practices, but frequently eliminates natural or semi-natural habitats that would otherwise be interspersed in the landscape matrix. A lack of habitats such as field margins, hedgerows, shrubs, tree lines, and remnants as well as other elements like downed wood or structures close to the crop field also serve as important nesting substrates for aboveground bees (Biesmeijer et al., 2006; Proesmans et al., 2019; Raderschall et al., 2021). Our results suggest that in highly disturbed landscapes, nesting habitat, particularly for aboveground bees, is a critically limited resource. Corroborating previous research, we found landscapes characterized by High-cultivation of crops were associated with decreased richness of aboveground nesting bees (Fig. 3B), but were positively associated with increases in woodland habitat (Table 2) (Evans et al., 2018; Palma et al., 2015). This suggests that woodland provides valuable nesting resources not otherwise present in more disturbed components of the landscape. Because crops are rotated and often tilled annually, aboveground nesting bees present in soybeans are likely a result of spillover from nearby woodland habitats (Blitzer et al., 2012) that act as a reservoir for these species (Kennedy et al., 2013). Increasing the prevalence of dispersed woodland shelterbelts may be an effective way to conserve bee biodiversity in landscapes with limited resources and high agricultural land use (Donkersley, 2019; Evans et al., 2018).

Although bees responded to landscape composition at all three spatial scales we measured, increases in wild bee communities were most strongly associated with landscape features at the 800 m scale (i.e., higher R^2; Table 2), indicating that most wild bee species were positively influenced by close proximity to non-crop landscape resources. Similar results have been observed with bees in oilseed rape fields, where proximity to non-crop resources has been shown to positively influence abundance of some bee species which nest in nearby habitat (Holzschuh et al., 2013). Floral specialist (i.e., oligolectic bee) richness was positively related with the proportion of grassland at the local scale (Table 2); grassland habitat adjacent to mass-flowering crops has been shown to increase nesting success and brood cell quantity in some bee species (Holzschuh et al., 2013). In general, the very limited impact of cultivation on either oligolectic or polylectic bees was surprising. We anticipated a greater response by oligolectic species to variation in cultivation and the presence of more perennial habitat. The lack of a strong response may be due to an already depauperate community of native bees with a narrow host range. Efforts to improve upon the abundance richness of these species will require adding more plant diversity in the form of native, perennial flowering species. Our data suggest that additions of grassland and woodlands would enhance the local bee community, and this community will not be immediately affected by small scale apiculture (Fig. 3 C; Table 2).

In our study area, the native habitat prior to European settlement was prairie, comprised of perennial grasses and flowering forbs (Smith, 1998). Re-establishing prairie near or within crop fields increases the abundance and diversity of bees (Kordbacheh et al., 2020; Schulte et al., 2017). However, the positive response of above and belowground nesting bees to woodland suggests that prairie alone may be insufficient to conserve the entire community of bee species. Ultimately, pollinator-targeted habitat enrichments in agricultural landscapes will depend on the goal(s)– conservation of bee biodiversity, supporting wild and managed bees for stability of pollination services, or apiculture in the form of honey production. In landscapes committed to production of crops, not requiring insect pollination, efforts to conserve pollinators may be limited, and there may be a reluctance to set aside marginal cropland or neighboring landscapes if there is an economic cost to the farmer. To conserve this community may require selecting practices that can deliver multiple benefits. For example, the addition of small patches of prairie to a crop field can achieve multiple goals including but not limited to pollinator conservation, topsoil retention, and reduced nitrogen and phosphorous runoff (Schulte et al., 2017).

Incorporating woodland shelterbelts can increase field productivity as a result of reduced wind erosion (Redei et al., 2020), reduced drift of insecticides (Ucar and Hall, 2001), and improving crop water use and increasing crop yields and economic returns (Kort, 1988). It is especially valuable in that perennial habitat and woodland shelterbelts can be modified and designed to fit specific cropping systems and landscapes (Redei et al., 2020; Sidhu and Joshi, 2016). An inference from these data is that, regardless of the initial goal, conservation of wild bee biodiversity, particularly rarer aboveground and oligolectic bee species, can be achieved in landscapes characterized by annual crop production via the addition of locally available woodland and grassland habitat.

This study may also have broader implications for pollinator conservation in the face of agricultural development globally. For at least the last decade, Iowa has been a top producer of maize and soybean in the USA, dedicating the highest percentage of its landscape (>66%; over 9 million ha of land) to their production (NASS-USDA, 2019). With most of the landscape taken up by crops that provide limited floral resources, this is an extreme example of how crop production can affect the food supply for bees. Many countries currently struggle to find a balance between food production and managing landscapes to limit losses of biodiversity (Dudley and Alexander, 2017). In our study, Iowa represents a 'worst-case scenario' for studying how landscape transformation affects wild bees. While many studies have focused on how these landscapes affect honey bees (Dolezal et al., 2019; Otto et al., 2016; Smart et al., 2018), we demonstrate that wild bees are also significantly impacted by the conversion of natural landscapes for annual crop production. Our results show that extensive agricultural land development, especially in the form of annual crops that are not insect dependent, may be a catalyst for reduced bee biodiversity. Landscapes currently undergoing agricultural conversions should focus on conservation of existing native perennial forbs and woodland habitats while existing agroecosystems should prioritize local reintegration of these features to mitigate biodiversity loss and preserve rarer bee species.

CRediT authorship contribution statement

AGD, ALT and MEO procured funding. AGD, ALS, ALT, and MEO designed the study. ALS and GZ collected the data. ALS identified bee specimens. ALS analyzed data and wrote the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2021.107826.

References

Angelella, G.M., McCullough, C.T., O'Rourke, M.E., 2021. Honey bee hives decrease wild bee abundance, species richness, and fruit count on farms regardless of wildflower strips. Sci. Rep. 11 https://doi.org/10.1038/s41598-021-81967-1 (3202).

Arduser, M., 2016. Key to the genera and species of the Midwestern United States with an emphasis on the Tallgrass Prairie region.

Ascher, J.S., Pickering, J., 2015. Discover Life bee species guide and world checklist (Hymenoptera: Apoidea: Anthophila) [WWW Document].

Baum, K.A., Wallen, K.E., 2011. Potential bias in pan trapping as a function of floral abundance. J. Kans. Entomol. Soc. 84, 155–159. https://doi.org/10.2317/JKES100629.1.

Biesmeijer, J.C., Roberts, S.P.M., Reemer, M., Ohlemüller, R., Edwards, M., Peeters, T., Schaffers, A.P., Potts, S.G., Kleukers, R., Thomas, C.D., Settele, J., Kunin, W.E., 2006. Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. Science 313, 351–354. https://doi.org/10.1126/science.1127863.

Blitzer, E.J., Dormann, C.F., Holzschuh, A., Klein, A.-M., Rand, T.A., Tscharntke, T., 2012. Spillover of functionally important organisms between managed and natural habitats. Agric. Ecosyst. Environ. 146, 34–43. https://doi.org/10.1016/j.agee.2011.09.005.

Brown, P.W., Schulte, L.A., 2011. Agricultural landscape change (1937–2002) in three townships in Iowa, USA. Landsc. Urban Plan. 100, 202–212. https://doi.org/10.1016/j.landurbplan.2010.12.007.

Cameron, S.A., Sadd, B.M., 2020. Global trends in bumble bee health. Annu. Rev. Entomol. 65, 209–232. https://doi.org/10.1146/annurev-ento-011118-111847.

Chao, A., Jost, L., 2012. Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. Ecology 93, 2533–2547. https://doi.org/10.1890/11-1952.1.

Crist, E., Mora, C., Engelman, R., 2017. The interaction of human population, food production, and biodiversity protection. Science 356, 260–264. https://doi.org/10.1126/science.aal2011.

Decourtye, A., Alaux, C., Le Conte, Y., Henry, M., 2019. Toward the protection of bees and pollination under global change: present and future perspectives in a challenging applied science. Curr. Opin. Insect Sci. 35, 123–131. https://doi.org/10.1016/j.cois.2019.07.008.

Dolezal, A.G., St Clair, A.L., Zhang, G., Toth, A.L., O'Neal, M.E., 2019. Native habitat mitigates feast-famine conditions faced by honey bees in an agricultural landscape. Proc. Natl. Acad. Sci. USA 116. https://doi.org/10.1073/pnas.1912801116 (25147).

Donkersley, P., 2019. Trees for bees. Agric., Ecosyst. Environ. 270–271, 79–83. https://doi.org/10.1016/j.agee.2018.10.024.

Droege, S., Tepedino, V., Lebuhn, G., Link, W., Minckley, R., Chen, Q., Conrad, C., 2010. Spatial patterns of bee captures in North American bowl trapping surveys. Insect Conserv. Divers. 3, 15–23. https://doi.org/10.1111/j.1752-4598.2009.00074.x.

Dudley, N., Alexander, S., 2017. Agriculture and biodiversity: a review. Biodiversity 18, 45–49. https://doi.org/10.1080/14888386.2017.1351892.

Evans, E., Smart, M., Cariveau, D., Spivak, M., 2018. Wild, native bees and managed honey bees benefit from similar agricultural land uses. Agric. Ecosyst. Environ. 268, 162–170. https://doi.org/10.1016/j.agee.2018.09.014.

Garibaldi, L.A., Pérez-Méndez, N., Cordeiro, G.D., Hughes, A., Orr, M., Alves-dos-Santos, I., Freitas, B.M., Freitas de Oliveira, F., LeBuhn, G., Bartomeus, I., Aizen, M.A., Andrade, P.B., Blochtein, B., Boscolo, D., Drumond, P.M., Gaglianone, M.C., Gemmill-Herren, B., Halinski, R., Krug, C., Maués, M.M., Piedade Kiill, L.H., Pinheiro, M., Pires, C.S.S., Viana, B.F., 2021. Negative impacts of dominance on bee communities: Does the influence of invasive honey bees differ from native bees? Ecology 102, e03526. https://doi.org/10.1002/ecy.3526.

Geldmann, J., González-Varo, J.P., 2018. Conserving honey bees does not help wildlife. Science 359, 392–393. https://doi.org/10.1126/science.aar2269.

Geslin, B., Gauzens, B., Baude, M., Dajoz, I., Fontaine, C., Henry, M., Ropars, L., Rollin, O., Thébault, E., Vereecken, N.J., 2017. Massively introduced managed species and their consequences for plant–pollinator interactions. Adv. Ecol. Res. 57, 147–199. https://doi.org/10.1016/bs.aecr.2016.10.007.

Giles, V., Ascher, J.S., 2006. A survey of the bees of the black rock forest preserve, New York (Hymenoptera: Apoidea). J. Hymenopt. Res. 15, 24.

González-Varo, J.P., Geldmann, J., 2018. Response—"Bee conservation: Key role of managed bees" and "Bee conservation: inclusive solutions. Science 360. https://doi.org/10.1126/science.aat3746.

Goulson, D., Sparrow, K.R., 2009. Evidence for competition between honeybees and bumblebees; effects on bumblebee worker size. J. Insect Conserv. 13, 177–181. https://doi.org/10.1007/s10841-008-9140-y.

Goulson, D., Nicholls, E., Botías, C., Rotheray, E.L., 2015. Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. Science 347. https://doi.org/10.1126/science.1255957 (1255957).

Greenleaf, S., Williams, N., Winfree, R., Kremen, C., 2007. Bee foraging ranges and their relationship to body size. Oecologia 153, 589–596. https://doi.org/10.1007/s00442-007-0752-9.

Grixti, J., Wong, L., Cameron, S.A., Favret, C., 2009. Decline of bumble bees (Bombus) in the North American Midwest. Biol. Conserv. 142, 75–84. https://doi.org/10.1016/j.biocon.2008.09.027.

Harrison, T., Gibbs, J., Winfree, R., 2019. Anthropogenic landscapes support fewer rare bee species. Landsc. Ecol. 34, 967–978. https://doi.org/10.1007/s10980-017-0592-x.

Henry, M., Rodet, G., 2018. Controlling the impact of the managed honeybee on wild bees in protected areas. Sci. Rep. 8, 1–10. https://doi.org/10.1038/s41598-018-27591-y.

Holzschuh, A., Dormann, C., Tscharntke, T., Steffan-Dewenter, I., 2013. Mass-flowering crops enhance wild bee abundance. Oecologia 172, 477–484. https://doi.org/10.1007/s00442-012-2515-5.

Horowitz, J., Ebel, R., Ueda, K., 2010. No-Till Farming Is a Growing Practice 70, 28.

Hudewenz, A., Klein, A.-M., 2013. Competition between honey bees and wild bees and the role of nesting resources in a nature reserve. J. Insect Conserv. 17 https://doi.org/10.1007/s10841-013-9609-1 (1275).

Kennedy, C.M., Lonsdorf, E., Neel, M.C., Williams, N.M., Ricketts, T.H., Winfree, R., Bommarco, R., Brittain, C., Burley, A.L., Cariveau, D., Carvalheiro, L.G., Chacoff, N. P., Cunningham, S.A., Danforth, B.N., Dudenhöffer, J.-H., Elle, E., Gaines, H.R., Garibaldi, L.A., Gratton, C., Holzschuh, A., Isaacs, R., Javorek, S.K., Jha, S., Klein, A. M., Krewenka, K., Mandelik, Y., Mayfield, M.M., Morandin, L., Neame, L.A., Otieno, M., Park, M., Potts, S.G., Rundlöf, M., Saez, A., Steffan-Dewenter, I., Taki, H., Viana, B.F., Westphal, C., Wilson, J.K., Greenleaf, S.S., Kremen, C., 2013. A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. Ecol. Lett. 16 https://doi.org/10.1111/ele.12082 (584).

Kleijn, D., Winfree, R., Bartomeus, I., Carvalheiro, L.G., Henry, M., Isaacs, R., Klein, A.-M., Kremen, C., M'Gonigle, L.K., Rader, R., Ricketts, T.H., Williams, N.M., Lee Adamson, N., Ascher, J.S., Báldi, A., Batáry, P., Benjamin, F., Biesmeijer, J.C., Blitzer, E.J., Bommarco, R., Brand, M.R., Bretagnolle, V., Button, L., Cariveau, D.P., Chifflet, R., Colville, J.F., Danforth, B.N., Elle, E., Garratt, M.P.D., Herzog, F., Holzschuh, A., Howlett, B.G., Jauker, F., Jha, S., Knop, E., Krewenka, K.M., Le Féon, V., Mandelik, Y., May, E.A., Park, M.G., Pisanty, G., Reemer, M., Riedinger, V., Rollin, O., Rundlöf, M., Sardiñas, H.S., Scheper, J., Sciligo, A.R., Smith, H.G., Steffan-Dewenter, I., Thorp, R., Tscharntke, T., Verhulst, J., Viana, B.F., Vaissière, B.E., Veldtman, R., Westphal, C., Potts, S.G., 2015. Delivery of crop pollination services is an insufficient argument for wild pollinator conservation. Nat. Commun. 6 https://doi.org/10.1038/ncomms8414.

Kline, O., Joshi, N.K., 2020. Mitigating the effects of habitat loss on solitary bees in agricultural ecosystems. Agriculture 10. https://doi.org/10.3390/agriculture10040115 (115).

Koh, I., Lonsdorf, E.V., Williams, N.M., Brittain, C., Isaacs, R., Gibbs, J., Ricketts, T.H., 2016. Modeling the status, trends, and impacts of wild bee abundance in the United States. Proc. Natl. Acad. Sci. USA 113. https://doi.org/10.1073/pnas.1517685113 (140).

Kordbacheh, F., Liebman, M., Harris, M., 2020. Strips of prairie vegetation placed within row crops can sustain native bee communities. PLOS One 15, e0240354. https://doi.org/10.1371/journal.pone.0240354.

Kort, J., 1988. 9. Benefits of windbreaks to field and forage crops. Agriculture, Ecosystems & Environment, In: Proceedings of an International Symposium on Windbreak Technology 22–23, pp. 165–190. https://doi.org/10.1016/0167-8809(88)90017-5.

Kovács-Hostyánszki, A., Espíndola, A., Vanbergen, A.J., Settele, J., Kremen, C., Dicks, L. V., 2017. Ecological intensification to mitigate impacts of conventional intensive land use on pollinators and pollination. Ecol. Lett. 20, 673–689. https://doi.org/10.1111/ele.12762.

Kremen, C., M'Gonigle, L.K., Ponisio, L.C., 2018. Pollinator community assembly tracks changes in floral resources as restored hedgerows mature in agricultural landscapes. Front. Ecol. Evol. 6 https://doi.org/10.3389/fevo.2018.00170 (170).

Kremen, C., Williams, N.M., Thorp, R.W., 2002. Crop pollination from native bees at risk from agricultural intensification. pp. 16812–16816.

LeBuhn, G., Griswold, T., Minckley, R., Droege, S., Roulston, T., Cane, J., Parker, F., Buchmann, S., Tepedino, V., Williams, N., Kremen, C., Messenger, O., 2003. A standardized method for monitoring Bee Populations – The Bee Inventory (BI) Plot. [WWW Document]. URL http://online.sfsu.edu/beeplot/pdfs/Bee%20Plot%202003.pdf.

Le Féon, Violette, Schermann-Legionnet, Agnès, Delettre, Yannick, Aviron, Stéphanie, Billeter, Regula, Bugter, Rob, Hendrickx, Frederik, Burel, Françoise, 2010. Intensification of Agriculture, Landscape Composition and Wild Bee Communities: A Large Scale Study in Four European Countries. Agriculture, Ecosystems & Environment 137 (1-2), 143–150. https://doi.org/10.1016/j.agee.2010.01.015.

Lerman, S.B., Milam, J., 2016. Bee Fauna and Floral abundance within lawn-dominated suburban yards in Springfield, MA. Ann. Èntomol. Soc. Am. 109, 713–723. https://doi.org/10.1093/aesa/saw043.

Littell, R.C., 2002. SAS for Linear Models, Fourth Edition, Fourth edition. ed, SAS for Linear Models. Place of publication not identified SAS Press Imprint.

Losey, J.E., Vaughan, M., 2006. The economic value of ecological services provided by insects. BioScience 56, 311–323. https://doi.org/10.1641/0006-3568(2006)56[311:TEVOES]2.0.CO;2.

Mallinger, R., Gibbs, J., Gratton, C., 2016. Diverse landscapes have a higher abundance and species richness of spring wild bees by providing complementary floral resources over bees' foraging periods. Landsc. Ecol. 31, 1523–1535. https://doi.org/10.1007/s10980-015-0332-z.

Mallinger, R.E., Gaines-Day, H.R., Gratton, C., 2017. Do managed bees have negative effects on wild bees?: A systematic review of the literature. PLOS One 12, e0189268. https://doi.org/10.1371/journal.pone.0189268.

Matteson, K.C., Ascher, J.S., Langellotto, G.A., 2008. Bee richness and abundance in New York City Urban Gardens. Ann. Èntomol. Soc. Am. 101, 140–150. https://doi.org/10.1603/0013-8746(2008)101[140:BRAAIN]2.0.CO;2.

Michener, C.D., 1994. The bee genera of North and Central America (Hymenoptera: Apoidea) / Charles D. Michener, Ronald J. McGinley, and Bryan N. Danforth. Washington: Smithsonian Institution Press, Washington.

Michener, C.D., 2007. The bees of the world / Charles D. Michener, 2nd ed. ed. Baltimore: Johns Hopkins University Press, Baltimore.

NASS-USDA, 2019. United States Department of Agriculture National Agricultural Statistics Service Iowa Ag News – Chemical Use Corn and Soybeans: Fall 2018.

Normandin, É., Vereecken, N.J., Buddle, C.M., Fournier, V., 2017. Taxonomic and functional trait diversity of wild bees in different urban settings. PeerJ 5, e3051. https://doi.org/10.7717/peerj.3051.

Otto, C.R.V., Roth, C.L., Carlson, B.L., Smart, M.D., 2016. Land-use change reduces habitat suitability for supporting managed honey bee colonies in the Northern Great Plains. Proc. Natl. Acad. Sci. USA 113. https://doi.org/10.1073/pnas.1603481113 (10430).

Paini, D.R., Roberts, J.D., 2005. Commercial honey bees (Apis mellifera) reduce the fecundity of an Australian native bee (Hylaeus alcyoneus). Biol. Conserv. 123, 103–112. https://doi.org/10.1016/j.biocon.2004.11.001.

Paini, D.R., Williams, M.R., Roberts, D.J., 2005. No short-term impact of honey bees on the reproductive success of an Australian native bee. Apidologie 36, 613–621.

Palma, A.D., Kuhlmann, M., Roberts, S.P.M., Potts, S.G., Börger, L., Hudson, L.N., Lysenko, I., Newbold, T., Purvis, A., 2015. Ecological traits affect the sensitivity of bees to land-use pressures in European agricultural landscapes. J. Appl. Ecol. 52, 1567–1577. https://doi.org/10.1111/1365-2664.12524.

Popp, J., Lakner, Z., Harangi-Rákos, M., Fári, M., 2014. The effect of bioenergy expansion: food, energy, and environment. Renew. Sustain. Energy Rev. 32, 559–578. https://doi.org/10.1016/j.rser.2014.01.056.

Portman, Z.M., Bruninga-Socolar, B., Cariveau, D.P., 2020. The state of bee monitoring in the United States: a call to refocus away from bowl traps and towards more effective methods. Ann. Èntomol. Soc. Am. 1–6. https://doi.org/10.1093/aesa/saaa010.

Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O., Kunin, W.E., 2010. Global pollinator declines: trends, impacts and drivers. Trends Ecol. Evol. 25, 345–353. https://doi.org/10.1016/j.tree.2010.01.007.

Proesmans, W., Bonte, D., Smagghe, G., Meeus, I., Decocq, G., Spicher, F., Kolb, A., Lemke, I., Diekmann, M., Bruun, H., Wulf, M., Van Den Berge, S., Verheyen, K., 2019. Small forest patches as pollinator habitat: oases in an agricultural desert? Landsc. Ecol. 34, 487–501. https://doi.org/10.1007/s10980-019-00782-2.

Raderschall, C.A., Bommarco, R., Lindström, S.A.M., Lundin, O., 2021. Landscape crop diversity and semi-natural habitat affect crop pollinators, pollination benefit and yield. Agric. Ecosyst. Environ. 306, 107189 https://doi.org/10.1016/j.agee.2020.107189.

Redei, K., Keseru, Z., Bach, I., Raso, J., Abri, T., Szabo, F., Gal, J., 2020. The multifunctional role of shelterbelts in intensively managed agricultural land - silvoarable agroforestry in Hungary. Acta Silv. Et. Lignaria Hung. 16, 9–18. https://doi.org/10.37045/aslh-2020-0001.

Rollin, O., Pérez-Méndez, N., Bretagnolle, V., Henry, M., 2019. Preserving habitat quality at local and landscape scales increases wild bee diversity in intensive farming systems. Agric. Ecosyst. Environ. 275, 73–80. https://doi.org/10.1016/j.agee.2019.01.012.

Roulston, T.H., Smith, S.A., Brewster, A.L., 2007. A comparison of pan trap and intensive net sampling techniques for documenting a Bee (Hymenoptera: Apiformes) Fauna. J. Kans. Èntomol. Soc. 80, 179–181. https://doi.org/10.2317/0022-8567(2007)80[179:ACOPTA]2.0.CO;2.

Russo, L., 2016. Positive and negative impacts of non-native bee species around the world. Insects 7. https://doi.org/10.3390/insects7040069.

Sánchez-Bayo, F., Wyckhuys, K.A.G., 2019. Worldwide decline of the entomofauna: a review of its drivers. Biol. Conserv. 232, 8–27. https://doi.org/10.1016/j.biocon.2019.01.020.

Scheper, J., Bommarco, R., Holzschuh, A., Potts, S.G., Riedinger, V., Roberts, S.P.M., Rundlöf, M., Smith, H.G., Steffan-Dewenter, I., Wickens, J.B., Wickens, V.J., Kleijn, D., 2015. Local and landscape-level floral resources explain effects of wildflower strips on wild bees across four European countries. J. Appl. Ecol. 52, 1165–1175. https://doi.org/10.1111/1365-2664.12479.

Schulte, L.A., Niemi, J., Helmers, M.J., Liebman, M., Arbuckle, J.G., James, D.E., Kolka, R.K., O'Neal, M.E., Tomer, M.D., Tyndall, J.C., Asbjornsen, H., Drobney, P., Neal, J., Van Ryswyk, G., Witte, C., 2017. Prairie strips improve biodiversity and the delivery of multiple ecosystem services from corn-soybean croplands. Proc. Natl. Acad. Sci. USA 114. https://doi.org/10.1073/pnas.1620229114 (11247).

Searchinger, T., Heimlich, R., Houghton, R.A., Dong, F., Elobeid, A., Fabiosa, J., Tokgoz, S., Hayes, D., Yu, T.-H., 2008. Use of U.S. croplands for biofuels increases greenhouse gases through emissions from land-use change. Science 319, 1238–1240. https://doi.org/10.1126/science.1151861.

Shackelford, G., Steward, P., Benton, T., Kunin, W., Potts, S.G., Biesmeijer, J., Sait, S.M., 2013. Comparison of pollinators and natural enemies: a meta-analysis of landscape and local effects on abundance and richness in crops. Biol. Rev. 88, 1002–1021. https://doi.org/10.1111/brv.12040.

Sidhu, C.S., Joshi, N.K., 2016. Establishing wildflower pollinator habitats in agricultural farmland to provide multiple ecosystem services. Front. Plant Sci. 7. https://doi.org/10.3389/fpls.2016.00363.

Smart, M.D., Otto, C.R.V., Carlson, B.L., Roth, C.L., 2018. The influence of spatiotemporally decoupled land use on honey bee colony health and pollination service delivery. The influence of spatiotemporally decoupled land use on honey bee colony health and pollination service delivery 13, 084016. https://doi.org/10.1088/1748-9326/aad4eb.

Smith, D.D., 1998. Iowa Prairie: Original Extent and Loss, Preservation and Recovery Attempts 104, 94–108.

Smith, G.W., Debinski, D.M., Debinski, N.A., Lange, C.J., Delaney, J.T., Moranz, R.A., Miller, J.R., Engle, D.M., Toth, A.L., 2016. Bee abundance and nutritional status in relation to grassland management practices in an agricultural landscape. Environ. Entomol. 45 https://doi.org/10.1093/ee/nvw005 (338).

St. Clair, A.L., Dolezal, A.G., O'Neal, M.E., Toth, A.L., 2020a. Pan traps for tracking honey bee activity-density: a case study in Soybeans. Insects 11, 366. https://doi.org/10.3390/insects11060366.

(St) St. Clair, A.L., Dolezal, A.G., Zhang, G., O'Neal, M.E., Toth, A.L., 2020b. Diversified farming in a monoculture landscape: effects on honey bee health and wild bee communities. Environ. Entomol. 49, 743–764. https://doi.org/10.1093/ee/nvaa031.

Tapia-González, J.M., Morfin, N., Macías-Macías, J.O., De la Mora, A., Tapia-Rivera, J.C., Ayala, R., Contreras-Escareño, F., Gashout, H.A., Guzman-Novoa, E., 2019. Evidence of presence and replication of honey bee viruses among wild bee pollinators in subtropical environments. J. Invertebr. Pathol. 168, 1–4. https://doi.org/10.1016/j.jip.2019.107256.

Tylianakis, J.M., Klein, A.-M., Lozada, T., Tscharntke, T., 2006. Spatial scale of observation affects α, β and γ diversity of cavity-nesting bees and wasps across a tropical land-use gradient. J. Biogeogr. 33, 1295–1304. https://doi.org/10.1111/j.1365-2699.2006.01493.x.

Ucar, T., Hall, F.R., 2001. Windbreaks as a pesticide drift mitigation strategy: a review. Pest Manag. Sci. 57, 663–675. https://doi.org/10.1002/ps.341.

USDA-NASS, 2015. United State Department of Agriculture-National Agricultural Statisitcs Survey: Upper Midwest Region – Iowa Field Office 2015 Iowa Crop Progress Review.

USDA-NASS, 2016. United States Department of Agriculture-National Agricultural Statistics Survey: Upper Midwest Region – Iowa Field Office 2016 Iowa Crop Progress Review.

Winfree, R., Aguilar, R., Vazquez, D.P., LeBuhn, G., Aizen, M.A., 2009. meta-analysis of bees' responses to anthropogenic disturbance. meta-analysis of bees' responses to anthropogenic disturbance 90, 2068–2076. https://doi.org/10.1890/08-1245.1.

Wojcik, V.A., Morandin, L.A., Davies Adams, L., Rourke, K.E., 2018. Floral resource competition between honey bees and wild bees: is there clear evidence and can we guide management and conservation? Environ. Entomol. 47, 822–833. https://doi.org/10.1093/ee/nvy077.

Zattara, E.E., Aizen, M.A., 2021. Worldwide occurrence records suggest a global decline in bee species richness. One Earth 4, 114–123. https://doi.org/10.1016/j.oneear.2020.12.005.

Zurbuchen, A., Landert, L., Klaiber, J., Müller, A., Hein, S., Dorn, S., 2010. Maximum foraging ranges in solitary bees: only few individuals have the capability to cover long foraging distances. Biol. Conserv. 143, 669–676. https://doi.org/10.1016/j.biocon.2009.12.003.