An ecological networks approach reveals restored native vegetation benefits wild bees in agroecosystems

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A B S T R A C T

Conservation of species that rely on mutualistic partners such as pollinators are often better studied using interaction networks and indicators of ecological functions. We used a novel systems-ecology approach using network analysis and bee morphological traits to investigate ecological structure and bee body condition in the context of a conservation practice known as prairie strips established within row-crop fields compared to un-restored field margins. We found the increased flower resources in prairie strips produced a network supporting higher bee abundance and a greater chance for bee-mediated plant pollination. Some, but not all, bee groups showed improved body condition at prairie strip sites with variation due to taxonomic group, foraging preferences, and body size. This study supports a growing body of literature on the utility of network analysis in more broadly assessing the effect of conservation practices on ecological communities.

1. Introduction

Poor nutrition and floral resource availability are leading causes of pollinator declines globally (Dicks et al., 2021; LeBuhn and Vargas Luna, 2021) especially in agricultural areas (Vasiliev and Greenwood, 2021). The highly farmed Midwestern US is a prime example; this landscape was extensively transformed from vast prairies to up 80 % farmland in some states over the course of the past two centuries (Smith, 1998). During that time, 15 % of Eastern US solitary bee species have declined (Bartomeus et al., 2013) and up to 50 % of Midwestern US bumble bee species are declining or locally extinct (Grixti et al., 2009). A major contributor to pollinator declines in these areas is lack of quality forage (Rowe et al., 2022; Dolezal et al., 2019; Kleijn et al., 2015). Practices that incorporate native vegetation patches into cropland have the potential to improve floral resources (Zhang et al., 2022; Schulte et al., 2017; Williams et al., 2015) and all levels of communities and ecosystems, from soil microbes (Brussaard et al., 2007) to higher trophic levels (Bardgett and Wardle, 2003; Corbet, 1997). However, it is not understood how such small patches of native vegetation improve ecosystem functions in the broader context of plant-pollinator interactions (Memtsas et al., 2022; Brittain et al., 2013).

Pollinators rely heavily on mutualistic partners and stand to benefit from a systems ecology approach to conservation (Borchardt et al., 2021). Research focused on interactions, such as network analysis, can provide deeper insights into how conservation can support communities of interacting species. In fact, host-plant interactions show resource availability and species use (Valido et al., 2019; Winfree et al., 2018), which precedes and often is indicative of future local species extinction (Valiente-Banuet et al., 2015). Measuring traits that are predictive of future species loss is even more important in the wake of global climate change, which can greatly affect mutualistic species (Rafferty and Ives, 2011; Tylianakis et al., 2008).

Specific structures of interaction networks are associated with ecosystem function and the ability to withstand environmental disturbances (Guimarães, 2020; Bascompte and Jordano, 2014). For example, "nested" networks show support for a diverse community of organisms through a core of interacting generalist species which can support specialized species that are connected to that core (Bascompte and Jordano, 2014). About 80 % of natural pollination networks show high nestedness (Bascompte et al., 2003) and therefore community persistence during environmental perturbations (Lever et al., 2014). In addition, network analysis can inform how generalist organisms are

behaving across the network. Generalists often specialize during a short time frame (Petanidou et al., 2008), potentially to decrease costs of switching between plant species (Goulson, 2000; Woodward and Laverty, 1992). However, pollinators may be forced to specialize when resources are limited due to lack of options (Lowe et al., 2022). Therefore, metrics such as "network-level specialization" can help us understand whether the floral community is sufficient to allow optimization of pollinator behavior. Finally, network analysis can relate to pollination success. For example, the "links per species" network metric (Dormann et al., 2009) can show if on average pollinators have few foraging options or plants have few chances for animal-mediated pollination services. By using community-wide data to analyze how interactions support species and pollination, we can better understand the quality of the ecosystem (Valiente-Banuet et al., 2015) and its ability to withstand disturbances (Guimarães, 2020; Bascompte and Jordano, 2014).

Despite their potential, interaction networks remain theoretical representations of ecological traits. Therefore, we paired network approaches with organismal body condition to show more direct effects of the habitat type on wild bee health. Organismal body condition can offer deeper insights relevant to conservation, such as how populations use or respond to their environment before they become locally extinct. For example, phenotypic condition is widely used in botanical and agricultural analyses of plant responses to stress (Sourour et al., 2017). In pollinators, wing traits can inform different aspects of body condition. First, wing area is lost as bees age (Mueller and Wolf-Mueller, 1993) and spend more time in flight, collide with vegetation, and forage (St. Clair et al., 2020; Foster and Cartar, 2011). Additionally, extreme loss of wing area can impede foraging activity (Higginson et al., 2011; Higginson and Barnard, 2004) and increase mortality risk (Dukas and Dukas, 2011). Second, fluctuating asymmetry is a common indicator of stress (Benítez et al., 2020) and poor nutrition during larval development (Szentgyörgyi et al., 2016; Beasley et al., 2013). Access to a greater diversity of native floral resources should enhance generalist wild bee nutrition by offering more options to provide an optimal mix of required nutrients (Parreño et al., 2022; Filipiak, 2018; Vaudo et al., 2015). Together, high wing wear and fluctuating wing vein asymmetry are predicted to negatively impact flight performance (Haas and Cartar, 2008).

In this study, we combined data on plant-bee networks and bee body condition to test the hypothesis that adding native vegetation to industrial row-crop production landscapes provides benefits to plant-bee community function and bee health (Table 1). We conducted a replicated, multi-site experiment to compare conventional farms with and without prairie strips in Iowa, one of the most highly farmed states in the US (Smith, 1998). Prairie strips are a recent federally subsidized conservation practice (CP-43, n.d.; USDA, 2018) gaining traction in the Midwestern US in which native species of grasses and forbs are planted on farm fields to increase soil retention and improve water quality while providing habitat for wild organisms. Crop fields with prairie strips are already known to have higher floral resources and pollinator abundance and richness (Murray, 2021; English, 2020; Kordbacheh et al., 2020; Schulte et al., 2017). However, our objectives are to determine if plant-bee networks show enhanced ecological functions on farms with prairie strips, and whether this is accompanied by improved body condition of multiple wild bee species, which remains unknown. This systems-ecology approach can provide a broader perspective on the conservation value of integrating native vegetation into large scale agriculture.

2. Materials and methods

2.1. Study area and study design

We used privately-owned row-crop fields in central Iowa, an agriculturally dominated Midwestern state in the US Corn Belt (Smith, 1998; Fig. 1). Iowa has a continental climate with cold winters (mean January temperature of −4.7 degrees Celsius), hot summers (mean July temperature of 25 degrees Celsius), and moderate annual precipitation (92.0 cm; US National Weather Service, 2000–2022). Study landscapes are topographically undulating and dominated by extensive agricultural production of corn (*Zea mays* [L.]) and soybean (*Glycine* max [(L.) Merr,]) grown in monocultures with typical practices of soil tillage, application of chemical fertilizers and pesticides, and winter fallow between crop years.

We surveyed wild bee communities in five prairie strips within row-crop fields ("Prairie Strips") and five grassy margins alongside roads or between row-crop fields ("Field Margins") (Fig. 1). We selected sites in pairs (one Prairie Strip with one Field Margin) based on same crop species (corn or soybean), similar management, and proximal location (Zhang et al., 2022) while also a minimum of 3.2 km apart to ensure bees were not foraging between sites, based on honey bee foraging range (Couvillon et al., 2014; Danner et al., 2014). Most crop fields in the Midwestern US have grassy field margins between farms or alongside roads, which functioned as the control in this study. We verified Field Margins sites were not documented to have areas purposefully planted with native grass and forb species, either through the USDA Conservation Reserve Program (CRP) or as roadside planting. However, the STO Field Margin site harbored species such as *Helianthus* spp. and *Oenothera* spp. (Murray, 2021), which usually occur only with restorative planting. Prairie Strips functioned as the restored treatment in this study; these are typically 1–5 strips that average around 6 m wide within fields, occupying approximately 10 % of the field area, and seeded with a mix of native grasses and forbs (CP-43, n.d., USDA, 2018). At the time of the study, prairie strips were a novel and uncommon conservation practice in the Midwestern US. All sites had apiaries of four honey bee colonies maintained as part of a companion study (Zhang et al., 2022). While honey bees can compete with wild bees for floral resources (Valido et al., 2019; Giannini et al., 2015), we chose to study farms with small apiaries (4 colonies) because honey bees are common non-native bee species present in working landscapes in this region.

2.2. Field collection

We surveyed the sites every other week from June 2019 to September 2019, a period of peak forb bloom (Murray, 2021). We intended to conduct bee surveys on days with ideal weather for sampling pollinators (*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 these sampling criteria due to too few ideal weather days in this region. Linear models for *Wild Bee Abundance* and *Richness* included average temperature, average wind speeds, and collection month as covariates to account for weather variation.

During bee surveys, we net-collected all bees observed touching the reproductive region of a flower (indicating potential for pollination) for a total of 10 observational minutes walking through the vegetation at a constant pace (Williams et al., 2015). Sites had different distributions of

Table 1

Predicted trends and overall results for the network metrics (Links per Bee Species, Links per Plant Species, Network-Level Specialization, and Weighted Nestedness) and body condition metrics (Wing Area and Wing Vein Asymmetry). Hypothesis and trends are shown for Prairie Strips ("PS"). Possible trends in Wing Area and Wing Vein Asymmetry are considered in the discussion.

| Metric	Hypothesis	Findings
Links per Bee Species	Higher in PS	No difference
Links per Plant Species	Higher in PS	Higher in PS
Network-Level Specialization	Higher in PS	No difference
Weighted Nestedness	Higher in PS	No difference
Wing Area	Higher in PS	Higher in PS (3 genera)
		No difference (2 genera)
		Lower in PS (1 genus)
Wing Vein Asymmetry	Lower in PS	Lower in PS (3 genera)
		No difference (2 genera)
		Higher in PS (1 genus)
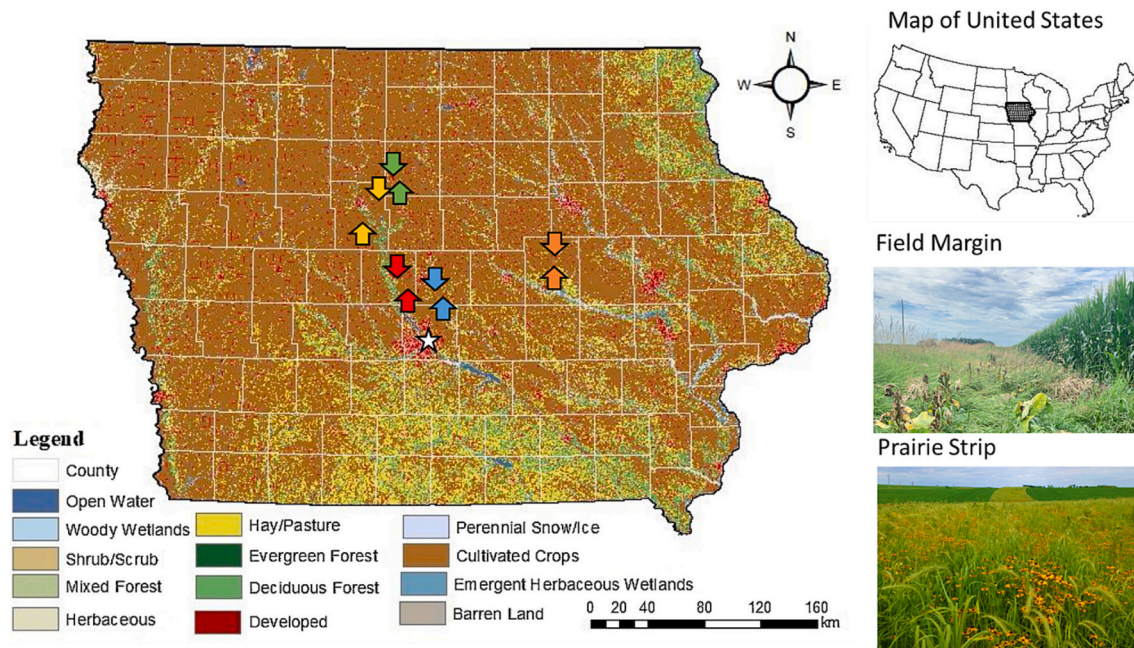
Fig. 1. Commercial farm fields served as study sites in central Iowa, a state in the US Midwest (map, top right). We paired sites with and without prairie strips based on sharing the same crop species, similar crop management, and proximal location while being a minimum of 3.2 km away from any other site to reduce bees foraging in multiple study locations. Prairie strips are on average 6 m wide and typically occupy about 10 % of the total field area, but sizes and shapes of strips vary by site. For sites without Prairie Strips, we surveyed Field Margins without known native species plantings (see images on right). The tip of each arrow indicates the sites and are colored according to their pairs. Site pairs from top to bottom of Iowa map: SMI (green, top center), SME (yellow, top left), STO (orange, farthest right), WOR (red, middle left), GUT (blue, middle right), and capital city of Des Moines, Iowa (star, bottom). Upadhaya et al. (2021) created the landscape map above using National Land Coverage Data (Dewitz, 2019). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

vegetation and terrain, therefore transects were not defined by a specific length or width but rather total time spent observing floral visitors. We stored collected bees in individual vials to prevent further pollen contamination following net-collection. Specimen processing and recording data did not count toward observation time. When few floral resources were present, we collected additional bees observed in flight to boost sample sizes for pollen interactions and bee body condition analysis, but these specimens were not included as observational data. "Observed interactions" were the plant species each collected specimen was observed visiting in the field. We recorded all missed bees by visual groupings for *Wild Bee Abundance* analysis, however visual identification was not reliable enough for species-level use in network or *Wild Bee Richness* analyses. Honey bees and queen bumble bees were caught, identified to species, and released. We also recorded all plants observed in bloom at each site to include in the network analysis.

We used a local database of plant species found both at the sites used as well as similar locations in the region to identify plants in the field (Murray, 2021; English, 2020). We also identified plant interactions *via* pollen grain microscopy using a local pollen library (Zhang et al., 2020). Since we used both field and pollen identification, some plant species were grouped at a higher taxonomic level if species identification was difficult using either method, such as *Melilotus* sp. or Asteraceae. We used DiscoverLife bee species guide (Ascher and Pickering, 2020) to identify collected bee specimens and verified the identifications with collections from the Iowa State University Entomological Museum. Only three genera were not identified to species: *Florilegus, Lasioglossum*, and one *Nomada* morph. While some studies have identified these genera to physically-similar morpho-species (St. Clair et al., 2020), we opted not to for this study due to issues such as inaccurately separating males and females from the same species into separate morpho-species, thereby artificially increasing species richness. Species richness is known to influence network analysis (Blüthgen et al., 2006; Fründ et al., 2016), therefore we did not want to inflate our species richness unnecessarily.

Further support for grouping by genera is that closely related species often have similar ecological roles (Cirtwill et al., 2020; Carvalheiro et al., 2014), which is preferable for our analysis of ecological functions.

We analyzed *Wild Bee Abundance* and *Richness* using a linear model to account for weather variables due to the difficulty of collecting specimens during good pollinator weather. The generalized linear model with a Poisson error distribution included average temperature and wind speeds, along with month, to account for weather outside of ideal pollinator climate (*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).

2.3. Pollen analysis

We collected pollen from each individual bee specimen using a modified version of MacGillivray's (1987) method (Tavares et al., 2015). Bee specimens placed in 80 % ethanol solution were vortexed to suspend pollen in the solution. We removed the bee specimens and added basic fuchsin dye to the solution and centrifuged the vial to embed the pollen in a solid gelatin-glycerol drop at the bottom of the centrifuge tube. We then decanted the supernatant and plated the gelatin-glycerol drop on a microscope slide using heat. We identified and counted at least 400 pollen grains along transects focused on the densest area of pollen or 15 transects of the densest region if few grains were present for each pollen slide. This is a higher threshold than other studies counting 100 to 200 pollen grains per specimen (Fisogni et al., 2018; Bosch et al., 2009). We visually identified pollen grains to species or morpho-group. Plant groups with >20 pollen grains were considered an additional interaction ("pollen interaction") if it was not the plant the specimen was collected on ("observed interaction"). This is comparable to other studies using 5 % (Fisogni et al., 2018) and 10 % (Bosch et al., 2009) of the total pollen grains measured as the cutoff minimums for pollen interactions. We cross-checked pollen interactions with the

bloom period of the plant species or recorded presence of the plant species at a particular site, and the date the specimen was collected.

2.4. Network analysis

We created network models using all collected bee species and recorded plant species as well as all observed and pollen interactions for all collected specimens across the entire season. All plant species observed in bloom at a site were included in the network even without any interactions with bee species. All bees had at least one interaction due to our collection methods. We analyzed networks using the 'bipartite' package (Dormann et al., 2009) in R (R Core Team, 2019) and calculated network metrics using the 'networklevel' function. We chose three network metrics to analyze which are more robust to differences in species richness between networks (Fründ et al., 2016; Blüthgen et al., 2006): *Links per Species, Network-Level Specialization (H_2')*, and *Weighted Nestedness (NODF)*.

Links per Species is the average number of interacting partners or links for all plant and bee species in the network. In plants, a mean value below one indicates some plants have no interacting partner (bee), and therefore a lower chance for bee-mediated pollination. In bees, the ecological interpretation behind *Links per Species* is more complicated due to a non-linear relationship dependent on resource availability. In low- or high-resource environments, bees specialize, however in moderate-resource environments they may forage more generally (Lowe et al., 2022; Memtsas et al., 2022). Therefore, *Links per Bee Species* may need to be considered with *Network-Level Specialization*, which calculates the deviation of the realized and expected number of links based on the number of interaction observations for each species. For *Network-Level Specialization*, a value of 0 indicates no specialization and a value of 1 indicates perfect specialization. Due to different interpretations, we analyzed *Links per Species* separately for plants and bees to facilitate ecological interpretation.

Weighted Nestedness (NODF) is a binary calculation of nestedness. To calculate *Weighted Nestedness*, each column in the plant-bee interaction matrix, representing a single bee species, is sorted by number of filled cells and marginal total of species interactions or "links" it had with the rows representing the plant species observed in bloom at a given site. Each column is then compared to all other columns with fewer links to determine the pairwise overlap measured as the percentage of links observed in both columns.

We used multiple statistical methods to determine if there are differences in the plant-bee interaction matrices between Field Margin and Prairie Strip sites and drew conclusions from the overall trends and significance. First, we analyzed the metrics without modification ("raw networks"). Second, we used randomized null models to verify if network metrics were likely from deliberate ecological structure. Null models ($n = 1000$) were created based on marginal totals of rows and columns (Pellissier et al., 2018) using the "mgen" function in the 'bipartite' package (Dormann et al., 2009). If the raw network metrics were similar to the null model metrics, then we concluded the metric value was produced by random assortment and does not have ecological meaning. Third, we created subsets of the network ($n = 1000$) so that all networks had the same number of plant and bee species to remove the influence of species richness ("rarified networks"; Pellissier et al., 2018). We intended to subsample all networks to match the size of the smallest network. The smallest network was too small to obtain sufficient variation in the network metrics (SMI Field Margin, bee species $= 5$, plant species $= 16$), so we subsampled all other networks to the size of the next smallest network (SME Field Margin, bee species $= 11$, plant species $= 16$) and left the smallest network unchanged. We used the non-parametric Mann-Whitney *U* test to describe the significance of differences in the network metrics between Field Margin and Prairie Strip sites.

2.5. Bee body condition

We analyzed external morphological traits in species with at least 5 specimens collected from each habitat type. We then grouped them by genus to further increase sample size, creating 6 bee genera comprised of 12 species total (Table S1). We imaged both forewings from each specimen using a Leica dissection microscope and collected morphometric data using tpsDIG (Rohlf, 2018). We excluded wings accidentally damaged during preparation ($\sim$0.5 % of total sample).

Body size is used to measure larval nutrition and therefore is lower in environments with scarce food or rampant disease (Baron et al., 2014; Burkle and Irwin, 2009; Roulston and Cane, 2000; Grab et al., 2019). We estimated individual size using *Wing Width* (from point A to B in Fig. 2), which can correlate to other size metrics such as intertegular distance and dry mass (Bullock, 1999) but this correlation can vary by environment (Peters et al., 2016). Therefore, a wing-based size measurement is more accurate at accounting for size when analyzing wing condition metrics. Linear models for *Wing Area* and *Wing Vein Asymmetry* included *Wing Width* as a covariate.

Wing Area is correlated with foraging effort, meaning *Wing Area* tends to be greater in environments with abundant, nearby food resources allowing bees to fly shorter distances (St. Clair et al., 2020; Nooten and Rehan, 2019; O'Neill et al., 2015). We measured apical wing area from a set point (Fig. 2; Foster and Cartar, 2011) and standardized the value by calculating the number of standard deviations the individual measurement was from the mean of the species and sex, to allow for easy comparison between species of different sizes and variation. We used caste instead of sex for social *Bombus* species. We then analyzed standardized wing area using a linear model to account for potentially confounding factors such as individual size, sex, and relative age within a bee genus (Mueller and Wolf-Mueller, 1993). We calculated relative age based on the number of days after the first observation of a given bee species. We also tested linear models including either site pair or measurement error as a random effect, but they did not produce a better fit
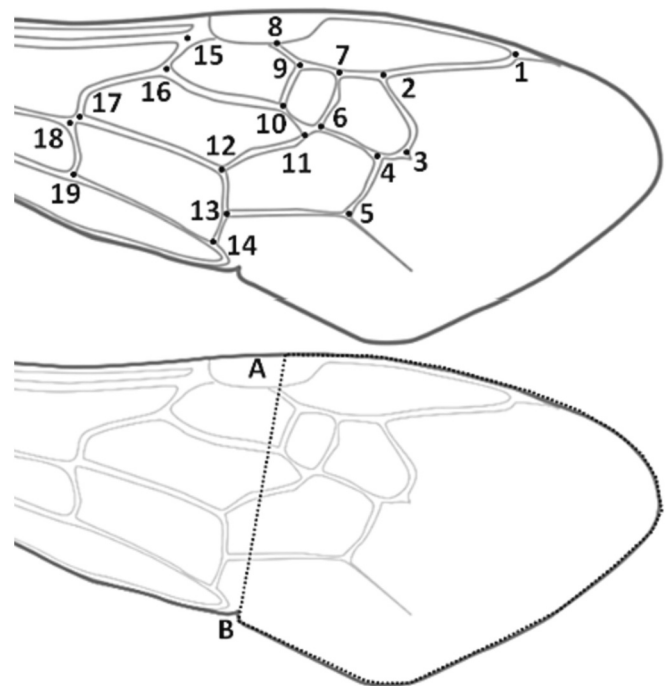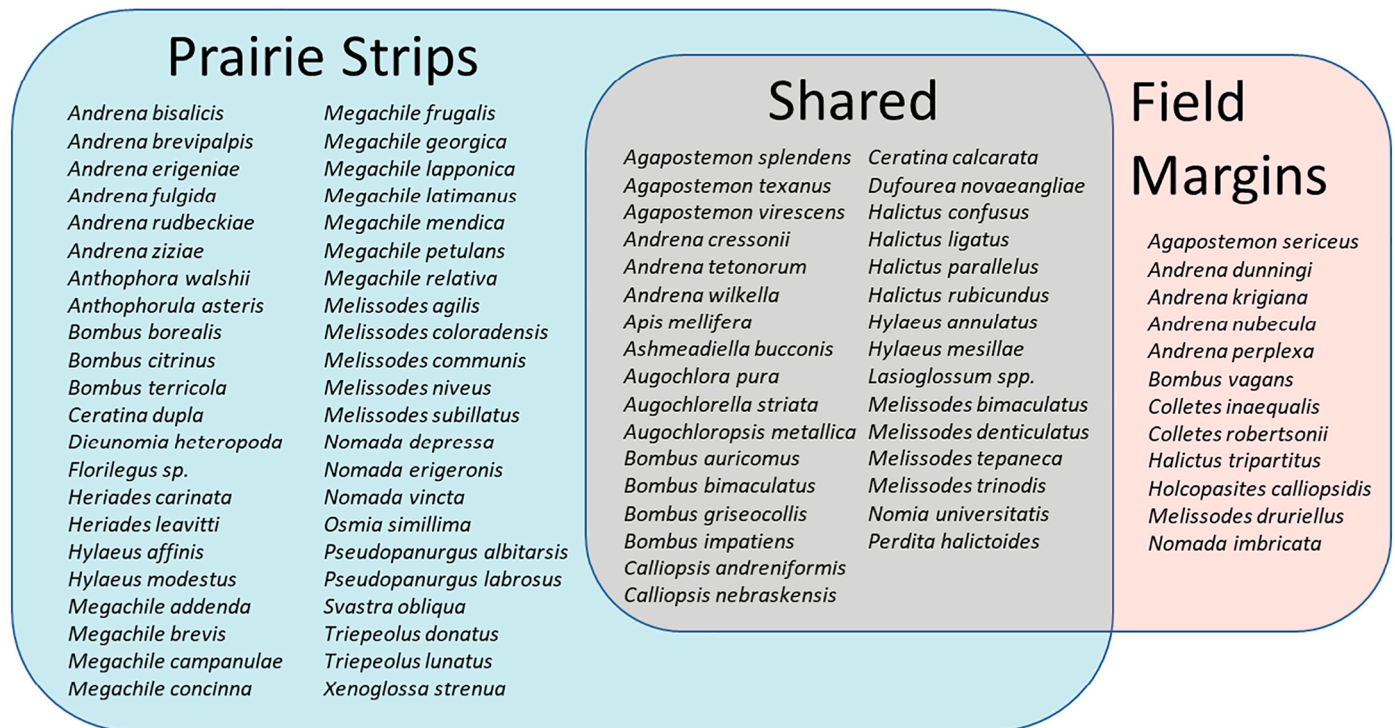

Fig. 2. We analyzed 19 landmarks to measure fluctuating Wing Vein Asymmetry (top; Szentgyörgyi et al., 2016) and measured the apex Wing Area right of the cropped line connecting the base of the marginal cell (A) to the wing indentation (B) (bottom; Foster and Cartar, 2011). The line from A to B measured Wing Width, a proxy for bee size.

(change in AIC or BIC > 10 points; Table S8). For *Augochlorella* sp., the model did not include sex because we didn't collect any males. We verified models showed a normal distribution both visually with a Q-Q plot and using an Anderson-Darling normality test. Two models reported a significant difference from a normal distribution, however visually appeared normally distributed. One possibility is that there is some environmental factor we did not account for, however the sample sizes were sufficient for non-normality to not cause major issues with the analysis (*Lasioglossum* spp., *n* = 84; *Nomia* sp., *n* = 52; Ghasemi and Zahediasl, 2012).

a) Bee Species

Prairie Strips

Andrena bisalicis
Andrena brevipalpis
Andrena erigeniae
Andrena fulgida
Andrena rudbeckiae
Andrena ziziae
Anthophora walshii
Anthophorula asteris
Bombus borealis
Bombus citrinus
Bombus terricola
Ceratina dupla
Dieunomia heteropoda
Florilegus sp.
Heriades carinata
Heriades leavitti
Hylaeus affinis
Hylaeus modestus
Megachile addenda
Megachile brevis
Megachile campanulae
Megachile concinna

Megachile frugalis
Megachile georgica
Megachile lapponica
Megachile latimanus
Megachile mendica
Megachile petulans
Megachile relativa
Melissodes agilis
Melissodes coloradensis
Melissodes communis
Melissodes niveus
Melissodes subillatus
Nomada depressa
Nomada erigeronis
Nomada vincta
Osmia simillima
Pseudopanurgus albitarsis
Pseudopanurgus labrosus
Svastra obliqua
Triepeolus donatus
Triepeolus lunatus
Xenoglossa strenua

Shared

Agapostemon splendens
Agapostemon texanus
Agapostemon virescens
Andrena cressonii
Andrena tetonorum
Andrena wilkella
Apis mellifera
Ashmeadiella bucconis
Augochlora pura
Augochlorella striata
Augochloropsis metallica
Bombus auricomus
Bombus bimaculatus
Bombus griseocollis
Bombus impatiens
Calliopsis andreniformis
Calliopsis nebraskensis

Ceratina calcarata
Dufourea novaeangliae
Halictus confusus
Halictus ligatus
Halictus parallelus
Halictus rubicundus
Hylaeus annulatus
Hylaeus mesillae
Lasioglossum spp.
Melissodes bimaculatus
Melissodes denticulatus
Melissodes tepaneca
Melissodes trinodis
Nomia universitatis
Perdita halictoides

Field Margins

Agapostemon sericeus
Andrena dunningi
Andrena krigiana
Andrena nubecula
Andrena perplexa
Bombus vagans
Colletes inaequalis
Colletes robertsonii
Halictus tripartitus
Holcopasites calliopsidis
Melissodes druriellus
Nomada imbricata

b) Plant Species

Prairie Strips

Asclepias incarnata
Asclepias syriaca
Asclepias tuberosa
Astragalus canadensis
Chamaecrista fasciculata
Convolvulus spp.
Desmodium canadense
Drymocallis arguta
Echinacea spp.
Eryngium yuccifolium
Euphorbia spp.
Gentiana alba
Lespedeza capitata
Parthenium integrifolium
Pycnanthemum tenuifolium
Silphium spp.
Tradescantia ohiensis
Trifolium hybridum

Shared

Amaranthus spp.
Ambrosia spp.
Cirsium spp.
Cirsium arvense
Dalea purpurea
Daucus carota
Erigeron spp.
Glycine max
Helianthus decapetalus
Helianthus grosseserratus
Heliopsis helianthoides
Lepidium campestre
Medicago sativa
Melilotus spp.

Monarda fistulosa
Pastinaca sativa
Ratibida pinnata
Rudbeckia spp.
Silphium spp.
Solanum spp.
Solidago spp.
Symphyotrichum spp.
Taraxacum officinale
Trifolium pratense
Trifolium repens
Verbena spp.
Zizia aurea

Field Margins

Anemone canadensis
Cannabis sativa
Cichorium intybus
Conyza canadensis
Iris sp.
Lactuca serriola
Leonurus cardiaca
Medicago lupulina
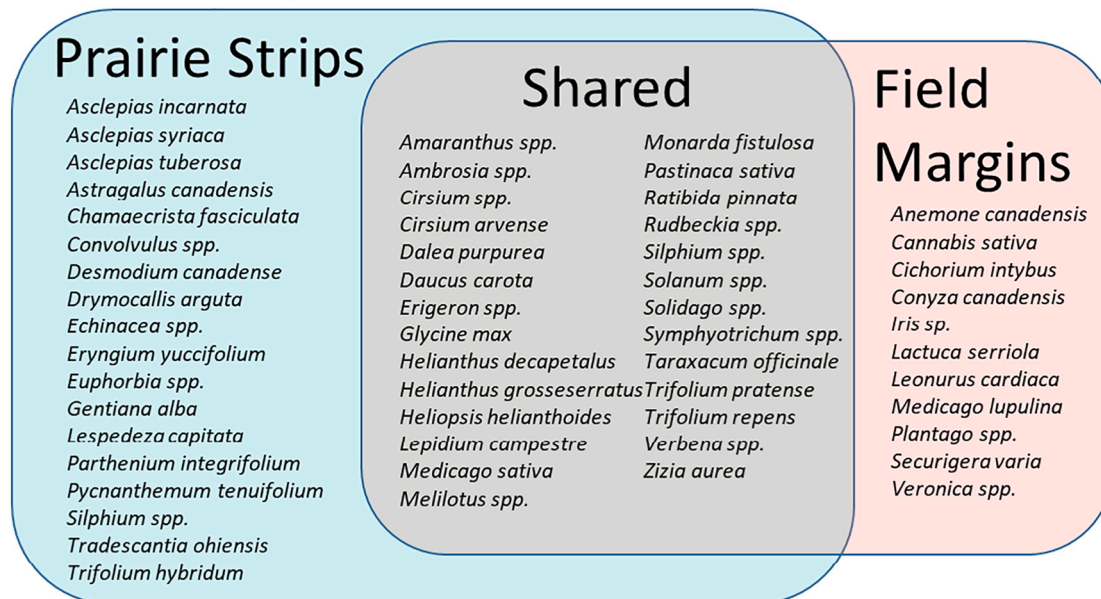Plantago spp.
Securigera varia
Veronica spp.

Fig. 3. Venn diagrams showing bee (top) and plant (bottom) species found only in Prairie Strips (left, blue), Field Margins (right, pink), or both vegetation types ("Shared"; middle purple). Plant species identified to family were excluded (Brassicaceae spp., Shared; Poaceae spp., Field Margins; Rubiales spp., Field Margins) and one bee species identified as a morph was excluded (Nomada sp. keb1). All plant groups found in the habitats are reported in Table S3. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Fluctuating asymmetry in wing veins can show stress during bee larval development, leading to higher fluctuating asymmetry when larvae are provided poor nutrition or are under poor environmental conditions (Vanderplanck et al., 2021; Banaszak-Cibicka et al., 2018; Szentgyörgyi et al., 2016; Nunes et al., 2015; Silva et al., 2009). We analyzed *Wing Vein Asymmetry* using nineteen landmarks for each wing, since all species analyzed had three submarginal cells (Szentgyörgyi et al., 2016). We conducted a generalized Procrustes analysis using least-squares to create an average wing configuration from which deviation of

individuals from that average shape can be calculated using the package 'geomorph' (Adams et al., 2013) in R (R Core Team, 2019; Fig. 2). If extreme wing loss or unintended folding of the wings when mounting on the slide caused landmarks to be missing or in incorrect locations, these wings were omitted from the analysis (about 1 % of samples). We analyzed *Wing Vein Asymmetry* using a linear model to account for differences in individual body size. We checked the data for outliers which were resampled and left in the analysis or omitted if there was cause for omission. We checked for normality using Q-Q plots.

Fig. 4. Cumulative network graphs by habitat type. Bee species are on the top and plant species are on the bottom, both coded with the first three letters of the genus and the first three letters of the species (see Tables S2 & S3 for decoding). Interactions are shown by the connecting lines (red or blue, outlined in black) with the relative width indicating the number of interactions relative to that specific network graph. Individual networks by site and habitat type are in the supplement (Fig. S1). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

3. Results

We observed a total of 88 bee taxa (86 to species, 2 to genera; Table S2) of which 36 % (32 species) were found in both habitat types, 50 % (4 species) were found only in Prairie Strips, and 14 % (12 species) were found only in Field Margins (Fig. 3). We observed 58 plant groups (38 to species, 18 to genera, 2 to family; Table S3) of which 48 % (28 groups) were found in both habitat types, 31 % (18 groups) were found only in Prairie Strips, and 21 % (12 groups) were found only in Field Margins (Fig. 3). There was no significant difference in *Wild Bee Abundance* (Table S4: linear model; estimate = 0.066 ± 0.088, t-value = 0.751, p-value = 0.453) and *Wild Bee Richness* (linear model; estimate = 0.812 ± 0.551, t-value = 1.475, p-value = 0.145) between the habitat types.

We analyzed a total of 1666 plant-bee interactions: 605 observed native bee interactions, 244 observed honey bee interactions, and 817 additional native bee pollen interactions (Table S5). Networks from Prairie Strips were visually more complex than those from Field Margins; Fig. 4 provides summary networks (for all sites within a treatment combined) that show these apparent differences. Network structures also differed statistically in several metrics, as revealed by different statistical methods, all demonstrating similar trends (Table 2). Despite the low number of sample sites, the raw network analysis revealed that Prairie Strips feature significantly more *Links per Plant Species* and *Network-Level Specialization* but showed mixed results for *Links per Bee Species* and *Weighted Nestedness* (Fig. 5). Interestingly, Field Margins had more variation in the network metrics between sites than Prairie Strip sites, suggesting species richness could be influencing the smaller Field Margin networks. The rarefied network analysis found significant differences in all network metrics; however, multiple subsampling of the networks led to a larger sample size in the significance test (n = 10,000), likely inflating *p*-values (Greenland, 2019; Cain and Zhang, 2019; Fig. 5). Rarefaction analysis is also sensitive to the number of interactions included in the subsampled network (Fig. S3) in a similar way that network metrics are sensitive to species richness between networks (Fründ et al., 2016; Blüthgen et al., 2006). However, rarefying networks to the same size is still recommended for comparing networks of different species richness (Pellissier et al., 2018). The rarefaction analysis provided further support for our raw network metric analysis; similar trends were observed with rarefaction and raw networks for *Links per Plant Species* and *Network-Level Specialization*. While *Weighted Nestedness* was higher in Prairie Strips than Field Margins in the rarefied networks, we still conclude there is no difference between the habitat types because there is no significant difference in the raw networks. For *Network-Level Specialization*, however, we found no significant difference when comparing *Network-Level Specialization* to randomly assorted null

Table 2

A summary of test results comparing Field Margins and Prairie Strips (PS) for each network metric. Due to subsampling and a high number of datapoints, all statistical tests of the rarefied networks were significant when using the usual $p < 0.05$ threshold. Raw network significance is reinforced when raw and rarified networks share similar directional trends. Null model analysis indicates whether the network shows a biologically meaningful result (significant difference) by comparing metric values of the raw network to randomized networks. Null model analysis is reported as the individual tests for each site studied (ten sites total), where each test compared a raw network to 1000 randomized null models created from the raw network (Fig. S2).

Network metric	Raw networks	Rarefied networks	Null models
Links per Bee Species	PS trends higher	PS lower	10 of 10 significant
Links per Plant Species	PS higher	PS higher	10 of 10 significant
Network-Level Specialization	Similar	PS higher	7 of 10 significant
Weighted Nestedness	Similar	PS higher	9 of 10 significant

models (Fig. S2: $p > 0.05$). We conclude that *Network-Level Specialization* did not show a true biological difference between the habitat types, and simply reflected an effect of random interaction assortment.

Most genera showed no difference in *Wing Width* (our size proxy) between the habitat types, except for *Halictus* spp. (two-sided *t*-test, $t = 2.741$, df = 14.9, $p = 0.0153$), mostly driven by a significant difference in *Halictus ligatus* which were larger in Prairie Strips compared to Field Margins (two-side t-test, $t = 2.505$, df = 10.6, $p = 0.0300$; Table S6). Linear model analysis for each of the six bee genera showed significant effects of habitat type on *Wing Area* in *Halictidae* genera, but not the *Apidae* genera (Table S7). Comparing the estimate effect of habitat type as a percentage of the range of measured *Wing Area*, *Halictus* spp. showed the largest increase in *Wing Area* when found in Prairie Strips (habitat type effect Prairie Strips = 0.17 ± 0.06, *Wing Area* range = 1.71–2.91 mm², percent area gain = 3.8 % - 13.5 %), followed by *Augochlorella* sp. (habitat type effect (Prairie Strips) = 0.13 ± 0.03, *Wing Area* range = 1.6–2.24 mm², percent area gain 4.5 % - 10 %) and *Lasioglossum* spp. (habitat type effect (Prairie Strips) = 0.05 ± 0.01, *Wing Area* range = 1.17–1.9 mm², percent area gain = 2.1 % - 5.1 %). However, *Nomia* sp. showed the opposite effect with more *Wing Area* in Field Margins than Prairie Strips (habitat type effect (Prairie Strips) = −0.74 ± 0.16, *Wing Area* range = 2.06–4.08 mm², percent area lost = 14.2 % - 43.7 %). In addition, *Halictus*, *Augochlorella* and *Lasioglossum* genera all had a significant interaction between sex and habitat type (Table S7).

Wing Vein Asymmetry differences between the habitat types appeared to be related to *Wing Width* (Table 3), a size proxy measurement from wing landmarks (Table S1). The three largest bee genera showed higher fluctuating asymmetry in Field Margins (*Bombus* spp., *Melissodes* spp., and *Nomia* sp.) while the next two large-bodied bee genera showed no significant difference (*Augochlorella* sp. and *Halictus* spp.) and the smallest-bodied bee genus (*Lasioglossum spp.*) showed the opposite trend: higher fluctuating asymmetry in Prairie Strips.

4. Discussion

Network analysis allows researchers to mathematically investigate ecosystems holistically to understand them as interconnected and complex communities. Using this method, we found ecological effects of integrating native vegetation into agricultural landscapes, using the prairie strips practice (CP43, USDA).

We hypothesized that adding native vegetation to industrial row-crop production landscapes would provide benefits to plant-bee community function and bee body condition. Using multiple statistical approaches, we found a consistent trend toward improved network functioning in Prairie Strips compared to Field Margins.

According to our interaction network analysis, *Links per Plant Species* was consistently higher at Prairie Strips compared to Field Margins, suggesting increased chance for animal-mediated plant pollination which may support organisms in higher tropic levels (Bardgett and Wardle, 2003; Corbet, 1997). In addition, there was some evidence for increased *Weighted Nestedness*, suggesting the possibility of increased ecological support for specialist species (Bascompte et al., 2003). We found less support for differences among *Links per Bee Species* and *Network-Level Specialization*. Since generalist bees can be seen as flexible foragers (Petanidou et al., 2008), we predicted they may specialize slightly more over a single season in Prairie Strips to optimize foraging (Goulson, 2000; Woodward and Laverty, 1992), but our data did not support this. It is possible that the prairie strip program may benefit from additional native vegetation to allow generalists to specialize more, however part of the appeal of this habitat program is improvement of some ecological functions while converting only part of the working field to conservation land (Schulte et al., 2017). We also note that our network-based analyses were able to uncover differences that may not have been detectable using traditional community metrics only. Although *Wild Bee Abundance* was significantly higher in Prairie Strips
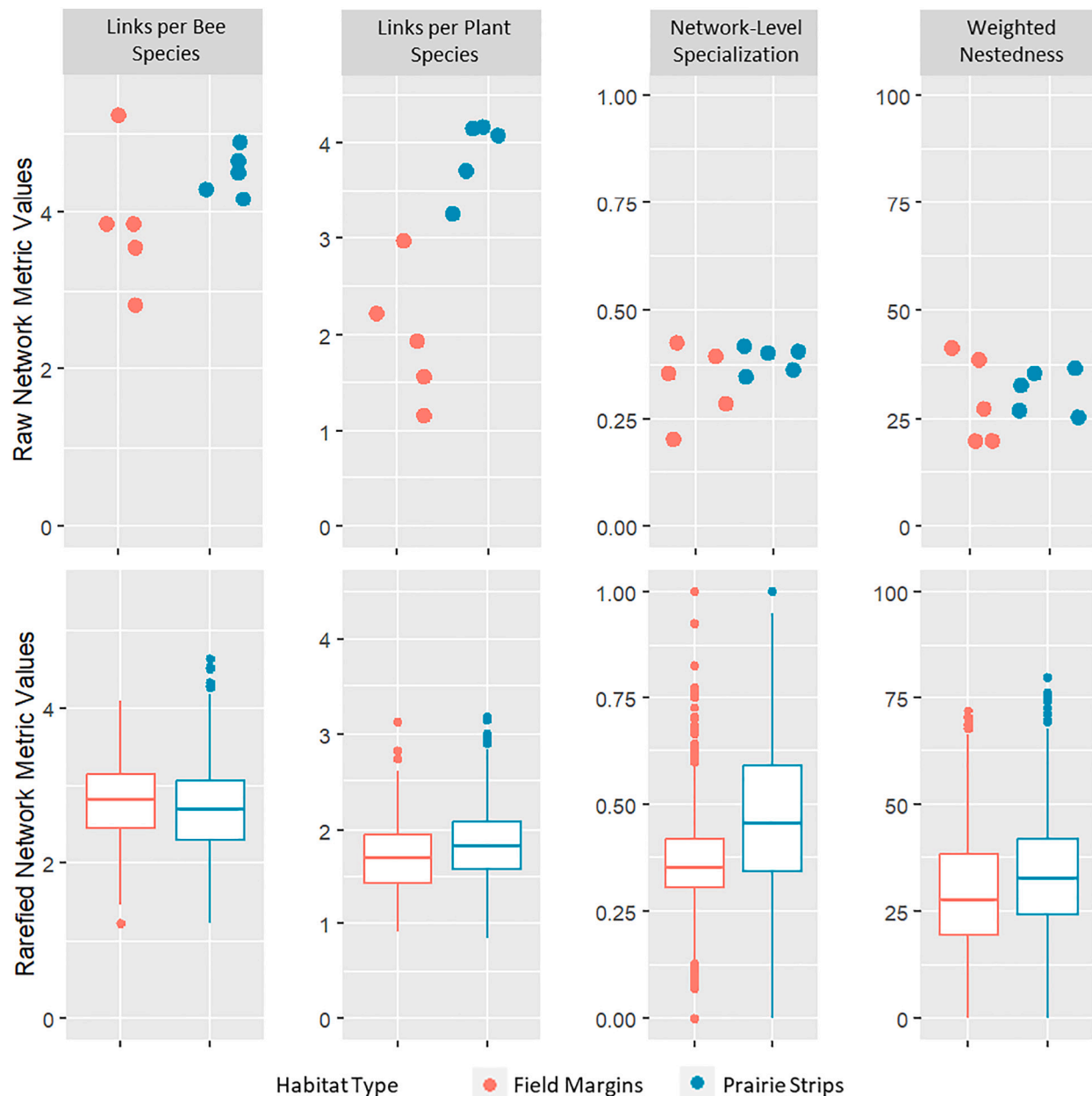
Fig. 5. Network metrics from the raw (top) and rarefied (bottom) networks. Raw networks are not standardized for different species richness between sites, which can affect metric values. Rarefied networks are subsampled 1000 times to maintain equal species richness across sites for better comparison. The middle line inside the box shows the median value, the upper and lower limits of the box showing the 75th and 25th quartiles respectively, and the whiskers extending up and down from the box range from the 75th and 25th quartile plus or minus 1.5 * Interquartile Range respectively. Points outside of the box and whiskers are plotted individually as outliers.

compared to Field Margins, *Wild Bee Richness* showed no difference. Neither *Wild Bee Abundance* and *Wild Bee Richness* were different between Prairie Strips and Field Margins, contradicting the beneficial community structure benefits we found with the network metrics. This underlines the value of network approaches as more sensitive species interaction metrics (Valido et al., 2019; Brosi et al., 2017; Valiente-Banuet et al., 2015).

In terms of bee body condition, we found some species and size classes of bees responded positively to prairie strips. Specifically, *Halictus* spp., *Lasioglossum* spp., and the *Augochlorella* sp. showed higher wing area in Prairie Strips; however, some genera showed no difference and *Nomia* sp. showed the opposite trend. Although the latter is contrary to our hypothesis, *Nomia* sp. mostly visits a non-native plant species, *Melilotus* spp., therefore increased native vegetation may not alter its

behavior. In addition, wing area is tightly linked with age (Mueller and Wolf-Mueller, 1993), and this may explain why the social *Bombus* spp. showed no effect. Since *Bombus* spp. workers are born continuously through the season, and a mixture of younger bees with more intact wings alongside older bees with more age-related wing wear might confound our results.

We also expected that environments with more floral resources would produce adult bees with lower fluctuating asymmetry. Prairie Strips were indeed associated with lower fluctuating asymmetry in the three largest-bodied genera (*Bombus* spp., *Melissodes* spp., *Nomia* sp.). However, there was no difference in the medium-bodied genera (*Halictus* spp., *Augochlorella* sp.), and the opposite effect in the smallest-bodied genus (*Lasioglossum* spp.) (Table 3). Larger bee species may need more resources for each larva, therefore nutritional stress may be

Table 3

We calculated the Procrustes variance using the formula Wing_Landmarks ~Wing Width + Species + Habitat_Type. Mann-Whitney *U* tests calculated the *p*-values reported from the Procrustes variances. Procrustes variances with significant p-values (* < 0.05, ** < 0.01, *** < 0.001) are bolded showing the value indicating the higher fluctuating asymmetry.

		Procrustes variance			
Bee group	Family	Field margins	Prairie strips	Difference PS-FM	P-value
Melissodes spp.	Apidae	**0.00375**	0.00127	$-2.47 * 10^{-3}$	0.001**
Bombus spp.	Apidae	**0.00136**	0.00106	$-3.08 * 10^{-4}$	0.001*
Nomia sp.	Halictidae	**0.00102**	0.00084	$-1.81 * 10^{-4}$	0.034*
Augochlorella sp.	Halictidae	0.00089	0.00108	$1.93 * 10^{-4}$	0.512
Halictus spp.	Halictidae	0.00095	0.00071	$-2.44 * 10^{-4}$	0.188
Lasioglossum spp.	Halictidae	0.00089	**0.00152**	$6.32 * 10^{-4}$	0.001**
Cumulative	*Na*	*0.01022*	*0.01030*	*$8.83 * 10^{-5}$*	*0.746*

more pronounced under resource limitation. Interestingly, we collected smaller-bodied species more often in Field Margins than larger-bodied bee species, especially when social bee species were removed (Fig. S4); however, there was little significant difference within a genus (5 of 6 genera tested show no difference; Table S6). Our results suggest not all bee species benefit equally from native vegetation enhancements; potential differences in the habitat needs of solitary *versus* social and smaller *versus* larger species requires further research. In addition, all the species chosen for body condition analysis are considered prevalent in agricultural environments (Kleijn et al., 2015), therefore more research is needed on rarer species, though this may be challenging due to their low abundance.

Our results do not support our overarching hypothesis in all instances, namely with regards to the traditional community metrics. Both *Wild Bee Abundance* and *Wild Bee Richness* were not significantly different between the habitat types although previous studies did find a significant difference in these metrics between Prairie Strips and Field Margins (Murray, 2021; Schulte et al., 2017). One possibility for these contradicting results could be different criteria for identifying the collected pollinators. For example, Murray (2021) surveyed only wild bees and identified *Lasioglossum* spp. to morpho-species, which increased the number of species but may not represent related taxonomic groups of similar ecological presence especially because males and females of the same species are often separated into different morpho-species. Schulte et al. (2017) surveyed all pollinator groups and identified them at least to family, and to species if able. It is possible we would've found a significant difference using morpho-species for *Lasioglossum* spp., however this would not necessarily mean there was a difference in richness of true bee species.

One concern with empirical network studies is low numbers of observed interactions. We used a similar sampling effort (70 total observation minutes per site) to previously published research (80 total observational minutes per plot; Brosi et al., 2017). However, we observed fewer interactions than other network studies (Valido et al., 2019; Brosi et al., 2017; Kaiser-Bunbury et al., 2017), but nearly doubled our total interactions by adding pollen interactions (Fisogni et al., 2018). Overall, our total interactions were still lower than comparable studies, and possibly due to biological depauperation of this highly agricultural environment compared to more natural, less disturbed environments used in some of the cited studies (Valido et al., 2019; Brosi et al., 2017). Therefore, we overcame these limitations in our analysis *via* multiple tests– analyzing raw metrics, null models, and rarefied networks allows us to consider confounding effects of random assortment, species richness differences, and drawing our conclusions from trends across multiple tests (Table 2). Importantly, investigating random assortment through null models led us to reject the finding for one of our metrics (network specialization). Random assortment or opportunistic attachment has been found in other small-scale agricultural restorations (Ponisio et al., 2017). Using this in-depth, redundant, and conservative statistical approach, we were still able to detect significant effects of native vegetation on plant-bee interactions, ecological functions, and bee body condition.

Our overall results support the idea that merging conservation with agriculture through prairie strips is correlated with network structures found in robust environments as well as improved native bee body condition in certain species. This study adds to an existing body of literature pointing to the benefits of network analysis of conservation habitat to detect differences in communities not identified with traditional ecological metrics (Borchardt et al., 2021; Valido et al., 2019; Kaiser-Bunbury et al., 2017; Giannini et al., 2015; Kaiser-Bunbury and Blüthgen, 2015; Valiente-Banuet et al., 2015). We suggest that in the future, it would be useful to create a standardized protocol for conservation habitat assessments, which includes using network approaches (as in this study) along with additional methods such as pan-traps or comparing with historical population data, if available for the studied environment. Given the precipitous loss of biodiversity and further threat of climate change, it is crucial that we use effective analytical methods in conservation to better sustain species, populations, and environments from further decline.

Statement on inclusion

Our study brings together authors from different disciplines from all from the country the study was conducted in. We shared research often with stakeholders and other researchers studying the conservation program CP43 (prairie strips). Whenever relevant, we cited research conducted in the region the study was conducted in, as well as studies from international scientists using our novel method.

CRediT authorship contribution statement

Kate E. Borchardt: Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing, Visualization, Project administration. **Claus Kadelka:** Formal analysis, Software, Writing – review & editing, Visualization. **Lisa A. Schulte:** Methodology, Validation, Writing – review & editing, Funding acquisition. **Amy L. Toth:** Conceptualization, Methodology, Validation, Resources, Writing – original draft, Writing – review & editing, Supervision, Funding acquisition.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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Data availability

Will be put on github after publication.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2023.110300.

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