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Debunking wasp pollination: Wasps are comparable to bees in terms of plant interactions, body pollen and single-visit pollen deposition

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Abstract

1. Wasps are understudied in their contribution to pollination services. In order to better understand the ecological contribution of wasp communities to plant pollination, we conducted three studies to compare bees and wasps by (1) the plant communities visited in agricultural and prairie environments, (2) body pollen composition as an indirect measure of pollination and (3) a single-visit deposition study as a direct measure of pollination in the plant species complex *Solidago canadensis*.
2. We found wasps visit a distinct early-blooming exotic plant community from bees but have overlapping use of late-blooming native plants and similar network interaction metrics. This suggests wasps may fill an ecological niche distinct from bees, while also serving as common native plant visitors. We also found that body pollen density and pollen fidelity in four and five (out of six) wasp families, respectively, were comparable to or greater than the bee family Colletidae. Three wasp families also showed comparable to or greater visit fidelity than two (out of five) bee families examined. These results suggest wasps may carry and potentially deliver substantial pollen to specific plants. In addition, controlled single-visit deposition revealed the paper wasp *Polistes fuscatus* deposits a similar amount of pollen grains as the bumble bee *Bombus impatiens*, suggesting surprisingly high pollination efficiency that warrants further investigation.
3. Our multi-pronged study shows the importance of investigating the role of wasps as pollinators, especially by focusing on direct plant-pollination metrics to determine wasp pollination efficacy.

KEYWORDS

bees, body pollen carriage, plant–insect interactions, pollination, single-visit deposition, wasps

INTRODUCTION

Interest in pollinator biology research and conservation has skyrocketed in recent years; however, not all groups of pollinators are equally represented in the literature (Knight et al., 2018; Sumner et al., 2018). Recent studies have highlighted the importance of less appreciated taxa such as flies, beetles and vertebrates in the pollination of both native plants and valued crops (Rader et al., 2020) with some of these taxa also providing multiple ecological services through the roles as predators or seed dispersers (Dunn et al., 2020). Nonetheless, there still remains a need to improve scientific awareness, published research and public perspectives of less-represented pollinators.

For instance, wasps have been one of the most poorly studied groups of pollinators, despite being the taxon of insects within which bees are evolutionarily nested. Wasps have the potential to provide multiple ecosystem services through pollination, managing insect pests (Brock et al., 2021; Southon et al., 2019) or acting as parasitoids (Wang et al., 2019). However, studies of their pollination ability have focused on a few model systems such as fig pollination (Herre et al., 2008) or plants with obvious pollinia (Coombs et al., 2009), creating a lack of knowledge of which plant species benefit from wasp pollination globally. One barrier to expanding research into wasp pollination stems from the fact that they are negatively perceived by lay people and scientists alike (Sumner, 2022), even though only a tiny subset of the immense diversity of wasps is highly defensive and deliver painful stings (i.e., *Vespula* yellow jacket wasps). In general, public opinion of wasps and their contribution to ecosystem services is much lower than other pollinator groups, and this is mirrored by a lower number of published scientific studies on wasps (Sumner et al., 2018) and fewer funding opportunities for wasp research. In addition, long-held misconceptions have created doubt about the role of a majority of wasp species as pollinators (Fægri & van der Pijl, 1979; Proctor, 1996). For example, scientists debate wasps' (1) fidelity and consistent visitation to specific plant species (Fægri & van der Pijl, 1979), (2) ability to be effective pollinators due to a lower capacity to carry pollen grains on their bodies (O'Neill, 2019) and (3) their ability to successfully fertilise flowers due to both of these traits.

Wasps are an incredibly diverse group of insects including a huge number of parasitoids, as well as medium- to large- bodied predatory wasps which are frequently observed floral visitors (O'Neill, 2019). Wasps have been described as 'unreliable and unsteady pollinators' based on perceptions that they are general nectar foragers (Fægri & van der Pijl, 1979; O'Neill, 2019), due to having less specialised nutritional needs than bees (Praz et al., 2008), and responding to more generalised floral cues that apply to broader taxa of plant species (Mazokin-Poshniakov & Grasvekaya, 1966). However, recent studies have identified plants often and reliably visited by specific wasp species (Bernhardt & Goldblatt, 2006; Goldblatt & Manning, 2006; Ollerton et al., 2003) and wasps may fill important ecological niches by visiting plant species less visited by other pollinators such as bees (Willmer et al., 2017).

There are also physical differences between wasps and bees that may relate to their ability as pollinators. Wasps lack specialised branched body hairs found in bees (O'Neill, 2019; Thorp, 1979; Thorp, 2000) and predatory wasps use prey items instead of pollen as a protein source (Sann et al., 2018). While this may result in wasps having lower body pollen carriage than bees, however body pollen carriage does not directly translate to pollination success. Bees often efficiently pack and store most of the pollen they collect to feed their larva (e.g., on the legs of corbiculate bees, Cerceau et al., 2019; Carvalho & Schlindwein, 2011; Pick & Schlindwein, 2011); therefore, only some of a bee's body pollen may be actually available for deposition (Adler & Irwin, 2006). This phenomenon has been reported with studies showing pollinator groups with lower pollen carriage than bees can still be effective pollinators (Dunn et al., 2020; Orford et al., 2015). Therefore, other traits such as the composition of body pollen may be more informative.

While plant visitation and body pollen carriage estimates provide valuable information, these traits do not always translate to actual pollination success (King et al., 2013). There is little information on the actual amount of pollen deposition from wasp visitation, as many of these plants are visited by other pollinator groups (Fægri & van der Pijl, 1979) and very few studies have investigated wasp pollen deposition (Willmer et al., 2017). This may be due to the difficulty in getting wasps to purposefully visit flowers since they switch between two distinct foraging behavioural modes—hunting prey and visiting flowers (Hunt, 2007). However, recent momentum towards researching wasp pollination (de Santos et al., 2010; Holm, 2021; Mello et al., 2011) has been ignited by previous studies demonstrating the beneficial potential of wasps in pest-management services (Brock et al., 2021; Southon et al., 2019; Wang et al., 2019), making wasp pollination a topic of renewed interest, especially in agricultural landscapes.

In this study, we perform a side-by-side analysis of several common pollination metrics, comparing wasps (especially medium- to large-bodied species) to their close relatives, the bees, within small native habitat plants in an agricultural landscape. We tested the historical assumptions that wasps are less loyal to plant species, carry less pollen on their body and do not deposit sufficient pollen on stigmas (Fægri & van der Pijl, 1979; Proctor, 1996). We investigated whether wasps and bees were comparable by analysing (1) the plant community visited, (2) indirect body pollen composition metrics and (3) direct metrics through single-visit deposition (SVD) of pollination efficiency. Comprehensively studying ecosystem-wide metrics as well as direct and indirect measures of pollination, this study aimed to gain a more holistic understanding of the role of wasps as pollinators in this environment.

MATERIALS AND METHODS

Study region

We conducted multiple studies in 2019 and 2021 in central Iowa, an agriculturally dominated state in the Midwestern United States (Smith, 1998). Iowa has a continental climate with cold winters (mean January temperature: -4.7°C), hot summers (mean July temperature: 25°C) and moderate annual precipitation (92.0 cm; US National Weather Service, 2000–2022). Iowa's general landscape is topographically undulating and extensively dominated by corn (*Zea mays* [L.]) and soybean (*Glycine max* [(L.) Merr,]) production, commonly grown as monocultures with soil tillage, chemical fertiliser and pesticide applications, and winter fallow between crop seasons.

Study 1a: Plant–wasp and plant–bee interaction networks and communities

Site selection

Wild bee and wasp communities were surveyed in 10 sites in central Iowa from June to September in 2019 (Borchardt et al., 2023) (Figure 1). We wanted to capture the plant communities visited by

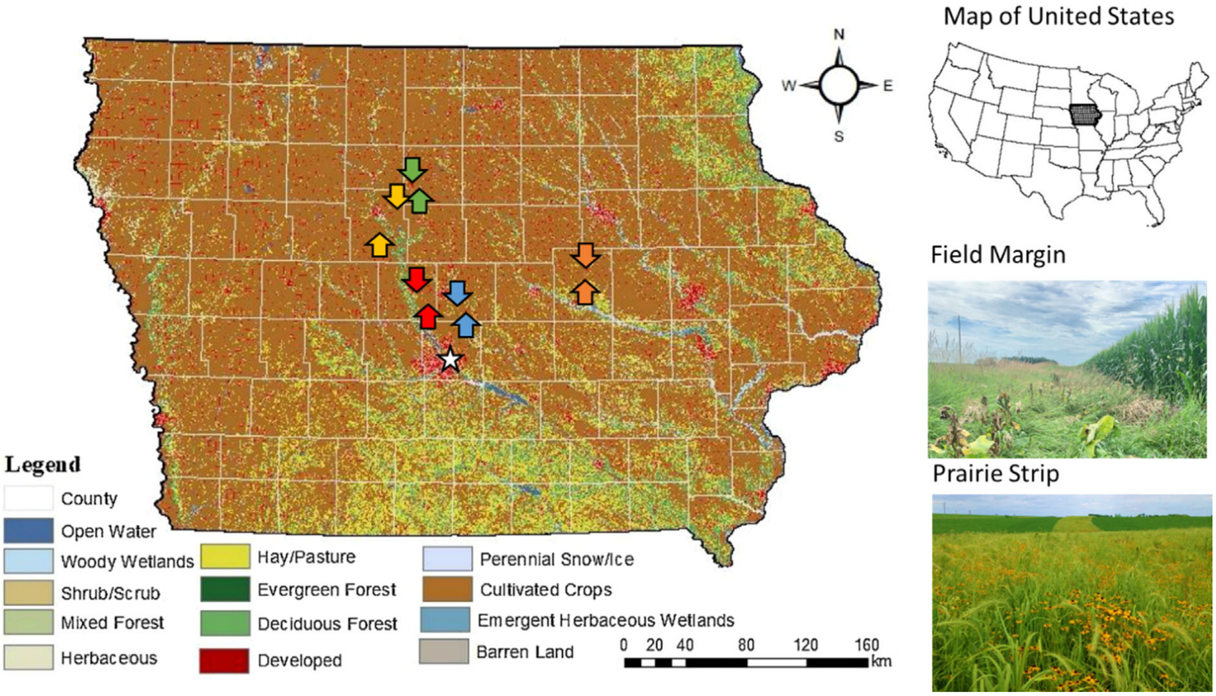


FIGURE 1 Ten sites were studied in central Iowa, a state in the US Midwest (map, top right). Sites were paired as one site with prairie strips (CP 43; USDA, 2019) and one site without, based on crop species, similar farm management and proximal location. Five sites were row-crop fields with prairie strips, and five sites were grassy field margins between fields or alongside roads. Site locations are indicated by arrows and were at least 3.2 km away from another site to reduce bees foraging in multiple study locations. Site pairs from top to bottom of the Iowa map and are abbreviated for landowner privacy: SMI (green, top centre), SME (yellow, top left), STO (orange, farthest right), WHO (red, middle left), GUT (blue, middle right) and capital city of Iowa Des Moines (star, bottom). Landscape map created by Upadhaya et al. (2021) using NLCD (Dewitz, 2019) data.

wasps and bees across two types of agricultural landscapes: (a) conventional rowcrop fields and (b) rowcrop fields with native vegetation. To capture a conventional agricultural landscape, we surveyed five grassy field margins commonly found between crop fields or alongside rows, often with weedy forb and grass species ('Field Margins'). Field Margin sites were not known to have native grass and forb species planted purposefully through the United States Department of Agriculture's Conservation Reserve Program (CRP) or other conservation programs such as roadside planting. However, we note that one site (named 'STO' Field Margin) contained species such as *Helianthus* spp. and *Oenothera* spp. (Murray, 2021), which are typically planted during restoration projects. To capture a recent movement towards including conservation within agricultural landscapes, we also surveyed five fields with prairie strips ('Prairie Strips'). Prairie Strips are native prairie grasses and forb plantings comprising 10% of the total row-crop field area in about 6 m wide strips (CP 43; USDA, 2019). Prairie strips were a novel and uncommon conservation practice in the Midwestern US at the time of the study but are shown to support increased insect pollinator populations (Schulte et al., 2017). However, prairie strips have gained popularity following federal support in 2019 through the CRP, the same year the specimens were collected. All sites had apiaries of four honey bee colonies as part of a companion study (Zhang et al., 2022). While honey bees are known to compete with wild bees for floral resources (Giannini et al., 2015; Valido et al., 2019) and likely compete with wild wasps as well, we chose to study farms with small apiaries (four colonies) because honey bees are common in agricultural landscapes of this region. In addition, the apiaries were smaller than the recommended limit in conservation habitat according to the Xerces Society for Invertebrate Conservation (fewer than 20 colonies; Hatfield et al., 2018).

Pollinator interactions

Bee and wasp specimens were collected by netting from each site every other week during samples of 10 observational minutes walking through the plant community at a constant pace (Borchardt et al., 2023; Williams et al., 2015). Transects were not defined by a specific length or width, but rather by total time spent observing floral visitors; this was necessary because of site differences in distributions of vegetation and terrain. Specimen processing and recording were not included in the 10 minutes of observation and across the season each site had 80 minutes of total observation time. We planned to conduct insect surveys on days with ideal pollinator weather (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); however, these conditions were relaxed due to too few ideal weather days in the sampled region. Collection via netting meant that we targeted large- to medium-bodied bees and wasps, and were not able to efficiently collect small-bodied wasps, many of which are likely to be parasitoids. Bees and wasps were identified as genus for consistency between the groups, due to the difficulty of identifying some wasp groups to species. Bees were identified using Ascher and Pickering (2020), and wasps were identified using both Holm (2021) and Goulet and Huber (1993) with some other smaller keys (Carpenter & Cumming, 1985). For difficult-to-identify specimens that required further confirmation, we uploaded images to Iowa State University's online insect identification service BugGuide, and confirmed or rechecked our identifications after they had been examined by an online community of wasp taxonomic specialists (VanDyk & Bartlett, 2020). We were unable to identify some wasps to genus and, therefore, identified them to the family—Braconidae (one specimen), Ichneumonidae (eight specimens), Mutillidae (one specimen; sole specimen in the family) and Tenthredinidae (one specimen; sole specimen in the family).

Two types of interactions were recorded to reduce sampling bias (Jordano, 2016)—'observed' interactions where the specimen was observed touching the reproductive region of a plant and 'pollen' interactions, which were estimated from the body pollen of that specimen (Borchardt et al., 2023; Fisogni et al., 2018). We collected pollen from individual specimens using a modified MacGillivray's (1987) method. First, the specimen was vortexed in an 80% ethanol solution with a drop of gelatin-glycerol at the bottom of the 1.5 mL centrifuge tube. Then, the specimen was removed, and basic fuchsin was added as a pollen dye. The solution was centrifuged to embed the pollen grains in the gelatin-glycerol, and the supernatant removed. The gelatin-glycerol was plated on a microscope slide using heat. Pollen was counted in a similar method to previous studies, using transects spanning the entire length of the coverslip in the densest pollen region of the slide until 400 total grains or 15 transects were counted (Borchardt et al., 2023; Bosch et al., 2009; Fisogni et al., 2018). Pollen was identified as the lowest possible taxonomic group using a reference collection from Iowa State University (Borchardt et al., 2023; Zhang et al., 2021; Zhang et al., 2022; Zhang et al., 2023), typically to genus or species except for Asteraceae, which was identified to family. We were unable to identify eight pollen types included in the analysis and named them 'Unknown' along with the specimen ID number they were first identified from (Table S1). Pollen species with more than 20 grains were considered a 'pollen interaction' if it was not the plant species the specimen was observed visiting ('observed interaction'; Borchardt et al., 2023; Fisogni et al., 2018; Bosch et al., 2009).

Networks were created and analysed using the 'bipartite' package in R (Dormann et al., 2009; R Core Team, 2019). Two sites (SMI Field Margin and SME Field Margin) did not have enough wasp interactions for network analysis and, therefore, were dropped from the analysis. We compared wasp, bee, and combined wasp and bee networks ('combined') in a matched-pairs design since they were collected from the same area and at the same times. We analysed network metrics in three ways. First, we analysed using the networks in their original form ('raw networks'). Second, we created randomised null models ('null models'; $N = 1000$) using the 'mgen' function in the 'bipartite' package in R to create random assortments of interactions based on the marginal totals of rows and columns (Dormann et al., 2009; Pellissier et al., 2018; R Core Team, 2019). If the raw network metric was not significantly different from the null models created from that network, then we concluded the network metric was caused by a random assortment of interactions and not an underlying biological pattern. Third, we subsampled the raw networks to the same size ($N = 1000$) for better comparison without influence from differences in species richness ('rarified networks'; Blüthgen et al., 2006; Fründ et al., 2016). While we chose metrics that are more robust to differences in species richness (Blüthgen et al., 2006; Fründ et al., 2016), we only considered results significant if there was a consistent trend between the raw and rarified networks. We subsampled networks to the size of the smallest network within a site and habitat type (Table S2). Two sites had two few pollinator species for accurate rarefaction (GUT FM wasps, plants $= 15$, pollinators $= 5$; SMI PS wasps, plants $= 19$, pollinators $= 2$); therefore, the next smallest network was used for rarefaction of the bee and combined networks (Table S2).

We analysed five network traits. Cluster coefficient is the average per-species connectance (realised links divided by all possible links; binary metric) and helps identify small-world networks where the distance between any pair of species is short (Watts & Strogatz, 1998). High cluster coefficient indicates the loss of a species will influence most other species in the network due to their tight clustering. This is calculated for both pollinators and plants separately, as well as overall in the network. Weighted nestedness (NODF) is a binary calculation of nestedness, where each column representing a single pollinator species is sorted by the number of filled cells representing interactions with rows representing available plant species (Almeida-Neto et al., 2008). Each column (or pollinator species) is then compared with all other columns with fewer links to determine the network's overall similarity to a perfectly nested network (Bascompte et al., 2003). High nestedness shows a core of interacting generalist species that can support more specialised species attached to that core. Interaction strength asymmetry is a measurement of the imbalance of interaction strength between a pair of interacting species based on weighted links. For example, a specialist pollinator species interacting with a sole generalist plant species has a high dependence on its sole interaction partner. However, the generalist plant species may be visited by many pollinator species, thereby having a low dependence on any one pollinator species, creating an asymmetric dependence between the specialist pollinator species and the generalist plant species. High interaction strength asymmetry indicates many rare species in the environment, each with few interactions (Vázquez et al., 2007). Links per species is the average number of interacting partners or binary links between all species in the network. In plants, a low number of interacting partners could mean a low chance of animal-mediated pollination services. In pollinators, the number of interacting partners has a non-linear relationship with resource availability. Low- and high-resource environments cause pollinators to specialise on a few plant species; however, in moderate-resource environments, pollinators may forage more generally as more options are available, but not abundant enough to support specialisation on one or a few species. Modularity is a measure of how isolated subsets of the weighted network are from each other. Often these subsets are connected by highly generalistic species, which if lost from the environment can isolate subsets of interacting plants and pollinators (Aslan et al., 2018; Valido et al., 2019) leading to increased extinction risk for the isolated subset (Bascompte & Jordano, 2014).

In addition to network metrics, we compared the community of plant interactions with wasp and bee families. We created nMDS plots using the 'vegan' and 'MASS' packages in R (Oksanen et al., 2022; Ripley et al., 2023) and calculated R^2 and *p*-value of the ordination between the wasp and bee families at both site types (Prairie Strips, Field Margins) and periods of the season (Early, June and July; Late, August and September).

Study 1b: Body pollen carriage and floral fidelity in wasp and bee families

Using the body pollen from the same wasps and bees collected for Study 1a and Borchardt et al. (2023), we compared overall body pollen density and floral fidelity. Body pollen density was determined by the density of pollen grains per microscope transect during the pollen counting procedure described in Study 1a, as a proxy for total body pollen carriage. We measured fidelity in two ways: 'Pollen fidelity' and 'Visit fidelity'. Pollen fidelity was determined by comparing the number of grains belonging to the most abundant plant group to the total number of grains counted for each specimen. Visit fidelity was determined by comparing the number of pollen grains belonging to the plant species the insect was observed visiting to the total pollen grains counted. Visit fidelity could have some observation bias (Jordano, 2016); however, it represents plants definitively visited by that pollinator.

We compared all pairwise combinations of bee and wasp families with more than five specimens (Table S3). Families with less than five specimens were excluded: Mutillidae (wasp, $n = 1$), Pompilidae (wasp, $n = 3$), Tenthredinidae (wasp, $n = 1$) and Thynnidae (wasp, $n = 3$). We conducted a *t*-test and calculated Cohen's D for effect size in order to determine if two families were similar or different calculated in R (R Core Team, 2019). Effect size determines how far two means are from each other according to their standard deviations and is not influenced by sample size like *t* tests. Typically, a value greater than 0.8 for Cohen's D indicates a large difference between two means. Our criteria for determining if the two groups were similar are that the absolute value of Cohen's D is less than 0.8 and the *p*-value is greater than 0.05, indicating in both of these values the groups are similar. If both of these criteria were not met, then the families were considered to be different in the direction indicated by Cohen's D (positive value, bee family has a higher metric value; negative value, wasp family has a higher metric value).

Study 2: Pollen deposition of *P. fuscatus* and *B. impatiens* on plant complex *Solidago canadensis*

In order to more directly measure pollination ability, we investigated single-visit deposition ('SVD') between a wasp and bee species. SVD studies on wasps exist but are uncommon (Willmer et al., 2017), and our study may be one of the first SVD studies to purposefully use a wasp species.

We used *Polistes fuscatus* [Fabricus], a social wasp species in the family Vespidae that can be reared in captivity for controlled experiments (Jandt et al., 2014; Walton & Toth, 2021). We chose to use the plant species complex *Solidago canadensis* [L.] (Melville & Morton, 1982), which is regularly visited by *P. fuscatus* (Figure S1; Blackwell & Powell, 1981) and potentially used as a mating location (Table S4; Toth, Borchardt, and Soto-Mendez, personal observations). We compared this to commercial *Bombus impatiens* [Cresson]. The plant complex *S. canadensis* is comprised of multiple difficult-to-differentiate species—*Soldiago canadensis*, *Solidago altissima* (Miller, 1981; Semple et al., 1984), *Solidago lepida* and *Solidago rupestris* (Semple et al., 2013)—sometimes with the additional inclusion of *Solidago gigantea* (Melville & Morton, 1982). The *S. canadensis* plant complex's native range spans throughout North America (Semple et al., 1984) and shares similar morphology including plants between 30 and 150 cm tall with narrow leaves and many small yellow disc florets arranged in multiple apical pyramidal-paniculiform arrays (Semple & Cook, 2006).

We performed these studies in a fine-mesh hoop house at the Horticulture Research Station in Ames, Iowa, from August 2021 to September 2021. Across this period, three wild-caught *P. fuscatus* nests and three *B. impatiens* boxes purchased through Koppert were allowed to acclimate in the hoop house. *P. fuscatus* colonies contained approximately 15–20 individuals, whereas *B. impatiens* colonies contained between 25 and 100 individuals. Both species coexisted in the hoop house for the duration of the study and were seen simultaneously foraging on the same floral resources. Colonies were given at least a week to acclimate to the hoop house and visit a bouquet of fresh flowering stems of the plant complex *S. canadensis* to reinforce floral visiting behaviour.

Single-visit study

We analysed pollen deposition on three groups of the plant complex *S. canadensis* floral bouquets: flowers made freely available to the insects at all times ('Unbagged'), flowers kept in insect-exclusion bagging to prevent any visit by an insect pollinator ('Bagged') and flowers that were only visited by a pollinator a single time ('Single-Visit'). The two latter treatments were bagged with fine-mesh insect exclusion bags during the bud stage, ensuring they had not been visited by an insect prior to being randomly placed in either the Bagged or single-visit treatments. We compared the number of pollen grains from the stigma due to self-pollination (Bagged treatment) and many visits from insect pollinators (Unbagged treatment) to our stigmas that were visited a single time (single-visit treatment) to determine the level of cross-pollination by our two insect visitors—*B. impatiens* and *P. fuscatus*. In addition, we also separately analysed male and female *P. fuscatus* to determine if there is a difference between the sexes. Single-Visit flowers were uncovered and allowed a single insect visitor to visit the flower, and then, the flowers were immediately moved away from the insects. Three flowers were randomly selected from where the insect visited the inflorescence and collected into centrifuge tubes. All instruments were cleaned between each flower to prevent inadvertent pollen transfer. We separated the Single-Visit flowers by the insect visitor: *B. impatiens*, male *P. fuscatus* and female *P. fuscatus*.

Pollen analysis

In the lab, three randomly selected stigmas were carefully removed from the collected flowers and placed on a microscope slide. Instruments were cleaned with ethanol between each stigma to prevent accidental pollen transfer. We recorded the number of *Solidago* spp. pollen grains attached to the stigmas on each slide. We excluded stigmas with abnormalities such as being occluded by other organic material that inhibited our ability to accurately count the pollen grains on the stigma (~6.7%). Analysis was done in R using the 'lme4' and 'emmeans' packages to analyse statistical contrasts from a linear model accounting for individual encounter and treatment, as a single pollinator visit may include multiple flowers (Bates et al., 2015; Lenth et al., 2023; R Core Team, 2019). Other linear models were tested; however, the Akaike Inofrmation Criterion (AIC) and Bayesian information criterion (BIC changes were not large enough to justify including additional variables. *p*-values were adjusted using a Tukey method. Contrasts were calculated from a linear mixed-effects model, as follows: total_pollen ~ (1|specimen_id) + treatment. *p*-values were adjusted using the Tukey method, and degrees of freedom were calculated using the Kenward–Roger method.

RESULTS

Study 1a: Plant–wasp and plant–bee interaction networks and communities

We observed a total of 31 bee genera in four families; wasps were identified to 24 genera in 10 families (noting that four taxa were not identified to genus level and only to family [Table S5]). We analysed 1669 bee interactions (737 observed native bee, 244 observed honey bee and 687 pollen interactions) and 321 wasp interactions (160 observed, 159 pollen interactions); wasp interactions made up 16.1% of the total observed interactions (Table S5). Between the site types, 78.7% of bee interactions and 61.7% of wasp interactions were observed at Prairie Strip sites, the remainder being at Field Margin sites. Visually, wasp networks were less complex than bee networks (Figure 2) potentially due to fewer wasp interactions observed. Overall, we found multiple instances where wasps showed similar or increased pollination potential than bees (Table 1).

Raw network comparisons indicate cluster coefficient of pollinators (one-way ANOVA, $F = 5.723$, $p = 0.010$) and links per species (one-way ANOVA, $F = 9.540$, $p = 0.001$) differ between the three types of networks (bee, wasp and combined); however, the rarified network comparison does not show a difference (cluster coefficient of pollinators, one-way ANOVA, $F = 0.440$, $p = 0.514$; links per species, one-way ANOVA, $F = 0.080$, $p = 0.780$; Table 2; Figure 3). The null model analysis did indicate that 1 of the 24 of the networks for cluster coefficient of pollinators was affected by a random assortment of interactions; however, this is not enough to discredit our other findings. The other metrics—cluster coefficient overall, cluster coefficient plants, interaction strength asymmetry, weighted nestedness (NODF) and modularity, did not show a difference in either raw networks or rarified network comparison. Null model analysis revealed a random assortment of interactions heavily influenced interaction strength asymmetry (18 of 18 networks were similar to the randomised null models; six were unable to run) and slightly influenced cluster coefficient overall and modularity (4 of 24 networks and 6 of 24 networks were similar to the randomised null models, respectively).

There were insufficient data points to test network differences between Prairie Strip and Field Margin Sites, nor was this the specific goal of this study. However, we note that the overall data patterns suggest there may be some differing trends (Figure S3).

Plant interaction composition comparisons show a significant difference in bee– and wasp–plant interaction communities overall ($R^2 = 0.3684$, $p = 0.0136$; Figure 4), in Field Margins ($R^2 = 0.4474$, $p = 0.0032$; Figure 5) and in the Early Season (June and July, $R^2 = 0.3774$, $p = 0.0125$). However, bees and wasps used similar plant communities in Prairie Strips ($R^2 = 0.1168$, $p = 0.2775$) and in the Late Season (August and September, $R^2 = 0.0878$, $p = 0.4298$).

Study 1b: Body pollen carriage and floral fidelity in wasp and bee families

We determined the body pollen carriage and floral fidelity of six wasp families and five bee families (limiting our analysis to those groups with at least five specimens, Table S3).

For the body pollen composition traits Pollen Density, Pollen Fidelity and Visit Fidelity, we concluded families had similar metric values if they had both a Cohen's D absolute value less than 0.8 and a *t*-test *p*-value greater than 0.05. If these criteria were not met, the families were considered to have different metric values (Figure 6 and Table S7). For Pollen Density, the bee family Colletidae showed lower pollen density than wasp families Sphecidae (Cohen's D $= -0.0115$, Mann–Whitney U, $W = 270$, $p < 0.0001$) and Vespidae (Cohen's D $= -0.0063$, Mann–Whitney U, $W = 464$, $p = 0.0142$). In addition, the bee family Colletidae was similar to wasp families Chrysididae (Cohen's D $= -0.0001$, Mann–Whitney U, $W = 148.5$, $p = 0.6977$) and Ichneumonidae (Cohen's D $= -0.0038$, Mann–Whitney U, $W = 148$, $p = 0.8178$). In all other pairwise combinations, bee families showed higher Pollen Density than wasp families.

For Pollen Fidelity, the bee family Colletidae had a lower Pollen Fidelity than the wasp families Sphecidae (Cohen's D $= -13.819$, Mann–Whitney U, $W = 488$, $p = 0.0735$) and Vespidae (Cohen's D $= -0.9181$, Mann–Whitney U, $W = 575$, $p = 0.2287$). In addition, the bee family Colletidae was similar to the wasp families Chrysididae

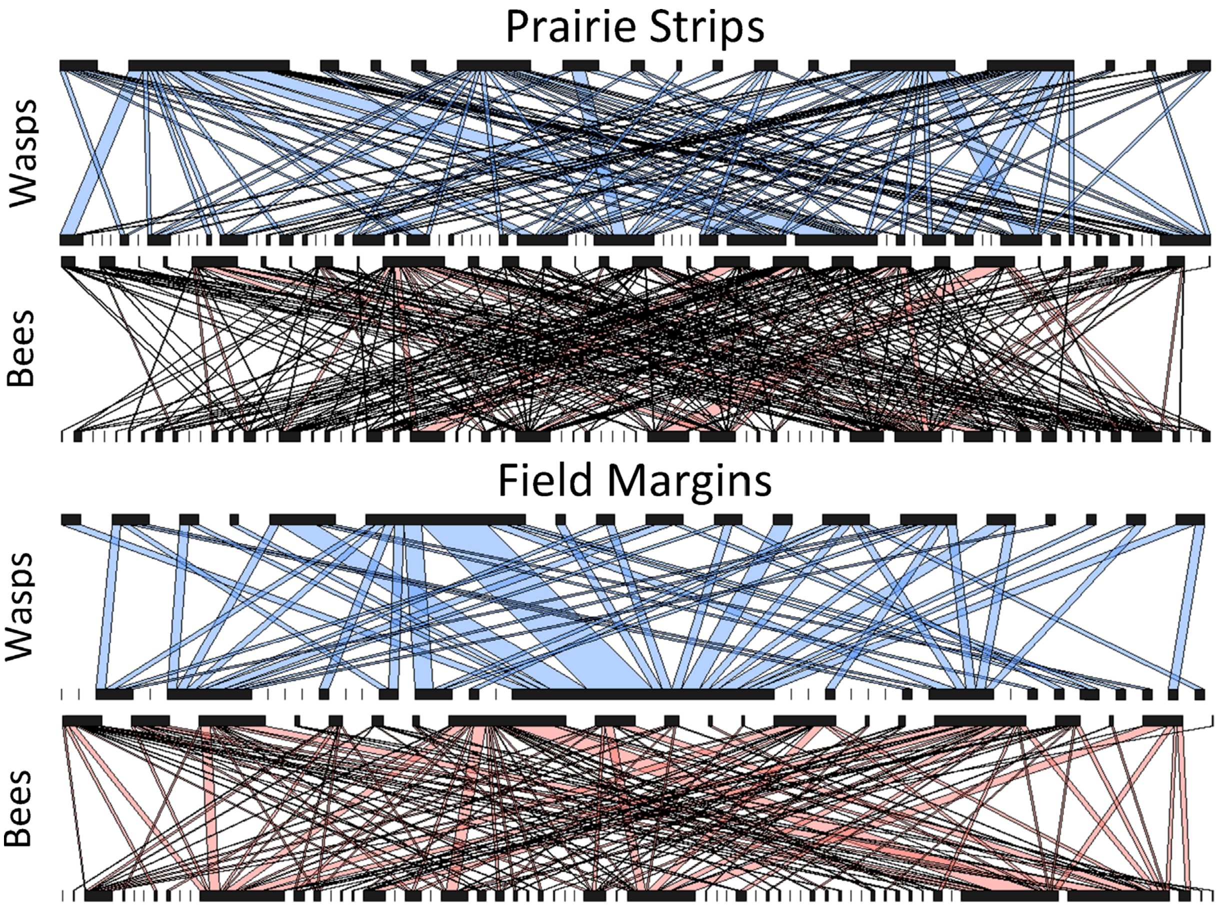


FIGURE 2 Wasp (blue) and bee (red) networks from Prairie Strips (top) and Field Margins (bottom). The connecting lines indicate interactions with thickness showing relative abundance of that interaction within that specific network. To see species names, refer to Figure S2.

TABLE 1 A chart showing the common assumptions about wasp pollination for each trait we analysed, followed by our findings.

Exp.	Metric	Common assumption	Results
1a	Cluster coefficient (CC)	Lower in wasp networks	No difference
1a	Weighted nestedness (NODF)	Lower in wasp networks	No difference
1a	Interaction strength asymmetry (ISA)	Lower in wasp networks	No difference
1a	Links per species	Higher in wasp networks	No difference
1a	Modularity	Higher in wasp networks	No difference
1a	Plant community overlap (nMDS)	High overlap between bees and wasps	Low overall overlap
1b	Body pollen density	Lower in wasp families	Wasp families similar to 1 of 5 bee families
1b	Pollen fidelity	Lower in wasp families	Wasp families similar to 1 of 5 bee families
1b	Visit fidelity	Lower in wasp families	Wasp families similar to 4 of 5 bee families
2	Single-visit pollen deposition	Lower in wasps	Wasps higher than freely visited flowers

Note: 'Exp.' indicates which experiment the metric was analysed in. 'Assumed Trend' describes the common view that wasps are not effective pollinators. 'Results' indicates what we found in our study.

(Cohen's D = 0.5173, Mann–Whitney U, W = 155.5, $p = 0.5317$), Crabronidae (Cohen's D = −0.6092, Mann–Whitney U, W = 1382, $p = 0.3532$) and Ichneumonidae (Cohen's D = −0.6537, Mann–Whitney U, W = 165, $p = 0.7939$). In all other pairwise combinations, bee families showed higher Pollen Fidelity than wasp families.

For Visit Fidelity, the wasp family Ichneumonidae had significantly higher Visit Fidelity than the bee families Colletidae (Cohen's D = −1.2206, Mann–Whitney U, W = 150.5, $p = 0.8642$) and Megachilidae (Cohen's D = −0.8492, Mann–Whitney U, W = 139.5, $p = 0.4718$). Three wasp families also showed similarity to multiple

TABLE 2 Results of ANOVA analysis between metric values of networks containing different pollinators (wasps, bees and combined) for raw and rarefied networks.

	Cluster coefficient pollinators	Cluster coefficient overall	Cluster coefficient plants	Interaction strength asymmetry	Links per species	Weighted Nestedness (NODF)	Modularity
Raw networks	$F = 5.723$	$F = 2.247$	$F = 1.216$	$F = 0.522$	$F = 9.540$	$F = 0.270$	$F = 0.540$
	$p = 0.010$*	$p = 0.131$	$p = 0.317$	$p = 0.601$	$p = 0.001$*	$p = 0.766$	$p = 0.591$
Rarefied networks	$F = 0.850$	$F = 0.011$	$F = 0.241$	$F = 0.022$	$F = 1.940$	$F = 0.369$	$F = 0.454$
	$p = 0.442$	$p = 0.989$	$p = 0.788$	$p = 0.979$	$p = 0.169$	$p = 0.695$	$p = 0.641$
Null models	$p > 0.05$	$p > 0.05$	$p > 0.05$	$p > 0.05$	$p > 0.05$	$p > 0.05$	$p > 0.05$
	$N = 1$ of 24	$N = 4$ of 24	$N = 0$ of 24	$N = 18$ of 18	$N = 0$ of 24	$N = 0$ of 24	$N = 6$ of 24

Note: The last row indicates the number of Null Model comparisons that were not significantly different (Table S6), and therefore suggest random assortment in those networks.

*Significance ($a < 0.05$).

bee families. The wasp family Ichneumonidae had similar Visit Fidelity to bee families Apidae (Cohen's $D = -0.4009$, Mann–Whitney U, $W = 1654$, $p = 0.2282$) and Halictidae (Cohen's $D = 0.4738$, Mann–Whitney U, $W = 1439.5$, $p = 0.0576$). The wasp family Chrysididae had similar Visit Fidelity to the bee families Apidae (Cohen's $D = 0.3871$, Mann–Whitney U, $W = 1432$, $p = 0.2856$), Colletidae (Cohen's $D = -0.3804$, Mann–Whitney U, $W = 134.5$, $p = 0.9551$) and Megachilidae (Cohen's $D = 0.0402$, Mann–Whitney U, $W = 118.5$, $p = 0.5921$). Finally, the wasp family Crabronidae had similar Visit Fidelity to the bee families Colletidae (Cohen's $D = -0.2185$, Mann–Whitney U, $W = 1436.5$, $p = 0.4922$) and Megachilidae (Cohen's $D = 0.4232$, Mann–Whitney U, $W = 1347$, $p = 0.2276$). In all other pairwise combinations, the bee family showed higher Visit Fidelity than the wasp family.

Study 2: Pollen deposition of *P. fuscatus* and *B. impatiens* on plant complex *Solidago canadensis*

We counted the pollen grains on a total of 345 stigmas of the plant complex *S. canadensis* after a single visit from an insect pollinator: 70 from *B. impatiens*, 210 from male *P. fuscatus* and 65 from female *P. fuscatus*. In addition, we counted pollen grains on 196 stigmas that were never visited by an insect ('Bagged') and 201 stigmas that were visited multiple times by insects ('Unbagged').

There were no statistically significant differences between pairwise comparisons of the Single-Visit treatments as well as between the Single-Visit treatments and our two controls—Bagged and Unbagged treatments. However, a single visit from a male *P. fuscatus* shows some evidence of higher pollen deposition than the Unbagged treatment that had multiple insect visitors (estimate $= -17.10 \pm 6.33$, $df = 81.5$, t-ratio $= -2.701$, $p = 0.0625$; Figure 7 and Table 3). While there is a trend towards higher pollen deposition in the Bagged treatment versus the Unbagged treatment, suggesting self-pollination (Figure S4), it was not significant. Additional visitation data from 2019 field observations from studies 1 and 2 show that *P. fuscatus* and *B. impatiens* appear to interact with *Solidago* spp. at similar rates (Table S4) although our data showed three times as many visits from *P. fuscatus* males than *B. impatiens*.

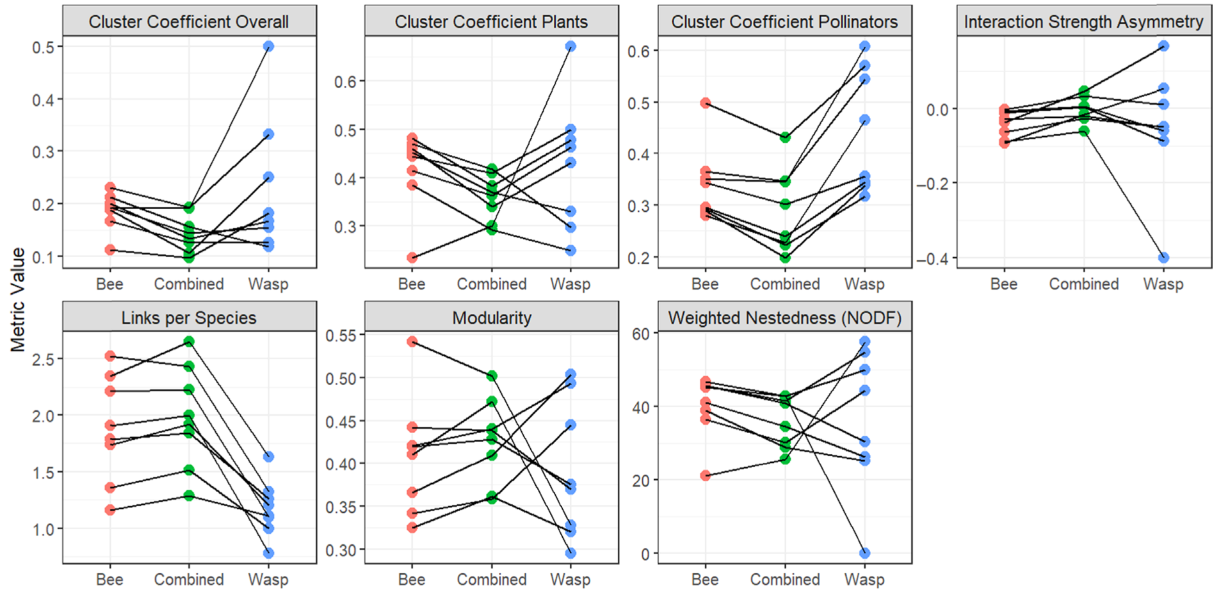
DISCUSSION

Wasps are recognised as pollinators; however, historically, their pollination ability has been discounted as generally less efficient compared with other pollinators. We aimed to determine the validity of these historical notions by measuring multiple pollination metrics in wasps compared with bees, a well-studied and relatively closely related taxon. Overall, we show that wasps can be effective pollinators and, in many aspects of pollination, are comparable to bee families, genera and species (Table 1). Although much more research needs to be done to confirm wasps' place as effective pollinators and the extent of their importance, our results support that wasp pollination should not be discounted.

Our results show that on an ecological level, wasps and bees have comparable plant interaction network structures than bees (Table 2). In fact, the only differences between the networks were due to differences in species richness, meaning studies focusing on one or a few pollinators instead of the entire pollinator community may have inaccurate findings (Blüthgen et al., 2006; Fründ et al., 2016). In addition, this supports that wasps play vital ecological roles in the pollination community in terms of ensuring plant pollination success, supporting rare species and maintaining stability within ecological communities of plants and pollinators.

Second, wasps and bees appear to visit distinct subsets of the plant community (Figure 4). Therefore, wasps may fulfill an ecological niche that is unique from other pollinator groups. However, in some environmental circumstances, wasp and bee plant community use overlapped, including during the late season (August–September) and in native habitat plantings (prairie strips; Figure 5). We believe the differences in plant community use were due to the presence of more weedy, exotic plant species that often bloom early in this region

(a) Raw Network Metrics



(b) Rarefied Network Metrics

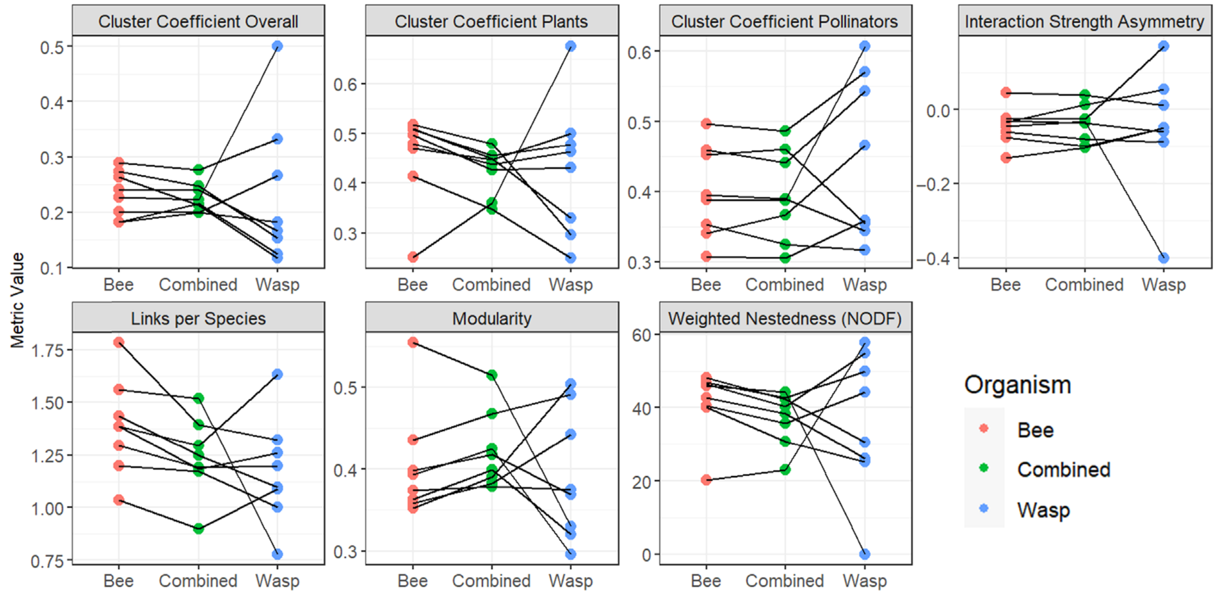


FIGURE 3 Network metrics from bee, wasp, and combined networks with black connecting lines indicating the matched pairs of site specimens were collected from. We analysed the networks in two ways: (a) as raw network values and (b) using rarefication to subsample networks ($n = 1000$) of the same species richness across the same site location.

(Zettlemoyer et al., 2019) and are found in unrestored Field Margins (Figure 5). While this might suggest that wasps could be contributing to exotic or invasive plant species proliferation, this does not negate our findings that they visit similar plant communities as bees when more native plant species are present and, therefore, may also be crucial to native plant pollination.

Third, we found that some wasp families are comparable to some bee families in terms of body pollen density and plant fidelity. For Pollen Density, the bee family Colletidae showed similar values to two wasp families Chrysididae and Ichneumonidae, and less Pollen Density than two other wasp families Sphecidae and Vespidae. This may be due to the composition of Colletidae in our study, which was 92% *Hylaeus* specimens; this genus is known to carry pollen internally (Proctor, 1996) and, therefore, is similar to wasps and does not have large external pollen stores. Pollen Fidelity again placed the bee family Colletidae within the same range of six wasp families. In fact, two wasp families Sphecidae and Vespidiae showed higher Pollen Fidelity than Colletidae, whereas three wasp families showed similar Pollen Fidelity to Colletidae: Chrysididae, Crabronidae and Ichneumonidae. Visit Fidelity values showed the most overlap between bees and

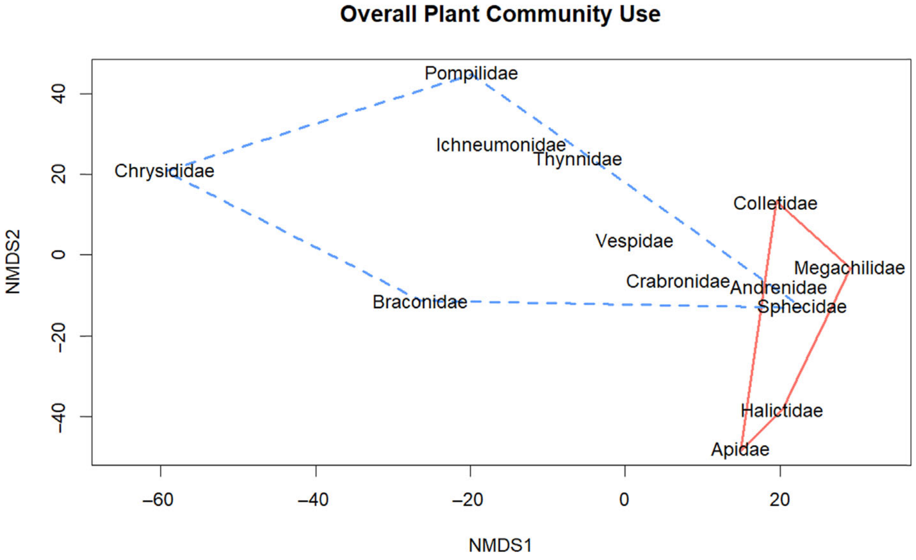


FIGURE 4 nMDS plot showing overall trends between the plant-interaction composition between bee (red solid outline) and wasp (blue dotted outline) families. Goodness of fit test reports an R^2 of 0.3684 and a corresponding *p*-value of 0.0136.

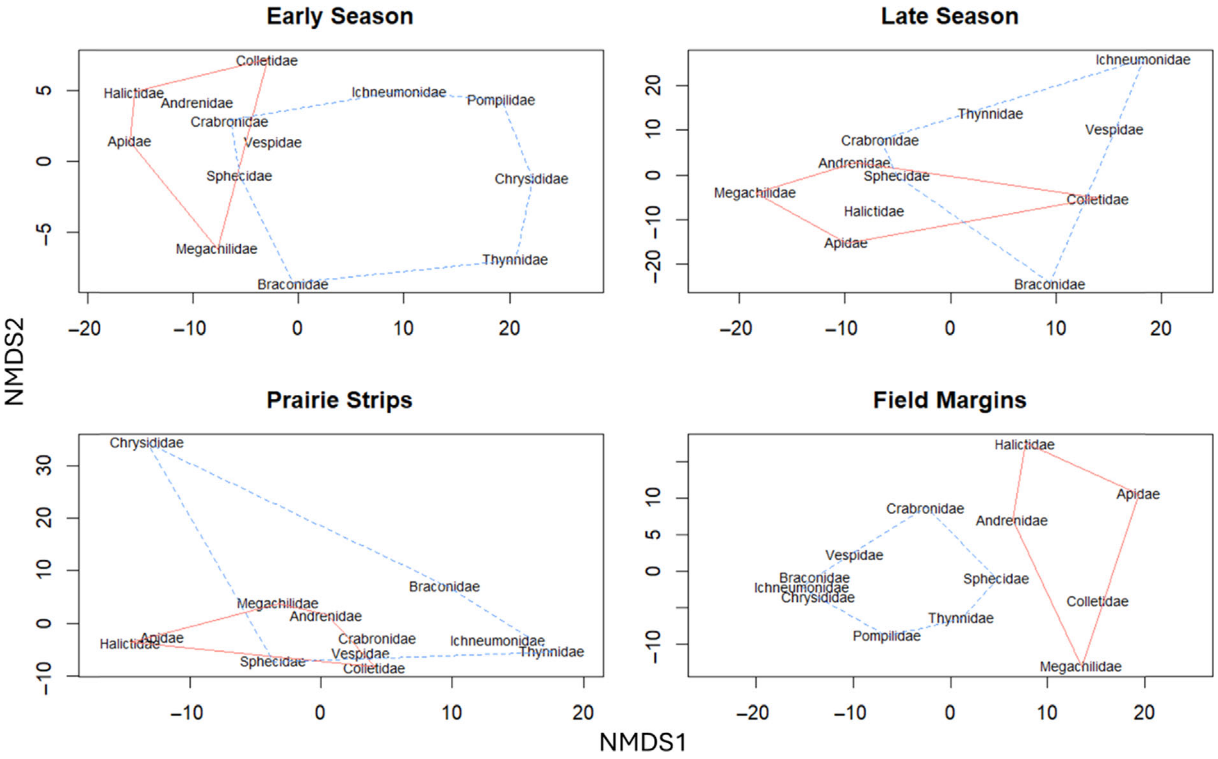


FIGURE 5 nMDS plots separated by site type (top row) and seasonality (bottom row). Outlines show plant-interaction composition between bee (red solid lines) and wasp (blue dotted lines) families. Goodness of fit tests on the ordination between wasp and bee families report the following statistical tests: Prairie Strips, $R^2 = 0.1168$, $p = 0.2775$; Field Margins, $R^2 = 0.4474$, $p = 0.0032$; Early Season, $R^2 = 0.3774$, $p = 0.0125$; Late Season, $R^2 = 0.0878$, $p = 0.4298$.

wasps, potentially because Visit Fidelity captures both nectar and pollen visits, which may reduce the bias of estimates of bee and wasp foraging patterns (Zemenick et al., 2019). The wasp family Ichneumonidae had higher Visit Fidelity than bee families Colletidae and Megachilidae, and similar Visit Fidelity to bee families Apidae and Halictidae. Ichneumonidae is a large wasp family comprised mostly of parasitoids (Gauld & Bolton, 1988), which, however, seems to have a wide range of floral specialisation and generalisation behaviours (Zemenick et al., 2019). The wasp family Chrysididae had similar Visit Fidelity as bee families Apidae, Colletidae and Megachilidae. Finally,

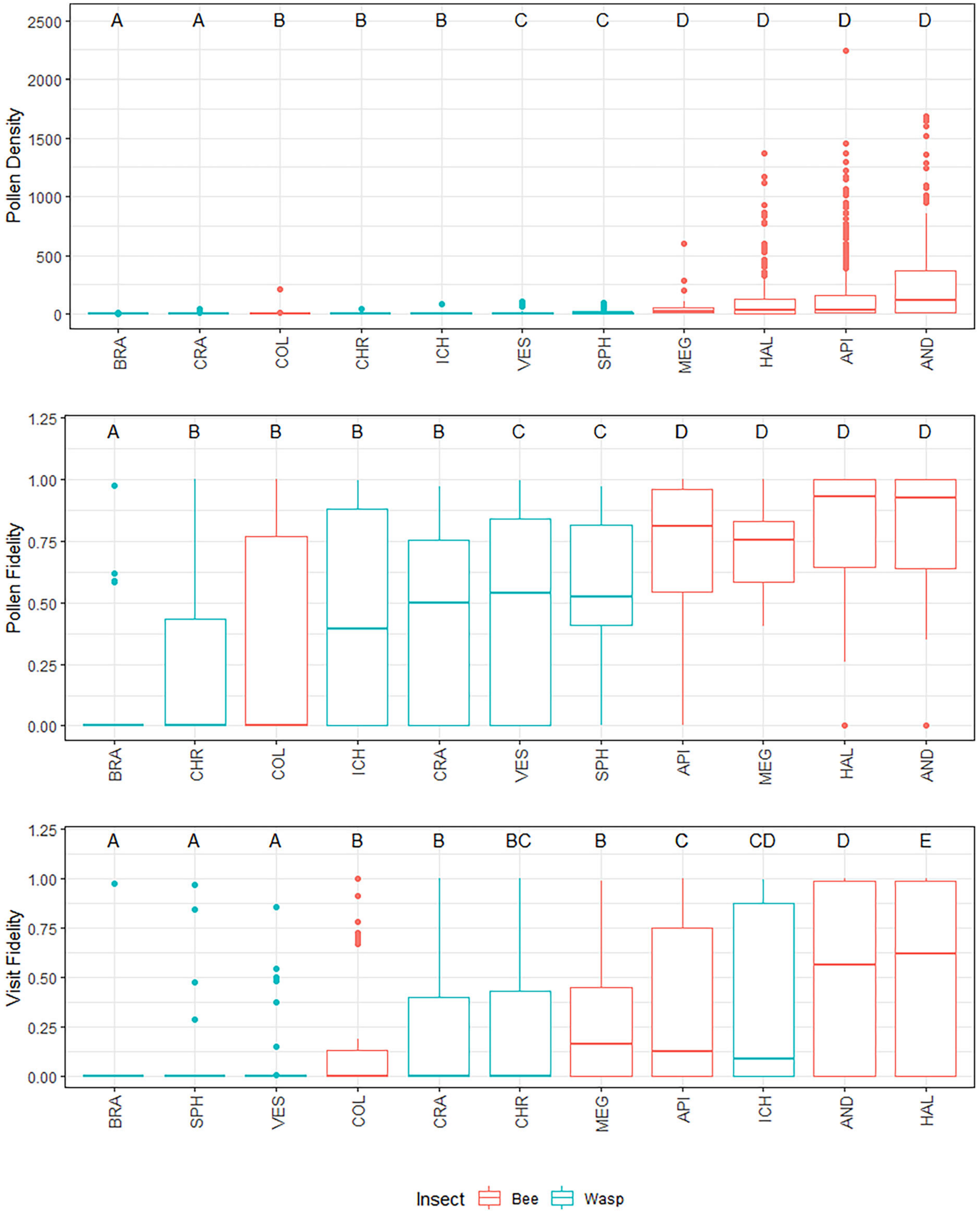


FIGURE 6 Comparison of wasp (blue) and bee (pink) families of increasing pollen density (top), pollen fidelity (middle) and visit fidelity values (bottom). Letters above the graph indicate which bee and wasp families are similar according to Cohen's D effect size and *t*-test results (Table S7). Families are shown by the first three letters of their family name (Table S2). Bee families are Andrenidae (AND), Apidae (API), Colletidae (COL), Halictidae (HAL), and Megachilidae (MEG). Wasp families are Braconidae (BRA), Chrysididae (CHR), Crabronidae (CRA), Ichneumonidae (ICH), Sphecidae (SPH) and Vespidae (VES). 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 each whisker extends to the most extreme value within 1.5 IQR from the box.

the wasp family Crabronidae had similar Visit Fidelity as the bee families Colletidae and Megachilidae. Altogether, these observations suggest that while overall bee families outperform wasp families in terms of pollen-carrying capacity, some wasp families are similar to or exceed specific groups of bees in pollen-carrying and plant fidelity. High fidelity can lead to more successful plant pollination and higher

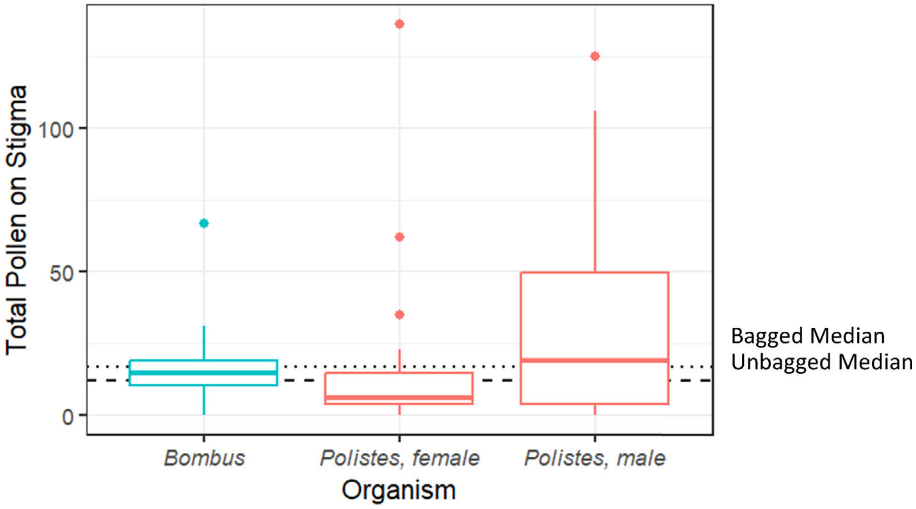


FIGURE 7 Distribution of the total pollen grains on *Solidago canadensis* species complex stigmas after a visit from a single insect. Lines show the median values of the Bagged (never visited) and Unbagged (visited multiple times) control groups. The middle line inside the box shows the median value, the upper and lower limits of the box showing the 75th and 25th quartiles respectively, and each whisker extends to the most extreme value within 1.5 IQR from the box.

TABLE 3 Summary of statistical contrasts comparing the pollen deposition of a single visit from an insect (male *P. fuscatus*, female *P. fuscatus* and *B. impatiens*) or a control treatment (Bagged, never visited; Unbagged, visited multiple times).

Contrast	Estimate	df	t ratio	*p* value
Unbagged—Bagged	−10.84 ± 6.41	81.8	−1.692	0.4443
Unbagged—*Bombus*	−3.68 ± 9.04	83.5	−0.408	0.9941
Unbagged—*Polistes* females	−1.75 ± 9.01	83.1	0.195	0.9997
Unbagged—*Polistes* males	−17.10 ± 6.33	81.5	−2.701	0.0625
Bagged—*Bombus*	7.16 ± 9.08	83.3	0.789	0.9332
Bagged—*Polistes* females	9.09 ± 9.05	82.9	1.004	0.8527
Bagged—*Polistes* males	−6.26 ± 6.39	81.2	−0.979	0.8639
Bombus—*Polistes* females	1.93 ± 11.07	83.7	0.174	0.9998
Bombus—*Polistes* males	−13.42 ± 9.03	83.2	−1.487	0.5740
Polistes males—*Polistes* females	15.35 ± 9.00	82.8	−1.706	0.4361

Note: Contrasts were calculated from a linear mixed-effects model: total_pollen ~ (1|specimen_id) + treatment. *p*-values were adjusted using a Tukey method and degrees of freedom were calculated using a Kenward–Roger method.

fruit set (Morales & Traveset, 2008) if it is made available for plant pollination (Adler & Irwin, 2006; Carvalho & Schlindwein, 2011; Cerceau et al., 2019). Therefore, this study provides evidence that wasps can carry comparable levels of pollen matching the plant species they often visit.

Fourth, our controlled study revealed that male paper wasps, *P. fuscatus*, may deposit more pollen grains in a single visit than multiple visits to a flower from both *B. impatiens* and *P. fuscatus* (Table 3). However, the true impact of this deposition requires further study due to similar pollen deposition in both the insect exclusion treatment (Bagged) and multiple insect visitation treatment (Unbagged), suggesting high levels of self-pollination. The plant complex *S. candensis* is largely self-incompatible (Blackwell & Powell, 1981; Melville & Morton, 1982); therefore, the Bagged treatment in this plant complex is uninformative due to the high chance of the pollen deposition we observed being incompatible pollen from self-pollination. Future studies should, therefore, analyse seed set alongside pollen deposition to more directly study plant pollination (Ne'eman et al., 2010). Seed set is more directly related to pollination than metrics commonly used for bees such as body pollen carriage and plant visitation (Carvalho & Schlindwein, 2011; Cerceau et al., 2019; King et al., 2013; Pick & Schlindwein, 2011). Importantly, this study introduces an effective method for quantifying wasp pollination in a controlled environment, which can be used for future studies. Our investigational approach allows researchers to decouple wasps' split attention between two very different resources—flowers and prey items—and focuses wasps' behaviour to floral visitation (Hunt, 2007), allowing scientists to perform detailed studies of wasp pollination biology.

Our study provides compelling evidence that wasps are important elements of the pollinator community, but more research is needed to fully understand their role in plant pollination. While we show that wasps are comparable to bees in terms of plant interactions, visited plant community composition, body pollen carriage and composition, and pollen deposition, our work represents only one study in one environment. This contributes to the increasing number of studies citing the importance of understudied taxa in pollination services (Rader et al., 2016; Rader et al., 2020) and highlights the need for a renewed focus on wasp pollination research. In addition, our study provides crucial methods for future studies on the ecological role of wasps as pollinators. One important contribution of this study is that we demonstrate that directed single-visit pollen deposition is possible to study in wasps; however, we suggest future studies should look at other plant species besides the plant complex *S. canadensis*. We chose this plant based on previous data indicating the plant complex *S. canadensis* is commonly visited by *P. fuscatus* (Table S4), which carries a high proportion of the plant complex *S. canadensis* pollen (Figure S1). However, while this plant complex is dependent on outcrossing for seed production (Blackwell & Powell, 1981; Melville & Morton, 1982), it often deposits pollen on its own stigmas, making pollen deposition complicated to assess. We suggest future studies should investigate seed set, in addition to pollen deposition to gain a more complete understanding of wasps' roles in plant reproduction.

Moving forward, more research attention at the community level that includes wasp taxa is also needed to establish the reliance of plants on wasp-mediated pollination. Wasps appear to visit a distinct plant community not utilised by other pollinator groups, potentially causing bias if excluded from pollination studies (Jordano, 2016). In addition, wasps' dual role as pollinators and pest predators (Brock et al., 2021; Southon et al., 2019; Wang et al., 2019) makes them underutilised beneficial insects in crop production. For example, social wasps in the genus *Polistes* have developed methods for rearing and attracting nests in the field and could be deployed in a similar manner as bumble bees and honey bees in agricultural landscapes. Overall, our data suggest that on a broad scale, wasps' pollination ability is more comparable to other pollinator groups than historically expected (Fægri & van der Pijl, 1979; Proctor, 1996) and research should focus on filling in our knowledge gap on wasps' true contribution to global plant pollination.

AUTHOR CONTRIBUTIONS

Kate E. Borchardt: Conceptualization; investigation; writing – original draft; methodology; validation; visualization; software; formal analysis; data curation. **Danielle Holthaus:** Conceptualization; investigation; methodology; writing – review and editing; data curation. **Paola A. Soto Méndez:** Writing – review and editing; investigation. **Amy L. Toth:** Conceptualization; writing – original draft; writing – review and editing; supervision; resources; project administration; funding acquisition.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Debunking Wasp Pollination at https://github.com/kateborc/Debunking-Wasp-Pollination.

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REFERENCES

Adler, L.S. & Irwin, R.E. (2006) Comparison of pollen transfer dynamics by multiple floral visitors: experiments with pollen and fluorescent dye. *Annals of Botany*, 97, 141–150.

Almeida-Neto, M., Guimarães, P., Guimarães, P.R., Jr., Loyola, R.D. & Ulrich, W. (2008) A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. *Oikos*, 117, 1227–1239.

United States Department of Agriculture. (2019) *Conservation Reserve Program Fact Sheet: Prairie Strip Practice (CP-43)*. Washington, D.C: Farm Service Agency.

Ascher, J.S. & Pickering, J. (2020) Discover life bee species guide and world checklist (Hymenoptera: Apoidea: Anthophila). *DiscoverLife*. Available from: http://www.discoverlife.org/mp/20q?guide=Apoidea_species&flags=HAS. [Accessed 2020]

Aslan, C.E., Liang, C.T., Shiels, A.B. & Haines, W. (2018) Absence of native flower visitors for the endangered Hawaiian mint Stenogyne angustifolia: impending ecological extinction? *Global Ecology and Conservation*, 16, e00468.

Bascompte, J. & Jordano, P. (2014) *Mutualistic networks*. Princeton, NJ, Princeton University Press.

Bascompte, J., Jordano, P., Melián, C.J. & Olesen, J.M. (2003) The nested assembly of plant–animal mutualistic networks. *Proceedings of the National Academy of Sciences*, 100, 9383–9387.

Bates, D., Mächler, M., Bolker, B. & Walker, S. (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67, 1–48.

Bernhardt, P. & Goldblatt, P. (2006) The role of phylogenetic constraints in the evolution of pollination mechanisms in Iridaceae of sub-Saharan Africa. *Aliso*, 22, 434–444.

Blackwell, W.H. & Powell, M.J. (1981) Observations on late season pollination of *Solidago canadensis* L. (Asteraceae) in Southwest Ohio. *Castanea*, 46, 136–139.

Blüthgen, N., Menzel, F. & Blüthgen, N. (2006) Measuring specialization in species interaction networks. *BMC Ecology*, 6, 9.

Borchardt, K.E., Kadelka, C., Schulte, L.A. & Toth, A.L. (2023) An ecological networks approach reveals restored native vegetation benefits wild bees in agroecosystems. *Biological Conservation*, 287, 110300.

Bosch, J., Martín González, A.M., Rodrigo, A. & Navarro, D. (2009) Plant–pollinator networks: adding the pollinator's perspective. *Ecology Letters*, 12, 409–419.

Brock, R.E., Cini, A. & Sumner, S. (2021) Ecosystem services provided by aculeate wasps. *Biological Reviews*, 96, 1645–1675.

Carpenter, J. & Cumming, J. (1985) A character analysis of the North American potter wasps (Hymenoptera: Vespidae; Eumeninae). *Journal of Natural History*, 19, 877–916.

Carvalho, A.T. & Schlindwein, C. (2011) Obligate association of an oligolectic bee and a seasonal aquatic herb in semi-arid north-eastern Brazil. *Biological Journal of the Linnean Society*, 102, 355–368.

Cerceau, I., Siriani-Oliveira, S., Dutra, A.L., Oliveira, R. & Schlindwein, C. (2019) The cost of fidelity: foraging oligolectic bees gather huge amounts of pollen in a highly specialized cactus–pollinator association. *Biological Journal of the Linnean Society*, 128, 30–43.

Coombs, G., Peter, C.I. & Johnson, S.D. (2009) A test for Allee effects in the self-incompatible wasp-pollinated milkweed Gomphocarpus physocarpus. *Austral Ecology*, 34, 688–697.

de Santos, G.M., Aguiar, C.M.L. & Mello, M.A.R. (2010) Flower-visiting guild associated with the Caatinga flora: trophic interaction networks formed by social bees and social wasps with plants. *Apidologie*, 41, 466–475.

Dewitz, J. (2019) National Land Cover Database (NLCD) 2016 Products (ver. 2.0, July 2020).

Dormann, C.F., Fründ, J., Blüthgen, N. & Gruber, B. (2009) Indices, graphs and null models: analyzing bipartite ecological networks. *The Open Ecology Journal*, 2, 7–24.

Dunn, L., Lequerica, M., Reid, C.R. & Latty, T. (2020) Dual ecosystem services of syrphid flies (Diptera: Syrphidae): pollinators and biological control agents. *Pest Management Science*, 76, 1973–1979.

Fægri, K. & van der Pijl, L. (1979) *The principles of pollination ecology*. Pergamon international library of science, technology, engineering and social studies, 3d rev. edition. Oxford: Pergamon Press.

Fisogni, A., Quaranta, M., Grillenzoni, F.-V., Corvucci, F., de Manincor, N., Bogo, G. et al. (2018) Pollen load diversity and foraging niche overlap in a pollinator community of the rare *Dictamnus albus* L. *Arthropod-Plant Interactions*, 12, 191–200.

Fründ, J., McCann, K.S. & Williams, N.M. (2016) Sampling bias is a challenge for quantifying specialization and network structure: lessons from a quantitative niche model. *Oikos*, 125, 502–513.

Gauld, I. & Bolton, B. (Eds.). (1988) *The Hymenoptera*. Oxford, UK: Oxford University Press.

Giannini, T.C., Garibaldi, L.A., Acosta, A.L., Silva, J.S., Maia, K.P., Saraiva, A.M. et al. (2015) Native and non-native supergeneralist bee species have different effects on plant-bee networks. *PLoS One*, 10, e0137198.

Goldblatt, P. & Manning, J.C. (2006) Radiation of pollination systems in the Iridaceae of sub-Saharan Africa. *Annals of Botany*, 97, 317–344.

Goulet, H., Huber, J.T. & Canada (Eds.). (1993) *Hymenoptera of the world: an identification guide to families*. Ottawa: Centre for Land and Biological Resources Research.

Hatfield, R., Jepson, S., Vaughan, M., Black, S. & Lee-Mader, E. (2018) *An overview of the potential impacts of honey bees to native bees, plant communities, and ecosystems in wild landscapes*. Portland, OR: Xerces Society for Invertebrate Conservation.

Herre, E.A., Jandér, K.C. & Machado, C.A. (2008) Evolutionary ecology of figs and their associates: recent progress and outstanding puzzles. *Annual Review of Ecology, Evolution, and Systematics*, 39, 439–458.

Holm, H. (2021) *Wasps: their biology, diversity, and role as beneficial insects and pollinators of native plants*. Minnetonka, MN: Pollination Press LLC.

Hunt, J.H. (2007) *The evolution of social wasps*. Oxford: Oxford University Press.

Jandt, J.M., Tibbetts, E.A. & Toth, A.L. (2014) Polistes paper wasps: a model genus for the study of social dominance hierarchies. *Insectes Sociaux*, 61, 11–27.

Jordano, P. (2016) Sampling networks of ecological interactions. *Functional Ecology*, 30, 1883–1893.

King, C., Ballantyne, G. & Willmer, P.G. (2013) Why flower visitation is a poor proxy for pollination: measuring single-visit pollen deposition, with implications for pollination networks and conservation. *Methods in Ecology and Evolution*, 4, 811–818.

Knight, T.M., Ashman, T.-L., Bennett, J.M., Burns, J.H., Passonneau, S. & Steets, J.A. (2018) Reflections on, and visions for, the changing field of pollination ecology. *Ecology Letters*, 21, 1282–1295.

Lenth, R.V., Bolker, B., Buerkner, P., Giné-Vázquez, I., Herve, M., Jung, M. et al. (2023) emmeans: estimated marginal means, aka least-squares means. R package version 1.8.6, https://github.com/rvlenth/emmeans.

MacGillivray, D.B. (1987) A centrifuging method for the removal of insect pollen loads. *Journal of the Entomological Society of Southern Africa*, 50, 521–523.

Mazokin-Poshniakov, G.A. & Grasvekaya, E.E. (1966) Recognition of colour combinations and the comparison of this ability in bees and wasps. *Zhurnal Obshchei Biologii*, 27, 112–116.

Mello, M.A.R., de Mendonça Santos, G.M., Mechi, M.R. & Hermes, M.G. (2011) High generalization in flower-visiting networks of social wasps. *Acta Oecologica*, 37, 37–42.

Melville, M.R. & Morton, J.K. (1982) A biosystematic study of the *Solidago canadensis* (Compositae) complex. I. The Ontario populations. *Canadian Journal of Botany*, 60, 976–997.

Miller, W.E. (1981) Composition of goldenrod (Solidago: Compositae) populations by species in the Upper Midwest. *Journal of the Minnesota Academy of Science*, 47, 15–17.

Morales, C.L. & Traveset, A. (2008) Interspecific pollen transfer: magnitude, prevalence and consequences for plant fitness. *Critical Reviews in Plant Sciences*, 27, 221–238.

Murray, C.J. (2021) *Pollinator response to prairie strips in the Iowa agricultural landscape*. Master of Science. Ames, IA: Iowa State University.

Ne'eman, G., Jürgens, A., Newstrom-Lloyd, L., Potts, S.G. & Dafni, A. (2010) A framework for comparing pollinator performance: effectiveness and efficiency. *Biological Reviews*, 85, 435–451.

Oksanen, J., Simpson, G.L., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R. et al. (2022) vegan: community ecology package. R package version 2.6-4, https://CRAN.R-project.org/package=emmeans.

Ollerton, J., Johnson, S.D., Cranmer, L. & Kellie, S. (2003) The pollination ecology of an assemblage of grassland asclepiads in South Africa. *Annals of Botany*, 92, 807–834.

O'Neill, K.M. (2019) Solitary wasps: behavior and natural history. In: *Solitary wasps*, Cornell series in Anthropod biology. Ithaca, NY: Cornell University Press.

Orford, K.A., Vaughan, I.P. & Memmott, J. (2015) The forgotten flies: the importance of non-syrphid Diptera as pollinators. *Proceedings of the Royal Society B: Biological Sciences*, 282, 20142934.

Pellissier, L., Albouy, C., Bascompte, J., Farwig, N., Graham, C., Loreau, M. et al. (2018) Comparing species interaction networks along environmental gradients. *Biological Reviews*, 93, 785–800.

Pick, R.A. & Schlindwein, C. (2011) Pollen partitioning of three species of Convolvulaceae among oligolectic bees in the Caatinga of Brazil. *Plant Systematics and Evolution*, 293, 147–159.

Praz, C.J., Müller, A. & Dorn, S. (2008) Specialized bees fail to develop on non-host pollen: do plants chemically protect their pollen. *Ecology*, 89, 795–804.

Proctor, M.C.F. (1996) *The natural history of pollination*. Portland, OR: Timber Press.

R Core Team. (2019) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Rader, R., Bartomeus, I., Garibaldi, L.A., Garratt, M.P.D., Howlett, B.G., Winfree, R. et al. (2016) Non-bee insects are important contributors to global crop pollination. *Proceedings of the National Academy of Sciences*, 113, 146–151.

Rader, R., Cunningham, S.A., Howlett, B.G. & Inouye, D.W. (2020) Non-bee insects as visitors and pollinators of crops: biology, ecology, and management. *Annual Review of Entomology*, 65, 391–407.

Ripley, B., Venables, B., Bates, D.M., Hornik, K., Gebhardt, A. & Firth, D. (2023) MASS: support functions and datasets for Venables and Ripley's MASS.

Sann, M., Niehuis, O., Peters, R.S., Mayer, C., Kozlov, A., Podsiadlowski, L. et al. (2018) Phylogenomic analysis of Apoidea sheds new light on the sister group of bees. *BMC Evolutionary Biology*, 18, 71.

Schulte, L.A., Niemi, J., Helmers, M.J., Liebman, M., Arbuckle, J.G., James, D.E. et al. (2017) Prairie strips improve biodiversity and the delivery of multiple ecosystem services from corn–soybean croplands. *Proceedings of the National Academy of Sciences*, 114, 11247–11252.

Semple, J. & Cook, J.C. (2006) Solidago Linnaeus. In: *Floral of North America*. Oxford, England: Oxford University Press. pp. 107–166.

Semple, J.C., Faheemuddin, H., Chong, Y.A., Sorour, M.K., Hood, J.A., Khamis, I. et al. (2013) A multivariate morphometric study of the *Solidago canadensis*/*S. lepida* complex of Solidago subsect. Triplinerviae. I. Northeastern taxa (Asteraceae: Astereae). *Phytoneuron*, 58, 280–292.

Semple, J.C., Ringius, G.S., Leeder, C. & Morton, G. (1984) Chromosome numbers of goldenrods, Euthamia and Solidago (Compositae: Astereae). II. Additional counts with comments on cytogeography. *Brittonia*, 36, 280–292.

Smith, D.D. (1998) Iowa prairie: original extent and loss, preservation and recovery attempts. *Journal of the Iowa Academy of Science*, 105, 94–108.

Southon, R.J., Fernandes, O.A., Nascimento, F.S. & Sumner, S. (2019) Social wasps are effective biocontrol agents of key lepidopteran crop pests. *Proceedings of the Royal Society B: Biological Sciences*, 286, 20191676.

Sumner, S. (2022) *Endless forms: the secret world of wasps*. Glasgow, Scotland: HarperCollins Publishers.

Sumner, S., Law, G. & Cini, A. (2018) Why we love bees and hate wasps. *Ecological Entomology*, 43, 836–845.

Thorp, R.W. (1979) Structural, behavioral, and physiological adaptations of bees (Apoidea) for collecting pollen. *Annals of the Missouri Botanical Garden*, 66, 788–812.

Thorp, R.W. (2000) The collection of pollen by bees. In: Dafni, A., Hesse, M. & Pacini, E. (Eds.) *Pollen and pollination*. Vienna: Springer, pp. 211–223.

Upadhaya, S., Arbuckle, J.G. & Schulte, L.A. (2021) Developing farmer typologies to inform conservation outreach in agricultural landscapes. *Land Use Policy*, 101, 105157.

US National Weather Service. (2000) *Des Moines, IA climate*. Washington, DC: National Oceanic and Atmospheric Administration.

Valido, A., Rodríguez-Rodríguez, M.C. & Jordano, P. (2019) Honeybees disrupt the structure and functionality of plant-pollinator networks. *Scientific Reports*, 9, 4711.

VanDyk, J. & Bartlett, T. (2020) *BugGuide—identification, images, & information for insects*. United States Geological Survey: Spiders & Their Kin for the United States & Canada.

Vázquez, D.P., Melián, C.J., Williams, N.M., Blüthgen, N., Krasnov, B.R. & Poulin, R. (2007) Species abundance and asymmetric interaction strength in ecological networks. *Oikos*, 116, 1120–1127.

Walton, A. & Toth, A.L. (2021) Resource limitation, intra-group aggression and brain neuropeptide expression in a social wasp. *Functional Ecology*, 35, 2241–2252.

Wang, Z., Liu, Y., Shi, M., Huang, J. & Chen, X. (2019) Parasitoid wasps as effective biological control agents. *Journal of Integrative Agriculture*, 18, 705–715.

Ward, K., Cariveau, D., May, E., Roswell, M., Vaughan, M., Williams, N.M. et al. (2014) Streamlined bee monitoring protocol for assessing pollinator habitat. 16 pp. Portland, OR: The Xerces Society for Invertebrate Conservation.

Watts, D.J. & Strogatz, S.H. (1998) Collective dynamics of 'small-world' networks. *Nature*, 393, 440–442.

Williams, N.M., Ward, K.L., Pope, N., Isaacs, R., Wilson, J., May, E.A. et al. (2015) Native wildflower plantings support wild bee abundance and diversity in agricultural landscapes across the United States. *Ecological Applications*, 25, 2119–2131.

Willmer, P.G., Cunnold, H. & Ballantyne, G. (2017) Insights from measuring pollen deposition: quantifying the pre-eminence of bees as flower visitors and effective pollinators. *Arthropod-Plant Interactions*, 11, 411–425.

Zemenick, A.T., Kula, R.R., Russo, L. & Tooker, J. (2019) A network approach reveals parasitoid wasps to be generalized nectar foragers. *Arthropod-Plant Interactions*, 13, 239–251.

Zettlemoyer, M.A., Schultheis, E.H. & Lau, J.A. (2019) Phenology in a warming world: differences between native and non-native plant species. *Ecology Letters*, 22, 1253–1263.

Zhang, G., Kersten, M., Owen, A. & Skidmore, A. (2023) Honey bee foraging and pesticide exposure in a desert urban agroecosystem. *Ecotoxicology and Environmental Safety*, 249, 114472.

Zhang, G., St. Clair, A.L., Dolezal, A.G., Toth, A.L. & O'Neal, M.E. (2021) North American prairie is a source of pollen for managed honey bees (Hymenoptera: Apidae). *Journal of Insect Science*, 21, 17.

Zhang, G., St. Clair, A.L., Dolezal, A.G., Toth, A.L. & O'Neal, M.E. (2022) Can native plants mitigate climate-related forage dearth for honey bees (Hymenoptera: Apidae)? *Journal of Economic Entomology*, 115, 1–9.

SUPPORTING INFORMATION

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

Data S1. Supporting Information.

Table S1. Total interactions by plant species and site. Site is shown as the three-letter site code and a treatment code (PS = prairie strip, FM = field margin). Some plant groups were not identified taxonomically, but were not one of the other plant groups. These were given a name "unk" for unknown and the number of the specimen from which it was first identified. Images of these pollen groups will be made available on github.

Table S2. Network sizes used for rarefaction analysis. Networks were subsampled to the smallest network size in their site and habitat type. Two sites were too small for accurate rarefaction analysis (indicated inside parenthesis with an asterisk), therefore the other networks were subsampled to the next smallest network (Pollinators species = 7, Plant species = 15).

Table S3. Genera, specimen counts (in parenthesis), and total specimens analyzed for the bee and wasp families used for the body pollen analysis in experiment 2. Only families with more than 5 specimens were included in this analysis.

Table S4. From the 2019 data used in experiment 1 and 2, analysis of the interaction frequency of bees and wasps to *Solidago* spp., with the two species used in experiment 3 bolded. *Apis mellifera* were recorded in the field but not collected, therefore they did not have their pollen interactions analyzed.

Table S5. Total count of wasp and bee interactions by interaction type (observed, pollen) and site. Site is shown by the three-letter site code and the treatment. Each bee and wasp genus was given an unique 3-4 letter code used in Figure S2's network graphs. Honey bees were identified and tallied in the field without collection ("Tallied").

Table S6. Z-scores and *P*-values from comparison of raw network traits to 1000 randomly created null models, in order to determine the likelihood of observed network traits being caused by random assortment of interactions. Habitat types are coded as "PS" for Prairie Strips and "FM" for Field Margins. Organism describes whether the network contained only bees, wasps, or both bees and wasps ("combined").

Table S7. Cohen's D and results of pairwise Welch two-sample *t*-tests for each wasp family and bee family for Pollen Density (top), Pollen Fidelity (middle), and Visit Fidelity (bottom). D-values and P-values are reported with the t-value and degrees of freedom in parenthesis. We used two criteria to determine if the bee and wasp family tested were similar: (a) the *p*-value of the *t*-test was greater than 0.05 and (b) Cohen's D was less than the absolute value of 0.8. Blue cells indicate the families were considered similar and yellow cells indicate when the families were considered different, but the wasp family had a greater metric value.

Figure S1. A companion study comparing the density of *Solidago* spp. pollen grains on one transect of the pollen slides, used as a metric for total body pollen carriage, between *Polistes fuscatus* to Goldenrod Soldier Beetle (*C. pensylvanicus*). The density of *Solidago* spp. pollen grains was statistically similar between the groups (Welch Two Sample *t*-test, $t = 0.0904$, $df = 79.25$, $p\text{-value} = 0.9281$). Specimens were collected from September 2020 to October 2020 on Iowa State University campus in a restored prairie that was mostly in the plant complex *Solidago canadensis*. Insects were netted from the plant complex *Solidago canadensis* patches during 10 minute observation periods for each patch.

Figure S2. Wasp and bee networks from Prairie Strips (top) and Field Margins (bottom). In each network, the pollinator species are at the top and plant species at the bottom (to decode, see Table S3 & S4). The connecting lines indicate interactions with thickness showing relative abundance of that interaction within that specific network.

Figure S3. Exploratory networks by site type (Prairie Strips top, Field Margins bottom). There was not enough data points for a statistical comparison.

Figure S4. Boxplot of pollen deposition on stigmas from the Bagged and Unbagged treatments. Not significantly different ($T\text{-ratio} = -1.692$, $p\text{-value} = 0.0944$).

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