

ARTICLE

Pollen–insect interaction meta-networks identify key relationships for conservation in mosaic agricultural landscapes

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Abstract

Flower visitors use different parts of the landscape through the plants they visit, however these connections vary within and among land uses. Identifying which flower-visiting insects are carrying pollen, and from where in the landscape, can elucidate key pollen–insect interactions and identify the most important sites for maintaining community-level interactions across land uses. We developed a bipartite meta-network, linking pollen–insect interactions with the sites they occur in. We used this to identify which land-use types at the site- and landscape-scale (within 500 m of a site) are most important for conserving pollen–insect interactions. We compared pollen–insect interactions across four different land uses (remnant native forest, avocado orchard, dairy farm, rotational potato crop) within a mosaic agricultural landscape. We sampled insects using flight intercept traps, identified pollen carried on their bodies and quantified distinct pollen–insect interactions that were highly specialized to both natural and modified land uses. We found that sites in crops and dairy farms had higher richness of pollen–insect interactions and higher interaction strength than small forest patches and orchards. Further, many interactions involved pollinator groups such as flies, wasps, and beetles that are often under-represented in pollen–insect network studies, but were often connector species in our networks. These insect groups require greater attention to enable wholistic pollinator community conservation. Pollen samples were dominated by grass (Poaceae) pollen, indicating anemophilous plant species may provide important food resources for pollinators, particularly in modified land uses. Field-scale land use (within 100 m of a site) better predicted pollen–insect interaction richness, uniqueness, and strength than landscape-scale. Thus, management focused at smaller scales may provide more tractable outcomes for conserving or restoring pollen–insect interactions in modified landscapes. For instance, actions aimed at linking high-richness sites with those containing unique (i.e., rare) interactions by enhancing floral

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corridors along field boundaries and between different land uses may best aid interaction diversity and connectance. The ability to map interactions across sites using a meta-network approach is practical and can inform land-use planning, whereby conservation efforts can be targeted toward areas that host key interactions between plant and pollinator species.

KEYWORDS

bipartite network, Diptera, ecosystem services, plant–pollinator networks, Poaceae, specialization, wind pollination

INTRODUCTION

Quantifying pollinator community responses to changes in land use is essential because both wild and managed species provide critical pollination services to plants in natural and modified landscapes (Garibaldi et al., 2013; Klein et al., 2007; Rader et al., 2016; Winfree et al., 2011). While many studies indicate that several ecosystem functions and/or services are at risk from land-use change and intensification (Kremen et al., 2002; Potts et al., 2010), responses of individual organisms to such changes are often variable (Bommarco et al., 2010; Cariveau et al., 2013; Rader et al., 2014; Stavert et al., 2017). This means detecting and understanding how plant and pollinator communities respond to land-use change is both species and context dependent. To date, most studies of pollinator community responses to land-use change have focused on species-level relationships with the amount or proximity to natural and seminatural vegetation (Banks et al., 2013; Greenleaf & Kremen, 2006; Hall et al., 2019; Holzschuh et al., 2016). While network studies exist that specifically link interactions with land-use change (e.g., exploring habitat fragmentation on calcareous grassland pollinator communities; Grass et al., 2018), few explore pollinator community interactions across different land-use types. Those that do tend to focus on mutualistic or antagonistic interactions with other insect groups (i.e., herbivores and parasites) (Hackett et al., 2019; Morrison et al., 2020) rather than pollen–insect interactions. Additionally, most studies on land-use impacts to pollinators fail to explore the direct contribution of non-bee pollinators (Senapathi et al., 2017, but see Weiner et al., 2014), despite the abundance of multiple arthropod groups that pollinate flowers (Wardhaugh, 2015).

The responses of pollinator species to more intensive land uses, such as agriculture, are dependent on a number of factors including body size, social structure, nesting requirements, feeding behavior and larval food availability (Hall et al., 2019; Henle et al., 2004; Rader et al., 2014). However, pollinator community composition is also directly influenced by changes in the availability of resources across space and time (Winfree &

Kremen, 2009). Different land-use types vary in the quantity and quality of resources, shaping use of these environments by pollinators based on if they can exploit available resources. For example, diverse bee communities are maintained by heterogeneous adjacent habitats that provide diverse food and nesting resources throughout the season (Winfree et al., 2011), while hover fly abundance and richness is dependent on food resources available for larval development and habitat connectivity within landscapes (Haenke et al., 2014; Power & Stout, 2011). These landscape attributes ultimately affect which pollen–insect interactions occur, where they occur, and how frequently.

In agricultural landscapes, knowledge of how pollen–insect interactions change across land uses is essential to understand the effects of intensive land management on the composition and performance of pollinator communities within the landscape. Understanding which floral resources are used by different taxa enables identification of agriculturally and ecologically important pollinators, as well as potential management actions to enhance the provision of pollination services. While linking the frequency of visits by pollinators to different plants at a particular site is the basic principle of plant–pollinator network studies (Memmott, 1999), the connection between species and sites through species-habitat networks (*sensu* Marini et al., 2019) allows for a landscape-scale view of species-habitat dependencies. This is important to inform conservation and management priorities by identifying pollinator species or habitats that are critical for network structure (Saunders & Rader, 2019). While this type of meta-network approach has been developed to examine, for example, bird seed dispersal or frugivory interactions (Emer et al., 2018; Li et al., 2020), it has not been widely used to understand pollinator community dynamics across multiple land-use types. Landscape-level meta-networks can identify ecosystem services provided by pollinators and inform conservation objectives in numerous ways. First, they can identify generalist pollen–insect interactions across multiple sites that may be important in dispersal across landscapes and land uses. Second, they can identify the importance of each

land use for maintaining unique pollen–insect interactions that may require conservation to ensure their persistence in modified environments. Finally, this approach enables identification of the scale (e.g., field or landscape) at which such interactions are important, ensuring conservation efforts can be targeted accordingly.

Here, we build on the species–habitat network approach, by connecting pollen transport networks (e.g., Alarcón, 2010; Popic et al., 2013) with the field-scale land uses in which they originate, to generate a pollen–insect interaction-site bipartite meta-network. Specifically, we use data comparing pollen–insect interactions across four different field-scale land uses that vary in management intensity, in a heterogeneous agricultural region of Australia, to test the utility of our approach. Specifically, we use the meta-network approach to ask:

1. How does field-scale land-use type influence insect abundance and the proportion of insect taxa that are pollen vectors?
2. At what scale do pollen–insect interactions respond most strongly to surrounding land use (field- or landscape-scale)?
3. Considering the scale that land use most strongly affects pollen–insect interactions, how do different land uses affect pollen–insect interactions?

METHODS

Site selection

Sites were located in the mosaic landscape of the Atherton Tablelands of northeastern Queensland, located inland from the city of Cairns (17°18' S, 145°29' E to 17°36' S, 145°44' E) in northeast Australia (Appendix S1: Figure S1). The area is known for its world heritage remnant vegetation and productive agriculture including horticulture, dairy, and arable cropping. Mean annual temperature is 20.2°C and mean annual precipitation is approximately 1700 mm/year, most of which falls between December and May. The Köppen classification for this region is “humid subtropical climate.” The pre-clearing vegetation type of the sampled vegetation remnants in the region was predominately of notophyll vine forest. These forests can be complex, simple, evergreen, semievergreen, and semideciduous and occur mostly from foothills to uplands. Trees have a canopy height of 24–33 m and communities occur generally on basalt and granite soils (Tracey, 1982).

Twenty-four replicates (six replicates per land use) were selected in four different land-use types: (i) remnant forest, (ii) avocado *Persea americana* Mill. orchard, (iii) dairy farm, and (iv) arable crop (potato *Solanum tuberosum* L.)

(Appendix S1: Figure S1). These represent the major conventional agriculture and natural land uses in the study area (DAF 2015) and exhibit different levels of land use intensity. For instance, forest sites receive very little disturbance to plants and soil, while avocado are a long-lived tree that can produce crops for 15–40 years (Goodall et al., 1971), thus requiring little regular mechanical disturbance (Appendix S1: Table S1). Dairy sites undergo more regular disturbance through grazing and trampling of plants by stock (Burgess et al., 2000), and potato crops require intensive soil disturbance for continual crop rotation (Honeycutt et al., 1996) (Appendix S1: Table S1). Sites were separated by at least 1.5 km, with most being ~3 km from the nearest neighboring site. These distances are greater than average foraging flight and pollen transport distances for our focal insect taxa, which are generally <1.5 km (Rader et al., 2011; Smith & Mayfield, 2015; Zurbuchen et al., 2010).

Insect collection

Flower visitors were sampled at the 24 sites for five consecutive days each sampling month using the same “window trap” design published in (figure 2 of Howlett et al., 2009). This design combines a yellow pan trap (34.7 cm L × 21.8 cm W × 6.0 cm depth) with a Perspex flight intercept trap (36.7 cm L × 23.8 cm W × 30.0 cm depth), arranged perpendicular to each other in one unit. We deployed two of these flight intercept pan traps (herein referred to as “insect traps”) for a total of 2880 trap nights in the months of February, April, and June 2008, to ensure the greatest diversity across wet, pre-dry, and dry seasons. Insect traps were placed at the centre of the focal site. At each site, two traps were positioned 2 m apart on stakes at a height of 1.2 m. To facilitate pollen collection on insects, we lined the insect traps with clear acetate sheets 22 cm × 30 cm and tangle foot paste (The Tanglefoot Company, Grand Rapids, MI, USA). Tanglefoot was applied as a thin film to the surface of the acetate sheet to maximize insect capture while preventing loss of pollen to excess drops of Tanglefoot. The acetate sheets with trapped insects were replaced daily. Insect samples from each trap pair for each month of sampling were combined, then were sorted into Orders and those carrying pollen (i.e., pollen vectors) were then pinned and identified to family level by experts, using appropriate keys (CSIRO, 2018; Marshall, 2017). Once identified, all insects were pooled across months for analyses. While species-level identification was not possible here, family-level resolution can support conservation decisions, particularly for arthropods which display a high family-species diversity correlation (Zou et al., 2020). Further, most insect families represented comprise multiple genera and species known to visit flowers and

provide some pollination service (see Appendix S1: Table S2 for a list of all families sampled and their ecosystem function). As many species within a family (e.g., Syrphidae) would have similar habitat requirements, conservation measures centered on a particular species or group would likely also benefit others within the same or closely related families.

Pollen identification

Insects mostly stuck to the Tanglefoot by their wings and ended up stuck upside down to the sheet. Thus, to standardize collection and identify pollen carried by potential pollinators between sites, the underside of every insect collected was pressed onto a 3 mm cube of gelatin-fuchsin agar gel on a glass slide (Kearns & Inouye, 1993). The agar was then melted, and a slide coverslip was placed on top. Pollen grains were observed at $\times 100$ magnification, with all visible grains on the slide counted. We then used $\times 400$ magnification to ensure appropriate pollen grain identification. Individual pollen grains were photographed and identified to family level, which was the highest taxonomic resolution attainable as determined by leading pollen experts. These pollen identifications were based on morphological characteristics using the Australasian pollen and Spore Atlas (APSA, 2007) and verified by an expert palynologist (SH). To determine a list of possible plant species visited by pollinating insects, known plant records encompassing the study region were downloaded from the Atlas of Living Australia (2021). We then used ArcGIS (v.10.6.1, ESRI, 2018) to identify all recorded plant species within a 100, 500, and 1000 m radius around each sampling site (Available at: 10.5281/zenodo.5157944).

Land-use mapping and analysis

We obtained the amount and composition of surrounding land-use types for each site, from a government data set for the wet tropics region (DSITI, 2016). We calculated land-use diversity (Shannon diversity) of these within two radii around each site: 100 m (field scale) and 500 m (landscape scale), using ArcGIS. We considered 500 m an appropriate landscape scale for this study region as it covers the typical flight range of most insects we recorded (Doyle et al., 2020; He et al., 2012), while avoiding overlapping radii around sites that would violate independence of records. Land use surrounding the sites comprised: natural, grazing (natural), grazing (modified), ground crops, tree crops, residential, commercial and water. We also calculated the proportion of natural habitat at the landscape scale (500 m radius) from aerial photographs using ArcGIS.

Construction of the bipartite interaction-site meta-network and calculation of network metrics

We constructed a bipartite meta-network, linking pollen–insect interactions among sites across the study region, by adapting the species-habitat network approach proposed by (Marini et al., 2019). Specifically, we produced an interaction-site network from the insect and pollen data using two steps. First, we listed pollen–insect pairs based on the pollen grains collected from individual insects. Each of these distinct pollen–insect pairs was assigned a unique identifier, i.e., Syrphidae–Poaceae (syrphid flies carrying Poaceae pollen) had a separate identifier to Syrphidae–Myrtaceae (syrphid flies carrying Myrtaceae pollen). If multiple pollen families were found on a pollinator, a unique pair was made for each. These unique identifiers were upper-level nodes in the network matrix. Second, we linked each unique pollen–insect pair to the lower-level nodes, which were the sites corresponding to the collection of each pollen–insect pair. Thus, values in cells of this weighted network were the frequency that each pollen–insect interaction (the sum number of pollen grains for each pollen taxa counted on each insect taxa) occurred at each site. Sampling completeness of interactions (i.e., based on pollen grains found on insects) was estimated following Devoto et al. (2012), details in Appendix S1: Section S1, Figure S2).

To identify how field-scale land-use type (remnant native forest, avocado orchard, dairy farm, rotational potato crop) alters pollen–insect interactions and to identify the most important sites for conserving interactions, we calculated several complementary metrics from our interaction-site network. First, we computed the richness of pollen–insect interactions at each site (typically referred to as species degree in traditional bipartite networks, Dormann et al., 2009) by summing the number of unique pollen–insect interactions recorded at each site. Second, to identify the importance of each field-scale land use for maintaining unique pollen–insect interactions, we quantified the number of pollen–insect interactions that only occurred at each site. Thus, interaction uniqueness contributes to the importance of each site for maintaining interaction richness across our study region. Third, we calculated the strength of interaction-site dependencies, which is a qualitative extension of species degree (sensu Bascompte et al., 2006), using the “strength” function in the *bipartite* package (Dormann et al., 2019). In traditional bipartite plant–pollinator networks, strength is defined as the sum of dependencies of pollinators on their plant partners or vice versa. However, in our interaction-site network, a site’s strength value is the sum of dependencies of pollen–insect interactions on that site. The combination of complementary network indices (richness, uniqueness, and strength) allowed us to identify the importance of different field-scale land uses for

maintaining pollen–insect interactions from both a qualitative and quantitative perspective.

Statistical analyses

Effects of field-scale land use on occurrence and abundance of pollen transport by insects

To examine the effect of field-scale land use (i.e., remnant native forest, avocado orchard, dairy farm, rotational potato crop) on insect abundance, abundance of pollen found on insects, and the proportion of pollen vectors, we constructed three generalized linear mixed-effects models (GLMM) using the *lme4* package (Bates et al., 2014). We ran models using only the four most abundant insect Orders (Coleoptera, Diptera, Hymenoptera and Lepidoptera), which represented 93.5% of pollen vectors and 94.5% of all sampled individuals, and are generally considered the most important pollinator groups (Wardhaugh, 2015). In general, sample sizes of the remaining taxa were too small to include in GLMM analyses, but were included in subsequent network analyses which are robust to sparse or infrequent data. We assigned a negative binomial distribution to models where the response variable was count data (insect abundance and pollen abundance on insects) after detecting overdispersion using a Poisson distribution. We assumed a binomial distribution for proportional data (proportion of pollen vectors). All models were validated by examining the distribution of residuals plotted against fitted values (Zuur et al., 2009). In all models, either the abundance of each of the four most common insect Orders, pollen abundance on those insect individuals or the proportion of pollen vectors, pooled across all sampling months, was the response variable, while field-scale land use (categorical) and insect order (categorical) were fixed effects in each. We included sampling site identity as a random effect to account for the dependent data structure of multiple sites within land-use categories. Post hoc multiple pairwise comparisons between land uses and insect Orders were tested using estimated marginal means (EMMs, in the *emmeans* package, Lenth, 2018). EMMs are generated using the fitted model to make predictions over a grid of predictor combinations to assess the effects of individual factors. These predicted differences in abundance of individuals, pollen abundance on insects and proportion of pollen vectors from each of the four dominant insect Orders between land uses. We estimated the significance of differences between terms, using Tukey's honestly significant difference (HSD) test with false discovery rate (FDR) corrected *p*-values (at $\alpha = 0.05$) (Verhoeven et al., 2005).

Relative effects of field-scale versus landscape-scale land use on pollen–insect interactions

We investigated the impact of land use on pollen–insect interactions (for the full data set), by comparing the effects of land use at the field scale (land-use type in the field where pollen–insect interactions were recorded) and landscape scale (diversity of land uses at 500 m radius). Specifically, we tested the effects of land use at different scales on pollen–insect interaction richness, uniqueness, and strength, using GLMMs with the “*glmmTMB*” function in the *glmmTMB* package (Brooks et al., 2017). In these models, either interaction richness, uniqueness, or strength, was the response variable (one value for each network metric per site) and field-scale land use (remnant native forest, avocado orchard, dairy farm, rotational potato crop; categorical), landscape-scale proportion of natural habitat (at 500 m radius; continuous) and landscape-scale land-use diversity (Shannon diversity index, continuous) were the fixed effects. We included site identity as a random effect to account for the dependent data structure of multiple sites within field-scale land-use categories. For strength, we repeated the model excluding singleton interactions and found that results were the same as those from the full data set. Therefore, we present the full data set results, including singleton interactions. We used a Poisson distribution truncated at zero for interaction richness, a Poisson distribution for interaction uniqueness, and a Gamma distribution for interaction strength. We did not detect overdispersion in the Poisson models. We also tested for covariance between fixed effects in each model using a modified version of the “*vif*” function in the *car* package (Fox et al., 2016). Variance inflation factor values were low (<3) in all models. Finally, to identify the best models for predicting interaction richness, uniqueness, and strength, we performed small sample corrected Akaike information criterion model selection on the global models, using the “*dredge*” function in the *MuMIn* package (Barton, 2011).

Effects of field-scale land use on pollen–insect interactions

We assessed differences in pollen–insect interaction richness, uniqueness, and strength among land uses using GLMMs (Brooks et al., 2017). In these models, either interaction richness, uniqueness, or strength, was the response variable and field-scale land use (remnant native forest, avocado orchard, dairy farm, rotational potato crop; categorical) was the fixed effect. We included sampling

site identity as a random effect to account for the dependent data structure of multiple sites within field-scale land-use categories. For strength, we repeated the model excluding singleton interactions and found that results were the same as those from the full data set. Therefore,

we present the full data set results, including singleton interactions. We then compared interaction richness, uniqueness, and strength among the different field-scale land uses (remnant native forest, avocado orchard, dairy farm, rotational potato crop) using pairwise least squared

TABLE 1 Differences in pollinator abundance, pollen abundance, and the percentage of pollen vectors by land use and insect Order, based on multiple pairwise comparisons

Response group	Contrast	Est.	SE	z_ratio	p-value
Pollinator abundance by land use	Forest–Avocado	−0.44	0.36	−1.22	0.61
	Forest–Dairy	−1.37	0.36	−3.83	<0.01
	Forest–Crop	−2.01	0.36	−5.62	<0.01
	Avocado–Dairy	−0.93	0.35	−2.64	0.04
	Avocado–Crop	−1.57	0.35	−4.50	<0.01
	Dairy–Crop	−0.64	0.33	−1.96	0.20
Pollinator abundance by insect order	Coleoptera–Diptera	−1.11	0.26	−4.32	<0.01
	Coleoptera–Hymenoptera	1.99	0.32	6.32	<0.01
	Coleoptera–Lepidoptera	1.05	0.28	3.72	<0.01
	Diptera–Hymenoptera	3.10	0.31	10.09	<0.01
	Diptera–Lepidoptera	2.16	0.27	7.98	<0.01
	Hymenoptera–Lepidoptera	−0.94	0.32	−2.99	<0.01
Pollen abundance by land use	Forest–Avocado	−0.20	0.46	−0.44	0.97
	Forest–Dairy	−1.70	0.43	−3.97	<0.01
	Forest–Crop	−1.98	0.42	−4.69	<0.01
	Avocado–Dairy	−1.50	0.42	−3.59	<0.01
	Avocado–Crop	−1.78	0.41	−4.33	<0.01
	Dairy–Crop	−0.28	0.37	−0.77	0.87
Pollen abundance by insect order	Coleoptera–Diptera	−0.92	0.22	−4.10	<0.01
	Coleoptera–Hymenoptera	1.40	0.31	4.46	<0.01
	Coleoptera–Lepidoptera	1.30	0.30	4.31	<0.01
	Diptera–Hymenoptera	2.32	0.30	7.70	<0.01
	Diptera–Lepidoptera	2.22	0.29	7.69	<0.01
	Hymenoptera–Lepidoptera	−0.10	0.36	−0.27	0.99
Pollen vectors by land use	Forest–Avocado	−0.44	0.32	−1.39	0.51
	Forest–Dairy	−1.29	0.31	−4.24	<0.01
	Forest–Crop	−1.96	0.30	−6.53	<0.01
	Avocado–Dairy	−0.85	0.29	−2.91	0.02
	Avocado–Crop	−1.52	0.29	−5.27	<0.01
	Dairy–Crop	−0.66	0.27	−2.44	0.07
Pollen vectors by insect order	Coleoptera–Diptera	−0.07	0.16	−0.44	0.97
	Coleoptera–Hymenoptera	−0.14	0.30	−0.47	0.97
	Coleoptera–Lepidoptera	0.48	0.26	1.84	0.26
	Diptera–Hymenoptera	−0.07	0.28	−0.25	0.99
	Diptera–Lepidoptera	0.55	0.24	2.26	0.11
	Hymenoptera–Lepidoptera	0.62	0.35	1.77	0.29

Note: Significant values ($p < 0.05$) in bold.

means contrasts in the *emmeans* package (Lenth, 2018) and determined significance with FDR corrected *p*-values (at $\alpha = 0.05$) (Verhoeven et al., 2005).

Specialization of pollen–insect interactions to different land-use types

To determine whether frequently occurring pollen–insect interactions (those that occurred ≥ 20 times in our network) were specialized to particular field-scale land uses, we calculated the Paired Difference Index (PDI) (Poisot et al., 2011) with the “PDI” function in the *bipartite* package (Dormann et al., 2019). PDI values are constrained between zero and one, wherein a value of one represents a perfect specialist and zero represents a perfect generalist. We tested the significance of each observed PDI value by comparison against a distribution of 999 PDI values, for each pollen–insect interaction, generated by a null model (for which we give a brief description, see Vázquez et al., 2007 for further details). The null model algorithm we used randomized the total number of pollen–insect interactions occurring at each site, as observed in the original network, by first creating a binary matrix and then filling matrix cells according to the probability of a pollen–insect interaction occurring at a given site. Therefore, each pollen–insect interaction and site occurred at least once in each randomly generated network. Following this, the remaining pollen–insect occurrences at each site were distributed to the filled cells, thus maintaining the original network connectance. All statistical analyses were conducted in R (v.3.6.0, R Core Team, 2019).

RESULTS

Effects of field-scale land use on occurrence and abundance of pollen transport by insects

We collected 1583 individual insects from 41 families, representing 10 Orders. Diptera were the most abundant insect order that we sampled (911 individuals; 57% of total abundance), followed by Coleoptera (372 individuals; 23.5%), Lepidoptera (139 individuals; 9%), and Hymenoptera (77 individuals; 5%) (Appendix S1: Table S3). The abundance of all insect groups was greater in dairy and cropping land uses than forests and avocado orchards (Table 1, Figure 1a). While there was a consistent trend across all insect groups, the relative abundance of each individual insect order differed across local land-use types (Table 1, Figure 1a).

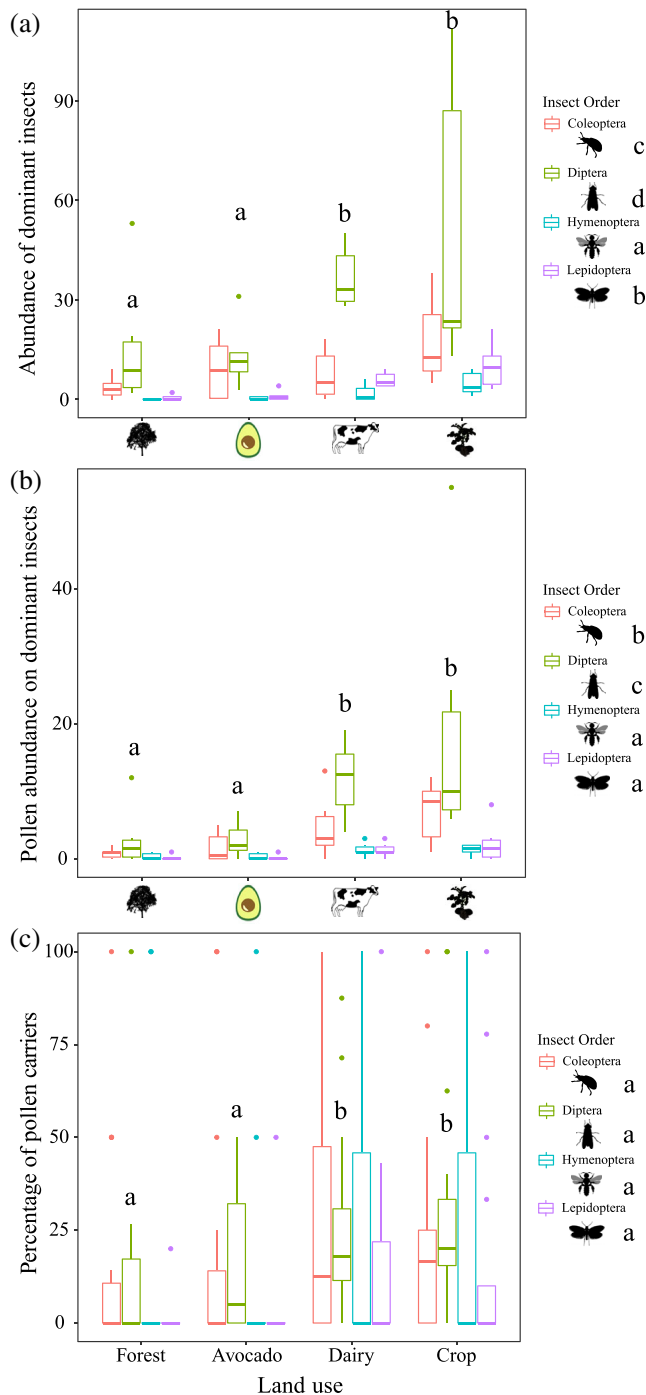


FIGURE 1 Abundance of the four most common insect Orders (a): Coleoptera, Diptera, Hymenoptera, and Lepidoptera pooled across all sites in each of the four different land-use types: remnant forest, avocado orchard, dairy farm, and potato crop. Pollen abundance carried across all sampled individuals (b) and variation in the proportion of pollen vectors from all individuals sampled (c) by each land-use type. Lettering above plots denotes significant groupings by land-use type and lettering next to insect order names denotes differences by Order based on multiple pairwise comparison. Graphical representation of land uses and insect Orders are also provided

TABLE 2 Model rankings for interaction richness, interaction uniqueness, and interaction strength, as determined by AIC_C model selection

Model formula	logLik	AICc	Δ AICc	Acc w_i
Interaction richness – field-scale land use	–65.53	144.59	0.00	0.61
Interaction richness – field-scale land-use + landscape-scale land-use diversity	–64.77	146.79	2.20	0.20
Interaction richness – field-scale land-use + landscape-scale natural habitat	–65.23	147.71	3.12	0.13
Interaction richness – field-scale land-use + landscape-scale land-use diversity + landscape-scale natural habitat	–64.65	150.77	6.18	0.03
Interaction richness – landscape-scale natural habitat	–72.42	152.11	7.52	0.01
Interaction richness – landscape-scale land-use diversity + landscape-scale natural habitat	–71.74	153.71	9.12	0.01
Interaction richness – landscape-scale land-use diversity	–73.77	154.80	10.21	0.00
Null	–75.26	155.13	10.53	0.00
Interaction uniqueness – field-scale land use	–43.87	101.28	0.00	0.63
Interaction uniqueness – field-scale land-use + landscape-scale land-use diversity	–43.74	104.72	3.44	0.11
Interaction uniqueness – field-scale land-use + landscape-scale natural habitat	–43.80	104.85	3.57	0.11
Null	–50.85	106.30	5.02	0.05
Interaction uniqueness – landscape-scale natural habitat	–49.66	106.59	5.31	0.04
Interaction uniqueness – landscape-scale land-use diversity	–50.08	107.43	6.15	0.03
Interaction uniqueness – field-scale land-use + landscape-scale land-use diversity + landscape-scale natural habitat	–43.54	108.54	7.26	0.02
Interaction uniqueness – landscape-scale land-use diversity + landscape-scale natural habitat	–49.36	108.93	7.66	0.01
Interaction strength – field-scale land use	–49.05	115.35	0.00	0.40
Null	–54.59	116.44	1.09	0.23
Interaction strength – landscape-scale natural habitat	–53.64	117.50	2.15	0.14
Interaction strength – landscape-scale land-use diversity	–53.97	118.16	2.81	0.10
Interaction strength – field-scale land-use + landscape-scale land-use diversity	–48.92	119.31	3.96	0.05
Interaction strength – field-scale land-use + landscape-scale natural habitat	–49.05	119.56	4.21	0.05
Interaction strength – landscape-scale land-use diversity + landscape-scale natural habitat	–53.52	120.58	5.23	0.03
Interaction strength – field-scale land-use + landscape-scale land-use diversity + landscape-scale natural habitat	–48.90	124.09	8.74	0.01

Note: Δ AICc is the difference in AIC_C values between the best model and each subsequent model. Acc w_i is the Akaike weight for each model.

We sampled a total of 3369 pollen grains from 16 plant families, the most prevalent being Poaceae (1233 grains; 37%), Asteraceae (960 grains; 29%), Myrtaceae (556 grains; 16%) and Amaranthaceae (407 grains; 12%) (Appendix S1: Table S4). The abundance of pollen transported was highest in dairy and cropping land uses (Table 1, Figure 1b). Diptera and Coleoptera carried the greatest pollen abundance respectively, while Hymenoptera and Lepidoptera carried significantly less pollen, but were not significantly different from each other (Table 1,

Figure 1b). Coleoptera carried eight of all recorded pollen families, Diptera carried 10, Hymenoptera carried 11, and Lepidoptera carried seven pollen families (Appendix S1: Table S4).

We found that 373 (~24%) insects collected were pollen vectors and this varied by field-scale land-use type (Appendix S1: Table S3). More than one pollen type was found on 48 (~13%) of pollen vectors collected. Dairy and crop sites again supported the greatest number of pollen vectors (Table 1, Figure 1c). On average, less than

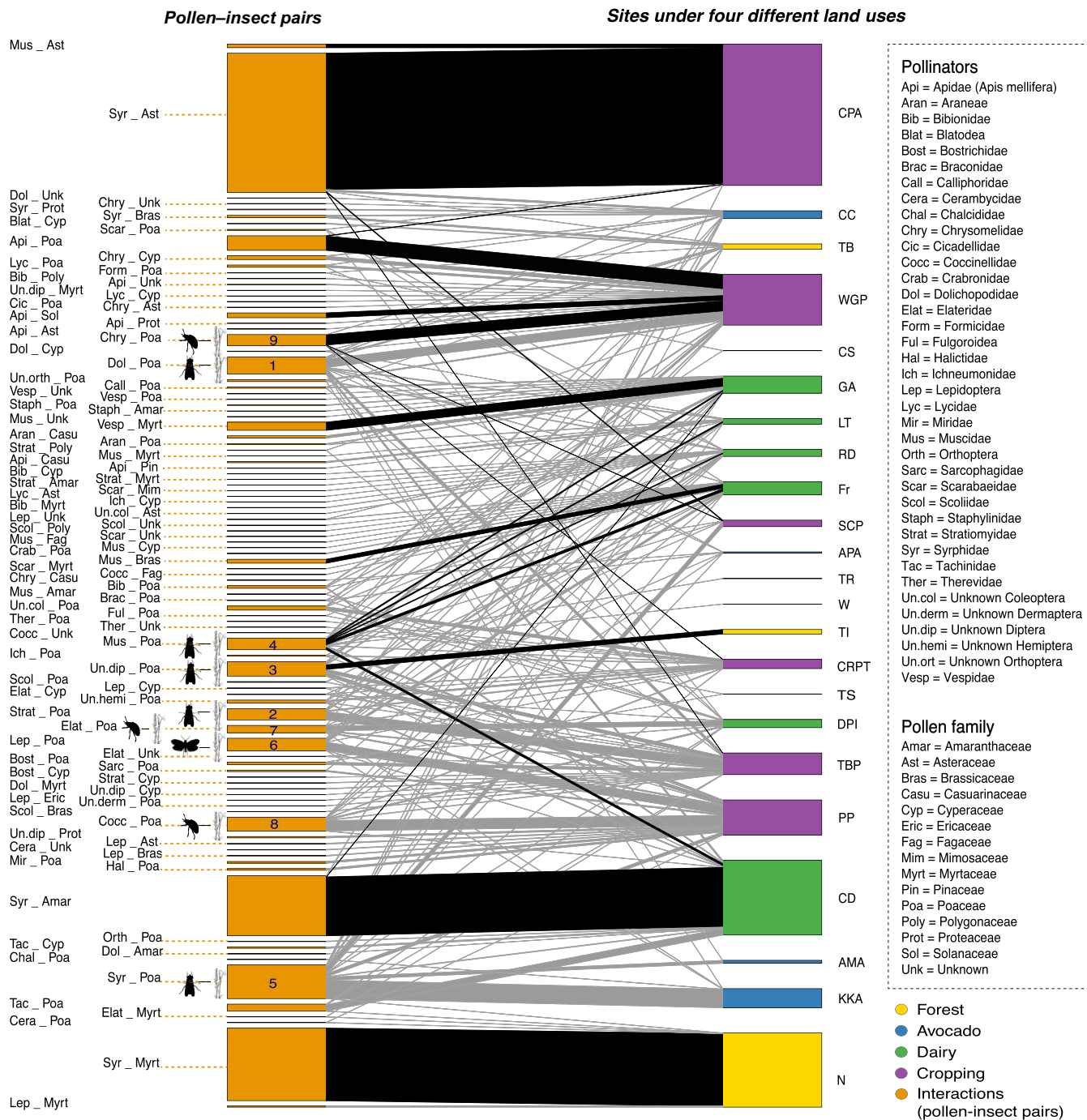


FIGURE 2 Visualization of the interaction-site bipartite meta-network, where nodes on the left side are pollen–insect interactions, and nodes on the right side of the diagram are sites, colored according to land use. Codes (e.g., CPA, WGP) indicate individual sites. Node thickness indicates the frequency (i.e., sum of pollen grains) that each pollen–insect interaction occurred at each site. Black links indicate highly specialized interactions of pollen–insect pairs with land use, as set out in Table 3. The identity of the most frequently occurring (most connected) pollen–insect pairs are indicated by silhouettes and numbers (also shown as an *igraph* in Appendix S1: Figure S3). Full names of pollinator and plant families are provided in the legend

25% of individual insects collected in each land-use type were carrying pollen (Figure 1c). Dominant pollen vectors comprised 10 families of Diptera (with 220 pollen vectors; 59% of all pollen vectors) nine families of Coleoptera (88 pollen vectors—23.5%), unclassified

Lepidopterans (24 pollen vectors—6%) and nine families of Hymenoptera (21 pollen vectors—5%). We also found non-traditional insect groups carrying pollen such as spiders (Arachnida) and bugs (Hemiptera), however these were sampled in low numbers and were not included in

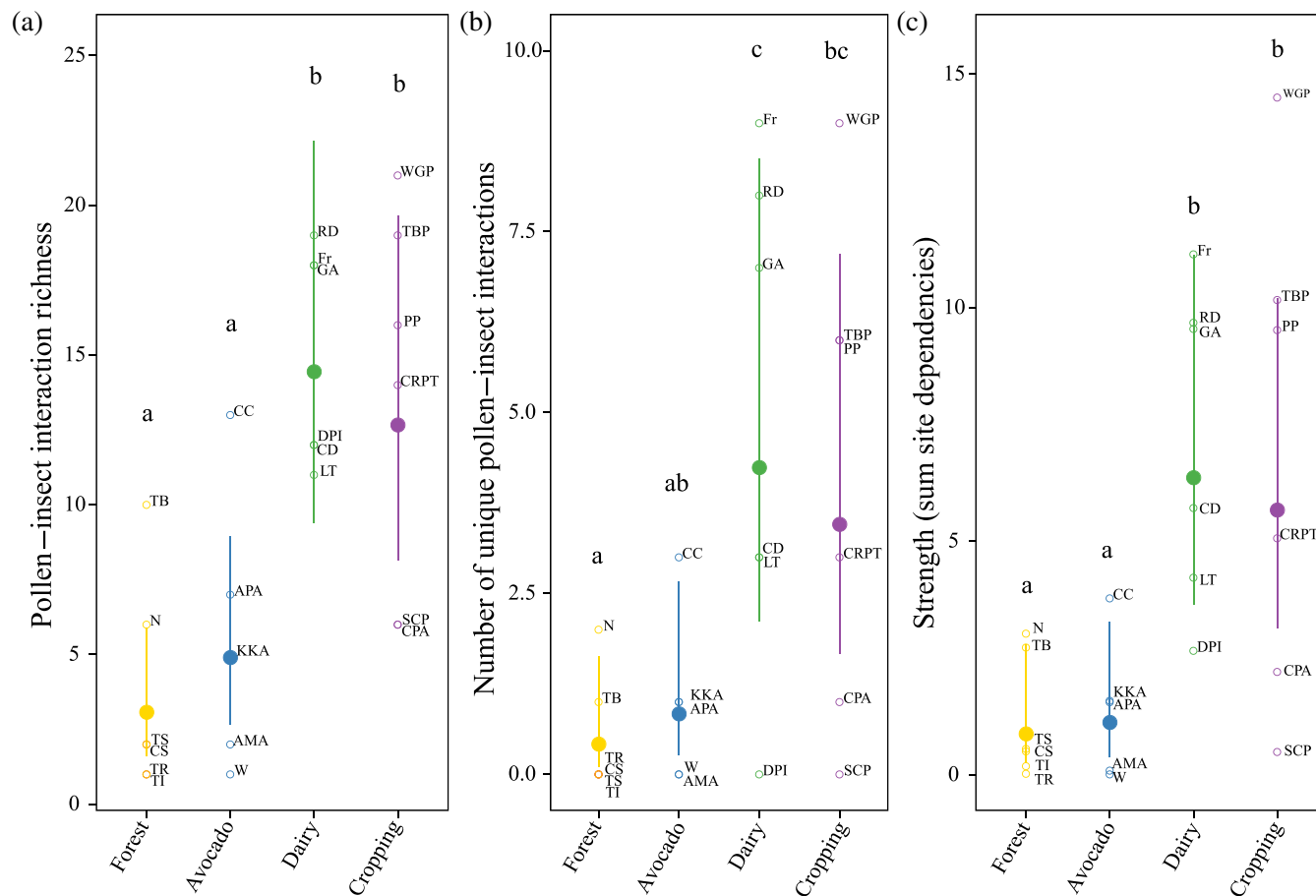


FIGURE 3 (a) Pollen–insect interaction richness, (b) the number of unique pollen–insect interactions and (c) differences in interaction strength (sum of site dependencies) at each site within different land uses. Large solid circles are the model-estimated interaction values for each land-use group and error bars denote the model-estimated 95% confidence intervals. Small open circles are metric values for each site. Large letters above each land-use group denote statistically significant differences, based on multiple pairwise comparisons ($\alpha = 0.05$; FDR corrected) between land uses

order-level analyses (Appendix S1: Table S3). There was no difference in the proportion of pollen vectors among insect Orders (Table 1, Figure 1c).

Relative effects of field-scale versus landscape-scale land use on pollen–insect interactions

We found that the best models for predicting interaction richness, uniqueness and strength all included the single fixed effect of field-scale land use (Table 2). However, for interaction strength, this model was marginally better than the null model, making determination of a real effect inconclusive. Conversely, landscape-scale land use (proportion of natural habitat and land-use diversity) was only weakly associated with pollen–insect interactions and were not retained in any of the best models (Table 2). In models that included proportion of natural

habitat and land-use diversity, both variables had weak, non-significant effects on interaction richness, uniqueness, and strength (Appendix S1: Table S5).

Effects of field-scale land use on pollen–insect interactions

Given the predictive capacity of field-scale land use in previous models, we used only field-scale analyses of interaction effects below. We found that sites used for cropping and dairy had the highest richness of pollen–insect interactions (Figures 2 and 3a, Appendix S1: Figure S3) and the highest interaction strength (Figure 3c), whereas avocado and forest land-use sites had relatively low interaction richness and strength. Similarly, cropping and dairy sites had the highest number of unique plant–pollination interactions (i.e., interactions not shared with any other site in the meta-network), although the number of unique interactions in cropping sites

TABLE 3 Specialization of pollen–insect interactions to specific land uses (those with ≥ 20 interactions recorded across all sites)

Interaction (pollen–insect pair)	Land-use	PDI	<i>p</i> -value
<i>Apis mellifera</i>–Solanaceae	Cropping	1.00	0.00
Muscidae–Asteraceae	Cropping	1.00	0.00
Muscidae–Brassicaceae	Dairy	1.00	0.00
Muscidae–Poaceae	Dairy	0.83	0.00
Syrphidae–Myrtaceae	Forest	1.00	0.00
Unknown Diptera–Poaceae	Forest	0.80	0.00
Vespidae–Myrtaceae	Dairy	1.00	0.00
Syrphidae–Amaranthaceae	Dairy	1.00	0.04
Syrphidae–Asteraceae	Cropping	1.00	0.04
<i>Apis mellifera</i>–Poaceae	Cropping	1.00	0.05
Chrysomelidae–Poaceae	Cropping	1.00	0.05
Tachinidae–Poaceae	Dairy	0.99	0.06
Chrysomelidae–Cyperaceae	Cropping	0.99	0.07
Stratiomyidae–Poaceae	Cropping	0.98	0.12
Coccinellidae–Poaceae	Cropping	0.98	0.13
Lepidoptera–Poaceae	Cropping	0.97	0.19
Elateridae–Poaceae	Dairy	0.97	0.23
Syrphidae–Poaceae	Avocado	0.96	0.34
Dolichopodidae–Poaceae	Cropping	0.95	0.47

Note: PDI values are bounded between one and zero, with one indicating perfect specialization to a particular land use and zero indicating perfect generalism across all land uses. Interactions in bold differ significantly ($p \leq 0.05$) from the distribution of PDI values obtained from null interaction-site networks.

was not significantly higher than for avocado sites (Figure 3b). Forest sites had the lowest number of unique interactions, but this was not significantly different from avocado sites (Figure 3b). The dairy and cropping sites that had greater pollen–insect interaction richness, uniqueness and strength were also more highly connected within the meta-network compared with those containing forest or avocado plantations (Figure 2; Appendix S1: Figure S3).

Specialization of pollen–insect interactions to different land-use types

We identified 19 distinct pollen–insect interactions (those that occurred more than 20 times), which were highly specialized to one field-scale land-use type (Table 3). Eleven of these 19 pollen–insect pairs (five in cropping, four in dairy, and two in forest) had PDI values greater than that of the distribution of null networks ($p < 0.05$, Appendix S1: Figure S2, Table 3). Seven of these specialized interactions involved fly species (Diptera), three involved bees or wasps (Hymenoptera), and one involved a beetle (Coleoptera). Pollen from these interactions came from six plant families, predominantly Asteraceae, Myrtaceae, and Poaceae (Table 3). Grass pollen (Poaceae) was carried in 11 of these

specialized interactions and by multiple insect Orders (three Coleopteran families, six Diptera, one Hymenoptera, and one Lepidopteran family; Table 3). Other wind-pollinated plant families (e.g., Cyperaceae) also occurred in highly site-specialized interactions with Chrysomelidae (Coleoptera).

DISCUSSION

Land-use change can have major impacts on pollinator communities, with knock-on effects to ecosystem function, yet limited knowledge of these relationships hinders understanding to inform management priorities for conservation. Here, we identified pollen vectors to family level and constructed pollen–insect interaction-site meta-networks to identify sites, taxa and interactions that are important to network richness and connectance in the focal landscape. We demonstrate through our case study of an agroecosystem comprising four different land-use types, that measures of interaction diversity, along with specialization (Berlow et al., 1999; Weiner et al., 2014), are powerful for informing management across mosaic agricultural landscapes to prioritize the conservation of important community interactions. Specifically, to increase diversity of interactions in these networks,

conservation efforts could focus on areas surrounding the most connected interactions and sites, or those with highly specialized interactions, and link them through the establishment of floral field margins and roadsides (Hevia et al., 2021; Phillips et al., 2020; Zamorano et al., 2020). Species-rich floral plantings, including forest species, will benefit multiple pollinator groups across all land uses (Kral-O'Brien et al., 2021). Such an approach may have flow on effects for crop pollination and other ecosystem services given that, in our study, the highly connected sites were often cropping land uses. Targeting conservation in this way would increase habitat connectivity across landscapes (Senapathi et al., 2017), and link with seminatural habitats, such as small forest blocks and low-intensity agriculture. These seminatural habitats for which insect abundance and pollen–insect interactions were limited, often have high habitat specialization (Smith et al., 2021).

Changes in land-use intensity often drive changes in abundance and diversity of plant and pollinating insect taxa (Clough et al., 2014; Harrison et al., 2017; Stavert et al., 2017). Here, we found that relatively low-intensity land uses (i.e., small intact forest patches and avocado orchards) consistently supported fewer individuals across the four main insect Orders that we sampled, compared with more intensively managed dairy and cropping landscapes. Furthermore, the more intensive land uses had a greater richness and number of unique interactions. Other studies have reported high solitary bee and syrphid fly abundance in such landscapes, but not necessarily greater species diversity (Haenke et al., 2009, 2014; Klein et al., 2002; Mogren et al., 2016; Stavert et al., 2018; Williams et al., 2010). Conversely, phytophagous beetle species, such as carabids, are more abundant and speciose in agricultural landscapes (da Silva et al., 2008). Our results demonstrate greater pollinator abundance in the more intensively managed land uses studied and indicate that a subset of these taxa is important to conserving unique pollen–insect interactions.

Several factors likely explain the greater insect abundance and number of plant interactions in more intensively managed land uses. Many pollinating insects frequently forage in open landscapes, such as grasslands, meadows or forest glades (Hanula et al., 2016; Memmott, 1999; Weiner et al., 2011). Floral abundance is also an important feature of open modified land-use types, particularly due to increases in mass flowering crops and wildflower enhancements (Westphal et al., 2003; Williams et al., 2015). It is also possible that trap visibility was greater in more open landscape elements, creating habitat-specific differences in sampling efficiency, however there is insufficient evidence that trapping location significantly alters insect catches (but see Abrahamczyk et al., 2010). It is unclear why field-scale

management was found to influence pollen–insect interactions more than landscape-scale, as other studies show conflicting results on the benefits of each for different pollinator taxa (Ferreira et al., 2013; Kremen & M'Gonigle, 2015; Westphal et al., 2003; Williams & Winfree, 2013). However, one possible explanation is that insects tend to forage on what is nearby (Pasquet et al., 2008; Rader et al., 2011; Zurbuchen et al., 2010), so we are likely detecting pollen from plants most recently visited, rather than from habitat in surrounding land uses. Although we did not measure plant species richness in our study landscapes, high pollen richness is often observed in land-use types that experience greater turnover of floral sources (i.e., those experiencing heavy cattle grazing or frequent cropping) and could also be associated with a high number of weeds in arable systems (Brenchley & Warington, 1933; Marshall et al., 2003). Weeds can also be an important pollinator food resource, particularly between periods of crop flowering (Bretagnolle & Gaba, 2015; Marshall et al., 2003; Requier et al., 2015). While we collected data from plant records for the region at different scales from sites (100, 500, and 1000 m radii), the coarse scale at which such records are usually collected, meant we were unable to detect many plant species at the field scale to elucidate our results.

Interestingly, we found the greatest abundance and richness of pollen taxa was carried by flies, including non-syrphid Diptera, which are often overlooked in pollination studies (Orford et al., 2015; Rader et al., 2020). Our pollen samples were also dominated by grass (Poaceae) pollen. These results are significant from the pollinator perspective. Grasses and three other plant families sampled here (Casuarinaceae, Cyperaceae, and Pinaceae) are considered to be anemophilous (wind pollinated) (Friedman & Barrett, 2009). Some studies dismiss wind-dispersed plant taxa as irrelevant to pollinators, both as a food source and because pollinating insects are not directly involved in their reproduction (Decourtye et al., 2010; Dupont et al., 2009). Other studies have identified insects either carrying or foraging upon anemophilous pollen, or recorded its presence in hives (Reemer & Rotheray, 2009; Sabugosa-Madeira et al., 2008; Saunders, 2018). We found the amount of pollen on insects from wind-pollinated species varied by land-use type, with more being transported in dairy and cropping land uses. While open land uses may have more airborne pollen due to a greater abundance of grass, which may attach itself to animals in air or on leaves and other structures, the higher loads on families with known pollinator species, along with the growing number of studies showing many insect species collect or eat anemophilous pollen, indicates it is likely being collected from, and moved between, flowers. Wind-pollinated plant taxa thus require greater attention in future

pollination studies, as they are being visited by insects across multiple land-use types and may be an important pollen source for many pollinator groups.

Although the majority of pollinator interactions are often reported among generalist species (Bosch et al., 2009; Waser et al., 1996), we found a number of interactions occurred far more frequently (i.e., were specialized) in particular land uses. For instance, the interaction between syrphid flies and three plant families were specialized to different land uses: Myrtaceae in forest, Amaranthaceae in dairy, and Asteraceae in cropping land uses. It is therefore possible that specialized interactions occur either by a requirement for that pollinator by the plant at the time of flowering, or a scarcity of resources for either the plant or pollinator in that land use. For instance, Myrtaceae are a characteristic plant family in Australian forests, including the iconic Eucalypts, that are a major food source for many generalist pollinator groups and some specialist bees, such as Colletids (Beardsell et al., 1993; Phillips et al., 2010). There is growing evidence that some bees are also forest specialists (Harrison et al., 2017; Smith et al., 2021). The very few interactions in forest habitats here would indicate that there are likely few pollinators available to visit Myrtaceae flowers when needed. Therefore, conservation measures aimed at promoting greater pollinator diversity, particularly in fragmented forest habitats that currently rely on specialized interactions with few species, may improve population persistence of plant and pollinator communities occurring primarily within that land-use type.

The interaction-site meta-network approach could be further improved in several ways. First, data relating to the richness and identity of plant species at the site level would increase our understanding of floral availability in the context of pollen carried by different taxa. While we would predict that most insects in the rotational potato crops would carry Solanaceae pollen and those from avocado farms would carry Lauraceae pollen, we found little evidence that this was the case. Furthermore, grass pollen (Poaceae) was a significant component of the specialized interactions across multiple insect Orders. This makes it difficult to understand where the pollinators were actually foraging, the traits of pollen collected, the distance insects moved across different habitats and land uses before being trapped, and whether grooming behavior impacted pollen carried.

Linking pollinators with a particular site is challenging. For instance, hoverflies (Syrphidae), who were involved in many important interactions here, can carry viable pollen over hundreds of kilometers during migration, but some also typically patrol a foraging area of 1–2 m at sites (Doyle et al., 2020). Bees in the family Apidae, most typically the western honeybee (*Apis mellifera* L.), typically forage to a distance of ~1.6 km, however this may be reduced in

tropical regions (He et al., 2012). *Apis* tend to display floral constancy, so would likely visit the one plant species within a single foraging bout (Free, 1963), thus can be more readily linked with a particular site. Second, while static traps are useful for collecting abundant data for multiple taxa (Hall, 2018; Hall & Reboud, 2019; Saunders & Luck, 2013), different bee communities are sometimes detected using transect or sweep netting methods (Gibbs et al., 2017). In the current study, only 20%–25% of all insects trapped were carrying pollen. It is possible the proportion of pollen vectors would have been greater using sweep netting, as individuals would have been collected while physically visiting flowers, rather than while visiting a particular site where they may not have been engaged in pollination flights. We therefore note that not all our sampled pollen vectors may act as pollinators. Recording the pollen carried specifically by flower visitors (as opposed to flight intercept traps) would provide greater detail in this regard.

Given many interactions recorded in this study involved flies, wasps, and beetles, the case study provided here highlights the importance of conserving non-bee pollinators in agroecosystems. Indeed, many of the families recorded across the four dominant Orders comprise known pollinators (e.g., Fenster et al., 2004, Ødegaard & Frame, 2007, Rader et al., 2020, Hall et al., 2020; see Appendix S1: Table S2 for greater detail). Yet, assigning functionality to many non-bee insects at the family level is difficult as numerous species in adult form require very different resources to larval stages (i.e., pollinators, predators, parasites, herbivores). Identifying interactions between plants and insects in intensive land uses (e.g., dairy and cropping landscapes) may highlight important management decisions such as the types of insects that transfer crop or weed pollen or those that visit rare or threatened native plant families in forested areas. Additionally, regular sampling through time is important to identify shifts in plants, pollinators, and their interactions and could be easily implemented using our approach. For instance, land use and climate continue to change at a rapid rate (Lambin & Meyfroidt, 2011; Loarie et al., 2009), which may alter pollen–insect communities and interactions through time. Given these landscapes may be subject to further land-use change, our approach could identify subsequent changes to pollen–insect interactions across multiple land uses and timepoints, to better inform adaptive management strategies at different sites across landscapes.

CONCLUSION

We advocate that interaction-site meta-networks can provide important insights into the types of relationships between pollinators, plants, and the land use in which

they occur. The identification of key pollen–insect interactions that only occur within certain land-use types suggests site management (i.e., at the field rather than landscape scale) may provide the best outcomes for conserving or restoring pollen–insect interactions in highly modified landscapes. Interactions among plants and insects are important to detect both for conservation of taxa as well as potentially identifying vectors for weed management. Incorporating species interactions into conservation planning is an important next step in conserving critical pollinator taxa and plants that sustain pollination ecosystem services in agroecosystems.

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CONFLICT OF INTEREST


The authors state they have no conflict of interest.

DATA AVAILABILITY STATEMENT

Data and code (Hall et al., 2021) are available in Zenodo at <https://doi.org/10.5281/zenodo.5157944>.

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