Interaction-site networks identify interactions for conserving key pollinators and plants in an agricultural mosaic landscape

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Abstract

Pollinators utilize different land-uses via the plants they visit, however these connections vary within and among land-uses. Identifying which insects are carrying pollen and from where can elucidate key plant-pollinator interactions and identify the most important sites for maintaining community-level interactions in different land-use types. We developed a novel interaction-site bipartite network approach to identify which land-use types at the field- and landscape-scale best conserve plant-pollinator interactions. We identified distinct pollen-insect interactions that were highly specialised to both natural and modified land-uses. Many interactions involved flies, wasps and beetles; groups requiring greater research effort. Field-scale land-use best predicted interaction richness, uniqueness and strength. Management at this scale may provide the best outcomes for conserving or restoring plant-pollinator interactions in modified landscapes. This novel, intuitive approach could inform land-use planning, whereby priority is afforded to conservation areas that represent significant links between plant and pollinator communities within mosaic landscapes.

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 (Klein et al. 2007; Winfree, Bartomeus & Cariveau 2011; Garibaldi et al. 2013; Rader et al. 2016). 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 different land-use types are often variable (Bommarco et al. 2010; Cariveau et al. 2013; Rader et al. 2014; Stavert et al. 2017). This makes it difficult to detect and understand how both plant and pollinator communities respond to land-use change. To date, most studies of pollinator community responses to changes in land-use intensity have focused on species-level relationships with the amount or proximity to natural and semi-natural vegetation (Greenleaf & Kremen 2006; Banks et al. 2013; Holzschuh et al. 2016; Hall et al. 2019).

The responses of pollinator species to land-use intensity are dependent on a number of factors including body size, social structure, nesting requirements, feeding behaviour and larval food availability (Henle et al. 2004; Rader et al. 2014; Hall et al. 2019). However, pollinator community composition is also directly influenced by changes in the availability of resources in 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 are able to 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 are dependent on food resources available for larval development, as well as habitat connectivity within landscapes (Power & Stout 2011; Haenke *et al.* 2014). These landscape attributes ultimately affect which plant-pollinator interactions occur, where they occur, and how frequently.

In agricultural landscapes, knowledge of how plant-pollinator 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 via 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 keystone pollinator species or habitats that are critical for network structure (Saunders & Rader 2019). Here, we build on this approach by connecting traditional pollen transport networks (e.g. Alarcón 2010; Popic, Wardle & Davila 2013) with the land-uses in which they originate to generate a plant pollinator interaction-site bipartite network. This novel approach enables identification of key sites and land-uses with high plant-pollinator interaction diversity. Specifically, we ask:

1. How does land use intensity influence the proportion of insect taxa that are carrying pollen and the taxonomic richness of pollen they carry?

2. How do richness, uniqueness and strength of plant-pollinator interactions respond to the spatial scale of the surrounding land-use (field or landscape-scale)?

3. Which plant-pollinator interactions are likely to have high conservation value (i.e. keystone interactions) within and between land-use types?

Materials and Methods

Site selection

Field sites were located on the Atherton Tablelands (17º 18' S, 145º 29'E to 17º 36'S, 145º 44' E) in northeast Australia (Fig. S1). Twenty-four sites were selected in four different land-use types (six replicates per land-use) within a mosaic agricultural landscape: remnant forest, avocado orchard, dairy farming, and arable rotation cropping (Fig. S1). These represent the major agricultural and natural land-uses in the study area. Sites were separated by at least 1.5 km, with most at a distance of 3 km from the nearest neighbouring site. These distances are greater than average foraging flight and pollen transport distances for our focal insect taxa, which are generally less than 1.5 km (Zurbuchen *et al.* 2010; Rader *et al.* 2011; Smith & Mayfield 2015).

Insect collection

Flower visitors were sampled for five days each month in 2008 using flight intercept and pan traps (Howlett *et al.* 2009). Insect traps were placed at the centre of the focal field. At each site, two yellow flight intercept pan traps were positioned 2 m apart on stakes at a height of 1.2 m. Each trap consisted of a pan measuring 22 cm x 35 cm x 6 cm attached to two vertical panes (flight intercept) that were arranged perpendicular to each other. To facilitate pollen collection on insects, we lined the traps with clear acetate sheets 22 cm x 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 maximise insect capture while preventing loss of pollen to excess drops of Tanglefoot. The acetate sheets with trapped insects were replaced daily. Insects were sorted into orders and those carrying pollen were then pinned and identified to family-level by experts, using appropriate keys (CSIRO 2018a, b; Marshall 2017).

Pollen identification

To identify pollen carried by potential pollinators, the underside of every insect collected in the months of February, April and June was pressed onto a 3 mm cube of gelatine-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 100X magnification, with all visible grains on the slide counted. We then used 400X magnification to ensure appropriate pollen grain identification. Individual pollen grains were photographed and identified to family-level—the highest taxonomic resolution attainable as determined by leading pollen experts—based on morphological characteristics using the Australasian pollen and Spore Atlas (APSA 2017) and verified by an expert palynologist (SH).

Land-use mapping

We calculated the surrounding land-use types, from a government dataset for the wet tropics region (DSITI 2016), within two buffer areas around each site: 100 m (field-scale) and 500 m (landscape-scale), using ArcGIS (v.10.6.1, ESRI 2018). We also calculated the proportion of natural habitat at the landscape-scale (500 m radius) from aerial photographs in ArcGIS.

Bipartite interaction-site network

We constructed a bipartite *interaction-site* network by adapting the species-habitat networks 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). 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 (based on the sum number of pollen grains for each pollen taxa counted on each insect taxa) that each plant-pollinator interaction occurred at each site.

To identify how land-use intensity alters plant-pollinator interactions and to identify the most important sites for conserving interactions, we calculated several metrics from our interaction-site network. First, we computed the richness of plant-pollinator 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 pairs recorded at each site. Second, to identify the importance of each land-use for maintaining unique plant-pollinator interactions, we quantified the number of pollen-insect pairs 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, Jordano, & Olesen 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 pairs on that site. Finally, to determine if frequently occurring pollen-insect interactions (those that occurred [?] 20 times in our network) were specialised to particular 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. Specifically, the PDI analysis allowed us to determine if a given plant-pollinator interaction occurred in the land-use with which it was most strongly linked more frequently than other land-uses in the landscape.

Statistical Analysis

The proportion of insect taxa carrying pollen and the taxonomic richness of pollen carried

To examine the effect of land-use intensity on the average abundance and proportion of pollen carrying insects in different land-use types and pollen richness present in each land-use and carried by different insect taxa, we constructed generalized linear mixed effects models using the*lme4* package (Bates *et al.*

2014). In these models, either average abundance of each of the four common insect orders, proportion of insect individuals carrying pollen or pollen richness on those insect individuals was the response variable and land-use (categorical) was the fixed effect. For the pollen carrying and pollen richness models, insect order was also included as a fixed effect. We included month as a random effect to account for repeated sampling across the three time periods. All models were validated by examining the distribution of residuals plotted against fitted values, and we set a negative binomial distribution to account for overdispersion where necessary (Zuur *et al.* 2009). We ran separate models for each of the four most abundant insect orders (Coleoptera, Diptera, Hymenoptera and Lepidoptera), which represented 93.5% of pollen carriers and 94.5% of all sampled individuals. The sample sizes of the remaining taxa were too small for further analyses. *Post-hoc* multiple pairwise comparisons between land-uses and insect orders were tested using estimated marginal means (EMMs, using the *emmeans* package, Lenth 2018). EMMs are generated using the fitted model to make predictions over a grid of predictor combinations in order to assess the effects of individual factors. These predicted differences in abundance of individuals and proportion of pollen carrying insects from each of the four dominant insect orders between land-uses, and differences in average pollen richness by land-use type and insect order. We estimated the significance of differences between terms, using Tukey's HSD (honestly significant difference) test with false discovery rate (FDR) corrected P values (at $a = 0.05$) (Verhoeven *et al.* 2005).

The richness, uniqueness and strength of plant-pollinator interactions at field and landscape scales

We investigated the impact of land-use on plant-pollinator interactions at different scales (field and landscape scales) by comparing the relative effects of land-use (proportion of natural habitat and habitat diversity) at the field-scale (100 m radius) and landscape-scale (500 m radius). Specifically, we tested the effects of land-use at different scales on pollen-insect interaction richness, uniqueness and strength using generalised linear mixed-effects models (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 and field-scale land-use (i.e. site where insects were collected, categorical), landscape-scale proportion of natural habitat (at 500 m radius) (continuous) and landscape-scale habitat 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 land-use categories. 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).

Plant-pollinator interactions that have high conservation value (i.e. keystone interactions) within and between land-use types

We assessed differences in 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 land-use (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 land-use categories. We then compared interaction richness, uniqueness and strength among land-uses using pairwise least squared means contrasts in the *emmeans* package (Lenth 2018) and determined significance with false discovery rate (FDR) corrected P values (at $a = 0.05$) (Verhoeven *et al.* 2005). Finally, we tested the significance of each observed PDI value by comparison against a null 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 random network. Following this, the remaining pollen-insect occurrences at each site were distributed to the filled cells, thus maintaining the original network connectance. The combination of complementary network indices (richness, uniqueness and strength) allowed

us to identify the importance of different land-uses for maintaining plant-pollinator interactions from both a qualitative and quantitative perspective.

All statistical analyses were conducted in R (v.3.6.0, R Core Team 2019).

Results

The proportion of insect taxa carrying pollen and the taxonomic richness of pollen carried

We collected 1,583 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%) (Table S1). Individual insect orders responded to changes in land-use intensity differently: Coleoptera, Diptera and Hymenoptera were more abundant in cropping and dairy land-uses compared with forest areas and avocado orchards (Figs. 1a-c).

We found that 373 (~24%) insects collected were carrying pollen and this varied by land-use type (Table S1). Dairy and crop sites supported the greatest number of pollinator families and individuals, but we found no statistically significant difference in the proportion of pollen carrying individuals among land-uses. Less than 25% of individuals sampled in each land-use were carrying pollen (Fig. 2a). Dominant pollen carrying insects comprised 10 families of Diptera (with 220 pollen carrying individuals - 59% of all pollen carriers) 9 families of Coleoptera (88 pollen carriers – 23.5%), unclassified Lepidopterans (24 pollen carriers – 6%) and 9 families of Hymenoptera (21 pollen carriers – 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 order-level analyses (Table S1). There was no difference in the proportion of pollen carriers among insect orders (Fig. 2b).

A total of 3,369 pollen grains were sampled from 16 plant families – the most prevalent being Poaceae (1,233 grains - 37%), Asteraceae (960 grains – 29%), Myrtaceae (556 grains - 16%) and Amaranthaceae (407 grains - 12%) (Table S2). The number of plant families carried as pollen was highest in dairy and cropping land-uses (Fig. 2c). Diptera and Coleoptera carried the highest richness of pollen respectively, while Lepidoptera carried significantly less pollen richness than Diptera (Fig. 2d). Coleoptera carried eight of all recorded pollen families, Diptera carried 10, Hymenoptera carried 11 and Lepidoptera carried seven pollen families (Table S2).

The richness, uniqueness and strength of plant-pollinator interactions at field and landscape scales

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 1). 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 habitat diversity) was only weakly associated with plant-pollinator interactions and were not retained in the best models (Table 1). In models that included proportion of natural habitat and habitat diversity, both variables had weak, non-significant effects on interaction richness, uniqueness and strength (Table S3).

We found that sites used for cropping and dairy had the highest richness of pollen-insect interactions (Figs. S1, 3, 4a) and the highest interaction strength (Fig. 4c), 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 (interactions not shared with any other site in the interaction-site network), although the number of unique interactions in cropping sites was not significantly higher than for avocado sites (Fig. 4b). Forest sites had the lowest number of unique interactions, but this was not significantly different from avocado sites (Fig. 4b). Sites from dairy and cropping land-uses that contributed to greater richness, uniqueness and strength were also more highly connected within the network than those containing forest or avocado plantations (Fig. 3).

Plant-pollinator interactions that have high conservation value (i.e. keystone interactions) within and between

land-use types

We identified 19 distinct pollen-insect interactions (those that occurred more than 20 times), which were highly specialised to one particular land-use type (Table 2). Eleven of the total 19 pollen-insect pairs (five in cropping, four in dairy and two in forest) had PDI values significantly higher than those obtained from the null distribution ($P < 0.05$, Fig. S2, Table 2). Seven of these interactions involved fly species (Diptera), three involved bees or wasps (Hymenoptera) and one involved a beetle (Coleoptera). Pollen carried in these interactions was from six plant families, predominantly Asteraceae, Myrtaceae and Poaceae (Table 2). Grass pollen (Poaceae) was carried in eleven of the total specialised interactions by multiple insect orders (three Coleoptera families, six Diptera, one Hymenoptera and one Lepidoptera family, Table 2). Other wind-pollinated plant families (e.g. Cyperaceae) were also involved in highly specialised 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 show how an *interaction-site* network approach can be used to identify keystone sites, taxa and interactions that are important in the focal landscape (Tylianakis *et al.* 2008; Schleuning *et al.* 2015). We demonstrate that measures of interaction diversity, along with specialisation (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.

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—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. Further, these intensive land-uses had a greater richness and number of unique interactions (both from a qualitative and quantitative perspective). Other studies have reported high solitary bee and syrphid fly abundance in such landscapes, but not necessarily greater species diversity (Klein *et al.* 2002; Haenke *et al.* 2009, 2014; Williams *et al.* 2010; Mogren *et al.* 2016; Stavert *et al.* 2018). 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 more intensively managed land-uses and indicate that a subset of these taxa is important to conserving unique plant-pollinator 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 (Memmott 1999; Weiner *et al.* 2011; Hanula *et al.* 2016). 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 unclear why field-scale management was found to influence plant-pollinator interactions more than landscape-scale, as other studies show conflicting results on the benefits of each for different pollinator taxa (Westphal *et al.* 2003; Ferreira *et al.* 2013; Williams & Winfree 2013; Kremen & M'Gonigle 2015). However, one possible explanation is that insects tend to forage on what is nearby (Pasquet *et al.* 2008; Zurbuchen *et al.* 2010; Rader *et al.* 2011), 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 (Marshall *et al.* 2003; Bretagnolle & Gaba 2015; Requier *et al.* 2015).

Interestingly, we found that the majority of pollen from different plant families was carried by flies, including non-syrphid Diptera, which are often overlooked in pollination studies (Orford *et al.* 2015; Rader *et al.* 2020).

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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 outright 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 (Dupont *et al.* 2009; Decourtye*et al.* 2010). Other studies have identified insects either carrying or foraging upon anemophilous pollen, or recorded its presence in hives (Sabugosa-Madeira *et al.* 2008; Reemer & Rotheray 2009; 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. The abundance and presence of pollen from Poaceae and other wind-pollinated plant families in these landscapes indicate that wind pollinated taxa require greater attention in future pollination studies, as they are being carried 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 (Waser *et al.* 1996; Bosch *et al.*2009), we found a number of interactions occurred far more frequently (i.e. were specialised) in particular land-uses. For instance, the interaction between syrphid flies and three plant families were specialised to different land-uses: Myrtaceae in forest, Amaranthaceae in dairy and Asteraceae in cropping land-uses. It is therefore possible that while insect taxa do not rely on these specialised interactions, the plant requires that particular pollinator at the time of flowering. Our approach provides an intuitive way to identify specialised interactions to a particular land-use and highlights the importance of maintaining all land-uses, including forest sites, despite these not being as critical to interaction diversity than more intensively managed land-uses. Unlike the specialisation of interactions to dairy and cropping landscapes, where the plant families likely comprise crop or weed species, interactions between pollinators and native plant families in forested areas (e.g., Myrtaceae) require careful management.

The interaction-site network approach could be further improved in a number of 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. Whilst we would predict that most insects in the potato cropping landscapes would carry Solanaceae pollen and those from avocado farms would carry Lauraceae pollen, we found little evidence that this was the case. This raises the question of whether pollinators trapped at a certain location were indeed carrying pollen from that location. In this study, only 20-25% of all insects that we trapped were carrying pollen. Whilst static traps are useful for collecting abundant data for multiple taxa (Saunders & Luck 2013; Hall 2018; Hall & Reboud 2019), different communities are often detected using transect or sweep netting methods (Gibbs *et al.* 2017). It is possible the proportion of pollen carriers would have been greater using sweep netting, as individuals would have been collected whilst physically visiting flowers, rather than whilst visiting a particular site where they may not have been engaged in pollination flights. Recording the pollen carried specifically by flower visitors (as opposed to flight intercept traps) would provide greater detail in this regard.

Conclusions

We advocate that interaction-site networks can provide important insights into the types of interactions between pollinators, plants and the land-use in which they occur. This study also highlights the importance of conserving non-bee pollinators in agroecosystems, given many interactions recorded in this study involved flies, wasps and beetles. Further, grass pollen (Poaceae) was a significant component of the specialised interactions across multiple insect orders. The identification of key plant-pollinator interactions that only occur within certain land-use types suggests field-scale management may provide the best outcomes for conserving or restoring plant-pollinator interactions in modified landscapes. 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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