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Adjacent crop type impacts potential pollinator communities and their pollination services in remnants of natural vegetation

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Abstract

Aim: Pollination plays a crucial role in the conservation of many plant species persisting in fragmented, human-dominated landscapes. Pollinators are known to be instrumental in maintaining genetic diversity and metapopulation dynamics for many plant species and are important for providing ecological services that are essential in agricultural landscapes where populations of native plants are highly isolated. Numerous studies have explored the value of remnant native vegetation for supporting pollination services to crop species, yet the effect of mass-flowering crops on the pollinator communities and the pollination services they provide to native plant communities persisting in fragmented landscapes are less well understood. Here, we assess the influence of the presence and phenology of a mass-flowering crop to pollinator community structure, abundance, and pollen load composition in remnant vegetation in complex agricultural landscapes.

Location: South-west Western Australia, Australia.

Methods: We recorded the composition and abundance of insect flower visitors and their pollen loads in isolated remnants of York Gum-Jam woodlands adjacent to canola (insect-attracting) or wheat (non-insect-attracting) fields over two years.

Results: All bees were much more sensitive to adjacent crop type (neighbouring canola or wheat) than non-bee pollinators. Honeybees were the most abundant pollinators in canola fields during peak flowering. Honeybee abundance increased in canola-adjacent reserves post canola bloom, potentially indicating a movement into reserves as crop flowering waned. Native bees were the most diverse in remnant vegetation. Pollen loads of native bees were more mixed (increased pollen richness and evenness) when sampled next to canola fields compared to wheat fields.

Main conclusion: The availability of potential insect pollinators to remnant wildflower communities in agricultural landscapes is context dependent. Whether sampled communities were adjacent to wheat or canola in a landscape significantly impacted the abundance of potential pollinators in certain landscape elements, but not others, and the composition of pollen loads carried by these insects. Results offer novel insights about the influence of landscape context on pollinator communities and the potential

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pollination services available for the conservation of native plant species in highly fragmented agricultural landscapes.

KEYWORDS

canola, flower visitor abundance, honeybee competition, mass-flowering crops, native plant communities, non-crop habitats, pollen loads, semi-natural habitats, unmanaged pollinators, wild plant pollination

1 | INTRODUCTION

Insect pollination is an important ecosystem service (Eilers et al., 2011; Gallai et al., 2009; Ollerton, 2017; Ollerton et al., 2011; Vanbergen et al., 2013). Though the economic value of pollinators has been used to motivate the protection of remnant vegetation in agricultural landscapes (Kennedy et al., 2013; Klein et al., 2007; Potts et al., 2016), crops are not the only plant species to benefit from wild pollinators. Insect pollinators also help many native plant species maintain genetic diversity and population structure (Kearns et al., 1998; Ollerton et al., 2011). It is also clear that these important aspects of diversity have been negatively impacted by extensive habitat fragmentation and landscape homogenization of ecosystems globally (Xiao et al., 2016). In many parts of the world, small vegetation remnants in large-scale agricultural landscapes are the only remaining habitat for many rare, threatened, and endemic plant species (Saunders et al., 1991; Yates & Hobbs, 1997). While the benefits of wild pollinators “spilling over” from natural vegetation into crop fields have been well explored (Garibaldi et al., 2011; Kennedy et al., 2013; Klein et al., 2007, 2012; Mandelik et al., 2012; Rader et al., 2012), the effect of mass-flowering crops on the plants and pollinators of conservation value in remnant natural vegetation have been studied much less. Thus, understanding how mass-flowering, insect-attracting crops impact pollinator communities in remnants and the pollination services they provide to persisting remnant populations of native plants is important for native plant conservation worldwide.

Of those studies that have explored the effects of mass-flowering insect-pollinated crops on native plant and pollinator communities in remnant vegetation, results vary from negative (Holzschuh et al., 2011; Lopezaraiza-Mikel et al., 2007; Magrach et al., 2017), to neutral (Diekötter et al., 2010; Stanley & Stout, 2014), to positive (Cussans et al., 2010; Kovács-Hostyánszki et al., 2013). Negative effects seem to occur when there is a reduction in visitation rates to non-crop species after pollinators are drawn away from plants in remnant vegetation by adjacent mass-flowering crops (Brown et al., 2002; Holzschuh et al., 2011, 2016; Riedinger et al., 2014). Some studies have also suggested that mass-flowering crops can negatively impact pollination outcomes of native plants via pollen clogging, which alters the way pollen is collected and deposited in a system. This is thought to occur when pollination networks are flooded with crop pollen, increasing cross-species pollen contamination and decreasing wild plant reproductive success (Brown et al., 2002; Lopezaraiza-Mikel et al., 2007; Stanley & Stout, 2014).

Wild pollinators and plants in remnant patches may also benefit from mass-flowering crops. Agricultural crops are typically grown in large, dense monocultures that produce great quantities of pollen and nectar; these additional resources may allow larger populations of wild pollinators to persist in a landscape, which can disperse into remnants and elevate native plant reproductive success (Ghazoul, 2006). This phenomenon is more likely to occur immediately after a mass-flowering crop blooms rather than during the mass crop bloom. In many systems, remnant natural plant communities flower concurrently with mass-flowering crops. In such cases, post-bloom spillover may be less likely to benefit native plants. To understand the conservation value of remnant vegetation in agricultural landscapes, more studies are needed to understand the consequences of insect-attracting crop species on the pollination of native plant species in such remnants. The few studies that have explored this relationship have focused on native plant pollination in urban landscapes (Williams & Winfree, 2013), hedgerows (which rarely support native plant species of conservation interest or are representative of original wild vegetation) (Kovács-Hostyánszki et al., 2013; Stanley & Stout, 2014), individual plant/pollinator species (Holzschuh et al., 2011), or pollinator densities in large-scale agroecosystems (Holzschuh et al., 2016). One study, Magrach et al. (2017), assessed the impact of mass-flowering crops to plant-pollinator network structure, finding networks to be resistant to pollinator spillover from natural vegetation to crops. More research is needed, however, to separate out the impacts of large-scale agriculture per se, from the attraction of the crop to insects across whole plant communities of conservation interest. Understanding this interplay between pollinators and natural and crop plants will allow us to develop better informed conservation practices for supporting pollination services in agroecosystems.

In this study, we explore the richness, composition, and abundance of potential pollinating insects and the composition of their pollen loads (as an indicator of the plant species they may be pollinating), in the York Gum-Jam woodlands (YGJW) of Western Australia. These remnants support diverse native wildflower communities that flower concurrently with the large-scale monocultural canola and wheat crops that dominate this region of Australia. This woodland type is currently listed as a Priority III Critically Endangered Ecological Community (DAWE, 2015). It is part of the plant biodiversity hotspot of SW Western Australia (Hopper & Gioia, 2004; Myers et al., 2000), and thus is of key value for plant conservation as well as for providing crop pollination services to the region's substantial canola crop (DAWE, 2015; Myers et al., 2000). We use data collected

over two years on potential insect pollinators and their pollen loads in 24 YGJW reserves, each surrounded by either canola (an insect-attracting mass-flowering crop) or wheat (a non-insect-pollinated crop), and ask the following questions about aspects of pollination systems in agricultural landscapes directly related to the availability of pollination services to native plant species:

1. Does pollinator diversity and community composition differ by adjacent crop type (canola or wheat) and remnant vegetation features (floral abundance, distance to crop, size of remnant)? If so, do differences suggest significant differences in potential pollination services due to reduced or increased availability of potential pollinators?
2. How do pollinator visitation patterns (as measured by body pollen load) differ between remnants adjacent to canola and wheat, as well as canola crop fields? Is there evidence that in some circumstances, large quantities of canola pollen have the potential to increase rates of pollen clogging in native plant species?
3. Is there evidence that the abundance and visitation patterns of common pollinators vary by canola flowering phenology in ways that may shift the potential pollination services to co-flowering native plant species in remnants?

2 | MATERIAL AND METHODS

2.1 | Study system

This study was conducted across 235 km of the central wheatbelt of SW Western Australia (distance from north-most to southeast-most remnant) in July–September of 2015 and 2016 (Figure S1). The Eucalypt woodlands of the Western Australian wheatbelt account for a substantial proportion of the native vegetation in the region (about 44.6%) though are made up of fragmented patches dispersed within an agricultural matrix of wheat, canola, barley, oats, and lupins (DAWE, 2015). A major sub-group of this woodland type in this region is the YGJW, currently listed as a Priority III Critically Endangered Ecological Community under the EPBC Act (DAWE, 2015). This woodland supports an overstorey dominated by two main tree taxa, *Eucalyptus loxophleba* subsp. *loxophleba* (York gum) and *Acacia acuminata* (Jam). The understorey in these woodlands is a mosaic of largely native shrubs, perennial grasses, and annual forbs (Dwyer et al., 2015). Annual forbs in this system are dominated by representatives of the Asteraceae, Goodeniaceae, and Araliaceae families with some common species known to require insects for pollination (Lai et al., 2015; Staples et al., 2016). The canopy trees in this system do not flower at the same time as canola and wheat, but the wildflower understorey does, with flowering starting at approximately the same time as canola (in July), extending up to two months after canola and wheat flowering stops in late August. In this study region, we selected 24 YGJW remnants (12 each year: 6 canola (*Brassica napus*), 6 wheat (*Triticum* sp.)), each greater than 0.1 km² and in intact condition (DAWE, 2015), supporting diverse

annual wildflower communities. Some remnants were included in both study years, but with swapped categories between years due to crop rotations, while others were only studied for one year (see Table S1). Across the two years, we established 324 sampling plots, with 252 sampling plots inside remnants, which were then divided into two groups: 108 core plots (>200 m from the agricultural edge) and 144 remnant edge plots. Remnant plots were divided among those adjacent to wheat and those adjacent to canola fields (<50 m from agricultural edge; Figure S1). The remaining 72 sampling plots were established in canola fields adjacent to each woodland remnant bordered by canola (Figure S1; Table S1). Initial surveys of wheat fields revealed no flower-visiting insects, so these were not surveyed further.

2.2 | Plot-level variables

In the 24 remnants, vegetation surveys and woodland “remnant” characteristics were recorded in 15 × 15 m plots during the months of July–September in 2015 and 2016. Measurements included: % bare soil within plot, proportion woody debris (i.e. dead logs) within each plot (from 0 to 1 – estimated as the amount of the plot containing woody debris that could be used as nesting substrate for solitary bees), % flower cover in the plot, and a categorization of the understorey community by dominant flowering plant life history strategy (i.e. predominately native forbs, exotic forbs, shrubs, or grasses). These measurements were repeated three times in each plot, one survey conducted during each flowering season. The same data were collected for remnants adjacent to canola, as well as an estimate of the canola flowering phenological stage in the relevant adjacent field, using three categories: “peak,” >70% inflorescences flowering; “past-peak,” between 40 and 70%; and “late,” end of the flowering period with <40% open flowers. Other variables included size of remnant (km²), size of the agricultural field adjacent to the study remnants (km²), and distance of each plot within the remnant to the nearest agricultural edge (m).

2.3 | Sampling of potential pollinators

Potential pollinators were collected three times from each plot across the canola flowering season (once during early canola bloom, peak canola bloom, and late canola bloom). We sampled only on sunny or partially cloudy, still days in 20-min time periods during peak insect activity times (10 am–3 pm). The 20-min timer was paused during insect capture and handling time. Preliminary surveys found minimal (often no) insect activity outside of this peak activity window possibly due to low temperatures (mean minimum temp of 6.1°C for July) early in the morning and late in these winter afternoons. Potential pollinators were collected only if they landed on a flower and were observed making contact with the anthers or stigmas of a flower. We were not able to directly assess whether each insect was actively pollinating during each visit, and thus note that collected insects in

this study are potential pollinators only. For conciseness, however, we refer to them as “pollinators.” Insects were captured using sterile plastic containers or bags to ensure all body pollen was accounted for and no cross-contamination of pollen from different individuals occurred. All insects were identified by experts to the lowest taxonomic level possible, using collected specimens. Given the limited taxonomic work that has been done on Western Australian bees and flies, most species were only identifiable to the family or genus level. For species whose taxonomy was unclear, we categorized them into morphospecies. Due to low samples sizes ($n = 36$ individuals), wasps were excluded from the study. Sampling efforts in canola fields were limited to the edge of the crop fields due to access restrictions. All honeybees collected in this study were considered to be feral (unmanaged), as managed honeybee hives were not used by the canola growers in this region during the study years, and feral honeybees are known to reach very high colony densities in Australia (Cunningham et al., 2022). This is a very sparsely populated region of Australia (Perenjori Shire has a population density of 0.07 people/km² (ABS, 2017)), and thus we are confident we were aware of all homesteads and know that no local farms or households were keeping honeybees during the study period.

2.4 | Pollen load collection

We recorded pollen load (the composition and number of pollen grains) found on 893 of the 923 individual pollinators collected in the 2015 season. The remaining 30 insects had no pollen on their bodies. Pollen loads were assessed by swabbing each collection bag and insect body with Fuchsin jelly, which was then melted on a glass slide and prepared as per Kearns and Inouye (1993) (see Material Methodology S1). We also created a pollen library to help with pollen compositional assessment, using the same Fuchsin jelly approach, where a voucher specimen of every flowering plant species in each remnant during each visit was collected. Details regarding pollen identification and counting can be found in Material Methodology S2.

2.5 | Statistical analysis

All statistical analyses were performed using R Statistical Software version 3.5 (R Core Team, 2021). Rarefaction curves (function `rarefy`, package “`vegan`”) were used to calculate and assess species richness, evenness, and diversity measures.

To answer questions 1 and 2, we ran generalized linear mixed-effect models using pollinator diversity and pollen load data from remnants only. For question 1, we used three common metrics of pollinator diversity, analysing each in separate models. Diversity measures were total pollinator abundance, species richness, and Shannon's diversity (calculated using the R package “`vegan`”) divided into the three major pollinator taxa: bees, flies, and beetles. For question 2, response variables were: pollen species richness per load and evenness (calculated as pollen species diversity divided by

the log(pollen species richness)). We ran models for each pollinator diversity and pollen load response variable separately with fixed effects: crop type, the amount of flower cover in the remnant, the size of the remnant, and the distance from the edge of the remnant (function `glmer`, package “`lme4`,” and function `glmmTMB`, package “`glmmTMB`”) with Poisson (abundance, richness) and Gaussian (Shannon's diversity, evenness). Preliminary analyses indicated that our measures of % bare soil and proportion of woody debris (i.e. dead logs) were not important terms in any of our models, thus were excluded in model construction and comparison. We included remnant and plot identity as nested random factors in all analyses, and year of data collection as a separate random factor for pollinator diversity models. While the year of data collection only contained two levels, we chose to include it as a random effect to help model the spatiotemporal autocorrelations in the observed data (Arnqvist, 2020; Barr et al., 2013; Harrison et al., 2018). Where overdispersion was evident (fly abundance), a zero-inflation factor was also included in model formulation. We also analysed model fit and residual interpretation plots to ensure model assumptions were met. Finally, we used log-likelihood and Akaike weight information criteria (function `model.sel`, package “`MuMIn`”) to identify the most parsimonious model for each pollinator and pollen load response variable from a set of 20 biologically feasible candidate models (Table S2).

To assess how the composition of pollen loads differed between canola fields and remnants adjacent to canola, we used NMDS ordination and PERMANOVA (see Material Methodology S2 for details).

To answer question 3, we focused on the six most abundant bee species in our study (*Apis mellifera* (honeybee), *Neopasiphae mirabilis*, and four different *Leioproctus* species (details in Table S3)) as sample sizes of other species were too small. We pooled together data on these six species and used generalized linear models (function `glm`, package “`stats`”) with Poisson distributions to examine canola phenology on common bee abundances by including predictor variables: stage of canola flowering (peak, past-peak, and late) and crop/plot type (canola field; remnant edge plots, <200 m from agricultural edge; and core plots, >200 m from agricultural edge). To assess the impacts of canola flowering phenology on the proportion of canola pollen in pollen loads, we used similar generalized linear models and predictor variables, but with a binomial distribution. This modelling approach was used due to the small sample size. We used the same approach to examine the effects of honeybees on the five most common bee pollinators in our study (excluding honeybees themselves).

3 | RESULTS

Over this two-year study, we captured 2175 pollinators (Table S4), including 1440 bees, 363 flies, and 372 beetles. The most common pollinators in remnants were: *Apis mellifera* (honeybee), *Neopasiphae mirabilis* (native bee), four *Leioproctus* species (native bees), and two beetles; a Melyridae species; and a *Phlogistus* species (Table S3). Honeybees (311 collected; Table S3) were by far the most common

visitor to canola flowers in fields. *Lasioglossum* bees were the second most common visitor, well-behind honeybees, at 20 individual canola visits (Table S3). We recorded a total of 3,441,441 pollen grains from the 893 pollinators captured in 2015. No pollinators carried any wheat pollen, and the proportion of canola pollen carried by pollinators varied by remnant and plot (Table 1). Pollinators in canola fields carried the largest proportions of canola pollen, but all pollinator taxa carried similar proportions of canola pollen in remnant edge plots adjacent to canola (Table 1 – an average of 5–7%). Native bees (all but *Apis mellifera*) carried the largest per individual proportion of wildflower pollen in core remnant plots when adjacent to wheat (Table 1 – an average of 97%), with less wildflower pollen in core remnant plots adjacent to canola (Table 1 – on average 78%).

3.1 | Do pollinator diversity and community composition differ by adjacent crop type and remnant vegetation features?

Looking at bee species captured across the whole study, the best-fitting model for bee abundance found significantly fewer bees in canola-adjacent remnants than those adjacent to wheat ($p < 0.05$; Table S5; Figure 1a). This pattern was largely driven by honeybees, which were significantly less abundant in canola-adjacent remnants than in plots adjacent to wheat (Figure 1b); there was no statistical difference for native bees (Figure 1c). Plots with more floral resources ($p < 0.001$; Table S5) and those further from the edge ($p <$

0.05; Table S5) had the highest abundance of bees (all bee species combined, Table S5). The best-fitting model for Shannon's diversity of bees (all species combined) in remnants included flower cover ($p < 0.01$; Table S5) and distance from the edge ($p < 0.01$; Table S5). For bee richness, it included distance from the edge only ($p < 0.05$; Table S5).

Models best explaining diversity patterns for flies and beetles varied substantially from that of bees (Table S5). For fly abundance, Shannon's diversity, and species richness, null models were best (Table S5). The null model was also the best-fitting model for beetle Shannon's diversity and richness, while for abundance the model contained significant landscape factors with significantly fewer beetles in wheat-adjacent remnants ($p = 0.001$; Table S5) and higher beetle abundances with increased distance from the edge ($p < 0.05$; Table S5).

The composition of pollinators in canola fields and adjacent remnants was significantly different ($p < 0.001$; Table S6). The canola pollinator community represented a small subset of the pollinator communities found in adjacent remnants (Figure 3a).

3.2 | How do pollinator visitation patterns (as measured by body pollen load) differ between remnants adjacent to canola and wheat?

The richness of pollen loads on bees (all species) from canola-adjacent remnants was significantly higher than from wheat-adjacent

TABLE 1 Pollen load composition (represented as the proportion of crop vs. wildflower pollen – the third category, shrub/tree pollen, was excluded from this table) of potential pollinators in the study system separated by plot type (remnant core, remnant edge, or crop field) and adjacent crop type (canola or wheat)

Pollinator	Proportion of canola pollen						Proportion of wildflower pollen				
	Type	N	Mean	SE	CI (L)	CI (U)	N	Mean	SE	CI (L)	CI (U)
Adjacent to WHEAT											
Honeybee	Core	10	0	0	0	0	10	0.70	0.15	0.35	1
	Edge	31	0	0	0	0	31	0.78	0.07	0.64	0.93
Native bee	Core	50	0	0	0	0	50	0.97	0.02	0.93	1
	Edge	49	0	0	0	0	49	0.93	0.03	0.87	1
Non-bee	Core	71	0	0	0	0	71	0.93	0.03	0.93	1
	Edge	97	0	0	0	0	97	0.87	0.03	0.87	0.97
Adjacent to CANOLA											
Honeybee	Crop	107	0.98	0.01	0.96	0.99	107	0.02	0.01	0.001	0.03
	Core	32	0.04	0.03	0	0.10	32	0.67	0.08	0.51	0.83
	Edge	38	0.05	0.02	0.01	0.08	38	0.80	0.06	0.68	0.92
Native bee	Crop	21	0.97	0.01	0.94	0.99	21	0.01	0.01	0.003	0.03
	Core	111	0.01	0.00	0	0.02	111	0.78	0.03	0.71	0.85
	Edge	75	0.05	0.01	0	0.08	75	0.81	0.04	0.72	0.88
Non-bee	Crop	123	0.86	0.04	0.89	0.96	123	0.12	0.03	0.03	0.10
	Core	149	0.01	0.00	0	0.02	149	0.90	0.03	0.81	0.91
	Edge	145	0.07	0.02	0	0.09	145	0.84	0.03	0.81	0.90

Abbreviations: N, sample size; SE, standard error; CI, confidence intervals (95% – L = lower bound, U = upper bound).

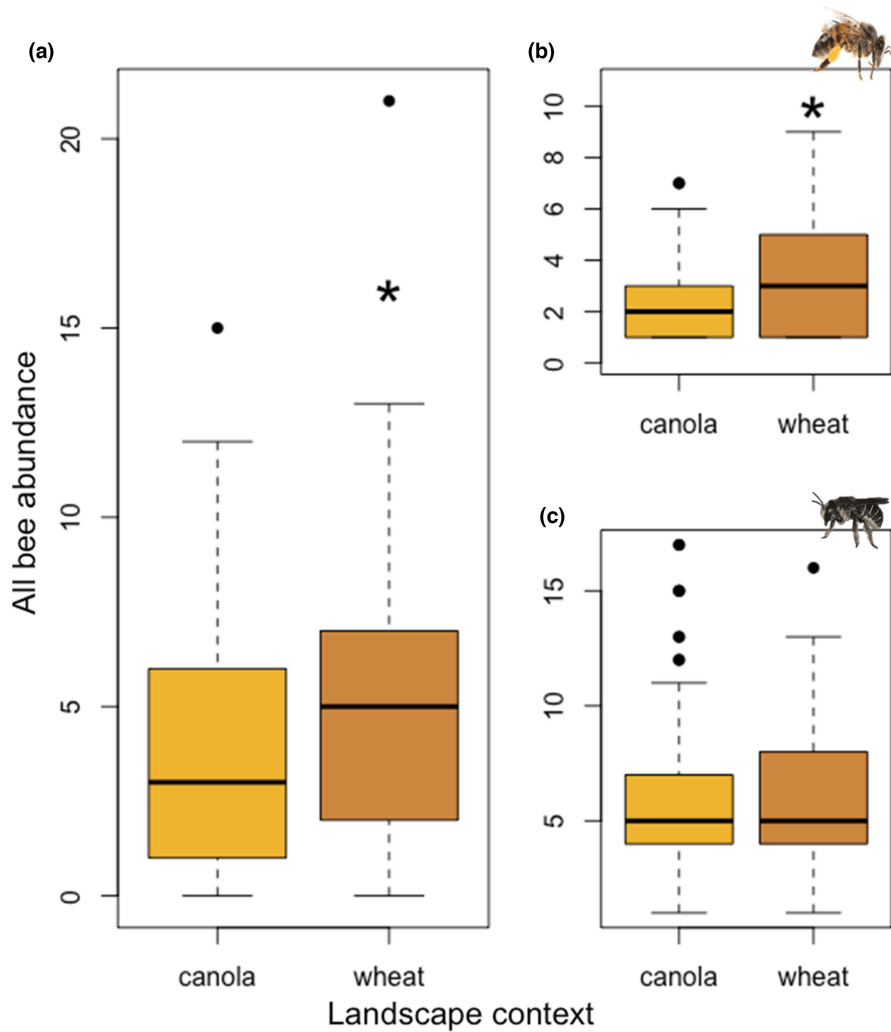


FIGURE 1 Mean abundance of bees in woodland remnants relative to neighbouring crop: (a) all bees, (b) honeybees, (c) native bees (36 different species – Table S2). p -value < 0.05*

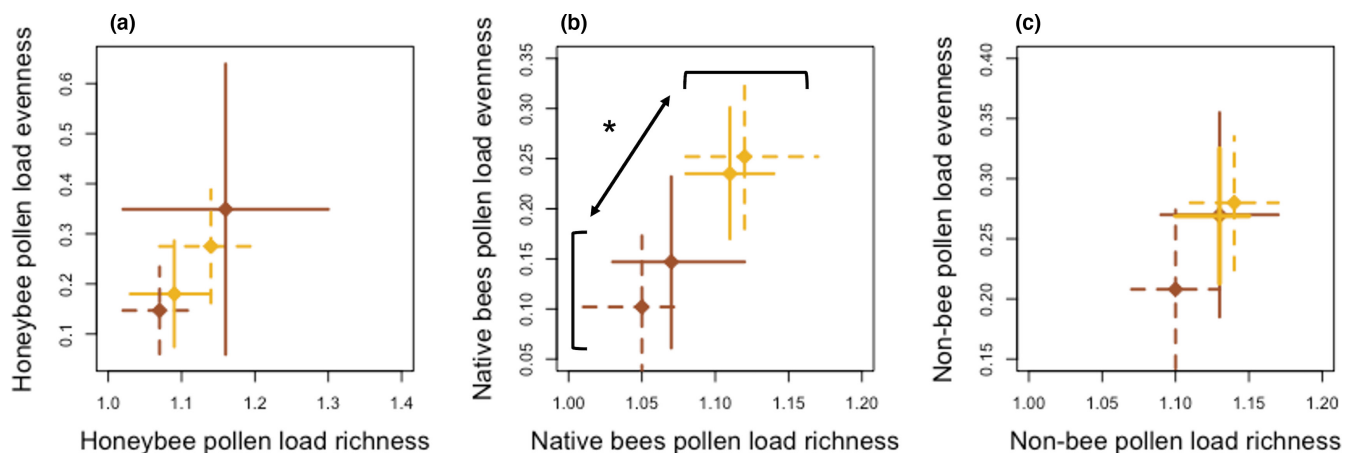


FIGURE 2 Pollen load richness and evenness from pollinators sampled in woodland remnants adjacent to canola (yellow) and wheat (tan) with respect to different distances from the agricultural edge (solid lines – core plots >200 m; dashed line – edge plots <200 m) for (a) honeybees, (b) native bee pollinators, (c) non-bee pollinator (flies, beetles, wasps). p -values < 0.05* signifies that there is a significant difference between native bee pollen load richness in canola-adjacent (yellow) compared to wheat-adjacent (tan) remnants

remnants ($p < 0.05$; Table S5) and with increasing flower cover ($p = 0.05$; Table S5). For flies, pollen load richness was significantly higher in canola-adjacent remnants ($p < 0.05$; Table S5), with increased

flower cover ($p = 0.05$; Table S5), and in large wheat-adjacent remnants ($p < 0.01$; Table S5). The null model was the best-fitting model for beetle pollen richness (Table S5).

Pollen load evenness for all bees was significantly higher in canola-adjacent rather than wheat-adjacent edge plots ($p < 0.05$; Table S5); but this was less so for honeybees than native bees (Figure 2a,b). Bee (all species combined) pollen load evenness increased with increased flower cover ($p < 0.05$; Table S5). There was no statistically significant difference between the pollen load richness and evenness of honeybees and native bees. Fly pollen load evenness also increased with increasing flower cover, regardless of adjacent crop type ($p < 0.01$; Table S5, Figure 2c). The null model was the best-fitting model for beetle pollen load evenness (Table S5).

The identities of the dominant pollinator taxa that carried canola and wildflower pollen differed among crop type and landscape contexts. Ten bee and non-bee taxa carried the most wildflower pollen in remnants (mean: >2500 pollen grains – Figure S2) including seven bee species (*Neopasiphæ mirabilis*, *Apis mellifera* and six *Leioproctus* species), one beetle species (*Phlogistus* species), and one fly species (*Choristus* species). Five pollinator taxa (*Apis mellifera*, a *Lasioglossum* species, two *Leioproctus* species, and a *Phlogistus* beetle species) from canola fields carried the most canola (*B. napus*) pollen (mean: 2000 pollen grains – Figure S3). Pollen loads from bees in canola fields predominately consisted of canola pollen, while remnant pollinators predominately carried pollen from Asteraceae and *Goodenia rosea* (Goodeniaceae – Syn: *Velleia rosea*) (Figure 3b,c). Mixed pollen loads containing both wildflower and crop pollen were evident mainly from insects that were collected in edge plots of canola-adjacent woodland remnants (Figure 3b,c). Body pollen from pollinators in canola fields and adjacent remnants were significantly different ($p < 0.001$; Table S6; Figure S5), and the proportion of canola pollen carried per pollinator decreased with distance from field edge into remnants, particularly for *Apis mellifera* and a *Lasioglossum* species (Figures S2, S3).

3.3 | Is there evidence that abundances and visitation patterns of common pollinators vary by canola flowering phenology?

There were significantly more honeybees (*Apis mellifera*) in canola-adjacent remnants during late-phase canola flowering ($p < 0.01$; Table S7, Figure 4a) than during peak and past-peak flowering periods. There were also significantly more individuals of the five most abundant native pollinators in the study (*Neopasiphæ* species, and four *Leioproctus* species) in remnants during later stage canola flowering than other stages (past-peak: $p < 0.05$, late: $p < 0.001$; Table S7, Figure 4b). An increase in honeybee abundances in remnants, particularly during the late canola flowering phase, corresponded with a significant reduction in the abundance of native bees found in remnants at the same time (past-peak stage flowering \times honeybee abundance interaction: $p = 0.04$, late-stage flowering \times honeybee abundance interaction: $p = 0.03$; Table S6, Figures S6, S7).

The proportion of canola pollen in honeybee (*Apis mellifera*) pollen loads in remnants did not vary significantly with flowering phase. There was slightly more canola pollen in honeybee pollen

loads during peak flowering (Figure 4c), with less pollen in late flowering season loads from both core and edge plots ($p = 0.07$; Table S7, Figure 4c). The proportion of canola pollen carried by the most common native bee pollinators in edge plots was significantly higher than those from core plots ($p < 0.05$; Table S7, Figure 4d).

As honeybees were the most common pollinator found in this study (Table S3: canola crops, remnant edge plots and core plots), we examined their pollen load compositions separately in relation to canola flowering phase. During the peak flowering phase, honeybees captured in canola fields predominately carried canola pollen (Figure 3d), while those captured in edge and core plots mainly carried wildflower pollen (especially Asteraceae and *G. rosea*). When the canola phase was past-peak (Figure 3e) and late (Figure 3f), compositional similarity of honeybee pollen loads was slightly higher from bees captured in canola field and remnant edge plots.

4 | DISCUSSION

4.1 | Overview

The long-term conservation of many native plant species surviving in agricultural landscapes relies, at least in part, on the continuity of pollination services. We found that the presence of a large-scale, insect-attracting crop (canola) next to wildflower remnants was associated with complex patterns of pollinator diversity and flower visitation activities, both important elements of pollination services. Notably, we found significantly fewer bees (honeybees and native bees) in canola-adjacent remnants than wheat-adjacent remnants, a pattern that weakened as the canola flowering season waned. Our results point to several avenues through which native plant species with concurrent flowering seasons to canola may be negatively impacted by the presence of canola, while some with later flowering seasons may benefit. Notably, during peak canola bloom, honeybees, the most abundant pollinator in this system, were more abundant on canola flowers than wildflowers. This suggests more limited potential for maximized fertilization of co-flowering native species flowering in remnants adjacent to canola fields. However, these same honeybees may benefit native plant species that bloom after canola as these species become more desirable resources for the large populations of honeybees left in the landscape post canola bloom.

Past studies have shown that a diversity of pollinators can provide the best pollination services, as different pollinator species offer many plant species non-redundant services (Kremen et al., 2002; Klein et al., 2009; Ricketts et al., 2004; Carvalheiro et al., 2011). Thus, our finding that native bee abundances dropped as honeybee abundances increased in remnants as canola flowering waned may have the more subtle negative impacts of reducing the diversity of pollination services available to native plants. As we did not test the directionality of pollinator movements or pollen limitation, our finding still points to the need for more detailed studies of the indirect effects of mass-flowering crops on the reproductive success of native plant species persisting in agricultural landscapes.

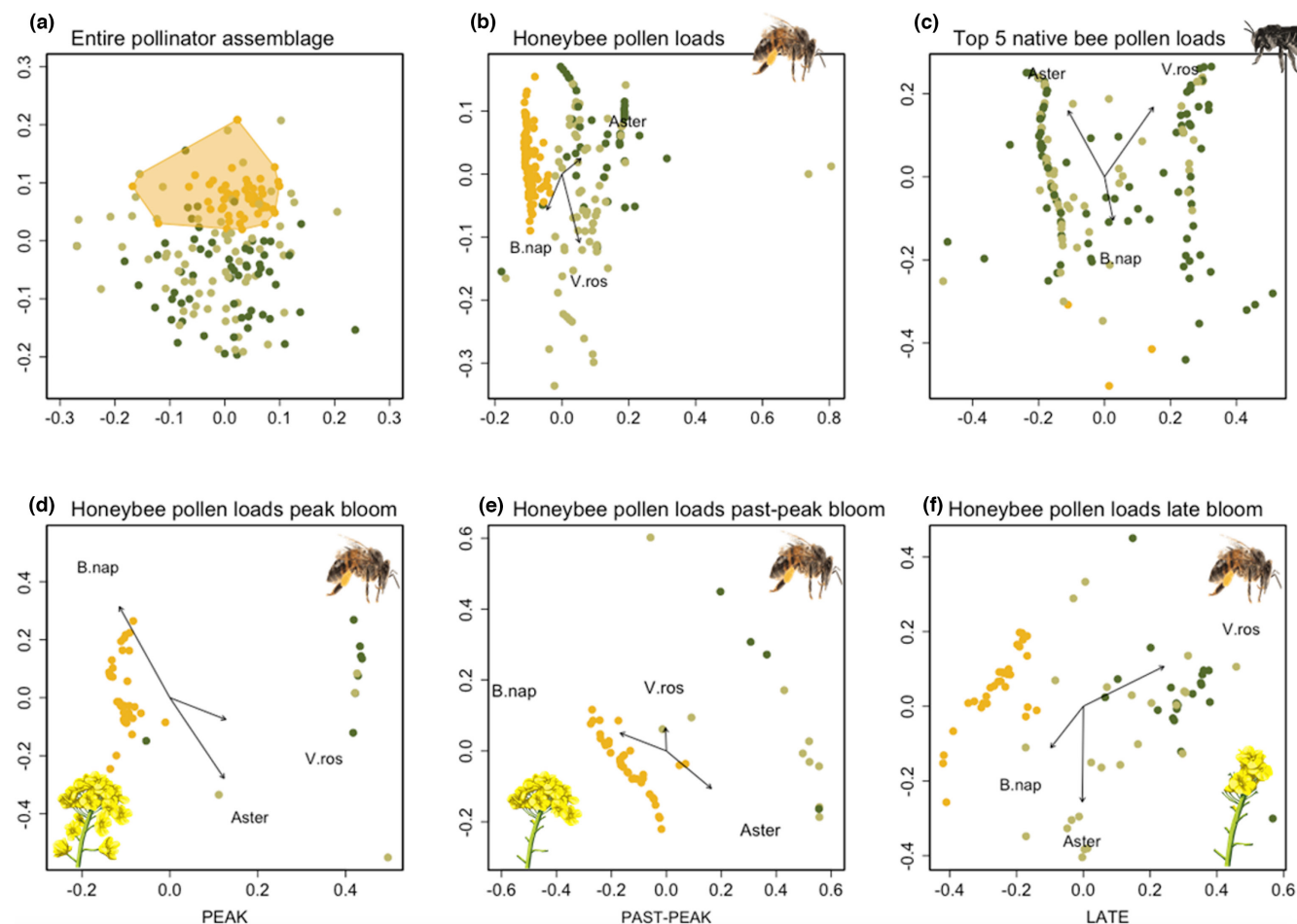


FIGURE 3 Nonmetric multidimensional scaling ordination of pollinator community assemblages (a) and pollen load compositions (b–f) in canola crop fields (yellow) and adjacent remnants (light green – edge remnant plots, dark green – core remnant plots). (a) The entire pollinator community in canola, remnant edge, and remnant interior plots. The yellow polygon encloses samples from the canola pollinator community. (b) Pollen load composition for honeybees (*Apis mellifera*) only. (c) Pollen load composition for the five most abundant native bee pollinators (*Neopasiphae mirabilis*, and four *Leioproctus* species). Honeybee pollen loads in (d) peak, (e) past-peak, and (f) late canola bloom. Vectors in b, c, d, e, and f indicate the association with the predominant pollen types in the system; *Goodenia rosea* (*V. ros*), Asteraceae spp. (*Aster*), and *Brassica napus* (*B. nap*; canola)

The outcomes of this study point to complex dynamics between pollinators, flowering crops, and non-crop flowering plant species in agricultural landscapes. By examining the pollen loads of pollinators across agricultural landscapes through space and time, we provide compelling evidence that at least some of the native wildflower species persisting in remnants of the critically endangered York um-Jam ecological communities may face a pollination challenge when canola dominates their landscapes. Our study suggests that changes in pollinator abundances, composition, and dominance associated with the canola bloom are likely mechanisms by which such effects occur.

4.2 | Pollinator communities, pollen loads, and potential pathways to reduced pollination services

There are several ways that the availability of canola pollen can impact on the pollination services received by native wildflower species in

remnant vegetation. First, high availability of canola pollen may reduce visitation of insects to wildflowers resulting in pollen limitation due to a lack of insect visitors. Alternatively, individual pollinators may limit wildflower reproductive success because of pollen clogging resulting from individual insects visiting canola and wildflower species during the same foraging trips. Though we did not measure pollen limitation or pollen tube clogging, many studies have shown a strong relationship between insect visitation rates and the quality and quantity of pollination services received by plants that benefit from insect pollination (Holzschuh et al., 2011; Loreau et al., 2001; Magrach et al., 2017; Morales & Traveset, 2008; Stanley & Stout, 2014). Thus, despite a lack of direct evidence linking insect pollinator behaviour to reproductive outputs, this study provides valuable insights about the complex relationship between insect pollinators and the pollination of native plants that benefit from insect pollination in agricultural landscapes (Lai et al., 2015; Staples et al., 2016). What makes this study unique is the focus on the juxtaposition of an insect-attracting monocultural crop with diverse natural vegetation – a common type of system that we

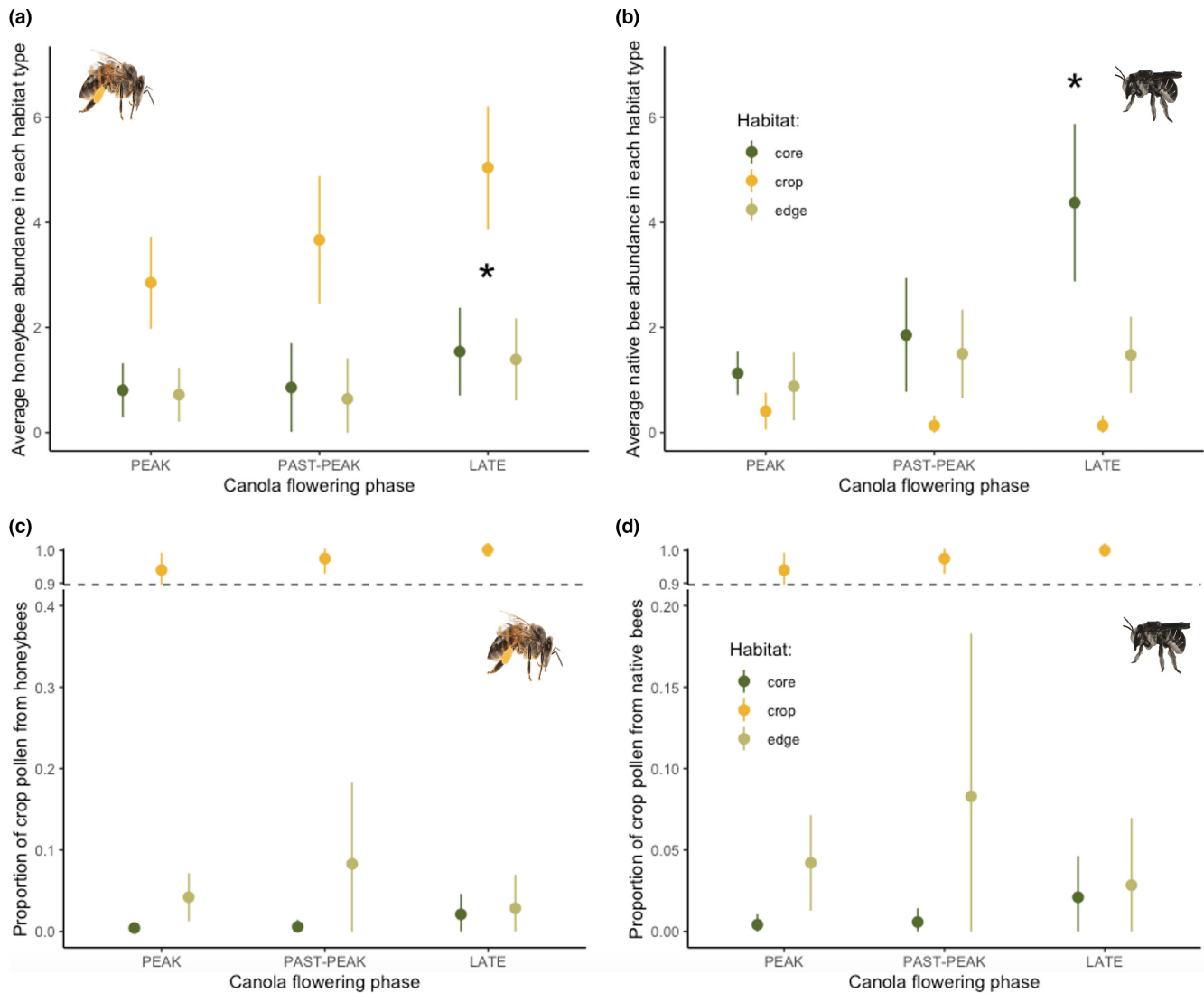


FIGURE 4 Bee abundances (a) honeybees only and (b) the five most common native bees only (*Neopisiphae mirabilis*, and four *Leioproctus* species) and the proportion of canola pollen on (c) honeybees and (d) native bees in canola crop fields (yellow) and canola-adjacent remnant core (>200 m from agricultural edge; core) and edge plots (<200 m from the agricultural edge; edge) at different stages of canola blooming (peak, past-peak, and late), plotted with 95% confidence intervals. p -value < 0.05 * indicates a significant difference (a) between the average honeybee abundance in canola fields compared to remnants (core and edge) during late canola bloom; (b) between the average native bee abundance in core remnants compared to edge and canola field sites during late canola bloom.

nonetheless poorly understand from the perspective of native plant access to insect-mediated pollination services.

4.3 | How visitation activities are impacted by the canola bloom

Honeybees, non-*Apis* bees, flies, and beetles were all found to forage in canola fields. This is not surprising as canola flowers are considered to be highly attractive to many insect pollinators (Rundlöf et al., 2014; Westphal et al., 2003). The diversity and abundance of non-*Apis* bees (and non-bees for that matter) were considerably lower in canola fields (24% were non-honeybee insects) than in adjacent remnant vegetation. This pattern is not surprising given that

solitary bees, flies, and beetles (especially those species with small- to medium-body sizes like most of the non-honeybee insects observed in this study) often have short foraging distances (Bommarco et al., 2010; Jauker et al., 2012; Lentini et al., 2012). Solitary bees also often have more complex floral visitation patterns, reflective of the need for each individual to obtain all resources for their broods. These pollinators also often require undisturbed and sparsely vegetated ground in which to create nests (Potts et al., 2010; Williams & Winfree, 2013) (though flies and beetles generally do not), a requirement that is largely incompatible with annual crop field management. Combined, limited local nesting sites, complex resource needs, and short foraging distances likely reduce the realized value of canola flowers to non-honeybee pollinators persisting in remnant vegetation in industrialized agricultural landscapes.

Fly and beetle pollinators varied markedly from bees in their response to the availability of floral resources across agricultural landscapes, frequently having little to no differences in their abundances across distinct vegetation types and landscape contexts. This lack of variation in non-bee pollinators may reflect flexible and diverse dietary needs and nesting habits (Raymond et al., 2014; Rader et al., 2016). Likewise, the variabilities in life history traits among non-bee pollinators make many of them less vulnerable to effects of agricultural land management (Rader et al., 2014), factors not so easily avoided by bee pollinators that are reliant on specific nesting sites and diverse dietary resources. The importance of these non-bee pollinators and their apparent ability to utilize a variety of habitat types and landscape contexts bodes well for ensuring the successful delivery of essential ecosystem services such as wild plant reproduction in systems dominated by mass-flowering crops (Rader et al., 2016, 2020).

The proximity of blooming canola to remnant vegetation appeared to impact honeybee visitation behaviour more than that of other pollinator insects. Bees (all) were significantly more abundant in remnants adjacent to wheat than canola. Honeybees, however, were largely the drivers of this difference as there were significantly more honeybees in wheat-adjacent remnants, perhaps due to the lack of mass-flowering canola resources nearby. The preference of canola pollen for honeybees is not surprising for a number of reasons. Notably, honeybees (the only eusocial bee in our study system) need to store large amounts of food to ensure colony growth and survival, and thus optimize foraging to exploit the best resources on offer at any given time (Keller et al., 2005; Rodney & Purdy, 2020; Rollin et al., 2013); a reality that likely shifts their importance as pollinators to different plant species over time (Stabentheiner & Kovac, 2016). However, for non-*Apis* pollinators, many factors are involved in determining the value of canola as a resource including foraging distance, competition with larger or more abundant pollinators (such as honeybees) and the availability of other resources in a landscape. Given the complex suite of factors impacting solitary insect pollinators in this study, it is, perhaps, not too surprising that these pollinators changed their interest in canola less over the flowering season than honeybees.

Though we did not track individual pollinator movements, or directly measure competition, one plausible interpretation of observed abundance patterns is that when canola is at peak flowering, honeybees are drawn into canola fields and away from remnants, releasing native bees from some competitive pressure in remnants. However, when canola wanes, the ability of honeybees to switch between resources could potentially force non-*Apis* pollinators to alter their foraging behaviour to avoid honeybees (Magrach et al., 2017; Montero-Castaño & Vilà, 2017; Thomson, 2016). This could explain our observations that native bee abundances in remnant edge plots were lower when honeybee abundances were higher. We also found a higher proportion of canola pollen in the pollen loads from remnant edge plot native bees – suggesting that mixed resource collection patterns may result from increased competition, altering short-term pollinator

floral fidelity (Brosi & Briggs, 2013). It is also possible that as the canola bloom waned, honeybees may shift into edge plots situated closer to the canola fields. To avoid this competition with the influx of honeybees, native bees may move to core remnant plots. Depending on the requirements of native plant species in this system, such changes in pollinator composition and visitation patterns may have positive, negative, or neutral changes in net pollination services. Though reduced pollinator diversity is known to result in losses of total pollination services in other systems (Garibaldi et al., 2011, 2016), it is worth exploring these dynamics in this system in the future. Likewise, future studies could investigate the overlap between pollinator phenology and resource phenology in the landscape, to further decipher the changes in bee abundance throughout a growing season.

4.4 | Shared pollen loads

Very few pollinators in this system were constant flower visitors, with most species holding mixed-species pollen loads. For wild plants in canola-adjacent remnants, the abundance of canola pollen present on pollinators suggests that the potential for interspecific pollen deposition and stigma clogging is high, particularly given the large size disparity between canola and wildflower pollen grains (Figure S4). As pollen deposition patterns were not recorded in this study, and thus we cannot know whether this threat translates into reduced fitness, our results do suggest that there is enough canola pollen on pollinators visiting native wildflowers to merit closer study of pollen deposition, pollination, and seed set in native plant species surviving in agricultural landscapes (Brown & Mitchell, 2001; Lanuza et al., 2021; Moragues & Traveset, 2005; Morales & Traveset, 2008).

The change in the canola bloom across our study system corresponded with significant differences in patterns of pollen load abundance and composition found on pollinators. The proportion of canola pollen present in remnant bee pollen loads remained relatively constant throughout the canola flowering season, suggesting that bees, particularly honeybees, readily exploited neighbouring mass-flowering canola fields, even when canola resources were waning. However, both remnant honeybees and native bees also consistently utilized wildflower floral resources. The increase in the compositional similarity of honeybee pollen loads in canola fields and those in remnant edge plots during the late canola flowering phase was reflective of an increase in wildflower pollen in honeybee loads over the season – a finding that could be positive or negative for native plant species restricted to isolated vegetation remnants; positive – as pollinators are still visiting (and potentially pollinating) native plant species, even when canola is present and in peak bloom, or negative – as the lack of floral fidelity between pollinators visiting native plant species and canola crops may result in increased interspecific pollen deposition, which could reduce native plant reproductive success (Loreau et al., 2001; Morales & Traveset, 2008).

5 | CONCLUSIONS

The composition of matrix environments in fragmented agricultural landscapes has been shown to have negative impacts on many taxa around the world (Lindemayer & Fisher, 2007). Despite the importance of maintaining pollination for the long-term conservation of insect-pollinated plant species, our study is one of the first to explore in detail the effects of a mass-flowering crop on the key elements of wild pollination services: pollinator community composition and pollinator visitation patterns. Our study showed that the presence of a mass-flowering crop – canola – alters total bee pollinator abundance but not pollinator diversity in vegetation remnants scattered through large-scale agricultural landscapes. Elevated abundances in certain landscape elements were short-lived, however, and aligned strongly with the peak flowering phase of the crop bloom. We also found that bee species were particularly disloyal to wildflower species when canola flowers were available. Honeybees often had high pollen load richness and evenness, while native bees exhibited even higher incidences of mixed-species pollen loads when canola was blooming adjacent to remnant vegetation. Overall, our results suggest that the major impact of canola on the pollination of native wildflowers in SW Western Australia resulted from lower honeybee abundances in remnant vegetation during the peak canola flowering phase. In so doing, canola increased the amount of pollination mediated by native bees in remnant vegetation during the peak bloom, while also increasing the risk wildflower species have of disrupted reproduction due to pollen clogging from mixed pollen loads. Our data reveal the potential for indirect and dynamic feedbacks between insect-attracting crops, insect pollinators, and remnant vegetation.

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CONFLICTS OF INTEREST

The authors declare there is no conflict of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available at Dryad at: <https://doi.org/10.5061/dryad.vdncjxswf>

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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