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# Variation in pollen load composition carried by wild bee species in native and nearby agricultural environments in south-eastern Australia

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## Abstract

1. Understanding the mechanisms by which wild bees survive in modified landscapes is important for their conservation and management as pollinators. Pollen is a critical resource for the completion of bee life cycles, so we investigated how the pollen loads carried by native bee communities change between natural forests and farms dominated by exotic crops and weeds in an agricultural region of south-east Australia.
2. We found that individual bees tended to carry higher proportions of exotic pollen on farms compared with forests (after accounting for whether they were captured on exotic or native flowers), and the diversity of pollen carried by bees did not differ significantly between native forest and farm sites or along native forest cover gradients. This suggests that the native bees found on farms, which are predominantly different species compared with those found in native forests, are not disadvantaged by the dominance of exotic plants in these habitats (though impacts on larval nutrition were not investigated).
3. While some native bees carried crop pollen, others almost exclusively carried the pollen of agricultural weeds (e.g., *Arctotheca* and *Brassica* species), such that some native bee species may pollinate and benefit from crops, whereas others may only persist on farms if agricultural weeds are tolerated.

## KEYWORDS

agriculture, bee, crop, forest, network, pollen, pollinator, weed

## INTRODUCTION

Conversion of natural vegetation to agriculture and other human uses is the leading cause of biodiversity decline globally (IPBES, 2019). This includes bees (Hymenoptera: Apoidea: Anthophila) that act as pollinators for many globally important crops (IPBES, 2016; Klein et al., 2007; Rader et al., 2020), which can experience declines in floral resources (pollen and nectar) and nesting sites when natural vegetation is converted to agriculture (Brown et al., 2022; Goulson et al., 2015; Harrison et al., 2018; Kleijn et al., 2015). Not all pollinator species are negatively

impacted by landscape modification (e.g., Harrison et al., 2018), and understanding the mechanisms by which they persist is important for conserving these species in modified landscapes.

One poorly understood aspect of bee responses to landscape modification is how it influences the pollen loads they carry. Some individual bees visit flowers for nectar without collecting or depositing pollen (Irwin et al., 2010; King et al., 2013; Praz et al., 2008), such that observations of flower visitation alone do not necessarily indicate whether pollination and pollen collection are occurring. Bees require pollen for larval development (Michener, 2007), and some species will

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cease pollen collection or be unable to complete normal development when non-host flowering species are the only ones present (e.g., Praz et al., 2008). Adaptation to consuming pollen from only particular plant species presumably requires long periods of co-occurrence between bee and host plant taxa, such that more specialised bees may experience declines in pollen availability when native plants are replaced by exotic plants (Brown & Cunningham, 2019; Brown & Cunningham, 2022). Alternatively, more generalist bee species may readily switch to collecting pollen from exotic plants when these replace native plants.

It is also important to understand how the diversity of pollen carried by bees changes with conversion of native vegetation to other land cover types, as pollen diversity can influence offspring production (Centrella et al., 2020; Filipiak et al., 2017; Klaus et al., 2021; Vaudo et al., 2015). Where mosaics of natural and agricultural patches exist, there may be a greater diversity of pollen (i.e., native and exotic species) available to generalist bees capable of exploiting exotic crops. Alternatively, pollen diversity may be lower at all degrees of conversion to agriculture compared with relatively intact landscapes if bees do not exploit crop pollen (e.g., Hass et al., 2019), or bees may adjust foraging ranges to maintain a fixed level of pollen diversity across gradients of landscape modification (Danner et al., 2017). Most studies exploring bee pollen diets in different landscapes so far have focused on eusocial bee species belonging to the Apidae family (Gervais et al., 2020; Jha et al., 2013; Machado et al., 2020; Piko et al., 2021; Schweiger et al., 2022), though Ritchie et al. (2016) studied two solitary Apidae species. It is, therefore, important to study species from families in addition to Apidae.

We investigate the influence of landscape composition on pollen loads carried by flower-visiting bee communities in mosaic landscapes of an agricultural region in south-east Australia to better understand how the pollen loads they carry change in modified landscapes. We first compare bee species-pollen interaction networks in native forest and farm sites, and then address the following questions about individual bee responses to land cover change: (1) do bees carry a higher proportion of exotic pollen on farms or in landscapes with less native vegetation; and (2) do bees carry more diverse pollen loads in landscapes with a greater diversity of cover types/less native vegetation. We also tested whether bee community composition varied between farm versus forest sites, and partitioned beta diversity into turnover and nestedness, to assess differences in pollen loads. Pollen diversity was measured in three different ways: richness, which increases with the number of pollen types; Shannon diversity, which increases with the number and evenness of pollen types; and the specialisation index  $d'$ , which takes into account the number and evenness of pollen types, as well as their availability (Blüthgen et al., 2006).

## MATERIALS AND METHODS

### Study area and sites

The study was undertaken in an approximately 400 km<sup>2</sup> area of the Highlands Southern Fall Bioregion in Victoria, Australia. Much of

the original vegetation has been cleared for agriculture since European people arrived after 1830, though some native forest remains on private land and public reserves. Agriculture in the area includes temperate fruits (predominantly pome and stone fruit, caneberrys, blueberries, and strawberries), wine grapes, cut flowers, meat, and dairy. Many of the cleared grassy areas support abundant exotic weeds such as capeweed (*Arctotheca calendula*) and *Brassica* species. Bees were collected from seven remnant native forest sites, seven berry farms (blueberry, *Vaccinium* sp.; caneberry, *Rubus* sp.) and six orchards (Apple, *Malus domestica*; Pear, *Pyrus* sp.; Cherry, *Prunus* sp.). Distances between sites ranged from 2 to 40 km (see Figure S1 in Supporting Information for site locations). Note that most farms and orchards (hereon collectively referred to as 'farms') contained native plants along roadsides and waterbodies, and these plants were included when surveying for bees.

### Bee collection and plant surveys

We collected native bees that were visiting flowers within a single circular sampling zone (100 m radius) at each site during spring (September–November) in 2017 and 2018 (though only 13 sites were sampled in both years). Sampling zones were positioned to avoid non-vegetated areas (e.g., farm dams and buildings) and represent the floral resources available at the site (e.g., sample zones included crops, weeds, and roadside native vegetation in small orchards bordering remnant vegetation). Each site was surveyed four times in 2017 and five times in 2018. Each survey was conducted between 10:30 and 16:30 when conditions were suitable for bee foraging (>17°, low wind and cloud cover), and lasted 40 min, giving a total of 2.6 survey hours per site in 2017 and 3.3 survey hours per site in 2018 (and a total of 100 survey hours across all sites and both years). Surveys were conducted by walking slowly around the sampling zone targeting floral resources. We were unable to survey overstories comprised of tall trees. Only bees observed contacting flowers were captured with plastic jars and later identified as species by Michael Batley (Australian Museum) and Michael Schwarz (Flinders University); bees were not captured or recorded if they were not contacting flowers. *Apis mellifera* is the only non-native bee in this area, and these were excluded from the study.

We also recorded all plant species present within each sampling zone so that plant community composition could be compared between farm and native forest sites. Plants were identified as species, or in some cases genus, in the field with reference to the Yarra Ranges local plant directory (<https://www.yarraranges.vic.gov.au/PlantDirectory/Home>).

### Pollen load analysis

Each bee was placed in a vial of 70% ethanol for 24 h. After this, the bee vials were placed in a Vortex machine and vibrated for 10 min at low speed. Both the bee and vial were rinsed with ethanol into a test

tube. If there was any visible pollen left on the bee, this was scraped off with forceps and washed into the test tube with ethanol. The forceps were washed and sonicated between each bee sample to ensure no cross-contamination. The samples were then centrifuged at 3000 rpm for 3 min after which the supernatant was removed. After spinning, the supernatant was carefully removed using separate plastic pipettes for each sample (to avoid cross-contamination), leaving approximately 1 mL of liquid per tube.

Flowers were collected from within the study sites and surrounding landscapes (within approximately 100 m of study sites), and the parent plant was identified to the lowest possible classification to establish a pollen reference collection. The anthers were removed and put through the same acetolysis procedure as the bee samples (outlined below), before being mounted on microscope slides. The pollen recovered from the bee samples as well as anthers from the pollen reference samples were processed using standard processing techniques (Bennett & Willis, 2002) (detail in Supporting Information S1).

Samples were slide mounted, and the pollen on the sample slide was identified by comparison to the reference library as well as the Australian Pollen and Spore Reference Collection (Haberle et al., 2021). An initial survey of the slide was conducted at 10 $\times$  magnification. We examined 653 bees, 16% (104 bees) yielded detectable pollen and were used for analysis. For slides with pollen, transect counts were conducted at 40 $\times$  magnification until at least 100 pollen grains were counted or the species accumulation curve appeared to reach saturation.

## Landscape measurement

We generated land cover maps in ArcGIS by drawing polygons corresponding to each cover type—native vegetation, cropland (predominantly perennial woody crops), pasture, residential, water, and exotic conifer—over the ‘Imagery’ base map, and subsequently ground-truthing polygons (i.e., determining whether imagery matched existing cover) during site visits. We defined ‘native vegetation’ as any area with an over-story of native trees (native tree plantations were not present). ‘Cropland’ consisted of pome and stone fruit orchards (52%), vineyards (21%), strawberry (15%), caneberry and blueberry (10%, all co-occurring), and greenhouse flowers (2%). ‘Pasture’ consisted of areas where the forest had been cleared and a grassy ground layer managed, typically with low-density grazing. Pasture comprised 95% of open agriculture in this study, strawberry (5% of open agriculture) was the only annual crop. ‘Residential’ comprised an area under human infrastructure. We used spatial analysis tools in ArcGIS to calculate two landscape metrics: the proportion of native vegetation within 250 m of sample locations (NV250), and the proportion of native vegetation within 1000 m of sample locations (NV1000).

We also examined scatterplots and tested correlations between native vegetation (NV250 and NV1000) and exotic land cover (crops + cleared grassy areas) with 250 and 1000 m to determine the strength of relationships between these land cover types. This was

done separately for each year as not all sites were surveyed in both years and there were minor changes in landscape composition between years (e.g., changes in crop composition). Native vegetation and exotic land cover were strongly negatively correlated in both years and at both spatial scales (Pearson correlation coefficient ranged from  $-0.88$  to  $-0.99$ ,  $p$ -values all  $<0.001$ ).

## Statistical analysis

We described pollen preferences of bees with two quantitative plant-pollinator interaction networks based on pollen load composition analysis; a native forest network and a farm network. Bipartite bee species-pollen interaction networks were created by pooling pollen load compositions across all sample periods and sites within each site category (forest vs. farm) for each bee species to create two matrices showing the number of pollen grains each bee species was carrying of each plant genus (genus being favoured for clarity, as there were 50 plant species). This was produced using the package ‘bipartite’ (Dormann & Strauss, 2014) in the R statistical environment.

Bipartite networks were also used to calculate the specialisation index  $d'$  for each bee for use in regression analysis (see below). Bee individual-pollen interaction networks were created for each site where more than one individual bee was collected ( $n = 16$ ) by pooling pollen load compositions across all sample periods within each site for each bee individual.

To address the main questions of whether pollen loads carried by bees change in modified landscapes in more detail we used generalised linear mixed models with individual bee specimens as observations, and different pollen load response variables—proportion of exotic pollen, pollen richness, Shannon diversity, and  $d'$ —for each model. We first determined the best random effects structure for each of these response variables using Akaike Information Criterion for small sample size (AICc) to compare models with all possible combinations of the following random effects: random intercepts for site (because multiple bees were collected from each site), random intercepts for the flower type (native vs. exotic) each bee was collected from, random intercepts for bee species, random site type slopes for bee species (i.e., responses to site type vary between bee species), random NV250 slopes for bee species (i.e., responses to NV250 vary between bee species) and random NV1000 for bee species (responses to NV1000 vary between bees species). Once the best (lowest AICc) random effects structure was determined for each response variable, model selection with AICc was used to determine the best fixed effects structure by comparing the following model sets comprising six models each (a separate set for each response variable): site type (native forest vs. farm), NV250, NV1000, site type plus NV250, site type plus NV1000 and a null model with random effects only. Different error distributions were used to meet model assumptions for different response variables as follows: beta for the proportion of exotic pollen and  $d'$  (both transformed to be  $>0$  and  $<1$  using  $= \frac{x(n-1)+0.5}{n}$ , where  $n$  = the number of bee specimens, according to Smithson and Verkuilen (2006)), Poisson for pollen richness, and Gaussian for pollen Shannon diversity.

All specimens with less than five pollen grains were excluded from regression analysis to provide more robust estimates of pollen diversity on specimens, as were all species and sites with fewer than three specimens to facilitate estimation of species and site random effects. This left 73 specimens belonging to eight species for regression analysis.

We also compared plant community richness and composition between farm and native forest sites. Richness was compared using simple linear regression with site type (farm vs. forest) as the explanatory variable. Composition was examined using PERMANOVA with site type as the explanatory variable, and an ordination plot. The site-by-plant species/genus matrix was binary (presence/absence) so we

used the raup-crck dissimilarity for PERMANOVA and the ordination plot, implemented in the R package 'vegan' (Oksanen et al., 2015).

## RESULTS

We surveyed 13,583 pollen grains belonging to more than 50 plant species from 104 individual bees (32 from native forest sites, 72 from farms) belonging to 26 bee species. Twenty species belonged to the Halictidae family, five to the Apidae family, and one to the Colletidae family (Table 1). Thirteen species were found only on farms, and six

**TABLE 1** The % exotic pollen, average pollen richness, and number of specimens of each species.

Bee specimens				Number of specimens		% exotic pollen		Average pollen richness	
Family	Genus	Species	Authority	Farms	Forests	Farms	Forests	Farms	Forests
Apidae	<i>Exoneura</i>	<i>robusta</i> <sup>a</sup>	Cockerell	6	6	72%	13%	4.2	3.3
Apidae	<i>Exoneura</i>	<i>sp3</i> <sup>a</sup>		1	2	100%	0%	2.0	2.5
Apidae	<i>Exoneura</i>	<i>sp4</i>		1	0	100%	NA	2.0	NA
Apidae	<i>Exoneura</i>	<i>sp1</i>		0	1	NA	0%	NA	3.0
Apidae	<i>Exoneura</i>	<i>sp2</i>		0	1	NA	1%	NA	6.0
Halictidae	<i>Homalictus</i>	<i>sphecoides</i> <sup>a</sup>	Smith	7	0	98%	NA	2.4	NA
Halictidae	<i>Homalictus</i>	<i>urbanus</i>	Smith	1	0	73%	NA	4.0	NA
Halictidae	<i>Lasioglossum</i>	<i>cf gilesi</i>		1	0	94%	NA	5.0	NA
Halictidae	<i>Lasioglossum</i>	<i>hemichalceum</i>	Cockerell	1	0	96%	NA	2.0	NA
Halictidae	<i>Lasioglossum</i>	<i>imitans</i>	Cockerell	1	0	85%	NA	3.0	NA
Halictidae	<i>Lasioglossum</i>	<i>lacthium</i>	Smith	2	0	98%	NA	8.0	NA
Halictidae	<i>Lasioglossum</i>	<i>lanarium</i> <sup>a</sup>	Smith	8	0	99%	NA	2.4	NA
Halictidae	<i>Lasioglossum</i>	<i>orbatum</i> <sup>a</sup>	Smith	6	0	92%	NA	5.3	NA
Halictidae	<i>Lasioglossum</i>	<i>clelandi</i> <sup>a</sup>	Cockerell	24	2	75%	1%	4.8	6.5
Halictidae	<i>Lasioglossum</i>	<i>littleri</i>	Cockerell	1	1	98%	0%	2.0	2.0
Halictidae	<i>Lasioglossum</i>	<i>sulthicum</i> <sup>a</sup>	Smith	5	8	75%	2%	4.6	4.4
Halictidae	<i>Lasioglossum</i>	<i>opacicolle</i> <sup>a</sup>	Cockerell	1	4	0%	4%	2.0	4.3
Halictidae	<i>Lasioglossum</i>	<i>seductum</i>	Cockerell	1	0	0%	NA	2.0	NA
Halictidae	<i>Lasioglossum</i>	<i>parasphecodes sp 2</i>		0	1	NA	0%	NA	2.0
Halictidae	<i>Lasioglossum</i>	<i>sturtii</i>	Cockerell	0	3	NA	0%	NA	2.0
Halictidae	<i>Lasioglossum</i>	<i>victoriellum</i>	Cockerell	1	1	37%	64%	6.0	3.0
Halictidae	<i>Lasioglossum</i>	<i>mundulum</i>	Cockerell	2	0	50%	NA	3.0	NA
Halictidae	<i>Lasioglossum</i>	<i>tamburinei</i>	Friese	1	0	42%	NA	6.0	NA
Halictidae	<i>Lipotriches</i>	<i>australiana</i>	Smith	0	1	NA	15%	NA	7.0
Halictidae	<i>Lipotriches</i>	<i>sp 2</i>		1	0	0%	NA	4.0	NA
Colletidae	<i>Leioproctus</i>	<i>sp3</i>		0	1	NA	0%	NA	8.0
All species				72	32	77%	6%	3.7	4.2

Note: The bottom row is % of exotic pollen across all specimens collected on farms versus forests, average pollen richness average across all species collected on farms versus forests and the total number of specimens collected on farms versus forests.

<sup>a</sup>Species included in regression analysis.

- , >66% native.
- , 31%–66% mixed.
- , >66% exotic.
- , more common on farm.
- , more common in forest.
- , pollen richness >3.

species were found only in forests (Table 1). The average number of pollen types carried by individual bees was 4.11 (standard deviation = 2.31). Almost half of the bee specimens (40%), comprising 12 species from 14 sites, carried pollen loads containing a mix of exotic and native pollen. Across all specimens, 55.67% of pollen grains carried by bees were from exotic plants (defined here as not being present before European colonisation).

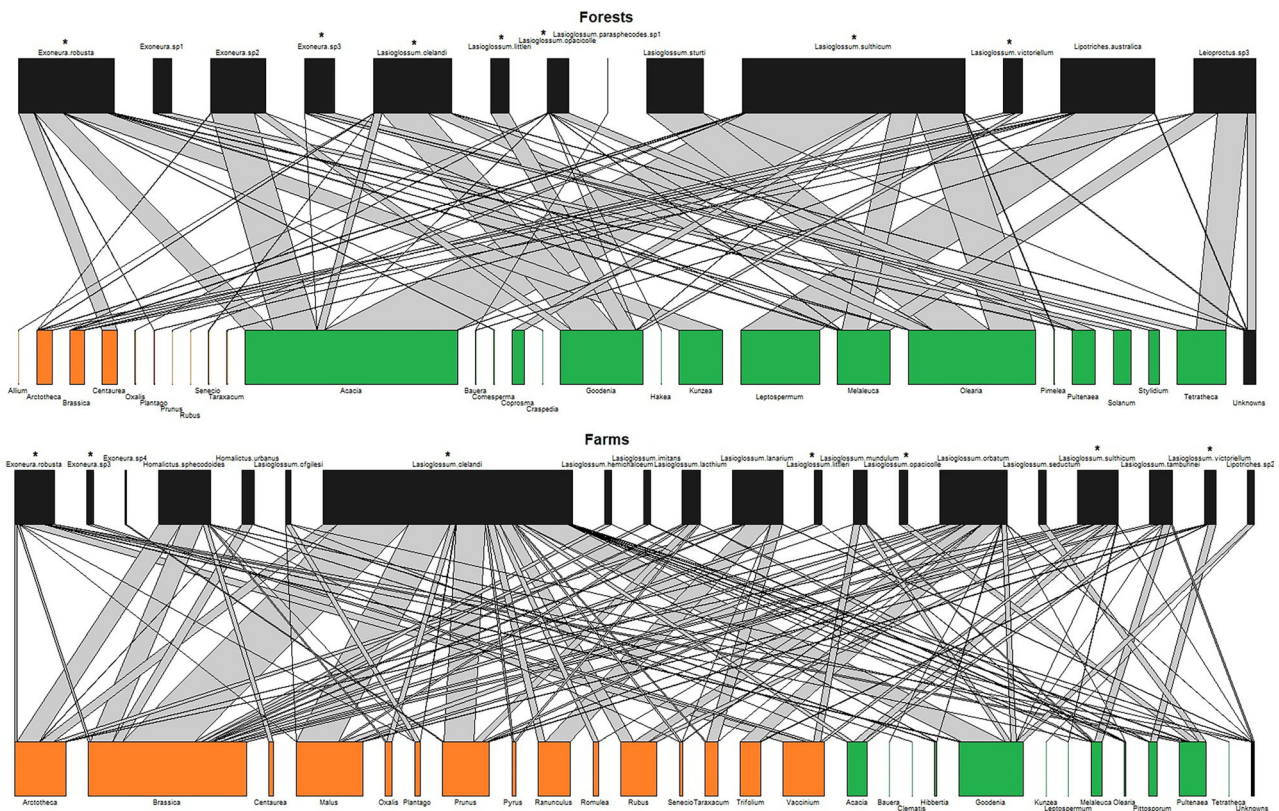
### Bee species-pollen interaction network

Overall the native forest network was dominated by native pollen and the farm network was dominated by exotic pollen, though pollen belonging to several native and exotic plant genera was found on bees in both farms and forests (e.g., native *Acacia*, *Goodenia* and *Pultenaea*; exotic *Arctotheca*, *Brassica* and *Centaurea*) (Figure 1). Most bee species found both in native forests and on farm sites (*Exoneura robusta*, *E. sp3*, *Lasioglossum clelandi*, *Lasioglossum littleri* and *Lasioglossum sulthicum*) carried predominantly pollen of the respective land cover type (i.e., native pollen in forests and exotic pollen on farms). The exceptions to this were *Lasioglossum opacicolle*, which almost exclusively carried native *Pultenaea* (Fabaceae) pollen in forests and on farms, and *L. victoriellum*, which carried evenly mixed loads in both habitats (Figure 1 and Table 1). The pollen load of bee species

presents only in native forests (*E. sp1*, *E. sp2*, *Lasioglossum parasphcodes sp1*, *Lasioglossum sturtii*, *Lipotriches australica* and *Leioproctus sp3*) was predominantly native pollen. Conversely, bee species present only on farms (*E. sp4*, *Homalictus sphaecodoides*, *Homalictus urbanus*, *Lasioglossum cf gilesi*, *Lasioglossum hemichalceum*, *Lasioglossum imitans*, *Lasioglossum lathium*, *Lasioglossum lanarium*, *Lasioglossum orbatum*, though not *Lasioglossum mundulum*, *Lasioglossum seductum* or *Lipotriches sp3*) tended to carry predominantly exotic pollen (Figure 1 and Table 1).

### Bee individual responses to land cover

Individual bees carried higher proportions of exotic pollen on farms compared with in native vegetation (Table S1). The best random effects structure included the site and type of flower (native vs. exotic) bees were collected from. The best model of the proportion of exotic pollen including fixed effects included site type (farm vs. native forest), and this model was substantially better than all other models except the model containing site type and the proportion of native vegetation within 250 m (the simpler model containing only site type was used for parameter estimation). The proportion of exotic pollen carried by bees was lower in native forests compared with farms (estimate = -1.519,  $p = 0.002$ ), after



**FIGURE 1** Bipartite networks showing interactions between bee species (top bars) and pollen species (bottom coloured bars; orange = exotic, green = native) for native forest and farm sites. Asterisk above bee species name indicates that species was collected on both native forest and farm sites.

accounting for whether the bee was collected from an exotic or native flower.

There was no evidence that pollen load diversity varied along gradients of landscape modification (Table S1). The best random effects structure included site and bee species for richness, and only site for Shannon diversity and  $d'$ . The richness, Shannon diversity and  $d'$  of pollen carried by individual bees did not respond to site type or the amount of native vegetation, with the null model being in the top-ranked models (the best or within 2 AICc of the best) for all three metrics.

## Plant community

Plant taxonomic richness and composition varied between farm and forest sites. Plant richness was statistically significantly ( $\alpha = 0.05$ ) higher on farms compared to forests (estimate =  $-5.319$ ,  $p = 0.002$ ), and site type explained a moderate amount of variation in plant richness (Adjusted- $R^2 = 38\%$ ). The effect of site type on plant community composition was a statistically significant ( $F = 31.74$ ,  $p = 0.001$ ) and explained more than half of the variation ( $R^2 = 64\%$ ). Farm and forest sites were clearly separated in ordination space (Figure S2). In addition to cultivated species found only on farms (e.g., apples, blueberries, cherries), there were a number of agricultural weeds that were common on farms but rare or absent from native forests (e.g., *Arctotheca calendula*, *Taraxacum officinale* and *Brassica* sp.).

## DISCUSSION

We found that individual native bees tended to carry higher proportions of exotic pollen on farms compared with forests (after accounting for whether they were captured on exotic or native flowers). Most bee species were found either on farms or forests, such that differences in pollen load composition were driven predominantly by the foraging patterns of different bee species, though individuals of species collected from both farms and forests also tended to carry a higher proportion of exotic pollen on farms. This reflected between-site differences in plant taxonomic composition, with farms being dominated by exotic crops and weeds while forests comprised mostly native species, suggesting that bee diets in different habitat types are restricted by the availability of different plant species. The diversity of pollen carried by bees did not differ significantly between native forest and farm sites or along native forest cover gradients, despite plant richness being higher on farms. Our study expands on previous analyses of pollen carried by bees, which typically focused on eusocial Apidae species, by including a larger number of predominantly solitary or semi-social Halictidae species (Hall et al., 2019; Walker, 1995).

Our results suggest that the orchards and berry farms in the Yarra Valley region, which was previously dominated by native forests provide habitat and are, therefore, of conservation value for some native bee species belonging predominantly to the Halictidae family.

Agriculture is relatively small-scale and heterogeneous in this region, and a diversity of herbaceous weeds is usually present on these farms, such that the conversion of native vegetation to relatively high diversity farming may have had minimal impact on the diversity of pollen types collected by these native bees. The Halictidae species that dominated communities we sampled are known to be the most tolerant of the conversion of native vegetation to agriculture in southeast Australia (Brown et al., 2020; Brown et al., 2022; Brown & Cunningham, 2022; Hall et al., 2019; Lentini et al., 2012; Neave et al., 2020), which our results suggest may be due to their ready acceptance of exotic pollen, particularly from agricultural weeds such as *Brassica* (Brassicaceae), *Arctotheca* (Asteraceae), *Ranunculus* (Ranunculaceae) and *Taraxacum* (Asteraceae) species. Tolerance of agricultural weeds on farms (or replacement by closely related native species) may, therefore, be an important component of native bee conservation in these agricultural landscapes.

Interestingly, a number of Halictid species present only on farms (*H. sphecodoides*, *H. urbanus*, *L. lanarium* and *L. orbatum*) that carried pollen from exotic herbaceous weeds almost exclusively were previously found to be more abundant in cleared landscapes than in landscapes dominated by native forests (Brown et al., 2020; Brown & Cunningham, 2022). Together these findings suggest that these Halictid species may have originally inhabited more open native vegetation dominated by herbaceous plants such as native grassland and grassy woodland that are now rare in southeast Australia and have expanded into ecologically similar agricultural systems as has been found for bees and other animals in the northern hemisphere (Brown et al., 2021; Harrison et al., 2018). Conservation of these bees may, therefore, also benefit from restoration of threatened native grassland and woodland ecosystems.

Our findings highlight the potential role of Australian bees as crop pollinators, justifying their conservation on economic grounds. *Lasioglossum* (Halictidae) and *Exoneura* (Apidae) species in south-eastern Australia deposit apple pollen on apple stigmas (Bernauer et al., 2022) and improve the quality of blackberry fruit (Coates et al., 2022). Our bee species-pollen type network revealed that some native *Lasioglossum* (Halictidae) and *Exoneura* (Apidae) species carried substantial amounts of blueberry (*Vaccinium*), cherry (*Prunus*) and *Brassica* (though a weed in our study landscapes, canola is a major crop in other parts of Australia) pollen and may, therefore, act as pollinators of these crops in addition to apple and blackberry.

While regression modelling did not support a strong effect of bee species on the proportion of exotic pollen carried by individuals, the species-level networks revealed that *L. opacicolle* predominantly carried native *Pultenaea* pollen on both forest and farm sites (though only one specimen was collected on a farm, whereas four were collected across two forest sites). This finding is interesting because Australian *Lasioglossum* species are typically generalists (Danforth & Ji, 2001; Walker, 1995), whereas our results and those of Hingston (1999) suggest *L. opacicolle* is a specialist of native *Pultenaea* species and is, therefore, vulnerable to loss of native vegetation (it was present at a number of native forest sites, but only one farm where *Pultenaea* was growing along a fence).

It is important to note that we were unable to include native bees of the Colletidae family, because only one specimen carried sufficient pollen for analysis (*Leioproctus sp3*). These species tend to specialise on ancient Australian plant lineages (e.g., Myrtaceae and Proteaceae) and so would be expected to be least capable of compensating for native plant decline through the utilisation of exotic pollen (Brown & Cunningham, 2022; Michener, 1965).

## CONCLUSIONS

Farms in our study region were characterised by exotic crops and weeds that were less common or absent in native forests. Generalist native bee species on farms collected pollen from a diversity of exotic plants, including crops and weeds, and many of these bee species were found only on farms. Tolerance of agricultural weeds may, therefore, be an important component of native bee conservation on farms, though this needs to be weighed against the negative impacts some of these exotic species have on agriculture and the environment.

## AUTHOR CONTRIBUTIONS

**Julian Brown:** Methodology; formal analysis; writing – original draft; conceptualization; data curation. **Helen Burke:** Investigation; methodology; data curation. **Janelle Stevenson:** Supervision; writing – review and editing; methodology. **Saul Cunningham:** Conceptualization; methodology; supervision; writing – review and editing.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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## SUPPORTING INFORMATION

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

**Data S1.** Pollen processing—acetolysis protocol.

**Figure S1.** Map showing the study area and sites from which bee were collected. Filled black square on map (in VIC) shows approximate location of study area. Circles in detailed study area map show locations of sites; blue = native forest, red = orchard, yellow = berry farm (note that some orchards also contained berries and vice versa).

**Figure S2.** Ordination plot showing separation of sites (blue circles) according to plant species composition. Coloured polygons are convex hulls (i.e., smallest polygons enclosing all points with each set) for farm sites (black polygon) and native forest sites (red polygon).

**Table S1.** Model structures, delta AICc, and Akaike weights for % exotic pollen, pollen richness, pollen Shannon diversity, and d'.

**Table S2.** Abundance of each pollen type collected from bees at each site.

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