





RESEARCH ARTICLE

Honey bees are the most abundant visitors to Australian watermelon but native stingless bees are equally effective as pollinators

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Abstract

1. Despite the benefits of a diverse approach to crop pollination, global food production remains reliant on a low diversity of managed pollinators, especially the European honey bee (*Apis mellifera*). To facilitate more robust pollinator management and improve the resilience of the production system, it is necessary to understand regional variation in the pollination ecology of global food crops. Watermelon (*Citrullus lanatus* [Thunb.] Matsum & Nakai) is a highly insect pollinator-dependent crop and even though it is grown globally across many different climate zones, little is known about its pollination ecology across the diverse growing regions of Australia, spanning from the tropics to the arid zone.
2. We compared the species composition, visitation rates and effectiveness of the dominant floral visitors on 15 farms across five major watermelon-growing regions of Australia.
3. We found that insect species composition differed significantly among regions, but honey bees were the dominant watermelon flower visitor, with relative abundance varying from 73% to 94%. However, native bees (including stingless bees *Tetragonula* sp., and bees from families Megachilidae and Halictidae such as *Lasioglossum*, *Homalictus* and *Lipotriches*) and flies (particularly Syrphidae sp.) also visited and transferred pollen onto watermelon flowers.
4. In particular, native stingless bees were common visitors in several growing regions and deposited similar amounts of pollen to honey bees.
5. Our findings indicate that the Australian watermelon industry utilizes honey bees, but the diverse assemblage of available native pollinating taxa provides an additional opportunity for growers in specific growing regions. Pollination service delivery could be increased by deploying managed populations (e.g., native

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stingless bee colonies), employing pollinator-safe land management practices as well as exploring methods for increasing the efficiency of managed honey bee colonies.

KEYWORDS

Citrullus lanatus, flower visitors, pollinator effectiveness, watermelon, wild pollinators

1 | INTRODUCTION

More than 75% of the world's crops are known to benefit from insect pollinators—many producing greater yields and/or higher quality produce with insect pollination, and some crops failing to set fruit altogether without pollinator visits (Aizen et al., 2019; Allen-Perkins et al., 2022; Klein et al., 2007). A diverse group of insects make important contributions to crop pollination (Breeze et al., 2011; Rader et al., 2020), and encouraging a variety of pollinator species can ensure system resilience and increase yields through complementary pollinator activity (Blüthgen & Klein, 2011; Hoehn et al., 2008; Rader et al., 2013) and synergistic interactions between pollinators (Brittain et al., 2013). Despite the understood benefits of pollinator diversity, pollination management remains reliant on a low diversity of pollinators (Garibaldi et al., 2017), in particular the European honey bee (*Apis mellifera*), the most widely recognized (Ollerton et al., 2012; Smith & Saunders, 2016) and utilized pollinator species (Aizen & Harder, 2009; Rollin & Garibaldi, 2019).

The current dependence on honey bees for crop pollination can be attributed to their widespread availability and relatively advanced management practices following a long history of management (Crane, 1999). However, the availability and cost of honey bees for pollination is volatile and subject to economic (Aizen & Harder, 2009; Evans et al., 2019), biotic (Neov et al., 2019) and climatic factors (Brown et al., 2017; Rader et al., 2013). This may be particularly true in Australia, where the honey bee parasite *Varroa destructor* has only recently arrived and not established—elsewhere in the world, the spread of this mite has severely altered beekeeping practices and hive availability (Iwasaki et al., 2015).

Concern about the reliability of honey bees as a pollination tool is one of the factors generating grower interest in pollinator diversity. An international survey of growers revealed that while most (59%) introduce managed honey bee colonies into their crops, 62% were keen to receive more information from scientists on pollination management that incorporates other species of pollinators (Osterman et al., 2021). However, for many crops/environments, baseline research has not been completed and firm recommendations for targeted management of diverse pollinators on farms and in surrounding landscapes are not available (Howlett et al., 2021; Rader et al., 2020).

The necessary first steps to providing biodiverse pollination management recommendations are clear; for any given crop, the effectiveness of different flower visitors at transferring pollen must be established to identify potential key pollinators, and the abundance

of these key species across growing regions must then be explored (Dymond et al., 2021; Pardo & Borges, 2020). With this information, growers can conduct their own abundance assessments for locally important species of wild pollinators and supplement natural pollination with honey bees or other managed pollinators accordingly. In this study, we establish the baseline pollinator data for Australian grown watermelon.

Watermelon (*Citrullus lanatus* [Thunb.] Matsum & Nakai; family: Cucurbitaceae) is a monoecious crop (producing both male and female flowers) which is entirely dependent on insects for pollination (Free, 1993; McGregor, 1976). Pollination deficits in watermelon have been widely reported by European growers (Breeze et al., 2019) and are known to limit yields in some countries (Layek et al., 2021; Sawe et al., 2020). Whilst watermelon is cultivated globally in a diversity of climates (Free, 1993; Stanghellini, 1997; Wijesinghe et al., 2020), most studies on its pollination ecology have been undertaken in the United States (Subasinghe Arachchige et al., Unpublished). The composition and importance of pollinator communities has yet to be explored in other important growing regions, including Australia which produces 176,279 tonnes of watermelon/year and contributes USD \$113 million annually to the Australian economy. Watermelon is grown across Australia largely as monoculture but sometimes with other crops in mixed cropping systems. The majority of marketable production comes from Queensland (32%), New South Wales (26%) and Northern Territory (25%) (FAO, 2019; Innovation, 2021).

Honey bees are prevalent in many watermelon-growing regions, but in open-growing environments the flowers are often visited by a diverse suite of insect pollinators (Garantonakis et al., 2016; Kremen et al., 2004; Layek et al., 2021; Njoroge et al., 2004; Pisanty et al., 2016; Winfree et al., 2007). Generally, agriculture in Australia is considered to be dependent on honey bees (Cunningham et al., 2002), but native insect richness is high, with 7000 dipteran and 10,000 lepidopteran species described (Britton, 2018) in addition to 1630 bee species in five families (Australian Faunal Directory, 2018 as cited in Smith, 2018). Australia's watermelon pollinator communities are expected to differ from other studied regions, due to continental variation in available fauna. For instance, Eucerini bees and bumble bees (*Bombus* spp.) are absent from mainland Australia, whereas *Peponapis pruinosa* Say (Apidae: Eucerini) and bumble bees are dominant flower visitors in U.S. watermelon fields (Campbell et al., 2018; Campbell et al., 2019; Rader et al., 2013; Spicer, 2007).

We conducted the following study to identify the insect taxa visiting watermelon flowers and their visitation rates and pollination efficiency

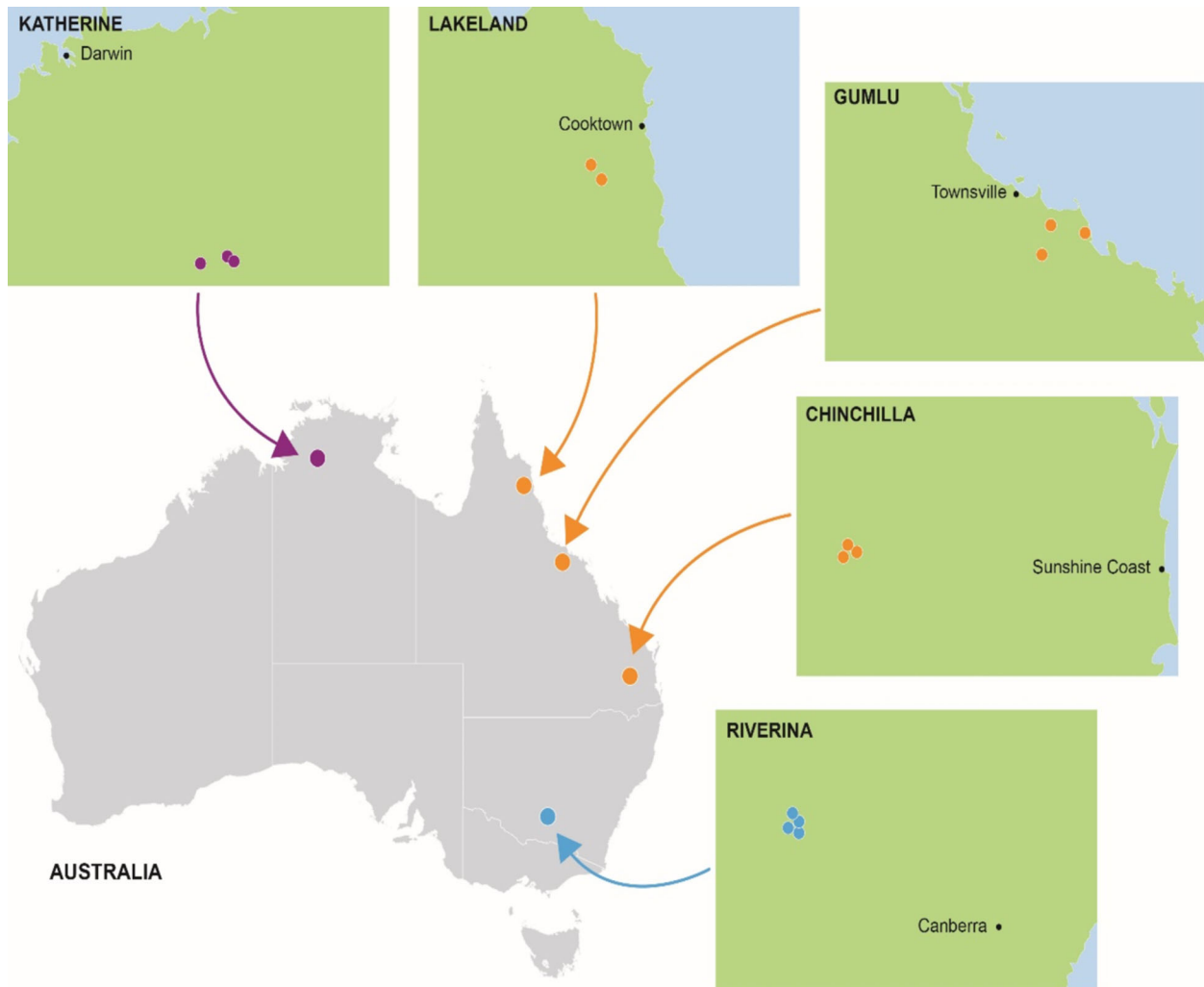


FIGURE 1 The location of the 15 watermelon farms from five major watermelon-growing areas across three different states in Australia: Katherine (Northern Territory); Lakeland, Gumlu and Chinchilla (Queensland) and Riverina (New South Wales). Each coloured dot on the five regional maps represents a separate farm.

in five major watermelon-growing areas across Australia. We asked the following research questions:

- (i) How does the composition and abundance of flower visiting insects vary among major watermelon-growing regions across Australia?
- (ii) Do flower visitation rates of key flower visiting insects vary temporally?
- (iii) How effective are different taxa at pollinating watermelon flowers and how do differences in their foraging behaviour influence their effectiveness?

2 | MATERIALS AND METHODS

2.1 | Study sites

We collected data from 15 commercial seedless watermelon farms, across five major watermelon-growing areas in three Australian states: Riverina ($n = 4$ farms) (NSW), Chinchilla ($n = 3$ farms) (QLD),

Lakeland ($n = 2$ farms) (QLD) and Gumlu ($n = 3$ farms) (QLD) and Katherine ($n = 3$ farms) (NT) (Figure 1). Climatic variation of selected watermelon-growing areas is given in Table 1. All farms in Lakeland and Chinchilla and one farm at Gumlu were adjacent to natural/semi-natural vegetation. The remaining two farms at Gumlu were bordered by sugar cane. In Riverina, watermelons were grown under intercropping system with some cucurbits (pumpkin, rockmelon and butternut squash) and other co-flowering species (purslane, caltrop and common heliotrope) flowering nearby. Farms at Katherine were adjacent to mango orchards, narrow hedge/tree rows, grass clearing lands or roads. All farms were located at least 2 km apart, which is beyond the typical foraging flight distance of honey bees and other large pollinators (Greenleaf et al., 2007). All the farms used an in-row planting system (3:1 seedless:pollinizer ratio), but the watermelon cultivars varied among farms. Managed honey bee hives were located in all farms at stocking rates between 2 and 7.5 hives/ha. Data were collected on sunny weather days with the average temperatures of 28°C (17.6–38°C) and wind speed of 3.6 m/s (0.8–6.4 m/s). All relevant permissions were obtained to use commercial farms sampled in this study.

TABLE 1 Variation of climate in selected watermelon growing regions in Australia based on three different climate classification schemes: Temperature/humidity, vegetation (as given in Köppen Classification) and seasonal rainfall

Region	Number of farms	Temperature/humidity	Vegetation (Köppen)	Seasonal rainfall
Lakeland (QLD)	2	Hot humid summer	Tropical savanna	Summer dominant (marked wet summer and dry winter)
Chinchilla (QLD)	3	Warm summer, cold winter	Temperate hot summer	Summer (wet summer and low winter rainfall)
Gumlu (QLD)	3	Hot humid summer	Tropical savanna	Summer dominant (marked wet summer and dry winter)
Katherine (NT)	3	Hot humid summer	Tropical savanna	Summer dominant (marked wet summer and dry winter)
Riverina (NSW)	4	Hot dry summer, cold winter	Grassland warm	Uniform (uniform rainfall)

Source: Climate classification maps (Kottek et al., 2006), Bureau of Meteorology, Australian Government web site.

2.2 | Community composition, relative abundance and insect visitation rates

To assess insect abundance and visitation rate to flowers, we conducted timed observations along a 50-m transect within each field. The starting point for all transects was from the edge of a block working towards the centre of the block. The compass direction of each transect and its proximity to managed honey bee hives varied between sites. We prioritized keeping the transect to the edge of blocks due to biosecurity concerns (to avoid mechanical damage to the vine to reduce the spread of viruses and other pathogens). Visitation rates were calculated from 45-s observation surveys of groups of flowers at 1-m-spaced points for a total of 50 observations along each transect (Winfree et al., 2007). On average, three flowers (range: 1–11) were observed at each point; the number and sex of flowers were recorded. Observations took place during three time intervals on two sunny weather days per farm, between 7:00 AM and 9:00 AM, 9:00 AM and 11:00 AM, and 11:00 AM and 1:00 PM, covering the period during which watermelon flowers were open. Altogether, the transect was walked between six and eight times at each farm. Insects were netted from watermelon flowers across the block and throughout the day for identification purposes. Then, insects were identified up to the lowest taxonomic level possible with the support of experts.

2.3 | Movement patterns among flowers

To determine the likelihood of different flowers' visitors moving between male and female watermelon flowers, the movement patterns of dominant taxa were recorded on all Queensland farms ($n = 8$). Observers used audio recorders to follow individual insects, annotating their visits to male/female flowers, distance travelled between flowers and stigma/anther contact. When choosing the insects to follow, less common insects (e.g., flies) were sought out, while the more common insects were chosen haphazardly on both male and female flowers. Their behaviour was observed as each insect was followed for as long as observer could view them, up until a maximum of 10 min. Insects were identified on the wing by the observer and assigned to one of six taxonomic groups: Honey bees, stingless bees, other medium-sized native bees (5–10 mm in length), other small-sized native bees (<5 mm in length), hover flies and other flies. These data

were collected throughout the day, over the 3–4 days we spent on each farm. Representative taxa from each taxonomic group were collected and identified in the laboratory upon completion of field work. All bees were identified by expert Tobias Smith. As watermelon flowers close in the early afternoon and in high temperatures, these data were collected only while watermelon flowers were open, that is from 7:00 AM until 1:00 PM.

2.4 | Pollinator effectiveness

Pollinator effectiveness was measured based on their single visit pollen deposition on stigmas (SVD) at farms in Chinchilla, Gumlu (QLD) and Riverina (NSW). Measures of SVD were collected using an active approach to obtain insect flower visits, as described by Howlett et al. (2017). Unopened mature female flower buds on triploid vines were enclosed with fine organza (jewellery) bags. Once open, the treatment flowers were picked and stems placed into a vial of water. After removing the bag, the flower was held close to a target insect visitor on a male flower. Once the insect moved onto the treatment flower, it was allowed to forage uninterrupted. After receiving an insect visit, each flower was kept moist in sealed plastic bags for at least 24 h, to allow pollen to germinate on the stigmas. After 24 h, the stigmas were excised and stored in 1.5-ml Eppendorf microcentrifuge tubes containing ethanol for later processing (Winfree et al., 2007).

To count the number of pollen grains on each stigma, the stigmas were either softened in 10% KOH for between 36 and 48 h and then washed and stained with 1% fuchsin and mounted on microscope slides (Campbell et al., 2018; Hart, 2007; Kremen et al., 2002; Sardinas et al., 2016; Winfree et al., 2007) or acetolysis was undertaken (Erdtman, 1953; Jones, 2014) and the solution obtained from each stigma was mounted on the microscope slides using a mixture of glycerol, ethanol and fuchsin (Jones, 2014). The number of pollen grains was counted at 40 \times magnification with a compound microscope (Kremen et al., 2002; Subasinghe Arachchige et al., 2022; Winfree et al., 2007). In a subsample of the softened stigmas, the remaining ethanol and KOH solutions were also checked for pollen grains that had not adhered to stigmas. Less than 20% of the total pollen grains (ethanol: 6.58% and KOH: 18.7%) were found in the solutions. In addition, bagged control flowers (remained covered in fine organza bags) and method control flowers (held next to a target insect visitor but

insect was prevented from moving onto the control flower) were also processed.

When possible, the foraging behaviour of a target insect immediately prior to the SVD visit was recorded, in order to determine whether pre-visit male flower type (diploid vs. triploid) and/or the foraging behaviour (nectar vs. pollen gathering) of an insect affects their ability to transfer pollen.

2.5 | Data analysis

Taxa were identified and grouped at the lowest taxonomic level possible in the field—beetles in the families Chrysomelidae, Coccinellidae and Staphylinidae; other coleopterans; lepidopterans as butterflies (Hesperiidae and Nymphalidae spp.) and moths; flies as Syrphidae sp. (hoverflies), Calliphoridae sp. and all other dipterans; true bugs: Miridae sp. and other hemipterans, bees: honey bees (*A. mellifera*), native bees (*Tetragonula* sp., *Lasioglossum* sp., *Homalictus* sp., *Megachile* sp., Halictidae sp. and other native bees) and wasps (including Pompilidae).

Insect community composition was compared among regions using Permutational multivariate analysis of variance (PERMANOVA) based on Bray–Curtis distance measure of dissimilarity (using function ‘adonis’ in package ‘vegan’ with subsequent permutation testing [999 iterations]) (Anderson, 2006; Beals, 1984; Clarke et al., 2006). We illustrated the dissimilarity in insect community composition by plotting the ordination scores from a non-multidimensional scaling ordination in ggplot with the ggorplots package and generated the ellipses according to standard deviations whereby regions with similar insect communities are placed closer together in ordination space (Wilson et al., 2016). Homogeneity of dispersion among regions was calculated using the abundance of insect groups using the function betadisper in the package ‘vegan’ (Dixon, 2003) with subsequent permutation testing (999 iterations). The cumulative contributions of the most influential species to the overall dissimilarity in each pair of regions were obtained using the function ‘simper’ (Vegan package: Dixon, 2003). Relative abundance of insect taxa in each region was calculated by dividing the number of individuals from one taxa by the total number of individuals from all insect taxa observed per day and then values were averaged for the region. For this analysis, insect taxa were grouped as honey bees, native bees (include all bee species except honey bees), flies and other taxa. We also calculated species richness, Shannon and Simpson’s diversity indices for each region (Vegan package: Dixon, 2003).

To assess flower visitation rates (number of visits per hour per flower) of the dominant insect taxa, we fitted a separate generalized linear mixed-effects model (GLMM) with a Poisson distribution, using the glmmTMB package (Bolker et al., 2009; Brooks et al., 2017). Number of visits was our response variable and insect species a categorical fixed effect, grouped as honey bees, native bees (all other bees) and flies. Time of day (categorical; three time intervals) and its interaction with insect species were also included as fixed effects. Transect point nested within site and date were included as random factors. To

account for differences in the number of flowers across transect points, log-transformed number of flowers/transect point was used as an offset. Pairwise comparisons of flower visitors and time of the day on visitation rate were performed using emmeans package (Tukey’s HSD) (Lenth et al., 2018).

Pollinator effectiveness was analysed by fitting a GLMM with a zero-inflated negative binomial distribution using the glmmTMB package (Bolker et al., 2009; Brooks et al., 2017). Insect taxa was included as a fixed factor, categorized as honey bees, stingless bees, other native bees and flies. To assess the effect of foraging behaviour and type of male flower previously visited on pollinator effectiveness, we fitted a separate GLMM model, similar to above while including both foraging behaviour (pollen or nectar) and male flower type (triploid or diploid) as fixed factors with a negative binomial distribution. The number of pollen grains deposited on the stigma was used as the response variable in both models. Pairwise comparisons were carried using R package emmeans (Tukey’s HSD) (Lenth et al., 2018). Site was included as random factor in all models.

We performed model diagnostics and validated the fit of all models with the DHARMA package (Hartig, 2018) and plotted using R package ggplot2 (Horton & Kleinman, 2010). All statistical analyses were performed in R statistical software version 4.0.0 (R Core Team, 2020).

3 | RESULTS

3.1 | Community composition and relative abundance of flower visitors

We observed 13 different genera, from 20 different families, visiting watermelon flowers across Australia (e.g. Figure 2). There were representatives from five orders: Hymenoptera, Diptera, Lepidoptera, Hemiptera and Coleoptera in all five regions (Table S1: List of insect taxa found in watermelon farms across five regions). The composition of flower visitors differed among the five watermelon-growing regions (PERMANOVA: $F_{4,26} = 5.11$, $R^2 = 0.44$, $p = 0.001$; Figure 3a). Differences in the contribution of honey bees were the highest contributor to the dissimilarity observed among regions (SIMPER, average dissimilarity: 72% [range: 57%–87%]; Figure 3b).

Honey bees were the most abundant flower visitors in all regions, representing among 73%–94% of all visitors (Figures 4a and S1; Table S2). The relative abundance of native bees (including stingless bees *Tetragonula* sp. and bees from family Halictidae such as *Lasioglossum*, *Homalictus*, *Lipotriches* and *Megachilidae*) was higher in our southernmost sampling regions: Chinchilla (21%) and Riverina (18%) (Figure 4a). Of the native bees, stingless bees (*Tetragonula* sp.) were the most abundant species, accounting for between 0% and 63% of the observed native bees (Figure 4b). However, stingless bees were not found in Riverina, which is beyond the natural range for *Tetragonula* spp. (Heard & Dollin, 2000). Flies (mostly family: Syrphidae) were present in low numbers across all the regions, although their abundance was comparatively high in Lakeland (4.6% of total observed insects). Other insect taxa including beetles, butterflies, moths and true

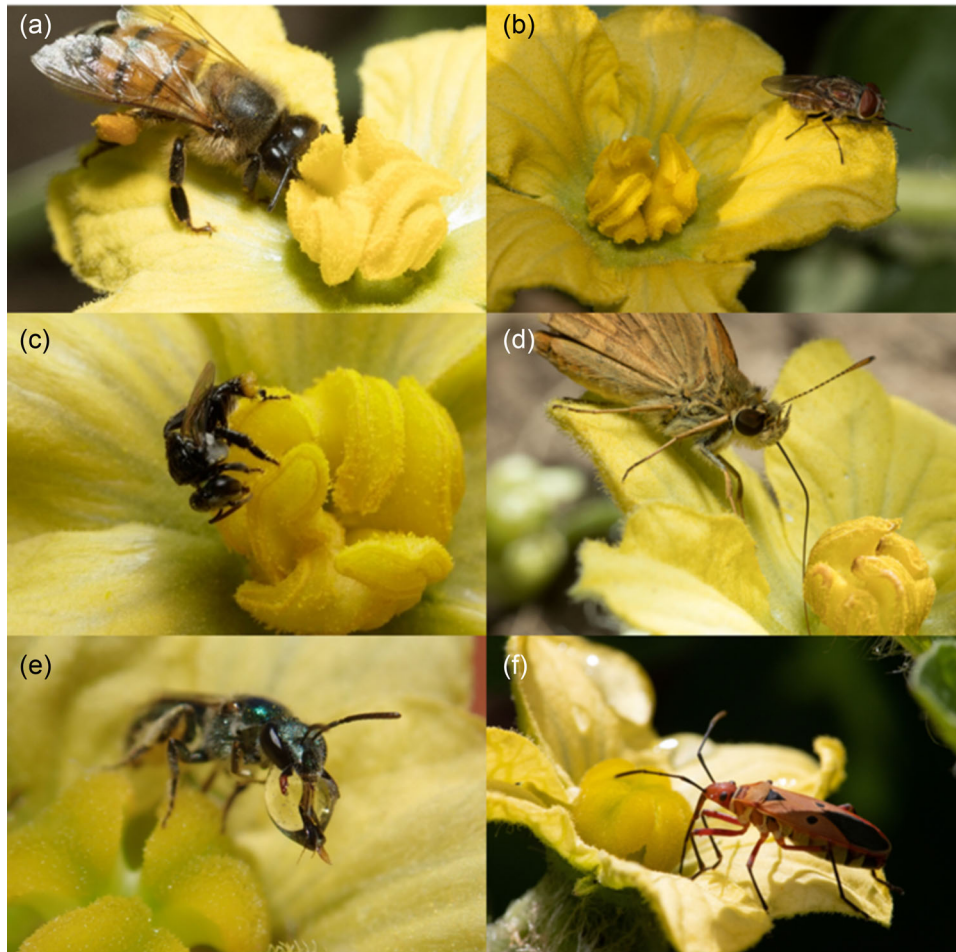


FIGURE 2 Flower visitors of watermelon in Australia: (a) honey bee (*Apis mellifera* feeding on nectar), (b) dipteran sp., (c) pollen foraging stingless bee (*Tetragonula* sp.), (d) lepidopteran sp., (e) sweat bee (*Homalictus* sp.) and (f) true bug (hemipteran sp.). Insects in panels (a–d) are on male flowers and panels (e) and (f) on female flowers. Photos: Brian Cutting

bugs were recorded in low numbers in all regions except Katherine. The relative abundance of other insect taxa was higher in Chinchilla (5.8%) and Riverina (5.7%) (Figure 4a). According to diversity indices, Chinchilla had the highest diversity of flower visitors, while Katherine had the lowest diversity among the selected regions (Table S3).

3.2 | Flower visitation rate

We observed 2873 insect visits to watermelon flowers over 15 farms. Honey bees, native bee species and flies were the most frequent visitors, while other taxa (beetles, moths, true bugs and wasps) were only occasionally observed visiting watermelon flowers. Honey bee visitation to watermelon flowers (mean \pm SE = 36 ± 0.8 visits/flower/h) was sevenfold higher compared to native bees ((mean \pm SE = 5.3 ± 0.4 visits/flower/h: model estimate (Est.) = 2.07, SE = 0.07, t. ratio (ratio of the two mean groups = 27.8, $p < 0.001$; Figure 5; Table S4)) and 36-fold higher than flies (mean \pm SE = 1 ± 0.2 visits/flower/h: Est. = 3.72, SE = 0.18, t. ratio = 20.4, $p < 0.001$; Figure 5; Table S4). The visitation

rate of native bees was also significantly higher compared to flies (pairwise comparison, Est. = 1.65, SE = 0.19, t. ratio = 8.5, $p = 0.01$).

There were some differences in the timing of watermelon flower visits across taxa/taxonomic groups ($\chi^2 = 15.4$, $df = 4$, $p = 0.003$; Figure 5; Table S5), with flies visiting flowers more frequently later in the day (11:00 AM to 1:00 PM) compared to early in the morning (two-way interaction, Est. = -1.61 , SE = 0.48, t. ratio = -3.29 , $p = 0.02$). However, time of the day had no significant effect on honey bees or native bee visits ($\chi^2 = 2.2$, $df = 2$, $p = 0.33$; Table S5 and Figure S2).

3.3 | Movement patterns among flowers

Our observations of insect movement among watermelon flowers indicate that honey bees visited the highest number of flowers per hour (scaled up from flower visits/min) and crossed between male and female flowers more frequently compared with other flower visiting insects (Table 2). All other flower visitors displayed longer visits to

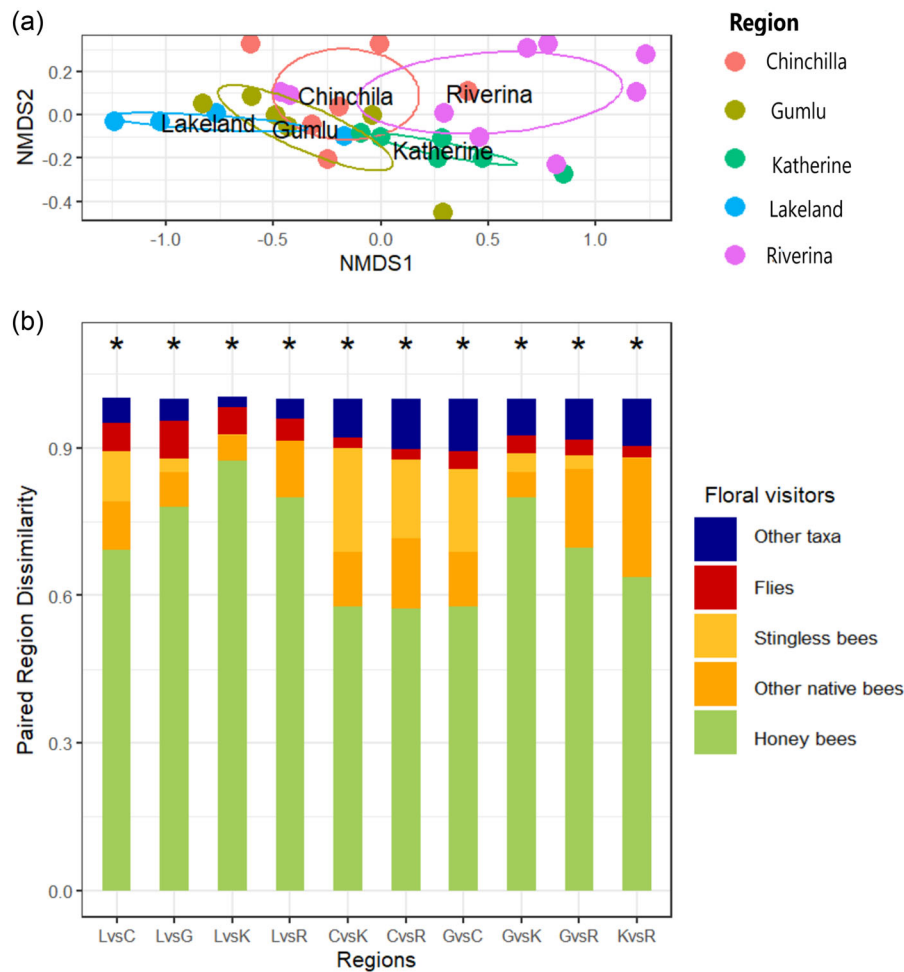


FIGURE 3 Insect community composition in five regions in Australia (Katherine, Lakeland, Chinchilla, Gumlu and Riverina) represented by (a) non-multidimensional scaling ordination in two dimensions (Stress = 0.050) based on Bray–Curtis dissimilarities. Each symbol represents insect composition on a given sampling day and those symbols of the same colour belong to a region. Insect community composition differed significantly ($p = 0.001$) among regions according to the PERMANOVA test. (b) Simper analysis shows the cumulative contributions of the taxon groupings to the overall dissimilarity in each pair of regions. Asterisks above bars indicate significance for within bar comparisons at the $\alpha = 0.05$ level. LvsC, Lakeland–Chinchilla; LvsG, Lakeland–Gumlu; LvsK, Lakeland–Katherine; LvsR, Lakeland–Riverina; CvsK, Chinchilla–Katherine; CvsR, Chinchilla–Riverina; GvsC, Gumlu–Chinchilla; GvsK, Gumlu–Katherine; GvsR, Gumlu–Riverina; KvsR, Katherine–Riverina

flowers and therefore visited fewer flowers overall. All taxonomic groups observed did, however, visit both types of flowers during their foraging. All bee groups and hover flies made contact with the anthers in >70% of their visits to male flowers. Honey bees, stingless bees and hover flies made contact with the stigma in >80% of their visits to female flowers (Table 2).

3.4 | Pollinator effectiveness

A total of 387 stigmas were used to estimate single visit pollen deposition for honey bees, stingless bees, other native bees (including *Homalictus* bees) and flies. There was no significant difference in the number of pollen grains honey bees and stingless bees deposited on stigmas during a visit (mean \pm SE = 39.7 ± 4.3 and 26.5 ± 5.5 for honey and stingless bees, respectively; Est. = -0.31 , SE = 0.22, $p = 0.16$;

Table S6). However, other native bee species (mean \pm SE = 17 ± 5.28 ; Est. = -0.77 , SE = 0.22, $p < 0.001$) and flies (mean \pm SE = $.75 \pm 1.41$, Est. = -2.11 , SE = 0.59, $p < 0.001$) deposited fewer pollen grains on stigmas compared with honey bees (Figure 6). Few pollen grains were found on bagged control flowers (mean = 0.25, $n = 4$) and method control flowers (mean = 0.65, $n = 34$).

More pollen grains were deposited on stigmas by bees (including honey bees and all native bees) that collected pollen compared to those that collected nectar (Est. = 0.46, SE = 0.21, t. ratio = 2.21, $p = 0.027$; Figure 7) and more pollen was deposited when a pollinator moved from a male flower on a diploid cultivar compared to a male flower on a triploid cultivar (Est. = 0.52, SE = 0.21, t. ratio = 2.54, $p = 0.01$; Figure 7; Table S7). Of our pollen-foraging bees, 69% were native bees, while 31% were honey bees. Honey bees represented higher proportion of our nectar-foraging bees (55%). However, as the bees used to assess pollinator effectiveness were selected

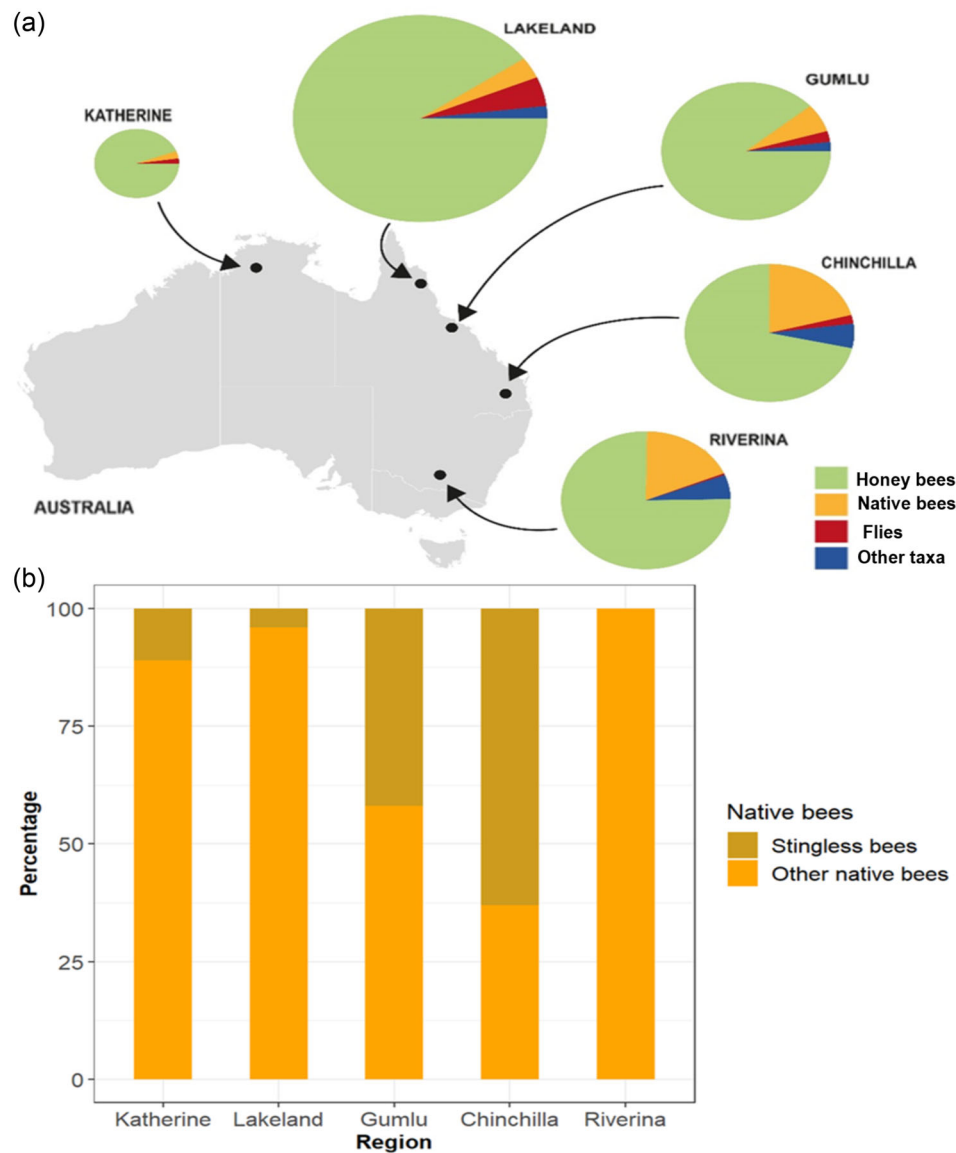


FIGURE 4 Abundance of insect visitors within five watermelon-growing regions in Australia (Katherine, Lakeland, Chinchilla, Gumlu and Riverina), shown as (a) the relative abundance of honey bees, native bees, flies and other taxa within each region and (b) the proportion of stingless bees (*Tetragonula* sp.) compared to other native bees

opportunistically, we did not collect data on the likelihood of pollen foraging for any given taxa.

4 | DISCUSSION

We found that the composition of insect visitors varied significantly across regions, but honey bees were the most abundant visitor in all regions, representing 73%–94% of all observed watermelon visitors. The high abundance of honey bees is not surprising as all growers deployed commercially managed honey bee hives, which is common practice in many watermelon-growing regions around the world (Layek et al., 2021; Stanghellini et al., 1998; Winfree et al., 2007). Still, their relative abundance is high compared to other watermelon-producing

countries (Garantonakis et al., 2016; Henne et al., 2012; Pinkus-Rendon et al., 2005; Subasinghe Arachchige et al.,), perhaps due to the presence of feral honey bees (Cunningham et al., 2002). Wild pollinator taxa were low in more isolated farms in some regions (e.g., Katherine), compared to other farms adjacent to semi natural vegetation or cropping fields—areas that may provide nesting sites and/or alternative food resources for wild pollinators.

The results of this study confirm that honey bees are effective pollinators of watermelon grown in Australia, moving frequently between flowers and depositing an average of 40 pollen grains per visit. Based on the 1000 pollen grains required for fruit set in seeded watermelons (Adlerz, 1966 reviewed in McGregor, 1976) (the precise number needed in seedless watermelons is unknown), approximately 25 flower visits by honey bees are needed for fruit production. We estimate that

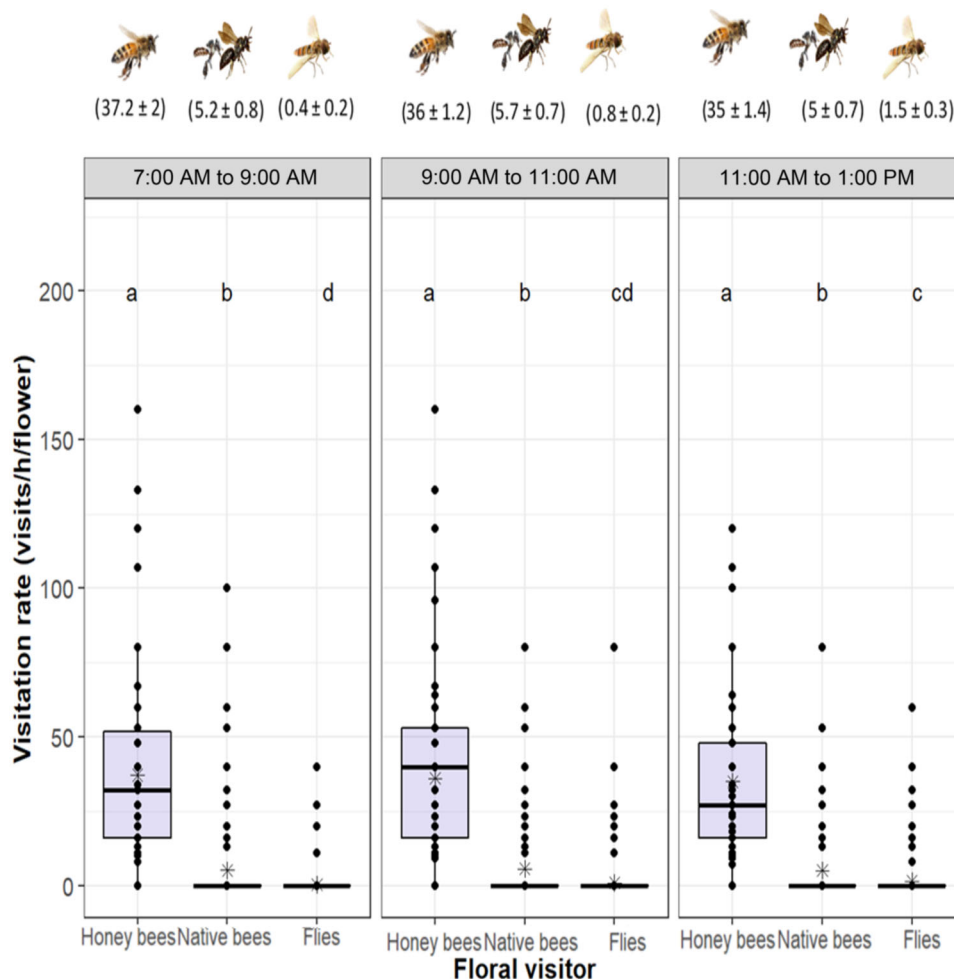


FIGURE 5 Visitation rate (number of visits per flower per hour) of honey bees, native bees and flies to watermelon flowers over the course of the daily flowering period. In each box, the bold horizontal line is the median, and means are shown with an asterisk (*). The lower and upper edges of the box represent the 25% and 75% quartiles, respectively. Whiskers indicate the maximum and minimum values that are not outliers (circular data points). Different letters indicate significant difference of floral visitors across time periods (interaction between floral visitors × time period interaction) (EMMeans pairwise comparisons at $\alpha = 0.05$ and Confidence Level = 0.95).

TABLE 2 Data on visitation frequency of different taxonomic groups to watermelon flowers and the percentage of visits that result in anther and/or stigma contact

Taxonomic group	N	Mean duration followed (min:s)	Predicted male flowers/h	Predicted female flowers/h	Percentage of anther contact	Percentage of stigma contact
Honey bees	375	01:59	314.16	34.72	79.40	82.32
Stingless bees	63	03:24	54.45	3.34	80.79	81.25
Other native bees (medium sized ^a)	28	02:22	51.16	5.59	76.67	66.67
Other native bees (small sized ^a)	10	02:52	48.46	9.52	80.95	40.00
Hover flies	11	03:17	41.30	1.72	83.33	100.00
Other flies	19	01:26	109.52	11.90	56.52	20.00

^aMedium-sized native bees were between 5 and 10 mm in length, and small sized bees were those <5 mm in length.

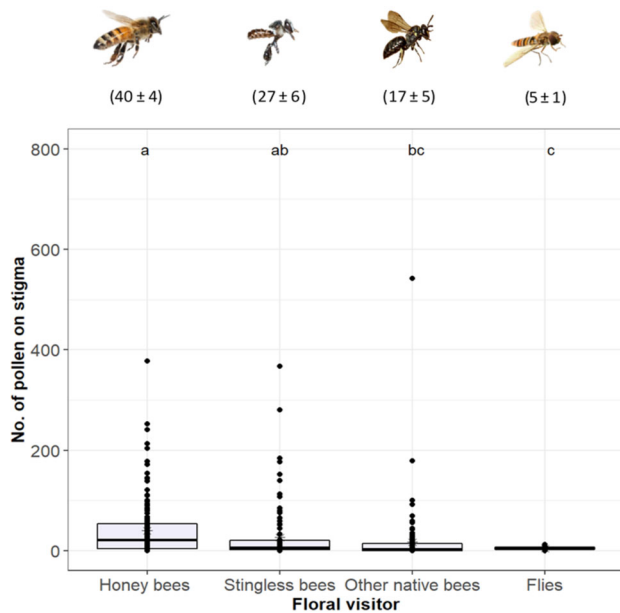


FIGURE 6 Pollinator effectiveness (single visit pollen deposition) including honey bees ($n = 82$), stingless bees ($n = 103$), other native bees ($n = 111$) and flies ($n = 8$) on watermelon. In each box, the bold horizontal line is the median, and means are shown with an asterisk (*). The lower and upper edges of the box represent the 25% and 75% quartiles, respectively. Whiskers indicate the maximum and minimum values that are not outliers (circular data points). The different letters indicate significant differences among floral visitors (EMMeans pairwise comparisons at $\alpha = 0.05$ and Confidence Level = 0.95).

this number of visits would have been achieved within 42 min in all the farms we surveyed, if pollen deposition and accumulation remains roughly uniform. Their high abundance and effectiveness at transferring pollen suggests that currently honey bees are responsible for the majority of watermelon pollination in the studied Australian regions.

Watermelon flowers were, however, also visited by a diversity of other insects across Australia, including native bees, flies, wasps, butterflies, beetles and true bugs. While many of these wild insects were only present in low numbers, native bees (including stingless bees *Tetragonula* sp., and bees from the families Megachilidae and Halictidae such as *Lasioglossum*, *Homalictus* and *Lipotriches*) were particularly abundant in the Southernmost sampling regions (Chinchilla and Riverina), making up 22% and 18% of the total visitors. Where assessed, a number of these taxa were also capable of pollinating watermelon flowers. For example, native stingless bees (including *Tetragonula hockingsi*, *Tetragonula carbonaria* and *Austroplebeia cassiae*) were the second most abundant species group observed overall, and despite being much smaller in body size they deposited pollen in similar quantities as honey bees.

Encouraging native bees and/or using a wider variety of managed species for watermelon pollination, alongside honey bees, has potential to benefit crop yields and improve the resilience of watermelon pollination services (Garantonakis et al., 2016; Garibaldi et al., 2013; Rader et al., 2013). In the farms/regions we surveyed, native bees visited watermelon flowers at the same times of day as honey bees

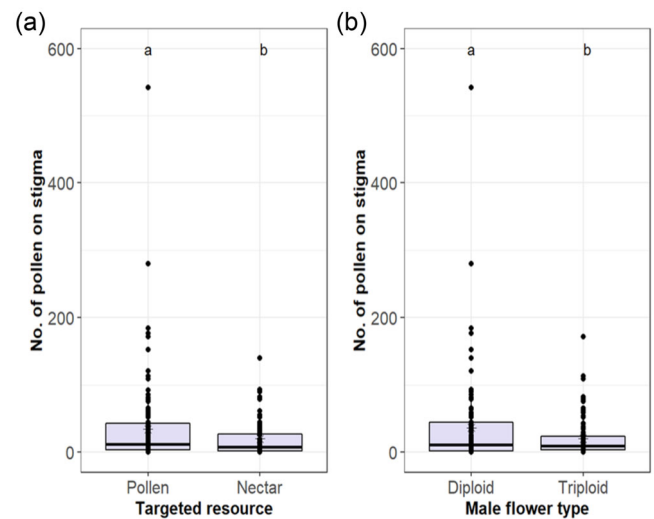


FIGURE 7 Variation of pollinator effectiveness (single visit pollen deposition) with foraging on targeted resources, shown with comparisons between (a) nectar ($n = 80$) and pollen ($n = 124$) collected bees (including honey bees and all native bees) and (b) previous male flower type visited by pollinators; diploid ($n = 105$) versus triploid ($n = 99$). In each box, the bold horizontal line is the median, and means are shown with an asterisk (*). The lower and upper edges of the box represent the 25% and 75% quartiles, respectively. Whiskers indicate the maximum and minimum values that are not outliers (circular data points). Different letters indicate significant differences between variables (EMMeans pairwise comparisons at $\alpha = 0.05$ and Confidence Level = 0.95).

and therefore provide pollination service redundancy—safeguarding against the failure of a single pollinating species. Other species may provide complementary (additive) pollination services, if their peak abundance differs from that of honey bees. In the current study, flies were most active on the crop late morning/early afternoon, although they were never more abundant than honey bees in the studied regions. As this study was conducted in fair weather conditions, it is possible that wild taxa may become more active than honey bees and provide pollination services in watermelon under variable and/or extreme climatic conditions (Rader et al., 2013).

Stingless bees are a good example of pollinators that display some niche overlap with honey bees (i.e., they offer redundancy in response to environmental conditions), and in many watermelon-growing regions across Australia these bees could be encouraged in fields. In Australia (and other countries), some species of stingless bee are commercially managed and are available for pollination services (Heard, 1999; Ramalho et al., 1994). The number of managed colonies deployed, and therefore the cost, would most likely be high compared to honey bees, given we show their movement between flowers is less frequent, they have fewer workers per colony (Heard, 1999; Oliveira et al., 2013) and they have a more localized foraging range (Evans et al., 2021). However, other studies have already demonstrated the utility of managed stingless bees in watermelon pollination, both in conjunction with honey bees (Layek et al., 2021), and as a sole pollinator (*Scaptotrigona* sp. nov.) of mini watermelons in protected cropping conditions

(Bomfim et al., 2015). Growers can also employ land and farm management practices, for example preserving native vegetation, in particular large trees which stingless bees use as nest sites (Oliveira et al., 2013), and maintaining other floral resources outside of crop bloom (Carvalho et al., 2010) to encourage wild stingless bees (and other wild taxa) to enhance free pollination services. Alternatively, growers can obtain their own stingless bee colonies and slowly build up a local population of these bees to assist with pollination.

Watermelon growers in Australia can also employ simple and inexpensive methods such as maintaining floral resources that exist in field margins or planting wildflower strips adjacent to crops. Similar approaches have been used in watermelon farms in the United States and positive impacts on pollinator visits are reported (Jenkins, 2019). However, care does need to be taken to ensure planting is based on known species-level relationships between insects, crops and non-crop vegetation because wildflower strips (and other types of plantings such as hedgerows and semi-native plantings) may not lead to improved crop pollination, and could create pest reservoirs (Howlett et al., 2021). Other farm management practices that are known to enhance wild pollinators include selective use of pesticide at times when pollinators are not active on the crop, for example in the late afternoon/evening after watermelon flowers have closed for the day (Njoroge et al., 2004). Integrated pest and pollinator management is another approach that can increase biodiversity while reducing input use (Lundin et al., 2021).

There may also be opportunities to manage honey bees in ways that increase their efficiency in watermelons, thus reducing the total number of colonies required per hectare. In other crops (e.g. European apples), reducing the number of managed honey bee hives has led to a greater abundance of other pollinators (Weekers et al., 2022). We found that pollen-foraging bees deposited significantly more pollen on watermelon stigmas compared with nectar-foraging bees. One strategy could be to increase the proportion of pollen foragers relative to nectar foragers within managed honey bee colonies. Other studies have achieved this when beekeepers have used supplemental feeding of sucrose within their hives—a technique used to increase pollen foraging (Free & Racey, 1966) and a pollination management strategy in other crops where pollen foragers are more effective (Free & Racey, 1966; Free & Spencer-Booth, 1961; Goodwin & Houten, 1991).

In conclusion, we show that Australia's watermelon crops are dominated by honey bees, but are also visited by a diverse assemblage of wild insects, and many of those assessed were effective pollinators. Given the diversity of available insect pollinators and the current reliance on a single managed species, growers would benefit from the following pollination management approaches: the inclusion of other managed pollinators such as stingless bees; encouraging other native bee species into their production system; and employing management techniques to improve the pollination efficiency of managed honey bees.

AUTHOR CONTRIBUTIONS

Lisa J. Evans and Romina Rader conceived the study. Erandi C. W. Subasinghe Arachchige, Lisa J. Evans and Romina Rader designed the trials and/or the analysis techniques and drafted the original manuscript.

Lisa J. Evans, Brian T. Cutting, Matthew Keir, Theo van Noort, Erandi C. W. Subasinghe Arachchige, Grant Fale and Brad G. Howlett conducted field experiments and collected data. Erandi C. W. Subasinghe Arachchige analysed data. All authors reviewed, edited and approved the final manuscript for publication.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.12jm63z24> (Subasinghe Arachchige et al., 2022).

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SUPPORTING INFORMATION

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

Table S1. Insect taxa recorded in watermelon farmer fields at Queensland (Chinchilla, Lakeland and Gumlu), Katherine (NT) and Riverina (NSW) in Australia.

Table S2. Relative abundance of insect groups recorded in five different watermelon-growing regions in Australia.

Table S3. Insect species richness, Shannon diversity index and Simpson's diversity index recorded in five different watermelon growing regions in Australia.

Table S4. Model parameters for visitation rate of floral visitors (honey bees, native bees and flies), time of the day (7:00 AM–9:00 AM, 9:00 AM–11:00 AM and 11:00 AM–1:00 PM and their interactions).

Table S5. Analysis of Deviance table for visitation rate of floral visitors (honey bees, native bees and flies), time of the day (7:00 AM – 9:00 AM, 9:00 AM – 11:00 AM and 11:00 AM – 1:00 PM and their interactions).

Table S6. Model parameters for pollinator effectiveness (single visit pollen deposition) of floral visitors (honey bees, stingless bees, other native bees and flies).

Table S7. Model parameters for pollinator effectiveness (single visit pollen deposition) on foraging behaviour (targeted resources: nectar and pollen) and previous male flower type visited (diploid and triploid).

Fig. S1. Overall relative abundance of insect groups; honey bees (84%), native bees (11%), flies (2%) and other taxa (3%) averaged in five watermelon growing regions, Australia.

Fig. S2. Visitation rates of floral visitors to watermelon flowers at three different times of the day. Box and whiskers indicates SE, bold lines indicates median and means are marked as asterisk marks (*); points are outliers (EMMeans pairwise comparisons at $\alpha = 0.05$ and Confidence Level = 0.95).

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