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REVIEW ARTICLE

A global assessment of the species composition and effectiveness of watermelon pollinators and the management strategies to inform effective pollination service delivery

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Abstract

For most food crops the identity and efficiency of pollinators across key growing regions remains a significant knowledge gap that needs to be addressed before we can develop crop-specific approaches for pollination service delivery. Here, we conducted a systematic literature review and meta-analysis on watermelon (*Citrullus lanatus* (Thunb. Matsum. & Nakai)), a globally important fruit crop, to identify the floral visitors and their efficiency across different growing regions. We found that 265 insect species visit watermelon flowers (including 5 orders, 18 families and 75 genera) across 17 countries and 6 continents. Bees and flies were the most abundant flower visitors overall, but show distinct regional differences. Honey bees were the majority visitor in 53% of growing regions (range: 0 − 94%), whilst wild bee species were more abundant in 42% of regions (range: 3.4 − 100%). Honey bees and other bees were equally effective at depositing pollen on stigmas, but varied in effectiveness for fruit set and seed set. Pollination data from global studies appear to be limited for the largest-scale watermelon producers, namely: China, Turkey, and India, with the majority (56%) of data available from North America. This synthesis identified four key themes for improving pollination in watermelon: increasing honey bee densities on crops where local polices and environmental conditions are suitable; introducing other managed pollinators; identifying key wild pollinator taxa to encourage within crops; and improving local and landscape management practices to support pollinators.

Keywords: *Citrullus lanatus*; Crop pollination; Honey bees; Pollinator diversity; Wild pollinators

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Introduction

Crop pollination is a fundamental ecosystem service that provides over US $ 200 billion to the global economy annually (Porto et al., 2020). One third of global food production depends on animal-mediated pollination (Klein et al., 2007), with insects playing a major role in improving the quantity and quality of fruits, vegetables, and seed crops (Goodwin et al., 2011; Garibaldi et al., 2013; Woodcock et al., 2013; Bartomeus et al., 2014; Abrol et al., 2019). Although over 19,900 bee species are described (Asher & Pickering, 2013), western honey bees (*Apis mellifera* L.) are the most dominant bees managed for crop pollination globally (Kremen et al., 2004; Potts et al., 2010; Garibaldi et al., 2017; Delaplane, 2021) along with 12 other bee species including species of bumble bees, stingless bees, and solitary bees, largely for use in enclosed systems (Potts et al., 2016; Garibaldi et al., 2017; Kendall et al., 2021). Other key wild crop pollinators (including wasps, flies, beetles, butterflies, and moths; Rader et al., 2016) are also important contributors to crop production and a combination of several pollinator species may increase yield due to spatiotemporal and behavioural complementarity among pollinators in their foraging activity (Winfree et al., 2007; Albrecht et al., 2012; Brittain et al., 2013a; Garibaldi et al., 2013; Pisanty et al., 2014; Pisanty et al., 2016).

While intensive agriculture has often resulted in homogenous landscapes, increased use of agrochemicals, and a low diversity of beneficial arthropod species (Kevan, 1999; Nicholls & Altieri, 2013), insect pollinators can often coexist in these modified systems if their resource needs are met (Garibaldi et al., 2013). Several studies have highlighted the contribution of wild pollinators to pollination (Garibaldi et al., 2013; Rader et al., 2016; Ramírez & Davenport, 2016; Ratto et al., 2018), but few have assessed how wild pollinator abundance and effectiveness varies relative to managed taxa, within a single crop and across growing regions (but see apple: Pardo & Borges, 2020; avocado: Dymond et al., 2021). Global evaluations of wild pollinator composition and effectiveness are required to ascertain the dominant and/or important pollinators for different crops. This will help to ensure their ongoing provision of service delivery in conjunction with managed taxa. Knowledge regarding the management of pollinators and pollinator diversity on farms across different landscapes is another significant knowledge gap for many crops (Rader et al., 2020; Howlett et al., 2021).

Watermelon (*Citrullus lanatus* [Thunb.] Matsum and Nakai*;* Family: Cucurbitaceae) is the third most important global fruit crop, contributing more than US$ 30 billion to the world economy (FAO, 2017). Watermelon is an ideal focal crop for assessing differences in pollinator contributions as it is cultivated in 119 countries and depends entirely on biotic pollination for fruit production (McGregor, 1976; Adlerz, 1996; Stanghellini et al., 1998b). Watermelon exhibits monoecy (separate male and female flowers but rarely bisexual flowers) and large sticky pollen grains, which require an insect vector for transport. Seedless watermelons are xenogamous (require cross-pollination) but seeded cultivars can be geitonogamous (pollen transfer may occur from the male to female flower of the same plant) (Bomfim et al., 2015b). However, most cultivars have a high male to female flower ratio throughout their bloom cycle, with the male flowers opening before the female flowers, encouraging outcrossing (Njoroge et al., 2004; Emuh & Ojeifo, 2012). In seedless cultivars, pollen grains need to be moved by insects from diploid flowers (polliniser/ pollen donor) onto triploid flowers (Fiacchino & Walters, 2003; Freeman et al., 2007). Fruit set and fruit size in seedless cultivars are determined by the phyto-hormones released by pollen tube growth and ovule fertilization (Gillaspy et al., 1993) as a result of insect pollination (reviewed in Wijesinghe et al., 2020). Inadequate pollination services are known to limit watermelon yields in some countries (e.g. northern Tanzania: Sawe et al., 2020; India: Layek et al., 2021).

Here, we conducted a systematic literature review and meta-analysis to identify watermelon floral visitors and their effectiveness in different growing regions around the world, and to identify suitable management strategies to support insect pollinators and improve watermelon production. Specifically, this study addressed the following research questions:

i) Which insect taxa are the dominant watermelon flower-visitors worldwide?
ii) How do honey bees and other bees compare in their effectiveness at transferring watermelon pollen and contribution to fruit and seed set?
iii) What pollination management strategies are likely to improve watermelon production?

Materials and methods

Systematic review and screening literature

We performed a systematic literature review in Scopus, Web of Science and Google Scholar using the search terms of watermelon OR "Citrullus lanatus*" AND pollinat*. Searches were current as of October 2021. We obtained 395 resources, which included journal articles, conference papers and published dissertations (Scopus = 201, Google Scholar = 356 and Web of Science = 191), after removing duplicates. Once the title, abstract, and full-text were screened, 53 published records were selected for the study (see Appendix A: Fig. 1). Relevant publications that provided data on flower visitor species composition, abundance, visitation rate or efficiency and that were available in English, were selected for the initial screening. We focused on empirical studies, and review papers were scanned for relevant information but datasets from these studies were not included directly in the study. We included studies conducted on commercial farms and experimental plots in either open or protected cropping systems. We also included one additional unpublished dataset accessible to authors, meaning altogether 54 records (published between 1974 and 2021) were used in the study.

Identify floral visitors

Studies that identified the insect taxa visiting flowers (male, female, or hermaphrodite) were used to populate datasets on watermelon flower visitors. We also extracted information regarding the geographic location of the study, floral visitor abundance, visitation rate and effectiveness, watermelon type (seeded or seedless) and cultivar if available (in seedless cultivars both main or polliniser cultivar), survey methods, management system (open field or protected cropping), and whether honey bee hives were introduced (see Appendix A: Table 1). When a study did not state the latter information, we assumed that experiments were conducted in the absence of managed pollinators.

Relative proportion of floral visitors

We used 21 studies (out of the 54 total studies) that recorded quantitative data on either visitation or abundance, to compare the relative proportions of each taxon/group (see Appendix A: Fig. 1). To extract data from publications presented only as figures and not presented in tables or files, we used Engauge digitizer 10.11 software (Mitchell et al., 2019). We categorised insect taxa found in each study into four groups; honey bees, other bees, flies, and other taxa. Only *A. mellifera* and *A. cerana* were included within the honey bee group (hereafter called honey bees), as they are the only truly domesticated and managed *Apis* species. Bees from all other genera (including *Bombus, Tetragonula, Lasioglossum, Halictus, Xylocopa* and *Ceratina* etc.,) and other *Apis* bees (e.g., *Apis florea* and *Apis dorsata)* were pooled into the 'other bees' category. All Diptera, predominately from the families of Syrphidae, Tabanidae and Muscidae were included as 'flies'. All other taxa (e.g., butterflies and moths, beetles, and dragonflies) were grouped as 'other taxa'. ArcGIS and Google earth software were used to prepare a world map showing the relative proportion of each group by region.

Effectiveness of floral visitors: a meta-analysis

For the meta-analysis we included studies that recorded one or more of the following pollination metrics after an insect visit: pollen deposition (number of pollen grains deposited on stigma) (n = 8), fruit set (proportion of flowers that set fruits) (n = 6), and seed set (number of seeds per fruit) (n = 4). Records that measured fruit weight (n = 5), seed weight per fruit (n = 1), fruit number per land area (n = 2), and seed yield per land area (n = 1) were removed due to low replication. Some studies comprised treatments with multiple insect species for a pollination metric. We obtained 65 comparisons from 16 studies. For consistency, only initial fruit set was extracted when both initial and final fruit set were provided in the studies (see Appendix A: Table 2 for the floral visitors that contributed watermelon pollination in recorded studies).

We extracted both the control (bagged/caged) and treatment (honey bees or other taxa) means/medians of pollination metrics and floral visitor taxon, their associated sample sizes and standard deviations (SDs) where available. When studies provided data as median, means were calculated following the procedure outlined by Wan et al. (2014). Engauge digitizer 10.11 software was used to extract data from the publications when data were presented only as figures (Mitchell et al., 2019). We grouped floral visitors into two categories - honey bees and other bees (including genera *Bombus, Agapostemon, Melissodes, Peponapis, Xylocopa, Lasioglossum, Halictus, Ceratina, Nomia, Augochlora, Hylaeus, Lipotriches* and *Tetragonula* etc.). We found only two records (from the USA and Australia) of pollen deposition by flies. This was considered insufficient for further analyses.

For each comparison of pollination metrics between honey bees and other bees, we used log response ratio (lnRR) as the effect size in our meta-analysis. The log response ratio was calculated using the following equation as given in Hedges et al. (1999) and Lajeunesse (2015).

$$lnRR = \ln(\mu\mathrm{T}/\ \mu\mathrm{C})$$

where μT is the treatment mean (honey bees or other bees) and μC is the mean of control (bagged/caged).

As we had a limited number of records and most of them were missing SDs (pollen deposition (42%), fruit set (67%) and seed set (80%)), we performed an unweighted analysis. An unweighted analysis enabled inclusion of data from a greater number of studies, therefore reducing potential biases due to using only a subset of available effect sizes (Englund et al., 1999). As watermelon is a well-known crop species that requires a biotic agent for pollination (Stanghellini et al., 1998a; Garantonakis et al., 2016), we used an average value for control treatments from studies that performed bagged/caged experiments (pollen deposition = 1.15, n = 137; fruit set = 6.9%, n = 98; using hermaphrodite flowers and caged experiments). To obtain log response ratios, we added a minimum value (+1) to both the control and treatment means to avoid undefined values when calculating the natural logarithm.

We performed three generalised linear mixed effects models (GLMMs), i.e. one for each pollination metric separately, to compare the effectiveness of honey bees and other bees with gaussian distribution using the glmmTMB package (Bolker et al., 2009; Brooks et al., 2017). We modelled the effect size as a function of floral visitor taxon (two levels: honey bees and other bees) and included this as a fixed effect in each model. We included Publication as a random effect, to control for the dependent data structure arising from obtaining multiple comparisons from the same study. All statistical analysis were performed in R statistical software version 4.0.0 (R Core Team, 2020).

Results

Geographical distribution and research focus of studies

Our search identified studies from 17 countries; 30 out of 54 studies (56% of total studies) were from the USA alone, followed by Asia (11), Africa (7), Europe (2), South America (1) and Australia (1; see Appendix A: Fig. 2). The majority of studies focused on floral visitor abundance, diversity, and visitation (72%, 39/54 studies) or floral visitor effectiveness (29/54 studies) (Fig. 1). Only 21 studies (37%) representing 11 countries (USA, Egypt, Cameroon, Kenya, Pakistan, Greece, Israel, Australia, India and Ghana) assessed both floral visitor abundance and effectiveness. Fourteen studies recorded foraging behaviour of floral visitors and the impact of landscape matrix (e.g., surrounding vegetation) and farm management practices (9 studies), mostly coupled with pollination efficiency and/or visitation or abundance of visitors. Three studies focused on the effect of agrochemical use on floral visitor health (Fig. 1).

With the exception of five studies conducted in greenhouses in Brazil (1) China (3) and Korea (1), all other studies were conducted in open fields. The majority (23) used seeded cultivars, 14 studies used seedless cultivars (with diploid pollinisers) and others (17) did not state the cultivar used. Some of the studies focused on a specific group of insects such as honey bees (8), wild native bees (7), bumble bees (3), stingless bees (2) or both honey bees and bumble bees (8) (see Appendix A: Table 1). Across all studies, 345 watermelon farms were assessed. Farms in Australia, Greece, India, and 86% of farms in USA all introduced managed honey bee colonies for watermelon pollination. Farms in Cameroon, Ghana, Indonesia, Tanzania, Israel and Pakistan did not report the use of managed honey bee taxa but rather utilised the pollination services of wild floral visitor species, including feral honey bee colonies (Fig. 2).

Floral visitors and distribution

We recorded 265 insect species representing five insect orders, 18 families, and 75 genera visiting watermelon flowers across 17 countries (see Appendix A: Fig. 2 and Table 1). Many flower visitors were identified to family or genus level only. Hymenopterans (243 species, 56 genera and 8 families) were the most abundant group of flower visitors, with some minor representation from other insect orders: Lepidoptera (10), Diptera (6), Coleoptera (4) and Odonata (2) (see Appendix A: Fig. 3).

The majority of species visiting watermelon flowers were from the Halictidae family (120 species), followed by Apidae (81), Megachilidae (21), Colletidae (17) and Andrenidae (3) (all Hymenoptera) (see Appendix A: Fig. 4). Honey bees (either *A. mellifera* L. or *A. cerana* L.) were recorded in 47 of 54 studies under field conditions, and found in all regions except Pakistan and Indonesia. Among the other bees, species from the large and widespread genus *Lasioglossum* (77)

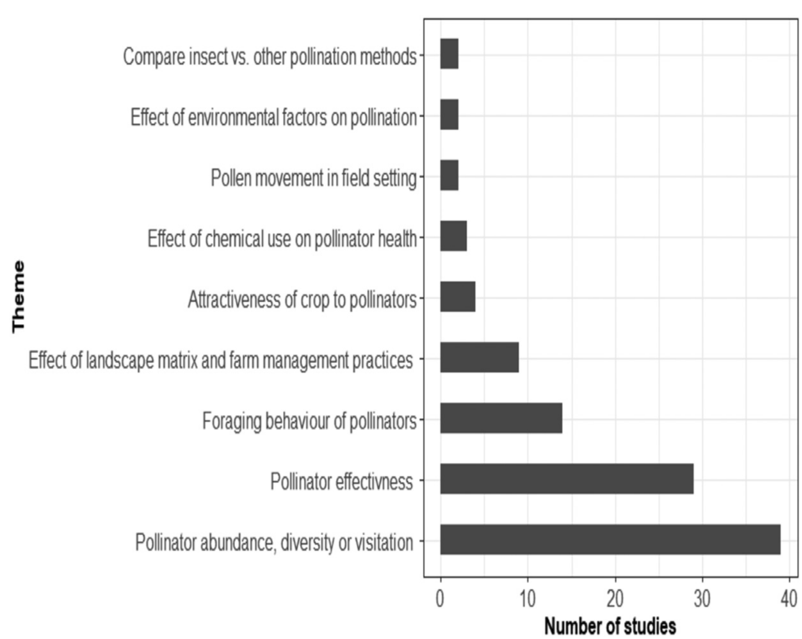

Fig. 1. Number of studies assessing watermelon insect pollination group by research theme.

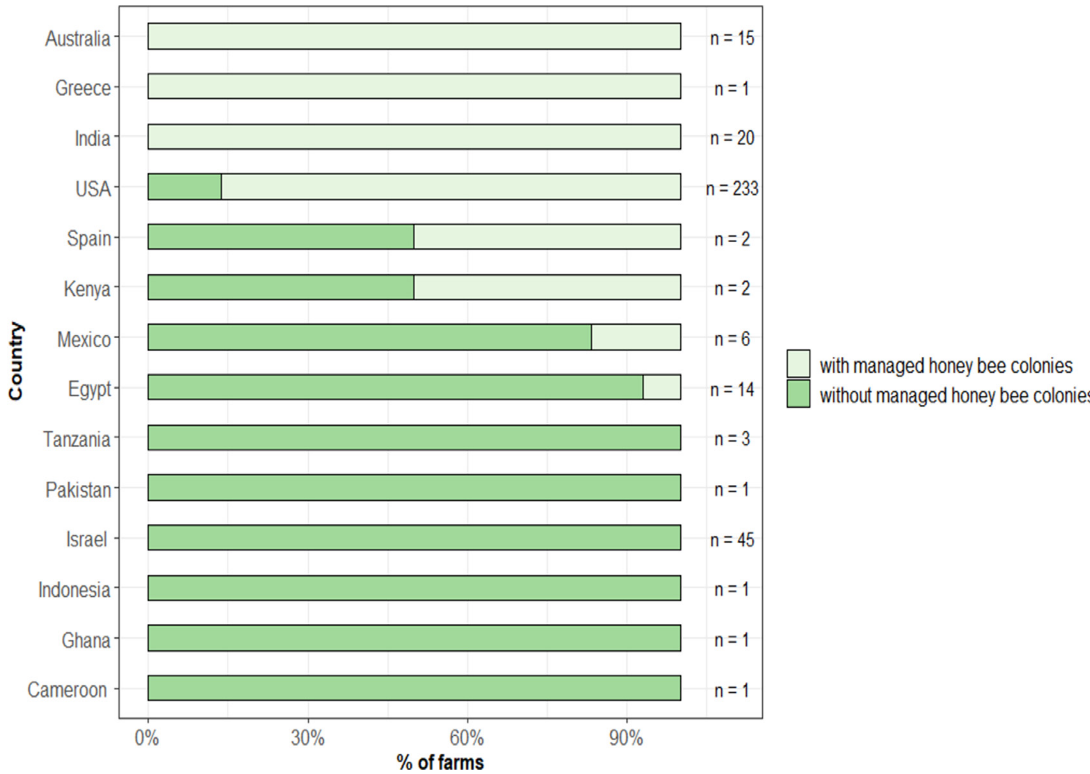

Fig. 2. Percentage of farms per country that used managed honey bees in watermelon crops, based on our reviewed studies. Farm numbers represent those assessed within a study and across studies. When a study did not state whether or not managed honey bee colonies were deployed (n = 11/54 studies) we assumed that they were not present. Only data from open fields are presented.

were the most common floral visitors (found in 21/54 studies and were recorded in nine countries), followed by species from *Hylaeus* (17), *Ceratina* (16) and *Halictus* (15) (Fig. 3). Bumble bees (*Bombus* spp.) were recorded only in USA. Flies (Diptera) were the next most common floral visitors (10/54 studies) and were found in Kenya, Ghana, Egypt, USA, Indonesia, and Australia. Hoverflies (Syrphidae) were the most common family among the dipterans (found in 8/10 studies). Both butterflies (Lepidoptera) and beetles (Coleoptera) were also found in Kenya, Egypt, USA, and Australia (see Appendix A: Table 1). Hemipterans (e.g. Family Miridae) were found in Australia and USA.

Relative abundance of floral visitors

Honey bees had the greatest relative abundance as a single floral visitor species in 14 out of 21 studies (53% on average; range: 0 - 94%). However, other bee species were dominant in a number of regions, including Khanewal, Pakistan (100%), Sulawesi, Indonesia (94%), North Carolina (76%), South Carolina (69%), Texas (54%), central New Jersey and eastern Pennsylvania (62%), Georgia (76%) in USA, India (74%) and Mexico (48%). The highest relative poportion of flies was recorded in Egypt (19%), followed by Ghana (11%), South Carolina, USA (6%), India (6%), Lakeland, Australia (2.5%), and Indonesia (2%). The relative abundance of other taxa (beetles, butterflies, bugs and wasps) was low ($\leq$ 6%) in all regions except Georgia USA (16%), Egypt (13%), India (13%), and Ghana (10%) (Fig. 4).

Effectiveness of floral visitors: meta-analysis

The meta-analysis indicated that honey bees and other bees were equally effective at depositing pollen on watermelon stigmas (92 $\pm$ 40 and 89 $\pm$ 14 pollen grains per visit $\pm$ SE respectively; model estimate = -0.053, SE = 0.41, P = 0.89). However, honey bees were more effective at contributing to fruit set than other bees, with 47 $\pm$ 13% of honey bee visited flowers resulting in fruit vs. 20 $\pm$ 9% by other bees (model estimate = -1.26, SE = 0.38, $P < 0.001$), while other bees were more effective than honey bees at contributing to seed set (model estimate = 0.20, SE = 0.06, P = 0.001 (Fig. 5).

Pollination management strategies to improve watermelon production

The available studies converged around four identifiable research themes for enhancing insect pollination of watermelon: (1) increasing honey bee density (4 studies),

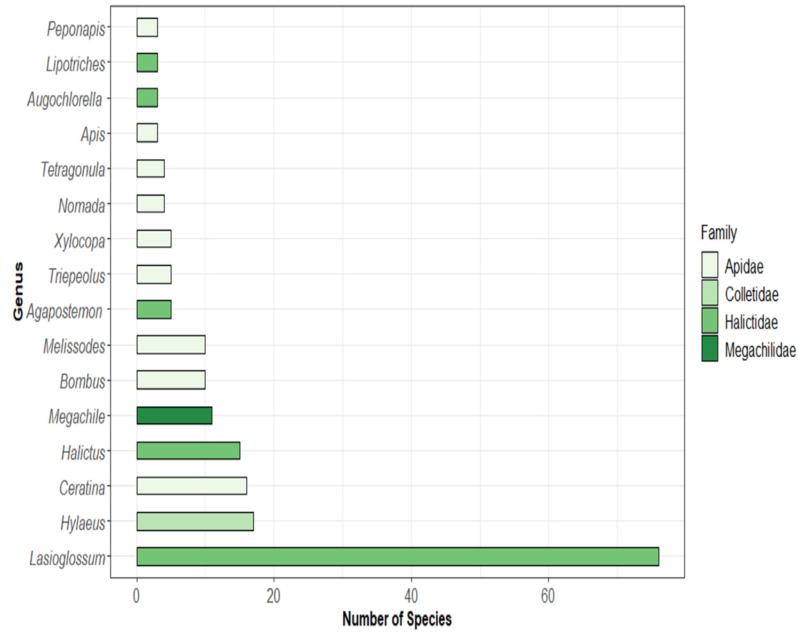

Fig. 3. Number of insect species recorded in order Hymenoptera according to genera; Note that only genera with ≥ 3 species are presented.

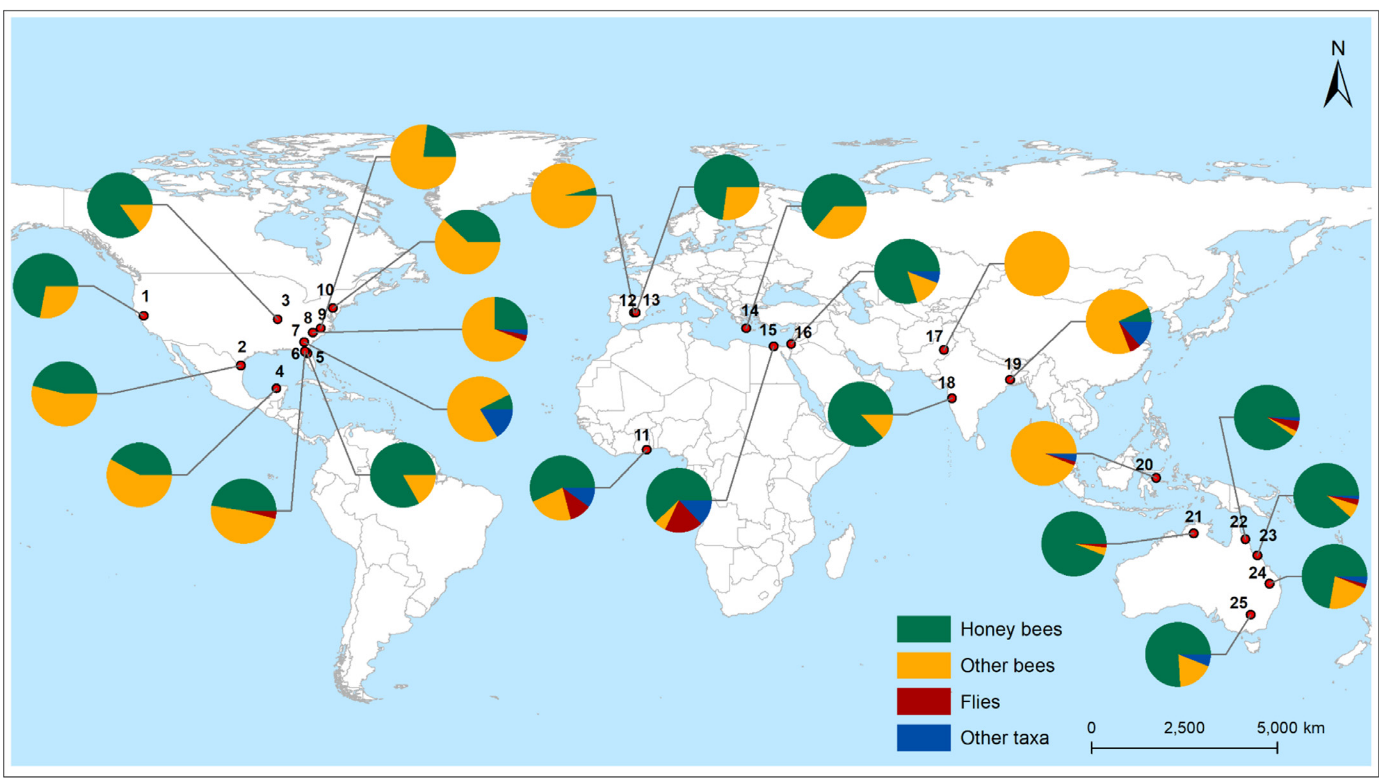

Fig. 4. World map showing the dominant flower-visiting taxa in watermelon. Each pie chart shows the relative proportion of honey bees, other bees, flies and other taxa (lepidopterans/coleopterans/odonates/hemipterans) for that location. Numbers given in the map show the different studies conducted at different regions and countries: (1) California (USA); (2) Texas (USA); (3) Illinois (USA); (4) Yucatán (Mexico); (5) and (6) north Florida (USA); (7) Georgia (USA); (8) South Carolina (USA); (9) North Carolina (USA); (10) New Jersey and Pennsylvania (USA); (11) Ayikuma (Ghana); (12) Castilla-La Mancha (Spain); (13) Villarrobledo (Spain); (14) Souda region (Greece); (15) Desouk (Egypt); (16) Judean foothills (Israel); (17) Khanewal (Pakistan); (18) Pune (India); (19) West Bengal (India); (20) Sulawesi (Indonesia); (21) Katherine (Australia); (22) Lakeland (Australia); (23) Gumlu (Australia); (24) Chinchilla (Australia) and (25) Riverina (Australia).

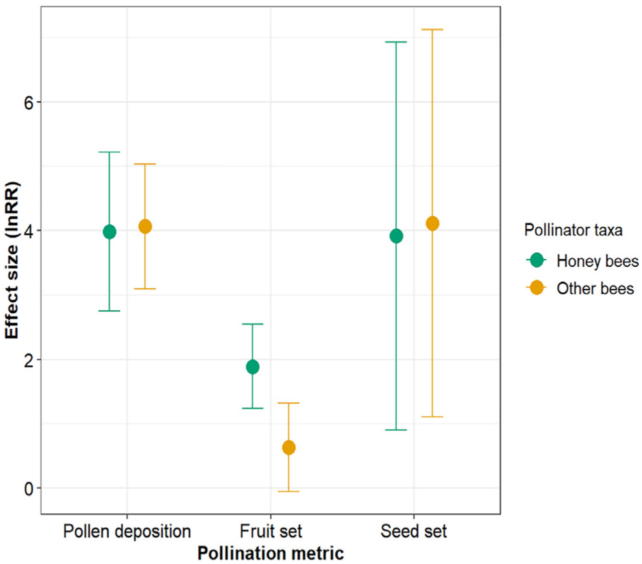

Fig. 5. Comparison of effect size (lnRR) of honey bees and other bees in pollination metrics: pollen deposition, fruit set and seed set. Solid points and whiskers represent the estimated marginal means and 95% Confidential Intervals.

including the use of chemical attractants (2), employing other managed pollinators (7 studies), (3) identifying promising wild pollinator taxa (8 studies), (4) manipulating land management practices (5 studies; Table 1).

Discussion

Our study demonstrates that a diversity of insect taxa may be important for watermelon production in major growing regions, however non-bee pollinator efficiency data was lacking so it is difficult to draw conclusions about the effectiveness of taxa other than bees. Worldwide, we found that 265 insect taxa visit watermelon flowers. The most abundant visitors were bees (Hymenoptera), wasps (Hymenoptera), and flies (Diptera). Visiting species varied widely in their morphology, from small stingless bees and hoverfly species, medium-sized honey bees and butterflies to large leaf-cutting bees and carpenter bees. This diversity likely reflects the presence of abundant nectar in watermelon flowers that is rich in sugars (sucrose, glucose and fructose) (Hawker et al., 1983; Wolf et al., 1999) available via a shallow nectary (Bomfim et al., 2015b), resulting in easy access to resources by a range of taxa (Stanghellini et al., 2002).

Overall, honey bees were the most dominant and frequent flower visitors (average abundance > 50%) in many regions. This is not surprising as managed colonies were deployed on 70% of farms in the reviewed literature, including all farms in Australia and India, and 86% of farms across the growing regions in North America. However, the relative abundance of honey bees did vary among production areas and it is clear that some regions are more heavily reliant on these bees. For example, in Australia, honey bees represented between 73-94% of flower visitors across five growing regions, compared to 7-85% across eight growing regions in the USA. The reason for higher abundance of honey bees in Australia may be due to the presence of both feral and managed honey bees on farms, as the honey bee parasitic mite, *Varroa destructor* (Cunningham et al., 2002; Owen et al., 2021) was only just recorded in Australia at the time of this study (2022). Still, even in regions where feral honey bee colonies are likely to be rare and no managed hives were deployed (e.g. central Israel), there were more visits by honey bees (80%) compared to other taxa. These high numbers could be due to honey bees from colonies in nearby cropping systems being attracted to melon flowers (Pisanty et al., 2016).

We show that wild bee species (including: bumble bees, sweat bees, squash bees, leafcutting bees, and carpenter bees) were more abundant than honey bees in 42% of regions (abundance ranging from 3.4% - 100%), including USA, Mexico, Indonesia and Pakistan. In the USA, regions with a higher proportion of wild bees in fields (such as 62% in New Jersey and Pennsylvania; Winfree et al., 2008) are areas where parasitic mites or/and colony collapse disorder have long been issues for honey bees. Other studies conducted in Mexico and in Asia (e.g. India, Indonesia, and Pakistan) found that watermelon fields were almost entirely dependent on wild bees. A more diverse group of wild taxa including bees, flies, butterflies and beetles were found as floral visitors in many African countries, such as Kenya, Egypt, and Ghana, perhaps due to the long coevolution of watermelon and pollinators in this region (Brown & Cunningham, 2019).

Results from the meta-analyses indicate that honey bees and other bees were equally effective at depositing pollen onto watermelon stigmas, but they differed in their contribution to seed and fruit set. Given the diversity of bees included in our ‘other bees’ category it is perhaps not surprising that there was no difference in their pollen deposition effectiveness compared to honey bees. Different wild bee species can vary markedly in their contribution to pollen deposition, with some depositing more pollen on stigmas than others. For example, *Lasioglossum* spp. deposited on average three times as much pollen as honey bees in Kenya (Njoroge et al., 2010) but only half as much as honey bees in New Jersey, USA (Rader et al., 2013). *Melissodes* spp. and *Bombus* spp. consistently deposited twice as much pollen compared to honey bees (Rader et al., 2013; Campbell et al., 2018). Both the variation in pollination effectiveness (within compared groups) and the observed differences in their contribution to seed and fruit set, could be due to variations in body size among species (Földesi et al., 2021), pollen viability and compatibility, behavioural differences, including their dispersal patterns and pollen-pistil interactions (Zhang et al., 2010). Differences in fruit set will also have been influenced by factors not related to the pollinators, including varietal differences, local weather conditions, and

Table 1. Summary of studies identified in our literature search which consider approaches of improving insect pollination in watermelons.

Study	Main themes	Key findings for improving insect pollination
(Njoroge et al., 2004)	Honey bee management	Managed honey bee colonies are a good option for growers but pesticides should be applied late in the evening when bees have left the flowers.
(Su et al., 2017)		Both managed *A. cerana* and *A. mellifera* can pollinate watermelon in tunnel greenhouses efficiently.
(Schultheis et al., 1994; Ellis & Delaplane, 2009)		No significant improvement in honey bee visitation, yield, fruit quality, or monetary returns when three different honey bee attractants were applied to flowers.
(Stanghellini et al., 1998b)	Honey bee management and other managed pollinators	Ensure abundant bees are available; 18 bee visits are needed to achieve around 300 seeds per fruit. Bumble bees (*Bombus* sp.) have great potential to serve as supplementary pollinators.
(Layek et al., 2021)		Deploying managed honey bees (*A. mellifera*) and/or stingless bees (*Tetragonula iridipennis*) improves pollination.
(Stanghellini et al., 1998a; Stanghellini et al., 2002)	Other managed pollinators	Bumble bees (*Bombus* sp.) are equally or more effective than honey bees (*A. mellifera*) and are another option for melon growers to deploy.
(Zhi-feng et al., 2011)		Mason bees (*Osmia cornifrons*) improve watermelon pollination beyond artificial means in greenhouses.
(Bomfim et al., 2015a)		Stingless bee (*Scaptotrigona* sp.) foragers are efficacious pollinators in mini watermelon.
(Campbell et al., 2018)		Bumble bees (*Bombus* sp.) can successfully pollinate watermelons and may be useful in greenhouses or high tunnels.
(Spicer, 2007)	Wild pollinators	Squash bees (*Peponapis pruinosa*), sweat bees (Halictidae sp.), and bumble bees (*Bombus* sp.) identified as watermelon pollinators.
(Winfree et al., 2007)		Native bees are the most important pollinators and their presence ensures that growers will not solely be reliant on managed pollinators.
(Taha & Bayoumi, 2009)		11 insect species identified as pollinators of summer seed watermelon.
(Njoroge et al., 2010)		Three wild bee species (*Lasioglossum* spp.) identified as important pollinators in watermelon.
(Ali et al., 2015)		*Apis florea* and *Nomia* sp. identified as watermelon pollinators.
(Garantonakis et al., 2016)		Native bee populations can provide an equivalent pollination service to that of managed honey bees
(Campbell et al., 2019)		Numerous insect species (e.g., *Agapostemon splendens, Dielis plumipes*) identified as contributors to watermelon pollination.
(Sataral & Rustiawati, 2019)		Seven species of insect visitors including *Amegilla* sp. identified as watermelon pollinators.
(Kremen et al., 2002; Kremen et al., 2004)	Land management	Pollination services from native bees is positively correlated with the proportion of natural habitat surrounding farms. Conservation of these habitats will allow farmers to diversify their pollination sources.
(Pisanty & Mandelik, 2015)		The amount of surrounding semi-natural habitat at 250-2500 m radii has a positive effect on wild bee diversity at field edge.
(Pisanty et al., 2016)		Wild bee visits are positively correlated with percentage shrub land and forest within 50 m, whereas honey bee visits were positively correlated the density of watermelon bloom.
(Jenkins, 2019)		Wildflower strips significantly increase the visitation rate of *Lasioglossum* spp.

plant/soil health (Garratt et al., 2016; Pisanty et al., 2016; Willcox et al., 2017).

The increasing demand for high quality hybrids globally will require specific pollination management practices as pollination may be a limiting factor for production (Sawe et al., 2020; Layek et al., 2021). Our study highlights four key areas likely to improve pollination success of watermelon: ensuring there is an adequate density of honey bees, introducing other managed pollinators, identifying wild pollinator taxa and encouraging them within watermelon fields, and the use of land management practices to better support pollinator populations.

Increasing honey bee densities in watermelon production systems can enhance pollination and production by increasing flower visitation rates. This may be achieved by increasing the stocking rates of managed colonies (five colonies/ha is the most common recommendation; Rollin & Garibaldi, 2019) or by employing plant management techniques to boost bloom density in watermelon crops − increasing the crop's attractiveness to honey bees (Stanghellini et al., 1998a; Stanghellini et al., 1998b; Rollin & Garibaldi, 2019; Layek et al., 2021). Chemical attractants have also been applied to flowers to increase honey bee visits, however they did not significantly increase visitation, yield, or fruit quality (Schultheis et al., 1994; Ellis & Delaplane, 2009). Increasing the stocking rates of managed bees does have potential to negatively impact the surrounding environment and native species (Mallinger et al., 2017), thus, local policies and environmental conditions need to be understood before increasing honey bee densities if they are considered a risk to other communities (OEH, 2018). Alternatively, better defined protocols for deploying managed honey bee colonies, including their spatial and temporal arrangement within watermelon production systems (Rollin & Garibaldi, 2019), could further increase their pollination efficiency, perhaps reducing the need to employ a larger number of colonies.

Other studies show that managed bee species other than honey bees also have potential as watermelon pollinators, these include bumble bees, stingless bees, and mason bees (Stanghellini et al., 1998a; Stanghellini et al., 1998b; Zhifeng et al., 2011; Bomfim et al., 2015a; Campbell et al., 2018; Layek et al., 2021). Bumble bees are consistently found to be more effective than honey bees at pollinating watermelon (Stanghellini et al., 1998a; Stanghellini et al., 1998b; Campbell et al., 2018), however, introducing managed bumble bees may have negative environmental impacts where they are not native (Delaplane, 2021). Stingless bees also have potential to be used for watermelon pollination, both in protected and open cropping systems (Bomfim et al., 2015a; Layek et al., 2021). These managed bee species may become increasingly important in some parts of the world, due to a growing tendency to cultivate watermelon under protected covers (Bomfim et al., 2015a; Bomfim et al., 2015b; Huang et al., 2018), which are known to be problematic for honey bees (Kendall et al., 2021). Other currently unmanaged taxa may also have potential as managed pollinators for watermelon in protected growing environments (Kendall et al., 2021).

Many studies have identified wild bee species that can be effective and abundant pollinators in watermelon fields and their presence could be encouraged to improve pollination and increase system resilience. This aligns with the recommendations of a large-scale review of data from 600 crop-fields worldwide (19 crops), which found that fruit set consistently increased with wild pollinator visitation, irrespective of the level of honey bee visitation (Garibaldi et al., 2013). The increased biodiversity in agro-ecosystems is important for ensuring pollinator taxa are available under a wide range of environmental conditions (Naeem, 1998; Senapathi et al., 2021). Enhancing bee diversity can also improve the pollination efficiency of honey bees (Greenleaf & Kremen, 2006; Brittain et al., 2013b). In watermelon, the pollination service of wild bees is positively correlated with the proportion and proximity of surrounding natural vegetation at farms (Kremen et al., 2002; Kremen et al., 2004; Pisanty & Mandelik, 2015). Resource-rich flower strips around cropping fields can also enhance watermelon flower visitation by wild insects in watermelon (Jenkins, 2019). Other farm management practices that are known to enhance wild pollinators include careful use of pesticides (Njoroge et al., 2004). Pesticide application can negatively affect diversity of floral visitors in watermelons (Tettey-Enyo, 2017), while organic watermelon farming systems are associated with effective pollination by wild bee taxa (Kremen et al., 2002). When used, pesticides should be applied at the recommended rates, at times when pollinators are not active on the crop, such as pre-flowering or late afternoon/ evening after flowers have closed for the day (Njoroge et al., 2004). These findings mean there is potential for farming landscapes to support wild pollinator taxa that provide free pollination services to enhance pollination and fruit production, while reducing the reliance on honey bees in watermelon cropping systems.

The results of our study indicate that the majority of studies investigating watermelon pollination originate from North America, which represents only a small portion of the world's production (3% on average 1961-2019). This synthesis did not locate large-scale field studies for the two largest producers: China, comprising 53% of world production on average 1961-2019 FAO (2019), and Turkey, the second largest producer. Only two studies originated from India, the third largest producer at present and just three studies assessed the contribution of insects to watermelon pollination in Europe and South America (13% of world production together, average 1961-2019, FAO (2019)). Further, only a limited number of studies were conducted in Africa, despite being the region of watermelon origin. While our review indicates a lack of data on insect pollinators in the major watermelon producing regions using Scopus, Web of Science, and Google Scholar, it is possible that studies exist in other languages and/or from other sources that were not indexed in these databases (Amano et al., 2021). Global reviews of pollinators in two other crop species, avocado (Dymond et al., 2021) and apple (Pardo & Borges, 2020), reveal a similar paucity of information in regard to the pollination ecology in the main crop-producing countries.

In conclusion, honey bees are frequent and important visitors to watermelon flowers in the many growing regions, but these flowers also attract a diverse group of insect species. Other bee species can be as or more effective than honey bees at pollinating watermelon and are the majority of visitors in over 40% of watermelon growing regions. This is evidence for distinct regional differences in the insect pollination services responsible for the production of a global crop. Our findings also highlight the potential for many regions to further decrease their dependency on one pollinating species, to achieve more resilient and stable pollination services. Future research should focus on addressing data deficiencies in major growing regions and refining pollination management practices to support and benefit from a wider range of pollinator species, in particular non-*Apis* bee species.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found in the online version at doi:10.1016/j.baae.2022.11.006.

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