

POLLINATION SERVICES OF MANAGED COMMON EASTERN BUMBLE BEES (*BOMBUS IMPATIENS*) IN SEEDLESS WATERMELON (*CITRULLUS LANATUS*)

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Abstract—Seedless watermelon is a highly pollinator-dependent crop; in consequence, growers stock fields with managed pollinators to ensure high yields. Historically, only western honey bees (*Apis mellifera*) were used, but, more recently, growers have begun adding common eastern bumble bees (*Bombus impatiens*) as further insurance. While bumble bees are efficient watermelon pollinators on a per-visit basis, the impacts of field-scale colony supplementation are unknown. We conducted two field studies in 2017-2018 and 2025 across 36 commercial watermelon fields that were either stocked or unstocked with bumble bees. Focal flower observations were then used to investigate pollinator visitation frequency (individuals recorded per observation) and visitation rate (flowers visited per minute per individual) across and within (i.e., near vs. far from colonies) fields. Additionally, in 2025, we dusted bumble bee colonies with fluorescent powder to more directly quantify their flower visitation, and in 2024-2025, we identified colony and foragers' pollen loads to estimate watermelon's relative contribution to foraging dynamics. Observations revealed that managed bumble bees did not increase visitation frequency to watermelon flowers at a whole field-scale, but only on plants adjacent to colonies within a field (3.6-fold increase within 10 m radius). Managed bumble bee presence also influenced other pollinators, with small solitary bees being, overall, most affected. Only 1.5% of flowers around bumble bee colonies contained fluorescent powder traces and 2.9% of pollen grains were identified as watermelon. Collectively, our data suggest that watermelon is not a preferred resource for managed bumble bees and thus stocking fields with colonies may not increase visits to crop flowers or contribute to enhancing yield.

Keywords—Colony hive, fluorescent powder, pollen analysis, pollinator-dependent crop, focal plant observations, quad nest-box

INTRODUCTION

Pollination is an essential ecosystem service in agroecosystems with over 75% of global crops relying, at least partially, on pollinators to secure commercial yield and food quality (Klein et al. 2007; Ollerton et al. 2011). Yet, the degree to which a crop depends on pollinators varies, from some crops depending little on pollinators (0-10%) such as guava (*Psidium guajava*), to some crops where pollinators are essential (> 90%) like watermelon (*Citrullus lanatus*) (Siopa et al. 2024). In recent decades, the need to secure pollination services has increased alongside the growing demand for

pollinator-dependent crops (Aizen et al. 2019; Porto et al. 2020). However, the expansion of agricultural areas, reduction of natural habitats, spread of parasites and pathogens and increase of management practices (e.g., chemical pesticide applications) among others have contributed to reducing the abundance and diversity of wild, native pollinators (Brunet & Fragoso 2024); potentially threatening food production through pollination deficits (Smith et al. 2022). Consequently, to overcome insufficient pollination services delivered by declining wild pollinating insect communities and achieve marketable yields,

growers typically use commercially available managed pollinators (Osterman et al. 2021). Insects, and especially bees, are the most frequent managed pollinators because they can provide efficient pollination services to a wide range of crops (Klein et al. 2007; Osterman et al. 2021).

The western honey bee (*Apis mellifera*) is by far the most important and widespread managed pollinator, which is used in multiple crops worldwide (e.g., grapefruit—*Citrus paradisi*—in Argentina, oilseed rape—*Brassica napus*—in Sweden, sunflower—*Helianthus annuus*—in South Africa; Rader et al. 2016). Despite the global use of honey bees, pollen limitation (i.e., pollination deficits as a result of insufficient pollination services) still occurs in multiple crops (Stroh et al. 2025). In addition, adverse weather conditions reduce honey bee foraging efficiency (Karbassioon et al. 2023). Thus, the inability of honey bees to maximise yields in many crops has contributed to the commercialisation of alternative managed pollinators (Bosch et al. 2006; Pitts-Singer & Cane 2011; Toni et al. 2021). For example, bumble bees are considered to be more efficient crop pollinators than honey bees based on their behaviour (Lyu et al. 2023; Bie et al. 2025) and single visit deposition (Campbell et al. 2018), although this depends on the crop. Moreover, their presence can improve the pollination efficiency of honey bees (Eeraerts et al. 2020). Bumble bees can also pollinate at different times of day and in inclement weather compared to honey bees, thereby providing more resilient pollination (Klein et al. 2007; Brittain et al. 2013a; Rader et al. 2016; Mateos-Fierro et al. 2022). Consequently, while many growers still rely exclusively on honey bees, combining honey bees with other commercially available bee species is an increasingly used practice (Boyle & Pitts-Singer 2019; Mateos-Fierro et al. 2023).

In North America, there are several commercially available managed bees that can be used in combination with (or as an alternative to) honey bees. These include the common eastern bumble bee (*Bombus impatiens*) for greenhouses (e.g., tomato—*Solanum lycopersicum*; Strange, 2015) and open fields (e.g., pumpkin—*Cucurbita pepo*; Petersen et al., 2013), the blue orchard bee (*Osmia lignaria*) for spring-blooming fruit tree crops (e.g., sour cherry—*Prunus cerasus*; Boyle & Pitts-Singer, 2019) and the leafcutter bee (*Megachile rotundata*)

for seed production (e.g., alfalfa—*Medicago sativa*; Pitts-Singer & Cane, 2011). The use of multiple managed pollinator species has generally contributed to increased pollination services and greater economic profits (Osterman et al. 2023). Yet, in some cases, a combination of managed pollinators may still not provide efficient pollination and thus fail to achieve optimal production (Osterman et al. 2023; Mateos-Fierro et al. 2023; Stroh et al. 2025). This failure may be caused, in part, by pollinator preference for non-crop forage (Gaffney et al. 2019; Zhou et al. 2024) or generalist managed pollinator species may not be as efficient as wild native pollinators (Larsson 2005). Thus, the benefits of adding new, non-honey bee managed species to existing pollination systems is unclear in many crops and regions.

Seedless watermelon is a triploid, monoecious crop, in which pollinators are essential to transfer viable pollen from compatible diploid pollinizers for fruit set (Wijesinghe et al. 2020). Consequently, in seedless watermelon systems in the Midwestern USA, honey bees are extensively used by all major producers and *ca.* 70% of them also use the common eastern bumble bee (*authors' personal observation*). This is a relatively new addition to the system; historically, honey bees were the only managed species added to fields. Bumble bees can potentially secure watermelon yields in the absence of honey bees (Stanghellini et al. 1998), as honey bees may not fly in adverse weather (Karbassioon et al. 2023). Supplementing fields with bumble bees is a balance between concerns of honey bees alone not being able to secure yields and managed bumble bee investment (i.e., cost-benefit). Indeed, the great efficiency of bumble bees to pollinate watermelon flowers has been demonstrated (Stanghellini et al. 2002; Campbell et al. 2018; Subasinghe Arachchige et al. 2023), but there is a growing concern among producers about the role of managed bumble bees in watermelon production, given their economic investment. For example, floral observation studies often show that bumble bees are small contributors (< 10%) to the total pollinator community in watermelon, even in fields stocked with commercial colonies (Henne et al. 2012; Campbell et al. 2019b; Bloom et al. 2021; Pecenka et al. 2023). Thus, despite their high per-flower efficiency on an individual visit scale, these benefits may not be realised if insufficient numbers of foragers visit flowers. Moreover, unlike honey

bees, bumble bees are complicated to evaluate since it can be difficult or impossible to differentiate wild vs. managed *Bombus* species co-occurring in the same field.

To better estimate the contribution of managed bumble bees to watermelon pollination and provide growers with management recommendations in commercial fields, we investigated: i) the visitation frequency (individuals recorded per observation), visitation rate (flowers visited per minute per individual) and community composition of pollinator species to watermelon flowers within and between fields stocked with managed bumble bee colonies, and ii) direct evidence for managed bumble bee use of watermelon flowers (via powder tracing) and relative preference for watermelon as a forage source (via pollen analysis). Combined, these approaches provide a holistic assessment of the foraging ecology of managed bumble bees in commercial watermelon production systems as proxies for their potential contribution to yield.

MATERIALS AND METHODS

STUDY SITE AND MANAGEMENT

We combined multiple field observations and manipulative experiments over four years (2017, 2018, 2024, 2025). All data collection was conducted in commercial seedless watermelon fields in Indiana, USA. Fields were mulched in black plastic and included multiple seedless and pollinizer watermelon cultivars common to the region (further details in Table S1). Fields were managed conventionally with standard pesticide programmes for the Midwestern USA (Phillips 2024), except for two fields, which were organically managed—one in 2017 and one in 2018. Within each year, fields were separated from one another by at least 2 km (except for four field pairs across 2017 and 2018, which were located ~1 km apart from each other) (Mola & Williams 2025).

DOES COLONY SUPPLEMENTATION INCREASE BUMBLE BEE VISITATION RATES TO WATERMELON FLOWERS?

An underlying assumption of pollinator supplementation strategies is that stocking fields will increase foraging rates on flowers compared to unstocked (control) fields. While relatively low foraging rates of bumble bees have previously been noted in watermelon fields, to our knowledge

no studies have compared fields with vs. without commercial bumble bee colonies to test for a visitation enhancement effect. To do so, we conducted two studies. The first study (observational study) was conducted in 2017–2018 and compared grower fields that were supplemented with bumble bee colonies with control fields that did not receive supplementation. The second study was conducted in 2025 and differed in two respects. First, we experimentally assigned and randomised colony placement in fields. The first study took advantage of natural variation in grower pollination programmes, whereas in the second study we identified fields not receiving bumble bees and stocked them with colonies, which allowed for stricter experimental control. A second difference is that, in the first study, bumble bees were stocked throughout entire fields (placed by growers), whereas in the second study we placed colonies in a smaller portion of fields. This allowed us to test for localised within-field effects (i.e., comparing the immediate vicinity around the colony area vs. more distant portions of the same field, 200 m into the field), in addition to between-field differences.

For study one (2017–2018), we used 30 commercial fields from 15 different growers—15 fields each year (Table S1). Due to watermelon field locations rotating each year, we considered the 30 fields individual units (i.e., 30 field-year combinations). All 30 fields were stocked with managed honey bees (honey bee hive rate: 1–2 hives acre⁻¹—2.5–5.0 hives ha⁻¹), clustered next to one field edge, but six fields (three each year) were also stocked with common eastern bumble bee (*B. impatiens*) quad boxes (bumble bee colony rate: 0.5–1 colonies acre⁻¹—1.25–2.5 colonies ha⁻¹; Koppert Biological Systems®; Howell, Michigan, USA), deployed throughout the fields. Each quad box consisted of four separate colonies clustered together. To better differentiate terminology for managed pollinator housing, we reserve the term “hive” for honey bees (e.g., honey bee hives), whereas we use “quad boxes” to refer to the commercially available bumble bee housing and “colonies” to refer to the individual units within them (e.g., bumble bee colonies within quad boxes). Quad boxes were shaded to improve colony survival (Marchese et al. 2015). Focal plant observations (3-minute each) were conducted

across two non-consecutive days for each field between July and August. We conducted four observation transects per field and day at four different distances within the fields (25, 100, 175, and 250 m from one field edge), irrespective of quad box locations. In total, this resulted in 16 observations per field per day (32 per season), resulting in > 900 total observations across all 30 field-years.

For study two (2025), we used six commercial fields from three growers (Table S1). All fields were stocked with managed honey bees (same hive stocking rate and placement as above), but none of the growers used bumble bees. We randomly assigned bumble bee supplementation to three of the fields (i.e., one of each farm field pair). In bumble bee supplemented fields, we deployed three quad boxes (12 colonies) per field (regardless of field size) and clustered them along one field edge within a 30-m range. Focal plant observations (5-minute each) were conducted across 8 non-consecutive days for each field between June and August. We conducted two observations per field and day at different distances within the field based on the location of quad boxes (i.e., two sampling locations). One sampling location was done within 10 m from the field edge (near the quad boxes when present) and the second in the field centre, > 200 m from the field edge (far from the quad boxes when present). We used over 200 m to consistently maximise the separation between the quad boxes (at the field edges) and the field centres across the six fields. In total, we conducted 16 observations per field (i.e., 1 observation $\times$ 2 sampling locations $\times$ 8 days $\times$ 6 fields = 96 total observations).

In both studies, each focal plant observation consisted of observing a watermelon plant (~1 m² quadrat) and recording the number of individual bumble bees and other pollinators visiting watermelon flowers (i.e., visitation frequency; the number of individuals recorded visiting watermelon flowers within quadrats, as a proxy for relative pollinator abundance). We recorded visitation frequency of other pollinators to test whether bumble bee supplementation negatively affected the foraging of non-*Bombus* species (Brittain et al. 2013b; Eraerts et al. 2020). We also investigated pollinator behaviour within the quadrats by recording the time pollinators spent

visiting flowers and the number of flowers they visited, from which we calculated visitation rate (the number of flowers visited per minute by each individual) and the transition from male to female flowers (essential for pollination in monoecious crops like watermelon). Prior to each observation, we recorded the number of male and female flowers in the quadrat. Observations were conducted on clear, low-wind days between 07:30 and 13:30 hours. Pollinators were not collected to avoid interference with their foraging behaviour and were identified to genus or species when possible. We categorised pollinators in five groups: i) bumble bees (managed *B. impatiens* + wild *Bombus* spp.), ii) honey bees (managed *A. mellifera*), iii) large solitary bees (*Agapostemon* spp. *Eucera* spp., *Melissodes bimaculatus* and *Xylocopa virginica*), iv) small solitary bees (*Augochlora* spp., *Augochlora aurata*, *Lasioglossum* spp. and *Halictus* spp.) and v) hover flies (Syrphidae). Other flower visitors such as wasps, beetles and butterflies were also recorded but excluded from analysis due to few individuals being observed.

DO MANAGED BUMBLE BEES USE WATERMELON FLOWERS AS A FOOD RESOURCE?

To provide direct evidence of watermelon floral use by managed bumble bees, we used two complementary techniques (each described below); first, powder tracing and, second, pollen analysis.

1) Fluorescent tracing experiment

We conducted a fluorescent powder experiment in 2025 to determine whether marked colonies left traces on watermelon flowers. We randomly selected three quad boxes across the bumble bee-stocked fields and used each quad once on three different occasions (i.e., one quad box per occasion round). Rounds were conducted in early-to-mid July (round 1), late July (round 2) and early August (round 3). In each round, we dusted the four colonies through the flight holes (colony entrances) with ~1.0 g of non-toxic, waterproof, blue, fluorescent powder (model: ANG-12G-GP, Art 'N Glow, USA). We applied the powder using a bulb dust applicator (414 mL Insect Buster, Dr. Killigan's, China) to mark the bumble bees inside the colonies (similar to Hagler et al. 2011) prior to 07:00 hours. Between 11:00 and 13:00 hours and within a 20-m radius around the quad box (in each quad box-round), we inspected

over 200 random watermelon flowers; ~100 flowers were inspected *in situ*, whereas ~100 flowers were collected and inspected in the laboratory. Additionally, in each round, we also inspected ~200 flowers (~100 *in situ* and ~100 in the laboratory) in a bumble bee-unstocked field. Inspection consisted of using an ultraviolet light torch (UV flashlight 51 LED, model: D61UV, Vansky, China) and recording whether the flowers contained fluorescent powder traces (Smith et al. 2012). To ensure the transfer of fluorescent powder from bumble bees to flowers after a visit, we sacrificed 10 bumble bees from the quad boxes where the powder was applied and then gently tapped the bumble bees on 50 watermelon flowers. All flowers presented fluorescent powder traces.

2) Pollen analysis

To explore the frequency of watermelon pollen collected by managed bumble bees in commercial fields, we collected 29 quad boxes across 2024 and 2025 between 19 of August and 01 of September each year. Nine quad boxes were collected from nine fields in 2024 whereas in 2025, 20 quad boxes were collected from seven fields. Each year, quad boxes were kept in a walk-in freezer (-20°C) until pollen extraction and analysis (~3-4 months afterwards). We extracted pollen from and within the wax pollen pots in the colonies and mounted microscope slides (O'Rourke & Buchmann 1991; Kearns & Inouye 1993; Silva Macêdo et al. 2025), since the common eastern bumble bee can use pollen as building material (Newhouse et al. 2021). First, we cut out small pieces from wax pollen pots which contained pollen, placed them on a porcelain mortar (model: 60316/60317, 14.87 ml, CoorsTek®, USA) with 70% ethanol (at a 1:3 pollen-ethanol ratio) and gently crushed them with a pestle to break apart the wax and pollen mixture. We transferred the solution to a 15 mL Falcon™ tube (Catalog No.: 14-959-49B, Fisher Scientific, Inc.) and left it to soak for 3 h. The solution then was vortexed (Vortex-Genie®2, Mo Bio Laboratories, Inc., USA) for 60-120 s. We used a 5 mL disposable transfer pipette (model: 13-711-5AMMD, Fisherbrand™, USA) to transfer ~50 µL of the solution to the centre of a clear glass microscope slide (75 × 25 mm, Catalog No.: 12-550D, Fisher Scientific, Inc.).

Additionally, between June and August 2025, we also harvested corbicular pollen (i.e., pollen

loads) from ~30 bumble bee individuals collected in seven watermelon fields stocked with quad boxes. Common eastern bumble bees foraging around and returning to the quad boxes (likely managed bumble bees) carrying pollen loads were caught using an insect net between 07:00 and 13:00 hrs. After collection, pollen loads were kept in a freezer (-80°C) until analysis (~3-4 months afterwards). Each individual pollen load was placed in a 1.5 mL Eppendorf™ tube (Catalog No.: 05-402-25, Fisher Scientific, Inc.), to which we then added 1.0 mL of 70% ethanol (Barth et al. 2010). The tubes were vigorously shaken manually until the grains of pollen were suspended in the ethanol and no clumps were visible. Next, as above, we used a pipette to transfer ~30 µL of the solution to a microscope slide. After the ethanol evaporated from the slide, ~20 µL of Glycerin Jelly with Basic Fuchsin stain (Brunel Microscopes Ltd.) was melted at 45-50°C and dropped over the dried pollen (Shivanna & Tandon 2014).

All slides (from quad boxes and pollen loads) were covered with a cover glass (22 × 22 mm, Catalog No.: 12-553-457, Fisher Scientific, Inc.), sealed by three coats of clear nail polish (Sinful Colors®, Bold Colour, clear coat), which was applied across the edges of the cover glass and were inspected using light microscopes (Olympus IX51 and Olympus CH-2). We mounted three separate slides per quad box (across the four colonies) but for the pollen loads, a portion of each slide was randomly selected three times. This resulted in three sub-samples (pseudoreplicates) for each quad box (2024: 9 quad boxes × 3 sub-samples = 27; 2025: 20 quad boxes × 3 sub-samples = 60) and pollen load sample (55 pollen loads × 3 sub-samples = 165). For each sub-sample, we randomly selected up to a total of 100 pollen grains and identified and counted all watermelon pollen grains. Watermelon pollen identification was done by comparing slides with freshly collected watermelon pollen and published literature (e.g., Subasinghe Arachchige et al. 2022a). While we did not identify the origin of all other pollen grains, for the 2025 sub-samples, we still identified pollen grains from five common plants found in the Midwestern USA. These included allium (*Allium* spp.), red clover (*Trifolium pratense*), white clover (*Trifolium repens*), vetch (*Vicia* spp.) and morning glory (*Ipomoea* spp.).

STATISTICAL ANALYSIS

All statistical analyses were performed in R (version 4.6.0) using RStudio (2026.05.0+218) (R Core Team 2026) with the ‘lme4’ package (Bates et al. 2015) and the ‘ggplot2’ package (Wickham 2016) for visualisation.

Analyses for the three response variables investigated during the observations—i) visitation frequency, ii) flowers visited (i.e., visitation rate) and iii) male-to-female transition—were done separately for each study (i.e., six total models). For the 2017-2018 study, pollinator group (five groups) and bumble bee stocking management (stocked vs. unstocked) along with their interaction were set as fixed factors, whilst in the 2025 study, we also added sampling location (edge vs. centre) and the three-way interaction. Non-significant interactions were removed to improve model parsimony ($\Delta AICc < 2.0$; Akaike Information Criterion; ‘MuMIn’ package; Bartoń 2025). Specifically, in the 2025 visitation rate model, the three-way interaction produced convergence warnings and unstable estimates; thus, to avoid overparameterisation, we excluded the sampling location interaction. All six models included: i) observation_id nested within field_id and week as random factors but random factors contributing negligible variance and not improving model fit (model summary and $\Delta AICc$ as above) were removed; ii) log-transformed floral availability as a covariate (total flowers per m² in the visitation frequency and visitation rate models and separate male and female flowers per m² in the male-to-female transition models; $m^{-2} + 1$); iii) either the log-transformed observation time (3 minutes in 2017-2018; 5 minutes in 2025) or visiting time (time in minutes that each pollinator was recorded visiting flowers in the quadrat) as an offset to standardise responses per minute and iv) the bobyqa (Bound Optimisation BY Quadratic Approximation) optimiser to maximise model convergence.

Visitation frequency and visitation rate were analysed using generalised linear mixed models (GLMM) with a negative binomial distribution and a log link (function ‘glmer.nb’), whereas male-to-female transition was analysed using binomial GLMMs with a logit link (function ‘glmer’, family = binomial). To investigate the floral transition probability, we transformed the counts to a binary response (0 = no transition, 1 = at least one

transition). Hover flies were excluded for the 2025 male-to-female transition model due to only one transition being observed.

Fluorescent powder tracing on watermelon flowers was analysed using a bias-reduced generalised linear model (GLM) with a Poisson distribution and a log link function (function ‘glm’, family = Poisson, method ‘brglmFit’, package ‘brglm2’; Kosmidis, 2025). Bumble bee management (stocked vs. unstocked) and inspection location (*in situ* vs. laboratory) were specified as fixed factors while the log-transformed number of flowers inspected was included as an offset.

The proportion of watermelon pollen grains was analysed using a GLM with a quasibinomial distribution (function ‘glm’, family = quasibinomial), which accounted for overdispersion. The response variable was the number of watermelon grains vs. total grains using the “cbind” function, while pollen source (quad box vs. pollen load) was included as a fixed factor.

For all models, we obtained model-based estimated marginal means (EMMs; package ‘emmeans’; Lenth, 2025) on the response scale (probability scale for binomial models). Tukey-adjusted pairwise comparisons were performed to further investigate significant differences among factor levels. Specifically, when interactions were present, comparisons of EMMs across combinations of factors were conducted (e.g., we compared sampling location levels within each pollinator group and bumble bee stocking levels) (Quinn & Keough 2002).

RESULTS

FOCAL PLANT OBSERVATIONS

We recorded 1,141 pollinators in the 2017-2018 study (58 bumble bees, 350 honey bees, 114 large solitary bees, 488 small solitary bees and 131 hover flies in 944 observations) and 438 pollinators in the 2025 study (72 bumble bees, 254 honey bees, 43 large solitary bees, 59 small solitary bees and 10 hover flies in 96 observations).

VISITATION FREQUENCY

In 2017-2018, visitation frequency (number of individuals recorded per observation) differed by group across bumble bee managed fields—stocked

vs. unstocked (pollinator group and bumble bee stocking interaction: $\chi^2 = 28.38$, $P < 0.001$; Table S2). Visitation frequencies of bumble bees (pairwise comparison: $Z = 2.14$, $P = 0.03$) and small solitary bees ($Z = 2.55$, $P = 0.01$) decreased by 74.8% and 52.1%, respectively, in fields stocked with bumble bees, but honey bee, large solitary bee and hover fly visitation frequencies remained similar (Fig. 1A; Table S3). Overall, honey bees and small solitary bees were the most recorded pollinator groups at 0.13 ± 0.02 (predicted mean $\pm$ SE) and 0.11 ± 0.02 individuals $\text{m}^{-2} \text{min}^{-1}$, respectively. Watermelon floral resources significantly increased pollinator visitation frequency ($\beta = 0.31 \pm 0.15$, $Z = 2.04$, $P = 0.04$).

The three-way interaction between bumble bee-stocked fields, sampling location (edge vs. centre) and pollinator group in 2025 was significant ($\chi^2 = 18.07$, $P < 0.01$; Table S2), indicating group-specific spatial responses to stocking. Within-field visitation frequencies of honey bees, large solitary bees, small solitary bees and hover flies were not affected by bumble bee stocking at either sampling

location. In contrast, bumble bee (wild + managed) visitation frequency was significantly greater in stocked fields, but only at the field edges, near quad box deployment, with a 3.6-fold increase ($Z = 3.57$, $P < 0.001$; Fig. 2; Table S3). Despite within-field visitation frequency of all other pollinator groups remaining similar, their visitation frequencies shifted across sampling locations due to stocking (i.e., no variation in visitation frequencies but relocation of individuals within the fields; Fig. 2). Honey bee visitation frequency was 35.1% lower at the edge than in the centre in stocked fields ($Z = 2.21$, $P = 0.03$; Table S3). In contrast, large solitary bees were more frequently recorded at the edge compared to the centre in stocked fields (169.0% increase; $Z = 2.04$, $P = 0.04$). Interestingly, small solitary bees were more often observed at the edge than in the centre only in unstocked fields (134.1% increase; $Z = 1.99$, $P = 0.046$).

Overall, honey bees were the most observed group at 0.42 ± 0.02 individuals $\text{m}^{-2} \text{min}^{-1}$

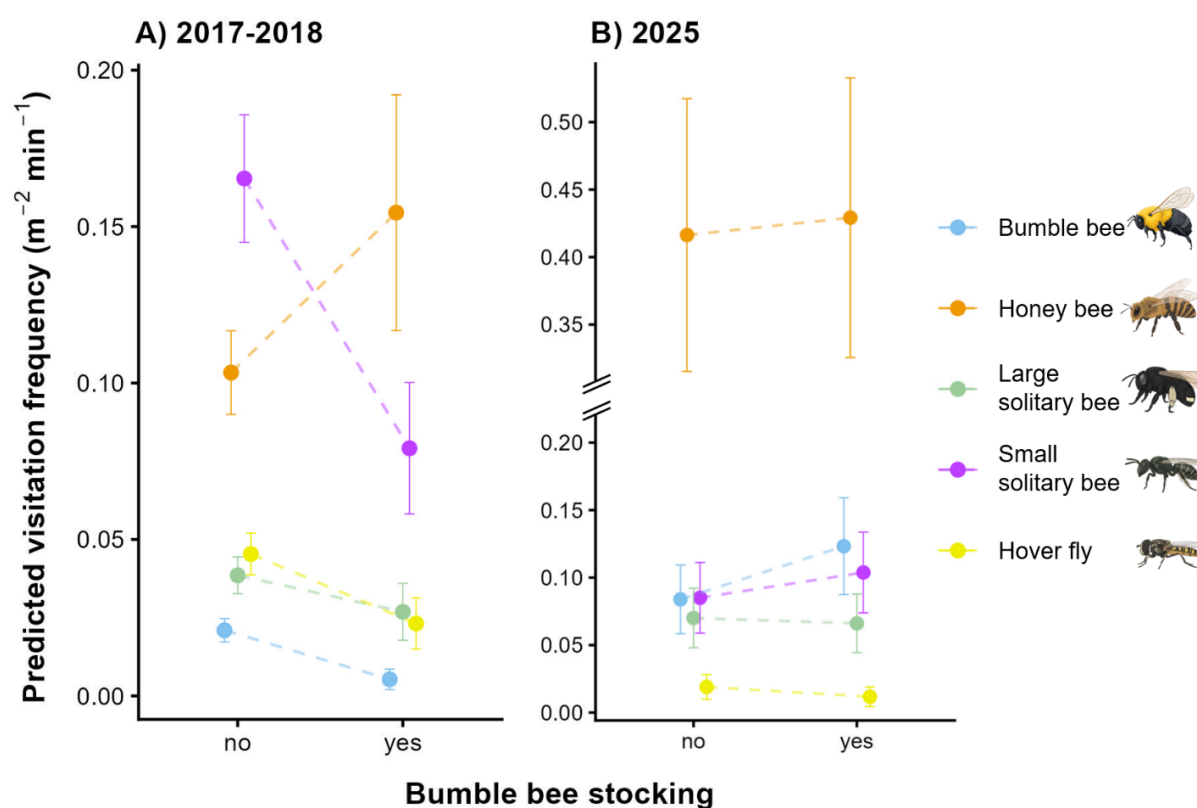


Figure 1. Predicted visitation frequency (number of individuals recorded $\text{m}^{-2} \text{min}^{-1}$) in the A) 2017-2018 and B) 2025 studies according to pollinator group and bumble bee stocking. Points and bars represent estimated marginal means $\pm$ SE, obtained on the response scale from negative binomial GLMMs. Note different y-axes and y-axis break in B (package 'ggbreak'; Xu et al., 2021).

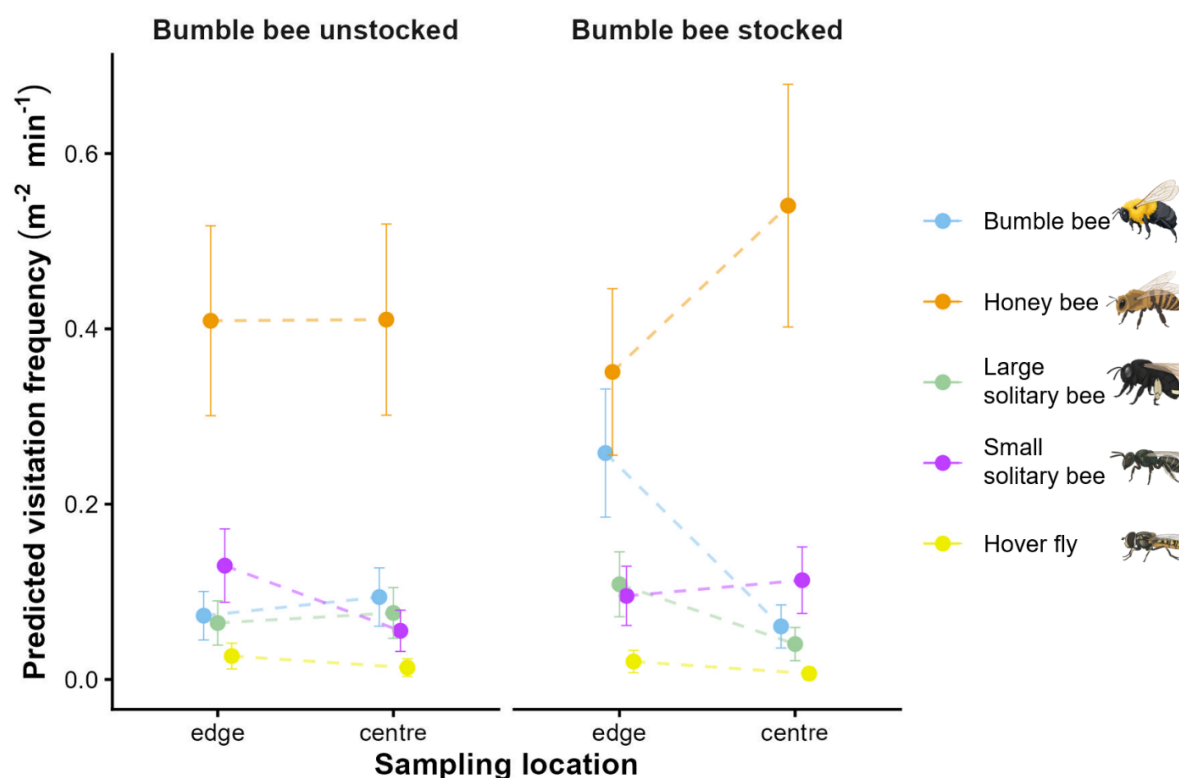


Figure 2. Predicted visitation frequency (number of individuals recorded $\text{m}^{-2} \text{min}^{-1}$) in the 2025 study according to pollinator group, bumble bee stocking and sampling location. Points and bars represent estimated marginal means $\pm$ SE, obtained on the response scale from a negative binomial GLMM.

(predicted mean $\pm$ SE) compared to all other groups (Fig. 1B). This represented a 3.3-fold increase for honey bees compared to the 2017-2018 study. Visitation frequencies of bumble bees (9.7-fold) and large solitary bees (2.1-fold) also increased in 2025 compared to 2017-2018, but visitation frequencies of small solitary bees (0.8-fold) and hover flies (0.5-fold) decreased. Similar to 2017-2018, floral resources significantly increased visitation frequency ($\beta = 0.40 \pm 0.20$, $Z = 2.06$, $P = 0.04$).

VISITATION RATE

In 2017-2018, visitation rate (number of flowers visited per minute per individual) significantly differed among pollinator groups ($\chi^2 = 442.95$, $P < 0.001$) and varied across fields with different bumble bee management practices ($\chi^2 = 6.49$, $P = 0.01$), but the interaction nor flower availability were significant factors (Table S2). Bumble bees, honey bees and large solitary bees visited more flowers ($9.7\text{--}11.2 \pm 0.5\text{--}1.2$ predicted mean flower visits $\pm$ SE $\text{m}^{-2} \text{min}^{-1}$) than small solitary bees (4.2 ± 0.2), which also had a greater visitation rate

compared to hover flies at 1.7 ± 0.2 (Fig. 3A; Table S3). Additionally, visitation rate of pollinators increased by 22.5% in bumble bee-stocked fields compared to unstocked fields.

However, in 2025, the interaction between pollinator group and bumble bee stocking was significant ($\chi^2 = 10.18$, $P = 0.04$; Table S2), but only small solitary bee visitation rate was greater (+62.1%) in bumble bee stocked fields compared to unstocked fields ($Z = 2.95$, $P < 0.01$; Fig. 3B; Table S3). Additionally, pollinator group had a significantly strong effect on visitation rates, which remained consistent regardless of bumble bee stocking. Bumble bees (13.0 ± 0.9 predicted mean flower visits $\pm$ SE $\text{m}^{-2} \text{min}^{-1}$) and large solitary bees (16.5 ± 1.7) visited significantly more flowers than honey bees (8.2 ± 0.5) (Table S3). These three groups had a greater visitation rate compared to small solitary bees (2.5 ± 0.2) and hover flies (1.5 ± 0.4), which were significantly similar. Interestingly, visitation rates in 2025 differed from those of the 2017-2018 study; specifically, bumble bees and large solitary bees increased their

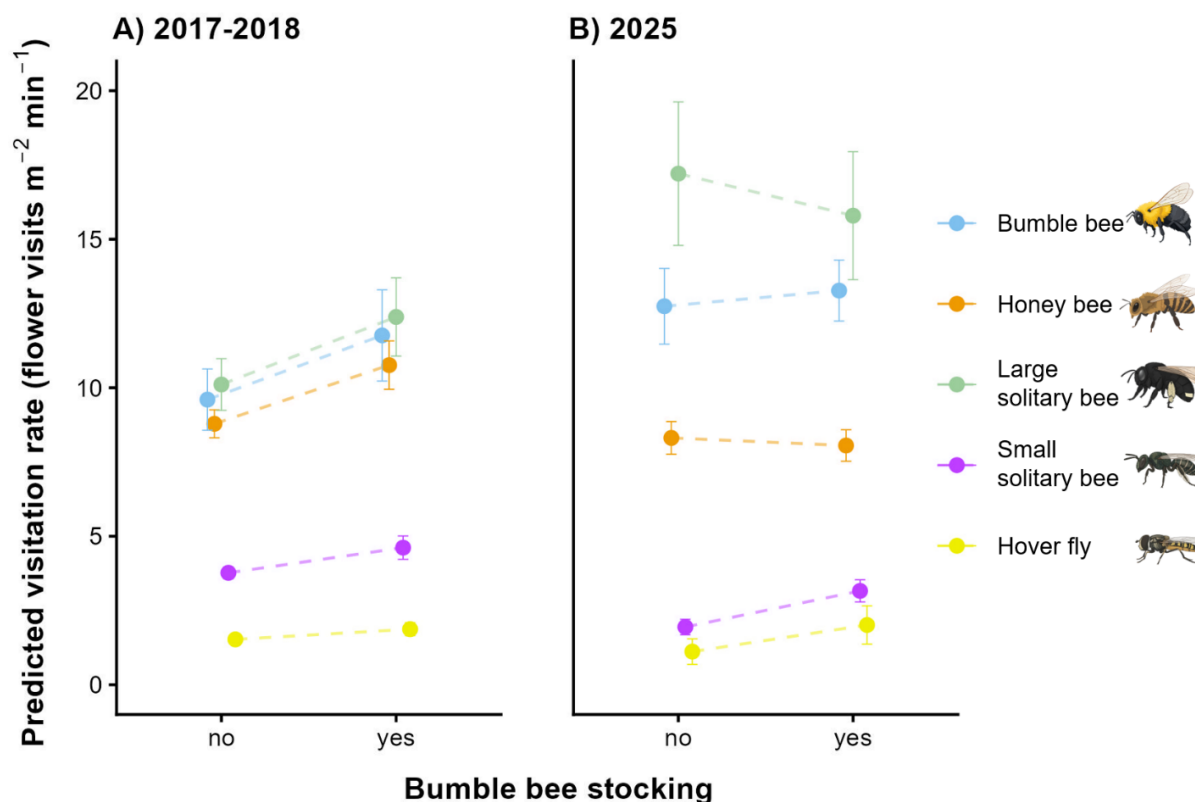


Figure 3. Predicted pollinator visitation rate (number of flowers visited $\text{m}^{-2} \text{min}^{-1}$) in the A) 2017-2018 and B) 2025 studies according to pollinator group and bumble bee stocking. Points and bars represent estimated marginal means $\pm$ SE, obtained on the response scale from negative binomial GLMMs.

visitation rates by 22.3% and 47.4%, respectively, whereas honey bee, small solitary bee and hover fly visitation rates decreased by 15.8%, 40.5% and 11.2%, respectively. Overall, sampling location was not a significant factor, but visitation rate increased with floral availability ($\beta = 0.31 \pm 0.09$, $Z = 3.33$, $P < 0.001$).

MALE TO FEMALE TRANSITIONS

In 2017-2018, the probability of a transition from a male watermelon flower to a female flower significantly differed among pollinator groups ($\chi^2 = 38.29$, $P < 0.001$), but it was consistent across bumble bee stocking management (neither bumble bee stocking nor the interaction were significant factors; Table S2). Similarly in 2025, the probability of transition was affected by pollinator group ($\chi^2 = 20.34$, $P < 0.001$) but not by bumble bee stocking, sampling location or the interactions (Table S2). In both studies, female flower availability strongly increased the probability of transition (2017-2018: $\beta = 3.30 \pm 0.38$, $Z = 8.80$, $P < 0.001$; 2025: $\beta = 1.65 \pm 0.53$, $Z = 3.13$, $P < 0.01$).

Bumble bees had the greatest probability of male-to-female transition in both studies (predicted probability $\sim 52\%$; Fig. 4; Table S3). Transition probabilities of honey bees and small solitary bees were also very stable across studies at $\sim 30\%$ and $\sim 14\%$, respectively. In contrast, large solitary bees varied the most, while they had a lower probability in 2017-2018 ($19.6 \pm 8.8\%$), male-to-female transition probability increased in 2025 to $30.9 \pm 13.6\%$. Transition probability of hover flies was lowest, but greater in 2025 than in 2017-2018 due to few observations recorded in 2025 (1 transition in 10 observations).

FLUORESCENT POWDER TRACING

The proportion of flowers with fluorescent powder traces was low, but significantly greater in bumble bee stocked fields ($1.5 \pm 0.5\%$; predicted mean $\pm$ SE) compared to the unstocked fields, where no flowers with traces were recorded ($\chi^2 = 12.47$, $P < 0.001$; Table S2). Within the stocked fields, a greater percentage of flowers with traces were detected in the laboratory ($2.5 \pm 0.6\%$)

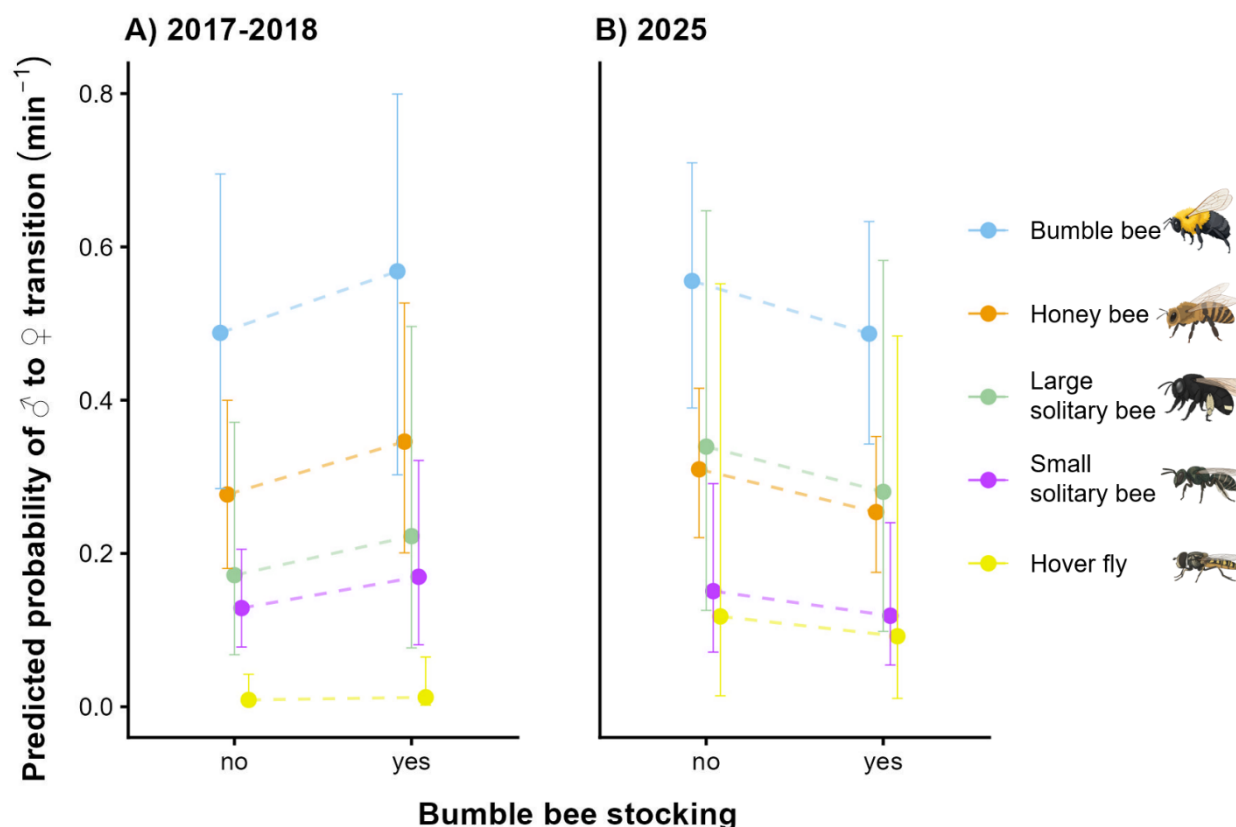


Figure 4. Predicted probability of a transition from a male watermelon flower to a female watermelon flower (min^{-1}) in the A) 2017-2018 study and B) 2025 study according to pollinator group and bumble bee stocking. Points and bars represent estimated marginal means $\pm$ CI, obtained on the response scale from binomial GLMMs.

compared to *in situ* field inspection ($0.7 \pm 0.7\%$), but this was only marginally significant ($\chi^2 = 3.32$, $P = 0.07$).

POLLEN ANALYSIS

The proportion of watermelon pollen collected by bumble bees was significantly greater in quad boxes compared to pollen loads ($\chi^2 = 6.56$, $P = 0.01$; Table S2), but it was overall low, at $4.2 \pm 0.1\%$ for quad boxes and $1.9 \pm 0.05\%$ for pollen loads (predicted mean $\pm$ SE). Of the non-watermelon pollen grains identified in 2025, white clover was the most frequent at 17.9%, followed by red clover (4.5%) and allium (4.0%). Vetch or morning glory represented $< 1\%$ of grains while 71.1% of pollen grains remained unidentified.

DISCUSSION

In this study, we investigated the contribution of the managed common eastern bumble bee to watermelon pollination in the Midwestern USA. Collectively, our data suggest that supplying watermelon fields with managed bumble bees

may not increase the number of bumble bees recorded on watermelon flowers and consequently may not contribute to improving yield profitability.

MANAGED BUMBLE BEE CONTRIBUTION TO WATERMELON POLLINATION

Both the 2017-2018 and 2025 studies highlighted the low visitation frequency of managed bumble bees to watermelon flowers in commercial fields (Henne et al. 2012), suggesting this pollinator species may not be a key contributor to watermelon production. Indeed, the mismatch between bumble bee stocking and visitation observed in 2017-2018 indicates that stocking did not reliably predict visits to watermelon flowers. Honey bee flower visitation also did not increase with hive stocking rate in blueberry, although the common eastern bumble bee did (Mallinger et al. 2021). The discrepancy in bumble bee flower visitation increasing with stocking in blueberry but not in our study in watermelon aligns with their potential preference for blueberry over

watermelon flowers (Campbell et al. 2019a). Additionally, spring blooming crops may be more likely to benefit from bumble bees compared to summer blooming crops, due to cooler conditions. Thus, stocking rates may differ across crops and managed pollinator species, and in watermelon, stocking managed bumble bees may not increase visits to crop flowers. Nonetheless, a study specifically investigating a gradient of bumble bee stocking rates in watermelon should be conducted to confirm whether higher colony rates result in greater number of crop flower visits.

Interestingly, while we did not observe an overall increase in bumble bee visitation throughout the fields, local increases around the quad boxes were observed in the 2025 study. Bumble bees tend to prioritise foraging within a small radius around their colony. In buff-tailed bumble bees (*B. terrestris*), for instance, almost 40% of workers forage within 100 m of their colony when resources are available (Wolf & Moritz 2008). Even though most bumble bee species are able to fly long distances (at least > 200 m), the fact that we only observed an increase in bumble bees next to their colonies suggest that they might prefer visiting other flowers and will only use nearby resources out of convenience (Mola & Williams 2025). While we clustered quad boxes on a single edge due to our 2025 study purposes, which would likely influence uniform visitation across the field, the recommended practice is to evenly distribute the quad boxes throughout the crop field (Marchese et al. 2013). Certainly, quad boxes were spread in the 2017-2018 comparative field study, but this still failed to increase overall bumble bee visits to crop flowers. Additionally, although bumble bee visits to watermelon flowers increased next to the colonies, this was inconsistent across fields, probably as a result of landscape composition. This suggests that when other preferred floral resources are available in the surrounding landscape, bumble bees may be drawn away from visiting crop flowers (Whittington et al. 2004; Foulis & Goulson 2014), but the extent to which landscape context affects managed bumble bee visitation should also be explored. Thus, watermelon growers who wish to continue using bumble bees should consider distributing the colonies throughout the field at regular distances, and while flowering plants can boost wild bees (including wild bumble bees), they

might also draw managed bumble bees away from watermelon flowers. Future research should consider observations across distance gradients from quad boxes to identify the average visitation distance, which we were unable to do in the 2017-2018 study because sampling distances did not account for quad box placement.

The scarce number of visits to watermelon flowers aligns with the low percentage of flowers with fluorescent powder traces (2025) and infrequent watermelon pollen grains collected from both quad boxes and bumble bee individuals (2024-2025). These data indicate that watermelon flowers may not be a preferred resource for this pollinator, as watermelon may not provide an optimal diet (Campbell et al. 2019a; Gauger et al. 2025). Our fluorescent powder experiment was specifically designed to discern visits between managed and wild bumble bees, as flowers would be visited by both, but only managed bumble bees could leave fluorescent powder traces. Specifically, we inspected flowers around the quad boxes, which were more likely to be visited by managed bumble bees (Wolf & Moritz 2008) and yet, the low percentage of flowers with traces observed is consistent with the infrequent visits of managed bumble bees to watermelon flowers. While the low percentage of flowers with traces aligns with low managed bumble bee visitation, detection sensitivity may not have been optimal and false negatives may have occurred (i.e., managed bumble bee visited flowers, but no detectable traces were left). Moreover, while the fluorescent powder must have originated in the managed colonies (the only known field source), theoretically, another pollinator (such as a wild bumble bee) could have picked up traces left on a flower by a managed bumble bee and subsequently leave new traces on a different flower. Consequently, additional methodologies, such as radio transmitters or video cameras, could help confirm managed bumble bee visitation in future studies.

The very small percentage of watermelon pollen collected by bumble bees further corroborates our flower visitation data, whereas the percentage of non-crop pollen grains identified from multiple plant species aligns with bumble bee predisposition for a balanced diet (Bain et al. 2025). Bumble bees normally prefer pollen with a high

protein-to-lipid (P:L) ratio, ranging from 5:1 to 10:1 (Vaudo et al. 2016). This preference may reduce the attractiveness of low protein pollen compared to other floral resources. Cucurbits typically have a P:L ratio of < 2:1, thus watermelon pollen may not meet bumble bee dietary requirements (Vaudo et al. 2020). Additionally, pollen of cucurbits like squash and pumpkin (*Cucurbita* spp.) has nutritional and chemical defence properties that are detrimental to the common eastern bumble bee (Brochu et al. 2020), which can lead to suboptimal colony health and thus diminished performance (Gauger et al. 2025). As a result, bumble bees may prefer visiting flowers with greater protein-rich pollen while avoiding the undesirable toxic effects of cucurbit pollen, although watermelon pollen, specifically, should be tested for macronutrient composition, and physical, nutritional and chemical traits to confirm this. Our data also showed differences in watermelon pollen percentage based on pollen source (quad boxes vs. pollen loads), and the greater percentage of watermelon pollen detected in the quad boxes compared to individual pollen loads could be a result of pollen collection varying throughout the season (Hemberger & Williams 2025). Nonetheless, the pollen in the quad boxes provides a more comprehensive view of bumble bee foraging behaviour across the entire season (Yourstone et al. 2023).

While our data on foraging behaviour suggest that managed bumble bees do not substantially contribute to watermelon pollination, comparing crop yields for stocked vs. unstocked fields is ultimately needed to more conclusively evaluate their economic impacts on the production system. While we collected watermelon yield data in 2025 (Table S1), this comparison suffers from insufficient replication, confounding effects of cultivar differences, and sub-optimal stocking rates (i.e., we only stocked on the field edge, not throughout the whole field). Future studies should also consider providing a cost-benefit analysis by accounting for bumble bee colony costs in comparison to potential yield increases.

EFFECT OF MANAGED BUMBLE BEES ON OTHER POLLINATORS

Of the wild pollinators, the small solitary bees *Lasioglossum* spp. and the large solitary bees *Melissodes bimaculatus*, were frequently recorded in watermelon fields, which aligns with previous

studies (Leach & Kaplan 2024; Stroh et al. 2024). These wild bees are often more efficient than honey bees (Garantonakis et al. 2016; Subasinghe Arachchige et al. 2023), with large bees typically being the most efficient along with bumble bees (Leach & Kaplan 2022; Subasinghe Arachchige et al. 2023). The presence of managed bumble bees only affected visitation frequency of some pollinators in 2017-2018, while in 2025, the strongest impact was on the relocation of pollinators within the fields. The effect of bumble bees on the presence and performance of honey bees has been previously reported; generally, bumble bee presence enhances the pollination services provided by honey bees (Brittain et al. 2013b; Eeraerts et al. 2020; Ternest et al. 2026). While the effects of managed bumble bees on wild native pollinators are less studied, they have, predominantly, negative implications by outcompeting and displacing foragers (Iwasaki & Hogendoorn 2022). In our study, we observed contrasting responses of wild pollinators to the presence of managed bumble bees, with small solitary bees most affected. Particularly, in the 2017-2018 study fewer small solitary bees were recorded visiting flowers in bumble bee stocked fields. This could be a consequence of their smaller size and inability to displace much larger bumble bees when visiting a flower, compared to large solitary bees (Graham et al. 2019).

Similar to visitation frequencies, the greater overall visitation rates of large bees compared to small solitary bees and hover flies is consistent with the literature (Stanghellini et al. 2002; Layek et al. 2021; Mateos-Fierro et al. 2026). Interestingly, regardless of the presence of managed bumble bees affecting pollinator visitation frequency and relocation, in general, visitation rates tended to increase in bumble bee stocked fields, whereas transition from male to female flowers was unaffected. This may be a consequence of the low number of bumble bees recorded visiting flowers throughout the fields; i.e., while visitation frequencies may be affected to some extent, effects on other behavioural traits are more associated with higher managed pollinator abundance (Mallinger et al. 2017). In turn, flower visit constancy (male-to-female transitioning) may be less dependent of managed pollinator presence (Lichtenberg et al. 2020; Soininen et al. 2025).

Aside from the direct effects of competition for floral resources between managed bees (both honey bees and bumble bees) and wild pollinators, other potential detrimental consequences may include the spread of pathogens, which might indirectly affect the abundance and performance of wild native pollinators (Licznier et al. 2025). This is particularly important when species are introduced outside their native range (Geslin & Morales 2015). Although the common eastern bumble bee is native to eastern North America, the use of western honey bees still raises concerns about being introduced outside their native range, as it contributes to wild pollinator declines (Geldmann & González-Varo 2018; Page & Williams 2023). Altogether, while the use of multiple pollinator species has generally contributed to economic profits, our data on visitation frequency and behaviour suggest that managed pollinators may not be providing an optimum pollination system in watermelon (Stroh et al. 2025). Due to the low efficiency of managed honey bees and scarce, albeit very efficient, visits of managed bumble bees, managed pollinators might not be the most promising tactic to maximise pollination (Trillo et al. 2018). Although honey bees can compensate for their inefficiency by a greater number of visits linked to the large number of individuals per colony (Subasinghe Arachchige et al. 2022b), wild native bees are very efficient at pollinating watermelon flowers and, if boosted in the fields, they may visit sufficient flowers to increase pollination (Garantonakis et al. 2016). Consequently, pollinator management practices should focus on enhancing wild pollinators rather than relying on managed bees. Habitat support, such as flowering cover crops, can help increase wild bee populations. A diverse pollinator community can, in turn, provide more efficient and resilient pollination services and enhance sustainable agriculture (Senapathi et al. 2015; Katumo et al. 2022). Future studies should investigate whether enough wild pollinator populations can be boosted sufficiently to maximise commercial yields within watermelon monoculture regions (e.g., southwestern Indiana).

CONCLUSION

Bumble bees excel at pollinating watermelon flowers, but visits to these flowers are infrequent and largely concentrated around their colonies.

Our data suggest that stocking fields with managed bumble bees, at least at currently recommended rates, does not increase watermelon flower visitation and thus likely contributes little to enhancing yields in commercial fields. Due to the potential detrimental effects of cucurbit pollen on bumble bee health, additional floral resources should be available within the field vicinity. Although additional resources will likely draw some foragers away, colonies may stay healthier and a greater number of watermelon flowers may be visited to complement their diet. Crucially, if managed bumble bees are used, colonies should be distributed throughout the field to help achieve more uniform flower visitation, but optimal stocking rates remain to be investigated. Altogether, our data suggest that bumble bees contribute little to watermelon pollination and are unlikely to serve as a surrogate for honey bees. Nonetheless, due to their potential ability to forage under adverse weather conditions, bumble bees may better complement honey bee stocking under these circumstances, although this has yet to be investigated. While honey bees are less efficient pollinators than bumble bees, they visit crop flowers more often and thereby may contribute more to securing commercial yields. However, wild pollinators are both highly efficient and frequently visit watermelon flowers, and consequently, they may help maximise yield. Critically, the presence of managed bumble bees affects other pollinators, but inconsistently across pollinator groups. It has yet to be explored whether these effects intensify under higher stocking rates and whether increased bumble bee abundance also enhances visitation frequency and subsequent contribution to watermelon pollination.

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AUTHOR CONTRIBUTION

Conceptualization: ZM-F, AL, JT, IK; Data curation: ZM-F, JT; Formal analysis: ZM-F; Funding acquisition: AL, IK; Investigation: ZM-F, DM, JT; Methodology: ZM-F,

AL, DM, JT, IK; Project administration: ZM-F, IK; Resources: ZM-F, IK; Supervision: ZM-F, AL, IK; Validation: ZM-F, JT; Visualization: ZM-F; Writing – original draft: ZM-F; Writing – review & editing: ZM-F, AL, DM, JT, IK.

DISCLOSURE STATEMENT

The authors declare no conflicts of interest.

GENERATIVE AI DISCLOSURE STATEMENT

The AI tool Gemini was used to generate three pollinator icons included in the figures: the large solitary bee, the small solitary bee and the hover fly.

DATA AVAILABILITY STATEMENT

Data are available on GitHub at <https://github.com/ZeusMF/Managed-bumble-bee-pollination-contribution> Mateos-Fierro.

APPENDICES

Additional supporting information may be found in the online version of this article:

Table S1. Commercial seedless watermelon fields used in the 2017–2018 and 2025 studies.

Table S2. Statistical summary of the eight models investigating response variables across studies.

Table S3. Statistical summary of post-hoc estimated marginal means (EMM) pairwise contrasts for fixed factors that significantly affected the response variables across studies.

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