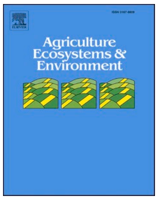
Agriculture, Ecosystems and Environment 396 (2026) 109965

Contents lists available at ScienceDirect

Agriculture, Ecosystems and Environment

journal homepage: www.elsevier.com/locate/agee



Honeybees are the most effective pollinators of mango, but only wild pollinators increase the yield of commercial fruits

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ARTICLE INFO

Keywords:
Fly pollination
Native bees
Pollination contribution
Self-incompatibility
Single-visit pollen deposition

ABSTRACT

Even when several crops depend on animals for their pollination, the effectiveness of each floral visitor remains largely unknown. With this information, conservation practices of the most effective pollinators could be implemented, improving the fruit yield of these crops. Specifically in mango, a globally valuable crop dependent on pollination by insects, little is known about the effectiveness of their floral visitors. Across five quantitative and qualitative metrics (abundance of floral visitors, visitation rate, proportion of legitimate visits, pollen deposition, and probability of tree change), and over two consecutive years, we compare for the first time the effectiveness of all the floral visitors of a self-incompatible mango cultivar ('Ataulfo') and evaluate whether the abundance of the exotic honeybee or wild pollinators influences the production of commercial (well-developed) and malformed fruits (known as nubbins) in one of the largest productive regions of mango in Mexico, the largest exporter worldwide. Our results clearly demonstrate that a diverse array of floral visitors, primarily hymenopterans and dipterans, were effective pollinators of 'Ataulfo' mango. Even when honeybees were the most effective pollinators in both years due to their greater abundance, only the the pollination effectiveness of wild pollinators was positively related to the yield of commercial fruits and negatively correlated with the incidence of nubbins, probably due to their greater mobility between cultivars. These findings highlight the importance of wild pollinators in the mango industry and the need to implement conservation practices to maintain these pollinators to ensure the growing global demand for this cultivar.

1. Introduction

The mango is one of the most economically important tropical crops worldwide (Michael et al., 2023). Although native to India, mango cultivation has spread worldwide and currently there are more than 1 000 cultivars in more than 100 countries (Sankaran et al., 2021). This crop relies heavily on insect pollination to ensure the production of well-developed fruits (Klein et al., 2007). Indeed, a recent study revealed that mango fruit production can decrease by up to 80 % in the absence of pollinators (Marcacci et al., 2023). Consequently, managed honeybees (*Apis mellifera* L.) have traditionally been employed to provide pollination services in mango in various regions (Carvalheiro et al., 2010; Cook et al., 2020). Nevertheless, mango flowers are visited by a wide variety of insects, including wild bees, wasps, beetles, ants, and flies (Carvalheiro et al., 2010; Dag and Gazit, 2000; Rader et al., 2020; Severiano-Galeana et al., 2024). However, the effectiveness of these

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https://doi.org/10.1016/j.agee.2025.109965
Received 12 March 2025; Received in revised form 19 July 2025; Accepted 4 September 2025

floral visitors as pollinators has rarely been evaluated.

Although many mango cultivars are self-compatible, in at least twelve cultivars (Dutta et al., 2013; El-habashy et al., 2016; Jain et al., 2023) varietal self-incompatibility has been reported, thus requiring cross-pollination with trees from other cultivars to produce well-developed fruits. In the case of 'Ataulfo' (another self-incompatible cultivar; Gehrke-Vélez et al., 2012; Lucas-García et al., 2021), pollen deposition from the same cultivar promotes the production of nubbins, which are malformed fruits characterized by their smaller size and weight compared to commercially viable fruits (Lucas-García et al., 2025). This entails a significant challenge for this mango industry, as nubbins hold little or no commercial value (Pérez-Barraza et al., 2007). Consequently, honeybees may not be the best pollinators for self-incompatible cultivars due to their limited mobility among trees of different cultivars (Brittain et al., 2013; Eeraerts et al., 2019). Albeit recent studies suggest that wild pollinators significantly contribute to mango pollination (Marcacci et al., 2023; Severiano-Galeana et al., 2024; Singh et al., 2024), no study has evaluated the contribution of each floral visitor to pollination in any self-incompatible mango cultivar. It is essential to identify which are the most effective pollinators of mango, to provide specific recommendations to protect these species to ensure their pollination services and enhance the yield and profitability of this crop.

Even when several studies provide useful approximations of pollinator performance by metrics such as visitor abundance, visitation rate, duration of visits, contact with reproductive parts (Dag and Gazit, 2000; Severiano-Galeana et al., 2024; Siqueira et al., 2008), or the pollen load carried by each floral visitor (Huda et al., 2015), they can yield imprecise results because they do not directly evaluate pollen deposition (Ne'eman et al., 2010). Therefore, it is crucial to combine both indirect and direct measures, such as pollen deposition, number of pollen tubes developed within styles, or fruit or seed set resulting from a single visit (Lucas-García et al., 2025; Mesquita-Neto et al., 2024) to generate a more accurate assessment of each floral visitor's contribution.

This study aims to compare the relative contribution of non-native honeybees and wild floral visitors as effective pollinators of the 'Ataulfo' mango in southern Mexico, the largest producer of mango in the Americas and the largest exporter worldwide (Rivera-Castro et al., 2022). It also evaluates the relationship between the pollination effectiveness of honeybees and wild pollinators on the yield of commercial fruits and the incidence of nubbins. Accordingly, the following hypotheses and predictions were proposed: **(1)** since mango floral traits are associated with pollination by flies and bees (i.e., myophily and melittophily, respectively; Table S1 in Rosas-Guerrero et al., 2014), both flies and bees are expected to contact the reproductive organs with equal frequency and to deposit similar amounts of pollen per visit; **(2)** given that honeybees have generalist feeding habits (Knowlton et al., 2022), a great capacity to colonize various habitats (Schneider et al., 2004), and their efficient recruitment communication (Shackleton et al., 2023), their abundance and visitation rate are expected to be greater than those of wild floral visitors; and **(3)** given the high floral constancy of honeybees (Eeraerts et al., 2019; Hung et al., 2023), their movements among trees are expected to be less frequent than those of wild floral visitors, and consequently, honeybees are expected to have a negative relationship with the yield and a positive association with the incidence of nubbins, unlike flies and native bees.

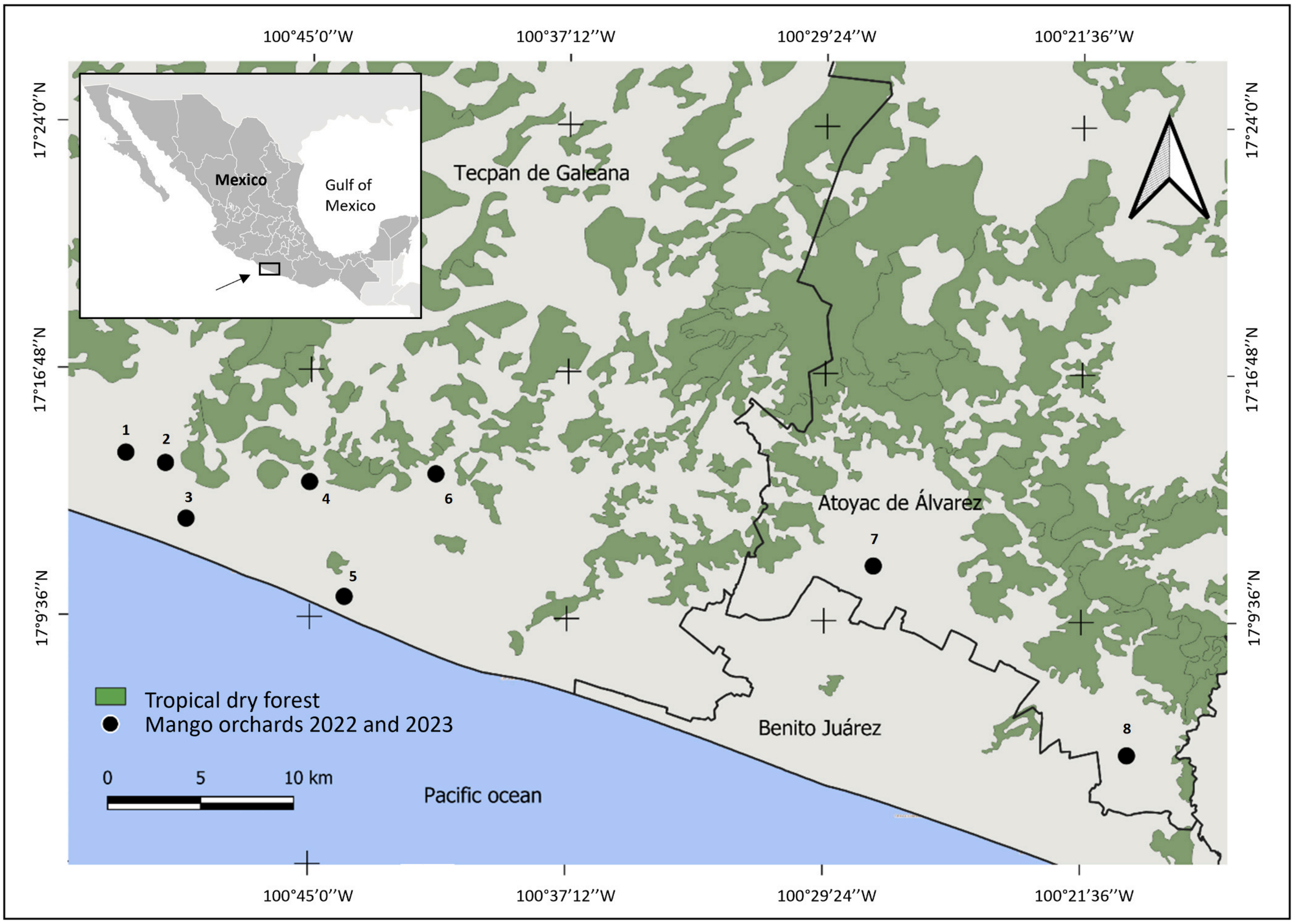

Fig. 1. Location of the eight selected orchards in the Costa Grande region, Guerrero, Mexico. The number of orchards are as in the Table A1.

2. Materials and methods

2.1. Study area

The fieldwork was conducted over two consecutive flowering seasons (November-December 2022 and 2023) in eight mango orchards located in the municipalities of Tecpan de Galeana and Atoyac de Álvarez, in the state of Guerrero, southern Mexico (Fig. 1). This region is one of the leading producers of the ‘Ataulfo’ mango in Mexico (SIAP, 2023).

This region has a warm subhumid climate, with an average annual precipitation of 1 100 mm. The rainy season extends from June to November (total precipitation ≈ 950 mm), while a dry period lasts from December to May (total precipitation < 70 mm). The average annual temperature is 27 °C, peaking at 32 °C in April-May and dropping to a minimum of 18 °C in December-January (INEGI, 2009). The predominant native vegetation type in the region is tropical dry forest (TDF), while the agricultural matrix comprises crops such as mango, coconut, and banana; subsistence agriculture (corn and beans); and pastures for livestock (Osorio et al., 2015).

2.2. Study system

The mango (*Mangifera indica* L., Anacardiaceae) is an andromonoecious tree with flowers easily accessible for pollen and nectar collection by several floral visitors (Siqueira et al., 2008). The natural flowering season in the region usually begins in November and lasts until January (Escalera-Mota et al., 2022). Given that ‘Ataulfo’ is a varietally self-incompatible cultivar, the selected ‘Ataulfo’ orchards included at least one tree of the compatible ‘Haden’ cultivar (Lucas-García et al., 2021). All selected orchards had trees with an average age of ~18 y, were planted under a square planting system and had similar conventional management practices (e.g., use of pesticides and synthetic fertilizers). Irrigation was performed by micro sprinklers and no honeybee hives were introduced. The orchards had an average size of 6.4 ± 1.44 ha and were spatially independent, being separated by an average distance of 23.0 km (range: 2.2–56.2 km; Table A1).

2.3. Floral visitors and pollination effectiveness

Five metrics were used to compare pollinator effectiveness (Ne’eman et al., 2010), two related to the quantity component (QNC) and three to the quality component (QLC). The QNC was estimated as the product of the abundance (**AB**) of floral visitors and the visitation rate (**VR**), while the QLC was estimated as the product of the proportion of legitimate visits (**LV**), the number of pollen grains deposited on the stigma (**PD**), and the probability of tree change (**TC**).

To estimate **AB**, observations of floral visitors were conducted in one day at each orchard along three transects measuring 60 × 2 m (see Carvalheiro et al., 2010), adjacent to rows of mango trees. For 10 min, three times a day during the peak activity of floral visitors (i.e., 10:00, 13:00, and 16:00 h; Severiano-Galeana et al., 2024), insect visits to mango flowers were recorded and floral visitors were collected using entomological nets and placed in a lethal chamber containing potassium cyanide. Insects were identified to the lowest possible taxonomic level using a stereoscopic microscope, dichotomous keys, and the help of a specialist (see acknowledgments).

To estimate **VR**, a focal floral visitor was followed while foraging for one minute and the number of flowers visited by each visitor was recorded. This was done in each orchard between 09:00 and 14:00 h on the same transects used for **AB**. At the end of each observation, a new floral visitor was followed.

To estimate **LV**, one panicle from each of four trees in each orchard was randomly selected and filmed with digital video cameras (Sony DCR-SR45, FDR-AX33, and HDR-CX455) during three 20-min intervals (i.e., 10:00–10:20, 13:00–13:20, 16:00–16:20 h). The total number of visits by each floral visitor and their contact frequency with the reproductive organs of the flower were recorded.

To estimate **PD**, six panicles from each of four trees (24 panicles per orchard) were randomly selected and enclosed in fine mesh bags (40 ×30 cm; mesh size ~0.5 mm) to exclude floral visitors. The next day, bags were carefully removed, and recently opened flowers were observed until they received a floral visitor. This procedure was conducted at 10:00 h, when anther dehiscence begins (Lucas-García et al., 2025), and stigma receptivity is optimal (Gehrke-Vélez et al., 2012). After a visit, the stigma was removed and placed in a gelatin-fuchsin cube (~3 ×3 mm) on a microscope slide and heat was applied until the gel melted (Kearns and Inouye, 1993). The number of pollen grains was counted with an optical microscope. This same procedure was applied to ten unvisited stigmas to serve as a control, and to ten stigmas exposed to visitors throughout the day to serve as a reference for natural pollen deposition. Floral visitors were classified into the following eight types: (1) honeybees (i.e., *Apis mellifera*), (2) yellow-banded wasps (i.e., *Polybia occidentalis*), (3) honey wasps (i.e., *Brachygastra azteca*), (4) stingless bees (e.g., *Frieseomelitta nigra*), (5) other wasps (i.e., *Polistes* spp.), (6) blowflies (flies of the family Calliphoridae), (7) hoverflies (flies of the family Syrphidae), and (8) other flies (flies of the families Muscidae, Sarcophagidae, Tabanidae and Tachinidae). Given that the **PD** records per species for several insects in 2022 were very low, these were grouped in the last five taxonomic groups mentioned above (Table A2).

To estimate **TC**, a focal floral visitor was followed while foraging for 3 min and it was recorded whether the visitor moved among the flowers of the same or different tree (Eeraerts et al., 2019). These pursuits were conducted in each orchard between 09:00 and 14:00 h. At the end of each observation, a new floral visitor was followed. The number of floral visitors tracked varied among orchards due to variations in the abundance of floral visitors.

Once these metrics were estimated, pollination effectiveness (**PE**) for each pollinator was calculated as the product of QNC and QLC (Liu et al., 2020; Rader et al., 2009), and standardized into percentages. To visualize this metric, each **PE** value was included in an “effectiveness landscape”, a two-dimensional graph represented by isoclines delineating possible combinations of QNC and QLC (see Schupp et al., 2017, 2010). Finally, the pollinator contribution (**PC**) was estimated as the proportion of **PE** of each pollinator in relation to the sum of **PE** performed by all pollinators. This metric was used to compare the pollination effectiveness among pollinators.

Differences among metrics for each pollinator, as well as between honeybees and all wild floral visitors (i.e., non-honeybees), were estimated using generalized linear mixed models (GLMMs). In all models, each metric was used as a response variable, with floral visitor treated as a fixed effect and orchards as a random effect (transect and tree were nested within orchard for **AB** and **LV**, respectively). A negative binomial distribution was used to compare **AB** and **PD** (with a logarithmic link function due to overdispersion), while a binomial distribution was used to compare **LV** and **TC** (with a logit link function suitable for proportional data). Finally, a Poisson distribution with a log link function (due to count data) was used to compare **VR**.

GLMMs were adjusted using the *glmmTMB* function from the ‘glmmTMB’ package (Brooks et al., 2017). Significance was estimated using likelihood ratio tests (ANOVA) between models that included the predictor of interest and their respective null models (simpler models without the predictor of interest) using a chi-square test. Each model was graphically validated using the ‘DHARMa’ package (Hartig, 2022). For post hoc comparisons, the ‘emmeans’ package was used with the Tukey method (Lenth, 2024) and the *ggemmeans* function from the ‘ggeffects’ package was used to obtain the means and standard errors of the models. All statistical analyses were performed using R software version 4.3.1 (R Core Team, 2023).

To construct the effectiveness landscape, 5 000 values for each metric were generated through bootstrap resampling

(Rodríguez-Rodríguez et al., 2013). These values were then multiplied to estimate the respective 5 000 values of QNC and QLC, which were subsequently multiplied to obtain 5 000 values of **PE**. Mean, standard deviation, and 95 % confidence limits were then calculated. To plot the location of floral visitors within the effectiveness landscape, the *effectiveness_plot* function from the 'effect.lndscp' package was used (Jordano, 2014).

2.4. *Pollination effectiveness and fruit production*

To evaluate the relationship between the pollination effectiveness of honeybees and wild pollinators on the yield of commercial fruits and the incidence of nubbins, we estimate pollination effectiveness (as described in 2.3) per orchard for each pollinator group. Because it was not possible to have data for each group in each orchard for the **PD** and **TC** metrics, we estimated the value of partial pollination effectiveness (**PPE**) as the product of **AB** x **VR** x **LV**. We considered two main groups of floral visitors: honeybees and wild pollinators, which included all non-honeybee floral pollinators. During both flowering periods, 20 panicles with similar characteristics (e.g., size and stage of development), located ~2 m from the ground, were selected from each of one of four trees per orchard (Severiano-Galeana et al., 2024). These trees were located within the transects used for pollinator observations (see 2.3) and positioned 7–10 m from a tree of the 'Haden' cultivar in order to maximize the likelihood of pollination with compatible pollen (Lucas-García et al., 2021). After 80 days, the total number of commercial fruits per tree was recorded, and the incidence of nubbins (i.e., number of malformed fruits/total fruits per panicle) for each tree was calculated (Severiano-Galeana et al., 2024). We multiply the total number of commercial fruits that were produced in the 20 marked panicles by the average weight of five commercial fruits selected at random to estimate the yield of commercial fruits in 20 panicles.

GLMMs were performed to examine the effects of the **PPE** of visitors on yield and the incidence of nubbins. **PPE** of honeybees and all wild floral visitors were used as explanatory variables, while the incidence of nubbins (binomial distribution with logit link function), and the yield in 20 panicles (Gaussian distribution with identity link function) were considered as response variables. The tree nested within the orchard was considered as a random effect. To avoid GLMM convergence issues, the two explanatory variables were standardized (mean = 0, SD = 1) before modeling with the 'scale' package. Residuals from the models were used to assess spatial autocorrelation via Moran's I test, implemented with the testSpatialAutocorrelation function from the 'DHARMa' package (Hartig, 2022). No significant spatial autocorrelation was detected ($P > 0.05$ in all cases; Table A3). Finally, marginal R-squared values were calculated using the r.squaredGLMM function in the 'MuMIn' package (Barton, 2023) to estimate the variance explained by fixed effects (Nakagawa and Schielzeth, 2013).

3. Results

3.1. *Floral visitors and pollination effectiveness*

A total of 6 447 insects visiting 'Ataulfo' mango flowers were observed across eight orchards (4 055 insects in 2022, and 2 392 insects in 2023; Table A4). As predicted, honeybees were the most abundant floral visitors in both years, comprising 84 % of the total, followed by hoverflies (5 %), and yellow-banded wasps (3 %) in 2022, and totaling 45 % in 2023, followed by blowflies (17 %), and other flies (11 %).

Unlike 2023, in 2022 the **AB** of honeybees was significantly higher than that of all other floral visitors together (left graph of Fig. 2A and B; Table A5). Specifically, in 2022 the **AB** of honeybees was several times larger than each of the other flower visitors ($\chi^2 = 278.44$, df = 7, $P < 0.0001$, right graph of Fig. 2A), while in 2023 the **AB** of honeybees

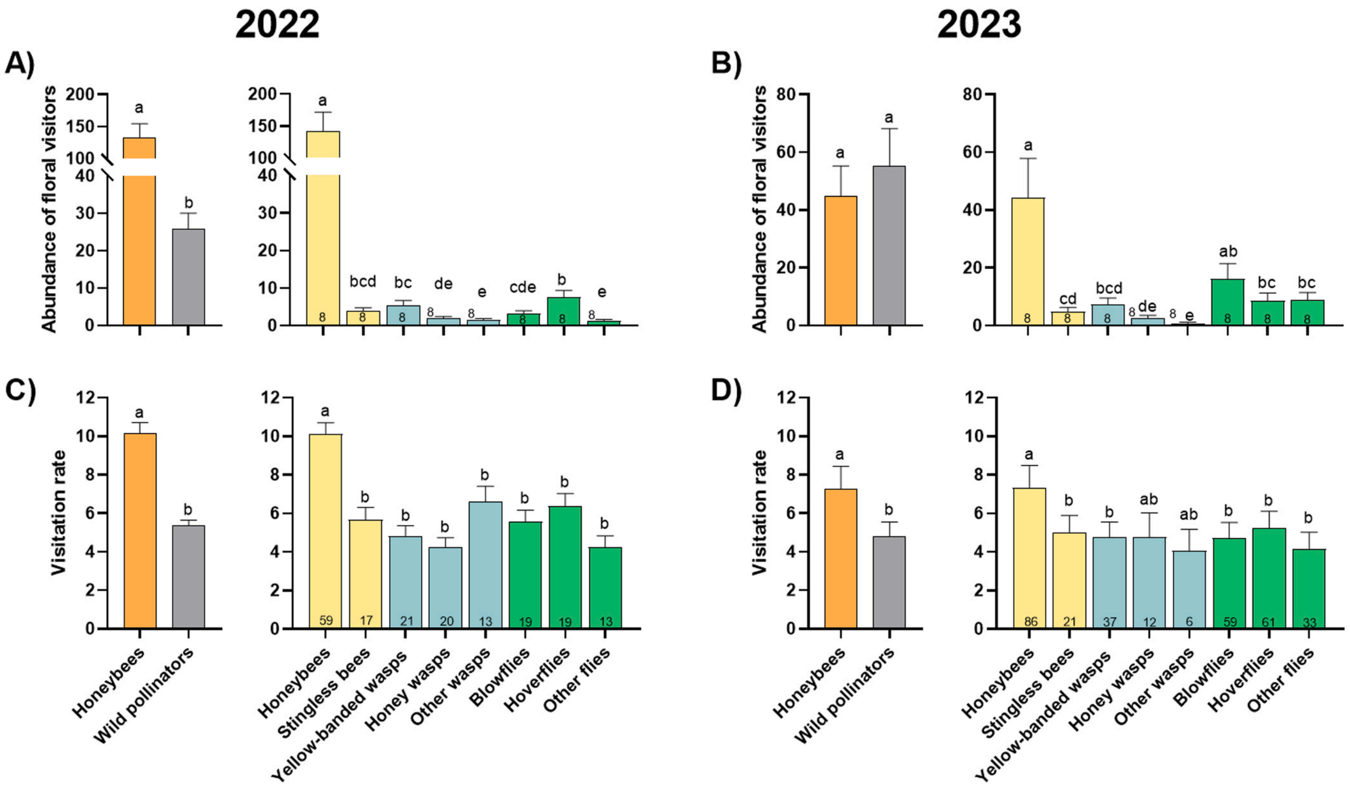

Fig. 2. Abundance (A, B) and visitation rate (C, D) of 'Ataulfo' mango floral visitors recorded in eight orchards during 2022 (left) and 2023 (right). On the left side of each graph, the values of honeybees and all wild floral visitors together are shown. Bar colors indicate honeybees (orange), all wild pollinators together (gray), bees (yellow), wasps (blue), and flies (green). The mean ± standard error is shown. Different letters denote significant differences between floral visitors according to Tukey's test. Numbers above the X axis indicate the sample size (i.e., number of orchards in A and B, and number of insects recorded in C and D).

was similar to those of blowflies but different from the rest of the other floral visitors ($\chi^2 = 98.76$, df = 7, $P < 0.0001$, right graph of Fig. 2B).

In both years, honeybees exhibited a higher **VR** compared to all wild pollinators together (left graphs of Fig. 2C and D; Table A5). Specifically, in 2022 honeybees had the highest **VR**, surpassing all other floral visitors ($\chi^2 = 140.37$, df = 7, $P < 0.0001$, right graph of Fig. 2C). In 2023, the **VR** of honeybees was only higher than the three groups of flies, stingless bees and yellow-banded wasps ($\chi^2 = 36.96$, df = 7, $P < 0.0001$, right graph of Fig. 2D).

In both years, honeybees contacted the stigma and anthers of flowers (**LV**) more often than all wild floral visitors together (left graphs of Fig. 3A and B; Table A5). Specifically in 2022, honeybees showed more **LV** than honey wasps, but similar to the other floral visitors ($\chi^2 = 20.71$, df = 7, $P = 0.004$, right graph of Fig. 3A). In 2023, the **LV** of honeybees was similar to that of hoverflies and honey wasps but higher than the rest of the other wild floral visitors ($\chi^2 = 80.47$, df = 7, $P < 0.0001$, Fig. 3B, right graph). It is also important to state that small ants were frequently observed but did not contact the reproductive organs of the flowers during any of their visits. Similarly, all the butterflies observed visiting mango flowers failed to contact the reproductive organs. Consequently, both groups were excluded from all analyses.

The number of **PD** by all floral visitors varied from 0 to 4 grains in 2022 (n = 134 stigmas; Table A2) and from 0 to 7 grains in 2023 (n = 300 stigmas; Table A2). No significant differences in **PD** were observed among the different floral visitors in both years (2022: $\chi^2 = 11.106$, df = 7, $P = 0.134$, Fig. 3C; 2023: $\chi^2 = 13.35$, df = 7, $P = 0.063$, Fig. 3D). On average, all floral visitors deposited fewer than one pollen grain per visit (0.39 ± 0.77 in 2022, and 0.33 ± 0.90 in 2023). All pollen grains deposited on the stigmas were conspecific; however, it was not possible to determine whether they belonged to a cultivar other than 'Ataulfo'. The stigmas of flowers that remained open throughout the day also received very low pollen deposition (0.6 ± 0.14 in 2022, and 0.7 ± 0.18 in 2023; n = 80 in each year), while flowers that were excluded from pollinators did not receive any pollen grains on their stigmas (n = 80 each year).

All wild floral visitors considered together exhibited a higher probability of **TC** compared to honeybees in 2022 (left graph of Fig. 3E), but not in 2023 (left graph of Fig. 3F; Table A5). Nevertheless, considering each pollinator, the probability of **TC** was similar among them in 2022 ($\chi^2 = 10.52$, df = 7, $P = 0.160$; right side of Fig. 3E) and in 2023 ($\chi^2 =$

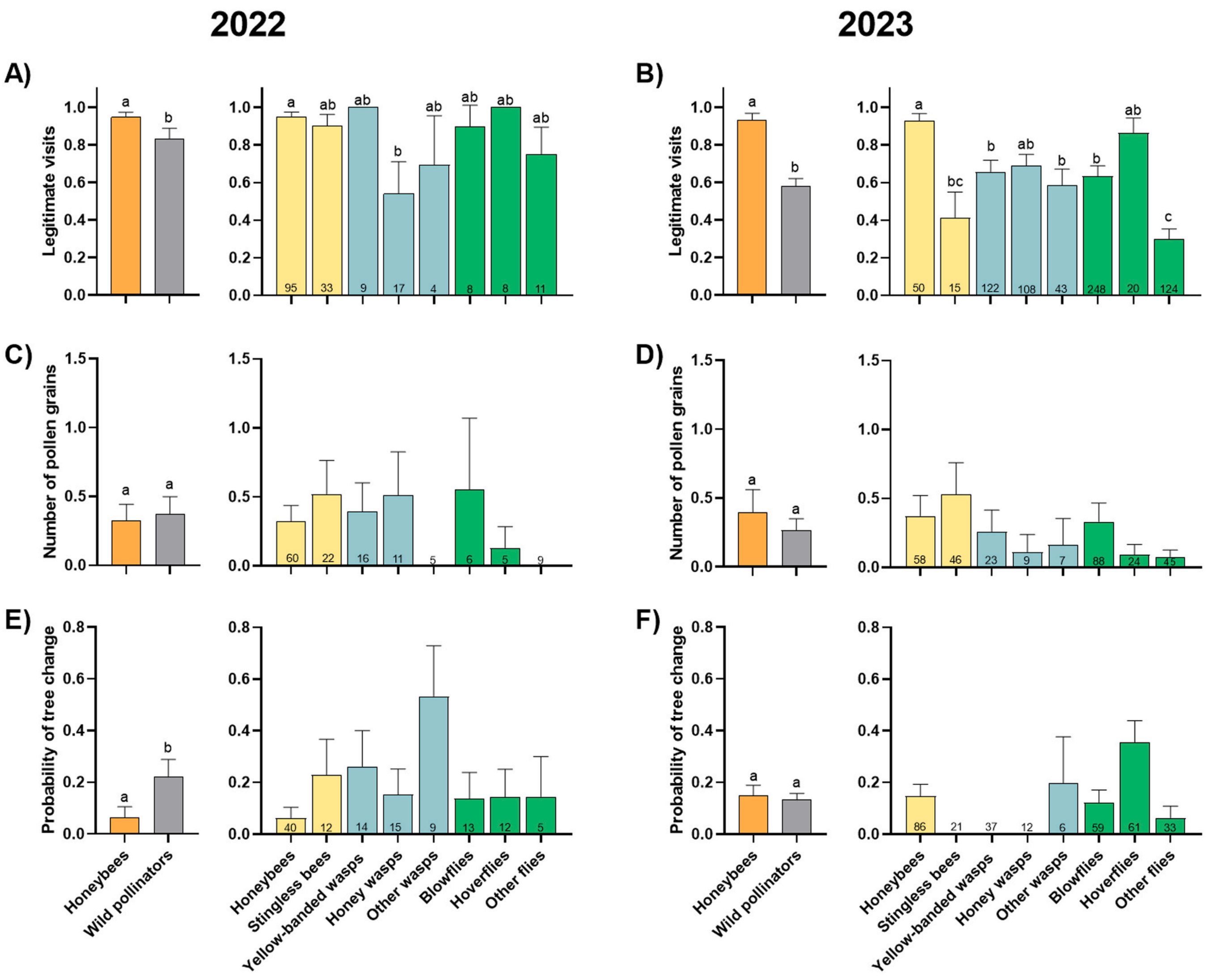

Fig. 3. Proportion of visits that contacted the reproductive organs (A, B), pollen deposition per single visit (C, D), and probability of visiting another tree (E, F) of 'Ataulfo' mango floral visitors recorded in eight orchards during 2022 (left) and 2023 (right). On the left side of each graph is shown the values of honeybees and all wild floral visitors together. Bar colors indicate honeybees (orange), all wild pollinators together (gray), all bees (yellow), wasps (blue), and flies (green). The mean ± standard error is shown. Different letters denote significant differences between floral visitors according to Tukey's test. Numbers above the X axis indicate the sample size.

13.48, df = 7, $P = 0.061$; right side of Fig. 3F).

As expected, honeybees were the most effective pollinators of mango in both years, followed by stingless bees and yellow-banded wasps in 2022 (Fig. 4A), and by blowflies and hoverflies in 2023 (Fig. 4B). Among all pollinators, the honey wasps, other wasps, and other flies, were among the less effective. Based on these results and considering values from both years, honeybees were considered the most important pollinators of 'Ataulfo', contributing to around 80 % of the pollination services (**PC**; Table A6), followed by blowflies and hoverflies, which contributed to 7 % and 5 % of the pollination services, respectively. The stingless bees, and yellow-banded wasps contributed 4 % each, while honey wasps, other wasps, and other flies, collectively contributed less than 1 % (**PC**; Table A6).

3.2. *Relationship between pollination effectiveness and fruit production*

As expected, the yield of commercial fruits was positively associated with wild pollinator **PPE** in 2022 ($Z = 5.96$, $P < 0.001$; Fig. 5A, Table 1) and 2023 ($Z = 2.389$, $P = 0.016$; Fig. 5B, Table 1), but negatively with honeybee **PPE** in 2023 ($Z = 2.389$, $P = 0.028$; Fig. 5D, Table 1). Moreover, the incidence of malformed fruits was negatively related to wild pollinator **PPE** in 2022 ($Z = -2.719$, $P = 0.006$; Fig. 5C, Table 1), but not in 2023 ($Z = -1.375$, $P = 0.169$; Table 1), while a marginally significant positive relationship was found between honeybee **PPE** and the incidence of malformed fruits in 2023 ($Z = 1.825$, $P = 0.068$; Table 1).

4. Discussion

The results of this study clearly demonstrate that a diverse array of floral visitors, primarily hymenopterans and dipterans, were effective pollinators of 'Ataulfo' mango in southern Mexico. Moreover, it was found that although honeybees were the most effective pollinators, their effectiveness was negatively associated with the yield of commercial fruits and positively with the incidence of malformed fruits. In contrast, the effectivity of wild pollinators was positively associated with the yield of commercial fruits and negatively with the incidence of malformed fruits. These findings highlight the crucial role that wild pollinators play in mango pollination and, consequently, in the yield and economic income of the mango industry. In addition, this study provides, for the first time, a comprehensive evaluation of the effectiveness of floral visitors of any mango cultivar in Mexico and the Americas.

4.1. *Honeybees were more abundant and visited more flowers than wild insects*

The 'Ataulfo' mango flowers were visited by bees, wasps, and flies, which coincides with several studies on mango (e.g., Cabrera-Asencio and Meléndez-Ackerman, 2021; Carvalheiro et al., 2010; Dag and Gazit, 2000; Severiano-Galeana et al., 2024; Willcox et al., 2019). This may be because their flowers have easy access to nectar and pollen (de Sousa et al., 2010). Of the insects visiting the mango flowers, honeybees were the most abundant in both years of this study, as found on different mango cultivars (Kumar et al., 2018; Siqueira et al., 2008). This high occurrence is probably due to their generalist feeding habits (Knowlton et al., 2022), the great capacity of honeybees to colonize various habitats (Schneider et al., 2004), and more probably, to their efficient recruitment communication, which enables them to rapidly mobilize numerous colony mates toward profitable floral resources (Shackleton et al., 2023). The lower abundance of wild pollinators, on the other hand, may be a consequence of the alteration and loss of natural and semi-natural habitats (Winfree and Kremen, 2009). Osorio et al. (2015) reported that from 2000 to 2011, the annual conversion rate of TDF to grassland and agriculture in this region was 4.5 %. Growing evidence suggests that agricultural practices, such as pesticide applications, also contribute to the decline of wild pollinators (Basu et al., 2024; Kremen et al., 2002; Siviter et al., 2023).

Even when the selected orchards in this study did not contain managed beehives, nor did the surrounding orchards, which was confirmed by visual inspection within the first 200 m around the orchards, the presence of beehives in other orchards could also explain their high abundance of honeybees observed in our study. While typical foraging distances under normal conditions are up to 2 km (Couvillon et al., 2014), honeybees can fly much longer distances, up to 9 km, when floral resources are scarce (Beekman and Ratnieks, 2000). It is important to consider that there are also colonies of feral honeybees in this region (Aguilar-Aguilar et al., 2024), and these might play a significant role in crop pollination (Cunningham et al., 2022). Although the density of feral colonies has not been studied in this region, other areas in Mexico have recorded approximately 5–9 colonies per km^2 (Ratnieks et al., 1991). Further studies are needed to explore the density of feral honeybee colonies in this region and to evaluate their contribution to mango pollination.

In this study, honeybees visited 'Ataulfo' mango flowers at a higher rate than other floral visitors in 2022 and outperformed most of them in 2023. Previous studies on other mango cultivars have also documented that honeybees exhibit higher **VR** than other pollinators (Chuttong et al.,

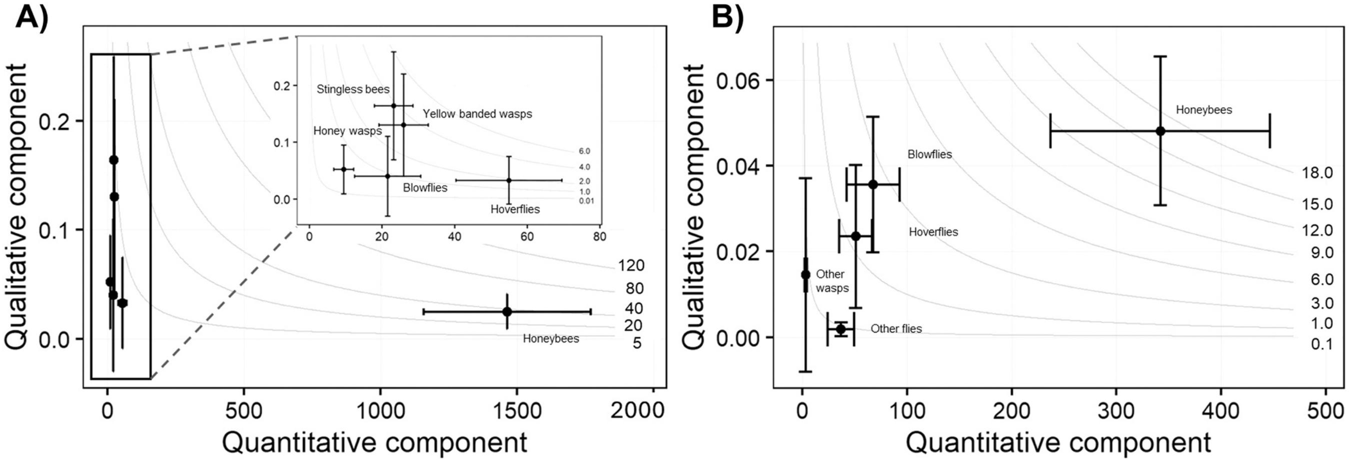

Fig. 4. Landscape showing the effectiveness of pollinators of 'Ataulfo' recorded in eight orchards during 2022 (A) and 2023 (B). The points represent the effectiveness of the pollinators, while the isoclines represent the same values of pollination effectiveness. Horizontal and vertical lines indicate ±1 SD. Note differences in scales among years.

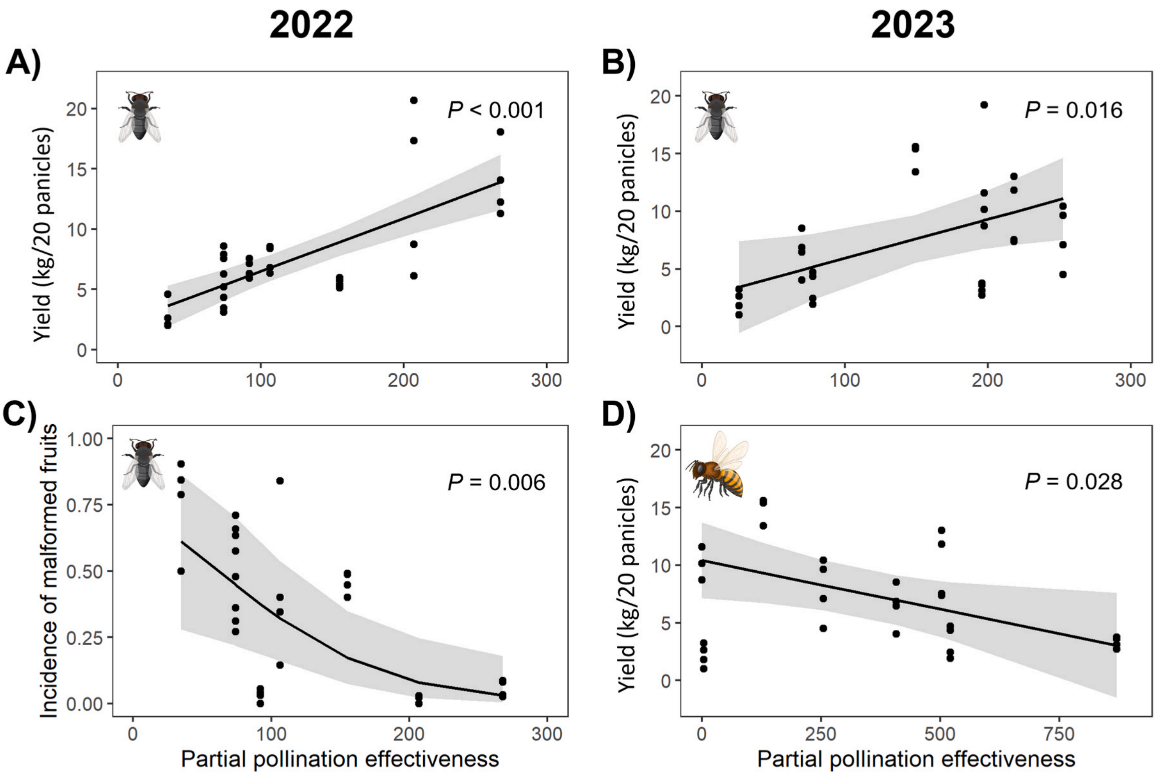

Fig. 5. Relationship between the PPE of wild pollinators and the yield of commercial fruits in 2022 (A) and 2023 (B) and the incidence of malformed fruits in 2022 (C), and of honeybees and the yield of commercial fruits in 2023 (D). Results based on GLMMs. The image of the fly and bee indicates data associated with the effectiveness of pollination of wild insects and bees, respectively. Black dots show raw data, and gray bands represent 95 % confidence intervals.

Table 1
Effect of the effectiveness (PPE) of honeybees and wild pollinators on the yield of commercial fruits (A) and on the incidence of malformed fruits (B) in eight 'Ataulfo' mango orchards in 2022 and 2023, after GLMMs. Marginal R squared (R^2m) values are shown for each model to represent the variance explained by the fixed effects. *P* values in bold are significant at the 0.05 level.

Explanatory variable	**2022**				**2023**			
	Estimate	***SE***	***Z***	***P***	***Estimate***	***SE***	***Z***	***P***
(A) Yield								
	$R^2m = 0.598$				**$R^2m = 0.434$**			
Intercept	7.671	0.535	14.337	**< 0.001**	7.573	1.060	7.144	**< 0.001**
Honeybees	0.830	0.548	1.516	0.130	−2.403	1.099	−2.188	**0.028**
Wild pollinators	3.271	0.548	5.969	**< 0.001**	2.624	1.099	2.389	**0.016**
(B) Incidence of malformed fruits								
	$R^2m = 0.554$				**$R^2m = 0.366$**			
Intercept	−1.088	0.445	−2.446	**0.014**	−1.066	0.703	−1.516	0.129
Honeybees	−0.510	0.457	−1.115	0.264	1.319	0.722	1.825	**0.068**
Wild pollinators	−1.249	0.459	−2.719	**0.006**	−0.977	0.710	−1.375	0.169

2022; Singh et al., 2024). Since **VR** depends on the number of flowers visited in a given time, differences in the behavior of floral visitors may be essential to understanding this metric. For example, pollen collectors have been reported to spend less time per flower and visit more flowers per unit of time than do nectar collectors (Estravis-Barcala et al., 2021; Henselek et al., 2018). In this study, we observed that flies and wasps visited 'Ataulfo' mango flowers primarily for nectar, while honeybees visited them mostly for pollen. Moreover, since honeybees exhibit high floral constancy (i.e., they restrict their visits to a single flower type during a foraging trip to optimize resource collection; Amaya-Márquez, 2009; Gautam et al., 2022), they are expected to spend less time per flower than other floral visitors.

4.2. *Honeybees contacted reproductive whorls and deposited pollen similarly to wild insects*

Several studies have indicated that body size is a key trait favoring contact with the reproductive parts of the flower, and smaller floral visitors tend to contact these structures less frequently than their larger counterparts (Mesquita-Neto et al., 2021; Solís-Montero and Vallejo-Marín, 2017). In the case of mango, it is suggested that floral visitors with a body size equal to or greater than 3 mm have a higher likelihood of contacting flower reproductive structures (de Sousa et al., 2010). However, we observed that insects between 8 and 13 mm (e.g., honeybees and hoverflies) have a more than 80 % probability of contact with the reproductive organs of mango flowers (Lucas-García et al., 2025). In contrast, smaller insects (<8 mm), such as honey wasps, stingless bees and ants, as well as the largest (>17 mm, i.e., other wasps and butterflies), were among the less legitimate floral visitors (Lucas-García et al., 2025). Similarly, Huda et al. (2015), found that hoverflies (*Eristalinus*: 8.9 ± 0.27 mm) had a much higher pollen load compared to smaller insects such as *Iridomyrmex* ants (3.9 ± 0.06 mm), which visited mango flowers but did not transport pollen.

Even when there were differences in the frequency of contact with the reproductive parts of the flower among all groups of pollinators, the number of pollen grains deposited in stigmas was similar. These results indicate that the most legitimate floral visitors were not necessarily the most efficient at transferring pollen. Grooming intensity has been shown to influence pollination success in several plant species (Holmquist et al., 2012). For example, bees are highly effective at collecting pollen due to their hairy bodies, but they groom the pollen stored in their corbiculae or scopae, which reduces its availability for deposition on stigmas (Parker et al., 2015). Similar to our results, a meta-analysis found that wild insects, including dipterans and wasps, deposited similar amounts of pollen than honeybees (Page et al., 2021). Similarly, Pérez-Balam et al. (2012) found that the number of pollen grains deposited per visit was similar among non-native bees (*A. mellifera*), flies (*Chrysomya megacephala*), and native wasps (*Brachygastra mellifica*) in avocado flowers in southern México. The only two studies (aside from ours), that have evaluated the effectiveness of floral visitors to mango, also found that, per visit, honeybees deposited similar amounts of pollen as hoverflies and blowflies, although they deposited less than stingless bees (Singh et al., 2024; Willcox et al., 2019).

4.3. *Honeybees were the most effective pollinators, followed by flies, stingless bees and wasps*

In this study, honeybees were found to be the most effective pollinators of ‘Ataulfo’ mango in two years. This finding aligns with other studies that detected that the dominant pollinator taxa provide the majority of pollination services for many crops (Singh et al., 2024; Willcox et al., 2019). However, it is important to recognize that wild insects, such as flies (including blowflies and hoverflies), stingless bees, and wasps, also contribute significantly to mango pollination, albeit with lower effectiveness than honeybees. Other studies have also shown that dipterans, including blowflies and hoverflies (Saeed et al., 2016; Sánchez et al., 2022; Singh et al., 2024; Willcox et al., 2019), and stingless bees like *Tetragonula mellipes*, *T. caronaria* and *T. laeviceps* (Chuttong et al., 2022; Singh et al., 2024; Willcox et al., 2019), were among the most effective pollinators of mango.

Our study provides the first empirical evidence that yellow-banded wasps (*Polybia occidentalis*) and honey wasps (*Brachygastra azteca*) function as effective pollinators of mango. These species were recently identified as two of the ten most important legitimate floral visitors of the ‘Ataulfo’ mango (Severiano-Galeana et al., 2024), and in our study, we confirmed their role by quantifying pollen deposition on stigmas during single visits, showing comparable values to those of other frequent floral visitors. Although their less hairy bodies might suggest lower pollen transport capacity (Sagwe et al., 2022), their behavior and effectiveness in depositing pollen on stigma support their potential contribution to mango pollination. These social wasps also serve as predators of various insects considered pests in agricultural systems (Borchardt et al., 2024; Detoni and Prezoto, 2021). For instance, *P. occidentalis* is a generalist predator and is considered a potential biological control agent for various crops, including mango (Hernández et al., 2009). Moreover, this species has shown tolerance to habitat disturbances, and its nests have been found in crops, grasslands, gardens, and human-made buildings (Hernández et al., 2009). Indeed, Severiano-Galeana et al. (2024) found that these wasps were present in nearly all orchards, even those located more than 1.5 km from patches of native vegetation.

It is important to highlight the temporal variation of the relative contribution of each pollinator. For instance, in 2022, yellow-banded wasps and stingless bees ranked as the second and third most effective pollinators, respectively, while in 2023, blowflies and hoverflies occupied the same positions. Probably the wetter conditions in the region during 2023, caused by intense rainfall from hurricanes Max (category 1) and Otis (category 5; SMN, 2024), provoked a more stressful environment for bees, which have greater sensitivity to rain, strong winds, and temperature fluctuations compared to other groups like dipterans (Goodwin et al., 2021). Given this context, future studies should explore the relationship between climatic conditions and the contributions of different groups of pollinators on mango and other crops.

4.4. *Only wild insects enhanced the production of commercial fruits and reduced the incidence of nubbins*

Despite the high scores of honeybees as effective pollinators of mango, they did not positively influence the yield of commercial fruits; in fact, it affected it in one year. Indeed, a previous study conducted in the same area found that the frequency of honeybee visits was negatively associated with mango fruit production (Severiano-Galeana et al., 2024). Two non-mutually exclusive explanations could be associated with these results. First, grooming behavior and the transfer of pollen to specialized transport structures in honeybees may diminish the quality of pollination, since the saliva and regurgitated nectar used to moisten the pollen (Koch et al., 2017; Parker et al., 2015) can lead to its deterioration or reduction of adhesion to the stigmas (Parker et al., 2015). Second, honeybees frequently forage within the same tree or move among nearby trees in the same row and cultivar (Brittain et al., 2013; Quinet and Jacquemart, 2017), and exhibit high floral constancy, that is, a tendency to repeatedly visit flowers of the same species or cultivar within a foraging bout (Gaffney et al., 2018; Kobayashi et al., 2010). While this behavior can enhance pollen transfer in self-compatible crops, it limits cross-pollination opportunities in varietally self-incompatible cultivars, such as ‘Ataulfo’ (Kendall et al., 2020; Severiano-Galeana et al., 2024), by promoting geitonogamous pollen transfer. In contrast, pollinators with lower floral constancy, such as certain wild insects, may promote greater inter-cultivar pollen movement (Gaffney et al., 2018; Kobayashi et al., 2010). On the other hand, lower levels of floral constancy may increase pollen deposition from other plant species, decreasing their efficiency as effective pollinators, as has been reported in other crops (Sagwe et al., 2022) and wild plants (Huang et al., 2015). However, given the massive flowering of mango, it is unlikely that insects will visit different species at the same time, which is confirmed by the null heterospecific pollen deposition recorded on the analyzed stigmas.

The effectiveness of wild pollinators, on the other hand, positively influenced the commercial fruit yield in both years and was negatively related to the incidence of malformed fruit in one year. Unlike honeybees, some species of flies display erratic movement patterns, which further increases the likelihood of movement between multiple cultivars planted in different rows (Gaffney et al., 2018; Inouye et al., 2015; Kobayashi et al., 2010). These results align with previous studies indicating that wild pollinators significantly improve mango production (Marcacci et al., 2023; Singh et al., 2024), and other crops, regardless of honeybee abundance (Garibaldi et al., 2013). A recent study on ‘Ataulfo’ mango also found that commercial fruit production increased with the visits of wild pollinators (Severiano-Galeana et al., 2024). The higher probability of **TC** by wild pollinators in 2022, may explain the stronger positive association between the effectivity of wild pollinators with the yield of commercial fruits, but also with the reduction in the incidence of malformed fruits in that year, since pollen deposition from other cultivars influences the development of fruits in this varietal self-incompatible cultivar (Gehrke-Vélez et al., 2012; Lucas-García et al., 2025, 2021). Even though honeybees and wild insects may be beneficial for the pollination of several self-compatible crops, the latter can perform better in self-incompatible crops (Garibaldi et al., 2013; Sáez et al., 2022). However, the quality of the pollen delivered by each pollinator, including its viability and compatibility, still needs a more detailed evaluation in future research.

One limitation of our study is that panicles were marked during the flowering period and evaluated 80 days later, but the initial fruit set was not monitored. Therefore, it is possible that post-pollination factors such as fertilization, irrigation, or climatic conditions may have influenced fruit set and retention (Groeneveld et al., 2010; Hünicken et al., 2020). Although the effects of pollination are typically more evident during the first weeks after flowering (Barda et al., 2024), subsequent physiological and agronomic processes can also affect the final outcome (Groeneveld et al., 2010; Hünicken et al., 2020). For this reason, future studies on mango could benefit from tracking both early and final fruit production to better isolate the effects of pollination. Nevertheless, from a production-oriented perspective, the final number of commercial fruits remains the most relevant indicator for farmers (Bos et al., 2007), as it directly determines yield and the economic value of the harvest (Severiano-Galeana et al., 2024). Therefore, our results provide valuable insights into the role of wild pollinators in the yield of 'Ataulfo' mango.

5. Conclusions and future directions

Through a detailed study of pollination effectiveness in multiple orchards over two consecutive years, we demonstrated that a diverse group of floral visitors, primarily hymenopterans and dipterans, are effective pollinators of 'Ataulfo' mango in southern Mexico. Even though non-native honeybees were the most important pollinators, contributing approximately 80 % of the pollination to this crop mainly due to their greater abundance and visitation rates, the effectivity of wild pollinators was the only associated with the upsurge of commercial fruits and the lessening of nubbins.

Our results highlight the key role of wild pollinators in the yield of commercial fruits and the reduction of nubbins in 'Ataulfo' mango. Thus, to increase the yield of this cultivar, practices that promote the conservation of these pollinators should be implemented at the local and landscape scales. This can be pursued through: **(1)** conserving native forest patches, which serve as a source of mango pollinators (Severiano-Galeana et al., 2024); **(2)** increasing the recovery of natural areas near orchards through restoration practices (López-Cubillos et al., 2023); **(3)** creating semi-natural habitats such as living fences and wildflower strips (Carvalheiro et al., 2012) that attract wild flies or bees to maintain them throughout the year; **(4)** decreasing the use of herbicides, pesticides, and other agrochemicals, which affect the survival of pollinators (Basu et al., 2024; Marcacci et al., 2023); and **(5)** introducing decomposing organic resources such as carrion to attract several types of fly pollinators (Dawson et al., 2025). With these practices, the productivity of the 'Ataulfo' mango could be improved considerably while promoting the conservation of pollinators and the tropical dry forest, which is one of the most endangered ecosystems worldwide (Stan et al., 2024).

CRediT authorship contribution statement

Rodrigo Lucas-García: Writing – review & editing, Writing – original draft, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Eduardo Cuevas:** Writing – review & editing, Supervision. **Rosas-Guerrero Victor:** Writing – review & editing, Writing – original draft, Supervision, Resources, Project administration, Methodology, Funding acquisition, Data curation, Conceptualization. **R. Carlos Almazán-Núñez:** Writing – review & editing, Supervision. **Carina Gutiérrez-Flores:** Writing – review & editing, Supervision. **Juan Violante-González:** Writing – review & editing, Supervision. **José Antonio Gama-Salgado:** Writing – review & editing, Investigation.

Funding

This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

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.

Acknowledgements

The authors thank M. López-Atanacio, L. Carmona-Barajas, S. I. Radilla-Mata, S. López-Gama, N. Abarca-Mato, J. E. Rendon-Caro, M. Rodríguez-Núñez, C. Cipriano-Pantoja, E. Viveros-Villa, A. Hernández-López and M. López-Maldonado, for their help in fieldwork and data collection, and E. Ramírez-García for his support in the identification of insects. The authors would also like to thank all the mango orchards owners who allowed access to their fields, and to Mariana Paola Mazzei and an anonymous reviewer for their valuable comments and suggestions that helped to improve earlier versions of this manuscript. The first author would like to thank the Secretaría de Ciencia, Humanidades, Tecnología e Innovación (SECITHI) for the scholarship awarded for PhD studies (CVU: 930153).

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2025.109965.

Data availability

The data and codes that support the findings of this study are available from figshare at https://figshare.com/s/97bb688cf511b03beb69.

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