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Orchards closer to forest patches produced fewer malformed fruits and more commercial fruits: The importance of legitimate floral visitors

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ABSTRACT

Mexico is the main mango exporter worldwide, making 'Ataulfo' one of the most preferred cultivars. However, fruit production has been drastically diminished due to the high incidence of malformed fruits, known as nubbins. One of the possible causes of this is the lack of pollinators, which are necessary to set developed fruits. Since many pollinators depend on forest patches, the proximity of mango orchards to these is expected to decrease the incidence of nubbins. However, no study has evaluated the effect of distance from forest patches on the production of malformed fruits in any mango cultivar. The present study evaluates the incidence of nubbins and the production of commercial fruits, as well as the richness, composition, and frequency of visits of legitimate floral visitors (i.e., those that contact both reproductive parts of the flowers) over two consecutive years on 'Ataulfo' mango orchards located at different distances from tropical dry forest patches. Our results indicate that mango orchards located closer to forest patches were visited more frequently and by more species of legitimate floral visitors, showed less incidence of nubbins, and had greater production of commercial fruits than those located further away from the forest patches. Moreover, we found that older mango trees and the absence of exotic honeybees are also key factors to increasing fruit production. Our results highlight the importance of the conservation of tropical dry forest patches to ensure the provision of pollination services and to maintain or increase the production of mango orchards.

1. Introduction

The mango (*Mangifera indica*) is one of the most important fruit trees in various tropical and subtropical agroecosystems across the world (Perea-Moreno et al., 2018; Zahid et al., 2022). Mexico ranks first in mango exports globally, with 20% of the total world trade (Menzel and Le Lagadec, 2017; FAO, 2021). Among all the cultivars produced in Mexico, the 'Ataulfo' cultivar generates the most profits in the national and international markets due to its organoleptic characteristics and its longer shelf life (Ornelas-Paz et al., 2008).

In recent years, however, the profitability of this cultivar has been decreasing, mainly due to the high incidence of nubbins (malformed fruits commonly known in Mexico as "mango niño") which are of smaller size and weight (Fig. A1A) compared to commercial fruits (Pérez-Barraza et al., 2007). These fruits have little or null commercial value, causing a reduction in the economic income of mango producers (García De Niz et al., 2014; Leyva-Mayo et al., 2016) by 50% to around 90% (Pérez-Barraza et al., 2015; Salazar-García et al., 2016).

The occurrence of nubbins has been attributed to various causes, including: (1) low temperatures in the flowering season (Salazar-García et al., 2016), which decreases pollen viability and pollen tube growth (Dag et al., 2000; Pérez-Barraza et al., 2007; Huang et al., 2010); (2) limited levels of boron, an essential element for the growth of the pollen tube (Lovatt and Dugger, 1984); (3) age of trees, mainly trees older than ten years (Pérez-Barraza et al., 2007); and (4) deposition of incompatible pollen grains on stigmas from the same cultivar (Gehrke-Vélez et al., 2012; Lucas-García et al., 2021). This last cause suggests that a decrease in the quantity and/or quality of pollinators may trigger an increase in

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the incidence of nubbins. However, the role of pollinator richness and visitation in the occurrence of nubbins is unknown.

It has been found that 'Ataulfo' trees located in close proximity (around 10 m) to other cultivars with compatible pollen, showed a lower incidence of nubbins (Lucas-García et al., 2021) and that the presence of animal vectors increases fruit set (80%) and fruit weight (8%; Marcacci et al., 2023). Given that forest patches serve as refuges or habitat for many pollinating insects (Kammerer et al., 2016; Franceschinelli et al., 2017; Ulyshen et al., 2023), it is expected that a short distance between the forest patches and the mango orchards will decrease the production of nubbins and increase the production of commercial fruits through the rise of pollinator activity. Indeed, it has been found that orchards located near forest patches has caused an increase in the richness and/or the visitation rate of floral visitors to various crops, including watermelon (Kremen et al., 2002; Power et al., 2022), macadamia, longan (Blanche et al., 2006), cucumber (Motzke et al., 2016), soybean (Huais et al., 2020), coffee (Ricketts, 2004; Klein, 2009; González-Chaves et al., 2020; Sitotaw et al., 2022), chili, tomato, eggplant (Power et al., 2022), grapefruit (Chacoff and Aizen, 2006), mustard (Devkota et al., 2020), and yellow passion fruit (Silva et al., 2019). Moreover, the yields of several crops (e.g., coffee, Klein et al., 2003; 'Kent' mango, Carvalheiro et al., 2010; rambutan and durian, Sritongchuay et al., 2016; soybean, Zelaya et al., 2018), have increased more in orchards located close to the forest patches than in those located further away.

Even though some studies have explored the impact of proximity to the forest on mango fruit production (Sritongchuay et al., 2016; Sitotaw et al., 2022), no study has evaluated the effect of the distance from forest patches on the production of malformed fruits in any mango cultivar and whether this is influenced by a decrease in the frequency of floral visits. It has been reported that the most frequent floral visitors are usually ineffective pollinators (Fenster et al., 2004) or even act as nectar or pollen robbers (i.e., visitors that consume floral rewards but do not pollinate them), and that non-legitimate floral visitors (i.e., visitors that do not contact both reproductive parts of flowers) may alter the behavior and quality of pollinators (Brittain et al., 2013). Therefore, it is very important to differentiate legitimate from non-legitimate floral visitors to avoid misidentification of the main pollen vectors of any plant.

This study aims to evaluate the influence of the proximity of tropical dry forest (TDF) patches on the incidence of nubbins and the production of commercial fruits in 'Ataulfo' mango orchards and their relationship with the composition, richness, and frequency of legitimate and non-legitimate floral visitors over two consecutive years. We hypothesize that TDF patches serve as sources of pollinators for mango orchards and predict that a greater distance of those orchards from TDF patches will cause change in the species composition and decrease the species richness and visits of legitimate floral visitors, causing a rise in the incidence of nubbins and a reduction in the production of commercial fruits. Moreover, given that the exotic honeybee (*Apis mellifera*) is considered to be less dependent on forest patches than wild insects due to its generalized habits and its ability to colonize diverse types of habitats (Gambino et al., 1990; Schneider et al., 2004; Villanueva and Roubik, 2004), and usually pollinate crops less effectively than such insects (Garibaldi et al., 2013), it is expected that the visits of honeybees will be less affected by the remoteness of TDF patches than other floral visitors, and that the number of visits by honeybees will be unrelated to fruit production. Finally, because the age of the trees influences the incidence of nubbins (Pérez-Barraza et al., 2007) and hermaphrodite flower production (Premalatha et al. 2023), it is expected that older trees will experience a higher incidence of nubbins, fewer visits to flowers, and fewer production of commercial fruits.

The results of this study will provide key information to evaluate the role of TDF as a source of pollinators for this important crop. In fact, TDF is considered to harbor a great diversity of native pollinators (Cortés-Flores et al. 2023), but it is also considered one of the most endangered ecosystems worldwide, with about 60% of its total extent vanished (Sánchez-Azofeifa et al., 2013), while around 97% of the remaining forest is at risk (Miles et al., 2006).

2. Materials and methods

2.1. Study area and selection of orchards

The study area included the municipalities of Atoyac de Álvarez (17°12' 28'' N, 100°26' 36'' W), Benito Juárez (17° 11' 00'' N, 100° 30' 00'' W), and Tecpan de Galeana (17° 14' 19'' N, 100° 38' 13'' W), on Costa Grande, Guerrero, southern Mexico, one of the most productive mango regions at the national level (SIAP, 2022). This region has a warm subhumid climate (Aw), with an average annual temperature of 28.5 °C, annual precipitation of 800–2 000 mm, and a mean altitude of 57 masl. The main vegetation type is TDF, distributed in patches in combination with extensive agricultural lands (INEGI, 2015).

Twenty-four 'Ataulfo' mango orchards of 1–3 ha, with similar characteristics (i.e., trees aged 8–20-years-old trees, irrigation through drip, flooding, or sprinklers, the same use of pesticides, without managed beehives, and tree density of 100–120 trees/ha), were selected throughout this region (Fig. A2). A check was carried out to ascertain that all the trees presented in each orchard were 'Ataulfo' and that there were no trees of another cultivar within 50 m around orchards. Different orchards were selected each year to include greater spatial variation: 13 during the flowering period of December 2018−January 2019 (hereafter 2019), and 11 during December 2019−January 2020 (hereafter 2020).

Each selected orchard was georeferenced with a GPS (Garmin ETrex 10) and imported into Google Earth (Google Inc., version 7.3) to measure the distance to the nearest TDF patch detected by satellite images. The proximity of the orchards to the TDF patches varied considerably, from 50 to 2 000 m (Table A1). Each patch was visited in the field to corroborate its presence and extent. For logistical reasons, only TDF patches of at least 1 ha were considered, even though there is an ongoing debate about whether several small patches hold more species than a few large patches (Valente et al., 2023, and references therein). Since TDF is the main vegetation type in this region, only patches of this ecosystem were considered.

2.2. Studied crop species

The mango cv. 'Ataulfo' was originated in the Soconusco region of Chiapas, Mexico (Infante et al., 2011). Natural and induced flowering of this cultivar in the study area occurs in the periods of November–January and August–October, respectively (Escalera-Mota et al., 2022). It is an andromonoecious species (Dag and Gazit, 2000) with panicle-shaped inflorescences (McGregor, 1976).

Their floral traits of this species (e.g., small yellow/white, dished-shaped flowers that open in the morning; Fig. A1B) match with the myophily (i.e., fly-pollination) and melittophily (i.e., bee-pollination) floral syndromes (according to the suite of traits in Table S1 in Rosas-Guerrero et al., 2014). Previous studies have shown that the species' main floral visitors are beetles, ants, flies, bees, and butterflies (Anderson et al., 1982; Jiron and Hedstrom, 1985; Dag and Gazit, 2000; De Siqueira et al., 2008; Carvalheiro et al., 2010; Huda et al., 2015; Deuri et al., 2018; Simba et al., 2018; Marcacci et al., 2023), and that insect pollination is required for higher yields (Dag and Gazit, 2000; De Siqueira et al., 2008; Carvalheiro et al., 2010; Ramírez and Davenport, 2016; Deuri et al., 2018; Simba et al., 2018; Marcacci et al., 2023).

Because 'Ataulfo' is varietally self-incompatible (Gehrke-Vélez et al., 2012), it depends on the proximity of compatible cultivars (Lucas-García et al., 2021). Previous studies indicates that the cultivars 'Joe Welch', 'Criollo' (Gehrke-Vélez et al., 2012), 'Haden' (Lucas-García et al., 2021), and 'Manila' (Rendón-Caro and Rosas-Guerrero, unpublished data) were compatible with 'Ataulfo'.

2.3. Floral visitors

In both years, the composition, richness, and frequency of visits of all floral visitors were estimated using camcorders (Sony DCR-SR45, FDR-AX33 and HDR-CX455). In each orchard, two to four hermaphrodite flowers from one panicle on each of six trees chosen at random were filmed for three 15-minute periods at 11:30, 14:30, and 17:30 h. These periods were selected according to the peak foraging times of the main legitimate floral visitors recorded in preliminary observations (see Fig. A3). Video recordings were conducted only on sunny days, and each orchard was filmed once (from December 5–31 of 2018 and from November 11 to December 27 in 2019). Cameras were placed close enough to the flowers to allow us to differentiate whether floral visitors acted legitimately (i.e., touched both reproductive parts of the flower) or as pollen/nectar thieves (i.e., without contact with the reproductive parts of the flower). The relative importance of each floral visitor species was estimated as the total number of visits per their frequency of contact with stamens and stigma and standardized to percentages. The frequency of visits was calculated as the number of visits per inflorescence per 45 minutes, whereas species richness was estimated as the number of distinct species or morphospecies found in each orchard.

Floral visitors were captured with entomological nets and placed in a lethal chamber with potassium cyanide for later identification using a stereoscopic microscope and dichotomous keys (i.e., Hull, 1925; Curran, 1930; Thompson, 1981; Morón and Terrón, 1988; Johnson and Triplehorn, 2020) and with the help of a specialist (see acknowledgments). The same mode of data capture was used (i.e., 20 min in 30 ×7 m transects, 30 min after each filming period) in all the orchards. The captured floral visitors were used for identification purposes, whereas data from the camera recordings were used to estimate the number of visits, species richness, floral visitor composition, and floral visitor importance.

2.4. Mango production

To estimate the production of commercial fruits and the incidence of nubbins in both years, 20 inflorescences per tree were tagged, which were at the same height from the ground and of similar size and stage of vegetative development. The same six trees selected for visitation data were used for the estimation of fruit production. Sixty days later, the total number of commercial fruits (number of commercial fruits harvested on the 20 panicles chosen per tree) and nubbins incidence (number of nubbins/total fruits on the 20 panicles chosen per tree) were recorded. Commercial fruits and nubbins were easily differentiated by their size and shape (see Fig. A1A). Only data from 12 of the 13 orchards in 2019 were considered in the analyses of fruit production because farmers harvested the fruits before data collection.

2.5. Statistical analysis

To visualize the relationships between floral visitor community composition and distance from forest patches in each orchard, an ordination analysis was performed separately per year. The total number of visits for each year (log10 transformed) and the frequency of occurrence per species (standardized as percentage) were averaged, and species up to the averages were included in the analyses. PCAs were calculated using the distance to forest patches and the total number of visits (previously transformed using the Hellinger transformation; Borcard et al., 2011), and then all the variables were normalized. The Hellinger transformation was performed using the 'vegan' package and the *decostand* function.

The frequency of all legitimate and non-legitimate visits (hereafter both types of visits) of honeybees, legitimate visits of honeybees, all visits of other floral visitors (hereafter native floral visitors), and legitimate visits of native floral visitors were analyzed separately. The age of mango trees and their interaction with the distance to the forest patches were included to account for possible variation between trees of different ages. All these analyses were made to evaluate which floral visitors were good predictors of the production of commercial fruits or nubbins incidence.

Generalized linear models (GLMs), in the case of the richness of all visitors (Poisson error distribution and *log link* function), or generalized linear mixed models (GLMMs, with the *glmer* function from the 'lme4' package; Bates et al., 2015), in the case of the frequency of visits, were used to test whether these were affected by the distance to forest patches. In these models, distance to forest patches, tree age, and their interaction were used as explanatory variables, whereas visitation frequency (Poisson error distribution and *log link* function) by all floral visitors, by honeybees, and by native floral visitors (e.g., flies, wasps, ants, and beetles) were used separately as response variables.

GLMMs were also performed to test whether nubbins incidence and production of commercial fruits were affected by the distance of forest patches, including distance to forest patches, tree age, species richness, frequency of honeybee visits, frequency of visits of native floral visitors, and the interaction between age of trees and distance to forest patches as explanatory variables, whereas nubbins incidence (binomial error distribution and *logit link* function) and production of commercial fruits (Poisson error distribution and *logarithmic link* function) were considered as response variables. Given that the frequency of visits of all floral visitors showed a high correlation with the frequency of visits of native floral visitors in both years (2019: $r = 0.91$ and 2020: $r = 0.96$), it was excluded from the models.

A multimodel inference approach (Burnham and Anderson, 2002) was applied for each response variable, and a global model that included all explanatory variables and two-way interactions was fitted. The *dredge* function of the 'MuMln' package (Bartonń, 2023) was used to select the best models derived from each global model with the values of the second-order Akaike Information Criterion (AICc). All models with a delta AICc < 2, taking as reference the best-fitting model (lowest AICc), were considered equally plausible. In this case, the subset of best models was averaged using the *model.avg* function to obtain a final model.

All predictor variables were standardized (mean $= 0$, SD $= 1$) before modeling to allow comparison of effect sizes. Each model was validated graphically by using the 'DHARMa' package (Hartig, 2022). To avoid multicollinearity, the correlation between all explanatory variables was previously explored, and only explanatory variables that were not strongly correlated ($r < 0.7$) were included in the models. To test for collinearity in the best models, variance inflation factors (VIF) with the 'car' package (Fox and Weisberg, 2018) were used. No collinearity between the explanatory variables included in the best models (VIF<2 for each response variable) was found. Residuals from the best fitted models were used to check for spatial autocorrelation using Moran's test with the *testSpatialAutocorrelation* function in the 'DHARMa' package (Hartig, 2022). None of the best models showed spatial autocorrelation ($P > 0.05$ in all cases; Table A2). Furthermore, the marginal R-squared values were estimated with the *rsquaredGLMM* function of the 'MuMin' package (Barton, 2023) for each model to represent the variance explained by the fixed effects (Nakagawa and Schielzeth, 2013).

With the exception of the PCA analyses that were done in the PRIMER-E v6 program (Clarke and Gorley, 2006), all statistical analyses were performed with R version 4.3.1 (R Core Team, 2023). In all GLMMs, tree IDs nested within the orchard were included as a random effect. All analyses were performed separately for each year to consider possible temporal variation.

3. Results

3.1. Composition of floral visitors

Throughout two consecutive years and through 316.5 h of observation of 422 (216 in 2019 and 206 in 2020) hermaphrodite 'Ataulfo' flowers, 712 visits were recorded by arthropods belonging to the orders of Diptera (families Calliphoridae, Muscidae, Sarcophagidae, Syrphidae, and Tabanidae), Hymenoptera (families Apidae, Eumenidae, Formicidae, and Vespidae), Hemiptera, Coleoptera, and Araneae (Table A3). Specifically, in 2019, 451 visits from 29 species were observed, of which only 15 were considered legitimate; meanwhile, in 2020, 261 visits from 21 species were recorded, of which only 10 were considered legitimate (Table A3). Relative importance values indicate that around 60% of the floral visits that contacted both reproductive parts of mango flowers in both years belonged to the honeybee, *Apis mellifera*, and the yellow-banded wasp, *Polybia occidentalis* (Table 1).

Hymenopterans were the most important legitimate floral visitors in both years, and their dominance in the first year was outstanding (92%) compared to the second year (57%), when dipterans became more apparent (40%; Table 1). Notably, some of the most important legitimate floral visitors were present in one year but were rare or absent in the other (e.g., *Frieseomelitta nigra*, calliphorid spp. 1, sarcophagid spp. 2), suggesting great interannual variation in the composition of floral visitors of ‘Ataulfo’ mango (Table 1, Fig. 1). Nevertheless, this variation could also be explained by inherent differences among orchards because floral visitor observations were made for different orchards each year.

Among the most important legitimate floral visitors recorded in both years in mango orchards, both *Apis mellifera* and *Polybia occidentalis* were found in almost all of the selected orchards (Figs. 1A, 1B). Calliphorid sp. 2 and *B. azteca* were absent from the orchards furthest from the forest, whereas *Musca domestica* showed the opposite trend. The sarcophagid sp. 1 showed great temporal and spatial variation since, in the first year, it was exclusively found in the orchards closest to TDF patches. In the second year, the distance to the TDF patches seems to have been irrelevant (Fig. 1B).

PCA results showed a model with the first two components explaining 50% and 64% of the variation for 2019 (Fig. A4A) and 2020 (Fig. A4B), respectively. The PCA biplot in 2019 showed much weight for the visits of *A. mellifera* and *B. azteca* for PC 1, and *P. occidentalis* and *Musa domestica* for PC 2. In 2020, the visits of *M. domestica* for PC 1 and sarcophagid sp. 2 and calliphorid sp. 2, as well as the distance to TDF patches for PC 2, showed the greatest weight (Fig. A4A, A4B; Table A4). Moreover, the PCA biplot revealed that the distance to TDF patches and visits of *A. mellifera* and *M. domestica* were positively correlated in 2019, but not in 2020, whereas the distance to TDF patches and the visits of sarcophagid sp. 2 were negatively correlated in 2020. In both years, the distance to TDF patches was not correlated with the visits of *B. azteca*. Regarding *P. occidentalis*, the distance to forest patches was negatively correlated with their visits in 2019 but not in 2020.

3.2. Richness and frequency of visits

The species richness of the floral visitors of ‘Ataulfo’ mango was significantly associated with the distance from forest patches, being lower for those located further than those located nearer forest patches, though only for the year 2019 ($Z = -2.76$, $P = 0.005$; Fig. A5, Table A5). Similarly, the frequency of visits of all legitimate floral visitors in 2019 (Fig. 2A), and in 2020 (Fig. 2B), legitimate visits of honeybees in 2020 (Fig. 2C), and legitimate visits of native floral visitors in 2019 (Fig. 2D), and in 2020 (Fig. 2E), diminished when the distance of orchards to forest patches increased ($|Z| > 2.03$, $P < 0.043$ for all comparisons; Table 2). Considering both types of visits, the same trend was observed for all floral visitors, honeybee visits, and native floral visitors in 2019 ($|Z| > 2.03$, $P < 0.042$, for all comparisons), but not in 2020 (Table A6). A significant interaction between forest distance and tree age only occurred in 2020 in the frequency of all legitimate floral visitors (Fig. 2B, Table 2). Finally, in 2019, the frequency of both types of visits from honeybees was positively correlated with tree age (Fig. A6, Table A6).

Table 1
Relative importance (%) of the main legitimate floral visitors found in mango ‘Ataulfo’ orchards in Costa Grande, Guerrero, Mexico, during two flowering seasons.

Species[1]	Family	2019[2]	2020[2]	Average
*Apis mellifera**	Apidae	41.2	29.6	35.4
*Polybia occidentalis**	Eumenidae	23.8	33.3	28.6
Calliphorid sp. 2	Calliphoridae	1.8	14.4	8.1
*Frieseomelitta nigra**	Apidae	14.8	0.0	7.4
Sarcophagid sp. 1	Sarcophagidae	2.3	7.7	5.0
*Brachigastra azteca**	Vespidae	6.2	1.1	3.6
Sarcophagid sp. 2	Sarcophagidae	0.0	5.9	3.0
Musca sp. 1	Musidae	1.3	4.3	2.8
*Polistes carnifex**	Vespidae	3.7	0.0	1.9
Musca domestica	Musidae	0.4	1.1	0.7

[1] The most important species or morphospecies were listed; those with an asterisk belong to the order Hymenoptera, and the rest to the order Diptera. [2] Since only the ten most important legitimate floral visitors were included, the sum of importance values does not necessarily equal 100%.

3.3. Incidence of nubbins and production of commercial fruits

The distance from forest patches was negatively associated with the production of commercial fruits per inflorescence in both years (2019: $Z = -7.87$, $P < 0.001$, Fig. 3A; 2020: $Z = -7.36$, $P < 0.001$, Fig. 3B; Table 3). Conversely, the incidence of nubbins was positively associated with the distance to forest patches in 2020 ($Z = 2.80$, $P = 0.005$; Fig. 3D, Table 3), but not significantly in 2019 ($Z = 0.91$, $P = 0.361$; Fig. 5 C, Table 3). That is, orchards located further from forest patches produced fewer commercial fruits and showed, at least in one year, a greater incidence of nubbins.

The age of the trees was also associated with the production of commercial fruits, yet contrary to expectations, the relationship was significantly positive in both years (2019: $Z = 8.27$, $P < 0.001$, Fig. A7A; 2020: $Z = 3.86$, $P < 0.001$, Fig. A7B; Table 3). Likewise, contrary to expectations, the age of the trees was not associated with the incidence of nubbins, at least in 2019 ($Z = 0.75$, $P = 0.454$; Table 3). In addition, an interaction between the age of trees and the distance to forest patches was found concerning the production of commercial fruits ($Z = 3.65$, $P < 0.001$; Fig. 3A) and nubbins incidence in 2019 ($Z = 2.06$, $P = 0.039$; Fig. 3C).

As expected, the production of commercial fruits per inflorescence was positively associated with the species richness of all floral visitors in 2019 ($Z = 4.82$, $P < 0.001$; Fig. 4A; Table 3), but surprisingly negatively associated in 2020 ($Z = 2.16$, $P < 0.031$; Fig. 4B; Table 3). Nonetheless, no association was found between species richness and the incidence of nubbins in any year (Table 3). Notably, the frequency of legitimate visits by honeybees was negatively associated with the production of commercial fruits in 2019 (Fig. 4C; Table 3). Unlike in 2019, in 2020 there was a positive association between the frequency of visits by legitimate native floral visitors and the production of commercial fruits (Fig. 4D; Table 3). Finally, in both years, there was no association between the frequency of visits by any legitimate floral visitor and the incidence of nubbins (Table 3).

4. Discussion

The results of this study support the hypothesis that forest patches function as a source of legitimate floral visitors to the ‘Ataulfo’ mango and that the proximity of orchards to these patches increases the production of fruits for commercial purposes while decreasing the incidence of malformed fruits. However, temporal variation was also detected in these associations, and the age of trees seems to play a main role in fruit production, as well as the species richness of floral visitors and the absence of honeybees.

In the study area, we found a diverse community of insects, mainly hymenopterans of the families Apidae and Vespidae and dipterans of the families Syrphidae, Calliphoridae, Sarcophagidae, and Muscidae, that visited ‘Ataulfo’ mango flowers in a legitimate way. This agrees with the

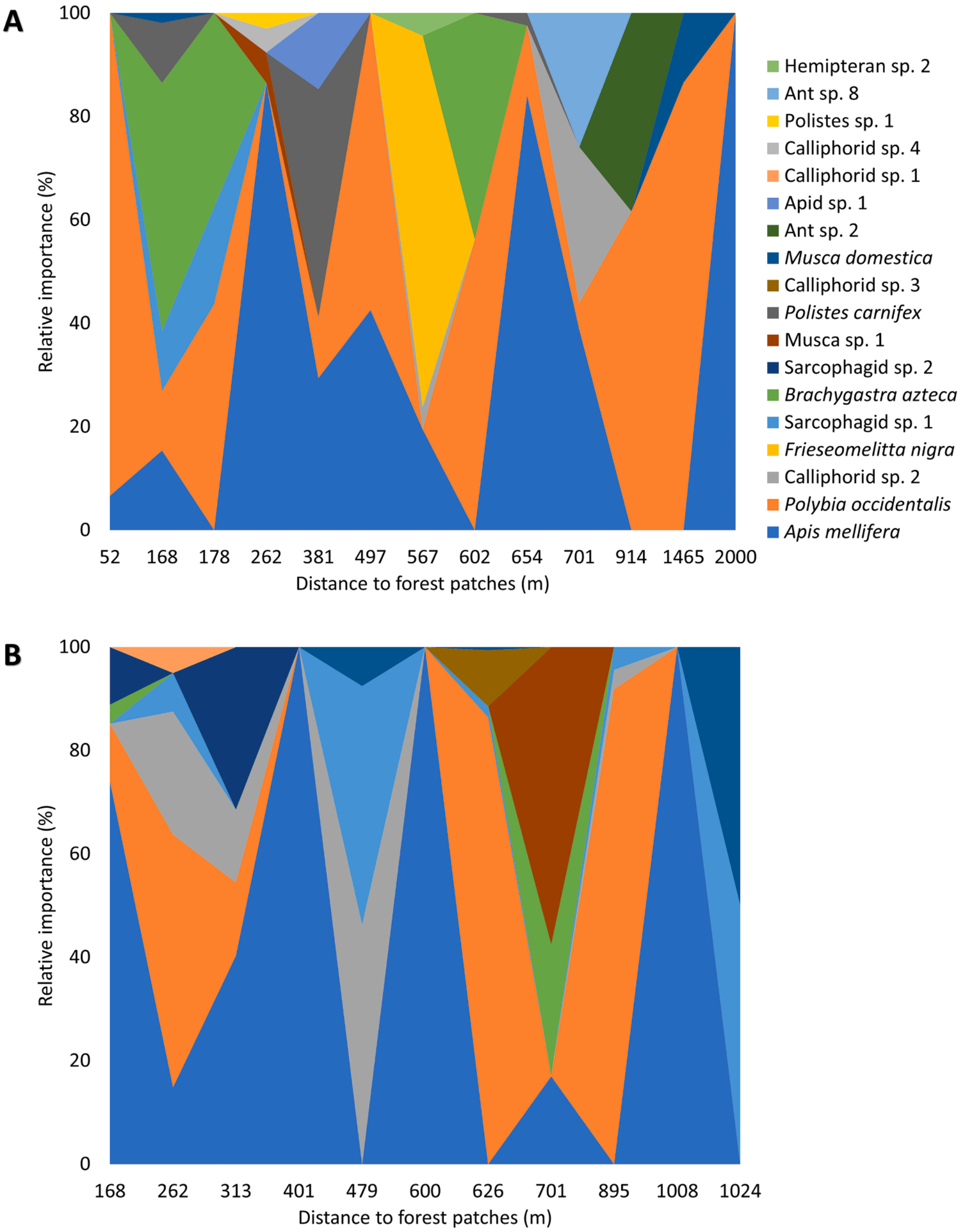

Fig. 1. Relative importance of legitimate floral visitors (estimated as the total number of visits per their frequency of contact with stamens and stigma and standardized to percentages) in mango orchards located at different distances from forest patches during the flowering season of December 2018 (**A**) and during November–December 2019 (**B**).

idea of pollination syndromes (see Rosas-Guerrero et al., 2014), since its floral traits suggest pollination mediated by flies and/or bees. Other studies have found that also insects from the orders Diptera and Hymenoptera were the most important floral visitors of other cultivars of mango, including 'Linn' in India (Kumar et al., 2012), 'Tommy Atkins' in Brazil (De Siqueira et al., 2008; Sousa et al., 2010), 'Keitt' in Israel (Dag and Gazit, 2000), 'Chok Anan' and 'Sala' in Malaysia (Huda et al., 2015), 'Osteen' in Spain (Sánchez et al., 2022), and 'Kent' in South Africa (Carvalheiro et al., 2010).

This study is the first record of the wasps *Polybia occidentalis*, *Polistes carniflex*, and *Brachigastra azteca*, as well as the stingless bee *Frieseomelitta nigra*, as floral visitors of mango flowers. Moreover, our study is one of the few (i.e., Dag and Gazit, 2000; De Siqueira et al., 2008) that differentiates illegitimate from legitimate floral visitors in situ. This differentiation is crucial for identifying the importance of each floral visitor as pollen vectors, devising plans for their conservation, and ensuring the maintenance of the mango industry. It is important to note that all floral visitors that were considered legitimate could not necessarily act as effective pollinators since they would need to deposit compatible pollen on stigmas. Thus, the number of effective pollinators of 'Ataulfo' could be lower than the number of legitimate visitors reported here. Moreover, it is unknown whether crepuscular or nocturnal floral visitors could act as pollinators for this crop. Therefore, more studies are needed considering the effectiveness of diurnal and nocturnal floral visitors.

We found a high spatial variation in the composition of the legitimate floral visitors of 'Ataulfo' mango orchards located at different distances from forest patches. For instance, *A. mellifera*, an exotic honeybee, was found in almost all orchards in both years, whereas native insects such as *B. azteca*, *F. nigra,* and sarcophagid and calliphorid flies were absent from many of them. The ubiquitous presence of *A. mellifera* may be related to its generalized habits and longer flight ranges compared to other legitimate visitors. This bee species can invade and colonize various types of habitats, and feed on native and exotic plant

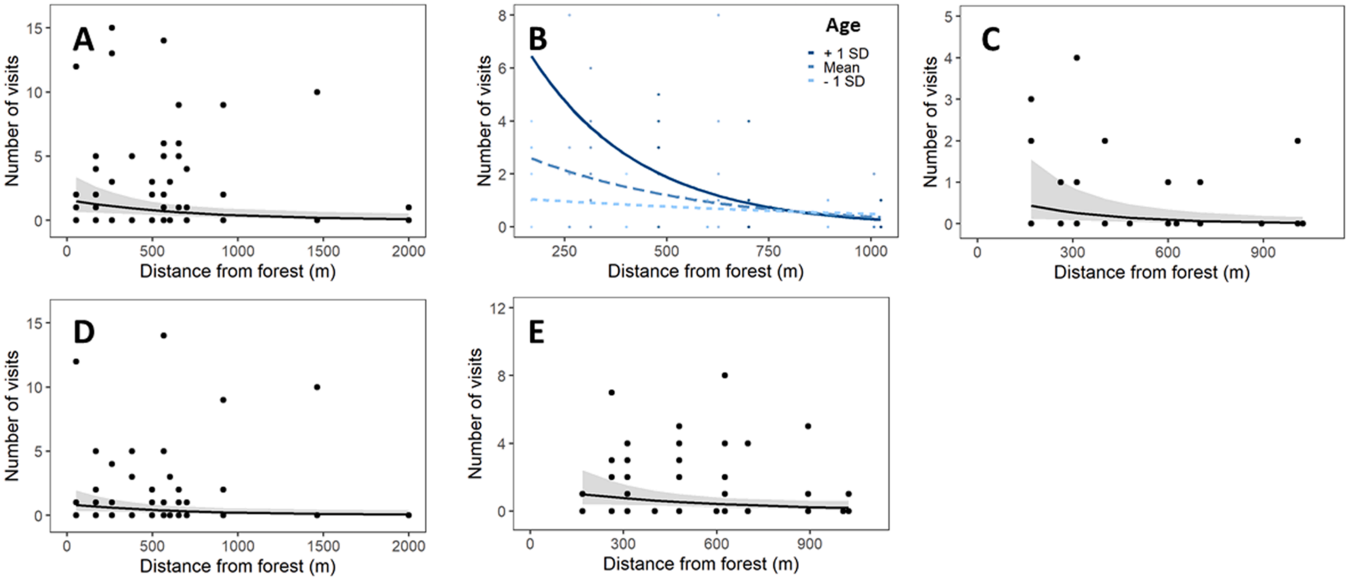

Fig. 2. Relationship between the distance of mango orchards from forest patches with the frequency of visits of all legitimate floral visitors in 2019 (**A**) and 2020 interacting with tree age (**B**), with the frequency of visits of legitimate visits of honeybees in 2020 (**C**), legitimate visits of native floral visitors in 2019 (**D**), and 2020 (**E**). The interaction plot show predictions for the mean, +1 SD, and −1 SD of trees' ages. Results are based on the correlations of the best GLMM. Black points show raw data, and gray bands represent the 95% confidence intervals.

Table 2
Effects of forest distance and age of tree on legitimate visits of all floral visitors (**A**), legitimate visits of honeybees (**B**), and legitimate visits of native floral visitors (**C**) of 'Ataulfo' mango orchards in 2019 (13 orchards) and 2020 (11 orchards) after a GLMM. Marginal R-square values (R^2m) are given for each model to represent the variance explained by the fixed effects. The *P*-values in bold are significant at the 0.05 level.

Response variable	**2019**				**2020**			
	Estimate	**Std. error**	***Z***	***P***	**Estimate**	**Std. error**	***Z***	***P***
(A) Visits of all legitimate floral visitors $R^2m = 0.152$ $R^2m = 0.244$								
Intercept	-0.506	0.330	-1.532	0.125	**-0.108**	**0.233**	**0.455**	0.649
Forest distance	-0.766	0.307	-2.497	**0.012**	-0.611	**0.207**	**2.889**	**0.003**
Age of tree	- -	- -	- -	- -	0.304	0.206	1.448	0.147
Forest distance x Age	- -	- -	- -	- -	-0.398	0.198	1.965	**0.049**
(B) Legitimate visits of honeybees $R^2m = 0.163$ $R^2m = 0.206$								
Intercept	-3.178	1.065	2.941	**0.003**	-2.286	0.638	-3.584	**< 0.001**
Forest distance	-0.833	0.580	1.601	0.157	-0.985	0.377	-2.613	**0.008**
Age of tree	0.833	0.499	1.414	0.109	- -	- -	- -	- -
Forest distance x Age	-0.516	0.563	0.899	0.368	- -	- -	- -	- -
(C) Legitimate visits of native floral visitors $R^2m = 0.146$ $R^2m = 0.104$								
Intercept	-1.109	0.376	2.895	**0.003**	-0.831	0.324	-2.563	**0.010**
Forest distance	-0.730	0.355	2.020	**0.043**	-0.560	0.275	-2.031	**0.042**
Age of tree	-0.068	0.187	0.361	0.718	0.409	0.266	1.537	0.124
Forest distance x Age	- -	- -	- -	- -	- -	- -	- -	- -

species (Schneider et al., 2004; Villanueva and Roubik, 2004), forage at distances greater than 9 km (Beekman and Ratnieks, 2000), and nest in several species of trees, dead trunks, ground, cliff faces, and artificial structures such as buildings and wells (Gambino et al., 1990). In addition, several farmers introduce the beehives of this species into their orchards, which favors an increase in their presence regionally, even when only those orchards without beehives were chosen in this study. By contrast, the stingless bee, *F. nigra*, nests almost exclusively in living trees (Cab-Baqueiro et al., 2022). Unfortunately, there is a lack of information about the flight range or habitat specialization of most of the other floral visitors to mango that could help us understand the causes of their spatial variation in mango orchards.

We also found considerable variation in the composition of the legitimate floral visitors of 'Ataulfo' mango flowers through time. For instance, the calliphorid sp. 1, 3, and 4, the sarcophagid sp. 2, the stingless bee *F. nigra*, and the wasp *P. carnifex* were absent from one of the two years considered. The unpredictability of some of the most important pollinators of the 'Ataulfo' mango may jeopardize the stability of their pollination service. Thus, it is important to explore the possible causes of this variability to lessen the instability of fruit production.

Similar to studies on other crops (e.g., Sritongchuay et al., 2019; Devkota et al., 2020; González-Chaves et al., 2020; Sõber et al., 2020; Viswanathan et al., 2020), our results showed that at least in one year, the richness of floral visitors was higher in orchards near forest patches than those farther away. This increase in the species richness of floral visitors could explain the greater fruit production in orchards near forest patches since it has been found that an increase in pollinator diversity increases the pollination effectiveness of dominant pollinators because other species alter their foraging activity (Brittain et al., 2013).

In both years, orchards near forest patches presented a higher frequency of visits by native legitimate floral visitors, similar to what has been found on coffee (Ricketts, 2004; Sitotaw et al., 2022), grapefruit (Chacoff and Aizen, 2006), apple (Joshi et al., 2016), and macadamia (Blanche et al., 2006). Probably as a consequence of this, we found that 'Ataulfo' mango orchards near forest patches produced more

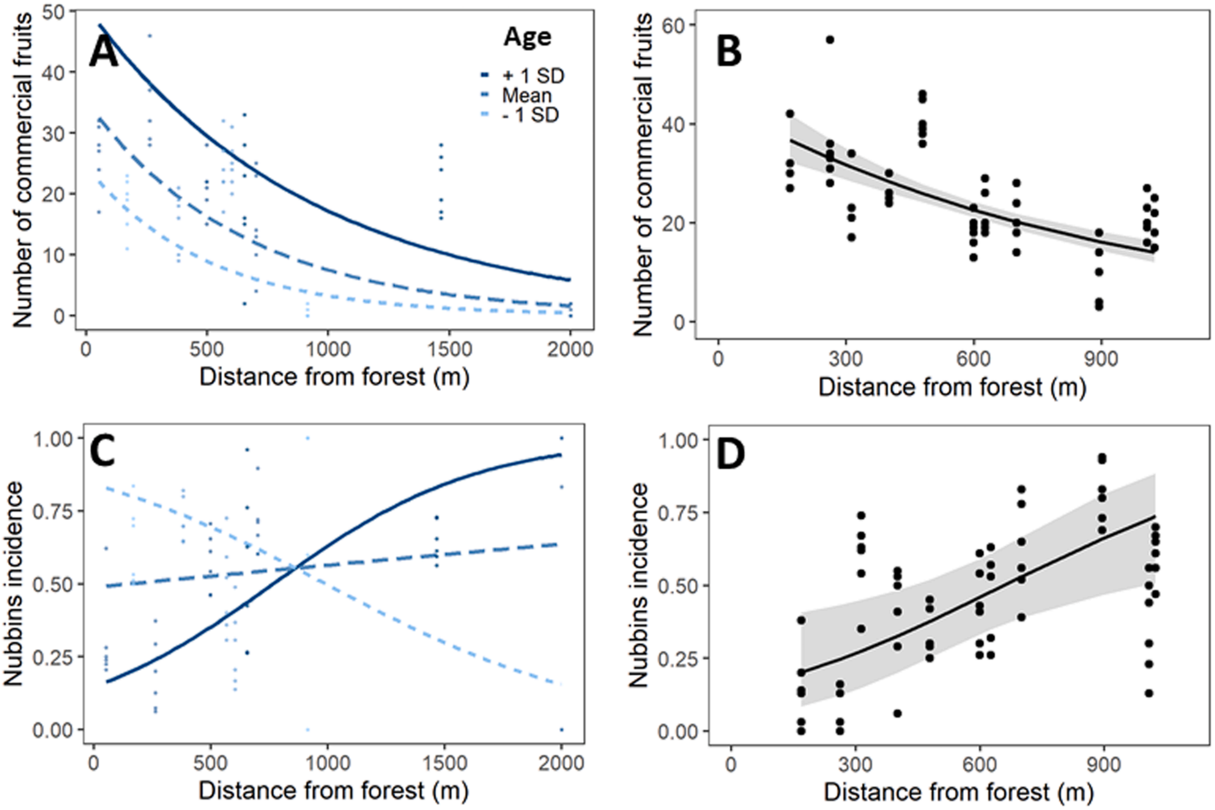

Fig. 3. Relationship between the distance of mango orchards from forest patches and the production of commercial fruits in 2019 and their interaction with the age of trees (**A**), the production of commercial fruits in 2020 (**B**), the incidence of nubbins in 2019 and their interaction with the age of trees (**C**), and the incidence of nubbins in 2020 (**D**). The interaction plot show predictions for the mean, +1 SD, and −1 SD of trees' ages. Results are based on the correlations of the best GLMM. Black points show raw data, and gray bands represent the 95% confidence intervals.

Table 3
Effects of forest distance, age of tree, species richness, legitimate visits of honeybees, and legitimate visits of native floral visitors on commercial fruit production (**A**) and nubbins incidence (**B**) of 'Ataulfo' mango orchards in 2019 (12 orchards) and 2020 (11 orchards) after a GLMM. Marginal R-square values (R^2m) are given for each model to represent the variance explained by the fixed effects. The *P*-values in bold are significant at the 0.05 level.

Response variable	**2019**				**2020**			
	Estimate	**Std. error**	***Z***	***P***	**Estimate**	**Std. error**	***Z***	***P***
(A) Commercial fruits		$R^2m = 0.817$				$R^2m = 0.817$		
Intercept	2.488	0.077	32.203	**< 0.001**	3.131	0.035	86.634	**< 0.001**
Forest distance	-0.842	0.107	-0.873	**< 0.001**	-0.316	0.042	7.364	**< 0.001**
Age of tree	0.669	0.080	8.268	**< 0.001**	0.161	0.041	3.859	**< 0.001**
Species richness	0.385	0.079	4.816	**< 0.001**	-0.089	0.040	2.156	**0.031**
Honeybees	-0.139	0.058	-2.370	**0.017**	-0.028	0.035	0.765	0.444
Native floral visitors	-0.029	0.057	-0.518	0.604	0.076	0.035	2.095	**0.036**
Forest distance x Age	-0.273	0.075	3.646	**< 0.001**	- -	- -	- -	- -
(B) Nubbins incidence		$R^2m = 0.281$				$R^2m = 0.222$		
Intercept	0.232	0.288	0.793	0.427	-0.199	0.269	0.727	0.467
Forest distance	0.377	0.407	0.913	0.361	0.814	0.285	2.801	**0.005**
Age of tree	-0.249	0.327	0.748	0.454	- -	- -	- -	- -
Species richness	-0.518	0.342	1.485	0.137	0.471	0.306	1.508	0.131
Honeybees	- -	- -	- -	- -	- -	- -	- -	- -
Native floral visitors	-0.190	0.277	0.674	0.500	-0.195	0.293	0.655	0.512
Forest distance x Age	0.950	0.453	2.059	**0.039**	- -	- -	- -	- -

commercial fruits than orchards located away from forest patches in both years. Indeed, there was a positive relationship between the frequency of visits by legitimate native floral visitors and the production of commercial fruits in 2020. The same trend of more production in orchards near forest patches has been reported in canola (Halinski et al., 2020), soja (González et al., 2020; Huais et al., 2020), rambutan (Sritongchuay et al., 2016), macadamia, and logan (Blanche et al., 2006).

Conversely, the frequency of honeybee visits in one year (precisely in the year when they were most frequent) was negatively associated with the production of commercial fruits. These results suggest that native pollinators, which depend on the proximity of forest patches, are crucial for the production of commercial mango fruits and that honeybees probably deposit less compatible pollen on stigmas and/or affect the behavior of native pollinators. Even when the honeybees were among the most frequent and ubiquitous of all the legitimate floral visitors, *F. nigra* and *P. carnifex* contacted the reproductive parts of the flower more frequently than the honeybees (86% and 83% vs. 66%, respectively; Table A3). Clearly, not only the quantity but also the quality of

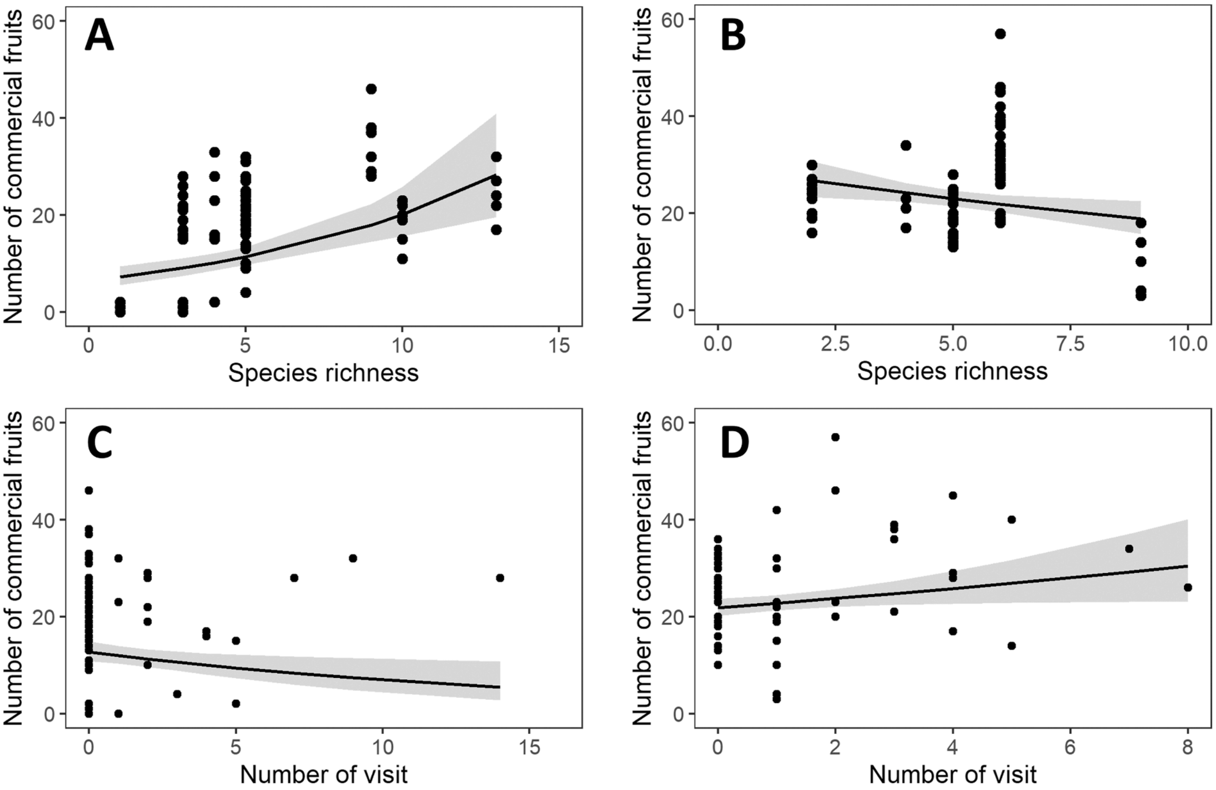

Fig. 4. Relationship between the production of commercial fruits and the species richness of floral visitors in 2019 (**A**), and 2020 (**B**), the frequency of visits by honeybees in 2019 (**C**), and the legitimate visits of native floral visitors in 2020 (**D**). Results are based on the correlations of the best GLMM. Black points show raw data, and gray bands represent the 95% confidence intervals.

legitimate visitors is important for understanding the production of pollinator-dependent crops.

Our results also showed that, contrary to our prediction, the age of mango trees was positively correlated with the production of commercial fruits in both years and was not related to the incidence of nubbins. Pérez-Barraza et al. (2007) revealed that in one of four localities, older trees (>10 y) showed a higher incidence of nubbins than younger trees (<10 y); however, they did not perform any statistical tests. The older trees probably produce more fruits because they are bigger and taller than younger trees. Bigger or taller plants increase the probability of being found by pollinators (Schlinkert et al., 2015) and have higher visitation by them (Hernández-Villa et al., 2020). Moreover, it is likely that older and bigger trees have more leaves than younger and smaller trees, which can increase the production of the photosynthates necessary for the proper development of fruits. Indeed, Sarron et al. (2023) found that older mango trees, which had wider canopies, were positively associated with mango yield.

The incidence of malformed fruits or nubbins in the year 2020 was higher in orchards farther away from forest patches. Nonetheless, no relationship was found between the frequency of legitimate visits by any floral visitor and the incidence of nubbins in any year. This could be due to at least two non-mutually exclusive factors: (1) nubbins produced by trees could be aborted before data collection, causing an underestimation of nubbins' incidence; and (2) the frequency of legitimate visits may not be a good predictor of good fruit development since not all floral visitors that touch anthers and stigma may deposit compatible pollen that fertilize the ovule and develop in fruit. Therefore, as mentioned above, it is essential to determine which floral visitors act as effective pollinators of mangos.

These findings highlight the importance of the quantity and quality of pollinators in setting fruits of commercial value. A recent study performed at the same study site (Lucas-García et al., 2021), revealed that the incidence of nubbins in 'Ataulfo' decreases with the proximity of a compatible cultivar (i.e., 'Haden'). Thus, to decrease the incidence of nubbins in orchards and to increase the yield and economic input of mango producers, a combination of proximity to forest patches and compatible cultivars is essential.

The differences found in the production of commercial fruits among orchards could help to estimate the economic losses per hectare of those orchards located far away from forest patches. By estimating the average fruit weight of 56 commercial fruits from three orchards in 2019 (239.8 ± 1 SD 51.66 g) and by estimating the average number of panicles in 48 trees [from six orchards (495 ± 338.85 panicles per tree); average tree age: 21.2 y], we calculate a rough estimate of the yield and economic income (USD $1.23 per kg) per hectare for each orchard. Comparing the average income per hectare in the three orchards closest (2019: $19,427; 2020: $22,429) and furthest (2019: $5,597; 2020: $12,167) to forest patches, an economic loss of $12,045 per orchard per hectare on average for both years could be estimated. If the restoration costs of a TDF were lower than the estimation of economic losses of all mango orchards located beyond 1 km from forest patches, priority should be given to restoration programs.

Particularly, TDFs in Mexico suffer one of the highest habitat losses, with around 300 000 ha converted annually to agricultural lands (Trejo and Dirzo, 2000). Therefore, it is crucial to reverse the loss of these forests through restoration programs and preserve the TDF remnants that still exist to favor the conservation of pollinators and our food security.

5. Conclusion

The results obtained in this study suggest that the presence of TDF patches favors the presence of animal species that act as important pollinators for a wide variety of crops (see Klein et al., 2007; Ollerton et al., 2011; Ulyshen et al., 2023). However, land use changes and habitat fragmentation of TDFs have threatened the existence of several pollinator species and, consequently, the maintenance of several crop industries and global food security (Kremen and Ricketts 2000; Potts et al., 2010; Aizen et al., 2019; Hall and Martins, 2020; Tscharntke, 2021; Ulvshen et al., 2023). Not only do we need to know which pollinator species depend on forests, but we also need to know which floral resources and nest sites they need (Ulyshen et al., 2023). We recommend that mango farmers invest in the conservation of forest remnants, the restoration of TDFs, the implementation of living fences with plant species that are attractive to native flies, bees and wasps, and avoiding including beehives in the orchards.

CRediT authorship contribution statement

Kuk-Dzul José Gabriel: Formal analysis, Supervision, Writing – review & editing. **Almazán-Núñez R. Carlos:** Supervision, Writing – review & editing. **Lucas-García Rodrigo:** Formal analysis, Methodology, Visualization, Writing – review & editing. **Alemán-Figueroa Lorena:** Conceptualization, Resources, Supervision, Writing – review & editing. **Rosas-Guerrero Victor:** Conceptualization, Funding acquisition, Methodology, Resources, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. **Severiano-Galeana Fernando:** Data curation, Investigation, Visualization, Writing – original draft, Writing – review & editing.

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.

Data Availability

The dataset presented in this study can be available in the following online repository: https://doi.org/10.6084/m9.figshare.24540940.v1 Dataset (Original data)

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2023.108872.

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