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Fruit production in coffee (*Coffea arabica* L.) crops is enhanced by the behaviour of wild bees (Hymenoptera: Apidae)

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Abstract

Changes in floral visitors' diversity and community composition have been reported to affect coffee production, which optimal growing conditions are cool to warm tropical climates found in the coffee belt. However, few studies have focused on understanding how insects' foraging behaviour (e.g., contact with floral reproductive organs) relates with coffee production. Thus, it is important to consider floral visitors' foraging behaviour, as this can influence the transfer of conspecific pollen required for plant fertilisation, the efficiency of floral visitors and improve the pollination service provided. Here, we assessed how foraging behaviour of honeybees and stingless bees affects coffee fruit set and fruit weight in conventional and agroecological managed crops. We quantified local floral resources and recorded diversity, abundance and behaviour of floral visitors at eight pairs of sites with agroecological and conventional management systems to assess how foraging behaviour of honeybees and stingless bees affects coffee fruit set and fruit weight in both types of managed crops. We found that the managed honeybee *Apis mellifera* and three wild bees *Tetragonisca angustula*, *Scaptotrigona mexicana* and *Partamona bilineata* are the principal floral visitors of coffee crops in Guatemala, whose total abundance but not richness was higher in agroecological areas. Regarding their behaviours, we observed that the average number of flowers visited by *P. bilineata* and its behaviour of touching the nectaries of coffee flowers were positively related to fruit set, while only the percentage of *A. mellifera* carrying pollen was positively related with fruit weight, suggesting that although *A. mellifera* is found in large quantities, wild bees are also efficient pollinators of coffee in the region. Our findings also suggest that in other tropical regions where coffee is grown and honeybees have been observed as a primary pollinator, wild bees may play an important role when considering their behaviour. In the same way, coffee farms in Guatemala are a representation of the diversity of agroecosystems found worldwide, and thus, the study of foraging behaviour of managed and wild bees and the conservation of wild bee species in different coffee agroecosystems should be emphasised to improve the production of coffee and other cash crops.

KEYWORDS

Apis mellifera, number of flowers, *Partamona bilineata*, pollen foraging, time spent on flowers, visit of anthers and nectaries

INTRODUCTION

Animal-mediated pollination is one of the essential ecosystem services that plays an important role in crop pollination, reproduction and outcrossing of wild and managed plant species and supports global diversity and human well-being (Klein et al. 2007; Mutavi-Katumo et al. 2022; Ollerton 2017). Honeybee, *Apis mellifera* Linnaeus, 1758, is considered an important crop pollinator worldwide (Hung et al. 2018; Osterman, Landaverde-González, et al. 2021). However, studies in different regions have reported how native pollinators' diversity and visitation rate have a greater contribution to the increase of pollination and yield of different crops than that of *A. mellifera* (Garibaldi et al. 2013; Osterman, Aizen, et al. 2021; Rader et al. 2016).

Pollination effectiveness measures help to understand the importance of different species of floral visitors on fruit development and production. Yet their importance is also a consequence of temporal and spatial change in abundance, the change of landscape structures at different scales and their foraging activity and behaviour (Mateos-Fierro et al. 2022; Saturni et al. 2016). It is also generally assumed that high flower visitation rate by bees is a strong indicator of high pollination efficiency (Gagic et al. 2021). However, given that some bee species may be inefficient in pollen transfer and some plants have physiological characteristics that require specialist pollinators, neither the abundance of floral visitors nor the rate of visits is equivalent to more successful pollination (Gagic et al. 2021). Foraging behaviour (e.g., flower visitation rate, contact with the stigma and anther, and visiting time in the flower) differs between non-apis bees and honeybees that may be due to variability in interspecific foraging behaviour. Specifically, some studies have shown that the foraging behaviour of wild pollinators (e.g., visiting more flowers per minute and high probability of stigma contact) increases their efficiency as observed in Fabaceae plants in Cameroon (Mazi et al. 2022), sweet cherry (*Prunus avium* L.) in the United Kingdom (Mateos-Fierro et al. 2022) and kiwifruit (*Actinidia deliciosa* (A. Chev.) C.F. Liang & A.R. Ferguson) in Spain (Miñarro & Twizell 2015). Gagic et al. (2021) also found that honeybees caused pollen limitation in cauliflower (*Brassica oleracea* var. *botrytis* L.) due to their preferences for hermaphrodite flowers and their high nectar thievery. Similarly, Boff et al. (2018) reported that a high visitation rate of oil bees increased the pollination efficiency of *Couepia uiti* (Mart. & Zucc.) Benth. ex Hook.f. (Uiti de Porco) in Pantanal wetland, Brazil. Together, these studies emphasise that to optimise crop pollination, it is necessary to investigate the pollination contribution of different floral visitor species and their foraging behaviour.

Further, the abundance, richness and density of flower resources have been observed to be a positive driver of pollinator diversity and visitation behaviour (e.g., increase of visitation rate) in both tropical (Caudill et al. 2017; Escobedo-Kenefic et al. 2020, 2022; Fisher et al. 2017; Hipólito et al. 2018; Landaverde-González et al. 2017; Vergara & Badano 2009) and temperate regions (Theodorou et al. 2017, 2020). However, some studies, mainly in coffee crops, also suggest that other floral resources and co-flowering crops may have no effect at the field scale or may compete for pollinators with mass flowering crops as coffee (Bänsch et al. 2021; Geeraert et al. 2019; Peters et al. 2013; Ricketts et al. 2008; Veddeler et al. 2006). It is also suggested that managed diversified agroforestry coffee systems (in our study, agroecological management), in contrast with conventional managed crops, could improve climate resilience on coffee crops and community of floral visitors (Chain-Guadarrama et al. 2019), which become important in the light of the high percentage (∼34%–51%) of areas with coupled decrease of coffee sustainability and bee richness suggested for the region (Imbach et al. 2017). Therefore, the relationship of coffee plantations with the management of other flowering crops and floral resources around the plantations should be also assessed. Floral visitors are often affected by pesticides (Crenna et al. 2020) used in crop management, via contact, through nectar feeding or pollen feeding. Further, insecticides have negative effects on bee diversity and worker foraging performance (Gill et al. 2012), as well as having an impact on bees' learning and foraging behaviours as in *Bombus* species, honeybee and *Osmia bicornis* (Linnaeus, 1758) (Boff et al. 2020, 2021; Siviter et al. 2019). This suggests that agricultural management (i.e., less use of pesticides or more ecological approaches) is paramount and should be also considered when analysing the service of pollination to crops.

Coffee, in particular *Coffea arabica* L. (Gentianales, Rubiaceae) variety, is native to Eastern Africa; it is grown in diverse tropical regions such as Oceania, the West Indies, Asia, Africa, Central America and South America (Xu 2003); and it was introduced in Central America due to the neotropical climate and soil characteristics (Coffee Research 2022). Coffee is one of the most cultivated cash crops in Guatemala with a variety of agricultural practices, ranging from large monoculture sun plantations with conventional management (i.e., large amount of pesticides and no shade) to less intensive agriculture, with agroecological approaches in smaller coffee plots, which is a representation of coffee cultivation worldwide where 79% are farms with less than 50 ha (reviewed in Siles et al. 2022). Although coffee is a plant capable of autogamy and self-fertilisation, it has been reported that the quantity and quality of fruit weight and fruit set are improved when fertilisation is mediated by pollinators (Classen et al. 2014; De Marco & Coelho 2004; Garibaldi et al. 2013; Klein et al. 2007; Martínez-Salinas et al. 2022; Moreaux et al. 2022; Ricketts 2004; Saturni et al. 2016). Klein et al. (2003a) showed that coffee fruit set in Indonesia increased by 12.3% with the contribution of honeybees and wild bees. Roubik (2002) indicated that Panamanian coffee fruit set had an increase of 50% provided by honeybee. Similarly, studies in Colombia (Bravo-Monroy et al. 2015), Mexico (Vergara & Badano 2009) and

Costa Rica (Ricketts 2004) show that higher bee diversity is a major driver for increasing pollination services for coffee crops. The species that primarily visit coffee flowers are *A. mellifera* in Panama (Roubik 2002) and species of the families Halictidae and Megachilidae in Indonesia (Klein et al. 2003a) and Costa Rica (Ngo et al. 2011; Ricketts 2004). Nevertheless, information on foraging behaviour and pollination efficiency of coffee pollinators in the tropics is scarce, and until now, the specific behaviour of pollinators visiting coffee flowers has been little studied and how these behavioural variables benefit coffee pollination remains an open question. Thus, it is necessary to determine the importance of species visiting coffee and also how their behaviours drive coffee pollination. In addition, the diversity of agricultural practices and the increase in its production when it is visited by insects make coffee crops ideal for studying the joint effect of management, environment variables, diversity and behaviour of floral visitors on the production of coffee fruits.

In this study, we analyse the effect of floral visitor diversity and behaviour on coffee pollination. We worked in eight pairs of coffee plantations with two management systems (agroecological and conventional) with the goal of determining (a) whether the management system affects the community composition, richness, abundance of floral visitors and the foraging behaviour of *A. mellifera* and the most abundant wild bee species visiting coffee flowers and (b) how diversity and behaviour influence the service of pollination to coffee in both management systems. We hypothesise that agroecological plantations will support a higher diversity and abundance of floral visitors than conventional plantations; additionally, floral visitors' foraging behaviour, mainly from wild bees, related with longer time spent and contact with nectaries and anthers on the flowers will show a positive relationship with fruit weight and fruit set.

MATERIALS AND METHODS

Area of study

We conducted the study in the departments of Guatemala, Quetzaltenango, Sacatepéquez, Sololá, Santa Rosa, Jalapa, El Progreso and Suchitepéquez, at the foothills of the Sierra Madre Mountain in Guatemala, ranging from 765 to 1800 m. asl, where coffee crops are cultivated, as seen in Figure 1. *C. arabica* variety is the

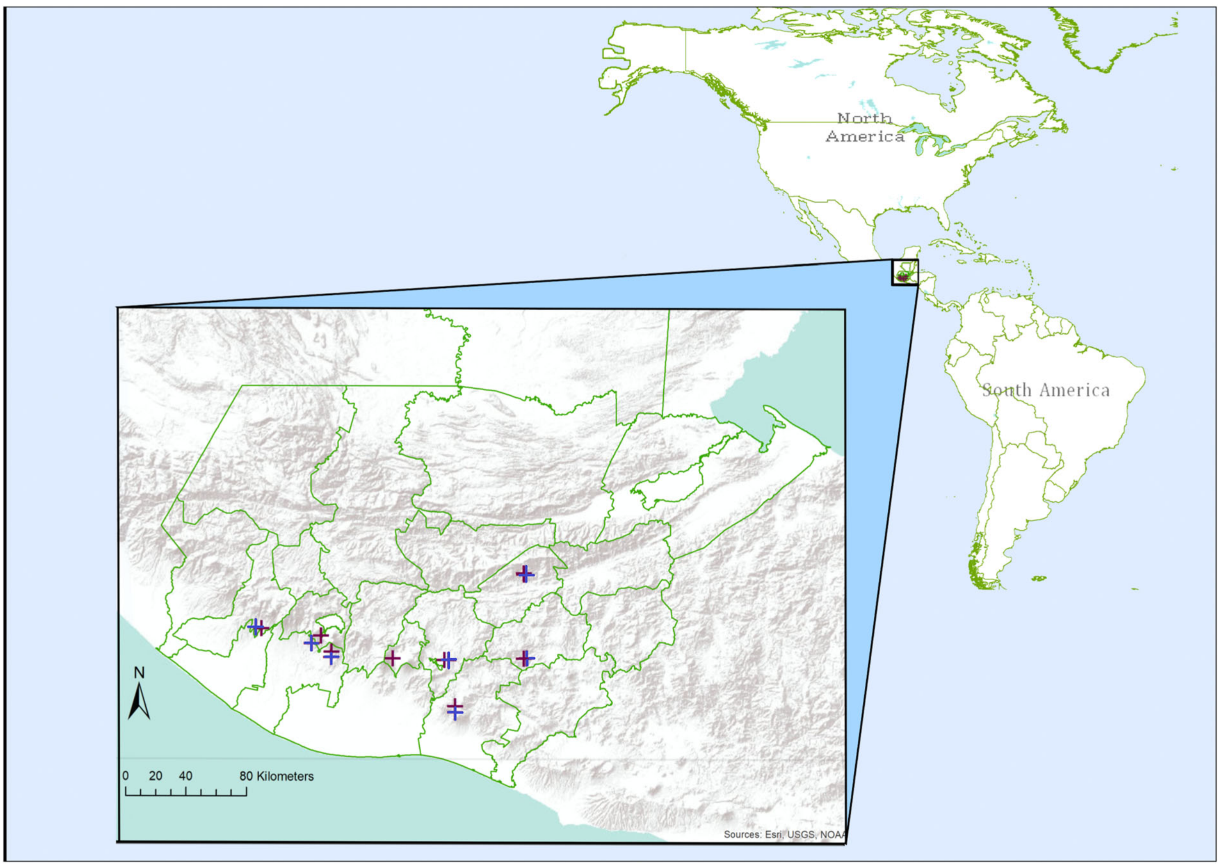

FIGURE 1 Location of all study sites. The map shows location of the study sites in the central and south-western regions of Guatemala, where pollination experiments and pollinator observations were performed. Blue crosses represent conventional sites, and lilac crosses represent agroecological sites.

principal coffee crop cultivated throughout the study site. Approximately 125 000 families drive the total country coffee production, of which 122 000 are smallholders (ANACAFÉ—Asociación Nacional del Café 2023; Fischer & Victor 2014). Guatemala has a diversity of ecosystems, which creates eight regions for *C. arabica* with a temperature that varies from a minimum of 15°C in Cobán to a maximum of 25°C in the east region, which includes El Progreso (Coffee Research 2022). In Guatemala, at least 98% of coffee cultivation is shade-grown mostly under the canopy of native tree species such as *Inga* spp. and the exotic tree *Grevillea robusta* A.Cunn. ex R.Br. Most of the selected coffee farms belong to the Association of Private Nature Reserves of Guatemala, in which crop cultivation and forest preservation are combined.

Experimental design

The experiments were conducted in eight pairs of sites, one per department mentioned above. Each pair of sites consisted of two coffee plantations with different management, one agroecological and one conventional (see description of management below), with a distance of at least 1 km. We randomly chose 30 coffee plants in each coffee plantation. In each coffee plant, we conducted an open and bagged (exclusion) pollination experiment and recorded the diversity of floral visitors and the foraging behaviour of species that visited the coffee flowers. We did both pollination experiments and recording of floral visitor's diversity on the same day, because the attractiveness of coffee flowers to pollinators only last 2 days (Camargo 1985), on sunny days without rain or strong wind. Behavioural observations were done for 5 min in each of the 30 coffee flowers from 8:00 AM to 2:00 PM, which varies for each coffee plantation depending on environmental conditions. In addition, fieldwork was carried out only once in each plantation during the flowering peak of coffee, in the following periods: in Quetzaltenango, Suchitepéquez, Sacatepéquez and Guatemala, from March to April 2018; in El Progreso, in April 2019; and in Jalapa, Santa Rosa and Sololá, from March to April 2021. In Sacatepéquez, we only sampled the conventional coffee site due to the eruption of the Fuego volcano in June 2018, which made the area inaccessible and destroyed all the crops. During the year 2020, the sampling could not be carried out because of restrictions imposed due to COVID-19 pandemic. Therefore, the data analysis included 15 coffee plantations, of which eight plantations corresponded to agroecological management and seven to conventional management (see Table S1 for location of each coffee plantation).

Management type in coffee plantations

To classify the type of management in the coffee plantations of our study in Guatemala, we defined the status of the following cultivation practices: (a) whether there was a regimen of low use of agrochemicals per harvest season (maximum one time a year); (b) that the richness of associated cultivated species is greater than at the paired site; (c) prioritisation of the use of organic compounds as fertilisers; (d) the existence of international certification of organic, ecological or sustainable or social production; (e) prohibition of the use of highly toxic pesticides; (f) presence of seminatural or natural vegetation surrounding the coffee plantation; and (g) density of high-level shade trees (Haggar et al. 2015; Moguel & Toledo 1999; see Table S2). We then compared the state of the seven practices described previously of a given plantation against its pair and scored them as follows. Whether if the practice was prevalent in the plantation, we scored each practice as one. In the opposite case, we scored each practice as zero. Based on this system, the coffee plantations with the highest score compared to their pairs were classified as agroecological management, whereas the coffee plantations with the lowest score compared to their pairs were classified as conventional management (Table S2).

Open and exclusion (bagged) pollination experiments

For each coffee plant, we selected and counted two clusters of flower buds, one for open pollination (14.89 mean of buds per cluster ± 6.08 SD) and the other for the exclusion 'bagged' (13.97 mean of buds per cluster ± 4.12 SD) experiments. Each cluster was marked with flagging tape so we could find it at the end of the experiment. Open pollination consisted in an experiment in which the buds were covered with bags, and the moment the flowers opened, the bags were removed and the visit of floral visitors was allowed. Exclusion (bagged) experiment consisted in an experiment in which flowers were let bagged during all the experiment as in Landaverde-González et al. (2017). To obtain the contribution provided by floral visitors, we subtracted the values from the exclusion experiment from open pollination values and consequently used the resulted value for the following analyses. Subsequently, we visited each plantation 4 months after, from July to August, and harvested the mature fruits. We then measured the weight of the fresh fruits and counted the total number of fruits produced per cluster. The fruit set was measured as the ratio between the total number of fruits produced and the initial number of floral buds counted per cluster, for a given plant. We calculated the average weight of the fruits and fruit set of the 30 plants for each coffee plantation. Lastly, because we performed the open pollination experiments and observations in different plant branches, our analysis is a general approximation of the pollination services provided by the overall flower floral visitors and must be taken with caution. We used a modification of the methodology created by Vergara and Badano (2009) and Landaverde-González et al. (2017).

Floral visitors and their foraging behaviour

With the goal to assess how behaviour and abundance of floral visitors affected fruit development, and whether these effects differed between management types, we selected a branch of flowers (57.65 mean ± 35.84 SD) located in a different side from the open pollination experiment and recorded which insect species visited the flowers and their foraging behaviour. For each coffee plantation, we measured the number of species of floral visitors (richness) and the frequency of visits of each floral visitor species to the same flower (abundance). The following behaviour variables for each floral visitor species were recorded: As the diverse species of floral visitors were observed in different periods of time (Figure S3) and temperature/time has been observed to change community composition of floral visitors in crops (Ludewig, Landaverde-González, et al. 2023), we used the time of the day they foraged on the flowers (Time) as a behavioural variable; pollen transported (PolTran) as the percentage of bees of each species that carried pollen on their legs/bodies before reaching the observed flowers (as these floral visitors were mainly observed within coffee plantations, we assumed that the pollen came from coffee flowers); pollen collected (PolCol) as the percentage of bees of each species that collected pollen from the observed coffee flowers; whether bees touched the anthers (Anther) as the percentage of individuals of a bee species that touched the anthers of the observed flowers; whether bees touched the nectary (Nectary) as the percentage of individuals of a bee species that touched the nectaries of the observed flowers; average number of flowers (NumFlow) as the average number of flowers visited by each floral visitor species in a specific branch observed during the 5-min observation time; and average time in seconds (TimeSec) spent by each individual of each species in the observed branch of flowers.

To describe floral visitors' diversity, we used total abundance and Chao-1 species richness (Chao-Richness) (Chao & Shen 2003). Additionally, we calculated the abundance of each of the four most abundant species visiting the coffee flowers (>10% from total visits): *A. mellifera* Linnaeus, 1758, *Tetragonisca angustula* (Latreille, 1811), *Scaptotrigona mexicana* (Guérin-Méneville, 1845) and *Partamona bilineata* (Say, 1837). We also used the mentioned behaviour variables from the most abundant species for the following analysis.

We performed each observation for five continuous minutes per plant in an area of 225 cm^2. In that way, we record visits of insects only on the selected cluster of flowers and we track the foraging behaviour of species in a reduced set of individuals at the same time. Floral visitors that could not be easily identified in the fields were sampled using a net and transferred into vials for further identification in the laboratory.

Statistical analysis

Community composition, diversity of floral visitors and the foraging behaviour

Community composition between conventional and agroecological management was evaluated by a paired permutational multivariate analysis of variance using the *adonis* function, with 999 permutations implemented in the R package *vegan* (Oksanen et al. 2018). The Euclidean distance matrix of species composition was the response variable, with management (conventional/agroecological) as the independent variable. The strata (block) argument was set to *site* so that randomisations were constrained to occur within each sample site, type of management and not across all sample sites. To determine whether management affected richness and abundance of floral visitors and the abundance of the most frequent species, we used paired *F* test.

Relationship between management type and the foraging behaviour of floral visitor's species

To evaluate whether the management type influences the foraging behaviour of the most frequent species, we executed generalised linear mixed models (GLMMs) with *Gaussian* distribution error using '*lme*' package Version 1.1-31 (Bates et al. 2015). We set site ($n = 8$) as a random factor and designated the management type (agroecological/conventional) as a fixed factor. Response variables were defined as foraging behaviour of the most frequent species *A. mellifera*, *T. angustula* and *P. bilineata*. We evaluated whether foraging behaviour variables per species were correlated using Spearman correlation test with Bonferroni correction in the PAST software (Hammer et al. 2001). We found that in *A. mellifera*, only the behaviour of collecting pollen was correlated with the transport of pollen ($p < 0.01$; Table S3). The abundance of *T. angustula* was correlated with the number of flowers visited ($p = 0.01$), and the number of flowers visited by *T. angustula* was correlated with the time in seconds spent on the flowers ($p < 0.01$). The number of flowers visited by *P. bilineata* was correlated with the visit to the nectary and the time spent on the flowers (all under $p < 0.03$). The behaviours of visit to the anther and visit to the nectary in *P. bilineata* were also correlated ($p = 0.01$; see more details in Table S3). Thus, we ran the models for these correlated variables independently. Model assumptions (non-overdispersion, linearity and homogeneity of variances) were verified visually using the '*DHARMa*' package Version 0.4.6 (Hartig 2022). We did not include the sampling year and elevation as a fixed factor effect in the model analysis, as the variation per year is included in the variation for each site. Management type remained a fixed factor in all the models. All models were run in R Version 2.3-1 (R Development Core Team 2022).

Relationship between diversity and foraging behaviour of floral visitor's species and coffee fruit weight and fruit set

To explore the relationship between the diversity and the foraging behaviour of floral visitor's species with coffee fruit weight and fruit set after removing the value from the exclusion experiments and considering management type, we performed linear mixed models with *Gaussian* distribution error and maximum likelihood adjustment, using the '*nlme*' package Version 3.1-160 (Pinheiro et al. 2022). We set the site ($n = 8$) as a random effect factor and designated the diversity and behavioural variables of the most frequent species and management type as fixed effect factors. The fruit weight and fruit set were set as response variables. As fruit weight did not follow a normal distribution (Shapiro–Wilk test $p < 0.05$), we normalised the variable using the ($1 + \mathrm{Log}_{10}$) transformation. In order to avoid multicollinearity in our models for *P. bilineata* behaviour variables, we run individual analysis, but for the rest, we run combined models' analysis for each species. Finally, model assumptions (normality, linearity and homogeneity of variances) were verified visually. All models were run in R Version 2.3-1 (R Development Core Team 2022).

RESULTS

Diversity of the floral visitors

We observed a total of 1170 individuals and identified 43 species. Overall, 1151 individuals were bees (98.50%), 12 individuals were flies (1.00%), and 7 individuals were wasps, lepidoptera and ant (0.50%) (see Table S4 and Figure S1 for more details). The most frequent species recorded throughout the observations of floral visitors were the non-native honeybee *A. mellifera* (31.02%), followed by the stingless bees *T. angustula* (17.52%), *S. mexicana* (15.04%) and *P. bilineata* (11.02%). These four species represented 75% of the total observation's floral visitors (Table S4 and Figures S1 and S2). *A. mellifera* was the only species present in all coffee plantations (Table S4), probably due to the preference of farmers to provide them for pollination assurance (Osterman, Landaverde-González, et al. 2021).

Behaviour of the floral visitors

Apis mellifera was the most abundant bee species in all coffee plantations, and it was the only species to be observed and captured at 8:00 AM and the only bee to be present at all observation times (from 8:00 AM to 4:00 PM) and to be present in all 15 sites (Figure S3). We observed that the highest number of visits to coffee flowers occurred by wild bees before noon, specifically between 10:00 AM and 12:00 PM, after the flowers had opened and before temperatures peaked at all the sites.

We recorded 363 visits for *A. mellifera* across all the sites (24.2 ± 20.13 SD; Table S4); however, its abundance of visits was significantly different only from that of *P. bilineata* (Mann–Whitney $p = 0.04$; Table S5). Similarly, *A. mellifera* was the species that was observed to touch nectaries significantly more often (22.07 ± 20.14 SD; Mann–Whitney $p < 0.05$; Tables S5 and S6), with the higher percentage of bees carrying pollen on their legs/bodies before reaching the observed flowers (19.2 ± 21.38 SD; Mann–Whitney $p > 0.03$; Tables S5 and S6), that touched the anthers the most (23.47 ± 20.34 SD; Mann–Whitney $p < 0.05$; Table S5) and that was significantly different only from *S. mexicana* (Mann–Whitney $p = 0.01$; Table S6).

T. angustula, compared to the other three species, was the bee with significantly longest average visiting time per cluster (14.18 ± 6.89 SD seconds per visit; Mann–Whitney $p < 0.04$; Table S5) and that most frequently collected pollen (12.33 ± 10.24 SD; Tables S5 and S6); however, it was not significantly different from the other bees (Mann–Whitney $p > 0.05$; Tables S5 and S6).

Relationship between management type, diversity and the foraging behaviour of floral visitor's species

We found that management type had no significant effect on species community composition (Adonis test $F = 1.29$, $p = 0.31$), Chao-1 corrected richness of floral visitors ($F = 2.53$, $p = 0.25$) and the abundance of *T. angustula* ($F = 4.98$, $p = 0.06$). Yet management type did have a significant relationship to floral visitors' abundance ($F = 8.86$, $p = 0.01$; Figure 2 and Table 1), *A. mellifera* abundance ($F = 6.65$, $p = 0.02$; Figure 2 and Table 1) and *P. bilineata* abundance ($F = 58.27$, $p < 0.01$; Figure 2 and Table 1). With respect to floral visitor behaviour, we found that management type was not significant for any behaviour variable of *A. mellifera* or the two stingless bees (GLMM $p > 0.05$ for all).

Relationship of diversity and foraging behaviour of floral visitor's species with coffee fruit weight and fruit set

We observed that Chao-1 corrected richness, total abundance of floral visitors and the abundance of the most frequent species *A. mellifera*, *T. angustula*, *S. mexicana* and *P. bilineata* did not have a significant relationship with the fruit weight (GLMM $p > 0.05$), and fruit set (GLMM $p > 0.05$). In addition, we found that only the percentage of *A. mellifera* that carried pollen on their bodies and legs had a positive relationship with fruit weight (GLMM: $t = 3.18$, $p = 0.02$; see Figure 3a and Table 2). For fruit

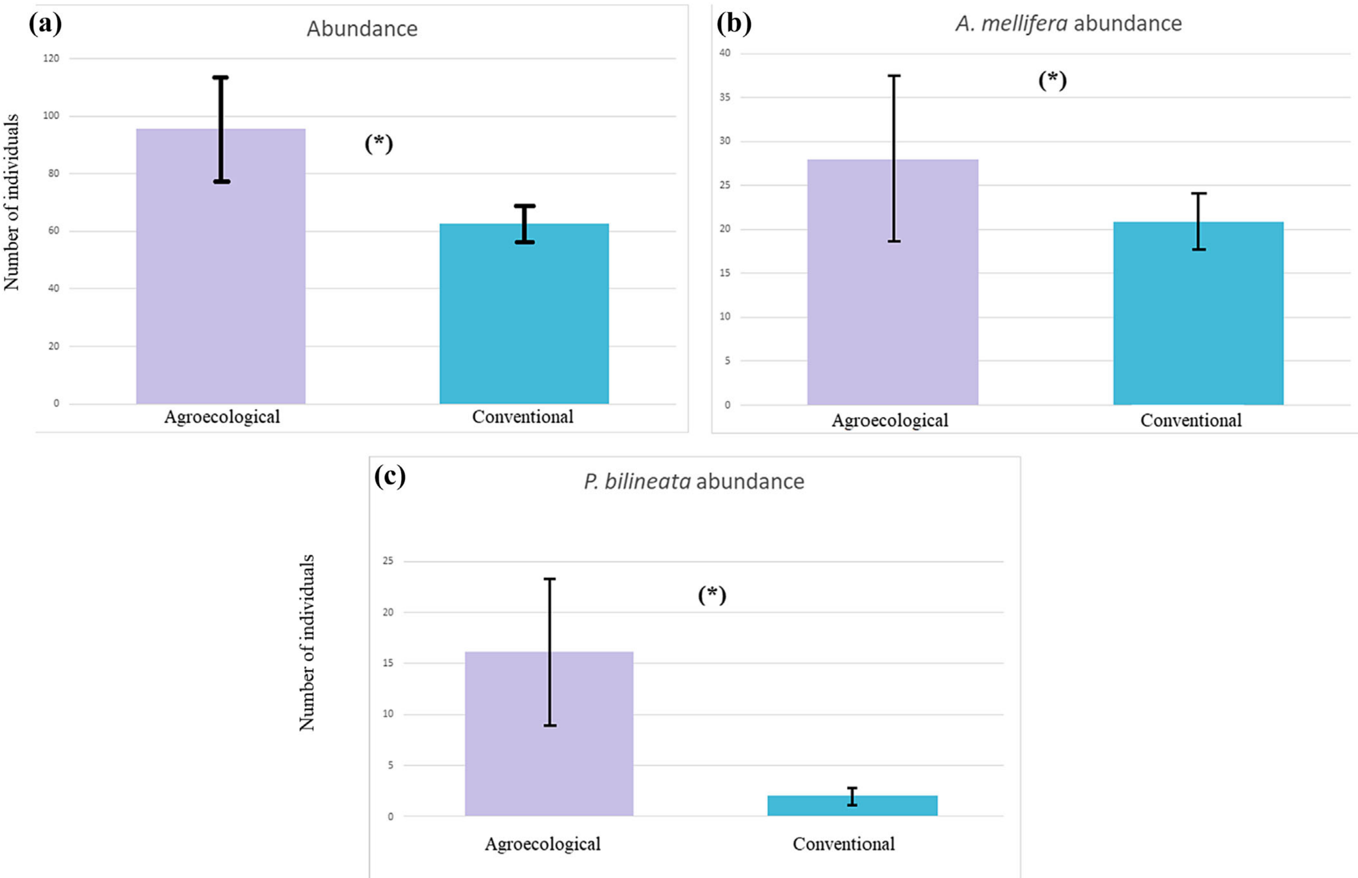

FIGURE 2 Distribution under conventional (blue) and agroecological (lilac) management of (a) abundance of floral visitors, (b) abundance of *A. mellifera* and (c) abundance of *P. bilineata*. The differences between variables considering management were analysed with paired -F-test. *$p < 0.05$.

TABLE 1 Relationship of management type (conventional and agroecological) on the diversity of floral visitors (abundance and Chao-1) and the most abundant floral visitors. Values in bold are those that were found to be statistically significant.

Response variable	*F* value	df	*p* value
Abundance	**8.86**	**7**	**0.01***
Chao-1	2.53	7	0.25
Apis mellifera	**6.65**	**7**	**0.02***
Partamona bilineata	**58.27**	**7**	**<0.01****
Tetragonisca angustula	4.98	7	0.06
Scaptotrigona mexicana	1.92	7	0.41

*$p < 0.05$.
**$p < 0.01$.

set, we found that the percentage of *P. bilineata* observed touching the nectary of the coffee flowers had a positive relationship with the fruit set (GLMM: $t = 3.35$, $p = 0.02$; see Figure 3b and Table 2). Lastly, the average number of flowers visited by *P. bilineata* individuals (NumFlow) also was found significantly related with the fruit set (GLMM: $t = 2.47$, $p = 0.04$; Figure 3c and Table 2). Management type did not influence the fruit weight (GLMM $p > 0.05$) and fruit set (GLMM $p > 0.05$).

DISCUSSION

Regarding our first question, we observed that management has an effect on abundance of floral visitors and abundance of *A. mellifera* and *P. bilineata*. Conversely, we found that management did not have a significant effect on the behaviour of floral visitors. Assessing our second goal, we observed that the percentage of *A. mellifera* individuals carrying pollen on body and legs had a positive relationship with fruit weight. Additionally, fruit set was positively related to the average number of flowers that were visited by each individual of *P. bilineata* and the behaviour of touching the nectary of the same bee. We discuss in detail our results in the following paragraphs.

Community composition and diversity of floral visitors on coffee

We found that the most frequent floral visitors to coffee were *A. mellifera* and three stingless bees *T. angustula*, *S. mexicana* and *P. bilineata*. Previous studies have pointed out that stingless bees might be playing a potential role as coffee pollinators in our region, as

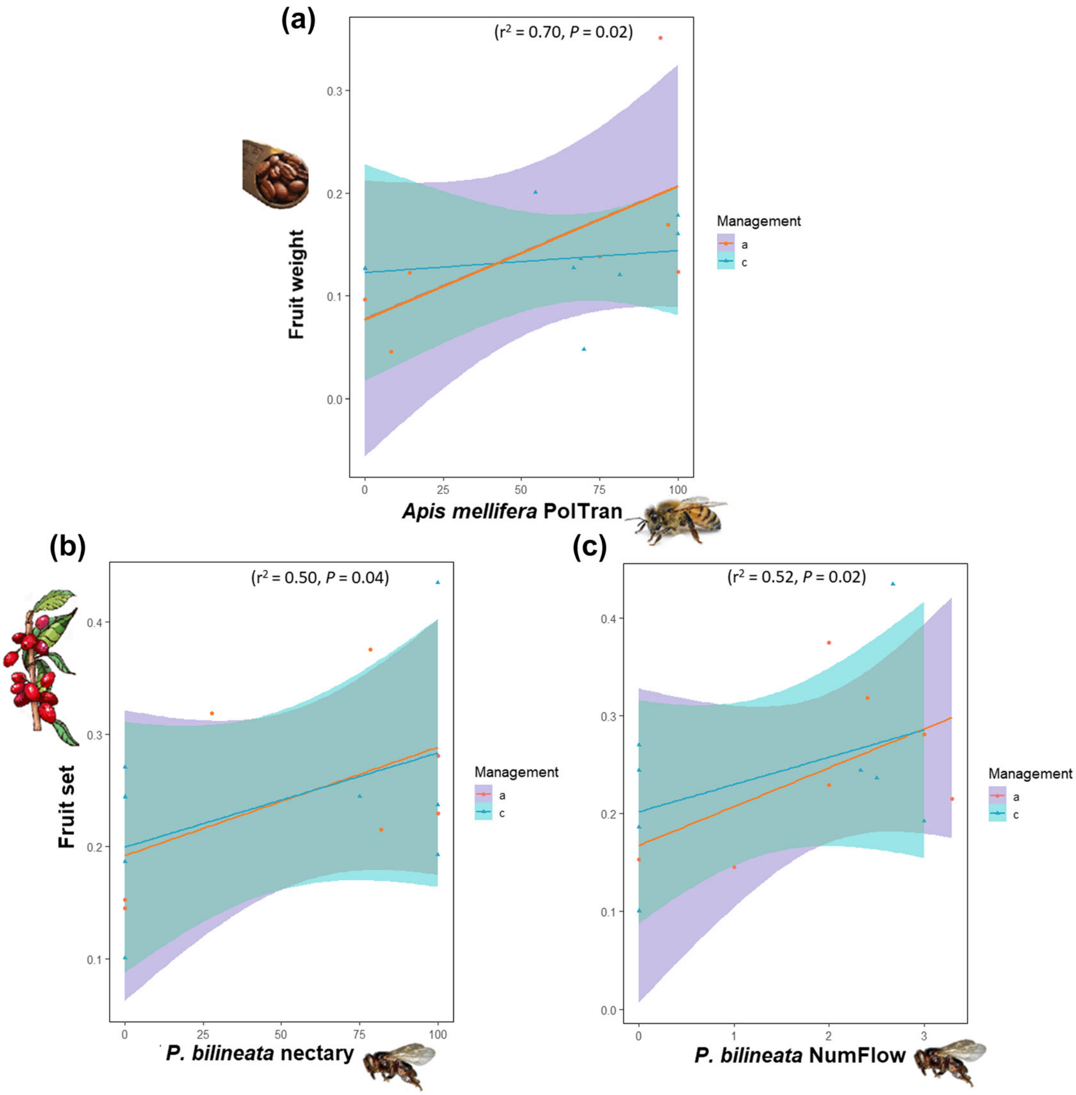

FIGURE 3 Relationship between the weight of fruits and (a) the percentage of *Apis mellifera* that carried pollen (PolTran) on their legs/bodies. Relationship between fruit set and (b) nectary, the percentage of *P. bilineata* observed touching the nectary of the coffee flowers, and (c) the average number of flowers visited by *P. bilineata*. Lilac colour is used for agroecological sites 'a', and blue is used for conventional sites 'c'. Shaded lines indicate 95% confidence interval.

TABLE 2 Relationship of foraging behaviour of *A. mellifera* and *P. bilineata* with coffee fruit weight and fruit set.

Response variable	Species	Behaviour	Estimate	SE	*t* value	*p* value
Fruit weight	*Apis mellifera*	PolTran	0.0014	0.0043	3.18	0.02*
Fruit set	*Partamona bilineata*	Nectary	<0.001	<0.001	3.35	0.02*
	Partamona bilineata	NumFlow	0.026	0.011	2.471	0.04*

Note: 'PolTran' indicates the percentage of bee's species that carried pollen on their bodies and legs. 'NumFlow' indicates the average number of flowers visited by each bee species in a specific branch observed. 'Nectary' indicates the percentage of bees observed touching the nectary of the coffee flowers.
*$p < 0.05$.
**$p < 0.01$.
***$p < 0.001$.

suggested by a review of 46 crops in Latin America (review in Real-Luna et al. 2022). It has also been observed that *A. mellifera* is an important pollinator on coffee crops (Manrique & Thimann 2002; Raw & Free 1977; Roubik 2002). Further, this pattern of floral visitors has been described previously in other studies from neotropical coffee plantations, principally in Mexico (Vergara & Badano 2009), Guatemala (Armas-Quiñonez et al. 2020), Costa Rica (Banks et al. 2013; Brossi et al. 2007; Ngo et al. 2013; Ricketts 2004), Colombia (Bravo-Monroy et al. 2015) and Brazil (Hipólito et al. 2020).

In addition, in our study, *A. mellifera* showed the highest values in most of the behavioural variables evaluated. Similarly, it has been described that the activity of *A. mellifera* on flowering crops began earlier (Can-Alonzo et al. 2005; Chuttong et al. 2022), honeybees were also the most prevalent and abundant floral visitors of diverse crops (Thompson et al. 2020) and their visitation rate to the butternut squash *Cucurbita moschata* Duchesne was higher than that of the stingless bees *S. mexicana*, *Trigona fulviventris* Guérin-Méneville, 1845 and *Frieseomelitta nigra* Cresson, 1978 (Delgado-Carrillo et al. 2018). Observations on *Macadamia integrifolia* Maiden & Betche of Heard (1994) showed that *A. mellifera* individuals looked for the nectary more often than the stingless bee *Tetragonula carbonaria* (Smith, 1854). However, in our study, some foraging behaviours of *A. mellifera* did not differ from the observed for wild bees, suggesting that *A. mellifera*, *P. bilineata* and *T. angustula* may be important pollinators of coffee in Guatemala; nevertheless, more investigation is needed to test adequately this hypothesis. Similarly, in other geographical areas where coffee is grown and *A. mellifera* has been reported as the main pollinator, the importance of wild bees could be emphasised by considering their behaviour and not just their abundance. Therefore, it is recommended to extend the study of the behaviour of floral visitors in coffee to other regions.

Relationship between management type, diversity and the foraging behaviour of floral visitor's species

We observed that agroecological plantations supported a greater abundance of floral visitors, although no differences were observed between management type for floral visitor community composition, richness and abundance of *T. angustula* and *S. mexicana*. In our sites, conventional plantations applied agrochemicals more often than those agroecological pairs; multiple applications of pesticides per harvesting season may explain the lower abundance of floral visitors in conventional plantations, which may negatively affect the diversity of floral visitors by reducing the efficiency of gathering pollen, the pollination efficiency and also the abundance of bee foragers (De Oliveira et al. 2019; Gill et al. 2012). Contrary, the reduced use of toxic pesticides in organic and agroecological systems may have a positive effect on the abundance of stingless bees and floral visitors in general (Xiu-Ancona 2007). Similarly, other studies have already shown that organic farms support a higher abundance of bees and flowering plants, even when bee community richness and composition did not differ (Austin et al. 2019; Rundlöf et al. 2008). A possible explanation for the difference in abundance observed may be that the abundance of floral visitors is driven by floral resource availability that can be greater in agroecological areas at specific time of the year during crop blooming (Austin et al. 2019).

Relationship of diversity and foraging behaviour of floral visitor's species with coffee fruit weight and fruit set

We observed a positive significant relationship between a greater percentage of *A. mellifera* observed carrying pollen on body and legs and the weight of coffee fruits. Previous studies already showed the positive effect of *A. mellifera* presence and foraging behaviour on coffee fruit weight and fruit set (Hipólito et al. 2020; Jha & Dick 2010; Klein et al. 2003a, 2007; Raw & Free 1977; Roubik 2002). However, we observed that fruit set was positively related with the behaviour of *P. bilineata* of touching the nectary of coffee flowers and a greater number of flowers visited by the same bee, which suggests that despite *P. bilineata* was found in smaller quantities than honeybee, both bees may play an important role. In addition, we observed that the relationship between behaviour variables and fruit production presented the same trend for both agroecological and conventional management, which is in line with the lack of effect of management on community composition, richness and behavioural variable of floral visitors observed in this study. Diverse studies had already showed that species richness was positively related to fruit production, where stingless bees were normally the second most abundant species after *A. mellifera* (Armas-Quiñonez et al. 2020; Garibaldi et al. 2013; Klein et al. 2003b; Munyuli 2014; Vergara & Badano 2009; Winfree et al. 2007), suggesting that wild bees are also responsible for pollination. Similarly, other studies comparing apis and non-apis behaviour showed that non-apis bees presented behaviour that was more efficient, even in the presence of large amounts of honeybees (Miñarro & Twizell 2015) and that an increase of 80% in crop yield was related to the density of non-managed, social floral-visiting bees per coffee shrub (Veddeler et al. 2008) and to their degree of sociability (Munyuli 2014). Species complementarity has been proposed as a hypothesis for greater fruit production in the presence of a greater diversity of floral visitors (Klein et al. 2003b; Saturni et al. 2016; Vergara & Badano 2009). Similarly, other studies in Mexico and Guatemala analysing relationship between pollen in honey and tree heterogeneity have shown that even with high abundance of coffee, *A. mellifera* tends to collect from different sources when the landscape is heterogeneous around coffee plantations (Zavala-Olalde et al. 2016). In addition, low-impact management systems of coffee plantations in central Veracruz, Mexico, showed higher species richness and high fruit production compared to high-impact management systems, where dominant species were predominant (Vergara & Badano 2009). In a posterior study in the same area, Badano and Vergara (2011) also observed a negative correlation with fruit production and diversity of native pollinators when honeybees' workers were in high abundance in coffee plantations. This suggested that there may be competition between honeybees and wild bees for the collection of floral resources. At the same time, the presence of other floral heterogeneous resources such as co-flowering crops can cause competition and stress within coffee crops, more strongly affecting the availability in coffee of social bees such as honeybees and stingless bees (Bänsch et al. 2021; Geeraert et al. 2019; Ludewig, Götz, et al. 2023; Peters et al. 2013; Ricketts 2004; Veddeler et al. 2006). However, these are hypotheses that are out of the scope of this study and future studies that consider the effect of floral heterogeneity at landscape and local scales (Escobedo-Kenefic et al. 2022) and competition between species in cash crops should be assessed.

Among the reasons that have been cited why *A. mellifera* may not always have a positive relationship with fruit production are as follows: (a) Honeybees are mass-recruiters that harvest pollen during the main flowering periods of coffee, causing the exclusion of other wild pollinators that are responsible for the transfer of quality pollen grains (Klein et al. 2003a; Roubik 2002) and limiting reproduction of coffee (Hipólito et al. 2020). In our study, we observed that honeybees presented high visitation time early in the morning, while *T. angustula* and *P. bilineata* appeared later, when the conditions were optimal for flower opening, which may cause honeybees to go to other crops to avoid competition and therefore reduce their relationship with fruit production. (b) Honeybees visit more flowers at a time compared with other wild bees and staying longer on branches with dense flowers, which may increase the probability of pollen transfer from the same coffee plant resulting in lower fruit set than the one from cross-pollination (Klein et al. 2003a, 2003b).

Additionally, most of our study sites belong to the system of private natural areas, a system that may favour the availability of resources for nesting and feeding of wild bees. Guatemalan farmers also manage distinct amounts of seminatural vegetation cover around and within coffee plantations even when they do not have sustainable certification (e.g., Rainforest Alliance and UTZ Certified Coffee), which contribute to increase the variability observed in coffee plantations (Coffee Research 2022; Haggar et al. 2015; Popper et al. 1996). Thus, even the conventional coffee plantation might have a large proportion of natural areas nearby, which contributes to the greater diversity of floral visitors in coffee. Several studies on coffee have already observed the positive effect of the proximity of natural areas on the diversity of floral visitors (Bravo-Monroy et al. 2015; Ricketts 2004; Ricketts et al. 2008). Other studies in coffee plantations have also shown that wild bees, especially the social ones as stingless bees, were enhanced in the presence of high shade coffee and tree diversity, as in our agroecological sites (González-Chaves et al. 2020; Jha & Dick 2010; Jha & Vandermeer 2009, 2010; Munyuli 2011) and floral resource availability (Escobedo-Kenefic et al. 2020, 2022; Landaverde-González et al. 2017). This proximity and higher proportion of natural areas in our study sites could have contributed to favoured pollination by wild bees. Worldwide, it has been reported that 60% of coffee farms are small producers with less than 5 ha and 19% of medium-sized producers between 5 and 50 ha, who have diversified their agroforestry systems in order to obtain a sustainable income, thus making their farms more ecologically diverse (reviewed in Siles et al. 2022). This means that the type of agroforestry systems used in Guatemala is a representation of what is observed worldwide, and therefore, the methods and findings can be extrapolated to coffee farms in other regions of the world.

In conclusion, we found that the managed honeybee *A. mellifera* and the wild bees *T. angustula*, *S. mexicana* and *P. bilineata* are the principal floral visitors of coffee. Further, abundance of floral visitors was positively related with the agroecological management, suggesting that the combination of availability of floral heterogeneous resources and low use of chemical may be positive for floral visitors' diversity. This underlines the importance of maintaining natural and heterogeneous areas that enhance a greater diversity of floral visitors that can provide pollination services. Even though foragers of *P. bilineata* are not as frequent as *A. mellifera*, the foraging activity of *P. bilineata* may be also efficient enough to promote cross-pollination in coffee plantations, which is only evidenced when considered pollinator foraging behaviour. In this way, the importance of native floral visitors for the pollination service in coffee is emphasised. Additionally, it is highlighted that natural forest cover is vital in tropical coffee plantations to maintain a richer assemblage of bee species and a high provision of pollination services for diverse cash crops and wildflowers; which is in line with the benefit that forested areas provide to other coffee plantations around the world.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no competing interests.

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