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Original article

Wild bees are key pollinators in organic tomato agroecosystems regardless of the presence of a managed stingless bee

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Abstract – While managing social bees is a well-documented strategy to enhance pollination services in controlled environments like greenhouses, this approach remains comparatively underexplored in open-field conditions. There is also a lack of empirical data on how managed bees affect wild bees and about minimally invasive methods for identifying and selecting healthy colonies for introduction into agroecosystems. We aimed to evaluate the potential of *Melipona quadrifasciata* for assisted pollination of tomato plants cultivated in open organic fields and its potential impacts on wild bees. We assessed nine *M. quadrifasciata* hives by monitoring foraging activity and qualitative parameters (brood cells, food storage, and pathogens) with environmental conditions (temperature and humidity). We then evaluated bee communities and pollination services across seven farms, four with introduced hives. We monitored bee activity on tomato flowers and non-crop plants to evaluate potential effects on wild bees. Pollination services were also evaluated along with fruit quality parameters. Monitoring foraging activity of hives alongside environmental data provides a practical, effective, and minimally invasive method for farmers to assess hive health. Open-pollination improved fruit quality, confirming that bee pollination enhances tomato production. However, the presence of *M. quadrifasciata* hives did not influence fruit quality, indicating that wild bees primarily drove pollination benefits. DNA metabarcoding analysis confirmed that *M. quadrifasciata* did not visit tomato flowers and relied mostly on pollen from arboreal plants. Our findings underscore the importance of conserving and promoting wild pollinators in organic agroecosystems by managing non-crop plants, which support diverse pollinator communities with complementary functional traits.

ecosystem services / *Melipona* / assisted pollination / organic farming / *Paratrigona* / Cerrado

1. INTRODUCTION

The demand for assisted pollination has increased, particularly for high-nutrition crops that form the basis of family farming (e.g., fruits and vegetables) and are highly dependent on animal pollination (Giannini et al. 2015; BPBES

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and REBIP 2019). This demand has also risen in landscapes where habitat changes have reduced the availability of bees for natural pollination (da Silva Carneiro et al. 2024). This trend reflects the growing recognition of pollination's contribution to fruit quality and productivity (BPBES and REBIP 2019), as well as advances in managing social bees for pollination in agroecosystems (Meléndez-Ramírez et al. 2018). Although managing social bees can enhance pollination services, most studies focus on the use of *Apis* and *Bombus* species (Iwasaki and Hogendoorn 2022), which are important for assisted pollination but are exotic to many regions. The introduction of exotic species can directly and indirectly impact interactions with native species, potentially compromising pollination dynamics (Page and Williams 2023; Aguiar et al. 2024; Assunção et al. 2025). This issue is particularly relevant in the Neotropical region, which plays a significant role in global food production and hosts a high diversity of native bees essential for crop pollination (Freitas et al. 2009).

New management strategies of native bees adapted to local contexts have been explored for assisted pollination, showing promising results across various crops (Giannini et al. 2015; Meléndez Ramírez et al. 2018; Maués et al. 2024). This is particularly true for native stingless bees of the tribe Meliponini (Apidae). For instance, *Melipona* species represent the second most economically important group of bees for agricultural pollination in Brazil, after the genus *Apis* (honeybee) (Giannini et al. 2020). Using Meliponini hives for assisted pollination in Brazil offers several advantages: (i) their natural occurrence in the Neotropical region; (ii) the availability of well-established management techniques for many species (Cortopassi-Laurino et al. 2006); (iii) their lack of a functional stinger, which reduces the risk of adverse incidents for farmers (Pedro 2014); (iv) their perennial and expansive colony growth, with a high number of individuals per hive (Roubik et al. 2018); and (v) their generalist foraging habits, floral constancy, and adaptability to diverse environmental conditions (Slaa et al. 2006; Roubik et al. 2018). Additionally, these bees exhibit morphological and behavioural diversity, including the ability to vibrate their bodies, which allows them to pollinate a wide variety of buzz-pollinated plants (BPBES and REBIP 2019).

The tomato plant (*Solanum lycopersicum* L.) is one of the cultivated species that requires specific pollination behaviours, such as licking and buzz behaviour (Gaglianone et al. 2015; Bartelli et al. 2024). Tomato cultivation is widespread across South America and holds significant socioeconomic importance, with Brazil, Argentina, and Chile progressively increasing both their cultivated areas and yield (FAO 2024). Although tomato plants are capable of self-pollination due to their hermaphroditic and self-compatible flowers, cross-pollination by bees significantly enhances fruit production (Del Sarto et al. 2005; Gaglianone et al. 2015). Among Meliponini bees, only species of the genus *Melipona*, such as *Melipona quadrifasciata* Lepeletier, 1836 and *Melipona bicolor* Lepeletier, 1836, can vibrate tomato flowers, making them efficient pollinators of tomato crops (Del Sarto et al. 2005; Gaglianone et al. 2015; de Moura-Moraes et al. 2021). Indeed, tomato productivity is clearly enhanced by assisted pollination from native bees in Brazil, including species of the genus *Melipona* (Del Sarto et al. 2005; Bartelli et al. 2014; Deprá et al. 2014; Silva-Neto et al. 2019).

To conserve natural resources and sustain farming practices in the long-term, it is crucial to explore strategies that enhance tomato production without expanding agricultural land use, particularly in megadiverse countries such as Brazil. In this context, organic production systems promote a more resilient and biologically diverse environment, supporting beneficial organisms (da Silva et al. 2022; Marins et al. 2024), including pollinators (Assunção et al. 2022). Maintaining species and functional diversity is important, as different bees play complementary roles, enhancing the resilience and effectiveness of pollination (Dainese et al. 2019; Assunção et al. 2022). Thus, although introducing non-native or native beehives can positively impact tomato crops, focusing solely on this approach may limit pollination services on agroecosystems (Garibaldi et al. 2021). The

success of managed hives depends on the compatibility between the introduced species and the target crop, on the adaptation of bees to the local environment, as well as the interactions between these managed bees and wild pollinators (Mallinger and Gratton 2015; Mallinger et al. 2017; Garibaldi et al. 2021). Given these complexities, a key concern regarding the introduction of hives into organic agroecosystems is their potential impact on wild pollinator communities due to the dominance and competition effects (Mallinger et al. 2017; Page and Williams 2023).

While the potential of managed beehives to mitigate pollination deficits on farms is increasingly recognized, significant knowledge gaps remain about their effective implementation, especially for stingless bees. First, studies on this practice have primarily focused on protected crops, leaving the complex ecological dynamics of open-field systems under-explored (Del Sarto et al. 2005; dos Santos et al. 2009). Second, there is a lack of empirical data on the ecological impacts of introducing managed hives on wild bee populations (Goulson et al. 2015; Geslin et al. 2017). Third, minimally invasive methodologies for identifying and selecting healthy colonies for introduction into agroecosystems are still lacking (Leão et al. 2024). Finally, a particularly problematic gap concerns the widespread practice of translocating native bee species across different habitats based solely on their reputation as effective pollinators elsewhere (Quezada-Euán et al. 2022; Roubik 2018). This practice typically lacks local, empirical validation, raising significant doubts about the efficacy of these bees on new target crops, their foraging preferences, and colony viability in new environments.

Given the need to understand the ecological implications of introducing hives into economically important crops, such as tomatoes, this study aims to evaluate the potential of *M. quadrifasciata* for assisted pollination of tomato plants grown in open organic fields. Specifically, we aimed to (i) assess the quality of *M. quadrifasciata* hives by evaluating bee activity to select healthy hives for assisted pollination strategies; (ii) examine the impact of introducing *M. quadrifasciata* hives on the diversity and abundance of wild bees in organic agroecosystems; (iii) determine whether the introduction of *M. quadrifasciata* hives enhances the productivity and quality parameters of tomato fruits; and (iv) characterize the foraging preferences of the managed *M. quadrifasciata* hives by identifying the floral resources that support their maintenance within the agroecosystem. We chose *M. quadrifasciata* to investigate whether its known efficiency as a tomato pollinator is maintained in an open-field setting in a region outside the species' native range. This approach enables an empirical evaluation of the ecological trade-offs associated with transporting and managing hives in novel environments, including a direct assessment of colony sustainability.

2. MATERIALS AND METHODS

2.1. Quality parameters of beehives for introduction in open-field organic tomato crops

Melipona quadrifasciata hives were maintained in an experimental area at Embrapa Genetic Resources and Biotechnology, Federal District, Brazil (15°46′48″S, 47°55′45″W), near a natural remnant of riparian vegetation in the Cerrado biome (the Neotropical savanna). The Cerrado is a biodiversity hotspot and the most diverse savanna in the world in terms of plant diversity (Myers et al. 2000; Sano et al. 2019). This biome supports 12% of the bee species in the Neotropical region, comprising approximately 820 species, with a significant proportion of endemic species (Raw 2007). The experimental area provided optimal conditions for hive development. To ensure additional resources for the colonies during the experiments, the hives were supplemented weekly with carbohydrates (50% sucrose solution) (Villas-Bôas 2018). The hives were sourced from local beekeepers who maintained these species in modular wooden boxes. Hive acquisition and subsequent management were conducted in strict accordance with Brazilian legislation for the scientific research

on native bees (BRASIL 2023). This legislation governs the scientific use of native bees and includes permissions for their transport outside their natural range, specifically for studies like ours that aim to assess the ecological risks and benefits of such introductions.

Approximately one month before the beginning of field experiments, in June 2023, we evaluated the behaviour of nine *M. quadrifasciata* hives to establish parameters for selecting healthy hives prior to their introduction into the farms. We assessed the foraging activity of the hives weekly. The number of bees entering and leaving the hives was recorded from 8 to 11 h at 30 min intervals. During this period, we observed individuals carrying pollen, resin, or discarding waste as they flew to and landed at the hive entrance, noting the masses of pollen and other materials, such as clay and resin, attached to the bees' corbiculae. Local temperature and relative humidity were recorded at 30-min intervals using online data from Google's weather forecast service, which provides short-term weather information on mobile devices (Google 2023). By identifying how factors such as temperature and humidity affect bee foraging activity, we aim to propose more effective, easy-to-implement management strategies for agroecosystems.

Qualitative parameters were assessed for all hives, including the presence of food storage pots containing pollen and honey, the absence of phorids or pathogens, and the existence of new and old brood cells. New brood cells are characterised by their lighter colour, smooth texture, and translucent appearance (Villas-Bôas 2018). Due to the invasive nature of this procedure for the colonies, qualitative parameters were measured only twice: on the day the hives were installed on the farms and again when they were returned to the experimental area approximately four months later.

2.2. Bee diversity and impacts of beehive introduction on local fauna

The introduction of *M. quadrifasciata* hives into agroecosystems was evaluated across seven farms from July to October 2023. These farms, located in the Federal District, Brazil (MS1 Figure S1), cultivate tomatoes in open fields. All farmers have been engaged in organic management systems for at least three years, with farms averaging 24,000 m^2 in size. Farm management relied predominantly on manual labour. The farms were situated within an agricultural matrix that included natural remnants of Cerrado vegetation, polyculture systems (simultaneous cultivation of multiple crop species, primarily vegetables), non-crop plants (commonly referred to as weeds), and fruit trees (MS1 Figure S2, S3). Farmers allowed non-crop plants to grow between crop rows and along field margins, removing them from cultivated areas as needed. These plants were typically used as live or dead soil cover, contributing to soil protection and nutrient cycling during both cropping seasons and fallow periods. Pest management was conducted using biological and natural products approved by Brazilian legislation, ensuring compliance with organic farming regulations (Togni et al. 2019).

The experiments were conducted using the Italian tomato cultivar (*S. lycopersicum* var. Matinella), widely cultivated by Brazilian farmers, particularly in organic systems (CONAB 2019). A previous study reported a higher frequency of *M. quadrifasciata* visits to this cultivar in greenhouse tomatoes compared to cherry tomatoes (Pires et al. 2024). We provided tomato seedlings and fertilisers to the farmers to standardise the number of plants cultivated per area and the nutritional conditions of the tomato plants. Tomato cultivation covered an average of 200 m^2 per farm, with approximately 380 plants. Soil preparation was carried out before planting, incorporating simple thermophosphate and poultry litter, in accordance with standard agronomic practices for local organic production. The tomato plants were supported using vertical staking and arranged in double rows with 60 cm spacing between rows to optimise light interception and airflow. Farmers used drip irrigation and sprinklers to maintain consistent soil moisture levels throughout the growing season. Seedlings were transplanted to the field 30 days after

germination. The experimental design ensured that hives were introduced approximately 10 days after transplanting, allowing the plants to acclimate and reach the early flowering stage, which typically occurs around 40 days after germination.

Pires et al. (2024) estimated that introducing one hive of *M. quadrifasciata* per 100 tomato plants at peak flowering resulted in approximately 90% of the flowers of the Italiano cultivar being visited in greenhouse conditions. Therefore, we established three hives per farm, considering that the cultivation area contained approximately 380 tomato plants. Bee hives were installed on four farms (+BH), while the remaining three farms did not have hives installed near the tomato crops (−BH). Farms with (II, III, V, and VII) and without (I, IV, and VI) hives were paired within the landscape to ensure comparable environmental conditions. The hives were installed in shaded areas adjacent to the field margins, 3–5 m from the tomato crop area. This introduction occurred shortly after the tomato plants were planted in early July, allowing the hives to acclimate before the tomato plants began flowering. Based on foraging activity results, hives with lower activity were excluded from the farms and replaced with new ones. Due to the inability to evaluate foraging activity in these new hives, they were randomly assigned to farms, ensuring that each farm received at least one active colony, previously assessed by foraging activity.

To characterise the community of flower-visiting bees on tomato flowers and assess the potential effects of introducing *M. quadrifasciata* hives, we conducted bee sampling throughout the tomato crop's flowering period from July to October. We evaluated the occurrence of introduced and wild bees in the tomato plants and on non-crop plants around the field margins, within a radius of up to 10 m from the cultivated area. Sampling bees on non-crop plants aimed to determine whether *M. quadrifasciata* also foraged on these plants, which are essential for maintaining wild bee interactions within tomato crop areas (Assunção et al. 2022). Each week, collectors walked through the area, actively capturing bees using plastic vials between 9 and 12 h. Only bees that landed directly on the flowers were collected. The collected specimens were immediately euthanized and preserved for subsequent identification in the laboratory. The daily sampling effort was quantified in minutes of collection and multiplied by the number of collectors. The total sampling effort was 20 h per farm, with 10 h spent on tomato plants and 10 h on non-crop plants, totalling 140 h across the seven sampled farms. The bees were identified to the lowest possible taxonomic level. Bee specimens were deposited in the Entomological Collection of the University of Brasília (DZUB) and the Entomological Collection of Embrapa Genetic Resources and Biotechnology, both located in the Brazilian Federal District.

2.3. Bee pollination in tomato crops

The pollination service provided by wild or introduced bees was evaluated in tomato plants. Two treatments were established in the tomato crops: (1) SP—self-pollination, where tomato inflorescences were bagged during the pre-anthesis stage using material that allows only wind passage, preventing bee visits; and (2) OP—open-pollination, where bees were allowed to visit the flowers (MS1 Figure S4). For each treatment on a given plant, three flowers were selected. Both treatments were applied simultaneously to each tomato plant on branches with flowers at the same developmental stage. A random sample of 100 plants was selected on each farm to implement the treatments, totalling 700 tomato plants per treatment (700 SP + 700 OP). The bags were removed from the SP inflorescences once fruit development began. In the OP treatment, flowers with necrotic marks on the anthers, caused by the insertion of mandibles of buzz-pollinating bees, were considered pollinated, indicating bee visitation (Pires et al. 2024).

The experiments were conducted from the 1 st to the 4th flowering cycles to avoid bias related to reproductive investment in flowers at different stages of plant development. The

tomato variety used in the experiment exhibits indeterminate growth, with the apical bud exerting dominance over the lateral buds. The plant continuously forms new buds and clusters along the main stem, and fruit development follows an ascending pattern, where the lowest-level clusters produce the most vigorous fruits. To account for these factors in the analysis of fruit quality, we recorded the level of the clusters and buds and marked the flower buds with water-based liquid paper.

We harvested up to two fruits per treatment from each tomato plant. After harvesting, fruit quality was evaluated in the laboratory by measuring fruit weight (mg), diameter (cm), number of seeds per fruit, and pest damage. Pest damage was quantified by counting the number of infestations per fruit, assigning a damage score of 1 for each distinct pest species affecting the fruit. For example, a healthy fruit received a score of 0, while a fruit infested by two pest species received a score of 2, and a fruit infested by three pest species received a score of 3. To identify pests and their respective damage, we followed a technical manual about tomato fruit quality (Michereff Filho et al. 2019).

2.4. Plants used as resources by *M. quadrifasciata*

We collected one or two samples of pollen from pot-pollen of at least one hive from each farm (hives B, C, J, K, L, and M—Figure S6), in July and August 2023, during the flowering period of the tomato plants. Pollen samples were stored at −20℃. For genomic DNA extraction, we weighed 100 mg of each pollen sample, homogenized in 800 µL of lysis buffer with three stainless steel beads (3 mm) in a FastPrep®−24 (MP Bio) at 4.0 m/s for 30 s three times, and we used the DNeasy Plant Mini Kit (Qiagen) following the manufacturer's instructions. We amplified the ITS2 region (internal transcribed spacer 2) using the dual-indexing strategy (Sickel et al. 2015) and primers S2F (Chen et al. 2010) and ITS4R (White et al. 1990). Each sample was amplified in three replicates. For each replicate, the PCR mix contained 1 × AmpliTaq Gold™ 360 Master Mix (Applied Biosystems™), each primer (0.25 µM), BSA (0.8 µg/ml), 6.84 µl of ultrapure water, and template DNA (5–20 ng/µL). In addition, a reaction containing ultrapure water instead of template DNA was performed to serve as a negative control and monitor for possible contamination. The amplification program consisted of an initial denaturation at 95 °C for 10 min, followed by 35 cycles of denaturation at 95 °C for 30 s, primer annealing at 56 °C for 30 s, extension at 72 °C for 40 s, and a final extension at 72 °C for 10 min. We pooled the samples, removed excess primers and unwanted fragment sizes, and added indexes to the samples with the Collibri™ PCR-free kit for Illumina platforms. The libraries were quantified using the Qubit dsDNA HS Assay Kit (Invitrogen™). Sequencing was performed using the Illumina MiSeqi100 platform, using the MiSeq i100 series 5 M Reagent Kit (600 cycles), following the manufacturer's protocol, to produce paired-end fragments.

The bioinformatic data analysis followed the dada2 pipeline in R (Callahan et al. 2016). We removed primers using cutadapt (Martins et al 2011), joined paired ends of forward and reverse reads, removed low-quality reads (maxEE = 2), removed chimeras, and defined amplicon sequence variants (ASVs). We compared each ASV to the NCBI nucleotide database to identify them at the species level using BLASTN version 2.17.0 (Camacho et al. 2009), with a minimum threshold of 100% for query cover and 98% of sequence identity. ASVs that corresponded to the same species were merged, and their read counts were summed. The unidentified ASVs were assigned to the lowest taxonomic level possible using the dada2 algorithm (Callahan et al. 2016) with a custom-made ITS2 reference database that included the Cerrado flora species lists (Flora e Funga do Brasil 2025) and all Spermatophyta entries from NCBI with vouchers deposited in a museum or herbarium. The reference database was created following the BCdatabaser pipeline (Keller et al. 2020). For each identified taxon, we listed the plant habit based on GBIF.org (2025). We normalized taxa count

per sample by rarefaction (Cameron et al. 2021). We subsampled up to 10,000 reads per sample 30 times, calculated the average count, and the relative frequency of each taxon in each sample.

2.5. Statistical analysis

To assess the correlation between explanatory variables (temperature, humidity, time of day) and response variables (number of bees leaving and entering the hive), we performed a Spearman correlation analysis, as the data did not follow a normal distribution. We used the Point-Biserial correlation coefficient (rpb) to evaluate the relationship between the binary variable (presence of bees entering the hive with pollen grains) and the continuous variable (number of bees leaving and entering the hive, which was square-root transformed to stabilise variances). Generalised Linear Mixed Effect Models (GLMMs) were fitted to evaluate the impact of explanatory variables on the response variable (Crawley 2012). Variables were selected based on observed correlations to avoid redundancy and multicollinearity. Given the well-documented relationship between temperature and humidity, we selected 'temperature' due to its established influence on bee foraging behaviour (Hilário et al. 2000; de Lacerda Ramos et al. 2024). This approach enhances the consistency and comparability of our findings across different seasons and study sites, irrespective of the time of observation. The variable 'hive' was included as a random factor in the analysis to account for specific variations among observed hives. This approach was justified by potential natural differences among hives, such as colony size, queen age, brood development rate, and foraging behaviour. To visualise differences among groups (different hives), we performed pairwise comparisons using estimated marginal means. The response variable data were log-transformed ($\log(x+1)$) to standardise variances.

We fitted Linear Mixed Effects Models (LMMs) and GLMMs to evaluate how richness, abundance, and diversity (Shannon-Wiener Index, H′) of wild bees (response variables) were affected by the introduction of hives in organic farms (+BH and −BH) (Crawley 2012). We included 'hive' as a random factor in the analysis to ensure that the observed effects were attributed to hive introduction rather than pre-existing differences among them (as mentioned above). Separate models were fitted for each response variable. The abundance and diversity (H′) data were log-transformed ($\log(x+1)$) to standardise variances.

To assess whether hive introduction affected pollination effectiveness on the farms, we fitted LMMs and GLMMs with fruit quality parameters (weight, diameter, number of seeds, and pest damage) as response variables, and hive introduction groups (+BH and −BH) and pollination treatments (SP and OP) as explanatory variables (Crawley 2012). We included 'hive', 'plants' (replicates), 'farms', 'clusters', and 'buds' as random factors in the analyses. 'Plants', 'clusters', and 'buds' were included to control for developmental variation in tomato fruits. Farms were included as random effects to account for environmental differences and bee diversity across study areas. Separate models were fitted for each response variable. Weight data were square-root transformed to standardise variances. One experimental farm (Farm VII) was excluded from the pollination analyses because all tomato plants were affected by disease shortly before fruit harvest. To ensure the validity of our comparisons, we restricted our analyses to the remaining six farms where plants completed their reproductive cycle.

Pairwise comparisons are estimated using the package 'emmeans' (Russell et al. 2018). Models were fitted using the 'lmerTest', 'lme4', and 'glmmTMB' packages (Bates et al. 2015; Kuznetsova et al. 2016; Brooks et al. 2017). Model fit was evaluated using residual plots and statistical tests from the 'DHARMa' package, ensuring the reliability of the fitted models (Hartig and Hartig 2017). The significance of variables in the models was assessed via an ANODEV using an F-test (Crawley 2012). For model comparison and selection, we used the Akaike Information Criterion (AIC). All analyses were performed using the software R (R Core Team 2018).

3. RESULTS

3.1. Quality parameters of beehives for introduction in open-field organic tomato crops

We identified a strong positive correlation between temperature and time of day ($\rho = 0.79$, d.f. = 214, $p < 0.001$); and a strong negative correlation for humidity in relation to both temperature ($\rho = -0.73$, d.f. = 214, $p < 0.001$) and time of day ($\rho = -0.81$, d.f. = 214, $p < 0.001$) (MS1 Figure S5). The data indicated an increasing trend in temperature and a corresponding decline in humidity over the time of day (MS1 Figure S5). We also found a significant correlation between the number of *M. quadrifasciata* individuals entering and leaving the hives ($\rho = 0.96$; d.f. = 214, $p < 0.001$) (Figure S5); and a positive correlation for the presence of individuals entering the hives with pollen grains in relation to both individuals leaving (rpb = 0.79; d.f. = 214, $p < 0.001$) and individuals entering (rpb = 0.73; d.f. = 214, $p < 0.001$) the hives. Given the significant correlations among these variables, we selected only the temperature and the number of bees leaving the hives to analyze the bee foraging activity.

The number of individuals leaving the hives exhibited considerable variation with temperature ($\beta = -0.05$, $F = 4.32$, d.f. = 1, $p = 0.038$) and among the hives evaluated ($F = 416.59$, d.f. = 8, $p < 0.001$) (Figure 1). The highest activity occurred at lower temperatures (18.28 ± 0.25 °C; mean ± SE) and high humidity (63.89 ± 0.91%; mean ± SE), with a gradual decline in foraging activity as the morning progresses and the temperature increases (21.78 ± 0.22 °C) and the humidity decreases (52.56 ± 0.78%). The mean number of individuals leaving the nest was higher in hive-B (110.29 ± 20.41; mean ± SE) and hive-C (105.42 ± 19.77) compared to the other *M. quadrifasciata* hives (Figure 1). In contrast, hive-F (1.75 ± 0.53) and hive-G (2.04 ± 0.48) exhibited considerably lower activity compared to the other hives (Figure 1). Based on these results, hives F and G were not introduced into the farms, and new hives were obtained to replace them.

Introducing hives on farms resulted in a general improvement of qualitative parameters related to their health and development. We observed the establishment of new food storage pots (pollen and honey) and brood cells (MS1 Figure S6, S7, S8, and S9), even in hives with less activity such as D and E (Figure 2; MS1 Figure S7). We also observed that the bees continued to forage on the farms, actively collecting pollen from floral resources, indicating that the hives acclimated to the farms within a relatively short period of time.

3.2. Bee diversity and impacts of beehive introduction on local fauna

We collected 2692 bees visiting tomato (1290 individuals) and non-crop (1402) flowers. They were identified into 60 species and five families (Table I). Overall, we recorded 8 species on tomato plants, 37 on non-crop plants, and 15 in both. The three most abundant species in tomato flowers were *Paratrigona lineata* Lepeletier, 1836 (77.83% of individuals collected), *Exomalopsis analis* Spinola, 1853 (9.84%), and *Pseudaugochlora* sp.2 (4.88%). The most abundant species on non-crop plants were *Apis mellifera* Linnaeus, 1758 (46.22%), *P. lineata* (12.13%), and *Trigona spinipes* Fabricius, 1793 (8.56%). Despite the observations of *M. quadrifasciata* workers leaving and returning to the hives with pollen grains, the species did not visit any tomato flowers or non-crop plants. Furthermore, there were no statistically significant differences between the farms with hives (+BH) and those without hives (–BH) in terms of bee richness, abundance, or diversity on tomato and non-crop plants (Figure 3).

3.3. Plants used as resources by *M. quadrifasciata*

Pollen analysis revealed that the diet of introduced *M. quadrifasciata* hives was composed of ten plant taxa belonging to the families Melastomataceae, Myrtaceae, and Solanaceae

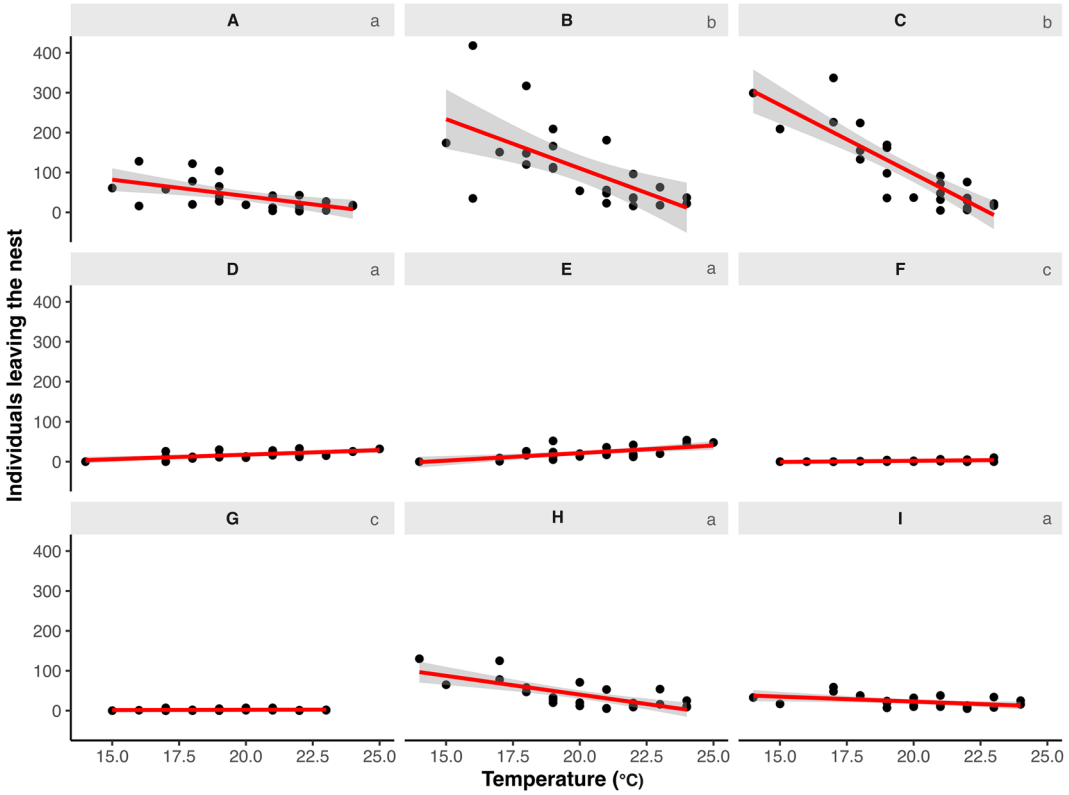

Figure 1. Relationship between temperature and the number of *Melipona quadrifasciata* individuals leaving the hive across different managed hives evaluated (**A**–**I**). The scatter plot displays observed data points (black dots), while the red line represents the fitted linear regression model, with the shaded area indicating the 95% confidence interval. Different grey letters indicate statistically significant differences between hives based on a post-hoc test. The data refer to observations of nine hives of *M. quadrifasciata* made in an experimental area at Embrapa Genetic Resources and Biotechnology, located in the Federal District, Brazil, in June 2023.

(Table II, MS2). Overall, woody plants, including species with shrub and tree habits, were the primary forage resources, with tomato accounting for a minimal portion of the collected pollen. Melastomataceae was the most important family, with *Miconia* spp. being the dominant pollen type in four of the six hives (C, J, K, and M). Myrtaceae also represented a key resource, particularly for hive L, which foraged heavily on *Psidium* sp. (69.4%), and hive C, which utilized *Siphoneugena* sp. (26.0%). Plants from the Solanaceae family, including the tomato flowers, were detected but at very low frequencies (0.1% in hives L and M) (Table II, MS2).

3.4. Bee pollination in tomato crops

A total of 769 tomato fruits were harvested on the six farms. The pollination treatments were the primary factor influencing fruit quality, with OP significantly increasing fruit quality compared to SP (Table III). However, no significant effect of managed colonies on the assessed fruit quality parameters was observed (Table III), showing that the benefits of open pollination were consistent across the introduction of hives. The SP had a significant negative effect on the fruit weight, length, and number of seeds produced per fruit (Table III). On average,

HIVE D

BEFORE:
New brood cell: no*
Old brood cell: yes
Honey pot: yes
Pollen pot: no
Pathogens: no
Activity: healthy

AFTER:
New brood cell: yes*
Old brood cell: yes
Honey pot: yes
Pollen pot: no
Pathogens: no
Activity: healthy

HIVE E

BEFORE:
New brood cell: no*
Old brood cell: no*
Honey pot: yes
Pollen pot: no
Pathogens: no
Activity: healthy

AFTER:
New brood cell: yes*
Old brood cell: yes*
Honey pot: yes
Pollen pot: no
Pathogens: no
Activity: healthy

HIVE H

BEFORE:
New brood cell: no*
Old brood cell: yes
Honey pot: yes
Pollen pot: no*
Pathogens: no
Activity: unhealthy*

AFTER:
New brood cell: yes*
Old brood cell: yes
Honey pot: yes
Pollen pot: yes*
Pathogens: no
Activity: healthy*

◂**Figure 2.** Evaluation of qualitative parameters in hives D, E, and H before and after their introduction into farms. The images depict internal hive conditions, showing the presence of pathogens, brood cells (both new and old), food storage pots (pollen and honey), and the overall activity of bees in the hives (healthy or unhealthy). The hives were installed on four farms with organic tomato crops located in the Brazilian Federal District, Brazil, from July to October 2023. Asterisks indicate the changes in hives following farm placement.

the weight of fruits from OP was 22.92% higher than that from SP; the length of OP fruits was 0.64% greater than that of SP fruits; the number of seeds was 29.46% higher in OP fruits. Of the total fruits harvested, 301 (39.15%) exhibited some degree of damage. SP had a slight positive effect on pest damage (Table III), with pest damage in SP fruits 0.11% higher than in OP. The majority of this damage was attributed to the presence of *Tuta absoluta* Meyrick, 1917 (Lepidoptera: Gelechiidae) (78.41% of fruits with damage), *Neoleucinodes elegantalis* Guenée, 1854 (Lepidoptera: Crambidae) (18.27%), *Helicoverpa zea* Boddie, 1850 (Lepidoptera: Noctuidae) (5.32%), and other types of damage caused by fungi or bacteria (29.92%).

4. DISCUSSION

Melipona quadrifasciata workers were not observed visiting tomato flowers, with pollen analysis showing a very low foraging preference for this crop. Hive introduction did not influence fruit quality, confirming that wild bees primarily drove the benefits of pollination, besides the role of wind. This suggests limited effectiveness of *M. quadrifasciata* for assisted pollination in open-field tomato crops. However, the introduction of selected hives into farms demonstrated a general improvement in hive quality parameters, including the establishment of brood cells and storage pots, indicating successful acclimatisation, potential for adaptation even in less active hives, and flower-visiting activity. This foraging success was sustained almost exclusively by pollen from the families Melastomataceae and Myrtaceae, sourced from the adjacent vegetation. On top of that, no differences in bee richness, abundance, or diversity were observed between farms with and without introduced hives, indicating that this practice had no direct effect on the local bee community. Additionally, the evaluation of hive quality confirmed that environmental factors, such as temperature, influenced bee activity.

Our findings reinforce the interaction between environmental conditions, hive quality, and colony performance (Pereboom and Biesmeijer 2003; Hrncir and Maia-Silva 2013). *Melipona quadrifasciata* workers exhibited a preference for foraging early in the morning (between 8 and 10 h), when temperatures ranged from 16 °C to 20 °C and relative humidity ranged from 55 to 70%. This aligns with the thermal foraging window of this species (12–22 °C, amplitude: 10 °C) and coincides with the peak of pollen collection activity recorded for the species in its natural habitat, the seasonal semi-deciduous forests of southeastern Brazil (Maia-Silva et al. 2014). Relative humidity exhibited the greatest fluctuations during the observation period, with a notable decline over time. Given that *M. quadrifasciata* prefers to forage under high humidity conditions (Maia-Silva et al. 2014; Oliveira-Abreu et al. 2014), we hypothesize that these fluctuations in humidity may explain the decline in bee foraging activity throughout the day.

From a management perspective, monitoring bees leaving the hive, combined with basic microclimatic data, particularly temperature and humidity, allows farmers to anticipate colony health without the need for frequent hive openings. This approach we developed here is essential for optimising hive performance in open-field cropping systems. The low activity levels observed in some hives must be considered critically, as bee foraging activity is essential for colony maintenance and survival through resource collection (Maia-Silva et al. 2014). A previous study demonstrated that foraging activity in stingless bees correlates with colony size, independent of species-specific life history traits (Leão et al. 2024). Furthermore, hives with a larger number of adults were positively correlated with the number of brood cells and food storage pots (Leão et al. 2024),

Table I Bee species collected from tomato and non-crop plants in organic farms. The table shows the total number of individuals (N) and their relative frequency (fr %) within each plant type (non-crop and tomato plants), as well as the overall total (2692 individuals) and frequency for each species. Species are listed within each bee family. The samples were made on farms located in the Brazilian Federal District, Brazil, from July to October 2023

	Non-crop-plants		Tomato-plants			
	N (1402)	fr (%)	*N* (1290)	fr (%)	Total *N* (2692)	Total fr (%)
Andrenidae						
Acamptopoeum prinii	1	0.07	-	-	1	0.04
Apidae						
Apis mellifera	648	46.22	1	0.08	649	24.11
*Bombus brevivillus***	5	0.36	7	0.54	12	0.45
*Bombus morio***	1	0.07	-	-	1	0.04
Ceratina (*Crewella*) sp.1	1	0.07	-	-	1	0.04
Ceratina fioreseana	4	0.29	-	-	4	0.15
Ceratina richardsoniae	13	0.93	-	-	13	0.48
*Eulaema nigrita***	-	-	1	0.08	1	0.04
*Exomalopsis analis***	23	1.64	127	9.84	150	5.57
*Exomalopsis auropilosa***	52	3.71	42	3.26	94	3.49
*Exomalopsis fulvofasciata***	1	0.07	2	0.16	3	0.11
Exomalopsis sp.2**	1	0.07	-	-	1	0.04
*Frieseomelitta doederleini**	8	0.57	-	-	8	0.30
Geotrigona mombuca	2	0.14	-	-	2	0.07
Geotrigona subterranea	21	1.50	-	-	21	0.78
Lophopedia sp.2	1	0.07	-	-	1	0.04
*Melipona quinquefasciata***	1	0.07	1	0.08	2	0.07
Paratetrapedia connexa	-	-	4	0.31	4	0.15
Paratetrapedia sp.1	3	0.21	12	0.93	15	0.56
*Paratrigona lineata**	170	12.13	1004	77.83	1174	43.61
Partamona sp.1	8	0.57	-	-	8	0.30
Partamona sp.2	11	0.78	-	-	11	0.41
Plebeia droryana	1	0.07	-	-	1	0.04
Scaptotrigona postica	105	7.49	-	-	105	3.90
Tapinotaspis sp.1	1	0.07	-	-	1	0.04
Tetragonisca angustula	38	2.71	-	-	38	1.41
Trigona spinipes	120	8.56	1	0.08	121	4.49
Colletidae						
Hylaeus sp.1	2	0.14	-	-	2	0.07
Hylaeus sp.2	1	0.07	-	-	1	0.04
Halictidae						
*Augochlora aurinasis***	7	0.50	-	-	7	0.26
*Augochlora morrae***	2	0.14	-	-	2	0.07
*Augochloropsis aurifluens***	4	0.29	-	-	4	0.15
Augochloropsis sp.1**	1	0.07	-	-	1	0.04

Table I (continued)

	Non-crop-plants		Tomato-plants			
	N (1402)	fr (%)	*N* (1290)	fr (%)	Total *N* (2692)	Total fr (%)
Augochloropsis sp.2**	-	-	2	0.16	2	0.07
Augochloropsis sp.3**	1	0.07	1	0.08	2	0.07
Augochloropsis sp.4**	-	-	8	0.62	8	0.30
Augochloropsis sp.5**	-	-	2	0.16	2	0.07
Augochloropsis sp.6**	1	0.07	3	0.23	4	0.15
Augochloropsis sp.7**	1	0.07	-	-	1	0.04
Augochloropsis sp.8**	-	-	2	0.16	2	0.07
*Augochloropsis wallacei***	-	-	2	0.16	2	0.07
Caenohalictus sp.1	2	0.14	-	-	2	0.07
Dialictus rostratus	21	1.50	-	-	21	0.78
Dialictus sp.1	14	1,00	1	0.08	15	0.56
Dialictus sp.2	34	2.43	-	-	34	1.26
Dialictus sp.3	2	0.14	-	-	2	0.07
Dialictus sp.5	7	0.50	1	0.08	8	0.30
Dialictus sp.6	3	0.21	-	-	3	0.11
Dialictus sp.7	35	2.50	2	0.16	37	1.37
Dialictus sp.9	1	0.07	1	0.08	2	0.07
Dialictus sp.10	1	0.07	-	-	1	0.04
Dialictus sp.11	4	0.29	-	-	4	0.15
Halictus lanei	1	0.07	-	-	1	0.04
Pseudagapostemon brasiliensis	12	0.86	-	-	12	0.45
Pseudaugochlora sp.2**	-	-	63	4.88	63	2.34
Sphecodini sp.1	1	0.07	-	-	1	0.04
Temnosoma metallicum	1	0.07	-	-	1	0.04
Thectochlora sp.1	1	0.07	-	-	1	0.04
Thectochlora sp.2	1	0.07	-	-	1	0.04
Megachilidae						
Coelioxys sp.1	1	0.07	-	-	1	0.04

*Bee species considered pollinators of tomato plants; ** Bee species considered pollinators of tomato plants and capable of buzz-pollinating (Deprá et al. 2014; Santos et al. 2014; Silva-Neto et al. 2016; Vinícius-Silva et al. 2017; de Moura-Moraes et al. 2021; Toni et al. 2021)

indicating healthy and active colonies (Hilário et al. 2000). We are confident that our approach provides a practical, effective, and minimally invasive alternative for farmers to monitor beehives, as it is directly related to bee foraging behaviour in a time-efficient manner (Leão et al. 2024). Despite the merits, it is necessary to consider that our samplings were made after the beginning of bee foraging activity, which is a caveat of our study in this regard. Our study was conducted during the dry season in the Cerrado, when relative humidity can fall below 15% (Oliveira and Marquis 2002). Therefore, further evaluations should be performed during other periods of the year and in different ecosystems.

The observed qualitative improvement in hives reinforces the idea that heterogeneous habitats can stimulate bee colony development

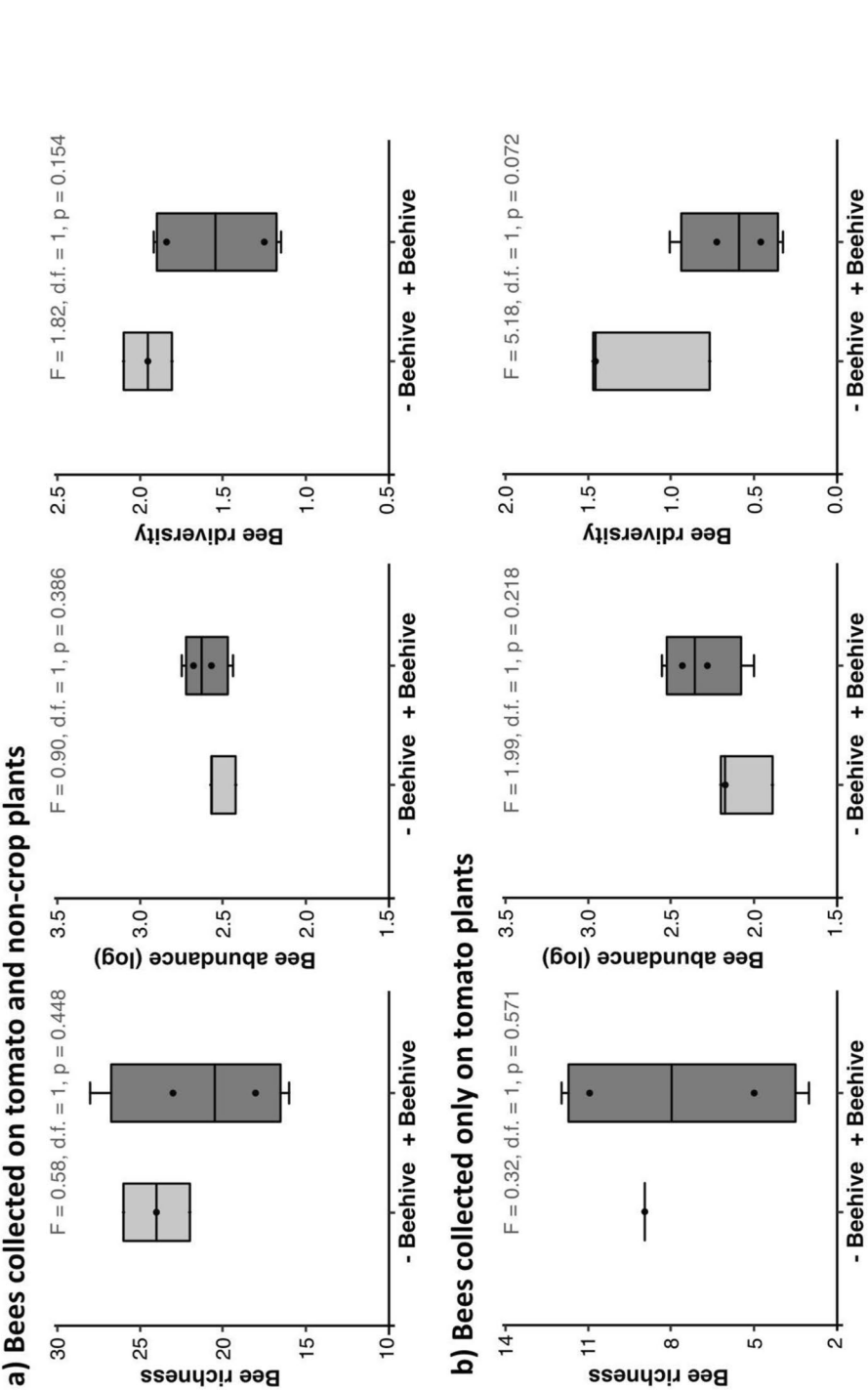

Figure 3. Boxplots showing bee richness, bee abundance and bee diversity (mean ± SE) in farms with (+BH) (dark gray bar) or without (−BH) (light gray bar) *Melipona quadrifasciata* managed hives. (a–c) bee data collected on tomato and non-crop plants; (d–f) bee data collected only on tomato plants. Statistical results from Generalized Linear Models (GLMs) are indicated in each panel, showing the F-value, degrees of freedom (d.f.), and p-value. No significant differences were observed in any comparison ($p < 0.05$). Data refer to bee samples from seven tomato-producing organic farms in the Federal District, Brazil, from July to October 2023.

Table II Quality of tomato fruits harvested from pollination treatments in farms with or without *Melipona quadrifasciata* managed nests. Quality parameters evaluated: weight (Mg), length (cm), number of seeds, and pest infestation damage. Pollination treatments: **SP**—self-pollination; tomato inflorescences were bagged to prevent bees from visiting the flowers; and OP—open-pollination; allowing bees to visit the flowers. Presence of nests: + **BH**—farms with nests installed near the tomato crop; **−BH**—farms without nests installed. Results of models and parameters used to test how the quality of tomato fruits (response variables) is affected by pollination treatments and introduction of nests (explanatory variables) are presented. We use data from tomato fruits harvested in organic fields in the Brazilian Federal District, Brazil. Significant values are indicated in bold ($p < 0.05$)

Fruit quality parameter	Presence of nest	Pollination treatment	Mean	Standard deviation	Sample (n fruits)		Effects			Model fit		
@	@	@	@	@	@	Coefficients	Est	z	p	F	d.f	p
Weight (mg)	−BH	OP	95.43	32.12	268							
		SP	69.41	29.28	221	Intercept	9.42	35.83	**> 0.001**	-	-	-
	+BH	OP	70.52	22.72	148	+BH	−1.01	−2.68	0.052	7.18	1	**0.007**
		SP	53.99	17.66	132	SP	−1.23	−12.37	**> 0.001**	152.96	1	**> 0.001**
Diameter (cm)	−BH	OP	7.66	1.04	268							
		SP	6.95	1.09	221	Intercept	7.56	30.85	**0.008**	-	-	-
	+BH	OP	6.72	0.96	148	+BH	−0.84	−1.23	0.347	1.52	1	**0.218**
		SP	6.24	0.90	132	SP	−0.56	−9.05	**> 0.001**	81.93	1	**> 0.001**
Number of seeds	−BH	OP	81.18	22.50	234							
		SP	51.70	28.70	189	Intercept	80.11	17.81	**> 0.001**	-	-	-
	+BH	OP	87.46	24.53	142	+BH	5.34	0.84	0.452	0.23	1	0.633
		SP	57.76	28.98	123	SP	−28.59	−15.08	**> 0.001**	222.70	1	**> 0.001**
Pest infestation damage	−BH	OP	0.43	0.62	268							
		SP	0.58	0.71	221	Intercept	−0.92	−2.36	**0.018**	-	-	-
	+BH	OP	0.45	0.68	148	+BH	0.12	0.22	0.826	0.05	1	0.826
		SP	0.50	0.75	132	SP	0.24	2.25	**0.025**	5.05	1	**0.025**

Table III Taxa identified in pollen samples from introduced hives, their habits and normalized occurrence frequencies (%) in each hive. We used data of *M. quadrifasciata* introduced in organic fields in the Brazilian Federal District, Brazil

Family	Genus/species	Habits	Hives					
			B	C	J	K	L	M
Melastomataceae	*Miconia*	Shrub	0.1	73.9	99.5	56.8		81.8
Melastomataceae	*Microlicia*	Subshrub, shrub or tree	88.3					
Melastomataceae	*Trembleya*	Shrub	10.5					
Myrtaceae	*Eucalyptus*	Tree	0.2			24.9	30.5	17.5
Myrtaceae	*Eugenia*	Subshrub, shrub or tree		0.1		0.4		
Myrtaceae	*Psidium*	Subshrub or shrub				7.2	69.4	0.1
Myrtaceae	*Siphoneugena*	Tree		26.0				
Myrtaceae	*Syzygium*	Tree				7.0		
Solanaceae	*Solanum*	Variable	0.8			3.6		0.6
Solanaceae	*Solanum lycopersicum*	Shrub					0.1	0.1

(Goulson et al. 2015; Timberlake et al. 2021). Although we observed workers returning to hives with pollen grains stored in their corbiculae and newly formed pollen storage pots, we did not observe *M. quadrifasciata* individuals foraging on tomato plants or nearby non-crop plants. *Melipona* bees can forage up to 2 km away and recruit over 1 km from their nest (Kuhn-Neto et al. 2009). Despite their generalist foraging behaviour, studies indicate that stingless bees prefer forest trees with mass flowering, even when these are available only at long distances (Ramalho 2004; Martins et al. 2023). Our pollen analysis confirms this foraging strategy, revealing a diet dominated by resources from trees and shrubs. Specifically, the high frequency of pollen from the genus *Miconia*, *Microlicia*, and *Psidium* demonstrates an apparent reliance on the surrounding native vegetation and fruit trees rather than the agricultural crop. Notably, the study farms were surrounded by natural vegetation patches, located up to 200 m from the tomato crops (MS1 Figure S3).

With 60 bee species identified, encompassing all bee families recorded in Brazil, this study highlights the ecological richness and sustainability of organic agroecosystems. Among these, native species such as *P. lineata*, *E. analis*, *Pseudaugochlora* sp., and *E. auropilosa* were the most abundant visitors of tomato flowers. Consistent with previous findings in the Cerrado, *P. lineata* accounted for a substantial proportion of flower visits (77.83%), demonstrating a strong preference for tomato flowers in this region (Assunção et al. 2022). Although this species does not perform buzz-pollination, it was seen using its glossa to access the poricidal anthers of tomato flowers (MS1 Figure S10). *Paratrigona lineata* can act as an effective pollinator of tomato flowers in the Cerrado, increasing fruit seed production by 30% (Bartelli et al. 2024). This is possible due to additional pollen-gathering behaviours that facilitate tomato pollination (e.g., 'scraping' and 'licking'; Gaglianone et al. 2015; Bartelli et al. 2024), as has also been observed in other stingless bee species, such as *Nannotrigona testaceicornis* Lepeletier, 1836 (de Moura-Moraes et al. 2021).

The composition of bee species differed between the two tomato and non-crop plants. Tomato plants were visited primarily by species with specific behavioural or morphological traits that enable their interaction with tomato flowers (Gaglianone et al. 2015). In contrast, non-crop plants were predominantly visited by eusocial generalist bee species that prefer plants with mass flowering and abundant nectar, such as *A. mellifera* (46.22%) and *T. spinipes* (8.56%)

(Page and Williams 2023; Assunção et al. 2025). However, the species shared between tomato and non-crop plants suggest that non-crop plants play a crucial role in attracting and sustaining tomato pollinators, as well as pollinators of other crops, in diversified agroecosystems (Assunção et al. 2022). By offering a diverse range of floral shapes, colours, traits, and sizes, non-crop plants support a broader assemblage of pollinator species with complementary functional traits (Bretagnolle and Gaba 2015; Escobedo-Kenefic et al. 2022).

Our findings on *M. quadrifasciata* pollen analysis provide a case study of this dynamic. The species adapted its foraging strategy to local floral availability around each farm, confirming that *Melipona* bees may meet their pollen requirements by foraging on pollen grains from a greater number of flowers (Antonini et al. 2006; Ramalho et al. 2007; da Luz et al. 2018). In addition to this foraging plasticity, our findings show that *M. quadrifasciata* exhibits a strong preference for some plant families, particularly Melastomataceae and Myrtaceae, suggesting that these families are essential for maintaining colonies in anthropized regions (Barth et al. 2020; Vieira et al. 2022). The near-absence of tomato pollen in their diet, despite its proximity, strongly corroborates this, showing that bees actively chose pollen resources from the surrounding native vegetation.

The absence of significant differences in the richness, abundance, or diversity of visitors to tomato and non-crop flowers suggests that the introduced *M. quadrifasciata* hives did not negatively impact wild pollinators. Increased competition for resources is a primary concern when introducing managed bees (Goulson et al. 2015). However, our results indicate that competition may have been avoided due to the distinct foraging preferences of the managed and wild bees in this heterogeneous agroecosystem, where non-crop plants provided high floral availability (MS1 Figure S2). Another key aspect is that studies on hive introduction focused, not surprisingly, on *A. mellifera* and *Bombus* species (Iwasaki et al. 2022). However, the introduction of non-native hives has negatively impacted natural pollinator populations, primarily due to the dominance effects of *A. mellifera* (Garibaldi et al. 2021; Page and Williams 2023; Aguiar et al. 2024).

Although the management of stingless bees has only recently been considered for assisted pollination (Osterman et al. 2021a), the limited available evidence suggests that some could serve as viable alternatives to exotic bees. For example, the introduction of *Tetragonula iridipennis* Smith, 1854 hives did not negatively affect the abundance, visitation rate, or foraging time of wild pollinators in open-field watermelon and fennel crops (Layek et al. 2021, 2022). This study thus represents a pioneering contribution to assessing the impacts of introduced native stingless bee hives on wild pollinators in open-field neotropical agroecosystems. Furthermore, we highlight the need for long-term impact assessments, as our study was limited to a single harvest season.

Managed hives of *M. quadrifasciata* did not directly contribute to tomato pollination in this study. Instead, wild bees provided the primary pollination service. This result highlights a critical distinction between a species' potential to serve as a pollinator and the ecological service it actually provides in a complex landscape with alternative resources. Thus, introducing managed hives in open fields may not necessarily enhance pollination services, particularly when wild pollinators are already established and performing effectively (Winfree et al. 2008; Mallinger and Gratton 2015). This is supported by the observed wild bee abundance and richness, as well as the impact of open pollination (OP), which improved fruit quality compared to self-pollination (SP). Pollinators facilitate more effective pollen transfer, promoting uniform fertilization and seed development, which in turn influences fruit size and weight (Giannini et al. 2015; Khalifa et al. 2021).

We also observed slightly lower pest damage rates in OP fruits compared to SP. *Tuta absoluta*, the tomato leaf miner, responsible for substantial tomato yield losses worldwide (Biondi et al. 2018), caused the highest incidence of fruit damage in our study. However, the minor reduction

in overall fruit quality may be attributed to *T. absoluta*'s low preference for oviposition in organic tomato plants (Medeiros et al. 2009). Additionally, it is reasonable to hypothesize that bee cross-pollination enhanced tomato plant vigour compared to self-pollination. Future research should therefore investigate the relationship between fruit development and pest infestation.

Assisted pollination may have a limited impact on farmers in organic and diversified agroecosystems, as natural pollination often does not require supplementation (Winfree et al. 2008; Mallinger and Gratton 2015) or introduced bees may forage on other crop and non-crop plants (Bänsch et al. 2020; Osterman et al. 2021b). Given this, rather than focusing solely on the introduction of managed hives, investing in habitat conservation and promoting naturally occurring pollinators may represent a more sustainable and cost-effective strategy for ensuring pollination services in diversified agroecosystems (Garibaldi et al. 2017; Isaacs et al. 2017; Jandt et al. 2025). Moreover, not all bee species are equally efficient at pollinating specific crops in open-field environments, where floral resources are abundant and bees may exhibit preferences for certain plants (Osterman et al. 2021b; Martins et al. 2023), as observed in our study. Therefore, further baseline studies are needed to better understand the foraging dynamics of bees in mass-flowering agroecosystems. Such knowledge will be valuable for designing farm landscapes that minimize competition among bees while maximizing species complementarity.

5. CONCLUSION

While introducing *M. quadrifasciata* hives did not directly enhance tomato fruit quality, it demonstrated the potential for hive acclimatisation and colony development in organic agricultural landscapes. We provided a practical and minimally invasive approach for farmers to assess hive health by monitoring bee foraging activity under appropriate weather conditions. The primary pollination services in tomato crops were provided by wild bees, particularly *P. lineata*, which exhibited a strong visitation rate for tomato flowers. This finding underscores the importance of conserving and promoting wild pollinator diversity in organic agroecosystems, as they play a critical role in sustaining pollination services. We highlight the need for habitat heterogeneity and the management of non-crop plants, which support a diverse assemblage of pollinators with complementary functional traits. Additionally, our findings point to three directions for future research. First, investigating the floral resources utilised by other stingless bees in agroecosystems and exploring the long-term impacts of hive introduction on wild pollinator communities across different cropping systems and ecosystems. Second, developing management techniques for *P. lineata* should be a promising alternative, although challenging. Finally, future work should also evaluate the potential of other managed stingless bees for assisted pollination in tomato crops, such as species of *Nannotrigona* and *Frieseomelitta*.

SUPPLEMENTARY INFORMATION

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AUTHOR CONTRIBUTION

All authors contributed to the study conception and design. Material preparation, data collection, and analysis were performed by Rafaela Mendes Assunção, Patricia Sanae Sujii, Isabelle Evangelista Gonçalves da Silva, Davi de Lacerda Ramos and. Pedro Henriqe Brum Togni and Carmen Sílvia Soares Pires supervised the study. The first draft of the manuscript was written by Rafaela Mendes Assunção, and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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DATA AVAILABILITY

Data will be made available from the first author upon request.

DECLARATIONS

Ethics approval Not applicable.

Consent to participate Not applicable.

Consent for publication Not applicable.

Competing interests The authors declare no competing interests.

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