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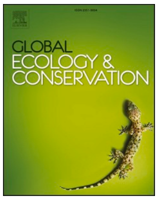

Original research article

Flower resource availability and *Tetragonisca fiebrigi* flower visits in two farming communities of Bolivian Chiquitanía

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ABSTRACT

This article describes the flower availability and resource use of the generalist stingless bee Tetragonisca fiebrigi at two farming communities (agroindustrial vs. traditional) of Bolivian Chiquitanía. Vegetation sampling was carried within the flight range of T. fiebrigi to characterize the habitats, life forms and richness of flowering plants present in each farming community. No significant differences were found in plant richness between the agroindustrial and traditional communities. However, the flowering plants in the agroindustrial community predominantly herbs, and the highest richness of plants was found in home gardens. In contrast, the flowering vegetation of the traditional farming community was characterized by the presence of shrubs and trees, with fallows contributing the most to overall plant richness. Bees of the agroindustrial community visited a higher and more variable median number of plant genera compared to the traditional one (15±6.57 vs. 10±2.04, respectively). In both communities, bees visited trees more frequently than other life forms, and they seem to prefer visiting trees in the traditional farming setting, as indicated by the use-to-availability ratio. Our findings highlight home gardens and fallows as important habitats contributing to flowering plant richness, and raise trees as potentially key resources for bee diets, independently of the farming context.

1. Introduction

Bees are among the most well-studied insects because of their vital ecological and cultural roles. As efficient pollinators, they support biodiversity and agricultural productivity (Potts, 2016). Their honey and other sub-products also serve as food and medicine to

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humans, while also contributing to cultural identity, particularly in Latin America (Aldasoro Maya et al., 2023; Maderson, 2023). Currently, there are global concerns about bee decline, which is mainly driven by land-use changes associated to agroindustrial expansion (Maderson, 2023; Potts, 2016). The shifts to the agroindustrial model modify the basic resources bees need for their survival, amongst which feeding resources (e.g. pollen) are a central one (Potts, 2016; Shanahan, 2022). This context underscores the urgent need to better understand how different farming models shape vegetation composition and bee foraging behavior, aspects that are still poorly understood for various bee species (Maderson, 2023; Kaehler et al., 2024; Kaluza et al., 2017; Roubik et al., 2005).

Industrial agriculture often leads to large-scale replacement of semi-natural habitats into extensive monocultures, simplifying the vegetation structure, functional diversity, and creating more homogenous landscapes (Perfecto et al., 2019; Siebert, 2002). In these landscapes the vegetation is dominated by herbs, or plants of first regeneration stages (Brosi, 2009; Cely-Santos and Philpott, 2019; Chévez et al., 2023; Potts, 2016; Potts et al., 2010). In contrast, traditional, small-scale, diversified agroecosystems have more of a mosaic composition, where people still manage the surrounding habitats, including crops, fallows, forests and other habitats (Maderson, 2023; Mahonya et al., 2019). These systems can retain a higher plant diversity, with higher structural complexity including shrubs, trees, and herbaceous plants that seem to be important for bees (Landaverde-González et al., 2017; Donkersley, 2019; Esquivel et al., 2023).

Bee foraging behavior is shaped by both genetic predispositions — such as whether a species is a specialist or a generalist— and environmental factors linked to availability, seasonality, climate and competition (Roubik et al., 2005; Rubenstein and Alcock, 2019; Roulston and Goodell, 2011). In undisturbed conditions, *Tetragonisca fiebrigi* — a common, abundant generalist stingless bee from tropical forests of high cultural importance (Kaehler et al., 2024; Adler et al., 2024) — exhibits a polylectic foraging behavior, visiting multiple flowering species within their flight range (Adler et al., 2024; Saravia-Nava et al., 2018), although they seem to present some specialization on certain resources that could be more rewarding (Adler et al., 2024; Saravia-Nava et al., 2018; Flores et al., 2021).

Amongst its foods, pollen is not only the main protein source of bees, but also provides amino acids, lipids, sterols and micronutrients to the whole colony. As such, it is an important food to be collected efficiently (Adler et al., 2025; Roulston and Goodell, 2011). The survival of bee colonies depends on achieving ideal diets, consequently, bees appear to select more nutritionally rewarding resources as shown by Adler et al. (2025) and Wood et al. (2022). Evidence suggests that woody vegetation (e.g. trees) might contain more nutritious pollen (Wood et al.,2022; Adler et al., 2025; Guimarães et al., 2021, Ramalho, 2004), and that their selection could be due to many factors including their density, size, volume or the presence of attractive or unattractive oils (Adler et al., 2025; Di Pascuale et al., 2016; Guimarães et al., 2021). Furthermore, Donkersley (2017), (2019), Ramalho (2004) and Bisui et al. (2019) have shown that trees were the most important items searched as food items by *Apis mellifera* and various species of stingless bees in England, Brazil and India, respectively.

In fact, the studies that link bee foraging behavior to land use frequently focus on the preference of vegetation cover type and the results indicate that, in general, bees seem to prefer semi-natural vegetation and agroforests or diversified crop systems - which is also where more tree cover is expected - over highly modified anthropogenic vegetation (Bottero et al., 2023; Cannizzaro et al., 2022; Shanahan, 2022; Vides-Borrell et al., 2019, Siebert, 2002; Roulston and Goodell, 2011). This underscores the potential tight relationship of bees with plants that might be found in less intensive, traditional farming systems (Ramalho, 2004; Guimarães et al., 2021). Additionally, Donkersley (2019) raises the importance of considering lifeforms types present in bee diets, which are often overlooked, particularly in agricultural studies, as it shows the structural complexity of the plant community (Ma and Herzon, 2014).

The ongoing transformation towards agroindustrial practices in Latin America (Oliveira, 2021; Colque and Vadillo, 2022), might have profound implications on the available flowering plant types and on the feeding characteristics of bees (Potts, 2016; Maurer et al., 2024; Lozada-Gobilart et al., 2025). In particular, Bolivia has experienced some of the world's highest deforestation rates, with most deforestation concentrated in the department of Santa Cruz, and more importantly in the Chiquitanía region, which are affecting biodiversity and bees (Global Forest Watch, 2023; Quintanilla et al., 2023, Townsend et al., 2021; Lozada-Gobilart et al., 2025; Colque and Vadillo, 2022, Vos et al., 2020). Between 1985 and 2021, this region lost 1.9 million hectares of forest, equivalent to 15.9 % of its surface area (Global Forest Watch, 2023; Proyecto MapBiomas-Bolivia, 2023). In this context, it would be relevant to study the characteristics of the flowering vegetation available to *T. fiebrigi* in agroecosystems under different land use regimes, as well as to understand which plants bees actually forage from.

The study of the characteristics of the available and used flower resources of culturally important bees present in the agroecosystems of Bolivia such as *T. fiebrigi* would provide a first general overview of the potential limiting resources of these insects' diets. In the future, such information could be used as a starting point to plan management and conservation strategies of these important insects, as well as to question the farming models promoted in the country. Our research was guided by the following research questions: (1) Which is the composition of the flowering plants (richness, habitats, life forms) at an agroindustrial vs. a traditional farming community? (2) Which is the composition (richness, life forms) of the floral resources used by *T. fiebrigi* as feeding sources at these farming communities and (3) do these stingless bees prefer certain life forms?

2. Methods

2.1. Study site

The Chiquitanía is an ecoregion that encompasses various ecosystems including the dry forest per se, the dry forest influenced by Amazonia, Cerrado, Chaco and Savannas. As a result of the encounter of these ecosystems a high vegetation diversity is found in this region, reaching a total of 237 shrub and tree species (Jardim et al., 2003). The Chiquitanía has an altitude range from 150 to 600 m.a.s.l, with a climate characterized by a dry season that lasts from April to September, followed by a wet season from October to March

(Jardim et al., 2003; Saravia-Nava et al., 2018). It extends over 12.4 million hectares (11.5 % of the surface of Bolivia), and still possess the best conserved dry forest of the continent, in spite of the drastic land use changes occurring in the last decades (Jardim et al., 2003; Proyecto MapBiomas-Bolivia colección 1.0, 2023).

Our study was conducted in two Indigenous smallholder farming communities situated at the Chiquitanía region (Fig. 1; S12). The first farming community is the Guaraní Indigenous District 16 de Marzo Cordillera (*Ind* hereafter), which belongs to the agroindustrial nucleus of eastern Bolivia, and has a total surface area of 2414 ha. *Ind* smallholders cultivate cash crops: soy, sunflower (pollen-nectar crops), as well as sorghum (pollen crops), which they started due to government incentives (Haas, 2019; S1). They sometimes cultivate pollen-nectar crops such as papaya, Cucurbitaceae, as well as corn (pollen crops) in small parcels of < 100 m^2 that are intended for self-consumption. While most of the land has been transformed to monocultures (Fig. 1) (Fundación TIERRA, 2023b), some patches of secondary forest remain in this community, making up an estimated 52 ha (2.15 % of the total surface area). Other semi-wild vegetation includes wetlands that are unsuitable for cultivation (287 ha; 12 %) (Fig. 1). Individual home gardens cover less than 9 ha, but are actively managed. Chicken, pigs, the native bee species *T. fiebrigi* and the introduced *A. mellifera* are often found in the home gardens (Fundación TIERRA, 2023b). Local people still harvest different plants and honey in the remnants of semi-natural vegetation. This vegetation is mainly composed of semi-deciduous forest species of the old alluvial plains of the San Julián River, which share several characteristics with the Bosque Chaqueño present in Argentina, Paraguay and Brazil (Table 1; Navarro and Maldonado, 2002, Fundación TIERRA, 2023b).

The second farming community is San Juan de Lomerío (*Trad* hereafter), which belongs to the Chiquitano Indigenous People. This farming community practices a "traditional" and local agricultural model that combines diverse crops mixed with cattle ranching. Each year, the families sow ≤ 1 ha. Their crops include various types of pollen crops, especially corn, sugar cane, rice, as well as pollen-nectar crops such as Cucurbitaceae, bananas, Manihot, sweet potato and fruit trees such as *Citrus* and papaya (Fundación TIERRA, 2023a). *Trad* has a total surface of 37,300 ha, of which 19,000 ha are part of their forest management zone and the rest is distributed in between the crops areas mixed with fallows, grasslands for animals and home gardens (Fig. 1). Wood logging, hunting, and forest harvest, including native honey harvest, are common activities. According to Vides-Almonacid et al. (2007) and Navarro and Maldonado (2002), the vegetation in this farming community could correspond to a semi-deciduous to low deciduous forest, with an average canopy height of four meters, although some areas are composed of trees reaching up to 10 m. Below the trees there is a stratum of shrubs and a dense inferior layer of thorny or spiny plants where the family Bromeliaceae dominates. Lianas and epiphytes are present, but they are not abundant. Economically important are present in the home gardens, fallows and crops surrounding the settlement area (Table 1; Fundación TIERRA, 2023a).

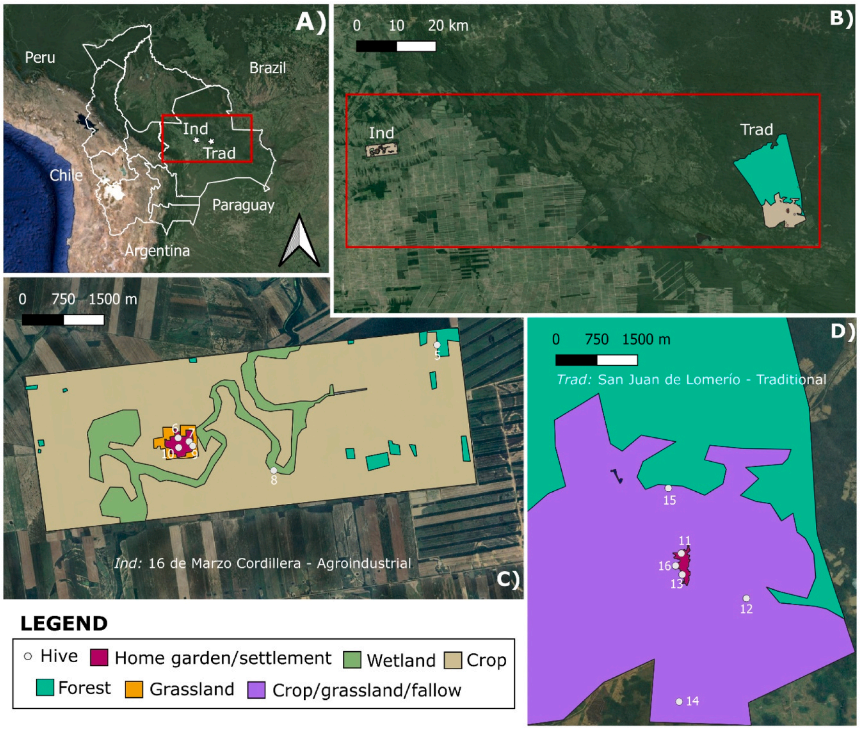

Fig. 1. a) Localtion of the study zone at the department of Santa Cruz in eastern Bolivia, the two farming communities: agroindustrial - 16 de Marzo/Cordillera (*Ind*) and traditional - San Juan de Lomerío (*Trad*) are shown in b). The main land uses identified using the satellite image are shown for *Ind* (c) and *Trad* (d), respectively. The first hives (5–10) were located at *Ind* and 11–16 at *Trad*. Own elaboration, the satellite image is from Bing.

Table 1
Main characteristics of the study sites *Ind* (agroindustrial) and *Trad* (traditional) farming communities.

Characteristics	Ind	Trad
Total surface	2414 ha	37,300 ha
Land use (habitats)	Mechanized or manual rotation monocultures, grasslands, home gardens, wetlands and patches of forest	Manually sown diversified crops mixed with pastures, home gardens, fallows of different ages and forest patches
Main crops	Soy, sunflower, sorghum	Corn, Cucurbitaceae, bananas, Manihot, sweet potato, *Citrus* papaya.
Median crop parcel size per household	3.5 ha (1–30 ha)	30 ha (1−65)
Forest related activities	Plant, honey harvest	Game meat, plant, honey harvest
Representative semi-natural vegetation	*Schinopsis brasiliensis Acosmium cardenasii, Aspidosperma tomentosum, Caesalpina pluviosa,* *Cereus tacuaralensis, Coccoloba paraguariensis, Diplokeleba floribunda, Melicocca lepidopetala*	*Astronium urundeuva,* *Tabebuia impetiginosa, Aspidosperma tomentosum, Terminalia obionga,* *Cereus tacuaralensis,* *Spondias mombin,* *Rhamnidium elaeocarpum,* *Genipa americana*
Use of pesticides	Yes	Rare

2.2. Data collection

2.2.1. Flower resource availability and reference collection

To understand the characteristics of the available flower resources at the two farming communities, we conducted botanical surveys around *T. fiebrigi* hives (sampling units), which were marked using a GPS (Fig. 1). We established four orthogonal transects of 500 m from the center of the hives (Fig. 1) (Saravia-Nava et al., 2018). Each transect faced a cardinal direction: North, South, East, West. The length of the transects was based on *T. fiebrigi's* flight range. This small stingless bee has been observed to fly 200 m of distance from their hives (Kaehler et al., 2024; Saravia-Nava et al., 2018). Our transects were longer than this, as the foraging range of stingless bees seems to expand depending on the landscape characteristics (Kaehler et al., 2024; Saravia-Nava et al., 2018; Smith et al., 2017; Araújo et al., 2004). We collected specimens from flowering plants as we walked along the transects. We only collected plants with open flowers or flower buds. At the end of the surveys, we summed the number of times we registered a species on each orthogonal transect. The total relative abundance of a given species was the sum of the counts in the four transects.

The available flowering plants collected were identified to the family, genus and species level. Nevertheless, we only considered the genus level in our analysis, as this was the finest level of identification obtained for the pollen survey (see the following 2.2.2). A botanical expert from the Natural History Museum Noel Kempff Mercado, Santa Cruz-Bolivia, performed the identifications. The plants, as well as the reference pollen identified were incorporated to the collection of the Herbario del Oriente Boliviano USZ, Herbario Nacional de Bolivia (LPB) and the Botanic Laboratory of the Universidad Autónoma Gabriel René Moreno (UAGRAM).

Taxonomic diversity alone is not enough to describe the links between biodiversity (Ma and Herzon, 2014), therefore, in order to better understand the resources available for bees we added the variables habitat (land use) and plant life form to our data set. Habitat type (land-use) allowed to gain further insights into *where* the flowering vegetation grew within the farming communities, and it was noted each time a plant was collected. Habitats included: fallows, home gardens, croplands, wetlands and forests. Once we had the total list of plants identified, we also added the plants life form of each species, to gain understanding of the structural complexity of the vegetation of the farming communities. For this, we searched for the name of the plant in Jørgensen et al. (2014) and added if they were: herbs, lianas, shrubs or trees.

2.2.2. Bee resource use

To understand the characteristics of the plants that were used as food sources by *T. fiebrigi* at both farming communities we collected pollen samples from the corbicula (i.e. leg pollen basket) of returning foragers. We considered the pollen types carried by bees as a proxy of the items that are part of their diet. However, we acknowledge the pollen stored pollen inside the hives, as well as nectar also constitute part of their feeding spectrum.

Corbicular pollen was collected during bees' greatest foraging activity: from 9:00 h to 12:00 h and from 15:30 h to 18:00 h, and only under optimal weather conditions (i.e., no rain or wind). From May to July (dry season) and then from October to November (wet season) we collected pollen samples from three to five individual bees per hive. We assembled pollen collections per month. That means we aimed at obtaining five pollen samples per hive overall.

Pollen was extracted by trapping an individual in a jar and brushing its corbiculae until the pollen pellet fell. Corbicular pollen samples were treated using the Acetolycis Method, with modifications to the technique of Erdtman (1986). The samples were decanted and stored in 1 ml of 90 % alcohol in Eppendorf tubes. We did descriptions of the palimorphs found and microphotographs were taken of the pollen samples. The images were processed using ImageJ 1.53. Pollen collections were treated and analyzed at the Botanic Laboratory of the UAGRAM.

The pollen was identified comparing morphological characteristics with the pollen library we built for this study, as well as with existing catalogs and taxonomic keys of zones similar to the study area (Colinvaux, 1999; Roubik and Moreno, 1992). The most reliable level of identification for the pollen samples that we reached was the genus level; thus, we present the results based on this taxonomic level. After pollen identification we also added the plant genera life form, in the same way we did for the flowering plants availability data set.

Availability and use data were collected in 2022, from May to July (dry season) and from October to November (wet season) from a total of seven *T. fiebrigi* hives from *Ind* and six from *Trad,* found in a period of one week. Our data was thus collected from a total 12 hives: *5–10* at *Ind* and *11–16* at *Trad* (Fig. 1). Additionally, four *Apis mellifera* hives were found at *Ind* and a total of 37 other native bee species, including parabita, obobosi, oro, suro, and plebeyas, at *Trad.*

We were unable to collect resource use data from hive *Ind4* as this harvested by people before we began data collection. For hives *Ind6* and *Ind8* we could not collect pollen samples for June, as bees returned to the nest without any pollen in their corbicula. A similar behavior was observed for *Ind10* in October and November. When not carrying pollen, bees were observed with nectar, water and/or resin in their legs, especially on cloudy days.

2.3. Data analysis

We employed multivariate, descriptive and inferential tests to answer our research questions. Our results are grouped by farming community (*Ind* or *Trad*), because our objective was to broadly understand how the adoption of different agricultural models (industrial vs. traditional) affected the availability and use of *T.fiebrigi* feeding resources. Our results are most likely influenced by the seasonal flowering patterns of the study zone (S14) (Danner et al., 2017), yet, we analyzed the pool of data to simplify the narrative of the manuscript. All analyses were executed using R 4.1.2 (R Core Team, 2024).

2.3.1. Available flowering plants

We used the information of the vegetation surveys to describe the available flower resources surrounding the hives at the two farming communities. We calculated the richness of flower resources around each hive and grouped them by farming community (*Ind* and *Trad*). The richness (S) was the total number of genera found around each hive. Then, we conducted a nonparametric Wilcoxon-Mann-Whitney test using the “wilcox.test” function in R (R Core Team, 2024) to assess whether there was a significant difference in floristic plant richness (S) between the two agricultural settings. Although our data was normally distributed, we employed this non-parametric text due to our small sample size ($n = 12$) (Shapiro-Wilk normality test $W_S = 0.92$, $p = 0.30$; S2).

We then performed a multivariate analysis using the presence-absence of the plant genera, to understand the composition of the vegetation surrounding the hives at the two farming communities. For this, we employed Principal Coordinate Analyses (PCoA; also known as Multi Dimensional Scaling). PCoA was chosen over PCA, one of the most frequently used unconstrained ordination methods, since our data set comprised zeros and ties (Ramette, 2007). In such cases, PCoA is a better method to represent inter-object dis-similarity. We applied the PCoA function of the Ape package (Paradis and Schliep, 2019). To calculate the distance measures, we used the used the Bray-Curtis method which is appropriate for count or abundance data. Following Kaiser’s criterion (Foguesatto et al., 2019) we focused on the interpretation of the first axis of the ordination, as the eigenvalues dropped below one after this axis. The results of the PCoA were used to visualize the flowering vegetation composition and to understand how the variables “habitat” and “lifeform” related to the plant communities.

As performed in spatial ecology, we then calculated the centroid of each group (farming community) (function Ordiellipse of Vegan, Oksanen et al., 2022). Centroids represent the average position of the data points of a particular group. We performed Permutational Multivariate Analyses of Variance (PERMANOVA) to test if the centroids of the vegetation of the two farming communities showed significant differences between each other. The centroids of the groups of the PCoA were significantly different: $F = 9.68$, $p = 0.007$.

Additionally, we tested if the richness (S) between pairs of similar habitat types from the two farming communities showed significant differences. We compared if the S of the fallows, home gardens, crops, forests and wetlands from *Ind* differed from those of *Trad.* We used the non- parametric Wilcoxon-Mann-Whitney test (function “wilcox.test”) (R Core Team, 2024) due to our sample size. The same was done with the variable life form.

Finally, we plotted the life form richness percentage per habitat, to explore the structural composition at each habitat type. We performed a Chi-square test to assess if there were differences in the proportion of life forms available between the two farming communities.

2.3.2. *T. fiebrigi* used resources

To understand the characteristic of resource use of *T. fiebrigi* we first estimated the overall genus richness (S) between farming communities (*Ind* and *Trad*). We tested for normality using the Shapiro-Wilk normality test, which showed a normal distribution for the richness data ($W_S = 0.94$, $p = 0.45$; S2). However, we performed the non-parametric Wilcoxon-Mann-Whitney test due to our sample size ($n = 12$), to understand if there were significant differences in the visited plants’ richness between the groups.

To further understand the types of plants used as feeding resources at the two farming communities, we plotted the proportion of the different life forms, grouped by the farming community. We first tested if there were differences between farming communities using the Wilcoxon-Mann-Whitney test. Then, we calculated Fisher’s Exact Test to identify differences in the total proportions of visited life forms between *Ind* and *Trad.* This test was preferred over the Chi-square test, given the expected low frequencies of the dataset.

Finally, in order to obtain an indicator of resource selection, we calculated a ratio between used and available flower resources. This ratio allowed exploring if bees visited the different life forms in relation to their availability. For this, we calculated the available and use proportion for each life form at each farming community, and then divided the used proportion to the availability proportion to obtain Manly's selection ratio (w_i) (Manly et al., 1993):

$$W_i = P_{use,i}/P_{ava,i}$$

Where, W_i is the ratio of a given life form "i". $P_{use,i}$ and $P_{ava,i}$ are the proportion of use and availability of a life form "i", respectively. For each life form, results of $W_i = 1$, indicated use was done in proportion to its availability. On the contrary, $W_i > 1$ indicated that a life form was preferentially used, whereas $W_i < 1$ indicated underuse.

Use–availability ratios lack a probabilistic interpretation and do not account for sampling uncertainty. The sampling uncertainty in W_i was quantified by Wald-type 95 % confidence intervals, following Manly et al. (1993). If Standard errors (SE) varied below one, their overall Wi was not considered as significant. SE were computed assuming a multinomial sampling distribution for use frequencies and fixed availability:

$$SE(Wi) = \surd\ P_{use,i}(1 - P_{use,i})/U(P_{ava,i})^2$$

We plotted the size effect (use/availability) and the SE per farming community using a scatter plot.

3. Results

3.1. Resource availability at two farming communities

A total of 2386 flowering plants were recorded, representing 203 genera across 61 families identified. The Wilcoxon-Mann-Whitney test showed non-significant differences in floral richness between two farming communities (*Ind*: 135 total genera, *Trad*: 132 total genera; Ws = 17, *p* = 0.94). The median values of richness were slightly lower for *Ind* with 68 ± 12.9 genera vs. 71 ± 14.7 for *Trad.*

The first axis of the ordination analysis (PCoA) explained 58 % of the variation of the data (Fig. 2). To the left, we observe a gradient structured by flowering plants of wetlands, croplands and home gardens, herbs and lianas. The right side of the gradient was structured by grasslands, forests and fallows flowering plants, as well as by trees and shrubs. The flowering plant composition of *Ind* and *Trad* were dissimilar, as they did not overlap in the ordination space: *Ind* was placed at the left side of the ordination gradient and *Trad* at the right (Fig. 2).

To the left side of the ordination - and thus associated with *Ind* – the most representative genera were *Helianthus* (herb)*, Ipomoea* (liana)*, Solanum* (shrub), as well as *Parthenium* and *Heliotropium* (herbs)*,* which were mainly present in croplands (Figure 2, S4). *Hibiscus* (shrub), *Solanum* (shurb), *Parthenium* (herb), *Croton* (herb, shrub), *Tecoma* (tree), were also frequent genus and were found at home gardens (Figure 2, S4). The composition on the right side of the ordination - associated with *Trad* - was characterized by the presence *Croton, Ruellia* (shrub), *Abutilon* (shrub), *Cantinoa* (herb), *Sida* (herb, shrub) and *Lippia* (shrub), and these were frequent in fallows. The shrub *Senna*, as well as the trees *Parthenium*, *Cantinoa*, *Samanea* were also frequent and found in home gardens, and *Croton* was common in grasslands (Figure 2, S4).

The highest richness of flowering plants was registered at home gardens and fallows at *Ind* and *Trad*, respectively (Table 2, Figure 3, S4). Home gardens at *Ind* had a median of 60 ± 28.8 genera and fallows 25 ± 9.37 genera. At *Trad*, fallows had the highest plant richness with 51 ± 18.2 genus, followed by home gardens with a median of 35 ± 12.5 (Table 2, Fig. 3). There were significant

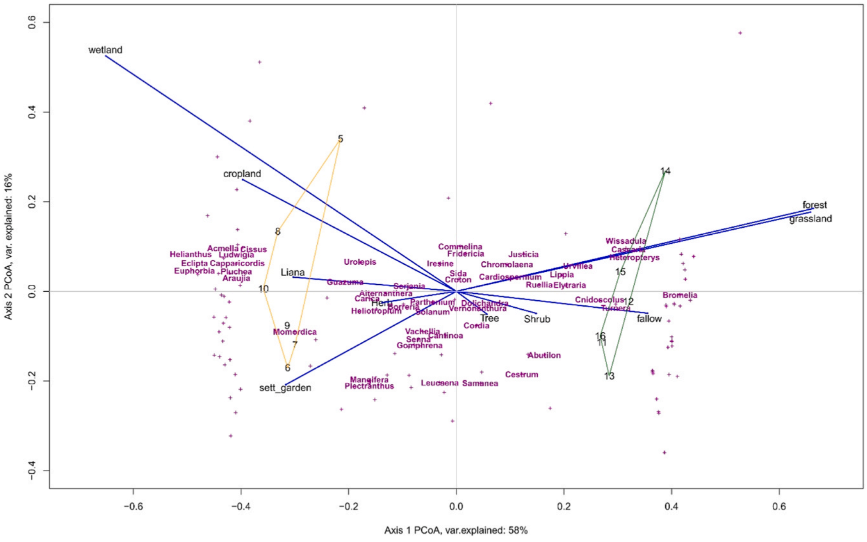

Fig. 2. Principal Coordinate Analyses (PCoA) of the available flower resources. The blue arrows represent the variables "habitat" and "life form", in violet are the names of the most frequent genera (relative frequency) and the plus sign "+ " represents less abundant genera. The yellow polygon represents the hives at *Ind* (agroindustrial) (5−10) and the green polygon the hives at *Trad* (traditional) (11−16).

differences between the richness of plants found in fallows between the two farming communities (U=4, n_{ind}= 6; n_{trad}= 6, $p = 0.03$; Table 2).

The highest overall richness was found for herbs and shrubs at Ind and shrubs and trees at Trad. We found significant differences between herbs, shrubs and liana richness between the communities (Table 2). However, there were no significant differences in the overall proportion of lifeforms between the between *Ind* and *Trad* when performing a Chi-square test (X^2= 6.59, p = 0.1, df= 3).

3.2. *T. fiebrigi's food*

T. fiebrigi visited a total of 72 flower genera belonging to 31 families. Of these, 54 genera belonged to *Ind* and 35 to *Trad*. We did not find significant differences in the richness of visited flowers between the farming communities (W_s= 25.5, $p = 0.25$), though, a higher, but more variable, number of flower genera were visited at *Ind*, with a median of 15 ± 6.57, compared to 10 ± 2.04 genera at *Trad*.

There were no differences between the richness of pairs of life forms visited between the communities *Ind* and *Trad* (Table 2). However, the total proportion of the life forms visited by *T. fiebrigi* significantly varied between the two farming communities (Fisher-Exact Test $p < 0.001$) (Figure 4, S8). At *Ind*, bees relied mostly on trees and herbs, whereas at *Trad* trees contributed the most to the proportion of plants visited (Fig. 4). The most important diet items were at *Ind* were the herbs *Chenopodium* and *Conyza,* as well as the shrub *Senna* and shrub-tree *Celtis* (S8). Other identified genera in the pollen samples included the trees *Androanthus*, *Ricinus* and the shrub-herb *Croton*. At *Trad,* bees mainly relied on tree *Zanthoxylum,* the shrub-tree *Celtis*, and the trees of the genus *Astronium* and *Citrus*. Other less important items included shrubs (e.g. *Hamelia*), shrubs-herbs (e.g. *Bauhinia*), herbs (e.g. *Pseudananas*) and lianas (e.g. *Arrabidea*) (S8).

The Manly selection ratio (Wi) indicated that the different life forms were used according to their availability at *Ind.* Although we observed the Wi values of *Ind* across lifeforms were above one, they presented a large variability and thus could not be interpreted as preference (Figure 5, S11). On the contrary, there was a consistent selection of trees at *Trad*. The other life forms were used according to their availability (Fig. 5; S11).

4. Discussion

Bees play vital social-ecological roles within agroecosystems, notably pollination (Vaidya et al., 2023). Despite extensive research of land-use impacts on bee communities, the ecology of tropical bee species remains understudied (Bottero et al., 2023; Shanahan, 2022; Vides-Borrell et al., 2019; Potts, 2016). Understanding the foraging ecology of bees in different agroecosystems is critical for conservation, as it can reveal how farming models affect the availability and use of floral resources — factors that largely determine pollinator survival (Roubik et al., 2005; Kaluza et al., 2017; Shanahan, 2022). This study compared the characteristics of floral resource availability and utilization in two farming communities of eastern Bolivia: agroindustrial (*Ind*) and traditional (*Trad*). Below, we discuss (a) the contribution of home gardens and fallows to plant richness and structural complexity, (b) the foraging differences of *T. fiebrigi,* and (c) situate these findings within the broader context of ongoing agroindustrial expansion in Bolivia.

Table 2

Detail of the richness (S), median S, and confidence interval of available and used flowering plant genera of the agroindustrial (*Ind*) and the traditional (*Trad*) farming communities. Data is separated by the habitat where plants were found, as well as by their life form. We also present the U-test – pairs: Wilcox-Mann Whitney test between pairs of habitats and life form types of the two farming communities, "*" indicates significant results, "n_i" are the sample sizes.

AVAILABLE	**S**		**Median S**		***U* test - pairs**
Per habitat	**Ind**	**Trad**	**Ind**	**Trad**	
Cropland	69	34	22 ± 11.4	19 ± 11	U= 12.5, n_{ind}= 6; n_{trad}= 3, p = 0.43
Fallow	80	105	25 ± 9.37	51 ± 18.2	U= 4, n_{ind}= 6; n_{trad}= 6, $p = 0.03$*
Forest	1	55	1	21.5 ± 7.4	U= 0, n_{ind}= 1; n_{trad}= 4, $p = 0.28$
Grassland	4	64	4	23 ± 17.9	U= 0, n_{ind}= 1; n_{trad}= 3, $p = 0.37$
Home garden	106	75	60 ± 28.8	35 ± 12.5	U= 11, n_{ind}= 5; n_{trad}= 3, p = 0.37
Wetland	28	0	9 ± 12.8	Na	Na
Per life form					
Herb	53	34	29 ± 6.05	17.5 ± 5.42	U= 33.5, n_{ind}= 6; n_{trad}= 6, p = 0.01*
Shrub	37	42	18.5 ± 2.79	26 ± 5.47	U= 5.5, n_{ind}= 6; n_{trad}= 6, p = 0.05*
Liana	18	12	10.5 ± 2.07	6 ± 2.17	U= 33.5, n_{ind}= 6; n_{trad}= 6, p = 0.01*
Tree	36	52	17.5 ± 7.28	23 ± 5.32	U= 8, n_{ind}= 6; n_{trad}= 6, p = 0.12
Total/median$S_{availability}$	135	132	68 ± 12.9	71 ± 14.7	
USED					
Per life form					
Herb	13	4	4.5 ± 1.97	1.5 ± 0.6	U= 18, n_{ind}= 6; n_{trad}= 4, p = 0.21
Shrub	8	4	2 ± 1.73	2.5 ± 2.12	U= 4.5, n_{ind}= 4; n_{trad}= 2, p = 1
Liana	6	1	1 ± 1.10	1	U= 3.5, n_{ind}= 5; n_{trad}= 1, p = 0.72
Tree	18	20	4 ± 2.8	6 ± 1	U= 10.5, n_{ind}= 6; n_{trad}= 6, p = 0.25
Shrub-herb	6	3	2 ± 1.15	1 ± 0.5	U= 11, n_{ind}= 4; n_{trad}= 4, p = 0.40
Shrub-tree	4	3	1 ± 0.8	1 ± 0.8	U= 10.5, n_{ind}= 5; n_{trad}= 5, p = 0.69
Total/median S_{use}	54	35	15 ± 6.57	10 ± 2.04	

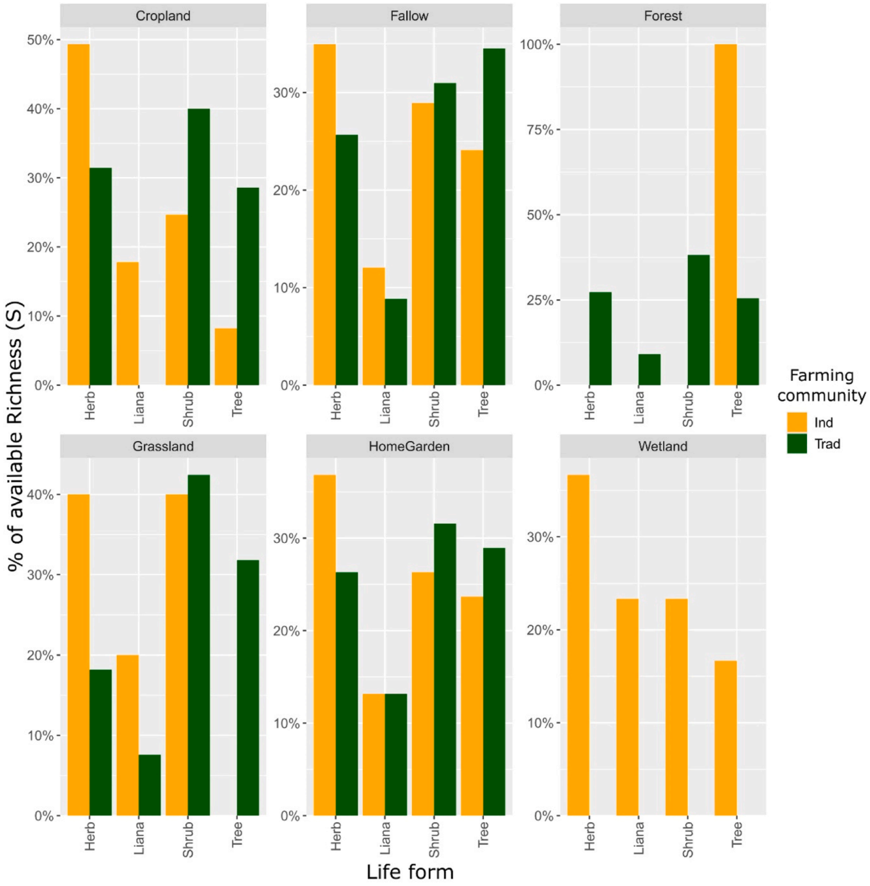

Fig. 3. Percentage of the richness (S) of available flowering plants grouped by habitat, life form and farming community *Ind* (agroindustrial) and *Trad* (traditional).

4.1. *Flower resource availability in two farming communities*

Ind and *Trad* exhibited a similar availability of flowering plants. We expected lower richness at *Ind*, due to the prevalence of monocultures and pastures surrounding most of the hives. It was therefore notable that its richness was comparable to *Trad*. Taxonomic diversity is not by itself a good indicator of the differences in plant communities, as it does not inform about the characteristics of the species that are part of a plant community (Ma and Herzon, 2014). However, looking at the plant life forms present at *Ind,* a simplified proxy of its structural complexity, we observe that all life forms were represented in the agroindustrial community *Ind*.

These results may have been influenced by the smaller extension of *Ind*. This study area did not exceed 3000 ha (Fundacion TIERRA 2023b), compared to more 37,000 ha at Trad (Fundacion TIERRA 2023a). As such, greater land use heterogeneity may occur within smaller areas, and thus within the bees' flight ranges. Nonetheless, consistent with the findings by Siebert (2002), a higher proportion of the flowering plants recorded at *Ind* were herbs, indicating a higher degree of vegetation disturbance (S6). Monoculture farming landscapes are typically dominated by herbaceous species because the high ambient temperatures in sun exposed crops (such as monocultures) can inhibit the establishment of other vegetation types. This effect is further intensified by management practices characteristics of agroindustrial monocultures, such as herbicide use (Siebert, 2002).

Furthermore, the overall high richness and other types of plant life forms (e.g. trees, lianas, shrubs) found at *Ind* were primarily influenced by the presence of flowering plants in home garden, which were often found within the bees' flight ranges. Home gardens can exhibit high structural complexity, comprising multiple vegetation layers even within small areas, and serve as key resource habitats for a variety of animals — including bees (Gibson et al., 2007; Roubik et al., 2005; Patel et al., 2022; Santos et al., 2022; Donald, 2004) — even in landscapes dominated by agroindustrial production (Cely-Santos and Philpott, 2019; Hinners et al., 2012; Kaluza et al., 2016).

Despite the richness of flowering plants that home gardens can harbor, these habitats are often composed of non-native and urbanophilic plants (Liira et al., 2008; Wood et al., 2022). Indeed, most of the flowering plants found in home gardens were herbs. However, they also exhibited the highest richness of trees, shrubs, and lianas (Table 2; Fig. 3). Our results thus underscore the importance of home gardens in promoting structural complexity and increasing floral availability, particularly at *Ind*. At the farming community *Trad*, the highest overall species richness was found in fallows, which were dominated by woody vegetation (shrubs and

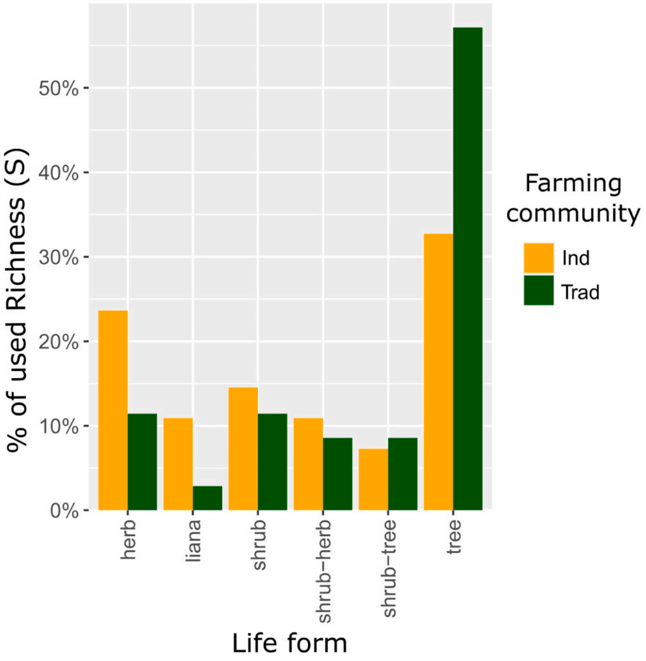

Fig. 4. Percentage of the richness (S) of used flowering plants grouped by habitat, life form and farming community *Ind* (agroindustrial) and *Trad* (traditional).

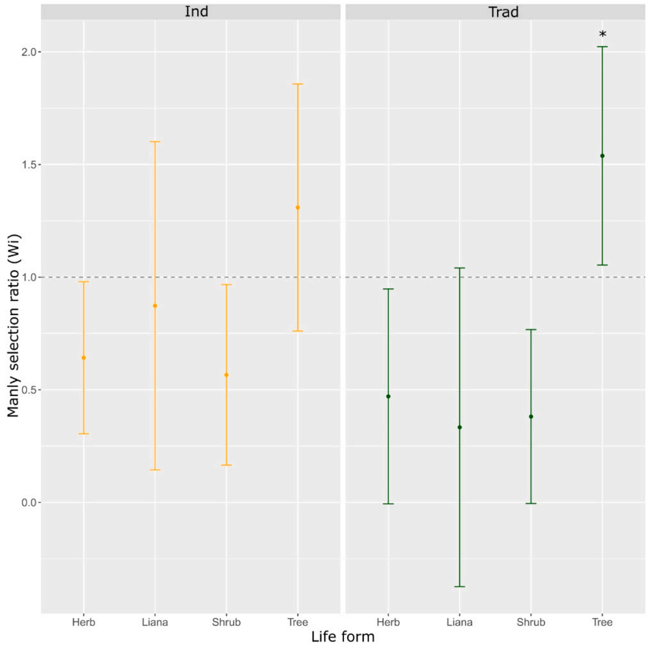

Fig. 5. Manly selection ratio (Wi) and confidence intervals for the different life forms used by bees, grouped by farming community: agroindustrial (*Ind*) and traditional (*Trad*). Significant selection of a life form is marked with an asterisk “*”.

trees). Habitats with intermediate levels of disturbance, such as fallows, often sustain high plant diversity and structural complexity (Siebert, 2002; Ma and Herzon, 2014).

The higher richness and diversity of life forms found in the fallows and home gardens likely reflect local plant-use practices. Indigenous farming communities, such as *Trad* and *Ind*, rely heavily on the resources of these habitats as integral components of their livelihoods, despite their integration to agroindustry (Mahonya et al., 2019; Galhena Dissanayake and Maredia, 2020; S15). In particular, woody plants provide valuable resources such as wood and medicine, and are therefore intentionally managed and conserved in such habitats, contributing to the overall plant diversity of agroecosystems (Mahonya et al., 2019; Ruelle et al., 2019, Perfecto et al., 2019).

4.2. *T. fiebrigi* foraging

We observed two main aspects of *T. fiebrigi* foraging in the studied farming communities: First, although no significant differences were detected in the richness of visited plants—likely due to our limited sample size (Well et al., 1990)—bees at *Ind* visited a greater, albeit more variable, number of genera than those at *Trad* (54 vs. 35 genera, respectively; Table 2). Second, the bees in the two farming communities seemed to focus on foraging different plant life forms. The bees from *Trad* foraged primarily on trees, whereas those at *Ind* visited mostly trees and herbs. Furthermore, the selection-ratio analyses indicated that bees at *Trad* seemed to prefer trees, while those at *Ind* used all plant types roughly in proportion to their availability, suggesting no marked preference for a resource type.

The global richness values align with the previously reported polylectic behavior of this species (e.g. López-Roblero et al., 2023; Saravia-Nava et al., 2018; Flores et al., 2021; Almeida Braga et al., 2012; Vossler, 2021; Adler et al., 2023). However, these previous studies did not compare resource use in between sites or farming contexts. In our results, the higher and more variable number of plant genera visited, as well as the lack of preference for a specific type of resource for the agroindustrial community (*Ind*), may reflect a compensatory strategy to obtain sufficient or high-quality resources. Each hive likely adjusts its foraging strategy to the resource availability within its flight range (e.g., Kaluza et al., 2017; Vaidya et al., 2023; Danner et al., 2017). When nutrient-rich sources are available, stingless bees may concentrate on few or even a single resource type (Adler et al., 2025). In fact, most of the studies involving *Tetragonisca* – which were carried in habitats with low levels of disturbance – show this bee species can exhibit some level of specialization on certain resources (Adler et al., 2024; Saravia-Nava et al., 2018; Flores et al., 2021). For instance, in the Amazon-Chiquitano Forest, *Tetragonisca angustula* was observed to visit 55 pollen types, but primarily forage on a small subset of plants, particularly on Fabaceae, Sapindaceae, Araliaceae, Euphorbiaceae (Saravia-Nava et al., 2018; Flores et al., 2021). Adler et al. (2023) reports fewer types of pollen (13 types from nine families) and also reports the presence of principal and secondary (less frequent pollen) sources.

Conversely, when preferred resources are scarce or of low nutritional quality, bees may broaden their dietary breadth to include less-preferred options (Pyke, 1977; Donkersley, 2019; Donkersley et al., 2017; Maurer et al., 2024). Indeed, resources that might otherwise be secondary (i.e. less rewarding) can become central when there is a reduction of food supply (de Novais and Absy, 2013). This adaptative response known as the “optimal diet” is central to the Optimal Foraging Theory (Jesmer et al., 2020; Pyke et al., 1977; Rubenstein and Alcock, 2019; Donkersley et al., 2017).

Woody plants – particularly trees – have previously been identified as potentially limiting resources for bees (Donkersley, 2019; Ramalho, 2004, Roubik et al., 2005). When these resources cannot be easily detected, bees could shift their diet visiting a broad variety of herbs and other life forms (Guimarães et al., 2021; Liira et al., 2008; Saravia-Nava et al., 2018; Donkersley, 2019; Donkersley et al., 2017). The previous studies on *T. fiebrigi* do not report specifically the plant life forms they collect, yet when looking at the plants reported as part of the diet spectrum, we observe that over 50 % of *Tetragonisca* pollen diet derived from various tree species (Saravia et al., 2018). Similar trends were observed in forest-agro-livestock systems of the Paraná Atlantic Forest in Brazil (Flores et al., 2021). In contrast, Adler et al. (2024), found that generalist bees such as *T. angustula* and *Scaptotrigona polysticta* often conditioned mono-floral honeys of lianas, herbs or trees. Our results show that *Trad* strongly focused on visiting trees and that they were also selected above their proportional availability. Furthermore, although *Ind* did not show preference for a resource type, trees were an important part of the resources they visited. These results support the importance of these types of resources for bees, even in farming communities distinct farming histories.

Although the studies pointing to the importance of different lifeforms, and particularly of trees for bee diets are still uncommon, these plants have been reported to have higher nutritional value (e.g. protein content) and larger pollen volumes, which may explain their significance as pollen sources in both farming communities (Cannizzaro et al., 2022; Hicks et al., 2016; Wood et al., 2022; Donkersley, 2019, Adler et al., 2025, Guimarães et al., 2021; Bisui et al., 2019).

While these findings provide valuable insights into potential variations in foraging behavior and the relative importance of certain plant types, they should be interpreted cautiously, particularly when considering management recommendations. First, future research should test our propositions with larger sample sizes to assess whether these observed patterns persist. Second, bees depend not only on trees –or any single life form– but complement their diets with a diversity of perennial and annual plants that vary seasonally according to climatic conditions and colony needs (Bueno et al., 2023; Donkersley, 2019; Adler et al., 2025; de Novais and Absy, 2013). Accordingly, feeding and preference studies should be conducted across multiple seasons, taking into account the flowering peaks, as well as precipitation and temperature, which are key factors influencing floral availability (Roubik et al., 2005; De Novais and Absy, 2013; Danner et al., 2017; Vaidya et al., 2023). Bees collect most of their feeding resources during flowering peaks (Roubik et al., 2005), yet our study did not coincide with these periods due to logistic limitations, which likely influenced our results. In the Chiquitanía, flowering occurs throughout the year, with distinct peaks during the rainy season (December-January) and again towards its end (April) (Justiniano and Fredericksen, 2000). Sampling during these periods could provide further insight into the selection of mass-blooming plants, such as trees.

Additionally, future studies should also examine the characteristics of flowers visited by bees — including flower density, abundance, nutritional content and other floral such as color, shape —to better elucidate the role of different plants in bee diets (Guimarães et al., 2021; Lozada-Gobilard et al., 2025; Adler et al., 2025).

Moreover, although we did not observe the presence of resins in our samples, the presence of nectar could go undetected and have influenced the results we presented. Unintentional pollen collection, which occurs when bees visit flowers for nectar or resin collection, should be accounted in the future. Stingless bees obtain most of their carbohydrates from nectar, and thus sometimes unintentionally collect pollen from plants they search for as nectar sources (Lozada-Gobilart et al., 2025). Resins are useful for other hive functions such as protection from parasites as well as communication (Villagómez et al., 2024; Adler et al., 2025) and could also lead to unintended pollen collection.

Furthermore, the sampling method for understanding the availability of flowering plants likely affected our results. We used straight transects around the hives record flowering plants, yet bees do not necessarily have circular or straight flight patterns (Wolf et al., 2016). Many of the plant genera that were visited by the bees were not present in the availability survey (S12). Thus, the ratios we presented may not accurately reflect true preferences but rather a limitation of the sampling method. Future research could also explore the flight characteristics of these bees, as it is difficult to measure which food sources are available without an understanding of the bee's motility (Kaehler et al., 2024; Wolf et al., 2016).

Finally, the foraging behavior of *T. fiebrigi*, was certainly modulated by the presence of other pollinators and bees (Nagamitsu and Inoue, 2005; Vaidya et al., 2023; Adler et al., 2025). The presence and behavior of more competitive or specialist species shapes which resources are accessible (Roubik et al., 2005, Nagamitsu and Inoue, 2005; Vaidya et al., 2023) and should be examined in different agroecosystems. At *Ind*, for instance, the growing presence of feral and managed *Apis mellifera* colonies could displace native bees from preferred foraging resources (Roubik et al., 2005, Nagamitsu and Inoue, 2005; Vaidya et al., 2023).

4.3. Counterbalancing the effects of agroindustry

Our results indicate that contrasting farming models did not result in different richness of flowering plants available but did influence the composition of both plant communities and bee diets. Although generalist bees such as *T. fiebrigi* can adapt their diets to changing environments through flexible exploitation of diverse floral resources (Bueno et al., 2023; Maurer et al., 2024), the advancement of deforestation in Bolivia, particularly in the Chiquitanía, could have significant implications for the future of biodiversity and of bees (Vos et al., 2020).

The *Ind* farming community is seeking to further transform the remaining semi-natural vegetation (e.g. wetlands) within their territory to arable land for landless farmers. However, the machinery required to drain wetlands is expensive and thus largely inaccessible, though it is perceived as essential for securing livelihoods. As Maurer et al. (2024) mention, bee communities can withstand certain levels of landscape transformation, but beyond a certain threshold, their persistence declines due to severe resource shortages (e.g. feeding). Even farming communities such as *Trad*, are projected to be incorporated into the expanding agroindustrial zone in the Chiquitanía within the next decade and are already subject to significant illegal deforestation (Fundación TIERRA 2023a). This may have already influenced the floral availability and the foraging strategies we observed in this community.

The effects of the ongoing land use changes will likely be aggravated by the recurrent use of pesticides associated with agroindustrial farming practices (Potts, 2016; Shanahan, 2022), factor that should be also accounted for in future research.

Despite this concerning context, some positive aspects were evident, particularly within the agroindustrial community. Contrary to expectations, *Ind* exhibited a high flowering-plant richness, largely driven by the presence of home-garden vegetation. This finding suggests that agroindustrial landscapes are not necessarily biodiversity dead ends (Ortiz-Przychodzka et al., 2025). However, home gardens only represented a small surface at Ind (<9 ha over 2414 ha) and will not be able to sustain alone the diets of a whole bee population or community. Bee populations require enough and continuous resources that can be accounted at the landscape scale, and not only within the flight range of some hives (Roulston and Goodell, 2011; Goddard et al., 2010).

Still, the characteristics of this habitat may inform strategies to restore diversity in this farming community. This community could, for instance, draw inspiration from existing home-garden management practices to produce diverse crops. For insects to thrive, and thus fulfill their ecological and cultural functions, an agroecological production that relies on on-farm inputs, and the inclusion and conservation of various plant types would be needed in large surfaces (Perfecto et al., 2019; Goddard et al., 2010).

The presence of different plant types, and particularly trees and shrubs, is often perceived as competing with agroindustrial productivity and is rarely integrated in mitigation strategies for bee conservation or livelihood diversification (Donkersley, 2019). However, structurally complex vegetation that mimics the natural systems is actually compatible with crop production and can achieve multifunctional outcomes, including improving resource availability for species such as bees (Perfecto et al., 2019; Vaidya et al., 2023; Vallejo-Ramos et al., 2016).

Given the alarming current and projected land-use changes projected in the Chiquitanía and Santa Cruz in general (Tejada et al., 2016; Czaplicki-Cabezas, 2024), documenting changes of the floral availability and bee resource use in different farming regimes is essential. Such information can reveal how management strategies influence ecological outputs such as foraging behavior, which ultimately determine bee survival (Shanahan, 2022). Understanding the current differences in available and used floral resources by *T. fiebrigi*, could guide management and conservation strategies to enhance access to key flowering plants, and recognize practices that already support bees, which act as important pollinators in agroecosystems (Maurer et al., 2024). Ultimately, farming practices will largely determine the future of this fundamental group of this insects in Bolivian Chiquitanía.

5. Conclusion

Both farming communities, *Ind* and *Trad,* exhibited a similar richness of flowering plants. The highest genera richness was found in home gardens at *Ind* and in fallows at *Trad*. While *Ind* was primarily composed of herbaceous plants, *Trad* was dominated by shrubs and trees. *T. fiebrigi* exhibited a higher – but more variable – richness of genera visited at *Ind*. The bees foraged mainly on trees and herbs at *Ind*, whereas trees were the most important food source at *Trad*. Bees at *Ind* did not show a preference for any particular life form, while at *Trad,* trees were selected above their availability.

Overall, our findings emphasize the key role of fallows and home gardens in sustaining floral resources for bees across different farming systems and suggest that trees are essential food sources for *T. fiebrigi*. These results underscore the importance of maintaining structurally diverse vegetation to support pollinator populations. Future research with larger sample sizes and multi-seasonal data is needed to confirm these patterns and guide management strategies that reconcile agricultural productivity with pollinator conservation.

Author contributions

Conceptualization was made by CBF and JH; data curation by CBF and AS; formal analysis by CBF, PR, PS and FB; funding acquisition JH; investigation CBF, AS and DM; methodology AS and CBF; project administration JH; resources JH; software CBF, PR, PS and FB; supervision JH; validation JH; visualization CBF, PR, PS; writing – original draft CBF; writing – review and editing CBF, PR, PS, AS, FB and JH.

CRediT authorship contribution statement

Felipe Benra: Writing – review & editing, Visualization, Validation, Software, Formal analysis. **Daniela Morón Aguilar:** Validation, Investigation. **Jan Hanspach:** Writing – review & editing, Validation, Supervision, Software, Resources, Project administration, Methodology, Funding acquisition, Conceptualization. **Paula Rodriguez:** Writing – review & editing, Visualization, Validation, Software, Formal analysis. **Ping Sun:** Writing – review & editing, Visualization, Validation, Software, Formal analysis. **Benavides Frias Camila:** Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Alexandria Saravia-Nava:** Writing – review & editing, Validation, Methodology, Investigation.

Ethics statement

X Not applicable: This manuscript does not include human or animal research.
If this manuscript involves research on animals or humans, it is imperative to disclose all approval details.
If Yes, please provide your text here:

Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work the author(s) used Chat GPT-pro in order to refine the R code for refining the plots and grammar of the text. After using this tool/service, the author(s) reviewed and edited the content as needed and take(s) full responsibility for the content of the published article.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2025.e03990.

Data availability

Data will be made available on request.

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