

Regional native plants visited by *Melipona beecheii* (Apidae, Meliponini) as nectar and pollen resources in the Yucatán Peninsula, Mexico

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Abstract

Although the Mayan bee *Melipona beecheii* is the most relevant stingless bee cultivated in the Yucatán Peninsula, few studies document the plants it visits to collect food resources. This work seeks to contribute to the knowledge of pollen spectra in pot-honey from *M. beecheii* in the Yucatán Peninsula, as well as to infer through a comparative palynological analysis between pot-honey and pot-pollen assemblages, whether, during storage, the Mayan bee includes pollen resources that could modify plant richness in pot-honey. We analysed 27 pot-honeys collected from meliponaries located in the Yucatán Peninsula: Quintana Roo (10), Yucatán (10) and Campeche (7). A total of 15,416 pollen grains were identified, belonging to 83 taxa across 38 botanical families. The highest species and family richness was found in Quintana Roo (62 taxa), followed by Yucatán (35 taxa) and Campeche (31 taxa). The most representative taxa in the palynological spectra were from the tree stratum: *Bursera simaruba*, *Cochlospermum vitifolium*, *Eugenia* aff. *axilaris*, *Melicoccus oliviformis*, *Mimosa bahamensis*, *Metopium brownei*, *Senna racemosa* var. *racemosa* and *Solanum erianthum*. In addition, 63% of the honey samples (n = 17) were identified by pollen overrepresentation from polliniferous taxa such as *C. vitifolium*, *S. racemosa* var. *racemosa*, *Solanum* and *Mimosa* species. Three species that produce both nectar and pollen due to their floral morphology were identified as key for bee nutrition, namely *B. simaruba*, *G. floribundum* and *M. oliviformis*. Palynological assemblages of stingless bee pot-honey suggest that *M. beecheii* workers exhibit a special pot-honey storage behaviour that increases its pollen diversity.

Implications for conservation practices: The conservation of natural ecosystems where native vegetation thrives is a fundamental pillar for the survival of stingless bees and for the quality, diversity and sustainability of pot-honey production. The palynological profiles of *M. beecheii* pot-honey encompass a high diversity of native nectariferous, nectar-polliniferous and polliniferous plants, underscoring the importance of well-preserved natural ecosystems in supporting year-round resource availability for native bees in tropical regions.

Introduction

Bees play a fundamental ecological role as the principal pollinators of flowering plants on the planet (Roubik 1989; González-Acereto 2008, 2012), yet several social bee species also possess the remarkable ability to collect nectar and transform it into honey within their colonies, a process that has been harnessed by humans for thousands of years. In Mexico, the Yucatán Peninsula is notable for the meliponiculture—stingless bee beekeeping—of *Melipona beecheii* (Quezada-Euan et al. 2001; Ayala et al. 2013), which has been done since pre-Columbian times and is part of our biocultural heritage (SEMARTAT 2023). Honey production with this stingless bee was of great importance to the ancient Mayans, who revered it through the deity *Ah Mucen Cab* and used its pot-honey to prepare *balché*, a ceremonial beverage made with the bark of *Lonchocarpus longistylus* (Quezada-Euán 2005, 2018; González-Acereto 2008; Guzmán et al. 2011; Avilés-Peraza 2015; Quezada-Euán et al. 2015).

However, recent changes in land use caused by natural resource exploitation, urban sprawl, deforestation and climate changes have transformed and deforested entire plant communities and led to the loss of biodiversity (Sánchez-Aguilar and Rebollar-Domínguez 1999; Jaureguiberry et al. 2022), directly threatening native bee populations and the continuity of ancestral meliponiculture (Quezada et al. 2015). Specifically, recent works have reported significantly decreased honey production in *M. beecheii* colonies (Villanueva-Gutiérrez et al. 2005; Quezada et al. 2015) which serves as an indicator of the environmental impact of human activity on the availability of food resources for native bees. Therefore, understanding the feeding resources of stingless bees is essential, as these species collect nectar and pollen from a wide diversity of plants found in forest ecosystems (Vit et al. 2025). In fact, *M. beecheii* pot-honey is known for its distinctive organoleptic characteristics, namely higher humidity and acidity, numerous bioactive components such as phenols, flavonoids and vitamin C, and also for its high antioxidant capability compared to *Apis mellifera* honey (Alvarez-Suarez et al. 2018; Vit et al. 2025). Additionally, the bioactive components contained in the pot-honey are presumed to be influenced by the native plants foraged by the bees, which may also underlie the multiple nutraceutical and curative properties attributed to *M. beecheii* honey in local medicine (Vit et al. 2025). Despite the long-standing cultural and ecological relevance of *M. beecheii* pot-honey, few melissopalynological studies have been conducted to identify the floral resources visited by this species in the Yucatán Peninsula to produce pot-honey.

Melissopalynology makes it possible to determine the floral origin of pot-honey stored in nests, and propolis, revealing bee foraging preferences and vegetation targets. This approach also helps elucidate the role of bees as pollinators in ecosystems, as these insects are the primary agents of cross-pollination in flowering plants. In Mexico, systematic melissopalynological research on different stingless bee species was conducted in the southeastern region during the 1990s; however, *M. beecheii* was not included in these studies (Martínez-Hernández et al. 1993). To address this gap, recent research carried out exclusively in the state of Yucatán analysed the palynological assemblages of pot-honey and pot-pollen samples from *M. beecheii* colonies (Bacab-Perez et al. 2024). This study identified several nectar-foraged plant taxa including *Alternanthera ramosissima*, *Bursera* spp. and members of the Fabaceae family such as *Lonchocarpus* and *Crotalaria*. Moreover, Pérez-Morfi et al. (2025) examined pot-pollen from deciduous, semi-deciduous and semi-evergreen tropical forests across the Yucatán Peninsula, finding that *M. beecheii* shows a preference for Fabaceae pollen and observing the highest species richness in samples from semi-evergreen tropical forests in the state of Quintana Roo. Nevertheless, a comprehensive analysis of the palynological assemblages of *M. beecheii* pot-honey across the Yucatán Peninsula has yet to be performed, which limits the comparative understanding of its nectar-foraging behaviour. Furthermore, it is essential to determine pollen grain concentrations in pot-honey using *Lycopodium* marker tablets, as this provides information on the proposed extraction methods and the storage behaviour of native stingless bees.

As with many husbandry activities, meliponiculture practices have evolved in an attempt at technical modernisation. In this regard, several meliponicultors have opted to keep their colonies in rational hives, in contrast to ancestral practices in which *M. beecheii* colonies were maintained in hollow logs called

hobones (Quezada-Euán 2018). Rational hives provide better access to the colony for management and, depending on the colony design, separate the brood area from the food reserve storage area, which facilitates pot-honey harvesting with syringes. Taking advantage of these features for standardised sample acquisition, we collected pot-honey samples from colonies in the Yucatán Peninsula to conduct palynological analyses. The objectives of this study were to contribute to the knowledge of pollen spectra in pot-honey and the foraging behaviour of *M. beecheii* by evaluating the representation of pollen from polliniferous plant species in honey samples, as well as to infer through a comparative palynological analysis between pot-pollen and pot-honey profiles, whether, during storage, the Mayan bee includes pollen resources that could modify plant richness in pot-honey. Our results contribute to the identification of key melliferous plant species for *Melipona beecheii*, which may be considered in reforestation and habitat restoration actions aimed at conserving this bee species, while also improving the understanding of its honey storage behaviour.

Materials and methods

Study areas

This study was conducted in meliponaries found in 22 localities from 12 municipalities in Quintana Roo, Yucatán and Campeche, across the Yucatán Peninsula (Fig. 1, Table 1 supplementary material). The peninsula is characterised by shallow soil with abundant karst rock as well as elevations that do not exceed 400 m above sea level; these characteristics play a fundamental role in shaping the spatial distribution and species composition of the plant communities, thereby conferring a distinctive ecological profile to the region (Duno de Stefano et al. 2018). The state of Yucatán is predominantly covered by deciduous and semi-deciduous tropical forest, while the states of Campeche and Quintana Roo are characterised by the presence of semi-deciduous tropical forest and semi-evergreen tropical forest (Durán and Olmsted 1999; Flores and Espejel 1994; Flores-Guido et al. 2010). Compared to other tropical regions in Mexico, the Yucatán Peninsula exhibits relatively low botanical diversity, with approximately 2300 documented species distributed among 956 genera and 161 plant families. This limited diversity is mainly attributed to the climatic, edaphic and topographical homogeneity of the region (Pérez-Sarabia et al. 2017).

Sample processing and palynological analysis

A total of 27 *M. beecheii* pot-honey samples were collected with syringes in the Yucatán Peninsula, Mexico, during 2023: 10 pot-honey samples from four municipalities in Quintana Roo, 10 pot-honey samples from seven municipalities in Yucatán and seven pot-honey samples from the municipality of Calkiní, in Campeche (Fig. 1 and Table 1). At the *Laboratorio de Palinología: Paleopalínología y Actuopalínología* (LABPALINO), *Instituto de Geología*, UNAM, 50 mL of honey per sample was chemically processed. Initially, each honey sample was diluted in hot distilled water and centrifuged to concentrate the pollen grains. Then a *Lycopodium* spore marker tablet was added, the sample was dehydrated with

acetic acid and the acetolysis technique of Erdtman (1960) was applied. Finally, slides were prepared with glycerine gelatine.

Slides were analysed using a Zeiss Axiolab photomicroscope with a 100X objective. Pollen grains were identified using references from pollen collections, palynological catalogues and previous melissopalynological studies (Palacios-Chávez et al. 1991; Roubik and Moreno 1991; Martínez-Hernández et al. 1993; Ramírez-Arriaga et al. 2018, 2020; Bacab-Pérez et al. 2024; Pérez-Morfi et al. 2025). Melissopalynological analyses consisted of the identification and random counting of 500 pollen grains per sample to estimate richness and the percentages of each taxon. Species were classified as predominant pollen ($P \geq 45\%$), secondary pollen ($S = 16-45\%$), important minor pollen ($I = 3-15\%$) and minor pollen ($M \leq 3\%$) in the pollen analysis (Louveaux et al. 1978). The predominant and secondary pollen grains recorded in the honey samples were photographed using a Canon camera and the AxioVision program.

Different sources were consulted in order to determine whether the species recorded in the palynological spectra were nectariferous, polliniferous or nectarpolliniferous (Martínez-Hernández et al. 1993; Pennington and Sarukhán 1998; Villanueva-Gutiérrez et al. 2009, 2018; Alfaro-Bates et al. 2010; González-Ramírez 2014; Ramírez-Arriaga et al. 2018, 2023).

Characterisation of samples by the absolute number of pollen grains

The absolute number of pollen grains in 10 mL of pot-honey was calculated and grouped into classes according to Maurizio's method (Louveaux et al. 1978; Der Ohe et al. 2004) with some modifications. Class I or pollen-poor honey (underrepresented pollen) contains $\leq 20 \times 10^3$ pollen grains in 10g of honey; in Class II ($21 \times 10^3-100 \times 10^3$) mostly multifloral honeys are included: honeydew honeys and mixtures of flower and honeydew honeys; Class III honey is rich in pollen (overrepresented pollen) and honeydew honeys ($101 \times 10^3-500 \times 10^3$); Class IV honey exhibits strongly overrepresented pollen and some pressed honeys ($501 \times 10^3-10^6$); Class V has only pressed honey ($> 10^6$) (Louveaux et al. 1978; Der Ohe et al. 2004).

Analysis of pollen assemblages

Palynological spectrum graphs were designed by state using the Tilia Graph program, and a CONISS analysis (Grimm 1987) was performed using the incremental sum of squares method to identify groups among samples from Quintana Roo, Yucatán and Campeche. To assess the diversity of *M. beecheii* in pot-honey, we calculated alpha diversity using Hill numbers (Hill 1973), following the estimation method proposed by Chao et al. (2014) and implemented in the *iNEXT* package in R (Hsieh et al. 2016). This framework extends both the sample-size-based approach (Colwell et al. 2012) and the coverage-based approach (Chao and Jost 2012) to generate rarefaction and extrapolation curves of species diversity derived from Hill numbers. Sample-size-based rarefaction and extrapolation curves were constructed in

order to obtain asymptotic diversity estimates with 95% confidence intervals calculated through a bootstrap procedure with 200 replications (Chao et al. 2014). For both coverage and diversity analyses, extrapolations were extended to twice the sample size recorded for each state in the Yucatán Peninsula (Chao et al. 2014).

A principal coordinates analysis (PCoA; Gower 1966) was performed on pollen data by constructing a dissimilarity matrix based on species composition and abundance. The matrix of species abundance across samples was transformed using the Hellinger correction for the double-zero problem, ensuring that the distance calculations were not affected by the absence of a species in two different samples. The Bray-Curtis dissimilarity coefficient was calculated for the composition and abundance matrix. A weighted principal coordinates analysis was then performed using two dimensions. An additive constant was added to the non-diagonal dissimilarities to ensure that all eigenvalues were non-negative. A *post hoc* permutational multivariate analysis of variance (ADONIS) was performed with 1000 permutations and the application of the Benjamini-Hochberg correction for multiple comparisons. This analysis sought to test differences in the overall species composition and abundance among the three states: Campeche, Quintana Roo and Campeche. A scatterplot was created to visualise the results using the first two PCo dimensions, highlighting sample groups by state. We identify the pollen species that structure the pollen spectra among states.

We also used a Shankey diagram (R library *ggsankey*) to illustrate the most abundant pollen types in the pot-honey samples of *M. beecheii* in the states of the Yucatán Peninsula. To analyse the influence of the main types of pollen grains (> 3%) on bee food in the Yucatán Peninsula, we constructed an interaction network with the *bipartite* package of R. For this, we used the data from Pérez-Morfi et al. (2025) on the morphotypes of pollen grains detected in pot-pollen samples and those identified in pot-honey from this study.

PCoA, Shankey diagram and interaction network analyses were performed using the R software (version 4.3.1; R Core Team 2023) along with the *vegan* (version 2.6–10; Oksanen et al. 2025) and *ggplot2* (version 3.5.2; Wickham 2016) libraries.

Results

Botanical composition and diversity of pot-honeys

Across the 27 pot-honey samples from the three states of the Yucatán Peninsula (Fig. 1, Table 1 supplementary material), a total of 15,416 pollen grains were counted, 570 per sample. A total of 83 pollen morphotypes representing 38 botanical families were identified, which encompass 42 tree species, nine shrub species, 15 herb species, six climbers and one parasitic plant. 10 pollen morphotypes remained undetermined. Pollen from tree species constituted 84% of the samples from Quintana Roo and 97% of the samples from Yucatán and Campeche (Table 2 supplementary material).

In terms of abundance, the most prevalent botanical families were Fabaceae, Bixaceae, Burseraceae, Sapindaceae, Polygonaceae, Myrtaceae, Solanaceae and Euphorbiaceae (Fig. 2A). When analysed by state, the Sapindaceae, Burseraceae, Fabaceae and Solanaceae families were the most abundant, with over 500 pollen grains recorded in the samples from Quintana Roo. In the state of Yucatán, the most prevalent families were Fabaceae, Bixaceae, Polygonaceae, Burseraceae and Myrtaceae, whereas in the state of Campeche, only Fabaceae and Bixaceae were represented with over 500 pollen grains in the pot-honey samples (Fig. 2A).

As for pollen diversity, the samples from Quintana Roo exhibited the highest richness with 62 species, while Yucatán and Campeche showed similar richness with 35 and 31 species, respectively (Fig. 2B $q = 0$). In terms of the diversity of equally common species ($q = 1$), the highest diversity was observed in Quintana Roo with 16 species, followed by Yucatán with 10 species and Campeche with only six, suggesting a low diversity in melliferous plants visited by *M. beecheii* in the Yucatán Peninsula. With regard to the number of dominant species ($q = 2$), once more the samples from Quintana Roo showed the highest values with 10 dominant species, followed by Yucatán with seven and Campeche with four (Fig. 2B).

Palynological profiles of pot-honey from Quintana Roo

Melissopalynological analyses of 10 samples of *M. beecheii* pot-honey from the state of Quintana Roo (Fig. 1, Table 1) recorded a total of 5679 pollen grains, with a species richness of 62 taxa: 38 determined at the species level, 17 at the genus level and four at the family level (Table 2), all belonging to 31 botanical families, while three pollen morphotypes remained undetermined. Considering results by individual pot-honey sample, species richness ranged from 16 to 32 taxa (Table 2).

The most representative taxa across the samples in Quintana Roo were *Bursera simaruba* and *Eugenia* aff. *axilaris*, *Melicoccus oliviformis*, *Senna racemosa* var. *racemosa*, and *Solanum erianthum* (Table 2, Fig. 3). Among these species, *B. simaruba* and *M. oliviformis* were predominant and secondary, while *Cochlospermum vitifolium*, *Croton* sp., *E. aff. axilaris* and *Metopium brownei* were recorded as secondary pollen grains (Table 2). The remaining botanical taxa were categorised as important minor or minor pollen (Table 2).

In the state of Quintana Roo, *M. beecheii* collected nectar mainly from trees (*B. simaruba*, *C. vitifolium*, *E. aff. axilaris*, *M. oliviformis*, *M. brownie*, *Mimosa bahamensis*, *S. racemosa* var. *racemosa* and *S. erianthum*). However, shrubs, herbs, lianas and an epiphyte species were also documented (Fig. 3). CONISS analysis differentiated the pot-honey samples from Quintana Roo into three groups. In group A, the samples shared essential elements such as *B. simaruba*, *Eugenia* aff. *axilaris*, *M. oliviformis* and *M. brownei*. In group B, *B. simaruba* and *M. oliviformis* were notable, followed in importance by *S. racemosa* var. *racemosa* and *S. erianthum*. Finally, in group C, the elements that stood out were *B. simaruba*, *M. oliviformis*, *Croton* sp. and *S. erianthum*.

Palynological profiles of pot-honey from Yucatán

Analyses performed on the 10 pot-honey samples of *M. beecheii* from Yucatán (Fig. 1, Table 1) recorded a total of 5665 pollen grains, with a species richness of 35 taxa: 25 pollen morphotypes identified at the species level and nine at the genus level, all belonging to 18 botanical families (Table 2); one pollen morphotype remained undetermined. Species richness at the level of individual samples varied from 13 to 21 taxa.

In the pollen spectra, both the predominant and secondary taxa were *C. vitifolium*, *B. simaruba*, *Eugenia* sp. and *Gymnopodium floribundum*. The species recorded as secondary pollen grains were *M. bahamensis* and *S. racemosa* var. *racemosa*, while the rest of the taxa were important minor or minor pollen grains (Table 2). As to the strata through which the Mayan bee moved, these insects preferred *B. simaruba*, *C. vitifolium*, *Eugenia* aff. *Axilaris*, *M. oliviformis*, *M. bahamensis*, *G. floribundum*, *Senna racemosa* var. *racemosa* and *Solanum erianthum* from the tree stratum (Fig. 4).

CONISS analysis identified three sample groups: in the first (group A), the Chaksinkín (CHA) sample is distinguished by the dominance of *Eugenia* sp. and *A. ramossisima*, while the remaining samples share important elements such as *B. simaruba*, *G. floribundum*, *M. bahamensis* and *S. racemosa* var. *racemosa*. In group B, *B. simaruba* and *C. vitifolium* were significant, and in group C, *M. oliviformis*, *G. floribundum* and *S. racemosa* var. *racemosa* were notable (Fig. 4).

Palynological profiles of pot-honey from Campeche

Palynological analyses of the seven pot-honey samples from Campeche generated a total of 4072 pollen grains, with a species richness of 31 taxa: 19 pollen morphotypes identified at the species level, eight at the genus level and four at the family level, all belonging to 18 botanical families (Table 2). Species richness among individual samples varied from 10 to 16 taxa. Predominant species were *C. vitifolium*, *B. simaruba* and *M. bahamensis*. *S. racemosa* var. *racemosa* and *G. floribundum* were recorded as secondary species (Table 2).

M. beecheii showed a preference for species in the tree stratum (*B. simaruba*, *C. vitifolium*, *G. floribundum*, *Mimosa bahamensis* and *Senna racemosa* var. *racemosa*) (Figs. 5 and 6). CONISS analysis identified three groups: the first (A) was primarily composed of *B. simaruba*, *C. vitifolium* and *S. racemosa* var. *racemosa*; group B mainly comprised *C. vitifolium* and *M. bahamensis*, whereas group C included *C. vitifolium*, *G. floribundum* and *S. racemosa* var. *racemosa* (Fig. 5).

Statistical comparison of pollen spectra among states

The first two dimensions of PCoA explained 32.2% of the total variation in the composition and abundance of pollen species. ADONIS analysis revealed three distinct sample groups based on the state of collection (Fig. 6), each of which showed significant differences in pollen species composition and abundance ($p = 0.001$). The post hoc ADONIS analysis using the Benjamin-Hochberg correction for multiple comparisons showed significant differences between Campeche and Quintana Roo ($p = 0.001$), Campeche and Yucatán ($p = 0.011$), and Quintana Roo and Yucatán ($p = 0.001$).

Pot-honey classes according to absolute number of pollen grains

Although our sampling process was done pot by pot and with syringes, we found a strong overrepresentation of pollen grains on *Melipona beecheii* pot-honey samples. In Quintana Roo, eight samples showed high concentrations of pollen, four samples exhibited strongly overrepresented pollen (Class IV) and four samples fell within the category of pressed honeys (Class V; Table 3). By contrast, one sample was classified as Class II (multifloral honey) and another as Class III (pollen-rich honey). In Yucatán, the absolute pollen counts indicated that six samples corresponded to pollen-rich honeys (Class III), while four samples had a high concentration of pollen, two from Class IV and another two from Class V (Table 3). In Campeche, five samples were classified as pressed honeys (Class V) and two were rich in pollen (Class III; Table 3).

Table 3. Group classes of honeys according to pollen concentration in 27 pot-honey samples from *Melipona beecheii* colonies in the Yucatán Peninsula.

Group classes of honeys (Louveaux et al. 1978)	Pollen concentration (Pollen grains in 10 g of honey)	Quintana Roo	Yucatán	Campeche
I - underrepresented pollen	$\leq 20 \times 10^3$	0	0	0
II- multifloral honeys	$21 \times 10^3 - 100 \times 10^3$	1	0	0
III - honey rich in pollen	$101 \times 10^3 - 500 \times 10^3$	1	6	2
IV - honey with strongly overrepresented pollen and some pressed honeys	$501 \times 10^3 - 10^6$	4	2	0
V - only pressed honey	$> 10^6$	4	2	5

Pollen overrepresentation of pot-honey samples from the Yucatán Peninsula was strongly influenced by the presence of substantial proportions of pollen from polliniferous plants. Across the 27 samples analysed, we recorded pollen from 29 exclusively polliniferous plant species, 28 pollen morphotypes from exclusively nectariferous plants and 16 morphotypes from nectar–polliniferous plants. The proportion of pollen grains derived from polliniferous plants varied among states, accounting for approximately one-third of the pollen counted in samples from Quintana Roo and reaching up to 76.57% in samples from Campeche (Table 4). Among the most prevalent pollen grains from polliniferous plants in the pot-honey samples were those of *Cochlospermum vitifolium*, *Mimosa bahamensis* and *Senna racemosa* var. *racemosa*, which were present in samples from all three states. *Solanum erianthum* pollen was also found, primarily in honey samples from Yucatán and Quintana Roo (Fig. 7).

Table 4. Mean percentage of pollen grains by plant resource type (polliniferous, nectariferous and nectar–polliniferous) in 27 pot-honey samples from *Melipona beecheii* colonies in the Yucatán Peninsula, by state.

Resource	Quintana Roo	Yucatán	Campeche
Pollen from nectariferous plants	30.32	9.96	1.44
Pollen from nectar–polliniferous plants	35.75	40.82	21.83
Pollen from polliniferous plants	33.1	49.21	76.57
Unidentified	0.83	0.02	0.16

Discussion

Conservation of landscapes inhabited by native bees

The conservation of natural ecosystems where native vegetation thrives is a fundamental pillar for the survival of stingless bees and for the quality, diversity and sustainability of pot-honey production. Tropical forests represent vegetation reserves that provide continuous and diverse sources of nectar, pollen and resins. Their loss and fragmentation, caused by land-use change, drastically reduce these resources. Fragmented landscapes have led to poor nutrition, which can be compounded by contaminated pollen and nectar from pesticides that may accumulate and reach every individual within the colony (Traynor et al. 2021; Bogo et al. 2023), thereby weakening honey-producing bees.

Landscape connectivity is vital for the genetic diversity of bees. In this sense, biodiversity also underpins “*meliponiculture*” (stingless beekeeping), a practice closely linked to tropical forests and strongly associated with Mayan communities; conservation planning and management must integrate diverse socio-ecological elements (Mesa-Sierra et al. 2022). In this regard, stingless bees, in addition to their ecological role as native pollinators of wild and cultivated plants, also hold high environmental, cultural and economic values for rural and semi-urban communities. Stingless beekeeping helps maintain the floristic richness of conserved landscapes, which underpin the production of monofloral and multifloral honeys highly recognised in speciality markets (Ayala et al. 2013; Aldasoro et al. 2023; Engel et al. 2023; Xolalpa-Aroche et al. 2024).

Knowledge of the botanical origin of pollen and honey from *M. beecheii* bees provides valuable information on the relationships among flowering patterns, forest management and honey production. Gómez-Ruiz et al. (2022) describe the relevance of local community participation in comprehensive and sustainable socio-ecosystem restoration processes, as well as the promotion of greater awareness of flowering cycles and forest management, which are crucial for honey production. Melissopalynological information about pollen and honey sources significantly contributes to the resilience of beekeepers and honey producers, which, at the same time, supports biological conservation.

Diversity of food resources for *M. beecheii* in southeastern Mexico

Despite the low botanical diversity of the Yucatán Peninsula (Quintana Roo, Yucatán and Campeche) compared to other regions of Mexico, this peninsula is the country's leading region for honey production, both in beekeeping and meliponiculture (Quezada-Euan et al. 2001). However, human activity primarily related to land-use change for agriculture and deforestation (Duran-García and García-Contreras 2010), has directly affected the availability of nectar resources for the region's bees. Thus, in this study, we evaluated, through palynological analysis, the floral resources present in the honey of *M. beecheii*, the main bee species used in meliponiculture on the Yucatán Peninsula.

When comparing the three states that make up the Yucatán Peninsula, we observed greater species richness and diversity of pollen grain morphotypes in the samples from Quintana Roo, while the values recorded for Yucatán and Campeche were similar to each other. This pattern may be related to differences in the vegetation surrounding the meliponaries where the *M. beecheii* pot-honey samples were collected. In this regard, Pérez-Morfi et al. (2024) recently reported in pot-pollen higher plant species richness at meliponaries located within semi-evergreen tropical forests in Quintana Roo compared to those situated in deciduous and semi-deciduous tropical forests in Yucatán and Campeche.

Despite these differences in diversity, tree species were the primary source of nectar for *M. beecheii* in all 27 samples analysed. This matches the results of a previous study, but in pot-pollen samples from *M. beecheii* from across the peninsula (Pérez-Morfi et al. 2025). Along with the prevalence of tree pollen, we also found a prevalence of Fabaceae pollen in our pot-honey samples from Quintana Roo, Yucatán and Campeche. This is consistent with a previous palynological study of pot-honey samples from *M. beecheii* carried out only in the state of Yucatán (Bacab-Pérez et al. 2024). In that study, the authors identified 12 pollen types from the Fabaceae family, accounting for over 50% of the pollen grains recorded. In agreement with our results, they also found a prevalence of pollen from the Burseraceae, Myrtaceae, Solanaceae and Bixaceae families. However, in the present study, honey samples from Yucatán showed a greater richness of plant taxa and families. Furthermore, when considering the palynological spectra of the peninsula as a whole, more species and families were recorded due to the inclusion of pot-honey samples from Quintana Roo and Campeche.

The high representation of pollen from the Fabaceae family in our samples may be due to the fact that this is the most diverse family in the Yucatán Peninsula (Duno de Stefano et al. 2010, 2012, 2018). The species *S. racemosa* var. *racemosa*, *M. bahamensis*, *C. vitifolium* and *B. simaruba* were recorded in honey samples from all three states (Fig. 7). By contrast, taxa recorded in the spectra of both Yucatán and Quintana Roo were *S. erianthum* and *M. oliviformis*. *G. floribundum* was observed in samples from Yucatán and Campeche (Fig. 7).

It should be noted that the plants which exclusively produce pollen are *S. racemosa* var. *racemosa*, *S. erianthum*, *M. bahamensis* and *C. vitifolium*, and that they are well represented in the palynological spectra (Table 2 supplementary material). Pérez-Morfi et al. (2025) reported that *C. vitifolium*, *S.*

racemosa var. *racemosa* and *Solanum* are abundant elements in pot-pollen samples from the Yucatán Peninsula, confirming their importance as resources that exclusively produce pollen. Moreover, all of these species were found in a previous palynological analysis of *M. beecheii* pot-pollen (Villanueva-Gutiérrez et al. 2018).

S. racemosa var. *racemosa* is characterised by heterantherous flowers that produce large quantities of pollen but no nectar, making this species an important food source for large bees such as *Xylocopa* spp. and medium-sized bees such as *Melipona*. These bee genera use a specialised mechanism known as vibration or buzz pollination (Amorim et al. 2017), whereby vibrations generated by the thoracic musculature release pollen from the anthers. This trait makes buzz-pollinating bees more effective pollinators than *Apis mellifera*—which lacks this ability—for several native and cultivated plant species, including members of the genus *Solanum* (Valadão-Mendez et al. 2025).

Overrepresentation of polliniferous plants in pot-honey

In the present work, pot-honey samples were classified according to the number of pollen grains calculated per gram of honey. Based on the classes defined by Maurizio's method (Louveau et al. 1978; Der Ohe et al. 2004), 63% of the honey samples ($n = 17$) were classified as pollen-overrepresented or pressed honeys, indicating the occurrence of pollen enrichment processes within *M. beecheii* colonies. In this context, several hypotheses can be proposed: (1) partial mixing of pot-pollen with pot-honey contents in the sampling process by pressing or decanting, with the exception of samples collected using syringes; (2) accidental or intentional incorporation of pollen loads collected by bees into the pot-honey, together with nectar regurgitated during honey processing; or (3) transfer of pollen adhering to the bees' bodies to the bees' crop after grooming or by ingestion, or to the honey during storage. A substantial proportion (30–75%) of the overrepresented pollen corresponds to exclusively polliniferous taxa, which supports the second hypothesis. The accidental or intentional inclusion of pollen loads deposited in pot-honey by workers may explain the pollen overrepresentation of exclusively polliniferous taxa, which may result from behavioural processes during resource storage. However, further observations are required to clarify this phenomenon, its frequency and whether there is any cause for this behaviour in worker stingless bees.

In our study, pollen overrepresentation from polliniferous plants was mainly associated with species of the family Fabaceae, particularly *Senna racemosa* var. *racemosa* and *Mimosa bahamensis*. Other highly represented taxa included were *Cochlospermum vitifolium* and *Solanum erianthum*. These findings are consistent with those reported by Bacab-Pérez et al. (2024) for pot-honey samples from *M. beecheii* colonies in the state of Yucatán, however, this is the first time that the absolute number of pollen grains per gram of *M. beecheii* pot-honey has been quantified. The influence of pollen grains from exclusively polliniferous plants on stored honey in *Melipona beecheii*, as well as in *Scaptotrigona mexicana* (Ramírez-Arriaga et al. 2003) and possibly other stingless bee species, suggests that this may be a characteristic phenomenon of stingless bees. These results also highlight the importance of determining pollen grain concentrations using *Lycopodium* marker tablets. This approach increases the informative power of palynological analyses by enabling the quantification of pollen input and providing insights not

only into the plant species, botanical families and vegetation strata visited by bees, but also into honey storage behaviour within stingless bee colonies and the extraction methods used during honey harvesting.

Relevant native plants required for pot-honey production in the Yucatán Peninsula

In general, *M. beecheii* forages heterogeneously on the Yucatán Peninsula, visiting secondary vegetation in both deciduous and semi-deciduous tropical forests and semi-evergreen tropical forests, with greater taxonomic richness in the latter (Bacab et al. 2024; Pérez-Morfi et al. 2025). Pollen representativeness in honey analyses reflects the availability and abundance of nectariferous, nectar-polliniferous and polliniferous resources in the landscape surrounding the meliponaries. When polliniferous taxa are excluded and only nectariferous and nectar–polliniferous elements are considered, *B. simaruba* is the only taxon shared among all three states. By contrast, *Melicoccus oliviformis*, *G. floribundum* and *Eugenia* sp. are shared between Yucatán and Quintana Roo. Taxa exclusive to the honeys from Yucatán included *T. paucidentata* and *Crotalaria* sp., whereas those exclusive to Quintana Roo were *M. brownei* and *Croton* spp.; in Campeche, only *P. piscipula* was recorded (Fig. 9). *Eugenia*, *T. paucidentata*, *Crotalaria*, *M. brownei* and *Piscidia piscipula* have previously been reported as nectar-producing taxa in analyses of *Apis mellifera* honey from the same region (Villanueva-Gutiérrez et al. 2009).

Bursera simaruba is a tree species locally known as *chakaj*, *chacáh* or *chaca* that is characterised by reddish-brown bark with translucent scales or, in some individuals, a reddish-green coloration and papery texture. This monoecious or dioecious species produces male and female flowers in separate panicles. Male flowers bear eight to ten stamens and a large annular nectary that occupies the central portion of the flower; female flowers possess a superior ovary surrounded by six stamens and a small annular nectary. These floral traits provide easy access to nectaries for medium-sized bees such as *Apis mellifera* and *Melipona* spp., and, together with this tree's abundant nectar production, make *B. simaruba* an important nectariferous and polliniferous species. It is abundant in tropical evergreen, sub-evergreen and sub-deciduous forests, as well as in low- and medium-deciduous forests and secondary vegetation derived from these plant communities (Pennington and Sarukhán 1998; Durán-García 2000).

Gymnopodium floribundum is one of the most important melliferous plants of the Yucatán Peninsula (Vicario-Mejía and Echazarreta 1999). Locally known as *ts'iits'ilche'* or *dzidzilché*, it is a tropical hermaphroditic tree with fissured grey to dark-brown bark. The species produces fragrant pale-green terminal inflorescences that may occur singly or in clustered pairs. Its flowers are protandrous, with the male phase maturing first, and they bear nine stamens and a superior ovary. Each flower produces approximately 1.28–1.64 μL of nectar per day, with a sugar concentration ranging from 54 to 68% (González-Ramírez 2014). Densities of up to 240 trees per hectare have been reported in the state of Yucatán, a pattern attributed to clonal reproduction (González-Ramírez 2014). In general, *G. floribundum* is abundant in low-deciduous forests (Paquini-Rodríguez et al. 2024), but also occurs in medium sub-deciduous, medium sub-evergreen, low evergreen and high evergreen forests (Durán-García 2000).

Finally, *Melicoccus oliviformis*, known locally as *chak wayuum*, *huayum* or *huaya* (Jiménez-Rojas et al. 2019; Durán-García 2000), is commonly found in the back yards of Mayan communities. It is a dioecious tree with male and female flowers borne in separate panicles, each featuring an extrastaminal nectary disc (Pennington and Sarukhán 1998; Acevedo-Rodríguez 2003). This species grows in sub-evergreen tropical forests as well as in deciduous and sub-deciduous forests (Pennington and Sarukhán 1998). *M. oliviformis* is widely distributed across the Peninsula due to the consumption of its fruits, a practice that dates back more than 3000 years (Jiménez-Rojas et al. 2019). The species is considered to be in an incipient stage of domestication (Clement 1999), since its average phenotypic traits remain within the range observed in its wild relatives.

Melissopalynological evidence to guide plant conservation and habitat restoration for stingless bees

A comparative analysis of the palynological assemblages from pot-honey in this study and pot-pollen from *M. beecheii* colonies in the Yucatán Peninsula (Pérez-Morfi et al. 2025) reveals complementary information on plant resources that is relevant for both bee nutrition and conservation planning (Fig. 8). The pot-honey samples exhibited several nectariferous and nectar–polliniferous taxa not previously identified in pot-pollen, including *Metopium brownei*, *Croton* sp., *Eugenia* aff. *axillaris*, *Melicoccus oliviformis*, *Eugenia* sp., *Gymnopodium floribundum* and *Piscidia piscipula*, highlighting their importance as nectar sources for *M. beecheii* (Fig. 8). At the same time, both pot-honey and pot-pollen spectra showed a consistent overrepresentation of exclusively polliniferous tree species, particularly *Cochlospermum vitifolium*, *M. bahamensis*, *Senna racemosa* var. *racemosa* and *Solanum erianthum*, which indicates their central role in pollen provisioning across the peninsula (Fig. 8).

Differences in the relative abundance of these taxa among states reflect underlying environmental gradients in rainfall and vegetation types, ranging from deciduous tropical forest in northwestern Yucatán to semi-evergreen forests in southeastern Quintana Roo. In this sense, the PCoA showed a greater similarity between the palynological assemblages of Campeche and Yucatán than between those of Campeche and Quintana Roo (Fig. 6). This pattern coincides with the distribution of rainfall (Espadas-Manrique and Orellana-Lanza 2020) and the vegetation types (Flores and Espejel 1994) that occur across the peninsula, which exhibits a precipitation gradient from northwest (mainly Yucatán) to southeast (mainly Quintana Roo). This gradient ranges from a dry area with less than 600 mm of annual rainfall in the northwest to a more humid area centrally with 1000–1100 mm of annual rainfall, to the wettest area, the south-southeast, with 1200 mm of annual rainfall. The vegetation types correspond to the rainfall regime: dry forest in the northwest part of the peninsula, tropical deciduous and semi-deciduous forests in the central zone, and semi-evergreen forest in the south-southeast region. In this regard, a portion of the samples collected in Yucatán were from localities within the same isohyet (1000 mm of rainfall) as those in Campeche, sharing pollen from secondary vegetation derived from deciduous tropical forests. The remaining honey samples from Yucatán are from localities within the 1100 mm isohyet in semi-deciduous forest areas; they do not share environmental conditions with Campeche or Quintana Roo (Fig. 1). The samples collected in Quintana Roo are unique because they do not share the

rainfall and vegetation conditions with Campeche and Yucatán; they are from localities within the 1200 mm isohyet in semi-evergreen tropical vegetation forests (Fig. 1) and contain pollen assemblages from a more diverse and better-preserved vegetation. Together, these patterns underscore the value of melissopalynological analyses for identifying key plant species and plant communities that sustain stingless bee populations, and they emphasise the need to prioritise the conservation and restoration of nectariferous, nectar–polliniferous and polliniferous tree species across environmental gradients in the Yucatán Peninsula.

Conclusion

The palynological spectra of *M. beecheii* pot-honeys reflect key characteristics of the secondary vegetation surrounding meliponaries and reveal clear differences in resource availability across the Yucatán Peninsula, with better-preserved habitats in Quintana Roo exhibiting greater richness and diversity of nectar and pollen resources than the more disturbed landscapes of Yucatán and Campeche. Since all pot-honey samples were collected using syringes, the observed overrepresentation of exclusively polliniferous taxa—such as *Cochlospermum vitifolium*, *Mimosa bahamensis*, *Senna racemosa* var. *racemosa* and *Solanum erianthum*—suggests that pollen enrichment results from the storage behaviour of *M. beecheii* workers rather than from sampling procedures. In addition, native tropical trees such as *Bursera simaruba*, *Gymnopodium floribundum* and *Melicoccus oliviformis*, which provide both nectar and pollen due to their floral morphology, were identified as key foraging resources. Overall, these findings highlight the high diversity of native polliniferous, nectariferous and nectar–polliniferous plants supporting *M. beecheii* populations and underscore the importance of conserving well-preserved natural ecosystems to ensure year-round resource availability for native stingless bees.

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Authors’ contributions. The study was conceptualised by Elia Ramírez-Arriaga, Azucena Canto, Alejandro Pérez-Morfi and Lorena Luna-Rodríguez. Aurora Xolalpa-Aroche, Lorena Luna-Rodríguez, Luciana Porter-Bolland and Juan Manuel Vargas-Romero were responsible for field pot-honey sample collection. Elia Ramírez-Arriaga contributed to sample preparation, palynological analysis and interpretation of pollen assemblages. Azucena Canto and Alejandro Pérez-Morfi performed the statistical analyses, prepared the

graphs and contributed to the interpretation of the results. All authors collaboratively drafted, reviewed and approved the final manuscript.

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Data availability. All data supporting the conclusions of the pot-honey study are included in the main text and supplementary information. Additionally, some data sources used in this work are publicly available: Comparative analysis of *Melipona beecheii* pollen foraging preferences in Deciduous, Semideciduous and Semi-evergreen Tropical Forests of the Yucatán Peninsula (Pérez-Morfi et al. 2025).

The authors declare no competing interests.

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Figures

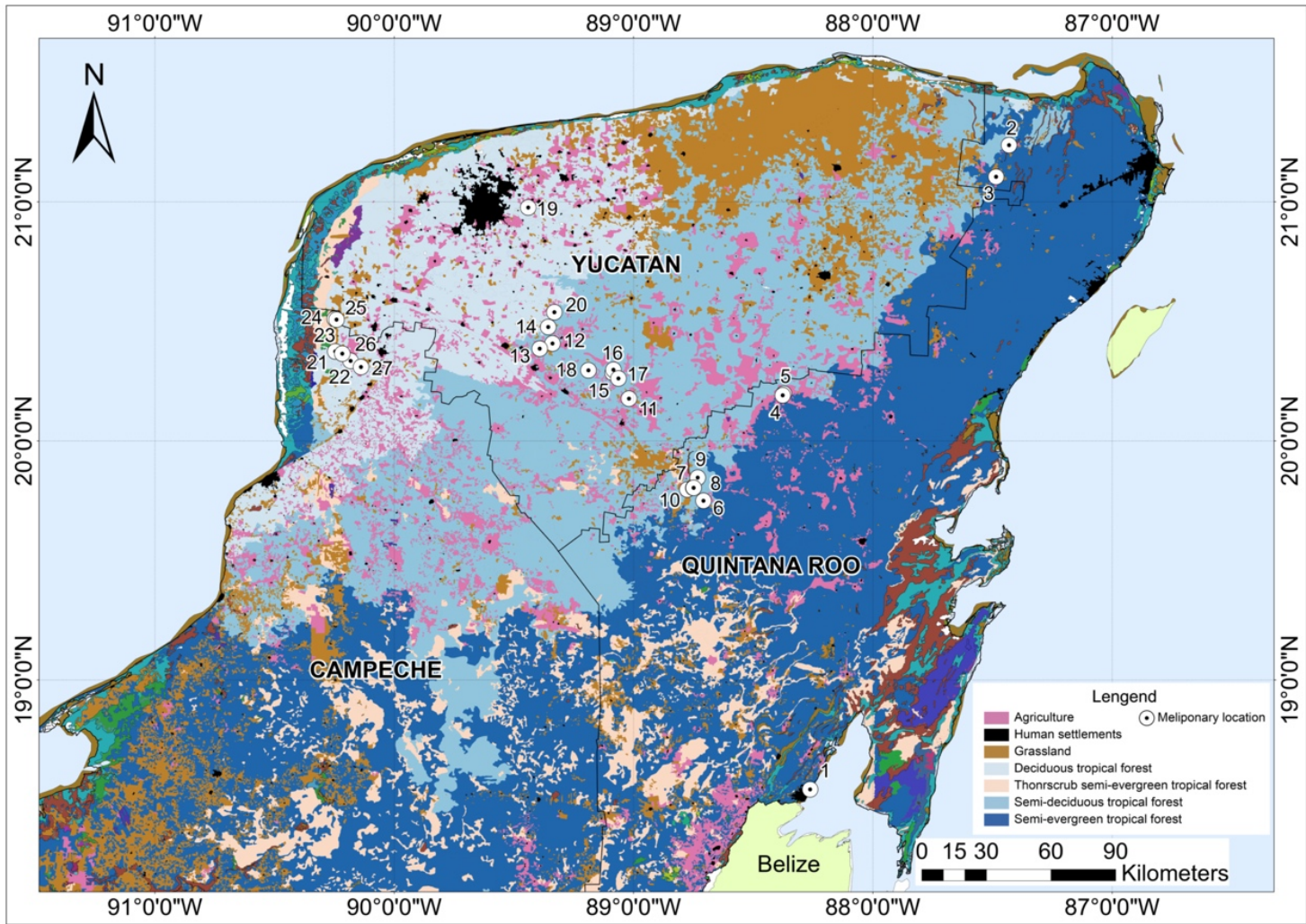


Figure 1

Location of the meliponaries where *M. beecheii* honeys were harvested in Quintana Roo, Yucatán and Campeche, in the Yucatán Peninsula, Mexico. Numbers correspond to the samples in Table 1.

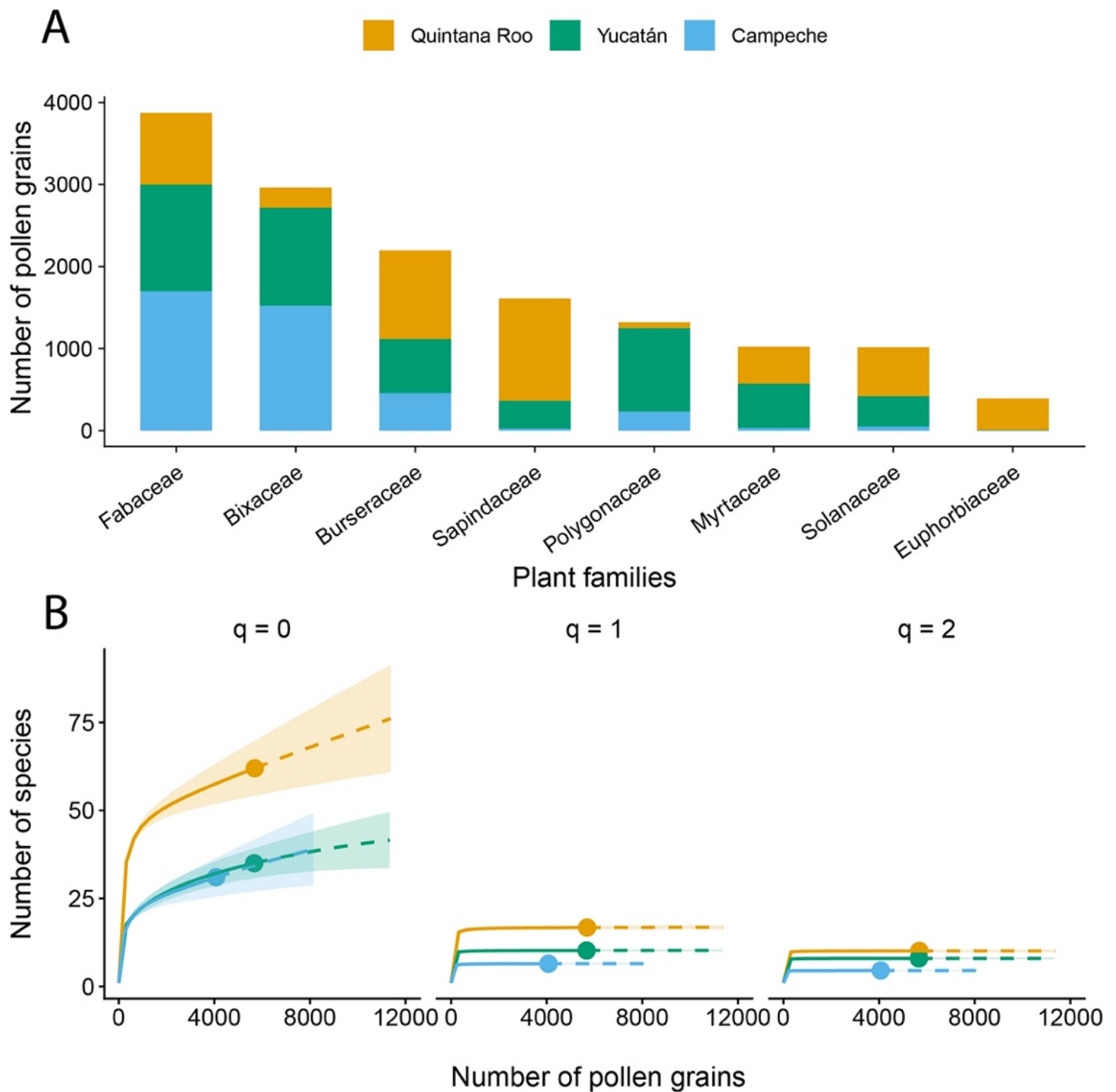


Figure 2

A: Number of pollen grains from each botanical family recorded in melissopalynological analyses of pot-honey samples. B: Estimates, based on Hill numbers, of pot-honey diversity in *Melipona beecheii* colonies in the three states of the Yucatán Peninsula. $q = 0$: species richness; $q = 1$: diversity of equally common species (exponential of the Shannon index); $q = 2$: diversity of dominant species (inverse of the Simpson index). Diversity curves were constructed from rarefaction (solid lines) and extrapolation (dashed lines) with estimates based on sample size. Each curve was extrapolated up to twice the

sample size achieved in our samplings. Shaded areas show the 95% confidence intervals obtained through a bootstrap method with 200 replications.

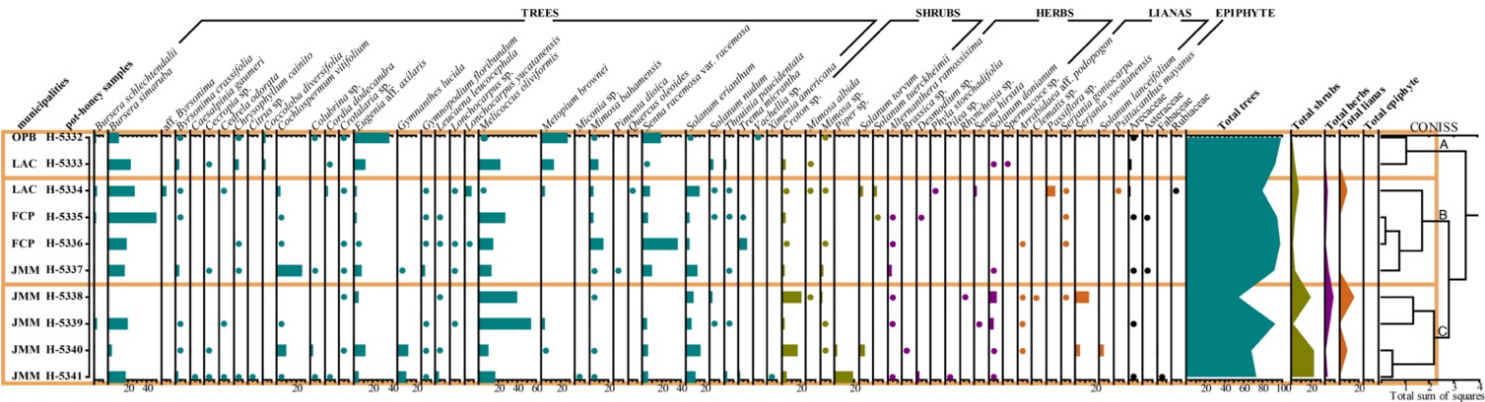


Figure 3

Pot-honey pollen assemblages from *Melipona beecheii* harvested in Quintana Roo in the municipalities of Othon P. Blanco (OPB), Lázaro Cárdenas (LAC), Felipe Carrillo Puerto (FCP) and José María Morelos (JMM).

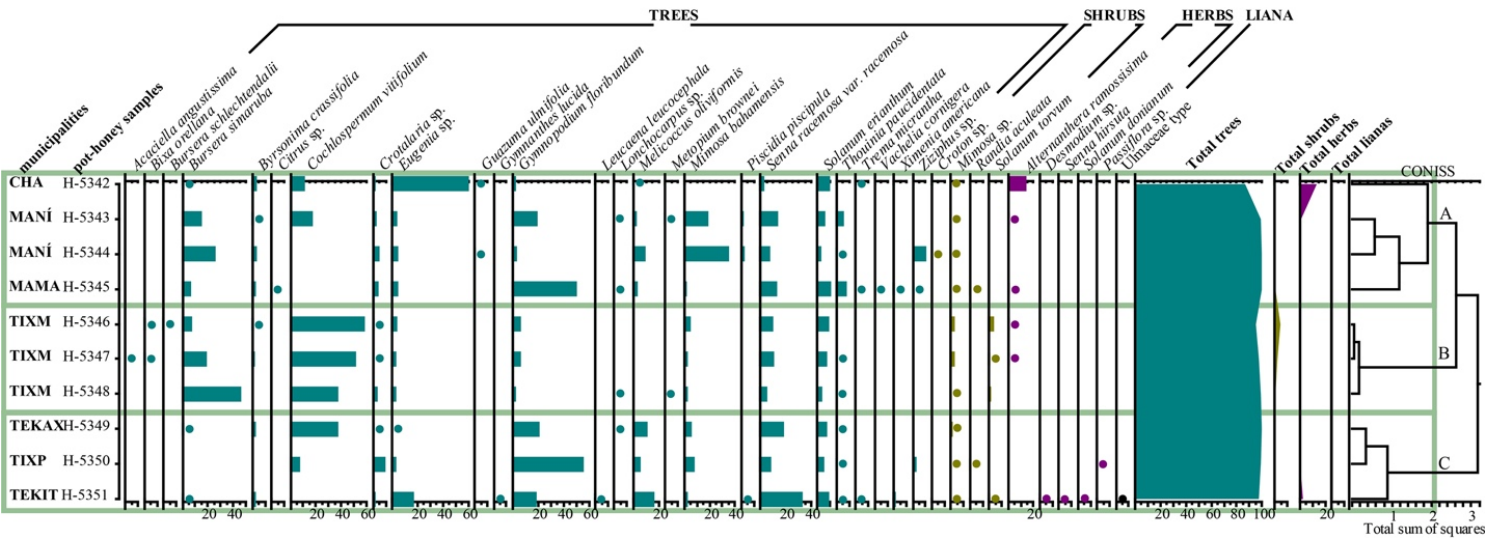


Figure 4

Pot-honey pollen assemblages from *Melipona beecheii* harvested in Yucatán in the municipalities of Chaksinkín (CHA), Maní, Mama, Tixmehuac (TIXM), Tekax, Tixpéhual (TIXP) and Tekit.

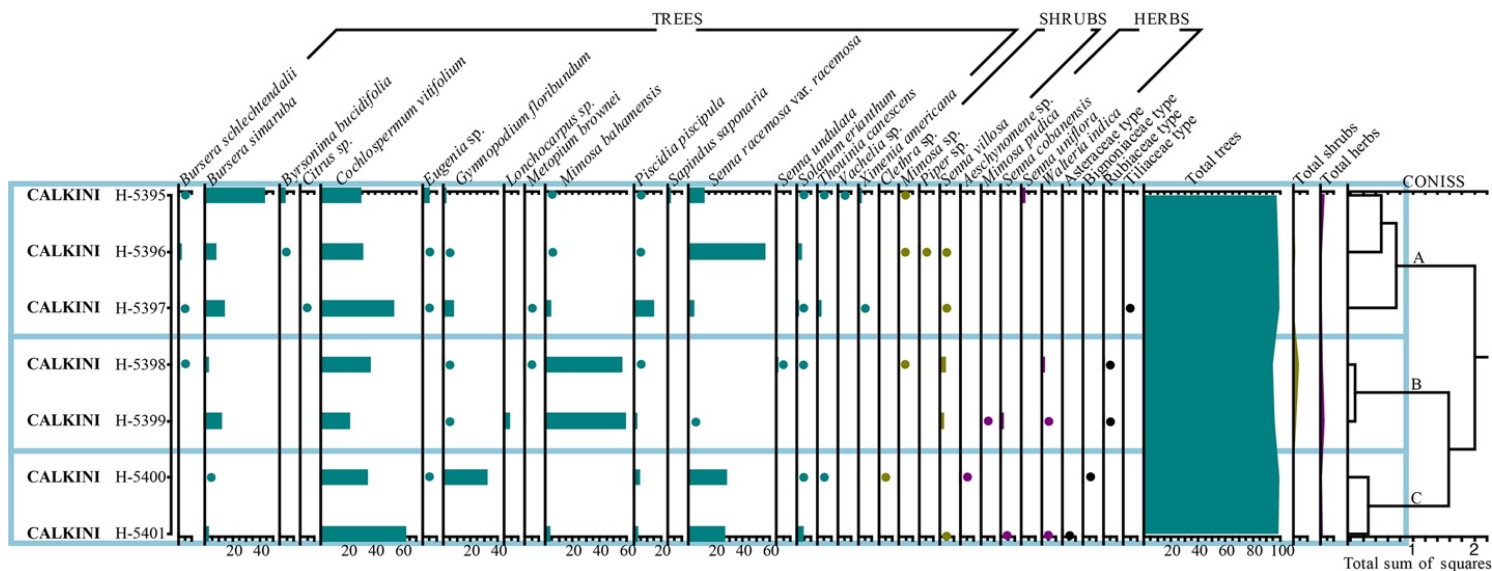


Figure 5

Pot-honey pollen assemblages from *Melipona beecheii* harvested in Campeche in the municipality of Calkini.

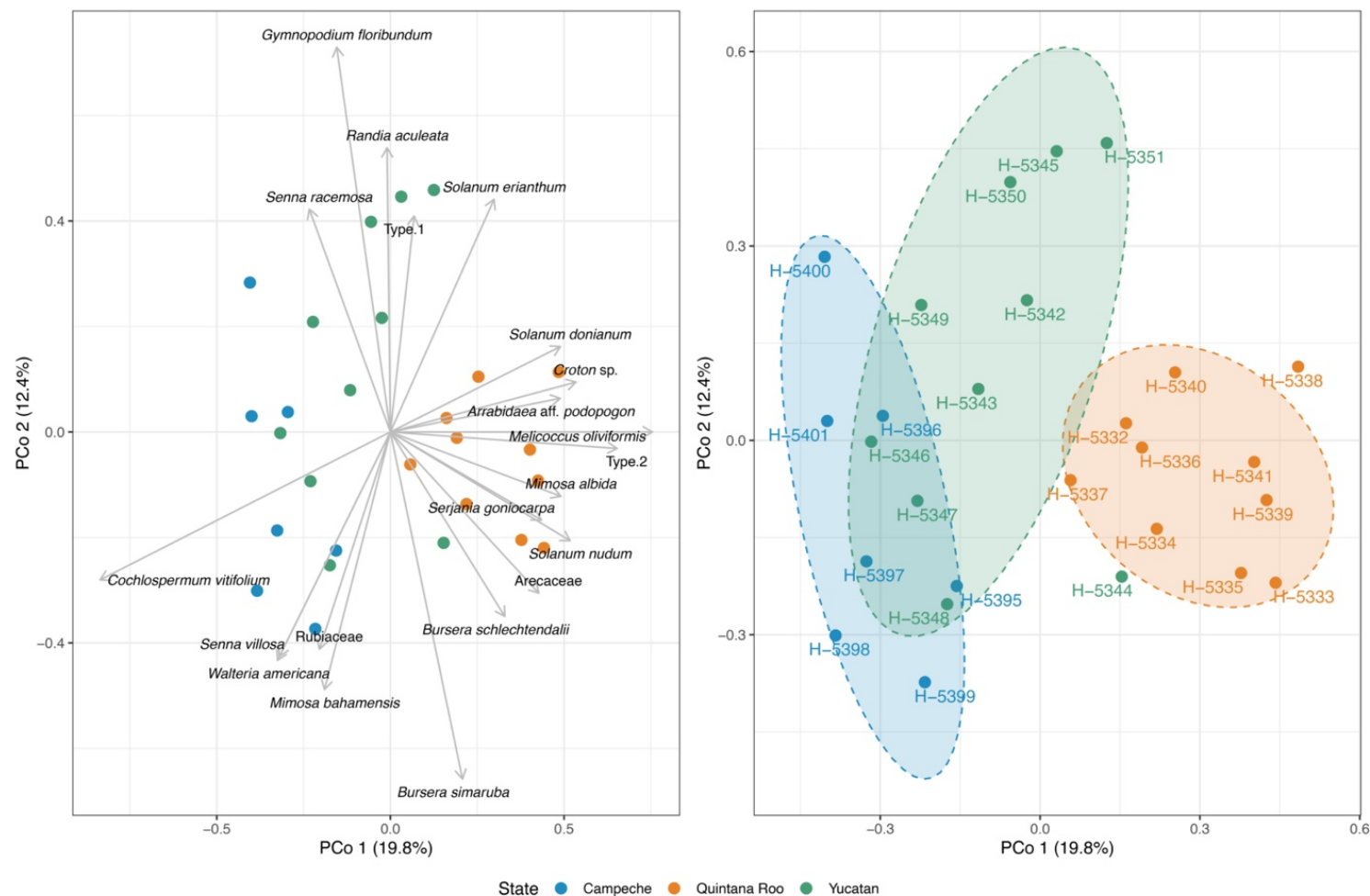


Figure 6

PCoA based on the palynological spectra of 27 samples of *Melipona beecheii* pot-honey from the three states of the Yucatán Peninsula. Pairwise comparisons were conducted to contrast between the states regarding their pollen spectra.

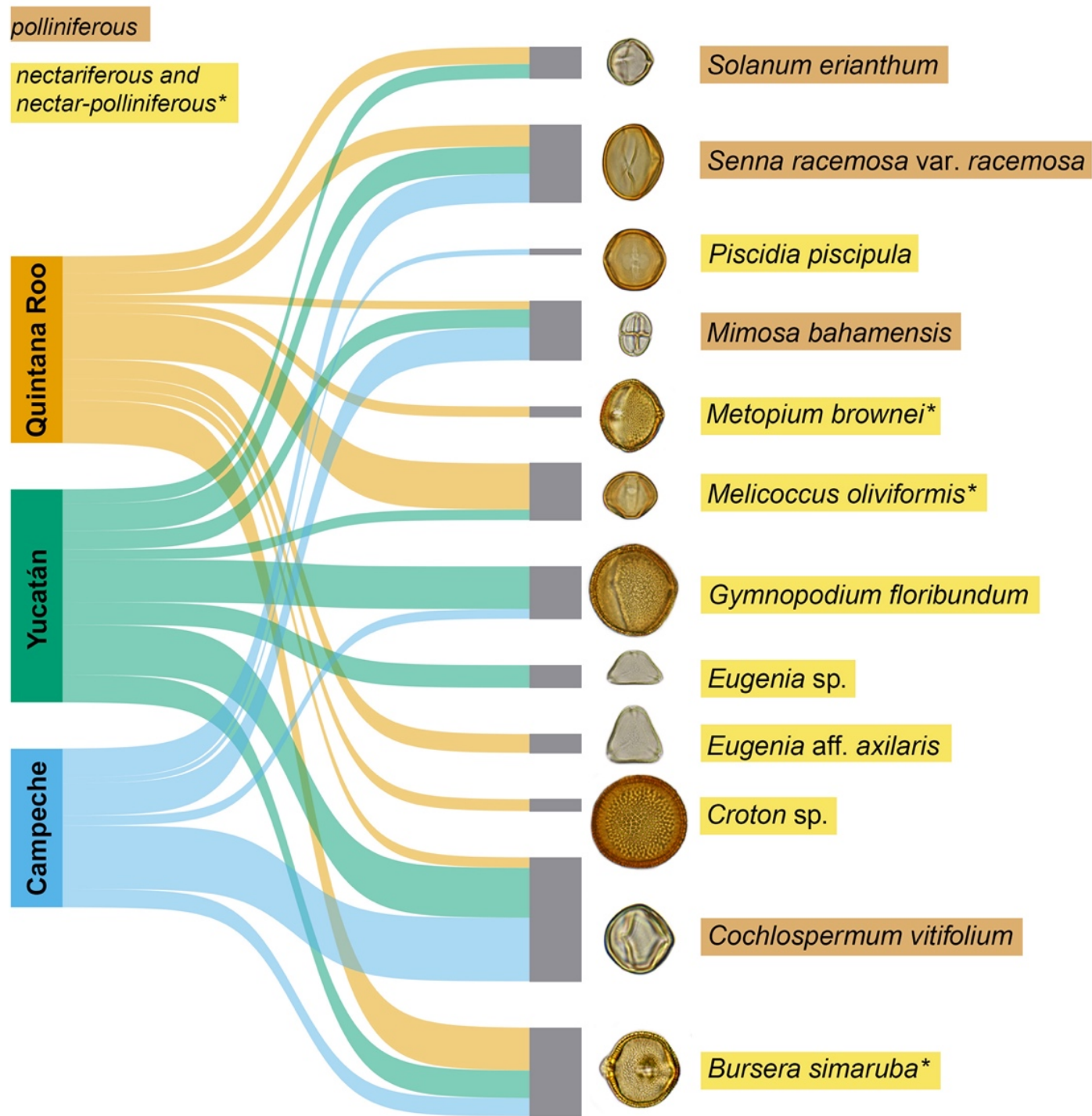


Figure 7

Relevant species recorded in the pollen spectra of *M. beecheii* pot-honey samples in Quintana Roo, Yucatán and Campeche.

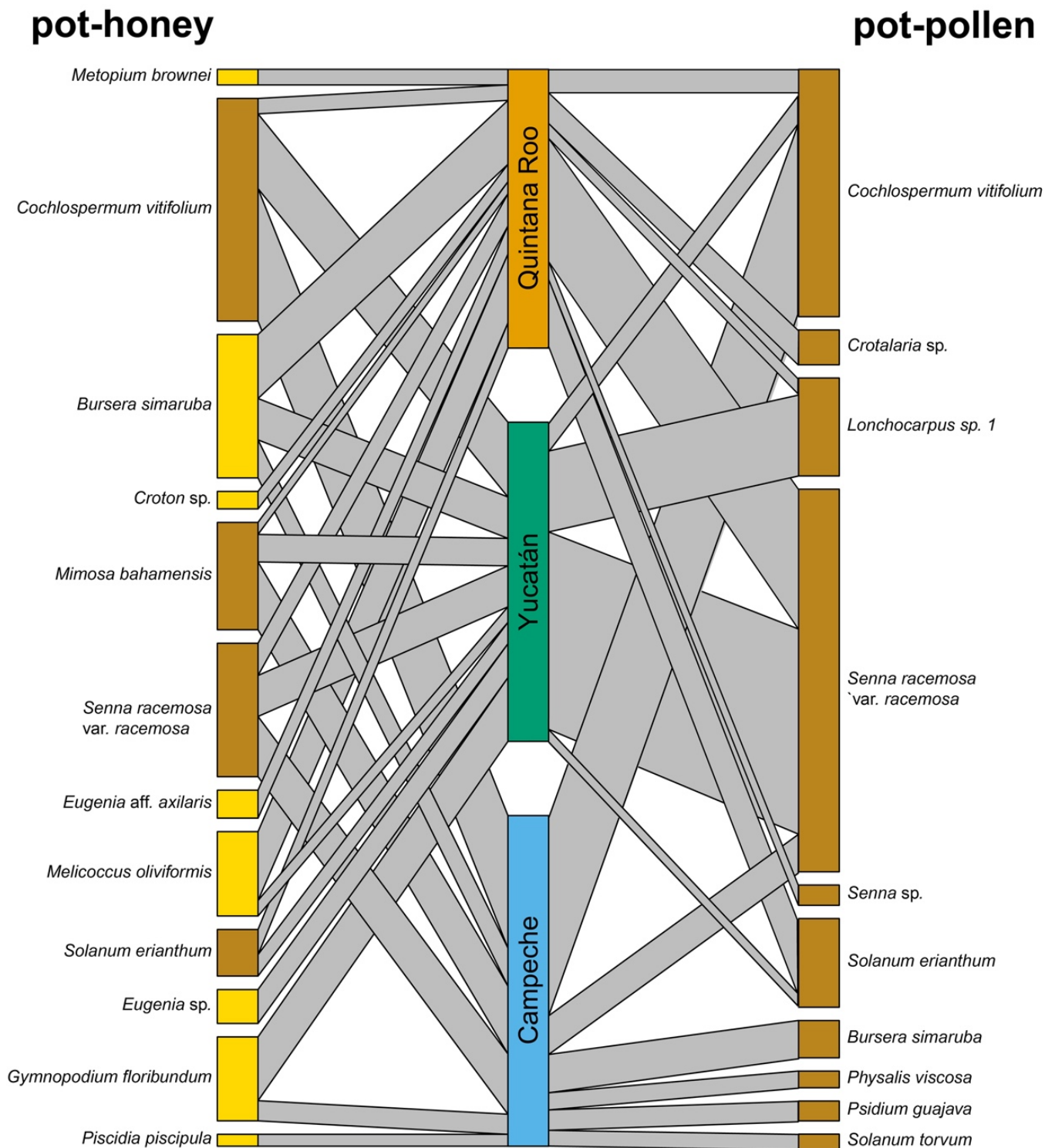


Figure 8

The most abundant species recorded in the pollen spectra of pot-honey in this study, and pot-pollen (Pérez-Morfi et al. 2025) from *M. beecheyi* in the Yucatán Peninsula.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [Table1MeliponaQRooYucCamp.docx](#)
- [Table2MeliponaQRooYucCamp.docx](#)