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Original article

Melissopalynology of pot-pollen and pot-honey of the Mayan stingless bee *Melipona beecheii* Bennett, 1831 (Apidae, Meliponini) in Yucatan, Mexico

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Abstract – The Mayan bee *Melipona beecheii* is one of the most important and widely cultivated stingless bees in Mexico. In order to document pollen and nectar resources for *M. beecheii* during the dry season, 25 pot-pollen and 25 pot-honey samples were collected from February to May 2021 at eight villages in Yucatan, Mexico. All samples were acetolysed, and 500 pollen grains were counted randomly for each sample. A total of 21 taxa belonging to eight botanical families were observed in the pot-pollen samples; in contrast, 32 pollen types from 16 botanical families were recorded in the pot-honey samples. According to PCA analyses, the pollen types that explained the maximum variance among the pot-pollen samples were *Senna racemosa* var. *racemosa*, *Lonchocarpus punctatum*, *Cochlospermum vitifolium*, *Bursera schlechtendalii* and *B. simaruba*, while *S. racemosa* var. *racemosa*, *C. vitifolium*, *Alternanthera ramosissima*, *Psidium guajava*, *B. schlechtendalii*, *B. simaruba*, *L. punctatum, Mimosa bahamensis* and *Solanum americanum* explained the greatest variance among the pot-honey samples. Our results confirm that *M. beecheii* displays polylectic foraging and targets for the secondary vegetation of tropical deciduous and tropical semideciduous forests. Diversity in the pot-pollen was found to be lower than that of the pot-honey samples. Since some pot-honey samples were overrepresented by the pollen grains of *S. racemosa* var. *racemosa*, PCA and cluster analysis grouped those pot-pollen and pot-honey samples together.

***Melipona beecheii* / melissopalynology / pot-pollen / pot-honey / mayan stingless bee**

1. INTRODUCTION

Currently, 46 stingless bee species have been reported in Mexico. One of the most important of these is *Melipona beecheii*, which has a wide distribution (Ayala 1999). Also known as the Mayan bee or *Xunan Kab*, *M. beecheii* is a stingless bee that is valued and cultivated by the Mayas for over 2100 years (Canto et al. 2021) in the Yucatan Peninsula, Mexico. Its honey, pollen and cerumen, this latter substance referred to as 'Campeche wax', and products derived from these resources are of biocultural importance. The Madrid Codex describes their importance in culture and traditional medicine, as well as the gods (e.g. *Ah Mucen Cab*) who were believed to take care of this native bee (Tozzer and Allen 1910).

More than 2327 species of vascular plants have been recorded in the aforementioned region, of which approximately 900 arboreal, shrub and herbaceous species are of melliferous importance for the 17 species of bees native to the same location (Ayala 1999; Duno et al. 2018; CONABIO

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2018). During pollen and nectar foraging, bees contribute to the cross-pollination of native and cultivated plants. Pollen is an essential resource in the diet of bees because it provides proteins, lipids, vitamins and essential amino acids (Yang et al. 2013). In addition, nectar is an aqueous solution consisting mainly of sugars, amino acids, mineral ions and essential oils (Baker and Baker 1983; Musicante and Galetto 2008). It is important to note that honey produced by stingless bees has particular physicochemical and organoleptic characteristics such as higher moisture and free acidity, and it is considered medicinally important in several Mexican regions (Rosales 2012).

Melissopalynological research helps us to determine the floral sources used for pollen and nectar collection, which are necessary for the larval diet and honey production. Among the most complete melissopalynological studies carried out in Mexican stingless bees, the investigation conducted in *Nannotrigona perilampoides*, *Plebeia* sp., *Scaptotrigona mexicana* and *Tetragonisca angustula* by Martínez-Hernández et al. (1993), who analysed pot-pollen, pot-honey and larval food during an annual cycle in Chiapas, emphasises the importance of native and cultivated plants in the diet of these polylectic bees. Ramírez-Arriaga and Martínez-Hernández (2007) conducted pollen spectra analysis of *S. mexicana* honey in Puebla; Pacheco-Palomo (2011) reported pollen recovered from *M. beecheii* pot-honey in Campeche as well as its physicochemical characteristics; Quiroz-García et al. (2011) investigated pollen spectra in *S. hellwegeri* in Jalisco; Espinoza-Toledo et al. (2018) studied at the family level pollen grains from the honey of *M. beecheii*, *M. solani* and *S. mexicana* in Chiapas; Villanueva-Gutiérrez et al. (2018) worked with *M. beecheii* pollen loads in Yucatan, citing *Bursera simaruba*, *Gliricidia sepium*, *Solanum*, *Senna*, *Metopium brownei*, *Cochlospermum*, *Viguiera dentata*, *Pouteria unicularis*, *Thrinax* and *Euphorbia* among the significant plant; López-Roblero et al. (2021) studied pollen recovered from the honey of *S. mexicana*, *M. beecheii*, *M. solani* and *Tetragonisca angustula* from Chiapas. Finally, Ortiz-Reyes et al. (2022) carried out melissopalynological studies and physicochemical analysis of *M. beecheii* and *Scaptotrigona mexicana* pot-honey samples in Veracruz.

More than 32 plant species have been reported in Mexico and Mesoamerica for *M. beecheii* and other stingless bees, which mainly forage on *Bursera simaruba*, *Gliricidia sepium*, *Solanum*, *Senna*, *Metopium brownei*, *Cochlospermum vitifolium*, *Viguiera dentata*, *Pouteria unicaris*, *Euphorbia*, *Thrinax* and *Psidium guajava*, among others (Enríquez and Dardón 2007; Ramírez-Arriaga et al. 2007, 2018; Villanueva-Gutiérrez et al. 2018).

In order to document pollen and nectar resources for the Mayan honey bee *M. beecheii*, we conducted melissopalynological analyses of pot-pollen and pot-honey samples collected from eight backyard meliponaries located in the state of Yucatan. This study also aimed to estimate foraging strategies and to propose a standardised method for the characterisation of *M. beecheii* pot-honey samples.

2. MATERIALS AND METHODS

2.1. Study area

The study was conducted from February to May 2021, during the dry season and in eight meliponaries where the native bee *M. beecheii* is cultivated. These privately owned meliponaries, located in back yards, were built with wooden roofs and concrete floors and housed 6 to 60 colonies, mainly of *M. beecheii* in wooden boxes (Table I). The meliponaries are located at a minimum distance of 7 km and a maximum distance of 191 km from each other (Figure 1). In general, the meliponaries were adjacent to agricultural crops and home gardens, which were surrounded by secondary low deciduous forest vegetation (trees 4 to 12 m tall) and secondary medium deciduous forest vegetation (trees 10 to 15 m tall). Both of these plant communities are dominant in the state of Yucatan (Figure 1).

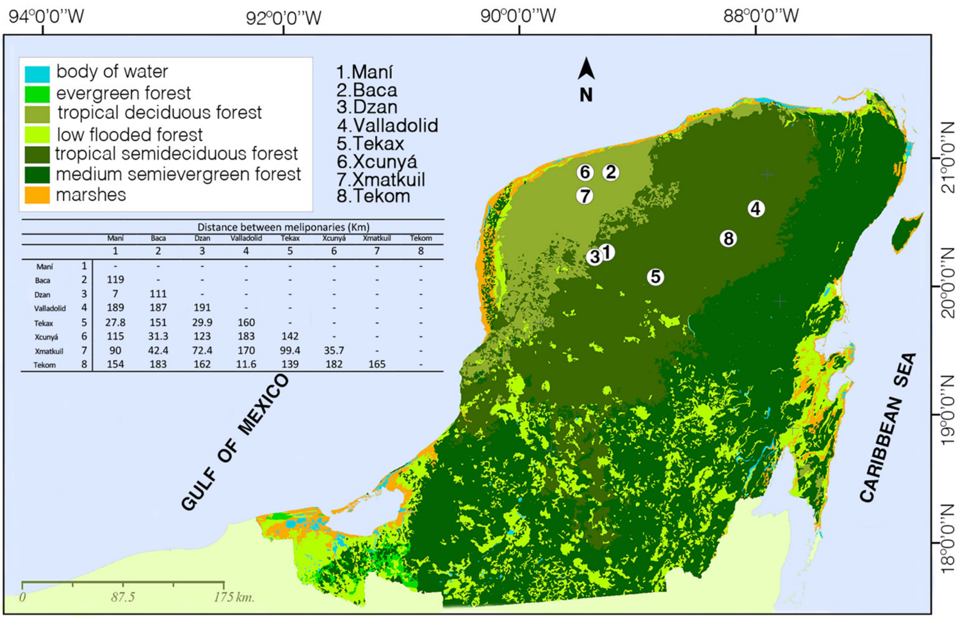
Table I List of towns where pot-pollen and pot-honey samples were collected in Yucatan, Mexico

Town	Coordinates	Number of nests	Site characteristics
1. Maní	20°22′46.956″ N 89°23′5.514″ W	22	The stingless bee boxes were in a back yard. The surrounding vegetation was secondary tropical semideciduous forest.
2. Baca	21°06′47.0″ N 89°24′25.2″ W	6	The stingless bee boxes were in a back yard. The surrounding vegetation was secondary tropical deciduous forest.
3. Dzan	20°22′46.1244″ N 89°26′41.132″ W	15	The stingless bee boxes were in a citrus grove, mainly lemon and orange. The surrounding vegetation was secondary tropical semideciduous forest.
4. Valladolid	20°40′42.3″ N 88°11′47.0″ W	5	The stingless bee boxes were in a back yard with the presence of *Trigona nigra* and *Scaptotrigona* sp. nests. The surrounding vegetation was secondary tropical semideciduous forest.
5. Tekax	20°11′56.4″ N 89°16′19.3″ W	17	The stingless bee boxes were in a back yard with the presence of *Scaptotrigona* sp. nests. The surrounding vegetation was secondary tropical semideciduous forest.
6. Xcunyá	21°7′57.2268″ N 89°36′45.6732″ W	17	The stingless bee boxes were in a back yard. The surrounding vegetation was secondary tropical deciduous forest.
7. Xmatkuil	20°52′01.2″ N 89°37′28.7″ W	60	The stingless bee boxes were in a back yard with the presence of boxes of *Partamona* sp., *Lestrimelitta* sp., *Cephalotrigona* sp., *Trigona* sp., *Scaptotrigona* sp., *Nannotrigona* sp. and *Frieseomelitta* sp. The surrounding vegetation was secondary tropical deciduous forest.
8. Tekom	20°36′28.9″ N 88°15′36.4″ W	23	The bee boxes were in a back yard. The surrounding vegetation was secondary medium semideciduous forest.

2.2. Sample collection and processing

Three samples of pot-pollen and three samples of pot-honey were collected from three nests of *M. beecheii* at each meliponary located in the villages of Baca, Dzan, Valladolid, Tekax, Xcunyá, Xmatkuil and Tekom, except for the one in Maní, where four pot-pollen and four pot-honey samples from four colonies were studied. The colonies were catalogued in good health and with good pollen and honey storage by the owners. Closed pot-pollen and pot-honey were sampled from each nest, and pollen samples were collected with sterile spoons and honey samples with sterile syringes. Subsequently, each extracted sample was placed separately in a sterile vial. Flowers were collected from the plants in the back yards of the meliponaries to obtain reference pollen.

At the Paleopalynology Laboratory: Paleopalynology and Actuopalynology of the Institute of Geology of the National Autonomous University of Mexico (UNAM), all samples were registered with a catalogue number, and then 6 ml of pot-honey samples and 1 g of pot-pollen samples were processed using Erdtman's acetolysis method (1960). After the samples were processed, permanent slides were made with glycerine gelatine.



		Distance between meliponaries (Km)							
		Maní	Baca	Dzan	Valladolid	Tekax	Xcunyá	Xmatkuil	Tekom
		1	2	3	4	5	6	7	8
Maní	1	-	-	-	-	-	-	-	-
Baca	2	119	-	-	-	-	-	-	-
Dzan	3	7	111	-	-	-	-	-	-
Valladolid	4	189	187	191	-	-	-	-	-
Tekax	5	27.8	151	29.9	160	-	-	-	-
Xcunyá	6	115	31.3	123	183	142	-	-	-
Xmatkuil	7	90	42.4	72.4	170	99.4	35.7	-	-
Tekom	8	154	183	162	11.6	139	182	165	-

Figure 1. Map of the Yucatan Peninsula, Mexico, location of the traditional meliponaries and distance between them in secondary tropical deciduous forest and tropical semideciduous forest vegetation (modified from Durán and García 2011).

2.3. Qualitative pollen analysis and characterisation of honey

First, pollen grains were described using a ZEISS AXIOLAB optical microscope with phase contrast at 100 × magnification. For the identification of pollen grains, reference pollen collections, palynological catalogues (Palacios-Chávez et al. 1991; Martínez-Hernández et al. 1993), melissopalynological studies (Ramírez-Arriaga 2007; Ramírez-Arriaga et al. 2016) as well as floristic lists of the Yucatan Peninsula were consulted.

To estimate the abundance of each pollen type in the samples in a standardised manner, 500 pollen grains were counted randomly for each sample. Following Louveaux et al. (1978), taxa were classified into predominant pollen ($P \geq 45\%$), secondary pollen ($S = 16–45\%$), important minor pollen ($I = 3–15\%$) and minor pollen ($M \leq 3\%$). Finally, the main pollen grains observed in the analysed samples were photographed.

2.4. Statistical analysis of pollen spectra

After the counts were performed, a data matrix was created and used for different analyses, in Tilia Graph to plot pollen diagrams in which the pollen types were classified by plant life form (tree, shrub, grass and vine or lianas). A CONISS analysis using the incremental sum of squares method was also performed to cluster the samples (Grimm 1987).

In order to analyse the most probable collecting behaviour of *M. beecheii*, the diversity (Shannon and Weaver 1949) and evenness (Pielou 1977) indices were calculated. When plants were foraged heterogeneously, J' values were close to zero. Conversely, if the resources were exploited homogeneously, the values were close to 1.

Moreover, a principal component analysis (PCA) was performed with variance–covariance data to explain the maximum variability among pot-pollen, pot-honey, and both pot-pollen and pot-honey spectra. The cluster analysis was carried out with the unweighted pair group method with arithmetic mean (UPGMA), using the Euclidean similarity index with Past 4 software (Hammer et al. 2007), which allowed us to analyse the samples of the different meliponaries by similarity.

3. RESULTS

3.1. Pot-pollen melissopalynological spectrum

A total of 12,542 pollen grains were counted in the 25 pot-pollen samples analysed, recording 21 taxa belonging to eight botanical families. The Fabaceae family exhibited the highest richness with 12 pollen types, followed by Bixaceae and Burseraceae with two pollen types each (Table II). As for abundance, the Fabaceae, Burseraceae and Bixaceae families recorded the highest values (Figure 2).

With regard to the abundance of pollen grains found in the pot-pollen samples collected in Maní, the predominant pollen types were *Senna racemosa* var. *racemosa* and *Cochlospermum vitifolium*. In Baca, *S. racemosa* var. *racemosa* was also predominant, followed by the minor pollen types *Mimosa* sp. (10%), *M. bahamensis* and *Desmanthus virgatus*. In all samples from Dzan, *S. racemosa* var. *racemosa* was predominant, followed by *Solanum americanum*, which was considered a minor pollen. In Valladolid, *S. racemosa* var. *racemosa* and *Lonchocarpus punctatus* predominated, while *S. racemosa* var. *racemosa* and *C. vitifolium* were recorded as the most prevalent pollen types in the samples collected in Tekax. Similarly, at the Xcunyá site, *S. racemosa* var. *racemosa* was the predominant pollen types, and *Bursera* spp. pollen was observed on a secondary level. The copal tree or *Bursera* pollen types were predominant in both Xmatkuil and Tekom (Figure 3 and Table II).

Finally, pollen types considered rare were *Leucaena leucocephala* ssp. *leucocephala*, *Caesalpinia gaumeri* and *Desmodium* sp. in Maní; *Solanum erianthum* in Baca; *Vachellia* sp. in Xcunyá; and *Desmanthus virgatus*, *Mimosa bahamensis* and *Pimenta dioica* in Tekom, all observed in the pot-pollen samples but not included in the pollen counts.

The Shannon–Weaver index (H') ranged from 0.19 to 1.24, most diversity values indicated a low diversity of species exploited by *M. beecheii* to obtain pollen, with the highest values in the samples from Tekax ($H' = 1.22$) and Xcunyá ($H' = 1.02$). Further, Pielou index (J') ranged from 0.16 to 0.88, most of the evenness values (J'), which were less than or equal to 0.67, suggest heterogeneous foraging behaviour (Figure 4).

In general terms, *M. beecheii* predominantly foraged in the arboreal stratum, followed by the herbaceous and shrub stratum. According to the foraging similarity observed in the meliponaries, the CONISS analysis formed two groups: group A included the Maní, Bacab, Dzan, Valladolid and Tekax sites, where the Mayan bee predominantly visited *S. racemosa* var. *racemosa* and *C. vitifolium*; group B included Xcunyá, Xmatkuil and Tekom, where the dominance of *Bursera simaruba* and *B. schlechtendalii* was notable, in addition to the presence of the cultivated tree *Psidium guajava* (Figure 3).

The principal component analysis (PCA) of the 25 pot-pollen samples indicated that the first three components explain 99.16% of the variance in the data. The first component explains 71.57%, the second 20% and the third 7.59%. The pollen types that explain the maximum variance among the samples are *S. racemosa* var. *racemosa*, *L. punctatum* and *C. vitifolium*, additional pollen types that contributed to a minor degree to explaining the percentage of variation were *B. schlechtendalii* and *B. simaruba* (Table III).

Three groups were differentiated in the PCA, and this was confirmed in the cluster analysis; in group A, there were three samples from Tekax and Maní in which *C. vitifolium* dominated, while group B associated twelve samples from the Maní, Baca, Dzan, Valladolid, Tekax and Xcunyá sites, defined mainly by *S. racemosa* var. *racemosa*. Group C congregated samples from Xcunyá, Xmatkuil and Tekom mainly because of the abundance

Table II Percentages of pollen spectra recorded in pot-pollen samples of *Melipona beecheii* in Yucatan

	Maní				**Baca**			**Dzan**			**Valladolid**			**Tekax**			**Xcunyá**			**Xmatkuil**			**Tekom**		
Number of samples: H-	**5058**	**5059**	**5060**	**5061**	**5062**	**5063**	**5064**	**5065**	**5066**	**5067**	**5068**	**5069**	**5070**	**5071**	**5072**	**5073**	**5074**	**5075**	**5076**	**5077**	**5078**	**5079**	**5080**	**5081**	**5082**
AMARANTHACEAE																									
Alternanthera ramosissima	0.2																								
ANACARDIACEAE																									
Astronium graveolens													3.6										0.4		
BIXACEAE																									
Bixa orellana													5.7												
Cochlospermum vitifolium		62.6	5.4	4.8		2.4					4.6	0.4		69.6	79	16.6									0.2
BURSERACEAE																									
Bursera simaruba		0.6							0.2			0.6			0.6	1.8		48.5	48.3	49.1	50.4	50.3	44.2	47.2	46.4
Bursera schlechtendalii		0.4									0.2	1			0.2	1.2		43.8	44.1	44	42.5	46	42.6	41.4	42.8
FABACEAE																									
Crotalaria sp.	4.4	0.2	3.6	1.4					0.6			1.4													
Desmodium sp.													3.2												
Desmanthus virgatus					1.6	0.2	7.6						4.3												
Enterolobium cyclocarpum																		0.6							
Leucaena leucocephala ssp. leucocephala													0.2												
Leucaena sp.							0.6												0.4						
Lonchocarpus punctatus													67.9												
Mimosa bahamensis		3.4	1.4	2.2	7.6	0.6	6.2			1.4	0.4						2.2								
Mimosa sp.	0.2	0.4	0.6	0.6	1.6	10		1.2	5	1		2		0.6											
Senna racemosa var. *racemosa*	94	31.6	87.4	88.6	85.2	82.6	85.5	90.2	82.6	96.4	91.2	94.6	6.0	29.4	20.2	80.4	95.2	7.1	6.4		0.4				0.4
Senna sp.1													6.6												
Senna sp.2													2.5												
MYRTACEAE																									
Psidium guajava						0.4														6.5	6.1	3.7	12.6	11.4	10.2
SAPINDACEAE																									

Table II (continued)

	Maní				Baca			Dzan			Valladolid			Tekax			Xcunyá			Xmatkuil			Tekom		
Number of samples: H-	5058	5059	5060	5061	5062	5063	5064	5065	5066	5067	5068	5069	5070	5071	5072	5073	5074	5075	5076	5077	5078	5079	5080	5081	5082
Thouinia paucidentata					0.2												2.6		0.8	0.4	0.6		0.2		
SOLANACEAE																									
Solanum americanum	1.2	0.8	1.6	2.4	3.8	3.8		8.6	11.6	1.2	3.6			0.4											

of *B. schlechtendalii* and *B. simaruba*. Finally, a sample from Valladolid (H-5070) was isolated owing to the dominance of *L. punctatum* (Figures 5 and 6).

3.2. Pot-honey melissopalynological spectrum

In the 25 honey samples analysed, a total of 12,696 pollen grains were counted and 32 different pollen types belonging to 16 botanical families were recorded. Fabaceae stands out with 14 pollen types, followed by Burseraceae, Solanaceae and Sapindaceae with two pollen types each (Table IV). With regard to pollen abundance, Fabaceae recorded the highest value, followed by Burseraceae, Myrtaceae, Amaranthaceae, Solanaceae, and Bixaceae (Figure 7).

In the pot-honey samples from Maní, *Alternanthera ramosissima* was predominant and the secondary elements were *Mimosa* sp., *S. racemosa* var. *racemosa*, *Solanum americanum* and *Lonchocarpus* sp. Honey samples from Baca showed *S. racemosa* var. *racemosa* as predominant and secondary taxa were *S. americanum* and *Mimosa bahamensis*, while *Waltheria rotundifolia* was of minor importance. In the case of Dzan, *S. racemosa* var. *racemosa* was predominant, followed by the secondary pollen types *S. americanum* and the less important *Serjania triquetra*. In Valladolid, *A. ramosissima* was recorded as predominant, with secondary pollen of *Lonchocarpus punctatus* and *S. racemosa* var. *racemosa*. In the Tekax pot-honey samples, *C. vitifolium* and *A. ramosissima* predominated, while *S. racemosa* var. *racemosa* was secondary. In Xcunyá, *S. racemosa* var. *racemosa* was also predominant, and *B. schlechtendalii*, *B. simaruba* and Fabaceae occurred as secondary pollen. The samples from Xmatkuil exhibited as secondary elements *B. simaruba*, *B. schlechtendalii* and *Psidium guajava*, while *Byrsonima* sp. was of minor importance. Finally, in the Tekom pot-honey samples, *P. guajava* predominated and *B. simaruba* was of minor importance.

The diversity indices recorded in the honey samples ranged from 0.88 to 2.35, with the highest value observed in Maní ($H' = 2.35$). Uniformity indices (J') oscillated between 0.35

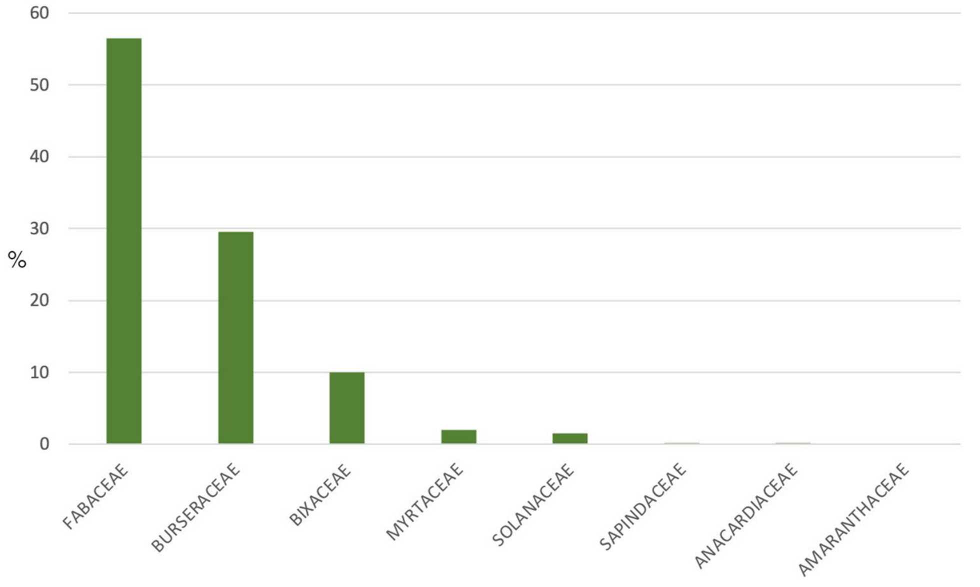


Figure 2. Percentages of the botanical families registered in the pot-pollen of *Melipona beecheii* collected in the backyard meliponaries in Yucatan, Mexico.

and 0.85, most of the *J′* values, which were less than or equal to 0.68 indicating heterogeneous foraging of resources (Figure 4).

The greatest number of pollen grains recorded in the pot-honey samples came mainly from arboreal plants of the Fabaceae family, followed by herbaceous, shrub and liana (Figure 8). The CONISS analysis showed three main groups with two subgroups each according to the similarity of pollen types recorded in each sample. Group A included Maní, Baca and Dzan; group B comprised Valladolid and Tekax. It should be noted that in groups A and B the collection in the arboreal and herbaceous stratum, and to a lesser extent the arboreal stratum,

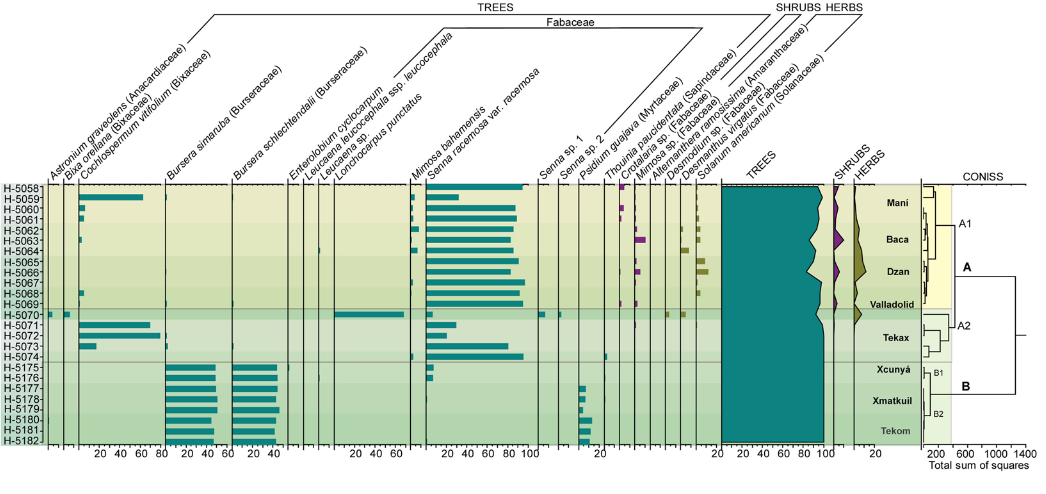


Figure 3. Melissopalynological spectrum of the pot-pollen samples from *Melipona beecheii* collected in Yucatan, Mexico.

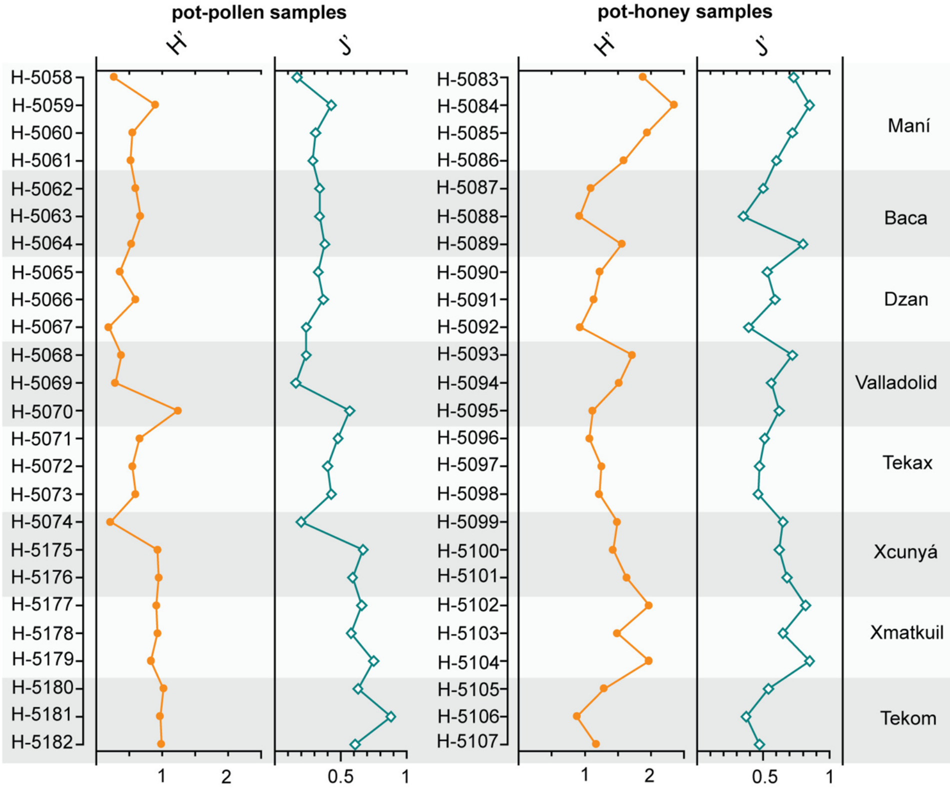


Figure 4. Diversity (*H*′) and evenness (*J*′) indices in the pot-pollen and pot-honey samples from *Melipona beecheii* collected in Yucatan, Mexico.

was predominant; in group C where samples from Xcunyá, Xmatkuil and Tekom are grouped, the arboreal stratum was dominant (Figure 8).

Table III Principal component analysis (PCA) of the *Melipona beecheii* pot-pollen spectrum

Eigenvectors PCA			
Eigenvalue	7.383	4.169	2.198
Variance (%)	71.566	20.003	7.5961
Cumulative variance (%)	71.566	91.569	99.1651
	PC 1	**PC 2**	**PC 3**
Senna racemosa var. *racemosa*	**−0.825**	−0.280	−0.230
Lonchocarpus punctatus	0.030	0.072	**0.821**
Cochlospermum vitifolium	0.007	**0.857**	−0.334
Bursera schlechtendalii	0.376	−0.285	−0.252
Bursera simaruba	0.417	−0.313	−0.280

The PCA of the 25 honey samples (Figure 9) showed that the first four components account for 83.58% of the variance. The first component explains 33.94%, the second 23.38%, the third 14.22% and the fourth component 12.04%. The pollen types that account for the maximum variance among the samples are *S. racemosa* var. *racemosa*, *C. vitifolium*, *A. ramosissima*, *P. guajava*, *B. schlechtendalii* and *B. simaruba*, other less significant taxa explaining the percentage of variation are *L. punctatus, M. bahamensis* and *S. americanum* (Table V).

The pot-honey samples were associated into six groups, and these groups as well as the relationship among the samples are detailed in the cluster analysis (Figures 9 and 10). Group A contains four samples from Baca, Valladolid and Tekax which were associated mainly by *A. ramosissima*; group B clusters five samples

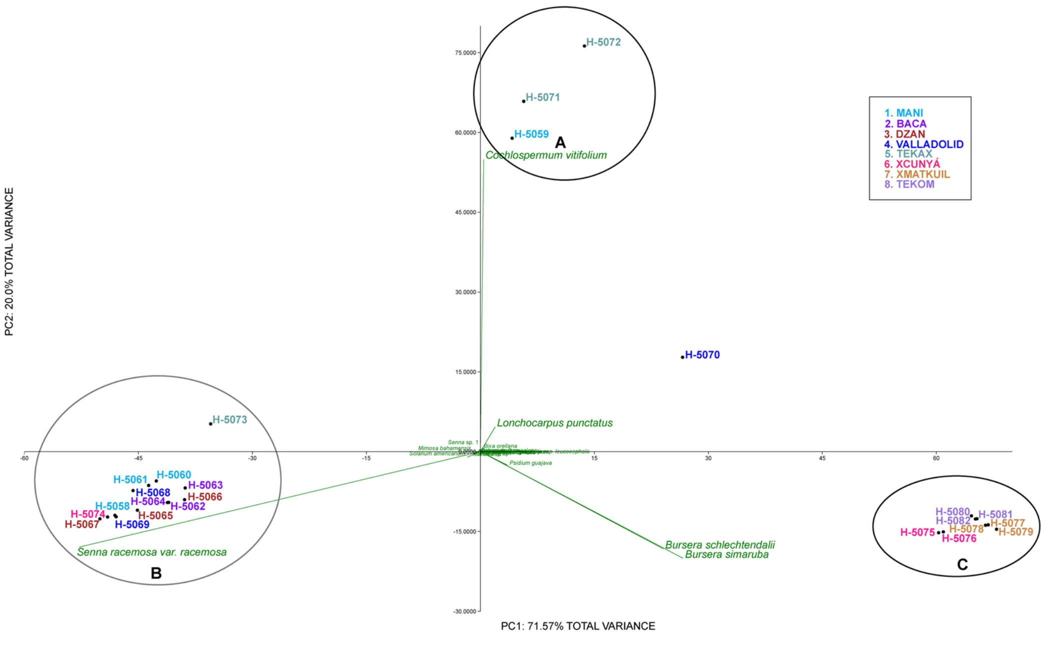


Figure 5. PCA of the *Melipona beecheii* pot-pollen samples collected in Yucatan, Mexico.

from Xcunyá and Xmatkuil which share an abundance of *B. schlechtendalii* and *B. simaruba*; group C contains only five samples from Maní, Baca and Valladolid where the significant elements were *S. americanum*, *M. bahamensis* among others; group D includes six samples from Baca, Dzan and Xcunyá associated by *S. racemosa* var. *racemosa*; group E contains two samples from Tekax by *C. vitifolium,* and group F relates the three samples from Tekom through *P. guajava* (Figures 9 and 10).

3.3. Comparative statistical analysis between the pot-honey and pot-pollen spectra

In order to determine the relationship between the pot-pollen and pot-honey samples, a primary component analysis was performed (Figure 11), which showed that the first three components explain 80.25% of the data variance. The first component accounts for 50.69%, the second component 17.76% and the third 11.80%. The pollen types explaining the maximum variance among the samples are *S. racemosa* var. *racemosa*, *C. vitifolium, A. ramosissima*, *B. simaruba* and *B. schlechtendalii*; besides, other taxa of minor importance are *P. guajava, L. punctatus*, *M. bahamensis* and *S. americanum* (Table VI).

A total of five groups were formed (Figures 11 and 12): group A includes a total of 19 samples: 6 pot-honey and 13 pot-pollen samples from Maní, Baca, Dzan, Valladolid, Tekax and Xcunyá, all associated mainly by *S. racemosa* var. *racemosa*; in group B, there are 3 pot-pollen and 2 pot-honey samples from Tekax and Maní in which *C. vitifolium* is significant; group C contains 3 pot-honey samples from Tekom that share the dominance of *P. guajava*; group D comprises 5 pot-honey samples and 8 pot-pollen samples from Xcunyá, Xmatkuil and Tekom, which share an abundance of *B. schlechtendalii* and *B. simaruba*; finally, group E includes 9 pot-honey samples and one pot-pollen sample from Valladolid, Maní, Tekax and Baca, with a primary dominance of *A. ramosissima* and *L. punctatus* (Figures 11 and 12).

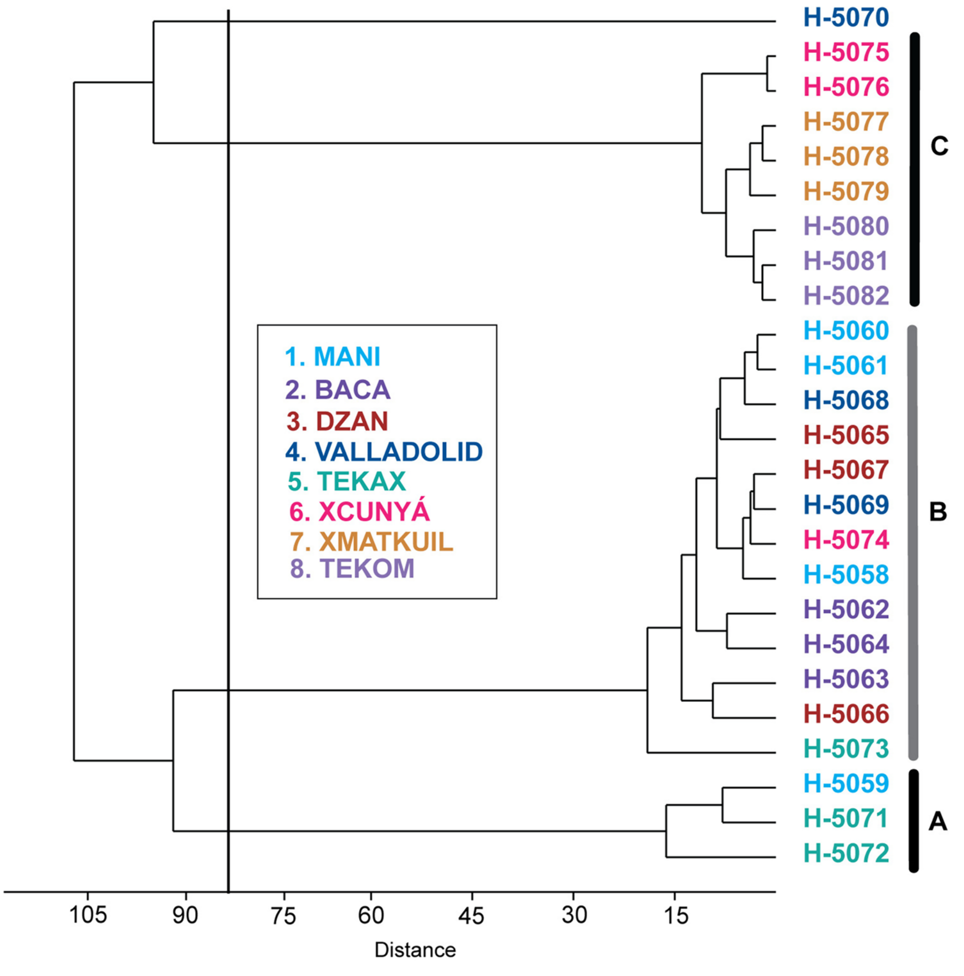


Figure 6. Cluster analysis of the pot-pollen samples from *Melipona beecheii* collected in Yucatan, Mexico.

3.4. Botanical characterisation of pot-honey samples

The characterisation of *M. beecheii* honeys was carried out considering only nectar-producing plants, *i.e.* elements were reported to be exclusively polliniferous were not included in this analysis, so abundances were recalculated considering only the plants reported as nectar-producing. It should be noted that not all of these plants have been confirmed as nectar producers through studies, despite being considered nectariferous.

A total of 16 nectariferous plants from the arboreal, herbaceous, shrub and liana strata were recorded (Table VII). The Fabaceae family was the most significant with ten pollen types. The most important nectariferous plants were *A. ramosissima*, *Thrinax radiata*, *B. simaruba*, *B. schlechtendalii*, *Crotalaria* sp., *Leucaena leucocephala* var. *leucocephala*, *L. punctatus*, *Lonchocarpus* sp., *M. bahamensis*, *Mimosa* sp., *W. rotundifolia*, *P. guajava*, *Thouinia paucidentata* and *Serjania triquetra* (Figures 13 and 14).

Table IV Percentages of pollen spectra recorded in pot-honey samples of *Melipona beecheii* in Yucatan

	Maní				**Baca**			**Dzán**			**Valladolid**			**Tekax**			**Xcunyá**			**Xmatkuil**			**Tekom**		
Number of samples: H-	**5083**	**5084**	**5085**	**5086**	**5087**	**5088**	**5089**	**5090**	**5091**	**5092**	**5093**	**5094**	**5095**	**5096**	**5097**	**5098**	**5099**	**5100**	**5101**	**5102**	**5103**	**5104**	**5105**	**5106**	**5107**
AMARANTHACEAE																									
Alternanthera ramosissima	0.6	12.2	6.6	52.5	0.8							50.3	63.4	65.1	5.7	3.6							0.6	0.6	0.4
ANACARDIACEAE																									
Astronium graveolens																							1.5	1	0.8
ARECACEAE																									
Thrinax radiata																			6.8						
ASTERACEAE																									
Viguiera dentata	0.2	1.4	7.6	4.1				0.4																	0.4
BIXACEAE																									
Cochlospermum vitifolium	7.2	5.3	2.4	0.6		0.4			2	1	8			13.1	67.4	65.5									
BURSERACEAE																									
Bursera simaruba	3.3	4.5	0.6	0.6		2		0.2			0.4				1.2	2.6	32.7	35.8	2	19.5	41.5	15.8	12	7.4	12.7
Bursera schlechtendalii	1.8	3.3				0.6									0.8	2	36.5	31.6	0.8	24.2	32.8	21.2	8.6	3.3	7.2
FABACEAE																									
Crotalaria sp.	5.7	7.3	5.2	3.7				4.3	1.2	1.6	4.8														
Caesalpinia gaumeri						1.4		0.2								0.2									
Desmodium sp.			1.2									0.8			0.6	0.6									
Desmanthus virgatus		1	0.2		0.6	0.4					1.2	0.6													
Leucaena leucocephala ssp. leucocephala	0.2	0.4	0.6	0.8	0.2	0.6						0.4			0.2	0.2	0.4	0.6	8.2	0.4		0.2			
Lonchocarpus punctatus		1	3	1.6	5.9	3.6	5.4				40.4	22.5	16.7												1
Lonchocarpus sp.	19.9	12	5.2	3.4	0.8	0.2					5				6	3.6								0.6	
Mimosa bahamensis	29.3	22.4	31.5	21.1	12.3	0.2	21.8		1.8	2	2.2	1		1	1.4		0.6	0.8	3.6	3.1	0.4	3.1	3.6	6.2	8
Mimosa sp.	1.4	2.2	1.2		3.2	8.8	0.8	2	5.5	1.4		0.6		0.8	0.6	0.6					0.4				
Fabaceae																	2.2	3.4	23.4						
Piscidia piscipula																		0.6	6.4	0.4					
Senna racemosa var. *racemosa*	5.9	10.2	30.3	6.5	69.3	79	23.4	54.9	58	76.8	25.6	12.3	8.6	16.4	12.1	18.4	19.4	23.9	46	3.3	3.4	4.8	1.9	0.2	0.4
Senna sp.1											0.2				0.2										

Table IV (continued)

	Maní				Baca			Dzán			Valladolid			Tekax			Xcunyá			Xmatkuil			Tekom		
Number of samples: H-	**5083**	**5084**	**5085**	**5086**	**5087**	**5088**	**5089**	**5090**	**5091**	**5092**	**5093**	**5094**	**5095**	**5096**	**5097**	**5098**	**5099**	**5100**	**5101**	**5102**	**5103**	**5104**	**5105**	**5106**	**5107**
Vachellia sp. 2																	2.8	0.8	0.6						
MALPIGHIACEAE																									
Byrsonima sp.																				15.7	4.3	15.8	1.1		0.4
MALVACEAE																									
Waltheria rotundifolia				2.2	6.9	0.4	15.6	0.4		1.6		0.8				0.2									
MYRTACEAE																									
Psidium guajava		2		0.8		0.8				0.6		0.6	0.6		0.8	0.4	1.4			18.2	10.7	23.1	64.8	78.6	66.9
PINACEAE																									
Pinus sp.							0.8					0.4													
POLYGONACEAE																									
Gymnopodium floribundum											5.4	2					3.4	1.8	1.4	3.1	1.2	2.3	5	1.6	1.6
PRIMULACEAE																									
Myrsine cubana	0.8													0.8	1										
RUTACEAE																									
Citrus sp.								0.4		0.4				0.2											
SAPINDACEAE																									
Thouinia paucidentata		1.8		0.4						1.2		1.4	1.8			0.4	0.6	0.6	0.8	6.2	0.8	8.7		0.4	
Serjania triquetra								11.3	3.1	1.4		0.4											0.4		0.2
SOLANACEAE																									
Solanum americanum	23.8	13	3.8	1.8		1.6	32.2	25.9	28.5	12.2	7	6.1	8.9	2.6	2.1	1.8				6	4.5	5.2	0.6	0.2	
Solanum erianthum			0.6																						

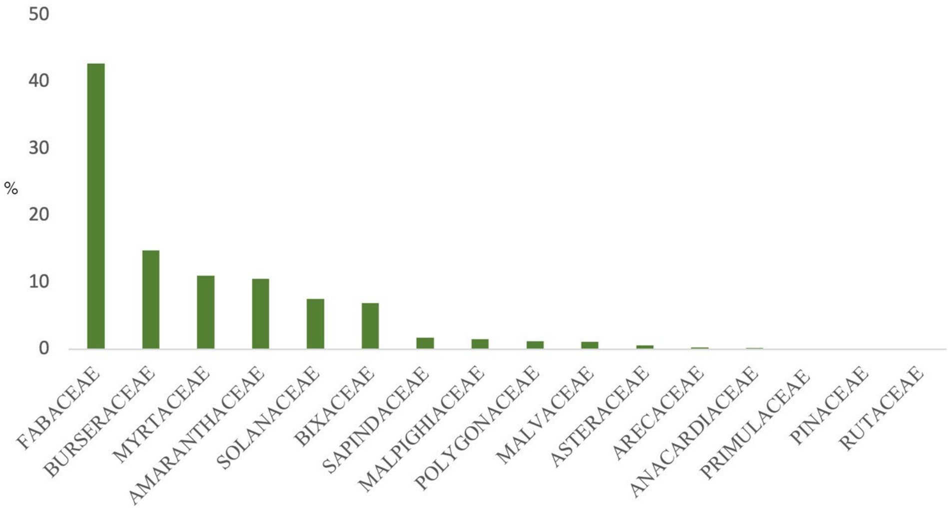


Figure 7. Percentages of the botanical families registered in the pot-honey of *Melipona beecheii* collected in the backyard meliponaries in Yucatan, Mexico.

A total of 15 honey samples were characterised as monofloral. Four samples were monofloral from *A. ramossisima*: H-5086 collected in Maní, H-5094 and H-5095 in Valladolid, as well as sample H-5096 in Tekax. In Xcunyá, honey H-5100 was monofloral from *B. simaruba*, as well as H-5103 from Xmatkuil. A monofloral sample (H-5099) from *B. schlechtendalii* was collected in Xcunyá. Sample H-5093 collected in Valladolid was monofloral from *L. punctatus*. In Maní, H-5083 and H-5085 were monofloral from *M. bahamensis*, just like H-5089 from Baca. All samples collected in Tekom (H-5105, H-5106 and H-5107) were monofloral from *P. guajava*. Finally, in Dzan, sample H-5090 was monofloral from *S. triquetra*.

By contrast, nine samples were classified as multifloral and one as bifloral. In the village of Maní, sample H-5084 was characterised as multifloral from *M. bahamensis*, *A. ramossisima, Lonchocarpus* sp. and *Crotalaria* sp., while in Baca, sample H-5087 was multifloral from *M. bahamensis*, *L. punctatus* and *Mimosa* sp.; H-5088 was multifloral from *L. punctatus*, *P. guajava* and *Mimosa* sp. In Dzan sample H-5091 was multifloral from *Crotalaria* sp., *Mimosa* sp. and *S. triquetra*, besides, sample H-5092 was multifloral of *Crotalaria* sp., *M. bahamensis*,

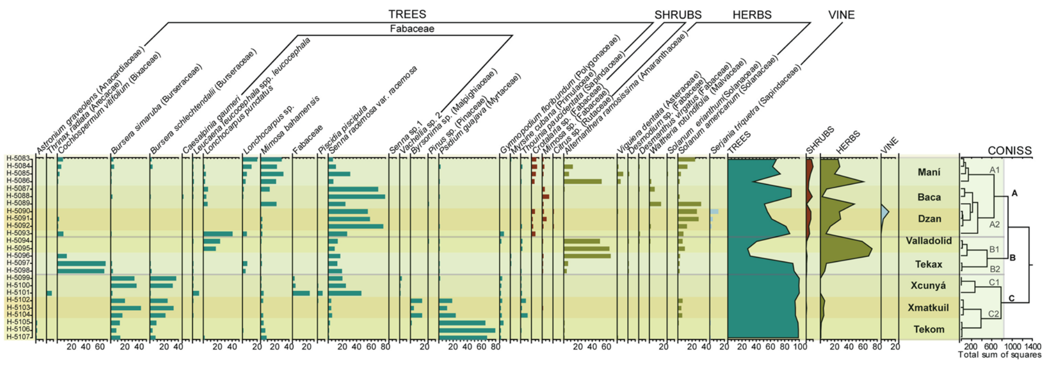


Figure 8. Melissopalynological spectrum of the *Melipona beecheii* pot-honey samples collected in Yucatan, Mexico.

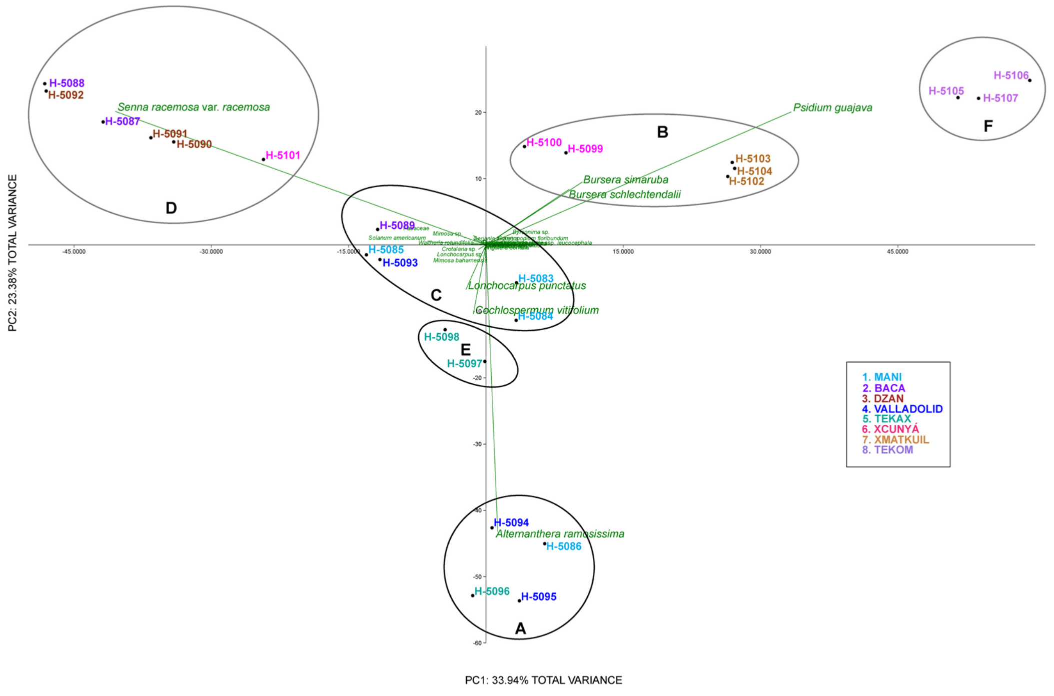


Figure 9. PCA of the *Melipona beecheii* pot-honey samples collected in Yucatan, Mexico.

Mimosa sp., *S. triquetra* and *W. rotundifolia*. In Tekax, sample H-5098 was multifloral from *A. ramossisima*, *B. simaruba*, *B. schlechtendalii* and *Lonchocarpus* sp., and sample H-5097 was bifloral from *A. ramossisima* and *Lonchocarpus* sp. In Xcunyá, sample H-5101 was multifloral from Fabaceae, *L. leucocephala*, *Thrinax radiata* and *P. piscipula*. In Xmatkuil, honey samples

Table V Principal component analysis (PCA) of the *Melipona beecheii* pot-honey spectrum

Eigenvectors PCA				
Eigenvalue	5.338	4.233	3.478	2.709
Variance (%)	33.94	23.38	14.22	12.04
Cumulative (%)	33.94	57.32	71.54	83.58
Variable	**PC 1**	**PC 2**	**PC 3**	**PC 4**
Senna racemosa var. *racemosa*	**−0.737**	0.367	−0.210	−0.170
Cochlospermum vitifolium	−0.025	−0.190	**0.836**	−0.351
Alternanthera ramosissima	0.023	**−0.788**	−0.378	−0.019
Psidium guajava	**0.607**	0.365	−0.278	**−0.539**
Bursera schlechtendalii	0.166	0.153	0.097	**0.531**
Bursera simaruba	0.192	0.173	0.089	**0.511**
Lonchocarpus punctatus	−0.040	−0.122	−0.088	−0.018
Mimosa bahamensis	0.010	0.070	0.147	−0.012
Solanum americanum	−0.116	0.009	−0.039	−0.007

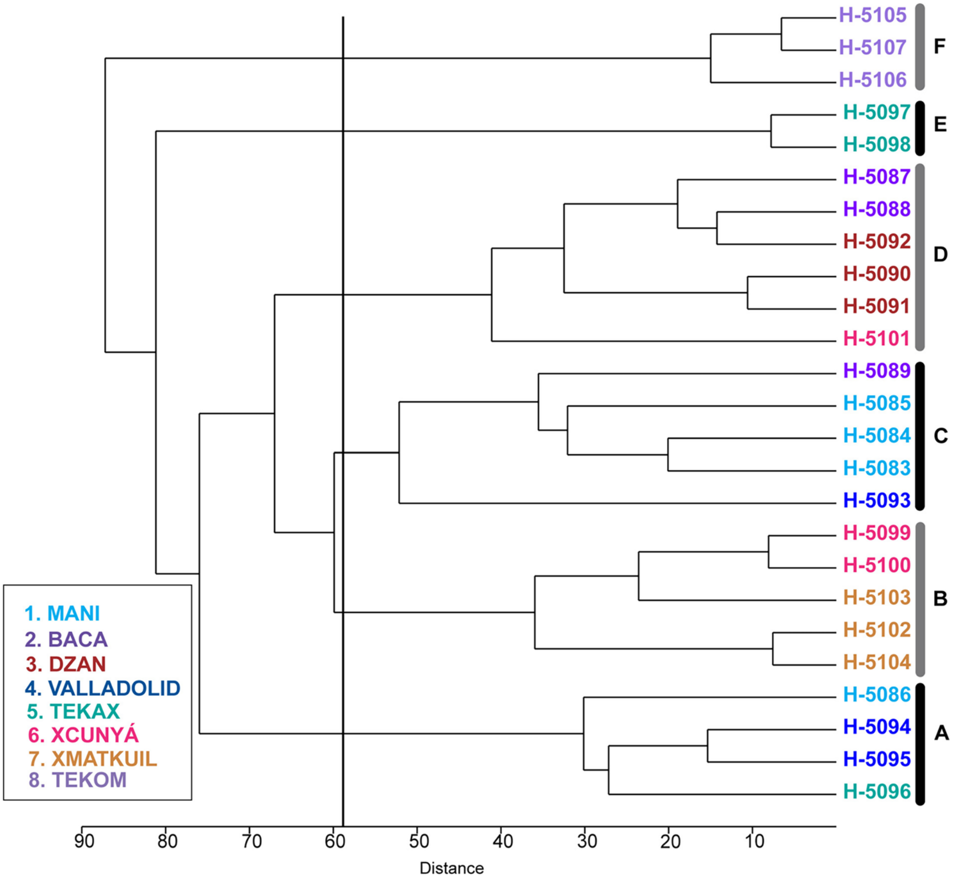


Figure 10. Cluster analysis for the pot-honey samples from *Melipona beecheii* collected in Yucatan, Mexico.

H-5102 and H-5104 were multifloral from *B. simaruba*, *B. schlechtendalii*, *Byrsonima* sp., *P. guajava* and *T. paucidentata* (Figure 13).

The CONISS analysis formed three main groups with subgroups: group A included the meliponaries in Maní, Bacab and Dzan where *M. beecheii* foraged at the arboreal, shrub and herbaceous strata; group B comprised Valladolid and Tekax, where the native bee predominantly collected from the arboreal and herbaceous strata; and in group C, consisting of the Xcunyá, Xmatkuil and Tekom meliponaries, the Mayan bee foraged at the arboreal stratum. A generally clear separation was observed among the samples from the different sites (Figure 13).

4. DISCUSSION

In the Yucatan Peninsula the floristic richness includes over 2300 species of vascular plants. Floristic studies carried out in Yucatan indicate that the most common families in low deciduous forest are Fabaceae, Bignoniaceae, Convolvulaceae, Orchidaceae and Euphorbiaceae, while the families Fabaceae, Rubiaceae, Sapotaceae, Myrtaceae and Ebenaceae are most abundant in medium subdeciduous forest (Miranda 1958; Zamora Crescencio et al. 2008).

The most abundant family in the studied region is Fabaceae, with 236 species and 78 genera (Duno de Stefano et al. 2018), which

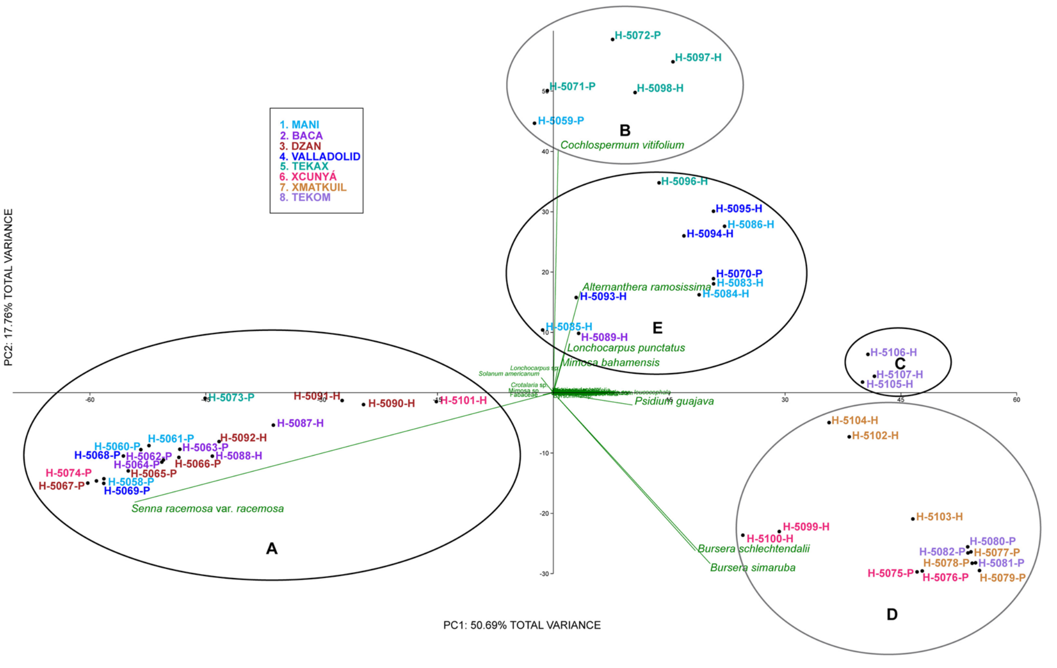


Figure 11. Comparative PCA between the *Melipona beecheii* pot-pollen and pot-honey samples collected in Yucatan, Mexico.

has been reported as one of the most important families in Mexico that include polliniferous and nectariferous plants (Martínez-Hernández et al. 1993; Roubik and Villanueva-Gutiérrez 2009; Ramírez-Arriaga et al. 2016, 2018; López-Roblero et al. 2021; Ortiz Reyes et al. 2022).

Table VI Comparative principal component analysis (PCA) between the *Melipona beecheii* pot-pollen and pot-honey spectra

Eigenvectors PCA			
Eigenvalue	5.697	4.347	3.966
Variance (%)	50.693	17.756	11.8
Cumulative (%)	50.693	68.449	80.249
Variable	**PC 1**	**PC 2**	**PC 3**
Senna racemosa var. *racemosa*	**−0.877**	−0.294	−0.127
Cochlospermum vitifolium	0.010	**0.654**	**−0.678**
Alternanthera ramosissima	0.057	0.272	**0.454**
Bursera simaruba	0.329	**−0.459**	−0.294
Bursera schlechtendalii	0.298	**−0.424**	−0.277
Psidium guajava	0.166	−0.033	0.271
Lonchocarpus punctatus	0.025	0.109	0.212
Mimosa bahamensis	0.010	0.070	0.147
Solanum americanum	−0.025	0.041	0.112

Five Fabaceae pollen types were notable in the present study: *L. punctatus*, *Lonchocarpus* sp., *M. bahamensis*, *Mimosa* sp. and *S. racemosa* var. *racemosa*. Pollen of *L. punctatus* has been recovered from *A. mellifera* honey samples in Quintana Roo (Córdova-Rodríguez et al. 2023), while *Lonchocarpus* sp. has been observed in pollen spectra of *A. mellifera* honey samples in Yucatan and Tabasco, as well as in pollen loads of *S. mexicana* and *Plebeia* sp. in Mexico and Brazil (Martínez-Hernández et al. 1993; Alfaro Bates et al. 2010; Villanueva-Gutiérrez 2002; Castellanos-Potenciano et al. 2012; Córdova-Córdova et al. 2013; da Silva Correia and Peruquetti 2023).

The *Mimosa* genus, which has 11 species in the Yucatan Peninsula, is an important pollen resource for stingless bees. It has also been reported in Panama, Brazil and Colombia (Aguilar-Sierra and Smith-Pardo 2009; Pinto da Luz et al. 2011; Barth et al. 2012; Roubik and Moreno Patiño 2018; da Silva Correia and Peruquetti 2023). As for the

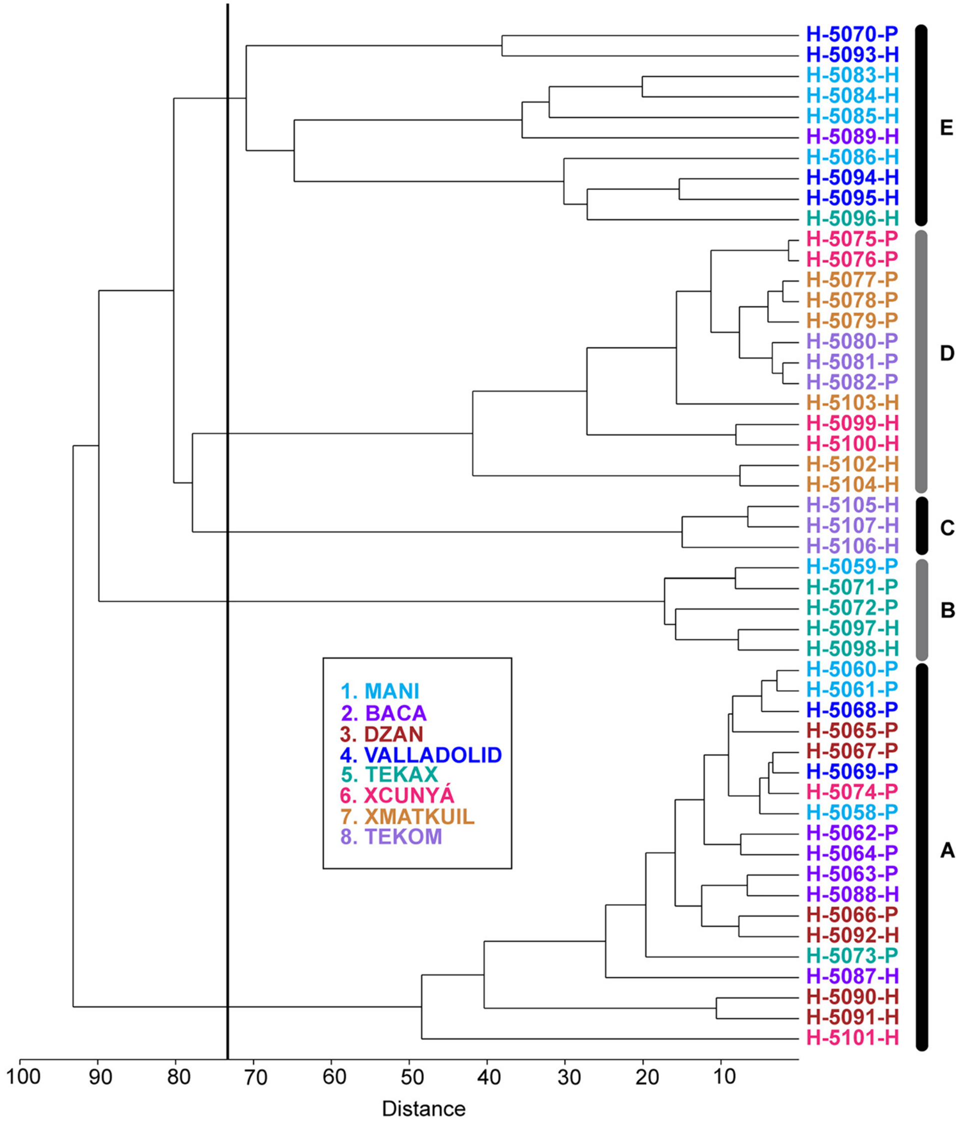


Figure 12. Comparative cluster between the *Melipona beecheii* pot-pollen and pot-honey samples collected in Yucatan, Mexico.

species *M. bahamensis*, it has been described as an important pollen and nectar resource for *A. mellifera* in Yucatan (Villanueva-Gutiérrez 2002; Villanueva-Gutiérrez et al. 2009; Alfato et al. 2010; Córdova-Rodríguez et al. 2023). All the pollen types we found in pollen and honey have been reported as key sources of nectar and pollen for bees.

The *Senna* tree is very diverse in the American continent, and in the Yucatan Peninsula, 23 taxa have been reported. It is important to mention that over 70% of the *Senna* species have extrafloral nectaries visited by ants and that bees do not collect these sugary secretions (Marazzi et al. 2006). Further, *Senna* has been considered an important pollen resource in Yucatan, Campeche, Quintana

Table VII Percentages of nectariferous plants recorded in pot-honey of *Melipona beecheii* samples in Yucatan

	Maní				Baca			Dzán			Valladolid			Tekax			Xcunyá			Xmatkuil			Tekom		
Number of samples: H-	**5083**	**5084**	**5085**	**5086**	**5087**	**5088**	**5089**	**5090**	**5091**	**5092**	**5093**	**5094**	**5095**	**5096**	**5097**	**5098**	**5099**	**5100**	**5101**	**5102**	**5103**	**5104**	**5105**	**5106**	**5107**
AMARANTHACEAE																									
Alternanthera ramosissima	0.9	17	10.4	57.5	7							61.9	76.8	95.9	31.1	25							0.6	0.6	0.4
ANACARDIACEAE																									
Astronium graveolens																							1.5	0.9	0.7
ARECACEAE																									
Thrinax radiata																			11.5						
ASTERACEAE																									
Viguiera dentata	0.3	1.9	12	4.5				1.4																	0.4
BURSERACEAE																									
Bursera simaruba	5.2	6.3	0.9	0.6		6.6		2.1			0.6				6.4	18	40.5	47	3.8	26	47.3	21.2	12.4	7.4	12.8
Bursera schlechtendalii	2.7	4.6				4.7									4.3	13.8	45.2	41.5	1.9	32.2	37.3	28.4	8.8	3.3	7.2
FABACEAE																									
Crotalaria sp.	8.9	10.1	8.2	4.1				20	12.3	11.1	8														
Caesalpinia gaumeri						3.1		0.7								1.3									
Desmodium sp.			1.9									0.9			3.2	4.1									
Desmanthus virgatus		1.3	0.3		4.3	2.3					2	0.7													
Leucaena leucocephala ssp. leucocephala	0.3	0.5	0.9	0.8	2	3.5						0.4			1	1.3	0.4	0.7	14.7	0.5		0.2			
Lonchocarpus punctatus		1.3	4.7	1.7	15.3	18.4	12.3				68.1	27.7	20.2												0.9
Lonchocarpus sp.	31.5	16.8	8.2	3.6	6	7.4					8.3				33.3	25								0.5	
Mimosa bahamensis	46.4	31.4	50.1	23.1	37.6	3.1	50		13.4	22.2	3.6	1.2		1.4	7.5		0.7	1	7.3	4.1	0.4	4.1	3.7	6.2	8
Mimosa sp.	2.1	3	1.9		11.6	27.4	1.8	11.4	42.6	19.6		0.7		1.1	3.2	4.1					0.4				
Fabaceae																	2.7	4.4	41.9						
Piscidia piscipula																		0.7	11.8	0.5					
Vachellia sp. 2																	3.4	1	2.2						
MALVACEAE																									
Waltheria rotundifolia				2.3	16	5.8	35.7	2.1		13.6		0.9				1.3									
MYRTACEAE																									

Table VII (continued)

	Maní				Baca			Dzán			Valladolid			Tekax			Xcunyá			Xmatkuil			Tekom		
Number of samples: H-	**5083**	**5084**	**5085**	**5086**	**5087**	**5088**	**5089**	**5090**	**5091**	**5092**	**5093**	**5094**	**5095**	**5096**	**5097**	**5098**	**5099**	**5100**	**5101**	**5102**	**5103**	**5104**	**5105**	**5106**	**5107**
Psidium guajava		2.7		0.8		17.2				5.1		0.7	0.7		4.3	2.7	1.7			24.2	12.1	31	67.1	78.9	67.4
POLYGONACEAE																									
Gymnopodium floribundum											9	2.4					4.2	2.3	2.8	4.1	1.3	3.1	5.1	1.5	1.5
PRIMULACEAE																									
Myrsine cubana	1.2													1.1	5.3										
RUTACEAE																									
Citrus sp.								2.1		5.9				0.2											
SAPINDACEAE																									
Thouinia paucidentata		2.4		0.4						7.6		1.6	2.1			2.7	0.7	0.7	1.6	8.2	0.9	11.6		0.3	
Serjania triquetra								60	31.4	14.5		0.4											0.3		0.1

Roo, Oaxaca, Veracruz and Brazil and is among the 10 important genera for *M. beecheii* and other stingless bees (Enríquez and Dardón 2007; Ramírez-Arriaga et al. 2011, 2018; Villanueva-Gutiérrez et al. 2018; Ortiz-Reyes et al. 2022; da Silva Correia and Peruquetti 2023). Although it is not a nectariferous plant, pollen grains of *S. racemosa* have been frequently recorded in *M. beecheii*, *Scaptotrigona mexicana* and *A. mellifera* honey pollen spectra in Veracruz, Tabasco, Yucatan, Campeche and Quintana Roo (Villanueva-Gutiérrez et al. 2009; Córdova-Córdova et al. 2013; Ortiz-Reyes et al. 2022; Córdova-Rodríguez et al. 2023).

Other important pollen sources rely on the Amaranthaceae family. *A. ramosissima* has been recovered from *A. mellifera* honeys in the Yucatan Peninsula, Brazil and Argentina (Cabrera 2006; Pereira-Oliveira et al. 2010; Ramos-Díaz et al. 2015).

In addition, the "copal" tree or *Bursera* spp. has been reported as a species of great nectar-polliniferous relevance for *M. beecheii*, *S. mexicana*, *S. hellwegeri*, *Cephalotrigona* sp., *A. mellifera*, among others, in the states of Puebla, Oaxaca, Tabasco, Yucatan, Campeche, Quintana Roo, as well as in Panama (Ramírez-Arriaga and Martínez-Hernández 2007; Villanueva-Gutiérrez et al. 2009, 2018; Alfaro et al. 2010; Quiroz-García et al. 2011; Ramírez-Arriaga et al. 2011, 2018, 2020; Castellanos-Potenciano et al. 2012; Roubik and Moreno 2018; López-Roblero et al. 2021).

Cochlospermum vitifolium has been reported as an important nectar-pollinator resource for *M. beecheii*, *Cephalotrigona* sp., *Tetragona* sp. and *A. mellifera* in the Yucatan Peninsula, in Panama, and in other regions of the Americas (Alfaro et al. 2010; CONABIO and AECID 2011; Villanueva-Gutiérrez 2018; Roubik and Moreno 2018; Córdova-Rodríguez et al. 2023).

The cultivated tree *P. guajava* is also considered a nectar-polliniferous plant for *M. crinita*, *M. scutellaris trinitatis*, *M. favosa*, *M. eburnea*, *Tetragonisca angustula*, *Trigona meldaria*, *Trigona nigra* var. *paupera* and *A. mellifera* in Colombia, Brazil and Trinidad; as well as for *Scaura*, *Cephalotrigona* and *Tetragona* in Panama (Sommeijer et al. 1983; Alfaro et al.

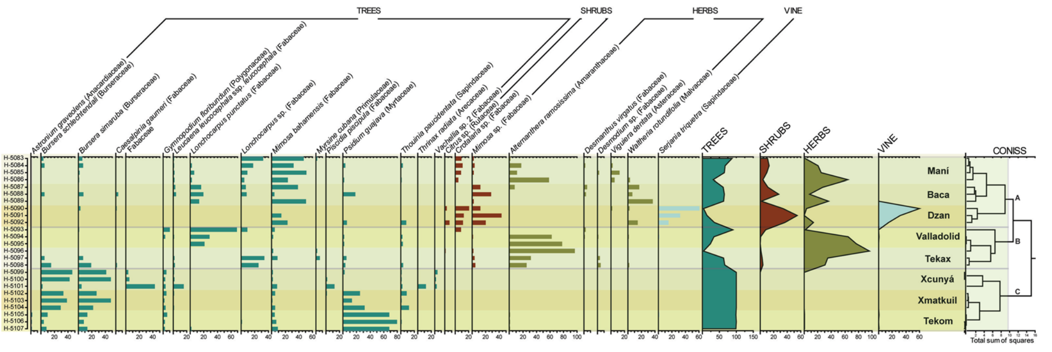


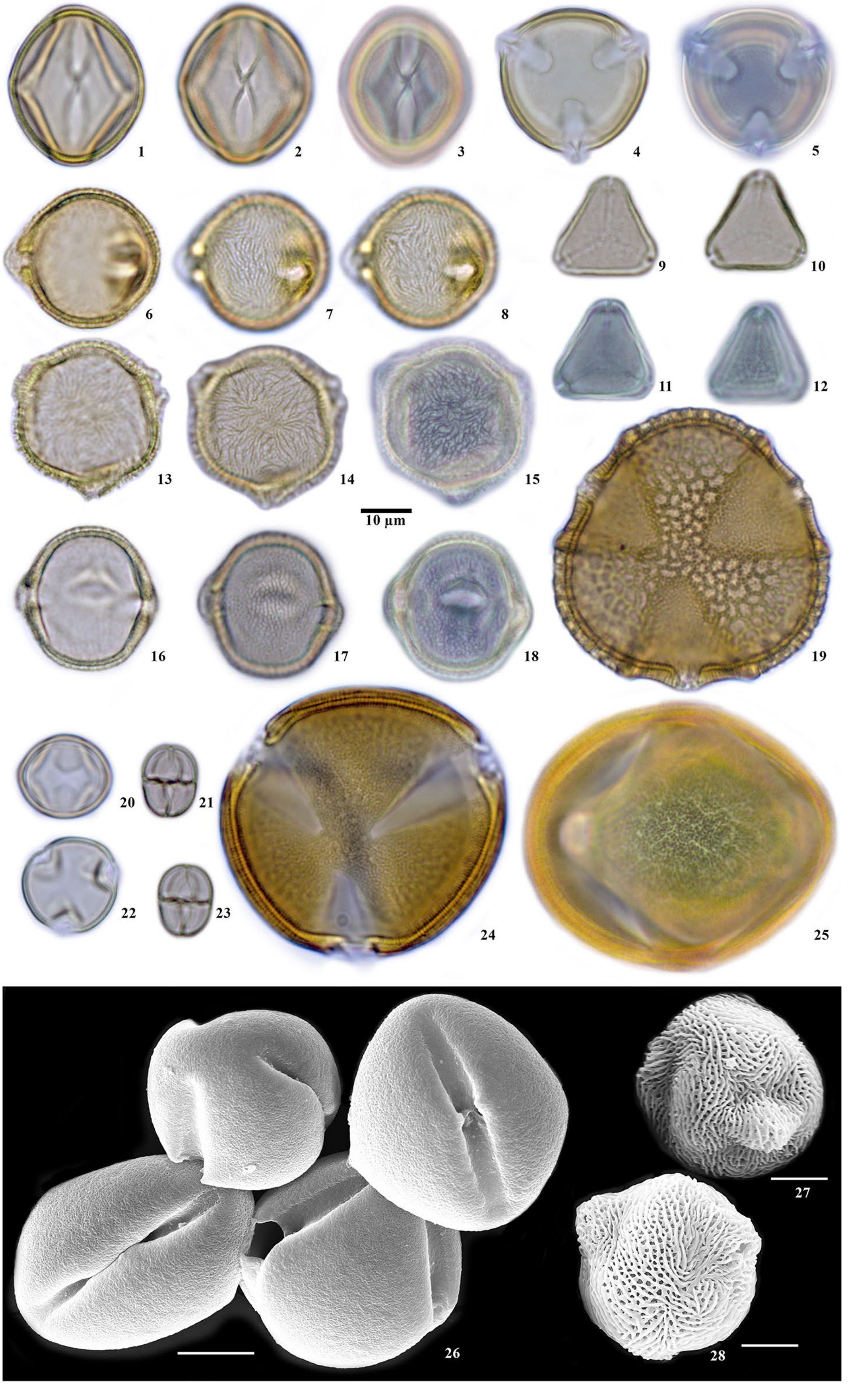
Figure 13. Melissopalynological spectrum of the nectariferous plants recovered from the pot-honey samples of *Melipona beecheii* collected in Yucatan, Mexico.

2010; Pereira-Oliveira et al. 2010; Obregón 2011; Córdova-Córdova et al. 2013; Roubik and Moreno 2018; Ortiz-Reyes et al. 2022; da Silva Correia and Peruquetti 2023).

The herbaceous *S. americanum* has been reported in Spain and Colombia in honeys and pollen loads of *A. mellifera* (Girón-Vanderhuck 1995; Díaz-Losada et al. 1997; Terrab et al. 2004). Also, *Solanum* sp. has been cited in studies of *M. beecheii*, *A. mellifera*, *Cephalotrigona* sp., *M. crinitaha*, *M. fasciata*, *S. pectoralis*, *Tetragona* sp., *Trigona* (*Tetragonisca*) *angustula*, *T.* (*Tetragona*) *dorsalis*, *T. fuscipennis* and *T. muzoensis* in Mexico, Brazil, Colombia and Panama (Aguilar-Sierra and Smith-Pardo 2009; Villanueva-Gutiérrez et al. 2009, 2018; Ramírez-Arriaga et al. 2016; Roubik and Moreno 2018; da Silva Correia and Peruquetti 2023).

The melissopalynological analyses of the present study suggested that *M. beecheii* workers incorporate pollen grains from polliniferous plants into honey pots only as an indirect action and probably during the packaging process. This is why it was possible to report pollen spectra of these honey samples and honey should only be characterised when nectariferous elements are included. In this sense, the recalculations we performed made it possible to characterise the monofloral honeys of *M. beecheii* from *A. ramosissima*, *B. simaruba*, *C. vitifolium*, *L. punctatus*, *M. bahamensis* and *S. americanum*. It should be noted that these resources have also been indicated as important for *A. mellifera* in Yucatan, Campeche and Quintana Roo (Cabrera 2006; Villanueva-Gutiérrez et al. 2009; Plan Rector 2011; Castellanos-Potenciano et al. 2012; Ramos-Díaz et al. 2015). By contrast, the pollen types *B. simaruba*, *B. schlechtendalii*, *M. bahamensis*, *L. leucocephala*, *L. punctatus*, *Lonchocarpus* sp., *M. bahamensis*, *P. piscipula*, *P. guajava*, *S. americanum*, *T. radiata* and *W. rotundifolia* were recorded in multifloral honey samples and in one bifloral honey.

Studies of the pollen spectrum show the polylectic behaviour of stingless bees, since they obtain their resources from diverse plant species belonging to local vegetation such as secondary and cultivated vegetation; in the analysis of pollen pots of *M. beecheii* in Campeche, monolectic and oligolectic temporal or local behaviour has been observed (Ramírez-Arriaga et al. 2018). Our results suggest polylectic foraging, since the foraging of *M. beecheii* includes diverse plant species; however, monolectic and oligolectic floral foraging were also observed in the Mayan stingless bee during the collection of pollen and nectar resources; this behaviour has been observed in *A. mellifera* and in diverse native bees (Ramírez-Arriaga and Martínez-Hernández 2007; Ramírez-Arriaga et al. 2018).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◂**Figure 14.** Pollen grains acetolysed from the pot-pollen and pot-honey samples of *Melipona beecheii* in Yucatan, Mexico. **1–5**, **26** *Senna racemosa* var. *racemosa*. **6–8**, **11–15**, **28** *Bursera schlechtendalii*. **16–18**, **27** *Bursera simaruba*. **9–12** *Psidium guajava*. **19** *Caesalpinia gaumeri*. **20**, **22** *Cochlospermum vitifolium*. **21**, **23** *Mimosa bahamensis*. **24**, **25** *Leucaena leucocephala* ssp. *leucocephala*. **1–25** optical photomicrographs. **3**, **5**, **11**, **12**, **15**, **18**, **25** photomicrographs in phase contrast. **26–28** photomicrographs taken with scanning electron microscopy (SEM), scales represent 10 µm.

5. CONCLUSIONS

Our research found that the primary source of pollen in the pot-honey and pot-pollen samples of *M. beecheii* is derived from the Fabaceae family. This family is known to be one of the most diverse across the peninsula. However, we also found that species from the Burseraceae family and other minor families that are commonly found in the area may also play a crucial role as pollen and nectar sources for this bee.

The Principal Component Analysis (PCA) revealed that *S. racemose* var. *racemose* and *C. vitifolium* were the most significant contributors to the variance in the pot-pollen samples. It is worth noting that the honey of *M. beecheii* has a high abundance of pollen grains from *A. ramosissima*, *S. racemose* var. *racemose*, and *P. guajava*. According to the PCA analysis, these plants also contributed significantly to the variance in the analysed pot-honey samples.

The results suggest that plant diversity is critical in conserving bee resources in the Yucatan Peninsula. Our research also provides valuable information on the sustainable management of stingless beekeeping in the Yucatan Peninsula. Furthermore, this research can aid in decision-making processes that prioritize flora conservation, which is of great importance to stingless beekeepers committed to the welfare of the Mayan bee.

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AUTHOR CONTRIBUTION

AIBP, ERA, and AC: study conception, experimental design, and manuscript revision; AIBP and AC: fieldwork; AIBP and ERA: melissopalynology work, statistical analysis, data interpretation, and drafting of the paper.

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AVAILABILITY OF DATA AND MATERIAL

Data availability is not applicable; All data are included in this manuscript.

CODE AVAILABILITY

Not applicable.

DECLARATIONS

Ethics approval Not applicable.

Consent to participate Not applicable.

Consent for publication Not applicable.

Conflict of interest The authors declare no competing interests.

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