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Diversity, structure, and composition of melliferous and non-melliferous vegetation surrounding meliponaries of the Yucatan Peninsula, Mexico

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Abstract

Background: Although the loss of *Melipona beecheii* colonies in meliponaries suggests insufficient availability of melliferous blooming plants, there is limited knowledge about the diversity and conditions of the surrounding vegetation.

Question: What is the diversity, structure, and composition of the melliferous and non-melliferous vegetation surrounding meliponaries, and how does it affect the availability of food sources for bees?

Study site and dates: The vegetation surrounding nine meliponaries, three in each political state of the Yucatán Peninsula encompassing the main vegetation types, was studied in 2022 and 2023.

Methods: Four 150-meter-long transects with the point-centered quadrants method were traced in each meliponary to estimate plant species composition, the availability of melliferous and blooming plants (IVI), diversity parameters (Hill-numbers), tree density, and diameter per strata.

Results: 312 taxa, 250 genera, and 73 plant families were recorded. In five meliponaries, blooming melliferous plants accounted for less than 9 % of the IVI, with one meliponary having no blooming species. The highest diversity was found in a meliponary surrounded by semi-evergreen forest. The high stratum had a mean tree height of 5.5 (SD ± 2.9) meters and 3,390 (SD ± 2,702) trees/hectare across vegetation types. The tree diameter was lowest in meliponaries located in the semi-deciduous forest.

Conclusions: The meliponaries are surrounded by young secondary vegetation with high density of small trees and predominance of the low stratum. We found a similar vegetation diversity among meliponaries and scarce blooming melliferous plants. Human activity seems to impact plant diversity and food availability for *M. beecheii*.

Keywords: Tropical dry forests, flower availability, human impact, meliponiculture, melliferous plants, secondary vegetation, stingless bees.

Resumen

Antecedentes: Aunque la pérdida de colonias de *Melipona beecheii* en meliponarios sugiere insuficientes plantas melíferas en floración, existe conocimiento limitado sobre la diversidad y condiciones de la vegetación circundante.

Pregunta: ¿Cuál es la diversidad, estructura y composición de la vegetación melífera y no melífera circundante a los meliponarios y cómo afecta a la disponibilidad de fuentes de alimento para las abejas?

Sitio de estudio y fechas: Vegetación circundante de nueve meliponarios, tres por cada estado de la Península de Yucatán, abarcando los principales tipos de vegetación en 2022 y 2023.

Métodos: Con cuatro transectos de 150-metros por meliponario y método de cuadrantes centrados en puntos, se estimó composición, disponibilidad de plantas melíferas y con flores (IVI), parámetros de diversidad (números de Hill), densidad y diámetros de árboles.

Resultados: 312 taxa, 250 géneros y 73 familias de plantas registradas. En cinco meliponarios, las plantas melíferas floreciendo representaron menos del 9 % del IVI y uno no tuvo especies floreciendo. La mayor diversidad fue en un meliponario rodeado de selva mediana subperennifolia. La altura promedio de árboles en el estrato alto fue 5.5 (DE ± 2,9) metros, con 3,390 (DE ± 2.702) árboles/hectárea en todos los tipos de vegetación. El diámetro de árboles fue menor en meliponarios en selva mediana subcaducifolia.

Conclusiones: Los meliponarios están rodeados de vegetación secundaria joven, alta densidad de árboles pequeños, predominio del estrato bajo, características similares y escasas plantas melíferas floreciendo, sugiriendo que, la actividad humana afecta la diversidad vegetal y disponibilidad de alimento para *M. beecheii*.

Palabras clave: Disponibilidad floral, impacto humano, meliponicultura, plantas melíferas, selvas tropicales secas, vegetación secundaria.

Meliponiculture is the breeding of stingless bees (tribe Meliponini) that are kept in small hives protected by shack-like structures called meliponaries. This activity was practiced in various tropical and subtropical regions of the Americas, Africa, Asia, and Australia (Cortopassi-Laurino *et al*. 2006). In Mexico, meliponiculture has been practiced since pre-Columbian times, and the Yucatan Peninsula is one of the areas where it has boomed, with *Melipona beecheii* Bennett as the main species (González-Acereto 2012, Quezada-Euán 2018). However, meliponiculture in this region has faced challenges over time due to changes in land use, including agriculture (especially sisal and sugarcane crops), deforestation, and urbanization (Quezada-Euán *et al.* 2015). These factors may be related to reports by *Melipona* beekeepers of colony deaths due to starvation (Villanueva-Gutiérrez *et al.* 2005). This suggests that the ecosystems where meliponaries are placed may not provide sufficient food for bee colonies. In this sense, the food sources available to bees are influenced by vegetation characteristics and local processes related to human activities around meliponaries.

In general, the Yucatan Peninsula is characterized by a lower floristic richness than other regions of Mexico (Duno-de Stefano *et al.* 2018). However, the diversity of native plants supports honey production activity in this region (Villanueva 1994, Flores-Guido & Vermont-Ricalde 2011). The vegetation of the Yucatan Peninsula and, therefore, the vegetation surrounding the meliponaries is determined by physiographic and climatic factors, mainly the rainfall regime and soil type (Hubp *et al.* 1992, Orellana *et al.* 1999, 2009). These tropical forests are classified according to the height of the canopy and the percentage of deciduous species (George-Chacón *et al.* 2022). The northern and drier zone, mainly occupied by the Yucatan state, is predominantly covered by deciduous and semi-deciduous tropical forests, characterized by tree heights of approximately 8 to 10 m in the former and 10 to 18 m in the latter; most trees in both forest types, shed their leaves during the dry season (Durán & Olmsted 1999, Flores-Guido *et al.* 2010). In contrast, the southern portion of the peninsula, occupied by the states of Campeche and Quintana Roo, is predominantly covered by semi-evergreen tropical forests. This vegetation type is characterized by a lower proportion of deciduous species, a more heterogeneous vertical structure, a canopy that reaches 15 to 25 m in height, and a higher species richness compared to the other forest types of the Yucatan Peninsula (Flores & Espejel 1994, Durán & Olmsted 1999, Duno-de Stefano *et al.* 2018). Therefore, the diversity of plant species surrounding meliponaries in semi-evergreen forest areas can be expected to be higher than in the other two forest types.

In the Yucatan Peninsula, meliponiculture is carried out in rural areas where the food resources for bees are found in a mosaic of secondary vegetation (59.4 % of the total area of the peninsula) and agricultural and urban areas (18.1 %; Islebe *et al*. 2015). This secondary vegetation emerges as a result of a successional process that allows the gradual recovery of the characteristics of native vegetation after the abandonment of agricultural or deforested areas. The availability of food sources for bees, *i.e.*, melliferous plants that provide nectar or pollen (Flores-Guido & Vermont-Ricalde 2011), is influenced by the structure of ecosystems (Beekman & Ratnieks 2000, Steffan-Dewenter *et al.* 2002, Steffan-Dewenter & Kuhn 2003). The habitat heterogeneity hypothesis suggests that ecosystems with a more complex structure provide a greater variety of niches and opportunities to exploit environmental resources (Bazzaz 1975). Plants play a central role in the structural heterogeneity of habitats due to their diverse growth forms and size ranges associated with ontogenic development, giving rise to a diversity of vegetation strata (Tews *et al.* 2004). Therefore, more diverse vegetation with more growth forms, plant sizes, and greater structural heterogeneity is expected to provide a greater availability of melliferous plants for bees (Gough *et al.* 2020).

In the Yucatan Peninsula, meliponiculture is carried out in the backyards of the houses of local honey producers (Villanueva-Gutiérrez *et al*. 2005, González-Acereto *et al*. 2006, Quezada-Euán *et al*. 2015). This practice places meliponaries in areas with disturbed vegetation due to their location in human settlements. Vegetation structure, particularly the size of plants, is adversely affected in rural areas close to human settlements (Banda *et al.* 2006, Jamil *et al.* 2022) due to human activities, such as the conversion of forests to agricultural land or pastures for livestock grazing, fuelwood extraction, charcoal production, which lead to deforestation, degradation, and biodiversity loss (Reyers 2004).

Some bee species may tolerate or benefit from moderate habitat disturbance (Winfree *et al.* 2009) because it increases environmental heterogeneity and, therefore, resource diversity and availability (Cane *et al.* 2006, Winfree *et al.* 2008). However, the opposite is true for stingless bees, which are sensitive to habitat disturbance (May-Itzá *et al.* 2021). In addition, vegetation disturbance or habitat degradation mainly affects bees through the loss of the flower resources they feed on (Biesmeijer *et al.* 2006, Carvell *et al.* 2006). A scarcity of melliferous plants in the vicinity of meliponaries is expected in this region, considering that *i*) *Melipona beecheii* depends on preserved vegetation (González-Acereto 2008); *ii*) there are reports that its colonies in the Yucatan Peninsula die from lack of food; and *iii*) meliponaries are located in areas with disturbed vegetation.

Despite efforts to promote the recovery of meliponiculture in the Yucatan Peninsula (González-Acereto *et al.* 2006, Martínez-Puc *et al*. 2022), the location of meliponaries in the backyards exposes colonies to changes in the availability of melliferous plants due to vegetation disturbance by human activities. This situation is aggravated by the loss of vegetation cover in the peninsula (Sánchez-Aguilar & Rebollar-Domínguez 1999, Duran-García & García-Contreras 2010), which puts more pressure on the vegetation on which bees depend. Despite this situation, the conditions of vegetation surrounding meliponaries in the Yucatan Peninsula have been scarcely investigated and require a detailed characterization to understand the relationships between colonies and vegetation.

Therefore, the objective of this study was to characterize the vegetation around meliponaries located within the main types of vegetation of the Mexican states on the Yucatan Peninsula. This characterization includes the diversity, composition and abundance of plant species, particularly melliferous plants, as well as vegetation structure, since heterogeneity influences the availability of food resources and affects the condition of bee colonies (Cepeda-Valencia *et al.* 2014, Ochungo *et al.* 2022).

We expect the plant diversity surrounding the meliponaries in localities with vegetation derived from deciduous and semi-deciduous forests to be lower than in localities derived from semi-evergreen forests. In addition, regardless of the type of forest from which the local vegetation derives, we expect to find low-height vegetation with a predominance of the low stratum and low availability of melliferous plants and flowers around the meliponaries. Data on the prevailing vegetation conditions in the location of meliponaries in the Yucatan Peninsula will facilitate the identification of those vegetation elements that need to be conserved or restored to sustain and strengthen *M. beecheii* colonies.

Materials and methods

Study area. This study was carried out in nine meliponaries located in villages and agricultural areas within the main tropical forest types in the three political states of the Yucatan Peninsula in southeastern Mexico (Figure 1). Our sampling strategy encompassed the range of environmental conditions and vegetation types in which meliponaries are found across the peninsula. According to the vegetation classification by Flores-Guido *et al*. (2010) and land-cover data for the region by INEGI (2018), the meliponaries of the towns of Baca, in Yucatan, and of Pucnachén, Chunkanán, and Lerma, in Campeche, are located in areas of deciduous tropical forests. Meanwhile, the localities of the other two meliponaries of Yucatan, Maní and Dzan, are located in semi-deciduous tropical forests. In addition to native vegetation, there are agricultural areas surrounding the Yucatan meliponaries and pastures near the Campeche meliponaries. On the other hand, the Quintana Roo meliponaries are surrounded by semi-evergreen tropical forest; two of these also include rainfed agriculture (Yaxché and Chanchén Palmar) and the third, cultivated pastures (San Juan de Dios; see Supplementary material Figure S1 for detailed maps of each meliponary).

In general, meliponaries are structures with wooden columns and a palm roof (Figure 2A). There can be low protective walls or fences between the columns that do not limit the flight of bees. The floor can be soil or cement, and water channels are common at the edges to prevent predators from entering the meliponary. Although the traditional method of keeping bee colonies in *jobones* (hollow tree trunks; Villanueva-Gutiérrez *et al*. 2005) is still common, many beekeepers currently use divisible wooden boxes that facilitate managing the colony. In the present study, *jobones* were found only in the meliponaries of Maní and Chunkanán.

Vegetation characterization. Fieldwork was carried out during the dry season (February to April) of 2022 and 2023. This season was selected because it is the time of the year when most melliferous plant species are blooming

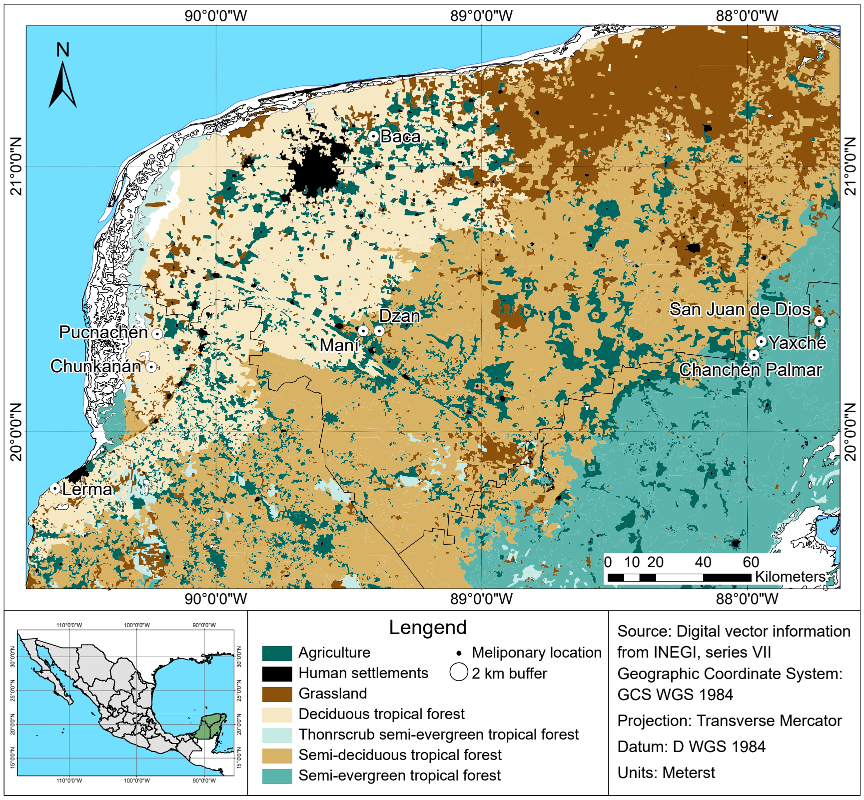

Figure 1. Map showing the locations of the nine meliponaries studied in the Yucatan Peninsula, Mexico, three in each sociopolitical state (Campeche, Yucatan, and Quintana Roo).

and, therefore, when the largest amount of nectar and pollen is collected and accumulated in *M. beecheii* colonies (Di Trani & Villanueva-Gutiérrez 2018), leading to peak honey production in the Yucatan Peninsula (Echazarreta *et al.* 1997). This made it possible to detect the species of melliferous plants that blossom in the study zones (CONABIO 2016).

To characterize the vegetation surrounding each meliponary, we traced four 150 meter-long transects running in the direction of the four cardinal points (north, south, east, and west), with the meliponary at the center. In cases where ground conditions or private land ownership did not allow tracing a straight line toward the respective cardinal point, we ensured that each transect was oriented to maintain the longest possible distance from the others, avoiding overlap and ensuring the greatest possible representativeness of vegetation cover in the area.

Fifteen evaluation points were selected along each transect (one every 10 m), and the point-centered quarter method (Figure 2B-C) was followed at each point (Brower *et al.* 1997, Mitchell 2010). Compared to other area-independent methods, this method allows for accurate estimations of plant density (Morisita 1978) and increases the sample size with a similar sampling effort (Cottam & Curtis 1956). The point-centered quarter method consists of tracing an imaginary line perpendicular to the transect at each evaluation point, thus creating four quadrants with the central point as the origin; in each quadrant, the plant closest to this central point was sampled (Figure 2B). For each plant, including herbs and climbers, we recorded its taxonomic identity, distance from the quadrant center, two perpendicular diameters of its crown to calculate its crown cover, its height, and whether it was blooming or not. Additionally, for trees and shrubs, we measured the diameter of the trunk in individuals with a diameter at breast height (DBH) of at least 1 cm. The DBH was recorded 1.3 m above the ground, and in trees with multiple stems, DBH was recorded for each stem with DBH of at least 1 cm. The height of each individual was measured in meters with a flexometer up to 2.5 m high; for larger plants, the height was visually estimated, always by the same trained evaluator to ensure consistency of the estimates. Since evaluations of vegetation around the meliponaries may have

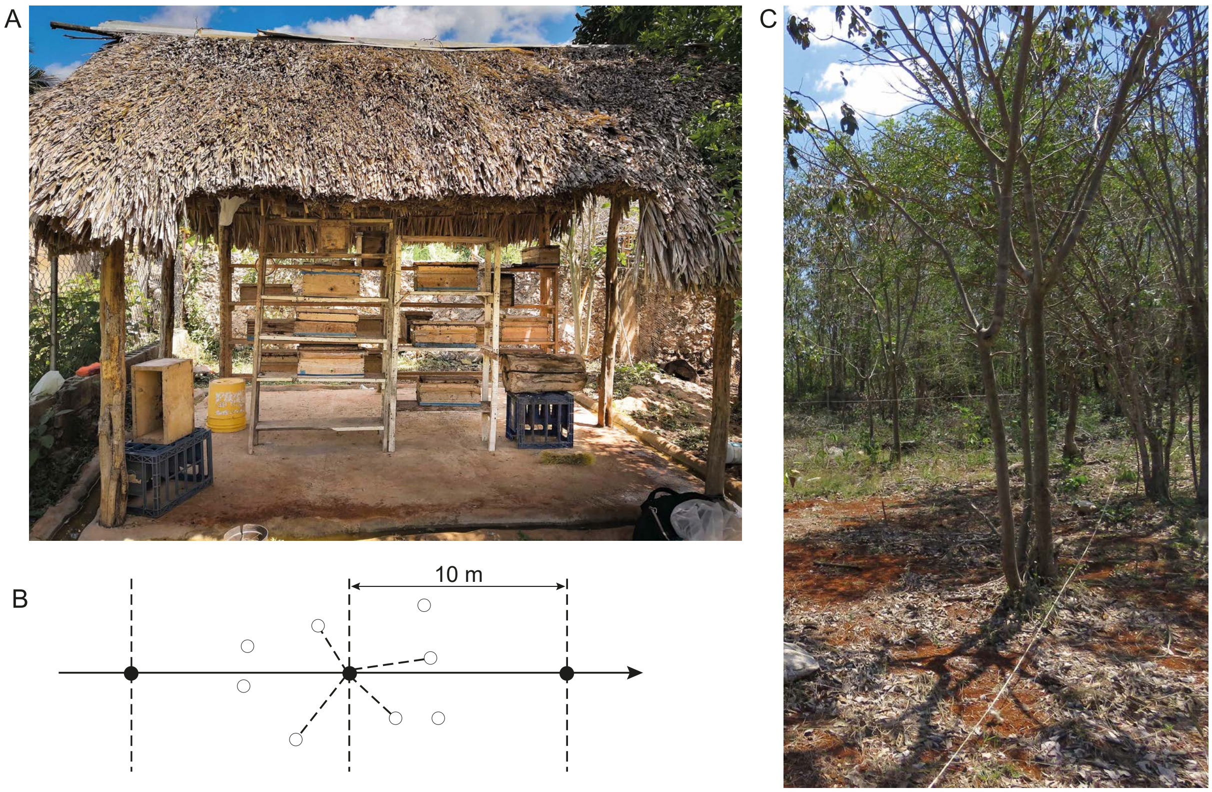

Figure 2. (A) A typical traditional meliponary in the Yucatan Peninsula, Mexico. This shack-like structure is a small bee house that serves as a home to the Mayan bee *Melipona beecheii* colonies. Most colonies are contained in rectangular wooden hives, while only a few are found in hollow logs called "jobón" (bottom right of the photograph). (B-C) Sampling scheme and picture illustrating the Point-Centred Quarter Method: Sample points (filled circles) were positioned every 10 meters along a 150-meter-long transect. Four quadrants (1, 2, 3, and 4) were outlined at each sampled point. Then, the distance (dashed lines), identity, height, and crown diameters of the nearest plant in each quadrant (open circles) to the sample point were recorded.

been carried out at different stages of the blooming period of the species, a given plant was considered to be in the blooming stage if it had at least one flower in any of the two census years. This allowed us to identify the species that were blooming in the days near (before or after) the sampling time.

Taxonomic identification was carried out in the field; when a given specimen could not be identified *in situ*, samples of branches and flowers or fruits were collected for comparison with voucher specimens deposited in the Herbarium of the *Centro de Investigación Científica de Yucatán, A.C*. for taxonomic identification.

Analysis of (melliferous) plant species composition. The species composition was analyzed considering all the taxonomic groups in the vegetation surrounding each meliponary, as well as the percentages of blooming species, in order to evaluate the availability of food sources for bees at each study site. We calculated the Importance Value Index (IVI; Curtis & McIntosh 1950) to analyze the composition of melliferous and non-melliferous species, based on the relative frequency, density, and cover of each species. The index is calculated as the sum of these three metrics in percentage per species, so those with the highest percentages are considered the most important and dominant species. As we used the point-centered quarter method for vegetation assessment, the IVI was calculated with the approximation of Mitchell (2010), adapted for this sampling method. The relative frequency was estimated as the proportion of sampling points in which a given species was found; the relative density was estimated as the proportion of quadrants in which a given species was found; and the relative cover was calculated as the proportion of the area occupied by a given species, including herbaceous, climbers, shrubs and trees. We calculated the relative cover using the formula $\pi \cdot r^2$, where r is the radius calculated from the average of the two crown diameters measured divided by 2.

To assess the representativeness of the melliferous species relative to the total number of species recorded per meliponary, we reviewed the lists of melliferous plants, that is, those serving as sources of nectar and pollen, reported for beekeeping and meliponiculture in the Yucatán Peninsula (Alfaro-Bates *et al.* 2010, Flores-Guido & Vermont-Ricalde 2011, Quezada-Euán 2018, Ramírez-Arriaga *et al*. 2018, Villanueva-Gutiérrez *et al*. 2018). From these studies, 114 melliferous species were identified (Supplementary material Table S1). In addition, to assess the availability of food resources for bees in the study period, blooming and non-blooming plant species were also considered.

Analysis of species richness and diversity indices. The alpha diversity or local diversity of the vegetation around the meliponaries was analyzed using the Hill numbers (Hill 1973). These are a family of diversity indices mathematically unified in a general equation, which differ from each other only by the value of the parameter q:

$$D^q = \left(\sum_{i=1}^{S} p_i^q\right)^{1/(1-q)}$$

Where D is the calculated diversity, S is the number of species in the community, and p_i is the relative abundance of species i. The parameter q regulates the sensitivity to the relative abundances of the species (Chao *et al.* 2014, Jost 2019). When $q = 0$, the Hill number of order 0 is calculated, which estimates species richness without considering the abundance of each species. When $q = 1$, the Hill number of order 1 is estimated, which is the exponential of Shannon's index and weighs each species exactly by its relative abundance; therefore, it estimates the diversity of equally common species. When $q = 2$, the Hill number of order 2 is estimated, which is the inverse of Simpson's index that gives more weight to the most abundant species and, therefore, estimates the number of dominant species. Hill numbers ($q = 0$, 1, and 2) were calculated using the approximation of Chao *et al*. (2014) implemented through the iNEXT package in R (Hsieh *et al.* 2016, R Core Team 2023), from which rarefaction/extrapolation curves of species diversity were produced.

To compare the diversity of plant species between meliponary localities by forest type, the sampling coverage was first estimated from the sample size. Sampling coverage indicates the proportion of the species richness of the analyzed community that was recorded through the sampling effort considering the abundance of each species (Chao & Jost 2012). Subsequently, rarefaction/extrapolation curves were constructed based on samples to provide asymptotic diversity estimators based on Hill numbers with their respective 95 % confidence intervals, using a bootstrap method with 200 repetitions. In both cases, that is, sampling coverage and diversity curves, extrapolations were made up to twice the sample size reached ($n = 240$, extrapolations up to 480 plants), as recommended by Chao *et al*. (2014).

Analysis of the vertical structure of vegetation. Five vegetation strata were established based on the main growth forms recorded (herbaceous, shrub, tree, and climbing) and plant height. The Low vegetation stratum grouped herbaceous species, as well as young trees and climbers less than 1 meter in height; the Middle stratum included shrub species, as well as young trees and climbers between 1 and 2 m in height; and the High stratum comprised only trees and climbing plants that exceeded 2 m in height. Furthermore, for better resolution in the analysis and because the semi-evergreen forest of the peninsula has three vertical strata (Flores-Guido & Vermont-Ricalde 2011), the High stratum was further divided into three height categories: High1: 2 - 10 m, High2: 10 - 15 m, and High3: >15 m.

The vertical structure of the vegetation was analyzed and compared between meliponaries by constructing graphs of the percentage of individuals by stratum. In addition, we analyzed the heterogeneity of the vertical structure of vegetation and the number of dominant strata using the Hill number of order two ($q = 2$), which gives more weight to the strata with higher frequency (Ehbrecht *et al.* 2016). Therefore, we used the five strata generated (Low, Middle, High1, High2, and High3) and the number of individuals per stratum to derive the effective number of dominant strata (ENDS) per meliponary. Finally, the mean height in the High stratum was compared between vegetation types using the Kruskal-Wallis non-parametric test, as these data were not normally distributed (Shapiro-Wilk normality test, $W = 0.9141$, $P < 0.001$).

Analysis of the horizontal structure of vegetation. Horizontal structure refers to the spatial distribution of individuals and their cover in the plant community. The horizontal structure was estimated using tree density (number of trees per unit area: 1 hectare) and basal area (area of the trunks obtained from DBH, expressed in m^2 per hectare). In addition, the mean DBH between plant forms and meliponaries was compared using the Kruskal-Wallis non-parametric test since these data were not normally distributed (Shapiro-Wilk normality test, $W = 0.81564$, $P < 0.001$). A Dunn test was also used to analyze the differences between meliponaries.

Results

Species composition and diversity. A total of 2,153 individuals were recorded in the 36 transects studied, of which 2,008 individuals were identified at the species level, 119 at the genus level, and 26 at the family level. This resulted in 312 taxa, 250 genera, and 73 families, considering all the localities studied. Meliponaries surrounded by fragments of the original type of vegetation (especially semievergreen tropical forest), rather than agricultural areas or human settlements, tend to have a higher taxonomic richness. For example, Baca and Dzan meliponaries, located in tropical deciduous and semi-deciduous forests, are mainly surrounded by agricultural zones, and showed the lowest taxonomic richness, with 15 families and 22 species, and 21 families and 36 species, respectively. In contrast, the meliponaries of San Juan de Dios and Chanchén Palmar in Quintana Roo, surrounded by relatively well-conserved semi-evergreen tropical forests, exhibited the highest taxonomic richness. A total of 47 families were recorded in each location, with 98 plant species in San Juan de Dios and 79 in Chanchén Palmar (Table 1, Supplementary material Figure S1).

Table 1. Frequency (n) of plant species and percentages (%) of blooming species in nine sampled meliponaries in the Yucatan Peninsula. The table shows data by locality, socio-political peninsular state (Yuc = Yucatán, Camp = Campeche, and Q. Roo = Quintana Roo), and vegetation type.

Vegetation type	Locality	Family (n)	Genus (n)	Species (n)	Blooming species (%)	Melliferous blooming species (%)
Deciduous tropical forest	Baca (Yuc)	15	25	22	22.7	9.1
	Pucnachén (Camp)	27	55	55	38.2	7.3
	Chunkanán (Camp)	36	81	77	19.5	1.3
	Lerma (Camp)	25	61	55	45.5	5.5
Semi-deciduous tropical forest	Maní (Yuc)	38	70	67	50.7	10.4
	Dzan (Yuc)	21	41	36	63.9	13.9
Semi-evergreen tropical forest	Yaxché (Q. Roo)	37	78	76	21.1	0
	Chanchén Palmar (Q. Roo)	47	82	79	39.2	6.3
	San Juan de Dios (Q. Roo)	47	101	98	32.7	5.1

Regarding the representation of blooming species, meliponaries located in semi-deciduous forests attained the highest percentages, with 63.9 and 50.7 % in Dzan and Maní, respectively (Table 1). The lowest percentages were observed in Chunkanán, located in a deciduous forest area (19.5 %), and Yaxché, in a semi-evergreen forest (21.1 %). We found that 50 out of the 114 melliferous plant species reported in the literature were present in the meliponaries. In terms of the blooming melliferous species, none were observed in Yaxché and in Chunkanán, only 1.3 % of plants were blooming melliferous species (a single species: *Ipomoea triloba*, Convolvulaceae). In all other meliponaries, the percentage of blooming melliferous species varied between 5.1 % in San Juan de Dios and 13.8 % in Dzan. The most common blooming melliferous species were *Waltheria indica* (Malvaceae) and *Tridax procumbens* (Asteraceae), present in five and four localities respectively. *Croton humilis* (Euphorbiaceae), *Jacquemontia pentanthos* (Convolvulaceae), *Piscidia piscipula* (Fabaceae), *Senna racemosa* (Fabaceae), and *Viguiera dentata* (Asteraceae), were all present in two localities. The remaining 13 blooming melliferous species were recorded in a single locality (Table 1).

Representation of melliferous species. The analysis of vegetation, as a whole, showed that non-melliferous species had a higher IVI than melliferous plants in most meliponary localities. In fact, in eight localities, non-melliferous species accounted for more than 58 % of the total IVI of vegetation, while melliferous species represented 28 to 42 % (Figure 3). The only exception was Dzan, where melliferous species accounted for 62.5 % of the IVI. However, this value was mainly due to the contribution of *Citrus* x *sinensis* (19.72 %), a cultivated melliferous species. On the other hand, when considering the blooming vegetation subset, the IVI of the melliferous species was remarkably low. In

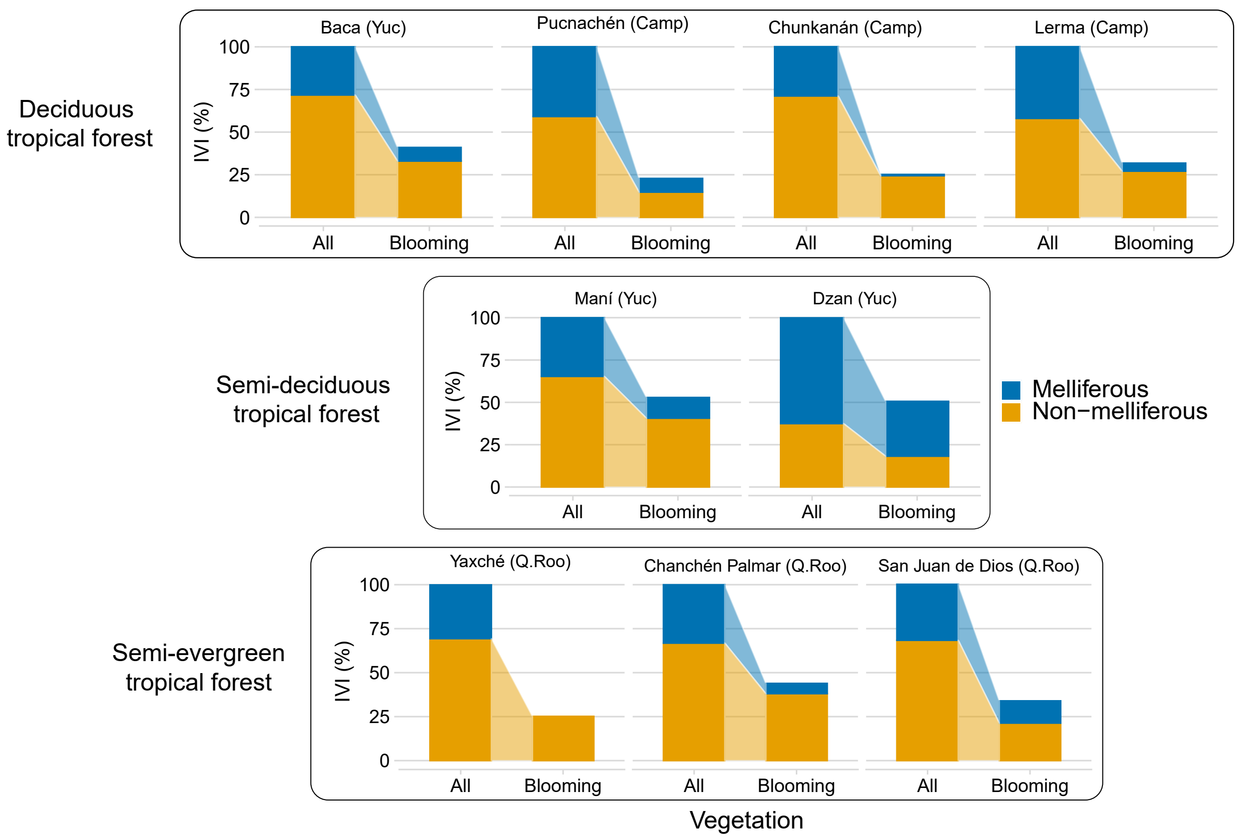

Figure 3. Representation of blooming melliferous and non-melliferous species in the Importance Value Index (IVI) of the plant community surrounding nine meliponaries in the three socio-political states (Yuc = Yucatán, Camp = Campeche, and Q. Roo = Quintana Roo) and in the three main types of vegetation of the Yucatan Peninsula, México. Melliferous and non-melliferous plant species were categorized according to Alfaro-Bates *et al.* (2010), Flores-Guido & Vermont-Ricalde (2011), Quezada-Euán (2018), Ramírez-Arriaga *et al.* (2018) and Villanueva-Gutiérrez *et al.* (2018).

fact, in the meliponary localities of Yaxché and Chunkanán, the IVI of the blooming melliferous species was 0 and 0.75 %, respectively (Figure 3). In the remaining localities, the IVI did not exceed 15 %, except in the meliponary locality of Dzan (32.4 %), where *C.* x *sinensis* was again the main blooming melliferous species. The other blooming melliferous species that stood out were *P. piscipula* (6.5 %), *T. procumbens* (5.82 %), and *S. racemosa* (4.8 %) in the localities of Baca, Maní, and San Juan de Dios, respectively (the list of all recorded plant species and their corresponding IVI is shown in the Supplemetary material Table S1).

Species richness and diversity indices. The overall coverage obtained in the sampling was 85.5 %. The lowest sampling coverage was recorded in San Juan de Dios, with 74.6 %, and the highest was observed in Baca, with 95.0 % (Figure 4A). Extrapolations from the sampling coverage curves indicate that doubling the current sampling effort, *i.e.*, using 300 m transects (n = 480), would result in an estimated sampling coverage of 93.28 %.

The mean plant species richness (q = 0) in the nine meliponaries evaluated was 70.8 species. The locality with the highest species richness was San Juan de Dios, with 109 effective species, located in a semi-evergreen forest area. In the same vegetation type, the Chanchén Palmar and Yaxché meliponaries showed 89 and 82 species, respectively. However, the species richness in the latter two localities showed no significant differences compared to the Maní meliponary (75 species), located in a semi-deciduous forest area, and compared to the Chunkanán (83 species) and Lerma (72 species) meliponaries, located in deciduous forests (Figure. 4B). In contrast, Baca, also located in a deciduous forest area, presented the lowest species richness with only 25 species.

Concerning the diversity of equally common species (q = 1), the San Juan de Dios meliponary (semi-evergreen forest) was also the most diverse locality with 79 effective species. In contrast, Baca (deciduous forest) and Dzan (semi-deciduous forest) were the least diverse localities with 8 and 16 effective species, respectively. The other localities showed intermediate diversity values that varied between 35 and 58 effective species, and the overlap of their confidence intervals showed no significant differences among vegetation types (Figure. 4B). Regarding the number of dominant species (q = 2), San Juan de Dios again was the locality with the highest value with 58 species. At the opposite end are the Baca and Dzan localities, with 5 and 8 dominant species, respectively (Figure. 4B). In the other localities, the overlap of confidence intervals showed similarities in the number of dominant species ranging from 23 to 35, regardless of the vegetation type.

Vertical structure of vegetation. In total, 116 taxa of herbaceous plants, 55 shrubs, 103 trees, 29 climbers, 6 palms, and 3 rosette species were identified. The Low stratum showed the highest percentage of individuals in six of the nine meliponary localities studied, with values exceeding 50 % in Baca, Pucnachén, Chunkanán, Lerma, Maní, and Yaxché (Figure 5). In the other three meliponaries, two of which are found in semi-evergreen forests (Chanchén Palmar and San Juan de Dios), a more even distribution of the percentages was observed between the Low, Middle, and High1 strata. The Dzan meliponary, located in a semi-deciduous forest area, was the only site where the High stratum exceeded 40 % of the recorded individuals. It is worth mentioning that Yaxché was the only locality that presented a plant in the High3 stratum, that is, measuring more than 15 m high (*Enterolobium cyclocarpum*, 17 m).

Although the percentage values indicate that the Low stratum prevails in most meliponary localities, the effective number of dominant strata (ENDS), derived from the Hill number of order 2, shows a different perspective (Figure 5). The analysis of these data highlights that only two localities, Baca (deciduous forest) and Yaxché (semi-evergreen forest), recorded less than two dominant strata, while the ENDS ranged from 2.1 to 2.8 in six meliponaries. Only San Juan de Dios (semi-evergreen forest) showed three dominant strata, with a more balanced distribution between the Low, Middle, and High strata, as mentioned above.

The analysis of species composition and abundance by stratum showed that, in general terms, the most abundant species in the Low stratum was *Parthenium hysterophorus* (Asteraceae), a non-melliferous plant, with a total of 90 plants. No melliferous species reached this abundance in this stratum (Table 2). In fact, the most abundant melliferous species in the Low stratum never exceeded 30 individuals. Among them, *T. procumbens* had 28 plants in Maní and *W. indica* had 21 in Pucnachén. In addition, these two were the most common melliferous species, recorded in

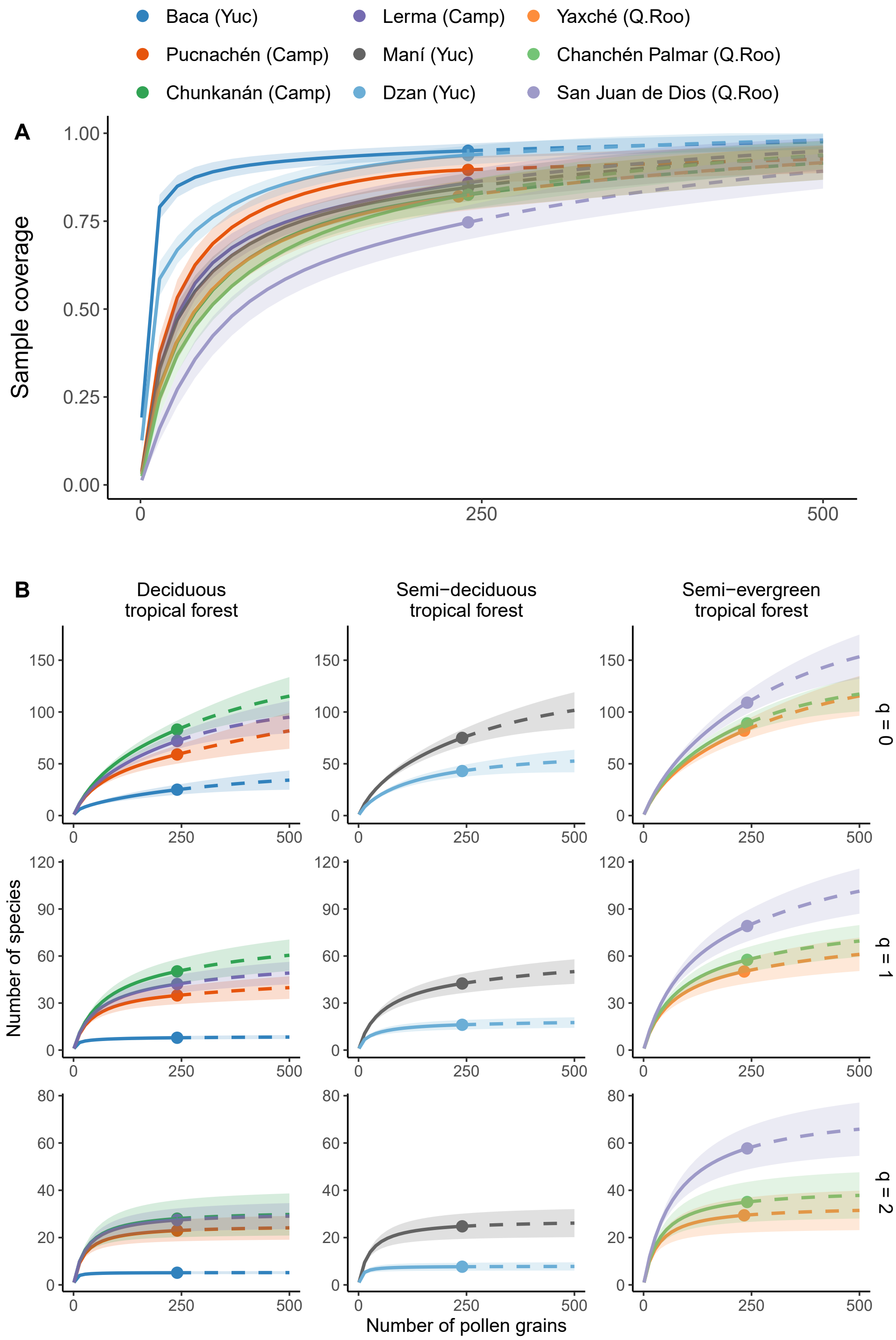

Figure 4. Diversity parameters based on the Hill numbers and species accumulation curves for plant communities of vegetation surrounding nine meliponaries on the Yucatan Peninsula. Data are presented by socio-political state (Yuc = Yucatán, Camp = Campeche, and Q. Roo = Quintana Roo) and by type of vegetation. (A) Sampling coverage curves for each meliponary area. (B) Comparison of diversity parameters among meliponaries: species richness ($q = 0$); equally common species diversity (exponential of Shannon's index, $q = 1$); dominant species diversity (inverse of Simpson's index, $q = 2$). Diversity curves were constructed using rarefaction (solid lines) and extrapolation (dashed lines) with estimations based on sample size. Shaded areas represent 95% confidence intervals obtained using a Bootstrap method with 200 replications.

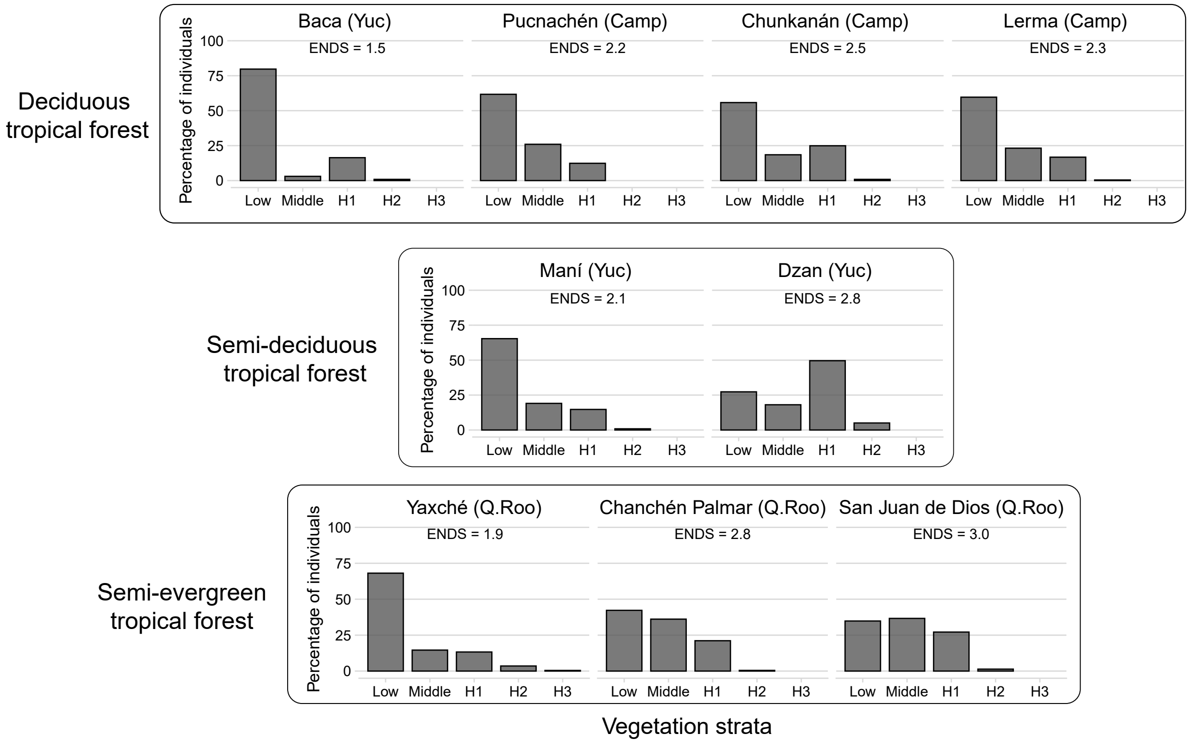

Figure 5. Percentage of plants in each vertical stratum in the vegetation surrounding nine meliponaries in the Yucatan Peninsula. Data are presented by socio-political state (Yuc = Yucatán, Camp = Campeche, and Q. Roo = Quintana Roo) and by type of vegetation. The High stratum category was subdivided into High1 - H1 (tress 2-10 m high), High2 - H2 (trees 10-15 m high), and High3 - H3 (trees > 15 m high). The effective number of dominant strata (ENDS), based on the abundance per species in each stratum (q = 2, Hill number), is shown for each meliponary.

two meliponaries each. At the opposite end, in the meliponary locality of Baca, no melliferous species were found in the Low stratum (Table 2). Interestingly, three tree species were identified among the most abundant melliferous species in the Low stratum: *Cedrela odorata* and *Metopium brownei* in San Juan de Dios and *P. piscipula* in Dzan.

As for the Middle stratum, the most abundant species was *Hamelia patens*, with 53 individuals. However, no melliferous species reached such abundance in the Middle stratum, the most abundant being the cultivated species *C* x *sinensis*, with 32 individuals, all in the vegetation of the Dzan meliponary (Table 2). In the rest of the meliponary localities, melliferous species in the Middle stratum were not very abundant, with numbers ranging between one and seven plants.

On the other hand, the High stratum had melliferous individuals in the three levels. However, the tree stratum in meliponary localities generally exhibited modest dimensions, with a mean height of 5.5 ± SD 2.9 m in the High stratum. The vegetation type with the highest trees was the semi-evergreen forest (6.3 ± SD 3.0 m), which differed from the deciduous forest (5.2 ± SD 2.6 m) and the semi-deciduous forest (5.2 ± SD 2.9 m), but the latter two did not differ from each other (Kruskal-Wallis rank sum test: $\chi^2 = 15.23$, df = 2, $P < 0.001$). Although 468 tree individuals were detected in the High stratum, only 40 individuals larger than 10 m in height were recorded, representing a mere 8.6 %. Of the total, 261 melliferous plants belonging to 32 species were identified, but only 22 plants (11 species) reached heights above 10 m. *Neomillspaughia emarginata* was one of the most abundant melliferous tree species, with 45 individuals in Dzan (Table 2). For the other species, the number of plants did not exceed 10 individuals, except for *Senna atomaria*, with 11 individuals in Baca.

Horizontal structure of vegetation. The tree vegetation of the meliponaries was characterized by a global mean DBH of 7.04 ± SD 3.2 cm. The comparison of vegetation types showed no differences in the DBH of trees between the deciduous forest (7.28 ± SD 6.6 cm) and the semi-evergreen forest (9.2 ± SD 5.8 cm), but the latter showed higher

Table 2. Frequency (n) of the most abundant melliferous plant species by vegetation stratum in the nine sampled meliponaries of the Yucatan Peninsula. The table shows data by locality, socio-political peninsular states (Yuc = Yucatán, Camp = Campeche, and Q. Roo = Quintana Roo), and vegetation type.

Vegetation type	Locality	Low stratum	Middle stratum	High stratum
		Species (n)	Species (n)	Species (n)
Deciduous tropical forest	Baca (Yuc)	-	*Piscidia piscipula* (1)	*Senna atomaria* (11)
	Pucnachén (Camp)	*Waltheria indica* (21)	*Gymnopodium floribundum* (6) *Mimosa bahamensis* (6)	*Gymnopodium floribundum* (7)
	Chunkanán (Camp)	*Tridax procumbens* (10)	*Mimosa bahamensis* (3) *Piscidia piscipula* (3)	*Guazuma ulmifolia* (6)
	Lerma (Camp)	*Viguiera dentata* (11)	*Mimosa bahamensis* (3)	*Leucaena leucocephala* (7)
Semi-deciduous tropical forest	Maní (Yuc)	*Tridax procumbens* (28)	*Piscidia piscipula* (5)	*Citrus* x *sinensis* (6)
	Dzan (Yuc)	*Piscidia piscipula* (8) *Waltheria indica* (8)	*Citrus* x *sinensis* (32)	*Neomillspaughia emarginata* (45)
Semi-evergreen tropical forest	Yaxché (Q.Roo)	*Corchorus siliquosus* (3)	*Piscidia piscipula* (1)	*Cedrela odorata* (6)
	Chanchén Palmar (Q.Roo)	*Boerhavia erecta* (3)	*Murraya paniculata* (6)	*Cedrela odorata* (5)
	San Juan de Dios (Q.Roo)	*Cedrela odorata* (3), *Metopium brownei* (3)	*Mimosa bahamensis* (7)	*Senna racemosa* (8)

values than the semi-deciduous tropical forest (5.7 ± SD 2.9 cm; Kruskal-Wallis rank sum test: $\chi^2 = 24.21$, df = 2, $P < 0.001$). This variation was also reflected at the level of individual meliponaries (Kruskal-Wallis rank sum test: $\chi^2 = 54.25$, df = 2, $P < 0.001$); the greatest difference was observed between Dzan and Yaxché, with mean DBH values of 5.34 (± SD 0.51) cm and 11.78 (± SD 2.15) cm, respectively (Table 3).

Regarding tree density in meliponaries, a global average of 4,496 (± 4,089) trees per hectare was recorded, with no significant differences among vegetation types (Kruskal-Wallis rank sum test: $\chi^2 = 8.35$, df = 2, $P = 0.015$). The Lerma and Baca meliponaries, both in deciduous forests, exhibited the highest densities with 9931 (SD ± 4,344) and 8,724 (SD ± 3,400) trees/ha, respectively. In contrast, San Juan de Dios, located in a semi-evergreen forest, showed the lowest density with 812 (SD ± 1059) trees/ha. We observed extreme values of tree basal area between meliponaries. Specifically, Baca recorded the highest value with 53.1 m^2/ha, followed by Lerma with 30.8 m^2/ha, while San Juan de Dios had the lowest value with 2.7 m^2/ha (Table 3). The global mean for the basal area of trees in the vegetation surrounding meliponaries was 23.4 (± SD 21.2) m^2/ha.

Discussion

Our results suggest that the impact of human activities, had a more pronounced effect on vegetation structure and diversity compared to the surrounding forest type, contrary to expectations. Since the meliponaries are located near human settlements, activities such as agriculture, horticulture, and urbanization may had an important effect on plant and structure diversity. The influence of human activities was evident in the mean tree height of trees in the high stratum of vegetation around the meliponaries, which was 5.5 m much lower than the reported tree heights in well-conserved deciduous (8-12 m), semi-deciduous (13-18 m), and semi-evergreen tropical (15-25 m) forests in the Yucatan Peninsula (Durán & Olmsted 1999, Flores-Guido *et al.* 2010). An in-depth analysis of the shifts in land use correlated with the surrounding vegetation of meliponaries will significantly bolster our findings.

We also found some evidence suggestive of an effect of biotic homogenization. This phenomenon occurs when human impacts (*e.g.,* deforestation) in the ecosystem promote the replacement of distinctive local species with others more resilient to disturbances or when the ecosystem conditions become more favorable for widely distributed species (McKinney 2006). We observed ruderal species, such as *P. hysterophorus* or *T. procumbens*, as well as widely distributed species, such as *P. piscipula* and *C. odorata* (both of economic interest), in the vegetation surrounding almost all meliponaries. Furthermore, we found crops, such as citrus fruits, in several of the meliponary localities, indicating a targeted selection of plants in areas adjacent to the meliponaries. The similarity in the effective number of equally common species (Hill number of order 1, $q = 1$) observed in six of the nine meliponaries studied encompassing different vegetation types further suggests an effect of biotic homogenization.

Table 3. Descriptive parameters (mean ± SD) of the horizontal structure of the vegetation around nine meliponaries of the Yucatan Peninsula. Socio-political peninsular states: Yuc = Yucatán, Camp = Campeche, and Q. Roo = Quintana Roo. Different letters in parentheses indicate significant differences (Dunn's test) in the breast height (SBH) among sites (vegetation surrounding the meliponaries).

Vegetation type	Locality	DBH (cm)	Tree density (n/ha)	Basal area (m^2/ha)
Deciduous tropical forest	Baca (Yuc)	8.1 ± 1.03 (ab)	8724 ± 3400	53.1 ± 9.3
	Pucnachén (Camp)	6.33 ± 2.64 (ac)	2039 ± 503	8.1 ± 4.1
	Chunkanán (Camp)	8.8 ± 5.33 (ac)	5922 ± 6093	27 ± 10.5
Semi-deciduous tropical forest	Lerma (Camp)	5.25 ± 2.55 (c)	9931 ± 4344	30.8 ± 21.6
	Maní (Yuc)	7.91 ± 0.7 (b)	3701 ± 2008	21 ± 12.2
	Dzan (Yuc)	5.34 ± 0.51 (c)	4061 ± 3141	10.7 ± 7.3
Semi-evergreen tropical forest	Yaxché (Q.Roo)	11.78 ± 2.15 (b)	3285 ± 1641	46.7 ± 30.3
	Chanchén Palmar (Q.Roo)	8.52 ± 2.92 (b)	1786 ± 742	10 ± 2.3
	San Juan de Dios (Q.Roo)	8.4 ± 3.75 (ab)	812 ± 1059	2.7 ± 0.8

Despite the similarities in the diversity between meliponaries, we observed the expected pattern of higher plant diversity in meliponaries located in semi-evergreen forests compared to other forest types, but only when comparing Baca and San Juan de Dios. These localities are in deciduous and semi-evergreen forests, respectively, characterized by contrasting precipitation levels (lower in Baca and higher in San Juan de Dios), which is consistent with the expected dissimilarities in species diversity between different types of vegetation (Flores & Espejel 1994, Flores-Guido *et al.* 2010). On the other hand, the low species diversity observed in the Dzan meliponary, located in a semi-deciduous forest (with intermediate precipitation levels) can be attributed to human activities rather than forest type since this meliponary was surrounded by a plantation of *C.* x *sinensis*.

The high vegetation stratum around the meliponaries showed a mean height of 5.5 m, a mean DBH of 7.04 cm, and a mean density of 4,496 (± 4,089) trees/ha. These values are characteristic of young secondary vegetation, which has high densities of small trees (Denslow & Guzman 2000, Guariguata & Ostertag 2001). Similarly, in Puerto Rico, Aide *et al*. (1996) reported tree heights of up to 5 m and a density of 4,000 trees/ha in secondary vegetation with 9.5 to 15 years of agricultural land abandonment. Additionally, in a semi-deciduous tropical forest of the Yucatan Peninsula, Saenz-Pedroza *et al*. (2020) found that the density of trees with DBH of 1 cm to 5 cm decreased from 12,000 to 6,000 trees/ha in areas with between 5 and 60 years of abandonment, while the density of trees with DBH > 5 cm increased from > 500 to 1,500 trees/ha in the same successional age range. Furthermore, considering compositional characteristics, we observed the presence of *Gymnopodium floribundum*, *M. brownei*, and *Bursera simaruba* mainly in the meliponaries of Quintana Roo. These three species, along with *Sabal yapa* (a genus recorded in our transects) and *Hampea trilobata* (undetected in the present study), form a plant community typical of early abandoned secondary vegetation in Quintana Roo State. Specifically, this community is associated with young secondary vegetation, 8 to 10 years of development (Sánchez & Islebe 2000).

The diversity of plants, including both melliferous and non-melliferous species, and their abundance and distribution by strata, suggest that the vegetation surrounding meliponaries is constantly influenced by human activities and may not ensure an adequate food supply for *M. beecheii* colonies. However, a study conducted by González-Avilés *et al*. (2023) in the Sierra del Abra Tanchipa Biosphere Reserve, San Luis Potosí, Mexico, found that disturbed areas of vegetation have a high richness of melliferous plant species. These areas consist of a mixture of both native and introduced melliferous species, which can serve as a rich source of food for bees, particularly *Apis mellifera*.

Although there are few studies on plant species used by *M. beecheii* as food sources in the Yucatan Peninsula, it has been observed that this bee species can visit approximately 114 species of melliferous plants in the region (Alfaro-Bates *et al.* 2010, Flores-Guido & Vermont-Ricalde 2011, Quezada-Euán 2018, Ramírez-Arriaga *et al*. 2018, Villanueva-Gutiérrez *et al*. 2018). These 114 plant species accounted for less than 43 % of the IVI of the surrounding vegetation in eight of the nine meliponaries evaluated. The exception was the Dzan meliponary, where the IVI of melliferous plants reached 62.5 %. However, this high value is largely due to the presence of C. x sinensis; if this species is excluded, the IVI of melliferous plants around the Dzan meliponary would be similar to values observed in other sites (42.78 %).

In addition to the low IVI values of melliferous plants around the meliponaries, the structure and young successional age of vegetation may limit food availability for bees, since some species of trees can take decades to start blooming (Hackett 1987). In addition, the age at first blooming is generally related to the final plant size; thus, the larger the tree, the larger the size it should reach to undergo its first blooming (Thomas 1996). Therefore, if the vegetation is young or the trees are cut and not allowed to grow, as in disturbed vegetation, the number of individuals that manage to flower is reduced, thus limiting food availability for bees. The low representation of blooming melliferous plants during the sampling time, which was carried out in the season of highest honey production in the Yucatan Peninsula agrees with this interpretation. Indeed, no blooming melliferous plants were observed in one meliponary and another five meliponaries had IVI values lower than 9 %.

The availability (abundance and species richness) of plants that produce nectar or pollen is essential to ensure sufficient food not only for *M. beecheii* but also for the other species of bees with which it coexists and competes. Additionally, the studies carried out to date evaluating the food resources used by *M. beecheii* have analyzed pollen collected by these bees but have not considered the surrounding vegetation; the response of this bee species to variations in the supply of food resources in the local ecosystem has not been addressed. Assessing the relationship between the diversity of available food sources in these meliponaries and those actually used by *M. beecheii* colonies is highly warranted (see González-Avilés *et al*. 2023).

There are two caveats to this study: the possible misclassification of some plant species as non-melliferous and the lack of information on the flight radius of bees. Some of the species may have been misclassified as non-melliferous in this work based on the literature on the melliferous flora of the Yucatan Peninsula, which may lead to underestimating the percentage of melliferous plants within the sampled flora. However, our list includes species such as *G. floribundum*, *P. piscipula*, *V. dentata*, *Lysiloma latisiliquum*, and *B. simaruba*, which are among the main melliferous species in the region in terms of the volume of food supplied to bees (Alfaro-Bates *et al.* 2010, Flores-Guido & Vermont-Ricalde 2011) and are widely represented in the forests of the Yucatan Peninsula (Miranda & Hernández-X. 1963, 2014, Rzedowski & Huerta 1994). Furthermore, our list covers species with different blooming periods, so it is possible that some of the species misclassified as non-melliferous are actually poorly represented melliferous species of little melliferous importance.

On the other hand, no data are currently available on the flight radius of *M. beecheii*. For other species of the same genus, the flight radius varies as follows: 1,120 m in *Melipona subnitida* (Silva *et al.* 2014), 1,800 m in *Melipona mandacaia* (Kuhn-Neto *et al.* 2009), and 2,470 m in *Melipona fasciculata* (Kerr 1987). This raises the possibility that the floristic diversity available to the bees studied here may have been underestimated, since our sampling was carried out within a radius of 150 m around the meliponaries. However, we believe that our results are indicative of the prevailing conditions in the peninsula due to its physiographic homogeneity, the widespread presence of the main agricultural activities (Flores & Espejel 1994, Duno-de Stefano *et al.* 2018), and the predominance of secondary vegetation (Islebe *et al.* 2015). These characteristics support the extrapolation of our results to greater distances around the meliponaries studied and other meliponaries of the Yucatan Peninsula.

To summarize, our results suggest that vegetation type has a low impact on the composition and structure of vegetation surrounding meliponaries. Rather, the influence of human activities, which was not directly assessed in this study, appears to be a more important factor. The low height of trees and high abundance of individuals in the low stratum indicate that the vegetation surrounding meliponaries is in early successional stages, possibly due to human impacts derived from agriculture and urbanization. However, it is necessary to analyze the relationship between current land use and the diversity and availability of plant species that serve as bee food resources. The availability of melliferous plant species observed around meliponaries cannot be fully explained by the analysis of vegetation structure and species diversity and composition alone. The effects of changes in land use on food availability for *M. beecheii* should be investigated to provide a more comprehensive explanation, as well as well-supported guidelines to foster meliponiculture in the Yucatan Peninsula.

Supplementary material

Supplemental data for this article can be accessed here: https://doi.org/10.17129/botsci.3497

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Literature cited

Aide TM, Zimmerman JK, Rosario M, Marcano H. 1996. Forest recovery in abandoned cattle pastures along an elevational gradient in northeastern Puerto Rico. *Biotropica* **28**: 537-548. DOI: https://doi.org/10.2307/2389095

Alfaro-Bates RG, Ortíz Díaz JJ, González-Acereto JA. 2010. Plantas melíferas: Melisopalinología, *In*: Durán García R, Méndez González M. *Biodiversidad y desarrollo humano en Yucatán*. Mérida: Centro de Investigación Científica de Yucatán A. C. (CICY), Programa de Pequeñas Donaciones (PPD) - Fondo para el Medio Ambiente Mundial (FMAM, Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO), Secretaría de Desarrollo Urbano y Medio Ambiente (SEDUMA) pp. 346-348. ISBN: 978-607-7823-08-7

Banda T, Schwartz,MW, Caro T. 2006. Woody vegetation structure and composition along a protection gradient in a miombo ecosystem of western Tanzania. *Forest Ecology and Management* **230**: 179-185. DOI: https://doi.org/10.1016/j.foreco.2006.04.032

Bazzaz F. 1975. Plant species diversity in old-field successional ecosystems in southern Illinois. *Ecology* **56**: 485-488. DOI: https://doi.org/10.2307/1934981

Beekman M, Ratnieks FLW. 2000. Long-range foraging by the honey-bee, *Apis mellifera* L. *Functional Ecology* **14**: 490-496. DOI: https://doi.org/10.1046/j.1365-2435.2000.00443.x

Biesmeijer JC, Roberts SPM, Reemer M, Ohlemüller R, Edwards M, Peeters T, Schaffers AP, Potts SG, Kleukers R, Thomas CD, Settele J, Kunin WE. 2006. Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science* **313**: 351-354. DOI: https://doi.org/10.1126/science.1127863

Brower JE, Zar JH, Von Ende CN. 1997. *Field and laboratory methods for general ecology*, 4th ed. Boston: WCB McGraw-Hill. ISBN: 0-697-24358-3

Cane JH, Minckley RL, Kervin LJ, Roulston TH, Williams NM. 2006. Complex responses within a desert bee guild (Hymenoptera: Apiformes) to urban habitat fragmentation. *Ecological Applications* **16**: 632-644. DOI: https://doi.org/10.1890/1051-0761(2006)016[0632:crwadb]2.0.co;2

Carvell C, Roy DB, Smart SM, Pywell RF, Preston CD, Goulson D. 2006. Declines in forage availability for bumblebees at a national scale. *Biological Conservation* **132**: 481-489. DOI: https://doi.org/10.1016/j.biocon.2006.05.008

Cepeda-Valencia J, Gómez PD, Nicholls C. 2014. The structure matters: bees visitors of coffee flowers and agroecological main structure (MAS). *Revista Colombiana de Entomología* **40**: 241-250.

Chao A, Gotelli NJ, Hsieh TC, Sander EL, Ma KH, Colwell RK, Ellison AM. 2014. Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. *Ecological Monographs* **84**: 45-67. DOI: https://doi.org/10.1890/13-0133.1

Chao A, Jost L. 2012. Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. *Ecology* **93**: 2533-2547. DOI https://doi.org/10.1890/11-1952.1

CONABIO (Comisión Nacional para el Conocimiento y Uso de la Biodiversidad). 2016. Mieles peninsulares y diversidad. Ciencias, núm. 118-119, noviembre 2015-abril, pp. 116-117.

Cortopassi-Laurino M, Imperatriz-Fonseca VL, Roubik DW, Dollin A, Heard T, Aguilar I, Venturieri GC, Eardley C, Nogueira-Neto P. 2006. Global meliponiculture: challenges and opportunities. *Apidologie* **37**: 275-292. DOI: https://doi.org/10.1051/apido:2006027

Cottam G, Curtis JT. 1956. The use of distance measures in phytosociological sampling. *Ecology* **37**: 451-460. DOI: https://doi.org/10.2307/1930167

Curtis JT, McIntosh RP. 1950. The interrelations of certain analytic and synthetic phytosociological characters. *Ecology* **31**: 434-455. DOI: https://doi.org/10.2307/1931497

Denslow JS, Guzman SG. 2000. Variation in stand structure, light and seedling abundance across a tropical moist forest chronosequence, Panama. *Journal of Vegetation Science* **11**: 201-212. DOI: https://doi.org/10.2307/3236800

Di Trani JC, Villanueva-Gutiérrez R. 2018. Annual foraging patterns of the Maya bee *Melipona beecheii* (Bennett, 1831) in Quintana Roo, Mexico, *In*: Vit P, Pedro S, Roubik D. eds. *Pot-Pollen in Stingless Bee Melittology*. Cham: Springer International Publishing. pp. 131-138. DOI: https://doi.org/10.1007/978-3-319-61839-5_10

Duno-de Stefano R, Ramírez Morillo IM, Tapia-Muñoz JL, Hernández-Aguilar S, Can LL, Cetzal-Ix W, Méndez-Jiménez N, Zamora-Crescencio P, Gutiérrez-Báez C, Carnevali-Fernández-Concha G. 2018. Aspectos generales de la flora vascular de la Península de Yucatán, México. *Botanical Sciences* **96**: 515-532. DOI: https://doi.org/10.17129/botsci.1868

Durán R, Olmsted I. 1999. Vegetación de la Península de Yucatán, *In*: Chico-Ponce de León PA, Alonzo-Aguilar A, García de Fuentes A, Jiménez-Osornio JJM, Orellana-Lanza R, Urzaiz-Lares E, eds. *Atlas de Procesos Territoriales de Yucatán*. Mérida: Universidad Autónoma de Yucatán. *PROEESA.* pp. 183-194.

Duran-García R, García-Contreras G. 2010. Distribución espacial de la vegetación, *In*: Duran-García R, Méndez-Gonzáles M, eds. *Biodiversidad y Desarrollo Humano en Yucatán*. Mérida: Centro de Investigación Científica de Yucatán A. C. (CICY), Programa de Pequeñas Donaciones (PPD) - Fondo para el Medio Ambiente Mundial (FMAM, Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO), Secretaría de Desarrollo Urbano y Medio Ambiente (SEDUMA). pp. 131-135. ISBN: 978-607-7823-08-7

Echazarreta CM, Quezada-Euán JJG, Medina LM, Pasteur KL. 1997. Beekeeping in the Yucatan peninsula: development and current status. *Bee World* **78**: 115-127. DOI: https://doi.org/10.1080/0005772X.1997.11099346

Ehbrecht M, Schall P, Juchheim J, Ammer C, Seidel D. 2016. Effective number of layers: A new measure for quantifying three-dimensional stand structure based on sampling with terrestrial LiDAR. *Forest Ecology and Management* **380**: 212-223. DOI: https://doi.org/10.1016/j.foreco.2016.09.003

Flores JS, Espejel I. 1994. Tipos de vegetación de la Península de Yucatán, *In*: Flores, JS, ed. *Etnoflora Yucatanense*. Mérida: Universidad Autónoma de Yucatán. ISBN: 9686843442

Flores-Guido JS, Durán-García R, Ortiz-Días JJ. 2010. Comunidades vegetales terrestres, *In*: Duran-García R, Méndez-Gonzáles M, eds. *Biodiversidad y desarrollo humano en Yucatán*. Mérida: Centro de Investigación Científica de Yucatán A. C. (CICY), Programa de Pequeñas Donaciones (PPD) - Fondo para el Medio Ambiente Mundial (FMAM, Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO), Secretaría de Desarrollo Urbano y Medio Ambiente (SEDUMA), pp. 125-129. ISBN: 978-607-7823-08-7

Flores-Guido JS, Vermont-Ricalde R. 2011. La vegetación de la península de Yucatán y su miel, *In:* Secretaría de Educación, ed. *La Miel y Las Abejas*. Mérida: Secretaría de Educación del Gobierno del Estado de Yucatán, pp. 31-46. ISBN: 6077824410

George-Chacón SP, Mas JF, Dupuy JM, Castillo-Santiago MA, Hernández-Stefanoni JL. 2022. Mapping the spatial distribution of stand age and aboveground biomass from Landsat time series analyses of forest cover loss in tropical dry forests. *Remote Sensing in Ecology and Conservation* **8:** 347-361. DOI: https://doi.org/10.1002/rse2.247

González-Acereto JA. 2008. *Cría y manejo de abejas nativas sin aguijón en México*. Secretaría de Fomento Agropecuario y Pesquero, Mérida: Impresiones Planeta. ISBN 970-9850-04-0

González-Acereto JA. 2012. La importancia de la meliponicultura en México, con énfasis en la Península de Yucatán. *Bioagrociencias*, México **5** 34-41.

González-Acereto JA, Quezada-Euán JJG, Medina-Medina L. 2006. New perspectives for stingless beekeeping in the Yucatan: results of an integral program to rescue and promote the activity. *Journal of Apicultural Research* **47**: 234-239. DOI: https://doi.org/10.1080/00218839.2006.11101356

González-Avilés BY, Reyes-Hernández H, Yañez-Espinosa L, Carranza-González E, De-Nova JA. 2023. La flora melífera del paisaje aledaño a la Reserva de la Biósfera Sierra del Abra Tanchipa, San Luis Potosí, México *Botanical Sciences* **101**: 775-803. DOI: https://doi.org/10.17129/botsci.3206

Gough CM, Atkins JW, Fahey RT, Hardiman BS, LaRue EA. 2020. Community and structural constraints on the complexity of eastern North American forests. *Global Ecology and Biogeography* **29**: 2107-2118. DOI: https://doi.org/10.1111/geb.13180

Guariguata MR, Ostertag R. 2001. Neotropical secondary forest succession: changes in structural and functional characteristics. *Forest Ecology and Management* **148**: 185-206. DOI: https://doi.org/10.1016/S0378-1127(00)00535-1

Hackett WP. 1987. Juvenility and Maturity, *In*: Bonga JM, Durzan DJ. *Cell and Tissue Culture in Forestry: General*

Principles and Biotechnology. Dordrecht: Springer Netherlands, pp 216-231. DOI: https://doi.org/10.1007/978-94-017-0994-1_13

Hill MO. 1973. Diversity and evenness: A unifying notation and its consequences. *Ecology* **54**: 427-432. DOI: https://doi.org/10.2307/1934352

Hsieh TC, Ma KH, Chao A. 2016. iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods in Ecology and Evolution* **7**: 1451-1456. DOI: https://doi.org/10.1111/2041-210X.12613

Hubp JL, Quesado JFA, Pereño RE. 1992. Rasgos geomorfológicos mayores de la Península de Yucatán. *Revista Mexicana de Ciencias Geológicas* **10**: 143-150.

INEGI [Instituto Nacional de Estadística y Geografía]. 2018. Conjunto de datos vectoriales de uso del suelo y vegetación. Escala 1:250 000. Serie VII. Conjunto Nacional. Mexico: INEGI. https://www.inegi.org.mx/app/biblioteca/ficha.html?upc=889463842781 (accessed May 11, 2022).

Islebe GA, Calmé S, León-Cortés JL, Schmook B. 2015. *Biodiversity and Conservation of the Yucatán Peninsula*. Switzerland: Cham: Springer International Publishing. ISBN: 978-3-319-06528-1.

Jamil A, Zubair M, Manzoor SA, Wali Muhammad M, Yasin G, Ur Rahman S, Alzain MN, Alqarawi AA, Abd-Allah EF. 2022. Impact of human settlements on diversity of range vegetation. *Sustainability* **14**: 2-15. DOI: https://doi.org/10.3390/su14010519

Jost L. 2019. What do we mean by diversity? The path towards quantification. *Mètode Science Studies Journal* **9**: 55-61. DOI: https://doi.org/10.7203/metode.9.11472

Kerr WE. 1987. *Biologia, Manejo e Genética de Melipona compressipes fasciculata Smith* (Hymenoptera, Apidae). PhD Thesis. Universidade Federal do Maranhão.

Kuhn-Neto B, Contrera FAL, Castro MS, Nieh JC. 2009. Long distance foraging and recruitment by a stingless bee, *Melipona mandacaia*. *Apidologie* **40**: 472-480. DOI: https://doi.org/10.1051/apido/2009007

Martínez-Puc JF, Cetzal-Ix W, Magaña-Magaña MA, López-Castilla HMJ, Noguera-Savelli E. 2022. Ecological and socioeconomic aspects of meliponiculture in the Yucatan Peninsula, Mexico. *Agro Productividad*. **15**: 57-65. DOI: https://doi.org/10.32854/agrop.v15i2.2108

May-Itzá W de J, de Araujo-Freitas C, Paxton RJ, Moo-Valle H, Medina-Medina LA, Quezada-Euán JJG. 2021. Stingless bees in urban areas: low body size and high frequency of diploid males at mating congregations of *Nannotrigona perilampoides* (Hymenoptera: Meliponini) in Mérida, Yucatán, México. *Apidologie* **52**: 755-766. DOI: https://doi.org/10.1007/s13592-021-00862-w

McKinney ML. 2006. Urbanization as a major cause of biotic homogenization. *Biological Conservation* **127**: 247-260. DOI: https://doi.org/10.1016/j.biocon.2005.09.005

Miranda F, Hernández-X E. 1963. Los tipos de vegetación de México y su clasificación. *Botanical Sciences* **28**: 29-179. DOI: https://doi.org/10.17129/botsci.1084

Miranda F, Hernández-X E. 2014. *Los tipos de vegetación de México y su clasificación edición conmemorativa* 1963-2013, 2015th ed. México: Ediciones Científicas Universitarias. ISBN: 6071618630

Mitchell K. 2010. Quantitative analysis by the point-centered quarter method. *arXiv Prepr*. arXiv1010.3303. DOI: https://doi.org/10.48550/arXiv.1010.3303

Morisita M. 1978. A new method for the estimation of density by the spacing method applicable to non-randomly distributed populations. *United States Department of Agriculture, Forest Service*. 1-20.

Ochungo P, Veldtman R, Abdel-Rahman EM, Muli E, Ng'ang'a J, Tonnang HEZ, Landmann T. 2022. Fragmented landscapes affect honey bee colony strength at diverse spatial scales in agroecological landscapes in Kenya. *Ecological Applications* **32**: e02483. https://doi.org/10.1002/eap.2483

Orellana R, Balam KM, Bañuelos I, García ME, González-Iturbe JA, Herrera CF, Vidal LJ. 1999. Evaluación climática, *In*: Chico-Ponce de León PA, Alonzo-Aguilar A, García de Fuentes A, Jiménez-Osornio JJM, Orellana-Lanza R, Urzaiz-Lares E, eds. *Atlas de Procesos Territoriales de Yucatán*. Mérida, Yucatán: Universidad Autónoma de Yucatán, pp. 163-182. ISBN: 9687556927

Orellana R, Espadas C, Conde C, Gay C. 2009. *Atlas - Escenarios de Cambio Climático en la Península de Yucatán*.

Centro de Investigación Científica de Yucatán A. C. (CICY: Unidad de Recursos Naturales); Universidad Nacional Autónoma de México (UNAM: Centro de Ciencias de la Atmósfera); Consejo Nacional de Ciencia y Tecnología (CONACYT: Fondo Mixto CONACYT-Gobierno del Estado de Yucatán); Secretaría de Desarrollo Urbano y Medio Ambiente (SEDUMA)-Gobierno del Estado de Yucatán; Sistema de Investigación y Desarrollo Tecnológico del Estado de Yucatán (SIDETEY); Organización de las Naciones Unidas- Programa de las Naciones Unidas para el Desarrollo (ONU-PNUD), Mérida, Yucatán, México.

Quezada-Euán JJG. 2018. *Stingless Bees of Mexico*. Cham: Springer International Publishing. DOI: https://doi.org/10.1007/978-3-319-77785-6

Quezada-Euán JJG, de Jesús May-Itzá W, González-Acereto JA. 2015. Meliponiculture in Mexico: problems and perspective for development. *Bee World* **82**: 160-167. DOI: https://doi.org/10.1080/0005772X.2001.11099523

R Core Team. 2023. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing. https://www.r-project.org/

Ramírez-Arriaga E, Pacheco-Palomo KG, Moguel-Ordoñez YB, Zepeda García Moreno R, Godínez-García LM. 2018. Angiosperm Resources for Stingless Bees (Apidae, Meliponini): A Pot-Pollen Melittopalynological Study in the Gulf of Mexico, *In*: *Pot-Pollen in Stingless Bee Melittology*. Cham: Springer International Publishing. pp. 111-130. DOI: https://doi.org/10.1007/978-3-319-61839-5_9

Reyers B. 2004. Incorporating anthropogenic threats into evaluations of regional biodiversity and prioritisation of conservation areas in the Limpopo Province, South Africa. *Biological Conservation* **118**: 521-531. DOI: https://doi.org/10.1016/j.biocon.2003.09.027

Rzedowski J, Huerta L. 1994. *Vegetación de México* (No. 582.16 R997r Ej. 1 002135), México: Limusa, Noriega Editores

Saenz-Pedroza I, Feldman R, Reyes-García C, Meave JA, Calvo-Irabien LM, May-Pat F, Dupuy JM. 2020. Seasonal and successional dynamics of size-dependent plant demographic rates in a tropical dry forest. *PeerJ* **8**: e9636. DOI: https://doi.org/10.7717/peerj.9636

Sánchez OS, Islebe G. 2000. La selva del noreste del estado de Quintana Roo: Distribución y dominancia de especies arbóreas. *Foresta Veracruzana* **2**: 11-17.

Sánchez-Aguilar RL, Rebollar-Domínguez S. 1999. Deforestación en la Península de Yucatán, los retos que enfrentar. *Madera y Bosques* **5**: 3-17. DOI: https://doi.org/10.21829/myb.1999.521344

Silva AG, Pinto RS, Contrera FAL, Albuquerque PMC, Rêgo MMC. 2014. Foraging distance of *Melipona subnitida* Ducke (Hymenoptera: Apidae). *Sociobiology* **61**: 494-501. DOI:

Steffan-Dewenter I, Kuhn A. 2003. Honeybee foraging in differentially structured landscapes. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **270**: 569-575. https://doi.org/10.1098/rspb.2002.2292

Steffan-Dewenter I, Münzenberg U, Bürger C, Thies C, Tscharntke T. 2002. Scale-dependent effects of landscape context on three pollinator guilds. *Ecology* **83**: 1421-1432. DOI: https://doi.org/10.1890/0012-9658(2002)083[1421:SDEOLC]2.0.CO;2

Tews J, Brose U, Grimm V, Tielbörger K, Wichmann MC, Schwager M, Jeltsch F. 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography* **31**: 79-92. DOI: https://doi.org/10.1046/j.0305-0270.2003.00994.x

Thomas SC. 1996. Relative size at onset of maturity in rain forest trees: A comparative analysis of 37 Malaysian species. *Oikos* **76**: 145-154. https://doi.org/10.2307/3545756

Villanueva R. 1994. Nectar sources of European and Africanized honey bees (*Apis mellifera* L.) in the Yucatán Peninsula, Mexico. *Journal of Apicultural Research* **33**: 44-58. DOI: https://doi.org/10.1080/00218839.1994.11100848

Villanueva-Gutiérrez R, Roubik DW, Colli-Ucán W. 2005. Extinction of Melipona beecheii and traditional beekeeping in the Yucatán peninsula. *Bee World* **86**: 35-41. DOI: https://doi.org/10.1080/0005772X.2005.11099651

Villanueva-Gutiérrez R, Roubik DW, Colli-Ucán W, Tuz-Novelo M. 2018. The value of plants for the Mayan stingless honey bee *Melipona beecheii* (Apidae: Meliponini): A pollen-based study in the Yucatan Peninsula, Mexico. *In*: *Pot-Pollen in Stingless Bee Melittology*. Cham: Springer, pp. 67-76. DOI: https://doi.org/10.1007/978-3-319-61839-5_5

Winfree R, Aguilar R, Vázquez DP, LeBuhn G, Aizen MA. 2009. A meta-analysis of bees' -responses to anthropogenic disturbance. *Ecology* **90**: 2068-2076. DOI: https://doi.org/10.1890/08-1245.1

Winfree R, Williams NM, Gaines H, Ascher JS, Kremen C. 2008. Wild bee pollinators provide the majority of crop visitation across land-use gradients in New Jersey and Pennsylvania, USA. *Journal of Applied Ecology* **45**: 793-802. DOI: https://doi.org/10.1111/j.1365-2664.2007.01418.x

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