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Diversidad de polen almacenado y su relación con la vegetación circundante a meliponarios de *Melipona beecheii* en la Península de Yucatán

Tesis que presenta

ALEJANDRO PÉREZ MORFI

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RECONOCIMIENTO

Por medio de la presente, hago constar que el trabajo de tesis de Alejandro Pérez Morfi titulado **Diversidad de polen almacenado y su relación con la vegetación circundante a meliponarios de *Melipona beecheii* en la Península de Yucatán**, fue realizado en la unidad de Recursos Naturales, en la línea de investigación de Servicios Ambientales, en el Laboratorio de Microbiología y Química Aplicada a la Ecología del Centro de Investigación Científica de Yucatán, A.C. bajo la dirección de la Dra. María Azucena Canto Aguilar dentro de la opción de Recursos Naturales, perteneciente al Programa de Posgrado en Ciencias Biológicas de este Centro y la codirección de la Dra. Elia Ramírez Arriaga del Instituto de Geología de la Universidad Nacional Autónoma de México.

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Este trabajo se llevó a cabo en la Unidad de Recursos Naturales del Centro de Investigación Científica de Yucatán, A.C, bajo la dirección de la Dra. María Azucena Canto Aguilar y en el Laboratorio de Palinología: Paleopalinología y Actuopalinología del Instituto de Geología de la Universidad Nacional Autónoma de México bajo la co-dirección de la Dra. Elia Ramírez Arriaga.

LISTA DE PRODUCTOS GENERADOS

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- Pérez-Morfi A, Ramírez-Arriaga E, Canto A (2024) Comparative analysis of *Melipona beecheii* pollen foraging preferences in Deciduous, Semi-deciduous and Semi-evergreen Tropical Forests of the Yucatan Peninsula. Apidologie (**En revisión**)

Artículos de divulgación

- Pérez-Morfi A y Canto A (2024) La alimentación de las abejas en los trópicos: meliponinos, ejemplo de buenos vecinos. Desde el Herbario CICY. (Aceptado)

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- Entrega de nueve infografías sobre las características de la vegetación y granos de polen más abundantes en colonias de *Melipona beechii* a los meliponicultores implicados en este trabajo

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RESUMEN

Melipona beecheii (Meliponini, Hymenoptera), una especie de abeja nativa sin aguijón que se distribuye desde el sur de Costa Rica hasta el sur de México. Esta especie es de gran importancia cultural y económica para los mayas de la Península de Yucatán donde es clave para la meliponicultura. Sin embargo *M. beecheii* y la meliponicultura en dicha región enfrentan amenazas debido a la deforestación y alteración del hábitat. Sin embargo, existe información limitada sobre las características de la vegetación de los meliponarios y los recursos poliníferos que utilizan. En este estudio, evaluamos la vegetación alrededor de nueve meliponarios ubicados en los tres principales tipos de vegetación de la Península de Yucatán y analizamos palinológicamente muestras de pan de abeja (polen almacenado en la colonia) recolectadas en 29 colonias. Encontramos un total de 268 especies de plantas de 73 familias alrededor de los meliponarios. En cinco meliponarios, las plantas melíferas representaron menos del 9 % del Índice de Valor de Importancia (IVI), y en un meliponario, no hubo plantas melíferas florecidas. La altura promedio de los árboles en el estrato alto fue de 5.5 metros, con una densidad promedio de 3,390 árboles/ha. El análisis de pan de abeja reveló 69 morfotipos de polen, con predominio de especies arbóreas, y de morfotipos de la familia Fabaceae. Además, no se encontró relación entre la densidad y la cobertura de especies vegetales y su representación en el polen de *M. beecheii*. Los meliponarios estaban rodeados de vegetación secundaria joven, caracterizada por una alta densidad de árboles pequeños, predominio del estrato bajo y escasez de plantas melíferas con flores. Esto sugiere que la actividad humana está afectando la diversidad vegetal y la disponibilidad de alimentos para *M. beecheii*, lo que contrasta con la preferencia de alimentación de la especie por un grupo reducido de especies arbóreas.

ABSTRACT

Melipona beecheii (Meliponini, Hymenoptera) is a native stingless bee species distributed from southern Costa Rica to southern Mexico. This species holds great cultural and economic importance for the Maya people of the Yucatán Peninsula, where it plays a key role in meliponiculture. However, *M. beecheii* and meliponiculture in this region face threats due to deforestation and habitat alteration. Nevertheless, there is limited information on the vegetation characteristics surrounding meliponaries and the pollen resources used by the species. In this study, we evaluated the vegetation around nine meliponaries located in the three main vegetation types of the Yucatán Peninsula and conducted palynological analyses of bee bread samples (stored pollen in the colony) collected from 29 colonies. We identified a total of 268 plant species from 73 families surrounding the meliponaries. In five meliponaries, melliferous plants represented less than 9% of the Importance Value Index (IVI), and in one meliponary, no flowering melliferous plants were found. The average height of trees in the upper stratum was 5.5 meters, with an average density of 3,390 trees/ha. The bee bread analysis revealed 69 pollen morphotypes, with a predominance of tree species and morphotypes from the Fabaceae family. Additionally, no relationship was found between the density and coverage of plant species and their representation in the pollen of *M. beecheii.* The meliponaries were surrounded by young secondary vegetation, characterized by a high density of small trees, a predominance of the lower stratum, and a scarcity of flowering melliferous plants. This suggests that human activity is affecting plant diversity and food availability for *M. beecheii*, which contrasts with the species' feeding preference for a limited group of tree species.

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INTRODUCCIÓN

En México se han descrito 18 géneros y 46 especies de abejas nativas sin aguijón pertenecientes a la tribu *Meliponini* (Ayala *et al.*, 2013). De estas, 19 especies habitan en la Península de Yucatán donde la cultura maya desarrolló ampliamente el manejo de los meliponinos desde tiempos precolombinos (Sotelo Santos y Alvarez Asomoza, 2018). *Melipona beecheii* (Bennett 1831) destaca como la especie más importante para los mayas, quienes la llamaron Xunan kaab (Señora de las abejas) y de la cual obtenían y comercializaban miel y cerumen (Chapman, 1959). La miel no solo la utilizaban como edulcorante sino que también tenía valor medicinal y espiritual al ser un elemento de rituales y ceremonias mágico-religiosas (Quezada-Euán *et al.*, 2018).

A pesar de la importancia histórica desde el punto de vista económico y cultural de *M. beecheii*, el número de colonias manejadas en la Península de Yucatán se ha reducido significativamente en las últimas décadas (Villanueva-Gutiérrez *et al.* 2005). Ello se le atribuye a la falta de interés de los lugareños por la meliponicultura, pero también a la muerte de las colonias por falta de alimento (Villanueva-Gutiérrez *et al.*, 2005). Se conoce que *M. beecheii* depende de vegetación poco perturbada (Villanueva-Gutiérrez *et al.* 2015) pero la Península de Yucatán destaca como una de las regiones más deforestadas de México, donde la reducción de la cobertura vegetal se estima en millones de hectáreas en las últimas dos décadas del siglo pasado (Duran-García y García Contreras 2010, Aguilar y Domínguez 1999). Además, al ser una especie de abeja sin aguijón las colonias manejadas se encuentran en meliponarios de traspatio y, por tanto, en zonas antropizadas. En este sentido, la estructura de la vegetación, en particular el tamaño de las plantas se ve afectado negativamente en áreas rurales cerca de asentamientos humanos (Banda *et al.*, 2006; Jamil *et al.*, 2022) debido a las actividades económicas, lo que provoca deforestación, degradación y pérdida de la biodiversidad (Reyers, 2004). Paradójicamente, existe poca información sobre las características de la vegetación a la que actualmente tiene acceso *M. beecheii* en los meliponarios de la Península de Yucatán y el uso que hacen de dicha vegetación.

Como otros meliponinos *M. beecheii* presenta hábitos de forrajeo generalistas que le permiten utilizar una amplia gama de recursos florísticos para cubrir las necesidades nutricionales de la colonia (Villanueva-Gutiérrez *et al.*, 2015). Sin embargo, muchas especies de abejas expresan preferencia por determinados grupos de plantas. Por ejemplo, las abejas de lengua larga como los meliponinos se ven más atraídas por las plantas perennes -árboles- posiblemente debido a que estas pueden destinar mayor cantidad de recursos a la reproducción y en consecuencia ofrecen recompensas más atractivas para las abejas (Corbet, 1995; Parrish and Bazzaz, 1979). Además, los meliponinos parecen visitar principalmente las familias de plantas con mayor riqueza de especies como Asteraceae, Euphorbiaceae, Lamiaceae y Fabaceae. En el caso de *M. beechii* la familia Fabaceae ha sido identificada como la predominante en el pan de abeja (polen almacenado en la colonia) de esta especie en Quintana Roo (Villanueva-Gutiérrez *et al.*, 2018). Sin embargo, otro estudio realizado en Campeche (Ramírez-Arriaga *et al.*, 2018) encontró abundancia del polen de la familia Solanaceae en el pan de abeja de esta especie. Las diferencias en los diseños y temporalidad de ambos estudios dificultan el análisis de los patrones de forrajeo de *M. beecheii* en la Península de Yucatán.

En este estudio nos proponemos evaluar la diversidad y características de la vegetación que rodea los meliponarios de la Península de Yucatán con el fin de conocer la disponibilidad de fuentes de alimento de las que disponen estas abejas. Además, nos proponemos caracterizar polínicamente el polen almacenado en colonias (pot-pollen en inglés) de la abeja nativa sin aguijón *M. beecheii,* en meliponarios establecidos en diferentes localidades de la Península de Yucatán. La información generada en esta investigación contribuirá al conocimiento de la biología alimentaria de *M. beecheii*, información que será de gran utilidad en planes de recuperación, reforestación o de manejo integral de esta especie de abeja en la región.

CAPÍTULO I

ANTECEDENTES

3.1. Abejas nativas sin aguijón (Apidae: Meliponini)

Las abejas nativas sin aguijón o meliponinos, pertenecen a la tribu Meliponini (Hymenoptera: Apidae) la cual a su vez forma parte de un grupo monofilético de cuatro tribus: Apini, Meliponini, Bombini y Euglossini; dicho grupo está conformado por abejas corbiculadas (Michener, 2013). La corbícula es una estructura que se encuentra en la tibia del tercer par de patas, es a menudo cóncava y marginada con pelos largos (Fig. 1.1). Esta estructura es utilizada por las obreras para transportar principalmente el polen acopiado, aunque también la utilizan para transportar otras sustancias como resinas. Actualmente hay descritas 552 especies de meliponinos pertenecientes a 58 géneros, de las cuales 426 especies y 31 géneros están presentes en el Neotrópico (Grüter, 2020). Ello representa una gran diversidad en comparación con las especies reportadas en la tribu Apini (8 especies) donde se encuentra la abeja melífera, Bombini (280 especies) que agrupa a los abejorros y Euglossini (251 especies) donde están las clásicas abejas polinizadoras de las orquídeas (ITIS, 2020). Las tribus Meliponini y Apini son las únicas que presentan abejas altamente sociales, es decir, eusociales (Michener, 2007).

En México se han descrito 18 géneros y 48 especies de meliponinos también llamados abejas sin aguijón (con aguijón vestigial) (Ayala *et al.*, 2013). De estas, 19 habitan en la Península de Yucatán (Ayala *et al.*, 2013), donde la cultura del manejo de las abejas sin aguijón, conocida actualmente como meliponicultura, ha existido desde tiempos precolombinos (Sotelo Santos y Alvarez Asomoza, 2018). Entre los meliponinos manejados por los mayas destaca *Melipona beecheii* Bennett 1831, especie de importancia económica y espiritual para dicha cultura. La miel y el cerumen cosechados por los mayas en las colonias de *M. beecheii* y otros meliponinos, eran los principales productos de intercambio de Yucatán después de la sal (Chapman, 1959). Desde el punto de vista espiritual los mayas le dedicaron la deidad Ah Muzen Kaab a sus abejas. Aunque *M. beecheii* se conoce principalmente por su importancia para la cultura maya, la distribución geográfica de esta especie se extiende de este a oeste de la Península de Yucatán hasta las costas mexicanas en el océano Pacífico y de Norte a Sur desde México hasta Costa Rica (Quezada-Euán, 2018a).

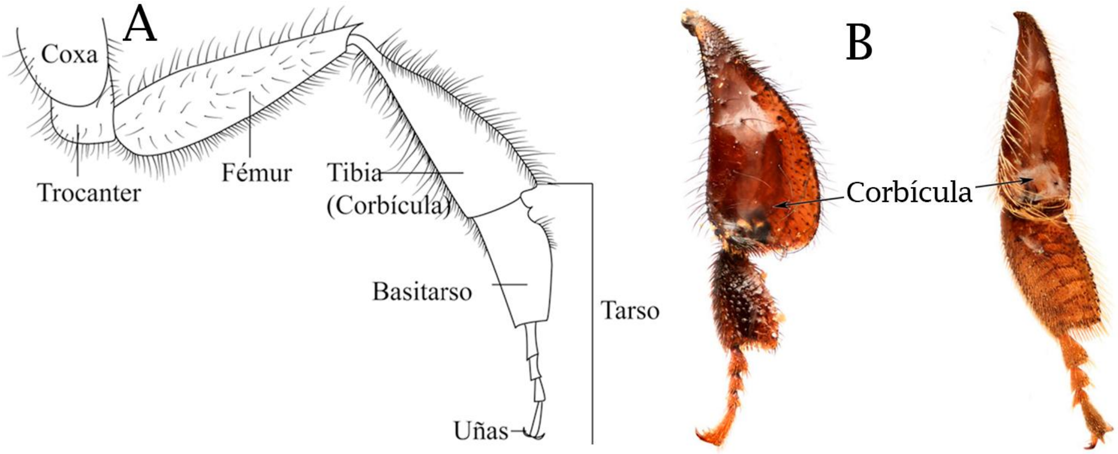

Figura 1.1: Corbícula de abeja, A: esquematización tomada de Farouk Miranda *et al.*, (2014) y B: fotografía modificada de Engel y Rasmussen (2020).

3.2. Meliponicultura en la Península de Yucatán

Históricamente la Península de Yucatán ha sido reconocida como una de las regiones melíferas más importantes de México (Coh-Martínez *et al.*, 2019; Güemes Ricalde *et al.*, 2003), de hecho, los meliponicultores plantean que décadas atrás se lograban hasta tres cosechas de miel de *M. beecheii* cuando en la actualidad solo se logra una. A pesar de esto, la meliponicultura en la Península de Yucatán ha sufrido un proceso de decadencia desde la llegada de los españoles. Durante la colonia, el incremento del área urbana, la ganadería y la expansión de la agricultura redujeron las selvas naturales. Además la introducción de la caña de azúcar y la utilización del azúcar como edulcorante, contribuyeron a reducir la demanda de miel de abeja sin aguijón (Quezada-Euán *et al.*, 2015). Después de la independencia de México, el cultivo del henequén (*Agave fourcroydes* Lem., Agavaceae), pero principalmente la introducción de la abeja melífera europea (*Apis mellifera* L.), acentuaron la tendencia a la disminución de la práctica de la meliponicultura. Por un lado, el henequén provocó la tala de aproximadamente 320 000 hectáreas de vegetación nativa (Ramírez-Carrillo, 2020) que servían de hábitat para los meliponinos de la región. Mientras que, debido a que *A. mellifera* produce mucha más miel que *M. beecheii,* la apicultura mejoró los ingresos de los campesinos (Quezada-Euán *et al.*, 2015) y acentuó el abandono de la meliponicultura (Villanueva-Gutiérrez *et al.* 2005).

La llegada de la abeja africanizada a la Península de Yucatán en 1987 (Quezada-Euán 2007) parece haber influido en el cambio de la tendencia al abandono de la meliponicultura (Quezada-Euán, 2018b). La defensividad de las abejas africanizadas provocó la reubicación de los apiarios fuera de las ciudades y centros urbanos, lo que dejó a las aldeas mayas prácticamente sin abejas productoras de miel a nivel de traspatio. Esto abrió una oportunidad para la recuperación de la meliponicultura en las comunidades mayas, la cual ha ganado popularidad desde entonces (Quezada-Euán, 2018b). Sin embargo, la pérdida de hábitat y de recursos alimenticios afectan tanto la supervivencia de los meliponinos en la región, como las cosechas de miel. De hecho, se conoce que *M. beecheii* depende de vegetación primaria o poco perturbada para su supervivencia (Villanueva-Gutiérrez *et al.* 2015) pero en las últimas décadas las pérdidas en la cobertura selvática de la Península de Yucatán se cuentan en millones de hectáreas (Céspedes- Flores y Moreno- Sánchez, 2010; Duran-García y García-Contreras, 2010; Ellis et al., 2024). Además, la meliponicultura se practica como una actividad de traspatio lo que posiciona los meliponarios en zonas antropizadas y por tanto con vegetación perturbada. Paradójicamente, existe gran desconocimiento sobre de qué recursos florísticos dispone y utiliza *M. beecheii* en la región, principalmente aquellos que aportan polen.

3.3. Vegetación en los meliponarios de la Península de Yucatán

Desde el punto de vista biogeográfico, los meliponarios que se encuentran en los tres estados políticos de la Península de Yucatán (Yucatán, Campeche y Quintana Roo) están emplazados en lo que se acota como Península Yucatán Mexicana (PYM; Duno-de Stefano *et al.*, 2018), la cual es parte de la Provincia Biótica Península de Yucatán. Esta última comprende, además, los departamentos del norte de Belice y el Departamento del Petén de Guatemala, (Barrera, 1962; Rzedowski, 2006).

En la PYM actualmente están descritas 2,327 especies de plantas vasculares de las cuales 99 son endémicas (Carnevali Fernández-Concha *et al.*, 2010, 2021). La familia de plantas más diversa de la PYM es Fabaceae seguida de Poaceae, Asteraceae y Orchidaceae (Carnevali Fernández-Concha *et al.*, 2010). En comparación con el resto de México, la PYM es una región con baja riqueza florística, en especial de helechos, licófitas y gimnospermas (Carnevali Fernández-Concha *et al.*, 2010). La baja riqueza florística de la PYM está influida por las pocas precipitaciones con fuerte estacionalidad (período lluvioso de mayo a octubre), los suelos poco profundos con afloramiento de material calizo, la homogeneidad fisiográfica y la ausencia de ríos (Duno-de Stefano *et al.*, 2018). Asimismo, la dificultad de acceso al agua y nutrientes constituyen factores de selección que influyen en la baja riqueza de especies de plantas que habitan en la península.

A pesar de la relativa homogeneidad de las condiciones ambientales de la PYM, existen variaciones que contribuyen a la diversidad local. En este sentido destaca principalmente la existencia de un gradiente geográfico de precipitaciones en dirección noroeste – suroeste. Lo anterior implica que la zona sur-suroeste de la península (Quintana Roo) es la más lluviosa con más de 1500 mm al año. Mientras que, hacia la zona norte de los tres estados de la península las precipitaciones rondan los 600 - 1000 mm (Orellana *et al.*, 2003).

El gradiente geográfico de precipitaciones hace que el estado de Yucatán, que se encuentra al norte, conforme una isla de vegetación seca rodeada de tipos más higrófitos de vegetación al sur (Duno-de Stefano *et al.*, 2018). Esta porción seca al norte se caracteriza por tener menor riqueza de especies, pero mayor endemismo y está cubierta principalmente por selvas bajas caducifolias y selvas medianas subcaducifolias, caracterizados por alturas de árboles de aproximadamente 8 m a 10 m en la primera y de 10 m a 18 m en la segunda (Duno-de Stefano *et al.*, 2018; Duno de Stefano *et al.*, 2010; Flores y Espejel, 1994). Mientras que por otro lado, la porción más al sur de la península es más húmeda, más rica en especies y tiene menor endemismo (Duno-de Stefano *et al.*, 2018; Espadas-Manrique *et al.*, 2003). Esta porción está ocupada por los estados de Campeche y Quintana Roo donde es la selva mediana subperenifolia la que ocupa la mayor extensión y se caracteriza por una menor proporción de especies caducifolias, una estructura vertical más heterogénea, con un dosel que alcanza de 15 a 25 m de altura (Flores y Espejel, 1994, Durán y Olmsted 1999, Duno-de Stefano *et al.* 2018).

Intercaladas con las selvas de gran extensión mencionadas anteriormente, existen otras formaciones vegetales de menor extensión que también contribuyen a la diversidad de los ecosistemas de la Península de Yucatán. Un ejemplo de ellas son las selvas bajas inundables, también conocidas como selvas bajas subperennifolias las cuales se distribuyen en forma de manchones dispersos al interior de las selvas medianas (Durán y Olmsted, 1999). Estas abundan principalmente en los estados Quintana Roo y Campeche y en menor medida en Yucatán (Flores Guido et al., 2010). Las selvas bajas inundables se caracterizan por presentarse en suelos pobres con poca materia orgánica y en ellas los árboles alcanzan entre 5 y 6 metros de altura. Por otro lado, en la Península de Yucatán también se pueden encontrar sabanas o pastizales naturales. Estas pueden estar asociadas a humedales costeros, mientras que tierra adentro se ecuentran en suelos profundos sin influencia marina (Flores Guido et al., 2010). En general, las sabanas están dominadas por gramíneas y ciperáceas, pero cuentan con un estrato arbóreo bajo cuya altura varía entre los 3 y los 6 metros.

Además de las plantas nativas de las selvas, *M. beecheii* también dispone de las plantas cultivadas por el hombre en sus asentamientos. Debido a que la mayor parte de los meliponarios en la región son de traspatio (Quezada-Euán *et al.*, 2015; Villanueva-Gutiérrez *et al.*, 2005) la vegetación con la que interactúa la colonia está influida por la actividad humana. De hecho, *M. beecheii* visita cultivos como el achiote, pepino, calabaza y melón (Meléndez-Ramirez *et al.*, 2002; Quezada-Euán, 2018a). Sin embargo, la propia actividad humana, con su efecto negativo en las zonas boscosas y la consecuente pérdida de hábitat -influida por las grandes extensiones dedicadas a la agricultura- parecen estar poniendo en peligro la supervivencia de *M. beecheii* (Villanueva-Gutiérrez *et al.*, 2005) y posiblemente a otros meliponinos. En este sentido se conoce que la abundancia de las abejas sin aguijón parece depender más de la disponibilidad de fuentes de alimento que de sitios de anidación (Eltz *et al.*, 2002; Hubbell y Johnson, 1977). No obstante, no existen estudios que evalúen las condiciones de la vegetación de los meliponarios en la Península de Yucatán. Teniendo en cuenta que la vegetación de los meliponarios de la Península de Yucatán está sujeta a características generales que influyen en la fitogeografía de la región, pero también depende de variaciones en las condiciones locales y de la actividad humana, se hace necesario estudiar la diversidad florística en meliponarios de la Península de Yucatán.

3.4. Hábitos de forrajeo y uso de recursos florales por los meliponinos

Los meliponinos han logrado aprovechar de manera eficiente los recursos florísticos en los trópicos, donde una de cada dos abejas observadas en las flores pertenece a este grupo (Heithaus, 1979; Roubik, 1989) y donde pueden coexistir varias docenas de especies en un mismo entorno (Roubik, 1989; Slaa, 2003). Ello se traduce en una superposición de la dieta, la cual, en términos de especies de plantas utilizadas, es generalmente considerable (Eltz *et al.*, 2001; Ramalho *et al.*, 1990; Roubik *et al.*, 1986). El éxito de los meliponinos se debe a estrategias de forrajeo generalistas que han desarrollado y que comparten con los apinos (Biesmeijer y Slaa, 2004).

En sentido general, las estrategias de *forrajeo* siguen una relación costo-beneficio entre la agresividad y la especificidad del forrajeo. Aquellas especies que son más agresivas en el reclutamiento y hacia otros visitantes florales (ejemplo: *Trigona* y *Oxytrigona*), no son muy buenas en encontrar nuevos recursos (Biesmeijer y Slaa, 2004). A partir de este tipo de estrategia aparecen variantes con disminución de la agresividad y el reclutamiento, pero con aumento en la diversidad de especies de plantas que visitan. Las abejas del género *Melipona* presentan un forrajeo no agresivo por lo que son capaces de explotar recursos florales a la vez que otras especies de abejas. De hecho, Ramalho *et al.*, (1990) reportan cuatro familias de plantas (Fabaceae, Myrtaceae, Arecaceae y Rubiaceae) que como fuentes de alimento, son igual de importantes para abejas de los géneros *Melipona* y *Trigona* y también para *Apis mellifera* africanizada. No obstante, estos autores reportan 52 especies exclusivamente importantes para las abejas del género *Melipona* en relación con los otros dos grupos.

En el Neotrópico americano, el uso que los meliponinos hacen de los recursos florales disponibles parece estar influido por factores taxonómicos. Las familias vegetales con mayor número de especies en la región (Anacardiaceae, Compositae, Euphorbiaceae, Lamiaceae, Fabaceae, Melastomataceae, Moraceae, Myrtaceae, Arecaceae, Rubiaceae y Solanaceae) constituyen también las fuentes más constantes de polen y néctar, desde el sur de Brasil hasta el sur de México (Ramalho *et al.*, 1990). Mientras que, en un contexto local determinado, los meliponinos obtienen la mayor parte de los alimentos de unos pocos grupos de plantas, a pesar de la gran cantidad de fuentes florales disponibles a escala regional y la gran diversidad de plantas en los hábitats de las selvas tropicales (Ramalho *et al.*, 1990). Esto se ha evidenciado en el análisis de las cargas de polen y el pan de abeja (polen almacenado en la colonia) de *Scaptotrigona hellwegeri* (Quiroz-García *et al.*, 2011), *Melipona beecheii* (Villanueva-Gutiérrez *et al.*, 2018) y otras especies de los géneros *Melipona* y *Trigona* (Ramalho *et al.*, 1990). A escala local, donde varias especies de abejas deben interactuar en un mismo paisaje, la partición de recursos parece explicar este fenómeno.

La partición de recursos entre especies puede ser mediada por diferencias interespecíficas en las preferencias de estrato de forrajeo y por la disponibilidad general de polen (Nagamitsu *et al.*, 1999). En situaciones en las que los recursos son diversos y abundantes, las abejas probablemente son capaces de ejercer una elección significativamente más activa con respecto a su dieta de polen (Eltz *et al.*, 2001). La diversidad y abundancia de recursos puede poner de manifiesto diferencias innatas en las preferencias de alimentación o la elección floral. Por ejemplo, se ha encontrado predominio del estrato arbóreo en cargas de polen de *Scaptotrigona hellwegeri* (Quiroz-García *et al.*, 2011; Bacab-Pérez *et al*., 2024). Además, se ha encontrado que los meliponinos pueden dividir los recursos florales de la misma especie vegetal a través de la variación temporal y espacial de los recursos florales (Hubbell y Johnson, 1978; Johnson, 1981; Johnson y Hubbell, 1975; Martínez-Hernández et al., 1993; Nagamitsu y Inoue, 1997) y a partir de variación en los rasgos florales entre diferentes especies de plantas (Nagamitsu *et al.*, 1999).

3.4.1. Hábitos de forrajeo de *Melipona beecheii*

Melipona beecheii tiene hábitos de forrajeo generalistas a nivel de colonia y especialistas a nivel de individuo (Slaa *et al.*, 2006). Esta última conducta se conoce como “constancia floral” y se debe a que los individuos tienden a especializarse en visitar las flores de una sola especie de planta durante su período de floración. La constancia floral y la capacidad de hacer polinización por sonicación hace de *M. beecheii* un excelente polinizador de cultivos (Quezada-Euán, 2018a). No obstante, en su estado natural *M. beecheii* depende de vegetación primaria o poco perturbada (Villanueva-Gutiérrez *et al.* 2015) para cubrir los requerimientos alimentarios de la colonia. Ramírez-Arriaga *et al.*, (2018) reportan también, que *M. beecheii* presenta un comportamiento de forrajeo poliléctico, además de una especialización monoléctica y oligoléctica temporal o local.

Las especies de abejas monolécticas usan una sola especie de huésped floral para la obtención de polen (Robertson, 1925). Tanto el comportamiento monoléctico como la constancia floral se evidencian en las cargas de polen extraídas de una sola especie de planta, pero el comportamiento monoléctico es un rasgo fijo y persistente específico de la especie, mientras que la constancia floral es un rasgo de comportamiento lábil de los recolectores individuales (Fig. 1.2) (Cane, 2021). Por otro lado, las abejas con dietas especializadas que exhiben una alta fidelidad para taxones de polen particulares se conocen como oligolécticas, y se cree que están restringidas fisiológica, temporal o ambientalmente a una amplitud de recursos limitada (Devictor *et al.*, 2010; Fox y Morrow, 1981), mientras que las abejas polilécticas buscan polen en una amplia variedad de especies de plantas. Por tanto, es posible que la especialización monoléctica reportada por Ramírez-Arriaga *et al.*, (2018) sea más bien a una reducción en la disponibilidad de recursos que forzó a las abejas a ir a solo una especie de planta.

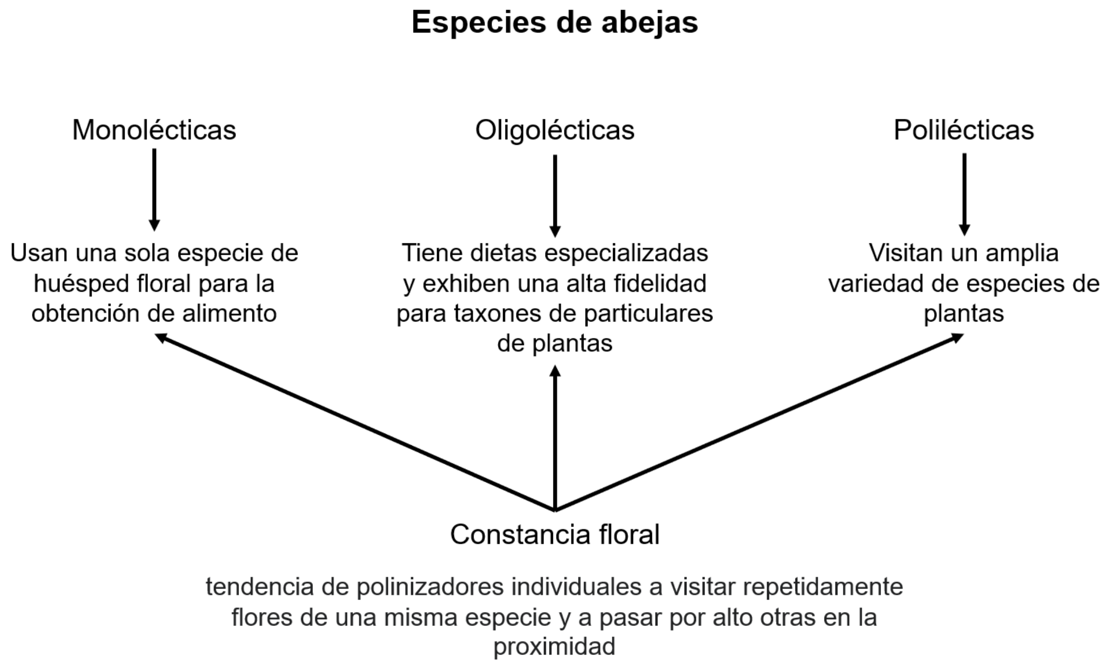

Figura 1.2: Esquematización las conductas de forrageo de las abejas.

3.5. Palinología

La forma más utilizada para investigar el uso que hacen las abejas de los recursos florares es a través de la melisopalinología. Esta disciplina se inserta dentro de la palinología la cual se refiere al estudio de los palinomorfos. Según Traverse, (2007) los palinomorfos son, entre otros, el polen, las esporas de helechos y hongos, las diatomeas, las algas, los foraminíferos y los dinoflagelados. El estudio de esta diversidad de palinomorfos posibilita que la palinología se aplique en multitud de campos de investigación. Por ejemplo, en la ciencia forense posibilita establecer relaciones entre personas, objetos y lugares. También existe la paleopalinología que analiza el polen fosilizado, permitiendo conocer la vegetación del pasado y su evolución, así como inferir las antiguas condiciones climáticas y ambientales de la Tierra (Traverse, 2007). Además, en arqueología y antropología la palinología contribuye en la interpretación de las actividades humanas y su efecto sobre el medio ambiente (Bryant Jr and Holloway, 1983).

En geología, la palinología se utiliza ampliamente para la prospección de petróleo (Talukdar, 1982). La copropalinología por otro lado, considera el contenido de polen en las heces (Callen y Cameron, 1960). La aeropalinología implica el estudio del contenido de polen en la atmósfera, su dispersión. distribución y sedimentación (Adeonipekun, 2012; Biesboer, 1977). La aeropalinología estudia el polen y fungosporas presentes en la atmósfera (Traverse, 2007), mientras que la iatropalinología considera exclusivamente las alergias al polen que afectan la salud humana (Sen *et al.*, 2003). La farmacopalinología enfatiza el uso de polen y esporas en la medicina y disciplinas relacionadas (Paunov *et al.*, 2007). Mientras que, la melisopalinología encuentra aplicación en la apicultura y la meliponicultura al estudiar el polen en la miel, polen almacenado, el alimento larval, polen en propóleos y geopropóleos (Nogueira *et al.*, 2012; Ramírez Arriaga *et al.*, 2016; Roubik y Moreno-Patiño, 2018).

3.5.1. Melisopalinologia

El estudio del polen en la miel, el polen corbicular, el pan de abeja, el alimento larval, polen de propóleos y geopropóleos se conoce como melisopalinología. A través del análisis melisopalinológico se puede conocer el origen botánico y geográfico de las mieles y de las cargas de polen acopiadas por las abejas. Se obtiene, además, información de los hábitos alimentarios de las abejas y sus estrategias de *forrajeo*. El análisis microscópico permite obtener información adicional sobre el contenido de levaduras así como de cualquier contaminación de la miel con cría, polvo, cenizas y otras partículas microscópicas que no suelen estar presentes en la miel (Louveaux *et al.*, 1978). La posibilidad de conocer el origen geográfico de las mieles también propició el desarrollo del control de calidad de las mieles con denominación de origen (d'Albore, 1997).

El análisis melisopalinológico consta de dos elementos, el cualitativo y el cuantitativo. El análisis cualitativo de los granos de polen consiste en su descripción a partir de un conjunto de caracteres morfológicos que permiten su identificación a nivel de familia, género o especie. Una vez identificados y/o descritos los morfotipos de granos de polen presentes en una muestra se procede a realizar el análisis cuantitativo. Este último consiste en realizar transectos en la preparación en los que se cuentan al azar 500 granos de polen. Esto posibilita cuantificar de la frecuencia de los morfotipos de granos de polen previamente identificados y/o descritos en cada muestra (Louveaux *et al.*, 1978). Dicha información permite identificar las especies de plantas de importancia nectarífera -según la abundancia de los tipos polínicos en la miel-, las especies de importancia polinífera -aquellas presentes en las cargas corbiculares de polen o en el pan de abeja almacenado en la colonia- y las de importancia nectaro-polinífera, es decir, que se encuentran tanto en la miel como en las cargas de polen acopiados por las abejas. El análisis cuantitativo también puede proveer información sobre la biología alimentaria de las abejas al analizar la abundancia relativa de las especies de plantas que visitan las abejas y evaluar si existen preferencias o tendencias en los hábitos alimentarios.

El análisis cualitativo se puede hacer con granos de polen acetolizados o no, sin embargo, la mayoría de las descripciones de polen en la literatura palinológica se basan en material acetolizado (Louveaux *et al.*, 1978). El método de acetólisis fue desarrollado por Erdtman (1960) y consiste en tratar químicamente los granos de polen lo que permite la elaboración de preparaciones permanentes para su mejor visualización e identificación. Brevemente, la acetólisis consiste en deshidratar los granos de polen con ácido acético, posteriormente se elimina el protoplasma y cubierta superficial de trifina o pollenkit con anhídrido acético y ácido sulfúrico (proporción 9:1) en baño María, se detiene la reacción con ácido acético y finalmente se lavan con agua destilada. Debido a las sustancias químicas fuertes que se utilizan, la acetólisis destruye hifas de hongos, levaduras, algas, algunos granos de polen de paredes delgadas como los de la familia Lauraceae y otras partículas que podrían ser útiles para evaluar la miel u otros productos de la colmena. A pesar de estas desventajas, la acetólisis tiene la gran ventaja de posibilitar la observación de la estructura y escultura de la exina de los granos de polen, lo que facilita la descripción e identificación del origen floral del polen.

3.5.2. Generalidades de la descripción de un grano de polen

El estudio de los granos de polen consiste en el análisis de su morfología con especial atención en el tipo y número de aperturas, la forma obtenida a partir de las dimensiones de los ejes polar (EP) y ecuatorial (EE) (Tabla 1.1), asi como la ornamentación y estructura de la pared (Tabla 1.2). Las aperturas son adelgazamientos de la exina que permiten la hidratación o deshidratación (procesos harmomegáticos) de los granos de polen así como su germinación (Thanikaimoni, 1986). Además, se calcula el área polar, característica propia de granos de polen colpados y colporados (Fig. 1.3 A, B), la cual se calcula considerando el índice obtenido a partir de la dimensión que existe entre los vértices de los colpos (d) entre el diámetro del eje ecuatorial (D) en vista polar (Fig. 1.3 C; Tabla 1.3).

Tabla 1.1: Forma de un grano de polen según Kremp, (1965).

EP/EE	Forma
<0.5	Peroblado
0.5-0.75	Oblado
0.75-0.88	Suboblado
0.88-1.00	Oblado esferoidal
1.00	Esferoidal
1.00-1.14	Prolado esferoidal
1.14-1.33	Subprolado
1.33-2.00	Prolado
>2.00	Perprolado

EP: Eje Polar, EE: Eje ecuatorial

Tabla 1.2: Caracteres morfológicos considerados en la descripción de un grano de polen.

Caracteres	Ejemplo de niveles de los caracteres
Tipo de asociación	Mónada, díada, tetráda, octada o políada
Polaridad	Apolar, isoplar o heteropolar
Simetría	Radial, bilateral o asimétrico
Tipos de aperturas	Poro, colpo, sulco o colporo
Exina Estructura	Tectada, subtectada, intectada o atectada Columelada, granular o alveolar
Ornamentación	Psilada, equinada, rugulada, verrugada, reticulada etc.
Dimensiones del grano de polen	Eje polar y eje ecuatorial. En el polen apolar se considera el diámetro.

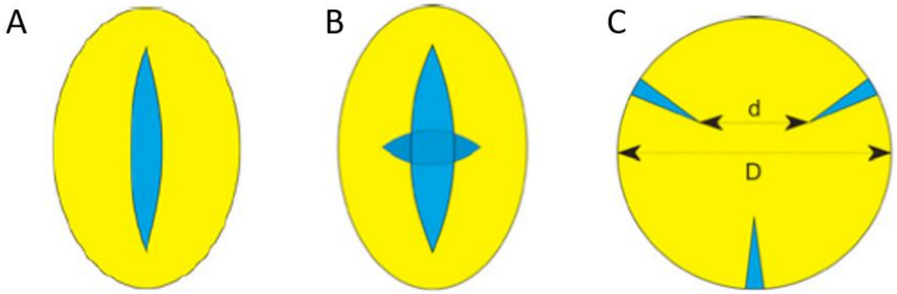

Figura 1.3: Esquematización de granos de polen colpado (A) y colporado (B), ambos en vista ecuatorial y colpado en vista polar (C). d: distancia entre colpos, D: Diámetro del Eje Ecuatorial (EE); tomado de Punt *et al.*, (2007)

Tabla 1.3: Índice apocólpico según Kremp, (1965).

d/D	Forma
0	Sin área polar
< 0.25	Área polar pequeña
0.25-0.50	Área polar media
0.50-0.75	Área polar grande
>0.75	Área polar muy grande

d: distancia entre colpos, D: Diámetro Ecuatorial

La pared del grano de polen presenta dos capas: la exina compuesta de esporopolenina y la intina de celulosa. Desde el punto de vista taxonómico la que más peso tiene es la exina. La nomenclatura empleada en Microscopía Electrónica de Trasmisión (MET) es la ectexina, endexina así como la intina. Mientras que con Microscopía Óptica (MO) se identifican la sexina y exina (Punt *et al.*, 2007; Fig. 1.4). Atendiendo a la ultraestructura de la exina, la ectexina está compuesta por: elementos de la escultura, tectum, columela y la capa basal; la endexina es una capa independiente. Cuando se utiliza MO se emplean los términos sexina y nexina (Fig. 1.4).

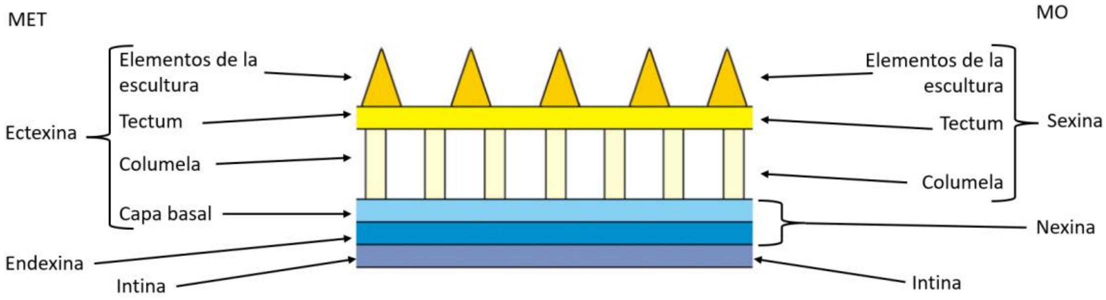

Figura 1.4: Estructura de la pared de grano de polen y sistemas de nomenclatura para describir la exina según el tipo de microscopía utilizada. MET: microscopio electrónico de transmisión; MO: microscopio óptico. Tomado de Punt *et al.*, (2007)

3.5.3. Estudios melisopalinológicos en meliponinos de México

Los estudios melisopalinológicos en México comenzaron en la década de 1980, enfocados en *A. mellifera* en regiones tropicales (Cárdenas-Chávez, 1985; Lobreau-Callen y Callen, 1982; Villanueva-Gutiérrez, 1984). Mientras que, el primer estudio melisopalinológico en el que se incluyen abejas sin aguijón fue de Roldán-Ramos, (1985) donde hace un análisis polínico de mieles de *A. mellifera* y *M. beecheii* en Yucatán. Pero no es hasta la década de 1990 que las investigaciones relacionadas con los granos de polen contenidos en el alimento de las abejas nativas sin aguijón comienzan a despuntar. Dichos estudios han estado enfocados en el análisis de polen en la miel, en las cargas corbiculares y en las provisiones de cría de varias especies de meliponinos entre ellos: *Nannotrigona perilampoides, Plebeia sp., Scaptotrigona mexicana* y *Tetragonisca angustula* (Martínez-Hernández *et al.*, 1993; Ramírez-Arriaga, 1989; Ramírez-Arriaga *et al.*, 1995). Además se ha trabajado en la caracterización palinológica anual de las provisiones de cría de *Scaptotrigona hellwegeri* (Quiroz-García *et al.*, 2011) y la miel de *Scaptotrigona mexicana* (Ramírez-Arriaga y Martínez-Hernández, 2007; Villamar, 2004). A ello se le añade el estudio de las reservas de polen en la colonia de *Melipona beecheii* (Quezada-Euán, 2018; Ramírez-Arriaga *et al.*, 2018; Villanueva-Gutiérrez *et al.*, 2018, Bacab-Pérez *et al.*, 2024) *Plebeia* sp. y *Scaptotrigona mexicana* (Ramírez-Arriaga *et al.*, 2018). Por último, se han realizado análisis de polen en propóleos y geopropóleos de *M. beecheii*, *Nannotrigona perilampoides*, *Plebeia frontalis*, *S. mexicana* y *S. pectoralis* (Ramírez-Arriaga *et al.*, 2024).

La melisopolinologia también se ha utilizado para comparar los hábitos de forrajeo de *A. mellifera* y Meliponinos (Martínez-Hernández *et al.*, 1993) encontrándose por ejemplo, mayor diversidad de recursos nectaríferos explotados por *Scaptotrigona mexicana* que por *Apis mellifera* (Ramírez-Arriaga y Martínez-Hernández, 2007). Además, se ha utilizado para describir las estrategias de alimentación de abejas solitarias como *Centris inermis* (García y Chávez, 1999) y abejas de las orquídeas del género *Euglossa* (Ramírez-Arriaga y Martínez-Hernández, 1998; Villanueva-Gutierrez *et al.*, 2013).

Los estudios melisopalonológicos en meliponinos en México abarcan desde el centro del país en la sierra de Puebla (Ramírez-Arriaga y Martínez-Hernández, 2007; Villamar, 2004); la costa del Pacífico, en Chamela, Jalisco (Quiroz-García *et al.*, 2011); y sureste en Chiapas (Martínez-Hernández *et al.*, 1993), Campeche y Veracruz (Ramírez-Arriaga *et al.*, 2018), así como Yucatán (Quezada-Euán, 2018; Bacab-Pérez *et al.*, 2024; Ramírez-Arriaga *et al*., 2024) y Quintana Roo (Villanueva-Gutiérrez *et al.*, 2018).

3.5.4. Recursos florales como fuentes de polen para *M. beecheii* en la Península de Yucatán

El presente trabajo se enfoca en la flora polinífera que usa *M. beecheii* por su importancia para la nutrición de la colonia y por ser a la que menos se le ha prestado atención, debido al interés económico asociado a la flora melífera para la producción de miel. En este sentido, existe poca información sobre la flora polinífera que visita *M. beecheii* en la Península de Yucatán. Con este precedente, Villanueva-Gutiérrez *et al.* (2018) analizaron el pan de abeja en colonias *M. beecheii* en la Reserva de la Biosfera Sian Ka´an, Quintana Roo. En coincidencia con el acotamiento de *forrajeo*, estos autores reportan que *M. beecheii* usa solo una porción de las especies de plantas con flores a las que potencialmente tienen acceso en la región (68 de 850). Las familias de plantas más importantes en cuanto a la cantidad de granos de polen fueron Fabaceae, Solanaceae, Burseraceae, Myrtaceae, Bixaceae. Mientras que, dentro de estas familias, el mayor volumen de polen lo aportaron *Bursera simaruba (L.) Sarg., Gliricidia sepium* (Jacq.) Kunth, y *Metopium brownei (Jacq.) Urb.* y especies de los géneros *Solanum* y *Senna*. Sin embargo, la disponibilidad de polen no es homogénea a lo largo del año ya que en Quintana Roo, la cantidad de polen almacenado en las colonias de *M. beecheii* alcanza el máximo en el mes de febrero y el mínimo en agosto-octubre (Di Trani y

Villanueva-Gutiérrez 2018). Lo cual contrasta con que los mayores volúmenes de miel almacenada ocurren en abril, pero los menores en febrero.

Para el estado de Yucatán Quezada-Euán (2018) reporta la identificación de 24 especies de plantas visitadas por esta especie de abeja aunque no incluye valores de abundancia de los granos de polen. Mientras que, más recientemente Bacab-Pérez *et al.* (2024) analizaron palinológicamente 25 muestras de miel y 25 muestras de pan de abeja de colonias provenientes de 8 meliponarios. Estos autores encontraron 21 taxones pertenecientes a ocho familias botánicas en las muestras de pan de abeja, mientras que, en las muestras de miel registraron 32 tipos de polen de 16 familias botánicas. En las muestras de pan de abeja el principal aporte polínico provino de *Senna racemosa* (Mill.) H.S. Irwin & Barneby var. *racemosa, Bursera schlechtendalii* Engl.*, Brusera simaruba* (L.) Sarg. y *Cochlospermun vitifolium* (Willd.) Spreng.; mientras que en las muestras de miel las especies nectaríferas más importantes fueron *Alternanthera ramosissima* (Mart.) Chodat & Hassl.*, Thrinax radiata* Lodd. ex Desf.*, B. simaruba, B. schlechtendalii, Leucaena leucocephala* var*. leucocephala* (Lam.) de Wit*, Lonchocarpus punctatus* Kunth*, Mimosa bahamensis* Benth.*, Waltheria rotundifolia* Schrank*, Psidium guajava* L.*, Thouinia paucidentata* Radlk. ex Millsp. y *Serjania triquetra* Radlk*.* En este último las colonias estaban ubicadas en vegetación secundaria de selvas baja y mendiana caducifolia.

Sobre las plantas poliníferas que visita *M. beecheii* en el estado de Campeche solo se conoce el trabajo de Ramírez-Arriaga *et al.* (2018). Estos autores encontraron polen perteneciente a 11 especies de plantas (cuatro familias), en muestras de pan de abeja colectado entre junio y septiembre de 2018. Según el aporte de granos de polen, las especies más importantes fueron *Solanum verbascifolium* L., *Physalis pubescens* L. y *Solanum lanceolatum* Ruiz & Pav.

Si se comparan los listados publicados para los tres estados de la Península de Yucatán se observa que la familia que más frecuentemente visitan estas abejas es Fabaceae. Mientras que las especies en común entre los tres estados peninsulares son: *Bursera simaruba, Caesalpinia gaumeri* Greenm.*, Gymnopodium floribundum* Rolfe*, Leucaena leucocephala* ssp*. leucocephala, Piscidia piscipula* (L.) Sarg.*, Viguiera dentata* (Cav.) Spreng.*, Cochlospermum vitifolium, Mimosa bahamensis, Thouinia* *paucidentata* y *Senna recemosa var. racemosa*. No obstante, debido a la relativa homogeneidad de las condiciones ambientales y la baja diversidad florística de la Península de Yucatán, es posible que existan más similitudes en los hábitos de forrajeo de *M. beecheii* en términos de especies de plantas poliníferas visitadas. Los diferentes diseños de trabajo en estas investigaciones dificultan hacer análisis precisos en cuanto a los hábitos de forrajeo de *M. beecheii* en la Península de Yucatán. Además, al no evaluar la vegetación circundante a los meliponarios, es limitada la información que brindan en cuanto a la disponibilidad y uso de fuentes de alimento a escala local.

PREGUNTAS DE INVESTIGACIÓN

1. ¿Cómo es la vegetación en los alrededores de los meliponarios de la Península de Yucatán y en qué estado de conservación se encuentran?
2. ¿Cómo se relacionan las características de la vegetación circundante a los meliponarios con el uso de recursos poliníferos en colonias de *M. beecheii* en la Península de Yucatán?

OBJETIVO GENERAL

Analizar las características de la vegetación contigua a los meliponarios de la Península de Yucatán, México y su relación con la diversidad polínica en el pan de abeja de *Melipona beecheii*.

OBJETIVOS ESPECÍFICOS

1. Caracterizar la diversidad y estructura de la vegetación circundante a meliponarios de la Península de Yucatán.
2. Identificar y cuantificar los morfotipos de granos de polen presentes en el pan de abejas de *Melipona beecheii* y estimar su frecuencia relativa en meliponarios de la Península de Yucatán.

3. Analizar la relación entre la disponibilidad y uso de recursos poliníferos en los meliponarios estudiados durante la temporada seca.

JUSTIFICACIÓN

Melipona beecheii es la especie de abeja sin aguijón más importante en la práctica de la meliponicultura en la Península de Yucatán. Sin embargo, en las últimas décadas los meliponicultores de la región han manifestado preocupación sobre la muerte de las colonias de *M. beecheii* por falta de alimento (Villanueva-Gutiérrez *et al.*, 2005). En este sentido, los recursos poliníferos revisten vital importancia ya que constituyen la principal fuente de proteínas y otros nutrientes necesarios para el desarrollo de la colonia. Paradójicamente existe poco conocimiento sobre la disponibilidad de recursos florales en los meliponarios y el uso que *M. beecheii* hace de estos.

Este trabajo tiene como propósito contribuir al conocimiento de las condiciones en las que viven las colonias de *M. beecheii* en la Península de Yucatán a partir de la evaluación de la vegetación aledaña a los meliponarios y el uso que las abejas hacen de la misma, específicamente de las plantas poliníferas. De ahí que esta investigación constituye un enfoque integral a la relación pan de abeja-vegetación atendiendo a la biología alimentaria. Los resultados de este trabajo contribuirán a entender el papel de la diversidad floral en la alimentación de *M. beecheii*. El estudio de las plantas visitadas para la recolección de polen será útil para futuros planes de reforestación o manejo de zonas selváticas, o incluso para que los propios meliponicultores planten en sus terrenos las especies de mayor importancia para *M. beechii* o abeja maya.

ESTRATEGIA EXPERIMENTAL

Para realizar esta investigación se seleccionaron 9 meliponarios en la Península de Yucatán distribuidos entre las tres principales formaciones vegetales de la región: selva baja caducifolia y selvas medianas subcaducifolias y sub-perennifolia. Durante la temporada seca (febrero a abril) de 2021 se hicieron las colectas de pan de abeja en tres colonias de *M. beecheii* por meliponario para un total de 29 muestras (se colectaron

4 muestras en dos meliponarios). Mientras que, durante la misma temporada, pero en 2022 y 2023, se hicieron las evaluaciones de la vegetación de los meliponarios con transectos aplicando el método de cuadrantes centrados en puntos. Cada transecto tuvo una longitud de 150 m con un punto de evaluación cada 10 m. Durante los transectos también se tomaron muestras de flores para facilitar la identificación de los granos de polen en el pan de abeja lo cual se hizo por análisis melisopalinológicos. En la Figura 1.5 se ilustra el esquema general de la estrategia experimental.

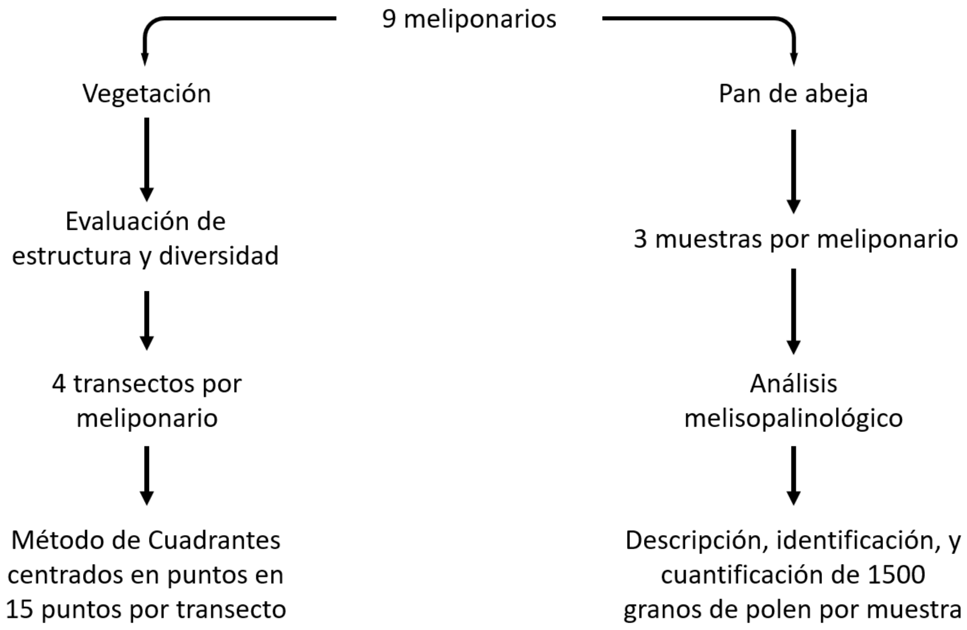

Figura 1.5: Estrategia experimental para el estudio de la vegetación y el pan de abeja de *Melipona beecheii* en meliponarios de la Península de Yucatán.

CAPÍTULO II

Diversidad, estructura y composición de la vegetación melífera y no melífera alrededor de meliponarios en la Península de Yucatán, México

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

Alejandro Pérez-Morfi, Alfredo Dorantes-Euan, Rosalina Rodríguez, Elia Ramírez-Arriaga, Juan Manuel Dupuy-Rada, Azucena Canto

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Resumen

Aunque la pérdida de colonias de *Melipona beecheii* en meliponarios (estructuras tipo choza) de la Península de Yucatán sugiere insuficientes plantas melíferas en floración en la vegetación circundante, existe un conocimiento limitado sobre las condiciones ecológicas de la vegetación. Por tanto, nos planteamos las siguientes preguntas ¿Cuál es la diversidad, estructura y composición de la vegetación melífera y no melífera que rodea los meliponarios tradicionales? ¿Cómo afectan estos componentes a la disponibilidad de fuentes de alimento para las abejas? Para responder estas preguntas se estudió la vegetación circundante de nueve meliponarios, tres en cada estado político de la Península de Yucatán, abarcando los principales tipos de vegetación en los años 2022 y 2023. En cada meliponario se trazaron cuatro transectos de 150-metros con el método de cuadrantes centrados en puntos en cada meliponario para estimar la composición de especies de plantas, la disponibilidad de plantas melíferas y con flores (índice de valor de importancia -IVI), parámetros de diversidad (números de Hill) y estructura vertical (estratos) y horizontal (densidad de árboles y diámetros). En general se registraron 268 especies, 262 géneros y 73 familias de plantas. En cinco meliponarios, las plantas melíferas en flor representaron menos del 9% del IVI, y un meliponario no tuvo especies floreciendo. La mayor diversidad de plantas se registró en un meliponario rodeado de selva mediana subperennifolia. La altura promedio de los árboles en el estrato alto fue 5.5 (DE ± 2,9) metros y la densidad promedio de árboles fue 3,390 (DE ± 2.702) árboles por hectárea en todos los tipos de vegetación. El DAP de los árboles fue menor en los meliponarios ubicados en la selva mediana subcaducifolia. Los meliponarios se encuentran rodeados de vegetación secundaria joven con alta densidad de árboles pequeños y predominio del estrato bajo. Encontramos vegetación con características similares entre los meliponarios, con escasas plantas melíferas en flor. La actividad humana parece afectar la diversidad de plantas y la disponibilidad de alimento para *M. beecheii*.

4.1. INTRODUCTION

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, 2018a). 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 (Flores-Guido and Vermont-Ricalde, 2011; Villanueva, 1994). 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.*, 2009, 1999). 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 m to 10 m in the former and 10 m to 18 m in the latter; most trees in both forest types, shed their leaves during the dry season (Durán and 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 m to 25 m in height, and a higher species richness compared to the other forest types of the Yucatan Peninsula (Duno-de Stefano *et al.*, 2018; Durán and Olmsted, 1999; Flores and Espejel, 1994). 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 and Vermont-Ricalde, 2011), is influenced by the structure of ecosystems (Beekman and Ratnieks, 2000; Steffan-Dewenter *et al.*, 2002; Steffan-Dewenter and 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 (González-Acereto *et al.*, 2006; Quezada-Euán *et al.*, 2015; Villanueva-Gutiérrez *et al.*, 2005). 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 (Duran-García and García-Contreras, 2010; Sánchez-Aguilar and Rebollar-Domínguez, 1999), 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.

4.2. MATERIALS Y METHODS

4.2.1. 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 2.1). 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 forests; two of these also include rainfed agriculture (Yaxché and Chanchén Palmar) and the third, cultivated pastures (San Juan de Dios; see Anexo I for detailed maps of each meliponary).

In general, meliponaries are structures with wooden columns and a palm roof (Figure 2.2A). 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.

4.2.2. 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 and, therefore, when the largest amount of nectar and pollen is collected and accumulated in *M. beecheii* colonies (Di Trani and 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, 2018).

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 so as 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 2.2 B-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 and 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 2.2 B). 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 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.

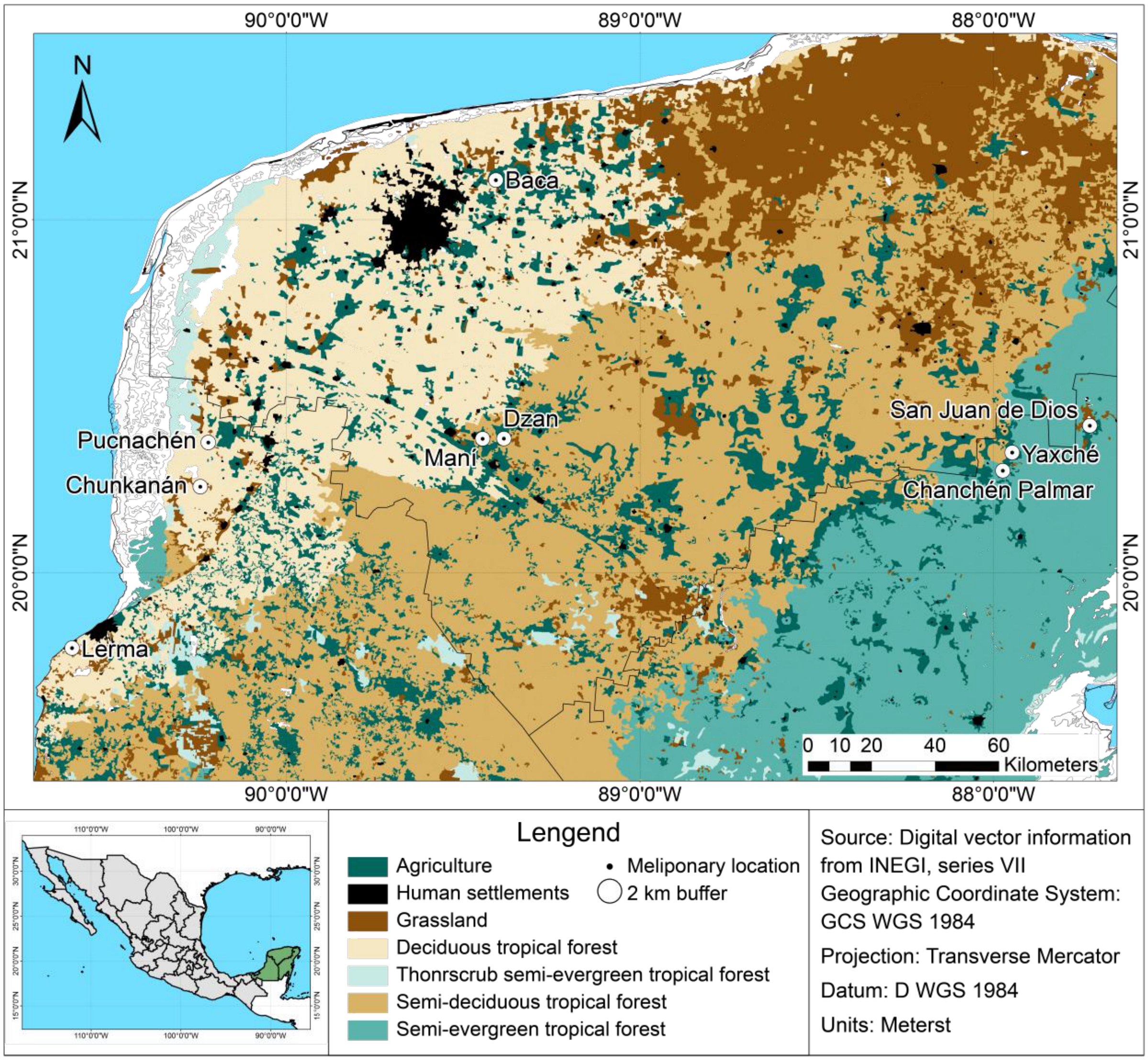

Figure 2.1. Map showing the locations of the nine meliponaries studied in the Yucatan Peninsula, Mexico, three in each sociopolitical state (Campeche, Yucatan, and Quintana Roo).

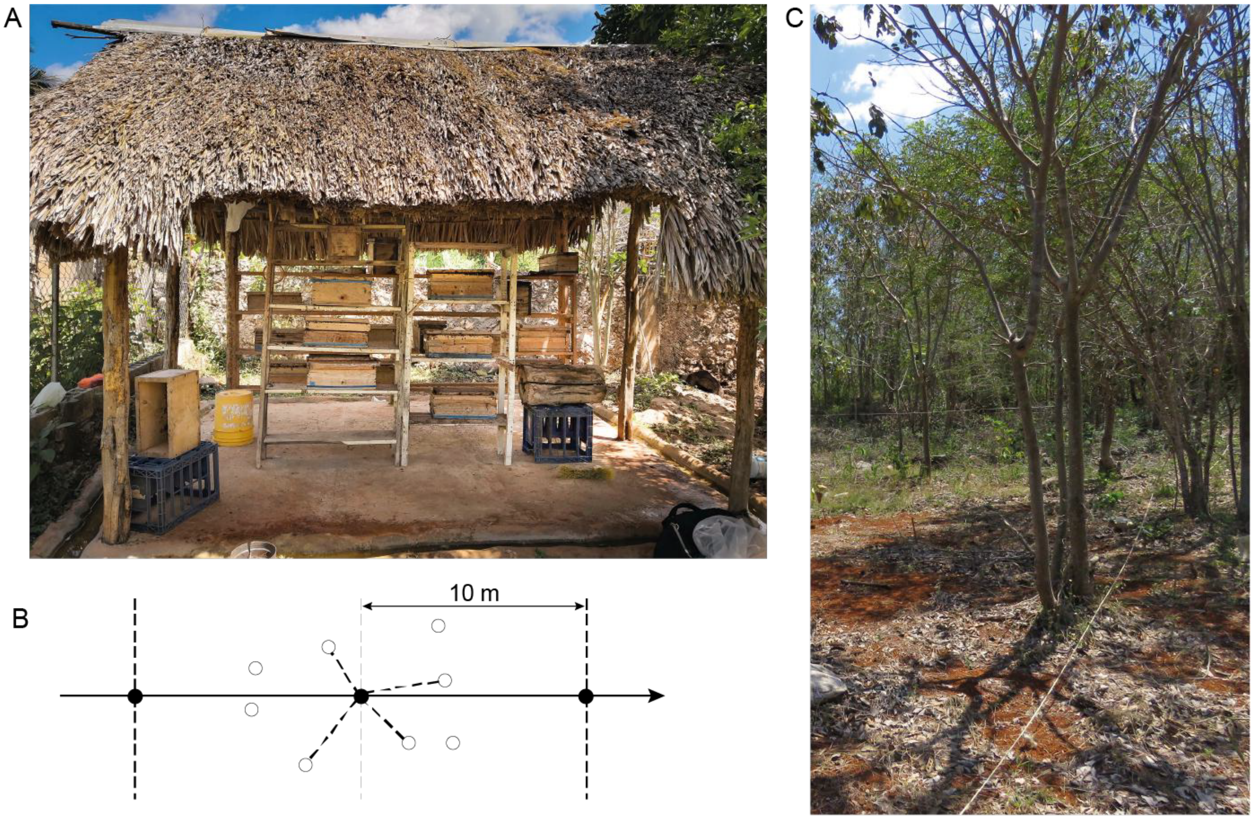

Figure 2.2. (A) A typical traditional meliponary that is frequently used in the Yucatan Peninsula, Mexico. This shack-like structure is a small bee house that serves as a home to the Mayan bee *Melipona beecheii* colonies. Most colonies are contained in rectangular wooden hives, while only a few are 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.

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.

4.2.3. Statistical analysis

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 and 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.*, 2010b; Flores-Guido and Vermont-Ricalde, 2011; Quezada-Euán, 2018a; Ramírez-Arriaga *et al.*, 2018; Villanueva-Gutiérrez *et al.*, 2018). From these studies, 114 melliferous species were identified (Anexo II). 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 and 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

Three 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 m 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 and Vermont-Ricalde, 2011), the High stratum was further divided into three height categories: High1: 2 m - 10 m, High2: 10 m - 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.

4.3. RESULTS

4.3.1. Species composition and diversity

A total of 2153 individuals were recorded in the 36 transects studied, of which 2008 individuals were identified at the species level (93%), 119 at the genus level, and 26 at the family level. This resulted in 268 species, 262 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 2.1)

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 2.1). 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* L. (Malvaceae) and *Tridax procumbens* L. (Asteraceae), present in five and four localities respectively. *Croton humilis* L. (Euphorbiaceae), *Jacquemontia nodiflora* G.Don. (Convolvulaceae), *Piscidia piscipula* (L.) Sarg. (Fabaceae), *Senna racemosa* H.S. Irwin & Barneby var. *racemosa* (Fabaceae), and *Viguiera dentata* (Cav.) Spreng. (Asteraceae), were all present in two localities. The remaining 13 blooming melliferous species were recorded in a single locality.

Table 2.1: 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 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

Yuc = Yucatán, Camp = Campeche, and Q. Roo = Quintana Roo

4.3.2. 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 2.3). 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 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 fact, in the meliponary localities of Yaxché and Chunkanán, the IVI of the blooming melliferous species was 0 % and 0.75 %, respectively (Figure 2.3). In the remaining localities, the IVI did not exceed 15 %, except in the meliponary locality of Dzan (32.4 %), where *C. sinensis* was again the main blooming melliferous species. The other blooming melliferous species that stood out were *Piscidia piscipula* (6.5 %), *Tridax procumbens* (5.82 %), and *Senna 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 Anexo II)

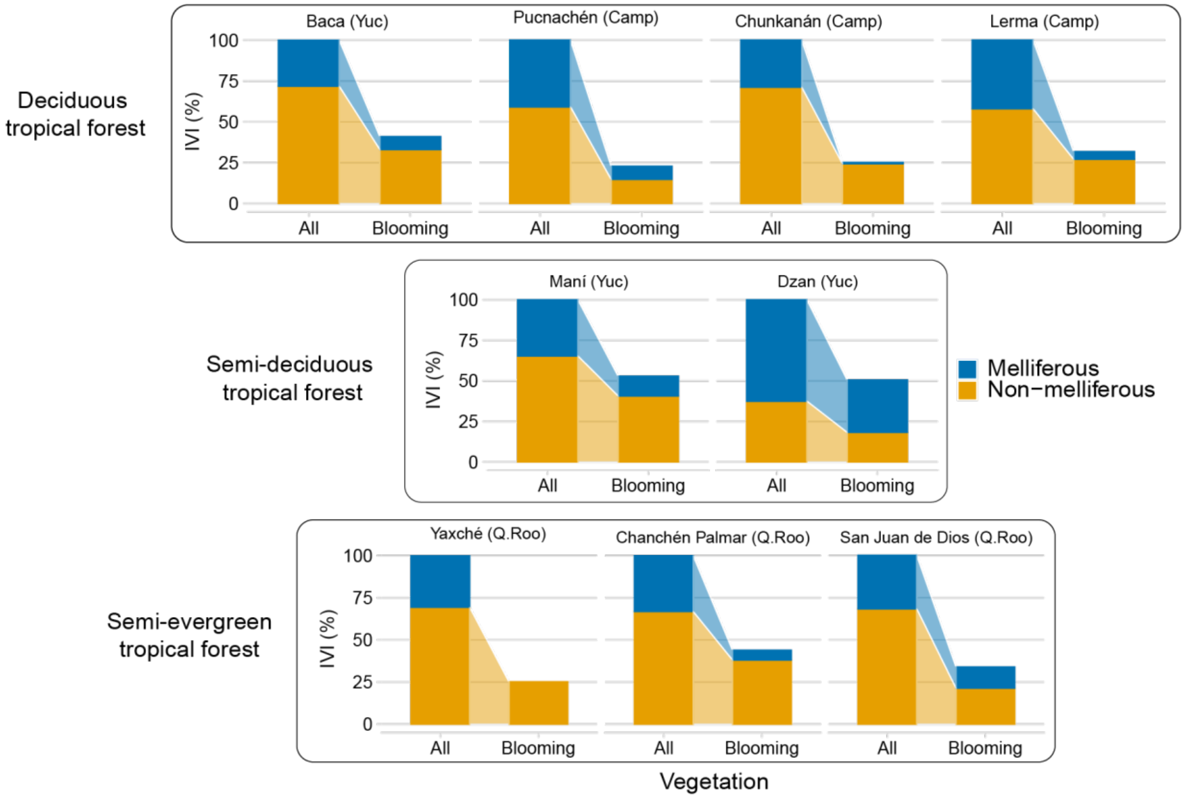

Figure 2.3: Representation of blooming melliferous and non-melliferous species in the Importance Value Index (IVI) of the plant community surrounding nine meliponaries in the three socio-political states (Yuc = Yucatán, Camp = Campeche, and Q. Roo = Quintana Roo)

and in the context of 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).

4.3.3. Species richness and diversity indices

The overall sampling coverage obtained 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 2.4A). 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 2.4B). 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 2.4B). 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 2.4B). 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.

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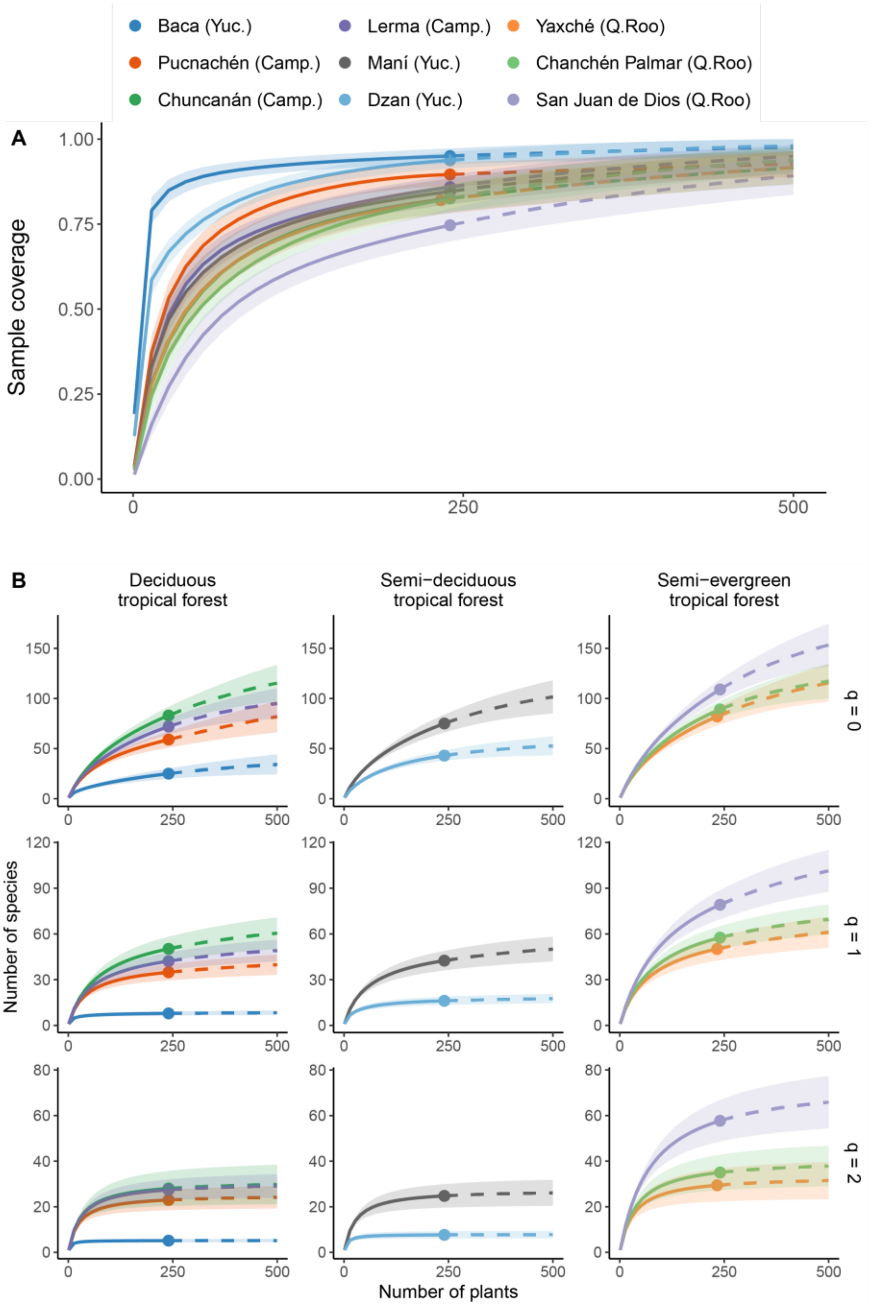


Figura 2.4: Diversity parameters based on the Hill numbers and species accumulation curves for plant communities of vegetation surrounding nine meliponaries on the Yucatan Peninsula. Data are presented by socio-political state (Yuc = Yucatán, Camp = Campeche, and Q. Roo = Quintana Roo) and by type of 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.

4.3.4. Vertical structure of vegetation

In total, 118 taxa of herbaceous plants, 51 shrubs, 107 trees, 28 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 2.5). 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).

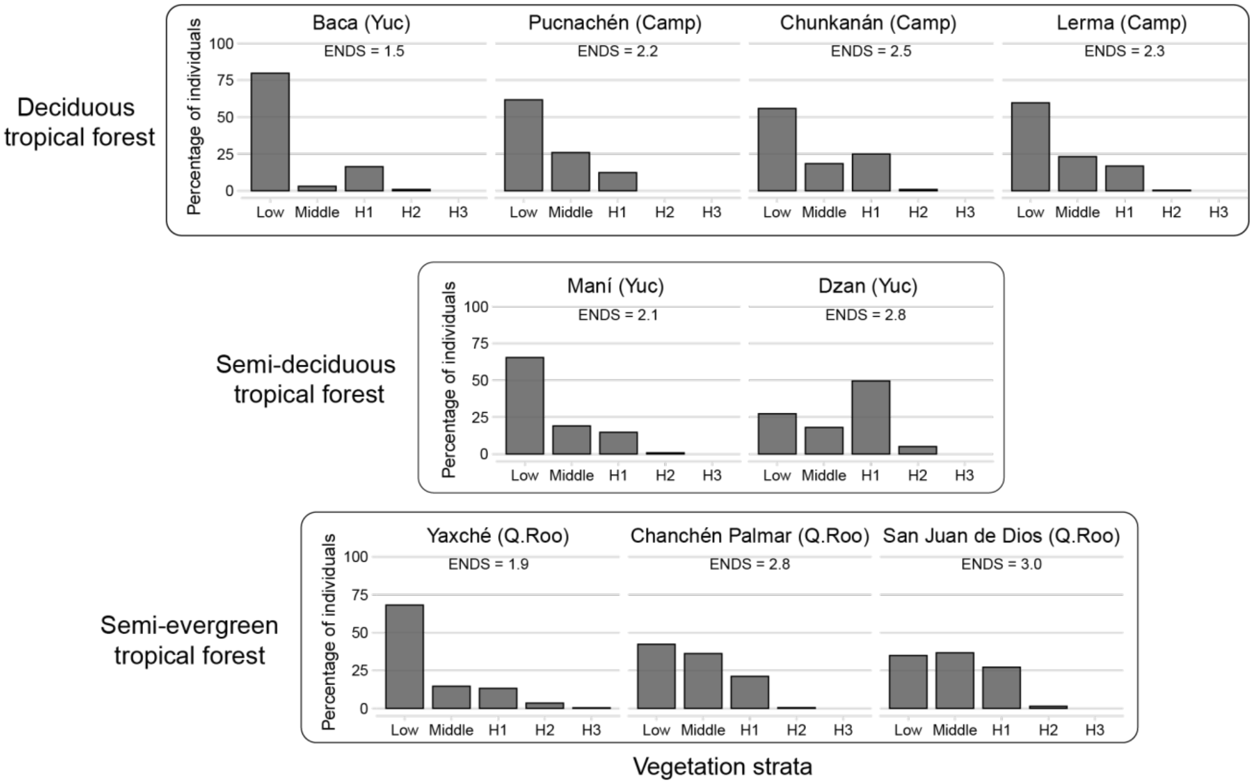


Figura 2.5: Percentage of plants in each vertical stratum in the vegetation surrounding nine meliponaries in the Yucatan Peninsula. Data are presented by socio-political state (Yuc = Yucatán, Camp = Campeche, and Q. Roo = Quintana Roo) and by type of vegetation. The High stratum category was subdivided 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.

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 2.5). 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* L. (Asteraceae), a non-melliferous plant, with a total of 90 plants. No melliferous species reached this abundance in this stratum (Table 2.2). In fact, the most abundant melliferous species in the Low stratum never exceeded 30 individuals. Among them, *Tridax procumbens* had 28 plants in Maní and *Waltheria indica* had 21 in Pucnachén. In addition, these two were the most common melliferous species, recorded in two meliponaries each. At the opposite end, in the meliponary locality of Baca, no melliferous species were found in the Low stratum (Table 2.2). 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 *Piscidia 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 *Citrus sinensis*, with 32 individuals, all in the vegetation of the Dzan meliponary (Table 2.2). 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 2.2). For the other species, the number of plants did not exceed 10 individuals, except for *Senna atomaria*, with 11 individuals in Baca.

4.3.5. 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 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 2.3).

Regarding tree density in meliponaries, a global average of 4496 (± 4089) 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 ± 4344) and 8724 (SD ± 3400) 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 2.3). The global mean for the basal area of trees in the vegetation surrounding meliponaries was 23.4 (± SD 21.2) m^2/ha.

Table 2.2. 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)
	Pucnanchén (Camp.)	*Waltheria indica* (21)	*Gymnopodium floribundum* (6) *Mimosa bahamensis* (6)	*Gymnopodium floribundum* (7)
	Chuncanán (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 sinensis* (6)
	Dzan (Yuc.)	*Piscidia piscipula* (8) *Waltheria indica* (8)	*Citrus 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 racemose* (8)

Table 2.3: Descriptive parameters (mean ± SD) of the horizontal structure of the vegetation around nine meliponaries of the Yucatan Peninsula. Differences in mean diameter at breast height (DBH) among meliponaries according to Dunn's test are presented in parentheses. Socio-political peninsular states: Yuc = Yucatán, Camp = Campeche, and Q. Roo = Quintana Roo. Different letters in parentheses indicate significant differences 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
	Pucnanchén (Camp)	6.33 ± 2.64 (ac)	2039 ± 503	8.1 ± 4.1
	Chuncanán (Camp)	8.8 ± 5.33 (ac)	5922 ± 6093	27 ± 10.5
	Lerma (Camp)	5.25 ± 2.55 (c)	9931 ± 4344	30.8 ± 21.6
Semi-deciduous tropical forest	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

4.4. 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 and 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 *Parthenium hysterophorus* or *Tridax procumbens*, as well as widely distributed species, such as *Piscidia piscipula* and *Cedrela 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.

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 Guido *et al.*, 2010; Flores and Espejel, 1994). 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 *Citrus 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 4496 (± 4089) trees/ha. These values are characteristic of young secondary vegetation, which has high densities of small trees (Denslow and Guzman, 2000; Guariguata and Ostertag, 2001). Similarly, in Puerto Rico, Aide *et al.*, (1996) reported tree heights of up to 5 m and a density of 4000 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 1500 trees/ha in the same successional age range. Furthermore, considering compositional characteristics, we observed the presence of *Gymnopodium floribundum, Metopium 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 and 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 and 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 *Citrus sinensis*. If *C. sinensis* were excluded from Dzan meliponary, the IVI of melliferous plants around it would be similar to values observed in other meliponaries (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 *Gymnopodium floribundum, Piscidia piscipula, Viguiera dentata, Lysiloma latisiliquum*, and *Bursera 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.*, 2010b; Flores-Guido and Vermont-Ricalde, 2011) and are widely represented in the forests of the Yucatan Peninsula (Miranda and Hernández-X., 2014, 1963; Rzedowski and 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: 1120 m in *M. subnitida* (Silva *et al.*, 2014), 1800 m in *M. mandacaia* (Kuhn-Neto *et al.*, 2009), and 2470 m in *M. 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 (Duno-de Stefano *et al.*, 2018; Flores and Espejel, 1994), 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.

4.5. ACKNOWLEDGMENTS

This research was funded by a CONAHCYT PhD scholarship (775415) and a CONAHCYT project grant (316771). We would like to express our gratitude to the Melipona beekeepers who provided valuable assistance from each state in the Yucatan Peninsula. Special thanks to Fátima Castillo Torres, María Cruz Torres, Diego Garza, and Rafael Dard from Yucatan; Stephane Palmieri, Patricio Tamay, Marcos Canché Ku, and Isabel May from Quintana Roo; and Luis Carrillo, Claudio Carrillo, Jorge Ramírez, and Pablo Hernández (ECOSUR), and Lucio Pat Fernández (ECOSUR), and Froylán Martínez (Technological Institute of Chiná) from Campeche.

Capítulo III

La importancia de la vegetación en la meliponicultura maya: un estudio de caso sobre las preferencias de alimentación por polen de *Melipona beecheii*

The Importance of Vegetation on Mayan Meliponiculture: A Case Study on the Pollen Foraging Preferences of *Melipona beecheii*

Manuscrito para someter en la revista *Apidologie*

Resumen

Melipona beecheii is the primary species used for meliponiculture in the Yucatan Peninsula. However, both the bees and meliponiculture are at risk due to deforestation and habitat disturbance. Although some studies have explored the food resources utilized by *M. beecheii* in the region, the relationship between these resources and the characteristics of the vegetation surrounding the meliponaries has not been examined. Consequently, we conducted a palynological study of pot-pollen from 29 colonies located across the three primary vegetation types of the Yucatan Peninsula. We analyzed our findings using existing descriptions of the meliponaries' vegetation. Approximately 1,500 pollen grains were counted per sample, comprising 69 pollen morphotypes. We identified 40 species, 45 genera, and 27 plant families, with Fabaceae and tree plants predominating. In general, similarities in pollen richness, the number of effective and dominant species were noted among the meliponaries in different vegetation types. We also observed varied pollen composition among vegetation types and a significant positive correlation between plant richness and pot-pollen richness. This relationship did not extend to the number of effective or dominant species, however. No relationship was found between the relative abundance of plant pollen in pot-pollen and the absolute density or coverage of these plants in the vegetation surrounding the meliponaries. Our findings indicate that *M. beecheii* selectively favors pollen from a small group of tree species mainly from Fabaceae y Bixaceae, while maintaining a diverse diet, probably in order to ensure that the colony obtains all essential nutrients.

Palabras claves: palinología, *Melipona beecheii*, México, flora, polen

5.1. INTRODUCTION

In the Yucatan Peninsula, *Melipona beecheii* Bennett (Hymenoptera: Apidae) is the emblematic species for Mayan meliponiculture, the traditional practice of stingless beekeeping (González-Acereto, 2012). This ancestral practice is approaching resurgence in the Mayan community, both as an economic venture and as cultural heritage (González-Acereto *et al.*, 2006; López Barreto, 2021). However, meliponiculture in the region faces challenges arising from agricultural expansion, urban sprawl (Quezada-Euán *et al.*, 2015), and intensive deforestation (Duran-García and García-Contreras, 2010; Sánchez-Aguilar and Rebollar-Domínguez, 1999). Additionally, as meliponiculture is predominantly practiced on a small scale near human settlements, it is consequently often situated in areas with disturbed vegetation. These circumstances impose significant alterations upon the natural habitat of *M. beecheii*, which leads to constrained food resource availability and results in colony death due to insufficient food (Villanueva-Gutiérrez *et al.*, 2005). Some studies have addressed the food resources used by *M. beecheii* in the region (Bacab-Pérez *et al.*, 2024; Ramírez-Arriaga *et al.*, 2018; Villanueva-Gutiérrez *et al.*, 2018), yet the link between these resources and the characteristics of the vegetation has not been examined. In this regard, pollen resources are important because they are the primary source of protein for the colony. Pollen scarcity can impact bee body size and colony performance in meliponines (Veiga *et al.*, 2013, May-Itzá *et al.*, 2021).

Like other meliponines*, M. beecheii* displays generalist foraging strategies (Villanueva-Gutiérrez et al. 2018; May-Itzá et al. 2021), which allows the species to exploit a broad diversity of resources and adapt to resource scarcity or competition (Villanueva-Gutiérrez *et al.*, 2015), although the quality and quantity of floral pollen do influence the bees' foraging preferences (Vaudo *et al.*, 2024). Perennial plants, for instance, seem more attractive to large and long-tongued bees such as meliponines, possibly because the perennials can allocate more resources to reproduction than annual plants and consequently offer more attractive rewards to the bees (Corbet, 1995; Parrish and Bazzaz, 1979). In addition, the foraging behavior of meliponines appears to be taxonomically influenced, because the families with the highest species richness in the neotropics (e.g. Asteraceae, Euphorbiaceae, Lamiaceae, Fabaceae, and Solanaceae) are also the most consistent sources of pollen and nectar from southern Mexico to southern Brazil (Ramalho *et al.*, 1990). In the Yucatan Peninsula, the most diverse plant families are Fabaceae (236 species), Poaceae (216 species), and Asteraceae (147 species) (Carnevali Fernández-Concha et al., 2010). Poaceae species exhibit wind pollination within the three plant families while bees typically favor Fabaceae pollen due to its elevated protein content (Ghosh *et al.*, 2020; Vaudo *et al.*, 2024). The Fabaceae family has been previously identified as the predominant family in *M. beecheii* pot-pollen in the state of Quintana Roo, on the Yucatan Peninsula (Villanueva-Gutiérrez *et al.*, 2018), while a study conducted in Campeche indicates that the Solanaceae family is the main source of pollen in *M. beecheii* pot-pollen in that region (Ramírez-Arriaga *et al.*, 2018). Differences in the design of these studies and the periods considered make it difficult to analyze the foraging patterns of *M. beecheii* on the peninsula.

The Fabaceae family also sheds light upon another important characteristic of the vegetation from the Yucatan Peninsula: the presence of common species among the different regions (Duno de Stefano *et al.*, 2012). The vegetation on the peninsula is greatly influenced by precipitation, resulting in greater plant diversity and taller vegetation in the southern areas (Durán and Olmsted, 1999; Duno-de Stefano *et al.*, 2018;). However, low orographic complexity, shallow soils with limestone outcrops, and the absence of rivers act as forces of selection that shape plant species diversity, with a general physiographic uniformity extending this tendency throughout the region. Thus, many common floristic elements may be visited by bees among the predominant types of tropical dry forests found on the peninsula, including deciduous, semi-deciduous, and semi-evergreen tropical forests (Flores and Espejel, 1994; Duno-de Stefano *et al.*, 2018; Pérez-Morfi *et al.*, 2024). At any rate, no large-scale research involving different vegetation types has been conducted in order to determine their influence on *M. beecheii* foraging.

On a local scale, since meliponiculture is a backyard activity, food availability for *M. beecheii* is influenced by human activities; vegetation structure and diversity are adversely affected in rural areas near human settlements (Banda *et al.*, 2006; Jamil *et* *al.*, 2022). In a previous investigation, we found that the vegetation surrounding nine meliponaries on the Yucatan Peninsula is characterized by young secondary vegetation and the dominance of the lower stratum (Pérez-Morfi et al., 2024a). Additionally, although we documented 268 plant species across all meliponaries, a deficiency of melliferous species—defined as plants offering nectar or pollen—was evident at all sites (Pérez-Morfi et al., 2024a). To cope with scarcity, social bees adapt through morphological changes (Veiga *et al.*, 2013) or by modulating fly span (Pope and Jha, 2018) to increase nectar and pollen collection. Maintaining pollen diversity is key for colony survival since no single pollen type can provide all the necessary nutrients. However, the specific trophic requirements of wild bees, especially native species, are not fully understood and may differ from those of honey bees (Leach and Drummond, 2018). Native bees exhibit some flexibility in foraging on exotic plants (Brown *et al.*, 2024), but the overall health and development of bees is influenced by the nutritional quality of pollen (Di Pasquale *et al.*, 2016, 2013; Schwarz *et al.*, 2024). Landscape composition plays a role in the availability of diverse pollen sources (Melin *et al.*, 2020), and conservation strategies should consider the habitat needs of native bees (Patrício-Roberto and Campos, 2014; Winfree, 2010). Understanding the foraging behavior and pollen diet of native bees is essential for identifying appropriate plant species that meet their food needs and support their conservation (Sentil *et al.*, 2022).

With our previous description of the vegetation as a guiding perspective (Pérez-Morfi et al., 2024a), we analyzed *M. beecheii* pot-pollen and vegetation characteristics at nine meliponaries on the Yucatan Peninsula. Both data sets (vegetation and pot-pollen) were collected during the dry season because that is when the maximum volume of pollen storage in *M. beecheii* colonies occurs in the region (Di Trani and Villanueva-Gutiérrez, 2018). We used these datasets to explore two questions related to *M. beecheii* foraging and the effect of vegetation characteristics on this behavior: 1. Does *M. beecheii* display a preference for some pollen types in its foraging? 2. What is the relationship between vegetation in the vicinity of the meliponaries and the foraging behavior of *M. beecheii*? This work aims to document the plant diversity of interest in the collection of pollen resources for *M. beecheii* on the Yucatan Peninsula.

5.2. MATERIALS Y METHODS

5.2.1. Pot-pollen collection, processing, and identification

We collected *Melipona beecheii* pot-pollen samples from nine meliponaries situated in municipalities across the main types of dry forest vegetation on the Yucatan Peninsula, encompassing its three socio-political states (Figure 3.1). In addition to native dry forests, the areas surrounding the meliponaries included human settlements, grasslands, and agricultural land. Samples were collected between February 22 and May 10, 2021, with three samples collected from seven of the meliponaries and four from those in Mani and Yaxché. Each sample comprised the entire pot-pollen content of one pot, which was placed into 20 ml tubes. A 100 mg aliquot was taken from each tube and subsequently acetolyzed (Erdtman, 1960). Four permanent slides with glycerinated gelatin were prepared from each sample, then recorded and incorporated into the collection of the Paleopalynology Laboratory at the Institute of Geology of the National Autonomous University of Mexico (UNAM).

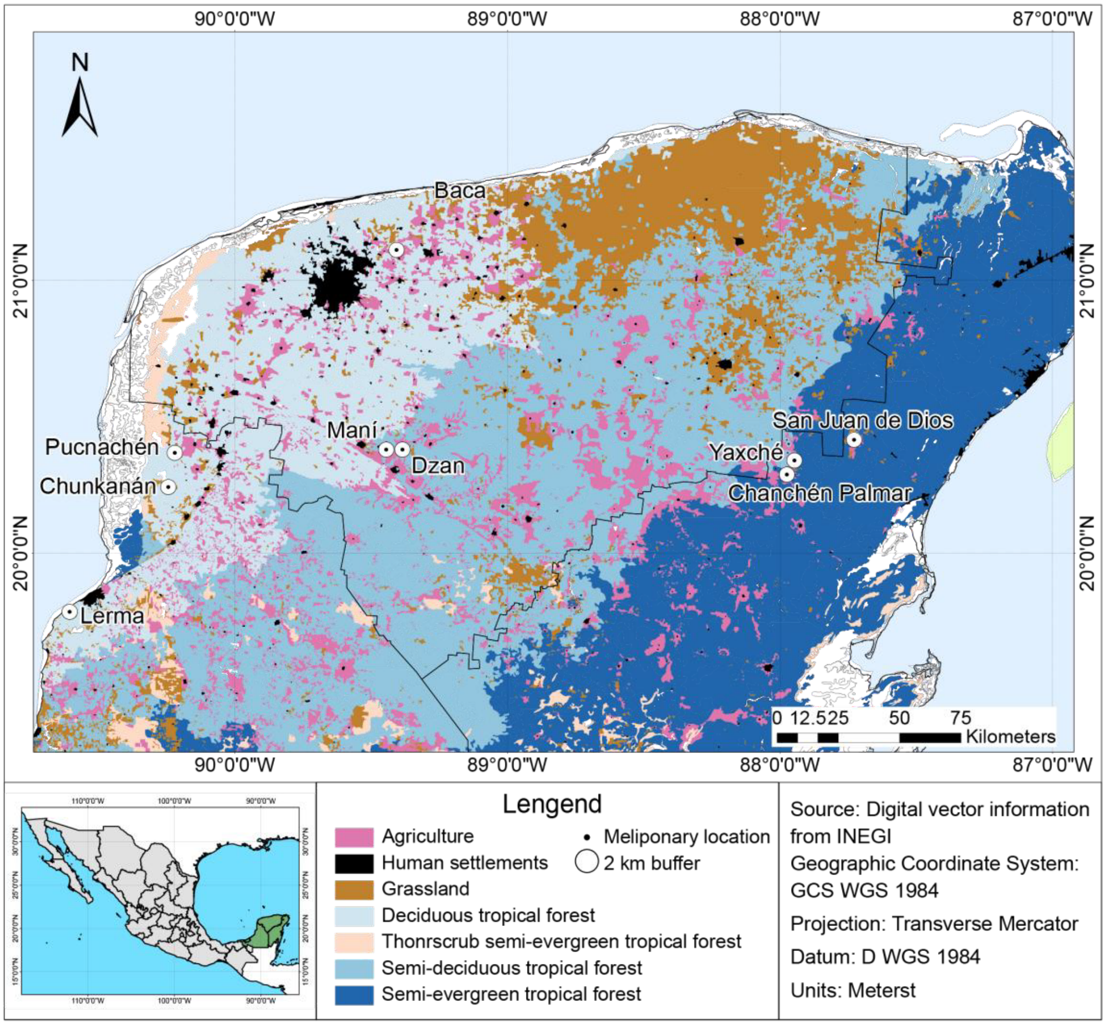


Figure 3.1: Location of the nine meliponaries sampled in the Yucatan Peninsula. Modified from (Pérez-Morfi et al. 2024).

Palynological descriptions were produced using a Zeiss Axiolab optical microscope (100x objective), considering the morphological characters of 15 pollen grains per morphotype following standard nomenclature (Punt *et al.*, 2007). We identified pollen morphotypes to the lowest taxonomic level possible using information reported in the literature for the region (Palacios-Chávez *et al.*, 1991; Martínez-Hernández *et al.*, 1993; Alfaro-Bates *et al.*, 2010a), as well as the palynological reference collection of the Institute of Geology at the UNAM. Once the pollen types present in each sample were differentiated, we conducted three random transects on the fixed preparations, each of approximately 500 pollen grains, to quantify the abundance of the detected morphotypes/taxa (Louveaux *et al.*, 1978).

Data analysis

5.2.2. Botanical composition and diversity of pot-pollen

We analyzed the botanical composition of the pot-pollen by considering all the taxonomic groups identified through palynological analysis. The growth form of the morphotypes identified at the species or genus level was determined using the website of the Herbarium of the Center for Scientific Research of Yucatan (CICY). This allowed us to calculate the relative abundances of the plant families and growth forms visited by *M. beecheii*. From these relative abundances, we identified the pollen grains most frequently collected (>16%) by bees per sample and per meliponary (Louveaux *et al.*, 1978). The results were illustrated in a heat map created with the R package "*tidyHeatmap*" (Mangiola and Papenfuss, 2020).

To evaluate *M. beecheii* pot-pollen diversity we estimated pot-pollen alpha diversity with Hill numbers (Hill, 1973) using the approximation proposed by Chao *et al.* (Chao *et al.*, 2014) and implemented in the "*iNEXT*" package (Hsieh *et al.*, 2016; R Core Team, 2023). This approach generalizes the sample-size-based (Colwell *et al.*, 2012) and coverage-based (Chao and Jost, 2012) approaches, to produce rarefaction-extrapolation curves of species based on Hill numbers. To assess the effectiveness of diversity estimations with our sampling effort, we estimated the sample coverage (Chao and Jost, 2012) based on the sample size. Subsequently, rarefaction-extrapolation curves based on sample size were generated to provide asymptotic estimators of diversity with 95% confidence intervals, constructed using a bootstrap method with 200 repetitions (Chao *et al.*, 2014). For both coverage and diversity curves, extrapolations were performed up to double the sample size reached per meliponary ($n \approx 4500$) (Chao *et al.*, 2014).

5.2.3. Vegetation and pot-pollen at the meliponaries

We compared the vegetation surrounding the meliponaries and the *M. beecheii* pot-pollen in terms of the relative abundance of species using vegetation data from Pérez-Morfi *et al.*, (2024). Based on these datasets, we constructed dissimilarity matrices using the Bray-Curtis index. The dissimilarity matrix was then visualized through a principal coordinate analysis (PCoA) using the "*cmdscale*" function from the "*vegan*" package (Dixon, 2003). To estimate and visualize species scores, we performed a PCA using the "*prcomp*" function from the "*stats*" package, applying it to Hellinger-transformed absolute abundance data. To compare differences in species relative abundance between foraged pollen and surrounding vegetation, we performed a permutational multivariate analysis of variance (PERMANOVA) with 1,000 permutations (Anderson, 2001).

5.2.4. Influence of vegetation characteristics on pollen resource utilization

We used a linear model to evaluate the effect of floristic diversity on palynological diversity, employing the Hill number diversity estimates (q = 0, 1, 2) with fixed coverage (Chao and Jost, 2012). For the floristic diversity in the vicinity of the meliponaries (Pérez-Morfi et al., 2024a), we based the fixed coverage (88.5%) on double the sampling effort of the site with the lowest coverage (San Juan de Dios, 74.6%) to estimate the diversity indices for the other meliponaries (Chao *et al.*, 2014). This was done using the "*estimateD*" function of the "*iNEXT*" package. For pot-pollen, we applied the common coverage of 99% for all meliponaries. Thus, the linear model used for the analysis was: q_i pollen diversity (99% coverage) ~ q_i vegetation diversity (88.5% coverage). Additionally, to evaluate the influence of the vegetation structural characteristics on *M. beecheii*'s foraging preferences, we ran linear models considering the log-transformed abundance of morphotypes identified at the species level and the corresponding log-transformed absolute density (trees/ha) and absolute coverage (m^2/ha) in the vegetation. The models were structured as follows: log (pollen abundance) ~ log (plant absolute density) and log (pollen abundance) ~ log (plant absolute coverage). Log transformations were applied to eliminate scale differences between variables.

5.3. Results

5.3.1. Botanical composition and diversity of pot-pollen

We performed a melissopalynological analysis of 29 pot-pollen samples, one per colony, distributed among nine meliponaries located in the three main vegetation types of the Yucatan Peninsula. In total, we counted 46,304 pollen grains, with a mean of 5,145 per meliponary and 1,597 per colony. We detected 69 pollen morphotypes comprising 40 at the species level, 18 at the genus level, 3 at the family level, and 8 unknowns. The identified pollen morphotypes included 27 families and 46 genera of plants, distributed among 34 trees, 9 shrubs, 16 herbs, and 2 climbers. Pollen from trees was not only the richest in species but also the most abundant in the pot-pollen of the *M. beecheii* colonies, accounting for over 67% of all pollen grains counted per meliponary and exceeding 89% in seven of them (Figure 3.2A).

In terms of abundance, the Fabaceae family notably represented between 52.5% and 95.5% of the pollen grains counted at six meliponaries (Figure 3.2B). However, in three meliponaries surrounded by deciduous tropical forest (Pucnachén, Lerma, and Chunkanán), the pot-pollen was characterized by a mix of pollen from Bixaceae with pollen from Fabaceae, Burseraceae, and Solanaceae. Considered with all families, again Fabaceae was salient, as it exhibited the highest richness with 19 taxa/morphotypes of pollen grains, followed by Solanaceae with seven and Malvaceae with four. Similarly, at the meliponary level, the Fabaceae family was the richest, presenting between seven and ten pollen morphotypes. It was matched only by the Solanaceae family at the meliponary in Lerma (deciduous tropical forest), which exhibited seven morphotypes (Anexo III).

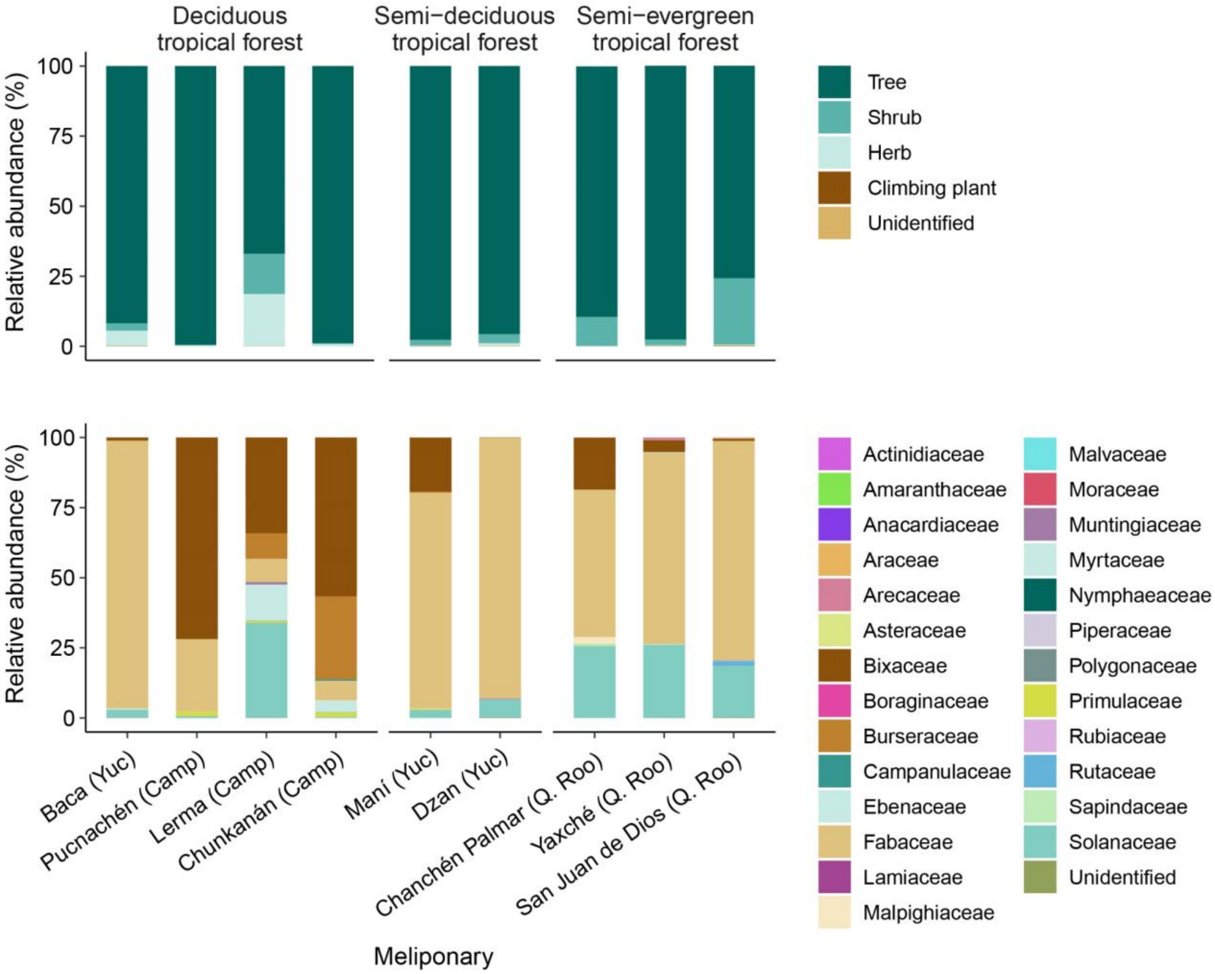
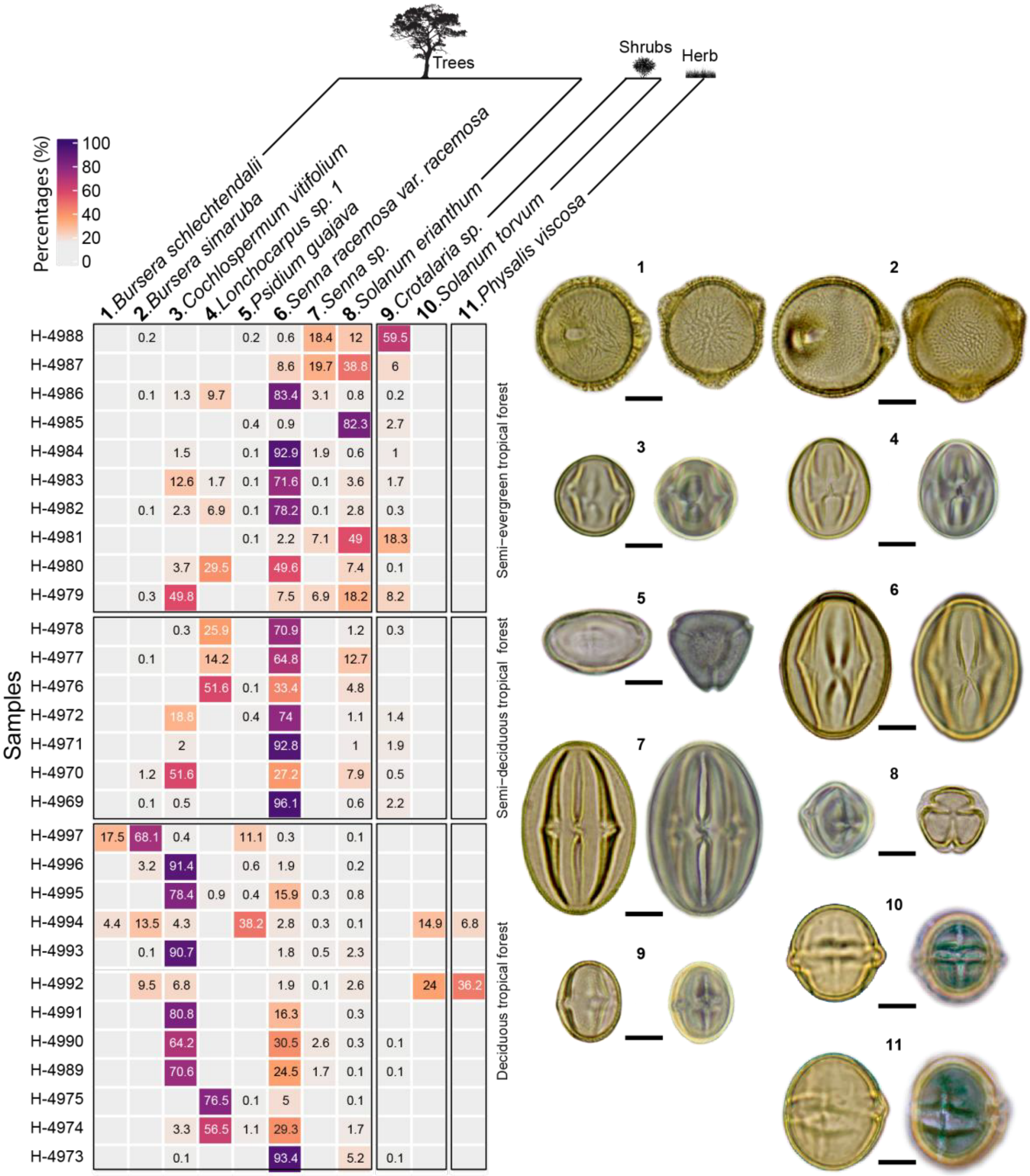


Figure 3.2. Percentage of pollen grains in the pot-pollen of *Melipona beecheii* from nine meliponaries in the Yucatan Peninsula, (*A*) by growth form of identified taxa and (*B*) by botanical family.

The strong representation of pollen from the Fabaceae and Bixaceae families was mainly due to the tree species *Senna racemosa* var. *racemosa* and *Choclospermum vitifolium* respectively. Pollen grains from these species were the most common and the most abundant among the 11 most abundant morphotypes, applying a threshold of 16% (Louveaux *et al.*, 1978) (Figure 3.3). However, the abundance of these two pollen species varied by vegetation type. *Senna racemosa* var. *racemosa* pollen grains were widespread and present at the meliponaries of all three vegetation types, though especially abundant in those located in semi-deciduous and semi-evergreen tropical forests. In contrast, *C. vitifolium* pollen was also present in every sample but was most prevalent in deciduous tropical forests.



Samples	1.Bursera schlechtendalii	2.Bursera simaruba	3.Cochlospermum vitifolium	4.Lonchocarpus sp. 1	5.Psidium guajava	6.Senna racemosa var. racemosa	7.Senna sp.	8.Solanum erianthum	9.Crotalaria sp.	10.Solanum torvum	11.Physalis viscosa
H-4988		0.2			0.2	0.6	18.4	12	59.5		
H-4987						8.6	19.7	38.8	6		
H-4986		0.1	1.3	9.7		83.4	3.1	0.8	0.2		
H-4985					0.4	0.9		82.3	2.7		
H-4984			1.5		0.1	92.9	1.9	0.6	1		
H-4983			12.6	1.7	0.1	71.6	0.1	3.6	1.7		
H-4982		0.1	2.3	6.9	0.1	78.2	0.1	2.8	0.3		
H-4981					0.1	2.2	7.1	49	18.3		
H-4980			3.7	29.5		49.6		7.4	0.1		
H-4979		0.3	49.8			7.5	6.9	18.2	8.2		
H-4978			0.3	25.9		70.9		1.2	0.3		
H-4977		0.1		14.2		64.8		12.7			
H-4976				51.6	0.1	33.4		4.8			
H-4972			18.8		0.4	74		1.1	1.4		
H-4971			2			92.8		1	1.9		
H-4970		1.2	51.6			27.2		7.9	0.5		
H-4969		0.1	0.5			96.1		0.6	2.2		
H-4997	17.5	68.1	0.4		11.1	0.3		0.1			
H-4996		3.2	91.4		0.6	1.9		0.2			
H-4995			78.4	0.9	0.4	15.9	0.3	0.8			
H-4994	4.4	13.5	4.3		38.2	2.8	0.3	0.1		14.9	6.8
H-4993		0.1	90.7			1.8	0.5	2.3			
H-4992		9.5	6.8			1.9	0.1	2.6		24	36.2
H-4991			80.8			16.3		0.3			
H-4990			64.2			30.5	2.6	0.3	0.1		
H-4989			70.6			24.5	1.7	0.1	0.1		
H-4975				76.5	0.1	5		0.1			
H-4974			3.3	56.5	1.1	29.3		1.7			
H-4973			0.1			93.4		5.2	0.1		

Figure 3.3. Relative abundance per sample of the 11 most abundant pollen grains (>16%) in *Melipona beecheii* pot-pollen from nine meliponaries located in the three main vegetation types of the Yucatan Peninsula. Pollen grains are grouped according to plant growth form. The numbers indicate the corresponding species.

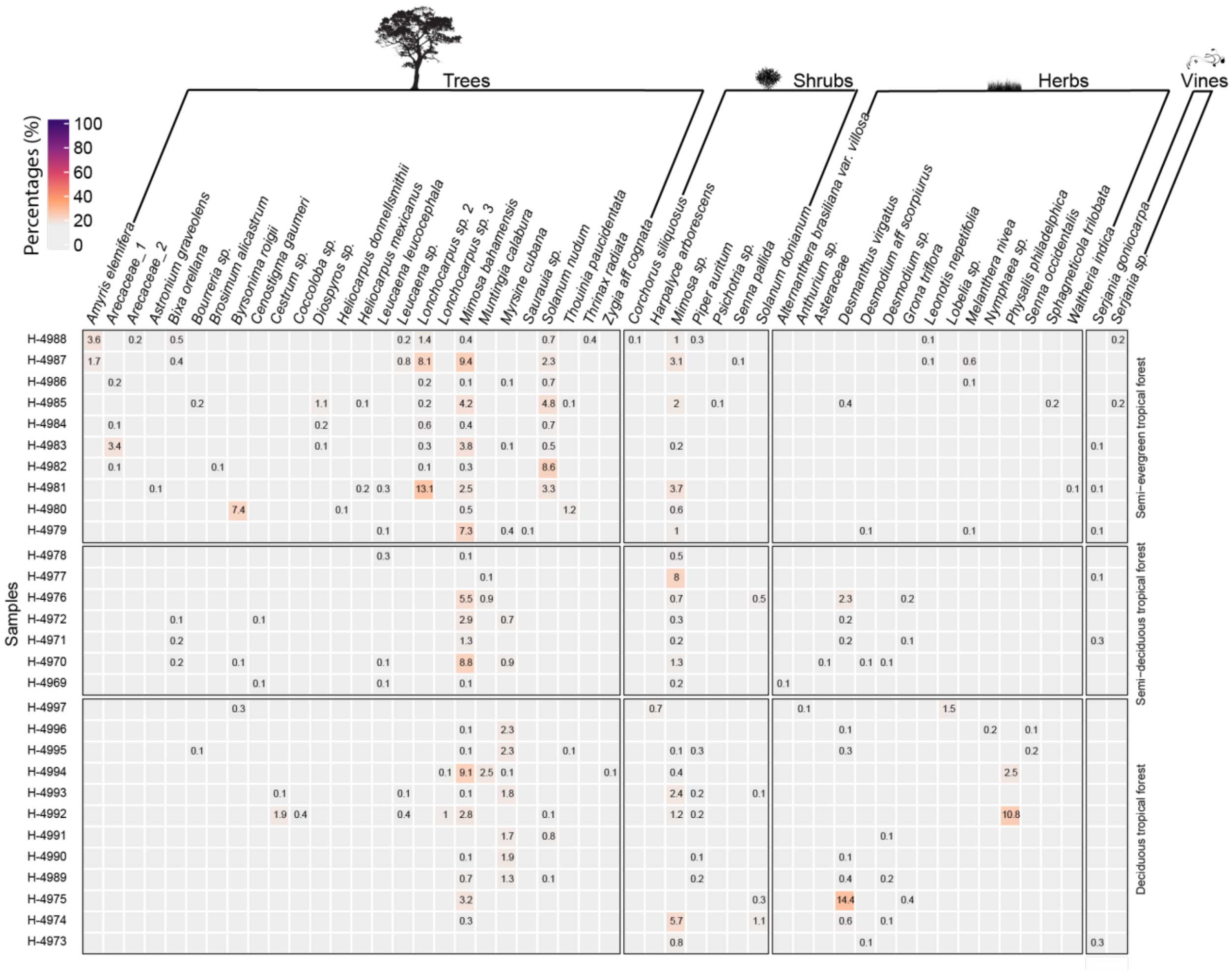


Figure 3.4. Pollen grains with <16% relative abundance in *Melipona beecheii* pot-pollen samples from nine meliponaries located in the three main vegetation types of the Yucatan Peninsula. Pollen grains are grouped according to plant growth form. Non-identified morphotypes are not shown.

The other highly abundant species were located at specific meliponaries, except for *Lonchocarpus* sp. 1 which was present in meliponaries located in all vegetation types. In deciduous tropical forest, *Bursera simaruba* and *Bursera schlechtendalii* (Burseraceae) were abundant only in Chunkanán. In Lerma (deciduous tropical forest), pollen from *Physalis pubescens* and *Solanum torvum* Sw. (both Solanaceae), and *Psidium guajava* (Myrtaceae) were conspicuous. In semi-evergreen tropical forest, pollen from *Solanum erianthum* (Solanaceae) was highly abundant at all three meliponaries. Additionally, pollen from *Crotalaria sp*. was notable in Chanchén Palmar and San Juan de Dios, and pollen from *Senna sp*. was also abundant at the latter. Details on the relative abundance of the 69 morphotypes detected in *M. beecheii* pot-pollen can be found in Figure 3.4.

To analyze pot-pollen diversity by vegetation type, we estimated the Hill numbers (Chao *et al.*, 2014; Hill, 1973) through the application of rarefaction and extrapolation curves (Hsieh *et al.*, 2016). Our sampling effort resulted in an average coverage of 99% per meliponary (Anexo IV). Although the meliponaries located in semi-evergreen tropical forests showed the highest morphotype richness values, with over 24 types, they did not exhibit significant differences compared to the other meliponaries located in deciduous (Chunkanán and Lerma) and semi-deciduous (Maní) tropical forests (Figure 3.5 q = 0). Thus, the pot-pollen showed a mean morphotype richness (q = 0) of 20.6 across the nine meliponaries evaluated. In terms of the diversity of equally common species (q = *1*), only three meliponaries, one in deciduous tropical forest (Lerma) and two in semi-evergreen tropical forest (Chanchén Palmar and San Juan de Dios), had more than four morphotypes. This suggests that there is a low diversity of plants visited by *M. beecheii* (Figure 3.5 q = 1). Meliponaries in Pucnachén (deciduous tropical forest) and Maní (semi-deciduous tropical forest) were the least diverse, both with two morphotypes. As for the number of dominant species (Figure 3.5 q = 2), again the meliponaries from Lerma, San Juan de Dios, and Chanchén Palmar showed the highest values, the first two with five species and the third with six.

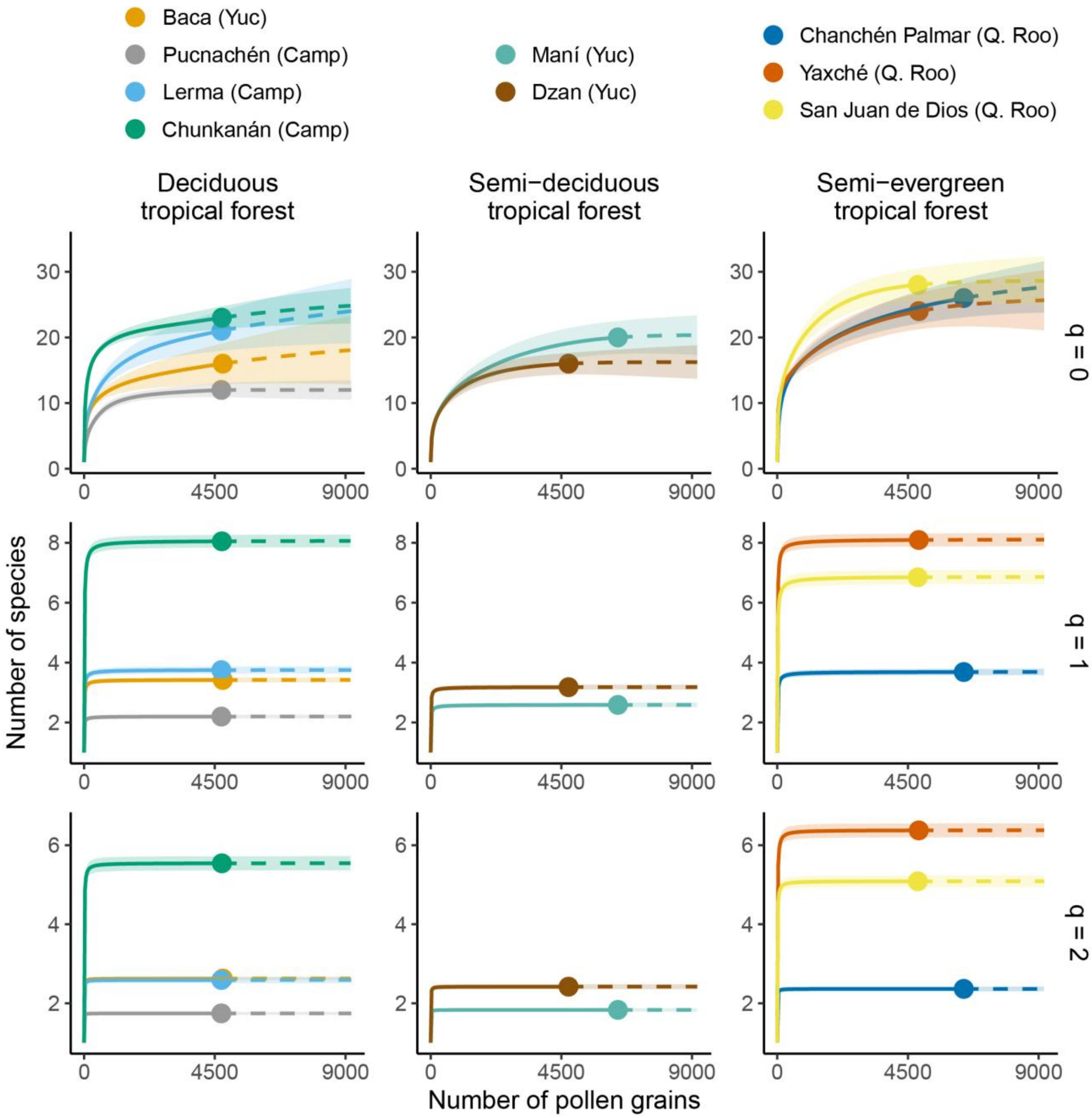


Figure 3.5. Estimates, based on Hill numbers, of pot-pollen diversity in *Melipona beecheii* colonies at nine meliponaries located on the Yucatan Peninsula by vegetation type (States: Yuc – Yucatan, Camp – Campeche, Q. Roo – Quintana Roo). *q* = 0: species richness; *q* = 1: diversity of equally common species (exponential of the Shannon index); *q* = 2: diversity of dominant species (inverse of the Simpson index). Diversity curves were constructed from rarefaction (solid lines) and extrapolation (dashed lines) with estimations based on sample size. Each curve was extrapolated up to twice the sample size achieved in our samplings. Shaded areas show the 95% confidence intervals obtained from a bootstrap method with 200 replications.

5.3.2. Vegetation and pot-pollen in meliponaries

When comparing plant and pot-pollen datasets, we found that bees visited only 18 out of the 266 plant species identified in the vicinity of the meliponaries. The number of plant species visited by the bees varied among the different vegetation types. At the meliponaries located in deciduous tropical forests, the bees had visited 8 of 151 species; in semi-deciduous tropical forests they had visited 4 out of 85 species. In semi-evergreen tropical forests, the bees had visited 15 out of 169 species. These low proportions in shared species were reflected in significant differences between the vegetation surrounding the meliponaries and the pot-pollen samples in terms of species abundance (perMANOVA test: $p < 0.001$, $R^2 = 0.46$) (Figure 3.6A).

Regardless of vegetation type, the vegetation samples from the meliponaries formed a tight cluster when considering species abundance. In contrast, pot-pollen exhibited greater distances to the centroid, especially between meliponaries in deciduous tropical forests and those in other vegetation types (Figure 3.6A). The PCA analysis for species abundance revealed the species that played a major role in shaping both pot-pollen and vegetation communities. In general, for plant species abundance the primary contributors to the meliponaries were *Petiveria alliacea*, *Neomillspaughia emarginata,* and *Citrus sinensis* (Figure 3.6B, Anexo VI) whereas *C. vitifolium, Lonchocarpus* sp. 1, and *S. r*. var. *racemosa* showed the greatest influence on pot-pollen (Figure 3.6C, Anexo V).

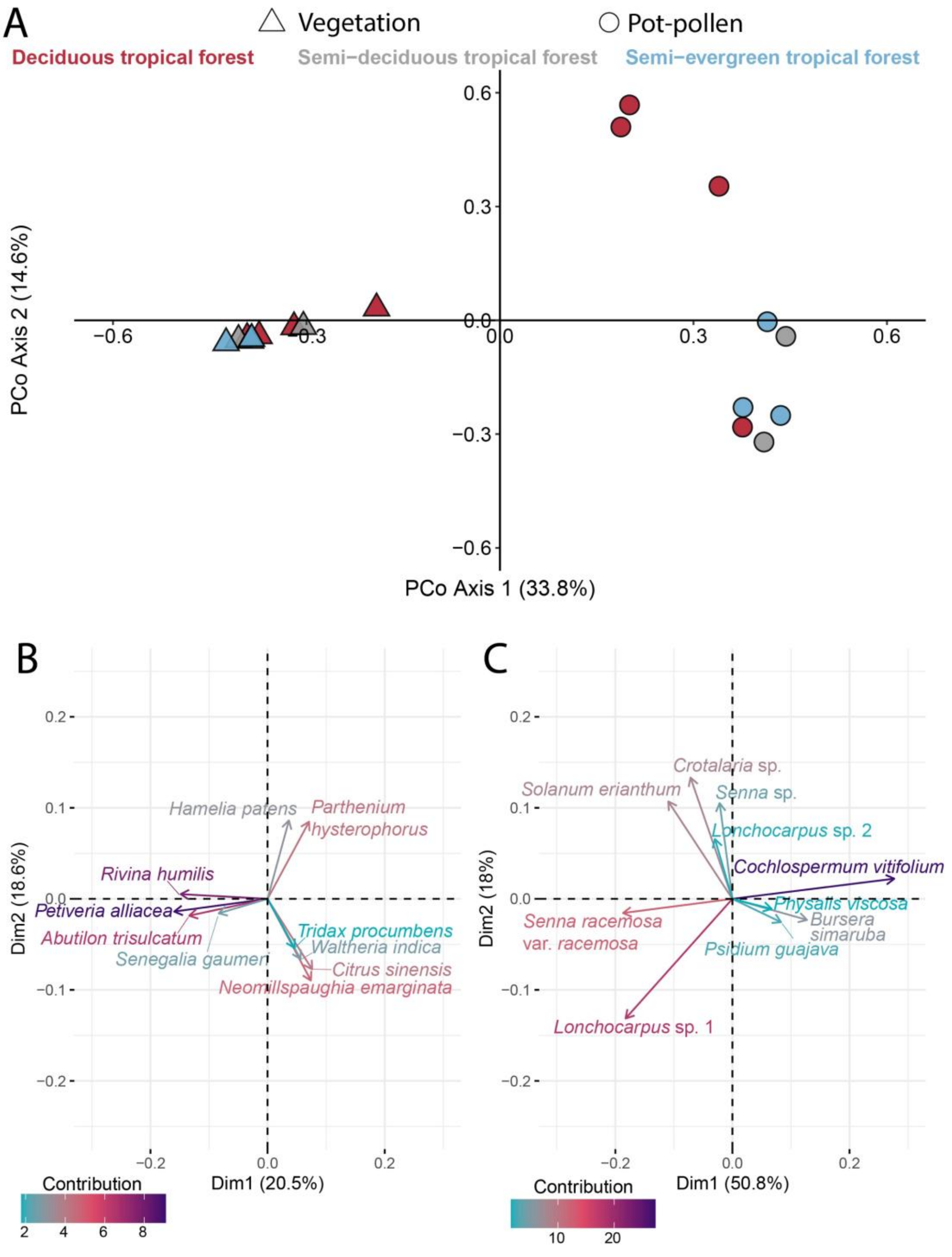


Figure 3.6. Multivariate analysis for plant species and *Mellipona beecheii* pot-pollen morphotypes/species considering (*A*) PCoA of species abundance and PCA of species scores based on their abundance in (*B*) vegetation and (*C*) pot-pollen samples. The vectors correspond to the 10 species with the greatest contribution to the arrangements. Data collected at nine meliponaries on the Yucatan Peninsula.

5.3.3. Influence of vegetation characteristics on pollen foraging

To analyze the effect of vegetation diversity on pot-pollen diversity, we generated three models (q_i pollen diversity ~ q_i vegetation diversity) corresponding to q = 0 richness, q = 1 equally common species, and q = 2 dominant species. Of these, only the richness model showed statistical significance (Figure 3.7), predicting a significant positive effect of plant richness on pot-pollen richness (P = 0.003). The plant richness surrounding the meliponaries accounted for 71% of the variance in pollen richness. However, the lack of significance in the models of equally abundant species and dominant species suggests a preference for a specific group of plants, irrespective of an increase in diversity and dominance of plants in the vicinity of the meliponaries. These preferences were further evidenced on regression analysis between the log-transformed abundance of pollen grains identified at the species level and their corresponding log-transformed absolute density and absolute crown coverage of those plant species in the vegetation. None of these two models were significant (Anexo VII), suggesting that *M. beecheii* collects certain plant pollen species over others regardless of their density and coverage in the surrounding vegetation.

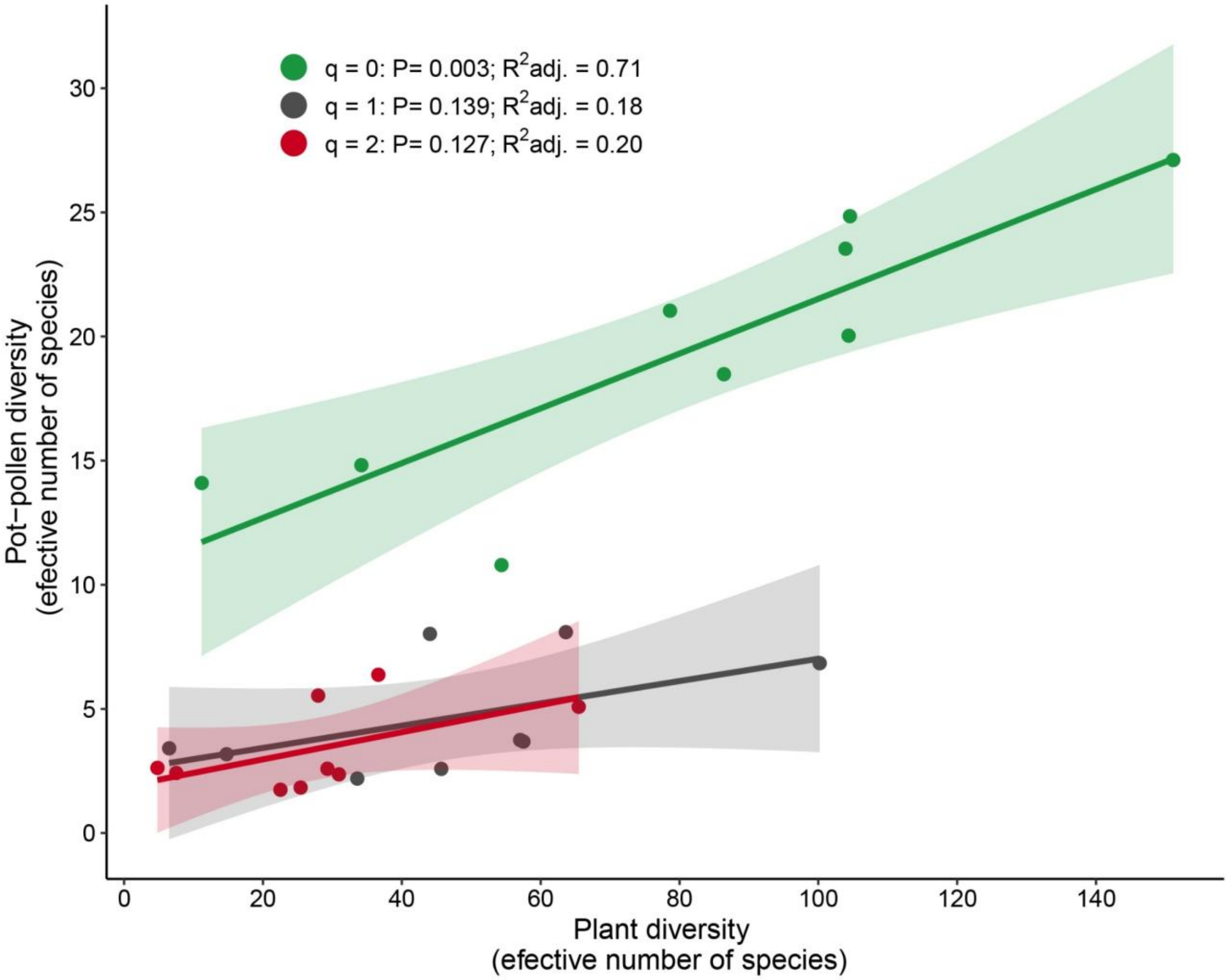


Figure 3.7. Linear regression model based on Hill numbers (*q* = 0, 1, 2) between plant diversity around nine meliponaries on the Yucatan Peninsula and the corresponding *Melipona beecheii* pot-pollen grain morphotype diversity from these meliponaries.

5.4. Discussion

Taxonomic patterns in host-plant foraging behavior are a fundamental topic in the study of the natural history of the bee (Cane and Sipes, 2006). There is a variety of research demonstrating that bees exhibit a range of foraging behaviors from generalist to specialist and that some species show preferences for certain plant taxa (Báez-Lizarazo *et al.*, 2021; Pardee *et al.*, 2023; Vaudo *et al.*, 2024). Meliponines show modular foraging depending on the scale; in the neotropics, they visit a wide range of botanical families, but at the local scale, they obtain most of their food from a few plant groups, despite the great diversity of plants in tropical forest habitats (Ramalho *et al.*, 1990). This wide foraging range coincides with our results regarding *M. beecheii* foraging in the Yucatan Peninsula, and we have expanded the range of known plant species visited by this bee to around 102 (Bacab-Pérez *et al.*, 2024; Ramírez-Arriaga *et al.*, 2018; Villanueva-Gutiérrez *et al.*, 2018). Our findings also show that *M. beecheii* has strong preferences for the pollen of a limited number of plants. Interestingly, these preferences do not seem to be affected by land use or the presence of exotic species, as evidenced by colonies in Dzan that are located in a citrus cultivation field, or those in Chunkanán close to a cucurbit (*Cucurbita moschata* Duchesne) field (Pérez-Morfi et al., 2024a). Although *Citrus* produces little pollen and is mainly nectariferous, if colonies are placed to pollinate, some of its pollen would be expected to be found in the pot-pollen, but this was not the case. We also found no Cucurbitaceae pollen in the pot-pollen. Similarly, in temperate regions, honey bees placed in almond orchards for cross-pollination have been observed to collect a significant amount of non-almond pollen, indicating that bees do not exclusively forage on the most abundant plants or the most economically valuable crops (Bezerra da Silva Santos et al., 2022; Carnevali Fernández-Concha et al., 2010).

5.4.1. Botanical composition of pot-pollen

Our results suggest that *M. beecheii* displays foraging preferences for pollen from tree plants, as evidenced by the dominance thereof in pot-pollen across all the meliponaries studied in the Yucatan Peninsula. Similar findings have been reported for the foraging of bees from various families, including Apidae (such as meliponines), Anthophoridae, Andrenidae, Colletidae, Halictidae, Megachilidae, and Melittidae (Hausmann *et al.*, 2016; Quiroz-García *et al.*, 2011; Splitt *et al.*, 2021; Steffan-Dewenter and Tscharntke, 2001). Trees, due to their life cycle and biology, can produce nectar and pollen even in adverse environmental conditions, which makes them a reliable source of nectar and pollen for bees throughout the year (Corbet, 1995).

Our results indicate that pollen from the *Senna* genus (4 species detected) from the Fabaceae family, especially from the tree *S. racemosa* var. *racemosa*, is of major importance for *M. beecheii.* The plants of the genus *Senna*—the most diverse Fabaceae genus in the peninsula—are reported to be nectarless and used by bees exclusively for pollen (Roubik and Patiño, 2013; Sabino *et al.*, 2019). Additionally, at the family level, Fabaceae pollen, represented by 19 taxa/morphotypes of pollen grains, was dominant in the *M. beecheii* pot-pollen. This result coincides with previous reports for the species in different areas of the Yucatan Peninsula (Bacab-Pérez *et al.*, 2024; Villanueva-Gutiérrez *et al.*, 2018) and is consistent with the fact that Fabaceae is one of the most diverse and abundant plant families on the same peninsula (White and Hood, 2004; Carnevali Fernández-Concha *et al.*, 2010; Duno-de Stefano *et al.*, 2018). The Fabaceae family has also been reported as an important source of pollen and nectar for other meliponines: *Tetragonisca angustula* (Roubik and Patiño, 2013), *Lepidotrigona terminata* (Chuttong *et al.*, 2018), and species of the genera *Frieseomelitta*, *Melipona*, *Plebeia*, *Scaptotrigona*, *Scaura*, and *Tetragonisca* (Vit *et al.*, 2018). The consistency of Fabaceae as a pollen source for bees could be explained by its protein content. Although nutrient availability varies among species within the same family, Fabaceae pollen is considered to be of higher nutritional value, with an average of 23% protein (Liolios *et al.*, 2015) compared to, for example, the second richest family of dicotyledons on the peninsula, Asteraceae (Duno-de Stefano *et al.*, 2018), the pollen of which has been found to contain approximately 18% protein (Tellería *et al.*, 2019).

5.4.2. Vegetation and pot-pollen in the meliponaries

Previous studies have shown that despite the high plant diversity of tropical habitats, meliponines rely on a limited number of plant groups for food resources (Quiroz-García *et al.*, 2011; Ramalho *et al.*, 1990). This aligns with our observation that *M. beecheii* collected pollen from only 18 of the 266 plant species identified in the vicinity of the nine meliponaries studied, and with Villanueva *et al.* (Villanueva-Gutiérrez *et al.*, 2018), who reported that *M. beecheii* collected pollen from 68 of the 850 angiosperm species in the Sian Ka'an Biosphere Reserve in Quintana Roo. The few species shared between the pot-pollen samples and the surrounding vegetation likely account for the distances observed in the PCoA groupings. However, species such as *Cochlospermum vitifolium* and *Senna racemosa* var. *racemosa* consistently appeared in the pollen collected by *Melipona beecheii*, irrespective of the vegetation type. The vegetation types on the Yucatan Peninsula are characterized by a northwest-southwest precipitation gradient, shallow soils, limestone outcrops, and physiographic homogeneity, which limits the plants' access to water and nutrients (Duno-de Stefano *et al.*, 2018). These environmental factors act as filters for plant diversity, creating similarities among the peninsula's vegetation formations (18). Our results suggest that these similarities also extend to the plant species visited by *M. beecheii* for pollen collection.

While the PCoA analysis showed greater dispersion among meliponaries based on pollen morphotype/species abundance, it is important to consider the nutritional implications. The variation in pollen species abundance across meliponaries was primarily driven by three species from distinct plant families: *Cochlospermum vitifolium* (Bixaceae), *Senna racemosa var. racemosa, and Lonchocarpus* sp. 1 (both Fabaceae). Furthermore, when analyzing the nutritional contributions of pollen, it is important to consider not only the dominant species but also their families, since closely related species tend to have similar protein and lipid content (Vaudo *et al.*, 2024). Thus, according to our findings, the main nutritional contributions to *M. beecheii* pollen on the Yucatan Peninsula come from the Fabaceae and Bixaceae families, with Fabaceae being dominant in six meliponaries. This suggests that differences in pollen foraging among most of the meliponaries may not be nutritionally significant. However, the meliponaries in deciduous tropical forests (Puchnachén, Chunkanán, and Lerma) are primarily influenced by *Cochlospermum vitifolium* (Bixaceae), which is accompanied in pot-pollen by species from Burseraceae (mainly *Bursera simaruba*), Myrtaceae (*Psidium guajava*), and Solanaceae (*Physalis pubescens* and *Solanum torvum*).

Although the pollen from *C. vitifolium* and the other companion species (*B. simaruba, P. guajava*, *P. pubescens* and *S. torvum*) has been previously reported as used by *M. beecheii* (Bacab-Pérez *et al.*, 2024; Villanueva-Gutiérrez *et al.*, 2018), there is currently no available data on their nutritional quality, which makes it difficult to hypothesize nutritional implications for bees. However, research indicates that it is the protein-to-lipid ratio in pollen rather than the absolute protein or lipid content that influences bee foraging and that it may be responsible for the formation of nutritional niches (Vaudo *et al.*, 2024). Therefore, it is possible that in the meliponaries at Puchnachén, Chunkanán, and Lerma, *M. beecheii might meet its* nutritional requirements by combining pollen from several botanical families rather than relying on one dominant family such as Fabaceae, as seen in the meliponaries at Baca, Dzan, and Maní.

Another explanation for the mix of Bixaceae and the pollen of other plant families could be related to a compensatory behavior intended to supplement the lack of nutritional contribution from Fabaceae pollen with that of species from different botanical families. It is known that *Apis mellifera* responds to deficiencies in the quantity or quality of its pollen reserves by increasing the number of bees collecting pollen and consequently the volume, rather than specializing in collecting pollen with a higher protein content (Pernal and Currie, 2001). Therefore, in environments where plant species with high-quality nutritional pollen are not abundant, collecting pollen from different botanical families could be an adaptive strategy to ensure an adequate supply of nutrients. This may explain the presence of multiple plant families in the pot-pollen from meliponaries where Fabaceae pollen did not predominate.

Additionally, changes in land use and vegetation disturbance may also help explain the presence of Bixaceae pollen mixed with pollen from other plant families. In this context, it is important to note that this mix includes *C. vitifolium*, an aggressive pioneer species commonly found in early successional vegetation (Fallas-Cedeño *et al.*, 2010; Huante *et al.*, 1995), *B. simaruba*, a species typical of early-stage secondary vegetation (8 to 10 years) on the Yucatan Peninsula (Sánchez and Islebe, 2000), and the cultivated plant *P. guajava*. Therefore, in the meliponaries of Puchnachén, Chunkanán, and Lerma, *M. beecheii* may be shifting its typical Fabaceae-dominated diet as a result of human-induced changes in vegetation. In any case, further research is needed for a complete understanding of the link between the nutritional quality of tropical pollen and the nutritional requirements and foraging behavior of *M. beecheii*.

5.4.3. Influence of vegetation characteristics on pollen resource utilization

Despite the previously mentioned variations in pot-pollen composition among different meliponaries, foraging preferences in *M. beecheii* in terms of diversity are evidenced by the lack of association between plant and pollen diversity regarding the equally common species and dominance. A positive relationship between plant and pot-pollen diversity in *M. beecheii* foraging was only found with regard to species richness. According to optimal foraging theory, this result can be attributed to the fact that herbivorous foragers tend to show selectivity in their food choices to maximize energy gain (Sinervo, 1997). However, the need for a balanced diet prevents herbivores from relying solely on energy-rich foods, as these may lack essential nutrients. Thus, herbivores seek to diversify their diet to obtain vital micronutrients, thereby complementing their diet with a variety of forage options that provide the necessary nutrients (Belovsky, 1984). In the context of social bees, this implies that the colony will use a group of plant species that optimize protein (or protein-to-lipid ratio) gain in the pollen, while also ensuring the acquisition of all necessary nutrients by diversifying foraging.

5.4.4. Implications for conservation

In Mexico, meliponiculture is still practiced by rural communities of Mayan descendants on the Yucatan Peninsula and by some Nahua groups in Puebla and Veracruz (Quezada-Euán *et al.*, 2015). It is estimated that there are around 720 meliponicultors on the Yucatan Peninsula, 100 in Campeche (Pat Fernández *et al.*, 2018), 500 in Yucatan (Echazarreta *et al.*, 1997), and 120 in Quintana Roo (Villanueva-Gutiérrez *et al.*, 2005), though there may be fewer as managed *M. beecheei* colonies are decreasing. In addition to the importance of economic drivers in the conservation of meliponiculture, biological and ecological factors are also of major consequence as meliponicultors report that their bees are starving (Villanueva-Gutiérrez *et al.*, 2005). In this regard, from a practical point of view, a reduction in pollen supply would have a greater impact on colony survival because 1) pollen quality affects colony performance (May-Itzá *et al.*, 2021; Veiga *et al.*, 2013), and 2) it is easier for meliponicultors to supply a sugar solution than a protein-lipid supplement.

Several alarming elements came to light upon analysis of our present results and our previous description of the meliponaries' vegetation in terms of the availability of melliferous resources (Pérez-Morfi et al., 2024a). First, we found that *M. beecheii* obtains most of its pollen from trees, but in the vicinity of the meliponaries, the vegetation consists of young secondary vegetation where the low stratum abounds, and the trees are smaller (mean height 5.5 m) than in natural vegetation, where they can reach from 8 to 25 m depending on the vegetation type (Durán and Olmsted, 1999). This may be a limiting factor because tree age and size influence flowering onset and therefore flower availability for bees (Hackett, 1987; Thomas, 1996). Second, we identified 266 plant species in the vicinity of the meliponaries, but *M. beecheii* collected pollen from only 6.2% of this richness. Third, the lack of effect of plant species density and crown coverage on pollen abundance in *M. beecheii* pot-pollen indicates a preference for a small number of species, regardless of their dominance in the environment. For instance, at the Dzan meliponary, *Senna racemosa* var. *racemosa* was one of the main pollen sources used by this bee, despite there being only 15 trees per hectare. In contrast, the pollen of *Citrus sinensis*, which had a density of 1015 trees per hectare, was absent from our samples, even though both species were blooming during the study period.

The location of the meliponaries near human settlements and the characteristics of the surrounding vegetation indicate a strong impact of human activity on food availability for *M. beecheii.* For bees, nest location regarding the ground and sociality is considered the most important trait moderating response to land use change (Williams *et al.*, 2010). Aboveground or underground nesting bees are sensitive to land use change because nest sites can be destroyed or access to bare soil can be increased (Williams *et al.*, 2010). Yet nest location can also be considered as the relative position of the colonies to food sources, which influences the bees' foraging distances (Steffan-Dewenter and Kuhn, 2003) and their ability to meet nutritional requirements (Roulston and Goodell, 2011). Moreover, social bees are more adversely affected by land use changes than solitary bees (Winfree *et al.*, 2009), possibly as a result of the bio-accumulation of pesticides in their nests, leading to exposure at all life-cycle stages (Williams *et al.*, 2010). At any rate, vegetation conditions should be also considered an important driver of meliponines' sensitivity to land-use change, as these bees rely on mature forest trees for nest sites (Winfree *et al.*, 2009), and, as our results suggest, for pollen resources.

5.5. Conclusions

Our study offers significant insights into the foraging behavior and pollen preferences of *Melipona beecheii*, emphasizing its reliance on tree pollen in the Yucatan Peninsula. Despite the rich diversity of plant species surrounding the meliponaries, *M. beecheii* selectively collects pollen from a limited number of species, showing a marked preference for Fabaceae, regardless of abundance in the surrounding vegetation. The presence of pollen from cultivated plants, pioneer species, and vegetation typical of early-stage secondary succession, as well as the proximity of meliponaries to human settlements, highlights the impact of anthropogenic factors on *M. beecheii*'s foraging resources. Given the nutritional importance of pollen and the challenges posed by habitat alteration, our findings underscore the need for conservation strategies that ensure access to diverse and nutritionally adequate pollen sources, which will support the sustainability of meliponiculture and the health of *M. beecheii* colonies on the Yucatan Peninsula.

CAPÍTULO IV

DISCUSIÓN, CONCLUSIONES GENERALES Y PERSPECTIVAS

6.1. Discusión general

En las últimas dos décadas estudios han reportado disminuciones locales y globales en la diversidad y abundancia de abejas silvestres (Biesmeijer *et al.*, 2006; Burkle *et al.*, 2013; Koh *et al.*, 2016). Aunque este fenómeno está influido por diversos factores (Cameron *et al.*, 2011; Forrest, 2015; Woodcock *et al.*, 2016), la pérdida de hábitat provocada por los cambios de uso de suelo se considera como el más importante (Dicks *et al.*, 2021; Kennedy *et al.*, 2013). En este sentido, la pérdida de sitios de anidación, así como la disminución de la densidad y diversidad de las fuentes de polen, son consecuencia de la tala, la urbanización, la agricultura y la pérdida de heterogeneidad de las tierras agrícolas (Herbertsson *et al.*, 2021; Winfree *et al.*, 2011). Las abejas nativas de la península de Yucatán, México, no escapan de dicha situación siendo esta una de las zonas más deforestadas del país (Duran-García y García Contreras 2010, Aguilar y Domínguez 1999). En este contexto se desarrolla la meliponicultura en la península, donde los meliponicultores reportan que las colonias de *M. beecheii* mueren por falta de alimento, pero se conoce poco sobre sus hábitos alimentarios. Por tanto, la finalidad de nuestro trabajo fue evaluar las características de la vegetación que rodea nueve meliponarios de la Península de Yucatán y analizar cómo estas características se relacionan con la disponibilidad y uso de recursos poliníferos para *M. beecheii*.

La descripción de la vegetación se realizó mediante el método de cuadrantes centrados en puntos, aplicado en cuatro transectos distribuidos alrededor de los meliponarios y orientados según los cuatro puntos cardinales (Capítulo II). Los resultados de esta evaluación indican que los meliponarios tradicionales de la península de Yucatán, generalmente situados cerca de las viviendas de los propietarios, están rodeados predominantemente de vegetación secundaria joven. Este tipo de vegetación se caracterizó por la prevalencia de árboles con alturas inferiores a 5 m, un estrato bajo denso, independientemente del tipo de vegetación circundante, y una notable escasez de plantas melíferas (fuente de polen y néctar).

La altura de la vegetación arbórea evaluada fue significativamente menor en comparación con las dimensiones reportadas para los árboles en tres tipos de vegetación predominantes en la península, analizados en este estudio: selva baja caducifolia (8–12 m), selva mediana subcaducifolia (13–18 m) y selva mediana subperennifolia (15–25 m) (Durán y Olmsted, 1999; Flores Guido *et al.*, 2010). Esta situación, junto con la escasez de plantas melíferas, probablemente afecta negativamente la disponibilidad de fuentes de alimento para las abejas, dado que la edad y el tamaño de los árboles influyen directamente en su capacidad de floración (Thomas, 1996). En este sentido, la importancia de los árboles como fuente de alimento para las abejas, especialmente como proveedores de polen, ha sido ampliamente documentada (Hausmann *et al.*, 2016; Quiroz-García *et al.*, 2011; Splitt *et al.*, 2021; Steffan-Dewenter y Tscharntke, 2001). El prolongado ciclo de vida y el mayor tamaño de los árboles en comparación con hierbas y arbustos les permite acumular nutrientes durante largos periodos, lo que a su vez posibilita la producción de néctar y polen incluso en condiciones ambientales adversas. Esto los convierte en una fuente confiable de alimento para las abejas (Corbet, 1995).

En términos de diversidad de plantas, se esperaba encontrar valores más altos en los meliponarios ubicados en zonas de selva mediana subperennifolia, dado el gradiente de precipitaciones que se extiende del noroeste al suroeste de la península (Orellana *et al.*, 2003). Sin embargo, entre los tres meliponarios localizados en este tipo de vegetación, únicamente el de San Juan de Dios se destacó por su elevada riqueza (109 especies) y diversidad florística (79 especies efectivas, Número de Hill de orden 1, q = 1). En el resto de los meliponarios no se observaron diferencias significativas en la diversidad de especies vegetales. Este resultado sugiere la existencia de un proceso de homogeneización biótica, caracterizado por el reemplazo de especies locales por especies más generalistas, resistentes o de interés económico (McKinney, 2006). Evidencia de este fenómeno fue la presencia de áreas de cultivo de cítricos y calabaza en los alrededores de los meliponarios de Dzan y Chunkanán, así como la proliferación de especies ruderales, entre ellas *Parthenium hysterophorus* y *Tridax procumbens*, alrededor de todos los meliponarios estudiados. Este proceso de homogeneización biótica podría estar contribuyendo a la reducción de la diversidad de fuentes de polen disponibles para *M. beecheii*, con posibles implicaciones negativas para su ingesta nutricional y, en consecuencia, para la salud de las colonias.

Por otro lado, el análisis palinológico de las muestras de pan de abeja (polen almacenado en la colmena “pot-pollen” en inglés) recolectadas en colonias ubicadas en los meliponarios estudiados (Capítulo III) reveló que las plantas arbóreas constituyeron la principal fuente de polen para *M. beecheii*, a pesar de la abundancia del estrato bajo alrededor de los meliponarios. En particular, nuestros resultados indican que las especies arbóreas *Senna racemosa* var. *racemosa*, *Lonchocarpus* sp. 1 (ambas Fabaceae), y *Cochlospermum vitifolium* (Bixaceae) se encuentran entre las más utilizadas por *M. beecheii* en la península. Este hallazgo es consistente con estudios previos que han señalado a la familia Fabaceae como una fuente importante de polen y néctar para la abeja maya y otras especies de meliponinos (Chuttong *et al.*, 2018; Roubik and Patiño, 2013; Vit *et al.*, 2018; Bacab-Pérez *et al.*, 2024). La relevancia de las fabáceas como fuente de polen para las abejas puede atribuirse a su alto contenido proteico (Liolios *et al.*, 2015; Vaudo *et al.*, 2024). Sin embargo, en la vegetación alrededor de los meliponarios solo encontramos individuos de *S. r*. var. *racemosa* en cuatro meliponarios y en ninguno encontramos ejemplasres de *C. vitifolium.*

A diferencia del polen de *S. racemosa* var. *racemosa*, que fue dominante en la mayoría de los meliponarios, el polen de *C. vitifolium* se registró en mayor abundancia en los meliponarios de Puchnachén, Chunkanán y Lerma, ubicados en zonas de selva baja caducifolia. No obstante, el polen de *C. vitifolium* estuvo acompañado por otras especies, como *Bursera simaruba* (Burseraceae), *Psidium guajava* (Myrtaceae), *Physalis viscosa* L. y *Solanum torvum* (ambas Solanaceae). Estudios previos han documentado que el polen de estas especies es utilizado por *M. beecheii* (Ramírez-Arriaga et al., 2018; Villanueva-Gutiérrez et al., 2018; Bacab-Pérez et al., 2024), aunque hasta el momento no se dispone de información detallada sobre su calidad nutricional ni sobre los requerimientos específicos de las colonias de esta especie. Sin embargo, la proporción entre proteínas y lípidos en el polen, más que su contenido absoluto, es un factor determinante en las preferencias alimentarias de las abejas y puede dar lugar a la formación de nichos nutricionales (Vaudo *et al.*, 2024). La evidencia disponible sugiere que, aunque las especies de plantas taxonómicamente relacionadas tienden a producir polen con proporciones similares de proteínas y lípidos, las abejas pueden cambiar de grupo taxonómico de plantas para mantener una proporción constante de estos nutrientes en el polen recolectado (Vaudo *et al.*, 2024). Es posible, entonces, que en los meliponarios de Puchnachén, Chunkanán y Lerma, *M. beecheii* satisfaga los requerimientos nutricionales de sus colonias mediante la combinación de polen proveniente de varias familias botánicas, en lugar de depender predominantemente de una sola familia, como las Fabaceae, como se observó en los meliponarios de Baca, Dzan y Maní.

Teniendo en cuenta los resultados de este trabajo, las estrategias de conservación de la meliponicultura en la Península de Yucatán deben considerar los impactos de las actividades humanas y los cambios en la vegetación sobre los requerimientos nutricionales de las abejas nativas y la disponibilidad de alimento. Proteger y restaurar hábitats forestales diversos y maduros es crucial para satisfacer las necesidades nutricionales de *M. beecheii* (González-Acereto, 2008) y de otras especies nativas (Traylor *et al.*, 2024). Los esfuerzos deberían centrarse en mantener la presencia de fuentes preferidas de polen y mitigar los efectos negativos de los cambios en el uso de la tierra. Por tanto, se debería propiciar a treves de incentivos gubernamentales, el cultivo y reforestación con especies nativas de los géneros *Senna* y *Buresera*, con *Cocholspermun vitifolium,* así como con especies de la familia Solanaceae. De esta forma se garantizaría la disponibilidad de recursos florales diversos y de alta calidad lo para sostener las poblaciones de abejas y los servicios esenciales de polinización que brindan. Junto con ello se deben hacer estudios de la calidad nutricional del polen de dichas especies para las abejas.

6.2. Conclusiones

1. La vegetación alrededor de los meliponarios se caracteriza por ser secundaria joven, en la que abunda el estrato bajo con árboles de pequeño tamaño y poca disponibilidad de plantas melíferas.

2. La presencia de especies ruderales ampliamente distribuidas cerca de los meliponarios sugiere un proceso de homogeneización biótica, que puede reducir aún más la disponibilidad de fuentes de polen preferidas para *M. beecheii*.

3. *Melipona beecheii* exhibe un forrajeo generalista en el que potencialmente puede visitar más de 100 especies de diferentes familias botánicas. A pesar del comportamiento generalista, *M. beecheii* exhibe preferencias específicas por ciertas fuentes de polen, particularmente de plantas arbóreas y de las familias Fabaceae y Bixaceae, especialmente *Senna* spp. y *Cochlospermum vitifolium* respectivamente. Esta preferencia fue consistente entre varios meliponarios a pesar de las diferencias en los tipos de vegetación, lo que indica una fuerte dependencia de ciertos taxones de plantas para el polen.

4. Las preferencias por algunas fuentes de polen son independientes de la densidad y dimensiones de estas plantas en los alrededores de los meliponarios.

6.3. Perspectivas

Las perspectivas generales de investigación giran en torno a la comprensión del comportamiento de búsqueda de alimento de las abejas nativas de México, los requerimientos nutricionales y el impacto de los cambios ambientales en sus hábitos de forrajeo. Esto incluye:

1. Evaluar el impacto del cambio de uso de suelo en la estructura y diversidad de la vegetación alrededor de los meliponarios

2. Investigar cómo las abejas nativas equilibran su dieta para satisfacer sus necesidades nutricionales y adaptarse a la disponibilidad variable de plantas.

3. Explorar los requerimientos nutricionales de las abejas nativas, en particular aminoácidos escenciales y lípidos en el polen y explorar cómo influyen en las decisiones de búsqueda y preferencia de alimento y la salud general de la colonia.

4. Estudiar la calidad nutricional del polen de las especies visitadas por *Melipona beecheii* en la Península de Yucatán
5. Estudiar las distancias de pecoreo de *Melipona beecheii*

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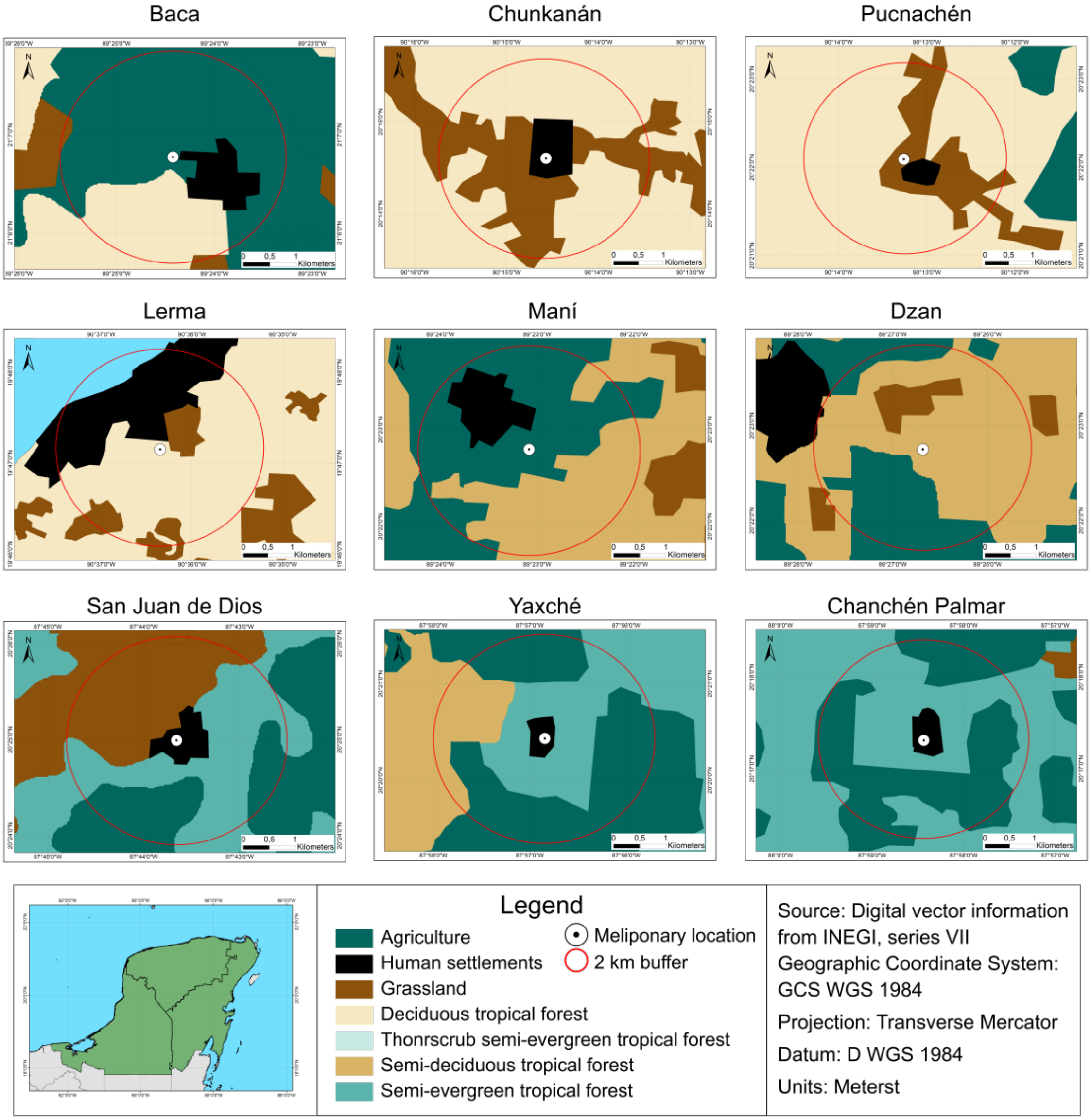
ANEXOS

ANEXO I. Land-cover maps of the areas surrounding each meliponary studied in the Yucatán Peninsula, México.



Baca

Chunkanán

Pucnachén

Lerma

Maní

Dzan

San Juan de Dios

Yaxché

Chanchén Palmar

Source: Digital vector information from INEGI, series VII

Geographic Coordinate System: GCS WGS 1984

Projection: Transverse Mercator

Datum: D WGS 1984

Units: Meterst

ANEXO II. Importance value index (IVI) of plant species recorded in the surrounding vegetation of nine meliponaries in the Yucatan Peninsula, Mexico. Cells highlighted in yellow indicate the species that were blooming during the study. Melif = Melliferous

Family	Taxa	Growth form	Mellif	Deciduous tropical forest				Semi-deciduous tropical forest		Semi-evergreen tropical forest		
				Baca	**Pucnachén**	**Chunkanán**	**Lerma**	**Mani**	**Dzan**	**Yaxché**	**Chanchén Palmar**	**San Juan de Dios**
Acanthaceae	Acanthaceae, unidentified species	Herbaceous	No	0	0	0	0.43	0	0	0	0	0
	Aphelandra scabra (Vahl) Sm.	Shrub	No	0	0	0	0.43	0	0	0.36	0	0
	Barleria cristata L.	Shrub	No	0	0	0	0	0	0	0	0.43	0
	Dicliptera sexangularis (L.) Juss.	Herbaceous	No	0	0	0	0.86	0	0	0	0	0
	Justicia carthaginensis Jacq.	Herbaceous	No	0	0.37	0.74	0	0.68	0	0	0	0
	Ruellia blechum L.	Herbaceous	No	0	0	0	3.83	0.67	0	0	0	0
	Ruellia inundata Kunth	Herbaceous	No	0	0	0	2.62	0	0	0	0	0
	Ruellia ciliatiflora Hook.	Herbaceous	No	0	0	0	0	0	1.74	0.36	0.32	0
	Tetramerium nervosum Nees	Herbaceous	No	0	0.37	1.48	0.46	0.34	0	0	0	0
Agavaceae	*Agave fourcroydes* Lem.	Rosette	No	0	0.6	0	0	0	0	0	0	0
Amaranthaceae	*Alternanthera flavescens* Kunth	Herbaceous	No	0	0	0	0	1.65	0	0	0	0
	Amaranthus sp.	Herbaceous	No	0	0	0	0	0	0	0	0	0.33
Amaryllidaceae	*Crinum × amabile* Donn ex Ker Gawl.	Herbaceous	No	0	0	0	0	0	0	0	0	0.4
Anacardiaceae	*Mangifera indica* L.	Trees	No	0	0	2.07	0	0	0	0	1.7	0
	Metopium brownei (Jacq.) Urb.	Trees	Yes	0	0	0.38	0	0	0	2.39	1.62	0.92
	Spondias purpurea L.	Trees	No	0	0	4.3	0	0	0	0	1.86	1.4
Annonaceae	*Annona muricata* L.	Trees	No	0	0	0.89	0	1.15	0	0	0	0
	Annona sp.	Trees	No	0	0	0	0.71	0	0	0	0	0
	Annona squamosa L.	Trees	No	0	1.01	2.47	0	0	0	0.72	1.36	1.38
Apocynaceae	Apocynaceae, unidentified species	Climber	No	0	0	0	0	0	0	0	0	0.31
	Asclepias curassavica L.	Herbaceous	No	0	0.37	0	0.43	0	0	0	0.64	0.31
	Cascabela gaumeri (Hemsl.) Lippold	Trees	No	0	0	0	0	0	1.13	0	0	0

Family	Taxa	Growth form	Mellif	Deciduous tropical forest				Semi-deciduous tropical forest		Semi-evergreen tropical forest		
				Baca	**Pucnachén**	**Chunkanán**	**Lerma**	**Mani**	**Dzan**	**Yaxché**	**Chanchén Palmar**	**San Juan de Dios**
Apocynaceae	*Cascabela thevetia* (L.) Lippold	Trees	No	0	0	0	0	0	0	0	0.32	0
	Cryptostegia grandiflora R.Br.	Shrub	No	0	0	0	0	0	0	0	0	0.36
	Cryptostegia sp.	Shrub	No	0	0	0	0	0	0	0	0.74	0
	Plumeria rubra L.	Trees	Yes	0	0	0	0	1.39	0	0	0	0
	Rauvolfia tetraphylla L.	Herbaceous	No	0	0.75	0	0	0	0	0.74	0.97	0
	Tabernaemontana divaricata (L.) R. Br. ex Roem. & Schult.	Shrub	No	0	0	0	0	0	0	0	1.19	0.52
	Pentalinon andrieuxii (Müll.Arg.) B.F.Hansen & Wunderlin	Climber	No	0	0	0	0.43	0	0	0	0	0
Araceae	*Anthurium schlechtendalii* Kunth	Herbaceous	No	0	0	0	0	0	0	0	0.98	0
Arecaceae	*Adonidia merrillii* (Becc.) Becc.	Palm tree	No	0	0	0	0	0	0	0.47	2.26	1.73
	Chamaedorea seifrizii Burret	Shrub	No	0	0	0	0	0	0	0	0	0.43
	Cocos nucifera L.	Palm tree	No	0	0	0	0	4.28	0	3.28	0	2.62
	Pseudophoenix sargentii H. Wendl. ex Sarg.	Palm tree	No	0	0	0	0	0	0	0	0.51	0
	Sabal sp.	Palm tree	No	1.06	1.73	0.54	0	1.04	0	0	1.06	2.72
	Thrinax radiata Lodd. ex Desf.	Palm tree	Yes	0	0	0	0	0	0	0.51	4.83	1.52
	Washingtonia sp.	Palm tree	No	0	0	0	0	0.77	0	0	0	0
Asparagaceae	*Beaucarnea pliabilis* (Baker) Rose	Trees	No	0	0	0	0	0.48	0	0	0	0.93
	Cordyline fruticosa (L.) A. Chev	Shrub	No	0	0	0	0	0	0	0	1.43	0
Asphodelaceae	*Aloe vera* (L.) Burm.f.	Rosette	No	0	0	0.4	0	0.38	0	0	0.33	0.31
Asteraceae	*Ageratum gaumeri* B.L. Rob.	Herbaceous	No	0	0	0	0	0	0	0	0	0.31
	Asteraceae. unidentified species	Shrub	No	0	0	0	0	0	0	0	0.32	0.32
	Bidens alba (L.) DC.	Herbaceous	No	0	0	0	0	0	0	0	0	0.65
	Calea sp.	Shrub	No	0	0	0	0	0	0	0	0.33	0
	Calea urticifolia (Mill.) DC.	Shrub	No	0	0	0	0	0	0	1.52	0	1.27
	Calyptocarpus vialis Less.	Herbaceous	No	0	0	0	0	0	0	0.36	0.32	0

Family	Taxa	Growth form	Mellif	Deciduous tropical forest				Semi-deciduous tropical forest		Semi-evergreen tropical forest		
				Baca	Pucnachén	Chunkanán	Lerma	Mani	Dzan	Yaxché	Chanchén Palmar	San Juan de Dios
Asteraceae	*Centratherum punctatum* Cass.	Herbaceous	No	0	0	0	0	0	0	0	0	0.31
	Chromolaena odorata (L.) R.M.King & H.Rob	Climber	No	0	0	0	0	0	0	0	0,32	0
	Cyanthillium cinereum (L.) H. Rob.	Herbaceous	No	0	0	1.1	0	0	0	0.36	0	0
	Delilia biflora (L.) Kuntze	Herbaceous	No	0	0	0.37	0	0	0	0	0	0
	Lagascea mollis Cav.	Herbaceous	No	0	0.74	0	0	0	0	0	0	0
	Melampodium divaricatum DC.	Herbaceous	No	0	0	0.37	0	1.39	0	0	0	0
	Melanthera nivea (L.) Small	Herbaceous	No	0	0	0	1.28	1.02	0.44	0.74	0	0.31
	Parthenium hysterophorus L.	Herbaceous	No	0	2.22	0.74	0	2.1	0.45	5.07	5.1	3.1
	Plagiolophus millspaughii Greenm.	Herbaceous	No	0	0.74	0	0	0	0	0.36	0	0
	Pluchea carolinensis (Jacq.) G. Don	Shrub	No	0	0	0	0.46	0	0	0	0	0
	Porophyllum punctatum S.F. Blake	Herbaceous	No	0	0	0	0.43	0.34	0	0	0.33	0
	Tithonia diversifolia (Hemsl.) A. Gray	Shrub	No	0	0	0	0	0	0	0	0.79	0.71
	Tridax procumbens L.	Herbaceous	Yes	0	1.49	2.24	0.86	5.82	1.3	0.36	0	0
	Viguiera dentata (Cav.) Spreng.	Herbaceous	Yes	0	0	0.37	2.57	2.22	0	0	0	0
	Wedelia acapulcensis Kunth	Herbaceous	No	0	0	0	0.44	0	0	0	0	0
	Zinnia elegans Jacq.	Herbaceous	No	0	0	0	0	0.35	0	0	0	0
Balsaminaceae	*Impatiens walleriana* Hook.f.	Herbaceous	No	0	0	0	0	0	0	0.36	0	0
Begoniaceae	*Begonia nelumbiifolia* Schltdl. & Cham.	Herbaceous	No	0	0	0	0	0.38	0	0	0	0
	Begonia sp.	Herbaceous	No	0	0	0	0	0.39	0	0	0	0
Bignoniaceae	Bignoniaceae, unidentified species	Climber	No	0	0	0	0.96	0	0	0	0	0
	Crescentia cujete L.	Trees	No	0	0	1.29	0	0	0	0	0	0
	Dolichandra unguis-cati (L.) L.G. Lohmann	Climber	No	0	0	0.53	0	0	0	0	0	0
	Parmentiera millspaughiana L.O. Williams	Trees	No	0	1.16	0.4	0	0	0	0	0	0

Family	**Taxa**	**Growth form**	**Mellif**	**Deciduous tropical forest**				**Semi-deciduous tropical forest**		**Semi-evergreen tropical forest**		
				Baca	**Pucnachén**	**Chunkanán**	**Lerma**	**Mani**	**Dzan**	**Yaxché**	**Chanchén Palmar**	**San Juan de Dios**
Bignoniaceae	*Tecoma stans* (L.) Juss. ex Kunth	Trees	No	0	0	0	0	0	0	0	0.52	0
Bixaceae	*Bixa orellana* L.	Trees	Yes	0	0	0	0	0	0	0.5	0.9	0.34
Boraginaceae	*Bourreria pulchra* Millsp.	Trees	No	0	0.88	0	0	0.36	1.29	0	0	0
	Cordia dodecandra DC.	Trees	Yes	0	0	0	0	0	0	0.97	0	0
	Cordia gerascanthus L.	Trees	Yes	0	0	4.68	0.81	0	0	0	0	0.64
	Ehretia tinifolia L.	Trees	No	0	0	0	0.43	0	0	0	1.08	0.45
	Heliotropium angiospermum Murray	Trees	No	0	0	0	0.42	0	0	1.08	0.97	0.63
	Tournefortia sp.	Climber	No	0	0	0	0	0	0.44	0	0.32	0
	Varronia curassavica Jacq.	Shrub	No	0	1.26	0.37	0	0.34	0	0.41	0	0.32
Brassicaceae	*Lepidium virginicum* L.	Herbaceous	No	0	0	0	0	0	0	0	0.32	0.31
Bromeliaceae	*Bromelia karatas* L.	Rosette	No	1.26	0	0	0	0	1.38	0	0	0
Burseraceae	*Bursera simaruba* (L.) Sarg.	Trees	No	0	1.52	2.18	0	0.71	2.02	0	0.64	0.39
Cactaceae	*Acanthocereus tetragonus* (L.) Hummelinck	Erect plant	No	3.74	0	0.39	0	0	0	0	0	0
	Selenicereus undatus (Haw.) D.R.Hunt	Climber	No	0	0	0	0	0	0	0	0	0.45
	Opuntia inaperta (Schott ex Griffiths) D.R.Hunt	Shrub	No	0.87	0	0	0	0	0	0	0	0
	Selenicereus grandiflorus (L.) Britton & Rose	Climber	No	0	0	0	0	0	0	0	0.32	0
Cannabaceae	*Celtis iguanaea* (Jacq.) Sarg.	Trees	No	0	0	0	0	1.12	0	0	0	0
Cannaceae	*Canna indica* L.	Herbaceous	No	0	0	0.38	0	0	0	0	0.32	0
Capparaceae	*Crateva tapia* L.	Trees	No	0.45	0	0	0	0	0	0	0	0
Caricaceae	*Carica papaya* L.	Shrub	No	0	0.38	0	0.44	1.02	0	0	1.68	0.68
Celastraceae	*Crossopetalum gaumeri* (Loes.) Lundell	Shrub	No	0	0	0	0	0.34	0	0	0	0
	Semialarium mexicanum (Miers) Mennega	Trees	No	0	0	0	0	1.91	2.29	0.36	0	0.62
Combretaceae	*Terminalia buceras* (L.) C. Wright	Trees	Yes	0	0	0	0	0	0	0	0	1.33

Family	Taxa	Growth form	Mellif	Deciduous tropical forest				Semi-deciduos tropical forest		Semi-evergreen tropical forest		
				Baca	**Pucnachén**	**Chunkanán**	**Lerma**	**Mani**	**Dzan**	**Yaxché**	**Chanchén Palmar**	**San Juan de Dios**
Combretaceae	*Terminalia catappa* L.	Trees	Yes	0	0	0	0	0	0	0.48	0	1.53
Commelinaceae	*Commelina erecta* L.	Herbaceous	No	0	1.89	0.74	0.43	0.7	0	0	0	0.31
	Tradescantia spathacea Sw.	Herbaceous	No	0	0	0	0	0	0	0	0	0.63
Convolvulaceae	*Camonea umbellata* (L.) A.R. Simões & Staples	Climber	No	0	0	0	0.44	0	0	0	0	0
	Distimake dissectus (Jacq.) A.R. Simões & Staples	Herbaceous	No	0	0	0	0	1.78	0	0	0	0
	Distimake quinquefolius (L.) A.R. Simões & Staples	Herbaceous	No	0	0	0	0.45	0	0	0	0	0
	Ipomoea crinicalyx S. Moore	Herbaceous	Yes	0	0	0	0	0.34	0	0	0	0.8
	Ipomoea hederifolia L.	Climber	No	0	0	0	0	0	0.43	0	0	0
	Ipomoea heterodoxa Standl. & Steyerm.	Herbaceous	No	0	0	0	0	0	0	0.36	0	0
	Ipomoea indica (Burm.) Merr.	Climber	No	0	0	0	0	0	0	0	0	0.66
	Ipomoea nil (L.) Roth	Herbaceous	Yes	0	0	0.37	0	0	0	0	0	0
	Ipomoea triloba L.	Climber	Yes	0	0	0.75	0	0	0	0	0	0
	Jacquemontia nodiflora G.Don	Climber	No	0	0.37	0	0	0	0	0	0	0
	Jacquemontia pentanthos (Jacq.) G. Don	Herbaceous	Yes	0	0	0	0	0.74	0.89	0	0	0.42
Crassulaceae	*Kalanchoe pinnata* (Lam.) Pers.	Herbaceous	No	0	0	0	0	0	0	0.72	0	0
	Kalanchoe sp.	Herbaceous	No	0	0	0	0	0.39	0	0	0	0
Cucurbitaceae	*Cucumis melo L.*	Herbaceous	No	0	0	0	0	0.71	0	0	0	0
	Cucurbita moschata Duchesne	Climber	No	0	0	2.29	0	0.7	0	0	0	0
	Momordica charantia L.	Climber	No	0	0	0	0	0	0	0.73	1.39	0
	Momordica sp.	Climber	No	0	0	0	0.43	0	0	0	0	0
Cyperaceae	*Cyperus* sp.	Herbaceous	No	0	0	0	0	0.38	0	0	0	0
Dioscoreaceae	*Dioscorea* sp.	Climber	No	0	0	0	0	0	0	0	0	0.76
Ebenaceae	*Diospyros anisandra* S.F. Blake	Shrub	No	0	0.77	2.5	1.31	0	0	0.36	0	0
	Diospyros salicifolia Humb. & Bonpl. ex Willd.	Trees	No	0	0	0	0	0.37	1.04	0	0	0
	Diospyros tetrasperma Sw.	Trees	No	0	0	0	0	0	0	0.37	0	0

Family	Taxa	Growth form	Mellif	Deciduous tropical forest				Semi-deciduous tropical forest		Semi-evergreen tropical forest		
				Baca	**Pucnachén**	**Chunkanán**	**Lerma**	**Mani**	**Dzan**	**Yaxché**	**Chanchén Palmar**	**San Juan de Dios**
Euphorbiaceae	*Acalypha leptopoda* Müll. Arg.	Shrub	No	0	0	0	0	0	0	1.1	0	0.36
	Acalypha sp.	Shrub	No	0	0	0	3.46	0	0	0.73	0	0.69
	Astraea lobata (L.) Klotzsch	Herbaceous	No	0	0	0	0	0.67	0	0	0	0
	Cnidoscolus aconitifolius I.M. Johnst.	Shrub	No	0	0	0.59	0	0.46	0	0.36	1.54	0
	Cnidoscolus souzae McVaugh	Shrub	No	0	1.13	0	0	0	0.46	0	0	0
	Croton ameliae Lundell	Shrub	No	0	0	0	0	0	0	0	0	0.31
	Croton arboreus Millsp.	Trees	No	0	0	0	0	2.19	2	0.71	0	0
	Croton ciliatoglandulifer Ortega	Herbaceous	No	0	0.37	0	0	0	0	0	0	0
	Croton humilis L.	Herbaceous	Yes	0	0.78	0	0	0.73	0	0	0	0
	Croton sp.	Shrub	No	0.43	1.2	1.19	0.42	0	0	0.36	0	0
	Dalechampia scandens L.	Herbaceous	No	0	0	1.14	0	0	0	0	0	0
	Euphorbia heterophylla L.	Herbaceous	No	0	0	0	0.42	0	0	0	0	0
	Euphorbia sp.	Herbaceous	No	0	0	0	0.43	0	0	0	0	0
	Ricinus communis L.	Shrub	No	0	0	0	0	0	0	0	0.34	0
	Tragia yucatanensis Millsp.	Herbaceous	No	0	0.38	0	0	0	0	0	0	0
Fabaceae	*Ctenodon fascicularis* (Schltdl. & Cham.) A. Delgado	Herbaceous	No	0	0	0	0.42	0	0	0	0	0
	Apoplanesia paniculata C. Presl	Trees	No	0	0	1.55	0	0	0	0	0	0
	Bauhinia divaricata L.	Trees	No	0	0	0	1.75	1.82	0	1.45	0.69	0.67
	Bauhinia monandra Kurz	Trees	No	0	0	0	0	0	0	0	0	0.37
	Caesalpinia pulcherrima (L.) Sw.	Shrub	No	0.53	0	0.45	0	0	0	0.57	0.91	0
	Tara vesicaria (L.) Molinari, Sánchez Och. & Mayta	Trees	No	0	0	0	0.67	0	0	0	0	0
	Cassia fistula L.	Trees	Yes	0	0	0	0	0	0	0	5.9	0.63
	Cenostigma gaumeri (Greenm.) Gagnon & G.P. Lewis	Trees	No	0	1.45	2.65	0	0	0	0.43	0	4.27
	Centrosema virginianum (L.) Benth.	Herbaceous	No	0	0	0	0	0	0.45	0	0	0

Family	Taxa	Growth form	Mellif	Deciduous tropical forest				Semi-deciduous tropical forest		Semi-evergreen tropical forest		
				Baca	Pucnachén	Chunkanán	Lerma	Mani	Dzan	Yaxché	Chanchén Palmar	San Juan de Dios
Fabaceae	*Chamaecrista glandulosa var. flavicoma* (Kunth) H.S. Irwin & Barneby	Shrub	No	0	0	0	0	0.44	0	0	0	1.42
	Chloroleucon mangense (Jacq.) Britton & Rose	Trees	No	0	0	0	0	0	0	4.24	0	0
	Coulteria mollis Kunth	Herbaceous	No	0	2.3	0	0	0	0	0	2.86	0.44
	Coursetia caribaea (Jacq.) Lavin	Herbaceous	No	0	0	0.37	0	0	0	0	0	0
	Coursetia greenmanii (Millsp.) Duno & Carnevali	Herbaceous	No	0	0	0	0	0	0	0.78	0	0
	Crotalaria sp.	Herbaceous	No	0	0	0	0	0	0	0	0	0.36
	Delonix regia (Bojer) Raf.	Trees	Yes	0	0	0	0	0	0	0.94	0	0
	Desmanthus virgatus (L.) Willd.	Herbaceous	No	0	0	0.37	0	0	0	0.36	0	0
	*Desmodium incanum (*Sw.) DC.	Herbaceous	Yes	0	0	0	0	0	0	0	0.32	0
	Desmodium sp.	Herbaceous	No	0	0	0	0	0	1.32	0	0	0
	Diphysa yucatanensis A.M. Hanan & M. Sousa	Trees	No	0	0.48	0	0.87	0	0	0	0	1.39
	Enterolobium cyclocarpum (Jacq.) Griseb.	Trees	Yes	0	0	0	0	0	0	9.83	0	0
	Erythrina standleyana Krukoff	Trees	No	0	0	0	0	0	0	0	0	0.34
	Erythrostemon yucatanensis (Greenm.) Gagnon & G.P. Lewis	Trees	No	0	0	0	0	0	0	0.55	0	0.9
	Gliricidia maculata (Kunth) Steud.	Trees	No	0	0	0	0	0	0	0	0	1.39
	Havardia albicans Britton & Rose	Trees	Yes	2.36	0.42	0	0	1.37	0.77	0	0	0.33
	Leucaena leucocephala (Lam.) de Wit *ssp. leucocephala*	Trees	Yes	5.99	0	0.38	5.24	1.02	0	0	0	2.98
	Lonchocarpus rugosus Benth.	Trees	Yes	0	0	0	0	0	0	0	0	0.31
	Lonchocarpus sp.	Trees	No	0	0	0	0.73	0.35	3.16	0	0	0
	Lysiloma latisiliquum (L.) Benth.	Trees	No	0	13.27	0.53	0	1.01	0	0	0	0.32
	Macroptilium sp.	Herbaceous	No	0	0	0	0.86	0	0	0	0	0
	Mimosa bahamensis Benth.	Trees	Yes	0	5.36	1.82	2.12	0.71	5.7	0	0	1.62

Family	Taxa	Growth form	Mellif	Deciduous tropical forest				Semi-deciduous tropical forest		Semi-evergreen tropical forest		
				Baca	Pucnachén	Chunkanán	Lerma	Mani	Dzan	Yaxché	Chanchén Palmar	San Juan de Dios
Fabaceae	*Mimosa* sp.	Shrub	No	0	0	0	1.04	0	0	0	0	0
	Phaseolus sp.	Climber	No	0	0	0	0	0	0	0	0.32	0
	Piscidia piscipula (L.) Sarg.	Trees	Yes	6.5	3.44	3.8	8.08	8.85	7.42	0.73	0.81	3.99
	Rhynchosia minima (L.) DC.	Herbaceous	No	0	0	0	0.43	0	0	0	0	0
	Rhynchosia sp.	Climber	No	0	0	0	0	0	0.44	0	0	0
	Senegalia gaumeri Britton & Rose	Trees	No	13.01	0	0	0.48	0	0	0	0	0
	Senna atomaria (L.) H.S. Irwin & Barneby	Trees	Yes	6.67	0	0	0	0	0	0	0	0
	Senna pendula (Humb. & Bonpl. ex Willd.) H.S. Irwin & Barneby	Climber	No	0	0	0	0	0	0	0	0.45	0
	Senna racemosa (Mill.) H.S. Irwin & Barneby *var. racemosa*	Trees	Yes	0	0.4	0	1.29	0	0.56	0	0	4.81
	Senna sp.	Trees	No	0	0	0	0.44	0	0	0	0	0
	Tamarindus indica L.	Trees	Yes	0	10.46	0	0	0	0	0	0	1.48
	Tephrosia cinerea (L.) Pers.	Herbaceous	No	0	0	0	0.43	0	0	0	0	0
	Vachellia collinsii (Saff.) Seigler & Ebinger	Shrub	No	0	0	0	0.54	0	0	0	0	0
	Vachellia pennatula var. parvicephala (Seigler & Ebinger) Seigler & Ebinger	Trees	No	2.74	0	0.52	0	0	1.61	0	0	0
	Vachellia sp.	Shrub	No	0	0.5	0	1.28	0	0	0	0	0
	Zapoteca formosa (Kunth) H.M. Hern.	Shrub	No	0	0.37	0	0	0	0	0	0	0
Lamiaceae	*Callicarpa acuminata* Kunth	Shrub	No	0	0	0	0	0	0	0	0.32	1.51
	Mesosphaerum pectinatum (L.) Kuntze	Herbaceous	No	0	0	0	0	0	2.72	0.4	0	0
	Ocimum campechianum Mill.	Herbaceous	No	0	1.48	0	0	0	0	0	0	0
	Salvia serotina L.	Herbaceous	No	0	0	0	0	0.34	0	2.89	0	0.31
	Salvia sp.	Herbaceous	No	0	0	0	0.46	0	0	0	0	0
	Vitex gaumeri Greenm.	Trees	Yes	0	0	0	0	0	0	0	0.32	0
Lythraceae	*Punica granatum* L.	Trees	No	0	0	0.5	0	0	0	0	0.4	0.62

Family	Taxa	Growth form	Mellif	Deciduous tropical forest				Semi-deciduous tropical forest		Semi-evergreen tropical forest		
				Baca	**Pucnachén**	**Chunkanán**	**Lerma**	**Mani**	**Dzan**	**Yaxché**	**Chanchén Palmar**	**San Juan de Dios**
Malpighiaceae	*Bunchosia swartziana* Griseb.	Shrub	No	0	2.28	0.4	0	0	0.6	0.37	0.33	0
	Byrsonima roigii Urb.	Trees	Yes	0	0	0	0	0	0	0	0.34	0
	Byrsonima crassifolia (L.) Kunth	Trees	Yes	0	0	0	0	0	0	0	3.09	0
	Stigmaphyllon lindenianum A. Juss.	Climber	No	0	0	0	0	0	0	0	0	0.32
Malvaceae	*Abutilon permolle* (Willd.) Sweet	Herbaceous	No	0	0	0	0	0	0	2.17	0	0
	Abutilon trisulcatum (Jacq.) Urb.	Herbaceous	No	10.17	0	0	2.28	0	0	0	0.32	0
	Anoda cristata (L.) Schltdl.	Herbaceous	No	0	0	0	0.85	0	0	0	0	0
	Ayenia abutilifolia (Turcz.) Turcz.	Herbaceous	No	0	0	0.74	0	0	0	0	0	0
	Ayenia aculeata (Jacq.) Christenh. & Byng	Climber	No	0	0	0	1.23	0	0	0	0	0
	Ceiba pentandra (L.) Gaertn.	Trees	No	0	0	0	0	0	0	1.19	0	0.69
	Corchorus siliquosus L.	Herbaceous	Yes	0	0	1.14	0	0	0.43	1.09	0.32	0.63
	Gaya calyptrata (Cav.) Kunth ex K. Schum.	Herbaceous	No	0	0	0.37	0	0.34	0	0	0	0.31
	Gossypium hirsutum L.	Shrub	No	0	0	0.85	0	0	0	0.39	0	0.91
	Guazuma ulmifolia Lam.	Trees	Yes	4.65	0	2.63	17.24	0	0	1.07	0	0.64
	Herissantia crispa (L.) Brizicky	Herbaceous	Yes	0	0.37	0.74	0	0	0	0	0	0
	Hibiscus poeppigii Garcke	Herbaceous	No	0	0	0	0	0	0	0	0	0.31
	Hibiscus rosa-sinensis L.	Shrub	No	0	0	0	0	0	0	1.28	0	0
	Malachra sp.	Shrub	No	0	0	0	0.43	0	0	0	0	0
	Malvastrum coromandelianum (L.) Garcke	Herbaceous	No	0	0	2.23	0.45	0.34	0	2.17	0	0.63
	Malvaviscus arboreus Dill. ex Cav.	Shrub	No	0	0	0	5.87	0	0	0	0	0.31
	Melochia tomentosa L.	Shrub	No	0	0.37	0	0	0	0	0	0	0.95
	Sida sp.	Herbaceous	No	0	0	0.39	0	0	0	0.36	0	0.31
	Sida spinosa L.	Herbaceous	No	0	0	0.74	0	0	0	0	0	0

Family	Taxa	Growth form	Mellif	Deciduous tropical forest				Semi-deciduous tropical forest		Semi-evergreen tropical forest		
				Baca	**Pucnachén**	**Chunkanán**	**Lerma**	**Mani**	**Dzan**	**Yaxché**	**Chanchén Palmar**	**San Juan de Dios**
Meliaceae	*Waltheria indica L.*	Herbaceous	No	0	4.1	0	0.42	1.01	3.07	0	0	0.65
	Waltheria rotundifolia Schrank	Herbaceous	No	0	0.38	0	0	0	0	0	0	0
	Wissadula amplissima (L.) R.E. Fr.	Herbaceous	No	0	0	1.12	0	0	0	0	0	0
	Azadirachta indica A. Juss.	Trees	No	0.47	0	0	0	0	0	0	0	0
	Cedrela odorata L.	Trees	Yes	0	0	0	2.83	0.8	0	7.74	2.67	3.58
	Melia azedarach L.	Trees	No	0	0	0	0	0	0	0	0.32	0
	Swietenia macrophylla King in Hook	Trees	No	0	0	0	0	0	0	1.51	0	0
Menispermaceae	*Cissampelos pareira* L.	Climber	No	0	0	0	0	0.68	0	0	1.02	0
Moraceae	*Brosimum alicastrum* Sw.	Trees	No	0.65	0	0.76	1.68	0	0	1.81	1.27	2.15
	Ficus cotinifolia Kunth	Trees	No	0	0	0.37	0	0	0	0	0	0
	Maclura tinctoria (L.) D. Don ex Steud	Trees	No	2.21	0	0.68	1.52	0	0	0	0	0
Moringaceae	*Moringa oleifera* Lam.	Trees	Yes	0	0	0	0	0	0	0	0.97	0
Musaceae	*Musa paradisiaca* L.	Herbaceous	No	0	0	0	0	0	0	0	1.13	0.4
Myrtaceae	*Eugenia* sp.	Trees	No	0	0	0	0	0	1.46	0	0	0
	Psidium guajava L.	Trees	Yes	0	0	2.17	0	0	0	0	0	0.61
	Psidium oligospermum Mart. ex DC.	Trees	Yes	0	0	0	0	0	2.88	0	0	0
Nyctaginaceae	*Boerhavia coccinea* Mill.	Herbaceous	No	0	0	0	0	0	0	0	0.33	0
	Boerhavia erecta L.	Herbaceous	Yes	0	0	0	0	0	0	0.36	0.96	0
	Bougainvillea sp.	Shrub	No	0	0	0.69	0	0	0	0	1.61	0.41
	Mirabilis jalapa L.	Herbaceous	No	0	0	0.76	0	0	0	0	0	0
	Neea sp.	Shrub	No	0	0	0.37	0.44	0	0	0	0	0
	Pisonia aculeata L.	Climber	No	0	0	0	1.44	0	0	0.36	0	0
Orchidaceae	*Vanilla* sp.	Climber	No	0	0	0	0	0	0	0	0.37	0
Oxalidaceae	*Oxalis frutescens* L.	Herbaceous	No	0	0.37	0	0	0	0	0	0	0
Passifloraceae	*Passiflora ciliata* Aiton	Climber	No	0	0	0	0	0.34	0	0	0	0

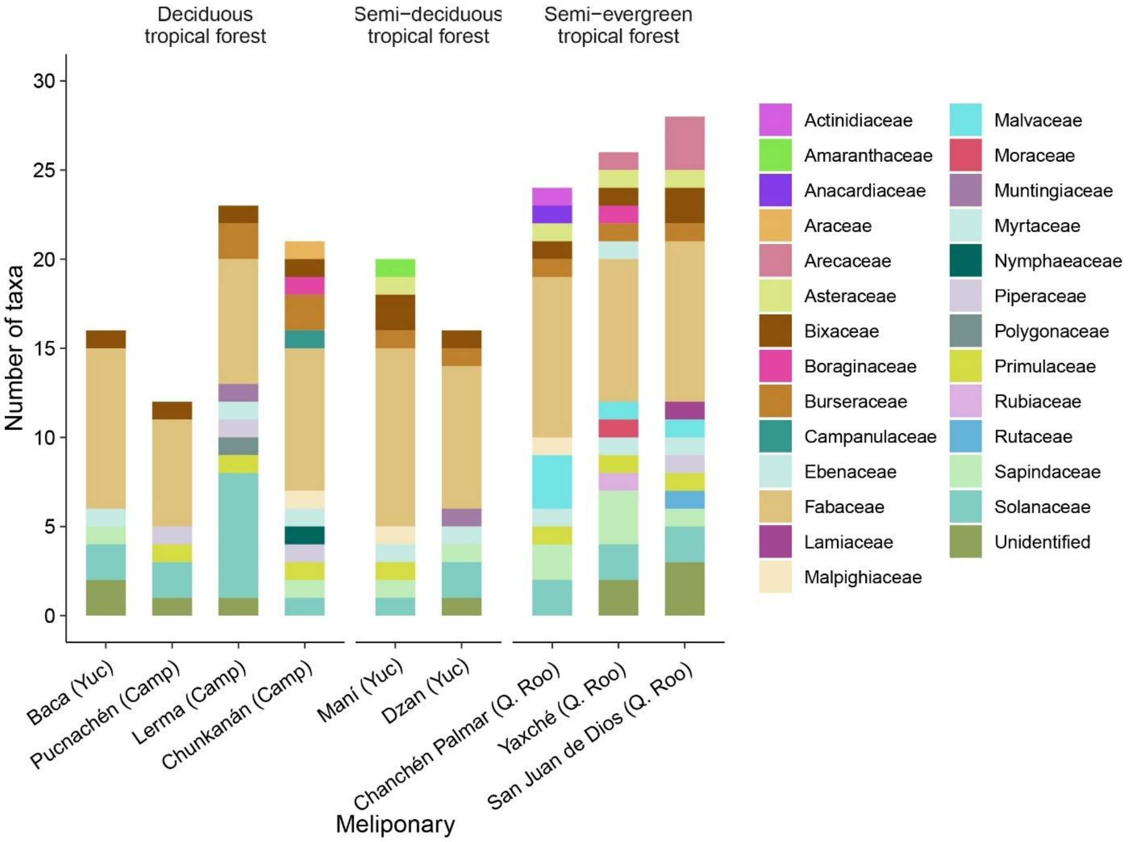
Family	**Taxa**	**Growth form**	**Mellif**	**Deciduous tropical forest**				**Semi-deciduous tropical forest**		**Semi-evergreen tropical forest**		
				Baca	**Pucnachén**	**Chunkanán**	**Lerma**	**Mani**	**Dzan**	**Yaxché**	**Chanchén Palmar**	**San Juan de Dios**
Passifloraceae	*Turnera ulmifolia* L.	Shrub	No	0	0	0.37	0	0	0	0	0	0
Phyllanthaceae	*Astrocasia tremula* (Griseb.) G.L. Webster	Trees	No	0	0	0	0.42	0	0	0	0	0
	Phyllanthaceae, unidentified species	Herbaceous	No	0	0	0	0.42	0	0	0	0	0
	Phyllanthus acidus (L.) Skeels	Trees	No	0	0	0.97	0	0	0	0	0.33	0
Phytolaccaceae	*Petiveria alliacea* L.	Herbaceous	No	17.27	0	0	0	0	0	0.37	0	0
	Rivina humilis L.	Herbaceous	No	14.89	0	0	0	0	0	2.56	0	0
Piperaceae	*Piper auritum* Kunth	Shrub	No	0	0	0	0	0	0	0	0.37	0.7
Plumbaginaceae	*Plumbago zeylanica* L.	Herbaceous	No	0.86	0	0	0	0	0	0.73	0	0
Poaceae	*Chloris* sp.	Herbaceous	No	0	0	0	0	0	0.9	0	0	0
	Dactyloctenium aegyptium (L.) Willd.	Herbaceous	No	0	0	0	0	0	0.47	0	0	0
	Lasiacis divaricata (L.) Hitchc.	Herbaceous	No	0	0	0	0.43	0	0	0	0	0
	Lasiacis sp.	Herbaceous	No	0.43	0	0.38	0	0.34	0	1.45	0	0
	Paspalum fimbriatum Kunth	Herbaceous	No	0	0	0	0	0	0.44	0	0	0
	Poaceae	Shrub	No	0	0	0	3.36	0	0	0	0.34	0
	Saccharum officinarum L.	Herbaceous	No	0	0	0	0	0	0	0	0	0.51
Polygonaceae	*Coccoloba spicata* Lundell	Trees	Yes	0	0	0	0	0.34	0	0	0.98	0
	Gymnopodium floribundum Rolfe	Trees	Yes	1.48	9.61	2.35	0	0	2.18	2.68	0.32	0.63
	Neomillspaughia emarginata S.F. Blake	Trees	Yes	0	1.87	0.62	0	1.05	17.57	0.53	0	0.34
Portulacaceae	*Talinum paniculatum* (Jacq.) Gaertn.	Herbaceous	No	0	0	0	0	0	0	1.82	0.66	0
Primulaceae	*Ardisia escallonioides* Schltdl. & Cham.	Trees	No	0	0	0	0	0.35	1.9	0	0	0.31
Rhamnaceae	*Colubrina arborescens* Sarg.	Trees	No	0	0	0	0	0	0	0	0	0.85
	Colubrina elliptica (Sw.) Brizicky	Trees	No	0	0.88	0	0	0	0	0	0	0
	Colubrina yucatanensis (M.C. Johnst.) G.L. Nesom	Trees	No	0	0	1.03	0	0	0	0	0	0

Family	Taxa	Growth form	Mellif	Deciduous tropical forest				Semi-deciduous tropical forest		Semi-evergreen tropical forest		
				Baca	Pucnachén	Chunkanán	Lerma	Mani	Dzan	Yaxché	Chanchén Palmar	San Juan de Dios
Rhamnaceae	*Karwinskia humboldtiana* (Schult.) Zucc.	Trees	No	0	0	0	0	0.42	0	0	0	0
Rosaceae	*Rosa* sp.	Shrub	No	0	0	0	0	0	0	0	0.35	0.33
Rubiaceae	*Chiococca alba* Hitchc.	Shrub	No	0	0	0	0	0	0.46	0	0	0.33
	Guettarda combsii Urb.	Trees	No	0	0	0	0	0.34	0	0	0	0
	Hamelia patens Jacq.	Shrub	No	0	0	1.34	0.68	4.01	0	2.98	4.48	2.49
	Ixora coccinea L.	Shrub	No	0	0	0	0	0	0	0	0	0.33
	Machaonia lindeniana Baill.	Trees	No	0	0.43	0	0	0	0	0	0	0
	Morinda citrifolia L.	Shrub	No	0	0	0	0	0	0	0	0.54	0.71
	Morinda royoc L.	Climber	No	0	2.6	7.63	0.42	2.04	1.31	0.74	2.28	0.31
	Psychotria sp.	Shrub	No	0	0	0	0	0	0	0	0	0.31
	Randia longiloba Hemsl.	Trees	No	0.71	0	0	0	0	0	0.88	0	0
	Randia obcordata S. Watson	Shrub	No	0	0.42	0.38	0	0	0	0	0	0
	Spermacoce sp.	Herbaceous	No	0	0	0	0	0	0.87	0	0	0
	Spermacoce tetraquetra A. Rich.	Herbaceous	No	0	0	0	0	0	0.87	0	0	0
	Spermacoce verticillata L.	Herbaceous	No	0	0	0	0	0	0	1.45	0	0.31
Rutaceae	*Citrus x aurantium* L.	Trees	No	0	0	0	0	2.82	0	1.5	1.47	0.69
	Citrus x latifolia Tanaka ex Q. Jiménez	Trees	No	0	3.17	0	0	10.31	0	0	0	0
	Citrus reticulata Blanco	Trees	No	0	0.54	0	0	4.77	2.93	0	0.35	0
	Citrus × aurantium var. *sinensis* L.	Trees	Yes	0	0.96	0	0	6.39	19.72	0	3.36	0.5
	Murraya paniculata (L.) Jack	Shrub	Yes	0	0	0.99	0	0	0	0	2.7	0
	Pilocarpus racemosus Vahl	Trees	No	0	0	0	0	0	0	0	0	0.31
	Zanthoxylum caribaeum Lam.	Trees	No	0	0	0.4	0.43	0	0	0	0	0
Salicaceae	*Casearia laetioides* Warb	Trees	No	0	0	0	0	0	0	0	0	0.94
Sapindaceae	*Allophylus cominia* Sw.	Trees	No	0	0	0	0	0.34	0	0	0	0
	Melicoccus bijugatus Jacq.	Trees	No	0	0	1.74	0	0	0	0.58	0	0
	Melicoccus oliviformis Kunth	Trees	No	0	0	5.29	0	0	0	0.4	6.3	0

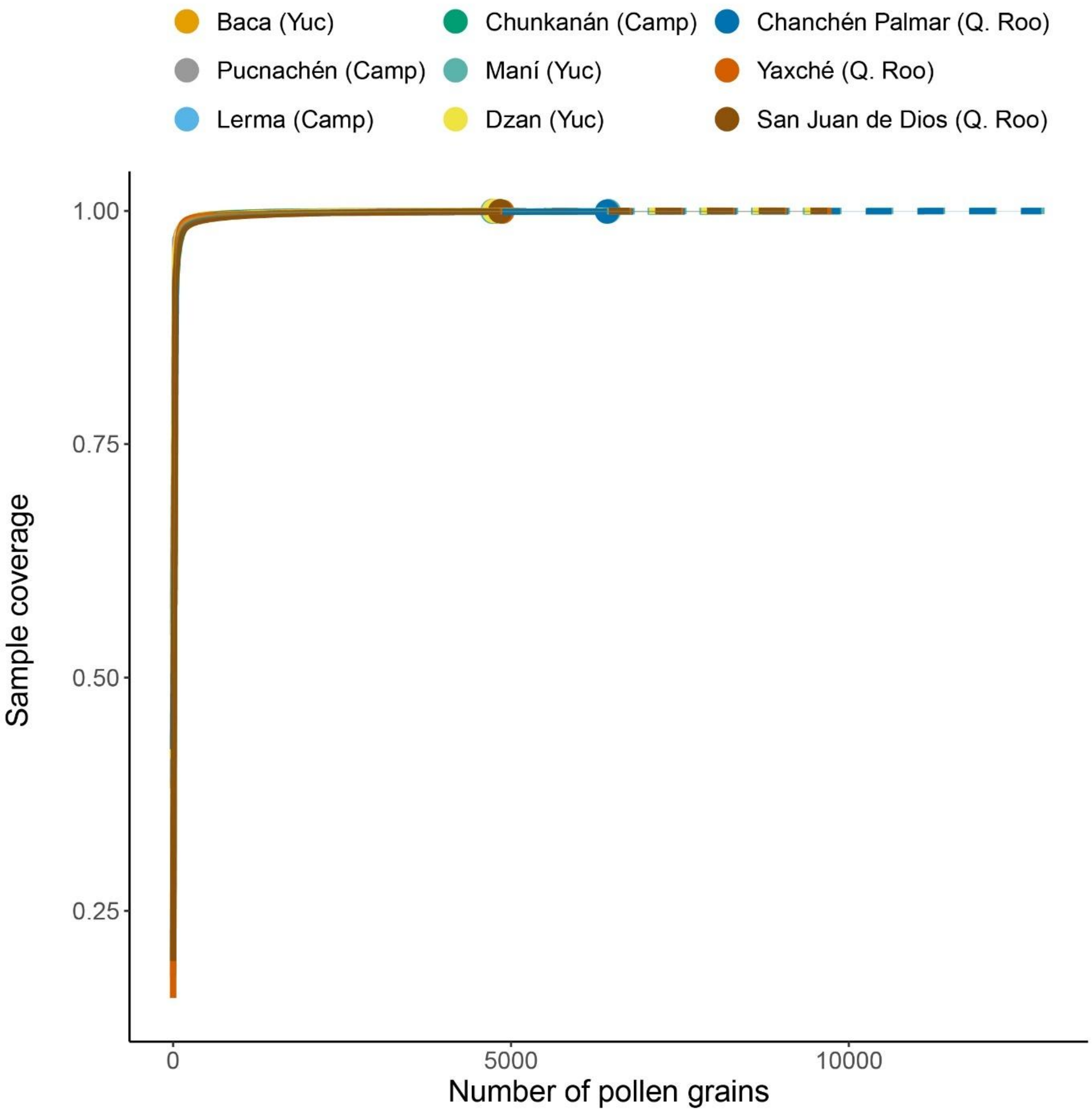
Family	**Taxa**	**Growth form**	**Mellif**	**Deciduous tropical forest**				**Semi-deciduous tropical forest**		**Semi-evergreen tropical forest**		
				Baca	**Pucnachén**	**Chunkanán**	**Lerma**	**Mani**	**Dzan**	**Yaxché**	**Chanchén Palmar**	**San Juan de Dios**
	Paullinia fuscescens Kunth	Climber	No	0	0	0.5	0	0	0	0	0	0
	Sapindaceae, unidentified species	Herbaceous	No	0	0.38	0	0	0	0	0	0	0
	Sapindus saponaria L.	Trees	No	0	0	0	0	0	0	0	0	1.03
	Thouinia paucidentata Radlk.	Trees	Yes	0	0	0	1.01	0	0	0	0.32	0
Sapotaceae	*Chrysophyllum cainito* L.	Trees	No	0	0	0	0	0	0	1.72	0	0
	Chrysophyllum mexicanum Brandegee ex Standl.	Trees	Yes	0	0	0.76	0	0	0	0	0	0.61
	Manilkara zapota (L.) P. Royen	Trees	Yes	0	0	2.01	0	0	0	0	1.7	0
Scrophulariaceae	*Capraria biflora* L.	Herbaceous	No	0	0	2.28	0	0.34	0	0.73	0.97	1.92
	Capraria frutescens (Mill.) Briq.	Herbaceous	No	0	0	0	0	0.33	0	1.44	0.32	0
Simaroubaceae	*Alvaradoa amorphoides* Liebm.	Trees	Yes	0.62	0	0	0	1.89	0	0.39	0.32	0
Solanaceae	*Capsicum annuum* L.	Herbaceous	No	0	0	0	0	0	0	0.36	0.32	0.63
	Schwenckia americana L.	Herbaceous	No	0	0	0.37	0	0	0	0	0	0
	Solanum donianum Walp.	Herbaceous	No	0	0	0	0.98	0	0	0	0	0
	Solanum erianthum D. Don	Trees	No	0	1.16	0	1.04	0	0	0	0	0
	Solanum hirtum Vahl	Shrub	No	0	0	0	0	0	0	0.38	0	0
	Solanum lycopersicum L.	Herbaceous	No	0	0	0	0	0	0	0	0.66	0
	Solanum sp.	Herbaceous	No	0	0	0	0	0	0	0.73	0	0
	Solanum houstonii Martyn	Herbaceous	No	0	0.37	0	0	0	0	0	0	0
Urticaceae	*Cecropia peltata* L.	Trees	No	0	0	0	0	0	0	0	0.36	3.14
Verbenaceae	*Aloysia virgata* (Ruiz & Pav.) Pers.	Shrub	Yes	0	1.66	0	0	0	0	0	0.44	0
	Verbena canadensis (L.) Britton	Herbaceous	No	0	0	0	0	0.35	0	0	0	0
	Lantana camara L.	Shrub	No	0	0.37	0.37	0	0.34	0	0	0	1.57
	Lippia origanoides Kunth	Shrub	No	0	3.65	0	0	0	0	0	0	0
	Priva lappulacea (L.) Pers.	Herbaceous	No	0	0	0	0	0	0.43	2.16	0.96	0
	Tamonea curassavica (L.) Pers.	Herbaceous	No	0	0.76	0.39	0	0	0	0	0	0

	Verbenaceae, unidentified species	Herbaceous	No	0	0	0	0	0	0	0.36	0	0
Vitaceae	*Cissus verticillata* (L.) Nicolson & C.E.Jarvis	Climber	No	0	0	0.44	0	0	0	0	0.34	0.36
Ximeniaceae	*Ximenia americana* L.	Trees	No	0	0.96	0	0	0	0	0	0	0
Zingiberaceae	*Alpinia* sp.	Shrub	No	0	0	0	0	0.58	0	0	0	0

ANEXO III. Number of morphotypes/species of pollen grains per botanical family in *Melipona beecheii* pot-pollen from nine meliponaries on the Yucatan Peninsula.



ANEXO IV. Sample coverage of pollen morphotypes in *Melipona beecheii* pot-pollen from nine meliponaries on the Yucatan Peninsula.



ANEXO V. Eigenvectors of species on the ordination axes for the species abundance of *Melipona beecheii* pot-pollen at nine meliponaries on the Yucatan Peninsula.

Species	PC1	PC2	Species	PC1	PC2
Alternanthera brasiliana var. *villosa*	-0,00018	0,00078	*Mimosa bahamensis*	-0,052	0,088661
Amyris elemifera	-0,02929	0,097514	*Mimosa* sp.	-0,08606	-0,04699
Anthurium sp.	0,00568	-0,00269	Morfo_43	-0,02085	-0,04793
Arecaceae_1	-0,02247	0,040934	Morfo_53	-0,00366	-0,01063
Arecaceae_2	-0,00547	0,018213	Morfo_62	-0,00221	0,002958
Asteraceae	-0,00013	0,000552	Morfo_65	-0,01126	0,027645
Astronium graveolens	-0,00115	0,006923	Morfo_74	-0,00632	0,02103
Bixa orellana	-0,01259	0,042286	Morfo_81	-0,00447	0,014871
Bourreria sp.	0,001848	0,002435	Morfo_85	0,003604	0,000949
Brosimum alicastrum	-0,00221	0,002958	Morfo_86	0,012708	-0,00352
Bursera schlechtendalii	0,141921	-0,05783	*Muntingia calabura*	0,018622	-0,04188
Bursera simaruba	0,279428	-0,0853	*Myrsine cubana*	0,101318	0,012571
Byrsonima roigii	-4,9E-05	0,070606	*Nymphaea* sp.	0,009839	-0,00466
Cenostigma gaumeri	-0,00018	0,00078	*Physalis philadelphica*	0,081769	-0,02264
Cestrum sp.	0,031643	-0,00876	*Physalis viscosa*	0,147329	-0,04079
Coccoloba sp.	0,013921	-0,00385	*Piper auritum*	0,02705	0,016607
Cochlospermum vitifolium	0,606687	0,08172	*Psichotria* sp.	-0,00221	0,002958
Corchorus siliquosus	-0,00316	0,010515	*Psidium guajava*	0,182432	-0,09458
Crotalaria sp.	-0,15686	0,49188	*Saurauia* sp.	-0,00115	0,006923
Desmanthus virgatus	-0,06564	-0,20892	*Senna occidentalis*	0,011361	-0,00538
Desmodium aff. *scorpiurus*	-0,00494	-0,00315	*Senna pallida*	-0,00447	0,014871
Desmodium sp.	0,004219	-0,00772	*Senna racemosa* var. *racemosa*	-0,40975	-0,05757
Diospyros sp.	-0,01014	0,013556	*Senna* sp.	-0,04779	0,388261
Grona triflora	-0,01714	-0,04075	*Serjania goniocarpa*	-0,01648	-0,01765
Harpalyce arborescens	0,01884	-0,00892	*Serjania* sp.	-0,0099	0,024129
Heliocarpus donnellsmithii	-0,00115	0,006923	*Solanum donianum*	-0,02337	-0,07332
Heliocarpus mexicanus	-0,00512	0,016174	*Solanum erianthum*	-0,24007	0,394879
Leonotis nepetifolia	-0,00447	0,014871	*Solanum nudum*	-0,04734	0,178504
Leucaena leucocephala	-0,01218	-0,00088	*Solanum torvum*	0,140598	-0,03892
Leucaena sp.	0,003844	0,036275	*Sphagneticola trilobata*	-0,00443	0,005916
Lobelia sp.	0,027242	-0,01289	*Thouinia paucidentata*	-0,00153	0,030446
Lonchocarpus sp. 1	-0,40029	-0,48445	*Thrinax radiata*	-0,00774	0,025757
Lonchocarpus sp. 2	-0,06543	0,242657	*Waltheria indica*	-0,00162	0,00979
Lonchocarpus sp. 3	0,023433	-0,00649	*Zygia aff cognata*	0,005683	-0,00157

Melanthera nivea	-0,0121	0,044665	

ANEXO VI. Eigenvectors of species on the ordination axes for the species abundance of vegetation surrounding nine meliponaries on the Yucatan Peninsula.

Species	PC1	PC2	Species	PC1	PC2
Abutilon permolle	-0,0063598	0,0902285	*Impatiens walleriana*	-0,0020111	0,0285328
Abutilon trisulcatum	-0,3484499	-0,0504149	*Ipomoea crinicalyx*	0,0266904	0,0162254
Acalypha leptopoda	0,0049754	0,0691262	*Ipomoea hederifolia*	0,0153058	-0,0307600
Acalypha sp.	-0,0503978	0,0306300	*Ipomoea heterodoxa*	-0,0028442	0,0403514
Acanthaceae	-0,0179448	-0,0113338	*Ipomoea indica*	0,0119626	0,0278685
Acanthocereus tetragonus	-0,1009240	-0,0175522	*Ipomoea nil*	0,0072242	-0,0001196
Adonidia merrillii	0,0315113	0,1401096	*Ipomoea triloba*	0,0102166	-0,0001692
Aeschynomene fascicularis	-0,0253778	-0,0160284	*Ixora coccinea*	0,0084588	0,0197060
Agave fourcroydes	0,0151787	-0,0188593	*Jacquemontia pentantha*	0,0556138	-0,0439616
Ageratum gaumeri	0,0084588	0,0197060	*Justicia cardinalis*	0,0485197	-0,0355323
Allophylus cominia	0,0147278	-0,0116431	*Kalanchoe pinnata*	-0,0028442	0,0403514
Aloe vera	0,0408291	0,0401669	*Kalanchoe* sp.	0,0147278	-0,0116431
Aloysia virgata	0,0288919	0,0056020	*Karwinskia humboltiana*	0,0147278	-0,0116431
Alpinia sp.	0,0147278	-0,0116431	*Lagascea mollis*	0,0214659	-0,0266711
Althernanthera flavescens	0,0294557	-0,0232862	*Lantana camara*	0,0578505	0,0176476
Alvaradoa amorphoides	-0,0190463	0,0499119	*Lasiacis divaricata*	-0,0179448	-0,0113338
Amaranthus sp.	0,0084588	0,0197060	*Lasiacis* sp.	-0,0304356	0,0375067
Annona muricata	0,0219520	-0,0117627	*Lepidium virginicum*	0,0158847	0,0519791
Annona sp.	-0,0179448	-0,0113338	*Leucaena leucocephala*	-0,1330610	-0,0326892
Annona squamosa	0,0423448	0,0748514	*Lippia graveolens*	0,0567935	-0,0705651
Anoda cristata	-0,0358896	-0,0226676	*Lonchocarpus rugosus*	0,0084588	0,0197060
Anthurium schlechtendallii	0,0128621	0,0558987	*Lonchocarpus* sp.	0,0352674	-0,1199514
Aphelandra scabra	-0,0273889	0,0125044	*Lysiloma latisiliquum*	0,0783725	-0,0467757
Apocynaceae	0,0084588	0,0197060	*Machaonia lindeniana*	0,0151787	-0,0188593
Apoplanesia paniculata	0,0144484	-0,0002392	*Maclura tinctoria*	-0,0665189	-0,0239441
Ardisia escallonioides	0,0606780	-0,0672833	*Macroptilium* sp.	-0,0253778	-0,0160284
Asclepias curassavica	0,0161946	0,0351540	*Malachra* sp.	-0,0179448	-0,0113338
Asteraceae	0,0158847	0,0519791	*Malvastrum coromandelianum*	0,0127657	0,0769193

Astraea lobata	0,0208283	-0,0164658	*Malvaviscus arboreus*	-0,0776014	-0,0346490
Astrocasia tremula	-0,0179448	-0,0113338	*Mangifera indica*	0,0177260	0,0455215
Ayenia abutilifolia	0,0102166	-0,0001692	*Manilkara zapota*	0,0177260	0,0455215
Azadirachta indica	-0,0483653	-0,0077961	*Melampodium divaricatum*	0,0401567	-0,0261543
Barleria cristata	0,0074259	0,0322731	*Melanthera nivea*	0,0188522	-0,0023372
Bauhinia divaricata	0,0234365	0,0824248	*Melia azedarach*	0,0074259	0,0322731
Bauhinia monandra	0,0084588	0,0197060	*Melicoccus bijugatus*	0,0116042	0,0401122
Beaucarnea pliabilis	0,0266904	0,0162254	*Melicoccus oliviformis*	0,0248103	0,1005285
Begonia nelumbiifolia	0,0147278	-0,0116431	*Melochia tomentosa*	0,0298298	0,0152725
Begonia sp.	0,0147278	-0,0116431	*Merremia dissecta*	0,0360757	-0,0285196
Bidens alba	0,0119626	0,0278685	*Mesosphaerum pectinatum*	0,0384842	-0,0528505
Bignoniaceae	-0,0253778	-0,0160284	*Metopium brownei*	0,0356360	0,1465285
Bixa orellana	0,0169495	0,0938798	*Mimosa bahamensis*	0,1127085	-0,1490331
Boerhavia coccinea	0,0105018	0,0456411	*Mimosa* sp.	-0,0253778	-0,0160284
Boerhavia erecta	0,0108509	0,0844314	*Mirabilis jalapa*	0,0125127	-0,0002072
Bougainvillea sp.	0,0285451	0,0754851	*Momordica charantia*	0,0120077	0,1048977
Bourreria pulchra	0,0626638	-0,0878095	*Momordica* sp.	-0,0179448	-0,0113338
Bromelia karatas	-0,0467533	-0,0545265	*Morinda citrifolia*	0,0158847	0,0519791
Brosimum alicastrum	-0,0454459	0,1140600	*Morinda royoc*	0,1589305	0,0155492
Bunchosia swartziana	0,0708766	-0,0234159	*Moringa oleifera*	0,0074259	0,0322731
Bursera simaruba	0,0890933	-0,0486349	*Murraya paniculata*	0,0254139	0,0789331
Byrsonima bucidifolia	0,0074259	0,0322731	*Musa paradisiaca*	0,0189606	0,0653471
Byrsonima crassifolia	0,0105018	0,0456411	*Neea* sp.	-0,0107206	-0,0114534
Byttneria aculeata	-0,0358896	-0,0226676	*Neomillspaughia emarginata*	0,1925918	-0,2447342
Caesalpinia pulcherrima	-0,0326504	0,0662581	*Ocimum micranthum*	0,0371801	-0,0461957
Caesalpinia vesicaria	-0,0179448	-0,0113338	*Opuntia inaperta*	-0,0683989	-0,0110254
Caesalpinia yucatanensis	-0,0179448	-0,0113338	*Oxalis frutescens*	0,0151787	-0,0188593
Calea sp.	0,0074259	0,0322731	*Parmentiera millspaughiana*	0,0335145	-0,0327849
Calea urticifolia	0,0144174	0,1078651	*Parthenium hysterophorus*	0,1846201	0,2312968
Callicarpa acuminata	0,0243435	0,0716851	*Paspalum fimbriatum*	0,0216456	-0,0435012
Calyptocarpus vialis	0,0054148	0,0608059	*Passiflora ciliata*	0,0147278	-0,0116431
Camonea umbellatus	-0,0179448	-0,0113338	*Paullinia fuscescens*	0,0072242	-0,0001196
Canna indica	0,0146501	0,0321535	*Petiveria alliacea*	-0,4152447	-0,0380772

Capraria biflora	0,0712877	0,1723859	*Phaseolus* sp.	0,0074259	0,0322731
Capraria frutescens	0,0181315	0,0776956	*Phyllanthaceae*	-0,0179448	-0,0113338
Capsicum annuum	0,0173773	0,0886744	*Phyllanthus acidus*	0,0146501	0,0321535
Carica papaya	0,0493182	0,0596377	*Pilocarpus racemosus*	0,0084588	0,0197060
Cascabela gaumeri	0,0153058	-0,0307600	*Piper auritum*	0,0158847	0,0519791
Cascabela thevetia	0,0074259	0,0322731	*Piscidia piscipula*	0,1094186	-0,1438401
Cassia fistula	0,0189606	0,0653471	*Pisonia aculeata*	-0,0273889	0,0125044
Cecropia peltata	0,0243435	0,0716851	*Plagiolophus millspaughii*	0,0242792	-0,0041325
Cedrela odorata	0,0168676	0,1767513	*Pluchea carolinensis*	-0,0179448	-0,0113338
Ceiba pentandra	0,0064477	0,0482388	*Plumbago zeylanica*	-0,0034834	0,0494202
Celtis iguanaea	0,0147278	-0,0116431	*Plumbago zeylanica*	-0,0683989	-0,0110254
Cenostigma gaumeri	0,0626945	0,0438441	*Plumeria rubra*	0,0208283	-0,0164658
Centratherum punctatum	0,0119626	0,0278685	*Poaceae*	-0,0643533	-0,0130621
Centrosema virginianum	0,0153058	-0,0307600	*Porophyllum punctatum*	0,0042090	0,0092962
Chamaecrista glandulosa var. *flavicoma*	0,0432082	0,0356713	*Priva lappulacea*	0,0232416	0,0950294
Chamaedorea seifizii	0,0119626	0,0278685	*Pseudophoenix sargentii*	0,0074259	0,0322731
Chiococca alba	0,0237646	-0,0110540	*Psidium guajava*	0,0156830	0,0195864
Chloris sp.	0,0265104	-0,0532778	*Psidium sartorianum*	0,0265104	-0,0532778
Chloroleucon mangense	-0,0028442	0,0403514	*Psychotria* sp.	0,0084588	0,0197060
Chromolaena odorata	0,0191079	0,0285887	*Punica granatum*	0,0231089	0,0518595
Chrysophyllum cainito	-0,0020111	0,0285328	*Randia longiloba*	-0,0503765	0,0207367
Chrysophyllum mexicanum	0,0156830	0,0195864	*Randia obcordata*	0,0224029	-0,0189789
Cissampelos pareira	0,0336904	0,0394329	*Rauvolfia tetraphylla*	0,0356690	0,0726536
Cissus verticillata	0,0231089	0,0518595	*Rhynchosia minima*	-0,0179448	-0,0113338
Citrus aurantium	0,0551789	0,1170986	*Rhynchosia* sp.	0,0153058	-0,0307600
Citrus latifolia	0,0793923	-0,0746450	*Ricinus communis*	0,0074259	0,0322731
Citrus reticulata	0,0851907	-0,0683836	*Rivina humilis*	-0,3861500	0,0141040
Citrus sinensis	0,1979642	-0,2111215	*Rosa* sp.	0,0158847	0,0519791
Cnidoscolus aconitifolius	0,0347927	0,0813163	*Ruellia blechum*	-0,0531600	-0,0631962
Cnidoscolus souzae	0,0415961	-0,0634253	*Ruellia inundata*	-0,0595162	-0,0375899
Coccoloba spicata	0,0252297	0,0339980	*Ruellia nudiflora*	0,0381673	0,0129119
Cocos nucifera	0,0287686	0,0684682	*Sabal* sp.	0,0429263	0,0356781
Colubrina arborescens	0,0119626	0,0278685	*Saccharum*	0,0084588	0,0197060

			officinarum		
Colubrina elliptica	0,0214659	-0,0266711	*Salvia serotina*	0,0162199	0,1069033
Colubrina yucatanensis	0,0144484	-0,0002392	*Salvia* sp.	-0,0179448	-0,0113338
Commelina erecta	0,0513060	-0,0591531	*Sapindaceae*	0,0151787	-0,0188593
Convolvulus nodiflorus	0,0151787	-0,0188593	*Sapindus saponaria*	0,0119626	0,0278685
Corchorus siliquosus	0,0437236	0,0785947	*Schwenkia americana*	0,0072242	-0,0001196
Cordia dodecandra	-0,0020111	0,0285328	*Selenicereus grandiflorus*	0,0074259	0,0322731
Cordia gerascanthus	0,0066678	0,0081047	*Semialarium mexicanum*	0,0734954	-0,0311534
Cordyline fruticosa	0,0166049	0,0721649	*Senegalia gaumeri*	-0,2173602	-0,0434779
Coulteria mollis	0,0695804	0,0454165	*Senna atomaria*	-0,1604096	-0,0258567
Coursetia caribaea	0,0102166	-0,0001692	*Senna pendula*	0,0074259	0,0322731
Coursetia greenmanii	-0,0028442	0,0403514	*Senna racemosa*	0,0331614	-0,0002903
Crateva tapia	-0,0483653	-0,0077961	*Senna* sp.	-0,0179448	-0,0113338
Crescentia cujete	0,0072242	-0,0001196	*Sida* sp.	0,0136719	0,0481191
Crinum amabile	0,0084588	0,0197060	*Sida spinosa*	0,0102166	-0,0001692
Crossopetalum gaumeri	0,0147278	-0,0116431	*Solanum donianum*	-0,0439556	-0,0277620
Crotalaria sp.	0,0084588	0,0197060	*Solanum erianthum*	0,0049796	-0,0537470
Croton ameliae	0,0084588	0,0197060	*Solanum hirtum*	-0,0020111	0,0285328
Croton arboreus	0,0682893	-0,0687682	*Solanum lycopersicum*	0,0105018	0,0456411
Croton ciliatoglandulifer	0,0151787	-0,0188593	*Solanum* sp.	-0,0028442	0,0403514
Croton humilis	0,0471186	-0,0491311	*Solanum tridynamum*	0,0151787	-0,0188593
Croton sp.	-0,0295183	-0,0234696	*Spermacoce* sp.	0,0216456	-0,0435012
Cryptostegia grandifolia	0,0084588	0,0197060	*Spermacoce tetraqueta*	0,0216456	-0,0435012
Cryptostegia sp.	0,0105018	0,0456411	*Spermacoce verticillata*	0,0024254	0,1053043
Cucumis melo	0,0255094	-0,0201664	*Spondias purpurea*	0,0291772	0,0651779
Cucurbita moschata	0,0375728	-0,0120213	*Stigmaphyllon lindenianum*	0,0084588	0,0197060
Cyanthillium cinereum	0,0096685	0,0401443	*Swietenia macrophylla*	-0,0020111	0,0285328
Cyperus sp.	0,0147278	-0,0116431	*Tabernaemontana divaricata*	0,0213209	0,0756047
Dactyloctenium aegyptium	0,0153058	-0,0307600	*Talinum paniculatum*	0,0083650	0,1196999
Dalechampia scandens	0,0144484	-0,0002392	*Tamarindus indica*	0,0236375	0,0008467
Delilia biflora	0,0102166	-0,0001692	*Tamonea curassavica*	0,0335145	-0,0327849

Delonix regia	-0,0020111	0,0285328
Desmanthus virgatus	0,0082054	0,0283636
Desmodium incanum	0,0074259	0,0322731
Desmodium sp.	0,0306116	-0,0615199
Dicliptera sexangularis	-0,0253778	-0,0160284
Dioscorea sp.	0,0119626	0,0278685
Diospyros anisandra	0,0088227	-0,0271384
Diospyros salicifolia	0,0363735	-0,0551442
Diospyros tetrasperma	-0,0020111	0,0285328
Diphysa yucatanensis	0,0141515	0,0092189
Distimake quinquefolius	-0,0179448	-0,0113338
Dolichandra unguis-cati	0,0072242	-0,0001196
Ehretia tinifolia	0,0010158	0,0540133
Enterolobium cyclocarpum	-0,0020111	0,0285328
Erythrina standleyana	0,0084588	0,0197060
Erythrostemon yucatanensis	0,0099514	0,0564012
Eugenia sp.	0,0265104	-0,0532778
Euphorbia heterophylla	-0,0179448	-0,0113338
Euphorbia sp.	-0,0253778	-0,0160284
Ficus cotinifolia	0,0072242	-0,0001196
Gaya calyptrata	0,0304109	0,0079433
Glandularia canadensis	0,0147278	-0,0116431
Gliricidia maculata	0,0146511	0,0341318
Gossypium hirsutum	0,0198642	0,0625449
Guazuma ulmifolia	-0,1068797	0,0105482
Guettarda combsii	0,0147278	-0,0116431
Gymnopodium floribundum	0,0536734	-0,0368103
Hamelia patens	0,0949107	0,2349421
Havardia albicans	0,0053058	-0,0493525
Heliotropium angiospermum	-0,0040365	0,1171589
Herissantia crispa	0,0276914	-0,0190665
Tecoma stans	0,0074259	0,0322731
Tephrosia cinerea	-0,0179448	-0,0113338
Terminalia buceras	0,0084588	0,0197060
Terminalia catappa	0,0064477	0,0482388
Tetramerium nervosum	0,0281156	-0,0421037
Thouinia paucidentata	-0,0179519	0,0162447
Thrinax radiata	0,0406306	0,1797421
Tithonia diversifolia	0,0158847	0,0519791
Tournefortia sp.	0,0074259	0,0322731
Tradescantia spathacea	0,0119626	0,0278685
Tragia yucatanensis	0,0151787	-0,0188593
Tridax procumbens	0,1197444	-0,1471189
Turnefortia sp.	0,0153058	-0,0307600
Turnera ulmifolia	0,0072242	-0,0001196
Urechites andreuxii	-0,0179448	-0,0113338
Vachellia collinsii	-0,0179448	-0,0113338
*Vachellia pennatula s*sp. *parvicephala*	-0,0258353	-0,0386757
Vachellia sp.	-0,0159026	-0,0384900
Vanilla sp.	0,0074259	0,0322731
Varronia curassavica	0,0653327	-0,0057442
Verbenaceae	-0,0020111	0,0285328
Viguiera dentata	-0,0132932	-0,0759134
Vitex gaumeri	0,0074259	0,0322731
Waltheria indica	0,1465389	-0,1803472
Waltheria rotundifolia	0,0214659	-0,0266711
Washingtonia sp.	0,0147278	-0,0116431
Wedelia acapulcensis	-0,0253778	-0,0160284
Wissadula amplissima	0,0161538	-0,0002675
Ximenia americana	0,0262903	-0,0326653
Zanthoxylum caribaeum	-0,0107206	-0,0114534
Zapoteca formosa	0,0151787	-0,0188593

Hibiscus poeppigii	0,0084588	0,0197060	*Zinnia elegans*	0,0208283	-0,0164658
Hibiscus rosa-sinensis	-0,0034834	0,0494202	*Zuelania guidonia*	0,0084588	0,0197060
Hylocereus undatus	0,0084588	0,0197060			

ANEXO VII. Regression linear models to analyze the effect of plant species absolute density and coverage on its pollen grains abundance on *Melipona beecheii* pot-pollen