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Melissopalynological Analysis Revealed a Higher Pollen Diversity in Stingless Bees than in Honey Bees

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ABSTRACT

Identifying floral resources used by honey bees and stingless bees is essential for sustainable beekeeping and understanding pollination ecology. This study compared the diversity of floral resources utilized by the honey bee *Apis cerana* and stingless bees *Geniotrigona thoracica* and *Heterotrigona itama* based on pollen in honey. Bee colonies were in the same Flora Nauli Beekeeping area, Pematang Siantar, North Sumatra, Indonesia, ensuring equal access to similar surrounding floral resources. Honey samples were collected, and pollen grains were extracted, acetolysed, and analyzed by counting 1,200 grains to determine frequency classes. Pollen diversity was calculated using the Shannon–Wiener index (H′). Stingless bee honey contained more diverse pollen than *A. cerana*, which only contained pollen from the Arecaceae family. *Heterotrigona itama* and *G. thoracica* honey contained pollen from 20 and 11 plant families, respectively. Each species had a distinct predominant pollen type (>45%): *Cocos nucifera* (*A. cerana*), Sapotaceae type (*G. thoracica*), and Casuarinaceae type (*H. itama*). A higher pollen diversity index was also observed in *H. itama* (1.05-1.83) than in *G. thoracica* (0.34–1.64) and *A. cerana* (0.66). These results indicate that stingless bees are more generalist than honey bees, highlighting their ecological role in supporting pollination networks in tropical agroecosystems.

1. Introduction

Honey serves not only as a nutritional and therapeutic substance but also as a valuable indicator of the floral source diversity utilized by bees (Das *et al.* 2024). The range of plant resources utilized by bees can be analyzed using melissopalynology, the study of pollen grains present in honey (Louveaux *et al.* 1978). This method offers a valuable approach to investigate the botanical (Salcedo *et al.* 2025) and geographical origin of honey (Sakač *et al.* 2024), providing insights into regional floral diversity (Karki *et al.* 2025), ecological interactions between bees and their environments (Ullah *et al.* 2025), bee foraging behavior (Daugaliyeva *et al.* 2024), and floral preferences (Adler *et al.* 2024). Such information is essential for understanding pollinator–plant relationships, supporting sustainable apiculture, and guiding the conservation of both bee species and the ecosystems they inhabit.

Comparing pollen composition contained in honey bees (*Apis* spp.) and stingless bees (Meliponini) honey is particularly important because these groups differ markedly in body size, tongue length, social structure, and foraging strategies (Michener 2007). These differences can shape the range of utilized floral resources, pollination efficiency, and resilience to

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environmental change (Hrncir and Maia-Silva 2013). From a practical perspective, both groups are managed for honey production in tropical Asia, including the Indo-Malayan Region. However, stingless bees are often favored in small-scale meliponiculture for their ease of management and adaptability to urban and agricultural landscapes. In contrast, honey bees are preferred for larger-scale honey yields. Understanding their floral usage in sympatric conditions can inform optimal resource management and enhance pollination services (Raffiudin *et al.* 2022).

The Indo-Malayan region is a global biodiversity hotspot with high plant endemism and complex floral assemblages shaped by tropical climate, varied altitudes, and island biogeography (Olson *et al.* 2001). Plant species richness in this region is among the highest in the world, and floral communities often differ significantly between islands (Roos *et al.* 2004) and elevations (Barthlott *et al.* 2005). These differences in plant distribution and phenology can influence the pollen spectra in honey, potentially revealing unique patterns of resource use that may not be observed in other tropical regions (Eltz *et al.* 2001). Thus, a melissopalynological study is relevant to be conducted in this region.

Indonesia, located within the Indo-Malayan region, hosts five native honey bee species, i.e., *Apis dorsata, A. cerana* (Ruttner 1988), *A. andreniformis* (Wu and Kuang 1987), *A. koschevnikovi* (Tingek *et al.* 1988), and *A. nigrocincta* (Maa 1953). Moreover, at least 46 species of stingless bees are primarily distributed across Kalimantan, Sumatra, Papua, and Java Islands (Kahono *et al.* 2018). Survey on the beekeeping and managed bee diversity in Indonesia, 22 species of bees, including three honey bee species (*A. mellifera, A. cerana,* and *A. nigrocincta*) and 19 species of stingless bees, are reared by Indonesian beekeepers (Buchori *et al.* 2022).

Previous melissopalynological analyses in Indonesia have mainly focused on single bee species, for example, *Tetragonula laeviceps* and *Heterotrigona itama* in Belitung Island (Priambudi *et al.* 2021), *T. sapiens* across different altitudes in Lombok Island (Rizqiani *et al.* 2025), *A. dorsata* in Belitung (Bramasta *et al.* 2023) and Sumatra (Raffiudin *et al.* 2024), and *A. cerana* in Central Sulawesi (Rasyiid *et al.* 2025). However, differences of floral diversity used by sympatric Indo-Malayan stingless bees and Asian honey bees within the same location, particularly in Sumatra, remain unexplored.

Sumatra is one of the Indonesian islands where beekeeping with both honey bees and stingless bees is becoming increasingly common. In this region, Asian honey bee *A. cerana* and stingless bees *H. itama* and *Geniotrigona thoracica* are predominantly managed (Buchori *et al.* 2022). These species often coexist in diversified agroecological settings, yet differences in their floral resource usage remain poorly understood. Therefore, we conducted a comparative melissopalynological analysis of honey samples collected from *A. cerana, G. thoracica*, and *H. itama* colonies managed within the same beekeeping area in Sumatra, Indonesia, to determine and compare the diversity of floral resources used by these sympatric bee species.

2. Materials and Methods

2.1. Sample Collection

Honey samples of three bee species, *A. cerana* (one colony), *G. thoracica* (two colonies), and *H. itama* (two colonies) were collected in August 2022 from the same beekeeping area at Flora Nauli Beekeeping, Setia Negara Village, Sub-district Siantar Sitalasari, Pematang Siantar City, North Sumatra, Indonesia. All colonies were located within a radius of less than 50 m of each other and thus had equal opportunities to access similar plant resources in the surrounding agroecological landscape. The use of only one *A. cerana* colony was due to the limited availability of managed *A. cerana* colonies at the farm during the sampling period. To minimize potential bias arising from unequal colony numbers, all honeys were sampled during the same flowering season, thereby reducing temporal and environmental variation in floral availability.

Honey of *A. cerana* was collected by cutting the honey portion of the comb, slicing through the wax capping to release the honey (Raffiudin *et al.* 2024). Honey from *H. itama* and *G. thoracica* was collected using a suction method: the tip of a suction hose was used to perforate the upper part of the honey pot, and the honey was extracted using a portable electric vacuum into a storage jar until melissopalynological analysis.

2.2. Melissopalynological Analysis

Pollen in honey was extracted following the acetic acid method (Louveaux *et al.* 1978). Three mL of honey in a 15 mL tube was homogenized with distilled water and centrifuged at 3,500 rpm for 5 minutes to obtain the pollen pellet. Four mL of glacial acetic acid was added to the pellet and centrifuged under the same conditions for further precipitation. The extracted pollen from honey was prepared using the acetolysis method

(Erdtman 1972). The acetolysis solution consisted of freshly mixed acetic anhydride ($C_4H_6O_3$, M = 102.09 g/mol) and sulfuric acid (H_2SO_4, M = 98.08 g/mol) in a 9:1 ratio. One mL of the solution was added to each pollen sample in a 1.5 mL microtube. The mixture was heated with the tube caps open in a water bath at 80°C for 5 minutes, centrifuged at 3,500 rpm for 10 minutes, and the supernatant discarded. The pellet was washed 2–3 times with distilled water until the suspension became clear. One mL of 30% glycerine was added, and the suspension was mixed. A drop of the pollen–glycerine suspension was mounted on a glass slide, covered with a cover glass, and sealed with clear nail polish.

Photomicrographs of pollen grains were taken using a Nikon Eclipse E100 compound microscope with an OptiLab camera (https://www.miconos.co.id/). Pollen types were identified based on polar and equatorial views for the following characteristics: size, shape, exine ornamentation, and aperture type (Huang 1972). Three online databases, i.e., the Australian Pollen and Spore Atlas (http://apsa.anu.edu.au/), the Global Pollen Project (https://globalpollenproject.org/), and the Palynological Database (https://www.paldat.org/) were used as pollen references during the identification process. In this study, a "pollen type" refers to a morphologically distinct pollen form identified to the lowest possible taxonomic level (species, genus, or family). When pollen could not be identified to species or genus level, it was classified as a morphotype of a family. However, it was considered a separate pollen type if it was morphologically distinct. For each honey sample, at least 1,200 pollen grains from 9-18 microscope slides were counted using OptiLab Viewer 4.0 software and assigned to one of four frequency classes (Louveaux *et al.* 1978): predominant (>45%), secondary (16–45%), important minor (3–15%), and minor (<3%).

2.3. Diversity Index Analysis

Pollen type diversity for each honey sample was calculated using the Shannon diversity index (H′), given by:

$$H' = -\sum_{i=1}^{S} p_i \ln(p_i)$$

Where S is the total number of pollen types, and p_i is the proportion of pollen type i relative to the total pollen count in the sample. Diversity categories were interpreted as follows: low diversity ($H' < 1.0$), moderate diversity ($1.0 \leq H' < 3.0$), and high diversity ($H' \geq 3.0$) (Shannon 1948).

3. Results

3.1. Pollen Diversity

We found a total of 39 pollen types in honey (Figure 1) with different pollen compositions in each honey sample (Figure 2). The results showed that stingless bee honey of *H. itama* and *G. thoracica* contained a higher variety of pollen types compared to *A. cerana* honey, which contained only two pollen types from a single family of Arecaceae, i.e., *Arenga* sp. and *Cocos nucifera* (Figure 2). *Heterotrigona itama* honey contained more diverse 17 and 26 pollen types from 20 plant families than *G. thoracica* honey, which contained 14 and four pollen types from 11 plant families, respectively, for colonies 1 and 2 (Figure 2). Shannon diversity index (H') analysis on pollen contained in honey also showed that *A. cerana* and *G. thoracica* colony 2 have a low pollen diversity with H' value, i.e., 0.66 and 0.34, respectively (Table 1). Moreover, honey samples of *G.* thoracica colony 1 and both *H. itama* colonies have moderate pollen diversity with H' ranging from 1.05 to 1.83 (Table 1).

3.2. Pollen Composition in Each Honey Sample

The pollen counting results showed that honey from *A. cerana, G. thoracica* colony 2, and *H. itama* colony 1 have predominant (>45%) pollen type of *C. nucifera*, Sapotaceae type-1, and Casuarinaceae type, respectively (Figure 2). Differences in predominant pollen types found in honey samples of *A. cerana, G. thoracica* colony 2, and *H. itama* colony 1 indicate that each species has a different nectar foraging preference. The last two honey samples of *G. thoracica* colony 1 and *H. itama* colony 2 revealed no predominant pollen type (Figure 2). *Geniotrigona thoracica* colony 1 has two secondary pollen types (16-45%), i.e., Casuarinaceae type and Verbenaceae type-1 (Figure 2), while the second *H. itama* colony has Asteraceae type-5 and Elaeocarpaceae type as the secondary pollen (Figure 2). The findings also indicate that both colonies have different nectar foraging preferences compared to other observed colonies.

Moreover, melissopalynological analysis also revealed that *A. cerana* has no specific pollen type, while *H. itama* has more diverse specific pollen types compared to *G. thoracica* (Figure 3). The total of 13 plant families was identified from 24 specific pollen types from *H. itama* honey, i.e., Asteraceae, Elaeagnaceae, Euphorbiaceae, Fabaceae, Lythraceae, Moraceae/Urticaceae, Myrtaceae, Nyctaginaceae, Rhamnaceae, Ranunculaceae, Rubiaceae, Verbenaceae,

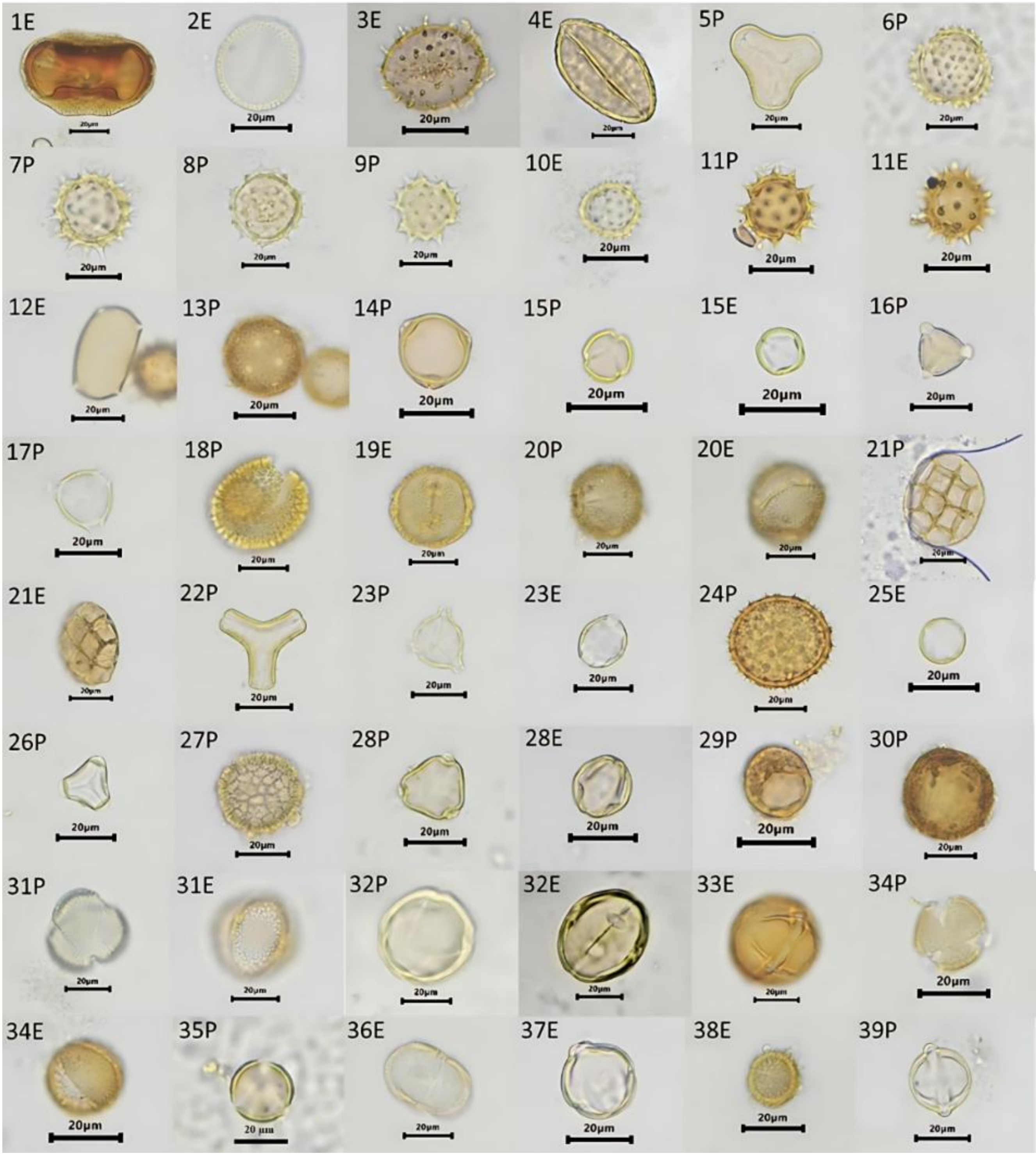

Figure 1. Photomicrographs showing the total of 39 pollen types (21 families) identified from honey samples of honey bee *A. cerana* and stingless bee *G. thoracica*, and *H. itama*. Achantaceae: 1. *Asystasia* sp.; Arecaceae: 2. *Areca* sp., 3. *Arenga* sp., 4. *Cocos nucifera*, 5. *Elaeis guineensis*; Asteraceae: 6. Asteraceae type-1, 7. Asteraceae type-2, 8. Asteraceae type-3, 9. Asteraceae type-4, 10. Asteraceae type-5, 11. Asteraceae type-6; Balsaminaceae: 12. *Impatiens* sp.; Caryophyllaceae: 13. Caryophyllaceae type; Casuarinaceae: 14. Casuarinaceae type; Elaeocarpaceae: 15. Elaeocarpaceae type; Elaeagnaceae: 16. Elaeagnaceae type-1, 17. Elaeagnaceae type-2; Euphorbiaceae: 18. Euphorbiaceae type-1, 19. Euphorbiaceae type-2, 20. Euphorbiaceae type-3; Fabaceae: 21. *Acacia* sp.; Loranthaceae: 22. Loranthaceae type; Lythraceae: 23. Lythraceae type; Malvaceae: 24. Malvaceae type; Moraceae/Urticaceae: 25. Moraceae/Urticaceae type; Myrtaceae: 26. *Eucalyptus* sp.; Nyctaginaceae: 27. Nyctaginaceae type; Rhamnaceae: 28. Rhamnaceae type; Ranunculaceae: 29. Ranunculaceae type-1, 30. Ranunculaceae type-2; Rubiaceae: 31. *Coffea* sp.; Sapotaceae: 32. Sapotaceae type-1, 33. Sapotaceae type-2; Verbenaceae: 34. Verbenaceae type-1, 35. Verbenaceae type-2, 36. Verbenaceae type-3; Violaceae: 37. Violaceae type, 38. Sp 1, 39. Sp2. P = polar view, E = equatorial view

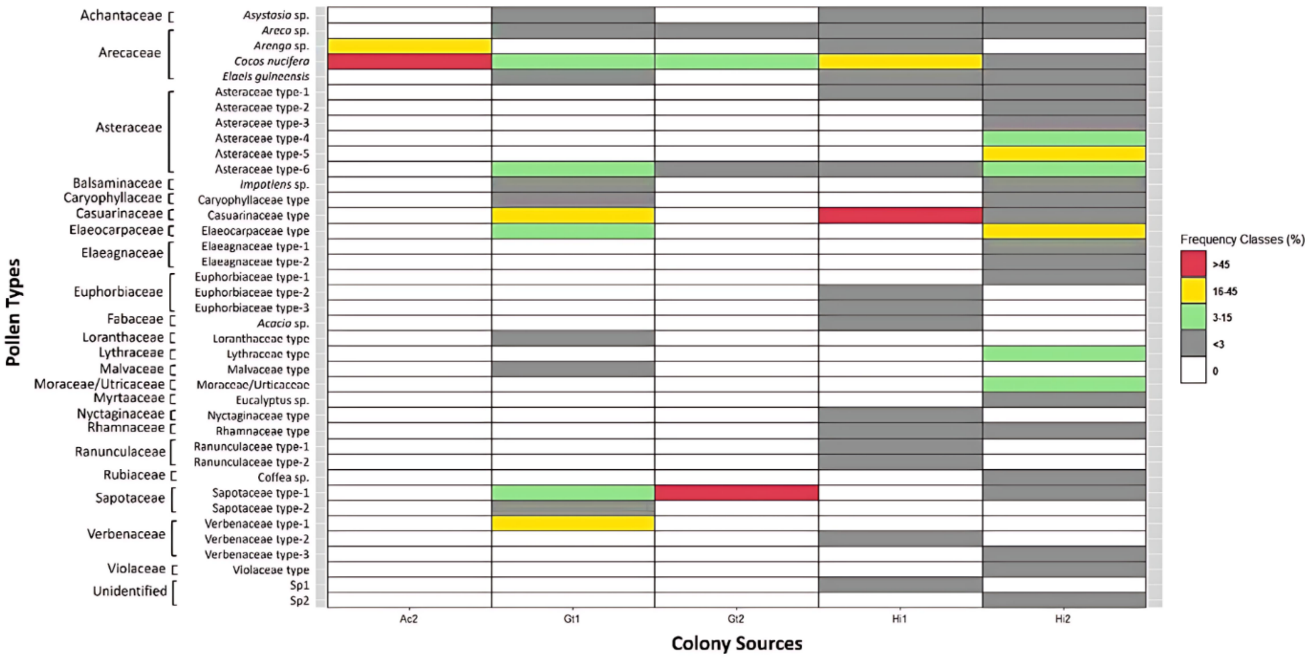

Figure 2. Pollen frequency in *A. cerana, G. thoracica*, and *H. itama* honey. Ac = *A. cerana*, Gt = *G. thoracica*, Hi = *H. itama*; the number after species abbreviation indicates colony number. Pollen frequency classes: predominant pollen type (>45%), secondary pollen type (16−45%), important minor pollen type (3−15%), and minor pollen type (<3%)

Table 1. Pollen diversity index calculated from pollen contained in the honey of *A. cerana, G. thoracica*, and *H. itama*

Honey samples	The number of pollen types	Diversity index (H')	Diversity level
Ac	2	0.66	Low
Gt1	14	1.64	Moderate
Gt2	4	0.34	Low
Hi1	17	1.05	Moderate
Hi2	26	1.83	Moderate

Ac: *A. cerana*, Gt: *G. thoracica*, Hi: *H. itama*; the number after species abbreviation indicates the colony number

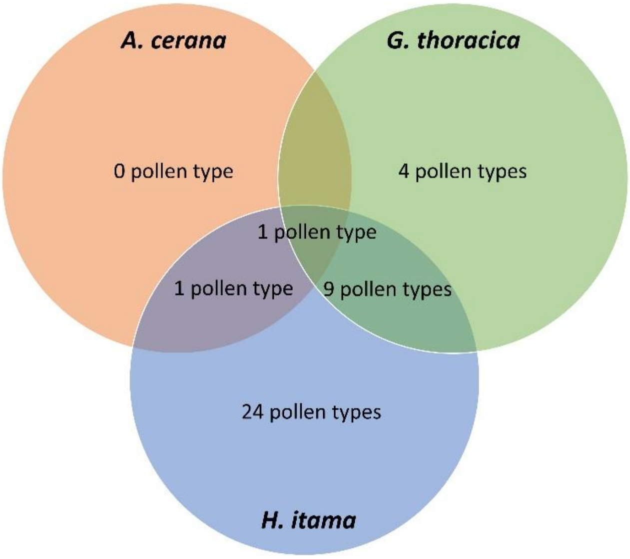

Figure 3. Pollen identification results showing the number of specific and shared pollen types used by honey bees and stingless bees. Resource partitioning among bee species is revealed by the specific pollen types contained in honey produced by each species, with the most specific pollen types found in *H. itama* honey

and Violaceae (Figures 2 and 3). Less specific pollen types from four plant families were identified from *G. thoracica*, i.e., Lorantaceae, Malvaceae, Sapotaceae, and Verbenaceae (Figures 2 and 3). The specific pollen types identified in each honey sample suggest the resource partitioning between the bee species. A single pollen type of *C. nucifera* was shared between all observed honey bee and stingless bee colonies. In contrast, pollen of *Arenga* sp. was only shared between *A. cerana* and *H. itama* (Figure 2 and 3). *Heterotrigona itama* shared more pollen types with *G. thoracica*, up to nine pollen types, i.e., *Areca* sp., Asteraceae type-6, Casuarinaceae type, Sapotaceae type-2, Caryophyllaceae type, *Impatiens* sp., Elaeocarpaceae type, *Elaeis guineensis*, and *Asystasia* sp. (Figures 2 and 3).

4. Discussion

Our melissopalynological analysis revealed clear differences in pollen diversity between honey collected from the stingless bee species *H. itama* and *G. thoracica*, and that of the honey bee *A. cerana*. The significantly higher pollen diversity in stingless bee honey, as shown by the Shannon diversity index (H', Table 1), suggests a broader range of floral resources utilized by stingless bees. Our findings parallel the patterns reported from the Neotropical region, where the stingless bee *Melipona mandacaia* frequently shows broader pollen spectra compared to *A. mellifera* (Santisteban *et al.* 2024). These convergent patterns across biogeographic regions suggest that the foraging flexibility of Meliponini often drives a high pollen diversity in stingless bee honeys (Martins *et al.* 2023).

The honey samples from *H. itama* demonstrated the highest pollen diversity, with up to 26 pollen types from 20 plant families, while *A. cerana* honey contained only two pollen types from a single family of Arecaceae (Figures 2 and 3). Such a narrow pollen profile in *A. cerana* may indicate a higher degree of floral constancy, in which foragers repeatedly visit the same plant species during a foraging trip. This behavior is often linked to the optimization of pollen collection efficiency and the facilitation of effective pollination for preferred plant species (Mondal *et al.* 2023). In social bees like *A. cerana*, which possess a sophisticated recruitment system (e.g., waggle dance) to communicate profitable floral sources to nestmates, floral constancy can enhance colony foraging efficiency by focusing collective effort on the most rewarding resources available at a given time (Mondal *et al.* 2023). In contrast, the broader spectrum in stingless bees reflects their more opportunistic foraging behavior, enabling them to visit a wider range of flower types (Martins *et al.* 2023).

The differences of foraging behavior between honey bees and stingless bees are influenced by morphological (Roubik 1989; Delgado *et al.* 2023) and physiological traits (Balbuena *et al.* 2024). Compared to honey bees, stingless bees generally have smaller body sizes, allowing them to access a wider variety of floral morphologies, including narrow or less accessible corollas (Roubik 1989; Delgado *et al.* 2023). As a result, stingless bees tend to visit a wider variety of flowers, which in turn increases the diversity of pollen carried into the honey. Moreover, the variation in proboscis length among stingless bee species enables them to exploit different floral niches (Hrncir and Maia-Silva 2013). These traits contribute to niche complementarity between coexisting pollinators and reduce direct competition (Hrncir and Maia-Silva 2013). From a physiological perspective, stingless bees possess enhanced olfactory sensitivity, which aids in detecting a broader array of floral scents, particularly in dense tropical forests (Balbuena *et al.* 2024). Their antennal sensilla are adapted for discriminating volatile organic compounds, allowing stingless bees to locate and evaluate diverse floral resources efficiently (Balbuena *et al.* 2024).

The presence of specific pollen types unique to *H. itama* and *G. thoracica* (Figure 3) further highlights the potential resource partitioning between these stingless bees and *A. cerana*. The more extensive list of pollen types found only in stingless bee honey suggests differential floral preferences and possible spatial or temporal partitioning in foraging behavior. Partitioning enhances pollination efficiency and supports higher biodiversity in tropical ecosystems (Kaluza *et al.* 2017). Furthermore, the variation in pollen composition between the two *G. thoracica* colonies observed in our study may reflect colony-specific foraging preferences (Elzt *et al.* 2001) or individual learning behavior among stingless bee foragers (Ludowici *et al.* 2024). Intra-specific variation aligns with earlier work demonstrating that different colonies of *Tetragonula collina* documented considerable variation in pollen type richness across colonies, suggesting flexible colony-level resource use responsive to local floral availability (Elzt *et al.* 2001). These intra-specific differences reinforce the idea that stingless bee colonies exhibit highly adaptable and flexible foraging strategies.

Our results revealed the important implications for pollination as they highlight the complementary role of stingless bees in supporting plant reproduction and biodiversity, particularly in areas with variable or fragmented floral resources. One limitation of this study is the relatively small number of colonies sampled for each bee species, which may not fully capture the range of intra-specific variability in foraging patterns and pollen diversity. Future research should also incorporate the examination of corbicular pollen and bee bread to provide a more comprehensive assessment of floral resource use and foraging dynamics.

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