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Diversity and nesting ecology of Indo-Malayan stingless bees (Hymenoptera: Apidae) in Aceh Province, Indonesia

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Abstract. *Emil MFP, Priawandiputra W, Kahono S, Atmowidi T. 2024. Diversity and nesting ecology of Indo-Malayan stingless bees (Hymenoptera: Apidae) in Aceh Province, Indonesia. Biodiversitas 25: 3617-3627.* The study of stingless bee diversity and nest ecology is needed as an integral part of beneficial insects. Information on stingless bees in the northern peninsula of Sumatra, Indonesia was limited. The study aimed to analyze the species richness and nest ecology of Indo-Malayan stingless bees in Aceh Province, Indonesia. Through exploratory surveys, data were collected from two observation sites, i.e., Aceh Besar and Bener Meriah Districts, between July and August 2023. Results showed that ten species of stingless bees were recorded. The stingless bees' body lengths ranged from 4.6 to 11.7 mm, and forewing lengths from 3 to 8.8 mm. Stingless bee nest substrates were found on natural substrates and those associated with settlements. Nest entrances varied in size (1.75-13.54 cm in length, 0.65-7.57 cm in horizontal diameter, 0.45-7.46 cm in vertical diameter), with long pipe funnel with dim gray, cavity shapes dominantly circular and irregular, soft textures with resin and pores. These nests were located 1-300 m from water sources in elevation ranges 0-600 cm. The cells in the stingless bee nest were composed of brood cells, honey cells, pollen cells, and stone layers. Variations in the nest entrance funnel may related to the adaptability to the environment and internal factors.

Keywords: Beneficial insects, nest entrance, nest internal structure, species richness

INTRODUCTION

Stingless bees (Hymenoptera: Apidae) are social insects distributed in the world's tropical and subtropical regions. These social insects are found across the Neotropical, Afrotropical, and Australasian regions, encompassing Asia, America, Africa, and Australia (Engel et al. 2023). A recent study indicated that 605 species belonging to 45 genera of stingless bees have been identified and described worldwide (Engel et al. 2023). The tropical regions are widely recognized as the dominant distribution areas for this insect group (Michener 2012). In Indonesia, stingless bees are distributed in three ecoregions, i.e., Indo-Malayan, Wallacea, and Australasian (Rasmussen 2008; Salatnaya et al. 2023). Forty-six species belonging to ten genera have been reported in Indonesia, particularly within the Sunda Shelf and Wallacea regions (Engel et al. 2018).

Sumatra is one of the five major islands of Indonesia with a unique geological history within the zoogeographic realm of the Sunda Shelf. Until now, twenty-three species of stingless bees have been recorded in Sumatra, twenty-eight species in Borneo, seven species in Java, three species in Sulawesi (Sakagami et al. 1990; Kahono et al. 2018), and three species in Ambon and West Halmahera (Salatnaya et al. 2022). Sumatra stingless bees belong to Indo-Malayan meliponini (Rasmussen 2008; Jalil et al. 2017). Comprehensive studies on the stingless bees of Sumatra and Northern Sumatra are crucial due to the limited data available. Limited knowledge due to the lack of available reports makes species conservation in natural habitats difficult.

Stingless bees are recognized as the primary pollinators for horticultural crops and wild plants and play a crucial role in enhancing human food availability. The bees have a small body size, high tolerance to climatic conditions, and high foraging activity, making them good pollinators. The stingless bees are essential for pollinating various plant species, such as snake fruit (*Salacca* sp.) (Atmowidi et al. 2021), pummelo (*Citrus maxima* (Burm.) Merr.) (Atmowidi et al. 2022a; Anisa et al. 2022), and orange fruit (*Citrus reticulata* var. RGL) (Nurdiansyah et al. 2023). Stingless bees also enhance seed formation in mustard (*Brassica rapa* L.) (Asmini et al. 2022) and kailan (*Brassica oleracea* var. *alboglabra*) (Wulandari et al. 2017). Additionally, stingless bee pollination improved the quality and quantity of crops, such as melon (*Cucumis melo* L.) (Bahlis et al. 2021; Atmowidi et al. 2022b), strawberry (*Fragaria* x *ananassa* Duch) (Alpionita et al. 2021; Atmowidi et al. 2022b), and okra (*Abelmoschus esculentus* L.) (Djakaria et al. 2022). Stingless bees have also been reported as one of the many insect visitors of crops in agricultural lands (Siregar et al. 2016; Jihadi et al. 2021). Several agricultural field experiments have demonstrated that stingless bee colonies significantly impact the pollination of tomatoes (*Solanum lycopersicum* L.) (Nurdiansyah et al. 2024a) and lemons (*Citrus limon* (L.) Burm.fil. Eureka) (Nurdiansyah et al. 2024b).

As integral parts of beneficial insects, the conservation of stingless bees must be prioritized. One challenge taxonomists face for supporting conservation efforts is identifying of stingless bees due to morphological characteristics (Sakagami and Inoue 1985). Therefore, studying the nest structures is essential as external characteristics for species identification (Mduda et al. 2023). Each stingless bee species has a nest-entrance variation in shape and size as external characteristics for that identification (Kelly et al. 2014; Anaktototy et al. 2021). Additional data, such as biotic characteristics (nest height from the ground and colony size), is also crucial for species identification (Reinhard-Jesajas et al. 2023). This research observed stingless bee species richness and nest ecology in Aceh province, Sumatra, Indonesia. This study provides additional data on the diversity of stingless bees in Sumatra, particularly in the northern peninsula region of Sumatra Island, Indonesia, and contributes to the sustainability of conservation and the management of stingless bees and their habitat. The increase in human population, along with the expansion of anthropogenic activities and land use, makes the conservation efforts of stingless bees an issue that needs attention. Nest ecology studies also provide foundational information for species conservation in the natural ecosystems.

MATERIALS AND METHODS

Study area

The sampling of stingless bee colonies was conducted from July to August 2023 at twelve observation sites in Aceh Province, i.e., in Aceh Besar (5°3'0"-5°45'0" S, 94°59'0"-95°55'0" E) (Peukan Bada, Darul Imarah, Lhoong, Mesjid Raya, Seulimeum, and Lembah Seulawah sub-districts) and Bener Meriah (4°33'50"-4°54'50" S, 96°40'75"-97°17'50" E) (Timang Gajah, Wih Pesam, Bukit, Gajah Putih, Bandar, and Permata sub-districts). The distance between Aceh Besar and Bener Meriah districts is 300.4 kilometers (Figure 1; Table 1).

Nest observations

The observations of bees were conducted in the forest and residential areas using an exploratory survey method (Silvy 2020). In each observation area, we tracked for three sunny days. We used information about the stingless bees from the local people using the phrase "*Linot*" (Aceh language). During bee observations, environmental parameters, i.e., temperature, humidity, light intensity, and wind velocity, were recorded using Lutron LM8000A four-in-one. All nests were examined using qualitative and quantitative parameters (Kelly et al. 2014; Rivaldy et al. 2023; Hora et al. 2023). Qualitative parameters observed were nest substrate, nest entrance shape, structure, size, and resin's existence. In contrast, quantitative parameters measured were the nest's height from the ground, the size of the entrance funnel, and the nest's distance from the water source. The dominant color of the nest entrance was also measured using an LS173 colorimeter. The internal structure of nests from six species of stingless bees was documented using hives from bee farms near the research sites to avoid damage or cut down of nesting trees.

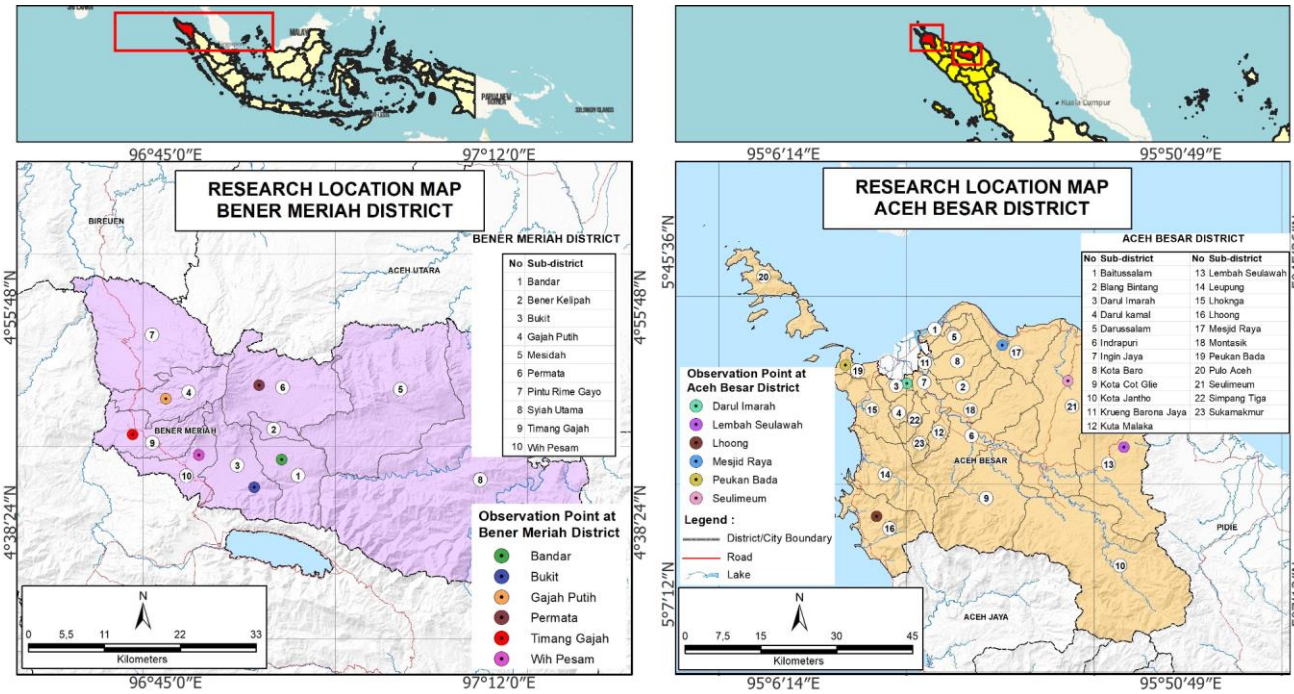

Figure 1. Observation sites of stingless bees in Aceh, Indonesia

Table 1. The species, number of colony, and nesting sites of stingless bees in Aceh, Indonesia: Gth. *G. thoracica*, Hit. *H. itama*, Lte. *L. terminata*, Lve. *L. ventralis*, Smo. *S. moorei*, Tco. *T. collina*, Tfu. *T. fuscobalteata*, Tge. *T. geissleri*, Tla. *T. laeviceps*, and Tmi. *T. minangkabau*

Location	Coordinate/altitude (m asl.)	Number of colony	Species code	Nesting sites	Nearest water source
Aceh Besar					
Peukan Bada	0532’33.6’’N & 09514’00.0”E/12	1	Tla	Termite nest (unknown species)	River
	0532’58.7’’N & 09513’49.1”E/7	2	Lte	Tree cavity (*Artocarpus heterophyllus*)	River
	0532’58.6’’N & 09513’49.2”E/24	3	Lve	Tree cavity (*Artocarpus heterophyllus*)	River
	0532’58.5’’N & 09513’50.0”E/19	4	Tla	House foundation	River
	0532’58.7’’N & E 09513’49.4”E/55	5	Hit	Tree cavity (*Sandoricum koetjape*)	River
	0532’58.5’’N & E 09513’49.4”E/2	6	Tla	Tree cavity (*Artocarpus heterophyllus*)	River
	0532’58.6’’N & 09513’49.4”E/33	7	Lte	Adventitious root (*Ficus elastica*)	Beach
	0534’10.7’’N & 09514’21.0”E/43	8	Lve	Rock crevice	Beach
Darul Imarah	0530’17.4’’N & 09519’32.5”E/-12	1	Hit	Tree cavity (*Cocos nucifera*)	Well
	0530’14.9’’N & 09519’29.4”E/2	2	Hit	Tree cavity (*Sandoricum koetjape*)	Brackish water
	0530’13.8’’N & 09519’24.6”E/4	3	Tge	Tree cavity (*Averrhoa bilimbi*)	Well
	0530’12.2’’N & 09519’29.2”E/-9	4	Hit	Tree cavity (*Nephelium lappaceum*)	Rice field
	0530’09.5’’N & 09519’19.3”E/7	5	Tla	Tree cavity (*Cocos nucifera*)	Irrigation
	0530’12.5’’N & 09519’35.1”E/12	6	Tla	House foundation	Irrigation
Lhoong	0517’08.0’’N & 09515’37.8”E/-9	1	Tco	Adventitious root (*tingkeum bui*: local name)	Waterfall
	0517’32.5’’N & 09513’24.9”E/-8	2	Gth	Tree cavity (*Pterocarpus indicus*)	Rice field
	0511’56.5’’N & 09518’22.1”E/3	3	Gth	Tree cavity (*Durio* sp.)	River
	0511’56.9’’N & 09518’22.3”E/25	4	Tco	Fallen trees (*Durio* sp.)	River
Mesjid Raya	0538’19.4’’N & 09527’58.7”E/-15	1	Hit	Tree cavity (*Mangifera indica*)	Beach
	0537’43.1’’N & 09528’08.3”E/-5	2	Hit	Tree cavity (*Azadirachta indica*)	Beach
	0536’49.7’’N & 09533’32.1”E/-2	3	Lte	Tree cavity (*Hibiscus tiliaceus*)	Beach
	0536’48.7’’N & 09533’23.4”E/5	4	Lte	Tree cavity (*Azadirachta indica*)	Beach
	0536’49.5’’N & 09533’21.2”E/6	5	Hit	Tree cavity (*Planchonella obovate*)	Beach
	0536’50.7’’N & 09533’21.2”E/15	6	Hit	Tree cavity (*Garcinia corallina*)	Beach
	0536’42.1’’N & 09533’26.9”E/25	7	Tla	Adventitious root (*Ficus elastica*)	River
	0535’35.8’’N & E09531’52.6”E/23	8	Gth	Tree cavity (*Spondias pinnata*)	River
	0535’34.5’’N & 09531’51.7”E/21	9	Gth	Tree cavity (*Spondias pinnata*)	River
Seulimeum	0536’38.7’’N & 0957’55.1”E/11	1	Hit	Tree cavity (*Azadirachta indica*)	River
	0535’11.8’’N & 09540’22.2”E/8	2	Gth	Tree cavity (*Celtis occidentalis*)	Aquaculture pond
	0535’12.2’’N & 09540’21.7”E/14	3	Tfu	House door and window frame	Aquaculture pond
	0535’12.1’’N & 09540’22.0”E/21	4	Tla	Tree cavity (*Spondias dulcis*)	Aquaculture pond
	0535’12.0’’N & 09540’22.0”E/23	5	Tla	Dead tree (*Spondias dulcis*)	Aquaculture pond
	05°35’12.4’’N & 095°40’22.0”E/16	6	Tfu	House door and window frame	Aquaculture pond
	0535’27.7’’N & 095’42.9”E/20	7	Gth	Tree cavity (*Cocos nucifera*)	Irrigation
	0534’59.9’’N & 095’35.0”E/75	8	Gth	Soil	River
	0535’00.7’’N & 095’34.1”E/72	9	Tfu	Tree cavity (*Vitex pinnata*)	River
	0535’00.7’’N & E 095’34.1”/72	10	Tla	Tree cavity (*Vitex pinnata*)	River
	0536’33.6’’N & 095’51.2”E/28	11	Hit	Pipe	Beach
Lembah	056’37.2’’N & 095’33.5”E/433	1	Tfu	Iron pillar	Pool
Seulawah	056’37.1’’N & 095’33.4”E/439	2	Tla	Concrete fence	Pool
	056’28.3’’N & 095’30.3”E/366	3	Tfu	House wall	River
	05’31.4’’N & 095’14.3”E/154	4	Tla	Tree cavity (*Parkia speciosa*)	Rice field
	05’10.1’’N & 095’32.5”E/181	5	Tla	Dead tree (*Parkia speciosa*)	Water reservoir
	05’10.0’’N & 095’33.3”E/185	6	Tfu	Dead tree (*Parkia speciosa*)	Water reservoir
Bener Meriah					
Timang Gajah	05’09.9’’N & 095’33.1”E/1042	1	Tla	Concrete fence	River
	0444’25.1’’N & 096’00.6”E/1051	2	Tla	Concrete fence	River
	0444’24.9’’N & E 096’00.7”E/1053	3	Tla	Concrete fence	River
Wih Pesam	04’51.0’’N & 096’29.1”E/1024	1	Tmi	Tree cavity (*Parkia speciosa*)	River
	0443’50.7’’N & 096’28.8”E/1022	2	Tmi	Tree cavity (*Morus alba*)	River
	043’50.9’’N & 09646’28.9”E/1025	3	Smo	Ant nest (*Crematogaster* sp.)	River
Bukit		Nol data available			
Gajah Putih	0440’54.0’’N & 09650’26.2”E/575	1	Tla	Fallen tree (*Areca catechu*)	River
Bandar		Nol data available			
Permata		Nol data available			
Total colony(s)		**51**			

Specimen collection and identification

An insect net collected thirty worker bees from each stingless bee colony. Then, the specimens were preserved in Eppendorf tubes containing 70% ethanol. Some samples of bees were preserved in the dry method (Koneri et al. 2021). The specimens were sent to the Laboratory of Animal Biosystematics and Ecology, Bogor Agricultural University in Bogor for identification process with approval from the Conservation of Natural Resources (BKSDA) Aceh Province with registration number BAP.402/K.20-TU/KSA.2.2/8/2023 and the Agricultural Quarantine Agency of Sultan Iskandar Muda International

Airport, Indonesia with registration number 2023.1.2404.0.K12.K.000229.

The morphological characters of bees were observed using a stereo microscope embedded with a camera. The stingless bee characteristics observed were body color, antennae (scape, pedicel, and flagellum), number of teeth in mandible, mesoscutum, scutellum, and propodeum, number of hamuli, wing, hind tibia, and basitarsus colors. Identification of stingless bees based on Sakagami et al. (1990), Jalil (2017), Engel et al. (2018), and Engel et al. (2023). The specimens were also verified using specimen collections of the Museum Zoologicum Bogoriense (MZB), National Research and Innovation Agency (BRIN), Bogor, West Java, Indonesia. Some specimens were deposited at the MZB as voucher specimens (registration number MZB Hymn 44666-MZB Hymn 44695). The specimens were also deposited at the Animal Biosystematics and Ecology Laboratory, Department of Biology, Bogor Agricultural University. The specimens were photographed using a VHX-7000 digital microscope.

Measurement of body size

Stingless bees' body and forewing lengths were measured using a VHX-7000 digital microscope at the Nano Imaging Laboratory of Bogor Agricultural University. Ten individuals of each species were measured. The body length was measured from the mandible to the metasoma's terga. Specimens were spread by inserting a pin from the clypeus to the end tergum of the metasoma. The forewing length was measured from the base of the tegula to the wing ends. Body length is the dynamic character being measured, while the static character is represented by forewing length.

Data analysis

The characteristics of the nest entrance were described and summarized in the table. The body size of ten bee species was analyzed using non-Metric Multidimensional Scaling (nMDS) using Paleontological Statistics (PAST) software version 4.09 (Hammer et al. 2001).

RESULTS AND DISCUSSION

Diversity of stingless bees

Ten species of stingless bees were found in two observation sites, i.e., *Geniotrigona thoracica* (Smith, 1857), *Heterotrigona itama* (Cockerell, 1918), *Lepidotrigona terminata* (Smith, 1878), *Lepidotrigona ventralis* (Smith, 1857), *Sundatrigona moorei* (Schwarz, 1937), *Tetragonilla collina* (Smith, 1857), *Tetragonula fuscobalteata* (Cameron, 1908), *Tetragonula geissleri* (Cockerell, 1918), *Tetragonula laeviceps* (Smith, 1857), and *Tetragonula minangkabau* (Sakagami and Inoue 1985) (Figures 2 and 3).

In Aceh Besar, eight species of stingless bees were found (86.28% of total colonies), i.e., *G. thoracica*, *H. itama*, *L. terminata*, *L. ventralis*, *T. collina*, *T. fuscobalteata*, *T. geissleri*, and *T. laeviceps*. Meanwhile, in Bener Meriah, three species were found (13.72% of total colonies), i.e., *S. moorei*, *T. laeviceps*, and *T. minangkabau* (Table 1). *T. laeviceps* was found in both observation sites (Table 2). Additionally, each observation site had different climatological conditions. In Aceh Besar, during the study period (July 2023), the air temperature was 32-34.6°C, humidity was 60-70%, light intensity was 823-900 lux, and wind speed ranged from 0.87 to 4 m/s. Furthermore, the climatological conditions recorded in Bener Meriah during this study (August 2023), the temperature was 16-23.6°C, humidity was 80-95%, light intensity was 700-738 lux, and wind speed ranged from 0.83 to 4 m/s.

Body size of stingless bees

The stingless bee species found in this study have varied body sizes (body and forewing lengths). *Tetragonula fuscobalteata* is the smallest body size (4.6 mm±0.52 and 3 mm±0.00). The larger species were *T. geissleri* (5.6 mm±0.52 and 4 mm±0.00), *S. moorei* (5.7 mm±0.48 and 4 mm±0.00), *T. laeviceps* (5.8 mm±0.79 and 4 mm 0.00), *L.ventralis* (6.4 mm±0.70 and 4.5 mm±0.85), *T. minangkabau* (6.5 mm±0.71 and 4.9 mm±0.32), *L. terminata* (6.8 mm±0.63 and 5 mm±0.47), *T. collina* (8.1 mm±0.74 and 6.1 mm±0.32), *H. itama* (8.8 mm±0.63 and 6 mm±0.00), and *G. thoracica* (11.7±1.06 mm and 8.8±0.42 mm). Based on nMDS analysis, ten stingless bee species were grouped into four clusters (stress value of 0.05297, <2.5). Cluster-1 was *G. thoracica*, the largest body size among the species analyzed. The cluster-2 was a group of *H. itama* and *T. collina*. Cluster-3 belongs to the species with small body sizes, i.e., *L. terminata*, *T. minangkabau*, *L. ventralis*, *T. laeviceps*, *S. moorei*, and *T. geissleri*. A close relationship occurred in *T. laeviceps*, *S. moorei*, and *T. geissleri* exhibit overlapping patterns. Cluster-4 belongs to *T. fuscobalteata* with the smallest body size (Figure 4).

Nesting ecology of stingless bees

Stingless bees construct their nests on natural and artificial substrates. A total of 40 colonies (78.43%) of stingless bees build nests on various natural substrates, such as plant parts, rocks, ant and termite nests, and soil. Additionally, 11 colonies of bees (21.57%) build nests in artificial substrates, such as foundations, door and window, wall, iron pole, and house pipe. The nest of *G. thoracica* was found in tree cavities (six colonies) and soil (one colony). The species tree for stingless bee nesting sites was *Artocarpus heterophyllus* Lam., *Mangifera indica* L., *Ficus elastica* Roxb., *Nephelium lappaceum* L., *Vitex pinnata* L., *Durio* sp., *Parkia speciosa* Hassk., *Pterocarpus indicus* Willd., *Spondias pinnata* (L.fil.) Kurz, *Spondias dulcis* Parkinson, *Morus alba* L., *Garcinia corallina* Vieill., and *Celtis occidentalis* L. Interestingly, we found the nest of *S. moorei* in an active arboreal ant nest (*Crematogaster* sp.) and the nest of *T. laeviceps* (one colony) in a termite nest (Figure 5). In addition, most stingless bee nests found close to the river ranged 1-300 m (*G. thoracica*, *L. ventralis*, *G. thoracica*, *S. moorei*, *T. collina*, *T. laeviceps*, and *T. minangkabau*). Other bee species built nests close to the beach (*L. terminata* and *L. ventralis*), close to the waterfall (*T. collina*), the pond (*T. fuscobalteata*), and the well (*T. geissleri*) (Table 1).

The nest funnel shapes found in this study are categorized as flat, short, and long, and tapering funnels based on the visual display. The dominant funnel shape was long (49.01%), followed by short (17.64%), flat (15.68%), tapering (15.68%), and other shapes (*S. moorei* nest). The cavity shape of the nest entrance (Figure 6.A) is dominated by circular (29.41%) and irregular (29.41%), followed by triangular (13.72%) and oval (5.88%). The entrance funnel with a soft texture was dominant (56.86%) compared to a hard texture (41.17%) (Figure 6.B). Other characteristics are pores and sticky resin in the nest entrance. About 52.93% of nest-entrance funnels have pores, and the remaining without pores (45.09%) (Figure 6.C) and most funnels with sticky resin (86.27%) (Figure 6.D).

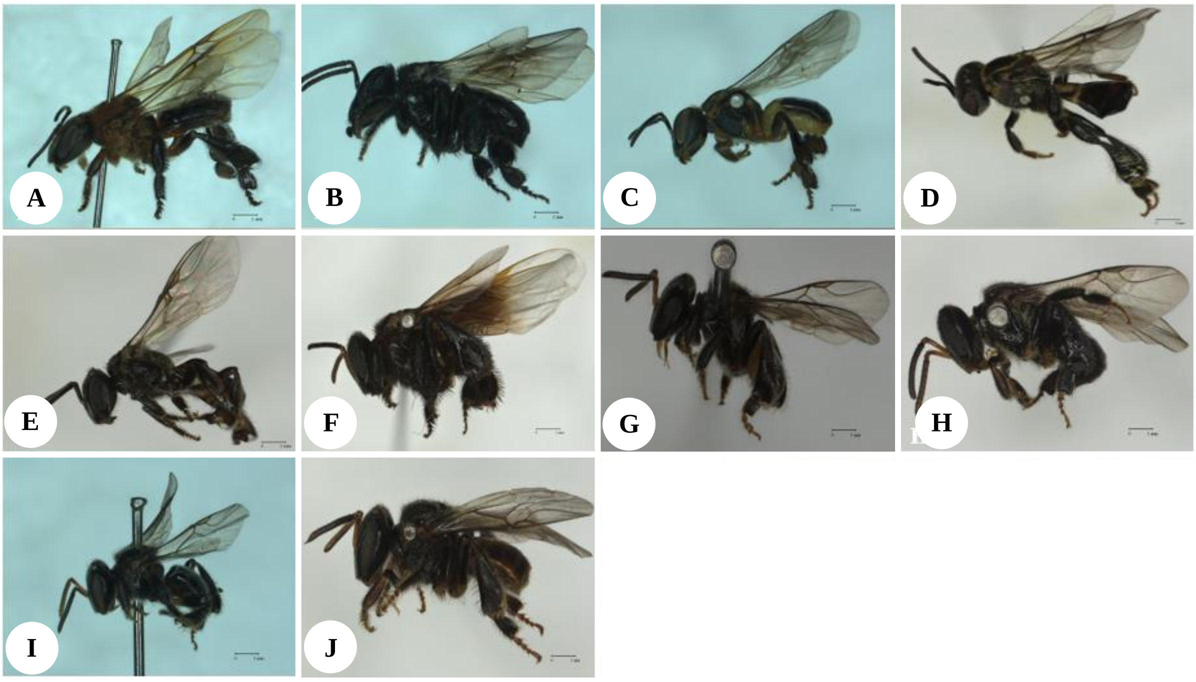

Figure 2. Stingless bee species found in Aceh, Indonesia: A. *Geniotrigona thoracica*, B. *Heterotrigona itama*, C. *Lepidotrigona terminata*, D. *Lepidotrigona ventralis*, E. *Sundatrigona moorei*, F. *Tetragonilla collina*, G. *Tetragonula fuscobalteata*, H. *Tetragonula geissleri*, I. *Tetragonula laeviceps*, and J. *Tetragonula minangkabau*

Figure 3. Frontal view of stingless bee species found in Aceh Province, Indonesia: A. *Geniotrigona thoracica*, B. *Heterotrigona itama*, C. *Lepidotrigona terminata*, D. *Lepidotrigona ventralis*, E. *Sundatrigona moorei*, F. *Tetragonilla collina*, G. *Tetragonula fuscobalteata*, H. *Tetragonula geissleri*, I. *Tetragonula laeviceps*, and J. *Tetragonula minangkabau*

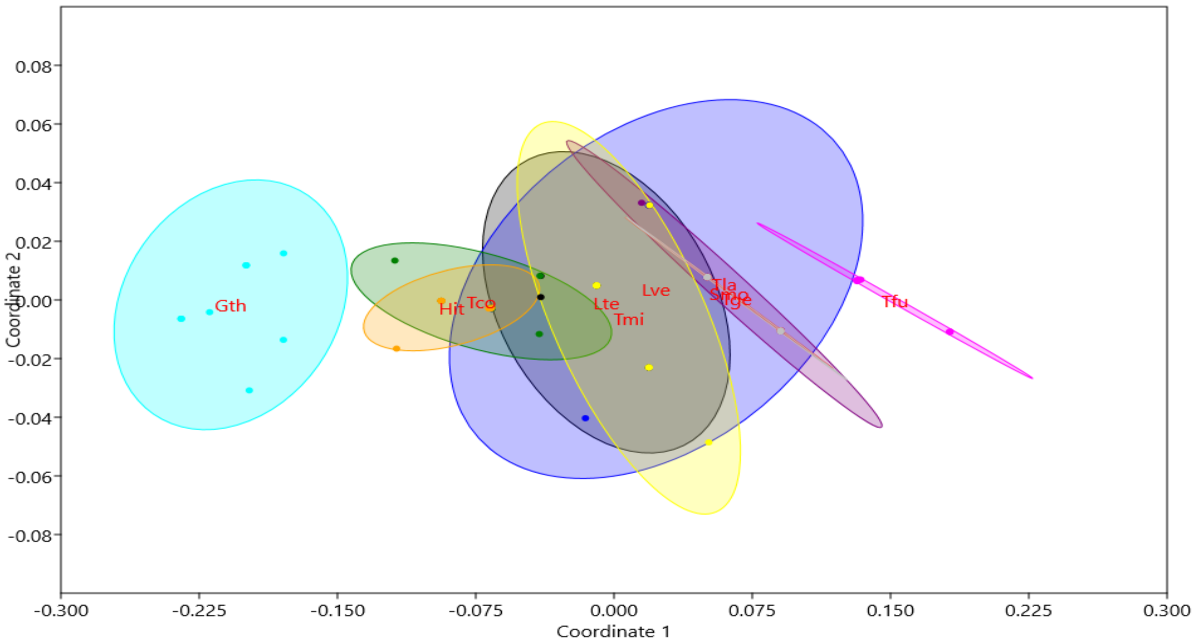

Figure 4. *Non-Metric Multidimensional Scaling* (nMDS) ordination of ten species of stingless bees found in Aceh (stress = 0.05297). Grouping patterns were shown based on species and the species code refers to Table 1

Table 2. Nest location and entrance size of stingless bees in Aceh, Indonesia. The numbers showed the average and ranged, (-) no data

Species	Nest entrance size (cm)			Nest height from ground (cm)	Distance of water source (m)
	Length	Horizontal diameter	Vertical diameter		
G. thoracica	13.54 (7-28)	7.57 (5-13)	7.46 (5-10)	167.20 (0-347.2)	66 (1-150)
H. itama	6.33 (0.7-10.3)	1.71 (0.7-3)	1.97 (1.2-3)	137.93 (37.6-416)	114 (2.7-300)
L. terminata	9.4 (7.9-11.2)	2.23 (1.3-2.9)	2.95 (2.1-3.4)	151.22 (19.7-270)	47,5 (30-60)
L. ventralis	3.55 (0.6-6.5)	0.65 (0.4-0.9)	0.45 (0.4-0.5)	74.5 (59-90)	45 (30-60)
S. moorei	-	-	-	600	145
T. collina	6.85 (3.7-10)	1.05 (0.9-1.2)	1.2 (1.1-1.3)	61.65 (3.3-120)	151 (2-300)
T. fuscobalteata	4 (0.3-11.6)	0.78 (0.4-1)	1.73 (0.5-3.6)	225.16 (134-350)	197.8 (3.5-70)
T. geissleri	5.3	1.1	2.2	77.6	11
T. laeviceps	1.75 (0.2-12.6)	1.18 (0.2-3.7)	1.78 (0.2-4.5)	111.57 (21.1-300)	36.18 (1-100)
T. minangkabau	2.2 (0.3-4.1)	2 (1.2-2.8)	4.25 (3.4-5.1)	60.7 (27.3-94.1)	151 (150-152)

Table 3. The color variation of stingless bee entrance funnels: L. brightness, A. red and green color components, B. blue and yellow color components. There is no data for *Sundatrigona moorei* due to the nest's position being inaccessible

Species	Colorimeter measurement			Color (*n* Nest)	Color display
	L	A	B		
G. thoracica	35.59	-0.90	1.28	Dim gray (4)	
	32.30	0.38	-0.82	Dark slate gray (3)	
H. itama	44.62	4.58	7.57	Dim gray (10)	
L. terminata	42.79	3.40	6.86	Dim gray (3)	
	45.06	1.92	9.27	Dark slate gray (1)	
L. ventralis	47.97	2.47	4.68	Dim gray (2)	
T. collina	37.16	6.95	8.41	Dim gray (2)	
T. fuscobalteata	39.47	2.93	8.01	Dim gray (5)	
	30.54	-0.77	-0.51	Dark slate gray (1)	
T. geissleri	30.80	-0.93	-0.49	Dark slate gray (1)	
T. laeviceps	34.69	1.76	1.63	Dim gray (3)	
	30.38	-1.05	-0.34	Dark slate gray (13)	
T. minangkabau	46.30	2.88	9.34	Dim gray (2)	

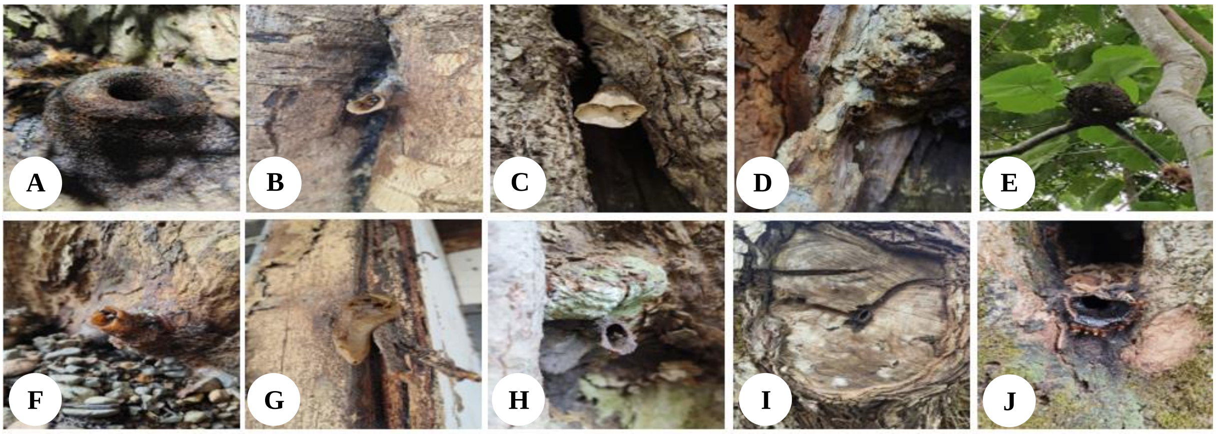

Figure 5. Nest entrance of stingless bee: A. *G. thoracica* (Mesjid Raya 8), B. *H. itama* (Darul Imarah 2), C. *L. terminata* (Mesjid Raya 3), D. *L. ventralis* (Peukan Bada 3), E. *S. moorei* (Wih Pesam 3), F. *T. collina* (Lhoong 1), *G. T.fuscobalteata* (Seulimeum 3), H. *T. geissleri* (Darul Imarah 3), I. *T. laeviceps* (Peukan Bada 1), and J. *T. minangkabau* (Wih Pesam 1)

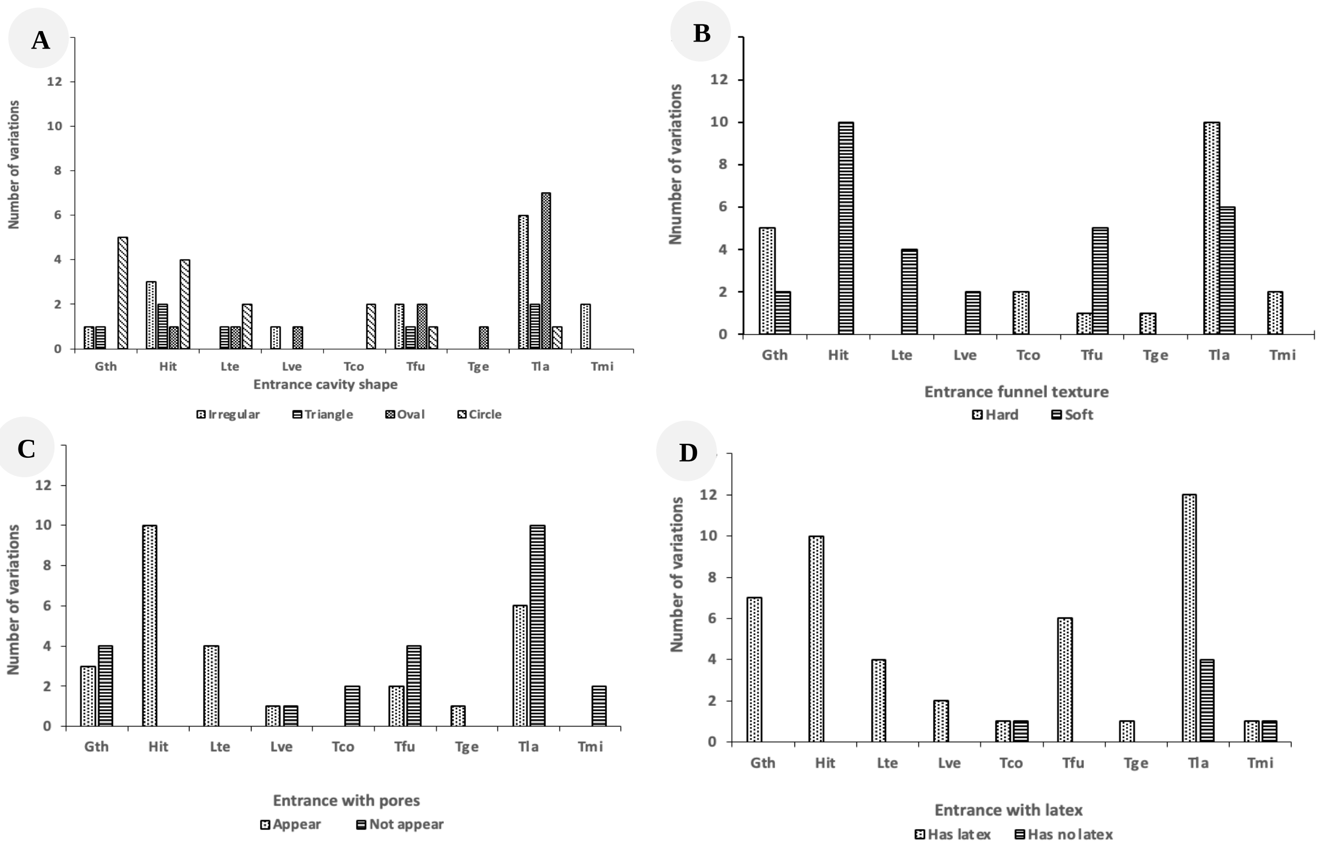

Figure 6. Variation of stingless bee nest entrance funnels: A. Entrance cavity shape, B. Entrance funnel texture, C. Entrance funnel with pores, D. Entrance funnel with resin. The species code refers to Table 1

The diameter of the nest entrance funnel varied among species. *Geniotrigona thoracica* has the largest funnel size (13.54 cm in funnel length, 7.57 in horizontal diameter, and 7.46 in vertical diameter). Meanwhile, small entrance sizes were found in *T. laeviceps* and *L. ventralis* (Table 2). Additionally, differences in nests are often found in the same species, even though they may show nearly similar visual characteristics. Most stingless bee nest entrances were bright in color, while dark color was found in *G. thoracica*, *L. terminata*, *T. fuscobalteata*, *T. geissleri*, and *T. laeviceps* (Table 3). Using a colorimeter, the bright color of the nest entrance was detected as dim gray and the dark color as dark slate gray. Additionally, the nest's heights from the ground ranged from 0 to 600 cm (Table 2), and the nest's distance from the water source ranged from 1 to 300 m. The internal structure of stingless bee nests consists of honey pots, pollen pots, brood cells, and stone layers (Figure 7).

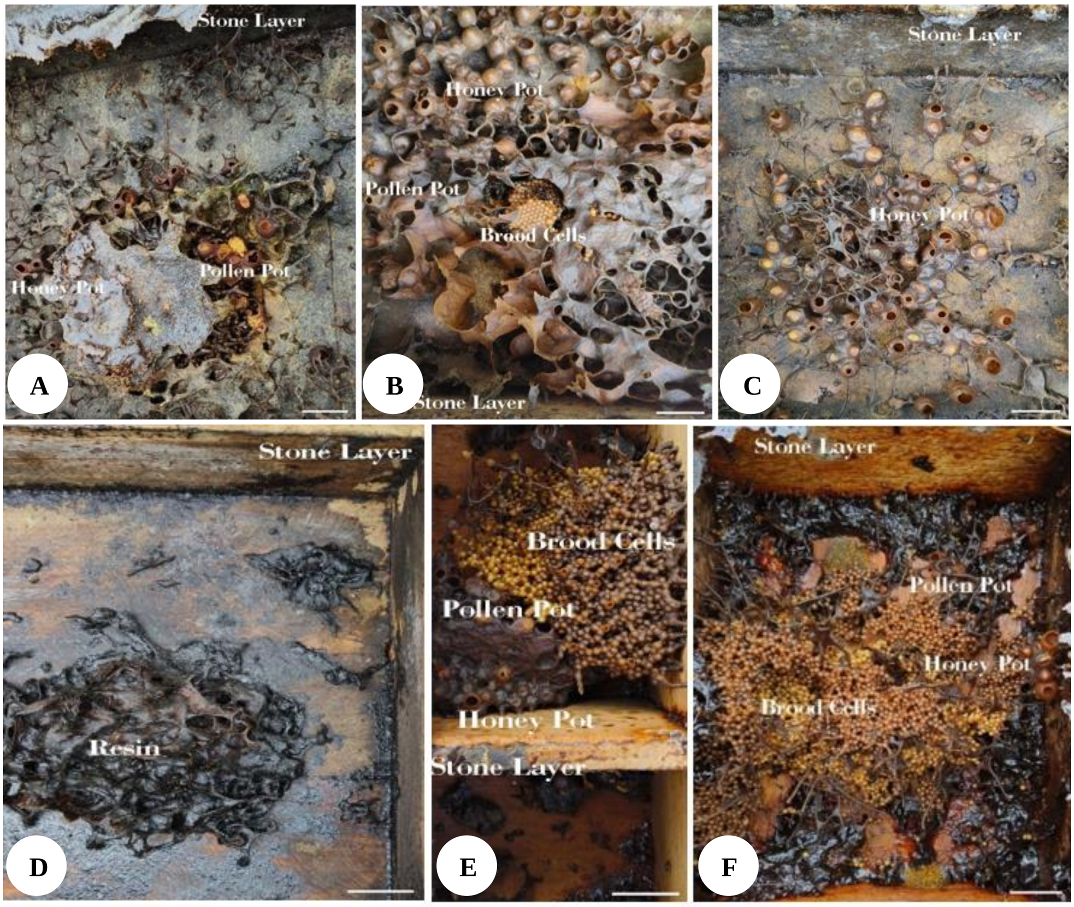

Figure 7. Nest internal structure of stingless bees: A. *G. thoracica*, B. *H. itama*, C. *L. terminata*, D. *L. ventralis*, E. *T. laeviceps*, F. *T. minangkabau*. Photos B, C, and D were documented from Mr. Khairil Fattah's farm (Peukan Bada, Aceh Besar), photos A, E, and F were documented from Mr. Ahlandi Saputra's stingless beehive collection (Timang Gajah, Bener Meriah). Scale bar = 5 cm

Discussion

This study found ten species of stingless bees of Indo-Malayan meliponini (Engel et al. 2023). A previous study reported 24 species of stingless bees in Sumatra (Sakagami et al. 1990; Herwina et al. 2020; Herwina et al. 2022). *Tetragonula geissleri* was reported in central Sumatra (Herwina et al. 2020; Herwina et al. 2022) and the Western Malaysian Peninsula (Salim et al. 2012). The historical land connection between Sumatra and Malaysia seems to contribute to the shared characteristics of the species in both regions (Li et al. 2023). Sundaland, comprising the Malaysian Peninsula, Sumatra, Java, Borneo, and Palawan, is part of Southeast Asia and features a mosaic of continental blocks, volcanic arcs, and suture zones that are remnants of closed ocean basins (Li et al. 2023). These are located on the shallow water of the Sunda Shelf, which was exposed as land during the low sea levels of the Pleistocene (Li et al. 2023). This region is recognized as a biodiversity hotspot (Li et al. 2023). Five species identified in this study, i.e., *G. thoracica*, *H. itama*, *L. terminata*, *T. fuscobalteata*, and *T. laeviceps*, have been reported in the southern peninsula of Sumatra, Indonesia (Priawandiputra et al. 2020). Six other species, i.e., *G. thoracica*, *H. itama*, *L. terminata*, *L. ventralis*, *T. collina*, and *T. laeviceps*, have been recorded in Lubuk Minturon, West Sumatra (Herwina et al. 2023). We supposed the distribution of Indo-Malayan stingless bees in Sumatra is across regions. This study confirms that the species identified belong to the Indo-Malayan stingless bees (Sakagami et al. 1990; Jalil et al. 2017; Herwina et al. 2020; Herwina et al. 2022; Engel et al. 2023).

Our results showed nests of stingless bees were found in diverse substrates. The selection of substrates for nesting sites of stingless bees has been widely reported, such as in dead tree cavity (da Costa Macedo et al. 2020), tree cavities (Chauhan and Singh 2021; Reinhard-Jesajas et al. 2023), soil, rock crevices, and ant nests (Sakagami et al. 1989; Suriawanto et al. 2017; da Costa Macedo et al. 2020; Reinhard-Jesajas et al. 2023). Our study also found the nest of *S. moorei* and *T. laeviceps* were in ant and termite nests, as myrmecophilous and termitophilous associations, respectively (Sakagami et al. 1989). The nest of stingless bees in pipes, door and window frames, house foundations, iron pillars, house walls, and concrete has been reported (Suriawanto et al. 2017; Reinhard-Jesajas et al. 2023). We did not find bamboo as a nesting substrate for stingless bees that have been reported by Qu et al. (2022).

The stingless bee nest was found on resin-producing trees, and this tendency is because resin-producing trees provide space for colony development (Reinhard-Jesajas et al. 2023). Resin-producing plants provide supply of resin for stingless bee colonies, as well as ease of access, along with empty spaces offered by these plants for nest building. The nest of stingless bees is located close to water sources. Lorenzon and Matrangolo (2005) observed the abundant flora and non-floral resources around the water source, revealing that worker bees visit this area. Noorahya et al. (2023) reported water is essential to honey production. The stingless bees are affected by temperature (Trianto and Purwanto 2022). The wide distribution of stingless bees in Aceh Besar provides information on how the insects tolerate air temperatures. The nesting site of *T. laeviceps* on various substrates showed high adaptability to environmental conditions (Priawandiputra et al. 2020; Herwina et al. 2020, 2022, 2023).

Nest entrance helps maintain the internal nest, defend against predators, and ventilate the nest (Rivaldy et al. 2023). The elongated tube-shaped entrance has been reported previously in *Homotrigona fimbriata* and *T. collina* (Rivaldy et al. 2023). The circular and irregular shapes of nest entrance have been documented for *Tetragonula sapiens*, *Tetragonula clypearis*, *T. fuscobalteata*, *L. terminata*, and *Wallacetrigona incisa*, with additional shapes, such as oval and triangular in Sulawesi stingless bee (Sayusti et al. 2021). The resin in the nest entrance deter ants (Alves et al. 2018; Purwanto et al. 2022). Formicidae is a major predator of stingless bees (Wicaksono 2017; Wicaksono et al. 2020). The variation of nest-entrance funnel size of stingless bees varied among species, and we supposed it related to body size. The entrance size enhances the efficiency of colony activity and is related to the number of workers in the colony (Couvillon et al. 2008). Additionally, the size of the entrance funnel is adjusted to defend against predators (Alvarez et al. 2018).

The nest entrance funnels of stingless bees observed were in two colors, i.e., bright and dark. Bright colors (dim gray) were dominant, whereas dark colors (dark slate gray) were observed in *G. thoracica*, *L. terminata*, *T. fuscobalteata*, *T. geissleri*, and *T. laeviceps*. The color of dim gray appears brighter compared to the color dark slate gray. This finding represents a novel contribution to scientific knowledge because the use of colorimeters in similar research is very limited and has never been used before. Previous studies on nest entrance coloration relied on visual observations, and the results depended on the observer, the time of observation, and environmental conditions. Azmi et al. (2019) reported that the entrance funnel of *H. itama* is lighter in color than that of *G. thoracica*. While in Baluran National Park, East Java, Rachmawati et al. (2022) reported brown and black nest-entrance funnels for *L. terminata* and *T. laeviceps*. The color variation in the nest entrance may be attributed to different resins. We supposed each location had resin-producing plants, and stingless bees selected resins from specific plants. The similarity in nest color is also believed to be due to the colonies selecting resin from the same resin-producing plant sources. The nesting site of stingless bees in higher locations aims to avoid predators and disturbances (Rivaldy et al. 2023). Woodcock et al. (2017) revealed that selecting a nest in a higher location in stingless bees is a mitigation strategy against pesticide exposure and other pollutants.

Our documentation of internal nest structure enhances information on nest ornamentation as an adaptation to the substrate. The internal structure displays the arrangement of nesting spaces and their placement. The inner nesting spaces play a role in double mitigation (bitumen layers), colony sustainability (broad cells), and food security for the colony (honey pots and pollen pots). Adaptation to nest substrate was observed in *G. thoracica*, *L. terminata*, and *L. ventralis*. This data supported Reinhard-Jesajas et al. (2023) that the nest structures of stingless bees were adapted to the nesting substrate. Variations in stingless bee nests are also influenced by genetics, nest age, and environmental factors, such as rainfall and sunlight (Kelly et al. 2014; Purwanto et al. 2022). In general, the internal structure of the nests found in this study is similar to stingless bee nests in Banten, as reported by Efin et al. (2019).

In conclusion, the northern peninsula of Sumatra (Aceh Province), Indonesia, represents a significant region for distributing Indo-Malayan stingless bees that are less attention. Our study showed a high diversity of stingless bees in Aceh province. Nest entrance variation in stingless bees is influenced by internal factors (such as the body size and the number of individuals in the colonies) and external factors related to mitigation and the colony's anti-predator behavior. Nest variation is related to the adaptation of the colony to its environment and resource availability. For future studies, we recommend a wider area of the Sumatra studies to explore other Indo-Malayan stingless bees. The conservation efforts of stingless bees and their ecosystem should be done to support the socio-bioeconomics of meliponiculture, agriculture, and the food industry.

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