Distribution, nest architecture, and forage plants of an endemic Wallacean species of stingless bee Wallacetrigona incisa (Apidae: Meliponini) in Sulawesi, Indonesia

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Abstract

Wallacetrigona incisa is a Wallacean species endemic to Sulawesi Island, Indonesia. To protect natural colonies, their habitat must be kept stable. Hunting in natural habitats and moving colonies to unsuitable environments causes stress. Information on their habitat distribution has been revealed; however, information on their distribution still needs to be improved, and aspects of their ecology that are currently poorly understood need to be studied for conservation and utilization. We conducted research on their additional distribution in different locations in South and West Sulawesi provinces, nest architecture, and food plants by direct observation. Each nest was found, the GPS position was measured, habitat conditions were characterized, and pollen was collected to determine the forage plants. Twenty-seven living nests were recorded in South Sulawesi, and two in West Sulawesi. The most prominent distinctive nest architecture for the defense of the colony from damage by predation is the strong entrance covered with a thick, hard resin of the *Agathis* plant. From the analysis of pollen balls on the feet of bees, it was found that forage plants from 19 families and 38 types of pollen, and the three dominant species were *Agathis celebica*, *Barringtonia asiatica*, and *Pigafetta elata.* This finding is important for supporting the conservation of this Sulawesi endemic species.

Implications for insect conservation

Our study reports new data on the natural habitat distribution, nest architecture and forage plants of an endemic Wallacean species of Sulawesi Island *W. incisa* that may help to protect this species in its natural habitat.

Introduction

Stingless bees are eusocial bees that are distributed abundantly in moist tropical countries (Michener 1990), one of which is that Indonesia has recorded as many as 46 species of stingless bees (Kahono et al. 2018). Indonesia, an archipelagic country, has flora and fauna distribution zones, including stingless bees, in at least three transitional zones (Hall 2009; Hall 2002). Sulawesi Island is the largest island in the transitional zone between Asia and Australia known as Wallacea (Wallace 1860; Mayr 1944) in which much of its fauna and flora originate from the Southeast Asian plate and from the eastern slice of New Guinea (Hall 2002; Hall 2009; Michaux 2010). Studies on stingless bees in the Wallacea region have shown that the endemic bee environment has been denuded and fragmented, and predation by natural predators and bee hunters can lead to a decline or even extinction of these bee populations in their habitat.

The majority of Sulawesi is located 500m above sea level, and approximately 20% of its total land area is above 1,000m. Mountainous regions in central and northern South Sulawesi have altitudes over 2,000m (Lobo and Halffter 2000; Stiegel et al. 2011). These heights are significant because they provide a refuge for diverse flora and fauna and serve as a source of genetic diversity (Hamilton and Miller 2016; Qodri et al. 2016; Syahriati et al. 2021). Sulawesi has many endemic species of flora and fauna, including honeybees, which have been better researched than other bee groups (Lohman et al. 2011; Myers et al. 2016), which play an important role as pollinators, and are key elements in the maintenance and conservation of natural ecosystems (Ollerton,et al. 2011; Slaa et al. 2006; Wratten et al. 2012).

Stingless bees have been recorded in Sulawesi Island namely *T. sapiens*, *T. clypearis*, *T. fuscobalteata*, *T. laeviceps*, *T. pagdeni*, *Lepidotrigona terminata*, and *Wallacetrigona incisa* (Engel & Rasmussen 2017; Kahono et al. 2018; Sayusti

et al. 2020; Suhri et al. 2021; Trianto et al. 2023). Most species are distributed in the lowlands of the island and spread to the eastern islands of Halmahera(Salatnaya et al.2021) and Ambon (Lamerkabel et al. 2021); however, *W. incisa* is endemic to the highlands at an altitude of 800–2200m on Sulawesi Island (Rasmussen et al. 2017; Suhri et al. 2021). Research on the distribution of *W. incisa* have been reported in several locations of the provinces of Central Sulawesi (Poso District, Lore Lindu National Park - Palu, and Todyamboe, Tokosa Mountain, North Sulawesi (Modoinding - Minahasa); and South Sulawesi (Tojambu); (Rasmussen et al. 2017). This species was successfully maintained in semi-natural habitats, but not in lowland habitats, which have different microclimate conditions, especially when the air temperature is warmer (Suhri et al. 2021). Further research on the different highland distribution locations of *W. incisa* will provide a better understanding of the geographical distribution of the species, which is essential for devising effective conservation and utilization strategies.

The main component of stingless bee nests is the resin secreted by plants. The nest architecture of the stingless bee species exhibits typical entrances, brood cells, food storage, and other outbuildings (Roubik 2006, 2022; Suriawanto et al. 2017; Pangestika et al. 2018; Sayusti et al. 2020; Suhri et al. 2021; Rachmawati et al. 2022; Reinhard et al. 2023) which are usually related to environmental conditions and nest defense behavior (Roubik 1983; De Camargo and De Menezes 1992; Rasmussen 2008). It is interesting to study the architecture of nests, especially the entrance of *W. incisa*, for defense of nests in their natural habitat and changes in their breeding environment.

Stingless bees select small-to-large flowers and find various nesting substrates (da Silva et al. 2019; Vossler 2019; Bisui et al. 2021). Bees play an important role as pollinators and are therefore a key element in the maintenance and conservation of natural ecosystems (Slaa et al. 2006; Ollerton et al. 2011; Wratten et al. 2012). Stingless bees generally have diverse food sources (Meléndez 2018; Prendergast and Bateman, 2021; Roubik 2006). However, information about the biogeographical aspects of *W. incisa* related to the interaction of bee feed plants that also facilitate their pollination is not yet known, so information about forage plants will assist in the formation of management and conservation policies. This study aims to add data on the distribution of *W. incisa* bees, nest architecture, and forage plants.

Materials and Methods

Study area

A study on the distribution, nesting patches, and forage plants of a species of the stingless bee *W. incisa* was carried out in the twenty-nine villages in five sub-districts of South Sulawesi and two villages of a sub-district of West Sulawesi (Fig. 1). All study sites were primary forests located at altitudes above 800 m above sea level, with the lowest temperature being 10°C at night. Bee samples were taken from each of the three colonies at each location.

Distributions

A Wallacetrigona incisa nest search at each study site was performed by experienced local beekeepers. The geographic position and habitat characteristics of the nests were measured. From each bee colony found, twenty worker bees were taken, ten were stored in 70% alcohol for morphometric analysis, and the other ten were stored in 96% alcohol for molecular identification.

Data on the distribution of *W. incia* were collected by measuring the GPS positions of flying bees and living nests using a global positioning system. All locations were visited directly by the divided team accompanied by local beekeepers. All recorded data were combined with previously known distribution data, including data from the

Museum Zoologicum Bogoriense collections and references (Rasmussen et al. 2017). Species distribution and geomorphological maps were created using ArcGIS 10.8. In this study, a geomorphological map was used to characterize the habitat related to the type of vegetation as the main food source of *W. incisa*. This is related to the type of vegetation available and is likely to be the main food source for *W. incisa* in the highlands.

Forage Plants

Forage plants of *W. incisa* were identified using pollen analysis methods. Pollen was collected from seven *W. incisa* nests at each sampling site (Table 1). Pollen was collected from inside the nest and stored in bottles under dry conditions. Pollen was analyzed using the acetolysis method described by Erdtman (1972) and was identified based on the pollen flora of Taiwan. Pollen analysis was performed using a binocular microscope, and digital images of the pollen grains were obtained using an Optilab viewer 2.2. To evaluate the trophic niches of *W. incisa*, Shannon-Wiener diversity (H') and uniformity per site (J') were estimated using the PAST program (Hammer et al. 2001). Pollen collection sites were selected based on the distribution of colonies in each sub-district. The decision to select locations was based on the proximity of villages and similar vegetation types; therefore, pollen sampling was conducted only on each of the seven colonies in each sub-district (Table 1).

Table 1
Pollen sampling locations

	Localities	Abbreviation	Longitude	Latitude	Altitude	N
1	Limbong village, North Luwu district, South Sulawesi Province	LBG	119,8326906	-2,592391588	1887,774245	7
2	Rampi village, North Luwu district, South Sulawesi Province	RMP	120,2040055	-2,116737333	1365,660086	7
3	Hoyane village, North Luwu district, South Sulawesi Province	HYN	119,6835138	-2,26084277	2207,118297	7
4	Saluseba village, North Luwu district, South Sulawesi Province	SLB	120,3627005	-2,363630138	894,1751349	7
5	Taupe village, Mamasa district, West Sulawesi Province	TPE	119,3526716	-2,918803132	1429,70335	7
6	Parombean village, Enrekang district, South Sulawesi	PRB	119,9911699	-3,31098318	1261,441727	7

Results

New record of natural habitat distribution of W. incisa

In South Sulawesi and West Sulawesi, *W. incisa* was found–894-2207m above sea level. 27 new sites in South Sulawesi and two new sites in West Sulawesi were identified as the natural habitats for *W. incisa*. The lowest altitude was recorded in Saluseba (894 m a. s.l.) on the hills of the Bayu Balease Mountain range, and the highest altitude was found in Hoyane (2207 m a. s.l.). In West Sulawesi, its habitat is found in the Tanete Gandang Dewata hill range, precisely in Taupe Village, at an altitude of 1429 meters above sea level (Fig. 2).

In South Sulawesi, *W. incisa* populations are distributed in the Latimojong and Bayu Balease Mountain ranges. In West Sulawesi, the habitat is scattered throughout the hilly range of Tanete Gandang Dewata. In northern Sulawesi, *W. incisa* habitat was scattered in the Torompupu hill range (Table 2). Based on topography, the Bayu Balease

Mountain, Tanete Gandang Dewata Hill, and Torompupu Hill ranges were connected in one series of hills. For the Latimojong Mountain range, the hill ranges are separate and do not connect with other distribution areas. Based on direct observations, all natural nests and wild bees of *W. incisa* were found in primary forests or forests undisturbed by human activities. Except for *W. incisa* colonies cultivated by the community, they were found around plantations or forest edges not far from residential areas.

Table 2

Natural habitat distribution of *W. incisa* propolis bees in South Sulawesi, West Sulawesi, and Central Sulawesi. Numbers 1-129 are the results of the direct observation. Numbers 30–36 are the locations that have been published by Rasmussen et al. (2017).

	Location		longitude	latitude	altitude	Habitat types	Landscape types
	Province	Sampling sites					
1	South Sulawesi	Kanandede	120.0222	-2.5187	1204.7702	primary forest	Strongly eroded mountains
2		Komba	119.9673	-2.5574	913.0520	primary forest	Strongly eroded mountains
3		Marampa	119.8326	-2.5923	1887.7742	primary forest	Volcanic fallout deposits
4		Minanga	119.9312	-2.5254	1503.5400	primary forest	Volcanic fallout deposits
5		Rinding Allo	119.8888	-2.5334	2031.2056	primary forest	Volcanic fallout deposits
6		Limbong	119.8428	-2.4674	2070.8741	primary forest	Volcanic fallout deposits
7		Pengkendekan	119.9451	-2.6340	2051.2782	primary forest	Volcanic fallout deposits
8		Tedeboe	120.1112	-2.1006	1602.5066	primary forest	Fault-block mountains
9		Rampi	120.2040	-2.1167	1365.6600	primary forest	Fault-block mountains
10		Dodolo	120.2682	-2.0756	981.8593	primary forest	Fault-block mountains
11		Onondowa	120.2450	-2.2077	1501.3539	primary forest	Fault-block mountains
12		Sulaku	120.3467	-2.1149	1483.3213	primary forest	Old fold mountains
13		Leboni	120.4502	-2.1435	1747.7768	primary forest	Old fold mountains
14		Wono	119.8233	-2.1998	1455.0527	primary forest	Fault-block mountains
15		Tirobali	119.7678	-2.4825	1882.3395	primary forest	Volcanic fallout deposits
16		Tanamakaleang	119.7533	-2.2583	1365.5624	primary forest	Fault-block mountains
17		Taloto	120.0064	-2.2334	1352.4827	primary forest	Strongly eroded mountains
18		Padang Raya	119.8918	-2.3046	1195.0619	primary forest	Volcanic fallout deposits
19		Padang Balua	119.8596	-2.2746	1317.0674	primary forest	Fault-block mountains

20		Marante	119.8907	-2.1203	1417.1014	primary forest	Fault-block mountains
21		Malimongan	119.7859	-2.3907	1526.6852	primary forest	Volcanic fallout deposits
22		Lodang	119.9684	-2.3802	1193.7998	primary forest	Strongly eroded mountains
23		Hoyane	119.6835	-2.2608	2207.1182	primary forest	Fault-block mountains
24		Embotanah	119.8262	-2.3480	1308.1409	primary forest	Volcanic fallout deposits
25		Beroppa	119.7379	-2.4065	1438.4957	primary forest	Fault-block mountains
26		Saluseba	120.3627	-2.3636	894.17513	primary forest	Strongly eroded mountains
27		Parombean	119.9911	-3.3109	1261.4417	primary forest	Fault-block mountains
28	West Sulawesi	Taupe	119.3526	-2.9188	1429.7033	primary forest	Strongly eroded mountains
29		Lambanan	119.5000	-2.8291	1604.5816	primary forest	Strongly eroded mountains
30	Central Sulawesi	Sedoa	120.345	-1.3356	1262.0422		Fault-block mountains
31		Kamarora	120.14	-1.22	1335.5223		Fault-block mountains
32		Minahasa	120.13	-2.93	712.37146		Strongly eroded mountains
33		Lindu	120.29	-1.42	1360.1645		Fault-block mountains
34		Lore Lindu	120.19	-1.47	1545.4447		Fault-block mountains
35		Tokosa Mountain	120.04	-1.35	1009.6738		Fault-block mountains
36		Tambing lake	120.31	-1.33	1714.7162		Strongly eroded mountains

In general, the landscape characteristics of *W. incisa* distribution areas are dominated by hilly mountains. In South Sulawesi, *W. incisa* habitats are distributed in Strongly Eroded mountains, fault-block mountains, volcanic fallout deposits, and old-fold mountains. In West Sulawesi, this habitat is found in mountainous areas characterized by strongly eroded mountains. In central Sulawesi, the habitat is found in fault blocks and strongly eroded mountains (Fig. 3).

Forage plants of W. incisa

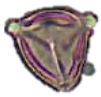
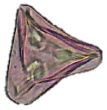
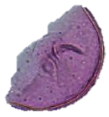
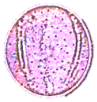
Pollen analysis revealed 38 pollen species from 19 families with 22,5±6,77 pollen species per site. *Agathis celebica*, *Barringtonia asiatica*, and *Pigafetta elata* were found at all sampling sites, whereas *Pinus merkusii*, *Quercus* spp., *Rhododendron rhodopus*, and *Vaccinium latissimum* were found at five of the six sampling sites (Table 4). The greatest pollen diversity was found in colonies from Limbong (LBG), Hoyane (HYN), Parombean (PRB), and Taupe (TPE) with H'_{LBG} = 2.125, H'_{HYN} = 2.054, H'_{PRB} = 1.975, and H'_{TPE} = 1.879, respectively. The lowest degree of pollen diversity was found in colonies from Rampi (RMP) and Saluseba (SLB) with H'_{RMP} = 1.256 dan H'_{SLB} = 1,166. High pollen diversity was found in LBG, HYN, and TPE. However, a low level of uniformity was observed at these three sites (J'_{LBG} = 0.39, J'_{HYN} = 0.343, and J'_{TPE} = 0.336). At other sites with lower levels of diversity, the RMP and PRB also had low levels of uniformity (J'_{RMP} = 0.444 and J'_{PRB} = 0.352). The low uniformity values indicate that *W. incisa* colonies at the five sites show selectivity for certain pollen sources and that there are dominant pollens that are frequently collected. In contrast, the SLBs with the lowest level of diversity had a high level of uniformity (J'_{SLB} = 0.825) (Table 3). The high uniformity value indicates that *W. incisa*colonies in the SLB do not show selectivity for a particular pollen source, that is, there is no dominant pollen type.

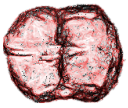
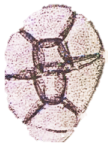
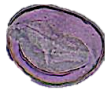
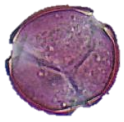
Table 3
Number of pollen types collected by *W. incisa*, pollen diversity (H'), and pollen uniformity (J'). These results were based on the analysis of pollen collected from workers at six randomly selected sites that were considered representative of all sites.

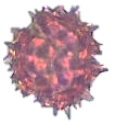
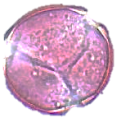
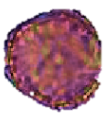
Localities	LBG	RMP	HYN	SLB	TPE	PRB
Number of pollen types	18	17	19	17	20	14
H'	2.125	1.256	2.054	1.166	1.879	1.975
J'	0.391	0.444	0.343	0.825	0.336	0.352

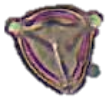
The dominant pollen types was LBG Rhododenron celebicum (80.35%), Barringtonia asiatica (RMP; 75.32%), HYN (*Rhododenron impositum*; 65.25%), PRB (*Vaccinium latissimum*; 65.10%), and TPE (*Rhododendron vanvuureni*; 75.15%). Pollen analysis revealed that *W. incisa* had visited 19 plant families. The most frequently visited families were Ericaceae (30.15%) and Myrtaceae (9.58%), which were present at all locations.

Table 4 Distribution of *W. incisa* food plants based on pollen identification results per sampling location (+ = present, - = absent)

Family	Spesies	Local name	Localities						Pollen morphology
			LBG	RMP	HYN	SLB	PRB	TPE	x1000
Pinaceae	*Pinus merkusii* et de Vriese	Tusam	+	+	+	-	+	+	
Arecaceae	*Pigafetta elata*	Wanga	+	+	+	-	+	+	
Araucariaceae	*Agathis celebica* (Lambert) L.C. Rich	Damar, Agatis, Kauri	+	+	+	+	+	+	
Fagaceae	*Quercus* spp	Pasang	+	+	+	+	-	+	
	Castanopsis acuminatissima (Bl.) A. DC.		+	+	-	+	-	+	
Ericaceae	*Vaccingium varingifolium* (Bl.) Miq.	Cantigi	+	-	+	-	+	-	
	Rhododendron celebecum (Blume) DC.	Azalea	+	-	+	-	+	-	
	Rhododendron arenicolum Sleumer	Saliyah	+	-	+	-	+	-	
	Rhododendron impositum J.J.Sm	Saliyah	+	-	+	-	+	-	
	Rhododendron nanophyton Sleumer	Saliyah	+	-	+	-	+	-	
	Rhodondendron vanvuurenii J. J. Sm	Azalea	+	-	+	-	-	+	
	Rhododendron	Azalea	-	+	+	+	+	+	

	rhodopus Sleumer								
	Vaccinium centrocelebicum Sleumer	Cantigi ungu	+	-	+	-	+	-	
	Vaccinium pilosilobum J.J.Sm.	Cantigi	+	-	+	-	+	-	
	Vaccinium latissimum J.J.Sm.	Cantigi	+	+	+	+	-	+	
	Cyrtandra tenuicarpa H. J. Aktins	Maleala	-	-	-	-	-	+	
	Diplycosia celebensis J.J.Sm.	-	+	-	+	-	+	-	
	Gaultheria celebica J.J.Sm.	-	+	-	+	-	+	-	
	Diplycosia aperta J.J.Sm.	-	-	-	-	+	+	+	
Podocarpaceae	*Podocarpus neriifolius* D.Don	-	-	-	-	+	+	-	
	Dacrycarpus imbricatus de Laub. blume	Jamuju	-	-	+	+	-	-	
Lecythidaceae	*Barringtonia asiatica* L.	Kalpataru, Bitung	+	+	+	-	+	+	
Myrtaceae	*Pimenta racemosa* (Mill.) JW Moore	Kayu bai	-	-	+	+	+	+	
	Euginia sulcata	-	-	-	-	+	+	-	

	(Kunth) DC.								
	Syzygium acuminatissimum Blume	Jambu talawe, copeng	+	+	+	+	+	+	
Lythraceae	*Cuphea ignea* A. DC	Bunga rokok	+	+	-	+	+	+	
Asteraceae	*Leontapodium alpinum* Cass.	Edelweis	-	-	+	-	-	-	
Primulaceae	*Ardisia* sp.	Kayu bai	-	-	-	-	-	+	
Melastomaceae	*Medinilla crassifolia* Blume	Kisun	-	-	-	-	-	+	
Zingiberaceae	*Alpinia* sp	Panak-panak	+	+	+	-	+	+	
Fabaceae	*Acacia celebica*	Mangga hutan	+	+	+	-	+	-	
Rosaceae	*Rubus fraxinifolus* Poir.	Langkiak kodo	+	+	-	+	+	+	
Symplocaceae	*Symplocos* sp.	Kayu anak	-	-	-	-	-	+	
Actinidiaceae	*Saurauia trystila* Burkill.	Jelatang gajah	+	-	+	-	-	+	

									
Cunoniaceae	*Caldcluvia celebica* Blume	-	-	+	-	+	+	+	
	Weinmannia blumei Planch.	Peris	+	-	+	+	+	+	
Pentaphylaceae	*Ternstroemia penangiana* Choisy.	-	+	+	+	+	-	-	
Lauraceae	*Litsea ochracea* (Blume) Boerl.	Lada gunung	+	-	+	-	+	+	

Characteristics of W. incisa nests

The nest entrance of *W. incisa* is mostly located at the center of the large trees. The *W. incisa* nest entrance had no funnels. The entire external nest entrance is composed of hardened resin (Fig. 4). The shape of the entrance is simple compared to that of other species, such as *Tetragonula biroi*, *T. sapiens*, and *T. laeviceps*, which generally have a funnel and soft texture. In *W. incisa*, the external nest entrance is 3.03±1.24 cm wide, dark in color and generally black, made of resin or tree sap mixed with soil or mud. All nest entrances found at 27 sites in South Sulawesi were black or dark brown, except for the white entrance to a *W. incisa* nest in Taupe Village, Mamasa. At the entrance, there–8–10 bees on the guard did not appear to be foraging.

Based on these observations, each nesting tree was inhabited by only one or two *W. incisa* colonies. No other bee species were found nesting in the same tree. Nests were made in tree cavities approximately 2–3 meters above the ground. The internal parts of the nest could not be seen in the *W. incisa* colonies because they were still active and could not be cut.

Discussion

New records of W. incisa distribution areas in South and West Sulawesi

Wallacetrigona incisa is distributed only at an altitude of 800–2200 masl (Rasmussen et al. 2017). However, *W. incisa* populations have never been found in the hilly mountain ranges of Lompobattang and Bawakaraeng, which also have altitudes > 800 masl. If analyzed based on geomorphology, *W. incisa* habitats are also potentially spread

throughout the hilly mountain ranges in Sulawesi, including the Lompobattang and Bawakaraeng Mountains. Few studies have been conducted on *W. incisa*, including its food plant species. Recent studies have been conducted on the nesting sites and nest architecture of *W. incisa* in South Sulawesi (Suhriet al., 2021). The habitat of *W. incisa* is entirely distributed in the highlands, which are dominated by hilly mountainous areas. The natural habitat of *W. incisa* is a primary forest undisturbed by human activities. Natural habitats, such as primary forests, are very important for *W. incisa* because they provide the right environment for them to breed and obtain the resources they need. Primary forests tend to exhibit high environmental stability. Factors, such as temperature, humidity, and food sources, are usually better maintained in primary forests (Gibson et al. 2011; Kormos et al. 2017). These stable environmental conditions can support the reproductive success and survival of *W. incisa*, which may depend on these factors. However, it is important to remember that natural habitats such as primary forests often face threats from deforestation, land-use change, and other human activities. Efforts to conserve and protect these natural habitats are essential to ensure the survival of endemic species, such as *W. incisa*, and maintain Sulawesi's overall biodiversity.

In South Sulawesi, the habitat of *W. incisa* is distributed in Strongly Eroded mountains, which are mountains or hills that experience strong erosion and significant shrinkage processes, forming steep and split soil patterns; the Fault-Block Mountains are a series of mountains formed by the movement of chunks of the earth's crust due to faults or faults; volcanic fall deposits are particles and materials of volcanic ash ejected by volcanic eruptions and then deposited around the eruption area; old folded mountains refer to mountain ranges that were formed millions of years ago as a result of folding and deformation of the earth's crust (Saroinsong 2020; Verkerk et al. 2020). They have undergone erosion and change over a long period of time, and alluvial plates formed due to geomorphological processes that are dominated by exogenous forces, including climate, rainfall, wind, rock type, topography, and temperature, all of which accelerate weathering and erosion (White et al. 2017).. Erosion results were deposited by water at lower locations or following the flow of the river. In West Sulawesi, its habitat is found in mountainous areas characterized by strongly Eroded mountains. In Central Sulawesi, this habitat is found in strongly eroded faults and mountainous areas.

The selection of these landscapes as habitats for *W. incisa* did not appear to be influenced by geological characteristics. However, habitat preference of *W. incisa* refers to the type of vegetation available for nesting sites, food sources, and resin sources. The landscape characteristics and vegetation types are interrelated (Deng et al. 2007; Franklin et al. 2003). Topography can provide a stable control of plants in mountainous areas. Information on the relationship between the landscape and vegetation availability is important for explaining vegetation properties. However, no previous studies have examined the distribution of *W. incisa* habitats based on landscape; therefore, this study provides the first information on the landscape and vegetation characteristics of *W. incisa* habitats.

Forage plants

Bee habitat preference is influenced by several factors, including vegetation. If *W. incisa* chooses its habitat in a particular location, the type of vegetation in that location can be analyzed. When referring to the types of landscapes that constitute the natural habitat of *W. incisa*, there were differences in the characteristics of each landscape. These differences in characteristics reflect the different types of vegetation. Each habitat has a distinctive type of vegetation and can characterize each landscape. The results showed that *Agathis celebica*, *Barringtonia celebica*, and *Pigafetta elata* pollen were identified in all bee samples from all sampling locations. The biodiversity of Sulawesi is linked to Sundaland to the west, the Philippines to the north, and Australia to the east. Although a few plant genera are endemic to Sulawesi compared with Borneo and New Guinea, their endemism at the species level is high.

Understanding the origins and affinities of the island's flora is critical for understanding the biogeography of an entire region with sparse plant collection (Atkins et al. 2020). The Latimojong Mountains are the highlands of Sulawesi, with the highest peak at Mount Rante Mario, 3478m above sea level (Kartonegoro 2014; Rahman and Rozak 2016). This area has more subalpine vegetation than other mountainous areas in Sulawesi; therefore, the presence of Ericaceae is dominant. The number of species recorded indicates that Ericaceae has a high level of endemism in the Latimojong Mountains.

The montane forest zone in the Gandang Dewata mountain range is divided into two types: lower montane forests (1500–2400 masl) and upper montane forests (2400–3000 masl). In the lower montane forest zone, trees tend to be relatively tall and less dense and support a wealth of epiphytes. Some tree species, such as *Lithocarpus* and *Castanopsis*, were present in high numbers. Some coniferous species grow in this zone. Interestingly, not all of these vegetation types are preferred food sources for *W. incisa*. The *Agathis* species was *Agathis celebica* is the main resin choice for nest buildings. In the upper montane forest zone, trees had more uniform crowns. The trees were relatively short, with twisted trunks, bumps, small and thick leaves, and trunks full of moss. The density of trees in this mountain tended to increase with increasing altitude. Common plants in this zone are members of the Ericaceae tribe such as *Rhododendron*, *Gaultheria*, and *Vaccinium* spp.. These three genera were identified as food sources for *W. incisa* at all the sampling sites.

The population of *W. incisa*, an endemic mountain species, is highly dependent on habitat temperature. The average ambient temperature in *W. incisa* habitat is 16°C, and there may be lower temperatures during the rainy season (Suhri et al. 2021). The presence of *W. incisa*, a species endemic to the tropics, allows for constant acclimatization to the environment. Apart from temperature, the type of vegetation available is also a factor in *the dependence of W. incisa* on resources in the Sulawesi Mountains. The main vegetation type crucial for *W. incisa* is *Agathis*. To the best of our knowledge, no previous publications have stated this. However, the identification results and observations of *W. incisa* colonies indicate its dependence on *Agathis* resin in nest building, particularly at the nest entrance. Some pollen source plants that are the main food sources for *W. incisa* are endemic, such as most of the Ericaceae family in the Latimojong mountain range. In addition, *Pigafetta elata* (local name: Wanga) is also the main food of *W. incisa* in North Luwu areas including Limbong (LBG), Rampi (RMP), and Hoyane (HYN). *Wallacetrigona incisa*'s need for large trees as nesting sites also forms an adaptation of *W. incisa* to socialize with the mountain environment. Tree species that often serve as nesting sites for *W. incisa* include *Shorea leprosula* (Dipterocarpaceae), *Lithocarpus sundaicus* (Fagaceae), and *Pigafetta elata* (Arecaceae) (Suhri et al. 2021). The selection of a large and tall tree with hardened resin and a small diameter nest door hole aims to avoid predators such as mountain rats, cusci, monkeys, and wild boars. Natural enemies of *W. incisa* are often found at night. Information on the natural enemies of *W. incisa* was described for the first time in this study.

Characteristics of nest entrances and their association with predation cases

Most stingless bee species are found in Southeast Asian nests in cavities of varying sizes, and some species are known to nest in large-canopy trees that are likely to be targeted by the timber industry (Roubik 1983; Sakagami et al. 1989; Vollet-Neto et al. 2015; Ragasa et al. 2015). Once established, stingless bee colonies are believed to remain stationary for the rest of the colony cycle as the queen loses its ability to fly. Although there are some exceptions, whole-colony escape in response to disturbances is extremely rare in stingless bees, indicating that colonies rely heavily on the persistence of their nest trees (Eltz et al. 2002; Maia-Silva et al. 2015; Suhri et al. 2021). In tree cavities, stingless bees build nests and place their main entrance into an available tree cavity. The size of the entrance may vary according to species and habitat. Habitat factors are related to the type of natural enemy that can potentially

invade bee colonies. In *W. incisa*, nest entrances in Rongkong District have funnel lengths at nest entrances ranging from 4.48 to 7.18 mm, and funnel diameters between 1.11 to 2.22 mm. The dominant color is solid black and blackish brown, with resin as the main constituent (Suhri et al. 2021). *Agathis* trees grow at high altitudes and are potential resin producers. Even for W. incisa in the mountains of Sulawesi, the presence of *Agathis* trees is crucial, because they are the main source of resin for nest construction and maintenance. *Agathis* resin, which dries and hardens when mixed with soil and bee saliva, greatly protects W. incisa colonies from predators in mountainous regions. In the highlands of Borneo, *Agathis borneensis* is the most attractive resin source for the stingless bees *Tetragonula collina* and *Tetragonula melanocephala* (Leonhardt and Blüthgen 2009).

In addition to their use in hive construction, bees benefit from the anti-predation properties of resins. Resins deposited around the hive entrance also entangle termites and ants, thereby preventing hive invasion (Bordoni et al. 2020; Leonhardt et al. 2010). In addition, resin allows some species of stingless bees to build and maintain their own nests inside ant nests without being attacked. In addition to the entrance, stingless bees, such as Austroplebeia australis and scaptotrigona bipunctata, also place resin on the bodies of non-nestmate intruders (Jungnickel et al. 2004; Halcroft et al. 2011). In addition to invertebrate deterrence, resin may also function as a germicide to prevent microbial and fungal growth. Apart from these potentially important resin functions, a resin structure not found in other stingless bee species is a stone-like hardened resin structure at the entrance of the W. incisa nest. This resin serves as a protective barrier against predatory mountain rats. The hard resin structure and small door holes make it difficult for mice to destroy *the W. incisa* nests (Suhri et al. 2021).

Resin is an important part of hive defense. Stingless bees use resin to build barriers, trap predators, and kill invaders. The choice of resin source by the bees also determines the character of the resin when attached to the hive. Resins are secreted by many plant families after wounding or are produced in flowers or seeds to attract pollinators or seed dispersers; therefore, a variety of resins may be available throughout the year in ecosystems with high plant diversity (Paiva 2016; Seyfullah et al. 2018). In contrast, in agricultural landscapes dominated by monocultures, bees may have limited access to diverse sources of resin. In an environment with multiple plant resins, bees have continuous access to a range of resins, some of which have similar functional properties (such as those of plants of the same genus) and are interchangeable. Not all resins accumulated both inside and outside the hive are equally effective in safeguarding bees from attack by natural enemies, despite the ability of bees to collect resins from various plants for defence purposes (Chui et al. 2022; Drescher et al. 2014; Shanahan and Spivak 2021). Therefore, we postulate that resins from different plant genera affect different organisms.

The antimicrobial properties of resins from one plant species can be very strong, effectively inhibiting potential pathogens, but have little effect on larger organisms such as ants or beetle predators. Conversely, resins from different plant species are effective at repelling ants but lack antimicrobial effects. *Agathis cunninghamii* resin did not inhibit the growth of *P. aeruginosa* and *S. Typhimurium*, whereas the resin from *C. torelliana* strongly inhibited the growth of these microbes. In other tests, *A. cunninghami* was able to prevent small hive beetle (SHB) infestation, while *P. caribaea* resin was unable to deter SHB (Drescher et al. 2014). The presence of terpenoids in the resin, particularly the more volatile mono- and sesquiterpenes, can explain its repellent effects (Leonhardt and Blüthgen 2009; Leonhardt et al. 2010; Pichersky and Raguso 2018). We argue that the selection of *Agathis* resin *by W. incisa* is adapted to the type of large predators present in its habitat; therefore, the fast hardening and extremely hard character of *Agathis* resin can provide protection for *W. incisa* colonies in the mountains. *Agathis* resin has a greater ratio of diterpenes and triterpenes than monoterpenes and sisquiterpenes; therefore, the viscosity of the resin increases more rapidly. When the resin is collected at the hive door and exposed to air, monoterpenes and sisquiterpenes evaporate, leaving larger non-volatiles that easily polymerize and produce a hardened resin (Chui et al.

2022; Drescher et al. 2014; Lyons et al. 2009; Razal et al. 2021). In addition to being repellent, resins can also be very sticky. However, the *Agathis* resin at the entrance of *W. incisa* nests has a smooth, slippery, non-sticky surface and thus cannot trap predatory ants and small beetles. The selection of *Agathis* resin by *W. incisa* is a means of protecting it from specific predators. It is also believed that reliance on *Agathis* resin limits the ability of *W. incisa* to thrive in areas where other resin types are present even at the same elevation.

Declarations

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Author's contribution AGMIS, SK: Study design, fieldwork, conceptualization, data analysis, Investigation, Methodology, Visualization, Writing – original draft. SK, SS, AGMIS: Conceptualization, Investigation, Methodology, Project administration, Visualization, Writing – review & editing. SS: Mapping, investigation, writing - original draft.

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Figures

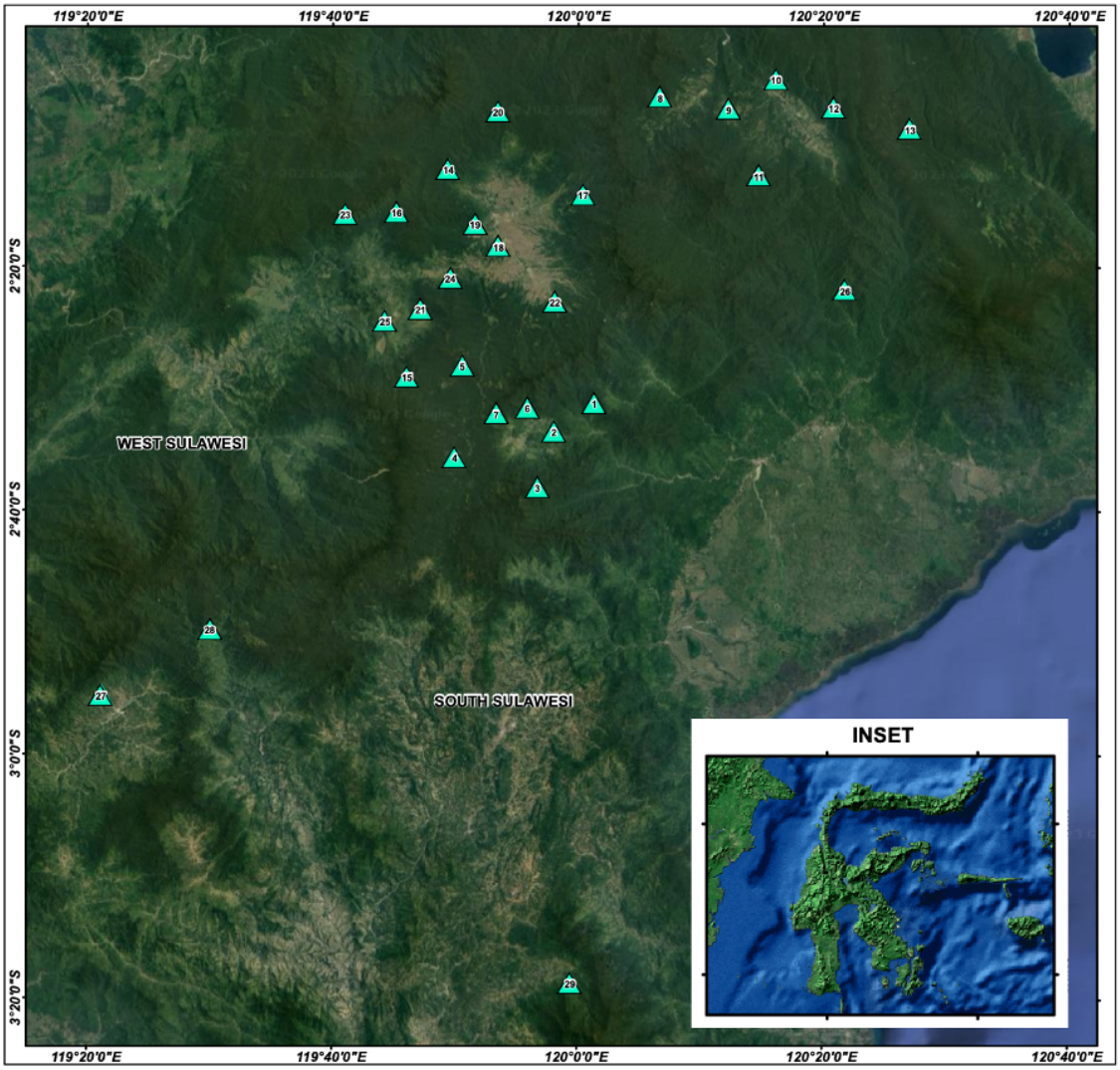

Fig. 1 Study area and sampling locations on the distribution and nesting patches the stingless bee *W. incisa.* The blue triangle marks (▲) are sampling locations to search and locate *W. incisa* habitat distribution in South Sulawesi and West Sulawesi. The number markers inside the blue triangle refer to Table 2.

Figure 1

See image above for figure legend

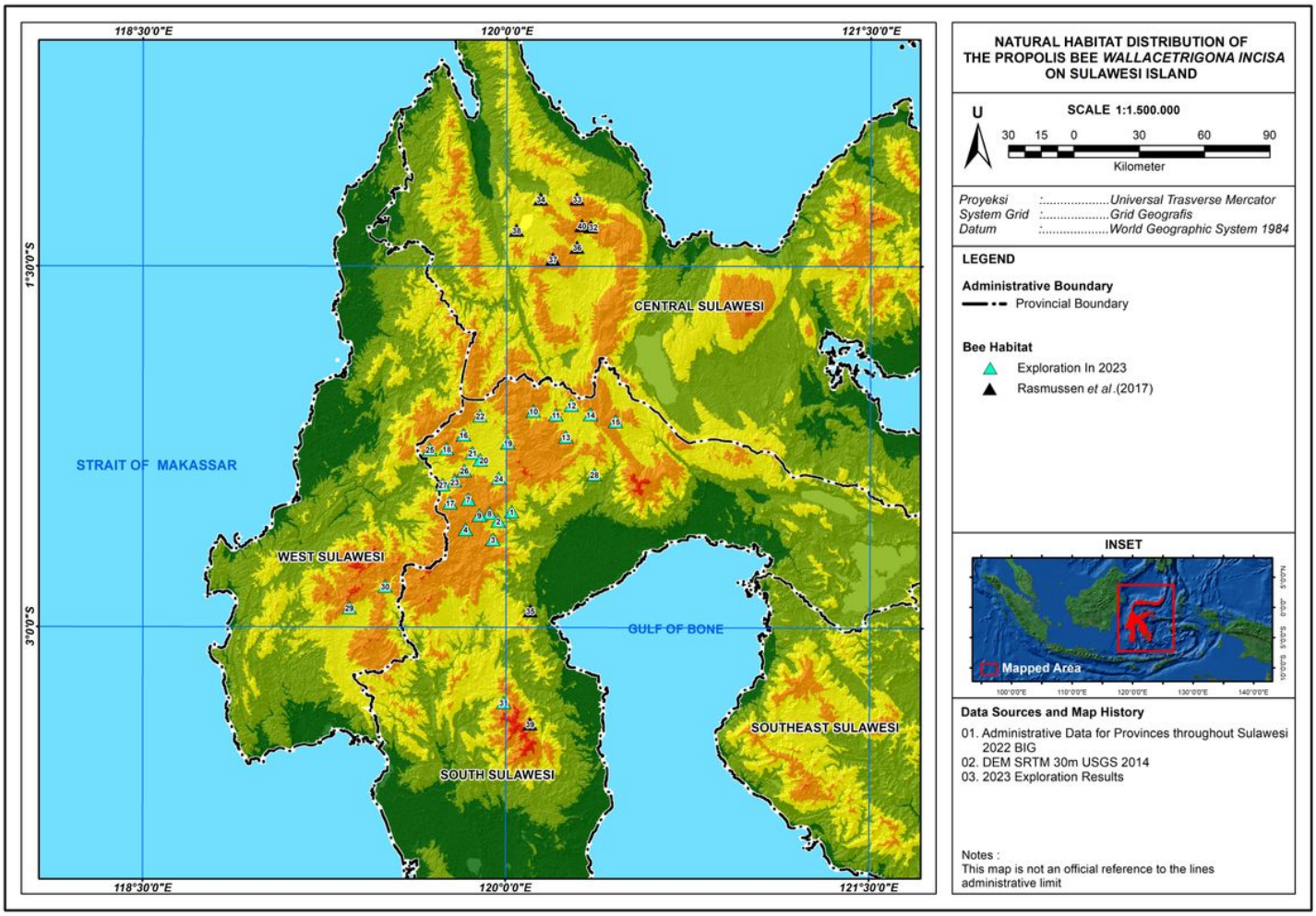

Figure 2

Map of natural habitat distribution of *W. incisa* based on exploration results in South Sulawesi and West Sulawesi. Black dots represent the distribution of *W. incisa* based on a study by Rasmussen et al. (2017).

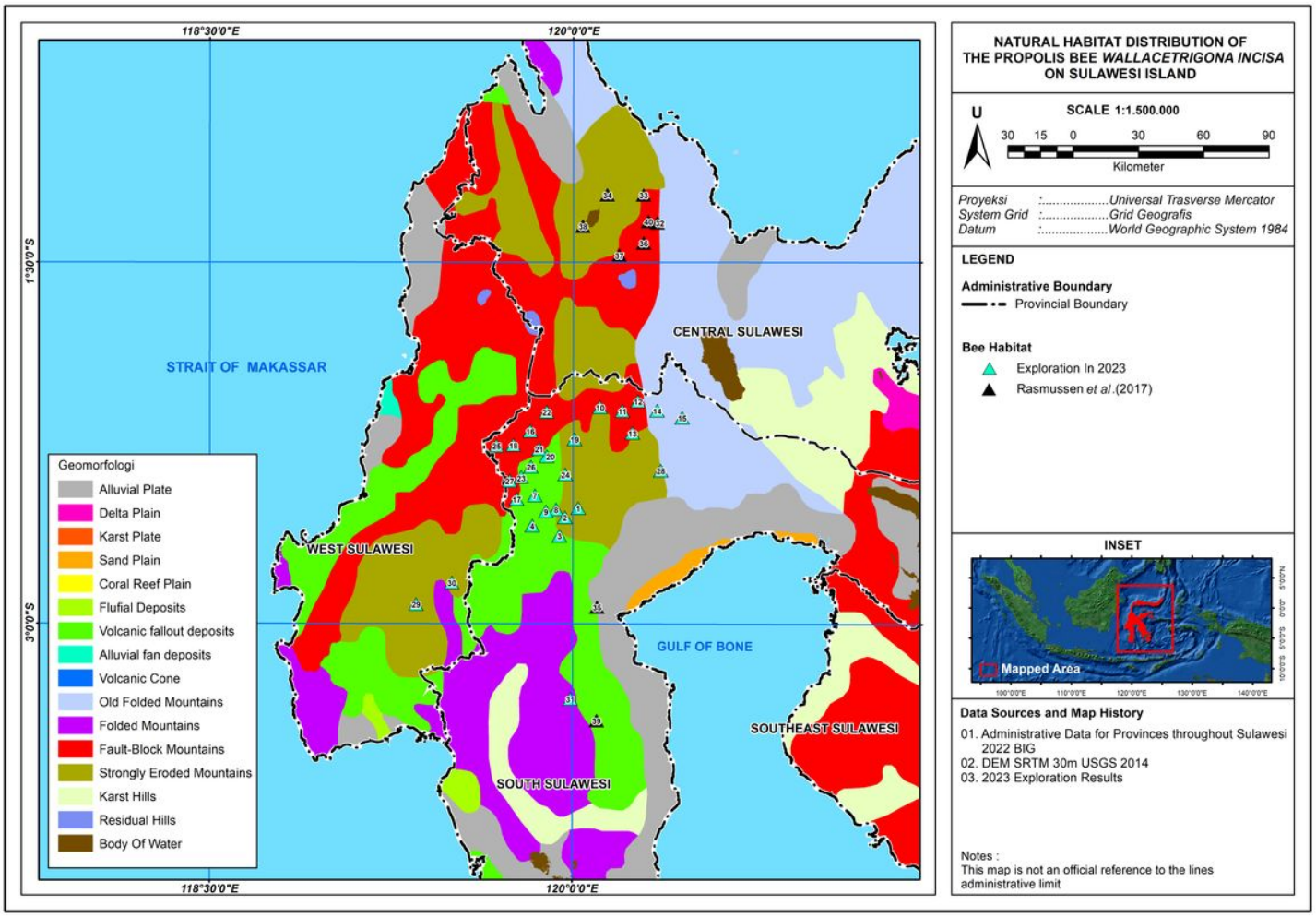

Figure 3

Landscape characteristics of natural habitats of *W. incisa* on Sulawesi Island. The blue circles represent new records of *W. incisa* locations, whereas the black circles represent data from Rasmussen's publication (Rasmussen et al.2017).

Figure 4

Shape and color characteristics of *W. incisa* nest entrance.