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Tropical lowland rainforest conversion to rubber monoculture affects flight activity and pollen resources of the stingless bees *Tetragonula laeviceps* (Smith)

Konversi hutan tropis dataran rendah menjadi lahan monokultur karet mempengaruhi aktivitas terbang dan asupan sumber daya lebah tanpa sengat *Tetragonula laeviceps* (Smith)

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ABSTRACT

Tropical lowland rainforest conversion leads to decreases diversity and population in insect pollinators, including stingless bees. However, how stingless bees respond to this conversion is still being studied. In this study we observed the number of flight activities of the *Tetragonula laeviceps* (Smith) in three converted land types in Jambi, Sumatra; identified the pollen resources of *T. laeviceps* from the collected pollen in the hind tibia; and exploring the flowering plants surrounding the *T. laeviceps* nests. Four flight activities were observed, i.e., flying out of the nest, returning with pollen, returning without pollen, and returning with resin. In addition to the flight activity, we observed flight direction and environmental factors and identified pollen composition from the hind tibia of stingless bees. This study showed that forest fragments had the highest number of bees flying out of the nest. Bees returning with or without pollen in the fragmented forest with high coverage were higher than in other habitats. The highest number of bees returning with resin was found in the rubber plantation with high coverage, while the lowest number of all flight activities were observed in the shrub with low coverage. The stingless bees mainly collected pollen from rubber flowers supported by their flight directions leading to blooming rubber trees. Our study showed that the conversion of tropical lowland rainforests in this case rubber plantation affects on decreasing the flight activities and pollen collecting of stingless bees, which may have a significant impact on the resources needed by the bees.

Key words: bee pollen, converted land, flight activity, pollen resource, *Tetragonula laeviceps*

ABSTRAK

Konversi hutan hujan tropis dataran rendah menyebabkan penurunan keanekaragaman dan populasi dari serangga penyerbuk, termasuk lebah tak bersengat. Namun, bagaimana lebah tanpa sengat mersespon konversi ini masih dipelajari. Pada penelitian ini kami mengamati jumlah aktivitas terbang *Tetragonula laeviceps* (Smith) di tiga tipe lahan yang dikonversi di Jambi, Sumatra;

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mengidetntifikasi sumber polen yang dikoleksi lebah *T. laeviceps* pada tungkai belakang; dan mengeksplorasi tumbuhan yang berbungan di sekitar sarang *T. laeviceps.* Empat aktivitas terbang lebah yang diamati, yaitu terbang keluar sarang, kembali dengan polen, kembali tanpa polen, dan kembali dengan resin. Selain aktivitas terbang, kami mengamati arah terbang lebah dan faktor lingkungan serta mengidentifikasi komposisi polen dari tibia belakang lebah. Studi ini menunjukkan bahwa hutan terfragmentasi memiliki jumlah lebah terbang keluar sarang tertinggi. Lebah yang kembali dengan atau tanpa polen di hutan terfragmentasi dengan tutupan tinggi lebih tinggi daripada di habitat lain. Jumlah lebah tertinggi yang kembali dengan resin ditemukan di perkebunan karet dengan tutupan tinggi, sedangkan jumlah terendah dari semua aktivitas terbang diamati di semak dengan tutupan rendah. Lebah tanpa sengat terutama mengumpulkan polen dari bunga karet yang didukung oleh arah terbangnya menuju pohon karet yang bunganya sedang mekar. Studi kami menunjukkan bahwa konversi hutan hujan tropis dataran rendah dalam hal ini menjadi perkebunan karet memengaruhi penurunan aktivitas terbang dan pengumpulan polen pada lebah tanpa sengat, yang dapat berdampak signifikan pada sumber daya yang dibutuhkan oleh lebah.

Key words: polen, lahan konversi, aktivitas terbang, sumber daya, *Tetragonula laeviceps*

INTRODUCTION

Land transformation into monoculture decreases vegetation diversity and ecological function (Barnes et al. 2014), leading to changes in biotic and abiotic factors (Drescher et al. 2016). It also threatens the tropical biota (Dirzo & Raven 2003) and reduces the species richness of plants and animals around the converted land (Schulze et al. 2004). Land transformation increasingly threatens insect pollinators (Ricketts et al. 2008) due to the reduction of trees needed for nesting, mating, oviposition, resting, and pollen and nectar resources (Kevan 1999).

Insect pollinators play an essential role in the stability of the ecosystem (Klein et al. 2007) because of the mutual interactions between insect pollinators and plants (Brandenburg et al. 2019). Pollination by *Tetragonula minangkabau* (Sakagami & Inoue) and *Tetragonula laeviceps* (Smith) on chilli pepper increased the fruit set by 79% and 82%, respectively (Putra et al. 2016). The insect pollinator in Jambi was a butterfly, fly, honey bees, and stingless bees (Siregar et al. 2016).

Stingless bees distribute in different environments in many regions, such as India, Singapore, Papua New Guinea, and Indonesia (Rasmussen 2008; Hrncir et al. 2019). In Indonesia, there are 46 species of stingless bees (Kahono et al. 2018), and seven species of stingless bees were found in Jambi, including *T. laeviceps* (Siregar et al. 2016). Jambi Province was dominated by lowland tropical forests (Mudiyarso 2002). However, the land cover has been converted into three different habitats, i.e., fragmented forest, rubber plantation, and shrub (Nurwanda et al. 2016) affecting the flight activities of stingless bees (Kaluza et al. 2015).

The flight activities of *Tetragonula carbonaria* (Smith) in Queensland displayed the highest amount of flight activity in gardens compared to the forest and Macadamia plantations (Kaluza et al. 2015). The flight activities of *Heterotrigona itama* (Cockerell) in Malaysia was observed around 8 am–5 pm, with the most nectar collection between 8 am–9 am. Pollen foragers appeared between 9 am–11 am, while the peak occurred at 10 am. Flight activities are also affected by temperature, humidity, and light intensity (Jaapar et al. 2018). The foraging behavior of stingless bees in oil palm and rubber plantations showed an increase in the number of returning stingless bees to the nest with pollen in the morning, followed by a decreasing flight in the afternoon. Different environmental factors influenced the foraging of the stingless bee species (Ramadani et al. 2021). There is no information about stingless bee flight activity in converted shrubland. Thus, our study aimed to observe the flight activities of stingless bee *T. laeviceps* in the fragmented forest, rubber plantation, and shrubland with three different forest coverages, i.e., high, medium, and low in the Jambi Sumatra. The correlation between flight activities of *T. laeviceps* and environmental factors, i.e., temperature, humidity, and light intensity in those habitats was also analyzed. Furthermore, the pollen composition collected by *T. laeviceps* in the hind tibia and flowering plants surrounding the nests were identified as well.

MATERIAL AND METHOD

Study sites

The research was carried out in July–September 2018 at the Sridadi, Pompa Air, Bungku, and Sengkawang Luar Villages, Batanghari District, Jambi Province, Indonesia (Figure 1 & Table 1). Eighteen colonies *of T. laeviceps* from meliponiculture in Bengkulu Province, Sumatra were placed in three types of habitats i.e., fragmented forest, rubber, and shrub (six colonies in each habitat type). These stingless bee colonies were used for observing flight activities in the different habitats and their surrounding forest coverage, i.e., high, medium, and low coverage (Table 1). The percentage of forest cover within a 500 m radius around these nine study sites was visually determined from SPOT 5/6 satellite imagery (CRC 990 EFForTS). Two colonies of stingless bees were used in each forest coverage in each habitat.

Observation of flight activity and flight direction

Prior to recording flight activities, we conducted bee behavior acclimatization until we obtained the normal flight activities. Four types of flight activities were observed: (1) the number of stingless bees flying out of the nest (FO), (2) the number of bees returning with pollen (RWP), (3) the number of bees returning without pollen

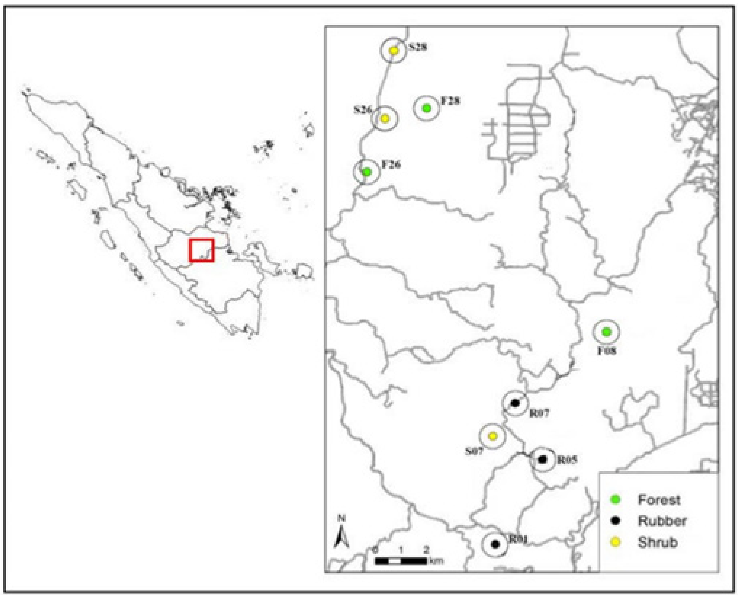

Figure 1. Map of Jambi Province showing the nine observation sites of *Tetragonula laeviceps* in the fragmented forest, rubber plantation, and shrub.

Table 1. Study site of stingless bee *Tetragonula laeviceps* observation in three different habitats with three coverage levels in Jambi Province

Habitat	Coverage levels	Sites	Village	GPS	Number of colonies
Fragmented forest	High coverage (FH)	F28	Sridadi	-1.78091’S 103.22663’E	2
	Medium coverage (FM)	F26	Sridadi	-1.86386’S 103.2893’E	2
	Low coverage (FL)	F08	Pompa Air	-1.80451’S 103.2053’E	2
Rubber plantation	High coverage (RH)	R05	Bungku	-1.91117’S 103.2668’E	2
	Medium coverage (RM)	R07	Bungku	-1.89032’S 103.2573’E	2
	Low coverage (RL)	R01	Bungku	-1.9428’S 103.2502’E	2
Shrub	High coverage (SH)	S07	Bungku	-1.90265’S 103.2494’E	2
	Medium coverage (SM)	S28	Sridadi	-1.75947’S 103.2148’E	2
	Low coverage (SL)	S24	Sengkawang Luar	-1.784667’S 103.2116’E	2
Total observed colonies					18

(RWoP), and (4) the number of bees returning with resin (RWR). Each flight activity was observed using a scan sampling method for 10 minutes with 10 minutes intervals from 8 am–3 pm (Martin & Batteson 1993). All observations were conducted with three replications of each colony in the fragmented forest, rubber plantation, and shrub habitats. All habitats are variously surrounded by high, medium, and low coverage forest. The environmental parameters included temperature, humidity, and light intensity, were measured every 10 minutes during the flight activity observations. We used a thermo-hygrometer for temperature and humidity measurement and a lux meter for light intensity measurement. Direct observation was conducted to study the flight direction (FD) every 10 minutes (Peng 2021).

Pollen collection and analysis

Bee pollen was collected from the hind tibia of *T. laeviceps* (five bees from each colony) to explore the pollen resources. We also collected the flowering plants around the stingless bee nest that will be used as the reference for the pollen collected by the returning bees. Bee pollen acetolyses were conducted based on Edrtman (1972) to remove the exin layer from pollen to observe the shape of the pollen. Pollen type was identified based on the polar and equatorial structure using the database of Australian pollen and spore atlas (ANU 2018).

Identification of flowering plants around the *T. laeviceps* nest

We identified the flowering plants around the *T. laeviceps* nests in the fragmented forest, rubber plantation, and shrubs habitat with three different coverage levels, which were based on the flight directions of the bees. Flowers were collected within 20 m x 20 m plot which located from 300 meters of bee nest. We determined the widely distributed plants found at least at four observation sites.

Data analysis

The effects of temperature, humidity, and light intensity on the four flight activities of *T. laeviceps* were analyzed using general linear models (GLM) with a Gaussian distribution. This analysis was performed using R (R Core Team 2019).

RESULT

Correlation of flight activity of *T. laeviceps* with environmental factors in three different habitats

Observation of *T. laeviceps* flight activities showed diverse responses in the three different habitats. In the fragmented forest with high coverage, the highest number of FO and RWP bees were 144 (Figure 2A) and 60 individuals (Figure 2B), respectively. In the rubber plantation with high coverage, the highest number of RWoP (Figure 2C) and RWR (Figure 2D) were 120 and 19 individuals, respectively. The lowest number of FO, RWP, and RWoP were in the shrub with low coverage, i.e., 4, 1, and 4 individuals, respectively (Figure 2A, 2B & 2C), and no flight activity of RWR in this habitat (Figure 2D).

The generalized linear model (GLM) of flight activities and environmental factors mostly correlated with temperature and humidity (Table 2A, B, & C). We found that the highest flight activity of FO and RWP bees in the fragmented forest with high coverage was affected by temperature, humidity, and light intensity ($p = 0.001$) (Table 2A). During the highest flight activity, we recorded the range of temperature, humidity, and light intensity were 26–32 °C, 43–69%, and 220–1598 lux. In medium-coverage fragmented forests, all flight activities of *T. laeviceps* were consistently affected only by humidity (FO and RWP bees; $p = 0.001$ & RWoP and RWR bees; $p = 0.01$) (Table 2A). In contrast, FO and RWoP in the fragmented forest with low coverage were affected by all environmental factors (Table 2A).

All flight activities except "RWP" in the rubber plantation with high coverage were affected by all the environmental factors ($p = 0.001$) (Table 2B). During the highest resin collection of the bees in the rubber plantation high coverage, we found that the range temperature, humidity, and light intensity were recorded at 2–35 °C, 38–70%, 7631–20768 lux. All environmental factors also affected FO ($p = 0.01$) and RWoP ($p = 0.001$) in low forest coverage of rubber plantations (Table 2B).

In the shrub with high coverage, FO and RWoP bees were affected by temperature and humidity (Table 2C). In the shrub with medium coverage, all the environmental factors affected these types

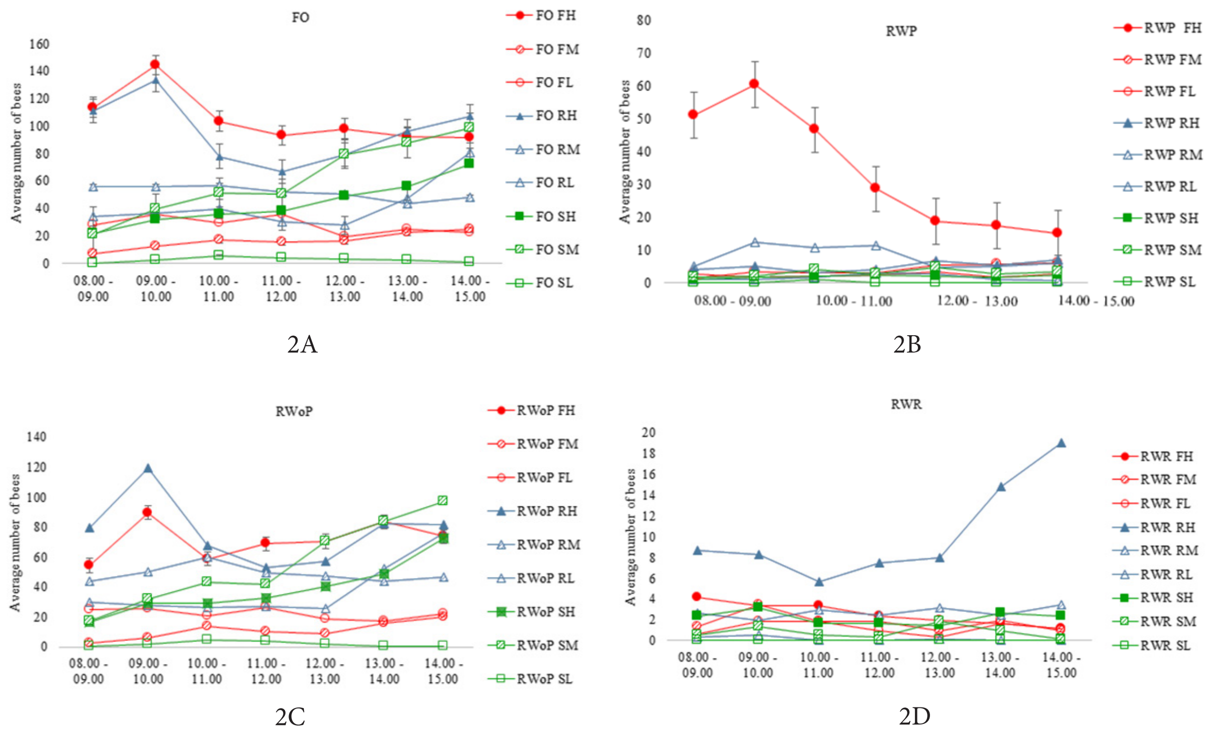

Figure 2. The average number of four flight activities of *Tetragonula laeviceps*. A: flying out (FO); B: returning with pollen (RWP); C: returning without pollen (RWoP); and d: returning with resin (RWR), in three habitats with three different coverage levels: fragmented forest (FH: fragmented forest high; FM: fragmented forest medium; FL: fragmented forest low), rubber plantation (RH: rubber plantation high; RM: rubber plantation medium; RL: rubber plantation low), and shrubs (SH: shrubs high; SM: shrubs medium; SL: shrubs low).

of flight activities, while RWP bees were only affected by temperature. All environmental factors in this habitat with low coverage only affected FO bees (Table 2C). Furthermore, the high temperature in shrub habitat i.e., 31–43 °C might affect the low number of FO, RWP and RWoP (Figure 2A–2C) and no bees were returned with resin (Figure 2D).

Flight direction of *T. laeviceps* in fragmented forest, rubber plantation, and shrub

Based on our observation, *T. laeviceps* generally flew in the same direction (Table 3). In the fragmented forest with high and medium coverage, we observed two flight directions for the two colonies, i.e., east and southeast, south and southeast, respectively. In contrast, the low coverage showed only one flight direction to the northeast (Table 3).

Flight direction in the fragmented forest habitat was varied compared to rubber plantation habitats. The two colonies of *T. laeviceps* in the rubber plantation with high and medium coverage showed one flight direction, i.e., northeast and southeast. Furthermore, we observed different flight directions of the two bee colonies in the low coverage of the rubber plantation, i.e., northeast and northwest (Table 3). However, in the medium coverage, we found different flight directions, i.e., south and southwest for the first colony and one flight direction to the southeast for the second colony (Table 3). The two colonies of bees in the shrub with high coverage have one different flight direction, i.e., west and southeast, respectively; the low coverage showed only one northeast bee flight direction for both colonies.

Pollen analysis and identification from the hind tibia of *T. laeviceps*

Based on the acetolyses and pollen identification from the hind tibia of *T. laeviceps*, we observed that seven individuals of *T. laeviceps* collected pollen from a single pollen type. *Tetragonula laeviceps* collected pollen 100% from *Hevea brasiliensis* in the high coverage fragmented forests and rubber plantation with high and low coverage (Table 4). This phenomenon was supported by the flight direction of *T. laeviceps* (Table 3), that the bees flew toward the

Table 2. Correlation between flight activities of *Tetragonula laeviceps* with temperature, humidity, and light intensity based on Generalized Linear Model analysis

A. Fragmented forest

Activity	Coverage levels	Temperature		Humidity		Light Intensity	
		Estimate	P	Estimate	P	Estimate	P
FO	High coverage (FH)	5.067×10^{-2}	0.001	1.348×10^{2}	0.001	2.589×10^{-4}	0.001
RWP		1.568×10^{-1}	0.001	4.060×10^{2}	0.001	6.750×10^{-4}	0.001
RWoP		1.056×10^{2}	1	2.390×10^{-3}	1	6.638×10^{-5}	0.5
RWR		1.274×10^{-1}	0.001	2.883×10^{2}	0.01	2.653×10^{-4}	1
FO	Medium coverage (FM)	3.320×10^{2}	0.001	1.134×10^{-2}	0.001	3.447×10^{-6}	1
RWP		9.734×10^{2}	0.001	3.359×10^{-2}	0.001	1.008×10^{5}	0.5
RWoP		2.566×10^{2}	0.5	9.502×10^{-3}	0.01	8.555×10^{-6}	0.5
RWR		7.840×10^{-2}	0.5	2.477×10^{2}	0.01	1.120×10^{-5}	1
FO	Low coverage (FL)	7.171×10^{2}	0.001	1.343×10^{-3}	0.001	6.24×10^{-5}	0.01
RWP		1.268×10^{2}	0.5	8.277×10^{-4}	1	1.416×10^{-4}	0.5
RWoP		5.215×10^{2}	0.01	1.534×10^{-3}	0.001	1.092×10^{-4}	0.001
RWR		1.014×10^{1}	1	2.422×10^{-4}	1	1.620×10^{4}	0.5

B. Rubber plantation

Activity	Coverage levels	Temperature		Humidity		Light Intensity	
		Estimate	P	Estimate	P	Estimate	P
FO	High coverage (RH)	3.082×10^{-2}	0.001	7.374×10^{3}	0.001	3.588×10^{-5}	0.001
RWP		5.026×10^{2}	0.5	1.328×10^{-2}	0.5	8.750×10^{-6}	1
RWoP		3.368×10^{-2}	0.001	8.004×10^{3}	0.001	3.637×10^{-5}	0.001
RWR		6.236×10^{2}	0.001	1.831×10^{-2}	0.001	3.366×10^{-5}	0.01
FO	Medium coverage (RM)	7.390×10^{-3}	1	4.811×10^{3}	0.01	3.755×10^{-6}	1
RWP		2.072×10^{3}	1	2.191×10^{-3}	1	2.048×10^{5}	1
RWoP		4.246×10^{3}	1	4.595×10^{-4}	1	2.823×10^{-6}	1
RWR		4.316×10^{2}	0.5	1.245×10^{-2}	1	7.262×10^{6}	1
FO	Low coverage (RL)	1.376×10^{2}	0.01	6.797×10^{-3}	0.001	5.099×10^{6}	0.01
RWP		1.131×10^{-2}	1	2.571×10^{3}	1	1.543×10^{-6}	1
RWoP		3.322×10^{2}	0.001	1.324×10^{-2}	0.001	1.156×10^{5}	0.001
RWR		1.592×10^{-1}	0.1	5.534×10^{2}	0.5	7.890×10^{-5}	0.1

C. Shrub

Activity	Coverage levels	Temperature		Humidity		Light Intensity	
		Estimate	P	Estimate	P	Estimate	P
FO	High coverage (SH)	4.328×10^{2}	0.001	1.598×10^{-2}	0.001	5.049×10^{-6}	0.1
RWP		6.252×10^{2}	0.5	2.209×10^{-2}	0.5	1.898×10^{5}	1
RWoP		4.620×10^{2}	0.001	1.733×10^{-2}	0.001	6.395×10^{-6}	0.5
RWR		2.773×10^{2}	1	1.414×10^{-3}	1	7.356×10^{-6}	1
FO	Medium coverage (SM)	1.102×10^{1}	0.001	3.973×10^{-2}	0.001	2.576×10^{5}	0.001
RWP		7.502×10^{2}	0.01	2.093×10^{-2}	0.5	1.553×10^{5}	1
RWoP		1.234×10^{1}	0.001	4.493×10^{-2}	0.001	3.034×10^{5}	0.001
RWR		2.313×10^{-3}	1	3.168×10^{-3}	1	1.864×10^{-5}	1
FO	Low coverage (SL)	6.308×10^{2}	0.01	3.465×10^{-2}	0.001	4.155×10^{5}	0.001
RWP		7.932×10^{2}	1	6.163×10^{-2}	1	7.716×10^{5}	1
RwoP		4.427×10^{2}	0.1	2.255×10^{-2}	0.5	3.338×10^{5}	0.01
RWR		8.368×10^{-16}	1	4.212×10^{16}	1	3.322×10^{19}	1

blooming flowers in the rubber plantation. In the fragmented forest with medium coverage, the bees also collected a single type of pollen that belongs to Rubiaceae and Capparaceae, while in the low coverage the bees collected pollen from Euphorbiaceae (Table 4). In the shrub habitat, the number of RWP bees was very low and the bee pollen cannot be collected. Thus, the pollen composition could not be determined.

The analysis of pollen collected by *T. laeviceps* also found that each individual carried a single pollen species (Table 4 & Figure 3). *Tetragonula laeviceps* mostly collected pollen in the time interval of 10 am–12 pm (Table 4), while in the rubber plantation with high coverage was observed from 8 am–10 am. In the fragmented forest with low coverage, the time interval of *T. laeviceps* to collect the pollen was from 10 am–3 pm (Table 4) and was shown by the different types of pollen from several habitats (Table 4 & Figure 3).

Flowering plants around the nest of *T. laeviceps* in three different habitats

Based on the flight direction of the bees, we found 32 flowering plants around the nest of *T. laeviceps* that comprised 19 families (Table 5). The pollen from Rubiaceae and Euphorbiaceae families was collected in the hind tibia of the returning bees (Table 4 & 5). Eight species of flowering plants around the nest were found in more than four sites in all habitats (Figure 4) i.e., *Clidemia hirta*, *Clibadium surinamensis*, *Melastomama labathrichum*, *Urena lobata*, *Stachytarpheta indica*, *Solanum jamaicense*, *Lantana camara*, and *Mussaenda frondose*.

DISCUSSION

Among all habitats, the fragmented forests with high coverage had the highest flight activities of FO (Figure 2A) and RWP (Figure 2B). This finding indicates that the abundance of stingless bees is closely linked to forest coverage and plant abundance (Brosi 2009; Buchori et al. 2019). FO, RWP, and RWoP activities in the fragmented forest were affected by all environmental factors, i.e., temperature (26–32 °C), humidity (43–67%) and light intensity (220–1598 lux) (Table 1A). This result is similar to the flight activities of

Table 3. Flight direction of the *Tetragonula laeviceps* in fragmented forest, rubber plantation, and shrub habitats

Habitat	Coverage levels	Site	Colony	Flight direction	
				Direction 1	Direction 2
Fragmented forest	High coverage (FH)	F28	1	E	SE
			2	E	SE
	Medium coverage (FM)	F26	1	S	SE
			2	S	SE
	Low coverage (FL)	F08	1	NE	–
			2	NE	–
Rubber plantation	High coverage (RH)	R05	1	NE	–
			2	NE	–
	Medium coverage (RM)	R07	1	SE	–
			2	SE	–
	Low coverage (RL)	R01	1	NE	–
			2	NW	–
Shrub	High coverage (SH)	S07	1	W	–
			2	SE	–
	Medium coverage (SM)	S28	1	S	SW
			2	SE	–
	Low coverage (SL)	S24	1	NE	–
			2	NE	–

E: East; S: South; NE: Northeast; SE: Southeast; NW: Northwest; W: West; SW: Southwest.

Table 4. Composition of pollen collected from hind tibia of seven samples of *Tetragonula laeviceps* with 3 collection time interval.

No. of bee pollen samples	Habitat and coverage levels	Family/Spesies	Percentage (%)	Time interval		
				08.00–10.00	10.00–2.00	12.00–15.00
1	FH	Euphorbiaceae/ *H. brasiliensis*	100	√	√	–
2	FH	Euphorbiaceae/ *H. brasiliensis*	100	–	√	–
3	FM	Rubiaceae	100	–	√	–
4	FM	Capparaceae/ *Maeru*a sp.	100	–	√	–
5	FL	Euphorbiaceae	100	–	√	√
6	RH	Euphorbiaceae/ *H. brasiliensis*	100	√	–	–
7	RL	Euphorbiaceae/ *H. brasiliensis*	100	√	√	–

F: fragmented forest; R: rubber plantation; H: high coverage; M: medium coverage; L: low coverage; √: pollen available.

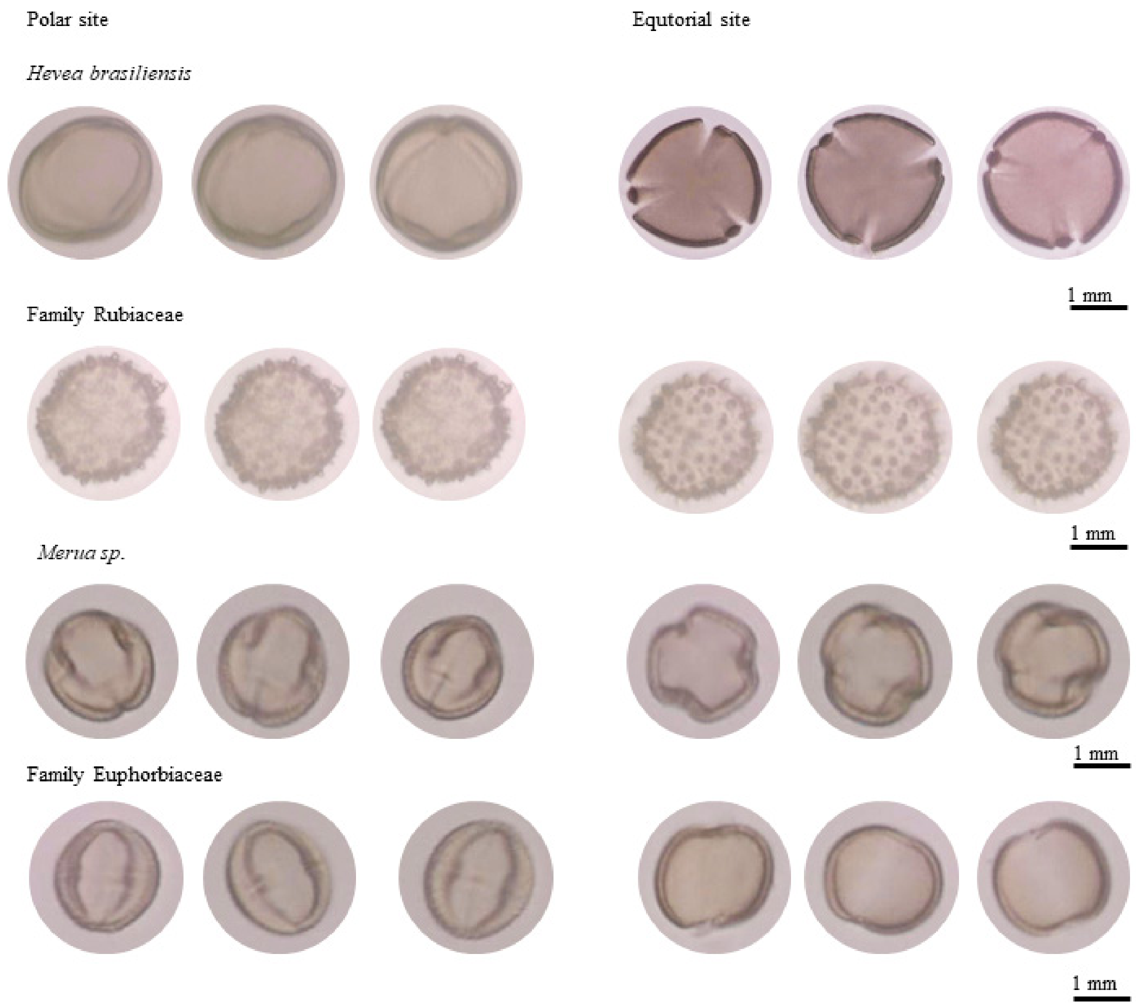

Figure 3. Pollen species identified from hind tibia of *Tetragonula laeviceps*. Black bar = 1 mm.

Table 5. Flowering plants around the nest of *Tetragonula laeviceps* in three different habitats. √: pollen available

Family	Species	Habitat									Number of existence
		Fragmented forest			Rubber plantation			Shrub			
		Coverage levels			Coverage levels			Coverage levels			
		High	Medium	Low	High	Medium	Low	High	Medium	Low	
Fabaceae	*Centrosema pubescens*	√	–	–	–	–	–	–	√	–	2
Fabaceae	*Mimosa pudica*	–	–	–	–	–	√	√	√	–	3
Fabaceae	*Saraca* sp.	–	√	–	–	–	–	–	–	–	1
Fabaceae	*Derris* sp.	–	√	–	–	–	–	–	–	–	1
Fabaceae	Species 1	–	–	–	–	–	–	–	√	–	1
Asteraceae	*Ageratum conyzoides*	–	–	–	√	–	√	√	–	–	3
Asteraceae	*Chromolaena odorata*	√	–	–	–	–	–	√	√	–	3
Asteraceae	*Clinadium surinamense*	–	–	√	√	√	√	–	√	√	6
Asteraceae	*Mikania micrantha*	–	–	–	–	–	√	√	–	–	2
Verbenaceae	*Lantana camara*	–	–	–	√	–	√	√	–	√	4
Verbenaceae	*Stachytarpheta indica*	–	–	–	√	–	√	√	√	–	4
Verbenaceae	*Stachytarpheta jamaicensis*	–	–	–	–	√	–	–	√	–	2
Melastomataceae	*Clidemia hirta*	√	–	√	√	√	√	√	–	√	7
Melastomataceae	*Melastoma malabathrichum*	√	–	√	√	√	√	√	√	√	8
Zingiberaceae	*Boesenbergia* sp.	–	–	√	–	–	–	–	–	–	1
Zingiberaceae	*Globba pendula*	–	–	–	–	–	–	√	–	–	1
Rubiaceae	*Mussaenda frondosa*	√	–	–	√	√	–	√	–	√	5
Rubiaceae	*Psychotria* sp.	–	√	√	–	–	–	√	–	–	3
Acanthaceae	*Asystasia gangetica*	–	–	–	√	–	√	√	–	–	3
Apocynaceae	*Tabernaemontana pauciflora*	–	–	–	–	√	√	–	–	–	2
Cleomaceae	*Cleome rutidosperma*	–	–	–	–	–	√	–	–	–	1
Cucurbitaceae	Species 2	–	–	–	–	–	√	–	–	–	1
Euphorbiaceae	*Hevea brasiliensis*	√	–	–	–	–	√	–	–	–	2
Lythraceae	*Cuphea carthagenensis*	–	–	–	–	–	√	–	–	–	1
Malvaceae	*Urena lobata*	–	–	–	√	–	√	√	√	–	4
Linderniaceae	*Lindernia crustacea*	–	–	–	–	–	√	–	–	–	1
Oxalidaceae	*Oxalis barrelieri*	–	–	–	–	–	√	–	–	–	1
Passifloraceae	*Passiflora foetida*	–	–	–	–	–	–	√	–	–	1
Polygalaceae	*Polygala paniculata*	–	–	–	–	–	√	–	–	–	1
Solanaceae	*Solanum jamaicense*	√	–	–	√	–	√	√	–	–	4
Simaroubaceae	*Eurycoma longifolia*	–	√	–	–	–	–	–	–	–	1
Oleaceae	*Jasminum multiflorum*	–	–	–	–	–	–	–	√	–	1
Total observed of flowering plants		7	4	5	10	6	19	15	10	5	81

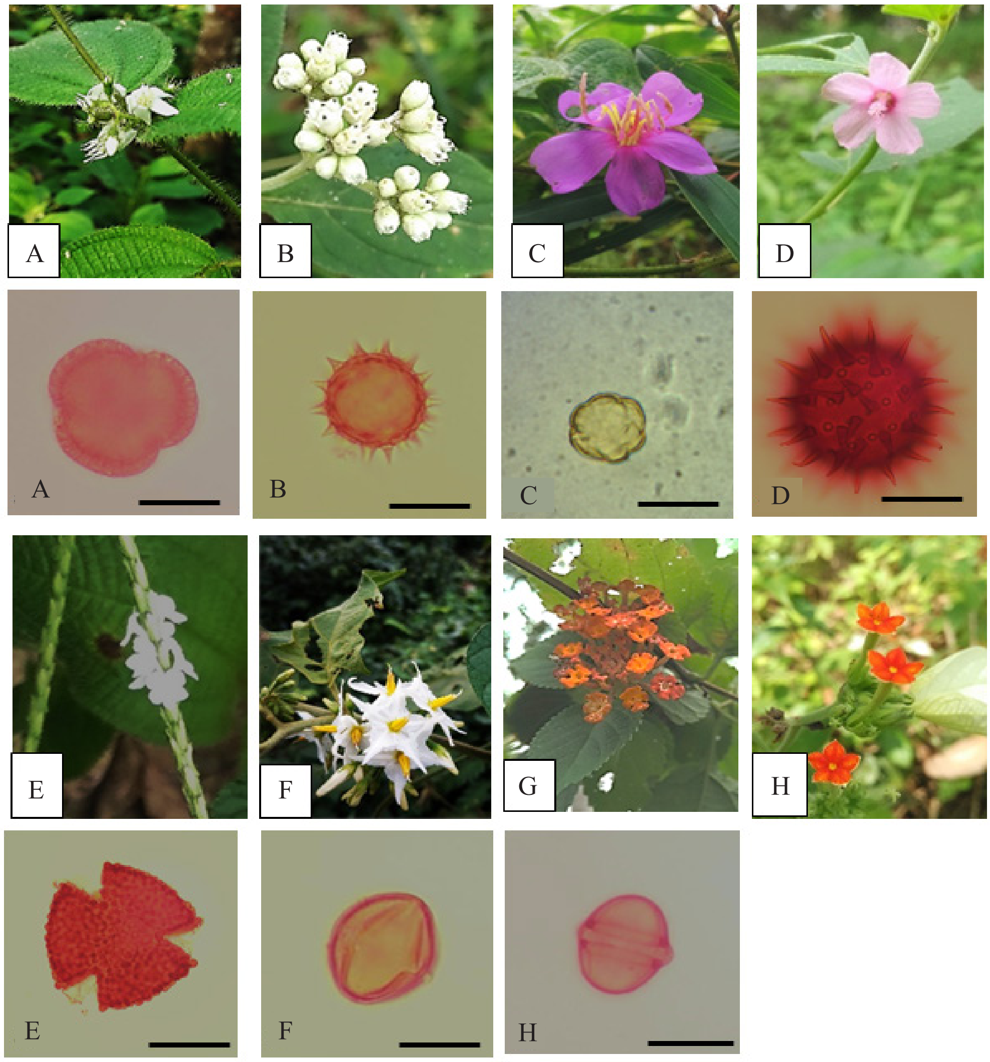

Figure 4. The flowering plants and their pollen that widely distributed around the nest of *Tetragonula laeviceps*. A: *Clidemia hirta*; B: *Clibadium surinamensis*, C: *Melastoma malabathrichum*; D: *Urena lobata*; F: *Stachytarpheta indica*; G: *Solanum jamaicense*; H: *Lantana camara*; and H: *Mussaenda frondosa* (pollen not available). Black bar = 10 µm.

Melipona subnitida Ducke in the Brazilian dry forest, where pollen foraging mainly occurred at temperatures between 22 °C and 34 °C and humidity between 50% and 65% (Maia-Silva 2015).

The flight activities of *T. laeviceps* and pollen collection were highest in the fragmented forest. Interestingly, we found a partition peak of time between pollen collection in the morning at 09 am–10 am (Figure 2B) and resin collection in the afternoon at 2 pm–3 pm (Figure 2D). Stingless bee *Meliponina bicolor* Lepeletier at Cunha, Atlantic Forest, Brazil, showed a similar pattern of pollen collection in the morning and resin collection in the afternoon (Hilario et al. 2000), and *T. laeviceps* at musk melon flower Gujarat, India (Gadhiya 2019). The circadian clock of flower affects pollen collecting activity of insects (Bloch et al. 2017). Observation of foraging behavior in honeybee *Apis mellifera* Linnaeus and bumblebee *Bombus lantschouensis* Vogt at the solar greenhouse in China revealed that pollen-collecting activity increased as the increasing of dehisced anthers followed by pollen release (Zhang et al. 2019). They also found that the number of dehisced anthers in the solar greenhouse peaked at 11:00 h to 14:00 h, in parallel with increasing temperature and decreasing relative humidity (Zhang et al. 2019). Thus, the peak of flight activities in *T. laeviceps* might be influenced by the nectar secretion of the surrounding flowers as their flower reward (Bloch et al. 2017). Research on the nectar secretion dynamics at the major honey plants, i.e., *Acacia* sp., Lamiaceae, and *Ziziphus* sp. in Saudi Arabia, showed an increasing trend in the early morning toward midday (Adgaba et al. 2017).

Overall, in the fragmented forest and rubber plantation habitat, we found that 4 individuals of 7 *T. laeviceps* collected pollen only from *H. brasiliensis* (Family Euphorbiaceae), while three other individuals also collected a single pollen type from Rubiaceae, Caparacae, and Euphorbiaceae families, respectively (Table 4). As predicted, the pollen collected by bees in the fragmented forest was more diverse than the other land uses (Table 4). A single type of *H. brasiliensis* pollen was collected by the bees in rubber plantations (Table 4), supported by Heard (1999), who found stingless bees usually forage in one plant species in each bout. It is presumably due to the blooming season; rubber plantations could supply adequate pollen resources for the stingless bees.

Our study supported that converting land into monoculture resulted in a decreasing diversity of flowering plants. It was indicated by the low number of pollen species collected by bees, half of which is the *H. brasiliensis* pollen (Table 4). This research was carried out during July-September, which is the rubber flowering period in Jambi (personal observation). This period is similar to the *H. brasiliensis* flowering in Bogor, Java, Indonesia (Madjid et al. 1976). Therefore, other plants should be available for sustaining pollen resources for bees during the non-flowering rubber season.

CONCLUSIONS

Land transformation and forest coverage affected the patterns of flight activities and pollen resources of *T. laeviceps* and resin. The highest flight activities were in the fragmented forest, and the lowest was found in the shrub habitat with almost no activity. Temperature and humidity significantly affected the flight activities of *T. laeviceps* in all habitats. We found that *T. laeviceps* brought one plant species, *H. brasiliensis,* pollen, to the nest in each foraging trip. Mass-flowering rubber trees thus strongly affect the food resources of *T. laeviceps* in our study region. The conversion of lowland tropical forests into rubber monocultures reduce the activity and pollen collecting of stingless bees, which may have important consequences for bee fitness and plant-pollinator interactions. In the future, the growth of stingless bee colonies should be examined over a longer period within the land transformation. Thus, we can understand the survival rate of the bee colonies.

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