

Bee diversity along a gradient of disturbance in tropical lowland forests of Southeast Asia

Lee Hsiang Liow

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Bees are believed to be dominant pollen vectors in tropical forests, yet studies specific to bees in Southeast Asia are rare. Regeneration and restoration of the rapidly disappearing lowland forests of this region are reliant on bees thus there is an urgent need for forest bee community-level data.

I surveyed bee communities of eight forested sites in Johor (Malaysia) and Singapore three times each from Feb–Aug 1999 at the below-canopy level. These sites ranged from relatively undisturbed primary lowland dipterocarp forests to late secondary forests and exotic forests, including an oil palm plantation.

I attempted to elucidate the environmental factors that determined the distribution of bees in these forests. I also attempted to determine if there was a correlation between bee and bird diversity.

Bee abundance, in particular that of Apidae, was significantly higher in larger primary forests than other types of forests. However, bee species richness was higher in disturbed forests. The distribution of bees in surveyed forests was influenced by variables closely related to forest disturbance and resource abundance such as the density of big trees (dbh 30–40 cm), temperature, and flowering intensity of trees and shrubs. Large trees and more constant ambient conditions are more conducive to many trigonid bees which may have the ability to survive inter-mass flowering conditions (tolerant of lower flowering intensities) and utilize abundant resources during mass flowering, which in turn allows cross-fertilization among con-specific trees. No significant correlations between bird and bee species richness and abundance were found, probably due to a small sample size.

The differences between the bee communities in forests of urban Singapore and primary forests in Johor may indicate that ecological processes, in particular pollination, in Singapore may be declining. However pollination may not be totally intact in the primary forests surveyed, as their bee communities seem to be depauperate.

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Introduction

Threats to tropical lowland forests of Peninsula Malaysia and Singapore

Deforestation in tropical Southeast Asia is rapid and the rate was 1.6% between 1981-1990 compared with 0.9% in the rest of the tropics (Groombridge 1992). In particular, the island state of Singapore has largely been urbanized except for small forested areas, totaling to about 20 km² or 3% of Singapore's total land area (Lum 1999). There are also intensive land-use changes in Peninsular Malaysia since the 1970s and now the total lowland evergreen broadleaf forest (including disturbed natural forests) stands at 31.7% of which only 9.0% (2.9% of the total land area of Peninsular Malaysia) is protected (Anon.1999). In Johor, Malaysia, most of the original dipterocarp forests have been logged for timber or cleared for plantations. Oil palm plantations alone accounted for 525 360 ha (26.3%) of land in Johor in 1990 (Sukaimi et al. 1993). Little is known how this extensive habitat loss will affect species diversity and ecological processes. Floral and faunal inventories have not been comprehensive even in Peninsular Malaysia and Singapore where biological research had a fairly long history.

Why insects?

Invertebrates, the bulk of which are insects, may be much more important than vertebrates for the maintenance of vital ecosystem processes (Wilson 1987). However, few intensive surveys of tropical insect diversity have been made (Holloway et al. 1992, Kremen et al. 1993). The direct conservation of tropical insect fauna is also rare (Janzen 1987) although there are recent efforts to generate interest in insect conservation (Collins & Thomas 1991, Samways 1994). It is also a recent trend to use insect taxa (including butterflies, tiger beetles and termites) as habitat or environmental quality indicators (e.g. Holloway & Barlow 1992, Pearson & Cassola 1992, Eggleton et al. 1996).

Why bees and pollination?

Anthropogenic changes such as the conversion

of native habitats and the introduction of exotic species will have more apparent effects through the loss of original vegetation architecture and native species than the loss of ecological processes (Kearns & Inouye 1997). However, the loss of ecological processes, e.g. pollination, is equally, if not more destructive than physical changes, to a natural ecosystem. Detrimental effects of pollinator declines (genetic erosion, decreases in species richness and ecological diversity) were discussed by Buchmann & Nabhan (1996) and Allen-Wardell et al. (1998). Threats of habitat alteration, agriculture, grazing, habitat fragmentation and alien introductions to native bees have also been recently reviewed (Kevan 1993, Verma 1993, Kearns & Inouye 1997). This study deals with bees also because they are believed to be the most dominant pollen vectors in tropical forests (Bawa 1990, Renner & Feil 1993, Roubik 1993a). For instance, 74% of the insects visiting flowers in Sumatra are apid bees (Inoue et al. 1990).

The bee fauna of the oriental region is the poorest (89 genera) in the world (Michener 1979) and accordingly, the bee fauna in tropical Southeast Asia is also species poor, despite an extremely high plant species richness (Whitmore 1984). However, tropical bee communities are more ecologically diverse (Roubik 1989, 1992). This means that each bee species in the tropics plays more roles in their ecosystem and may have a greater part in maintaining the angiosperms than bees in other regions (Michener 1979).

Despite their purported roles as dominant pollen vector, studies specific to bees in tropical Southeast Asia are rare, in contrast to the neotropics (e.g. Bawa et al. 1985, Roubik 1993b, Frankie et al. 1997 and references therein). There are many botanical and anecdotal accounts of bee-pollinated plants in Southeast Asia (e.g. Jackson 1981, Appanah 1987, Momose et al. 1997) but few studies specifically deal with the pollinators themselves. Exceptions include studies done in Sarawak (Kato 1996, Inoue & Hamid 1997, Nagamitsu & Inoue 1997), Peninsular Malaysia (Appanah 1981), Brunei (Roubik 1996) and Sumatra (Sakagami et al. 1990, Salmah et al. 1990), but these are concerned mainly

with the family Apidae.

Objectives of this study

There is no comprehensive inventory, systematic comparison between sites or study on the habitat requirements of bees in Malaysian and Singaporean forests. We attempt to partly fill these gaps.

First, I ask if there are differences in the assemblage of bee species found at the different sites, in particular between undisturbed and disturbed sites. I test the hypothesis that primary forests are richer than disturbed forests in species richness and abundance of bees. Second, I ask whether there are habitat preferences for bees. I test whether vegetation structure and/or microclimate variables affected the distribution of the bee species. Third, I ask whether both total bird species richness and richness in different feeding guilds correlated with bee species richness and abundances to determine if both these taxa show similar distribution patterns. Finally, I attempt to make generalizations on the bees found at the below-canopy level in forests of varying disturbances in the southern Malay Peninsula and discuss what the results of this study spell for the conservation of this region.

Materials and methods

Study sites

Eight sites were surveyed, five in Singapore and three in Johor, Malaysia (Fig. 1), to represent a range of tropical lowland forests of varying degrees of anthropogenic disturbances. A summary of the forest types (definitions based on Whitmore 1984) and background information of the eight sites are given in Table 1.

Bee surveys

Preliminary studies were conducted between December 1998 and January 1999 to optimize sampling methods. Three yellow funnel traps and three yellow floating platforms on petri dishes were set up at MacRitchie, Singapore with baits (honey solutions, sugar solutions and banana pulp)

in December (1998) to test the feasibility of trapping and/or attracting bee individuals. The traps were set 50 m apart with funnels alternating with the petri dishes. Some bees were trapped after entering the funnel or by the surface tension of the liquid. Both methods rendered the bees wet, making taxonomic identification difficult. The average trap rate (\pm S.E.) were 9.0 ± 2.4 and 8.3 ± 4.3 for individuals/trap/day for funnel traps and petri dishes respectively. Bees were not attracted to banana pulp.

Honey baiting on vegetation was also tested. Honey-salt-water and sugar-salt-water solutions of varying concentrations were made and sprayed on vegetation 1–2 m from the ground at both sites. At MacRitchie there were three baiting spots of about 1 m in diameter for different concentrations of honey or sugar solutions while at Bekok there was one of each. The baiting spots were about 10 m apart at each site.

It was found that a solution of honey diluted in the ratio of 1:2 (honey:water, V:V) and solutions diluted in the ratio of 1:4 (honey:water and sugar:water), with salt concentration constant at 2 cm³ in 500 ml of solution sprayed on vegetation, did not have significantly different recruitment rates for different morphospecies of bees. It was also found that the method of baiting on vegetation was more efficient at attracting bees than that of baited funnels type traps and petri dishes. During each check, approximately 20.0 ± 2.8 trigonid bees were counted at individual vegetation baiting spots.

For the actual bee surveys, one to three transects of 0.5–1 km were set-up at each site (see Table 1 for transect lengths). Honey solution (1:4, honey:water) with 2 cm³ salt/500 ml of solution, standardized with a hand refractometer was used to attract bees. Thirty jets (20 ml) of this solution were sprayed on the vegetation marked with colored flagging tape every 100 m along the transects. The baited spots were about 1 m in diameter and between 1–2 m above the ground. The baits were replenished every other time the transects were checked by spraying 15 jets of the solution on the same previously sprayed spots. If the solution was washed away



Fig. 1. The eight study sites where BK = Bekok, BL = Belumut, BT = Bukit Timah Nature Reserve, HW = Holland Woods, KR = Kent Ridge, MC = MacRitchie, NS = Nee Soon, and UMP = UMP oil palm plantation.

by rain, the baiting spots were sprayed at least half an hour before the transects were surveyed again. Bees attracted to each of these baited spots were caught with a standard insect net four times a day (between 0730 and 1700h), during a maximum of three minutes. The time lapse between bait application and collection ranged from 30 minutes to 16 h (e.g. when the bait was left over-night). I waited at each baited spot for 20 seconds to scan the area for bees and moved on if there were none. Bees spotted when I was walking along the transects were also collected and the substrates on which they were caught were recorded. Each collection cycle at a particular site ran for three consecutive days. I visited each study site three times between February and August 1999 (Table 1). Temperature, humidity

and light intensity were measured every 200 m of a transect during the first and the third check of the transect during the day using a thermo-hygrometer and an illumination meter.

The collected bees were identified with the help of R. W. Brooks (Snow Entomological Museum at the Kansas State University) and are now deposited at the Raffles Museum of Biodiversity Research (RMBR) of the National University of Singapore and the Snow Entomological Museum of the Kansas State University.

Floral resource availability

To determine if floral resource availability affected the numbers of bees caught, the flowering intensity every 200 m along the transects were

recorded on the second day of each bee collecting cycle. Binoculars were used to scan a circular area (8 m radius = approx. 200 m² ground area) and trees (more than 2 m in height) with open flowers were counted. A 50 m² area was divided into ten sectors and the number of sectors with flowering shrubs recorded. In both cases, open flowers are defined as single flowers or parts of inflorescence with anthers and/or stigmas no longer being concealed by the corolla and/or calyx but before the corolla and/or calyx falls off. When the perianth was not obvious, open flowers were taken to be single flowers or parts of the inflorescence with mature anthers or stigmas.

Vegetation sampling

To determine if vegetation structure is a factor in determining bee species distribution, the following variables were measured and recorded along transects at 150 m intervals.

- 1) The canopy cover of the forest, using a spherical densiometer, according to Lemmon (1957)
- 2) The dbh (density at breast height) of trees having more than 2 cm. I also visually estimated if these trees are more or less than 10 m in height.
- 3) The number of trees having less than 2 cm dbh.
- 4) The number of dead trees.
- 5) The number of palms.
- 6) The percentage ground cover.
- 7) The leaf litter depth that was obtained by gently inserting a ruler vertically into the leaf litter at twelve random points in each plot.

Bird surveys

To determine if bee species diversity correlated with resident bird species diversity, bird surveys were carried out on four days (between about 0730-1100 h) at each site. The bird species recorded during these surveys were used to generate a species list (Appendix 1) for each of the eight study sites. Only resident birds (including introduced bird species that are known

to have established breeding populations in the study sites) were used for analyses.

Data analyses

The Kruskal-Wallis test was used to determine if the catch-rate of bee species and number of bee individuals at the eight study sites were significantly different. On finding that there were significant differences, the catch-rates were manually ranked and Duncan's multiple range test was used to determine which sites were different from the others. The two catching methods (netting at baits and netting along transects) were compared using the Mann-Whitney U test. All these tests were performed using SAS version 6.12. Bee diversity indices (Margalef's, Menhinick's, Simpson's, Berger-Parker, McIntosh's, Brioullin's and Shannon's indices) were hand calculated according to Magurran (1988). Each set of indices was ranked and Kendall's coefficient of concordance, W, calculated according to Siegel & Castellan (1988).

The bee species presence-absence data from 21 transects in the eight study sites were subjected to a Cluster Analysis using PC-ORD version 2.0. This analysis used Euclidean distance and Ward's method. Similarly, the presence-absence data of the Apidae species from my eight study sites and those from Brunei (Roubik 1996) and Sumatra (Salmah et al. 1990) were also subjected to a Cluster Analysis. Twenty-four environmental variables (the mean dbh and density of trees < 10 m height/plot, the mean density of palms < and > 10 m height/plot, the mean dbh and density of trees > 10 m height/plot, the mean number of trees < 2 cm dbh/plot, the mean number of dead trees/plot, shrub and canopy cover, leaf litter depth, the density of trees with dbh < 10 cm, between 10-20 cm, 20-30 cm, 30-40 cm and > 40 cm, the number of flowering trees/m², the flowering density index of shrubs, mean and standard deviation of temperature, humidity, and light intensity) were correlated using SAS. From all groups of variables with a Pearson correlation coefficient > 0.50, only one variable was retained for ordination analysis. The retained variables were the ones that were most

biologically relevant: the mean density of trees < 10m height per plot, leaf litter depth, the mean density of trees with dbh between 30-40 cm, the number of flowering trees/m², flowering density index of shrubs and the mean temperature.

To determine the factors affecting the distribution of bee species, Canonical Correspondence Analysis (CCA) (ter Braak 1986) in PC-ORD 2.0 was performed using data matrices of log-transformed bee species abundance data and the six environmental variables retained. Axis scores were standardized using Hill's (1979) method and scaled to optimize the representation of species.

The number of bird and bee species recorded, the absolute number and rate of collection of bees were correlated using Spearman correlation coefficients (SAS). Similarly, the number of bee species recorded and the rate of collection of bees were correlated with the number of insectivorous, nectarivorous and frugivorous birds (data from del Hoyo et al. 1992, Jeyarajasengam & Pearson 1998) recorded during this study.

Results

Overall species diversity

Forty-five morphospecies and 1613 individuals from five bee families (Anthophoridae, Apidae, Colletidae, Halictidae and Megachilidae) were collected during 71 days (279 h). The three most abundant species in the eight sites combined were *Trigona* (*Tetragonula*) *geissleri* Friese 1918, *T. (T.) melina* Gribodo 1918 and *T. (T.) laeviceps* Smith 1857 with 412, 202 and 546 individuals collected, respectively, while seven species, *T. (Lepidotrigona) ventralis* Smith 1857, *T. (Geniotrigona) thoracica* Smith 1857, two species of *Nomia* (*Maculonomia*), two species of Lipotriches and one species of Halictidae were collected only once each during the collection period (Appendix 2). The total number of species collected at each site ranged from four at Nee Soon to 22 at MacRitchie. The total number of individuals collected ranged from 63 individuals at Kent Ridge Park to 444 individuals at Belumut (Appendix 2).

One nest each of five species was encountered at three sites. The nests of *Trigona* (*Heterotrigona*) *itama*, *T. (Tetrigona)* *apicalis*, *T. (Tet3ragonula)* *melina* and *T. (Lepidotrigona)* *terminata* were found in trees with dbh from 50 cm while that of *T. (Tetragonula)* *laeviceps* was found in the ground (Appendix 3).

The cumulative collection curves (Fig. 2) at Bekok, Belumut, Bukit Timah, Holland Woods, Kent Ridge appear to have reached their asymptotes during this study. However, those at MacRitchie, Nee Soon and the UMP oil palm plantation are still rising. Only bees of the honeybee family, Apidae, were encountered at the two large primary forest tracts in Johor while the family Halictidae dominated in the oil palm plantation, an exotic forest (Figs. 3a and 3b). *Apis mellifera* Linn. 1758, the globally widespread exotic honeybee, was not found.

Comparisons between bee capturing methods

The mean numbers (\pm SE) of bees caught at baits and along transects were 5.62 ± 2.65 and 1.08 ± 0.39 inds. h⁻¹, respectively. The baiting method was significantly more efficient at catching bees than just netting bees sighted along transects (Mann Whitney's U = 10.426, df = 7, P < 0.0012). The mean number of Apidae caught at baits (3.83 ± 4.63 individuals per hour) was significantly higher than the mean number of non-Apidae bees caught at baits (0.09 ± 0.07) (U = 29.011, df = 7, P < 0.0001). Of the all bees caught while they were approaching or foraging on flowers, 80.2% were caught on only four species of continuously flowering plants. These were *Dillenia suffruticosa* (Griff.) Martelli, *Melastoma malabatricum* Linn., *Asystasia instrusa* Blume and *Stacytarpbeta indica* Vahl., of which the first two are plants of early secondary forests and the last two are weeds found in open areas. All are native plants except *S. indica* that originated from South America.

Bee diversity

The number of individuals and species collected per hour varied from 1.63 ± 0.22 and 0.38 ± 0.11

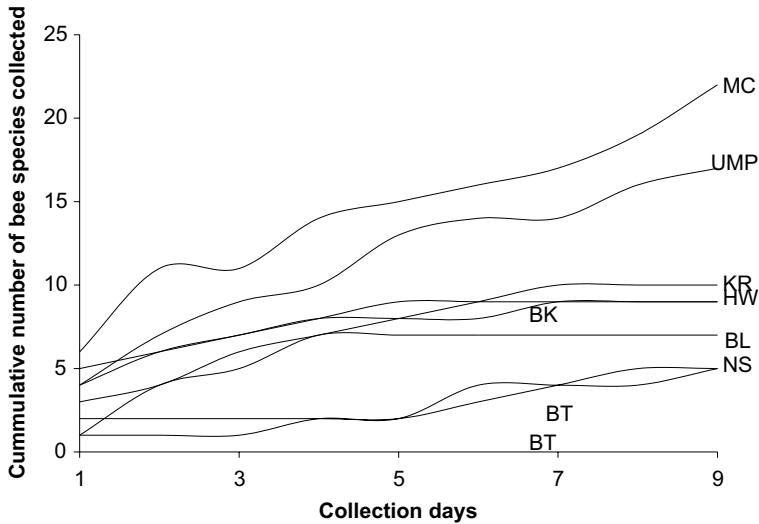


Fig. 2. The cumulative number of bee species collected at the eight study sites. For site abbreviations see Table 1.

(Holland Woods and Bukit Timah) and that of individuals varied from 12.15 ± 1.48 to 0.95 ± 0.26 (Bekok and Bukit Timah), respectively (Figs. 4a and 4b). The mean numbers of bee species caught per hour differed significantly among sites ($KW = 44.763$, $df = 7$, $P < 0.0001$). Duncan's multiple range test showed that the ranked mean number of bee species caught per hour at Belumut, NeeSoon and Bukit Timah were significantly lower than that at Holland Woods, MacRitchie, Bekok and Kent Ridge ($P < 0.05$). The mean numbers of bee individuals caught per hour differed significantly among sites ($KW = 40.673$, $df = 7$, $P < 0.0001$). Duncan's multiple range test showed that the ranked mean number of bee individuals caught per hour at Bekok and Belumut were not significantly different from each other but were significantly higher than that at the remaining sites ($P < 0.05$), with the exception of Nee Soon.

Bee diversity indices for sites

Of the eleven diversity indices calculated, six gave the most disturbed forest, the oil palm plantation the highest diversity value and Nee Soon, a late secondary forest the lowest diversity value (Table 2). The Kendall coefficient of concordance, W was significant ($W = 0.453$, $P < 0.0001$),

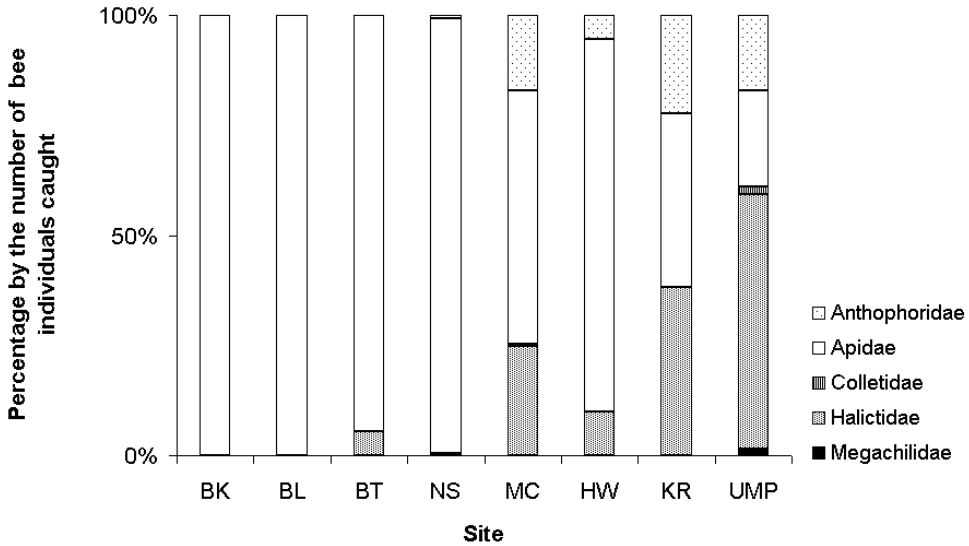
indicating reasonably good consensus among indices. Averaging the ranks of the sites (using the 11 indices and the total number and species of bees collected at each site), the most diverse site was MacRitchie, a secondary forest while the least diverse site was Bukit Timah Nature Reserve, a small primary forest (Table 2).

Bee community similarity among sites

Three of the more disturbed forests (Kent Ridge, Holland Woods and the UMP Oil Palm Plantation) and transects A and B from MacRitchie (a secondary forest) formed the first main cluster in the dendrogram drawn using presence-absence data of all bee species found. The remaining sites consisting of the three primary forest sites (Bekok, Belumut and Bukit Timah), one secondary forest site (Nee Soon) and transect C from MacRitchie formed another main cluster. Five out of six transects from the two large tracts of primary forests (Bekok and Belumut) were very similar while many transects from the closed forests in Singapore grouped together (Fig 5).

A dendrogram of bees of the family Apidae (including *Trigona* and *Apis*) was drawn using presence-absence data separated the sites from this study (Singapore and Johor) from the

a)



b)

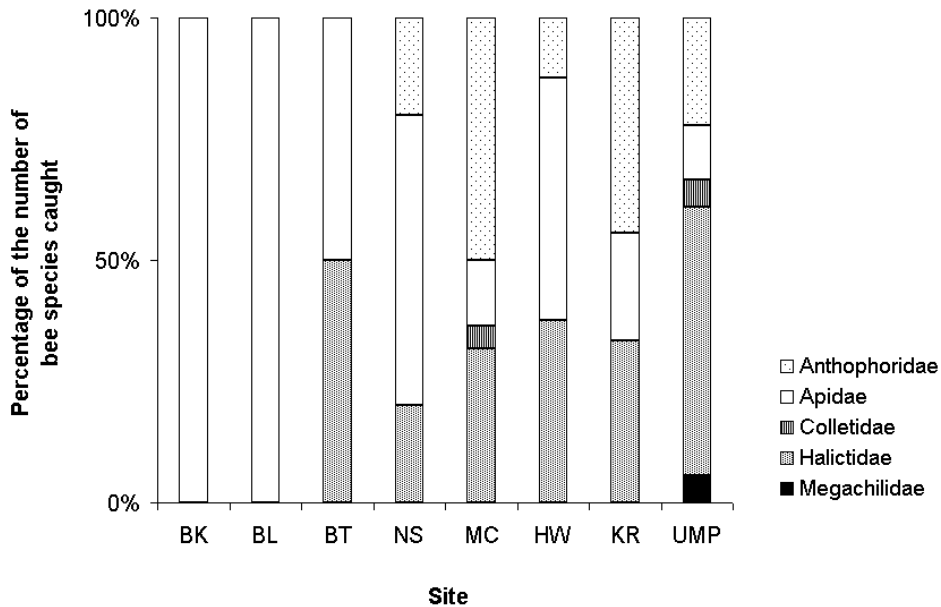


Fig. 3. a) Proportion of bee families collected at each site (based on number of individuals collected) and b) Proportion of bee families collected at each site (based on number of species collected). For site abbreviations see Table 1.

Table 1. Summary of information on study sites surveyed for bees from February to August 1999 including: 1) The names, state and countries of the study sites and abbreviations used in the text; 2) the description of the forest type (based on Whitmore 1984); 3) the landscape of the matrix surrounding the surveyed forest; 4) the geographical co-ordinates of the sites; 5) the size of the sites; 6) the dates of the bee surveys; transact lengths at each site and 7) approximate age of the forests.

Name and location of site and abbreviation used in text	Description	Surrounding matrix	Coordinates	Size (ha)	Dates of bee surveys (1999)	Transact Length, km (hrs surveyed)	Approx. age
Belumut, Johor Malaysia (BL)	primary hill Dipterocarp forest	Oil palm and rubber plantations and logged forests	2°03.90N 103°31.57E	>2000	9-11 Feb; 25-27 May; 3-5. Aug	1.2 (16.04) 1.1 (4.63) 0.5 (13.99)	Never logged
Bekok, Johor Malaysia(BK)	primary lowland /hill Dipterocarp forest	Oil palm and rubber plantations and logged forests	02°20.84N 103°09.41E	>2000	17-19 Jun; 13-15 Jul; 11-13 Aug	1 (13.80) 1 (16.59) 1 (13.26)	Never logged
Bukit Timah Nature Reserve, Singapore (BT)	Primary hill Dipterocarp forest	Urban areas 103°50'E	1°20'N	87 20-22 Apr; 1 (12.80) 28-30 Jun 1 (11.39)	3-5 Mar; 20-22 Apr; 1 (12.80) 28-30 Jun 1 (11.39)	1 (12.24)	Never logged
MacRitchie, Singapore (MC)	Secondary forest with primary patches	Urban areas and secondary forest		521	24-26 Feb; 12-14 Apr; 22-24 Jun.	1 (12.04) 1 (10.32) 1 (12.41)	60-80 yrs
Nee Soon, Singapore (NS)	Secondary forest with primary patches	Urban areas and secondary forest		794.6	16-18 Mar; 26-28 Apr; 6-8 Jul	1 (16.16) 1 (14.34) 1 (14.64)	60-80 yrs
Holland Woods, Singapore (HW)	Secondary forest mixed with (<i>Albizia</i> spp.) exotic forest	Urban areas		41.5	5-7 May; 8-10 Jun; 26-28. Jul	1.8 (24.42)	20-40 yrs
Kent Ridge Park, Singapore (KR)	Secondary forest and open parkland	Urban areas		27.2	30 Mar-1 Apr; 18-20 May; 1-3 Jul	1 (10.96) 1 (11.88)	20-40 yrs
UMP , Oil Palm Plantation Johor (UMP)	Uniform oil palm) stand(<i>Elaeis guineensis</i>)	Pineapple,rubber and fruit trees plantations	1°35.81N 103°27.57E	2105.6	12-14 Mar; 12-14 May; 20-22 Jul	1 (11.75) 1 (12.45) 1 (13.13)	Cleared: 1946/7

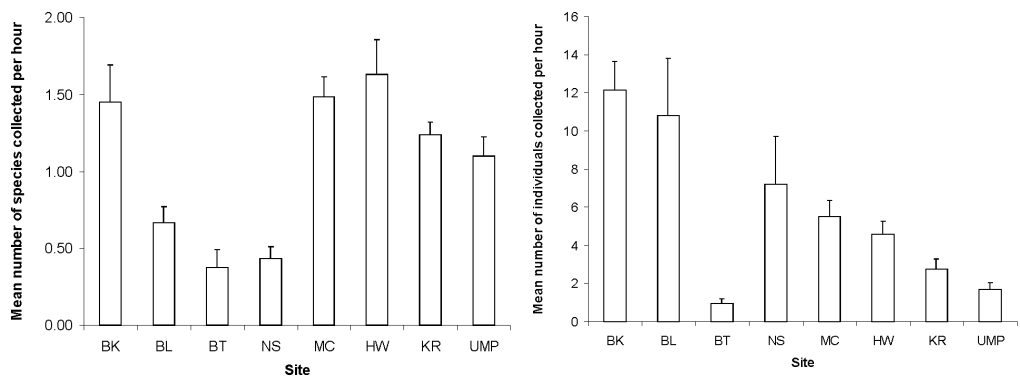


Fig. 4. a) Mean number of species collected per hour at each site and b) Mean of number of individuals collected per hour at each site. For site abbreviations see Table 1.

Sumatran sites (data from Salmah et al. 1990) and those in Brunei (data from Roubik 1996) (Fig. 6). Within the sites from the present study, the primary forests in Johor were clearly distinguished from the rest of the sites in Singapore and the oil palm plantation in Johor. Within the Sumatran and Bornean sites, the pristine primary forests formed a separate cluster (Fig 6).

Environmental factors affecting bee distribution

A Canonical Correspondence Analysis (CCA) was performed on a primary data matrix consisting of log transformed numbers of bee individuals

collected per hour for 45 bee species and a secondary matrix with six environmental variables. The first two CCA axes explained 28.2% and 22.4% of the variation in the data sets, respectively (Table 3). Both the first and second axes had high loadings of the mean temperature of the sites and the flowering density index of shrubs (Table 3). Five groups of bees can be distinguished, namely the honey bees (group 1), the 1st group of stingless bees (group 2, including *melina*, *ita-ma*, *reepeni*, *ventra* and *terminata*), the 2nd group of stingless bees (group 3, including *geisslerei* and *laeviceps*), the 1st group of Megachilids and Anthophorids (group 4, including *Nomia*, *Cerat-*

Table 2. Bee species richness (S), absolute numbers of bees (N) collected at each site (see Table 1 for abbreviations) and diversity indices calculated according to Magurran (1988). D (Mg) = Margalef's index, S (Mn) = Menhinick's index, 1/D(S) = inverse of Simpson's index, N/Nmax = inverse of Berger-Parker's index, U (McIn) = McIntosh's index in general form, D (McIn) = McIntosh's dominance measure, E (McIn) = McIntosh's evenness, HB = Brillouin index, E of HB = Brillouin's evenness index, H? = Shannon's index and E of H? = Shannon's evenness index.

Sites	S	N	D (Mg)	D (Mn)	1/D (S)	N/ Nmax	U	D (McIn)	E (McIn)	HB (McIn)	E of HB	H?	E of H?
BK	9	419	1.32	0.44	3.39	2.07	228.07	0.48	0.68	0.373	0.71	1.543	0.256
BL	7	444	0.98	0.33	2.12	1.77	305.59	0.33	0.5	0.66	0.27	0.881	0.145
BT	5	42	1.07	0.77	1.6	1.27	33.44	0.24	0.36	0.282	0.2	0.765	0.205
NS	5	232	0.73	0.33	1.1	1.05	221.09	0.92	1.55	0.098	0.14	0.249	0.046
MC	22	242	3.83	1.41	4.96	2.95	109.48	0.59	0.7	0.819	0.65	2.018	0.368
HW	9	111	1.7	0.85	3.85	2.41	57.3	0.53	0.73	0.643	0.76	1.598	0.339
KR	10	63	2.17	1.26	4.12	3	31.73	0.57	0.73	0.622	0.74	1.608	0.388
UMP	17	64	3.86	2.13	8.88	4.92	22.58	0.74	0.85	0.881	0.82	2.259	0.543

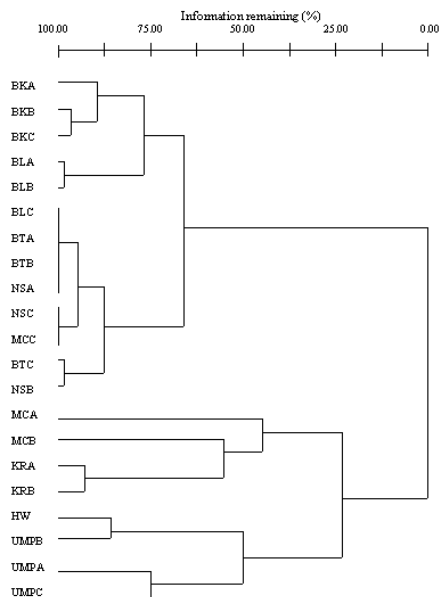


Fig. 5. A dendrogram of bee species recorded along the transects of the eight study sites (See Table 1 for abbreviations).

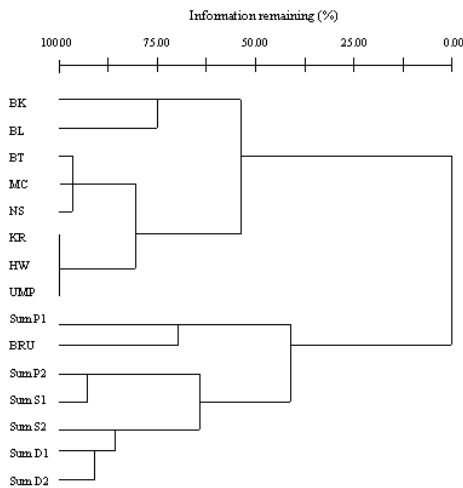


Fig. 6. A dendrogram of the distribution of Apidae in 14 sites, where BK, BL, BT, MC, NS, HW, KR, UMP are from this study, (see Table 1 for abbreviations), Sum P1= Primary forest, Sum P2 = Primary forest mixed with secondary forest, Sum S1 = Secondary forest, Sum S2 = Secondary forest mixed with other disturbed habitats, Sum D1 = coconut plantations and orchards, Sum D2 = villages (Sumatran sites from Salmah *et al.* 1990) and Bru = Brunei primary forest (Roubik 1996).

ina, *Amegilla*, *Xylocopa*) and the 2nd group of Megachilids and Anthophorids (group 5, including *Lipotriches* and *Lassioglossum*) (Fig. 7). Both the groups of stingless bees increased in abundance with the increase in the number of big trees (the density of trees with dbh between 30-40 cm), and decreased with increasing temperature and flowering intensity of both trees and shrubs. The honey bees appear to prefer average conditions or may not be strongly affected by the measured variables. Group 5 increases in abundance with increasing flowering intensity and temperature and tolerates the low density of larger trees (Fig 7).

Correlation of birds and bees

The species richness of birds and bees, and the absolute abundance and catch rate of bees were not correlated. However, bird species richness increases with bee abundance. There are also no significant correlations between the number of insectivorous, nectarivorous, frugivorous birds and the bee species richness or catch rates of bees. Although, again, the number of insectivorous bird species increases with the abundance of bees. This may be due to the limitation of a small sample size ($N = 8$). Plotting bird richness and bee abundance along a disturbance gradient shows that both values decrease with disturbance (Fig. 8), especially when the outlier, BT (Bukit Timah) is removed.

Discussion

Bee community characteristics at the eight sites

Within the limitations of the collecting methods used, it can be seen that disturbed forests tend to have greater absolute bee species richness. These disturbed habitats may also attract more "tourists", i.e. bees that do not reside within the habitat under investigation and those with potentially greater foraging ranges (e.g. the trap-lining *Amegilla* and *Xylocopa* spp.). However, the relatively undisturbed lowland Dipterocarp primary and secondary forests have greater absolute abundance of bees.

The Apidae, especially the genus *Trigona*, is

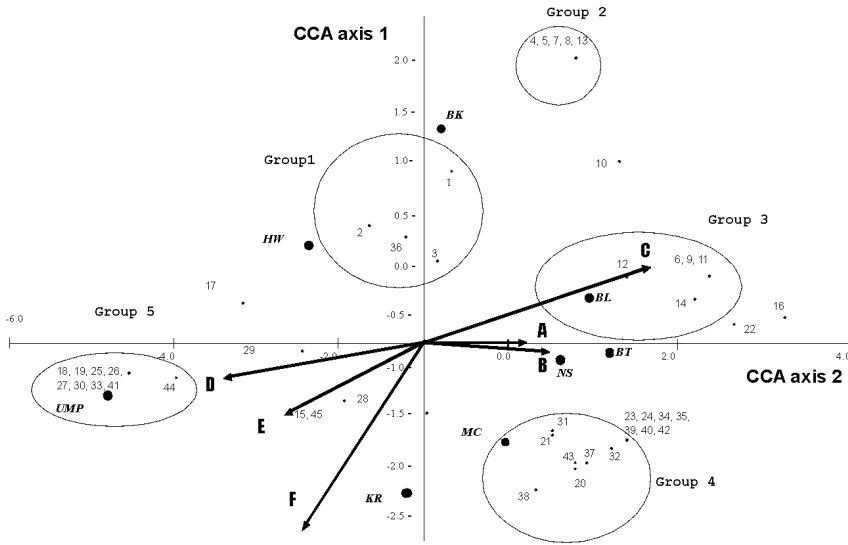


Fig 7. The ordination diagram from the CCA of a primary matrix of the log transformed numbers of bees collected per hour and a secondary matrix of six environmental variables and their canonical coefficients. Solid circles refer to sites (for abbreviations, refer to Table 1), small diamonds refer to bee species (refer to Appendix 2), the arrows A-F refer to environmental variables where A = Density of trees < 10 m in height, B = leaf litter depth, C = density of trees with dbh between 30-40 cm, D = flowering tree/m², E = flowering density index of shrubs and F= temperature.

ubiquitous in the rain forest (Appanah et al. 1986) and are important pollinators, especially in the under-story (Bawa & Opler 1975, Appanah 1981). Both the primary and secondary forests harbour a much greater proportion of Apidae: the more undisturbed by human activity the forests, the fewer non-Apidae bees can be found

in the under-story. In fact, only *Apis* and *Trigona* of the family Apidae were recorded in Bekok and Belumut. In similar but smaller forests in Singapore, the Apidae were also relatively dominant (99.1% of all bees caught in Nee Soon and 95.2% in Bukit Timah Nature Reserve). MacRitchie, another late secondary forest in

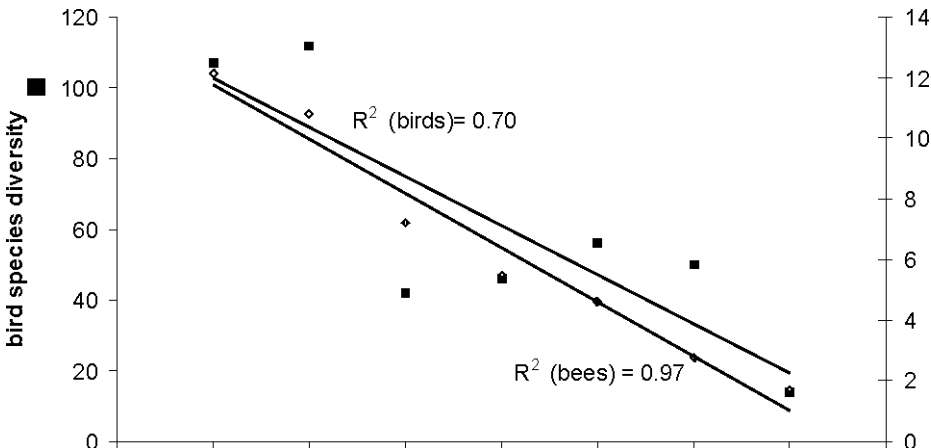


Fig. 8. Birds and bees along a disturbance gradient (minus outlier BT)

Table 3. Summary statistics of the 1st two CCA axes of the CCA performed with a primary matrix of the log transformed numbers of bees collected per hour and a secondary matrix of six environmental variables and their canonical coefficients.

Canonical Axis	1	2
Eigenvalue	0.668	0.529
% of variance in species data explained	28.2	22.4
Cummulative % of variance in species data explained	28.2	50.6
Pearson Correlation (Spp- Env)	0.995	0.999
Environmental variables (Abbreviation)	Canonical	coefficients
Density of trees <10m height (A)	-0.121	0.6
Leaf litter depth (B)	0.499	-0.326
Flowering trees/m ² (D)	2.08	-1.896
Flowering density index of shrubs (E)	-2.013	1.67
Temperature (F)	2.935	-4.204

Singapore has a somewhat mixed habitat. Two of its transects (A and B) were more open and haboured more weedy, constantly flowering shrubs and early pioneer species (pers. obs.). This observation is supported by the analysis which clustered these two transects with those from Kent Ridge Park a relatively young, open forest (Fig. 5). The two more abundant families of non-Apidae bees were the Anthophoridae and the Halictidae. The remaining two families (Colletidae and Megachilidae) were rarely collected or observed during this study. The Anthophoridae and Halictidae favoured the more open and disturbed forests. They are frequently caught on flowers of common early secondary plants and widespread weeds in open habitats. This is in contrast to Kato's (1996) observation in Sarawak where *Amegilla* of the Anthophoridae was noted as shade-loving. This may indicate that these bees are more adaptable than previously reported.

There is no reason to believe that Sumatra and Brunei have a different bee composition from Peninsular Malaysia with the exception of a few endemic species. But 13 out of 27 species of *Trigona* and *Apis* found in Sumatra and Brunei, and thus expected during this study, were never encountered. It is not known why this was so, despite a comparatively lengthy collection period that included months with a higher flowering intensity in the lowland forests (March to July, Medway 1972) and similar collection

methods. Perhaps some species are becoming so rare, even in the primary forests of Johor, that chance encounters are very low. It must be born in mind that these primary forests of Johor are also forest fragments, albeit large ones, and they are surrounded by plantation forests. The alternative explanation is that population numbers of certain species may be low during inter-mass flowering periods, hence decreasing the number of chance encounters. On a positive note however, the feral *Apis mellifera* was never encountered during this study even in the most disturbed forest habitats.

The inadequacy of classical diversity indices

Diversity indices such as the ones calculated in this study are not adequate in reflecting the biological status of the habitat in consideration. The primary forest sites are ranked less diverse by these indices when the absolute abundance of bees may be more important in maintaining the ecosystem than the absolute number of species. The ecological roles of the species involved must be considered when deciding how undisturbed a habitat is.

Resources for foraging bees

Mass flowering in the lowland Dipterocarp forests of West Malesia is a well-known phenomenon (Appanah 1985), although it is

little understood (Corlett 1990). During the inter mass flowering years, however, the level of flowering is kept more or less constant by a changing assortment of species and the peak flowering period during any year appears to be between March to July (Medway 1972). This study spans this period of high flowering intensity although it did not coincide with a mass flowering period, hence it sheds light on the bee community structure during 'normal' periods of flowering intensity in Bekok, Belumut, Bukit Timah, Nee Soon and MacRitchie, all of which have at least some resemblance to the forests described by Medway (1972). The Apidae must have some mechanisms for tiding over periods of low flowering and these may include storage of resources and/or the use of resources other than nectar and pollen (e.g. extra-floral nectaries) to maintain densities large enough to utilize efficiently the mass flowering phenomenon when it occurs.

In the three remaining sites, where plant species composition is different and species diversity lower, flowering of both trees and shrubs is quite constant. We may speculate that many solitary bee species from the Anthophoridae and Halictidae found in these forests need not be adapted to store food because of a constant supply of open flowers.

Different species or even genera and families of bees are sometimes not very specific in their choice of resource. One of us (Liow) has seen bees from all the four major families (Apidae, Halictidae, Megachilidae and Anthophoridae) foraging on *D. suffructocisa*, *M. malabathricum*, *A. instrusa* and *S. indica* flowers despite differences in the architecture of the flowers. *Trigona* have been reported to be polylectic, visiting flowers of many different plant species (e.g. Kato 1996). This may be due to the unpredictability of flowering in the West Malesian tropics (Roubik 1992), requiring bees to be flexible in their resource use and thus to be primarily generalists instead of specialists (Waser et al. 1996).

However, the honey baits tended to attract mainly the honey bees (*Apis*) and stingless bees (*Trigona*). This could be indicative that the

concentration and method of presentation of the sugars was attractive only to the Apidae.

Environmental parameters, forest disturbance and the distribution of bees

Many of the environmental variables, thought to be important in defining the habitat for bees, are related to the level of disturbance in the forest. In the relatively undisturbed forests, temperature and light intensity were lower, humidity higher, and all the three variables more constant than in the rest of the sites. This is due to a closed canopy that results from the higher density of sub-canopy and canopy trees. Hardly any under-story plants or trees were observed flowering during this study. Under these conditions, only bees of the Apidae were collected in the under-story. The species richness within Apidae in Bekok and Belumut were higher (nine and seven respectively) than that in the other sites. Out of the total of 14 species of Apidae collected at these two sites, eight were not collected elsewhere. In particular, *T. melina*, an abundant species collected at Bekok appears to be a species restricted to primary forests, as also indicated by the Sumatran study (Salmah et al. 1990). This species may be restricted by its small foraging range, (common to most if not all trigonids e.g. Roubik & Aluja 1983, van Nieuwstadt & Iraheta 1996) and fragile nest structure (Appendix 3).

The CCA indicates that many of the stingless bees favour forests with larger trees and lower temperatures. In the case of some *Trigona* it has been shown that nest sites are limiting factors for their density (Inoue et al. 1990). In other words, these stingless bees characterize the bee community in closed native forests. They seem to be tolerant of the apparent lack of flowering resources. This may be due to their ability to store food in their nests to tide over times of meagre resources during inter-mass flowering episodes.

Many of the trigonid nests observed during this study had nest entrances made of resinous material and trigonids have been observed to collect resins from trees. There appears to be much more available resin on trees in the primary

forests of Johor. This may be because the trees are older, larger and more frequently utilized by beetles, woodpeckers and fungi, causing the resins to be exposed and available for bees to collect. It is not known if bees are specific in the choice of resins for nest building.

In the intermediately disturbed forests of Singapore, the physical parameters were more variable as there were more gaps in the canopy. Growth of open area species such as *Dicranopteris linearis*, a fern and *Clidemia hirta*, an exotic shrub, were also apparent. MacRitchie in particular was abundant in shrubs and treelets constantly flowering. Both Nee Soon and Bukit Timah are in a physiognomic and a bee compositional sense (mainly Apidae) similar to the primary forests in Johor although species richness is lower. MacRitchie, consisting of a mix of open and closed habitats, is much more bee species rich, as can be expected of a mixed habitat. It has also a more even distribution of bee families. Bukit Timah Nature Reserve deserves a separate mention because despite its primary forest status, it is very small (87 ha with a lot of edge habitats) and apparently very poor in both species richness and abundance. *Trigona laeviceps*, which has been described to the most commonly found trigonid species (Inoue et al. 1984) especially in disturbed areas, dominated both Bukit Timah and Nee Soon.

At the other end of the spectrum, Kent Ridge, Holland Woods and the UMP oil palm plantation are more or less dominated by exotic plants (by ornamental plants in Kent Ridge, *Albizia* sp. in Holland Woods and *Elaeis guineensis* in the oil palm plantation). Under these conditions, the family Halictidae and Anthophoridae were more commonly caught. They seem to require higher temperatures and light intensity, and lower humidity levels. They also increase in abundance with greater flowering intensities both in the low-lying vegetation and in trees. They apparently do not require larger trees.

The relationship between bird diversity, forest condition and the bee community

Correlations between species richness in different taxa have been found to be significant (e.g. Pearson & Cassola 1992) or absent (Lawton et al. 1998). In this study no correlation was found between birds and bees although one might speculate that the number of insectivorous birds should be positively correlated with bee abundance, if bees can act as an indicator of insect diversity in general. One might also speculate that the number of nectarivorous birds should reflect positively the number of nectar collecting bees since they are using the same resource. There is a trend that bird diversity and bee abundance decrease with disturbance.

Conservation implications

It has been reiterated that baiting methods are biased (Southwood 1978). In particular, this study could not investigate the bee community in the canopy of trees, especially in the less disturbed forests where trees were commonly more than 20 m in height. It was also biased by the non-randomness of the transects chosen. However, the collection methods were standardized throughout the eight sites and it is possible to compare the bees collected from the sites of varying disturbances. The physical architecture of forests is determined mainly by plants but the underlying perpetuation of plants is dependent on pollinators especially in the tropics where many plants are dioecious (Renner & Feil 1993) and where wind-pollination is very rare (Whitmore 1984). Animal pollination is an important ecological process dominated by bees. It is still not known how bees are affected by habitat change though inferences can be made from this study and some other previous studies. In particular, larger trees and more constant ambient conditions are more conducive to many trigonid bees that may have the ability to survive inter-mass flowering conditions and utilize abundant resources during mass flowering. This in turn allows cross-fertilization among con-specific trees. Nest sites/materials (e.g. resins) and foraging sites may be limited when forest

conversions occur.

Are there enough pollinators surviving for the process of pollination to continue in regenerating forest fragments or logged forests? If, as this study show, the bee community composition is largely different in disturbed and undisturbed forests, are disturbed forests such as secondary forests adequate to meet the pollination requirements of regenerating forests? During the period of study, it has been observed that there are many more *T. laeviceps* individuals immediately outside the forest of Bukit Timah foraging on exotic, ornamental flowering plants along the road than in the interior of the Nature Reserve. This may indicate that *T. laeviceps* is favouring a richer and more constant food source in the matrix of the small forest fragment and may hence neglect to visit forest plants that flower much less frequently. The five Singaporean forest sites studied are quite different in bee community structure as compared with the primary forests in Johor. This is probably an indication that ecological processes in forests of Singapore are changing. Trigonids, dominant in closed forests, were absent from the oil palm plantation, a habitat that is rapidly becoming all pervading in Peninsular Malaysia. However, even in the primary forest sites in Johor, the bee community is not as complete as it should be. There is a need to study the bee community in relation to the matrix surrounding these undisturbed forests. We can only speculate at this moment that the matrix (i.e. plantations) surrounding these forests, may not provide adequate nest sites for many forest bee species. These negative trends, which can also be seen in the South American tropics (Frankie et al. 1997), should be rectified before the process of pollination grinds to a dangerous low. The only way of rectification that can be suggested based on our present knowledge of tropical ecology is to preserve larger tracts of undisturbed tropical lowland forests.

Research directions

We need to study the mechanisms of resource storage by social bees, especially during the mass flowering periods which may allow them to

maintain a steady population throughout the long inter mass flowering period. Do these bees forage more intensively during mass flowering periods and are there mechanisms through which they increase their worker populations to tap nectar and pollen resources? We also need to study the effects of forest fragmentation on bees and their pollination functions. Exactly how selective are bees for nest sites and are they limiting for bees? Is it true that the bees found in disturbed habitats cannot respond to mass flowering in native forests? What are the consequences of small forests with differing matrices for bees with various foraging ranges? How important is the recruiting behaviour in social bees like trigonids for utilizing fluctuating resources in the mass flowering tropics?

All these questions should be answered to help us manage the remaining bee populations and understand the role of pollination in regeneration and restoration of mass-flowering lowland tropical Southeast Asian forests.

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Appendix 1 . Table of the bird species recorded at the eight study sites (see Table 1 for abbreviations), their dates of survey and the habitat preference of the bird species where FW = fresh water habitat, P = Primary forest, S = Secondary forest and forest edge, GR =grassland and open areas.

	Common Name Resident Species	Scientific Name	Site								Habitat			
			NS	MC	BT	HW	KR	UMP	BL	BK	FW	P	S	GR
1	Purple Heron	<i>Ardea purpurea</i>					1				1			
2	Striated Heron	<i>Butorides striatus</i>					1				1			
3	Brahminy Kite	<i>Haliaastur indus</i>				1	1				1		1	
4	White-bellied Sea-Eagle	<i>Haliaeetus leucogaster</i>	1	1	1		1	1			1			
5	Grey-headed Fish-Eagle	<i>Ichthyophaga ichthyaetus</i>	1								1	1		
6	Crested Serpent-Eagle	<i>Spilornis cheela</i>		1					1	1	1	1	1	1
7	Changeable Hawk-Eagle	<i>Spizaetus cirrhatus</i>	1	1	1				1			1	1	1
8	Black-thighed Falconet	<i>Microhierax fringillarius</i>							1			1	1	1
9	Red Junglefowl	<i>Gallus gallus</i>							1	1		1	1	
10	Great Argus	<i>Argusianus argus</i>							1	1		1	1	1
11	Red-legged Crake	<i>Rallina fasciata</i>				1					1	1	1	
12	White-breasted Waterhen	<i>Amaurornis phoenicurus</i>				1	1	1			1			1
13	Thick-billed Pigeon	<i>Treron curvirostra</i>							1	1		1		
14	Little Green Pigeon	<i>Treron olax</i>							1			1		
15	Pink-necked Green-Pigeon	<i>Treron vernans</i>	1	1	1	1	1				1		1	1
16	Green Imperial Pigeon	<i>Ducula aenea</i>							1			1	1	
17	Spotted Dove	<i>Streptopelia chinensis</i>			1	1	1	1	1				1	1
18	Peaceful Dove	<i>Geopelia striata</i>						1					1	1
19	Green-winged Pigeon	<i>Chalcophaps indica</i>							1	1		1	1	
20	Long-tailed Parakeet	<i>Psittacula longicauda</i>	1	1	1	1			1		1	1	1	1
21	Blue-rumped Parrot	<i>Psittinus cyanurus</i>	1		1				1	1	1	1		
22	Blue-crowned Hanging-Parrot	<i>Loriculus galgulus</i>			1	1				1	1			1
23	Indian Cuckoo	<i>Cuculus micropterus</i>					1		1			1	1	
24	Banded Bay Cuckoo	<i>Cacomantis sonneratii</i>			1	1						1	1	1
25	Rusty-breasted Cuckoo	<i>Cacomantis sepulchralis</i>				1						1	1	
26	Violet Cuckoo	<i>Chrysococcyx xanthorhynchus</i>	1	1	1					1		1	1	
27	Drongo Cuckoo	<i>Surniculus lugubris</i>	1		1							1	1	
28	Common Koel	<i>Eudynamys scolopacea</i>			1		1						1	1
29	Black-bellied Malkoha	<i>Phaenicophaeus diardii</i>								1		1	1	
30	Chestnut-bellied Malkoha	<i>Phaenicophaeus sumatranus</i>		1	1							1	1	

Appendix 1. Continued.

	Common Name	Scientific Name	Site								Habitat				
	Resident Species		NS	MC	BT	HW	KR	UMP	BL	BK	FW	P	S	GR	
31	Raffles's Malkoha	<i>Phaenicophaeus chlorophaeus</i>							1	1		1	1		
32	Chestnut-breasted Malkoha	<i>Phaenicophaeus curvirostris</i>								1		1	1		
33	Short-toed Coucal	<i>Centropus rectunguis</i>								1		1	1	1	
34	Greater Coucal	<i>Centropus sinensis</i>	1			1		1		1			1	1	
35	Lesser Coucal	<i>Centropus bengalensis</i>		1		1							1	1	
36	Reddish Scops-Owl	<i>Otus rufescens</i>							1	1		1			
37	Collared Scops-Owl	<i>Otus lempiji</i>			1				1	1		1	1		
38	Barred Eagle-Owl	<i>Bubo sumatranus</i>								1		1	1		
39	Brown Hawk-Owl	<i>Ninox scutulata</i>			1							1	1		
40	Spotted Wood-Owl	<i>Strix seloputo</i>							1			1	1	1	
41	Gould's Frogmouth	<i>Batrachostomus stellatus</i>								1		1			
42	Javan Frogmouth	<i>Batrachostomus javensis</i>								1		1			
43	Malaysian-Eared Nightjar	<i>Eurostopodus temminckii</i>							1			1			
44	White-bellied Swiftlet	<i>Collocalia esculenta</i>							1			1	1	1	
45	Brown Needletail	<i>Hirundapus giganteus</i>							1		1	1	1	1	
46	Silver-rumped Swift	<i>Rhaphidura leucopygialis</i>							1	1	1	1			
47	House Swift	<i>Apus affinis</i>			1	1	1							1	
48	Asian Palm-Swift	<i>Cypsiurus balasienis</i>				1	1					1	1	1	
49	Grey-rumped Treeswift	<i>Hemiprocne longipennis</i>				1	1		1	1		1	1		
50	Whiskered Treeswift	<i>Hemiprocne comata</i>								1		1	1	1	
51	Red-naped Trogon	<i>Harpactes kasumba</i>							1			1	1		
52	Diard's Trogon	<i>Harpactes diardii</i>							1	1		1	1		
53	Scarlet-rumped Trogon	<i>Harpactes duvaucelii</i>							1	1		1	1		
54	Blue-eared Kingfisher	<i>Alcedo meninting</i>							1		1	1			
55	Blue-banded Kingfisher	<i>Alcedo euryzona</i>								1		1			
56	Oriental Dwarf Kingfisher	<i>Ceyx erithacus</i>			1					1	1	1			
57	Banded Kingfisher	<i>Lacedo pulchella</i>							1	1		1			
58	Stork-billed Kingfisher	<i>Halcyon carpensis</i>		1							1				
59	White-throated Kingfisher	<i>Halcyon smyrnensis</i>	1	1	1	1	1	1			1		1	1	
60	Collared Kingfisher	<i>Halcyon chloris</i>				1	1				1		1	1	
61	Rufous-collared Kingfisher	<i>Actenoides concretus</i>							1	1		1			
62	Blue-tailed Bee-eater	<i>Merops philippinus</i>	1		1	1	1				1			1	

Appendix 1. Continued.

	Common Name	Scientific Name	Site								Habitat				
	Resident Species		NS	MC	BT	HW	KR	UMP	BL	BK	FW	P	S	GR	
63	Blue-throated Bee-eater	<i>Merops viridis</i>	1	1	1	1	1		1	1	1	1		1	
64	Red-bearded Bee-eater	<i>Nyctornis amictus</i>							1			1	1		
65	Dollarbird	<i>Eurystomus orientalis</i>	1	1	1	1	1					1	1		
66	White-crowned Hornbill	<i>Berenicornis comatus</i>								1		1			
67	Bushy-crested Hornbill	<i>Anorrhinus galeritus</i>								1		1			
68	Wreathed Hornbill	<i>Rhyticeros undulatus</i>							1	1		1			
69	Rhinoceros Hornbill	<i>Buceros rhinoceros</i>							1	1		1			
70	Helmeted Hornbill	<i>Rhinoplax vigil</i>							1	1		1			
71	Gold-whiskered Barbet	<i>Magalaima chrysopogon</i>							1	1		1			
72	Red-crowned Barbet	<i>Megalaima rafflesii</i>	1	1	1					1		1	1		
73	Red-throated Barbet	<i>Megalaima mystacophanos</i>								1	1	1	1		
74	Blue-eared Barbet	<i>Megalaima australis</i>							1	1		1	1		
75	Coppersmith Barbet	<i>Megalaima haemacephala</i>				1	1					1		1	
76	Brown Barbet	<i>Calorhampbus fuliginosus</i>							1		1	1	1		
77	Rufous Woodpecker	<i>Celeus brachyurus</i>	1	1		1	1		1	1		1	1	1	
78	Laced Woodpecker	<i>Picus vittatus</i>				1						1	1		
79	Crimson-winged Woodpecker	<i>Picus puniceus</i>							1	1		1	1		
80	Chequer-throated Woodpecker	<i>Picus mentalis</i>							1	1		1			
81	Banded Woodpecker	<i>Picus miniaceus</i>	1	1	1	1	1		1	1		1	1		
82	Common Goldenback	<i>Dinopium javanense</i>	1			1	1					1	1		
83	Buff-rumped Woodpecker	<i>Meiglyptes tristis</i>							1			1	1		
84	Buff-necked Woodpecker	<i>Meiglyptes tukki</i>								1		1	1		
85	Great Slaty Woodpecker	<i>Mulleripicus pulverulentus</i>							1			1	1		
86	White-bellied Woodpecker	<i>Dryocopus javensis</i>		1								1	1		
87	Maroon Woodpecker	<i>Blythipicus rubiginosus</i>								1		1	1		
88	Dusky Broadbill	<i>Corydon sumatranus</i>								1		1			
89	Black-and-red Broadbill	<i>Cymbirhynchus macrorhynchus</i>								1	1	1	1		
90	Banded Broadbill	<i>Eurylaimus javanicus</i>							1	1		1	1		
91	Black-and-yellow Broadbill	<i>Eurylaimus ochromalus</i>							1	1		1	1		
92	Green Broadbill	<i>Calyptomena viridis</i>							1	1		1	1		
93	Pacific Swallow	<i>Hirundo tabitica</i>	1	1	1	1	1				1			1	
94	Red-rumped Swallow	<i>Hirundo daurica</i>		1	1						1			1	

Appendix 1. Continued.

	Common Name	Scientific Name	Site							Habitat				
	Resident Species		NS	MC	BT	HW	KR	UMP	BL	BK	FW	P	S	GR
95	Bar-winged Flycatcher-Shrike	<i>Hemipus picatus</i>							1			1	1	
96	Black-winged Flycatcher-Shrike	<i>Hemipus hirundinaceus</i>							1	1		1	1	
97	Large Wood-Shrike	<i>Tephrodornis virgatus</i>							1	1		1	1	
98	Bar-bellied Cuckoo-Shrike	<i>Coracina striata</i>							1			1	1	
99	Lesser Cuckoo-Shrike	<i>Coracina fimbriata</i>							1	1		1	1	
100	Pied Triller	<i>Lalage nigra</i>			1		1						1	1
101	Fiery Minivet	<i>Pericrocotus igneus</i>							1	1		1		
102	Scarlet Minivet	<i>Pericrocotus flammeus</i>			1				1	1		1		
103	Green Iora	<i>Aegithina viridissima</i>							1	1		1	1	
104	Common Iora	<i>Aegithina tiphia</i>	1	1		1	1						1	1
105	Great Iora	<i>Aegithina lafresnayei</i>								1		1	1	
106	Lesser Green Leafbird	<i>Chloropsis cyanopogon</i>			1				1	1		1	1	
107	Greater Green Leafbird	<i>Chloropsis sonnerati</i>			1				1			1	1	
108	Blue-winged Leafbird	<i>Chloropsis cichinchinensis</i>	1	1	1				1	1		1	1	
109	Straw-headed Bulbul	<i>Pycnonotus zeylanicus</i>			1						1	1	1	
110	Black-headed Bulbul	<i>Pycnonotus atriceps</i>							1			1	1	
111	Black-crested Bulbul	<i>Pycnonotus melanicterus</i>			1							1	1	
112	Grey-bellied Bulbul	<i>Pycnonotus cyaniventris</i>							1	1		1	1	
113	Red-whiskered Bulbul	<i>Pycnonotus jocosus</i>					1						1	1
114	Yellow-vented Bulbul	<i>Pycnonotus goaivier</i>	1	1	1	1	1	1	1				1	1
115	Olive-winged Bulbul	<i>Pycnonotus plumosus</i>	1	1	1	1	1			1		1	1	1
116	Cream-vented Bulbul	<i>Pycnonotus simplex</i>	1	1	1				1	1		1	1	
117	Red-eyed Bulbul	<i>Pycnonotus brunneus</i>			1	1			1	1		1	1	
118	Spectacled Bulbul	<i>Pycnonotus erythrophthalmos</i>							1	1	1	1	1	
119	Finsch's Bulbul	<i>Criniger finschii</i>								1		1		
120	Grey-cheeked Bulbul	<i>Criniger bres</i>							1	1		1	1	
121	Yellow-bellied Bulbul	<i>Criniger phaeocephalus</i>							1	1		1	1	
122	Hairy-backed Bulbul	<i>Hypsipetes criniger</i>							1	1		1	1	
123	Buff-vented Bulbul	<i>Hypsipetes charlottae</i>							1	1		1	1	
124	Streaked Bulbul	<i>Hypsipetes malaccensis</i>							1	1		1		
125	Ashy Bulbul	<i>Hypsipetes flavala</i>	1		1		1		1			1	1	
126	Bronzed Drongo	<i>Dicrurus aeneus</i>								1		1	1	

Appendix 1. Continued.

	Common Name	Scientific Name	Site								Habitat				
	Resident Species		NS	MC	BT	HW	KR	UMP	BL	BK	FW	P	S	GR	
127	Greater Racquet-tailed Drongo	<i>Dicrurus paradiseus</i>	1	1	1	1			1	1	1	1	1		
128	Dark-throated Oriole	<i>Oriolus xanthonotus</i>							1	1		1	1		
129	Black-naped Oriole	<i>Oriolus chinensis</i>	1	1	1	1	1	1					1	1	
130	Asian Fairy-Bluebird	<i>Irena puella</i>	1	1	1				1	1	1	1	1		
131	Crested Jay	<i>Platylophus galericulatus</i>								1		1			
132	Large-billed Crow	<i>Corvus macrorhynchos</i>	1	1	1	1	1	1	1		1			1	
133	Sultan Tit	<i>Melanochlora sultanea</i>							1	1		1	1		
134	Velvet-fronted Nuthatch	<i>Sitta frontalis</i>				1			1		1	1			
135	Black-capped Babbler	<i>Pellorneum capistratum</i>							1	1		1	1		
136	Short-tailed Babbler	<i>Trichastoma malaccense</i>	1	1					1		1	1	1		
137	Horsfield's Babbler	<i>Trichastoma sepium</i>							1			1			
138	Abbott's Babbler	<i>Trichastoma abbotti</i>			1		1					1	1		
139	White-chested Babbler	<i>Trichastoma rostratum</i>	1						1		1	1	1		
140	Moustached Babbler	<i>Malacopteron magnirostre</i>							1	1	1	1	1		
141	Sooty-capped Babbler	<i>Malacopteron affine</i>								1		1	1		
142	Rufous-crowned Babbler	<i>Malacopteron magnum</i>							1	1		1			
143	Grey-breasted Babbler	<i>Malacopteron albogulare</i>								1	1				
144	Chestnut-backed Scimitar-Babbler	<i>Pomatorhinus montanus</i>							1			1			
145	Striped Wren-Babbler	<i>Kenopia striata</i>							1		1	1			
146	Large Wren-Babbler	<i>Napothera macrodactyla</i>							1			1			
147	Eyebrowed Wren-Babbler	<i>Napothera epilepidota</i>							1			1			
148	Rufous-fronted Babbler	<i>Stachyris rufifrons</i>							1			1	1		
149	Grey-headed Babbler	<i>Stachyris poliocephala</i>								1		1	1		
150	Chestnut-rumped Babbler	<i>Stachyris maculata</i>							1	1		1			
151	White-necked Babbler	<i>Stachyris leucotis</i>							1			1			
152	Black-throated Babbler	<i>Stachyris nigricollis</i>								1		1			
153	Chestnut-winged Babbler	<i>Stachyris erythroptera</i>	1	1					1	1		1	1		
154	Striped Tit-Babbler	<i>Macronus gularis</i>	1	1	1	1	1		1	1		1	1		
155	White-bellied Yuhina	<i>Yuhina zantholeuca</i>							1	1		1	1		
156	Malaysian Rail-Babbler	<i>Eupetes macrocerus</i>							1	1		1	1		
157	Oriental Magpie Robin	<i>Copsychus saularis</i>					1	1	1	1			1	1	

Appendix 1. Continued.

	Common Name	Scientific Name	Site								Habitat				
	Resident Species		NS	MC	BT	HW	KR	UMP	BL	BK	FW	P	S	GR	
158	White-rumped Shama	<i>Copsychus malabaricus</i>	1							1	1		1	1	
159	Chestnut-naped Forktail	<i>Enicurus ruficapillus</i>									1	1			
160	Flyeater	<i>Gerygone sulphurea</i>					1		1	1		1	1		
161	Common Tailorbird	<i>Orthotomus sutorius</i>				1	1	1					1	1	
162	Dark-necked Tailorbird	<i>Orthotomus atrogularis</i>	1	1	1	1	1		1	1	1	1	1		
163	Ashy Tailorbird	<i>Orthotomus sepium</i>			1			1			1		1	1	
164	Rufous-tailed Tailorbird	<i>Orthotomus sericeus</i>				1			1	1		1	1		
165	Yellow-bellied Prinia	<i>Prinia flaviventris</i>				1					1		1	1	
166	Grey-chested Flycatcher	<i>Rhinomyias umbratilis</i>							1		1	1	1		
167	Grey-headed Flycatcher	<i>Culicicapa ceylonensis</i>							1	1		1			
168	Spotted Fantail	<i>Rhipidura perlata</i>							1			1	1		
169	Pied Fantail	<i>Rhipidura javanica</i>				1							1	1	
170	Blacked-naped Monarch	<i>Hypothymis azurea</i>							1	1		1	1		
171	Rufous-winged Monarch	<i>Philestoma pyropterus</i>							1	1	1	1			
172	Asian Paradise-Flycatcher	<i>Terpsiphone paradisi</i>		1	1							1	1		
173	Philippine Glossy Starling	<i>Aplonis panayensis</i>	1	1	1	1	1						1	1	
174	Common Myna	<i>Acridotheres tristis</i>					1						1	1	
175	Hill Myna	<i>Gracula religiosa</i>	1	1		1	1		1	1		1	1		
176	Brown-throated Sunbird	<i>Anthreptes malaccensis</i>	1	1		1	1			1	1		1	1	
177	Red-throated Sunbird	<i>Anthreptes rhodolaema</i>								1		1	1		
178	Ruby-checked Sunbird	<i>Anthreptes singalensis</i>								1		1	1		
179	Purple-naped Sunbird	<i>Hypogramma hypogrammicum</i>							1	1		1	1		
180	Purple-throated Sunbird	<i>Nectarinia sperata</i>	1	1		1						1	1	1	
181	Olive-backed Sunbird	<i>Nectarinia jugularis</i>				1	1				1		1	1	
182	Crimson Sunbird	<i>Aethopyga siparaja</i>	1	1	1	1	1					1	1		
183	Little Spiderhunter	<i>Arachnothera longirostra</i>	1	1	1				1	1		1	1		
184	Long-billed Spiderhunter	<i>Arachnothera robusta</i>							1			1	1		
185	Spectacled Spiderhunter	<i>Arachnothera flavigaster</i>								1		1	1		
186	Grey-breasted Spiderhunter	<i>Arachnothera affinis</i>							1	1		1	1		
187	Yellow-breasted Flowerpecker	<i>Prionochilus maculatus</i>							1	1		1	1		
188	Crimson-breasted Flowerpecker	<i>Prionochilus percussus</i>							1	1	1	1	1		
189	Orange-bellied Flowerpecker	<i>Dicaeum trigonostigma</i>	1	1	1				1	1		1	1	1	

Appendix 1. Continued.														
Common Name		Scientific Name	Site								Habitat			
Resident Species			NS	MC	BT	HW	KR	UMP	BL	BK	FW	P	S	GR
190	Scarlet-backed Flowerpecker	<i>Dicaeum cruentatum</i>		1	1	1	1					1	1	
191	Everett's White-eye	<i>Zosterops everetti</i>							1	1		1	1	
192	White-rumped Munia	<i>Lonchura striata</i>							1		1		1	1
193	Scaly-breasted Munia	<i>Lonchura punctulata</i>		1			1	1			1		1	1
Introduced species (naturalized)														
194	Red Lory	<i>Eos bornea</i>					1						1	
195	Rainbow Lorikeet	<i>Trichoglossus haematodus</i>				1							1	
196	Blossom-headed Parakeet	<i>Psittacula roseata</i>				1							1	
197	Rose-ringed Parakeet	<i>Psittacula krameri</i>		1		1	1						1	1
198	Red-breasted Parakeet	<i>Psittacula alexandrii</i>				1							1	
199	Tanimbar Corella	<i>Cacatua goffini</i>				1							1	
200	White Cockatoo	<i>Cacatua alba</i>				1							1	
201	House Crow	<i>Corvus splendens</i>		1		1	1							1
202	Greater Necklaced Laughingthrush	<i>Garrulax pectoralis</i>					1						1	
203	White-crested Laughingthrush	<i>Garrulax leucolophus</i>			1	1	1					1	1	
204	Hwamei	<i>Garrulax canorus</i>				1							1	
205	White-vented Myna	<i>Acridotheres javanicus</i>	1	1	1	1	1	1	1				1	1
206	Oriental White-eye	<i>Zosterops palpebrosa</i>				1	1					1	1	
Total			42	46	52	56	50	14	112	107				
Transect length (km)			4.5	5.5	1.9	1.7	2.6	3.0	3.0	2.5				
Dates of surveys (d-m-y)			9.2.98	14.7.97	22.10.97	1.6.99	17.7.97	12.5.99	27.7.99	29.7.99				
			10.2.98	16.8.97	30.12.97	29.9.98	2.11.97	13.5.99	28.7.99	30.7.99				
			7.7.98	7.1.98	17.4.98	30.11.98	15.1.98	21.7.99	15.8.99	5.8.99				
			7.8.98	27.11.98	3.7.98	25.3.99	5.8.98	22.7.99	16.8.99	6.8.99				

Appendix 2. Absolute abundance of 45 bee morphospecies collected at each transect in the eight study sites. (See Table 1 for site abbreviations).

Family	Species Transects	BK			BL			BT			NS			MC			HWKR				UMP			
		A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	A	A	B	A	B	A	C
1	Apidae	<i>Apis cerana</i> Fabricius 1793	40	0	19	0	3	3	0	0	0	0	0	0	0	0	29	0	0	4	3	6		
2		<i>A. dorsata</i> Fabricius 1793	0	0	0	0	0	0	0	0	0	0	0	0	0	0	15	0	0	1	0	0		
3		<i>A. adreniformis</i> Smith 1858	0	0	0	0	0	0	0	0	5	0	0	0	0	0	44	1	3	0	0	0		
4		<i>Trigona (Leipdotrigona) terminata</i> Smith 1878	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
5		<i>T. (L.) ventralis</i> Smith 1857	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
6		<i>T. (Homotrigona) fimbriata</i> Smith 1857	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
7		<i>T. (Tetragonula) reepeni</i> Friese 1918	0	0	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
8		<i>T. (Heterotrigona) itama</i> Cockerell 1918	0	0	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
9		<i>T. (Genotrigona) thoracica</i> Smith 1857	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
10		<i>T. (Tetrigona) apicalis</i> Smith 1857	0	10	5	2	6	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0		
11		<i>T. (Tetragonula) atripes</i> Smith 1857	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
12		<i>T. (T.) geissleriei</i> Friese 1918	37	7	33	95	118	38	1	1	0	1	0	2	18	8	26	6	10	11	0	0	0	
13		<i>T. (T.) melina</i> Gribodo 1893	39	41	122	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
14		<i>T. (T.) laeviceps</i> Smith 1857	25	1	9	42	88	44	12	14	7	72	36	113	20	15	47	0	0	0	0	0		
15	Halictidae	<i>Halictus</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1		
16		Halictidae?	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0		
17		<i>Lassioglossum (Ctenonomis)</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	4	5		
18		<i>Lassioglossum (Eurylaeus)</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	8	3		
19		<i>Lassioglossum</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0		
20		<i>Pachyhalictus</i> sp.	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	2	0	0	0		
21		<i>Nomia (Curvinomia)</i> sp.	0	0	0	0	0	0	0	0	1	0	0	0	27	14	6	4	7	14	0	2	0	
22		<i>Nomia (Maculonomia)</i> sp. 1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0		
23		<i>Nomia (Maculonomia)</i> sp. 2	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0		
24		<i>Nomia (Maculonomia)</i> sp. 3	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0		
25		<i>Lipotriches</i> sp.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0		
26		<i>Lipotriches</i> sp. 2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0		
27		<i>Lipotriches</i> sp. 3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1		
28		<i>Lipotriches (Lipotriches)</i> sp.	0	0	0	0	0	0	0	0	0	0	0	1	3	0	0	0	0	1	0	1		
29		<i>Pseudapis</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	0	2	0	1	1	1	3		

Appendix 2. Continued.

Family	Species Transects	BK			BL			BT			NS			MC			HWKR			UMP		
		A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	A	B	A	B	C
30 Megachilidae	<i>Chalicodoma</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
31 Anthophoridae	<i>Amegilla</i> (<i>Zonamegilla</i>) <i>korotonensis</i> (Cockerell)	0	0	0	0	0	0	0	0	0	0	0	0	8	0	0	0	0	0	1	0	0
32	<i>A. (Z.) andrewsi</i> (Cockerell)	0	0	0	0	0	0	0	0	0	0	0	0	10	1	0	0	0	1	0	0	0
33	<i>A. (Z.) flammeozonata</i> (Dours)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
34	<i>A. (Glossamegilla) insularis</i> (Smith)	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0
35	<i>A. (G.) fulvobirta</i> (Meade-Walde)	0	0	0	0	0	0	0	0	0	0	0	0	4	1	0	0	0	0	0	0	0
36	<i>Thyreus himalayns</i> Radcloz.	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	6	0	0	0	0	0
37	<i>Ceratina</i> (<i>Ceratinidia</i>) <i>nigrolateralis</i> Cockerell	0	0	0	0	0	0	0	0	0	0	0	0	2	3	0	0	1	1	0	0	0
38	<i>Ceratina</i> sp.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
39	<i>Ceratina</i> sp.2	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
40	<i>Ceratina</i> sp. 3	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
41	<i>Ceratina</i> (<i>Pithitis</i>) sp.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
42	<i>Ceratina</i> (<i>Pithitis</i>) sp.2	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
43	<i>Xylocopa</i> (<i>Platynopoda</i>) <i>latipes</i> (Drury)	0	0	0	0	0	0	0	0	0	0	0	2	2	2	1	0	3	7	0	0	0
44	<i>Xylocopa</i> (<i>Kortortosoma</i>) sp.	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	6	0	2
45 Colletidae	<i>Hylaeus</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0

Appendix 3: Descriptions of trigonid nests encountered during this study. See Table 1 for site abbreviations

Species	Site	Description of nest entrance	Description of nest location
<i>Trigona (Teragonula) melina</i>	BK	Delicate, extensive, resinous tube with a total length of 33.8 cm. Mouth of entrance 1.8 by 3.3 cm.	In trunk of tree (dbh 180 cm, ht. >20 m), entrance 81 cm above ground.
<i>T. (Lepidotrigona) terminata</i>	BK	Solid tubular structure 5 cm in length opening out into a delicate, resinous trumpet like exit 4.2 cm in length. Mouth of entrance 1.9 by 2.0 cm.	In trunk of tree (dbh = 222 cm, ht. > 20m), entrance 60 cm above ground
<i>T. (Heterotrigona) itama</i>	BK	Solid tubular structure 7 cm in length. Mouth of entrance 1.2 by 1.2 cm.	In trunk of tree (dbh = 100 cm, ht. > 20 m), entrance 103 cm above ground.
<i>T. (Tetrigona) apicalis</i>	BTNR	Vertically flattened trumpet like opening without a tube, 18.0 by 2.5cm.	In trunk of tree (dbh = 50 cm, ht. ca. 20 m) entrance 47 m above ground.
<i>T. (Tetragonula) laeviceps</i>	NS	Solid short tube inserting into loose soil. Mouth of entrance 1.0 by 1.0 cm.	In loose soil camouflaged by leaf litter.