Ecology of stingless bees (Apidae, Meliponini) in lowland dipterocarp forests in Sabah, Malaysia, and an evaluation of logging impact on populations and communities

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1 INTRODUCTION

1.1 Tropical forest management and conservation of biological diversity

There is an ongoing debate on the potential of Natural Forest Management (NFM) for the conservation of tropical biodiversity (Bawa and Seidler 1998, Chazdon 1998, Putz et al. 2001). In broad generalization, Natural Forest Management involves the harvesting of timber trees in such a way as to allow the forest to regenerate naturally before the next round of extraction (Bawa and Seidler 1998). The conceptual or implemented forms of NFM vary widely in extraction intensity, selective logging cycles and the kinds of silvicultural treatments applied before and after logging (Kleine and Heuveldop 1993, Hartshorn 1995, Bruenig 1996, Ong et al. 1996), but all share the common aim of long-term sustainability. The important role of NFM in the conservation of tropical forest biota is mainly derived from the rapid decline of undisturbed lowland forests (Soule and Sanjayan 1998) and an increasing realism concerning the protective effects of isolated reserves: Even if 10-12 % of the area in tropical latitudes would be appropriately preserved, up to 50 % of tropical species would still be expected to become extinct during the next decades (Soule and Sanjayan 1998). Commercial forest reserves harboring logged forests could serve as additional refuges for endangered species and may be of prime importance in preserving species with restricted distributions (see Prendergast et al. 1993). Thus, NFM has become a main focus of political and research organizations concerned with tropical conservation. However, it has been debated whether NFM will live up to the high expectations. Lines of criticism are twofold: First, indirect consequences of logging (increased susceptibility to fire, increased access by poachers and settlers) may severely reduce the benefits of commercial forests for conservation (Holdsworth and Uhl 1997, Chazdon 1998). Second, and more to the scope of the present work, the effects of forest disturbance on populations and communities are not sufficiently understood to warrant long-term predictions on maintenance of tropical biodiversity (Linsenmair 1995, Linsenmair 1997, Bawa and Seidler 1998).

Responses of animals and plants to logging have been the subject of an increasing number of ecological studies. Structural alterations of the forest vegetation can be substantial (Thiollay 1992, Bawa and Seidler 1998, Seidler and Bawa 2001), ranging up to 75 % canopy loss in case of exploitative operations in dipterocarp forests in Asia (Cannon et al. 1994). In the same locality, reduced stem density also resulted in decreased per-area species richness of trees

eight years after logging, but the number of tree species per number of individuals sampled was similar to primary forest controls (Cannon et al. 1998). Generally, the direct impact on trees and tree species richness is likely to depend on logging intensity and methods. Reduced Impact Logging in Sabah, Malaysia, has been shown to reduce negative effects on residual stem density by more than 50% in comparison with conventional logging (Marsh et al. 1996), implying a likewise reduction of effects on per-area tree species diversity. Logging affects the relative abundance of trees in favor of widespread pioneer species, suggesting that logged forests become increasingly homogeneous on a regional scale (Wyatt-Smith 1987).

Results of studies on responses of animals are varied, partly because of variation in site parameters (e.g. logging intensity) and scale and intensity of sampling, but also because different groups of organisms have different ecological requirements. E.g., different feeding guilds of birds consistently differ in their response to selective logging. Understory insectivores are reduced in number and species richness (Thiollay 1992, Johns 1996, van der Hoeven et al. 2000), whereas generalist feeders have been shown to increase at the same time (Thiollay 1992, Mason 1996). Proximate causes of differences in responses remain speculative and include different microclimatic adaptations of species as well as alterations of the specific resource base (Thiollay 1992, Mason 1996). Respective patterns in mammals are very diverse and specific responses range from local extinction to pronounced increases in abundance after logging (Laidlaw 1996, Bawa and Seidler 1998, van der Hoeven et al. 2000). Insects and other invertebrates have received increasing attention from ecologists during the last decade. Most studies have shown alterations of abundance, species richness and/or species composition in logged versus undisturbed forests (Inoue et al. 1990, Salmah et al. 1990, Burghouts et al. 1992, Holloway et al. 1992, Eggleton et al. 1995, Eggleton et al. 1996, Eggleton et al. 1997, Hill 1999, Beck and Schulze 2000, Chung et al. 2000, Vasconcelos et al. 2000, Beck et al. in press), but generalizations are difficult to make (Lawton 1998). A reduction of numbers and species as a response to disturbance appears to be the most frequent result, whereas increases in diversity seem rare (but see Nummelin and Borowiec 1991). Most studies that included plantations or clear-felled sites reported that the observed reduction in diversity was mainly found between forests and open habitats and to a lesser degree between selectively logged forests varying in disturbance history (Eggleton and al. 1995, Eggleton and al. 1996, Lawton 1998, Chung et al. 2000; and see Floren and Linsenmair in press and Floren et al. in press for re-growth forest). Information on proximate causes of the observed alterations is generally scant. Most studies were confined to speculations based on distinct diversity patterns in certain subgroups of study organisms. E.g., the consistent decrease of the

soil feeding guild among termites was attributed to the likely alteration of soil microclimate in logged forests (Eggleton et al. 1997). Only few studies have attempted to measure a range of environmental variables in order to identify causative relationships (Chung et al. 2000, Beck et al. in press), and only one was able to relate diversity of the study taxon (geometrid moths) to a habitat variable (diversity of understory vegetation) closely linked to relevant resource requirements of the insect group studied (Beck et al. in press).

Although data are scant, forest disturbance is likely to alter biotic interactions and related processes in complex forest systems, making it difficult to predict long-term stability of populations and communities (Linsenmair 1997, Seidler and Bawa 2001). Logging has been shown to lead to insufficient regeneration of forest trees due to reduced seed production and an increased proportion of predated seeds in Bornean forests (Curran et al. 1999). Similarly, logging increased the likelihood of egg predation in a natural experiment using artificial bird nests in mainland Malaysia (Cooper and Francis 1998). Perhaps the greatest danger to disturbed habitats arises from a disruption of plant-pollinator interactions (Kearns et al. 1998, Kremen and Rickets 2000). In case of selective logging two factors may combine in their negative effects on reproduction of self-incompatible forest plants. First, logging increases nearest-neighbor distances to conspecific trees and has been shown to reduce inter-tree movement of pollinators, thereby reducing the amount of viable pollen for seed set (Ghazoul et al. 1998). Pollen flow and outcrossing was low in low-density situations in some forest trees in Panama (Murawski et al. 1990, Murawski and Hamrick 1991, Stacy et al. 1996). Second, the pool of available pollinators can be reduced as an effect of habitat change (Frankie et al. 1990, Frankie et al. 1997), further reducing between-plant pollen flow.

Stingless bees (Apidae: Meliponini) are among the most predominant flower-visiting insects in both Old and New World tropical forests (Heithaus 1979a, Heithaus 1979b, Roubik 1979a, Roubik 1989, Appanah 1990, Inoue et al. 1990, Roubik 1990, Momose and Inoue 1994, Nagamitsu and Inoue 1994, Momose et al. 1998). Although their effectiveness as pollinators has rarely been demonstrated experimentally, stingless bees frequently come in contact with the sexual organs of the flowers they visit, and are therefore likely pollinators of a substantial fraction of plant species in both canopy and understory (Roubik 1979a, Momose and Inoue 1994). It is the aim of the present work to elucidate responses of stingless bees to selective logging in forests of Sabah, Malaysia. Before outlining research approach and specific questions (see 1.3), I will briefly review relevant aspects of stingless bee biology, with special reference to Southeast Asian species.

1.2 Biology of stingless bees

Together with honey bees (Apini), bumble bees (Bombini), and orchid bees (Euglossini) stingless bees (Meliponini) form a distinct clade (subfamily Apinae) within the Apidae (Hymenoptera: Apoidea)(Roig-Alsina and Michener 1993). Meliponines are highly eusocial bees that live in perennial colonies of a few hundred to tens of thousands of individual bees, normally descendants of a single queen (Michener 1974, Sakagami 1982, Wille 1983).

1.2.1 Nesting, brood production and recource requirements

Nests of most stingless bees are mainly constructed with cerumen, a mixture of wax with resins and gums (propolis) collected from plants and brought to the nest (Sakagami 1982, Wille 1983). Species vary in nest site, ranging from exposed nests constructed in vegetation (aerial nests, only in the Neotropics), over nests established within aerial nests of termites and ants (e.g. Sakagami et al. 1989) and subterranean nests built in underground cavities, to nests in preexisting cavities in trees (Darchen 1992, Roubik 1979b, Roubik 1983, Sakagami et al. 1983b, Salmah et al. 1990). In all cases the central brood and storage area is enclosed within a layer of cerumen, except for the entrance hole (Sakagami 1982, Sakagami et al. 1983a, Sakagami and Yamane 1984). Within this envelope brood cells are constructed in clusters or combs. In contrast to honey bees, brood rearing in stingless bees is always done by mass provisioning cells (Sakagami 1982). In most neotropical (see Roubik 1982a for exceptions) and all Asian species brood is raised on pollen as the major source of protein (Sommeijer and De Bruijn 1985, Sommeijer et al. 1985). Both pollen and nectar (floral and extra-floral) are collected in quantities by foraging workers and deposited in special storage pots within the nest (Roubik 1989). Food storage allows colonies to survive for months without incoming food (Roubik 1989).

1.2.2 Colony cycle, swarming and longevity

New colonies are founded by swarming. In contrast to honey bees, where swarming involves more or less instantaneous departure of the old mother queen and a large mass of workers (Michener 1974, Winston 1978, Lee and Winston 1985), colony founding is a gradual process in meliponines: After scout bees have located a new nest site, nest material and food is first translocated by workers from the old colony. Later, a virgin queen arrives with the actual

swarm, makes her nuptial flight, and brood cell construction and oviposition are initiated in the new nest (Moure et al. 1958, Sakagami 1982, Inoue et al. 1984b). Several weeks or even months can pass until complete independence of the daughter colony (Wille 1983). Due to the lasting relationship between old and new nest, the dispersal radius of stingless bees is more restricted than in honey bees (to a few hundred meters, Nogueira-Neto, 1954, cited in Sakagami 1982), a fact that may have consequences for meliponine re-colonization of disturbed areas or forest fragments. Once safely established, individual meliponine colonies are known to survive for 10 to 26 years (Wille 1983, Roubik 1989).

1.2.3 Regulation of colony foraging

Social bee colonies are subject to a continuously changing internal state and external environment to which they need to respond adequately to survive (Biesmeijer et al. 1999a). Internal factors such as the amount of pollen stored or brood in the nest have been shown to influence total foraging effort, the relative proportion of nectar and pollen foraging, foraging frequency and trip duration in honey bees (Free 1967, Fewell and Winston 1992, Camazine 1993, Camazine 1998, Fewell and Bertram 1999). The effect of resource availability in the habitat has not been studied in detail in honey bees. Only two studies have addressed related questions in stingless bees: Roubik (1982b) found that when food reserves were low in colonies of *Melipona* at the end of the wet season in tropical Guyana, brood cannibalism occurred and brood production ceased. Foragers did not increase their foraging effort in response to low food reserves. At the same time, life-spans of individual workers doubled (Roubik 1982b). In a study on *Melipona beecheii*, a relatively larger fraction of foragers were allocated to pollen foraging when pollen stores were experimentally reduced, but the total forager force remained unchanged. Pollen foraging mainly depended on positive cues related to pollen availability in the habitat, e.g. the number of successful pollen foragers returning to the nest (Biesmeijer et al. 1999a). In summary, the response of stingless bees to internal or (perceived) external resource dearth seems more conservative than that of honeybees. This strategy is probably facilitated by the long individual life-spans and long larval development times of meliponines, as well as by the fact that large amounts of pollen are stored within developing brood cells (Biesmeijer et al. 1999a).

1.2.4 Foraging strategy and recruitment

Stingless bees are generalist flower visitors. On the population level some species are known to use floral resources from more than a hundred plant taxa over the course of several seasons in a given habitat, with considerable overlap of plant spectra between species of bees (Wilms et al., 1996). It has been suggested that resource partitioning between species is partly mediated by differences in foraging strategy and communication of food resources. Johnson (1983) distinguished solitary and group foragers among neotropical species of stingless bees, with solitarily foraging species exploiting resources scattered in space and time, whereas group foragers concentrate on rich and clumped resources. The latter are able to recruit large numbers of nest mates and can dominate resource patches by sheer numbers or by means of aggressive interactions (Johnson and Hubbell 1974, Johnson and Hubbell 1975, Hubbell and Johnson 1978, Roubik 1980, Roubik 1981, Johnson 1983). Relatively little is known about foraging strategies of Southeast Asian meliponines (Nagamitsu and Inoue 1997). The mechanisms used by meliponines to communicate food resources include scent-trails, piloting, and relatively complex dances involving sound emissions (Lindauer and Kerr 1960, Nieh 1998, Aguilar and Sommeijer 2001). A combination of cues and signals enables some species to communicate locations in three spatial dimensions (Nieh and Roubik 1995).

1.2.5 Diversity and community structure

There are approximately 200 described species of stingless bees in tropical areas worldwide (Sakagami 1982). However, species are not distributed equally within the tropics. Local and regional diversity is high in the Neotropics, where up to 60 meliponine species can be found in a single forest locality (Roubik 1989). Asian communities generally have less than thirty species (Salmah et al. 1990, Roubik 1996). The apparent compression of stingless bee assemblages in Asia is paralleled by an equally reduced diversity of solitary bee taxa (Roubik 1990), and has been attributed (i) to the competitive pressure exerted by Asian honeybees and (ii) to extreme temporal fluctuations of floral resource levels in Asian tropical forests (Roubik 1992). This interpretation assumes that competition for food is a strong structuring agent in tropical bee communities. Competition for food resources among stingless bees is indicated by behavioral studies reporting direct interference competition between colonies at food patches (Johnson and Hubbell 1974, Johnson 1983, Nagamitsu and Inoue 1997), and by uniform nest dispersion of colonies of some neotropical *Trigona* (Hubbell and Johnson 1977).

1.3 Stingless bees and forest disturbance: questions

To date there has been only one study that addressed responses of tropical apids to habitat disturbance. In equatorial Sumatra Salmah et al. (1990) found that both species richness and abundance of stingless bees was negatively related to the degree of habitat alteration. In this study the disturbance gradient encompassed a large variety of habitat conditions ranging from primary lowland forest, over plantations close to forest fragments, to city areas. The highest diversity of meliponines was found in sites that included primary forest. Due to the large heterogeneity involved in both sampling protocol and sites it is difficult to draw conclusions on the potential impact of forest management on bee communities. The proximate causes of variation in bee richness remained unexplored.

The present thesis describes results of studies on stingless bee diversity and abundance in differentially logged and unlogged forests in Sabah, Malaysia. In order to evaluate effects of logging on bee populations and communities, particular emphasis was given to investigating the proximate causes of observed patterns. The following specific questions were asked:

1. **What are the patterns of meliponine species richness and abundance in differentially logged and unlogged lowland dipterocarp forests?** The forest sites studied are characterized in chapter 2. Section 4.1 and 4.2 describe patterns of stingless bee richness obtained by honey-water baiting assays and quantitative nest surveys.

2. **What are the direct, instantaneous effects of logging on stingless bee populations?** Section 3.4 analyzes nest trees of meliponines and estimates the proportion of likely harvest trees among those.

3. **What are the ecological factors involved in determining stingless bees population density and species richness in undisturbed or regenerating forests?** Sections 3.1, 3.2, 3.4 and 4.2 describe food and nesting resources of stingless bees, evaluate logging-independent nest mortality, and (4.2) relate the findings to nest density in the different sites. Section 3.3 describes a new method for assessing pollen diets of natural colonies of meliponines.

2 STUDY BACKGROUND AND RESEARCH SITES

2.1 Forest management in Sabah

Sabah has a long history of timber exploitation. Since the issue of the first timber concession in 1879, annual log production has constantly increased until 1978, when the volume exceeded 13 million m^3. Depletion of forest resources led to reduced productivity afterwards (Kleine and Heuveldop 1993). Today, 40 % of the state area are designated commercial forest reserves (Marsh et al. 1996), harboring mostly logged-over forest with severely reduced timber stocks (Lohuji and Taumas 1998). During the last decade increasing emphasis has been given to managing rather than exploiting natural forests in Sabah. Reduced Impact Logging methods have been tested that reduce damage to the residual stand in order to promote natural regeneration (Marsh et al. 1996), and management concepts have been developed that integrate technical and planning procedures (Kleine and Heuveldop 1993). The research presented in this thesis was conducted within the Malaysian-German Sustainable Forest Management Project (M-G-SFMP), installed by the German GTZ and the Sabah State Forestry Department and aimed at introducing sustainable forest management to Sabahan forests. Hereby, environmental impact assessment of management operations is an integral aspect in evaluating sustainability (Kleine and Heuveldop 1993). Part of the research was conducted in the Deramakot Forest Reserve, the model area of the M-G-SFMP (see section 2.2). Parallel to the investigations on bees the research sites were also surveyed for leaf-litter ants (Brühl et al. 1998, C. Brühl in prep.), ants of the lower vegetation (Gossner 1999), nymphalid butterflies (Mohd. Fairus 2000) and moths (Chey in prep).

2.2 Study Sites

Between 1997 and 2000 we studied stingless bees at a total of 14 research sites located in primary and logged forests in lowland Sabah, Malaysia. At each site we established a transect grid covering an area of 600 x 600 m (Fig. 4). Research sites were situated in three localities in eastern and central Sabah (Fig. 1, Fig. 2, Fig. 3).

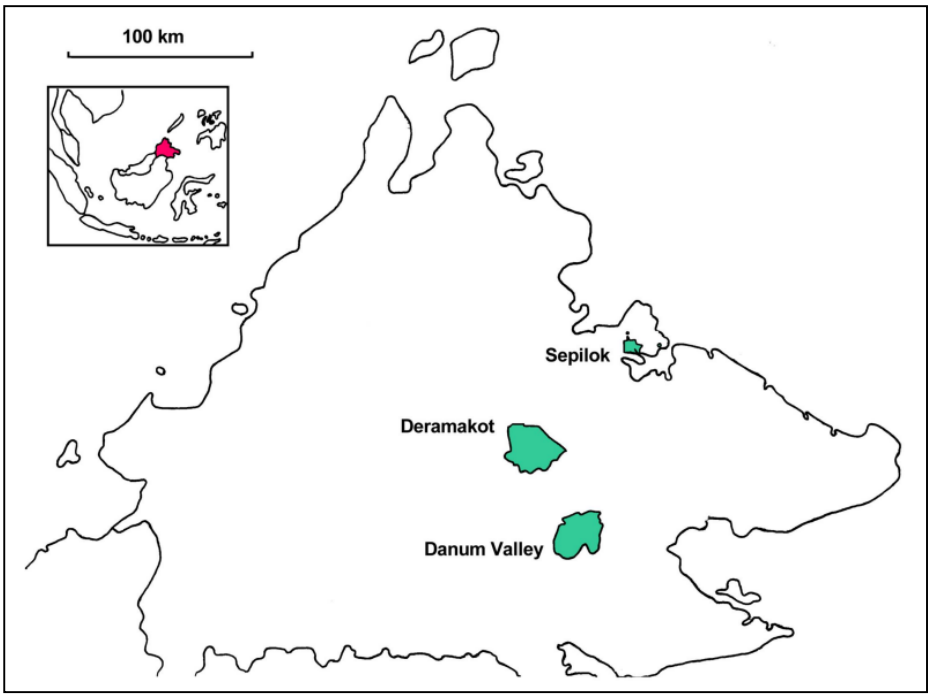

Fig. 1 Map of Sabah. Research localities are green.

Danum Valley (4°50‘N-5°00‘N and 117°35‘E-117°45‘E): Two sites. The Danum Valley Conservation Area (DVCA) is situated about 70 km west of Lahad Datu and includes 43.800 ha of largely undisturbed dipterocarp forest, with *Parashorea malaanonan*, *P. tomentella* and *Shorea johorensis* dominating the canopy around the Danum Valley Field Centre (Marsh and Greer 1992). The Segama River forms the eastern and southern boundary of DVCA. The two research sites were located in rugged terrain (at about 250 m a.s.l.) within walking distance from the Field Centre (4^{O} 57.7’ N, 117^{O} 48.2’E): one was situated along the West Trail (Plot L: W10-W16) and the other at the 1.5 km mark along the Waterfall trail (Plot M). The forest at these sites has never been used for any commercial purpose and can be considered as primary within the context of this study. The distance between sites L and M is about 2,5 km. Both sites are surrounded by large tracts of continuous forest with distances of more than 5 km to large-scale forest openings in all directions.

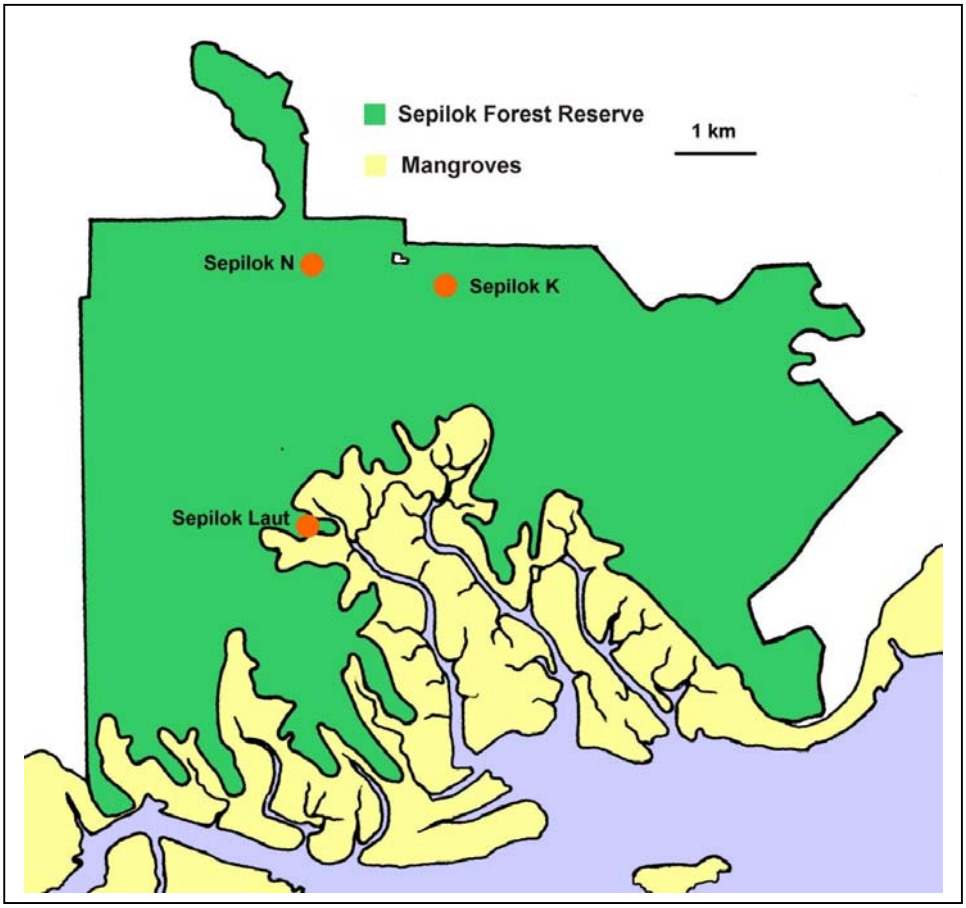

Fig. 2 Map of Kabili-Sepilok Forest Reserve and locations of study sites. White surrounding areas are plantations.

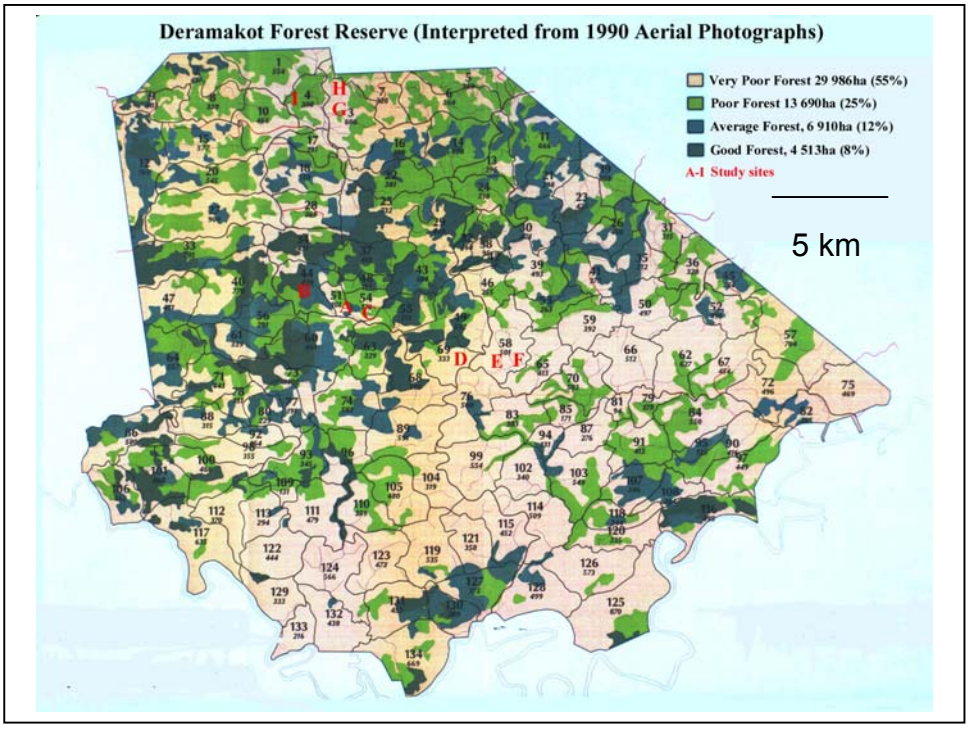

Fig. 3 Map of Deramakot Forest Reserve and locations of study sites.

Sepilok (5°54‘N, 118°04‘E): Three sites. The Kabili-Sepilok Forest Reserve is a coastal forest fragment of 4294 ha, with more than one third of that area consisting of mangrove forest fringing Sandakan Bay. On elevated ground, lowland mixed dipterocarp forest of the *Parashorea tomentella-Eusideroxylon zwageri* type is dominant. On steep ridges it is replaced by sandstone hill dipterocarp forest with a somewhat different floristic composition (Fox 1973). Kerangas of varying height exist in a few locations. To the east, north and west the reserve is bordered by plantations. Although Sepilok was partly logged 50 to 100 years ago, the areas in and around our sites (K, N, Sepilok Laut) probably remained undisturbed. Plots K and N are situated in the north of the reserve, approximately 500 m distant from the forest edge, on undulating to rugged terrain. The cultivated land bordering the forest north of K is highly heterogeneous, including old orchards (with Rambutan and other fruit trees), patches of corn, cassava and oil palm, as well as gardens with ornamental plants. Most of the land bordering the forest north of N is covered by old oil palm plantations. The third site, Sepilok Laut (laut = sea, ocean (Malay)), directly borders the mangroves in the South of the reserve. The nearby mangroves are mixed stands of *Rhizophora apiculata*, *Ceriops tagal*, *Xylocarpus granatum* and *Lumnitzera littorea*, with *R. apiculata* being the dominant species (Fox 1973). Due to the specific topography the total length of the transect system in Sepilok Laut was only 60% that of the other sites. Data on tree stand structure and stingless bee nest density were corrected accordingly.

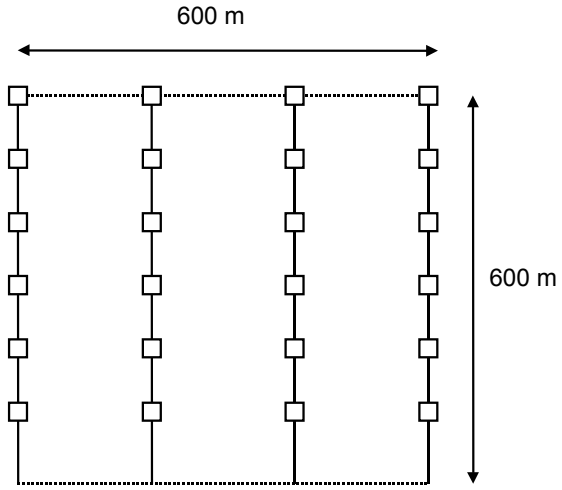

Fig. 4 Schematic view of transect grid established in each of the 14 forest sites. Squares indicate locations for relaskop angle-count sampling for assessment of stand structure (this section). Transects were also used for honey-water baiting (4.1) and quantitative nest surveys (4.2).

Deramakot (5°19‘N-5°20‘N and 117°20‘E–117°42‘E): Nine sites. The Deramakot Forest Reserve is a 55.000 ha class II commercial forest estate and has been established as a model area for the introduction of sustainable management practices by the Malaysian-German Sustainable Forest Management Project (Kleine and Heuveldop 1993). It is situated in the Centre of Sabah (60 km north of Danum Valley) and is covered by lowland mixed dipterocarp lowland forest of the *Parashorea tomentella-Eusideroxylon zwageri* type. The terrain is undulating to rugged. The entire area has been subject to timber extraction since 1956 (Chai and Amin 1994) and harbors a wide range of logged-over forests with varying degree and history of disturbance. The selected sites can be grouped according to their location within Deramakot and, related to location, logging history and current stand structure (see below).

- *Old* logged-over forests, *slightly* disturbed: selectively logged once between 1974 and 1976; largely intact canopy; sites A, B, C all situated in the still well stocked area around the Deramakot Base Camp (Compartments 44, 51, 54) at about 250 m a.s.l..

- *Old* logged-over forests, *heavily* disturbed: logged once or twice between 1968 and 1970; partly subjected to detrimental silvicultural treatment; very heterogeneous, with uneven canopy; heavily infested with vines and climbers; sites D, E, F located in the South of Deramakot (250 m a.s.l.) that was the first area to be exploited by the timber industry (Compartments 58, 69).

- *Young* logged-over forests, *heavily* disturbed: logged up to three times between 1980 and 1989; uneven canopy; heavily infested with vines and climbers; sites G, H, I situated in the northern areas of Deramakot (Compartments 3, 4) at 100 m a.s.l..

With the exception of A, that is close to the Deramakot base camp clearing, all sites were situated within large continuous forest tracts. In order to quantify site characteristics we measured tree size distribution using angle-count sampling with a custom-made Spiegel relaskop (Schreuder et al. 1987). Individual counts with basal area factor four were taken every 100 m along the transect grids (Fig. 4). All in-trees above 5 cm dbh were counted and counts were recorded separately for five dbh-classes: 5-15 cm, 15-30 cm, 30-60 cm, 60-100 cm, and trees above 100 cm. In addition, we separately recorded trees of the pioneer genus *Macaranga*. For statistical analysis we combined primary sites of Danum Valley and Sepilok and consecutively tested for effects of forest type on tree diameter distribution using ANOVA (with four levels of disturbance: primary and the three levels of disturbed forests described above). There were significant differences in all variables tested: the skewness of the diameter

distribution (N=14, F_3=4.98, $p<0.05$), the total number of large trees above 60 cm dbh (F_3=15.65, $p<0.001$), and the total number of *Macaranga* trees (F_3=24.3, $p<0.001$). No consecutive pairwise tests between disturbance types were undertaken. Generally, the presence of larger trees decreased from primary forests towards more heavily and more recently disturbed sites. Primary sites of Danum Valley and Sepilok were similar (Fig. 5).

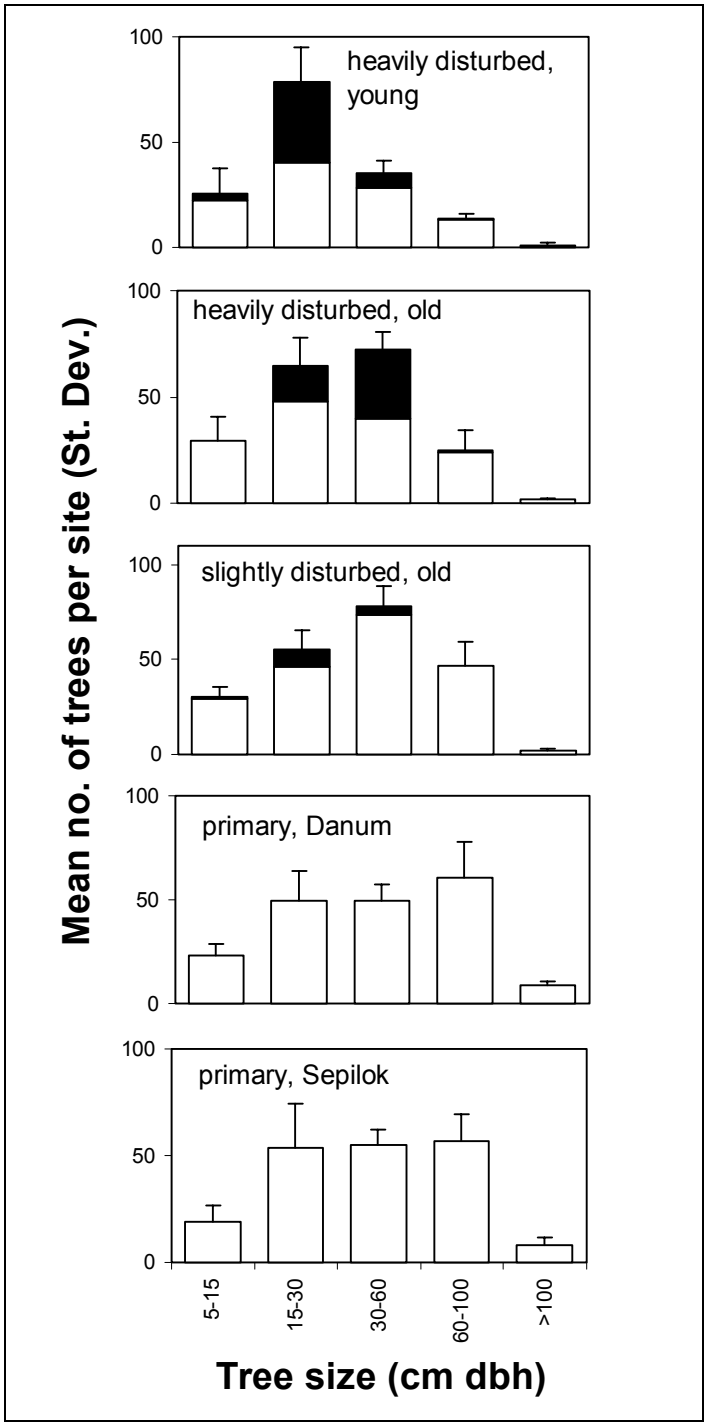

Fig. 5 Tree diameter distribution in primary and logged forest sites measured by angle-count sampling along transect grids. Black sections of bars represent the pioneer genus *Macaranga*. All disturbed sites were in Deramakot Forest Reserve and are grouped by logging history. See text for further specifications and statistics.

3 BACKGROUND STUDIES: FOOD RESOURCES AND NESTING OF STINGLESS BEES IN SABAH

3.1 Pollen foraging and resource partitioning of stingless bees in relation to flowering dynamics in a Southeast Asian tropical rainforest

(T. Eltz, C. A. Brühl, S. van der Kaars, Chey V. K. and K. E. Linsenmair, in press)

3.1.1 Introduction

Stingless bees (Apidae, Meliponini) live socially in perennial colonies of a few hundred up to several thousands of individuals (Wille, 1983). They are generally polylectic and forage on an array of food plants that provide some pollen and nectar over much of the year rather than being highly specialized flower visitors. On the population level some species are known to use floral resources from more than a hundred plant taxa over the course of several seasons in a given habitat (Wilms et al., 1996). Niche overlap between different stingless bee species was frequently found to be high in studies of flower visitation, although some selectivity has been reported, at least on the sub-tribal level (Heithaus, 1979; Ramalho, 1990; Wilms et al., 1996). Results from a study in Sarawak, Malaysia, using a canopy access system suggest that resource partitioning between species may be mediated by interspecific differences in foraging stratum preferences (Nagamitsu et al., 1999).

The analysis of colony pollen stores or forager pollen loads has proven to be a useful tool in assessing bee diet as it is independent of flower accessibility and allows for equally high resolution in the forest canopy and understory (Engel and Dingemans-Bakels, 1980; Sommeijer et al., 1983; Ramalho et al, 1989; Nagamitsu et al., 1999). Sommeijer et al. (1983) studied pollen loads of homing foragers of stingless bees in farmland in Trinidad and found that the variability of pollen spectra was greater between two species of *Melipona* than between colonies of the same species. Nagamitsu et al. (1999) found quite pronounced seasonal fluctuations of the between-species similarity of pollen diets of five species of stingless bees and speculated that the amount of resource partitioning may be related to general pollen resource availability. To our knowledge there has been no study so far that has linked pollen foraging and resource partitioning to floral resource availability in the habitat.

We report on our findings from a study on three closely related species of Southeast Asian *Trigona (Tetragonula)*. The study took advantage of the specific spatial arrangement of two aggregations of bee nests at our study site as well as of the continuous increase of flowering activity in the habitat during the course of the field season. We asked the following questions:

1. Is there species specificity of both qualitative and quantitative aspects of pollen resource diversity?

2. What is the relationship between flowering activity in the habitat and (i), the diversity of foraged pollen, and (ii), pollen resource overlap between colonies and species?

3.1.2 Material and Methods

Study site

The study was carried out in the Deramakot Forest Reserve (site A, Fig. 3) in central Sabah, Malaysia, northern Borneo (117°30‘ E, 5°19‘ N). The commercial forest reserve is covered by still large areas of old-growth (25 years since last major disturbance) slightly disturbed lowland mixed dipterocarp forest (*Parashorea tomentella/Eusideroxylon zwageri* type)(Chai and Amin, 1994). The climate is normally only slightly seasonal with reduced rainfall in March and April, but in early 1998 was heavily influenced by the onset of the local effect of the Pacific El Nino event that resulted in an exceptional dry spell in the whole of Southeast Asia. The particular flowering phenology observed during the study period from March until May 1998 was probably caused in part by this exceptional dry spell (see results).

Bees and bee nests

The study took advantage of the species composition and spatial arrangement of two aggregations of nests (see Fig. 6a): One (monospecific) aggregation consisted of three nests of *Trigona (Tetragonula) collina* Smith that were situated underneath the base of two large trees growing in close proximity (less than 5 m apart. The other (mixed) aggregation consisted of one nest of each of the following three species: *T. (Tetr.) collina*, *T. (Tetr.) melanocephala* Gribodo, *T. (Tetr.) melina* Gribodo. These nests were also situated underneath two large trees that were in close proximity (less than 30 m apart). The two aggregations were located in old logged-over forest at a distance of approximately 250 m from each other. Due to the close proximity of the nests it was guaranteed that the colonies of each of the aggregations had widely overlapping foraging ranges and, at least potentially, were able to use overlapping sets

of flowering plants. The species are small to medium-sized stingless bees that do not seem to exhibit any obvious morphological differences potentially related to pollen foraging. *T. collina* is the largest species (head width ~ 2.3 mm) followed by *T. melina* (~ 2,1 mm) and *T. melanocephala* (~ 2.0 mm).

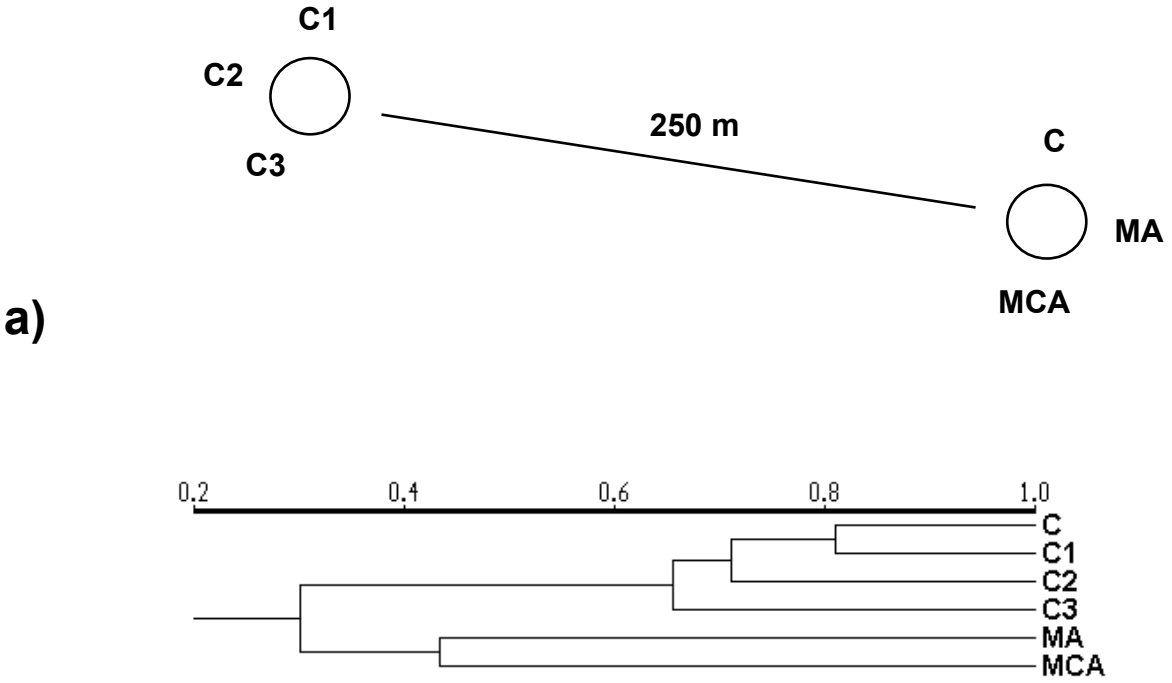

Fig. 6 (a) Schematic view of the relative position of nests of two aggregations of stingless bees. The first aggregation is monospecific and consists of three colonies of *T. collina* (C 1-3), the second is mixed and has one colony of each of the three species: *T. collina* (C), *T. melina* (MA), and *T. melanocephala* (MCA). (b) Dendrogram based on qualitative similarity of all pollen types present in all samples of the respective colony over the entire study period. Distances are Sørensen-Index, clustering was done with UPGMA.

Flowering phenology

In an attempt to quantify the floral resource availability in the habitat we repeatedly ran a 2 km flower phenology transect that criss-crossed through the bees‘ nesting area. We counted all flowering woody plants visible from the transect and collected specimens to assess species diversity. In the case of large trees binoculars were used for the confirmation of the presence of flowers and decayed flowers were collected from the forest floor. Assessment of flowering

activity normally took place immediately following pollen sampling. Due to its limited scope and lack of canopy access the transect was likely to miss much of the actual flowering in the area. Therefore, the results should be regarded as an index of flowering intensity and diversity rather than a detailed survey of potential bee resources.

Pollen samples

Returning pollen foragers were captured at the nest entrances using a hand-held exhaustor. For any given date pooled 20-forager samples were collected from each colony between 6:30 and 12:30 depending on weather conditions and foraging activity. Repeated samples were taken on six consecutive points in time during March, April, and May 1998 (12/13.3., 18.3., 1.4., 16./17.4., 29.4., and 7.5.). On 2.2., 17.2., 17.4., 8.5., and 9.5. we additionally collected individual samples from all three species (N=53 for *T. collina*, N=28 (*T. melina*), and N=21 (*T. melanocephala*)) in order to assess individual within-foraging trip resource use.

Pollen treatment and analysis

Standard palynological protocols (KOH digestion, acetolysis, glycerin jelly mounting) were followed for slide making. The slides were then analyzed in a standardized way. First, the core area of each slide was thoroughly searched for pollen types and types were characterized by size, shape, number and shape of the apertures, and ornamentation. High resolution light micrographs were made from polar and equatorial views of all pollen types. For quantitative analysis pollen grains of all types encountered repeatedly in the core area were then counted within the boundaries of 14 quadrants situated along a transect across the cover slip. Particularly abundant grains were counted in the smaller subunits of various (suitable) sizes of the same quadrants and counts of all types were finally transformed into per-area densities. Density data were consecutively transformed into per-slide percentages for each pollen type by multiplying the densities with a type-specific volume correction factor inferred from size and shape of the respective grains. Grains represented with less than 0.5 volume-% were considered as contaminations and omitted from further analysis. Using this area- and volume-based approach allowed for a sufficiently high level of standardization between samples without the tedious task of counting thousands of minute grains situated among small numbers of giants (Biesmeijer and Sommeijer, 1992).

Taxonomic identifications of types to the level of plant family, genus or species (or taxonomic ‘type’) wherever possible were done from micrographs by S. v. d. Kaars (see Appendix 1).

To describe pollen type diversity of samples we used simple pollen type richness (number of types per sample) as well as Shannons J' (Pielou 1966), a measure of the evenness of the quantitative representation of types in a sample. Effects of colony and time on sample richness and evenness were analyzed using ANCOVA with time as a covariate.

Between-sample similarity was calculated as the qualitative Sørensen-index that ranges between 1 (identical) and 0 (no match)(Magurran 1988). For the comparison of within-aggregation similarity of samples in relation to time we selected a focal colony in each aggregation (in case of the mixed aggregation it was the *collina*-colony C) and calculated Sørensen-values between the focal colony and the two other colonies for each point in time. Means were used for Linear Regression Analysis with time as the independent variable.

3.1.3 Results

Individual pollen loads

Individual bees of all three species seemed to be highly constant pollen foragers. Samples were defined as pure if more than 95 volume-% of the sample consisted of the same pollen type. Based on this definition, all but two loads (from 102) were found to be pure, and even higher purity standards (e.g. 98 volume-%) would not significantly alter that result. Thus, the presence of a range of different pollen types in the pooled samples of a given colony described below is largely a result of different foragers specializing (at least temporarily) in different pollen plants.

Total between-colony similarity

A total of 74 different pollen types were recorded (see Appendix 1) in the pooled samples of all six stingless bee colonies, with the number of types being almost identical for all *T. collina* colonies (20 to 26) and *T. melanocephala* (25), and being slightly higher in *T. melina* (32). Fig. 6b shows the results of a cluster analysis that was done on a qualitative presence/absence matrix (74 pollen types x 6 colonies) pooling all samples for each colony. It is evident that intraspecific similarity is much greater than interspecific similarity. The *collina*-nest C that is situated within the distant mixed aggregation is actually nested within the cluster of the three other *collina*-colonies.

Within-sample pollen diversity

At a given point in time 20-forager samples contained between 2 and 10 different types above the 0.5%-volume threshold. Table 1 summarizes the results of within sample diversity of pollen sources for all colonies. Between colonies there was significant variation in the number of pollen types per sample (N=36; df=5; F=3.15; $p<0.05$), a result that was almost entirely based on the slightly elevated numbers in the *T. melina* colony. No differences were apparent between different colonies of *T. collina*. There was no between-colony effect on the evenness of pollen type representation (F=1.11; N.S.). Generally, the rank-predominance distributions of samples of different colonies were similar (Fig. 7).

Table 1 Summary of pollen analysis of 20-forager samples (N=6) of six colonies of stingless bees.

	Mean no. pollen types/20 bees (std. deviation)	Mean eveness (J´) of volume distribution (std. deviation)	Total no. of pollen types
T. collina (**C1**)	4.67 (2.34)	0.61 (0.29)	20
T. collina (**C2**)	5.67 (2.25)	0.70 (0.18)	24
T. collina (**C3**)	5.34 (1.51)	0.60 (0.28)	26
T. collina (**C**)	5.83 (1.60)	0.77 (0.13)	22
T. melina (**MA**)	8.50 (1.05)	0.55 (0.18)	35
T. melanocephala (**MCA**)	6.67 (1.63)	0.69 (0.05)	25

Flowering activity and pollen diversity

Both species diversity and abundance of blooming plants significantly increased during the study period (Linear Regression with time as independent variable; species diversity: $R^2=0.86$, F=31.86, $p<0.01$; number of individuals: $R^2=0.68$, F=11.84, $p<0.05$)(Fig. 8d). This confirms our impression of a continuously increasing flowering activity accompanying the severe dry spell that was experienced by the whole Deramakot area from February until May 1998. Flowering involved all strata of the forest and finally, in the end of April, turned into a minor mass flowering event including several species of Dipterocarpaceae. This finding is contrasted with the lack of any change in the number of pollen types per sample over time

(R^2=0.030; F=0.895; N.S)(Fig. 8a). There was, however, an slight increase of sample evenness (R^2=0.179; F=6.33; $p<0.05$).

Within the two aggregations the similarity of pollen samples showed a strikingly different pattern over time. Whereas similarity significantly increased over time within the monospecific *collina*-aggregation (R^2=0.90; F=35.18; $p<0.01$)(Fig. 8b), there was no change of similarity at all between colonies in the mixed aggregation (R^2=0.005; F=0.02; p=0.90)(Fig. 8c).

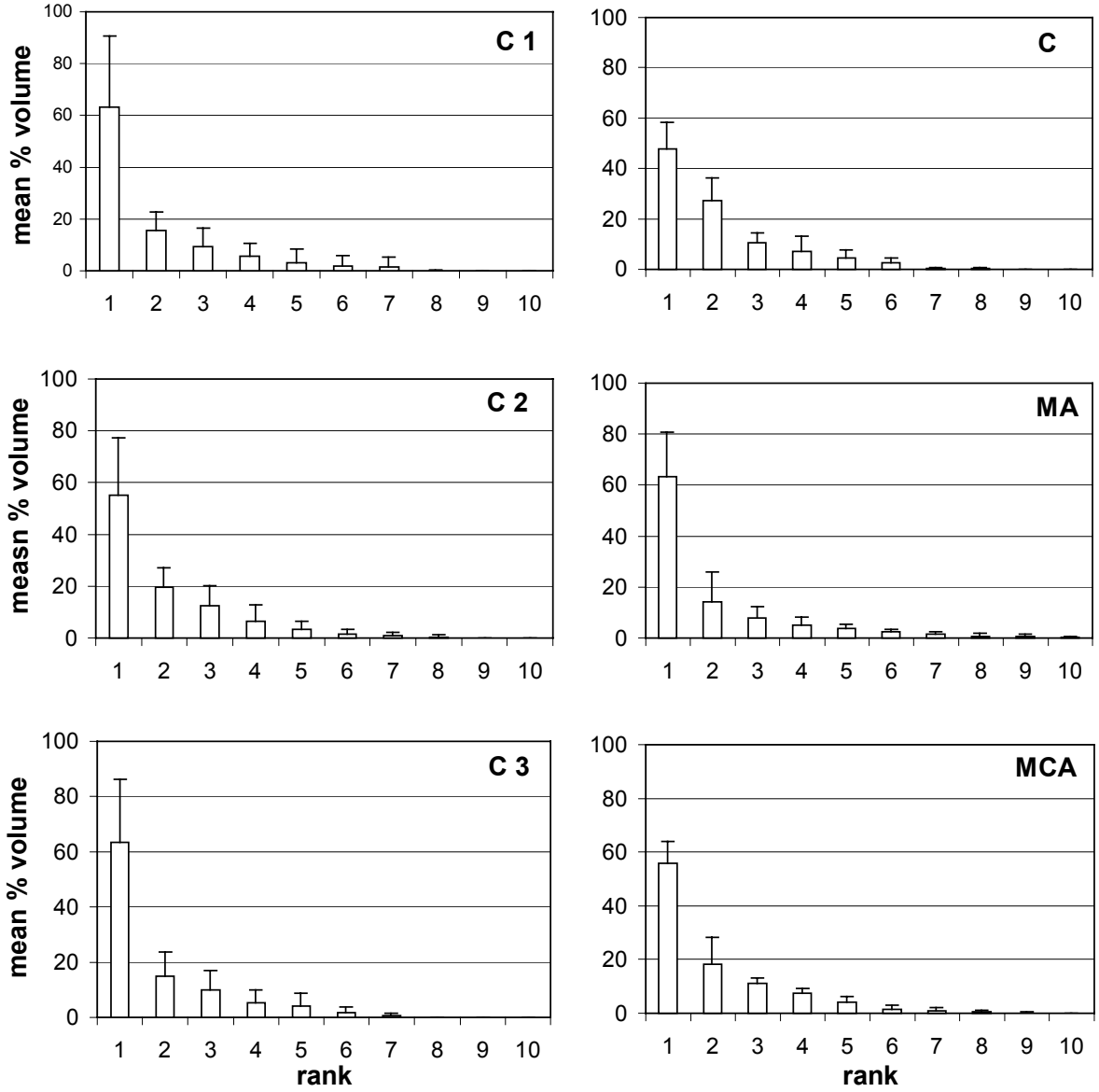

Fig. 7 Mean rank-predominance distribution of volume-representation of pollen types in 20-forager samples of six colonies of stingless bees belonging to three different species: *T. collina* (C, C1-3), *T. melina* (MA), and *T. melanocephala* (MCA). Error bars are standard deviations

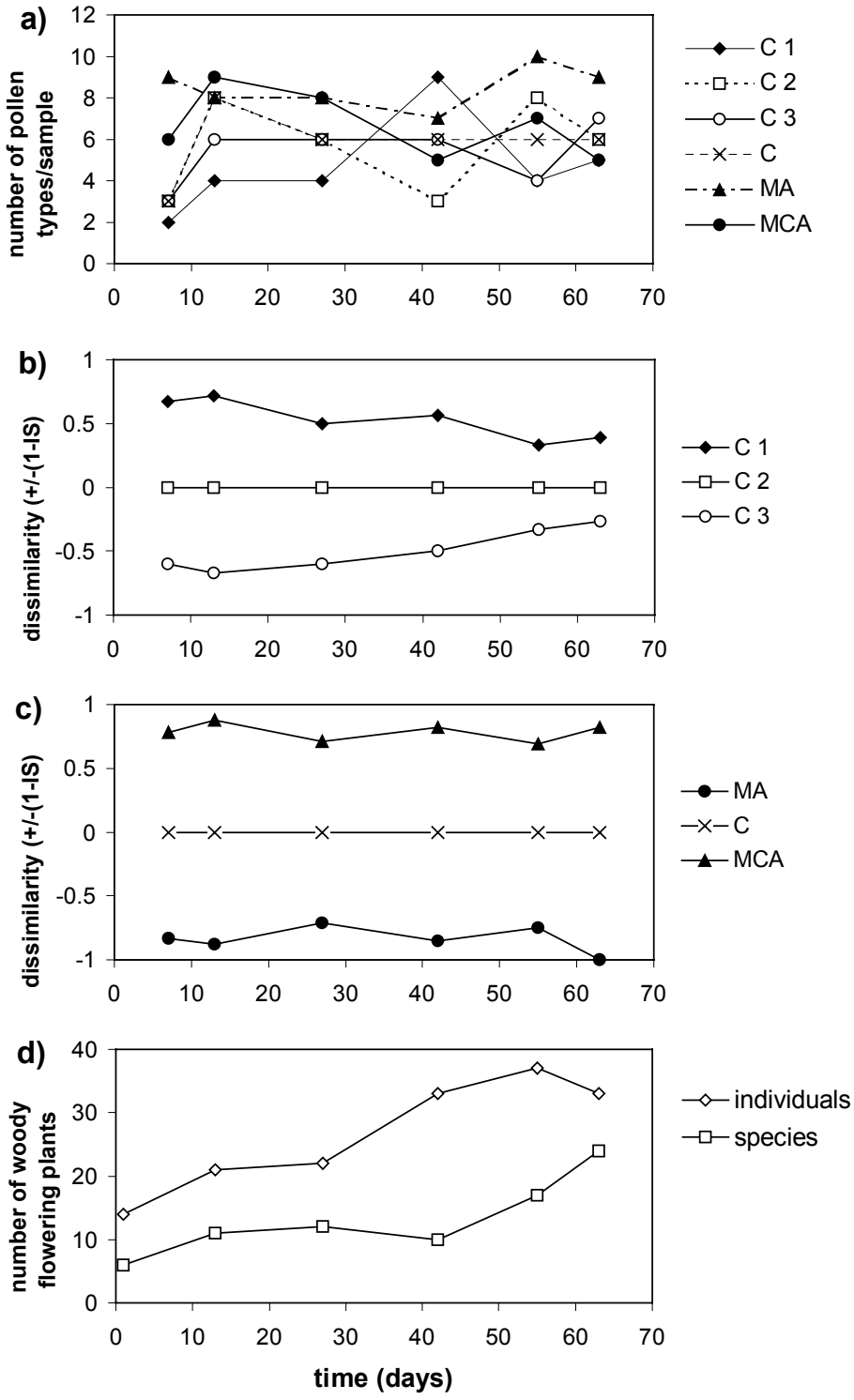

Fig. 8 (a) Pollen type richness of samples between March and May 1998 from different colonies of stingless bees (C=*T. collina* (4 colonies); MA=*T. melina*; MCA=*T. melanocephala*), (b) dissimilarity of pollen samples within the monospecific *collina*-aggregation over time (dissimilarity is calculated as (1-Sørensen-Index) and plotted as positive and negative deviation from 0 (focal colony), (c) dissimilarity of pollen samples within the mixed aggregation, and (d) flowering activity as a function of time in the habitat.

3.1.4 Discussion

Specificity of pollen sources

Our results suggest that some species specificity exists in pollen plant preferences of the *Trigona (Tetragonula)* species investigated. Judged by their pollen source plants all four colonies of *T. collina* were clustered according to their species rather than their spatial location and were clearly distinct from those of the colonies of *T. melanocephala* and *T. melina*. Our findings add strength to the view that some floral resource partitioning occurs even between closely related species of social bees in tropical habitats (Sommeijer et al., 1983; Nagamitsu et al. 1999).

We can only speculate on the proximate causes of diverging floral preferences of the species investigated. As there seem to be no significant distinguishing morphological features that might lead to differential patterns of pollen collection between species, the causes are likely to be found in the context of flower search behavior and/or foraging strategy. Johnson (1983) distinguished solitary and group foragers among neotropical species of stingless bees, with solitarily foraging species exploiting resources scattered in space and time whereas group foragers concentrate on rich and clumped resources. These are only extremes of a range of strategies that are further specified through interspecific differences in aggressiveness and speed of recruitment (Johnson and Hubbell, 1975; Johnson, 1983). In our study the rather uniform rank-predominance distributions of pollen sources of all three species suggest that there are no drastic differences between species concerning diversity and degree of clumping of food patches. At any time, even during times of high flowering activity, the colonies were foraging on a relatively broad array of pollen plants, a finding that does not plead for the existence of an effective mass recruitment system like those present in other Meliponines (Hubbell and Johnson, 1978; Johnson, 1983). Possible interspecific differences in foraging behavior are revealed by studies using artificial feeder experiments (Nagamitsu and Inoue, 1997). In their study the authors report that *T. melanocephala* is relatively quick to arrive at fresh honey baits, whereas *T. melina* is significantly slower, and *T. collina* is generally reluctant to visit baits at all (Nagamitsu and Inoue, 1997). The speed of detecting new food resources may thus affect the choice of pollen sources.

Part of the differences in pollen sources between the species may result from foraging stratum preferences. Nagamitsu et al. (1999) studied flower visitation of 11 stingless bees in a rainforest in Sarawak with the help of a canopy observation system. Their findings suggest

that, in contrast to all other species, *T. melanocephala* is foraging predominantly in the understory. Feeder experiments seem to confirm this view (Nagamitsu and Inoue, 1997). Our own results are difficult to interpret in this respect because most pollen identifications are not accurate enough to allow deduction of plant stratum. Typical understory taxa as Palmae are indeed present in *T. melanocephala*, but occur even more frequently in *T. melina*. On the other hand, the pollen diet of *T. melanocephala* also includes typical canopy taxa like Dipterocarpaceae and Bombacaceae (see Appendix 1), suggesting that possible stratum preferences are not exclusive.

Pollen foraging and general resource availability

Floral resource availability of bees is difficult to quantify in natural forest habitats due to the difficulty of judging the relative importance of certain flowering plant species to the bees in question. Acknowledging this we are nonetheless confident that our approach of relating general flowering activity to bee foraging is justified because (i) the bee species in question did obviously use a broad range of flowering plants, and (ii) because the evident increase of flowering equally concerned both abundance and diversity of woody plants in all strata of the forest. Thus, it seems justified to assume that pollen resource availability in the habitat did indeed vary accordingly for the three bee species.

In our study pollen resource overlap between colonies, conspecific or not, was generally low at the beginning of the study period when floral resources were scarce. Much of this effect is probably due to extrinsic factors such as a highly scattered distribution of food patches at the time. If flower patches are at low density in the habitat foragers will have to cover long distances to find them. The larger the diameter of the foraging range, the more likely are foraging bees from different colonies to forage at different sets of patches. In many cases this will also lead to exploitation of different plant taxa. This may explain why intra- and interspecific similarities of pollen diets were almost equally low at times of low food availability.

When resources became more available, however, foraging bees were probably capable of exerting significantly more active choice concerning their pollen diet. According to optimal foraging theory foragers are expected to consecutively drop non-profitable food items/patches from their diet in favor of more profitable ones (MacArthur and Pianka, 1966). In case of the conspecific colonies of *T. collina* this potential for choice may have led to the observed increase of pollen diet similarity as foragers settled on a selection of highly profitable and

nearby flower patches. The same scenario is likely to have applied for the mixed aggregation as well, but with a somewhat different outcome. Here, innate differences in foraging preferences or floral choice (e.g. stratum preferences, color preferences, etc.) between species seem to have counteracted any effect of diet convergence.

In contrast to Nagamitsu et al. (1999) we did not find occasional sharp increases in diet overlap between different species, a difference that is likely to be related to the particular flowering characteristics present at the time and location of the respective studies. In our case, flowering diversity increased together with general flowering activity, thus creating a multitude of profitable foraging opportunities for bees to choose from. In a flowering situation that is more heavily biased in favor of one or a few overabundant plant taxa, diet overlap between bee species is bound to be more pronounced.

Appendix 1 Pollen types represented by more than 0,5 volume-% in 20-forager samples of six colonies of stingless bees of three species: *T. collina* (C 1-3, C), *T. melina* (MA), and *T. melanocephala* (MCA).

.	apertures	family	genus/type	C 1	C 2	C 3	C	MA	MCA
1	inaperturate	Euphorbiaceae	*Croton* type					x	
2	inaperturate	Euphorbiaceae	*Croton* type	x	x		x	x	x
3	inaperturate	Hernandiaceae			x				
4	inaperturate, tetrade	Mimosaceae	*Mimosa pudica* type	x		x	x		
5	inaperturate, polyade	Mimosaceae	*Accacia/Albizia* type			x			
6	inaperturate, tetrade			x	x	x	x		
7	inaperturate			x		x	x		
8	monocolpate	Palmae	*Cocos nucifera* type					x	x
9	monocolpate	Palmae	*Eugeissona* type					x	
10	monocolpate	Palmae ?						x	
11	monoporate	Palmae ?						x	
12	monocolpate							x	
13	monocolporate				x			x	x
14	monoporate	Pandanaceae	*Pandanus*					x	
15	monoporate	Typhaceae	*Typha* type					x	
16	dizonoporate	Moraceae						x	x
17	triaperturate	Passifloraceae		x	x	x	x		
18	triaperturate	Passifloraceae	*Passiflora*					x	
19	triaperturate	Passifloraceae	*Passiflora*	x	x	x	x	x	
20	trizonocolpate	Convolvulaceae	Merremia type						x
21	trizonocolpate	Dipterocarpaceae	*Shorea* type	x	x	x	x		x
22	trizonocolpate	Thecaceae		x	x	x	x		x
23	trizonocolpate				x	x	x		
24	trizonocolpate				x				
25	trizonocolporate	Anacardiaceae		x	x	x	x	x	x
26	trizonocolporate	Anacardiaceae				x			
27	trizonocolporate	Bombacaceae		x	x	x	x	x	x
28	trizonocolporate	Bombacaceae		x	x	x			
29	trizonocolporate	Bombacaceae						x	
30	trizonocolporate	Bombacaceae						x	
31	trizonocolporate	Bombacaceae		x		x	x		
32	trizonocolporate	Bombacaceae		x	x	x	x	x	
33	trizonocolporate	Euphorbiaceae	*Macaranga* type					x	
34	trizonocolporate	Euphorbiaceae	*Blumeodendron* type	x	x				
35	trizonocolporate	Euphorbiaceae	*Blumeodendron* type					x	x
36	trizonocolporate	Guttiferae	*Antidesma* type ?					x	
37	trizonocolporate	Leguminosae		x	x	x	x		
38	trizonocolporate	Leguminosae ?						x	
39	trizonocolporate	Loranthaceae							x
40	trizonocolporate	Rubiaceae		x	x	x	x	x	x
41	trizonocolporate	Rubiaceae ?				x			
42	trizonocolporate	Rubiaceae ?	*Ixora* ?						x
43	trizonocolporate	Sanzaniaceae ?	*Sanzania* ?						x
44	trizonocolporate	Sapindaceae ?						x	
45	trizonocolporate					x			
46	trizonocolporate							x	
47	trizonocolporate			x	x		x	x	x
48	trizonocolporate				x				
49	trizonocolporate							x	x
50	trizonocolporate								x
51	trizonocolporate							x	
52	trizonocolporate							x	x
53	trizonocolporate								x
54	trizonocolporate					x			
55	trizonocolporate				x				
56	trizonocolporate				x				
57	trizonocolporate			x	x	x	x	x	x
58	trizonocolporate								x
59	trizonocolporate			x		x			
60	trizonocolporate			x	x	x	x		
61	trizonocolporate								x
62	trizonocolporate						x		
63	trizonoporate	Loganiaceae	*Fagraea*				x		
64	trizonoporate	Loganiaceae ?	*Fagraea* ?			x			
65	trizonoporate	Moraceae						x	
66	trizonoporate	Sterculiaceae	*Pterospermum* type ?			x			
67	trizonosyncolporate	Myrthaceae	*Eugenia*					x	
68	tetrazonocolporate	Rutaceae			x		x		
69	tetrazonocolporate	Sapotaceae/Meliaceae					x	x	
70	tetrazonocolporate	Sapotaceae/Meliaceae						x	
71	tetrazonocolporate	Sapotaceae/Meliaceae							x
72	octozonocolporate	Polygalaceae	*Xanthophyllum* type						x
73	polypantoporate	Malvaceae	*Hibiscus* type			x			
74	?-aperturate							x	x

3.2 Collection of mold (*Rhizopus sp.*) spores in lieu of pollen by the stingless bee *Trigona (Tetragonula) collina* (T. Eltz, C. A. Brühl & C. Görke, submitted)

Pollen is the principal source of nitrogen for most bees and is normally collected in quantities in order to provision brood cells. The occasional collection of fungal spores in lieu of pollen has been reported in a fair number of cases all over the world. The fungi concerned were either rust fungi (Basidiomycota), powdery mildews or members of *Neurospora* (Ascomycota), whereas the bees collecting the spores were exclusively honeybees of the genus *Apis* (Shaw & Robertson, 1980; Wingfield et al., 1989; Shaw, 1990 and references therein). Data on the performance of brood raised on fungal spores is scant and it remains controversial whether the bees actually benefit from spore collection. In some cases, however, the sheer quantity of spores collected as well as the fact that spore collection takes place over considerable periods of time suggests that some nutritional benefit is likely to be obtained (Shaw 1990).

Here we report on observations made on homing foragers of the stingless bee *Trigona (Tetragonula) collina* (Apidae: Meliponini) in lowland rain forest in Sabah, Malaysia. Our findings are notable in two respects: first, they involve the first case of fungal spore collection of bees other than honeybees, and second, the source fungus is a mold of the Zygomycota (Mucorales) that, to our knowledge, have never been shown to be of interest to foraging bees.

Our observations were made in the context of a study aimed at assessing pollen diets of six colonies of meliponines belonging to three species (*T. collina* (4 colonies), *T. melina* (1), *T. melanocephala* (2)) in selectively logged forest in Deramakot Forest Reserve (Eltz et al., in press-a; see section 3.1). To assess pollen diets we took repeated biweekly samples of corbicular loads of 20 homing foragers between March and May 1998. For this purpose we briefly closed the nest entrances and captured pollen foragers with the help of hand-held exhaustors. When collecting samples on May 7 we noted that substantial numbers of foragers of three of the four colonies of *T. collina* were carrying large loads of a fluffy black smear that could easily be distinguished from 'regular' pollen loads that were more compact and either white, yellow or orange. On May 7 12,5%, 25%, and 50% of the collected samples were of the black type for the three different colonies of *T. collina*. Although no quantitative

observations were made, the continued collection of the black smear was confirmed for all three colonies on the two following days.

Microscopic analysis showed that the loads were almost pure samples of globular, partly elongate spores that were characterized by a distinctly striate ornamentation and variable size of 7 to 18 microns (Fig. 9). Samples were frozen and finally transported to the Mycology laboratory at Tübingen. Here the spores were transferred to MA-medium (Gams et al., 1987). Germination was followed by growth of mycelium and finally the production of sporangia. The culture was identified to genus level by the shape of its stolones and rhizoids as well as by the characteristic striate ornamentation of the sporangiospores (Zycha et al., 1969). Spore morphology of the culture was identical to that of the spores in corbicular load samples taken from the bees.

Rhizopus sp. are mostly saprophytic molds on a wide range of substrates such as feces and decaying parts of animals and plants (Domsch et al., 1980). Among other fungi they have also been found to spoil provisions in brood cells of soil nesting bees and are suspected to cause some mortality among brood (Lindsley & MacSwain, 1952; Batra et al., 1973). This effect, however, is mostly associated with bees ground-nesting in moist substrate, whereas mold-caused mortality of brood is apparently rare in honeybees (Batra et al, 1973). Unfortunately, we have no data on the fate of the mold spores within the colonies of *T. collina*. No detrimental effect was evident, however, and all colonies were alive and populous one and two years after the observations were made. Thus, it is likely that the spores were mixed with pollen reserves within the colony and, at least partly, introduced into the intra-colony flow of liquid food (Sommeijer et al, 1985). Generally, bees possess various potential defenses against microbial infections including cephalic gland secretions, chemicals of nest materials, and possibly colony thermoregulation (Cane et al., 1983; Seeley, 1985).

Several authors have speculated on the benefits of fungal spore collection for bees. Protein content of spores seems low in comparison to pollen (Shaw 1990), but spores may warrant harvesting simply because they are available in huge quantities (Kempf-Mercado 1955, Shaw 1990). Unfortunately, we could not locate the source of the mold spores collected by *T. collina* in our study. However, we speculate that spore collection was indeed related to mass-production of fungal spores triggered by flowering phenology. At the time of our observations the entire study area experienced a heavy dry spell that was accompanied by a regional mass flowering event that involved all strata of the forest and included many canopy trees (Eltz et al., in press-a; section 3.1). Thus, mold spore collection took place at a time when large

amounts of deceased petals and flower parts were accumulating on the forest floor. Stingless bees can be observed to continue foraging from flowers dropped on the ground (T. Eltz, pers. obs.) and may thus have come in contact with sporangia of *Rhizopus* growing on the decaying flower material. If this scenario is correct, spore-collection may have been favored initially by regular pollen collection from the same site.

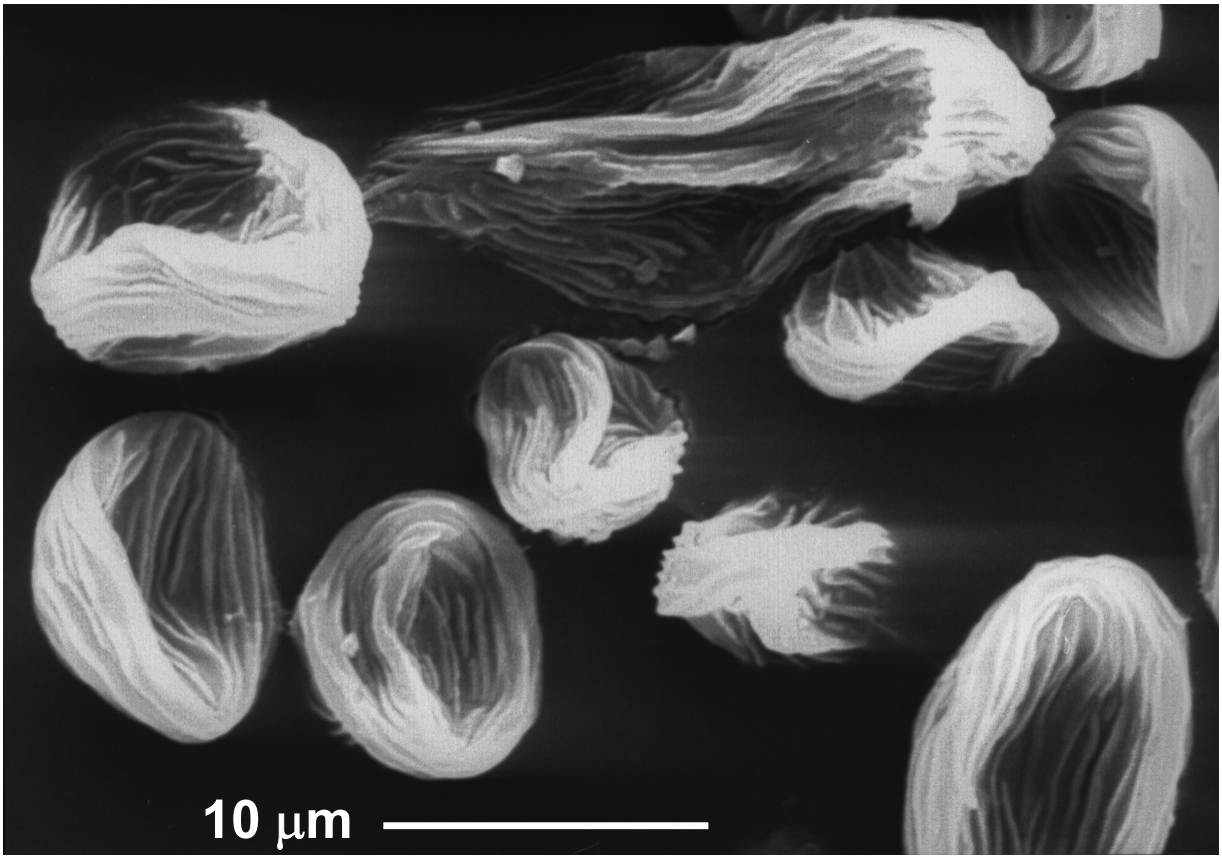

Fig. 9 Scanning Electron Micrograph of *Rhizopus* sp. spores taken from corbicular loads of homing *Trigona collina* workers in Deramakot Forest Reserve, Sabah, Malaysia. The material was dried at room temperature.

3.3 **Assessing stingless bee pollen diet by analysis of garbage pellets: a new method** (T. Eltz, C. A. Brühl, S. van der Kaars and K. E. Linsenmair, in press)

3.3.1 Introduction

Pollen is the principal source of nitrogen for most stingless bees and is collected in large quantities by workers for provisioning brood cells or storage in colony pollen pots (Roubik, 1989). Palynological methods allow detailed analyses of pollen samples (Biesmeijer and Sommeijer, 1992), and pollen diets of stingless bee colonies have been investigated in several studies of floral resource use and partitioning (Engel and Dingemans-Bakels, 1980; Sommeijer et al., 1983; Absy et al., 1984; Appanah et al., 1986; Roubik et al., 1986; Ramalho et al., 1989; Lobreau-Callen et al, 1990; Ramalho, 1990; Nagamitsu et al., 1999; Roubik and Moreno, 2000; Eltz et al. in press-a). To obtain pollen samples these authors either directly collected corbicular pollen from incoming workers or, more frequently, extracted pollen from colony storage pots or deposits in the nest. Whereas the first method is generally time-consuming and requires frequent sampling, the second often suffers from lack of accessible colonies. Therefore, low or unequal sample size and/or lack of sufficient colony replicates has been a problem of studies of stingless bee pollen diet.

Alternative methods of sample acquisition are required that can be applied to reasonable numbers of wild colonies of bees. Unfortunately, permanent pollen traps similar to those used for honeybees (Imdorf, 1983; Imdorf and Wille, 1983) are of little use in case of meliponines due to their tendency to use resin to obstruct any device imposed on their nest entrances. Many stingless bees, however, expel from their nests small parcels of garbage that have been reported to contain larval feces (Roubik, 1989; D. W. Roubik, pers. comm.). This garbage, potentially rich in pollen exines, is either directly dropped from the nest entrance or, more frequently, scattered in the vicinity of the nest by airborne workers (Roubik, 1989; T. Eltz, pers. obs.). It is the aim of this article to (i) introduce an efficient way of trapping garbage from wild colonies of stingless bees in Malaysia, and (ii) to investigate whether and how pollen obtained from garbage samples can be used to indicate bee pollen diet.

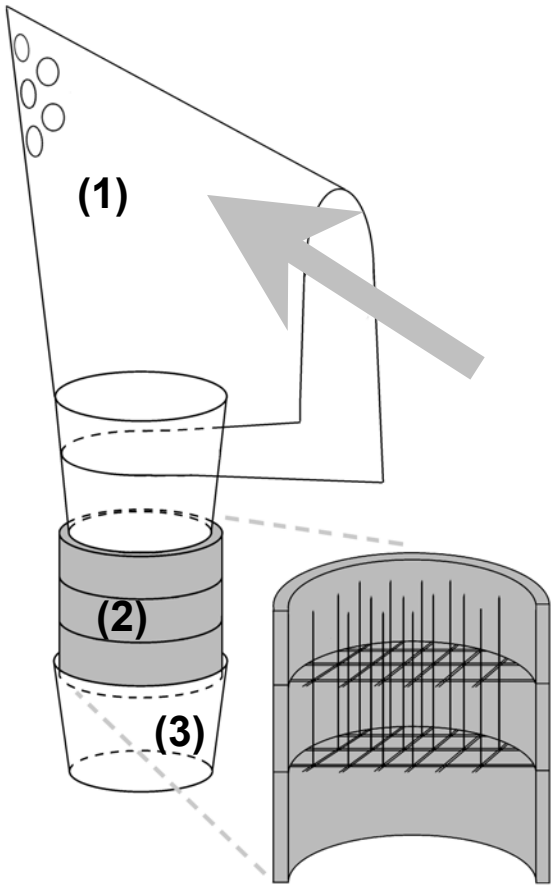

Fig. 10 Schematic view of the garbage trap: (1) Transparent funnel made from clear DIN A4 overhead transparency, (2) garbage sieve (grey) that consists of a dense array of household pins suspended in PVC tubing by a double layer of nylon mesh (mesh width ~ 0,5 cm), and (3) sampling jar. The trap is placed in front of the nest entrance and exiting bees enter the funnel as indicated by the arrow. Bees can escape from the funnel through punctures in the tip (diameter ~3 mm) unless carrying garbage pellets (see text for further specifications).

3.3.2 Materials and Methods

Bee garbage were collected from stingless bee nests situated in the bases of large trees in lowland mixed-dipterocarp forest in Sabah, Malaysia. Our study focused on *Trigona (Tetragonula) collina*, an abundant, medium-sized species in the study area. Unless stated otherwise, all information given concerns this species.

The garbage trap

Garbage pellets were sampled using funnel traps that were installed in front of nest entrances. Traps consisted of (i) a transparent funnel, (ii) a garbage sieve made of pins suspended by a double layer of nylon mesh within a PVC tube, and (iii) a sampling jar (Fig. 10). Bees exiting

the nest inevitably enter the transparent funnel, crawl towards the tip guided by increasing light levels and finally leave the funnel through one of a series of holes (diameter ~ 3 mm) punched into the tip area. In the case of bees carrying garbage pellets in their mandibles, the holes were too small to serve as escape routes and the bees instead sought to circumvent the trap. In attempting to do so, most of the individuals sooner or later fell onto the pin cushion of the garbage sieve and, unable to comfortably walk on the spaced pins (distance ~ 0,5 cm), released their garbage loads. The pellets dropped through the sieve and into the sampling jar. In the course of one day a trap collected between a dozen and several hundred garbage pellets, depending on colony size and status (T. Eltz, pers obs.). In our study pellets were placed singly or in tens (pooled samples) in Eppendorf cups and frozen until further analysis.

Macroscopic examination

For general description garbage pellet contents were first studied by dissecting single pellets (dissolved in water or 70% EtOH) under a stereomicroscope. In addition to pellets from *T. collina* we also examined samples obtained from colonies of the following species: *T. (Tetr.) melanocephala*, *T. (Tetr.) melina*, *T. (Lepidotrigona) terminata*, and *T. (Tetrigona) binghami*.

Pollen content

In order to obtain a quantitative estimation of total pollen content of pellets, we used acetolysis for pollen concentration. Twelve pooled samples of ten pellets each, collected from twelve different colonies of *T. collina* were dried for 24 h at 60°C, weighed, and consecutively acetolysed (Moore et al., 1991). Acetolysis removes all but the chemically most resistant components and reduces garbage pellets to sediments of almost pure pollen exines. The proportional weight of the treated sample (after drying, in %) can therefore be used as a conservative but standardized measure of garbage pollen content.

Microscopic pollen analysis

For a more detailed analysis of pollen type composition of garbage of *T. collina* we investigated the following sets of samples:

Single-pellet garbage samples taken from two colonies (colony A and B) at Deramakot Forest Reserve at three consecutive points in time separated by approximately three weeks (10 single-pellet samples for each colony on each of April 10, May 2, and May 25 in 1999). The colonies were located in logged-over forest at two different sites separated by 8 km and

almost certainly had non-overlapping flight ranges (see van Nieuwstadt and Ruano Iraheta, 1996).

Ten-pellet (pooled) garbage samples taken from one of the colonies (colony B) at four points in time separated by four to six months (one pooled sample in April 1999, September 1999, March 2000, and July 2000).

Ten-pellet (pooled) garbage samples *and* corbicular pollen samples taken from a colony (colony C) at Sepilok Forest Reserve in intervals of 12 days (average) between February 27 and July 23 in 2000. In this case we used a modified version of the trap that maximized sampling of corbicular pollen loads from incoming pollen foragers in addition to outbound garbage pellets. This was achieved by increasing the diameter of the sampling jar in order to capture corbicular pollen that is stripped off worker bees attempting to enter through the punctured funnel from the outside (most of the loads drop off on the outside rather than the inside of the funnel wall). Due to the fact that garbage pellets as well as corbicular pollen loads are quite compacted and stable it was possible to collect both items separately for each consecutive sample. Cross-contamination of pollen between corbicular loads and garbage pellets probably occurs but is considered to be low enough to be eliminated by the 0,5%-volume threshold applied for analysis (see below). All corbicular loads of one sampling day were pooled. Even the modified traps do not normally collect large quantities of corbicular pollen and substantial amounts were obtained only because colony C was exceptionally populous.

Standard palynological protocols (KOH digestion, acetolysis, glycerin jelly mounting) were followed for slide making. The slides were analyzed in a standardized way. First, the core area of each slide was thoroughly searched for pollen types and types were characterized by size, shape, number and shape of the apertures, and ornamentation. Digital images were made from polar and equatorial views of all pollen types and images were entered into a pollen database that served as a working reference. Taxonomic identifications of types to the level of plant family, genus or species (or taxonomic ‘type’) were made from original slides by S. van der Kaars, partly by comparison with reference pollen collected from flowers in the bees’ habitat.

For assessing pollen type representation on a slide we used a volume-based approach similar to Biesmeijer and Sommeijer (1992) that corrects for the huge size differences between different pollen species (the volume and, presumably, the amount of digestible protoplasm

can vary over more than five orders of magnitude). A type-specific volume was assigned to each pollen type based on size and shape of the respective grain (geometric formulas for sphere or elipsoid volume were used for calculations). Grains were then counted in quadrants situated along transects across the center of the slides and counts/type/quadrant were immediately typed into Excel spreadsheets that continuously calculated cumulative volume for each type as well as total volume of pollen counted. In previous tests we had found that sampling a total pollen volume of $6x10^6$ cubic microns per slide would reflect pollen slide diversity with reasonable accuracy (concerning both type diversity and percentage representation). Thus, for standardized comparisons of pollen contents between slides we invariably stopped counting grains as soon as the total volume of grains counted exceeded $6x10^6$ cubic microns. Grains represented with less than 0,5 volume-% were considered as contaminations and omitted from further analysis.

For comparisons of pollen composition between samples we calculated the Steinhaus coefficient S (Legendre and Legendre, 1998), with S=2W/(A+B), where W is the sum of minimum percentages of the various types, and A and B are the sums of the percentages of all types in each of two samples. Note that differences between dominant types reduce S to the same extent as do differences between minor types. For convenience we multiplied S with 100 to present values reflecting *percentage similarity*.

To estimate pollen type saturation in increasing numbers of garbage pellets sampled on a given day we plotted type accumulation curves using the software EstimateS 5.0.1 by Robert K. Colwell.

3.3.3 Results

General description of garbage pellets

Garbage pellets of *T. collina* are dark brown, roughly spherical particles of about 2mm in diameter that have a conglomerate appearance. When dissected in water or EtOH almost all pellets reveal large quantities of pollen grains that make up most of the pellet volume. Other contents include the remains of old brood cells as well as parts of dead bees or parts of bee larvae and pupae. The spherical shape and the compactness of the pellet is maintained by layers and threads of resinuous material that are worked around and into the pellet. Due to these inclusions the garbage pellets are quite stable items that are normally trapped intact and can easily be counted and preserved.

Garbage pellets of *T. melanocephala*, *T. melina*, *T. terminata* and *T. binghami* also contained large quantities of pollen and differed from those of *T. collina* only in respect to pellet size (depending on bee size) and, partly, color.

Pollen content

Mean dry weight of pooled ten-pellet garbage samples was 25.4 mg (+/-4.6 mg; N=12). After acetolysis treatment this was reduced to 5.2 mg (+/- 1.4 mg), thus indicating a content of pure pollen exines of 20.3 % (+/- 1.5 %) of the dry weight. This value certainly underestimates the true pollen content of garbage pellets because acetolysis does dissolve the less resistant parts of pollen grains such as remaining cellular contents, the pollen kit and also parts of the pollen wall (Moore et al., 1991).

Pollen composition of single pellets

Microscopic slides made from garbage samples were very clear, almost devoid of non-pollen material, and invariably showed well preserved and evenly spread assemblages of pollen grains. Single garbage pellets of *T. collina* (colonies A and B) contained between seven and 11 different morphotypes of pollen above the 0,5%-volume threshold (Fig. 11). Volume representations were strongly skewed towards dominant grains, and between 84 and 96% of the sample volume consisted of the four most dominant grains of the sample.

Pellets collected on the same day from one colony were very similar in pollen composition, with mean percentage similarities (S*100) between pairs ranging from 71 to 90 % (mean: 80.1 +/- 8). This high degree of similarity is also reflected by the type accumulation curves shown in Fig. 12. Single garbage pellets already contained between 60 and 80% of the pollen types found in the entire set of samples taken from one nest on a given day (10 to 15 types total), and all but one set of samples (nest B, May 2) showed rapid type saturation within the observed range of replicates.

Temporal variation of pollen composition

The pollen composition of single garbage pellets collected at different times in April and May 1999 is shown in Fig. 11. Although some differences are apparent between sampling dates in both nests, the similarities were still high. Average percentage similarities between samples of consecutive dates are given in Table 2. Many of the dominant pollen types (e.g. Leguminosae A, *Durio* type, *Convolvulus* type, Leguminosae B) were present in variable

quantities at all times in one or both colonies. In contrast, very few major types were restricted to one particular point in time (e.g. Leguminosae C).

This pattern partly changed when samples were separated by more than a few weeks. The pollen composition of pooled ten-pellet samples collected from colony B at intervals of 4 to 6 months in 1999 and 2000 is given in Table 3. Each sample contained between 11 and 15 different types, summing up to a total of 28. Similarity was low between samples of consecutive points in time in two cases (14.0% between April and September 1999; 13.6% between September 1999 and March 2000) and relatively high between March and July 2000 (58.5%). Although total similarity over time was partly low, a reasonable number of types (*Durio* type, *Manihot esculenta*, Leguminosae B, Leguminosae ? A, Bombacaceae A) was found in substantial quantities at two or three points in time (Table 3).

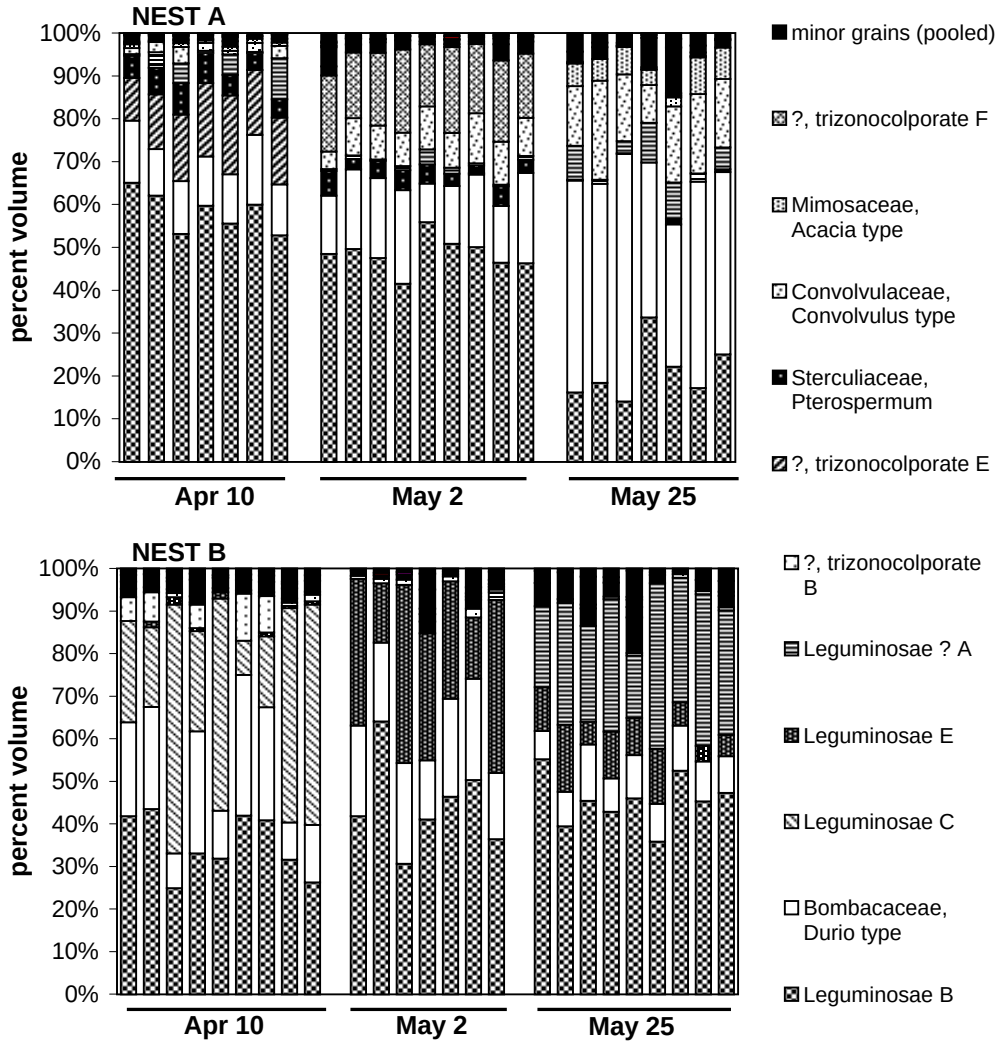

Fig. 11 Pollen composition of single garbage pellets taken from two different colonies of *T. collina* (nest A and B, both in Deramakot Forest Reserve) at three different points intime in 1999. Only dominant pollen types are shown in detail.

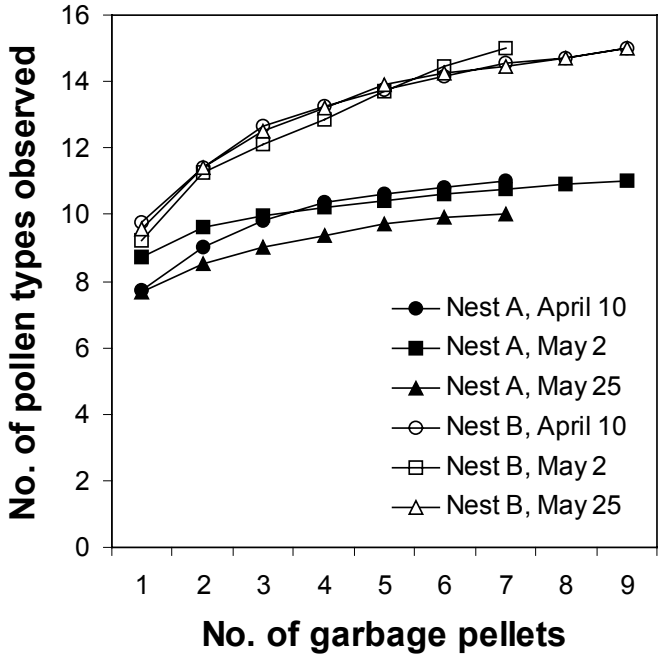

Fig. 12 Pollen type accumulation in samples of garbage of two colonies of *T. collina* (Nest A and B) collected at three different points in time in 1999. Note the rapid type saturation after adding relatively small numbers of garbage pellets. Curve parameters were calculated with EstimateS 5.0.1 software using 50 randomizations.

Comparison between corbicular and garbage pollen

The modified trap collected sufficient amounts of incoming corbicular pollen to allow comparisons with garbage pollen. Between 15 and 136 (mean: 52.7; N=13) corbicular loads were counted on any sampling day, with pollen type diversity being dependent on the number of loads in pooled samples (Fig. 13)(Nonlinear Regression, S model: R^2=0.61; F=15.59; p<0.01). The shape of the saturating curve suggests that the daily pollen import of colony C at the time of the study comprised about ten different types.

The number of types found in samples of garbage at the same time was twice as high on average (20.8 +/- 2.61), and there was no relationship between the number of types found in corbicular load samples and garbage samples at a given day (Fig. 14). Almost all (94%) of the types that were collected as pollen (total: 32) did also appear in the garbage samples but only 65% of the types found in garbage samples (total: 46) were also detected in pollen loads during the study period. Generally garbage pollen diversity was much higher in colony C than in colony A and B from Deramakot Forest Reserve (see above).

Table 2 Similarity of pollen composition of single garbage pellets taken at consecutive points in time from a given colony of *T. collina* (for colonies A and B). Values are Steinhaus-Index * 100 and represent percentage similarity. All possible pairwise comparisons between single pellets were included and means were calculated across these comparisons.

Colony	Dates compared	Number of pellets and pairwise comparisons	Mean % similarity	Minimum % similarity	Maximum % similarity
A	April 10 with May 2	7 x 9 = 63	75.4	67.8	83.1
A	May 2 with May 25	7 x 9 = 63	52.0	36.0	71.7
A	April 10 with May 25	7 x 7 = 49	38.9	27.8	58.2
B	April 10 with May 2	7 x 7 = 49	52.8	36.3	72.1
B	May 2 with May 25	7 x 7 = 49	60.1	45.8	71.7
B	April 10 with May 25	9 x 9 = 81	46.4	34.9	59.5

Table 3 Pollen composition of pooled ten-pellet garbage samples taken from *T. collina* colony B at intervals of 4 to 6 months in 1999 and 2000 (Deramakot Forest Reserve). Values are percent volume of the entire sample.

No.	Pollen type/species	April	September	March	July	Mean
		1999		2000		
1	Leguminosae ? A		7.80	49.80	26.97	21.14
2	Rubiaceae, *Neonauclea* type ?		60.46	1.86		15.58
3	Leguminosae B	34.10	5.73			9.96
4	Bombacaceae A			22.89	15.19	9.52
5	Leguminosae C	32.96				8.24
6	Bombacaceae, *Durio* type	18.95	5.38		2.88	6.80
7	Euphorbiaceae, *Manihot esculenta*			6.02	18.57	6.15
8	Mimosaceae, *Mimosa pudica* type	0.56	1.35	5.83	7.08	3.70
9	Oleaceae, *Jasminium* type	0.84			10.91	2.94
10	?, trizonocolporate A	1.08	6.47	0.84	1.51	2.47
11	Asteraceae, Tubulifloreae A type		0.53	6.60	1.92	2.26
12	Leguminosae D		6.86			1.72
13	Leguminosae E	0.86		0.79	4.90	1.64
14	Symplocaceae, *Symplocos* type		0.65		5.15	1.45
15	Passifloraceae, *Passiflora ?*	1.29	1.12	1.84	0.63	1.22
16	?, trizonocolporate B	4.35				1.09
17	Caesalpiniaceae, *Caesalpinia* type			2.49		0.62
18	Bombacaceae B		2.19			0.55
19	Combretaceae, *Terminalia* type	1.70				0.42
20	Leguminosae ? F	1.46				0.36
21	?, trizonocolporate C				1.21	0.30
22	Rutaceae, *Clausena* type				1.02	0.25
23	?			0.69		0.17
24	?, trizonocolpate				0.68	0.17
25	?, trizonocolporate D	0.61				0.15
26	Euphorbiaceae, *Croton* type				0.59	0.15
27	Rutaceae, *Citrus* type	0.51				0.13
28	Sterculiaceae, *Sterculia* type		0.50			0.13
	No. of types/sample	13	12	11	15	28

Fig. 15 shows the phenology of major pollen types over time in samples of garbage as well as corbicular pollen. Although patterns are varied, the data allow two generalizations: (i) Representation of types in corbicular load samples is usually much more restricted in time than representation in garbage, and (ii) representation in garbage tends to peak at times when types are also present in corbicular loads. In some cases major grains were present in garbage samples long before (e.g. *Zea mays*, Bombacaceae A) or after (Mimosaceae ? type) any sign of import of those types was apparent in the corbicular load samples, and in one case (Cucurbitaceae type) a major grain was not present in corbicular loads at all.

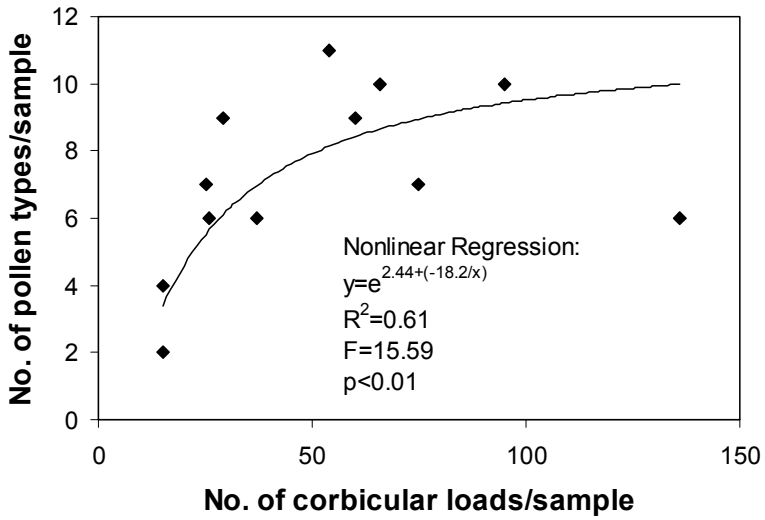

Fig. 13 Relationship between the number of corbicular loads per pollen sample and type diversity. A non-linear S model produced the best fit among models offered by the SPSS statistical package. The model saturates at 11.4 pollen types for very large load numbers.

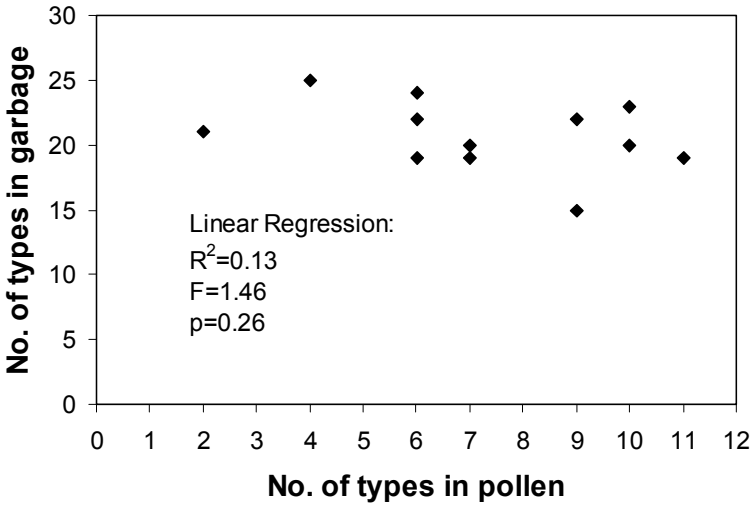

Fig. 14 Relationship between the number of pollen types in garbage samples and that in corbicular samples collected at the same day. No effect was observed.

3.3.4 Discussion

Our results show that garbage pellets of *T. collina* contain large quantities of pollen. Although the origin of pollen in garbage has not been directly demonstrated by our study it is very likely that it is derived from feces previously deposited in the nest by bee larvae and adults. Pollen exines have been shown to remain largely unharmed by digestive (Stanley and Linskens, 1974; Klungness and Peng, 1984; Crailsheim et al., 1992), a finding that can explain the high degree of preservation of garbage pollen.

Dynamics of garbage pollen composition

Temporal patterns of pollen type representation in samples of garbage and corbicular pollen are varied and suggest that several factors interact in determining when foraged pollen is likely to appear in garbage pellets. The processes involved work on a range of different time scales and are likely to include (i) defecation of pollen directly consumed by workers, (ii) inclusion of fecal pellets (meconia) removed from brood cells after a lag-time of several weeks for larval development, and (iii) consumption and defecation of pollen from long-term storage pots. The flow of pollen in stingless bee colonies can be complex and has been studied in detail by Sommeijer et al. (1985) for *Melipona favosa*. After being deposited in pollen pots by foragers pollen is first ingested by workers of a wide range of ages which then pass it to others in liquid form (trophallaxis). The flow is finally directed to a limited number of younger workers that are eventually provisioning empty brood cells (Sommeijer et al., 1985). It is unknown how much of the pollen is actually digested and consumed by adult workers during the process of trophallaxis, but amounts could be substantial. We believe that direct pollen consumption and defecation by workers in the nest is responsible for our finding that some pollen types synchronously peaked in both garbage and corbicular pollen samples. In contrast, inclusion of larval feces and consumption of pollen from long-term storage is likely to lead to the pronounced time-lags as evidenced in some dominant pollen types. Generally, the temporal dynamics of pollen appearing in garbage is likely to depend on the nutritive state of the colony and may therefore vary considerably over time. Consequently, garbage trapping cannot easily be used for studies on short-term temporal dynamics of pollen foraging. On a time scale of weeks there will be no straightforward relationship between the time of collection of certain pollen species and their appearance in garbage samples. However, if long-term patterns of resource use are of interest, repeated garbage trapping can be used for measuring pollen turnover over seasons and years.

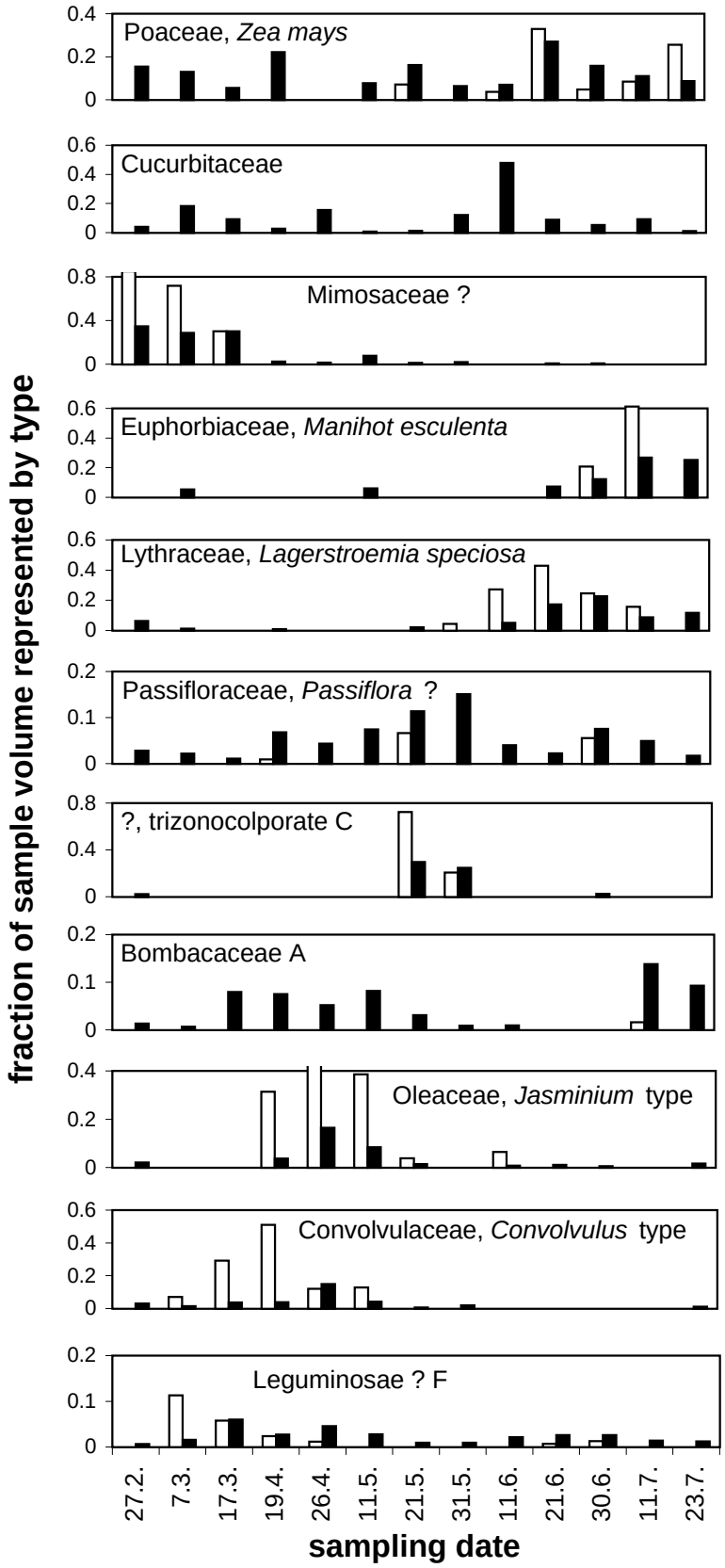

Fig. 15 Temporal distribution of major pollen types in samples of garbage (black) and corbicular pollen (white) taken from colony C between February and July in 1999.

Sampling efficiency

Pollen contents of garbage pellets collected at one point in time from a given colony were surprisingly similar in type composition and relative abundance. This implies that sampling small numbers of pellets will already provide a good estimate of garbage pollen composition at the time. Moreover, the turn-over of garbage pollen was low, presumably because the processes described above are integrating harvested pollen over a range of time scales. Thus, it seems that even sampling at relatively long intervals (4-6 months as for colony B in this study) will be sufficient for a crude assessment of long-term colony pollen diet.

So far garbage samples have been collected from colonies of five species of stingless bees in Malaysia, but the method is likely to be applicable to a much wider range of meliponines (see Roubik, 1989). Non-invasive sampling of garbage pollen will prove especially advantageous in studies on natural bee populations and communities because of the fact that it is not necessary to fell entire nest trees in order to access colony pollen stores. Therefore, and because the described garbage traps allow automated synchronous sampling from large numbers of colonies, the analysis of garbage pollen should be useful in future studies of stingless bee resource use, interspecific resource partitioning or competition.

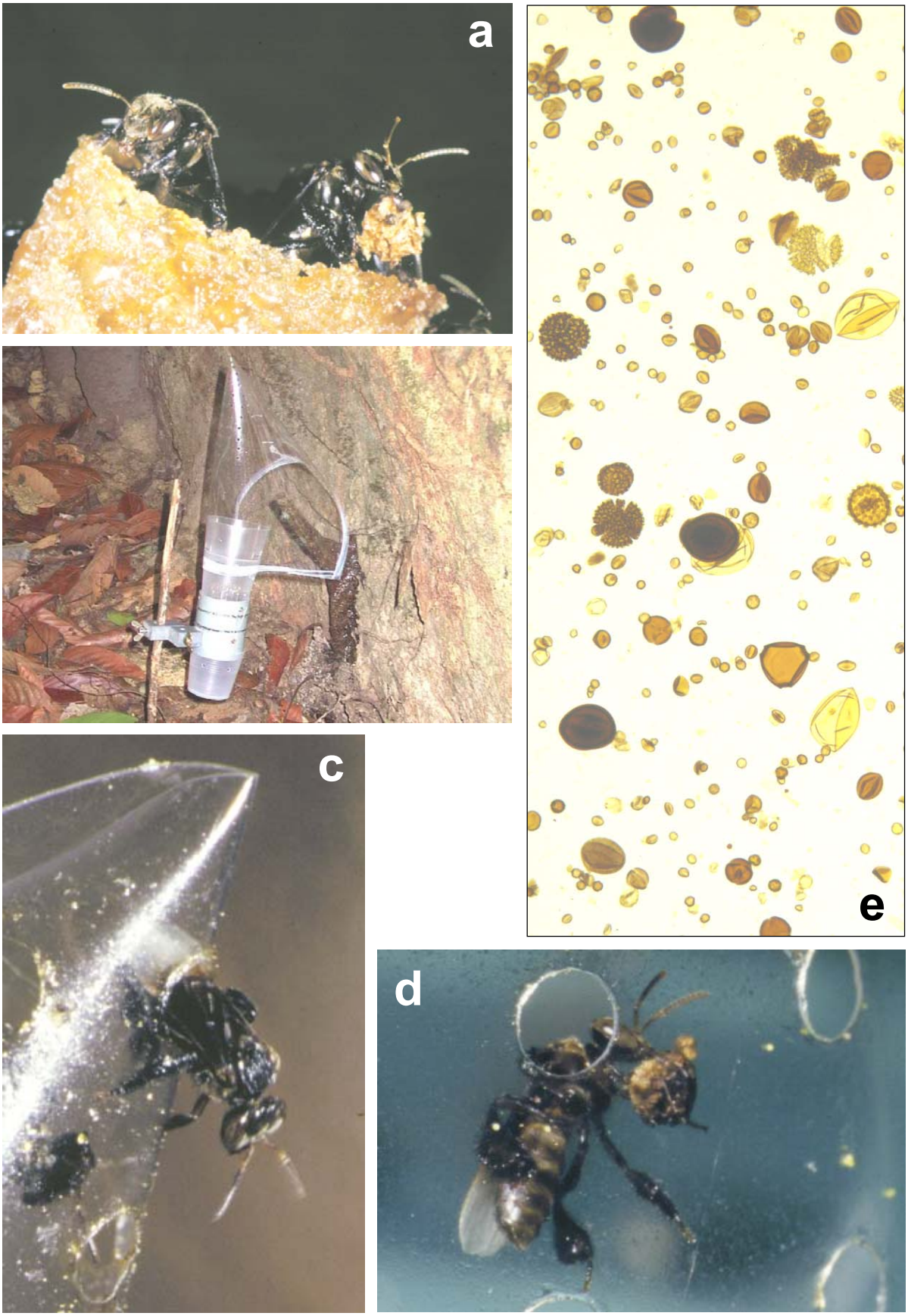

Plate 1 a) Worker bee of *T. collina* carrying a garbage pellet, shortly before taking off. b) Operational garbage trap at nest entrance. c) *T. collina* worker escaping through puncture in the trap funnel. d) Garbage bee stuck in funnel. e) Microscopic slide with garbage pollen.

3.4 **Nesting and nest trees of stingless bees (Apidae: Meliponini) in lowland dipterocarp forests in Sabah, Malaysia, with implications for forest management** (T. Eltz, C. A. Brühl, I. Zamrie & K. E. Linsenmair, submitted)

3.4.1 Introduction

Cavities in trees are an important structural feature of natural forests, and a wide range of vertebrates and invertebrates depend on them for varying purposes, e.g. nesting and roosting (Lindenmayer et al., 1997; McComb and Noble, 1982; Newton, 1994, Oldroyd et al., 1994). Forest management is expected to pose considerable threat to both cavity-bearing trees as well as the fauna associated with them. Populations of cavity-dwelling animals could be (i) directly affected by management operations, e.g. through mortality resulting from felling of the tree, or (ii) indirectly, as a result of decreased availability of suitable cavities in managed stands. So far, most research has concentrated on measuring or estimating indirect effects on populations of forest birds and marsupials in temperate forests: Forest management has been shown to severely reduce the availability of tree cavities for hole-nesting birds in North America (van Balen et al., 1982; Newton, 1994 and references therein), as well as the availability of tree hollows in Southern Australia (Saunders et al., 1982; Bennett et al., 1994; Gibbons and Lindenmayer, 1996). In some cases reduced availability of cavities was related to reduced population densities of cavity-dependent fauna (Lindenmayer et al., 1991; Newton, 1994; Saunders et al., 1982), suggesting that nest or den sites can become a limiting resource in managed forests. Direct effects of management operations on cavity-dwelling animals have received much less attention, presumably because of difficulties quantifying logging-induced mortality in relatively mobile taxa like birds or other vertebrates. Direct effects, however, could have considerable impact on populations of long-lived organisms with low fecundity.

Stingless bees (Apidae: Meliponini) of Asian dipterocarp forests might be such organisms. Meliponines are eusocial and live in colonies of a few hundred to several thousand workers (Sakagami 1982). Individual colonies are generally perennial and reported maximum life-spans range from 10 to 26 years (Wille, 1983; Roubik, 1989). Most species found in Southeast Asia nest in pre-existing cavities of variable sizes (Sakagami et al., 1983a; Sakagami et al., 1983b; Salmah et al., 1990), and at least some species are known to nest in

association with large canopy trees (Sakagami et al., 1983b; Roubik, 1996) that are likely to be targeted by the timber industry. Furthermore, once established, stingless bee colonies are believed to remain stationary for the rest of the colony cycle because the queen looses the ability to fly (Michener 1974). Although there have been some exceptions to that rule (Inoue et al. 1984a), absconding of entire colonies as a response to disturbance is extremely rare in stingless bees, suggesting that colonies are heavily dependent on the persistence of their nest trees. Meliponines are among the most predominant flower-visiting insects in the canopy and understory of Asian tropical forests (Inoue et al. 1990, Momose et al. 1998), probably providing important pollinator services during both general and non-general flowering seasons (Momose et al., 1998). Their conservation in commercial forests should be of considerable concern to forest managers.

In the present study we analyzed the nesting habits and characteristics of nest trees of stingless bees in lowland forests in Sabah, Malaysia, in order to estimate the potential direct impact of logging operations on bee populations and communities. Using information on taxonomic composition, size and expected log quality of nest trees, we discuss potential effects of disturbance imposed by different harvesting systems (Reduced Impact Logging (RIL) versus conventional harvesting) and highlight areas of conflict between natural forest management and the conservation of stingless bees and other cavity-dependent fauna.

3.4.2 Methods

Study sites and nest searching

During 20 months of field work between September 1997 and July 2000 we searched for stingless bee nests in all three research localities (Fig. 1; see section 2.2). Nests were located either by chance during field trips or by inspecting trees located along forest trails (57 % of nests), and by standardized nest surveys along transect grids established for quantitative measurements of stingless bee nest density (43 %; see section 4.2). We pooled data sets for the analyses presented below.

Nests and nest trees

For bee nests (= colonies in the present context) and nest trees we recorded the following data:

1. Bee species: Identification of hand-netted vouchers was done using descriptions in Schwarz (1937, 1939), the key for Sumatran species given by (Sakagami et al. 1990) and by comparison with reference material. Colonies nesting in more elevated sections of tree trunks could frequently be identified by visual inspection (using binoculars) of bee size and color, as well as the highly characteristic shape of the nest entrance tube. However, colonies nesting at the upper canopy level (30-50 m high) could not be identified and are treated as *Trigona spp*..

2. Nest type: We distinguished two general modes of nesting.'Cavity nests' were situated within hollows in the tree trunks and are characterized by entrance tubes emerging from those hollows via openings in the wood. Cavity nests could be at any height of the tree trunk. 'Base nests', on the other hand, were always situated under or in the bases of trees and are characterized by an entrance tube attached to the outer wall of the tree base, running down the tree until concealed from sight by surrounding soil. Most base nests are probably located within the upper root system of the tree (this was the case in two excavated nests of *Trigona collina*, T. Eltz, pers. obs., and in comparable neotropical *T. cilipes* and *T. fulviventris*, D. W. Roubik, pers. comm.), but in some cases the entrance tube may also curve up into the lower section of the trunk, frequently hollow in large trees (Panzer 1976).

3. Diameter of nest trees: Diameter at breast height was measured (using measuring tape) or estimated by comparison with machetes of known length. In the case of trees with large buttresses dbh-recordings were made for the height above the buttresses. Tree diameter is an important criterion for harvesting. Under conventional forestry guidelines in Sabah all timber trees above 60 cm dbh were considered harvestable (Marsh et al. 1996). Recently an upper cutting limit (120 cm) has been promoted by the Sabah Forestry Department RIL guidelines (Lohuji and Taumas, 1998).

4. Taxonomy of nest trees: Trees were either identified in the field by experienced forestry staff, or, in most cases, using dropped leaves originating from the respective trees. Leaf samples were identified by Mr. Leopold Madani (Forest Research Centre, Sepilok), partly by cross-referencing with specimens deposited in the FRC herbarium. Based on these identifications and in accordance to the relevant literature (Burgess, 1966; Hing, 1986; Lemmens et al., 1995; Soerianegara and Lemmens, 1994; Sosef et al., 1998) we classified nest trees as commercial or non-commercial species.

5. Estimated log quality: The commercial potential of a subset of nest trees (N=47) as well as that of randomly chosen control trees (no nest, >60 cm dbh, N=75) was estimated by an

experienced forest ranger, Mr. Hussin Achmad (Wilaya, Sandakan). In addition to tree size and species, judgements were based on a range of characters including the form and integrity of the trunk, crown shape, presence or absence of epiphytic fungi, and signs of broken branches. Hollowness was also indicated by sound emissions evoked by knocking on buttresses and accessible sections of the trunk using parangs (machetes). Trees were then assigned to one of three quality classes:

- Good: no visible flaws, solid and straight log over the entire length, prime quality
- Medium : minor flaws, but substantial trunk segments harvestable
- Bad: major flaws, no commercially valuable segments of sufficient length to warrant harvesting

In combination with other criteria (tree size, tree species) this classification was used to estimate the percentage of nest trees that were likely to be harvested in case of selective logging.

The classification is likely to suffer from inaccuracies and should only be regarded as an approximation of the true harvest potential of nest trees. In particular, the judgement of hollowness could be biased due to the fact that our estimations were based on uninvasive methods. During logging operations, in contrast, tests for hollowness are made by pushing the blade of the chain saw vertically into the stem. If the resistance to the saw abruptly changes, the tree is considered hollow (Trockenbrodt et al., 2001). Judgements are somewhat subjective and decisions made by fellers have been shown to be incorrect in many cases (Trockenbrodt et al., 2001). Thus, the extent of bias in our own judgements is difficult to estimate. On average, however, our classification in harvest trees (good, medium) and non-harvest trees (bad) is likely to be reasonably close to that made during logging operations.

3.4.3 Results

Nests and nest aggregations

We found a total of 275 natural nests of 12 species of stingless bees in the three different forest reserves. Stingless bees of all but seven nests could be identified to species. Without exception the nests were closely associated with living or dead trees (142 trees, see nest tree analysis below) and could easily be classified as ‘cavity nests’ or ‘base nests’. Table 4

summarizes the results of nest type and height for the different species. It was obvious that the different species had distinct preferences in nesting. The majority of species (7) were cavity nesters, but the majority of detected nests (81 %) belonged to predominantly base-nesting species: Among those, *Trigona (Tetragonula) collina*, a medium-sized black bee (~6.5 mm body length), was by far the most common species (52 % of all nests), followed by *T. (Tetr.) melanocephala* (~5.5 mm; 13.8 %) and *Hypotrigona pendleburyi* (~3 mm; 13.4 %). The pronounced imbalance in favor of base-nesting species is probably due to difficulties in detecting colonies situated close to or within the canopy. Accordingly, the most common cavity-nesting species, *T. (Lepidotrigona) terminata* (~6 mm; 7 %), has a tendency to nest at relatively low height (Table 4).

Table 4 Number of nests, nest type, and nest height of nests of stingless bee species.

	No. of nests	No. of base nests	No. of cavity nests	Height of cavity nests (m)		
				Mean	Min	Max
T. (Tetragonula) collina	143	134	9	2.9	1	15
T. (Tetragonula) geissleri	1		1	?		
T. (Tetragonula) laeviceps	7		7	3.1	0.3	10
*T. (Tetragonula) laeviceps-group**	2		2	0.8		
T. (Tetragonula) melanocephala	38	37	1	0.5		
T. (Tetragonula) melina	6	6				
T. (Odontotrigona) haematoptera	5		5	4.7	2	10
T. (Lepidotrigona) terminata	19	1	18	3.1	0.3	15
T. (Homotrigona) fimbriata	6		6	15	1	35
T. (Tetrigona) binghami	3		3	9.3	3	20
T. (Tetrigona) apicalis	1		1	6		
H. (Pariotrigona) pendleburyi	37	35	2	1.5	1.5	1.5
Trigona spp.	7		7	25.7	10	40
Total	275	213	62			

* represents a probably undescribed species of the subgenus *Tetragonula* that is slightly smaller than *T. laeviceps*. Possibly identical with the small variety of *T. laeviceps* mentioned in (Sakagami et al., 1990).

Fifty-seven of 142 individual nest trees (40.1 %) harbored more than one (maximum: 8) bee nests (mean 1.94 nests/tree), and 64 % of the aggregations consisted of more than one (up to three) bee species (mean of 1.3 species/nest tree; Table 5). All species observed in appreciable numbers were sometimes found to be part of aggregations, but the likelihood to aggregate and the tendency to form conspecific versus mixed aggregations seemed to vary

among species. We tested for differences among the three most abundant base-nesting species, *T. collina*, *T. melanocephala* and *H. pendleburyi*. Frequencies of numbers of nests in a 3x3 contingency table (species x type of aggregation) were clearly heterogeneous (χ^2=49.28; N=218; df=4; p<0.001; Fig. 16). Whereas *T. collina* and *T. melanocephala* frequently nested alone, all but one colony of *H. pendleburyi* were found in aggregations with other nests. Interestingly, these were mostly mixed aggregations where up to five colonies of *H. pendleburyi* were associated with one or two of the other base-nesting species. In contrast, the majority of aggregated *T. collina* nests were found in association with conspecifics only, although mixed aggregations were also common. Colonies of *T. melanocephala* either nested alone, or singly in association with other species (Fig. 16).

Nest trees: taxonomy

Twelve (8.5 %) of the 142 nest trees were dead, the remaining (91.5 %) were living trees of which 80 were identified to species or genus (Table 6). The family Dipterocarpaceae was predominant (43.7 %), followed by Lauraceae (26.3 %), Leguminosae (5.0 %), Anacardiaceae, Euphorbiaceae, Olacaceae (each 3.8 %) and others. Among Dipterocarpaceae the genus *Shorea* (Red and Yellow Seraya, Selangan Batu) was most common. The vast majority of nest trees belonged to genera and species that are considered commercial timber trees under both conventional (95.0 % of trees) and RIL (88.7 %) guidelines. The difference between RIL and conventional guidelines is due to the fact that some nest trees belonged to species protected under RIL (*Shorea pinanga*, *Shorea mecistopteryx*; Table 6).

Generally, nest tree diversity was high (22 genera with at least 38 species), and many tree species were only represented by a single individual. By far the most common single species (20.0 %) was the Bornean Ironwood or Belian (*Eusideroxylon zwageri*, Lauraceae), a tree that is famous for having exceptionally hard and durable wood (Burgess, 1966; MacKinnon et al., 1996). Seventeen of 30 nests associated with *E. zwageri* were cavity nests (57 %), a frequency that is significantly different from that found in the whole of the remaining tree community (18 %; χ^2=22.45; N=275; df=1; p<0.001). Notably, several bee nests were also found in dead Belian trees (five out of the 12 dead nest trees) which, due to the durability of their wood, can escape decay for years or even decades.

Generally, across all species, nest trees tended to harbor either cavity nests or base nests. Only three individual trees were home to both types of bee nests.

Table 5 Degree of nest clustering and the tendency to form monospecific and/or mixed nest aggregations in individual nest trees of stingless bee species. Species associated in aggregations are indicated by abbreviations: b=*T. binghami*; c=*T. collina*; f=*T. fimbriata*; g= *T. geissleri*; h=*T. haematoptera*; l=*T. laeviceps*; l*=*T. cf. laeviceps*-group; mca=*T.melanocephala*; ma=*T.melina*; p=*H. pendleburyi*; t=*T. terminata*.

	Nests	Nest trees	No. of nests in aggregations (%)	Nests in aggregations		Associated species
				Mono-Specific	Mixed	
T. (Tetragonula) collina	143	72	113 (79.2)	60	53	c, b, f, g, h, ma, mca, p, t
T. (Tetragonula) geissleri	1	1	1		1	c, f
T. (Tetragonula) laeviceps	7	5	3 (42.9)		3	l, b, t
*T. (Tetragonula) laeviceps-group**	2	2	1 (50.0)		1	t
T. (Tetragonula) melanocephala	38	36	21 (55.3)	2	19	mca, c, h, ma, p
T. (Tetragonula) melina	6	6	3 (50.0)		3	c, mca
T. (Odontotrigona) haematoptera	5	5	2 (40.0)		2	c, mca, t
T. (Lepidotrigona) terminata	19	19	8 (42.1)		8	b, c, h, l, l*, ?
T. (Homotrigona) fimbriata	6	6	1 (16.7)		1	c,g
T. (Tetrigona) binghami	3	3	2 (66.7)		2	c,l,t
T. (Tetrigona) apicalis	1	1				
H. (Pariotrigona) pendleburyi	37	20	36 (97.3)	4	32	p, c, mca
Trigona spec.	7	7	1 (14.3)			t

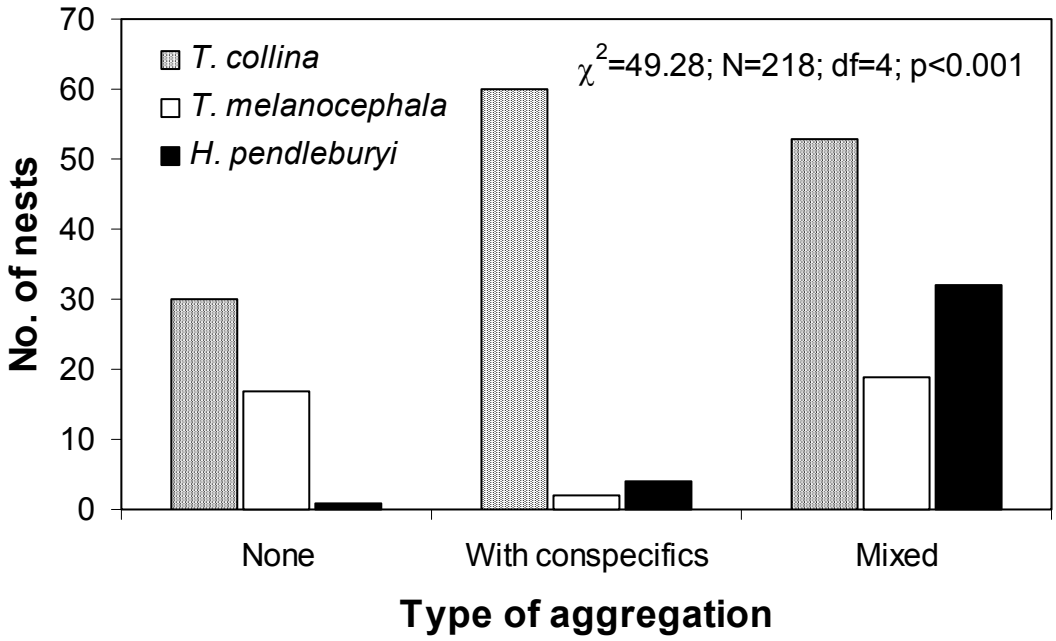

Fig. 16. Frequency of nests of three base-nesting species of stingless bees found singly or in aggregation with other colonies.

Table 6 Taxonomic composition, local common names and commercial affiliation of nest trees of stingless bees in Sabah.

Tree species	Family	Trade name	No. of nest trees	Commercial species	Protected (RIL)
Gluta oba	Anacardiaceae	Rengas	1	**x**	
Gluta sabahana	Anacardiaceae	Rengas	1	**x**	
Gluta sp.	Anacardiaceae	Rengas	1	**x**	
Lophopetalum beccarianum	Celastraceae	Perupok	1	**x**	
Lophopetalum sp.	Celastraceae	Perupok	1	**x**	
Dipterocarpus grandiflorus	Dipterocarpaceae	Keruing	1	**x**	
Dipterocarpus sp.	Dipterocarpaceae	Keruing	1	**x**	
Shorea acuminatissima	Dipterocarpaceae	Yellow Seraya	2	**x**	
Shorea atrinervosa	Dipterocarpaceae	Selangan batu	1	**x**	
Shorea beccariana	Dipterocarpaceae	Red Seraya	1	**x**	
Shorea exelliptica	Dipterocarpaceae	Selangan batu	1	**x**	
Shorea falciferoides	Dipterocarpaceae	Selangan batu	2	**x**	
Shorea fallax	Dipterocarpaceae	Red Seraya	1	**x**	
Shorea ferruginea	Dipterocarpaceae	Red Seraya	1	**x**	
Shorea gibbosa	Dipterocarpaceae	Yellow Seraya	1	**x**	
Shorea johorensis	Dipterocarpaceae	Red Seraya	1	**x**	
Shorea macroptera	Dipterocarpaceae	Red Seraya	1	**x**	
Shorea mecistopteryx	Dipterocarpaceae	Kawang	1	**x**	**x**
Shorea multiflora	Dipterocarpaceae	Banjutan	3	**x**	
Shorea parvifolia	Dipterocarpaceae	Red Seraya	2	**x**	
Shorea pauciflora	Dipterocarpaceae	Oba suluk	2	**x**	
Shorea pinanga	Dipterocarpaceae	Kawang	3	**x**	**x**
Shorea smithiana	Dipterocarpaceae	Red Seraya	1	**x**	
Shorea waltonii	Dipterocarpaceae	Red Seraya	1	**x**	
Shorea sp.	Dipterocarpaceae	div.	8	**x**	
Chaetocarpus castanocarpus	Euphorbiaceae	Kayu dusun	2	**x**	
Trigonopleura malayana	Euphorbiaceae	Gambir hutan	1		
Lithocarpus, Quercus sp.	Fagaceae	Mempening	1	**x**	
Hydnocarpus woodii	Flacourtiaceae	Karpus wood	1	**x**	
Callophyllum sp.	Guttiferae	Bitangor	1	**x**	
Dehassia sp.	Lauraceae	Medang	1	**x**	
Eusideroxylon zwageri	Lauraceae	Belian	16	**x**	
Litsea caulocarpa	Lauraceae	Medang	1	**x**	
Litsea sp.	Lauraceae	Medang	2	**x**	
Phoebe macrophylla	Lauraceae	Medang	1	**x**	
Dialium sp.	Leguminosae	Keranji	1	**x**	
Intsia palembanica	Leguminosae	Merbau	1	**x**	
Sympetalandra borneensis	Leguminosae	Merbau Lalat	2	**x**	
Ficus sp.	Moraceae	Kayu Ara	2		
Syzigium sp.	Myrtaceae	Obah	2	**x**	
Scorodocarpus borneensis	Olacaceae	Bawang hutan	3	**x**	
Scaphium affine	Sterculiaceae	Kembang semangkok	1	**x**	
Wikstroemia sp.	Thymelaeaceae	Tindot	1		

All bees species that were recorded in number nested in or under a variety of nest tree taxa, and nest tree diversity per bee species was strongly dependent on the number of identified nest trees (R^2=0.96; N=11; p<0.001) (Fig. 17). The two cavity-nesting species *T. terminata* and *T. haematoptera* had relatively low nest tree diversity, a finding that is due to their apparent preference for *Eusideroxylon zwageri*. In *T. terminata*, six out of 11 identified trees were *E. zwageri*, and in *T. haematoptera* all four identified nest trees belonged to this species.

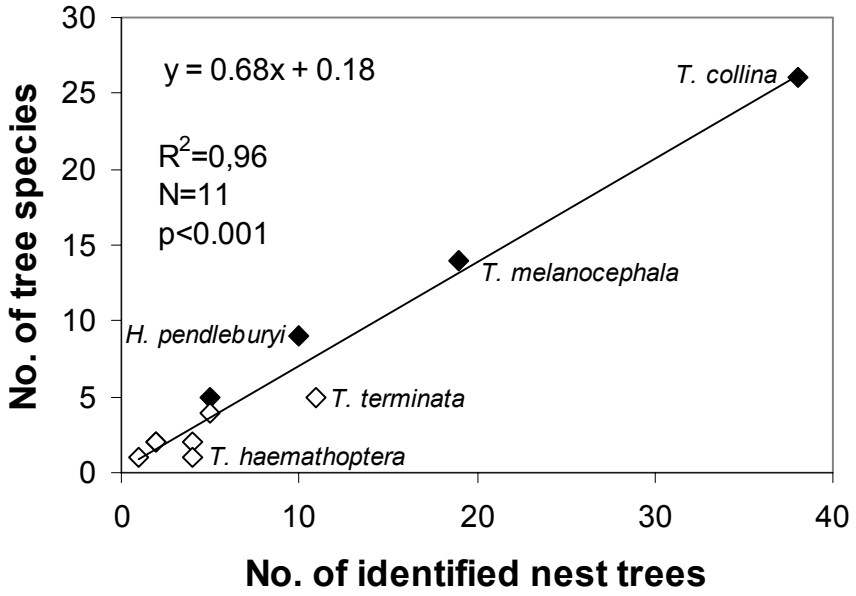

Fig. 17. Relationship between the number of identified nest trees and nest tree species richness for different stingless bee species. Solid diamonds are (predominantly) base-nesting species, open diamonds are cavity-nesting species.

Nest trees: size

Most bee nests were situated in or under large to very large canopy trees, with trees harboring base nests being larger on average than trees harboring cavity nests (ANOVA: F=8.88; N=120; df=1; p<0.01; Fig. 18). A total of 86.1 % of nest trees were larger than 60 cm dbh, and 73.0 % were between 60 and 120 cm dbh, the size range considered fit for harvesting according to official RIL guidelines.

The number of nests associated with a given tree was positively correlated with tree diameter in base-nest trees (R_s=0.37; N=81; p<0.0001), but not among cavity-nest trees (R_s=0.01; N=38; p=0.93). Trees larger than 120 cm dbh (13.1 % of all nest trees) were home to 19.1 % of all stingless bee colonies (Fig. 19).

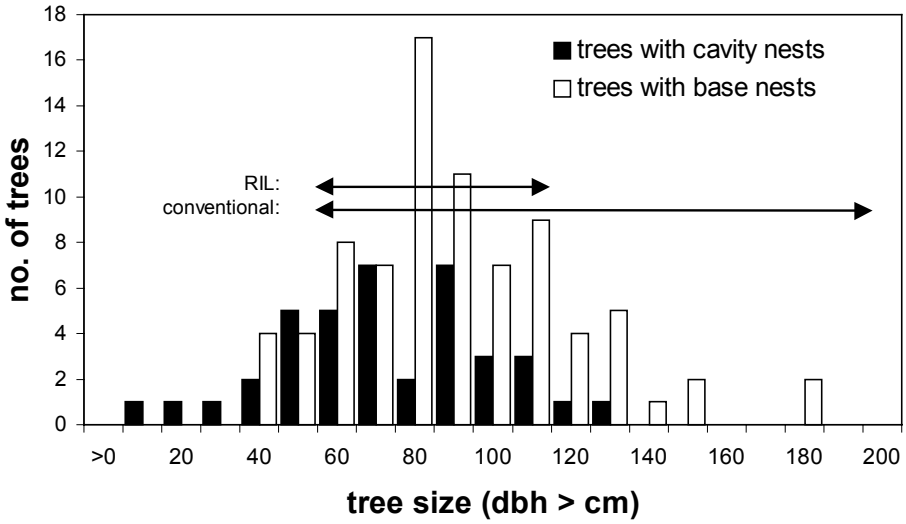

Fig. 18. Size distribution of living nest trees of stingless bees. Note difference in size between trees with cavity nest and trees with base nests. Trees harboring both nest types are not shown (N=3). The arrows indicate harvesting size under conventional and Reduced Impact Logging (RIL) guidelines.

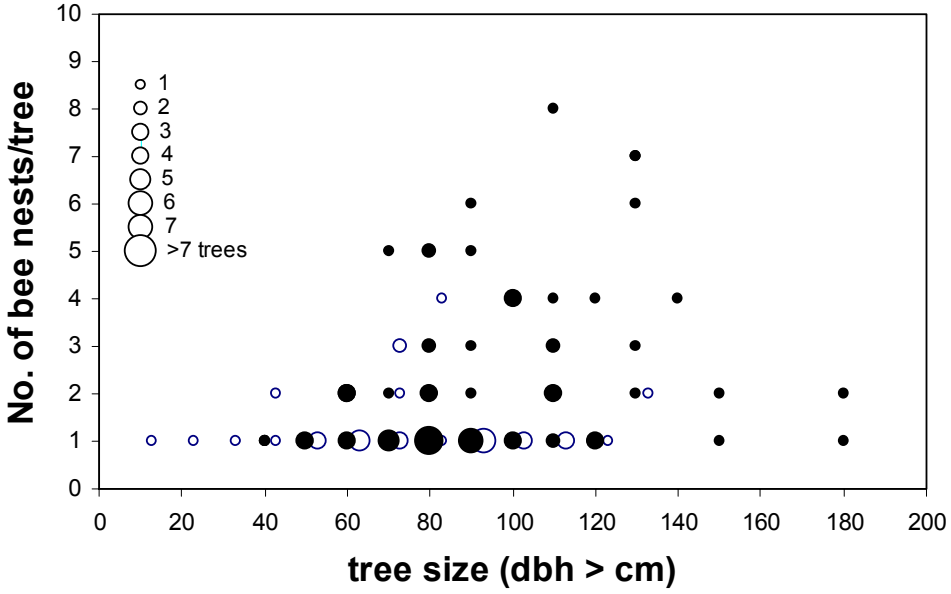

Fig. 19. The number of nests per nest tree as a function of tree size. Data are shown separately for trees with cavity nests (open circles) and trees with base nests (solid circles). Trees harboring both nest types are not shown (N=3).

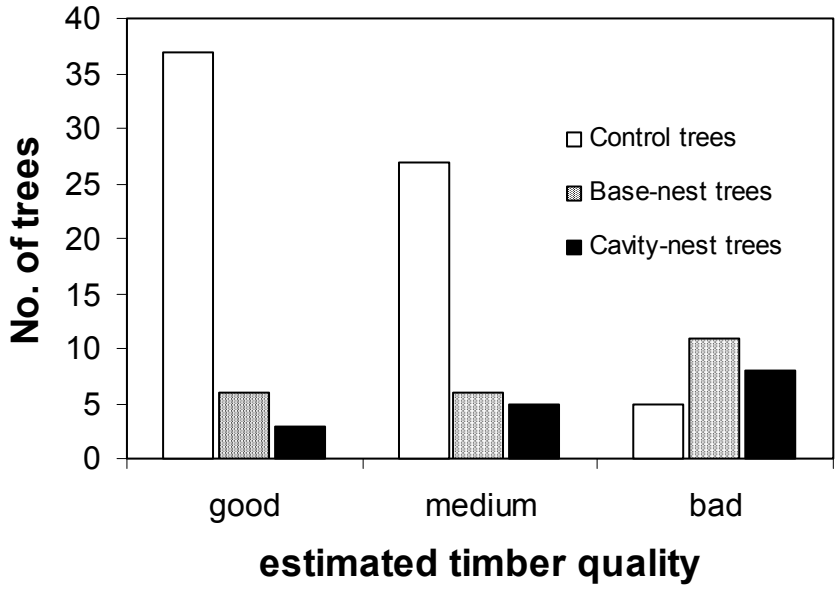

Fig. 20. Wood quality classification of nest and control trees. Frequencies of base-nest trees and cavity-nest trees are shown separately.

Nest trees: timber quality

108 of the 122 nest and control trees inspected by Mr. Hussin Achmad were potential timber trees above 60 cm dbh. For these, estimates of log quality were analyzed. 51.2 % of the nest trees were classified as 'good' or 'medium' timber quality and would qualify for harvesting given they complied with other criteria (harvest size, commercial species). Generally, nest trees were of significantly lower timber quality than control trees (χ^2=25.59; N=108; df=2; p<0.001; Fig. 20). In order to test whether this effect was due to the larger size of nest trees, we compared frequencies of a subset of nest and control trees that were matched for size by random sub-sampling. Neither direction nor magnitude of the effect was altered (χ^2=16.29; N=58; df=2; p<0.001), suggesting that tree size and timber quality were largely independent in trees above 60 cm dbh. The estimated timber quality did not differ between trees harboring cavity nests and trees with base nests (χ^2=0.32; N=39; df=2; N.S.; Fig. 20).

Percentage of potential harvest trees among nest trees

Sixteen of the 47 nest trees (34.0 %) inspected by Mr. Hussin Achmad were considered harvest trees under the official RIL guidelines for selective logging published by the Sabah Forestry Department. The remaining trees were either too small (3), too large (4), had been classified as having 'bad' timber quality (21), belonged to non-commercial taxa (3), or showed combinations of these characters (5). When we applied conventional standards the

number of potential harvest trees was raised to 20 (42.6 %), because four very large nest trees (dbh > 120 cm) were now considered fit for harvesting.

These estimates are based on a limited sample of nest trees, but percentages of likely harvest trees are roughly confirmed by results of calculations based on the entire data set. Here, we multiplied the mean likelihood of a nest tree belonging to a harvestable species (see above) with the mean probability of having the correct size for harvesting (see above) and being of sufficient timber quality (see above). Respective percentages of potential harvest trees were 35.5 % (RIL) and 41.9 % (conventional). This approach assumes that taxonomy, size and timber quality vary independently among nest trees, an assumption that will not strictly apply in reality.

3.4.4 Discussion

Nest surveys and the stingless bee community

The present study provides the first detailed account of stingless bee nests, nest aggregations and nesting resources from natural forest areas in Southeast Asia. It is based on a total of 275 nests belonging to 12 species of meliponines. Sakagami et al. (1990) list 28 species of Meliponini from the whole of Borneo, and data from honey-baiting suggests that up to 22 species can occur sympatrically in a Bornean lowland rain forest locality (Roubik 1996). Thus, our nest surveys located about one half of the regional stingless bee assemblage. Among the species not located by our surveys, at least six are known to be cavity-nesting species whose nests have been recorded by previous authors from Borneo or Sumatra (Sakagami et al, 1983b; Salmah et al., 1990; Roubik, 1996). Some of theses (e.g., *T. canifrons* and *T. thoracica*) are large species that form huge colonies (Salmah et al. 1990) and probably occur in relatively low population densities, but others may have escaped detection because their nests are restricted to the higher canopy. Lack of canopy access and difficulties of detecting canopy colonies may have particularly biased our data for species nesting in small cavities in major branches of canopy trees. Species of the *laeviceps*-species group (including *T. laeviceps*, *T. fuscobalteata*, and a probably undescribed species (see Sakagami et al., 1990), are particularly likely to exploit this nesting resource. The same species are more frequently found nesting in various artificial structures (house walls, pillars, palm fronds) in close contact with humans (Salmah et al., 1990; Starr and Sakagami, 1987; D. W. Roubik, pers.

comm.), but nests found in dropped branches (Eltz, unpublished data) suggest they are present in mature forests as well.

Aggregated nesting

Generally, stingless bee nests were heavily aggregated within individual nest trees in Bornean forests. Although this trend was apparent in all species that were found in number, aggregated nesting was particularly pronounced in *T. collina*, favoring conspecific aggregations, and in *H. pendleburyi*, showing a tendency to form mixed aggregations with any of the other base-nesting species. Clustering of nests in trees or artificial structures has been reported by several authors (Starr and Sakagami 1987, Salmah et al. 1990, Roubik 1996), but the reasons for aggregating are poorly understood. Limited availability of suitable nest sites may be one possible cause, especially in degraded areas that lack sufficient numbers of natural tree cavities. In those situations, presence of cavities and crevices in construction material of farm houses can permit phenomenal concentrations of colonies (Starr and Sakagami 1987). In undisturbed forests, however, nest cavities are less likely to be limited. Here, clustering may be favored by mechanisms related to how new nest sites are located by bees. In stingless bees colony multiplication is started by scout bees that search for suitable nest sites (Michener 1974, Inoue et al. 1984b). In forests in Sabah one can frequently observe single workers of *T. collina* circling the bases of large canopy trees, presumably in search of suitable nest sites (see also Hubbell and Johnson, 1977, for *T. fulviventris* in Costa Rica). It is possible that these scout bees are guided by cues that include (or are enhanced by) the presence of other bee colonies. Specifically, odor of bee brood or nest material (resin) may indicate a particularly suitable nest tree. If no adverse effects are connected to nesting in aggregation bees should favor those nest trees because of reduced searching costs. We hypothesize that scouts of the mixed-aggregation specialists *H. pendleburyi* are guided by cues provided by colonies of other species.

The tendency of some Bornean stingless bees to nest in aggregations is markedly different from patterns found in the Neotropics. In a dry-forest in Costa Rica four out of five species of meliponines studied in detail showed a uniform pattern of dispersion, and multiple nests per tree were a notable exception restricted to a single species, *Nannotrigona perilampoides* (Hubbell and Johnson, 1977). Hubbell and Johnson (1977) argue that aggressive competition for food is the ultimate reason for uniform nest dispersion in group-foraging neotropical meliponines, and that nest spacing is proximately mediated by aggressive encounters between colonies competing for new nest sites. The idea is based on the finding that antagonistic

interference between colonies of *Trigona* is strong in neotropical bee communities (Hubbell and Johnson, 1977; Johnson and Hubbell, 1974, 1975). Nest clustering may prevail in Borneo because interspecific aggression between bees is less pronounced. We have spent many weeks observing stingless bees at honey-baits and flowers in Sabah and were rarely aware of antagonistic interactions between individuals or colonies. Instead, our general impression was that of a relatively peaceful coexistence between foragers that were mostly concerned with the exploitation of resources (but see Nagamitsu et al. 1997).

Nest trees

Stingless bee nests were situated in or underneath a large variety of trees. Selectivity in favor of certain species of trees was apparently low as indicated by a proportional increase of nest tree diversity/bee species with nest tree sample size. A similar relationship was found by (Hubbell and Johnson 1977) in a Costa Rican dry-forest. Thus, stingless bees seem to be quite opportunistic in their selection of nest sites and are likely to colonize any tree that offers a suitable cavity of the right size. It is likely, however, that tree species differ in their tendency to form suitable cavities due to differences in wood and growth characteristics. Based on our data the only obvious example of an above-average nest tree is the Bornean Ironwood or Belian, *Eusideroxylon zwageri* (20 % of identified nest trees). Although we lack large-scale quantitative tree inventories for our research areas, it is highly likely that *E. zwageri* is over-represented among samples of nest trees (see Fox, 1973). Belian is characterized by exceptionally durable wood that is commercially used for many purposes including heavy construction in marine environments (Burgess 1966) and, for the bees, may serve as a effective shield against predator attacks. Additionally, Belian has a tendency to form hollows that can be accessed by bees through crevices between living and dead parts of the trunk (T. Eltz, pers. obs.).

Trees may differ in their likelihood of serving as nest trees due to differences in acquiring hollow cores due to stem rot. Panzer (1976) measured core decay of 3586 trees in mixed dipterocarp forests in Sarawak. Across all tree sizes (>30 cm dbh) and species an average of 46% of trees were found to be hollow. Hollowness increased initially with tree size in the smaller size classes, but remained relatively constant (around 54 %) in trees above 60 cm dbh. This result is in agreement with our finding that estimated nest tree quality was largely independent of tree size. Notably, the percentage of hollow trees also varied between tree genera. Among dipterocarps Keruing (*Dipterocarpus*) had fewer hollow individuals than expected, perhaps because of specific wood characteristics (e.g. decay inhibitors; Panzer,

1976). Our finding that only two stingless bee nests were associated with the relatively common genus *Dipterocarpus* may be related to its apparent resistance against decay. On the other hand, Kapur (*Dryobalanops*) was relatively prone to core decay according to Panzer (1976), and was not represented among nest trees in this study. Other characters related to tree architecture, e.g. the accessibility of the hollow trunk sections, may influence the quality of different taxa as nest trees.

We have shown that a large fraction of bee nests are situated in commercial timber trees, many of which are members of the principal timber family Dipterocarpaceae. It is of special interest to see how nest frequencies relate to the representation of dipterocarps and other commercial timbers in Sabahan forests. On a coarse taxonomic level quantitative stock data are available for Deramakot Forest Reserve. During a planning inventory, trees in several hundred temporary plots were classified according to diameter and taxonomic as well as commercial affiliation (Chai and Amin 1994). Table 7 shows the percentages of trees classified as (i) dipterocarps, (ii) non-dipterocarp timber trees and (iii) non-commercial trees for trees larger than 60 cm dbh. Frequencies are contrasted with the respective percentages for stingless bee nest trees. The strong affiliation of nest trees with commercial trees roughly reflects general representation in the forest. Within the commercial classes, nest trees seem to be particularly well represented among non-dipterocarps, a finding that is partly based on the fact that *Eusideroxylon zwageri* (20 % of all identified nest trees) is part of this class.

Table 7 Percentage of dipterocarps, non-dipterocarp timbers and non-commercial trees among nest trees (this study) and among trees recorded during the medium-term planning inventory in Deramakot Forest Reserve (Chai and Amin, 1994).

	% of nest trees	% of trees in Deramakot inventory (only >60 cm)
Dipterocarpaceae	43.75	64.42
Commercial non-Dipterocarpaceae	51.25	28.85
Non-commercial species	5.00	6.73

Nest trees, logging, and stingless bee conservation

Harvesting of nest trees is very likely to cause mortality in bee nests, either directly because the nests are destroyed during felling, or indirectly because nests loose protection from predators or adverse effects of the environment (e.g. rain and/or termites). Even nests situated within tree bases that are left in place after harvesting are likely to suffer because predators can gain access to the colony through the hollow base core. This view is supported by the fact that we have very rarely found nests in tree stumps. In case of dead trees with base nests, the trees were still standing (so-called 'snags'), thus providing structural integrity.

Calculations based on our data on tree taxonomy, size and estimated log quality suggest that at least one-third of the nest trees would be considered potential timber trees for logging. The likelihood of whether a given nest tree will indeed be harvested is influenced by a range of factors including the intensity of timber extraction and the harvesting regulations followed by operators. Extraction intensity in forests in Sabah has varied considerably during past decades, partly depending on management system, but normally resulted in logged-over forests with drastically altered stand structure (Marsh et al., 1996). More recently, efforts have been made to shift practices towards Sustainable Forest Management (SFM) using Reduced Impact Logging (RIL)(Kleine and Heuveldop, 1993; Marsh et al., 1996). Current RIL guidelines published by the Sabah Forestry Department require detailed stock mapping, road and skid trail planning, and restrict harvesting to trees marked for felling by trained foresters (Lohuji and Taumas 1998). In order to maintain seed sources commercial trees are supposed to be retained if they are oversized (>120 cm dbh). According to our data this size restriction alone will reduce the proportion of harvested nest trees from 42,6 to 34,0 % in comparison to conventional regulations lacking an upper diameter limit. The positive effect on bee populations will be even greater because nests tend to be more heavily aggregated in oversized trees. If RIL guidelines are followed by operators the impact on bees will be further reduced by restricting harvesting to slopes below 25° and by retaining harvestable trees in areas with insufficient regeneration. Furthermore, RIL has been demonstrated to reduce operational damage on non-harvest trees (Marsh et al. 1996), an effect that may be particularly beneficial for bees that nest in dead or low-quality trees with reduced structural stability. In summary, the strict implementation of existing RIL guidelines is highly recommendable in the light of stingless bee conservation and the maintenance of meliponine pollination in managed forests.

Other feasible measures to reduce the direct impact of harvesting on bee colonies, e.g. marking of nest trees for retention, are desirable but probably unrealistic in view of the current situation of the forestry sector in Sabah and Southeast Asia in general. The current steep decline of commercially manageable forests in Sabah has led to intensified timber exploitation in the remaining fragments (Putz et al. 2000). In order to meet the planned forest productivity (annual allowable cut (AAC)) in sustainably managed forests, Trockenbrodt et al. (2001) suggest to increase the use of timber in intact fractions of hollow trunks as well as large branches. The approach is aimed at (i) reducing logging waste, and (ii) at increasing the use of timber resources available in poorly stocked management compartments. Whereas the first incentive is clearly recommendable from both economic and ecological points of view, the second implies increased harvesting of hollow trees. This, in turn, may partly offset some of the benefits of SFM and RIL for cavity-dependent wildlife (see above). An obvious trade-off exists between increasing timber productivity and maintaining aspects of ecological integrity in managed forests. More applied studies like that of Trockenbrodt et al. (2001) are needed in order to judge whether the amount of timber volume gained by an increased use of hollow trees justifies the additional damage imposed on the forest ecosystem.

3.4.5 Conclusions

We have shown that stingless bees in dipterocarp forests are closely linked to potential harvest trees due to their way of nesting. Selective logging is likely to cause direct mortality to a substantial fraction of residual bee colonies because harvesting of nest trees will destroy or expose bee nests. Due to the fact that meliponine colonies are long-lived and have low fecundity, impact from logging may have lasting effects on bee populations. However, our data also show that potential conflict between timber extraction and bee conservation is reduced when RIL guidelines were applied for estimating logging impact. Harvesting guidelines that retain high proportions of large and hollow trees should be promoted in order to preserve stingless bee pollination in Sustainable Forest Management.

4 BETWEEN-SITE COMPARISONS OF SPECIES RICHNESS AND ABUNDANCE: PATTERNS AND CAUSES OF VARIATION

4.1 Survey of stingless bees and honey bees using honey-water baits

4.1.1 Introduction

How to measure apid bee abundance and species richness in different forest types and localities? The number of nests per bee species per site (nest density) is likely to be the closest possible correlate of true bee abundance in a given area. However, nest surveys are of limited value in assessing bee diversity due to very high efforts involved in locating sufficient numbers of cryptic nests. Alternative methods are required. Potential methods include (i) flower monitoring and (ii) honey-water baiting. Flower monitoring has been successfully used to study bee communities in selected locations in the Neotropics (Heithaus 1979a, Wilms et al. 1996). In a comparative study, Rincon et al. (1999) surveyed understory bees at flowers in logged and silviculturally treated rainforest plots in Costa Rica. Their results are symptomatic for problems implicit with the use of flower monitoring: Numbers of species and individuals of bees strongly depended on numbers of flowering plants present in plots at the time of the study, but not on plot treatment (Rincon et al. 1999). Due to the spatial and temporal variation of flowering, flower monitoring for between-site assessment of bee diversity is bound to require large efforts over extensive periods of time. Additional problems arise from restricted access to the forest canopy where most flowering is likely to occur (Appanah 1990, Momose et al. 1998).

Honey-water baiting was introduced by (Wille 1962, ‘A technique for collecting stingless bees under jungle conditions’), upon noticing that flowers and visiting bees are difficult to access in closed forest. The method consists of spraying diluted honey (honey-water) on ground-level vegetation. Bees, mostly apines, and other flower-visiting insects arrive after minutes or hours and consume droplets from leaves. Although easily applicable, there have been only few studies that used the method for bee surveys (Inoue et al. 1990, Salmah et al. 1990, Roubik 1996). Salmah et al. (1990) used honey-water spraying along with flower monitoring to study apid bee diversity along altitudinal and disturbance gradients in fragmented landscapes of Sumatra. 22 of 29 species present in the research area were attracted

to honey baits in variable numbers. Combining data from flower monitoring with those of honey-water spraying, the study found that high species richness and abundance of apid bees was associated with the proximity of primary forest habitats (Salmah et al. 1990). Based on these promising results, and after failed trials with sticky and flight intercept traps, it was decided to use honey-water spraying for an assessment of apid bee richness in the primary and disturbed forests in Sabah.

4.1.2 Methods

Honey-water spraying was used to attract foraging stingless bees and honeybees in twelve sites in 1998, with partial replication in 1999 (see below). An individual assay consisted of spraying 30 marked spray stations positioned along a pair of two neighboring transects of a given forest site (Fig. 4; section 2.2). A 33 % (volume) honey-water solution was used for spraying. At each spray station ten thrusts (~150 ml) of honey-water from a custom-made insecticide vaporizer were sprayed on a patch of vegetation, adding up to a total of 4.5 l of honey-water per assay. Spraying started between 8.00 and 9.00 hours and was completed after approximately 90 minutes, the duration of a walk around one 600 x 200 m grid mesh. Bees were recorded at the spray stations during a second circulation that started 150 minutes after spraying was initiated, and was completed within 240 minutes. This time schedule had proven to yield maximal numbers of species and individuals of stingless bees during previous tests. Normally bees could be identified directly at the stations. In uncertain cases vouchers were collected and later identified using published keys and descriptions (Schwarz 1937, Schwarz 1939, Sakagami 1978, Sakagami and Inoue 1985, Rinderer et al. 1989, Ruttner et al. 1989, Sakagami et al. 1990), as well as reference material provided by D. Roubik and the FRC Entomological Collection. On each spraying station numbers of individuals of each species were counted or estimated and recorded in five abundance classes: 1, 2-5, 6-20, 21-50, >50 individuals. Honey-spraying was generally restricted to clear or slightly cloudy days. In case of afternoon rainfall before completion of the assay, accumulated data were discarded and the assay was repeated on a different day.

Using this sampling regime all pairs of transects of all forest sites (except Sepilok Laut and N; see section 2.2) except were sampled once between February and May in 1998. Repeated spraying of a subset (one transect pair per site) was done between February and May in 1999. In 1999, transect pairs of selected sites (A, C, E, G, M) were sprayed repeatedly over the entire field season. For those, means of measured parameters were calculated across temporal

replicates. The following measures of bee diversity and abundance were analyzed: The number of bee species per transect-pair (assay), the mean number of bee species per spray station, and the mean number of bee individuals per spray station. All three measures were analyzed separately for stingless bees and for honeybees. ANOVA with repeated measures design was used to test for effects of forest type and year on bee diversity and abundance.

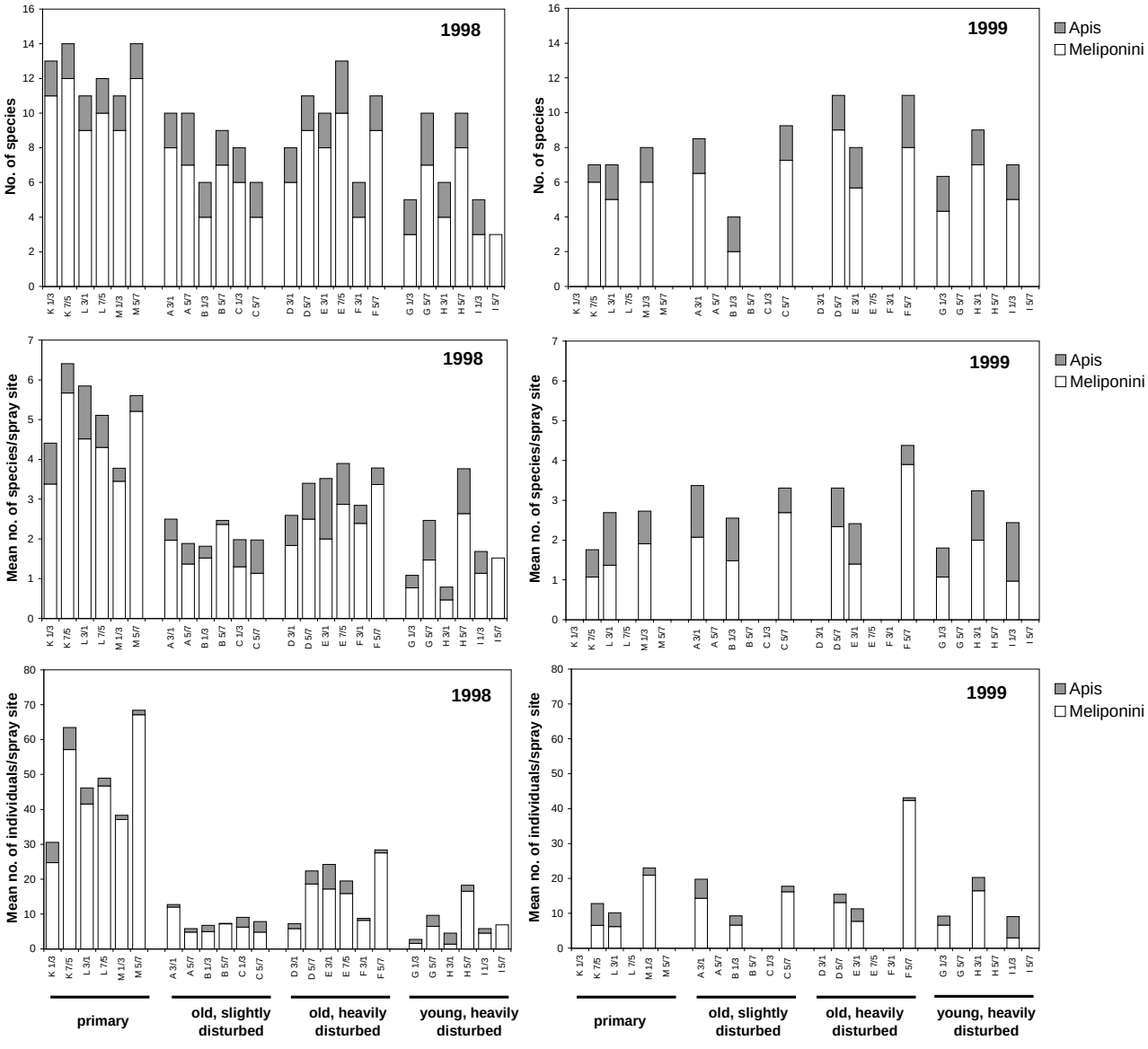

Fig. 21 Summary of results of honey-water spraying assays in twelve forest sites grouped by locality and disturbance regime. Data are shown separately for stingless bees (Meliponini) and honey bees (Apis). Note differences between years (left and right).

Table 8 ANOVA effects of forest type (disturbance regime) and year on stingless bee species richness and abundance at honey-water spray stations in twelve forest sites. Forest type was used as the independent variable (four levels), with year (two levels) as repeated measures factor.

Dependent variable: No. of species/site

Effect	FG	N (valid)	FG (Error)	F	p-Wert
Forest type	3.00	12.00	8.00	5.28	0.027
Year	1.00	12.00	8.00	2.49	0.153
Forest type x year	3.00	12.00	8.00	6.74	0.014

Dependent variable: Mean no. of species/bait

Effect	FG	N (valid)	FG (Error)	F	p-Wert
Forest type	3.00	12.00	8.00	5.47	0.024
Year	1.00	12.00	8.00	2.04	0.191
Forest type x year	3.00	12.00	8.00	8.92	0.006

Dependent variable: Mean no. of individuals/bait

Effect	FG	N (valid)	FG (Error)	F	p-Wert
Forest type	3.00	12.00	8.00	3.99	0.052
Year	1.00	12.00	8.00	1.14	0.316
Forest type x year	3.00	12.00	8.00	5.95	0.020

Table 9 ANOVA effects of forest type (disturbance regime) and year on honeybee (*Apis*) species richness and abundance at honey-water spray stations in twelve forest sites. Forest type was used as the independent variable (four levels), with year (two levels) as repeated measures factor.

Dependent variable: No. of species/site

Effect	FG	N (valid)	FG (Error)	F	p-Wert
Forest type	3.00	12.00	8.00	2.05	0.185
Year	1.00	12.00	8.00	0.06	0.811
Forest type x year	3.00	12.00	8.00	2.05	0.185

Dependent variable: Mean no. of species/bait

Effect	FG	N (valid)	FG (Error)	F	p-Wert
Forest type	3.00	12.00	8.00	0.18	0.910
Year	1.00	12.00	8.00	5.29	0.050
Forest type x year	3.00	12.00	8.00	2.67	0.119

Dependent variable: Mean no. of individuals/bait

Effect	FG	N (valid)	FG (Error)	F	p-Wert
Forest type	3.00	12.00	8.00	0.40	0.756
Year	1.00	12.00	8.00	0.92	0.365
Forest type x year	3.00	12.00	8.00	1.91	0.206

4.1.3 Results

Species richness and abundance of social bees

A total of sixteen species of stingless bees (including one undescribed form, see Table 11) and four species of honeybees were attracted to honey-water spray stations. Of those, the giant honeybee *Apis dorsata* was excluded from further analysis because its presence and abundance was likely influenced by patterns of regional migration (Dyer and Seeley 1994). Results for the remaining species are presented in Fig. 20. Patterns of stingless bee species richness and abundance were clearly different between years. Whereas there were pronounced differences between forest types in 1998 in all parameters analyzed (see Eltz et al., 1998), no differences were apparent in 1999. The results of ANOVA are presented in Table 8 (for stingless bees) and Table 9 (for honeybees). In stingless bees, there were significant or marginally significant effects of forest type on all three parameters analyzed. However, significant interactions between year and forest type in all cases indicated that the findings cannot be regarded as conclusive. Obviously, much of the observed variation in stingless bee diversity and abundance could be attributed to temporal fluctuations rather than between-site effects. Changes between years were most striking in primary sites in Danum and Sepilok: Whereas honey-spraying had produced large numbers of species and individuals in 1998, corresponding spray stations were almost devoid of bees one year later.

Table 10 Number of spray stations visited by the different species of bees. Totals are given, as well as numbers of stations visited by a given species for each of the five abundance classes. Total number of sites sprayed was 1800. Data include all assays in 1998 and 1999.

	No. of baits visited by species						Percent of baits
Species	1 individual	2 - 5	6 - 20	21 - 50	> 50	Total	visited
Apis andreniformis	7	7	10	3	1	28	1.6
Apis cerana	241	348	211	18	3	821	45.6
Apis koschevnikovi	182	251	132	15	2	582	32.3
T. (Geniotrigona) thoracica	3	0	1	0	0	4	0.2
T. (Heterotrigona) erythrogastra	1	0	0	0	0	1	0.1
T. (Heterotrigona) itama	75	61	59	16	4	215	11.9
T. (Homotrigona) fimbriata	53	42	35	26	1	157	8.7
T. (Lepidotrigona) terminata	97	85	72	20	5	279	15.5
T. (Lepidotrigona) ventralis	41	23	29	12	7	112	6.2
T. (Odontotrigona) haematoptera	5	4	8	1	0	18	1.0
T. (Tetragonula) collina	54	10	0	1	0	65	3.6
T. (Tetragonula) fuscobalteata	37	57	50	9	4	157	8.7
T. (Tetragonula) laeviceps	112	314	483	201	75	1185	65.8
*T. (Tetragonula) laeviceps-group**	10	11	15	7	2	45	2.5
T. (Tetragonula) melanocephala	271	434	220	21	0	946	52.6
T. (Tetragonula) melina	30	45	31	9	1	116	6.4
T. (Tetragonula) rufibasalis	14	2	1	0	0	17	0.9
T. (Tetrigona) apicalis	12	27	24	6	4	73	4.1
T. (Tetrigona) binghami	66	106	119	90	87	468	26.0

* represents a probably undescribed species of the subgenus Tetragonula that can only be distinguished from *T. laeviceps* by its smaller size. Possibly identical with the small variety of *T. laeviceps* mentioned in (Sakagami et al., 1990).

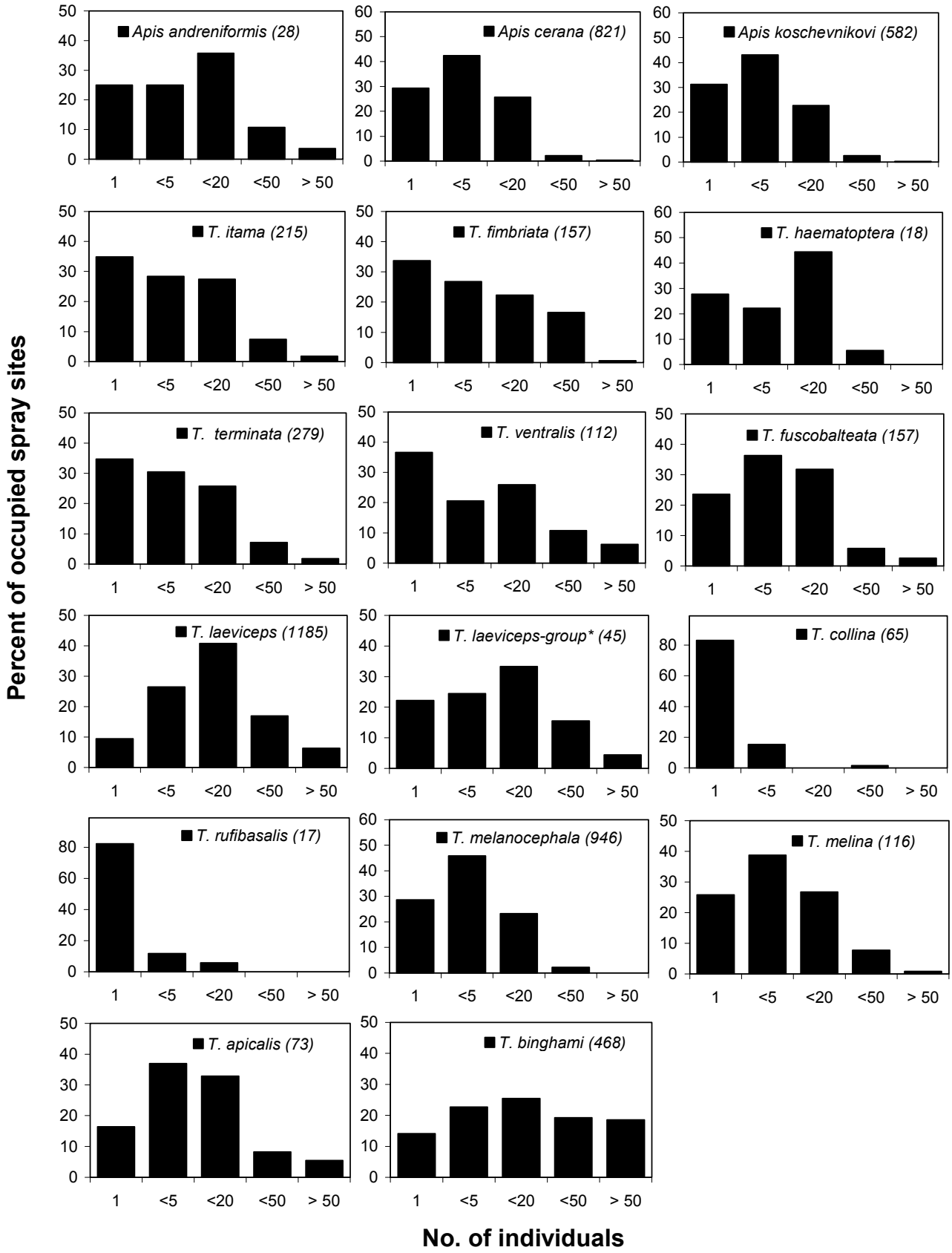

Fig. 22 Numerical presence of apid bee species at honey-water spray stations (total N=1800) in 1998 and 1999 (all sites pooled). Percentages of baits are shown that were visited by species according to the number of individuals present (five abundance classes). Numbers in parentheses behind species names are totals of visited baits.

Honeybees, mostly *A. cerana* and *A. koschevnikovi*, represented only a small fraction of bees at the spray stations. In contrast to stingless bees no effects of forest type and/or year were observed.

Patterns of relative abundance of apid bee species

Species of bees varied drastically in their incidence at honey spray sites. Table 10 summarizes the results across all localities and over both years. *T. laeviceps* was most frequently encountered (65.8 % of spray stations), followed by *T. melanocephala* (52.6 %), *Apis cerana* (45.6 %) and *A. koschevnikovi* (32.3 %). Other species visited spray stations less frequently. Species also differed in the number of individuals that were present at visited stations (Table 10, Fig. 22). Generally, the incidence and frequency of different species of meliponines at honey baits is probably *not* closely related to their relative abundance in the forest. For instance, *T. collina* was the most common species during quantitative nest surveys (see section 4.2), but the species was rare at honey baits. Six other species evidently present in the area (see Table 11) were not recorded at spray stations at all: Of those *H. pendleburyi* was also relatively common during nest surveys (see section 4.2). Incidence and frequency of bee species probably depends mostly on foraging behavior and recruitment system. In the neotropics, the speed of discovering artificial honey baits varied drastically between different species of meliponines (Hubbell and Johnson 1978, Johnson 1983). The differences were related to foraging strategy: Pheromone-using group-foragers were slow to discover baits, whereas solitary foraging species were relatively quick. In Borneo, *T. melanocephala* is normally the first meliponine bee to arrive at freshly sprayed stations, followed by *T. laeviceps*. Both species also located large fractions of spray stations. *T. melanocephala* was mostly present in small numbers (Fig. 22), suggesting that the species forages solitarily without using pheromone communication. *T. laeviceps* sometimes arrived in large numbers, perhaps indicating a facultative group-foraging strategy (Johnson 1983). Other species like *T. ventalis*, *T. apicalis* and *T. binghami* take considerably more time to discover spray stations and visited fewer baits. If present, however, they frequently arrived in considerable numbers (hundreds of bees, see Fig. 22). These species probably represent group-foragers that use scent-trails to communicate food sources. *T. canifrons*, a large and aggressive species (Nagamitsu and Inoue 1997) of Borneo, is perhaps most extreme in terms of mass recruitment. It was frequently observed at patches of road-edge flowers in Deramakot and also came to dominate nearby honey baits. However, the species was never attracted to the more cryptic and perhaps less rewarding spray stations of the regular assays. Other factors

influencing numerical presence at spray stations may include specific stratum preferences (Nagamitsu and Inoue 1997, Nagamitsu et al. 1999) and differences in selectivity for certain nectar (honey-water) concentrations (Roubik and Buchmann 1984, Nagamitsu and Inoue 1998, Biesmeijer et al. 1999b).

Table 11 Presence or absence of species of Apidae in primary and disturbed forests in Sabah. Incidences are pooled for sites with the same degree and history of disturbance.

	primary			disturbed		
	total	Sepilok	Danum	old, slightly disturbed	old, heavily disturbed	young, heavily disturbed
No. of sites	3	1	2	3	3	3
Sites	K, L, M	K	L, M	A, B, C	D, E, F	G, H, I
Apis andreniformis	**x**	**x**		**x**	**x**	**x**
Apis cerana	**x**	**x**	**x**	**x**	**x**	**x**
Apis koschevnikovi	**x**		**x**	**x**	**x**	**x**
T. (Geniotrigona) thoracica	**x**	**x**		**x**	**x**	
T. (Heterotrigona) erythrogastra				**x**		
T. (Heterotrigona) itama	**x**	**x**	**x**	**x**	**x**	**x**
T. (Homotrigona) fimbriata	**x**	**x**	**x**	**x**	**x**	**x**
T. (Lepidotrigona) terminata	**x**	**x**	**x**	**x**	**x**	**x**
T. (Lepidotrigona) ventralis	**x**	**x**	**x**	**x**	**x**	
T. (Odontotrigona) haematoptera	**x**	**x**		**x**	**x**	**x**
T. (Tetragonula) collina	**x**	**x**	**x**	**x**	**x**	**x**
T. (Tetragonula) fuscobalteata	**x**	**x**	**x**	**x**	**x**	**x**
T. (Tetragonula) laeviceps	**x**	**x**	**x**	**x**	**x**	**x**
*T. (Tetragonula) laeviceps-group**	**x**	**x**	**x**		**x**	
T. (Tetragonula) melanocephala	**x**	**x**	**x**	**x**	**x**	**x**
T. (Tetragonula) melina	**x**	**x**	**x**	**x**	**x**	**x**
T. (Tetragonula) rufibasalis	**x**		**x**	**x**	**x**	
T. (Tetrigona) apicalis	**x**	**x**	**x**	**x**	**x**	
T. (Tetrigona) binghami	**x**	**x**	**x**	**x**	**x**	**x**
Sum	18	16	15	18	18	13

* represents a probably undescribed species of the subgenus *Tetragonula* that can only be distinguished from *T. laeviceps* by its smaller size. Possibly identical with the small variety of *T. laeviceps* mentioned in (Sakagami et al., 1990).

Not recorded during regular honey-spraying assays, but found on other occasions (n=nest; fl=at flowers; hs=honey spraying)

Hypotrigona (Pariotrigona) pendleburyi	**x** (n)	**x** (n)	**x** (n)	**x** (n)
T. (Lepdotrigona) nitidiventris			**x** (fl)	
T. (Lophotrigona) canifrons			**x** (fl, hs)	**x** (fl, hs)
T. (Tetragonula) drescheri		**x** (hs)		
T. (Tetragonula) geissleri	**x** (n)			

Additonal meliponine species listed for Borneo (Sakagami et al. 1990, partly based on Schwarz 1937, 1939)

Hypotrigona (Lisiotrigona) scintillans	
T. (Platytrigona) hobbyi	
T. (Tetrigona) peninsularis	perhaps only variety of *T. apicalis* (Schwarz 1939)
T. (Tetrigona) melanoleuca	
T. (Trigonella) moorei	nests within *Crematogaster* carton-nests (Sakagami et al. 1989), perhaps confined to open habitats
T. (Tetragonula) atripes	
T. (Tetragonula) fuscibasis	probably only variety or even callow stage of *T. collina* (Schwarz 1937, 1939)
T. (Tetragonula) reepeni	
T. (Tetragonula) sarawakensis	

Stingless bee communities

Data from honey-spraying assays were extremely variable over time for sites that were sampled repeatedly. Accordingly, it is difficult to draw conclusions concerning bee community composition in different forest types. Table 11 lists all apid species recorded during honey spraying in the respective sites and localities, neglecting differences in numbers of sites and temporal replicates. Thirteen of 19 species were recorded in primary as well as in all three disturbed forest types. No differences in species richness or composition were apparent between primary and old disturbed forest (all having a total of 18 species). However, the young, heavily disturbed sites (G, H, I) in Deramakot were comparatively low in species number (13 species), a finding that corresponded to generally low values of bee numbers in both years (see Fig. 20). Species missing from samples in young, heavily disturbed sites are species that were generally rare at honey baits. It is hypothesized that their absence is due to a general reduction of social bee nest density (rarefaction, thinning) in recently logged forests rather than representing a directional shift in community composition (local extinction of sensitive species). Additional honey-spraying assays, or an increase of the area sprayed, would probably yield most or all species recorded from other sites. However, in combination with data from nest surveys (very low nest densities in G, H, I, see section 4.2), low species richness at honey baits suggests that bee populations have not yet recovered in recently logged sites.

Comparison with the regional species pool

During assays of honey-spraying 16 species of meliponines were recorded. An additional six species were found at their nest sites, at flowers or during non-regular honey-spraying, resulting in a total of 22 species of stingless bees. Of those, all but one (the undescribed small form within the difficult laeviceps-group) were also listed for Borneo by Sakagami et al. (1990). The same authors list eight additional species or forms from Borneo, mostly based on publications by H. F. Schwarz (1937, 1939; Table 11).

4.1.4 Discussion

Between-year variation was pronounced in results of honey-spraying assays in the present study. Whereas clear effects of disturbance and forest type were evident in 1998, no such effects were found one year later. On average, fewer bees came to spray stations in 1999. Reasons for the observed patterns remain obscure. The two years were certainly different in

climatic conditions during the respective field seasons. Between March and May 1998 the whole of Borneo experienced a severe dry spell caused by the Pacific ENSO event. Dry and sunny weather conditions were accompanied by increasing flowering activity, at least in Deramakot (see section 3.1). In contrast, the same months in 1999 were conceivably rainy. However, honey-water spraying was confined to days with reasonably good weather in both years (in case of rainfall data were discarded). Thus, diverging results of the two years are not likely explained by weather as such. Instead, it is hypothesized that different climatic conditions interacted with other parameters that in turn affected bee incidence at spray stations. Those parameters are likely to include (i) flowering and floral resource availability during months prior to spraying, (ii) corresponding colony strength (bees/nest) of stingless bees, and (iii) natural resource availability at the time of spraying. Stingless bees are known to be energy-conservative foragers that reduce foraging effort in case of low floral resource levels (Roubik 1982b, Biesmeijer and Toth 1998). Thus, reduced colony strength and low foraging effort could explain low bee numbers in rainy 1999.

No simple explanation exists for the pronounced effects of forest type on bee numbers in 1998. Two arguments suggest that the effect was *not* based on real differences in bee abundance and diversity in the respective sites: First, data from nest surveys show that most variation in bee abundance is found between Sepilok and the remaining forests (see section 4.2), and not between forest types. Second, the extreme reduction of bee numbers from 1998 to 1999 in primary sites is certainly not based on colony mortality. Mortality of bee colonies was very low over the entire study period (1997 to 2000; see section 4.2). Instead, it is hypothesized that the effect of forest type is due to local differences in flowering between groups of sites and localities. As outlined in the site descriptions (section 2.2), forest type (disturbance regime) of sites was not independent of location. Primary sites were located in completely different forest reserves (Sepilok, Danum Valley), and differentially disturbed forest sites were at least grouped locally within Deramakot. Although no quantitative flowering data were collected in the different locations it was the general impression that local to regional scale differences in phenology do exist. Perhaps, these differences led to differences in foraging activity of bee colonies (see above). Differences in natural nectar availability at the time of the study may also have influenced the relative attractiveness of baits, creating additional variation in bee incidence. Thus, the extremely high bee numbers in primary sites in 1998 could have been the result of a combination of high colony levels (due to previously high resource availability) and high a attractiveness of honey-water baits to bees (due to currently low levels of flowering).

The reasons for observed variation in baiting results remain speculative. However, it is clear that pronounced temporal effects severely reduce the applicability of the method in bioassessment. It has become clear that acquiring meaningful data on local bee diversity would involve frequent repeated spraying over extensive periods of time. The required effort is likely to be outside the scope of most applied projects concerned with assessing management impact on biodiversity. Low temporal repeatability of baiting results was also evident in two studies on neotropical meliponines (Baumgartner and Roubik 1989, Breed et al. 1999), and fluctuations in bait attractiveness may be a general problem of resource-based baiting methods (Pearson and Dressler 1985, Ackerman 1989).

In summary, rapid but accurate assessment of stingless bee abundance and diversity seems impossible with available methods. At present, there are no alternatives to measuring nest density in studies of population and community ecology of stingless bees.

4.2 Factors limiting stingless bee nest density in primary and regenerating dipterocarp forests of Sabah, Malaysia

4.2.1 Introduction

It is a major goal of ecology to understand what factors determine the abundance of individuals in their habitats. Food supply often has a limiting effect on animals (Power 1984, Martin 1987, Butynski 1990, Deslippe and Savolainen 1994), but other factors like climatic conditions or predation may keep local population densities below those at which food shortages occur (Franks and Fletcher 1983, Andrewartha and Birch 1984). In the case of social insects that frequently live in permanent and populous colonies, local colony density may be limited by the availability of suitable sites for nesting. Evidence for nest site limitation has been obtained for some populations of ants (Herbers 1986, Kaspari 1996).

To date only one study has addressed ecological factors that are potentially limiting stingless bee populations (Hubbell and Johnson 1977, see below). Stingless bees are distributed throughout the tropics and live in perennial colonies of a few hundred to several thousands of workers (Sakagami 1982, Roubik 1989), with the majority of species nesting in pre-formed cavities in live trees (Roubik 1979b, Roubik 1983, Sakagami et al. 1983b, Salmah et al. 1990). All are generalist foragers, and some species are known to use floral resources (nectar, pollen) from more than a hundred plant taxa over the course of several seasons in a given habitat (Wilms et al., 1996). Diet overlap between different stingless bee species is often high as determined by studies of flower visitation and pollen foraging (Heithaus 1979a, Ramalho 1990, Wilms et al. 1996, Eltz et al. in press-a, section 3.1), indicating high potential for interspecific competition for food. Hubbell and Johnson (1977) intensively studied nest sites and nest dispersion of five species of stingless bees in a tract of dry-forest in Costa Rica. Bee species were rather indiscriminant in their choice of nest trees, and suitable cavities seemed not to be in short supply. Instead, two lines of evidence suggested that population densities were primarily limited by food. First, nest density of the different species of bees was negatively related to the specific colony weight, suggesting that nest densities were influenced by metabolic requirements. Second, four out of five species showed uniform patterns of nest dispersion, indicating that competition for food may set limits to nest densities (Hubbell and Johnson 1977). Patterns of intraspecific and interspecific nest dispersion were particularly pronounced in group-foraging species that are known to behave aggressively towards alien

individuals of their own and/or other species during encounters at food resources (Johnson and Hubbell 1974, Johnson and Hubbell 1975, Hubbell and Johnson 1978, Johnson 1983). Meliponine nest dispersion has received less attention in the Paleotropics, but emerging data from Bornean rain forests suggest that patterns are quite different to those found in Central America: nests of the more frequently encountered species are often aggregated in nest trees (Roubik 1996, Nagamitsu and Inoue 1997, Eltz et al. in press-a, Eltz et al. submitted-b, sections 3.1 and 3.4).

Very little is known about how stingless bees respond to forest disturbance imposed by human activities. Selective logging for timber extraction can drastically reduce the abundance of large trees in residual stands (Cannon et al. 1994, Marsh et al. 1996) and may thus create a situation in which nest sites become a limiting resource for cavity nesting bees. Forest management has been shown to severely reduce the availability of tree cavities as well as population densities of hole-nesting birds and marsupials in temperate areas of North America and Australia (Saunders et al. 1982, van Balen et al. 1982, Lindenmayer et al. 1991, Bennett et al. 1994, Newton 1994, Gibbons and Lindenmayer 1996). Hubbell and Johnson (1977) speculated that the colonization of second-growth forest by stingless bees will depend on tree size, and that species depending on large cavities will be excluded from early successional stages. By changing stand structure, light environment and microclimatic conditions, forest disturbance may also affect flowering plants and floral resource availability (Rincon et al. 1999). To date, the only study that has addressed the influence of human disturbance on stingless bees is that of (Salmah et al. 1990) in Central Sumatra, covering a wide range of habitats from primary forests to city areas. Stingless bees were censused at flowers and honey baits, and both species diversity and abundance of meliponines decreased along the disturbance gradient.

In the present study we measured nest density of stingless bee populations and communities in fourteen sites situated in primary and logged dipterocarp forests in lowland Sabah, Malaysia. A factorial design was used and selected sites were grouped within four disturbance regimes according to logging history and intensity. In order to evaluate hypotheses on causal factors involved in creating the observed variation in nest density, we collected large amounts of background data on bee nests, pollen diet and habitat parameters in the different sites. We focussed on three main hypotheses of population control, potentially interacting to varying degrees with human disturbance:

1. Stingless bees are chiefly limited by nest predation. In contrast to a shortage of food that will mostly reduce colony growth and reproduction, intensive nest predation is likely to increase mortality of existing colonies. If predation is responsible for variation in nest densities, survival of existing colonies should also vary between sites. In order to test this prediction we monitored colony survival over up to four years.

2. Stingless bees are chiefly limited by nest sites. In order to evaluate nest site limitation we related stingless bee nest density to a relative estimate of nest tree availability in the different sites.

3. Stingless bees are chiefly limited by food resources. Diets of Asian meliponines principally consist of two kinds of substances: nitrogen-rich pollen and sugar-rich nectar, both collected separately or synchronously by foraging workers from floral and non-floral sources in the habitat. The availability of floral resources is highly variable over time in Bornean forests (Sakai et al. 1999), and food is probably in short supply at least occasionally during the life of an individual colony. In order to evaluate the importance of food resources in limiting bee populations we used two different approaches. First, nest density was related to qualitative aspects of pollen diet (composition, diversity, origin) that may be indicative of differences in resource levels. Second, we monitored foraging activity and the amount of pollen harvested by colonies. Data from studies in the Neotropics suggest that stingless bees are employing an energy-conservative foraging strategy, e.g. reduce foraging activity in favor of individual longevity in the case of low resource levels (Roubik 1982b, Biesmeijer and Toth 1998). This strategy is supposed to increase colony survival at the cost of productivity. Given that resource availability is indeed variable between sites with high and low nest density, foraging activity and pollen harvest of colonies should also vary accordingly.

4.2.2 Methods

Study Sites

Between 1997 and 2000 we studied stingless bees in a total of 14 research sites located in primary and logged forests in lowland Sabah, Malaysia. Localities and sites are described in Section 2.2.

Nest survey

Most stingless bee nests in Southeast Asian forests are found in association with large living trees, situated either in pre-existing cavities in the trunk or underneath the tree bases (Salmah et al. 1990, Roubik 1996, Eltz et al. submitted). In order to quantify nest density in our sites we searched for bee traffic and nest entrance tubes in bases and trunks of all trees larger than 30 cm dbh situated in 20m-corridors along the established transects (see section 2.2, Fig. 4). Nest counts were transformed into nest density per hectare by incorporating area searched (length of transect x 20 m). The total area searched was 4.8 ha per site except in Sepilok Laut where only 2.8 ha were covered. Nest trees and individual nests were marked with spray paint and flagging tape. Whenever possible we made bee species identifications at the site or collected voucher specimens. In case of colonies high up in trees, identifications could normally be made by inspection of bee size and color as well as the characteristic shape of the resinous entrance tubes using binoculars. Due to the impressive height of many trees in dipterocarp forests (up to 60 m) we certainly missed bee nests, especially those situated close to or within the canopy. Thus, nest densities can only be considered as relative indices for between-site comparisons. So far, absolute nest densities have never been determined for entire stingless bee communities in any tropical forest.

Stingless bee nests located during nest surveys as well as additional nests found in and around our research sites were checked repeatedly over up to four years. Presence or absence of bees in the entrance tubes of known nests indicated colony survival or death. Mean yearly colony mortality was calculated for localities with sufficient numbers of nest.

Pollen diet of a focal bee species

We quantified pollen diets of colonies of *Trigona (Tetragonula) collina* in five sites that encompassed the complete range of observed nest densities (see below). *T. collina*, a medium-sized black bee, is the most frequently found stingless bee species in forests in Borneo (Roubik 1996, section 3.4, this section). Nests are frequently aggregated underneath large trees (see section 3.4). Pollen diets were assessed by microscopic analysis of pollen in colony garbage. Workers of *T. collina* and many other stingless bees expel from their nests small pellets of refuse that contain substantial amounts of pollen exines (~ 20% of pellet dry weight in *T. collina*), and these pellets can be collected with the help of special funnel traps that are installed in front of nest entrances (Eltz et al. in press-b, section 3.3). Garbage pollen closely resembles pollen import, but with a certain time-lag. The ways collected pollen grains

take until their exines are expelled as bee garbage are likely to include direct consumption and defecation by adult bees, delayed defecation of brood provisions by bee larvae (meconia are probably a major fraction of the expelled pellets), as well as consumption and defecation of pollen that has been stored for some time in pollen pots. Consequently, the temporal turn over of pollen in garbage is much slower than that of foraged pollen taken from the corbiculae of returning foragers (Eltz et al. in press-b, section 3.3). In practice this means that sampling garbage pollen at relatively long intervals (up to several months) will yield reasonable estimates of long-term colony pollen use. Between April 1999 and November 2000 we collected one to five (mean: 2.6) repeated garbage samples from each of a total of 38 colonies of *T. collina* situated at Sepilok Laut (8 colonies), Sepilok K (8), Danum Valley M (3), Deramakot A (8) and Deramakot G (11). Sampling dates were clustered over time within five distinct sampling periods: April-May 1999, September-October 1999, March-May 2000, July 2000, and November 2000. Total observation time and periods differed between sites (7 to 19 months, see Fig. 27).

An individual sample consisted of ten garbage pellets. Sample processing, microscopic slide making and the grain volume-based analysis of pollen composition followed the protocol described in Eltz et al. (in press-b) and section 3.3. The analysis yielded values of the relative representation (in % volume) of different pollen types in a given sample as well as measures of pollen type richness and evenness (Shannons J; Pielou 1966) per sample. Grain volume is a good indicator of grain mass and protein content across both zoophilous and anemophilous plant taxa (Roulston et al. 2000). Taxonomic identifications of morphotypes to the level of plant family, genus or species (or taxonomic 'type') were made from original slides by S. v. d. Kaars, partly by comparison with reference pollen collected from flowers in the bees' habitat. Similarity of pollen composition between samples was quantified using the Steinhaus-coefficient S (Legendre and Legendre 1998), with S=2W/(A+B), where W is the sum of minimum percentages of the various types, and A and B are the sums of the percentages of all types in each of two samples (see also section 3.3). Turn-over (dissimilarity) was calculated as 1-S.

Foraging activity and pollen foraging of *T. collina*

We obtained estimates of foraging activity of 22 colonies of *T. collina* situated in three sites encompassing part of the observed range of nest densities (sites A, G, K). Foraging activity was estimated by measuring entrance tube traffic with the help of electronic bee counters developed in the Department of Animal Ecology and Tropical Biology in Würzburg (G.

Vonend and T. Eltz, in preparation). An individual counter unit consisted of an infrared light barrier attached to the entrance tube of a bee colony (Fig. 23) and an interface module that controlled the barrier and cumulatively counted interceptions (regardless of direction) by bees. Accumulated counts were read in five-minute intervals by a controller/data logger (Tiny Tiger, Fa. Wilke Technologies, Germany). Up to four interface units could be synchronously attached to one controller/data logger. The controller/data logger and associated interface modules were housed in a robust and water proof aluminium box permanently attached to a given nest trees. From there cables led to one to four bee nests (and light barriers) aggregated in the base of the nest tree. The energy consumption of stations was minimized by pulsing light barrier operation (1:99 at 65 Hz) and by automatically switching off the controller/data logger between reading intervals. Configured in this way, stations could be run independently for ten to 14 days on three rechargeable batteries (C type, 1.5 V). A total of nine stations (three per site) were operated between February 27 and July 23 2000, almost permanently recording tube traffic of 22 colonies (8, 7 and 7 in the respective sites, see example curves in Fig. 24). Manual control counts of bees passing through the light barrier box were done repeatedly in all colonies in order to detect counter malfunction. Across all nests there was a tight almost 1:1 linear relationship between electronic and manual counts (Fig. 25), and counter sensitivity did not vary between sites (ANOVA: $N=67$, $F_2=1.52$, $p=0.23$). A linear relationship was also found between electronic counts and airborne bee traffic (manual counts of bees taking off and landing) ($N=44$, $R^2=0.93$, $p<0.001$). The proportion of bees that were actually departing or returning foragers decreased over the day ($R^2=0.52$, $p<0.001$). It was generally high in the morning (81% on average between 7:00 and 10:00), and daily sums of interceptions between 7:00 and 10:00 a.m. were used as an index of foraging activity for comparisons between nests and sites.

We used modified garbage traps (Eltz et al. in press-b, section 3.3) in order to quantify pollen import of the 22 colonies. In addition to collecting garbage, the modified traps strip off corbicular pollen from returning foragers and pollen pellets are collected in sampling buckets. Traps were placed before nest entrances between 8:30 and 14:30 on nine to 12 sampling days per nest between February and July. Only a small fraction of incoming pollen loads is stripped off bees and the trap is most efficient during the first two hours of its daily operation. The total number of pollen pellets collected per colony over the five months (corrected for the number of sampling days) was used as a relative index of colony pollen intake.

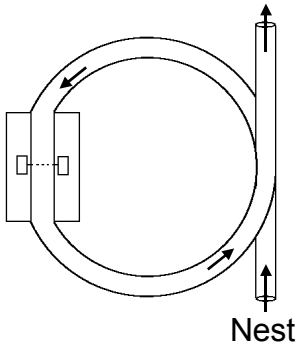

Fig. 23 Light barriers of electronic bee counters were housed in small (6 x 5 x 4 cm) PVC boxes. Bees passed between emitter and sensor crawling through a piece of clear plexiglass tubing (inside diameter: 9.5 mm) that was connected to the nest entrance with silicon hose. The circular arrangement of the hose was quickly accepted by the bees and successfully kept them from idling within the light barrier box. The setup was shaded from direct sunlight.

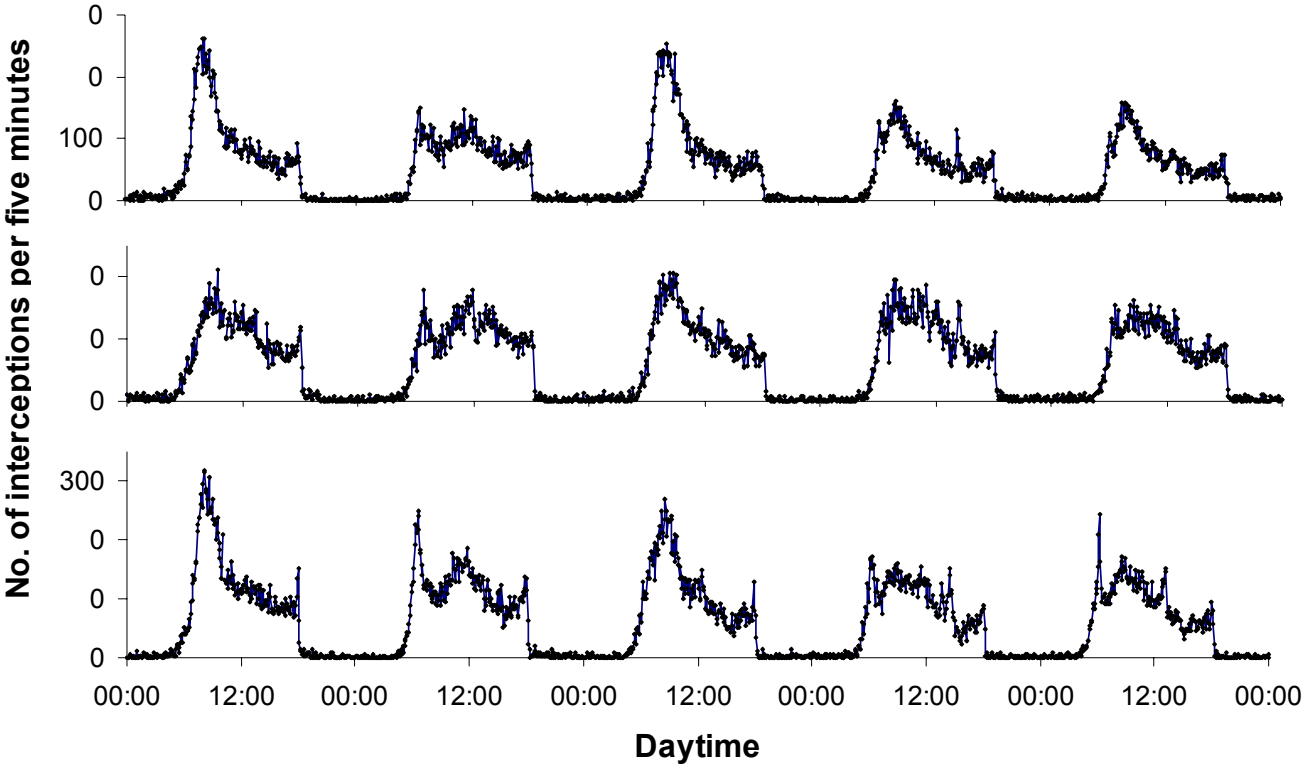

Fig. 24 Entrance tube traffic logged in five-minute intervals for three nests of *T. collina* (all in Sepilok K) over five consecutive days in March. All days were sunny. One strong rainfall event took place around 21h on day one.

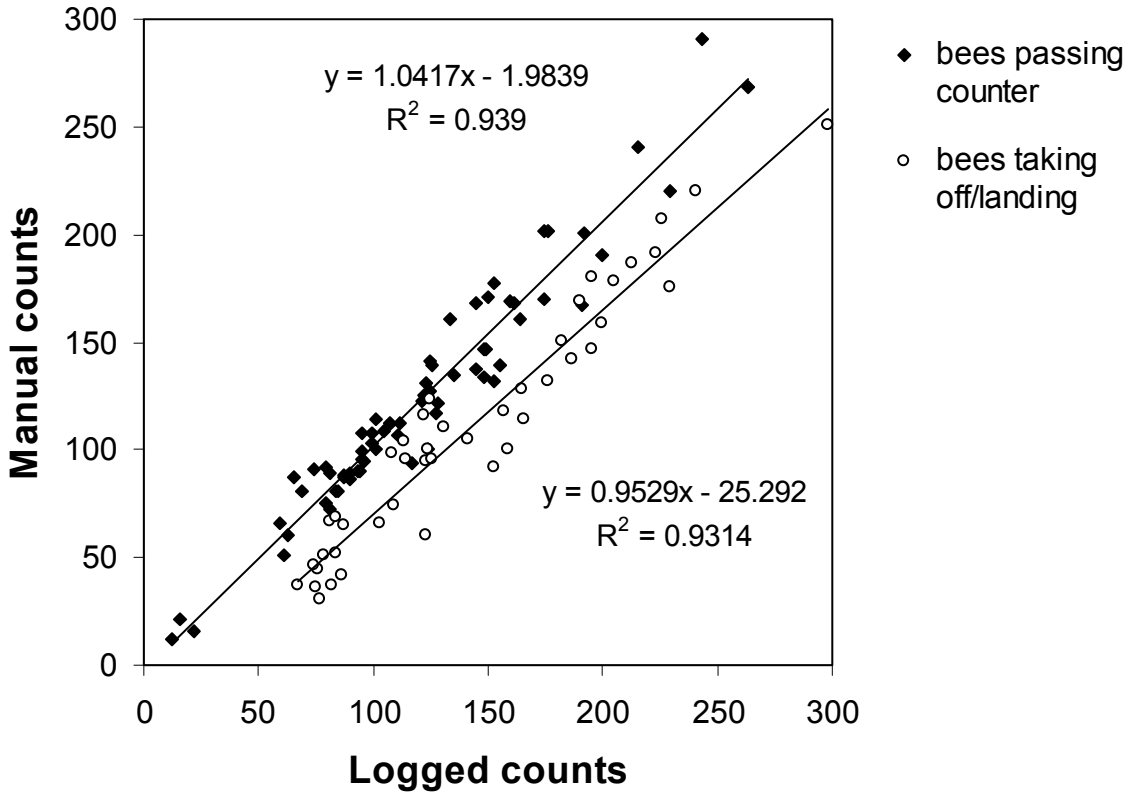

Fig. 25 Relationship between logger-counts and manual control counts of *T. collina* workers passing through the light barrier box (black diamonds) as well as control counts of bees landing and taking off at the end of the tube (open circles). Values refer to 5-minute intervals.

We did not attempt to quantify flowering in our research sites because reasonable measures would have required immense efforts due to the spatial scale and patchiness of the variation involved. Differences in the vertical stratification of the different sites (see Fig. 5) would also have constrained meaningful comparisons of floral resources. It was our impression that flowering levels were low to intermediate, with no clear increase or decrease over the five months at all three sites. On a longer time scale, the study period was part of the non-general flowering period following local and regional mass flowering in 1996 and 1998 (Sakai et al. 1999, Eltz et al. in press-a, section 3.1).

4.2.3 Results

Nests and nest density

A total of 117 stingless bee nests of 11 species were located during the quantitative nest survey (Table 12) Among those *T. collina* was by far the most abundant species (54.7 % of nests), followed by *T. melanocephala* (16.2 %) and *H. pendleburyi* (12.0 %). All three are

species that predominantly nest in and under tree bases, and we probably found a large proportion of their nests in the searched areas. All but one (*T. melina*) of the other species nest in tree cavities at variable height and are probably underrepresented to varying degrees.

Nest densities (all species pooled) varied drastically between sites and ranged from 0 to 16.2 nests/ha (Table 12). Densities varied significantly between localities (Sepilok, Danum, Deramakot; Kruskal-Wallis-Test: N=14, H_2=7.04, p=0.03), an effect that was almost exclusively based on the elevated nest densities in Sepilok Forest Reserve. The 16.2 nests/ha of the Sepilok Laut site were outstanding and represent the highest stingless bee nest densities that have so far been recorded in any tropical site (see references in the Discussion). Possible effects of forest disturbance (not consecutively tested) were obviously dwarfed by those of locality. Primary forests in Danum Valley had much lower numbers of nests than that of Sepilok and were comparable with disturbed sites in Deramakot. Within Deramakot the lowest nest densities were found in the *heavily disturbed*, *young* sites (only one nest in three sites). However, no pair-wise comparisons were done between different classes of disturbed forests because of insufficient numbers of replicates.

Table 12 Counts and densities of nests and nest trees of stingless bees found during quantitative nest surveys fourteen forest sites in central and eastern Sabah, Malaysia.

	Sepilok			Danum		Deramakot									Sum	% of nests
Site	Laut	K	N	L	M	A	B	C	D	E	F	G	H	I		
Area searched (ha)	2.8	4.8	4.8	4.8	4.8	4.8	4.8	4.8	4.8	4.8	4.8	4.8	4.8	4.8	65.2	-
No. nest trees	21	12	6	1	3	2	2	3	1	5	0	0	0	1	57	-
No. nests	45	30	13	1	6	5	2	3	1	10	0	0	0	1	117	-
Nest trees/ha	7.55	2.5	1.25	0.21	0.63	0.42	0.42	0.63	0.21	1.04	0	0	0	0.21	-	-
Nests/ha	16.2	6.25	2.71	0.21	1.25	1.04	0.42	0.63	0.21	2.08	0	0	0	0.21	-	-
T. (Tetragonula) collina	30	19	8		1	4		1						1	64	54.70
T. (Tetragonula) melanocephala	3	2	3	1	1	1	1	2		5					19	16.24
H. (Pariotrigona) pendleburyi		6	1		3					4					14	11.97
T. (Lepidotrigona) terminata	3		1						1						5	4.27
T. (Tetragonula) laeviceps	3									1					4	3.42
T. (Odontotrigona) haematoptera		2													2	1.71
T. (Homotrigona) fimbriata	2														2	1.71
T. (Tetrigona) binghami	2														2	1.71
T. (Tetragonula) melina	2														2	1.71
*T. (Tetragonula) laeviceps-group**		1													1	0.85
Trigona spec.					1										1	0.85

The locality effect on nest density was evident for *T. collina* alone (N=14, H_2=7.64, p=0.02), and also for the rest of the stingless bee community (N=14, H_2=6.30, p=0.04), suggesting that various species responded similarly to factors causing the observed variation in nest densities. Across all sites, the number of species of stingless bees present was correlated with nest density (R_S = 0.95, p<0.0001). However, shifts in relative abundance were also evident: The proportion of *T. collina* in relation to other species varied significantly between localities (Chi^2=14.9, N=117, df=2, p<0.001) and seemed to increase with overall nest density (Sepilok>>Deramakot>Danum Valley).

Patterns of nest density were paralleled by patterns of nest tree density (Table 12). On average, 2.0 nests were clustered in a given tree (N=57 nest trees), and the degree of clustering did not vary between the three localities (N=11, H_2=4.18, p=0.12).

Nest survival and predation

For an analysis of nest survival we pooled information on nests located during the quantitative surveys with that of nests found on other occasions in or close to the research sites. Even so the number of nests with repeated observations on colony state (alive or dead) allowed comparisons only between Sepilok (N=52, mean observation time per nest 1.42 years) and Deramakot (N=51, 1.3 years) (nest from all sites pooled for the two localities). Only 10 colonies evidently died in each locality during the observation time resulting in similarly low yearly mortality rates of 0.135 (Sepilok) and 0.150 (Deramakot). Survival times did not vary between localities in a Survival Analysis (Gehan's Wilcoxon-Test, test-statistic= -0.013, p=0.99). Also, no differences were observed when only *T. collina* was considered (yearly mortalities of 0.130 in Sepilok (N=36) and 0.082 in Deramakot (N=27)). Thus, differential mortality of established nests is unlikely to explain the pronounced differences in nest density between Sepilok and Deramakot.

It was our general impression that stingless bee colonies, once firmly established in or under protective trees, were very stable over years and did not seem to suffer much predation. Potential vertebrate nest predators of meliponines in Sabah include the sun bear (*Helarctos malayanus*), yellow-throated marten (*Martes flavigula*), tree shrews (*Tupaia* sp.), monkeys (Shelford 1917, Seeley et al. 1982 and references therein), and possibly the pangolin (*Manis javanica*). Of those, the sunbear is likely to pose the greatest threat to colonies situated in or underneath live trees, and sun bears undoubtedly cause some mortality to stingless bees (Wong Siew Te, Wildlife Biology Program, Montana, pers. comm.). *Helarctos* is present in

all three localities but generally occurs at low population densities (Wong Siew Te and Elis Tambing (Sabah Wildlife Department), pers. comm.). Over four years of studying meliponines in Sabah, we became aware of only one case of likely sun bear nest predation: at some point between May and October 1999 a large animal had excavated two nests of *T. collina* that were situated in the root system of an emergent tree (dbh 100 cm) in Deramakot. A huge cavity had been created, with probably more than 2 m^3 of substrate removed. All other cases of nest mortality were not clearly attributable to predation. Animals occasionally damaged the entrance tubes of nests of *T. collina*, probably consuming small numbers of worker bees present there. In one case a vertebrate, perhaps a monkey, succeeded in getting limited access to a nest of *T. collina* through a small hole (diameter ~ 8 cm) in the base of the nest tree. Some brood was consumed, but the nest survived. No attacks of ants (e.g. driver ants) on stingless bee nests were observed. Generally, stingless bees are believed to be relatively immune to ant predation due to their use of sticky resins for colony defense (Seeley et al. 1982, Khoo and Yong 1987, Salmah et al. 1990).

Availability of nest trees

In order to evaluate the hypothesis of nest site limitation, it is first necessary to consider what constitutes stingless bee nesting resources. Most stingless bee nests (whole community: 86 %; *T. collina*: 97 %) found in our research sites were situated in or under live canopy trees larger than 60 cm dbh (section 3.4). Apart from the evident preference for large tree size, the selection of nest sites seemed to be quite opportunistic, and nests were found in a large variety of hard wood tree taxa (section 3.4; Eltz et al. submitted-b). No nests were found associated with pioneer trees of the genus *Macaranga*. Nest trees comprised the entire range of estimated tree qualities (ranging from prime timber to completely hollow), making it difficult to judge suitability of potential nest trees. Therefore, we used the most simple approach and calculated an index of nest tree availability that was exclusively based on tree size: Stingless bee nest density across sites was positively correlated with the mean number of trees above 60 cm dbh present in angle-count samples (Spearman R_s=0.601; N=14; p=0.023)(Fig. 26). No significant correlation was observed for *T. collina* (R_s=0.357; N=14; p=0.21). Note that the presence of large trees leaves much of the observed variation in nest density unexplained, especially the large variation between well stocked primary sites in Danum and Sepilok (Fig. 26). The outstanding nest density in Sepilok Laut was not paralleled by an exceptional presence of large trees. We were unaware of any other characteristic of the tree community that could explain the high nest density. Nest tree diversity was similar to other sites and localities (13

different taxa among 19 identified trees), with no pronounced bias in favor of a single tree species. None of the nest trees in Sepilok Laut were Bornean Ironwood (*Eusideroxylon zwageri, Lauraceae*), a tree that may have superior qualities as a nest tree (section 3.4; Eltz et al. submitted-b).

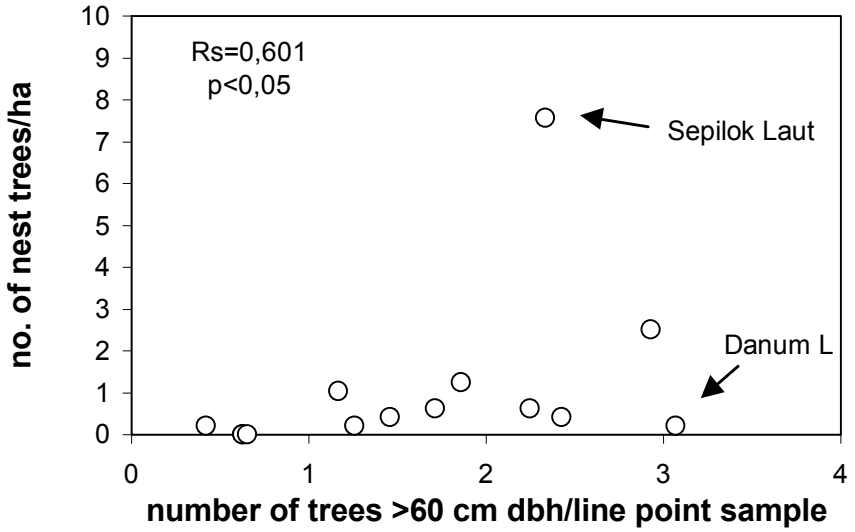

Fig. 26 Relationship between the presence of large trees (> 60 cm dbh) and stingless bee nest density across 14 forest sites in Sabah.

Table 13 Summary of pollen type richness, evenness and turn-over in garbage samples of *T. collina* colonies in five different sites in Sabah. Values in brackets are standard deviations. F-values and significance levels of ANOVA are given for between-site effects. Note exceptionally low diversity and high turn-over in Sepilok Laut.

	Sepilok		Danum	Deramakot			
	Laut	K	M	A	G	df	F values
No. of nests sampled	8	8	3	8	11		
Mean no. of pollen types in sample per nest	5.3 (1.6)	20.7 (1.7)	14.0 (1.4)	12.3 (3.3)	10.0 (2.5)	4, 33	48.2 ***
Mean evenness of pollen types in samples per nest (J)	0.4 (0.1)	0.8 (0.04)	0.6 (0.2)	0.7 (0.1)	0.7 (0.1)	4, 33	26.7 ***
Mean monthly turnover of pollen types per nest (% volume; 1-Steinhaus) §	7.5 (3.5)	16.3 (2.5)	12.7 (2.7)	14.6 (3.4)	16.0 (3.8)	4, 22	8.1 ***

§ only nests with repeated samples included (N=27)

*** P < 0.001

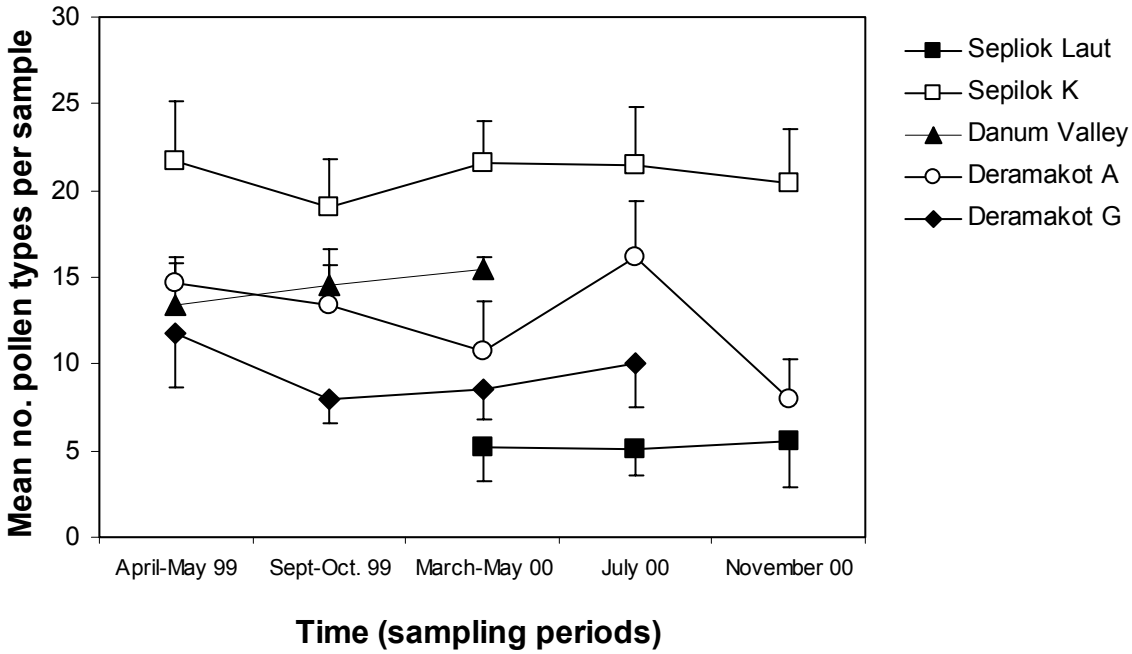

Fig. 27 Pollen type richness of garbage samples collected from colonies of *T.collina* at five consecutive sampling periods between April 1999 and November 2000. Note differences between sites. Error bars are either positive or negative standard deviations.

Pollen resources of *T. collina*

T. collina garbage contained a total of 148 different morphotypes of pollen, belonging to at least 38 plant families. Samples collected from colonies at the same site at a given point in time were normally similar in composition (55.8 +/- 24.6 % similarity; Steinhaus-coefficient), whereas large differences in pollen diet were evident between localities and sites (see below, Appendix 2). There were significant differences between sites in grand means of the number of pollen types per nest over all sampling periods (ANOVA: N=38, F_4=48.16, p<0.0001). Samples of nests in Sepilok Laut (mean of 5.3 different types/sample) had much fewer types than those in Sepilok K (20.7). Means of nests in Danum Valley (14.0) and Deramakot (A: 12.3; G: 10.0) were intermediate (Table 13). These patterns in pollen type richness were very stable over time (see Fig. 27). Aside from type richness, samples of nests in different sites also differed in the mean evenness (Shannons J) of pollen type representation (N=38; F_4=26.66, p<0.0001), suggesting that differences exist between sites concerning quantitative aspects of the source plant community (Table 13). The effect was mostly based on the fact that samples of nests in Sepilok Laut were heavily dominated by a single pollen type, that of the mangrove tree *Rhizophora apiculata*. Individual samples collected in May, July and November 2000 contained relative volumes of *R. apiculata* grains between 59 and 98 %

(means across nests of 79.6, 83.5 and 81.3 % for each of the three sampling periods; see Appendix 2). In all other sites, the mean representation of the most dominant grain rarely exceeded 30% of the pollen volume. Sepilok Laut colonies also had exceptionally low temporal variability in pollen composition. We calculated mean monthly turn-over rates (1-Steinhaus-coefficient) of pollen type composition for nests with repeated samples. Turn-over in Sepilok Laut (7.5% per month) was only half of that found in nests of other sites (Table 13; ANOVA: N=26, F_4=8.15, p<0.001).

Generally, the two sites in Sepilok, both characterized by high nest density, could not have been more different in terms of pollen type richness, evenness and turn-over. However, pollen identifications did reveal one similarity: colonies in both sites used large amounts of pollen from external non-forest sources. Whereas mangrove pollen was heavily collected by bees in Sepilok Laut, pollen of cultivated plants from nearby plantations was common in samples in Sepilok K. Between April 1999 and November 2000 these sources included corn (*Zea mays*; mean of 15.6 % across sampling periods), manioc (*Manihot esculenta*; 5.7%), water melon (*Citrullus lanatus*; 5.0 %) and an alley tree (*Lagerstroemia speciosa*; 2.5 %)(see Appendix 2). Nests situated in continuous forest in Danum Valley and Deramakot had either no pollen sources of evidently external origin, or (in Deramakot A) were confined to minor sources present among roadside plants (*Mimosa pudica*; 1.8 %) and plants grown in the Deramakot Base Camp clearing (manioc 4.5 %, ornamental Polemoniaceae 1.6 %) (Appendix 2).

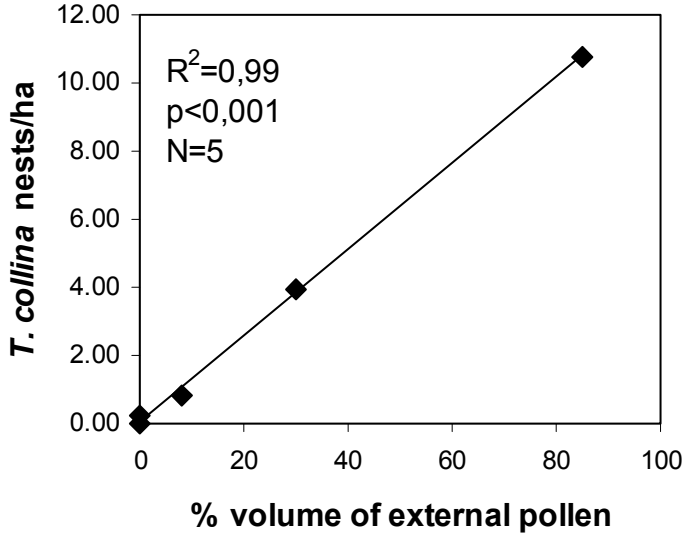

Fig. 28 Relationship between the mean proportion of external non-forest pollen in garbage samples of *T. collina* and *collina*-nest density in five different forest sites in Sabah.

Evidently, *T. collina* colonies exhibited a strong tendency to include non-forest pollen in their diets. Across sites (N=5) there was a positive relationship between the mean proportion of non-forest pollen in garbage (grand means across nests and time) and nest density of *T. collina* (R^2=0.99; p<0.001)(Fig. 28).

Pollen use of other meliponine species in Sepilok Laut

In order to investigate whether our findings on *T. collina* allow more generalized interpretations for stingless bee communities, we repeatedly collected garbage samples from colonies of *T. (Lepidotrigona) terminata* (2 colonies), *T. (Tetragonula) melanocephala* (1), *T. (Tetragonula) melina* (1) and *T. (Tetrigona) binghami* (1) in Sepilok Laut. Sampling took place over the same three sampling periods, and treatment and analysis followed the same standards as in *T. collina*. Garbage of all four species contained large quantities of pollen of *Rhizophora apiculata* (Table 14), suggesting that the mangrove tree represented an important resource for most if not all meliponine species in the area.

Table 14 Percent volume of *Rhizophora apiculata* pollen in garbage samples of four additional meliponine species (five colonies) in Sepilok Laut

	Apr-May 99	Sep-Oct 99	Mar-May 00	July 00	Nov 00	Mean
T. (Tetragonula) melina	no data	no data	60.0	71.2	27.7	53.0
T. (Tetragonula) melanocephala	no data	no data	71.7	44.4	51.5	55.9
T. (Lepidotrigona) terminata 1	no data	no data	85.4	92.8	70.5	82.9
T. (Lepidotrigona) terminata 2	no data	no data	89.7	91.5	26.9	69.4
T. (Tetrigona) binghami	no data	no data	no data	82.6	100.0	91.3

Foraging activity and pollen foraging of *T. collina*

Morning tube traffic of colonies of *T. collina* (means over five months) varied significantly between sites (Kruskal-Wallis-Test: N=22, H_2=7.79, p=0.020)(Fig. 29 a), with traffic in Sepilok K being almost twice as high as in the two Deramakot sites. The same pattern of variation was found in the number of trapped pollen pellets (N=22, H_2=6.31, p=0.043, Fig. 29 b).

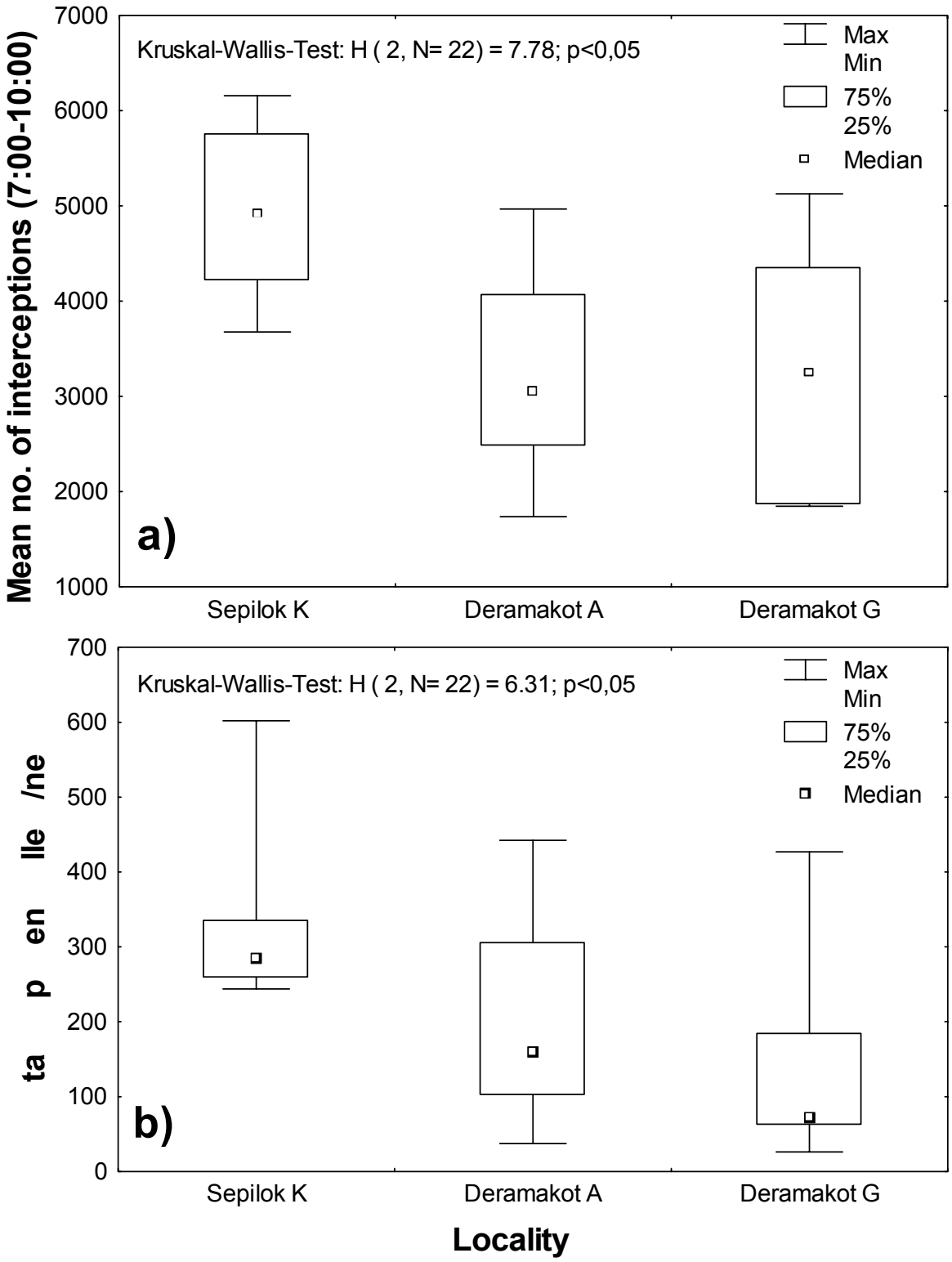

Fig. 29 Indices of morning foraging activity (a) and pollen import (b) of colonies of *T. collina* (N=22) situated in three research sites in Sabah. See text for details.

Variation in foraging activity as indicated by tube traffic may originate from three partly interrelated variables: (i) the number of bees present in a given colony (colony strength), (ii) the proportion of bees in a nest that participate in active foraging, and (iii) the number of trips

made by these workers per unit time (trip frequency) (Robinson 1992, Thom et al. 2000). Applied to our results, all three possibilities are in general agreement with the idea of differential availability of floral resources to bees in Sepilok and Deramakot. However, (ii) and (iii) are short-term responses of individual workers to internal and external cues designed to maximize colony fitness, whereas colony strength (i) is a colony-level character that may itself represent a fitness component. Thus, it is of interest to separate the three variables. Unfortunately our attempts to measure colony strength using mark-recapture techniques have failed due to difficulties of marking sufficient numbers of workers. However, the relative importance of short-term regulation (ii and iii) is indicated by site-specific diurnal patterns of tube activity. Fig. 30 suggests that colonies in Sepilok were particularly active between sun rise and 10.00 am. Differences between sites decreased later in the day. Several studies, including our own observations on *T. collina* (T. Eltz, unpublished data), have shown that most pollen foraging by meliponines is done during early morning hours (Roubik and Buchmann 1984, Inoue et al. 1985, Roubik 1989). This and the higher amount of pollen collected by Sepilok colonies (Fig. 29 b) suggests that at least part of the increased morning traffic is related to a regulatory increase of pollen foraging.

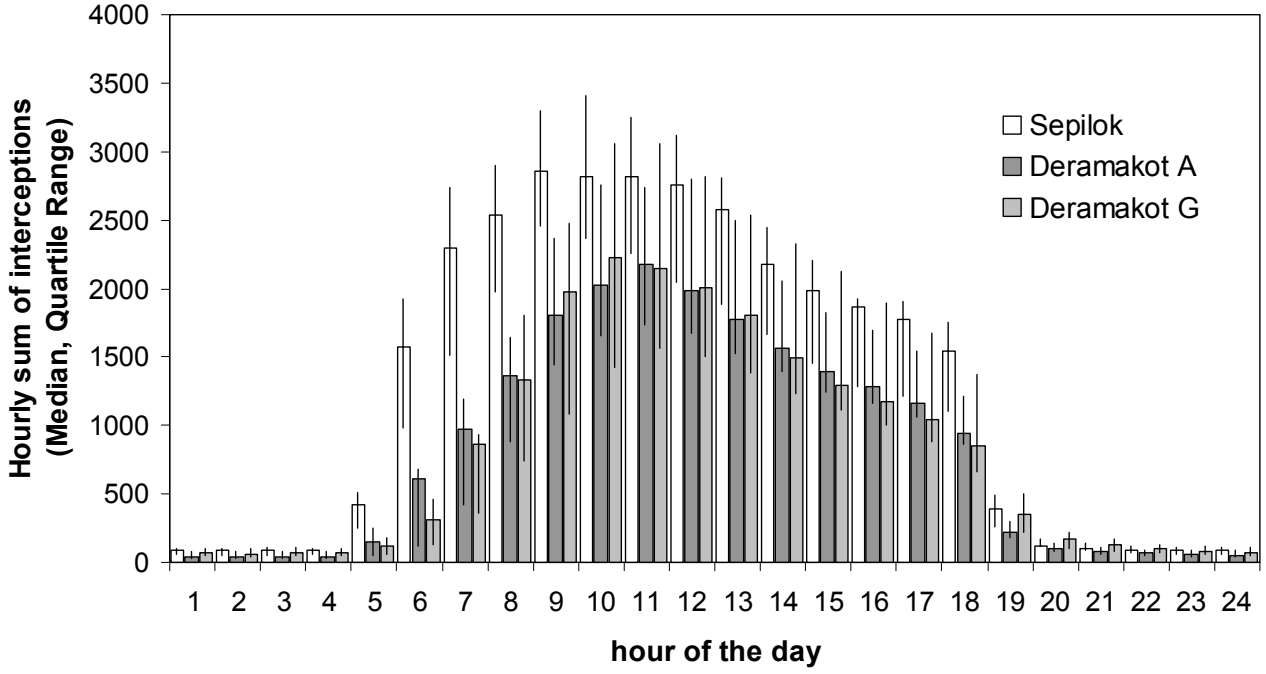

Fig. 30 Mean hourly tube traffic in colonies of *T. collina* in Sepilok K, Deramakot A and Deramakot G.

4.2.4 Discussion

Evidence for food limitation

Nest density of stingless bees in dipterocarp forests in Sabah varied more than 20-fold between sites in our study, ranging from a mean of 0.5 to 0.7 nest/ha in Deramakot and Danum Valley to a phenomenal 16.2 nests/ha in mangrove-bordering forests in Sepilok. Variation in nest density was not explained by differences in nest mortality (indicative of predation), nor closely related to logging history and the availability of potential nest trees. Instead, three lines of evidence suggest that meliponine populations densities in Sabah are chiefly determined by the availability of food resources.

First, the presence of extremely high nest densities in Sepilok Laut is paralleled by an equally distinctive pollen diet of the local bee nests: Diets of the focal species, *T. collina*, as well as colonies of four other meliponine species, were heavily dominated by pollen of the mangrove tree *Rhizophora apiculata*, the most abundant tree species of the nearby mangroves. *R. apiculata* is mainly wind-pollinated and produces copious quantities of pollen in open flowers (Tomlinson et al., 1979, T. Eltz, pers. obs.). The fact that the predominance *of R. apiculata* pollen in bee garbage was maintained over seven months of observation suggests that the tree represented a superabundant pollen source. Its continued exploitation may have substantially increased the carrying capacity for bees in nearby forests.

Second, and more generally, a positive relationship was found between density of bee nests and the proportion of non-forest pollen resources of *T. collina* colonies. We hypothesize that dietary inclusion of alternative pollen sources from a variety of habitats reduces the extent of temporal fluctuations of floral resource levels to bees. This may be crucial in Asian dipterocarp forests that are characterized by extreme and partly unpredictable fluctuation in flowering (Sakai et al. 1999, Wich and van Schaik 2000). Although data from our research sites are lacking, flowering phenology in plantations, road sides and mangroves is likely to differ markedly from that inside the forest. In many mangrove trees, including *Rhizophora*, flowering normally covers substantial parts of the year (Christensen and Wium-Andersen 1977, Tomlinson et al. 1979, Wium-Andersen 1981). In mangrove areas in southern Thailand flowering of *R. apiculata* had distinct seasonal peaks, but some flowers were present at any point in time over 16 months (Christensen and Wium-Andersen 1977). Relatively constant availability of *R. apiculata* pollen probably explains much of its observed predominance in bee diets. Additionally, flowering peaks in mangroves are likely to be out of phase with that

in nearby forests, thus enhancing potential benefits to stingless bees. Tomlinson et al. (1979) speculated that *Bruguiera* (Rhizophoraceae) in Queensland, Australia, must constitute a major nectar source during its peak flowering season in May and August, a time when terrestrial plants are generally not flowering. Distinct flowering phenologies of mangrove trees and correlated peaks of insect abundance have been shown to influence foraging patterns and breeding seasons of insectivorous birds in Venezuela (Lefebvre et al. 1994). Temporal reliability of floral resources is also a characteristic of many crop plants, and pollen from Sepilok plantations has evidently supplemented diets of meliponine colonies in Sepilok K. Evidence from other studies supports the idea of increased nest densities mediated by alternative food sources: Floral resources from mediterranean farmland have been suggested to increase bee abundance due to their availability during times when natural habitats become dry and unproductive (Banaszak 1992, Kremen and Rickets 2000). In some situations crop plants with extended flowering seasons may even represent keystone resources for certain bumblebees (Corbet 2000). In this context it should be emphasized that the positive effect of crop plants on bee populations will depend heavily on the kind of plantation. Diverse agricultural landscapes like those bordering Sepilok K are likely more beneficial to bees than monocultures. Specifically, the vast and even-aged stands of oil palm (*Elaeis guieneensis*), already covering more than 15% of lowland Sabah (Forest Research Centre, Sabah), are not likely to benefit bees. Although oil palm pollen is occasionally collected by certain species of meliponines and honeybees (Kiew and Muid 1991), oil palm is not considered a good forage plant for bees (Roubik 1995). Despite being present in plantations bordering Sepilok K, oil palm pollen was only a minute component of diets of local *T. collina* (Appendix 2; Rank 66).

Thirdly, increased pollen import and foraging activity suggest that the intensity of pollen foraging per colony of *T. collina* was indeed greater in bee-rich Sepilok than in bee-poor Deramakot, indicating differences in pollen availability at the time of the study. It is of course arguable whether an observation period of five months is sufficient for a sound comparison of resource levels, and we cannot rule out the possibility that the observed differences would level out over several years. However, the finding does make sense in combination with the data on pollen diets and strengthens the view that pollen resources are in better supply in areas with high nest density.

On the whole, our findings in Borneo are in broad agreement with the conclusions of Hubbell and Johnsons (1977) from Costa Rica, that stingless bees live in saturated communities that are chiefly limited by food resources. Among food items our results hint to the special

importance of pollen. Pollen is the prime source of nitrogen for Asian meliponines and brood production is proximately dependent on pollen availability. It is an intriguing fact that pollen is also the only floral resource that is exclusively provided by flowers. Nectar, in contrast, is also available from extra-floral nectaries (Roubik 1989) and levels of supply are probably less variable over time.

Direct and indirect effects of logging

Our results lack clear indications of a negative influence of selective logging on stingless bee nest density. Although floral resource levels were not directly measured in sites with different degree of degradation, data on foraging activity and pollen foraging of *T. collina* colonies suggest that resource levels did not vary drastically between slightly logged old (A) and heavily logged young (G) forests in Deramakot. This is perhaps surprising because sites were characterized by greatly differing canopy structure. Heavily logged sites had lost large fractions of upper canopy layers, a finding that is typical for logged-over forests in Borneo (Cannon et al. 1994). However, loss of flower production in the forest canopy could be compensated by increased flowering in lower strata that experience increased light levels (Seidler and Bawa 2001). Among Venezuelanian forest birds, nectar-feeding guilds were favored by logging in the short-term, probably as a result of increased floral resources in the understory (Mason 1996). Generalist flower visitors like social bees may quickly adjust to alterations in forest stratification. In addition, their evident foraging in open habitats like plantations and mangroves suggests that foragers of most species can adjust well to altered microclimatic conditions encountered in heavily disturbed forests.

The availability of potential nest trees varied substantially along the disturbance gradient, but explained only minor fractions of the variation in nest density. This suggests that suitable cavities are not in short supply over a large range of nest densities and forest stand structures. However, the apparent lack of evidence for nest site limitation does not rule out direct negative effects of logging on stingless bees. In a different study (Eltz et al. submitted-b, section 3.4) we analyzed the commercial potential of 142 nest trees of stingless bees in dipterocarp forests in Sabah and concluded that roughly one third would qualify for harvesting in case of a commercial logging operation. Because absconding of bee colonies as a response to disturbance is extremely rare in stingless bees (Michener 1974, Inoue et al. 1984a), felling of the nest tree is very likely to kill associated colonies. Residual effects of logging-induced mortality were possibly weak in our study because logging had taken place more than two decades ago in most Deramakot sites. However, the extremely low nest

densities in the most recently logged areas in Deramakot (G, H, I) may still indicate direct logging impact.

Stingless bee carrying capacity, competition and community structure

Reported meliponine nest densities were very low in continuous tracts of dipterocarp forests in Borneo (0.5 and 0.7 nest/ha in the present study and 2.8 nest/ha in Belalong forest in Brunei (Roubik 1996)). Although comparisons across continents and forest types have to be regarded with caution these, densities seem well below the 4 to 6 nests/ha found in the Neotropics (Hubbell and Johnson 1977, Roubik 1996). We hypothesize that the apparent differences are related to differences in floral resource availability between the Old and New World tropics. Two factors are likely to create low resource levels in Southeast Asia. First, flowering in dipterocarp forests is characterized by extreme temporal fluctuations, specifically by long periods of relatively little flowering interrupted by rare supra-annual bursts of mass-blooming (Appanah 1985, Sakai et al. 1999, Wich and van Schaik 2000). It is likely that bee colonies cannot take sufficient advantage of the occasional superabundance of resources during mass-flowering, but are instead limited by low intervening resource levels. Data from Lambir Hills in Sarawak suggest that forests in Borneo have fewer plant species that flower continuously across seasons than neotropical forest (Sakai et al. 1999). Thus, it is reasonable to assume that floral resource levels are also lower most of the time. Second, the availability of pollen and nectar to Asian meliponines could be further reduced by competition with up to four sympatric species of honeybees (*Apis* sp.). In contrast to the Paleotropics, honeybees have been absent from most of tropical America until very recently (Roubik 1989). Honey bees are believed to be superior competitors for floral resources due to their quick and efficient recruitment behavior (Roubik 1989), and the competitive effect exerted by their populous colonies is likely to dwarf that of meliponine species (Roubik et al. 1986, Roubik 1992). Both extreme fluctuations of flowering as well as competition by honeybees has been suggested to explain depauperate bee communities (solitary and social) in Southeast Asia (Roubik 1990, Roubik 1992). We suggest that the same factors are responsible for low nest density of extant meliponines in Bornean forests.

Overall nest density is likely to have influenced the evolution of competitive traits and could have led to diverging structures of stingless bee communities in different parts of the tropics. In neotropical bee communities two lines of evidence suggest a strong structuring effect of interspecific interference competition: First, behavioral studies reported aggressive encounters and dominance hierarchies at artificial feeders and flower patches (Johnson and Hubbell 1974,

Johnson and Hubbell 1975, Hubbell and Johnson 1978, Roubik 1980, Johnson 1983). Second, interspecific uniform nest spacing of colonies in a Costa Rican dry forest was restricted to those species that were also known to have frequent antagonistic encounters at food sources (Hubbell and Johnson 1977). Although quantitative data are lacking (but see Nagamitsu and Inoue 1997) interference at food patches between colonies and species seems generally less pronounced in Southeast Asian communities (D. W. Roubik, pers. comm.). We have spent many weeks observing stingless bees at honey-spray sites and flowers in Sabah and were rarely aware of direct interference between individuals or species. Instead, our general impression was that of a relatively peaceful coexistence between foragers that were mostly concerned with the exploitation of resources (T. Eltz, unpublished data, see section 4.1). No indication exists for interspecific or intraspecific nest spacing. On the contrary, several studies found Asian stingless bee nests commonly aggregated in individual nest trees (Roubik 1996, Nagamitsu and Inoue 1997, Eltz et al. in press-a, Eltz et al. submitted-b, section 3.4). In the present study up to eight nests were situated in a given tree, and aggregations consisted of up to three different species of bees. In summary, we suggest that foraging and nesting of social bees in low-density/low-resource environments like Bornean forests requires low-density strategies. Finding ephemeral resources scattered within large tracts of forests has been the main problem here, and natural selection could have favored strategies of efficient exploitation over strategies of resource defense and aggressive interference. Potential mechanisms that increase exploitative efficiency without involving aggressive dominance include specialization on certain floral traits (e.g. flower depth) or foraging stratum preferences. Suggestive evidence has been found for both by studies on bee morphology (Nagamitsu and Inoue 1998) and flower visitation (Nagamitsu et al. 1999) in Bornean forests. So far the theory of differences in foraging strategies and community structure between tropical America and Asia awaits to be addressed in a quantitative way.

Appendix 2 Pollen type representation in garbage samples collected from *T. collina* colonies at five consecutive sampling periods between April 1999 and November 2000. Only types that were above the 0.5%-volume threshold in at least one sample are shown. Values are means of percentages calculated across all nest (N) sampled at a given point in time.

Sepilok Laut

		1999		2000				
Rank	Pollen type	April-May	Sept.-Oct.	March-May	July	November	Mean	Remark
		No data	No data	N=8	N=8	N=8	%	
1	Rhizophora apiculata			79.65	83.49	81.26	81.46	Mangrove
2	Anacardiaceae, Gluta type B			13.99	2.28	0.47	5.58	
3	Rhizophoraceae, Carallia ?			2.31	6.68	--	3.00	Mangrove
4	?, trizonocolporate L			--	--	5.84	1.95	
5	Asteraceae, Tubuliflorae A type			0.13	--	5.35	1.82	
6	Leguminosae E			0.10	3.77	--	1.29	
7	Euphorbiaceae			--	--	1.80	0.60	
8	Meliaceae			0.10	0.28	1.10	0.49	
9	Euphorbiaceae, Croton type			1.15	0.12	0.15	0.47	
10	Combretaceae, Lumnitzera littorea			0.79	0.35	0.10	0.41	Mangrove
11	Scrophulariaceae ?			--	0.83	0.20	0.34	
12	Loganiaceae, Fagraea			0.77	--	--	0.26	
13	Combretaceae, Terminalia type B			--	0.21	0.53	0.25	
14	?, trizonocolporate N			--	--	0.68	0.23	
15	Leguminosae N			--	0.48	0.10	0.19	
16	Euphorbiaceae, Baccaurea type A			--	--	0.52	0.17	
17	Anacardiaceae ? B			0.18	0.17	0.12	0.15	
18	Sapindaceae, Allophylus type B			0.07	--	0.38	0.15	
19	?, trizonocolporate H			0.21	0.24	--	0.15	
20	Leguminosae ? A			0.21	0.12	--	0.11	
21	Dilleniaceae, Dillenia			--	0.23	--	0.08	
22	?, trizonoporate C			--	--	0.21	0.07	
23	?, trizonocolporate M			--	--	0.20	0.07	
24	Rutaceae ? A			--	--	0.12	0.04	
25	Leguminosae O			--	0.09	--	0.03	
26	?, trizonocolporate U			--	0.08	--	0.03	
27	?, trizonocolporate V			--	0.07	--	0.02	
28	?			0.06	--	--	0.02	

Sepilok K

		1999		2000				
Rank	Pollen type	April-May	Sept.-Oct.	March-May	July	November	Mean	Remark
		N=3	N=4	N=7	N=4	N=5	%	
1	Poaceae, Zea mays	26.44	16.74	8.49	14.71	11.65	15.60	Crop plant
2	Bombacaceae A	--	30.96	9.83	14.72	2.79	11.66	
3	Euphorbiaceae, Manihot esculenta	--	2.44	3.55	13.76	8.62	5.68	Crop plant
4	Asteraceae, Tubuliflorae A type	3.17	0.19	4.16	0.32	17.72	5.11	
5	Cucurbitaceae, Citrullus lanatus	--	15.87	4.43	2.52	2.18	5.00	Crop plant
6	Mimosaceae	3.87	0.24	16.08	--	2.98	4.63	
7	Convolvulaceae, Convolvulus type A	11.73	2.59	4.84	0.73	0.87	4.15	
8	Malvaceae, Hibiscus type	--	1.30	2.50	--	15.67	3.90	
9	Leguminosae ? A	0.33	--	2.23	--	11.15	2.74	
10	?, trizonocolporate H	--	--	--	11.20	2.47	2.73	
11	Lythraceae, Lagerstroemia speciosa	2.37	1.08	1.71	6.31	1.15	2.52	Alley tree
12	Leguminosae ? F	1.19	0.39	5.93	2.96	1.75	2.45	
13	Passifloraceae, Passiflora ?	5.44	1.32	1.84	1.71	0.13	2.09	
14	Leguminosae E	3.04	1.77	1.38	4.24	--	2.08	
15	?, trizonocolporate F	4.18	0.88	0.68	3.45	0.46	1.93	

Sepilok K continued

16	Rutaceae, Citrus type B	--	--	7.37	1.12	0.86	1.87	
17	?, trizonocolporate C	5.22	0.42	0.17	1.31	0.50	1.52	
18	Rutaceae ? A	--	--	2.12	1.30	3.85	1.45	
19	Theaceae, Schima type B	1.63	1.33	1.41	0.67	1.09	1.23	
20	Caesalpiniaceae, Caesalpinia type B	1.58	0.17	2.54	0.60	0.65	1.11	
21	Theaceae, Schima type A	4.11	1.33	--	--	--	1.09	
22	Poaceae	1.64	1.10	1.13	0.55	0.79	1.04	
23	Rubiaceae, Neonauclea type ? A	--	4.19	0.76	--	0.25	1.04	
24	?, trizonocolporate J	--	--	4.66	--	0.13	0.96	
25	Rhizophora apiculata	3.36	0.26	0.72	--	0.14	0.90	Mangrove
26	Rutaceae, Citrus type A	0.47	2.40	0.33	0.74	0.50	0.89	
27	Cyperaceae	--	--	1.49	0.92	1.95	0.87	
28	?, trizonocolporate B	3.60	0.59	--	--	--	0.84	
29	Mimosaceae, Adenathera type	--	--	--	4.01	--	0.80	
30	?, trizonocolporate Q	--	--	0.92	1.79	0.79	0.70	
31	Palmae, Cocos nucifera type	0.34	0.77	1.26	0.25	0.87	0.70	
32	Rutaceae ? B	0.58	2.89	--	--	--	0.69	
33	Leguminosae O	--	--	3.26	0.19	--	0.69	
34	Euphorbiaceae, Croton type	--	2.01	0.54	0.19	0.69	0.69	
35	Oleaceae, Jasminium type	1.63	0.61	0.08	0.63	0.30	0.65	
36	?, tetrazonocolporate	0.22	1.19	0.71	0.96	--	0.62	
37	Bombacaceae B	0.76	1.92	--	0.40	--	0.62	
38	Leguminosae, Intsia type A	--	--	0.24	1.90	0.70	0.57	
39	Symplocaceae, Symplocos type	--	0.16	--	1.99	--	0.43	
40	Mimosaceae, Acacia type	0.19	0.18	0.56	1.01	--	0.39	
41	Convolvulaceae, Ipomoea type	1.33	--	--	--	0.59	0.38	
42	Bombacaceae, Campnostemon type	1.33	0.37	--	--	0.14	0.37	
43	Bombacaceae, Durio type	1.46	--	--	0.21	--	0.33	
44	Euphorbiaceae	--	--	--	0.14	1.45	0.32	
45	Leguminosae B	1.34	--	--	--	--	0.27	
46	Leguminosae P	1.19	--	--	--	--	0.24	
47	Rubiaceae, Ixora ?	--	--	--	--	1.07	0.21	
48	Leguminosae, Intsia type B	0.96	--	--	--	--	0.19	
49	Rubiaceae, Randia type D	0.87	--	--	--	--	0.17	
50	Theaceae, Schima type C	--	--	0.59	0.15	0.14	0.17	
51	Anacardiaceae, Gluta type A	--	--	--	0.72	--	0.14	
52	Rubiaceae, tetrade type	0.70	--	--	--	--	0.14	
53	Sterculiaceae, Pterospermum	--	--	--	0.69	--	0.14	
54	Polemoniaceae, Bunga pagi	0.38	0.29	--	--	--	0.13	Ornamental
55	Leguminosae I	--	0.35	--	0.18	0.12	0.13	
56	Convolvulaceae	0.45	0.14	--	--	--	0.12	
57	?, trizonocolporate P	--	--	--	--	0.37	0.07	
58	Dilleniaceae, Dillenia	--	--	--	--	0.36	0.07	
59	Rubiaceae, Brachytome type ?	--	0.32	--	--	--	0.06	
60	Rubiaceae, Randia type C	0.29	--	--	--	--	0.06	
61	Aquifoliaceae, Ilex	--	--	--	0.28	--	0.06	
62	?	0.25	--	--	--	--	0.05	
63	?, trizonoporate B	0.25	--	--	--	--	0.05	
64	?, trizonocolporate R	--	--	0.23	--	--	0.05	
65	?, trizonocolpate B	--	--	0.21	--	--	0.04	
66	Palmae, Elaeis guineensis	--	--	--	0.21	--	0.04	Crop plant
67	Leguminosae ? L	0.20	--	--	--	--	0.04	
68	Sterculiaceae, Sterculia type	--	--	--	--	0.19	0.04	
69	?, polycolpate	--	--	--	--	0.15	0.03	
70	?, monocolpate	--	--	--	0.15	--	0.03	
71	Onagraceae, Ludwigia type	--	--	--	--	0.13	0.03	
72	Myrtaceae, Eugenia type A	--	--	--	0.13	--	0.03	
73	?, inaperturate B	--	--	0.11	--	--	0.02	
74	Mimosaceae, Mimosa pudica type	--	--	0.09	--	--	0.02	Road edge

Danum Valley M

Rank	Pollen type	1999		2000			Mean	Remark
		April-May	Sept.-Oct.	March-May	July	November		
		N=3	N=2	N=7	No data	No data	%	
1	Bombacaceae, Durio type	4.30	15.57	21.83			13.90	
2	Leguminosae E	33.13	5.18	1.67			13.33	
3	Convolvulaceae, Convolvulus type B	10.18	16.33	--			8.84	
4	Bombacaceae A	14.05	10.83	1.17			8.68	
5	Asteraceae, Tubuliflorae A type	7.72	1.49	9.31			6.17	
6	?, trizonocolporate F	8.40	4.36	--			4.25	
7	Malphigiaceae, Hiptage type	--	--	12.55			4.18	
8	Rutaceae, Citrus type C	0.26	10.45	1.15			3.95	
9	Leguminosae, Intsia type B	4.42	4.35	3.07			3.95	
10	Theaceae ?	--	10.91	--			3.64	
11	Rubiaceae, Randia type C	0.81	--	6.81			2.54	
12	Tiliaceae, Grewia type ? B	0.57	--	6.86			2.47	
13	?, trizonocolporate Ac	--	--	5.11			1.70	
14	Malvaceae, Hibiscus type	1.93	3.14	--			1.69	
15	?, inaperturate A	--	--	4.51			1.50	
16	Rutaceae, Clausena type C	--	--	4.44			1.48	
17	Stercullariaceae ?	3.78	--	0.65			1.48	
18	Leguminosae ? A	--	1.97	2.33			1.43	
19	Euphorbiaceae, Baccaurea type ? B	3.09	1.11	--			1.40	
20	Rutaceae ? A	--	--	4.07			1.36	
21	Rubiaceae, Randia type A	--	--	3.78			1.26	
22	?, trizonocolporate Y	0.50	--	2.52			1.01	
23	Solanaceae	--	--	2.78			0.93	
24	Sterculiaceae, Pterospermum	0.91	1.76	--			0.89	
25	Rubiaceae, Neonauclea type ? A	--	2.48	--			0.83	
26	Rubiaceae, Neonauclea type B	0.38	1.92	--			0.77	
27	Convolvulaceae, Convolvulus type A	--	0.90	1.30			0.73	
28	Rubiaceae, tetrade type	--	--	2.19			0.73	
29	Euphorbiaceae	0.58	0.73	0.67			0.66	
30	Bombacaceae B	--	0.85	0.85			0.57	
31	Anacardiaceae, Gluta type A	--	1.57	--			0.52	
32	Rubiaceae, Randia type ? B	--	1.21	--			0.40	
33	?, trizonocolpate D	--	1.17	--			0.39	
34	?, trizonocolporate Ab	--	0.79	--			0.26	
35	?, trizonocolporate K	0.71	--	--			0.24	
36	Euphorbiaceae, Antidesma typ	0.69	--	--			0.23	
37	?	0.48	--	--			0.16	
38	Symplocaceae, Symplocos type	0.48	--	--			0.16	
39	Combretaceae, Terminalia type A	0.18	0.28	--			0.15	
40	?, trizonocolporate H	--	0.45	--			0.15	
41	Anacardiaceae ? B	0.29	--	--			0.10	
42	Sterculiaceae, Pterocymbium type	0.27	--	--			0.09	
43	?, trizonocolporate Z	0.26	--	--			0.09	
44	?, trizonocolporate Aa	0.22	--	--			0.07	
45	Tiliaceae, Pentace type	0.21	--	--			0.07	
46	Dipterocarpaceae, Hopea type B	0.21	--	--			0.07	
47	Euphorbiaceae, Croton type	0.19	--	--			0.06	

Deramakot A

Rank	Pollen type	1999		2000			Mean	Remark
		April-May	Sept.-Oct.	March-May	July	November		
		N=3	N=3	N=8	N=6	N=4	%	
1	Leguminosae ? A	9.52	10.53	38.87	16.38	59.58	26.98	
2	Leguminosae B	30.62	18.82	7.53	1.79	--	11.75	
3	Rubiaceae, Neonauclea type ? A	--	27.78	7.28	3.43	6.35	8.97	
4	Bombacaceae A	--	--	7.68	18.29	7.31	6.66	
5	Euphorbiaceae, Manihot esculenta	--	--	1.54	9.24	11.64	4.48	Crop plant
6	Bombacaceae, Durio type	14.92	4.74	0.43	1.67	0.18	4.39	
7	Asteraceae, Tubuliflorae A type	0.73	0.18	6.95	1.00	10.35	3.84	
8	Leguminosae D	--	16.52	0.27	--	--	3.36	
9	Rutaceae, Clausena type A	--	--	1.46	11.26	--	2.54	
10	Anacardiaceae A	--	--	10.76	0.10	--	2.17	
11	Leguminosae C	9.87	--	0.54	0.20	--	2.12	
12	Bombacaceae B	--	1.18	0.41	7.64	--	1.85	
13	Mimosaceae, Mimosa pudica type	2.28	2.19	2.60	2.01	--	1.82	Road edge
14	Combretaceae, Terminalia type A	2.47	3.53	1.66	1.32	--	1.80	
15	Leguminosae E	0.48	--	5.15	2.36	0.21	1.64	
16	Polemoniaceae, Bunga pagi	3.05	3.85	0.52	0.40	0.35	1.63	Ornamental
17	Oleaceae, Jasminium type	0.78	--	--	5.91	0.24	1.38	
18	?, trizonocolporate D	5.07	0.59	0.39	--	--	1.21	
19	Dipterocarpaceae, Hopea type B	2.12	1.37	1.48	0.31	--	1.06	
20	Malphigiaceae, Hiptage type	5.14	--	--	0.09	--	1.05	
21	Passifloraceae, Passiflora ?	1.59	1.09	0.23	1.27	0.50	0.94	
22	Malvaceae, Hibiscus type	--	--	--	3.91	--	0.78	
23	?, trizonocolporate B	3.25	0.52	--	--	--	0.75	
24	Leguminosae M	2.32	0.88	--	--	--	0.64	
25	Leguminosae G	2.20	0.73	--	--	--	0.59	
26	Rutaceae, Citrus type A	--	0.39	--	2.03	--	0.48	
27	Convolvulaceae, Ipomoea type	--	1.22	0.19	--	0.77	0.44	
28	Tiliaceae, Pentace type	0.57	--	0.33	0.79	--	0.34	
29	Leguminosae, Intsia type B	--	1.55	0.14	--	--	0.34	
30	Symplocaceae, Symplocos type	0.20	0.22	--	1.10	--	0.30	
31	Caesalpiniaceae, Caesalpinia type A	--	--	1.50	--	--	0.30	
32	Proteaceae, Heliciopsis type	--	--	--	1.50	--	0.30	
33	Tiliaceae, Grewia type ? B	--	--	0.73	0.54	--	0.25	
34	Euphorbiaceae, Croton type	0.27	0.18	--	0.41	0.28	0.23	
35	?, trizonocolporate F	--	--	--	0.55	0.47	0.20	
36	Passifloraceae, Passiflora type	0.20	0.40	--	0.24	--	0.17	
37	?, trizonocolporate H	0.17	--	--	0.61	--	0.16	
38	Sterculiaceae, Sterculia type	--	0.17	0.19	0.22	0.13	0.14	
39	?, trizonocolpate A	--	--	--	0.67	--	0.13	
40	?, trizonoporate D	--	--	--	--	0.54	0.11	
41	Myrtaceae, Eugenia type B	--	--	--	0.48	--	0.10	
42	Mimosaceae, Acacia type	--	--	0.17	0.21	--	0.08	
43	Anacardiaceae, Gluta type A	0.37	--	--	--	--	0.07	
44	Theaceae ?	--	--	--	--	0.36	0.07	
45	Anacardiaceae ? B	--	--	--	0.29	--	0.06	
46	Leguminosae ? F	--	0.24	--	--	--	0.05	
47	?, trizonocolpate C	--	--	--	0.23	--	0.05	
48	?, trizonocolporate C	--	--	--	0.20	--	0.04	
49	Guttiferae, Garcinia cuspidata type	--	--	--	0.14	--	0.03	
50	Euphorbiaceae, Blumeodendron type	--	--	--	0.12	--	0.02	
51	Convolvulaceae, Convolvulus type A	--	--	0.11	--	--	0.02	
52	?, trizonocolporate X	--	--	0.09	--	--	0.02	
53	Boraginaceae, Tournefortia type	--	--	0.08	--	--	0.02	
54	?, trizonocolporate W	--	--	0.05	--	--	0.01	
55	Euphorbiaceae	--	--	--	0.01	--	0.002	

Deramakot G

Rank	Pollen type	1999		2000			Mean	Remark
		April-May	Sept.-Oct.	March-May	July	November		
		N=4	N=2	N=7	N=6	no data	%	
1	Convolvulaceae, Convolvulus type B	14.08	--	36.55	12.51		15.79	
2	Rubiaceae, Neonauclea type ? A	--	26.62	16.59	9.97		13.30	
3	Asteraceae, Tubuliflorae A type	3.75	32.78	6.65	1.03		11.05	
4	?, trizonocolporate F	17.99	2.92	0.76	18.13		9.95	
5	Bombacaceae B	--	3.79	1.97	26.35		8.03	
6	Leguminosae B	6.54	12.06	5.17	5.43		7.30	
7	Rutaceae, Clausena type A	13.85	0.35	3.76	9.53		6.87	
8	Leguminosae D	--	13.19	6.05	1.75		5.25	
9	Combretaceae, Terminalia type A	10.64	--	3.72	4.21		4.64	
10	Bombacaceae, Durio type	9.21	0.90	1.62	3.64		3.85	
11	Leguminosae E	1.69	--	7.28	0.28		2.31	
12	Leguminosae ? A	0.99	5.25	1.74	--		1.99	
13	Sterculiaceae, Pterospermum	4.05	--	0.78	0.47		1.33	
14	Leguminosae Q	3.96	--	--	0.30		1.06	
15	Myrtaceae	--	--	3.00	--		0.75	
16	Leguminosae G	--	--	0.35	1.95		0.57	
17	Oleaceae, Jasminium type	--	0.66	1.42	--		0.52	
18	Tiliaceae, Grewia type ? B	1.89	--	0.09	--		0.49	
19	Malphigiaceae, Hiptage type	0.13	--	1.69	0.09		0.48	
20	Leguminosae H	1.74	--	--	--		0.44	
21	Leguminosae I	0.85	--	0.22	0.54		0.40	
22	Rubiaceae, tetrade type	1.51	--	--	--		0.38	
23	Passifloraceae, Passiflora ?	1.27	--	--	0.11		0.35	
24	Symplocaceae, Symplocos type	--	--	--	1.36		0.34	
25	Mimosaceae, Acacia type	1.31	--	--	--		0.33	
26	Leguminosae J	0.96	0.33	--	--		0.32	
27	Rutaceae C	--	0.77	--	--		0.19	
28	Euphorbiaceae, Croton type	0.15	--	--	0.55		0.17	
29	Rutaceae, Clausena Type B	0.66	--	--	--		0.16	
30	Leguminosae K	--	--	--	0.46		0.11	
31	Leguminosae ? L	0.37	--	--	--		0.09	
32	?, trizonocolporate I	0.34	--	--	--		0.09	
33	Euphorbiaceae, Discocleidion type	0.34	--	--	--		0.08	
34	Anacardiaceae A	--	--	0.30	--		0.08	
35	Sterculiaceae, Pterocymbium type	--	--	--	0.30		0.07	
36	Tiliaceae, Pentace type	0.29	--	--	--		0.07	
37	Rhamnaceae, Ziziphus type	0.28	--	--	--		0.07	
38	?, trizonocolporate D	0.23	--	--	--		0.06	
39	?, trizonocolpate A	--	--	--	0.23		0.06	
40	?, trizonocolporate H	0.22	--	--	--		0.05	
41	Leguminosae, Intsia type B	--	--	--	0.17		0.04	
42	?, trizonoporate A	0.13	--	--	--		0.03	
43	?, trizonocolpate C	--	--	--	0.09		0.02	

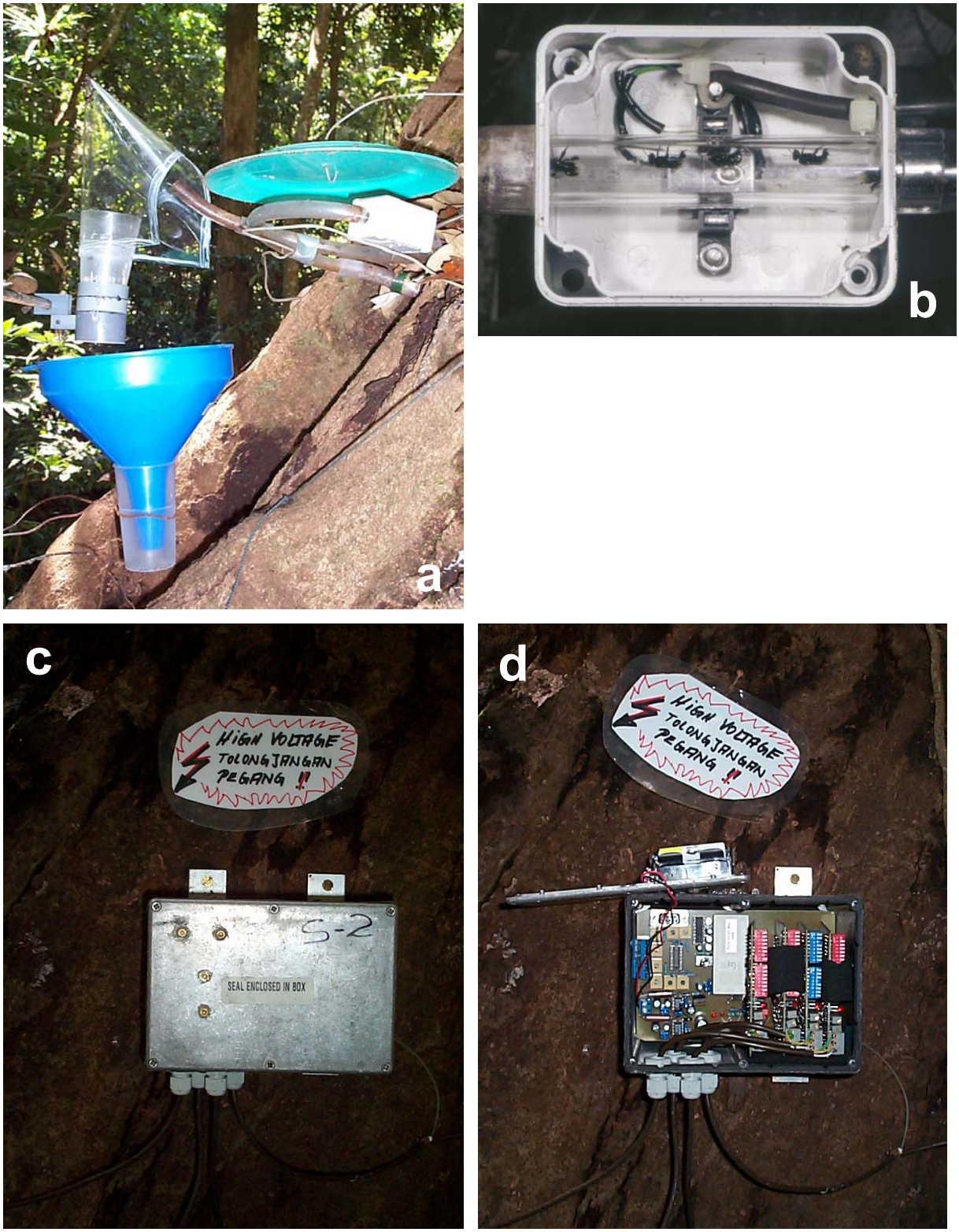

Plate 2 a) Pollen trap and light barrier installation at the nest entrance of a colony of *T. collina*. Before leaving the nest bees walked through a circle of silicon hose and cross light barriers installed in small PVC boxes (b). The circular arrangements of the hose kept bees from idling inside the light barrier box. Interceptions were registered by a controller/data logger (d) housed in water proof aluminium boxes (c).

5 SYNTHESIS

Stingless bees of Sabah nest in large, living and partly commercial trees (3.4). Therefore, and because harvesting of nest trees is likely to cause colony mortality in most cases, the direct impact of logging could be substantial. The direct impact will strongly depend on logging intensity and harvesting regulation. Estimations suggest that roughly 30 to 40 % of nests would be affected in a full-scale selective logging operation (3.4). However, the present study could not detect a clear relationship between logging history and stingless bee population density in unlogged and regenerating forests 10 to 30 years after logging (4.1, 4.2). This may be due to the following reasons:

1. Data derived from surveys are not sufficient to detect effects of logging history. This is certainly true for results of honey-water spraying assays that suffered from extreme between-year variation (4.1). Nest surveys are more reliable, but produced only small numbers of nests in sites relevant for an evaluation of logging effects (4.2).

2. Populations of bees have recovered since logging took place. Although the effects could not be confirmed statistically, both honey-water spraying and nest surveys consistently produced minimal numbers of bees and nests in the most recently logged forest sites G, H and I (4.1, 4.2), perhaps indicating residual effects of logging-induced mortality on bee populations.

3. Meliponine populations and communities are regulated by factors that may not be closely related to forest disturbance. It is evident that bee populations are mostly limited by food resources and not by the availability of nest trees (4.2). Judged by circumstantial evidence, the availability of food did not differ greatly between continuous forest sites, logged or unlogged. Instead, food availability was apparently maximal in edge situations with access to non-forest flowers (mangrove or plantation plants). The resulting 20-fold variation in nest density was in part (positively) related to forest fragmentation, but not to logging-related alterations of the residual stand.

Stingless bee species were found to be opportunistic foragers that use variable ranges of pollen plants, depending on flowering dynamics in the habitat (3.1) as well as on the local composition of the flowering plant community (3.3, 4.2). Even fungal spores were collected instead of pollen by one species (*T. collina*, 3.2). Two species (*T. melanocephala and T.*

collina) had clearly distinct preferences for pollen plants in continuous forest in Deramakot (3.1), but converged in their diets when the accessible range of pollen resources was dominated by one constantly available and rewarding plant species, the mangrove tree *Rhizophora apiculata* (4.2). Stingless bees also used crop plants (e.g. corn, manioc, water melon) as pollen sources, deliberately foraging in open plantation areas (4.2). Thus, the evident flexibility in exploitation of floral resources suggests that meliponines can adapt to a wide range of habitat conditions. However, the conservation of stingless bees and their pollination services in Sabah will ultimately depend on the conservation of meliponine nesting habitat. For all but a handful of anthropophilous species (see 3.4), this means preservation of remnants of old-growth forest. Although nest sites (large trees appropriate for nesting, 3.4) seemed not to limit populations over the range of logged and unlogged forests covered in the present study (4.2), the situation is certainly different in forest plantation and agricultural land. Two questions will have to be addressed in future studies in order to provide guidance for landscape-level planning:

- What is the minimal forest fragment size for maintaining stingless bee populations?
- How is the answer to that question influenced by characteristics of the surrounding area, e.g. the type and diversity of crop plants grown?

Stingless bees seem hopeful candidates for providing pollination of crop plants in agricultural landscapes in Asia. Their performance in this respect is likely to be highest in heterogeneous and diverse habitat mosaics including sizable patches and corridors of natural forest.

The lack of a clear response to disturbance from logging in the investigated sites cannot be generalized across other insect taxa. In contrast to stingless bees, leaf-litter ants were clearly reduced in species richness and density in logged forests. This decline is related to a deterioration of microclimatic conditions and a reduction of the leaf-litter habitat following logging (Brühl et al. 1998, Brühl in prep.). Whereas meliponine populations were favored by edge effects and occurred in highest densities in the 4294 ha forest fragment of Sepilok, inverse patterns were found in ants. These contrasting results strengthen the view that a meaningful evaluation of disturbance impact on biodiversity has to include information on a wide range of taxa with variable ecological requirements.

6 SUMMARY

The present thesis reports on four years of field research on stingless bee ecology in Sabah, Malaysia. Hereby, it was the main focus to evaluate the effect of selective logging for timber extraction on communities of bees, and to elucidate the relevant causative relationships involved in regulating bee populations. Included were background studies on resource use (3.1, 3.2, 3.3) and nesting biology (3.4) as well as comparative studies on stingless bee diversity and abundance in logged and unlogged lowland rainforest sites (4.1, 4.2). The results are summarized by chapter.

Background studies: food resources and nesting of stingless bees in Sabah:

(3.1) Pollen foraging and resource partitioning of stingless bees in relation to flowering dynamics in a Southeast Asian tropical rainforest. We used microscopic pollen analysis to investigate the diversity and similarity of pollen diets of six colonies of stingless bees (Apidae; Meliponini) located within one monospecific (three colonies of *Trigona collina*) and one mixed nesting aggregation (one colony of *T. collina*, and one colony of each of the close relatives *T. melina* and *T. melanocephala*) in lowland tropical rain forest in Sabah, Malaysia. Samples of 20 corbicular loads, collected six times over a period of three months from each colony, contained a total of 74 different morphotypes of pollen grains with an average between 4.7 to 8.5 per sample for the different colonies. In an analysis on total diet composition intraspecific similarity was much greater than interspecific similarity. The focal colony of *Trigona collina* from the mixed aggregation distinctly clustered according to species rather than nest location, suggesting that some interspecific resource partitioning occurs. The sampling period was accompanied by a drastic increase in flowering activity as evidenced by data from a flower phenology transect. At times of limited flowering similarity of pollen diets was generally low, both within and between species. It is hypothesized that this is so because bees are forced to forage from scattered subsets of flower patches spread out over a large foraging range. In times of increased flowering pollen diet similarity significantly increased between colonies of the monospecific aggregation, presumably because colonies concentrated on more profitable sources in closer proximity. In contrast, similarity remained low within the mixed aggregation, suggesting that innate differences in foraging preferences precluded any effect of diet convergence.

(3.2) Collection of mold (*Rhizopus sp*.) spores in lieu of pollen by the stingless bee *Trigona (Tetragonula) collina.* In the course of a study on pollen diets of three sympatric species of stingless bees (Apidae: Meliponini) in Sabah, Malaysia (3.1), we made the observation that large fractions of the foragers of three colonies of *Trigona (Tetragonula) collina* collected large loads of fungal spores in lieu of pollen. Collection of spores continued for at least three consecutive days. The spores were brought to germination in the laboratory and the culture was identified as mold of the genus *Rhizopus* (Zygomycota, Mucorales). Our observations represent the first reported case of the collection of mold spores in lieu of pollen by bees as well as the first reported case of the collection of fungal spores by bees other than honeybees (*Apis*).

(3.3) Assessing stingless bee pollen diet by analysis of garbage pellets: a new method. Studies on pollen resource use of stingless bees frequently suffer from low sample size due to difficulties concerning the acquisition of adequate samples of harvested pollen. Here we describe a funnel-trap that allows non-invasive and automated sampling of pollen-rich garbage pellets that are expelled from colonies by workers bees. Single garbage pellets of *Trigona collina* from Sabah, Malaysia, contained between 7 and 11 different morphotypes of pollen and the similarity of the pollen composition of pellets expelled by a given colony on a given day was very high (quantitative Steinhaus index: 71 to 90 %). The turn-over of pollen types in samples taken at consecutive points in time was relatively low over periods of three weeks (52 to 75 % similarity) and variable over periods of four to six months (13,6 to 58,5 % similarity). The comparison of pollen in corbicular loads and garbage pellets indicates that garbage pollen is derived from both feces of pollen-consuming workers and larval feces (meconia). The slow turn-over of pollen in garbage suggests that sampling at relatively long intervals (4-6 months) will be sufficient for a crude assessment of long-term pollen resources of stingless bee colonies.

(3.4) Nesting and nest trees of stingless bees (Apidae: Meliponini) in lowland dipterocarp forests in Sabah, Malaysia, with implications for forest management. Nesting habits of highly social stingless bees (Meliponini) were studied in lowland dipterocarp forests in Sabah, Borneo. A total of 275 nests of 12 species of bees were located. All nests were closely associated with living (91.5 %) or dead (8.5 %) trees, either within pre-formed cavities in the trunk (cavity nests) or situated in or under the tree base (base nests). Species of bees differed in nesting. The majority (7) were cavity nesters, but the majority of nests (81 %) were base nests. Nests were often aggregated (mean of 1.94 nests/ nest tree), with up to eight colonies

and three species in a single tree. Nest trees were mostly large to very large (86.1 % above 60 cm dbh) commercial timber trees. 47.3 % of nest trees were dipterocarps. According to visual inspection nest trees were of significantly lower expected timber quality then randomly chosen control trees. Taking into account information on tree species, size and expected timber quality, we estimated that 34.0 % or 42.6 % of nest trees were potential harvest trees, depending on harvesting regulations (Reduced Impact Logging versus conventional). Lower percentages under RIL guidelines were mostly due to size restrictions that protect very large trees (> 120 cm dbh). Harvesting is likely to kill bee colonies associated with the respective tree. Therefore, and because meliponine colonies are long-lived and have low fecundity, direct impact from logging may have lasting effects on bee populations. Harvesting guidelines that retain high proportions of large and hollow trees should be promoted in order to preserve meliponine pollination in Sustainable Forest Management.

Between-site comparisons of species richness and abundance: patterns and causes of variation

(2.2) Sudy sites. Stingless bees were surveyed in a total of 14 research sites located in primary and logged forests in lowland Sabah. In each site we established a transect grid covering an area of 600 x 600 m. Research sites were situated in three localities in eastern and central Sabah. Sites included continuous undisturbed forest (Danum Valley, two sites: L, M), fragmented undisturbed forest (Sepilok, three sites: Laut, K, L) and three types of selectively logged forest varying in history and intensity of logging (Deramakot, three sites in each of the types: A, B, C (slightly disturbed, old); D, E, F (heavily disturbed, old); G, H, I (heavily disturbed, young)) (see 2.2).

(4.1) Survey of stingless bees and honey bees using honey-water baits. Stingless bees were sampled at honey-water spray stations along transects in twelve of the fourteen sites between February and May in 1998. Partial replication followed during the same months in 1999. A total of sixteen species of stingless bees were attracted to the spray stations, representing about two thirds of the local species pool. The number of species per assay, the number of species per spray station and the number of individual bees at spray stations all varied significantly between forest types in 1998, with highest measures for all parameters in undisturbed forests. In 1999, however, the patterns were partly reversed, and significant interaction between forest type and year (two-way ANOVA) indicated that more temporal replicates would be required for conclusive results. Heavily and recently logged sites (Deramakot G, H, I) were relatively consistent in having low numbers of bees and bee species, however, indicating lasting effects of logging-induced mortality (see 3.4). The high

temporal variability of baiting results is probably derived from (i) fluctuations in stingless bee colony strength, (ii) variable foraging activity of individuals and colonies, and (iii) changes in the attractiveness of baits due to variable availability of natural nectar sources at the time of baiting. Extreme temporal fluctuations of bee incidence limit the potential of honey-water baiting as a tool for stingless bee bio-assessment.

(4.2) Factors limiting stingless bee nest density in primary and regenerating dipterocarp forests of Sabah, Malaysia. We searched for stingless bee nest trees and nests along 20-meter corridors along the transect grids in all 14 forest sites. A total of 117 stingless bee nests of 11 species were located, with 54.7% of the nests belonging to *Trigona collina*. Per-area nest density varied twenty-fold across sites and was dependent on locality (Danum, Sepilok, Deramakot), but not clearly on degree and history of disturbance. Nest density was generally high in the Sepilok Forest fragment (mean 8.4 nests/ha). Hereby, the 16.2 nests/ha in mangrove-bordering Sepilok Laut represented the highest stingless bee nest density recorded for any tropical forest. In contrast, nest densities in continuous forests (Danum and Deramakot) were all low (between 0 and 2.1 nests/ha, mean 0.55 nests/ha). Proximate causes of differences in nest density may include (i) differential mortality of established colonies due to predation, (ii) differential limitation of nest sites (nest trees) in different forest sites, or (iii) differences in stingless bee carrying capacity mediated by differential availability of food resources. Data were collected in order to evaluate each of these possibilities: Nest mortality (i) did not vary accordingly between forest localities. The presence of potential nest trees (>60 cm dbh)(ii) was positively correlated with nest density, but explained only a minor fraction of the observed variation. Instead, nest density was best explained by differences in the pollen resources (iii) available to the bees (quantified with the help of garbage analysis, see 3.3). In Sepilok Laut, the site with the highest nest density, diets of colonies of five species of stingless bees included large proportions of mangrove pollen (*Rhizophora apiculata*, 28 to 100 % volume of garbage pollen), suggesting that *R. apiculata* constitutes a super-abundant resource for bees in nearby forests. Similarly, bees in Sepilok K foraged on crop and ornamental plants grown in nearby plantation areas. Across five selected sites (Sepilok Laut, Sepilok K, Danum M, Deramakot A and G) the amount of non-forest pollen included in diets of *T. collina* was closely correlated with *T. collina* nest density. It is hypothesized that external pollen sources effectively supplement bee diets at times when little flowering occurs inside the forest, thus increasing overall bee carrying-capacity. The idea of pollen limitation is strengthened by direct measurements of pollen import and foraging activity in three selected sites between February and June 2000: Pollen traps installed at *T. collina* nests in high-density

Sepilok K captured significantly more corbicular pollen than colonies in low-density Deramakot A and G. At the same time, morning foraging activity (measured by electronic bee counters) was also greater in Sepilok, indicating a regulatory increase of foraging in response to high pollen availability.

It is concluded that the abundance of stingless bees in forests in Sabah is chiefly dependent on the local availability of food resources. Hereby, bee populations strongly benefit from edge effects and increased habitat diversity. Although direct negative effects of selective logging are strongly indicated by a close association of bee nests with commercial trees, no clear effects were detected in regenerating forests ten to 30 years after logging.

7 ZUSAMMENFASSUNG

Die vorliegende Dissertation umfaßt die Ergebnisse einer vierjährigen Studie zur Ökologie von Stachellosen Bienen in den Regenwäldern von Sabah, Malaysia. Hauptziel war es dabei, mögliche Auswirkungen der selektiven Holznutzung auf Bienengemeinschaften zu erforschen und, falls sich ein Effekt nachweisen läßt, die dafür verantwortlichen Wirkfaktoren zu identifizieren. Die Arbeiten schlossen sowohl Hintergrundstudien zur Nahrungsökologie (3.1, 3.2, 3.3) und Nistbiologie (3.4) ein, als auch vergleichende Erfassungen der Bienenabundanz und -diversität in primären und durch Holznutzung gestörten Tieflandregenwäldern. Die Ergebnisse werden hier einzeln für die jeweiligen Kapitel zusammengefaßt.

Hintergrundstudien: Nahrungsnutzung und Nistbiologie

(3.1) Pollennutzung und Ressourcenteilung bei Stachellosen Bienen in Abhängigkeit der Blühphänologie in einem Südostasiatischen tropischen Regenwald. Die Diversität und Ähnlichkeit von Pollentrachten von sechs Kolonien Stachelloser Bienen (Apidae; Meliponini) wurden mittels mikroskopischer Pollenanalyse untersucht. Die Kolonien befanden sich in einer monospezifischen (drei Kolonien von *Trigona collina*) und einer gemischten (eine Kolonie von T. collina und jeweils eine von *T. melina* und *T. melanocephala*) Aggregation. Proben von jeweils 20 corbicularen Ladungen, sechs mal im Verlauf von drei Monaten von jeder Kolonie abgesammelt, enthielten insgesamt 74 verschiedene Pollen-Morphotypen (4.7 bis 8.5 pro Probe und Kolonie). Die Ähnlichkeit der Typen-Zusammensetzung der Pollennahrung von Kolonien war größer innerhalb der Art *T. collina* als zwischen den Kolonien verschiedener Arten, ein Befund, der auf interspezifische Ressourcenteilung hinweist. Die Blühaktivität (Anzahl von blühenden Pflanzen und Pflanzenarten) stieg während der Untersuchungsperiode stark an. Bei geringer Blütenverfügbarkeit war die Ähnlichkeit der Pollenzusammensetzung zwischen Kolonien generell niedrig, sowohl innerhalb als auch zwischen den Arten. Es wird vermutet, daß dies durch die Notwendigkeit bedingt wird, Pollen von ‘Subsets’ weit verstreuter Blütenvorkommen zu sammeln. Mit zunehmender Blütenverfügbarkeit nahm die Ähnlichkeit der Trachten innerhalb der monospezifischen Aggregation zu, vermutlich weil die Sammelbienen ihre Aktivität auf näherliegende, stärker belohnende Quellen konzentrierten. Im Gegensatz dazu blieb die Ähnlichkeit innerhalb der gemischten Aggregation niedrig. Dies legt nahe, daß artspezifische Fouragier-Präferenzen einer Konvergenz der Nahrungsspektren entgegenwirkte.

(3.2) Eintrag von Schimmelpilzsporen (*Rhizopus sp.*) an Stelle von Pollen durch Sammlerinnen der Stachellosen Biene *Trigona (Tetragonula) collina*. Während einer Untersuchung des Polleneintrags von drei sympatrischen Stachellosen Bienen (Apidae: Meliponini) in Sabah, Malaysia (siehe 3.1), beobachteten wir, daß ein großer Teil der Arbeiter von drei Kolonien der Art *T. collina* Ladungen von Pilzsporen anstatt Pollen ins Nest trugen. Das Sammeln der Sporen dauerte über mindestens drei aufeinander folgende Tage an. Die Sporen konnten im Labor zum Keimen gebracht werden. Die Kulturen wurden als Schimmelpilz der Gattung *Rhizopus* (Zygomycota, Mucorales) identifiziert. Unsere Beobachtungen stellen den ersten Nachweis für den Eintrag von Schimmelpilzsporen durch Bienen dar. Außerdem handelt es sich um den ersten Nachweis für das Pilzsporen-Sammeln bei Meliponinen.

(3.3) Die Erfassung der Pollennahrung von Stachellosen Bienen durch die Analyse von Bienenmüll: Eine neue Methode. Die zur Zeit gebräuchlichen Methoden zur Erfassung der Pollennahrung von Stachellosen Bienen sind mit Schwierigkeiten verbunden, da sie entweder sehr arbeitsaufwendig sind oder den direkten Zugang zu den Pollenvorräten der Kolonien voraussetzen. In dem vorliegenden Artikel beschreiben wir eine einfache Falle, mit deren Hilfe es gelingt, die von Arbeiterbienen aus dem Nest geworfenen, pollenhaltigen Müllballen aufzufangen. Im Falle unserer hauptsächlichen Untersuchungsart, *Trigona (Tetragonula) collina* aus dem Tiefland von Sabah (Malaysia), bestehen etwa 20 % des Trockengewichts der Müllballen aus gut erhaltenen Pollenexinen, die als Grundlage für eine mikroskopische Pollenuntersuchung dienen können. Einzelne Müllballen von zwei Untersuchungskolonien von *T. collina* enthielten zwischen 7 und 11 verschiedene Pollen-Morphotypen. Die Pollenzusammensetzung von Ballen, die am selben Tag von einer Kolonie abgesammelt wurden, war sehr hoch (71 – 90%, quantitativer Steinhaus-Index). Die zeitliche Dynamik von Pollen in Müllproben war dagegen niedrig. Exemplarisch verglichen wir bei einer Kolonie von *T. collina* über einen Zeitraum von fünf Monaten den Pollen-Eintrag (corbicularer Pollen) mit dem Müllpollenauswurf. 94 % der eingetragenen Pollentypen wurden auch im Müll gefunden, aber der Müll enthielt zusätzlich weitere Typen, die zur Untersuchungszeit nicht nachweislich eingetragen wurden. Die zeitliche Verteilung verschiedener Pollentypen in Eintrag und Auswurf legt nahe, daß die Zusammensetzung des Müllpollens von mehreren Prozessen beeinflußt wird, die auf unterschiedlichen Zeitskalen wirken: Bienenmüll enthält (i) Pollen, der direkt von Arbeiterbienen verzehrt und wieder ausgeschieden wird (bzw. dessen Exinen), (ii) Pollen aus den Exkrementen (Meconia) der Larven, und (iii) Pollen, der nach Einlagerung in Pollenbehältern nach geraumer Zeit konsumiert und schließlich ausgeschieden

wird. Die beschriebene Müllfalle könnte sich in zukünftigen Studien als ein nützliches Hilfsmittel zur Erfassung der Pollenressourcen von Meliponinen erweisen. Der geringe Turn-over impliziert, daß für eine grobe, langfristige Erfassung der Pollenressourcen bereits Probennahmen in mehrmonatigen Abständen (bis zu 4-6 Monaten) ausreichend sind.

(3.4) Nistbiologie und Nistbäume von Stachellosen Bienen (Apidae: Meliponini) in Dipterocarpaceen-Wäldern im Tiefland von Sabah, Malaysia: Implikationen für die Bewirtschaftung von Nutzwäldern. Die Nistweise hochsozialer Stachelloser Bienen wurde in Sabah, Borneo, untersucht. Insgesamt wurden 275 Nester von zwölf Arten gefunden. Alle Nester waren eng mit lebenden (91.5 %) oder toten (8.5%) Bäumen assoziiert und befanden sich entweder in Hohlräumen im Stamm (Höhlen-Nester) oder unter bzw. in der Stammbasis (Basis-Nester). Verschiedene Arten zeigten unterschiedliche Präferenzen. Die Mehrheit der Arten (7) nistete hauptsächlich in Stammhöhlen, aber die Mehrheit der Nester (81%) waren Basis-Nester. Oft fanden sich mehrere Nester aggregiert in einzelnen Nistbäumen (Durchschnitt 1.94 Nester/Baum, Maximum: 8). Die Nistbäume waren fast immer sehr groß (86.1% über 60 cm Stammdurchmesser) und gehörten oft (88.7%) zu kommerziell nutzbaren Arten. Bei visueller Inspektion ergab sich, daß Nistbäume eine geringere Holzqualität besaßen als zufällig ausgewählte Kontrollbäume. Unter Berücksichtigung der taxonomischen Zugehörigkeit, Baumgröße und der erwarteten Holzqualität wurde geschätzt, daß zwischen 34% und 42.6% der Nistbäume der kommerziellen Holznutzung zum Opfer fallen würden (je nach verwendeten Einschlagmethoden: Reduced Impact Logging (RIL) oder konventionell). Der niedrigere Wert für RIL ergab sich hauptsächlich aus der hierbei geförderten Erhaltung übergroßer Bäume (>120 cm Stammdurchmesser). Das Fällen von Nistbäumen würde wahrscheinlich den Tod der meisten assoziierten Bienenkolonien bewirken. Deshalb, und weil Meliponinen sehr langlebig sind und nur geringe Fortpflanzungsraten aufweisen, könnte der Einfluß von selektivem Holzeinschlag langfristige Folgen für die Bienenpopulationen haben. Verbindliche Nutzungsvorschriften, die den Erhalt von großen und hohlen Bäumen bewirken, sollten im Zusammenhang mit dem Schutz von Meliponinen (und deren Dienste als Bestäuber) gefördert werden.

<u>Vergleichende Untersuchungen zur Bienenabundanz und –diversität: Muster und mögliche Wirkfaktoren</u>

(2.2) Untersuchungsflächen. Zur Erfassung Stachelloser Bienen wurden 14 Untersuchungsflächen in primären und selektiv eingeschlagenen Wäldern im Tiefland von Sabah ausgewählt. In allen Flächen wurden Transektsysteme mit 600 x 600 m Kantenlänge

angelegt. Die Flächen beinhalteten kontinuierlichen, ungestörten Wald (Danum Valley, zwei Flächen: L, M), ungestörten Wald in Randlage eines Waldfragments (Sepilok, drei Flächen: Laut, K, L) und drei Typen von holzwirtschaftlich genutzten Wäldern mit unterschiedlicher Nutzungsgeschichte (Deramakot, drei Flächen von jedem der drei Typen: A, B, C (leicht gestört, alt); D, E F (stark gestört, alt); G, H, I (stark gestört, jung)). Siehe Karten in Sektion 2.2.

(4.1) Erfassung der Stachellosen Bienen mit Honigwasser-Ködern. Wir sprühten Honigwasser auf Vegetation entlang der Transektsysteme in allen 14 Flächen und erfaßten die numerische Präsenz und Artenzahl der angelockten Bienen. Insgesamt wurden sechzehn Meliponinenarten an den Köderstellen festgestellt. Die Artenzah pro Sprüheinheit (Sprühtag), die Artenzahl pro Köderstelle und die Anzahl individueller Bienen pro Köderstelle waren im Jahr 1998 signifikant vom Waldtyp abhängig (mit den höchsten Werten in ungestörten Wäldern). Im darauffolgenden Jahr lagen zum Teil umgekehrte Verhältnisse vor (signifikante Interaktion zwischen den Effekten von Waldtyp und Jahr), so daß die Befunde der Untersuchung keine klaren Schlußfolgerungen erlauben. Nur die stark gestörten, jungen Flächen (Deramakot G, H, I) wiesen in beiden Jahren ähnlich niedrige Werte auf, ein Befund, der möglicherweise auf eine noch bestehende Reduzierung der Bienendichte durch die Waldnutzung (direkt verursachte Nestmortalität) hinweist. Die hohe zeitliche Variabilität der Ergebnisse der Honigköderstudie legt nahe, daß die Methode für eine schnelle Erfassung von Meliponinen (Stichwort ‘Bioassessment’) nicht geeignet ist.

(4.2) Limitierende Faktoren für die Nestdichte Stachelloser Bienen in primären und regenerierenden Wäldern in Sabah, Malaysia. Die Meliponinen-Nestdichte wurde durch quantitative Nestsuche in 20-m-Korridoren entlang der Transektsysteme in allen 14 Untersuchungsflächen bestimmt. Insgesamt wurden 117 Nester von 11 Arten gefunden. Ein Großteil davon (54.7%) waren Nester der basis-nistenden *T. collina*. Die Nestdichte variierte 20-fach zwischen den Untersuchungsflächen und war signifikant abhängig von der Lokalität (Danum, Sepilok, Deramakot), aber nicht von der Nutzungsgeschichte des Waldes. Hohe Dichten wurden nur im Sepilok-Waldfragment gefunden (Mittel: 8.4 Nester/ha). Die mangrovennahe Fläche Sepilok Laut wies dabei die höchste jemals in einem tropischen Wald gemessene Meliponinendichte auf. Im Gegensatz zu Sepilok waren die Nestdichten in kontinuierlichen Waldgebieten (Danum, Deramakot) sehr niedrig (zwischen 0 und 2.1 Nester/ha; Mittel: 0.55). Mögliche proximate Ursachen (Wirkfaktoren) der Variation der Nestdichten sind (i) ungleiche Nestmortalität, z. B. durch Nestprädation, (ii) ungleiche

Limitierung durch Nistmöglichkeiten (Nistbäume), oder (iii) ungleiche Limitierung durch Nahrungsressourcen. Wir bestimmten die Nestmortalität, genutzte Pollenquellen und Fouragieraktivität von Meliponinen-Kolonien in den unterschiedlichen Lokalitäten um die relative Bedeutung dieser Faktoren abzuwägen. Die Nestmortalität (i) war generell niedrig (13.5 bis 15.0% pro Jahr) und wies keine Unterschiede auf, die die unterschiedlichen Nestdichten erklären würden. Auch die Anwesenheit von potentiellen Nistbäumen (>60 cm Stammdurchmesser)(ii) konnte nur einen sehr kleinen Teil der beobachteten Variation erklären. Die hohe Nestdichte in Sepilok wurde am besten durch die dort verfügbaren Nahrungsressourcen (iii) erklärt. In der extrem bienenreichen Fläche Sepilok Laut bestand die Pollennahrung (bestimmt mit der unter 3.3 beschriebenen Methode der Bienenmüllanalyse) von fünf untersuchten Arten zu sehr hohen Anteilen (28 bis 100% des Gesamtvolumens) aus Pollen des Mangrovenbaums *Rhizophora apiculata*. *R. apiculata* dominiert die lokalen Mangroven, produziert große Mengen von leicht zugänglichem Pollen und stellt so eine superabundante Nahrungsquelle für Bienen benachbarter Wälder dar. Nester der plantagennahen Fläche Sepilok K griffen in ähnlicher Weise auf Pollen von kultivierten Pflanzen zurück. Über fünf untersuchte Flächen (Sepilok Laut, Sepilok K, Danum M, Deramakot A und G) hinweg gab es eine signifikante Korrelation zwischen dem Anteil externer Pollenquellen im Bienemüll von *T. collina* und der Nestdichte dieser Art. Vermutlich stellen externe Pollenquellen eine wichtige Ergänzung der Bienennahrung zu Zeiten geringer Blühaktivität im Wald dar. Die 'Carrying capacity' des Waldes für Meliponinen könnte somit erhöht sein. Die Theorie der Limitierung durch Pollenquellen wird durch direkte Messungen von Polleneintrag und Fouragieraktivität in drei ausgewählten Flächen zwischen Februar und Juni 2000 gestützt: Pollenfallen vor *T. collina*-Kolonien in der bienenreichen Fläche Sepilok K fingen mehr Pollen auf als Fallen vor Kolonien der selben Art in den Flächen Deramakot A und G. Zur gleichen Zeit war die morgendliche Fouragieraktivität (gemessen mit Hilfe elektronischer Bienenzähler) ebenfalls in Sepilok K höher, ein Befund, der auf erhöhtes Pollenfouragieren und erhöhte Pollenverfügbarkeit hinweist.

Zusammenfassend läßt sich schließen, daß die Abundanz von Stachellosen Bienen in Sabahanischen Wäldern hauptsächlich von der lokalen Nahrungsverfügbarkeit abhängt und Bienenpopulationen hierbei stark von Randeffekten und erhöhter Habitatdiversität profitieren. Ein Einfluß von anthropogener Störung durch selektive Holznutzung ist aufgrund der Nistbiologie von Meliponinen kurz und mittelfristig zu erwarten, konnte aber in regenerierenden Wäldern zehn bis 30 Jahren nach dem Einschlag nicht eindeutig nachgewiesen werden.

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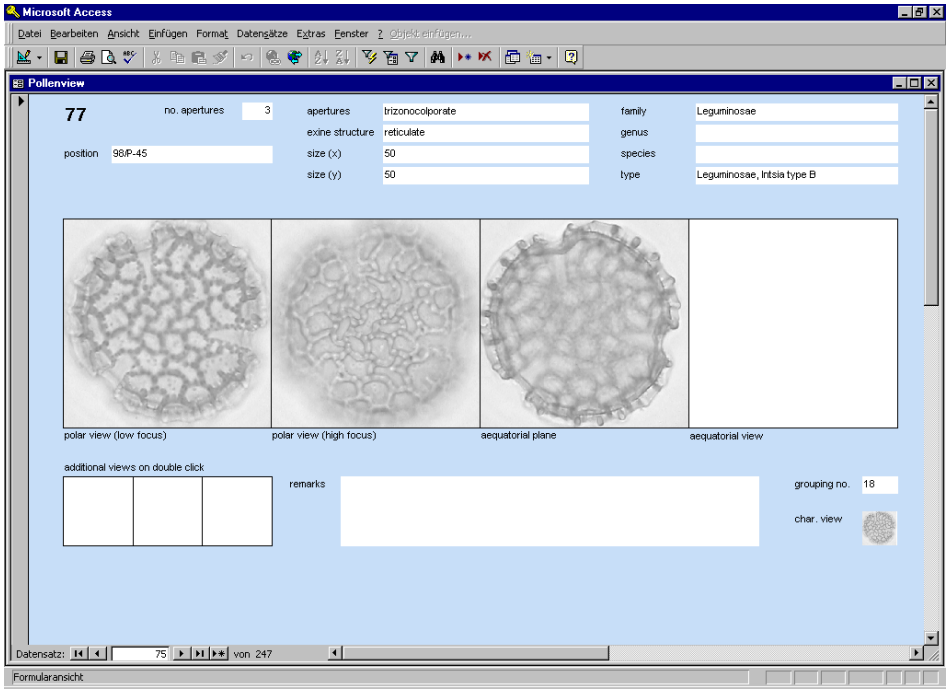
9 APPENDIX

Appendix 1 → Section 3.1, page 36

Appendix 2 → Section 4.2, page 107

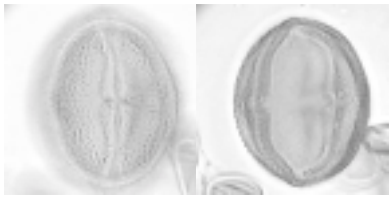
Appendix 3 Pollen image data base in Microsoft Access

Since 1999 all microscopic pollen slides were analyzed with the help of a computerized image and data base using Ms Access 97. Images of new pollen types (polar and/or equatorial views) were scanned directly from microscopic slides using a Sony digital video camera mounted on a Leitz Laborlux microscope, and Snappy 3.0 hardware and software (Play Inc.) for capturing video snapshots. Image files were saved as gray scale .GIF with 800x600 pixels and entered into Access tables using the 'Objekt einfügen' function. At present, the data base contains more than 200 grain types with almost 700 individual pictures. Images and data can be accessed using the following interface:



The following pages show pollen types that were above the 0.5% volume threshold in samples of bee garbage of *T. collina*, *T. melina*, *T. melanocephala* and *T. terminata*. Types names cross-reference with those in sections 3.3 and 4.2 (garbage pollen samples), but not with those in section 3.1. The data base contains pollen types found in garbage of nests of *T. melanocephala* in Deramakot A, Deramakot G and Sepilok K (N=1 nest/site) that are not mentioned in the text. Pollen types are sorted by plant family in alphabetical order. Grain diameter is given in microns (x=polar axis; y=equatorial axis). Values in gray fields represent mean percent volume in samples of the respective species in a given location (sample size varies).

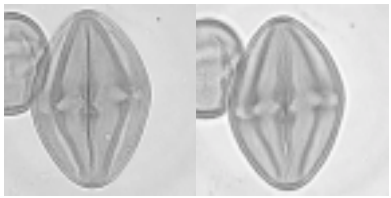
198 Anacardiaceae A



x: 34
y: 47

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K				
Danum M				
Deramakot A	2,17			
Deramakot G	0,08			

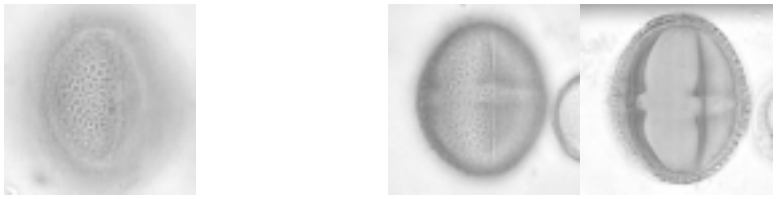
174 Anacardiaceae ? B



x: 44
y: 31

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut	0,15		0,19	
Sepilok K				
Danum M	0,10			
Deramakot A	0,06			
Deramakot G				

199 Anacardiaceae ? C



x: 34
y: 41

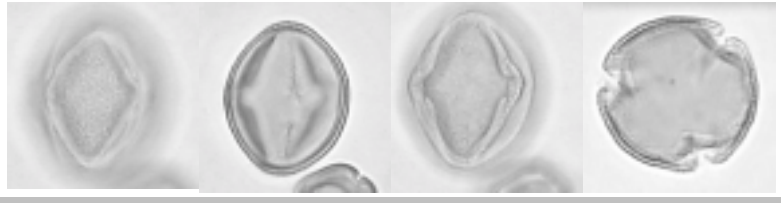
	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K				
Danum M				
Deramakot A		9,67		
Deramakot G				

73 Anacardiaceae, Gluta type A

x: 28
y: 39

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K	0,14			
Danum M	0,52			
Deramakot A	0,07			
Deramakot G				

175 Anacardiaceae, Gluta type B



x: 31
y: 25

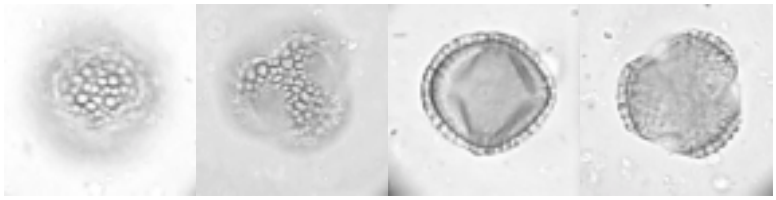
	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut	5,58	0,58	0,28	3,25
Sepilok K				
Danum M				
Deramakot A				
Deramakot G				

192 Annonaceae, Meiogyne type

x: 56
y: 56

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K		9,18		
Danum M				
Deramakot A				
Deramakot G		3,36		

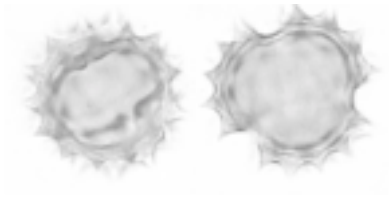
185 Aquifoliaceae, Ilex



x: 22
y: 22

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut			1,38	
Sepilok K	0,06			
Danum M				
Deramakot A				
Deramakot G				

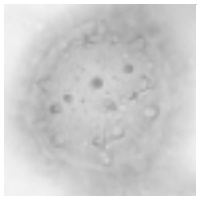
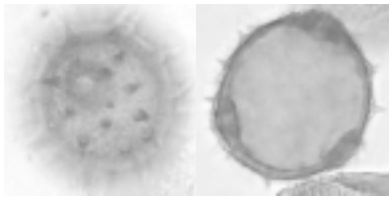
12 Asteraceae, Tubuliflorae A type

x: 23
y: 23

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut	1,82		9,17	
Sepilok K	5,11	1,50		
Danum M	6,17			
Deramakot A	3,84			
Deramakot G	11,05			

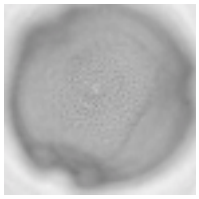
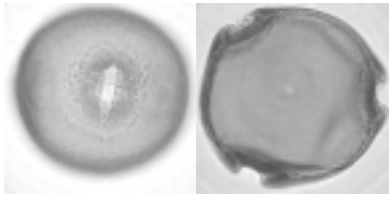
143 Bombacaceae, Campnostemon type

x: 27
y: 27

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K	0,37			
Danum M				
Deramakot A				
Deramakot G				

3 Bombacaceae, Durio type

x: 63
y: 63

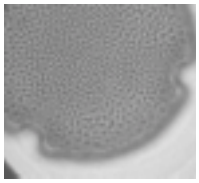
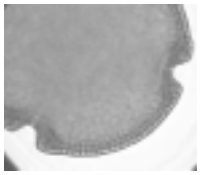
	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K	0,33			
Danum M	13,90			
Deramakot A	4,39			
Deramakot G	3,85			

220 Bombacaceae A

x: 83.7
y: 83.7

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K	11,66			
Danum M	8,68			
Deramakot A	6,66			
Deramakot G				

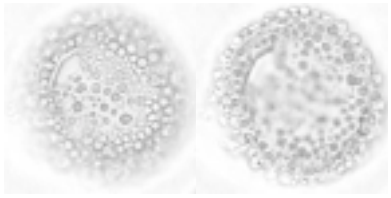
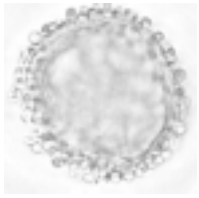
52 Bombacaceae B

x: 86
y: 86

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K	0,62			
Danum M	0,57			
Deramakot A	1,85			
Deramakot G	8,03			

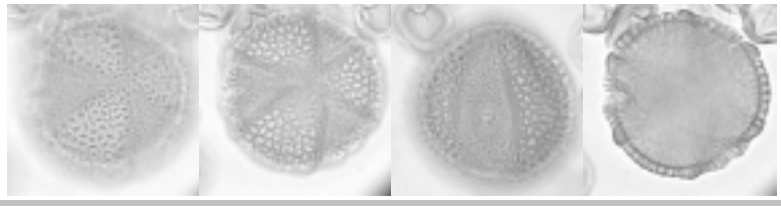
95 Boraginaceae, Tournefortia type

x: 34
y: 34

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K				
Danum M				
Deramakot A	0,02			
Deramakot G				

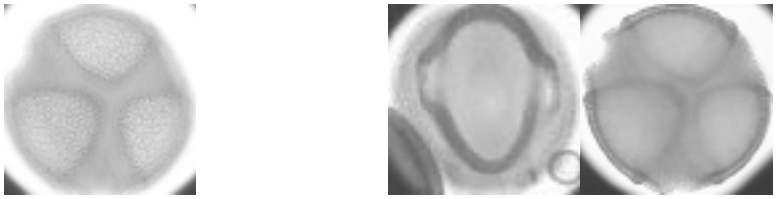
197 Caesalpiniaceae, Caesalpinia type A



x: 38
y: 38

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K				
Danum M				
Deramakot A	0,30			
Deramakot G				

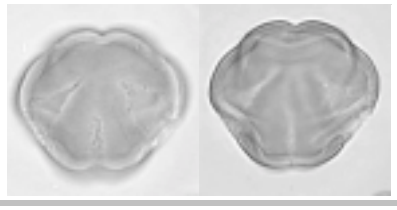
142 Caesalpiniaceae, Caesalpinia type B



x: 85
y: 85

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K	1,11			
Danum M				
Deramakot A				
Deramakot G				

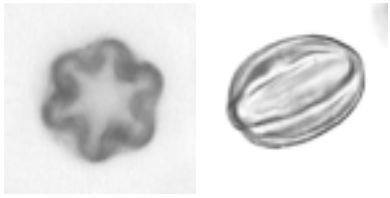
177 Combretaceae, Lumnitzera littorea



x: 36
y: 36

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut	0,41	1,52	1,51	0,56
Sepilok K				
Danum M				
Deramakot A				
Deramakot G				

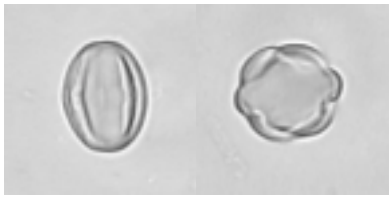
98 Combretaceae, Terminalia type A



x: 15
y: 21

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K				
Danum M	0,15			
Deramakot A	1,80			
Deramakot G	4,64	2,44		

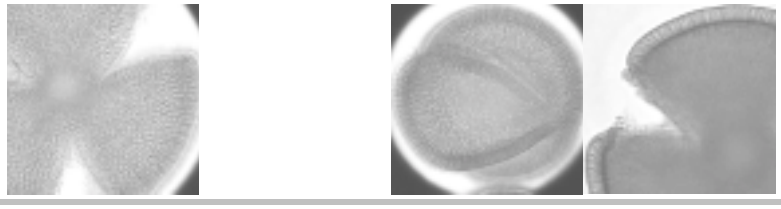
173 Combretaceae, Terminalia type B



x: 17
y: 14

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut	0,25			
Sepilok K				
Danum M				
Deramakot A				
Deramakot G				

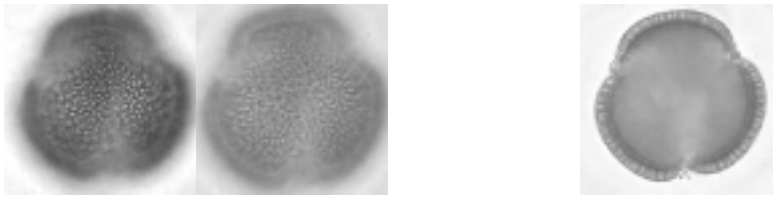
46 Convolvulaceae, Convolvulus type A



x: 87
y: 87

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K	4,15	30,66		
Danum M	0,73			
Deramakot A	0,02			
Deramakot G				

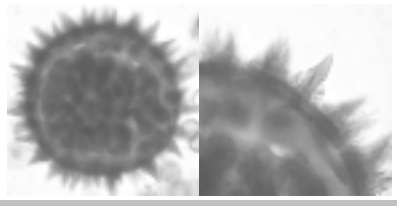
107 Convolvulaceae, Convolvulus type B



x: 40
y: 40

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K				
Danum M	8,84			
Deramakot A				
Deramakot G	15,79	2,80		

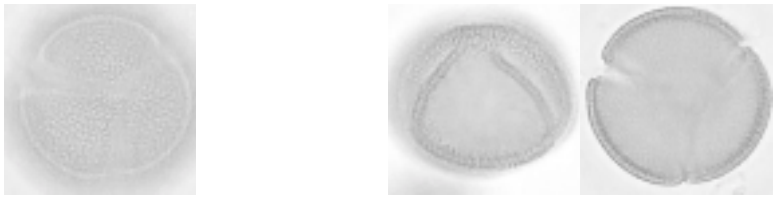
126 Convolvulaceae, Ipomoea type



x: 105
y: 105

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K	0,38			
Danum M				
Deramakot A	0,44			
Deramakot G				

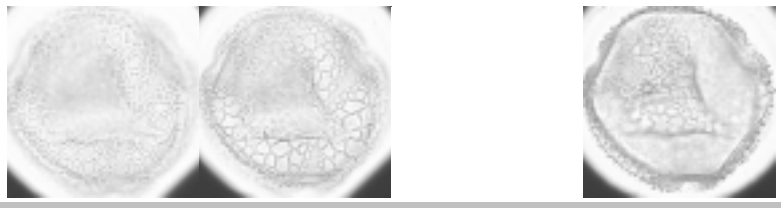
146 Convolvulaceae



x: 34
y: 34

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K	0,12			
Danum M				
Deramakot A				
Deramakot G				

154 Cucurbitaceae, Citrullus lanatus



x: 84
y: 84

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K	5,00			
Danum M				
Deramakot A				
Deramakot G				

61 Cyperaceae

x: 38
y: 38

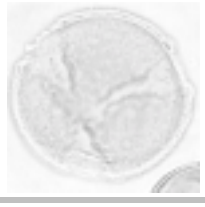
	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut		1,52		
Sepilok K	0,87			
Danum M				
Deramakot A		1,21		
Deramakot G				

171 Dilleniaceae, Dillenia

x: 31
y: 25

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut	0,08			
Sepilok K	0,07			
Danum M				
Deramakot A				
Deramakot G				

40 Dipterocarpaceae, Hopea type A



x: 28
y: 28

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K				
Danum M				
Deramakot A				
Deramakot G		13,91		

105 Dipterocarpaceae, Hopea type B

x: 26
y: 38

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K				
Danum M	0,07			
Deramakot A	1,06			
Deramakot G				

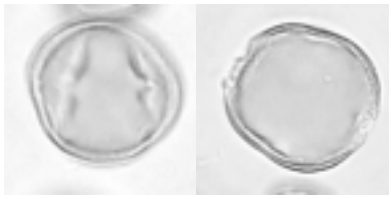
48 Euphorbiaceae, Antidesma typ

x: 13
y: 28

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K				
Danum M	0,23			
Deramakot A		2,64		
Deramakot G				

183 Euphorbiaceae, Baccaurea type A

x: 25
y: 25



	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut	0,17		6,25	
Sepilok K				
Danum M				
Deramakot A				
Deramakot G				

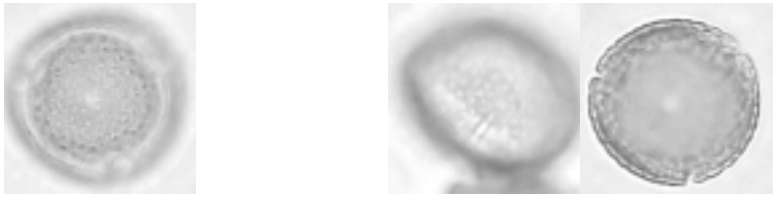
212 Euphorbiaceae, Baccaurea type ? B

x: 23
y: 23

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K				
Danum M	1,40			
Deramakot A				
Deramakot G				

64 Euphorbiaceae, Blumeodendron type

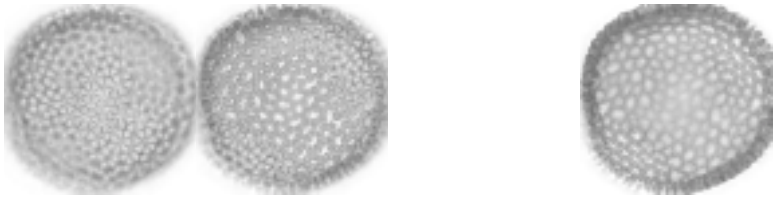
x: 22
y: 26



	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K				
Danum M				
Deramakot A	0,02			
Deramakot G				

57 Euphorbiaceae, Croton type

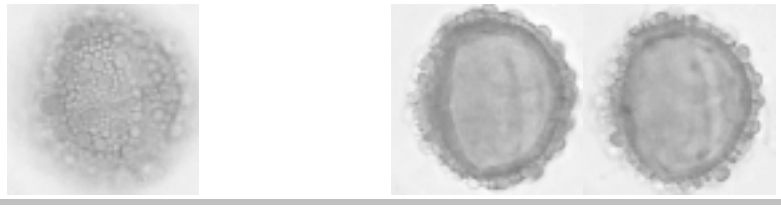
x: 60
y: 60



	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut	0,47		0,79	0,53
Sepilok K	0,69			
Danum M	0,06			
Deramakot A	0,23			
Deramakot G	0,17			

136 Euphorbiaceae, Discocleidion type

x: 25
y: 33



	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K				
Danum M				
Deramakot A				
Deramakot G	0,08			

74 Euphorbiaceae, Macaranga/Mallotus

x: 22
y: 6

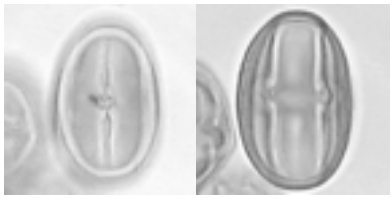
	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K				
Danum M				
Deramakot A		51,13		
Deramakot G		2,35		

9 Euphorbiaceae, Manihot esculenta

x: 165
y: 165

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K	5,68			
Danum M				
Deramakot A	4,48			
Deramakot G				

182 Fagaceae, Nothophagus/Castanopsis type



x: 18
y: 28

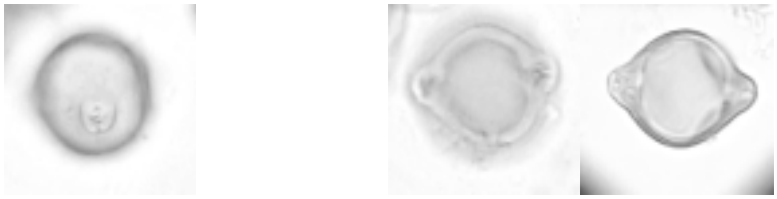
	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut			0,33	
Sepilok K				
Danum M				
Deramakot A				
Deramakot G				

66 Euphorbiaceae

x: 25
y: 18

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut	0,60			
Sepilok K	0,32	1,12		
Danum M	0,66			
Deramakot A	0,00			
Deramakot G				

206 Guttiferae, Garcinia cuspidata type



x:
y:

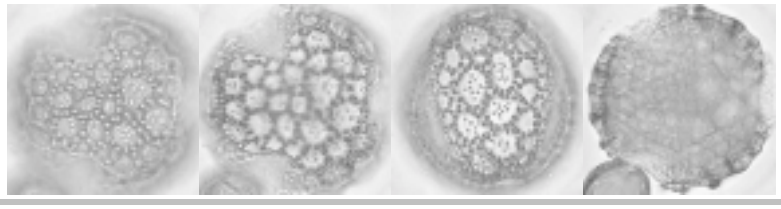
	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K				
Danum M				
Deramakot A	0,03			
Deramakot G				

193 Leguminosae, Crudia type

x: 31
y: 44

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K		1,81		
Danum M				
Deramakot A				
Deramakot G				

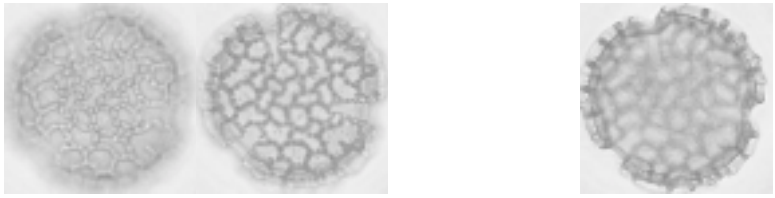
166 Leguminosae, Intsia type A



x: 69
y: 69

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K	0,57			
Danum M				
Deramakot A				
Deramakot G				

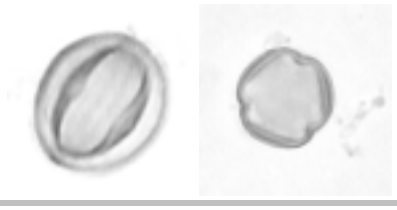
77 Leguminosae, Intsia type B



x: 50
y: 50

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K	0,19			
Danum M	3,95			
Deramakot A	0,34			
Deramakot G	0,04			

97 Leguminosae ? A

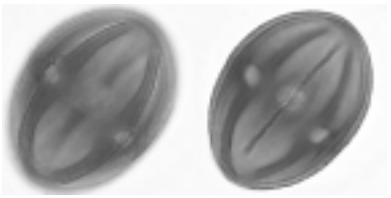


x: 14
y: 14

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut	0,11			
Sepilok K	2,74			
Danum M	1,43			
Deramakot A	26,98	6,82		
Deramakot G	1,99			

96 Leguminosae B

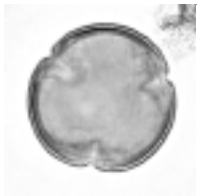
x: 54
y: 80

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K	0,27			
Danum M				
Deramakot A	11,75	10,29		
Deramakot G	7,30	42,45		

104 Leguminosae C

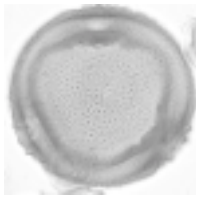
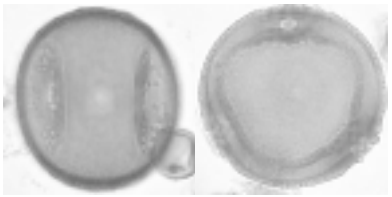
x: 23
y: 36




	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K				
Danum M				
Deramakot A	2,12			
Deramakot G				

115 Leguminosae D

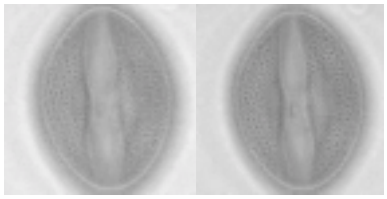
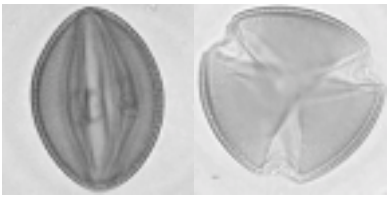
x: 54
y: 54

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K				
Danum M				
Deramakot A	3,36			
Deramakot G	5,25			

103 Leguminosae E

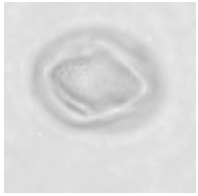
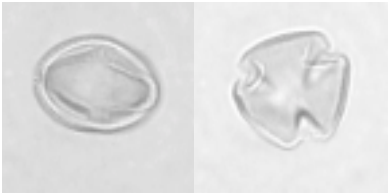
x: 42
y: 56

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut	1,29			
Sepilok K	2,08	1,74		
Danum M	13,33			
Deramakot A	1,64			
Deramakot G	2,31	0,92		

111 Leguminosae ? F

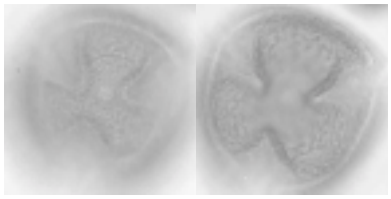
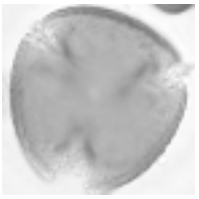
x: 13
y: 19

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K	2,45			
Danum M				
Deramakot A	0,05			
Deramakot G				

118 Leguminosae G

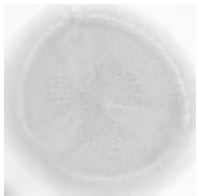
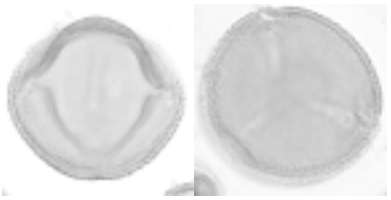
x: 47
y: 38

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K				
Danum M				
Deramakot A	0,59			
Deramakot G	0,57			

132 Leguminosae H

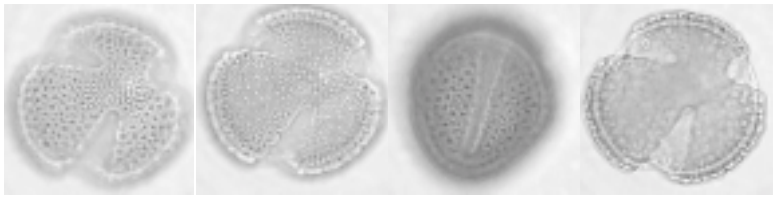
x: 42
y: 44

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K				
Danum M				
Deramakot A				
Deramakot G	0,44			

110 Leguminosae I

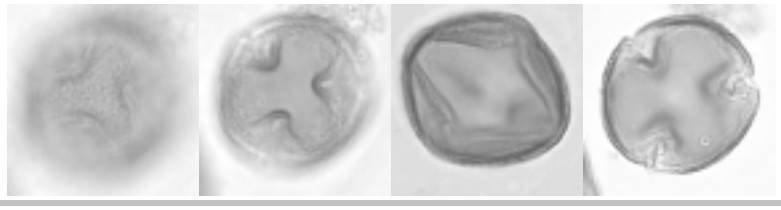
x: 33
y: 33



	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K	0,13			
Danum M				
Deramakot A				
Deramakot G	0,40			

109 Leguminosae J

x: 31
y: 31



	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K				
Danum M				
Deramakot A				
Deramakot G	0,32			

208 Leguminosae K

x: 38
y: 38

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K				
Danum M				
Deramakot A				
Deramakot G	0,11			

72 Leguminosae ? L

x: 36
y: 36

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K	0,04			
Danum M				
Deramakot A				
Deramakot G	0,09			

121 Leguminosae M

x: 39
y: 78

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K				
Danum M				
Deramakot A	0,64			
Deramakot G				

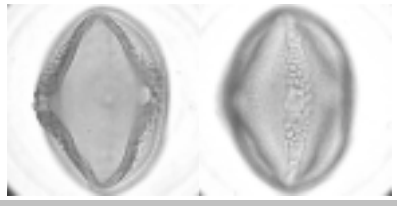
170 Leguminosae N

x: 51
y: 35

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut	0,19			
Sepilok K				
Danum M				
Deramakot A				
Deramakot G				

161 Leguminosae O

x: 54
y: 81



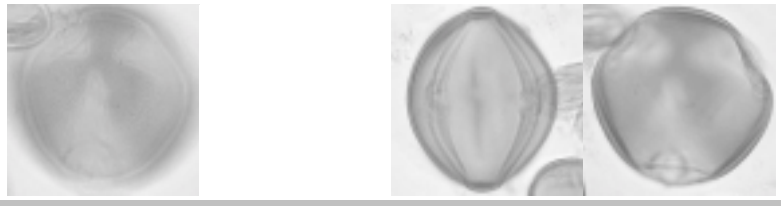
	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut	0,03			
Sepilok K	0,69			
Danum M				
Deramakot A				
Deramakot G				

148 Leguminosae P

x: 32
y: 32

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K	0,24			
Danum M				
Deramakot A				
Deramakot G				

134 Leguminosae Q



x: 36
y: 58

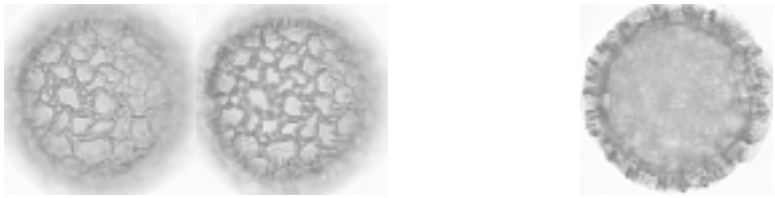
	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K				
Danum M				
Deramakot A				
Deramakot G	1,06			

155 Lythraceae, Lagerstroemia speciosa

x: 35
y: 45

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K	2,52			
Danum M				
Deramakot A				
Deramakot G				

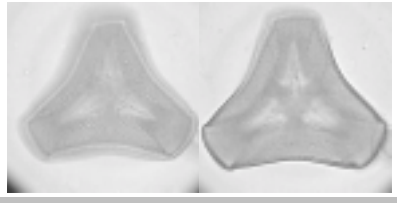
92 Loganiaceae, Fagraea



x: 44
y: 44

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut	0,26	1,64		0,78
Sepilok K				
Danum M				
Deramakot A				
Deramakot G				

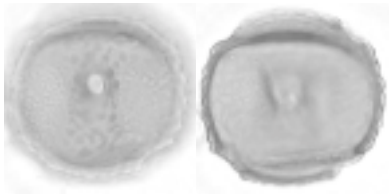
201 Loranthaceae



x: 63
y: 20

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K				
Danum M				
Deramakot A		0,80		
Deramakot G		1,27		

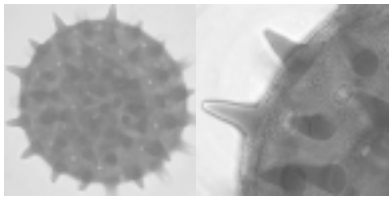
117 Malphigiaceae, Hiptage type



x: 40
y: 40

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K				
Danum M	4,18			
Deramakot A	1,05			
Deramakot G	0,48			

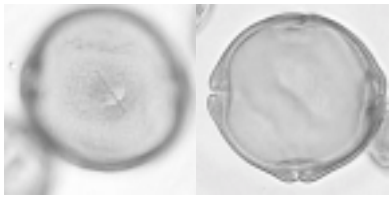
14 Malvaceae, Hibiscus type



x: 166
y: 166

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K	3,90			
Danum M	1,69			
Deramakot A	0,78			
Deramakot G				

178 Meliaceae



x: 36

y: 36

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut	0,49			
Sepilok K				
Danum M				
Deramakot A				
Deramakot G				

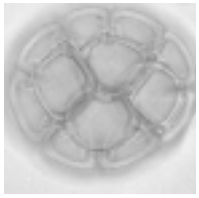
69 Mimosaceae, Acacia type

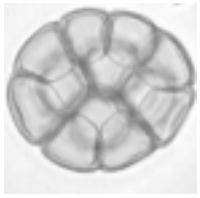
x: 46

y: 25

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K	0,39			
Danum M				
Deramakot A	0,08			
Deramakot G	0,33			

167 Mimosaceae, Adenathera type





x: 50

y: 63

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K	0,80			
Danum M				
Deramakot A				
Deramakot G				

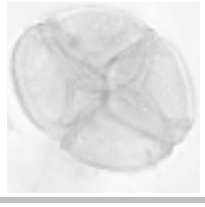
13 Mimosaceae, Mimosa pudica type

x: 9.6

y: 9.6

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K	0,02			
Danum M				
Deramakot A	1,82	1,62		
Deramakot G				

149 Mimosaceae



x: 29

y: 29

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K	4,63			
Danum M				
Deramakot A				
Deramakot G				

67 Myrtaceae, Eugenia type A

x: 22

y: 15

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K	0,03			
Danum M				
Deramakot A				
Deramakot G				

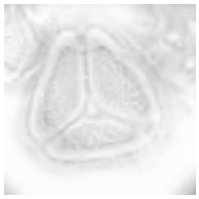
63 Myrtaceae, Eugenia type B

x: 19

y: 12

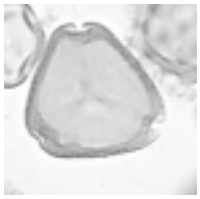
	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K				
Danum M				
Deramakot A	0,10			
Deramakot G				

207 Myrtaceae



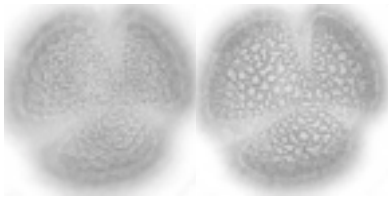
x: 25

y: 16



	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K				
Danum M				
Deramakot A				
Deramakot G	0,75			

21 Oleaceae, Jasminium type

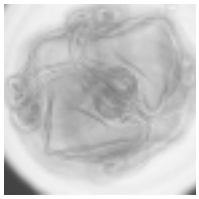


x: 62

y: 62

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K	0,65			
Danum M				
Deramakot A	1,38			
Deramakot G	0,52	11,26		

191 Onagraceae, Ludwigia type

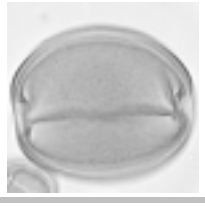


x: 50

y: 38

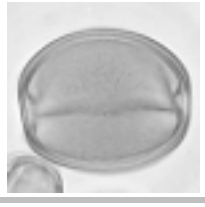
	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K	0,03	12,95		
Danum M				
Deramakot A				
Deramakot G				

186 Palmae, Calamus type



x: 41

y: 31



	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				0,82
Sepilok K				
Danum M				
Deramakot A				
Deramakot G				

194 Palmae, Caryota type

x: 22

y: 25

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K		0,53		
Danum M				
Deramakot A				
Deramakot G				

16 Palmae, Cocos nucifera type

x: 43

y: 60

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K	0,70			
Danum M				
Deramakot A		6,28		
Deramakot G				

187 Palmae, Elaeis guineensis

x: 31

y: 31

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				0,56
Sepilok K	0,04	28,85		
Danum M				
Deramakot A				
Deramakot G				

181 Palmae, Proxapertites operculatus type


x: 34
y: 22

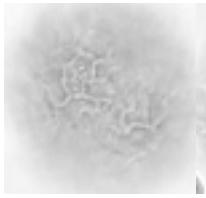
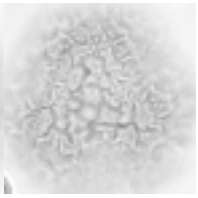
	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut		0,26		
Sepilok K				
Danum M				
Deramakot A				
Deramakot G				

179 Pandanaceae, Pandanus

x: 19
y: 19

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut		6,64		38,83
Sepilok K				
Danum M				
Deramakot A				
Deramakot G				

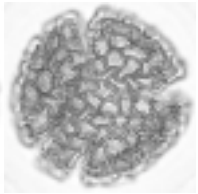
85 Passifloraceae, Passiflora type


x: 35
y: 35

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K				
Danum M				
Deramakot A	0,17			
Deramakot G				

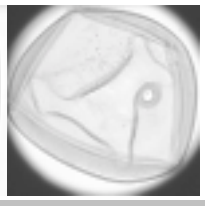
53 Passifloraceae, Passiflora ?

x: 76
y: 76

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K	2,09			
Danum M				
Deramakot A	0,94			
Deramakot G	0,35			

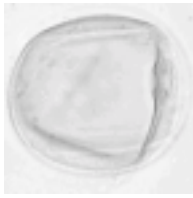
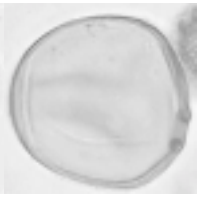
139 Poaceae, Zea mays

x: 85
y: 85

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K	15,60			
Danum M				
Deramakot A				
Deramakot G				

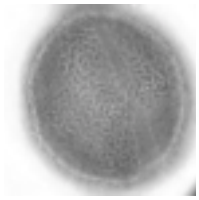
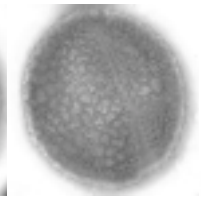
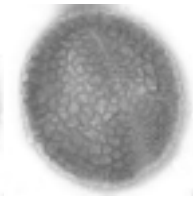
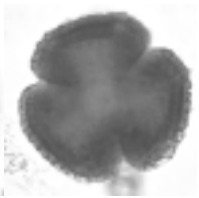
145 Poaceae

x: 35
y: 35

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K	1,04	7,93		
Danum M				
Deramakot A				
Deramakot G				

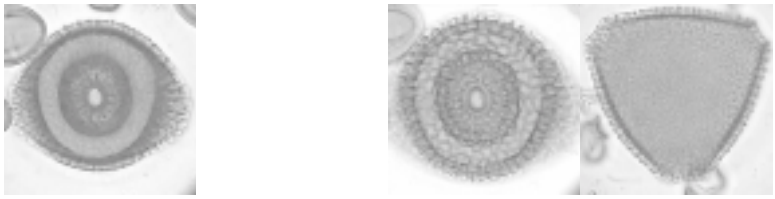
102 Polemoniaceae, Bunga pagi

x: 44
y: 44

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K	0,13			
Danum M				
Deramakot A	1,63			
Deramakot G				

204 Proteaceae, Heliciopsis type



x:
y:

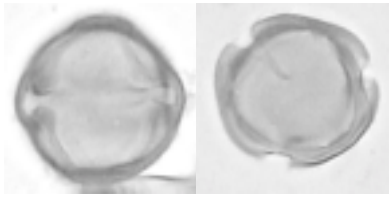
	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K				
Danum M				
Deramakot A	0,30			
Deramakot G				

138 Rhamnaceae, Ziziphus type

x: 22
y: 22

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K				
Danum M				
Deramakot A				
Deramakot G	0,07			

147 Rhizophoraceae, Rhizophora apiculata



x: 23
y: 24

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut	81,46	55,89	76,16	52,97
Sepilok K	0,90			
Danum M				
Deramakot A				
Deramakot G				

176 Rhizophoraceae, Carallia ?

x: 16
y: 16

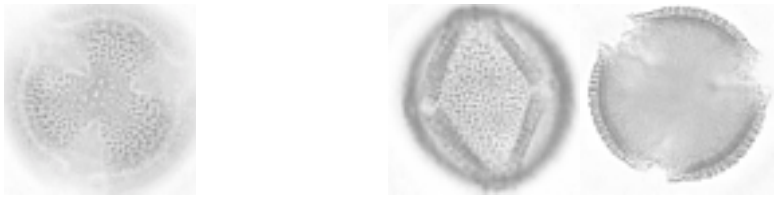
	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut	3,00		1,21	
Sepilok K				
Danum M				
Deramakot A				
Deramakot G				

158 Rubiaceae, Brachytome type ?

x: 59
y: 59

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K	0,06			
Danum M				
Deramakot A				
Deramakot G				

19 Rubiaceae, Ixora ?



x: 32
y: 32

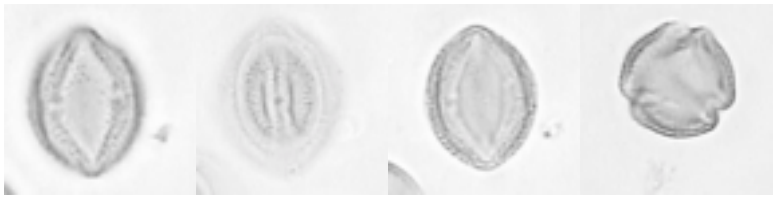
	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K	0,21			
Danum M				
Deramakot A				
Deramakot G				

114 Rubiaceae, Neonauclea type ? A

x: 14
y: 14

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K	1,04			
Danum M	0,83			
Deramakot A	8,97	6,94		
Deramakot G	13,30	18,64		

210 Rubiaceae, Neonauclea type B



x: 16
y: 19

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K				
Danum M	0,77			
Deramakot A				
Deramakot G				

217 Rubiaceae, Ramdia type A

x: 23
y: 19

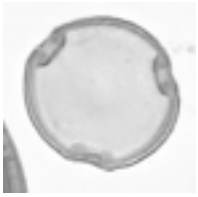
	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K				
Danum M	1,26			
Deramakot A				
Deramakot G				

215 Rubiaceae, Ramdia type ? B

x: 16
y: 16

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K				
Danum M	0,40			
Deramakot A				
Deramakot G				

144 Rubiaceae, Ramdia type C



x: 18
y: 17

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K	0,06			
Danum M	2,54			
Deramakot A				
Deramakot G				

125 Rubiaceae, Randia type D

x: 18
y: 17

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K	0,17			
Danum M				
Deramakot A				
Deramakot G				

135 Rubiaceae, tetrade type

x: 51
y: 51

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K	0,14			
Danum M	0,73			
Deramakot A				
Deramakot G	0,38			

164 Rutaceae ? A

x: 23
y: 26

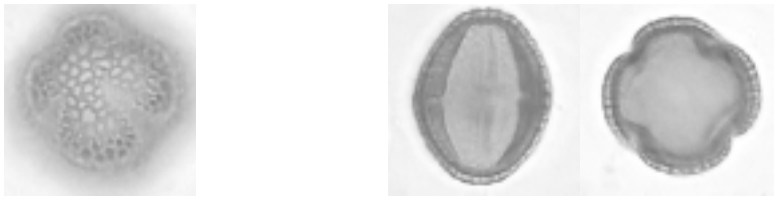
	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut	0,04			
Sepilok K	1,45			
Danum M	1,36			
Deramakot A				
Deramakot G				

159 Rutaceae ? B

x: 18
y: 29

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K	0,69			
Danum M				
Deramakot A				
Deramakot G				

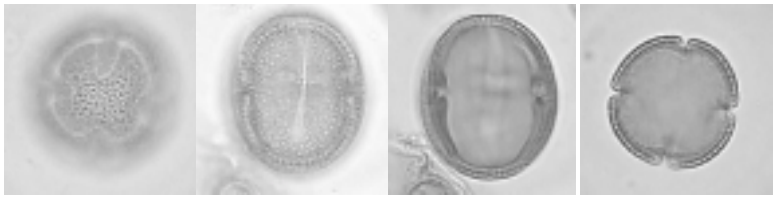
54 Rutaceae, Citrus type A



x: 27
y: 33

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K	0,89			
Danum M				
Deramakot A	0,48			
Deramakot G				

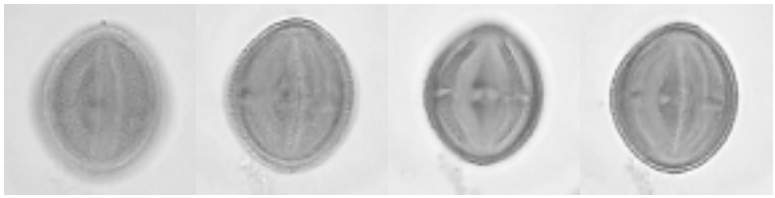
190 Rutaceae, Citrus type B



x: 30
y: 34

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K	1,87			
Danum M				
Deramakot A				
Deramakot G				

213 Rutaceae, Citrus type C



x: 28
y: 34

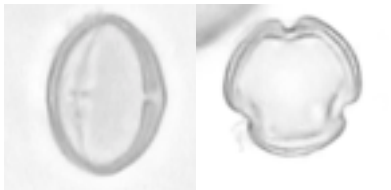
	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K				
Danum M	3,95			
Deramakot A				
Deramakot G				

20 Rutaceae, Clausena type A

x: 18
y: 24

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K				
Danum M				
Deramakot A	2,54			
Deramakot G	6,87			

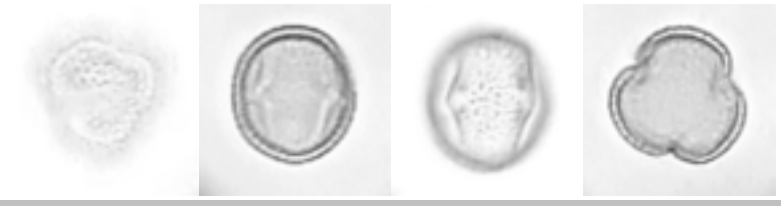
131 Rutaceae, Clausena Type B



x: 14
y: 17

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K				
Danum M				
Deramakot A				
Deramakot G	0,16			

219 Rutaceae, Clausena type C



x: 16
y: 16

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K				
Danum M	1,48			
Deramakot A				
Deramakot G				

129 Rutaceae C

x: 19
y: 23

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K				
Danum M				
Deramakot A				
Deramakot G	0,19			

200 Sapindaceae, Allophylus type A

x: 26
y: 16

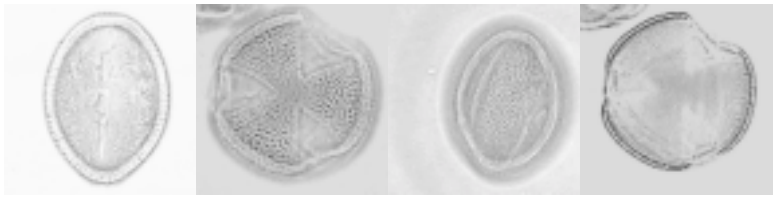
	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K				
Danum M				
Deramakot A		1,05		
Deramakot G				

153 Sapindaceae, Allophylus type B

x: 34
y: 16

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut	0,15			
Sepilok K				
Danum M				
Deramakot A				
Deramakot G				

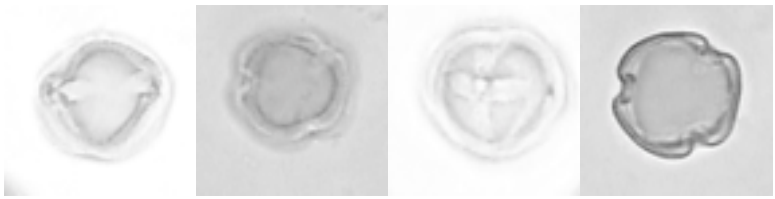
172 Scrophulariaceae ?



x: 38
y: 25

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut	0,34			
Sepilok K				
Danum M				
Deramakot A				
Deramakot G				

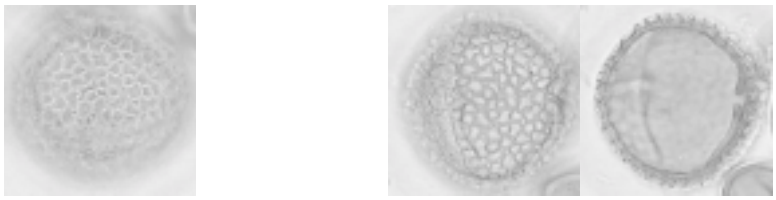
218 Solanaceae



x: 18
y: 18

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K				
Danum M	0,93			
Deramakot A				
Deramakot G				

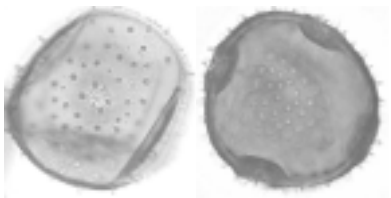
209 Sterculiaceae, Pterocymbium type



x: 47
y: 47

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K				
Danum M	0,09			
Deramakot A				
Deramakot G	0,07			

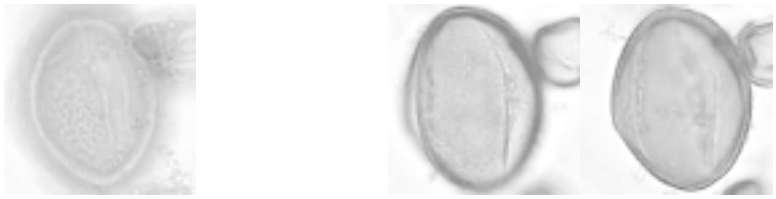
91 Sterculiaceae, Pterospermum



x: 54
y: 54

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K	0,14			
Danum M	0,89			
Deramakot A				
Deramakot G	1,33			

116 Sterculiaceae, Sterculia type



x: 28
y: 38

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K	0,04			
Danum M				
Deramakot A	0,14			
Deramakot G				

214 Stercullariaceae ?

x: 19
y: 31

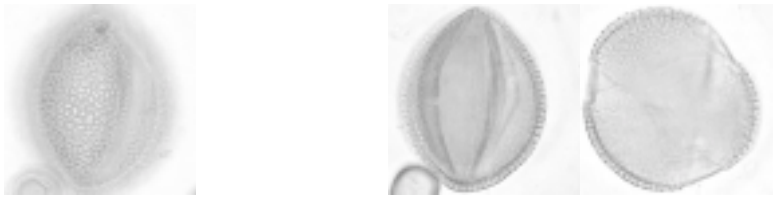
	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K				
Danum M	1,48			
Deramakot A				
Deramakot G				

2 Symplocaceae, Symplocos type

x: 50
y: 40

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K	0,43			
Danum M	0,16			
Deramakot A	0,30			
Deramakot G	0,34			

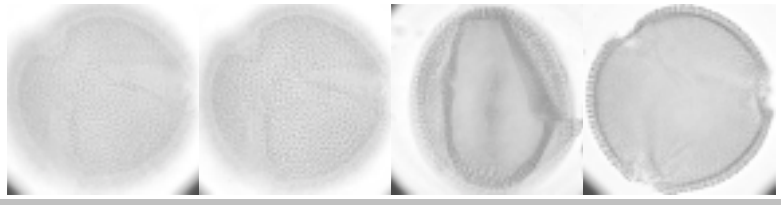
140 Theaceae, Schima type A



x: 36
y: 49

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K	1,09			
Danum M				
Deramakot A				
Deramakot G				

141 Theaceae, Schima type B



x: 65
y: 65

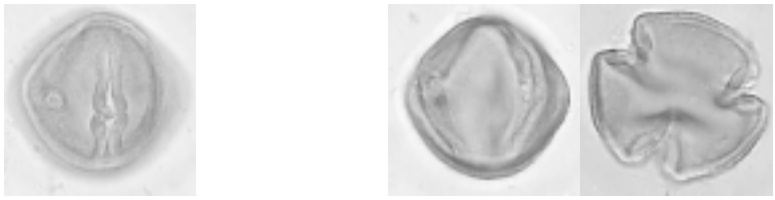
	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K	1,23			
Danum M				
Deramakot A				
Deramakot G				

162 Theaceae, Schima type C

x: 44
y: 44

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K	0,17			
Danum M				
Deramakot A				
Deramakot G				

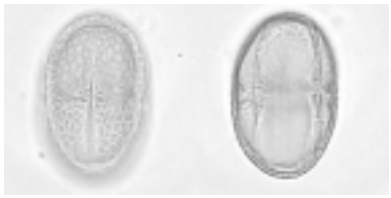
216 Theaceae ?



x: 41
y: 41

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K				
Danum M	3,64			
Deramakot A	0,07			
Deramakot G				

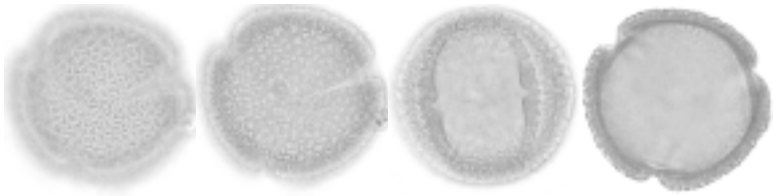
196 Tiliaceae, Grewia type A



x: 25
y: 38

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K		1,05		
Danum M				
Deramakot A				
Deramakot G				

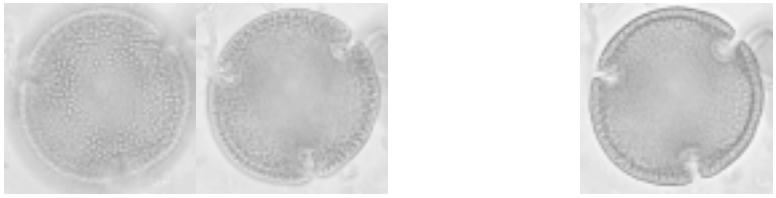
71 Tiliaceae, Grewia type ? B



x: 42
y: 42

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K				
Danum M	2,47			
Deramakot A	0,25			
Deramakot G	0,49			

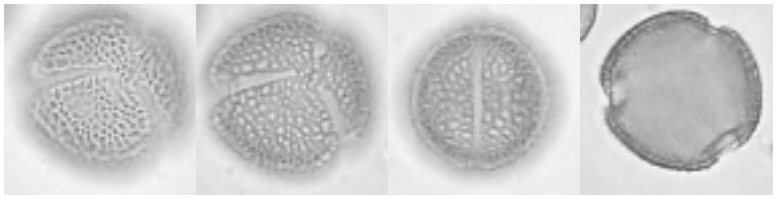
127 Tiliaceae, Pentace type



x: 39
y: 19

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K				
Danum M	0,07			
Deramakot A	0,34			
Deramakot G	0,07			

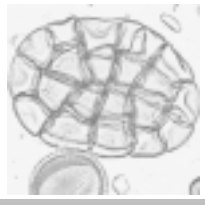
180 Verbenaceae, Avicennia



x: 34
y: 35

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut		14,97		0,61
Sepilok K				
Danum M				
Deramakot A				
Deramakot G				

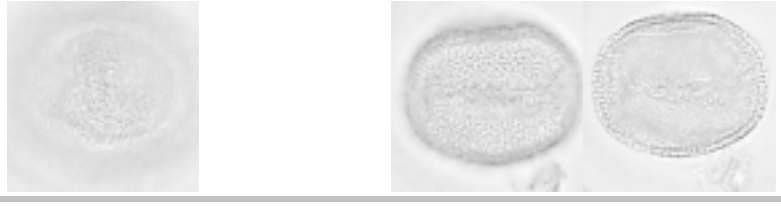
163 ?, inaperturate B



x: 163
y: 119

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K	0,02			
Danum M				
Deramakot A				
Deramakot G				

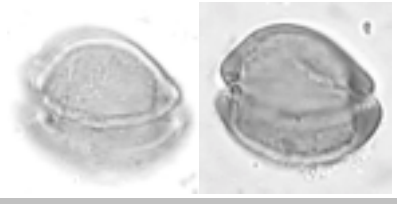
94 ?, monocolpate



x: 32
y: 38

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K	0,03			
Danum M				
Deramakot A				
Deramakot G				

226 ?, dizonocolporate

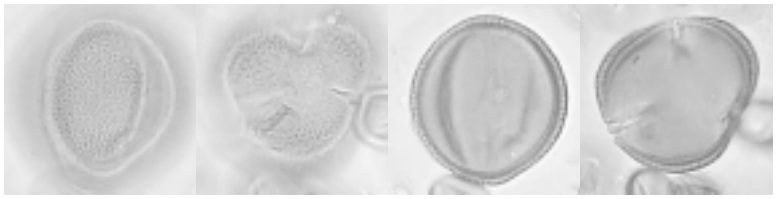


x: 28
y: 22

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut			0,20	
Sepilok K				
Danum M				
Deramakot A				
Deramakot G				

203 ?, trizonocolpate A

x: 44
y: 44



	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K				
Danum M				
Deramakot A	0,13			
Deramakot G	0,06			

75 ?, trizonocolporate B

x: 29
y: 36

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K	0,84			
Danum M				
Deramakot A	0,75			
Deramakot G				

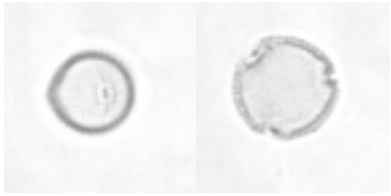
157 ?, trizonocolporate C

x: 53
y: 53

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K	1,52			
Danum M				
Deramakot A	0,04			
Deramakot G				

17 ?, trizonocolporate D

x: 11
y: 11



	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K				
Danum M				
Deramakot A	1,21	1,15		
Deramakot G	0,06			

128 ?, trizonocolporate F

x: 23
y: 22

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K	1,93			
Danum M	4,25			
Deramakot A	0,20			
Deramakot G	9,95			

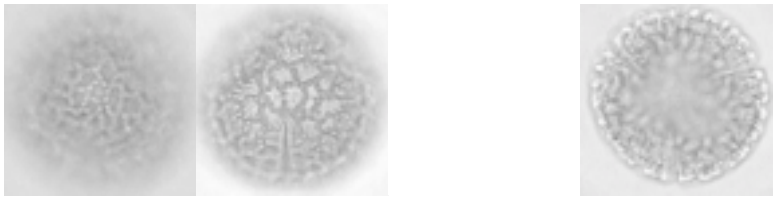
195 ?, trizonocolporate G

x: 16
y: 22

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K		0,95		
Danum M				
Deramakot A				
Deramakot G				

18 ?, trizonocolporate H

x: 33
y: 33



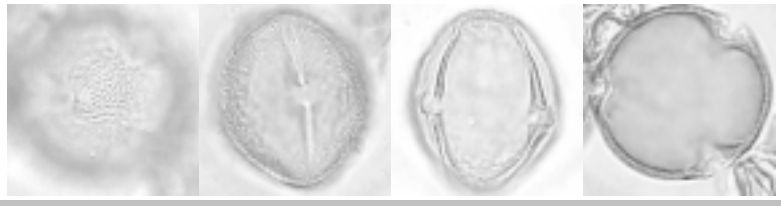
	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut	0,15			
Sepilok K	2,73			
Danum M	0,15			
Deramakot A	0,16			
Deramakot G	0,05			

130 ?, trizonocolporate I

x: 15
y: 16

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K				
Danum M				
Deramakot A				
Deramakot G	0,09			

160 ?, trizonocolporate J



x: 40
y: 44

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K	0,96			
Danum M				
Deramakot A				
Deramakot G				

211 ?, trizonocolporate K

x: 19
y: 19

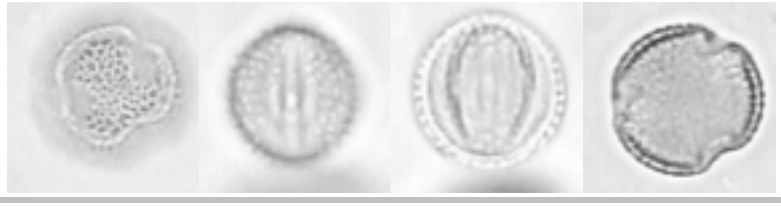
	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K				
Danum M	0,24			
Deramakot A				
Deramakot G				

221 ?, trizonocolporate L

x: 18
y: 18

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut	1,95		0,49	
Sepilok K				
Danum M				
Deramakot A				
Deramakot G				

222 ?, trizonocolporate M



x: 16
y: 16

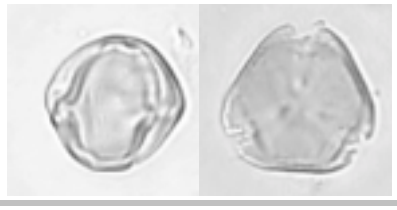
	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut	0,07			
Sepilok K				
Danum M				
Deramakot A				
Deramakot G				

224 ?, trizonocolporate N

x: 32
y: 32

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut	0,23	9,51		
Sepilok K				
Danum M				
Deramakot A				
Deramakot G				

225 ?, trizonocolporate O

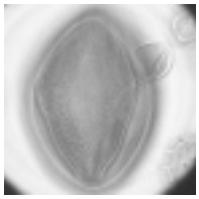


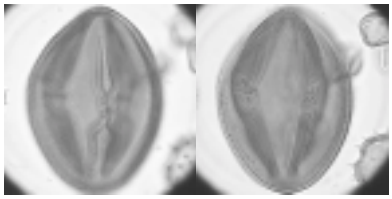
x: 19
y: 16

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut		0,94		
Sepilok K				
Danum M				
Deramakot A				
Deramakot G				

228 ?, trizonocolporate P

x: 75
y: 56

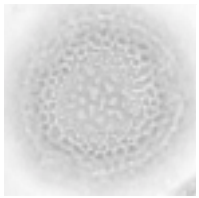


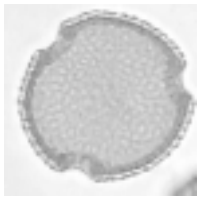


	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K	0,07			
Danum M				
Deramakot A				
Deramakot G				

137 ?, trizonoporate A

x: 31
y: 19

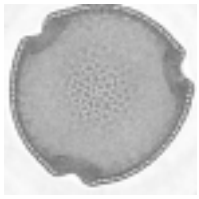




	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K				
Danum M				
Deramakot A				
Deramakot G	0,03			

156 ?, trizonoporate B

x: 47
y: 30



	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K	0,05			
Danum M				
Deramakot A				
Deramakot G				

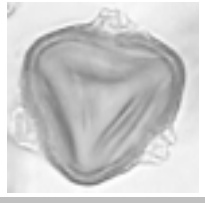
223 ?, trizonoporate C

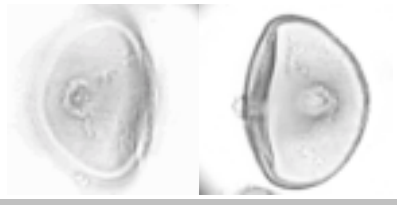
x: 75
y: 75

	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut	0,07			
Sepilok K				
Danum M				
Deramakot A				
Deramakot G				

227 ?, trizonoporate D

x: 28
y: 20

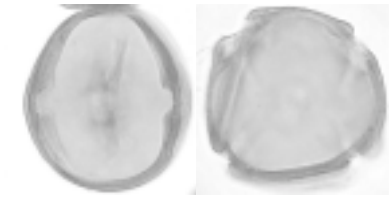




	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K				
Danum M				
Deramakot A	0,11			
Deramakot G				

151 ?, tetrazonocolporate

x: 46
y: 46



	collina	*melano-cephala*	*melina*	*terminata*
SepilokLaut				
Sepilok K	0,62			
Danum M				
Deramakot A				
Deramakot G				

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Familienstand:	ledig, keine Kinder

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Eltz, T., C. A. Brühl, S. van der Kaars, V. K. Chey, and K. E. Linsenmair, 2001. Pollen foraging and resource partitioning of stingless bees in relation to flowering dynamics in a Southeast Asian tropical rainforest. Insectes Soc., in press.

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Eltz, T., C. A. Brühl, I. Zamrie, and K. E. Linsenmair, submitted. Nesting and nest trees of stingless bees (Apidae: Meliponinae) in lowland dipterocarp forests in Sabah, Malaysia, with implications for forest management.

Eltz, T., C. A. Brühl, S. van der Kaars, and K. E. Linsenmair, submitted. Determinants of stingless bee nest density in lowland dipterocarp forests of Sabah, Malaysia.

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ERKLÄRUNGEN

Hiermit erkläre ich ehrenwörtlich, daß ich die vorliegende Arbeit selbständig angefertigt und keine anderen als die angegebenen Quellen und Hilfsmittel verwendet habe.
Ich habe diese Dissertation weder in gleicher noch in ähnlicher Weise in einem anderen Prüfungsverfahren vorgelegt.
Ich erkläre ferner, daß ich bisher noch keinen weiteren akademischen Grad erworben oder zu erwerben versucht habe.

Würzburg, Juni 2001

Thomas Eltz