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BAT DIVERSITY IN THE VEGETATION MOSAIC AROUND A LOWLAND DIPTEROCARP FOREST OF BORNEO

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ABSTRACT. **–** Tropical rainforests in Southeast Asia are decreasing rapidly because of conversion to agricultural lands, which in turn leads to an increase in mosaic landscapes. Little is known about the effects of these anthropogenic changes on bat fauna or feeding behaviour. To better explore anthropogenic effects on bats (Chiroptera), we investigated the diversity and feeding habits of bats in an intact lowland dipterocarp forest and surrounding areas of varying vegetation types. The total sampling effort using mist nets (32,795 m^2h) resulted in the capture of 495 bats, representing 28 species. Simpson's index of diversity was relatively high in primary forests (7.86) compared to secondary forests (3.38), orchards (3.65), and oil palm plantations (1.24). The capture rate of two frugivorous bats clearly differed among the four vegetation types, and these species were never caught in orchards or oil palm plantations. In addition, the capture rate of microchiropterans was notably lower in oil palm plantations than in the other three vegetation types. These results indicate that many bat species rarely use agricultural land for feeding, and these plant communities are not suitable for maintaining bat diversity. However, the data on the feeding habits of three megachiropterans that were frequently captured in orchards and oil palm plantations indicate that agricultural plants are their primary food sources. Orchards and oil palm plantations may be inadequate habitats for most frugivorous and insectivorous bats, but these plant communities may provide important food sources for certain species of megachiropterans.

KEY WORDS. **–** Lambir Hills National Park, megachiropterans, oil palm plantation, orchard, secondary forest, Sarawak.

INTRODUCTION

Tropical forest landscapes are changing rapidly because of human activities. Approximately half of the potential tropical closed-canopy forest has already been removed and converted to other uses (Wright, 2005). Deforestation rates were 3.9 × 10^6 ha/yr in tropical America, and 2.3 × 10^6 ha/yr in tropical Asia during the 1990s (Hansen & DeFries, 2004). Wright (2005) predicted that in the near future, tropical landscapes will only remain as islands of secondary and protected old-growth forests isolated within a sea of land converted for human use and agriculture.

The effects of these anthropogenic changes on mammals have been studied across several taxonomic groups (e.g., Ickes, 2001; Cox et al., 2003; Kinnaird et al., 2003; Naughton-Treves et al., 2003). Among these groups, bats (Chiroptera) are regarded as one of the most vulnerable taxa. There are about 1,000 known species of bats, nearly 25% of which are globally threatened (Mickleburgh et al., 2002). According to the IUCN Red List (IUCN, 2007), nine bat species are confirmed extinct and 247 species are threatened (i.e. categorized as "Critically Endangered", "Endangered" or "Vulnerable"). Major threats to bat populations include the loss or reduction in quality of foraging habitat and habitat fragmentation (Racey & Entwistle, 2002).

The order Chiroptera is divided into two suborders: the Megachiroptera with a single family, Pteropodidae (ca. 163 species) and the Microchiroptera with 17 families (ca. 814 species in total; Corbet & Hill, 1992). Megachiropterans are known as Old World fruit bats and are distributed across Africa, tropical Asia, India, Australia and their surrounding oceanic islands. Megachiropterans are relatively large (20–1,500 g) and predominantly feed on plants (fruits, nectar, pollen, flowers, and leaves). In contrast, microchiropterans are found on every continent except Antarctica, are relatively small (1.5–150 g), and exhibit more diverse feeding habits (e.g., insectivorous, frugivorous, nectarivorous, ichthyophagous, and sanguivorous; Altringham, 1996).

Recent studies have indicated that many bat species play important roles in tropical rainforests. For example, pollination by bats is a phenomenon restricted to the tropics and subtropics. Megachiropterans visit at least 141 plant species, including a number of commercially important plants (e.g. *Durio*, *Ceiba* and *Parkia*) for nectar or pollen (Fujita & Tuttle, 1991; Marshall, 1985). Bats may be more energetically costly to attract than other plant pollinators, but these costs are offset by the extensive distribution of pollen provided by widely foraging bats (Start & Marshall, 1976). Some species of bats travel long distances in one night (e.g., *Eonycteris spelaea* travels at least 38 km, *Rousettus amplexicaudatus* travels 25 km; Marshall, 1983). Megachiropterans feed upon 145 genera of fruits and presumably disperse the seeds of the majority of the fruits consumed (Marshall, 1985). Small seeds ingested by megachiropterans are transported over substantial distances, and larger seeds are frequently carried with fruits to feeding roosts. In Palaeotropical regions, flying foxes (family Pteropodidae) likely play a unique role in the longer-distance dispersal of the large-seeded fruits of dominant canopy trees on oceanic islands (Rainey et al., 1995). In the Neotropics, where megachiropterans do not occur, nectarivorous or frugivorous microchiropteran species belonging to the family Phyllostomidae act as pollinators or seed dispersers. In addition, approximately 70% of extant bat species are insectivorous and prey on a diverse range of insects (e.g., Lepidoptera, Diptera, Coleoptera and Hemiptera; Jones & Rydell 2002).

Southeast Asia is a hotspot of bat diversity. Like many groups of organisms, the number of bat species per unit area is large in tropical zones, especially in the Amazon basin and Southeast Asia (Altringham, 1996). In Borneo, bat is the most diverse order of mammals in terms of the number of species, accounting for 42% of all mammal species (Payne & Francis, 1998).

Southeast Asia also has the highest deforestation rate of any major tropical region, and currently, more than 50% of the land area in Asia is under agriculture (Zhao et al., 2006). The conversion of forests to cash-crop plantations (e.g., oil palm, rubber, and cocoa) is thought to be one of the major causes of the current high deforestation rates in the region (Primack & Corlett, 2005). Since the 1970s, areas planted with African oil palm (*Elaeis guineensis*), which is native to West Africa, have expanded in both Malaysia and Indonesia. In Malaysia, as of 2003, oil palm plantations covered 3.5 $\times 10^6$ ha, and this number continues to increase. These plantations constitute 11% of the total land area of the entire country and 62% of all cultivated agricultural land (Brown & Jacobson, 2005).

Such anthropogenic changes can create mosaics of fragmented vegetation, thereby greatly affecting the diversity, abundance, and feeding behaviour of bats. Megachiropterans that inhabit these mosaic landscapes are expected to feed on crops, because some agricultural plants may serve as food sources, and the bats can fly long distances from mosaic to mosaic. However, little is known about the effects and extent of the impacts of these anthropogenic changes. Although several studies have investigated bat fauna in Southeast Asia (e.g., Zubaid, 1993; Francis, 1994; Abdullah et al., 1997; Hall et al., 2004; Heaney et al., 1991, 1999; Rickart et al., 1993), few study have compared bat fauna among plant communities under different land-uses including agricultural fields within a single landscape.

We investigated the bat community in mosaic landscapes formed by the expansion of agricultural lands. Specifically, we explored differences in the density and diversity of megachiropterans between primary forests and agricultural lands within a single landscape. These bat species are important pollinators and seed dispersers of many plant species and are critical to the regeneration of forests. We also discuss the impact of increasing mosaic landscapes on bat-plant interactions, focusing on nectarivorous bats.

METHODS

Study site. **–** We conducted our research in and around the Lambir Hills National Park (LHNP), Sarawak, Malaysia (Fig. 1; 4°2'N,113°50'E, ca. 150 m in altitude). One characteristic of the site was the high heterogeneity of vegetation. We selected four types of vegetation for bat censuses: primary forests, secondary forests, orchards, and oil palm plantations. The primary forests were intact lowland mixed dipterocarp forests within the LHNP. The park covers an area of 6,949 ha (69.49 km^2) and the height of emergent trees sometimes exceeds 70 m. Shanahan & Debski (2002) recorded 10 species of bats (five megachiropterans and five microchiropterans) in the park. The secondary forests were young forests that had developed after slash-and-burn agriculture conducted by Iban villagers. Census points were established in three forests of varying ages: a 7-year-old forest dominated by *Vitex pinnata*, a ca. 30-year-old forest dominated by *Artocarpus elasticus*, and a > 60-year-old forest dominated by *Artocarpus elasticus* (Nakagawa et al., 2006). Forest height varied among census points (2–25 m). These forests were surrounded by ponds, paddy fields, isolated intact forests, and rubber (*Hevea brasiliensis*) forests. The orchards were small [< 5 ha (< 0.05 km^2)] areas with many cultivated plants (e.g., *Durio kutejensis*, *Nephelium lappaceum*, *Carica papaya*, *Cocos* sp., *Musa* sp., *Parkia* sp., *Artocarpus integer*, *Lansium domesticum*, *Piper* sp., and *Saccharum* sp.) established by Iban villagers. Tree height ranged from 1 to

10 m. The orchards were located near villagers' houses and were surrounded by ponds, paddy fields, rubber forests, and bamboo groves. The oil palm plantations were large-scale [ca. 4,000 ha (40.0 km^2)], continuous plantations of mature African oil palm managed by a corporation or Iban villagers. Vegetation consisted of a complete monoculture, and the heights of oil palms were 10–20 m. The plantations shared borders with the primary and secondary forests.

Field methods. **–** Censuses were conducted four times between Apr.2005 and Aug.2006 in all vegetation types except oil palm plantation. In the oil palm plantation we conducted censuses only for twice according to the availability of permission. We set mist nets on the ground along trails in the forests or forest edges. In the primary forests, we also set nets on canopy walkways (at a height of 15–35 m) for five nights. There were no significant differences between data from the ground and the walkways, so the data were combined. We used two to four nets (24 to 36-mm mesh; 6–12 m long; 6.0 m high; eight shelves) per night and occasionally harp traps (The Austbat Harptrap, Faunatech and Austbat, Australia; 4.2 m^2 in area; four nights in primary forests and two nights in orchards). Traps were set at sunset and checked at 15-min intervals. Sampling continued until 2300 hrs unless it rained. We recorded age, sex, morphological measurements, and reproductive state of the captured bats. Age class was determined by the degree of fusion of the epiphyseal plates on the phalanges (Kunz, 1988). Bats with unfused epiphyseal plates were regarded as juveniles. The number of census points and sampling effort varied among vegetation type: 14,179 m^2h [area of traps (m^2) × sampling time (h)] in the primary forests (six census points), 8,707 m^2h in the secondary forests (three census points), 6,526 m^2h in the orchards (three census points), and 3,382 m^2h in the oil palm plantations (five census points).

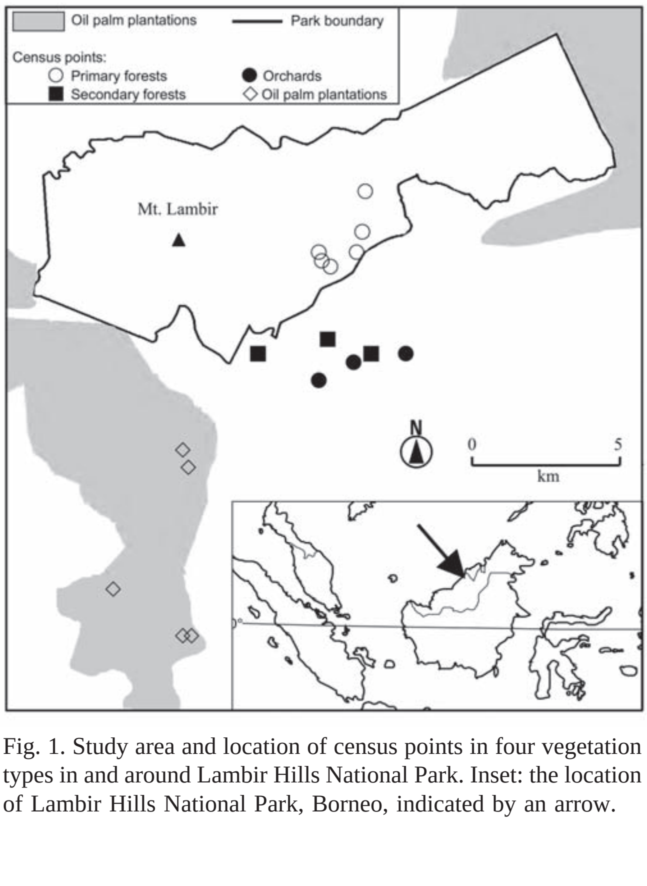

Fig. 1. Study area and location of census points in four vegetation types in and around Lambir Hills National Park. Inset: the location of Lambir Hills National Park, Borneo, indicated by an arrow.

We identified bat species according to Payne & Francis (1998). Because some studies have suggested the presence of two cryptic species within *Cynopterus brachyotis* that differ significantly in genetic and morphological characteristics as well as habitat preferences (Francis, 1990; Abdullah et al., 2000; Abdullah, 2003), we divided the species into two categories (*C. brachyotis* I and *C. brachyotis* II). We classified individuals of *C. brachyotis* based on their forearm length: in adult *C. brachyotis* I (larger form), the forearm length ranged from 60 to 66 mm, and for adult *C. brachyotis* II (smaller form), the forearm length was approximately 55 mm, but < 60 mm (M.T. Abdullah, pers. comm.). If individuals of the species were juveniles and their forearm lengths were less than 60 mm, they were recorded as 'C. *brachyotis* (unidentifiable)'. We also used mark-recapture methods to assess bat movements and fidelity to a vegetation type. Prior to releasing bats, we attached aluminum bands with running numbers (Lambournes Ltd., Leominster, UK) to the forearm.

Feeding habits of megachiropterans. **–** We surveyed the feeding habits of megachiropterans to determine the availability of cultivated plants as food sources. Pollen samples were collected from the faces of captured megachiropterans using transparent sticky tape (18 × 57 mm) immediately after the removal of bats from the traps. We also collected pollen from 21 species of plants growing in the vicinity of the census points as reference samples. Pollen from the megachiropterans were observed under a light microscope and identified to genus by comparison to reference samples. Morphological features of the pollen were recorded following Erdtman (1966). Prior to identification, we washed the pollen sample with 10% KOH at 55°C for 10 min, mounted it on glass slides with glycerin jelly, and sealed the cover glass with clear nail polish. We recorded a pollen genus only when > 10 grains of that type were present.

In the oil palm plantations, we tested if *C. brachyotis* I consumed fruits of the oil palm. An individual of the species and the fruit were placed into a cloth bag. After one hour, we checked whether the fruit was bitten or not. This test was repeated for three individuals.

Data analysis. **–** A Chi-square test (Sokal & Rohlf, 1973) was used to compare the number of captures of megachiropterans, microchiropterans, and each individual species among vegetation types. In the Chi-square tests, the observed and expected numbers of captures were compared. The expected number of captures was calculated assuming the capture rate was equal for each vegetation type. We did not distinguish seasons and census points, since we did not detect any significant differences.

Species accumulation curves were depicted to examine saturation of species numbers. Simpson's index of diversity (Simpson, 1949) was calculated for each vegetation type.

Table 1. Capture rate of bats (individuals per 10,000m^{2}h). Data for species with small sample sizes (< 20 individuals) are not shown. The rightmost column presents results of the Chi-square test: * = P < 0.05; ** = P < 0.01; *** = P < 0.001; - = test not carried out to due insufficiently large sample size.

	Primary forests	Secondary forests	Orchards	Oil palm plantations	Significance
Megachiropterans	55	86	208	272	***
Microchiropterans	40	26	49	6	**
Each species					
Megachiroptera					
Balionycteris maculata	16	2	0	0	–
Cynopterus brachyotis I	4	49	106	201	***
C. brachyotis II	8	11	6	9	–
Eonycteris spelaea	4	1	44	12	***
Macroglossus minimus	5	3	31	0	***
Penthetor lucasii	13	3	0	0	–
Microchiroptera					
Hipposideros cervinus	23	13	11	3	*
Glischropus tylopus	4	1	31	0	–

Unidentifiable individuals of *C. brachyotis* (see above) were assigned to *C. brachyotis* I and *C. brachyotis* II based on the proportion of the two forms in the community.

RESULTS

Capture rate of bats. **–** The total sampling effort (32,795 m^{2}h) resulted in the capture of 495 bats representing 28 species in five families (Appendix 1). The capture rate of megachiropterans differed significantly (P < 0.001) among the four vegetation types and was particularly high in the oil palm plantations and orchards compared to the primary and secondary forests (Table 1). The capture rate of microchiropterans also differed significantly (P < 0.001) among vegetation types and was lower in the oil palm plantations compared to the other three plant communities (Table 1).

For the eight bat species with relatively large sample sizes (> 20 individuals), capture rate varied among vegetation types (Table 1). The capture rates of *Balionycteris maculata*, *Penthetor lucasii*, and *Hipposideros cervinus* were the highest in primary forests. Capture rates were lower in secondary forests than in primary forests for all species except *C. brachyotis* I and II. In the orchards, the capture rates of *Eonycteris spelaea*, *Macroglossus minimus* and *Glischropus tylopus* were very high compared to the other three vegetation types. In contrast, *B. maculata* and *P. lucasii* were not observed in the orchards. In the oil palm plantations, the capture rate of *C. brachyotis* I was notably higher than in the other vegetation types. However, the capture rates of other bat species were low or zero in the plantations.

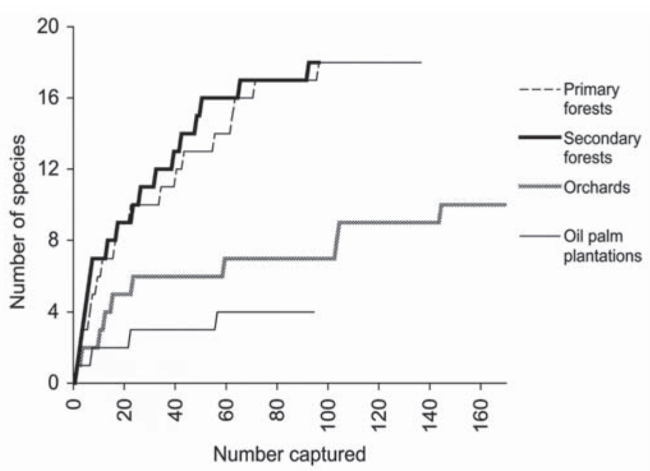

Fig. 2. Species accumulation curves indicating the cumulative number of species encountered relative to the total number of individuals captured in each vegetation type.

Diversity of the bat community. **–** The species accumulation curves did not reach asymptotes but demonstrated clear differences among the four vegetation types (Fig. 2). Simpson's index of diversity also varied among plant communities (Table 2). Simpson's index for megachiropterans was highest in primary forests, lower in secondary forests and orchards, and lowest in the oil palm plantations.

Cynopterus brachyotis I was the most common and abundant species in all vegetation types, except primary forests. This species accounted for 44% of all bats in the secondary forests, 41% in the orchards, and 72% in the oil palm plantations. In the primary forests, the dominant species was *Hipposideros cervinus* (24% of all bats), and *C. brachyotis* I accounted for only 4% of bats.

Recaptures. **–** We recaptured 25 bats of eight species (Table 3). Nineteen recaptures of seven species occurred at the same census point, and 16 of these were recaptures after 31 days or longer. This result indicate that some individuals of captured species have strong site fidelity. Recaptures at different census points in a short time (< 5 days) occurred four times. We also observed bat movement from orchards to the secondary forest twice. Even though the data were scarce, long-distance recaptures (> 1 km) demonstrated that *C. brachyotis* I and *M. minimus* are capable of long distance travel.

Table 2. Simpson's index of diversity in the four vegetation types. (*N*: number of individuals, *S*: number of species, *1/D*: Simpson's index of diversity). Note that *1/D* was not calculated for microchiropterans in oil palm plantations due to the insufficiently large sample size.

		Primary forests	Secondary forests	Orchards	Oil palm plantations
Megachiropterans	*N*	78	75	136	92
	S	8	10	6	3
	1/*D*	5.00	2.09	2.54	1.19
Microchiropterans	*N*	57	23	32	2
	S	11	8	5	2
	1/*D*	2.95	3.50	2.24	
All bats	*N*	135	98	168	94
	S	19	18	11	5
	1/*D*	7.86	3.38	3.65	1.24

Table 3. Recaptures of bats. Numbers indicate the distance (m) between the original and recapture census points. * = transfer from the orchard to the secondary forest.

Species	Days from first capture to recapture				
	1–5	6–30	31–100	101–300	> 300
Megachiroptera					
Balionycteris maculata			0	0, 0	0
Cynopterus brachyotis I	0, 170, 1,600*	0, 0	0	0, 0	0, 0
C. brachyotis II	210	430*			
C. brachyotis (unidentifiable)	210				0
Macroglossus minimus		1,320	0	0, 0	
Microchiroptera					
Glischropus tylopus				0	
Rhinolophus trifoliatus			0		
Megaderma spasma			0		

Table 4. Proportion of individuals with pollen (> 10 grains), total number of pollen types, and number of pollen types per individual (mean ± SD and ranges in parenthesis) for each species. Data for species with small sample sizes (< 10 individuals) are not shown.

Species	No. of sampled-individuals	Individuals with pollen (%)	Total no. of pollen types	No. of pollen types/individual
Balionycteris maculata	25	0		
Cymopterus brachyotis I	146	5	4	1
C. brachyotis II	24	0		
C. brachyotis (unidentifiable)	37	8	3	1
Eonycteris spelaea	38	58	5	1.7 ± 0.72 (1–3)
Macroglossus minimus	29	76	5	1.7 ± 0.84 (1–3)
Penthetor lucasii	19	0		

Feeding habits of megachiropterans. **–** Pollen samples were collected from 85.3% of megachiropteran individuals. At times, pollen adhesion to the rostrums of nectarivorous bats (*E. spelaea* and *M. minimus*) was apparent upon visual examination. The high rates of pollen adhesion to samples from *E. spelaea* (58%) and *M. minimus* (76%) indicated that these species frequently visited flowers (Table 4). In contrast, pollen rarely adhered to the other bat species (0–8%). Five types of pollen were found on *E. spelaea*, of which three were identified as *Durio*, *Musa* and *Parkia*. In total, these three plants accounted for 64% of the total pollen adhesions on *E. spelaea* (36 total adhesions). In *M. minimus*, five types of pollen were observed, of which two were identified as *Musa* and *Parkia*. In total, these two plants accounted for 32% of the total pollen adhesions in *M. minimus* (37 total adhesions). Both *E. spelaea* and *M. minimus* used *Musa* and *Parkia*, while four types of pollen (*Durio* sp., Unidentified 2, 3, and 4) were unique to each species.

Fruits of the oil palm were bitten by *C. brachyotis* I each time they were enclosed with the bats. The exocarp and mesocarp of the fruit were heavily gnawed.

DISCUSSION

The diversity of the bat community in LHNP did not differ greatly from bat diversity in other old growth lowland dipterocarp forests, although comparable studies are limited. When accounting for differences in sample size, the number of megachiropteran species in LHNP (eight species; 78 individuals) was roughly similar to other study sites in Malaysia: Krau Wildlife Reserve (8; 352; Hodgkison et al., 2004a), Sepilok Forest Reserve (6; 75; Francis, 1994), and Pasoh Forest Reserve (4; 23; Francis, 1994). In addition, the number of microchiropteran species in LHNP (11 species; 57 individuals) did not differ greatly from the diversity in Sepilok (14; 53) or Pasoh (13; 71). The capture rate of megachiropterans in LHNP (55 individuals per 10,000 m^2h) was nearly equal to that in Krau (49) but higher than in Sepilok (32) and Pasoh (14). The capture rate of microchiropterans in LHNP (40) was nearly equal to that of Pasoh (44) and higher than in Sepilok (23). Because there were no large differences in bat diversity or capture rates between LHNP and other sites, our sampling method appears valid. Thus, the bat community in LHNP can be regarded as representative of old growth lowland dipterocarp forests.

To our knowledge, ours is the first study to demonstrate clear differences in the diversity and abundance of bats among forests and agricultural lands within a single landscape in Southeast Asia. Relative to primary and secondary forests, the number of megachiropteran species was somewhat low in orchards and notably low in the oil palm plantations. In addition, the capture rates of two frugivorous bats (*B. maculata* and *P. lucasii*) clearly differed among the four vegetation types, and these two species were not recorded in the orchards or the oil palm plantations. These results indicate that these megachiropteran species rarely use agricultural lands for feeding; thus, the vegetation is not suitable for maintaining a diversity of megachiropterans. Moreover, there may be no species unique to agricultural lands, because those species for which more than two individuals were captured were also recorded at least once in the primary or secondary forests (Appendix 1). Megachiropteran diversity in natural forests is thought to be maintained by various factors, including the diversity of food sources (Hall et al., 2004; Hodgkison et al., 2004a), the availability of roosts for tree-roosting bats (Zubaid, 1993), and the heterogeneity of forest structure (Hall et al., 2004; Hodgkison et al., 2004b). The oil palm plantations clearly lacked these characteristics.

Orchards and oil palm plantations may be inadequate habitats for most frugivorous and insectivorous bats; nevertheless, the capture rates of some species were high in these plant communities. The high capture rate of *G. tylopus* in the orchards may have been due to an abundance of bamboo groves in the vicinity of the census points. This bat roosts in the hollow stems of dead or damaged bamboo (Payne & Francis, 1998; Yasuma & Andau, 2000). Two species of nectarivorous bats (*E. spelaea* and *M. minimus*) were captured at significantly higher rates in orchards than in the other vegetation types, and *E. major* was only captured in an orchard. One cause of these high capture rates of nectarivorous bats may be the abundance of flowers in the orchards. The pollen examination indicated that three species of cultivated plants (*Durio* sp., *Musa* sp., and *Parkia* sp.) were the primary food sources of *E. spelaea* and *M. minimus*, although we did not distinguish between wild and domestic species within the genera. The particularly high capture rate of *C. brachyotis* I in the oil palm plantations may indicate that they feed on oil palm fruits, as indicated by the preliminary feeding experiment, although we do not know to what extent the bats depend on oil palm fruits. As Kinjo et al. (2003) noted, agricultural lands can be important feeding locations for certain species of megachiropterans.

The capture rate of megachiropterans differed significantly among vegetation types, with high rates in the oil palm plantations and orchards and low rates in the secondary and primary forests. This trend was nearly opposite to the pattern of bat diversity. The observed high capture rate and low species diversity of megachiropterans in agricultural lands were similar to the pattern reported by Hall et al. (2004) although their sampling sites were scattered across Southeast Asia, and the crop species studied differed from those in our study. In the Philippines, Heaney et al. (1989) also measured high capture rates and low diversity of megachiropterans in agricultural lands relative to lowland forests. Thus, these patterns may be common throughout Southeast Asia. Similar patterns have also been found in the Neotropics. For example, Medellin et al. (2000) observed both low species richness of phyllostomid bats and high dominance of particular bat species in agricultural lands (shaded cacao plantations and cornfields with other crops) compared to adjacent rainforests. Phyllostomid bat diversity was also low in coffee plantations relative to small fragmented forests (Numa et al., 2005).

The capture rate of microchiropterans was lower in the oil palm plantations but did not differ among the other three vegetation types. One possible cause of the strikingly low capture rate of microchiropterans in the oil palm plantations may have been the low abundance of insects. Although studies concerning the abundance of prey insects in this vegetation type are rare, Chung et al. (2000) reported low beetle abundance and diversity in oil palm plantations compared to logged and primary forests in Sabah, Malaysia.

The drastic increase of *C. brachyotis* I in the oil palm plantations was a particularly intriguing result. The population size of *C. brachyotis* I in the oil palm plantations may indeed be large, considering that its capture rate was extraordinarily high and the plantations cover a vast area (ca. 388,500 ha in Sarawak as of 2004; Brown & Jacobson, 2005). High capture rates and dominance of *C. brachyotis* in agricultural lands have been reported repeatedly in other regions (Abdullah et al., 1997; Hall et al., 2004). For example, Abdullah et al. (1997) measured a very high capture rate of *C. brachyotis* (570 individuals per 10,000 m^2h) in *Cocos* and *Musa* plantations in Indonesia, where *C. brachyotis* accounted for 93% of total captures. Our recapture data indicated that *C. brachyotis* was capable of movement between vegetation types. In addition, a fecal analysis suggested movement between the oil palm plantations and adjacent forests. *Ficus* seeds were found in approximately half of the feces samples of *C. brachyotis* I captured in oil palm plantations (n = 11), but no *Ficus* trees were present in this vegetation type (D. Fukuda, pers. obs.). Since the census points of the plantations are located within the maximum distance of recapture of the species (1600 m, Table 3) from the edge, the bats might have eaten *Ficus* fruits outside of the plantation. We can not deny the possibility that the original composition of the forest bat community would be altered by expanding bat populations in surrounding oil palm plantations. Such situation has not been reported for bats in Southeast Asia, but Ickes (2001) noted hyper-abundance of wild pigs (*Sus scrofa*) at a lowland dipterocrp forest that was probably caused by an abundant year-round food supply of oil palm fruits from plantations bordering the forest.

Cultivated plants in orchards may be abundant and consistent food sources, contributing to the maintenance of nectarivorous bats populations. This may be especially true in the lowlands of Southeast Asia, because lowland dipterocarp forests in the region are known for the supra-annual flowering and fruiting phenologies of many tree species (Appanah, 1985; Sakai et al., 1999; Sakai, 2002). Megachiropterans may rely on cultivated plants in agricultural lands during inter-flowering periods. Hodgkison et al. (2004a) reported seasonal fluctuations in the capture rates of certain megachiropteran species that consumed 'big bang' phenology food items in an old-growth lowland mixed dipterocarp forest. However, if the majority of a bat population is drawn to cultivated plants, this food supply in orchards may actually reduce both bat density and ecological services such as pollination and seed dispersion in surrounding areas. This study suggests significant changes in megachiropteran population densities and feeding habits among natural and cultivated vegetation types. Therefore, the effects of human activities on plant reproduction in natural forests as a result of changes in pollination and seed dispersion by megachiropterans are important subjects for future research.

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Appendix 1. Species list of bats captured in and around Lambir Hills National Park during this study.

Scientific name	Forearm length (mm) (mean, ± SD)[a]	Body weight (g) (mean, ± SD)[a]	Diet[b]	No. captured				
				Primary forests	Secondary forests	Orchards	Oil palm plantations	Total
Megachiroptera								
PTEROPODIDAE								
Balionycteris maculata	41.63 ± 1.75	14 ± 2.2	Fruit	23	2	0	0	25
Chironax melanocephala	45.50 ± 1.20	19 ± 0.5	Fruit, nectar, pollen	1	1	0	0	2
Cynopterus brachyotis I	62.36 ± 1.87	33 ± 4.0	Fruit, nectar, pollen	6	43[c]	69[c]	68[c]	186
C. brachyotis II	57.80 ± 1.37	27 ± 3.8	Fruit, nectar, pollen	11	10	4	3	28
C. brachyotis (unidentifiable)	NA	NA	Fruit, nectar, pollen	6	9	9	17	41
Dyacopterus spadiceus	77.5	74	Fruit	0	1	0	0	1
Eonycteris major	76 ± 0	76 ± 1.0	Nectar, pollen	0	0	2	0	2
Eonycteris spelaea	63.61 ± 2.58	48 ± 7.4	Nectar, pollen	5	1	29	4	39
Macroglossus minimus	39.98 ± 1.45	15 ± 1.5	Nectar, pollen	7	3	20	0	30
Penthetor lucasii	59.63 ± 3.80	35 ± 5.7	Fruit	18	3	0	0	21
Rousettus amplexicaudatus	NA	NA	Fruit, nectar, pollen	1	1	0	0	2
Rousettus spinalatus	86.16 ± 2.67	89 ± 8.8	Fruit, nectar	0	1	3	0	4
Microhiroptera								
HIPPOSIDERIDAE								
Hipposideros cervinus	47.45 ± 1.16	9 ± 1	Insects	32[c]	11	7	1	51
Hipposideros diadema	84.18 ± 0.13	38 ± 5.0	Insects	2	0	0	0	2
Hipposideros dyacorum	39.55 ± 0.05	6 ± 0	Insects	2	0	0	0	2
Hipposideros galeritus	49.19 ± 1.01	9 ± 1	Insects	0	3	0	0	3
Hipposideros ridleyi	48.15	NA	Insects	0	1	0	0	1
VESPERTILIONIDAE								
Glischropus tylopus	28.89 ± 0.90	4 ± 0	Insects	5	1	20	0	26
Hesperoptenus blanfordi	25.05 ± 0.05	6 ± 0	Insects	2	0	0	0	2
Kerivoula pellucida	29.91 ± 0.09	4 ± 0	Insects	0	1	1	0	2
Murina suila	31.09	4	Insects	0	1	0	0	1
Philetor brachypterus	32.70	11	Insects	1	0	0	0	1
Pipistrellus tenuis	29.20	5	Insects	1	0	0	0	1
Tylonycteris pachypus	NA	NA	Insects	0	1	0	0	1
Tylonycteris robustula	26.80	5	Insects	0	0	0	1	1
RHINOLOPHIDAE								
Rhinolophus borneensis	42.12 ± 0.20	8 ± 1	Insects	2	0	2	0	4
Rhinolophus sedulus	42.35 ± 0.34	9 ± 0	Insects	4	0	0	0	4
Rhinolophus trifoliatus	49.98 ± 1.51	14 ± 2.0	Insects	2	4	2	0	8
MEGADERMATIDAE								
Megaderma spasma	54.32 ± 0.27	19 ± 3.6	Insects, spiders, small vertebrates	4	0	0	0	4
Total				135	98	168	94	495

NA = data not available; [a] = data of juveniles were excluded; [b] = based on Yasuma & Andau (2000), although the literature does not distinguish between the two forms of *C. brachyotis*; [c] = dominant species in the vegetation type.