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SMALL MAMMAL SPECIES DIVERSITY AND COMPOSITION IN TWO ECOLOGICALLY DISTINCT RAIN FOREST SITES IN NORTHERN SUMATRA, INDONESIA

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Most organism groups reach their maximum diversity in the tropics and most of these in tropical rain forests. For consumers, higher diversity can be expected the greater the range of resource types from the trophic level below such that species can be more specialized (with narrower niches) with the result that more species can coexist in the community (Pianka 1983). The types and quality of food resources produced at the first trophic level should also be considered, because plant species vary in the types of fruits produced and seed dispersal mode (Pijl 1982). As a consequence, it should be expected that the floristic composition of a forest site affects the availability of food resources to consumers, indirectly affecting their diversity.

In northern Sumatra, Indonesia, two forest sites, Ketambe and Bukit Lawang, less than 60 km apart, differ markedly in tree species composition. In Ketambe, the forest is characterized by an abundance of trees of the Meliaceae and Moraceae that produce fleshy, animal-dispersed fruits (Palombit 1992). Its most striking feature is the high density of strangling figs (Schaik 1996). Bukit Lawang is a hill Dipterocarp forest (*sensu* Whitmore 1984) dominated by trees of the Dipterocarpaceae, which are characterized by the production of dry, wind-dispersed fruits. Strangling figs are rare at that site.

Both forests compared in this study, Ketambe and Bukit Lawang, are in the Gunung Leuser National Park, part of the Leuser Ecosystem, Sumatra, Indonesia. Table 1 gives an overview of the physical and ecological characteristics of the compared sites. Due to their proximity and similar elevation, both sites are climatically similar and potentially have the same pool of species. Thus, differences in animal species composition between the two sites are expected to be related to local ecological conditions. We lived-trapped small mammals in Ketambe and Bukit Lawang to search for differences in small consumer species richness and composition between these sites.

Ketambe is composed of a series of Holocene alluvial terraces in the valley of the Alas River and on the lower slopes of the adjacent mountain range (Schaik & Mirmanto 1985). Bukit Lawang is characterized by a network of hills and narrow valleys fanning out from a mountain ridge. Preliminary soil analysis (J.P.B., unpublished data) reveals that Ketambe soils are more fertile, as indicated by a higher pH (6.5 vs. 4.8 in Bukit Lawang) and concentration of macronutrients (Ca, Mg, Na, K, P and S).

To compare both sites in terms of small mammal diversity, 80 live traps were placed at each site and baited with ripe bananas and peanut butter every

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TABLE 1. Physical and ecological contrast between Ketambe and Bukit Lawang (source, van Schaik, unpublished report, and Palombit 1992).

Site	Ketambe	Bukit Lawang
Coordinates	3°41'N, 97°39'E	3°33'N, 98°06'E
Altitude (m)	350–550	450–700
Major landscape unit	alluvial terraces +mountains	network of hills
Soils pH	5–7.5	4–4.5
Annual rainfall (mm)	3229	4675
Driest month 1st dry season	Feb	Feb
Driest month 2nd dry season	Aug	Jul
Wettest month 1st rainy season	Apr	Apr
Wettest month 2nd rainy season	Nov	Nov
Major forest type	Non-dipterocarp lowland	Hill dipterocarp
Large strangler figs (n/km)	9.2	0
Small strangler figs (n/km)	4	3.7
Dominant tree families	Meliaceae , Moraceae and Euphorbiaceae	Dipterocarpaceae

morning (09:00h). Traps were locally made 20 x 10 x 10 cm live traps (Indonesian). They were equipped with a hook release mechanism and covered by a fine wire mesh. All trapping was done during the rainy season of 1999 (October to December)

Live traps were placed in two locations about two km apart in Ketambe, on a high terrace near the slopes of the mountain range (28/10/1999 to 06/11/1999) and at a lower terrace near the Alas River (12/12/1999 to 19/12/1999). At both sites, the 80 traps were set in three lines of 20 stations each, totaling 60 trap stations per location. At each trap station one trap was placed on the ground, the 'ground traps', and 20 others ~1.5 m above the ground, the 'tree traps'. Trap stations were placed in three parallel straight lines running north-south in terrace 6 and east-west in terrace 3. Stations and lines were 15 m apart. Tree traps were placed at every other station for the first 40 stations (there were only 20 tree traps).

In Bukit Lawang, traps were placed in two locations, on a hill-crest (21/11/1999 to 27/11/1999) and in a valley (28/11/1999 to 4/12/1999). Locations were approximately 500 m apart. Due to the steepness of the terrain, traps were placed on a single file in both locations. Again, 80 traps were set, 60 on the ground at 15 m intervals and 20 others on trees at ~1.5 m above ground. As in Ketambe, there were 60 trap stations per trap line.

Because the fauna of the region is poorly known taxonomically, most captures were collected and deposited at the Bogor Zoological Museum, Bogor, Indonesia and the Museum of Vertebrate Zoology (MVZ) at University of California, Berkeley, USA. Released individuals were marked by clipping their right ears. Dr. Agustinus Suyanto from Bogor and Dr. Jim Patton from MVZ identified the animals deposited at their museums, confirming our field identifications. Finally, a few trapped individuals escaped while emptying the traps. The Shannon diversity index (H') was calculated as $H = -\Sigma(pi \log pi)$ where pi was the proportion of the *ith* species in the total sample. Differences between the diversity indices for Ketambe and Bukit Lawang were tested with a Student's *t*-test formulated for diversity indices (Zar 1999).

Because it has been documented that small mammals can be affected by habitat structure (August 1983, Malcolm 1995), we contrasted structural complexity of the study sites. We used six of the 11 habitat parameters adopted by August (1983); canopy height, canopy density, mid-story density, connectivity, density of herbs and density of ground cover. Description of each category is given in August (1983). Except for canopy height, which was estimated in meters, all other measurements consisted of subjective estimations on a scale of 0–4, from low (0) to high (4) complexity. At each sampling location, habitat complexity was assessed by J.P.B. at every other trap station or 30 per trap line and 60 per site. Differences between the samples were tested with a Mann-Whitney U-test. Significance levels were set at $p < 0.05$.

TABLE 2. Summary of trapping results in Ketambe and Bukit Lawang.

Location	Number of trap-nights	Number of captures	Trap success	Number of species
Ketambe, high terrace	771	18	2.3%	7
Ketambe, low terrace	640	23	3.6%	8
Bukit Lawang, hill crest	540	18	3.3%	4
Bukit Lawang, valley	556	17	3.1%	4
Total	2507	76	3.0%	11

Trapping results are summarized in Tables 2 and 3. In total, 76 individuals were captured during 2507 trap-nights. Overall, trapping success was 3 % : 3.1 % for Bukit Lawang and 2.9 % for Ketambe (Table 3). Fifty-three of the individuals captured were collected and the remaining 23 either escaped while the trap was being emptied (three individuals in Ketambe and two in Bukit Lawang) or were released (18 individuals in Bukit Lawang). Only three of the released individuals were recaptured.

Despite their proximity, the two sites sampled here showed a significant difference in small mammal species diversity and composition as assessed by live trapping. In the two sites combined, 11 species of small mammals were captured. Species richness in Ketambe was considerably higher than in Bukit Lawang (10 *vs.* 4, Table 3). The Shannon diversity index for Ketambe was significantly greater than that for Bukit Lawang ($t = 2.6$, $p < 0.01$). Three species were captured in both habitats; one species was exclusive to Bukit Lawang and seven to Ketambe (Table 3). *Maxomys rajah*, the only species exclusive to Bukit Lawang, was also the dominant species at that site, accounting for 60 % of all captures. Second in number of captures in Bukit Lawang was *Tupaia glis*, accounting for 23 % of the captures.

In Ketambe, captures were more evenly distributed among the trapped species. The two most trapped species, *Tupaia glis* and *Niviventer rapit*, accounted for 29 % and 24 % of captures respectively. *Niviventer rapit* was practically exclusive to Ketambe since only two individuals of this species were captured in Bukit Lawang. Apart from *Sundasciurus tenuis* all other small mammals captured were primarily ground-dwelling forms (Harrison 1957, Medway 1978). Although considered to be the most trappable species in Malaysia (Harrison 1969, Medway 1972, 1978, Kemper & Bell 1985), in this study *Leopoldamys sabanus* represented less than 4 % of total captures.

In terms of habitat structure, the forest in Bukit Lawang was significantly taller (40.7 +/– 7 vs. 33.4 +/– 8; $p < 0.01$), whereas the forest in Ketambe had denser ground vegetation (1.9 +/– 1 vs. 2.5 +/– 1, $p < 0.01$) and higher connectivity (2.7 +/– 1 vs. 3.1 +/– 1; $p = 0.02$). The differences in the other three estimated parameters were not significant (Table 4).

In a seminal paper, August (1983), following a tradition of bird ecologists initiated by MacArthur & MacArthur (1961), proposed that habitat structural complexity and heterogeneity affected the abundance and diversity of mammals. Following August (1983) several authors demonstrated, to a greater or lesser ex-

TABLE 3. Summary of captures.

Species	Ketambe	Bukit Lawang
Leopoldamys sabanus	3	0
Lariscus insignis	1	0
Leopoldamys edwardsii	2	4
Maxomys rajah	0	21
Maxomys sp.	2	0
Maxomys whiteheadi	6	0
Niviventer rapit	10	2
Sundamys muelleri	2	0
Sundasciurus tenuis	2	0
Tupaia glis	12	8
Tupaia tana	1	0
Number of individuals	41	35
Number of species	10	4
Diversity (H’)	0.85	0.46
Total trap effort	1411	1096
Trap success	2.9%	3.1%

TABLE 4. Average for measures of habitat complexity. Mann-Whitney U-test was used with the combined data to compare the two sites.

Habitat complexity	Ketambe, terrace 3	Ketambe, terrace 6	Bukit Lawang, hill crest	Bukit Lawang, valley	Ketambe combined	Bukit Lawang combined	p
Canopy height	31.5+/–6.7	35.3+/–8.6	43+/–5.8	38.3+/–7.0	33.4+/–7.9	40.7+/–6.8	<<0.01
Canopy density	2.4+/–0.9	2.4+/–1.0	2.3+/–0.5	2.4+/–0.7	2.4+/–1.0	2.4+/–0.6	0.66
Mid-story density	3.3+/–1.0	3.0+/–1.0	3.2+/–0.6	3.3+/–0.7	3.2+/–1.1	3.3+/–0.8	0.83
Connectivity	3.3+/–1.0	2.9+/–1.0	2.3+/–1.0	3.1+/–0.9	3.1+/–1.0	2.7+/–1.1	0.02
Herbs	2.5+/–1.0	2.6+/–0.9	2.4+/–0.9	2.5+/–0.9	2.6+/–0.9	2.5+/–0.9	0.50
Ground cover	2.9+/–1.3	2.2+/–1.1	1.9+/–0.9	1.8+/–0.9	2.5+/–1.2	1.9+/–0.9	<0.01a

tent, the importance of habitat structure and heterogeneity in determining the abundance and diversity of small mammal communities (e.g., Rosenzweig & Winakur 1969, Kemper & Bell 1985, Fonseca and Robison 1990, Malcolm 1995, Paglia *et al.* 1995). Despite the efforts devoted to testing this idea, the underlying mechanism behind this relationship remains largely unexplored.

Although structurally complex habitats may offer a greater variety of support for locomotion, more hiding places and more and safer connections between food patches, greater diversity in consumer species should be expected when the range of resource types from the trophic level below is abundant enough to allow species to be more specialized and more species can coexist in the community (Pianka 1983).

In this study, small mammal species richness was higher in Ketambe. Primate species richness follows the same trend with six diurnal primate species coexisting in Ketambe (*Pongo pygmaeus*, *Hylobates lar*, *H. syndactylus*, *Presbytis thomasi*, *Macaca nemestrina* and *M. fascicularis*) in contrast to a mere four species in Bukit Lawang (*P. pygmaeus*, *H. lar*, *P. thomasi*, *M. nemestrina*, pers. obs.). The observed difference in habitat structure however, was subtle. We suggest that the paucity in consumer species in Bukit Lawang, the hill dipterocarp forest site, results from the overall low habitat quality as indicated by the low abundance and diversity of fleshy fruits at that site (e.g., Howe & Westley 1986, Adler 1998, Ganesh & Priya 1999, Stevenson 2001). We believe that factors such as soil condition, primary productivity, structural complexity and floristics (and the availability of fleshy fruits) all interact, affecting to a greater or lesser degree the consumer assemblage. To better understand this relationship, however, it is necessary to investigate how these ecological factors interact and to what extent they affect the diversity of animals at the second trophic level.

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