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Effects of rain forest logging on species richness and assemblage composition of small mammals in Southeast Asia

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ABSTRACT

Aim The effects of logging and habitat degradation on the richness and abundance of small mammals in Asian rain forests are largely unknown. This work compares the species richness, dominance and evenness of small non-volant mammals between logged and unlogged forests, and assesses whether assemblage variability (β-diversity) is similar between forest types.

Location Southeast Asia, northern Borneo (Sabah, Malaysia), Sunda-shelf.

Methods We surveyed species-rich assemblages of small non-volant mammals in three unlogged and three logged forests for 2 years. At each forest site, we sampled a permanently marked transect and two additional sites in three trapping sessions. All analyses were performed at both levels to include the effects of local abundances and point estimates, separately from the relative abundances of species on a more regional scale.

Results We trapped a total of 1218 individuals of 28 species. Eleven common species accounted for 95% of all captures. Species richness and diversity were significantly higher in unlogged forest (27 species) than in logged forest (17 species). This was mainly attributable to the smaller number of rarely recorded species in logged forest (five compared with 16 in unlogged forest, with a total of fewer than 10 captures). However, all common species were present in both logged and unlogged forests, and our analyses revealed similar patterns of dominance, evenness and fluctuations in abundance. Hence overall assemblage composition in multivariate space did not differ greatly between forest types. Assemblages of Muridae and Tupaiidae showed similar population fluctuations in space and time, indicating that the ecology of these taxa may be partially driven by the same environmental factors.

Main conclusions Although species were distributed patchily within sites, analyses at local and regional scales revealed similar patterns in diversity and assemblage variability, suggesting that effects of forest modification did not differ extensively locally and regionally, but had a profound effect on rare species. Our results emphasize the importance and conservation value of logged forest stands that are able to hold a large proportion of the small mammals also found in unlogged forests. Rare and more specialized species are more vulnerable to forest degradation than commonly caught species, resulting in the complete loss, or a decrease in numbers, of certain groups, such as arboreal small mammals and Viverridae.

Keywords
Community structure, forest structure, logging impacts, Sabah, small mammals, spatial scale, Sunda region, Tupaia.

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INTRODUCTION

The species diversity and structure of local assemblages of rain-forest animals are influenced by many factors, including habitat complexity and patch heterogeneity, leading to differences in the spatio-temporal availability of resources. Tropical rain forests, in which tree diversity provides the essential resources of food and structural heterogeneity, consist of dynamic patches that are frequently affected by local disturbances such as tree-fall (Denslow, 1995; Condit *et al.*, 2000; Schnitzer & Carson, 2001). The impact of naturally occurring, low-to-intermediate disturbance levels is not necessarily negative; it can also enhance diversity through an increase in heterogeneity and patchiness of the environment (intermediate disturbance hypothesis: Connell, 1978; Molino & Sabatier, 2001). However, large-scale and high-intensity disturbances, which are prominent in many commercially logged forests, often have negative overall effects on species assemblages, even though logging can resemble naturally occurring large tree-fall gaps if reduced-impact logging is applied (Sist *et al.*, 2003).

Given the ever-increasing anthropogenic pressure on natural environments, and in view of the continuing degradation of rain forests, ecologists and conservationists face a growing challenge in trying to understand more fully the effects of human land-use on species, assemblages and ecosystem functioning. Borneo contributes considerably to the high biodiversity of Southeast Asia (Myers *et al.*, 2000), although many functional groups of flora and fauna have only rarely been subjected to detailed studies (Sodhi & Liow, 2000). Deforestation in this area is progressing more rapidly than in any other rain-forest biome worldwide (Curran *et al.*, 2004; Sodhi *et al.*, 2004). Most forests in Borneo will probably be logged in the foreseeable future, leaving the largest proportion of land area either deforested, or covered with logged forest of reduced economic and ecological value. The recovery and succession of the remaining forest stands depend on the availability of plant resources such as seeds, and on the presence of herbivores and their predators (Howlett & Davidson, 2003; Brearley *et al.*, 2004). Following the loss or alteration in numbers of resources, species or functional groups, the interactions of the remaining species will probably be negatively affected.

Because of their seed and seedling consumption, small mammals are assumed to play a central role in changes occurring within logged rain forest in terms of the composition and succession of plant species (Asquith *et al.*, 1997; Blate *et al.*, 1998; Lambert *et al.*, 2005; Wells & Bagchi, 2005). Increases in the abundance of some small mammals can lead to an increase in seed predation, which may suppress forest regeneration (Struhsaker, 1997). Moreover, the consumption of plant material and herbivorous arthropods by small mammals will have a further impact on plant regeneration. As small mammals are versatile and exploit tropical rain forests in three-dimensional space, including a wide variety of habitat patches that are inaccessible to larger vertebrates (Bourliere, 1989), they may even influence forest structure in areas that are at an early stage of succession.

Although the effects of forest fragmentation on small non-volant mammal assemblages (Laurance, 1994; Lynam & Billick, 1999; Goodman & Rakotondravony, 2000) and the surrounding matrices (Gascon *et al.*, 1999; Pardini, 2004) have been intensively studied, less work has been done that addresses the effects of logging on small-mammal communities in Asian tropical forests (Wu *et al.*, 1996; Laidlaw, 2000; Yasuda *et al.*, 2003; Bernard, 2004) or elsewhere in the tropics (Laurance & Laurance, 1996; Malcolm & Ray, 2000; Lambert *et al.*, 2005). As a result, our current knowledge of the impact of habitat degradation on small-mammal assemblages is still poor for many areas, particularly for dipterocarp rain forests. Most studies in the dipterocarp rain forests of Southeast Asia have included only two sites (logged vs. unlogged) and no replication, although it is becoming increasingly evident that the effects of habitat degradation on species diversity and animal dynamics are strongly dependent on the spatial scale of sampling and landscape heterogeneity (Condit *et al.*, 2002; Hill & Hamer, 2004). These aspects thus require multi-site approaches and a larger sampling effort.

Within unlogged dipterocarp rain forests, a large proportion of small mammals are generalists (e.g. some abundant murids and tupaiids) with overlapping dietary composition and microhabitat use (Langham, 1983; Emmons, 2000; Wells *et al.*, 2004, 2006). This large overlap and flexibility in habitat use might blur possible scale-dependent effects on the occurrence of species within a heterogeneous forest matrix, although patchiness in the distribution of key resources might influence demography, even in generalist species (Adler, 2000). The demography of small mammals is also expected to differ along habitat gradients according to the degrees of specialization and colonization ability of the species (Seamon & Adler, 1996), including preferences for small-scale perturbations such as tree-fall gaps (Beck *et al.*, 2004).

The floral composition of logged forests differs from that of unlogged forests. These differences affect not only overall structure and resource availability, but also the scale of habitat heterogeneity (Cannon *et al.*, 1998). On one hand, logging may lead to simultaneous changes in species composition and a strong increase in species that are tolerant to logging-induced habitat changes (Cottingham *et al.*, 2001); on the other hand, species composition might change but compensatory changes in species populations might maintain certain community properties, such as overall abundance, at a relatively constant level (Ernest & Brown, 2001). Whether the effects of habitat alterations are largely compensated for at the local or regional level, or whether they are chiefly influenced by habitat conditions, depends on the extent of environmental perturbation and tolerance of key species (Brown *et al.*, 2001). The assessment of what species persist in logged forests, and an examination of whether and under what conditions certain properties of small-mammal assemblages are maintained (and at what level) are therefore particularly important. The collection of these data may prove crucial in unravelling whether, and in what manner, functional groups or taxa respond to logging, eventually allowing generalizations about

particular sets of species and the creation of conservation strategies that preserve as many species as possible.

To fill these gaps in our knowledge of the species richness and assemblage dynamics of small mammals in Southeast Asia, we compared species richness, dominance and evenness of small non-volant mammals between logged and unlogged forests, and assessed whether assemblage variability (β-diversity) is similar between forest types. Furthermore, we investigated factors that lead to changes in assemblage composition and analysed the ways that specific taxonomic groups (Tupaiidae and Muridae) react to forest degradation.

METHODS

Study area

Borneo is the second largest tropical island after New Guinea. It harbours a diverse flora and fauna of approximately 3000 tree species (MacKinnon *et al.*, 1996) and around 130 non-volant mammal species (Payne *et al.*, 1998), comprising both Sundaic elements and a high degree of endemism. The moist tropical climate, with annual average rainfall of 2670 mm and annual mean temperature of 26.7°C (Danum Valley Conservation Area), is characterized by two periods of pronounced rainfall in May–June and October–January (Walsh & Newbery, 1999). Droughts induced by El Niño events affect fruit production by triggering synchronous fruiting of dipterocarp trees, a key resource for many vertebrates (Curran & Webb, 2000). Despite extensive and ongoing clearance, the remaining forest areas at present are estimated to cover half (48%) of the land surface; this includes large forest patches (Sabah Forest Department, personal communication). However, extensive areas of forest have previously been logged at least once and are thus altered to some extent.

We selected a total of six study sites: three in unlogged lowland rain forest and three in logged lowland rain forest, all situated in northern Borneo (Sabah, Malaysia) at altitudes of 200–900 m (Fig. 1). All forest stands were at least 1000 ha and between 17 and 236 km (mean 130 ± 80) apart. Unlogged forests: Danum Valley Conservation Area at 04°57′ N, 117°48′ E, 'Uf1'; Poring, Kinabalu NP at 06°02′ N, 116°42′ E, 'Uf2'; Tawau Hills NP at 04°23′ N, 117°53′ E, 'Uf3'; logged forests: Luasong Field Centre at 4°36′ N, 117°23′ E, 'Lf1'; Kg. Monggis at 06°13′ N, 116°45′ E, 'Lf2'; Kg. Tumbalang at 06°08′ N, 116°53′ E, 'Lf3'. Whereas the unlogged forest stands were characterized by relatively undisturbed vegetation, with emergent trees rising up to 60 m, canopy heights at the logged forest sites, which had been selectively logged *c.* 15–25 years prior to our study, reached only *c.* 25–30 m, and the few remaining larger trees (e.g. *Ficus* spp.) were of no commercial value. Harvesting practice in the highly productive Bornean forests may exceed 10 trees ha^{-1}, damaging more than 50% of the original stand (Sist *et al.*, 2003).

Details of the logging histories at the various sites were not available, although all logged sites were structurally similar.
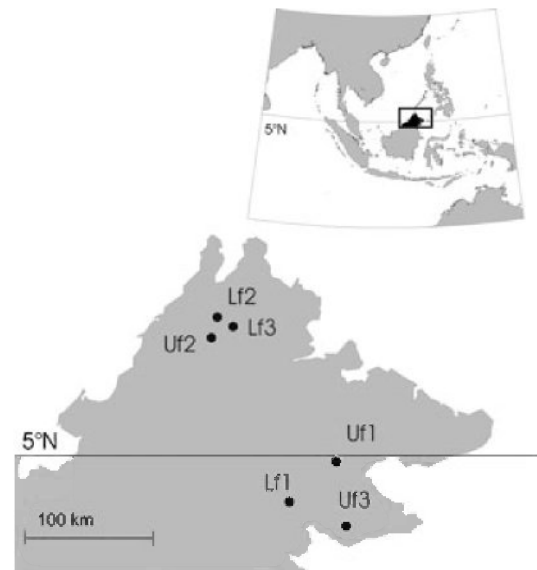
Figure 1 Map of Borneo with the six study sites. Unlogged forests: Danum Valley Conservation Area 'Uf1'; Kinabalu NP 'Uf2'; Tawau Hills NP 'Uf3'; logged forests: Luasong Field Centre 'Lf1'; Kg. Monggis 'Lf2'; Kg. Tumbalang 'Lf3'.

Half the original stands were damaged to a certain degree, as is usual in conventional logging practice where trees are cut and then transported through the unlogged areas to nearby roads. Compared with unlogged forest, disrupted canopies and pronounced gaps in logged forest lead to differences in plant composition and understorey, in which fast-growing plants such as climbing bamboo (*Dinochloa* spp.), sago palms (*Metroxylon* spp.) or rattan (*Calamus* spp.) dominate. The hunting of most vertebrates is common in nearly all forest areas. Small, non-volant mammals in particular are hunted in logged forests because of the large number of rural villages nearby and easy access via logging roads (K.W., personal observation). However, these influences were assumed to have little effect on our sampling, as the hunting of small mammals did not take place near our study locations.

Animal capture and handling

Animals were captured with locally made wire-mesh live traps equipped with a plastic roof for rain protection (280 × 140 × 140 mm) between September 2002 and November 2004. We conducted 18 trapping sessions, alternating between six study sites with a mean interval of 103 ± 50 days between consecutive trapping sessions at the same forest site, giving a total of three sampling units per site. Trapping was carried out at equal intervals throughout the seasons and year for both forest types (Uf1: Mar 03, Dec 03, Sep 04; Uf2: Dec 02, Jun 03, Feb 04; Uf3: Oct 02, Aug 03, Apr 04; Lf1: Apr 03, Sep 03, May 04; Lf2: Nov 02, May 03; Jan 04; Lf3: Jul 03, Mar 04, Nov 04). At each forest site, we established a randomly located and permanently marked transect of 40 traps set 20 m apart in two parallel lines on the forest floor. Additionally, 60–116 traps

were placed arbitrarily at two additional locations about 0.5–1.1 km away from the transects, except in Poring where the distance was only 300 m because of the topography. Additional traps were set at various places to enhance data on species diversity. The traps were baited with banana and checked every morning for 16 consecutive days during each trapping session.

The mean trapping effort was 2148 ± 408 trap-nights (traps active for 24 h) per session. Captured animals were briefly anaesthetized (we used diethylether, which had no apparent long-term impact on animal sedation), marked with a pit tag (ARE 162 transponders, AEG, Germany), measured, then released at the point of capture. Although some rats at arbitrarily sampled sites were marked only by ear punching, they could be identified reliably as recaptures during the entire study period. Species identification was based on Payne et al. (1998) and on comparison with specimens from the Sabah Parks Museum (Kundasang, Sabah, Malaysia). Specimens of accidentally killed animals, or individuals collected during the last trapping sessions, were deposited either at the Sabah Parks Museum or at the Senckenberg Museum, Frankfurt, Germany.

Data analysis

We examined species richness in logged and unlogged forests by using sample-based rarefaction curves based on the total trapping effort throughout the study period. This approach incorporated spatial heterogeneity, which is inherent to almost all samples (Colwell et al., 2004). We then estimated the expected number of species for logged and unlogged forest with Chao2 and Jack1 species-richness estimators (Colwell et al., 2004).

We established data matrices that included the number of individuals of each species trapped in transects during the 16-day periods (483 individuals in 18 transects, 'trans') and the first 54 individuals from a trapping session pooled from captures in transects and additional locations ('sess'). Two trapping sessions were excluded from analysis because of small sample size, leaving 864 individuals in 16 sessions for analysis. We analysed our data at the assemblage level and with respect to two taxonomic groups, murids and tupaiids, which dominated in all of our samples. All analyses were performed at both levels to include the effects of local abundances and point estimates (trans), separately from the relative abundances of species on a more regional scale (sess). As some immature spiny rats (Maxomys rajah and M. surifer) were not distinguishable in the field, we added the unidentified individuals proportionally to the number of identified individuals of both species for analyses (45 out of a total of 171 individuals, Table 1).

For each matrix, we used the coefficient of variation (CV = SD/average number of individuals) to describe variations in species abundances within sites, and the non-parametric Shannon–Wiener index H' to analyse species diversity (Magurran, 2004). Bray–Curtis (quantitative Sørensen) similarity matrices were used for comparisons across species assemblages from local and regional estimates. Based on these matrices, we conducted a two-dimensional non-linear ordination with multidimensional scaling (NMDS), which is a particularly robust ordination technique (Clarke, 1993). Axes scores for axis 1 of the NMDS were correlated to features of assemblages and taxonomic groups, respectively, using Spearman's correlation. We tested similarity matrices of species assemblages for possible relationships of temporal (chronological time differences in days), seasonal (shortest time differences between months of respective sessions), and geographical (kilometres between sites) distances between all trapping sessions by using Mantel statistics with 1000 permutations. We approximated species-specific relative persistence rates of individuals in consecutive sessions as $PR = re \times \Delta t / (N_t \times N_{t-1})$, where re is the number of recaptured individuals, Δt is the time lag [days] between sessions, N_t is the number of individuals in the session, and N_{t-1} is the number of individuals in the previous session. Diversity estimates were calculated with the software ESTIMATES (ver. 7.5, R. K. Colwell, http://purl.oclc.org/estimates), Mantel tests were conducted with PC-ORD 4.0 (B. McCune & M.J. Mefford, 1999), and further non-parametric statistics [Mann–Whitney (MW) U, Kruskal–Wallis (KW) ANOVA, Spearman's correlation, χ^2 test] were performed with STATISTICA 6.0 (StatSoft, 2001). Values are given as means ± 1 SD.

RESULTS

α-Diversity in logged and unlogged forests

During the entire study, we trapped a total of 1218 individuals (trapped at 3809 different times in total) from 28 species, representing 17 genera from eight families, with a sampling effort of 40,552 trap-nights (Table 1). In the unlogged forests, we found more species but fewer individuals (27 species, 547 individuals) than in the logged forests (17 species, 671 individuals). The only species that was not recorded in unlogged forests was the shrew Chimarrogale himalayica, but this was captured only once in logged forest. Being an insectivore, it was probably not attracted to our bait.

Accumulation curves indicated that the unlogged forests contained a richer small non-volant mammal assemblage, with a steeper accumulation curve, than the logged forests (Fig. 2). Estimates of predicted species richness were higher for unlogged forests, with 29 ± 3 (Chao2) to 32 ± 2 (Jack1) estimated species, than for logged forests, with 22 ± 6 to 21 ± 2 estimated species. These estimates confirmed that species richness was lower in logged forests (Fig. 2). Estimates of species richness for data sets from the transects (Chao2: 17 ± 3 for Uf, 14 ± 1 for Lf; Jack1: 19 ± 1 for Uf, 16 ± 1 for Lf) or standardized sessions (Chao2: 27 ± 4 for Uf, 14 ± 0.2 for Lf, Jack1: 28 ± 3 for Uf, 15 ± 1 for Lf) were in part lower than the total number of documented species; this was probably the consequence of rare and therefore slowly accumulating species that were under-represented in single trapping sessions.

Table 1 Number of individuals of all species trapped in the various study areas. Total trap effort for each area in parentheses. Additional trapping efforts in Uf2 and Uf3 during the period of field work that was not part of the analyses are included to provide a more complete species record.

| Species	Latin name authority	Total number of individuals	Unlogged forest (Uf)			Logged forest (Lf)		
			Uf1 (7092)	Uf2 (7545)	Uf3 (8115)	Lf1 (6469)	Lf2 (6040)	Lf3 (5291)
Rodentia								
Muridae								
Chiropodomys major	Thomas 1893	1	1	–	–	–	–	–
Lenothrix canus	Miller 1903	2	–	2	–	–	–	–
Leopoldamys sabanus	Thomas 1887	175	9	76	18	12	39	21
Maxomys baeodon	Thomas 1994	5	1	–	–	1	1	2
Maxomys ochraceiventer	Thomas 1894	2	–	2	–	–	–	–
Maxomys rajah	Thomas 1894	76	25	1	3	37	9	1
Maxomys surifer	Miller 1900	50	7	4	10	14	9	6
Maxomys cf. surifer/rajah		45	25	4	4	3	8	1
Maxomys whiteheadi	Thomas 1894	73	12	10	26	18	3	4
Niviventer cremoriventer	Miller 1900	265	28	26	9	19	55	128
Rattus rattus	Linnaeus 1758	4	2	–	2	–	–	–
Sundamys muelleri	Jentink 1879	41	3	1	1	–	–	36
Sciuridae								
Lariscus hosei	Thomas 1892	1	–	–	1	–	–	–
Callosciurus notatus	Boddaert 1785	11	–	5	–	1	4	1
Callosciurus prevostii	Desmarest 1822	4	–	3	1	–	–	–
Sundasciurus brookei	Thomas 1892	1	–	1	–	–	–	–
Sundasciurus hippurus	Geoffroy 1831	7	1	1	4	–	–	1
Sundasciurus lowii	Thomas 1892	45	8	2	21	5	5	4
Hystricidae								
Trichys fasciculata	Shaw 1801	2	–	–	2	–	–	–
Insectivora								
Chimarrogale himalayica	Gray 1842	1	–	–	–	–	–	1
Erinaceidae								
Echinosorex gymnura	Raffles 1822	4	–	–	2	2	–	–
Scandentia								
Tupaiidae								
Ptilocercus lowii	Gray 1848	1	–	1	–	–	–	1
Tupaia gracilis	Thomas 1893	24	1	9	4	4	2	4
Tupaia longipes	Thomas 1893	117	28	10	42	23	4	10
Tupaia minor	Günther 1876	76	1	25	2	–	4	44
Tupaia tana	Raffles 1821	173	22	15	12	15	54	55
Carnivora								
Viverridae								
Arctogalidia trivirgata	Gray 1832	2	–	1	1	–	–	–
Paradoxurus hermaphroditus	Pallas 1777	6	4	–	2	–	–	–
Viverra tangalunga	Gray 1832	3	3	–	–	–	–	–
Total		1218	181	199	167	154	197	320
Number of species		28	17	19	19	12	12	16

Eleven species, each represented by more than 20 captures, were classified as commonly caught. These species accounted for 95% of all captures and were recorded at all forest sites, except for *Sundamys muelleri*. Murids were most abundant in both forest types, accounting for 57% and 63% of all captures in unlogged and logged forests, respectively. Tupaiids were recorded with lower capture rates (31% and 33% of all captures) in unlogged and logged forest.

Shannon–Wiener diversity estimates showed no clear differences between single site estimates from logged vs. unlogged

forest sites (MW U test, trans: $U = 4.0$, $P = 0.83$; sess: $U = 3.0$, $P = 0.51$) but the overall diversity between both forest types was significantly lower in logged forest (trans: $H'_{Uf} = 2.35 \pm 0.02$, $H'_{Lf} = 2.08 \pm 0.05$; sess: $H'_{Uf} = 2.43 \pm 0.03$, $H'_{Lf} = 2.12 \pm 0.04$).

Dominance and abundance of common species

The most abundantly trapped species recorded in the sessions were *Niviventer cremoriventer* (most abundant in $n = 5$
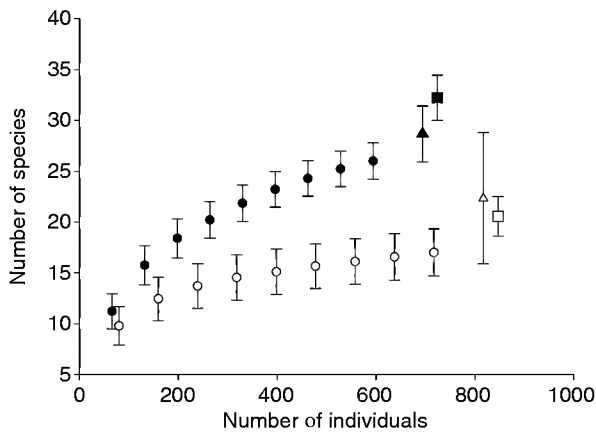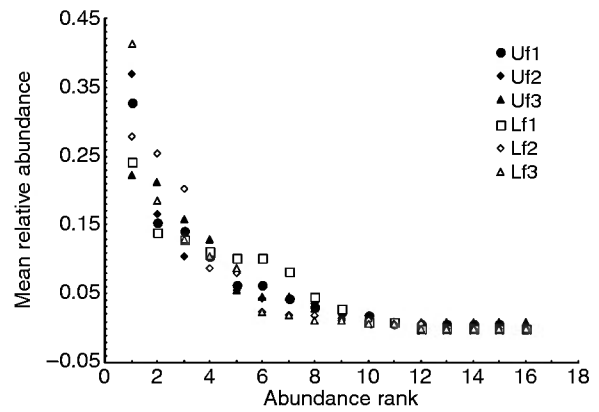
Figure 2 Rarefied species-accumulation curves representing the average number of species for a given number of captured individuals for the entire regional trapping effort (sessions) in unlogged forest (●) and logged forest (○). Triangles and squares refer to the estimated number of species based on Chao2 and Jack1 estimators, respectively. Bars are 95% CI.

Figure 3 Mean relative abundances of species pooled over trapping sessions at various study sites. No significant differences in the shape of the rank abundance curves were detectable (all Kolmogorov–Smirnov two-sample tests, $P > 0.10$). Note that the numbers of species are lower than actually recorded in some sessions because of data standardization.

sessions), *M. rajah* ($n = 4$), *Leopoldamys sabanus* ($n = 3$), *Tupaia longipes* ($n = 3$), *Tupaia tana* ($n = 2$) and *Maxomys whiteheadi* ($n = 1$). The three most abundantly trapped species varied within and between study sites. Whereas they were mostly the same within a study site (Sørensen index, S_{mean} (site) $= 0.70 \pm 0.19$), the abundant species differed more often between sites of the same forest type (S_{mean} (Uf) $= 0.39 \pm 0.26$, S_{mean} (Lf) $= 0.50 \pm 0.29$) with no obvious differences in dominance patterns between Uf and Lf (S_{mean} (Uf × Lf) $= 0.42 \pm 0.27$).

Fluctuations in the abundance of the 11 most commonly caught species, as determined by the CV from each site, did not differ across sites (MW *U* test, trans: $U \leq 3.0$, $P > 0.08$; sess: $U \leq 3.0$, $P > 0.08$). Mean CVs ranged from 0.65 at Uf3 to 1.14 at Uf1 for transect data, and from 0.33 at Lf1 to 1.07 at Lf3 for sessions, with no recognizable difference in abundance fluctuations between species (KW ANOVA$_{trans}$, $H_{10,53} = 12.00$, $P = 0.28$; KW ANOVA$_{sess}$, $H_{10,60} = 10.73$, $P = 0.38$). Overall, the mean abundance fluctuations pooled for the different forest types did not differ between logged and unlogged forests (MW $U = 397.0$, $P = 0.43$). Likewise, the relative abundance of the 11 most dominant species did not differ between sessions in logged and unlogged forests (MW $U = 36$, $P = 0.79$), while the overall abundance distributions as indicated by rank abundance curves were not distinct between logged and unlogged forests (all Kolmogorov–Smirnov two-sample tests ($n = 15$) $P > 0.10$) (Fig. 3). However, mean capture frequencies were significantly larger for *N. cremoriventer* and *T. tana* in logged than in unlogged forest (both MW $U > 15$, $P < 0.05$).

Spatio-temporal variation in assemblage structure

NMDS ordinations of species assemblages and seasonal/temporal similarities between trapping sessions extracted

two-dimensional solutions in which all raw stress factors, ϕ, were ≤ 0.15, indicating that the original relationships in matrices were represented sufficiently by the resulting NMDS axes (Clarke, 1993). Changes in assemblage structure at the local level based on transect data (trans, Fig. 4) were significantly correlated with changes at the regional level based on data from complete sessions (Mantel test, $r = 0.79$, $P < 0.01$).

Although the number of tupaiid species was correlated with the composition of assemblages (NMDS axis 1) at the local level based on transect data (trans: Spearman $R_{n=18} = -0.60$, $P < 0.009$), the number of murid species was correlated with species composition at the regional level, based on data from complete sessions (sess: Spearman $R_{n=18} = 0.68$, $P < 0.004$; Fig. 5a). Changes in the regional assemblage composition of murids and tupaiids were significantly correlated (Mantel test, $r = 0.27$, $P < 0.05$), suggesting that part of this pattern was
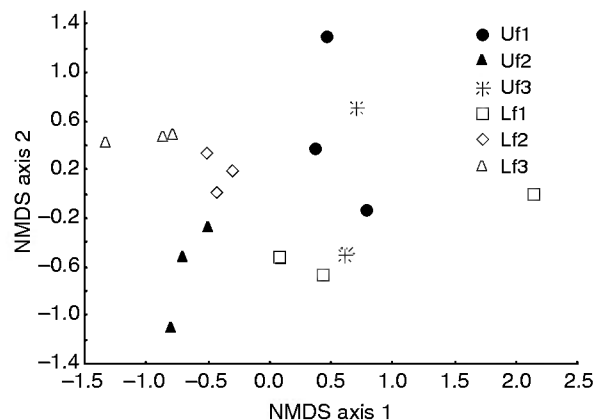
Figure 4 Multidimensional scaling plot of small non-volant mammal assemblages based on local censuses (trans) during the 18 trapping sessions.

(a)

(b)
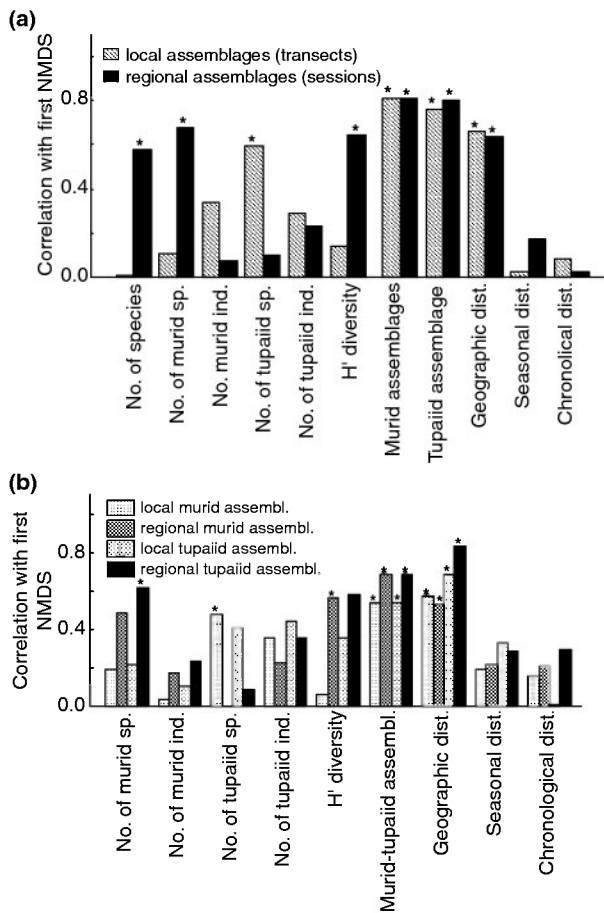
Figure 5 Impact of selected variables on changes in community composition in (a) assemblages of all species and (b) murid and tupaiid assemblages, on both local and regional scales. Bars represent R values from Spearman's correlations for numbers of species and individuals and for H' diversity, and r values from Mantel statistics for murid/tupaiid assemblages and geographical/temporal distances. Note that we considered only the first non-linear ordination with multidimensional scaling (NMDS) axes in these figures. *Significant correlations ($P < 0.05$).

driven by similar environmental fluctuations (Fig. 5b). We traced this relationship down to the species level and found that murid assemblages described by NMDS axis 1 scores were correlated with the relative abundances of *T. minor* and *T. longipes* (sess: both Spearman $R_{n=16} > \pm 0.75$, $P < 0.0006$). Tupaiid assemblage scores (NMDS axis 1) were correlated with the relative abundances of *N. cremoriventer*, *M. rajah* and *M. whiteheadi* (sess: all $R_{n=16} > \pm 0.50$, $P < 0.05$). Species assemblages were also correlated with respective H' diversity estimates, but not with number of captured individuals (Fig. 5a,b).

An impact of geographical distance between sites on assemblage similarity (quantitative Sørensen distances) was detectable for both local and regional species assemblages and for murid and tupaiid assemblages (Mantel tests, all $r > 0.29$, $P < 0.01$).

Capture success was lowest during fruiting seasons in September and October (Fig. 6), although we found no significant general impact of seasonal or temporal differences on assemblage compositions (Mantel tests, all $r < 0.18$, $P > 0.05$). Composition of species assemblages as described by NMDS axis 1 scores was most similar within sites and less similar across sites (site as fixed factor: KW ANOVA axis 1, trans: $H_{5,18} = 14.45$, $P < 0.02$; sess: $H_{5,16} = 14.01$, $P < 0.02$). NMDS axis 1 scores of assemblages in unlogged and logged forest were indistinguishable from each other at the local level (trans: both MW $U > 25$, $P > 0.17$). However, NMDS scores of assemblage composition at the regional level differed between unlogged and logged forest on the first ordination axis (sess: MW $U = 11$, $P < 0.03$).

Distribution of species

The spatial distribution of species was heterogeneous among localities (transects and additional locations) within a study site. A comparison of observed and expected distributions of commonly caught species, based on the total number of captures at different locations, revealed significant deviations from a random distribution among locations within each site in 20 out of 146 cases ($\chi^2 > 6.1$, $P < 0.05$). These patterns of spatial heterogeneity regarding species distribution were similar for unlogged and logged forest, and were most pronounced for *L. sabanus*, *Sundasciurus lowii* and *Tupaia gracilis*.

Persistence of individuals

We recaptured 15% ($n = 120$ individuals) of 784 marked individuals. Persistence rates of individuals in consecutive
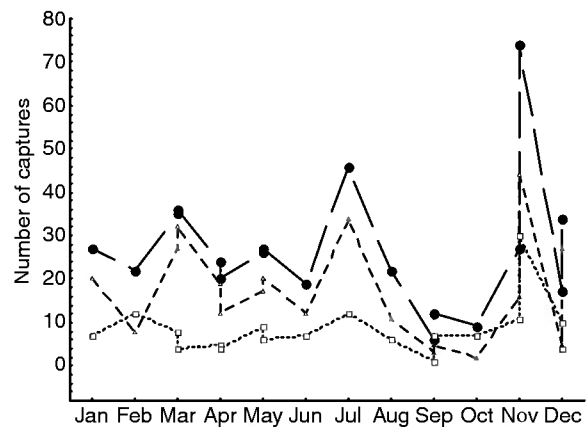
Figure 6 Number of captures in transects throughout the year. Total numbers of captured individuals (●), murids (△) and tupaiids (□) are given. Although the trap success for murids and tupaiids was not correlated (Spearman $R_{(n=18)} = 0.16$, $P = 0.54$), and the verification of general seasonal patterns was weak, the trapping success for both taxa was lowest during the fruiting season in September/October. Note that some months contain more than one sample.

trapping sessions differed between forest sites (KW ANOVA $H_{5,110} = 18.15$, $P < 0.003$), as persistence rates were relatively high in Uf3 but low in Lf1. They were marginally lower in logged than in unlogged forest (MW $U = 1203$, $P = 0.07$). The mean persistence rate was highest for *M. surifer*, *M. rajah* and *T. gracilis*. However, the means differed only slightly between species because of the large variability of persistence rates between sites (KW ANOVA $H_{5,110} = 18.15$, $P = 0.08$) (Table 2). The longest persistence was recorded for a *T. minor* individual, which had been marked in a previous study in 2001 (Wells *et al.*, 2004) and was recaptured after 636 days.

DISCUSSION

Small mammal diversity in logged and unlogged forests

In tropical forests, a high structural diversity and great variability in resources are considered key elements in the maintenance of diverse small-mammal assemblages (August, 1983). Furthermore, occurrence and assemblage patterns of small mammals are determined by the degree of specialization, flexibility and general demography of the constituent species (Adler, 2000). Species flexibility should not only ensure persistence and abundance in spatially and temporally heterogeneous forest matrices, but also tolerance of logging and habitat disturbance. Although rain-forest logging resulted in a significant loss of rare small mammal species in our study, the ubiquitous presence of commonly caught species at all forest sites, both logged and unlogged, suggests that assemblage dynamics are mainly determined by these species. Multiple comparisons of replicates within and between sites have revealed that fluctuations in abundance and assemblage variability appear to be little affected by logging, raising the question of how far synchronous responses to environmental fluctuations account for variation in local species assemblages, and whether this can be traced to the same dominant species.

Table 2 Maximum recorded persistence times for commonly caught species.

Species	Max. persistence (days)	Site of record	Total number of recaptured individuals	Mean persistence rate PR ± SD
L. sabanus	534	Uf3	14	3.8 ± 5.8
N. cremoriventer	494	Lf3	20	0.5 ± 0.9
M. rajah	573	Uf1	23	20.8 ± 41.0
M. surifer	537	Uf3	5	20.1 ± 37.8
M. whiteheadi	273	Uf1	5	7.4 ± 14.6
S. muelleri	250	Lf3	1	0.2 ± 0.7
S. lowii	262	Uf3	3	0.6 ± 1.8
T. gracilis	287	Uf3	4	19.3 ± 33.1
T. minor	636	Uf2	6	0.4 ± 1.0
T. longipes	590	Uf3	9	2.2 ± 2.8
T. tana	547	Uf3	19	6.9 ± 13.7

The pronounced decline in species richness and diversity in logged forests was mainly attributable to the reduction in rare species, whereas commonly caught species of omnivorous murids or tupaiids were recorded almost equally often at all sites. This pattern is consistent with other studies on small non-volant mammals in Australia (Laurance & Laurance, 1996), Malaysia (Zubaid & Ariffin, 1997; Yasuda *et al.*, 2003) and Venezuela (Ochoa, 2000).

Common vs. rare species

In our study, species affected by logging could be arranged in various functional groups, but no evidence was found for a single factor explaining the lack of certain species in logged forests. Four of the rare species we recorded only in unlogged forests are endemic to Borneo (*Chiropodomys major*, *Maxomys ochraceiventer*, *Lariscus hosei*, *Sundasciurus brookei*), and their restricted geographical distribution might be associated with less tolerance to environmental variability compared with species that inhabit a larger geographical area. Species decline in logged forest was most evident in civets, which are known to be sensitive to habitat degradation (Heydon & Bulloh, 1996; Colon, 2002). The mainly arboreal rats (*C. major*, *Lenothrix canus*) and squirrels (*Callosciurus prevostii*, *S. brookei*) are less prevalent in logged forests, which might be because of reduced canopy space and altered tree composition and texture (Saiful *et al.*, 2001; Yasuda *et al.*, 2003; Wells *et al.*, 2004) compared with unlogged forest. The question remains as to whether resource availability, or structure and habitat space, is the main determinant of reduced species richness in logged forest, and whether these proximate parameters affect particular species groups more than others. Some studies have suggested that the consequences of habitat disturbance differ with the type and spatial extent of disturbance. Favourable circumstances, such as an increase in herbaceous vegetation, a decrease in canopy and sapling density, and more abundant arthropods and fruits (Malcolm, 1997; Struhsaker, 1997; Lambert *et al.*, 2003) may lead to increases in small non-volant mammal densities in disturbed habitats (Malcolm & Ray, 2000; Lambert *et al.*, 2005). We found an increased abundance of *N. cremoriventer* and *T. tana* in logged forests. Although it has been suggested that *T. tana* prefers dense undergrowth and gap structures (Emmons, 2000; Wells *et al.*, 2004), whether structural features or particular resources are important *per se* remains unclear. Furthermore, whether conclusions from gap vs. understorey dynamics are applicable to logged forest conditions is also uncertain.

Species richness and resource aggregation

If the decline in species in logged forests is mainly attributable to resource specialization, a consideration of whether the occurrence and abundance patterns of species are driven by the presence of particular resources and/or by certain patterns of resource allocation would be of interest. For instance, tree species that play a significant role in overall forest architecture

and resource availability are often not randomly distributed within tropical forests (Condit *et al.*, 2000). Rather than overall forest structure, such patchy distribution patterns of key resources have been shown to influence the demography of the Neotropical *Proechimys* rat, which concentrates its activity mainly around fig (*Ficus*) trees, one of its main food resources (Adler, 2000). Therefore small mammals with specialized feeding habits and a dependence on spatially clumped resources seem to be mostly aggregated. Conversely, common species with omnivorous diets cope well with a wide range of resources and exhibit greater tolerance towards spatio-temporal resource availability. If the area covered by the spatial variability of plant and other resources exceeds the foraging areas of generalist feeders, then more specialized species should be able to cope more efficiently with a subset of the resources in some localities. This, in turn, might lead to a balanced overall dynamic of the assemblage, as the number and abundance of specialist and generalist species might compensate each other. High resource diversity and its specific distribution in heterogeneous forests therefore should promote the presence and abundance of both specialist and generalist species. With respect to capture probabilities, the chances of capturing a specialized species should be lower because of its reduced abundance, and higher for more generalist species.

Plant composition and distribution differ in logged forests (Cannon *et al.*, 1998). The proportion of animal-dispersed and mammal-pollinated trees, as well as arthropod assemblages that may serve as food sources for small mammals, may be affected by logging (Davis *et al.*, 2001; Chazdon *et al.*, 2003; Cleary, 2003). For instance, the reduced availability of particular fruit resources in logged forests has been reported as negatively influencing densities of the fruit-eating mouse deer *Tragulus* spp. (Heydon & Bulloh, 1997). As outlined above, such resource alteration should mostly influence the occurrence and density of more specialized small non-volant mammals. This is in agreement with our results, as analysis of commonly caught species reveals some aggregation at the level of individuals, but they are also widely dispersed in different locations and forest sites. Reduced species richness in logged forests probably occurs mostly as a consequence of reduced overall species densities and/or lower abundance of rare species, as most of the rare species that we trapped only in unlogged forests are known also to be present in logged forests (*L. canus, C. prevostii, Trichys fasciculata*, all civets; personal observation).

Tolerance of logging by common species, and the pronounced prevalence of rare species in unlogged forests, have also been found for birds in the same geographical region (Sodhi, 2002; Lammertink, 2004). However, other studies conducted at different spatial scales with birds and butterflies led to contrasting results, with both decreased and increased diversity (Hill & Hamer, 2004).

The amount of intraspecific aggregation of a species within a set of assemblages should concomitantly decrease α-diversity and increase β-diversity (Veech, 2005). Therefore the spatially clumped distribution of species should also be considered in the interpretation of variability in assemblages both within and among forest types. Surprisingly, the variability in assemblages from unlogged vs. logged forest, as determined by multivariate analysis, differed at neither the local nor the regional level. Furthermore, we found no differences in abundances of commonly caught murids and tupaiids within a forest type, and no evidence for differential impacts of logging on these functional groups. However, some fluctuations in the assemblage of both taxa are evident: while the number of tupaiid species were associated with assemblage fluctuations at the local level, murid species had more influence on assemblage fluctuations on a regional scale (Fig. 5a).

Logging effects on small-mammal assemblages

Based on the observation that different plant or invertebrate taxa respond inconsistently to anthropogenic habitat alteration (Lawton *et al.*, 1998; Ricketts *et al.*, 2002), we conclude that habitat disturbance in the form of logging may not necessarily lead to the synchronous alteration of food availability for different groups of small mammals. Unfortunately, the diet of murids and tupaiids is not well known, although they are thought to include a large range of arthropods and plant material (Langham, 1983; Emmons, 2000). However, interesting differences exist in their morpho-physiological traits related to food processing. Tupaiids have weak jaws in combination with short intestinal transition times and simplified colons (Emmons, 1991) that do not allow the processing of the hard dipterocarp and lithocarp fruits that are favoured by murids during the fruiting season in unlogged forests (Curran & Webb, 2000; Wells & Bagchi, 2005). Surprisingly, although these fruits comprise a key resource in unlogged forests, differences in local abundance related to habitat disturbance resulted neither in detectable differences in murid fluctuations between unlogged and logged forest, nor in any asynchronous changes in murid and tupaiid assemblages. Nevertheless, some impact of season in relation to fruiting can be inferred from the reduced trapping success during the main fruiting peak; this time interval also coincides with the main reproductive period of murids in unlogged forests (personal observation).

Another factor contributing to the observed assemblage structure patterns in our study could be the geographical locality and the distance between study sites. Geographically distinct areas differ in climate, altitude and edaphic factors that influence plant and resource composition on a regional scale (Ashton & Hall, 1992; Newbery *et al.*, 1996). Three of the sites, one unlogged and two logged (minimum distance between sites 17–24 km; Uf2, Lf2, Lf3), were close to Mount Kinabalu, a mountain that strongly influences the topography, soil mineral content and climate of this region (Kitayama, 1992). Such geographically related factors might be of greater importance than factors sensitive to logging in influencing abundance fluctuations and assemblage dynamics. Overall, the similarities in assemblage features between forest types suggest that fundamental ecological or abiotic features of the biome,

rather than profound differences between unlogged and logged forest, are major driving forces in shaping assemblage structure and abundance patterns.

Although logged forests are generally characterized by distinctly altered plant composition and physical structure compared with unlogged forest, many kinds of logging damage might in some ways be equivalent to the naturally occurring perturbations and alterations to which a large proportion of common non-volant small mammal species are well adapted. Most of the commonly caught species from our study, such as *L. sabanus*, *M. surifer* or *M. whiteheadi*, have inhabited a wide geographical range in the Sunda region of Southeast Asia throughout their evolutionary history (Gorog *et al.*, 2004). This supports the idea of the long-term adaptation to, and tolerance of changes in, habitat conditions by these species.

CONCLUSIONS

Logging does not appear consistently to cause strong changes in species assemblages with respect to ubiquitously present generalist species. We know little about the multiple interactions of small non-volant mammals with other components of the ecosystem. Further work is required to determine whether fundamental ecosystem processes in logged forests are altered by changes in resource availability, competitors or carnivorous predators, even if the same small mammal species are present (Terborgh *et al.*, 2001). The role of rare species remains even more elusive, although the reduced species richness in our study clearly suggests that some species are vulnerable to severe population reductions or extinction by logging-induced changes. The inconsistency in logging responses among species, and the large habitat variability that is intrinsic to rain forests and that is further generated by various anthropogenic impacts, present a challenge when selecting areas for conservation. Hitherto, general statements on logging effects can be made for different species groups. Although logged rain forests might house large proportions of the small-mammal assemblages found in undisturbed forests, some rare species will remain unprotected if unlogged forests are not conserved, as these forests remain the major source of the region's immense species richness.

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BIOSKETCHES

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