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The effects of selective logging on the distribution of moths in a Bornean rainforest

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The effects of selective logging on the diversity and species composition of moths were investigated by sampling from multiple sites in primary forest, both understorey and canopy, and logged forest at Danum Valley, Sabah, Malaysia. The diversity of individual sites was similar, although rarefied species richness of logged forest was 17% lower than for primary forest (understorey and canopy combined). There was significant heterogeneity in faunal composition and measures of similarity (NESS index) among primary forest understorey sites which may be as great as those between primary understorey and logged forest. The lowest similarity values were between primary forest understorey and canopy, indicating a distinct canopy fauna. A number of species encountered in the logged forest were confined to, or more abundant in, the canopy of primary forest. Approximately 10% of species were confined to primary forest across a range of species' abundances, suggesting this is a minimum estimate for the number of species lost following logging. The importance of accounting for heterogeneity within primary forest and sampling in the canopy when measuring the effects of disturbance on tropical forest communities are emphasized.

Keywords: beta diversity; canopy; Lepidoptera; light trap; Sabah; understorey

1. INTRODUCTION

There is widespread concern for the effects of tropical forest disturbance on biodiversity (Whitmore & Sayer 1992) and the principal cause of disturbance in South-East Asia has been selective logging (Collins *et al.* 1991). As a sustainable method of forest management, selective logging needs to be economically viable, provide a sustained yield of timber and conserve biodiversity (Bawa & Seidler 1998). While the consequences of logging have been studied for some of the fauna, notably birds and mammals, there is a critical lack of information on the response of invertebrate communities to disturbance (Sutton & Collins 1991; Grieser Johns 1997). In particular, there is a shortage of long-term, quantitative data which incorporate canopy sampling (DeVries *et al.* 1997).

Several recent papers have examined the extent to which insect diversity is maintained in secondary forest or plantations, but without samples from the canopy of the primary forest 'control' site (e.g. Chey *et al.* 1997; Hill *et al.* 1995; Holloway *et al.* 1992). Biodiversity assessment is likely to sample only the fauna on or near to the ground due to the practical difficulties of canopy access. If a large number of canopy specialists are missed in the process, then the species richness of the primary forest may be severely underestimated or the taxonomic composition misjudged. Furthermore, there is some evidence that canopy insects may fly closer to the ground in logged or secondary forest where the canopy is lower (Davis & Sutton 1998). If these are detected in ground-based sampling in the secondary habitat, but not the primary, then the estimate of species richness in the former will be inflated relative to that of the latter, confounding any comparisons.

Approximately 60% of the state of Sabah, Malaysian Borneo, is under forest cover of some sort (Marsh 1995). Of this, around 20% is plantation or scheduled for conversion to agriculture and 16% is in parks or reserves now protected from logging. The remaining 64% is production forest subject to selective logging which, in theory, follows a 35-year cycle (Collins *et al.* 1991). So on a landscape scale the most important question for the preservation of rainforest biodiversity in Sabah, and south-east Asia in general, is how species are maintained in periodically logged production forest.

2. METHODS

(a) *Site description*

Fieldwork was based at the Danum Valley Field Centre (DVFC), Sabah, Borneo (4°58′ N, 117°48′ E, altitude *ca.* 170 m). The field centre is on the edge of a 438 km^2 conservation area of primary lowland dipterocarp rainforest (*sensu* Whitmore 1984) within a 9730 km^2 timber concession, the Ulu Segama Forest Reserve, most of which had been selectively logged. Average annual rainfall is approximately 2700 mm and is not strongly seasonal, although the area is within the drought-prone north-east of Borneo (Walsh 1996). Further details of the local geography and land use may be found in Marsh & Greer (1992), and of the forest structure and composition in Newbery *et al.* (1992).

Forestry in Sabah involves harvesting all healthy, commercially valuable tree species with a diameter at breast height (dbh) >60 cm occurring on slopes of less than 20° (Marsh 1995). These are usually extracted from the felling site by bulldozers (forming 'skid trails') or overhead cable systems to a central 'log-landing site' from where they are removed on

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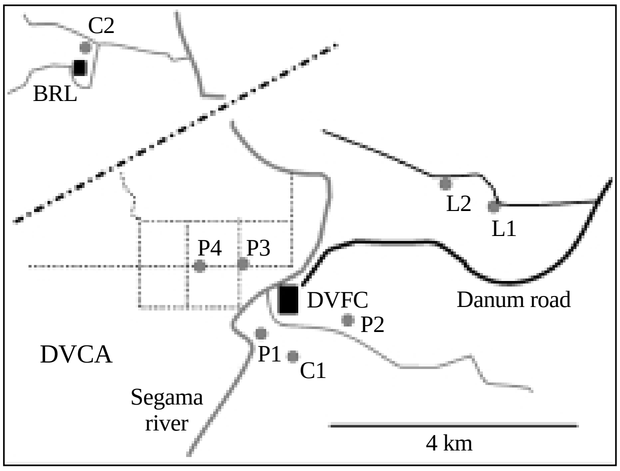

Figure 1. Locations of primary understorey (P1–4), canopy (C1–2) and logged (L1–2) forest sites. Key: DVCA, Danum Valley Conservation Area; DVFC, Danum Valley Field Centre; BRL, Borneo Rainforest Lodge.

lorries. While only 3–7% of trees are harvested, over 50% of trees >30 cm dbh may be destroyed by the logging and road building process (Johns 1988, 1992). Since 1980, the average area logged in the Ulu Segama Forest Reserve has been around 2000 ha yr^{-1} and the average volume of timber extracted in the 1980s was 70 $\mathrm{m}^3\,\mathrm{ha}^{-1}$ (Marsh & Greer 1992). This translates to about 8 trees ha^{-1}, which is lower than the average extraction of 12–15 trees ha^{-1} typical in the rest of Malaysia (Marsh 1995). Following logging, there remains a mosaic of vegetation types, from relatively undisturbed forest, through areas dominated by pioneer trees (e.g. *Macaranga*, *Octomeles*, *Neolamarkia* and *Duabanga*), to more open areas of grasses, ferns, vines and climbing bamboo (*Dinochloa* spp.) and finally, exposed and compacted mineral soil with little or no vegetation.

The study was carried out between August 1993 and July 1995 at eight sites within the Danum Valley Conservation Area (DVCA) and in adjacent forest selectively logged in 1988 (figure 1).

Primary forest understorey sites: four sites were located in closed-canopy forest on the system of trails around DVCA and the unlogged water catchment surrounding DVFC. P1 was on the Nature trail, and P2 on the East Ridge trail. P3 was at W5, 500 m from the Segama river along a trail due west of DVFC, and P4 was at W9, 900 m along the same trail.

Primary forest canopy sites: C1 comprised a 40 m high platform built onto a *Shorea johorensis* (Dipterocarpaceae) tree in relatively flat terrain approximately 200 m from the field centre, close to P1. C2 was a 35 m high platform built onto a *Koompasia excelsior* (Leguminosae) tree approximately 9 km north of DVFC near Borneo Rainforest Lodge.

Logged forest sites: the logged forest sites, L1 and L2, were located approximately 4 km east of DVFC and 600 m apart. In both cases, traps were located 10–20 m from a logging road within a relatively open stand of pioneer trees and vegetation. Towards the road there were more grasses, ferns and herbaceous vegetation, and away from it, an area of relatively undisturbed remnant forest. Thus the sites had all of the logged forest habitat types, from undisturbed forest through to exposed soil, close by.

The mean canopy height in primary forest was approximately 45 m (with emergents to >60 m), and in logged forest, 15 m. Logged forest canopy openness at a site adjacent to L2 was 10.7%, significantly more open than primary forest at 5.3% (Zipperlen & Press 1996).

(b) *Sampling and identification*

All 'macro-moths' (Cossoidea, Zygaenoidea, Bombycoidea, Noctuoidea, Geometroidea) were collected at light traps run on rain-free nights from 19.00 (dusk) to 20.00. There is no evidence that this represents a biased subsample of the moths active between dusk and midnight (S. J. Willott, unpublished data). Each trap comprised a white sheet illuminated by a 125 W mercury vapour bulb powered by a portable generator, and moths were collected from the sheet into killing bottles charged with ethyl acetate. Sites were visited haphazardly through time to avoid biases due to daily and seasonal variation in activity, and collecting continued until at least 1000 individuals had been obtained from each site. Light traps draw in moths from a radius of 10–25 m (Muirhead-Thomson 1991), so at this site, a trap on the ground would attract moths from the canopy of the logged forest, but not that of the primary. Trap efficiency depends to some extent on environmental conditions and on light-throw, with more individuals collected per unit time in an open location relative to dense vegetation. This was compensated for by sampling until comparable numbers of individuals were collected from each site, rather than equalizing the number of hours of trapping.

Nomenclature and higher classification follows Holloway (1983–1998), with identification based on these volumes and on specimens in the Natural History Museum, London. Species were determined by dissection of their genitalia where necessary. Species which could not be named are referred to in the text by a code number. Specimens are deposited at the Forestry Research Centre, Sandakan, Malaysia, and the Natural History Museum, London, UK.

(c) *Analyses*

A randomized species accumulation curve was generated for the total community by randomly sampling from the data set, taking the mean of 500 replicates drawn without replacement for each sample size. Alpha of the log-series was used as a diversity index as it is not unduly biased by either very common or rare species and is widely used in the entomological literature (Magurran 1988). However, there is some evidence that alpha increases with sample size (Robinson & Tuck 1993) which is potentially a problem in this study as more samples were taken in the primary forest understorey. So to provide a comparative estimate of the rarefied species richness of each site (or combination of sites) independent of sample size, the mean number of species expected in a sample of 1000 individuals (S_{1000}) was generated from the mean of 500 random samples of 1000 individuals drawn without replacement. Faunal similarity of sites was quantified using normalized expected species shared (NESS) (Grassle & Smith 1976; Wolda 1983) using the correction of Trueblood *et al.* (1994). In calculating NESS, the size of the random subsample, m, was set to 20. The NESS index varies from 0–1, a value of 1 indicating that the two samples come from the same population. Sites were clustered using group-mean averaging of the NESS indices. Spatial correlation among sites was evaluated by means of Mantel tests (Manly 1998) on matrices of the NESS index and distance between sites.

3. RESULTS

(a) *Diversity*

A total of 9482 moths comprising 1238 species was collected. The most abundant species was *Nirmides basalis* (Limacodidae), represented by 368 individuals (3.9% of the total), while 460 species (37%) were represented by a

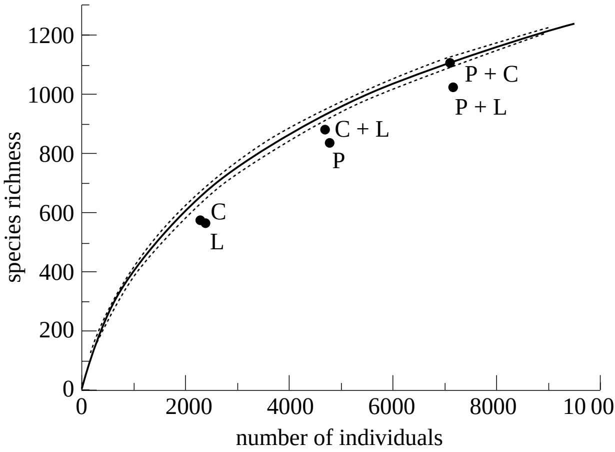

Figure 2. Randomized species accumulation curve (solid line) and 95% confidence intervals (dashed line) for the total community of moths, and observed species richness for the primary understorey (P), canopy (C) and logged (L) forest sites, and combinations of these sites.

single individual ('singletons'). The abundance of singletons and the steepness of the species accumulation curve (figure 2) suggests a very large species pool from which the samples were drawn. The observed species richness of the pooled samples from each individual habitat type (primary forest understorey, P, canopy, C and logged forest, L) were significantly lower than for the total community, indicating that there was significant turnover in species between habitat types. The pairwise combinations of samples C + L and P + L were also significantly lower than the curve for the total community, but the combination of P + C was not (see figure 2), suggesting that there were no species added in logged forest. Using the Chao estimator (Colwell & Coddington 1994) on the present data set, and further quantitative samples from the primary forest at Danum (S. J. Willott, unpublished data), the predicted number of species of macrolepidoptera at Danum is in excess of 1850, compared to the known Bornean fauna of 4500 species (Holloway 1987).

The diversity of individual sites varied widely (table 1), but with no evidence that the canopy was more diverse, or the logged forest less diverse, than the primary forest understorey. The lowest and highest diversities were recorded in the primary forest understorey. When replicate sites within each habitat were combined, the primary forest understorey apparently had the highest alpha diversity, although this would seem to be a function of sample size as the expected number of species in 1000 individuals, S_{1000}, was similar for P and C, and marginally lower for L. However, a true estimate of the diversity of forest should include both undestorey and canopy samples. When these were combined (P + C), alpha diversity was approximately 26% higher and rarefied species richness 12% higher than the understorey samples alone. In comparison with the 'true' primary forest, alpha in the logged forest was approximately 57% lower, and the rarefied species richness approximately 17% lower.

Table 1. *Number of species and individuals collected from each site, or alpha of the log-series and rarefied species richness, S_{1000} (both ± 95% CI)*

site	species	individuals	alpha	S_{1000}
P1	458	1485	226 ± 19	367 ± 12
P2	344	1115	170 ± 16	323 ± 6
P3	375	1058	207 ± 20	362 ± 6
P4	352	1128	176 ± 17	329 ± 7
primary (P)	835	4786	292 ± 14	370 ± 17
C1	391	1174	205 ± 19	356 ± 9
C2	390	1138	210 ± 20	363 ± 17
canopy (C)	571	2312	244 ± 16	368 ± 13
L1	393	1323	189 ± 16	338 ± 10
L2	368	1061	200 ± 20	355 ± 5
logged (L)	564	2384	234 ± 15	353 ± 16
P + L	1026	7170	328 ± 13	382 ± 19
C + L	881	4696	320 ± 15	401 ± 17
P + C	1106	7098	367 ± 15	413 ± 18
total	1238	9482	382 ± 14	413 ± 18

Table 2. *Similarity of moth faunas (NESS index) of sites within primary forest understorey (P1–4), canopy (C1–2) and logged forest (L1–2) at Danum Valley*

	P1	P2	P3	P4	C1	C2	L1
P1	—	—	—	—	—	—	—
P2	0.767	—	—	—	—	—	—
P3	0.663	0.677	—	—	—	—	—
P4	0.604	0.674	0.859	—	—	—	—
C1	0.475	0.364	0.302	0.264	—	—	—
C2	0.385	0.301	0.303	0.281	0.780	—	—
L1	0.688	0.658	0.614	0.578	0.588	0.500	—
L2	0.609	0.577	0.596	0.498	0.579	0.487	0.750

(b) *Faunal similarity of sites*

NESS similarity indices tend to be higher within habitats than between them (within-P mean ± s.d., 0.707 ± 0.037; within-C, 0.780; within-L, 0.750; table 2), although there is only one comparison within the canopy and logged forest habitats. Between habitats, similarity was highest between P and L (mean 0.602 ± 0.057), intermediate between C and L (0.539 ± 0.052) and lowest between P and C (0.334 ± 0.075). There is a significant difference (Mann–Whitney *U*-test; $U = 7$, $p < 0.05$) between values of the NESS indices for within-P and between P and L comparisons, although there is considerable overlap, indicating that differences among individual sites in the primary forest understorey may be as great as those between primary and logged forest. There is no significant correlation between the NESS index between sites and their distance apart, either for all sites (Mantel test; $p = 0.09$), or P sites only ($p = 0.22$). The dendrogram of group-average cluster analysis of the similarity values (figure 3) shows that the P and L sites group closely, with the C sites forming a distinct cluster.

At the family level, there was no evidence for strong differences in the species composition of sites (figure 4*a*). At each site, the most speciose families were, in descending order, Noctuidae, Geometridae and Arctiidae. The Nolidae were more speciose in the canopy, with 41 species recorded from each site (11% of the total in each).

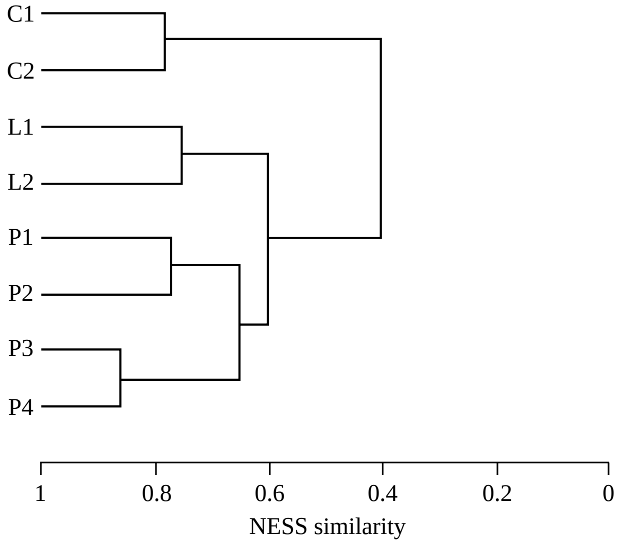

Figure 3. Dendrogram of group-mean cluster analysis of NESS similarity indices among primary understorey (P1–4), canopy (C1–2) and logged (L1–2) forest sites.

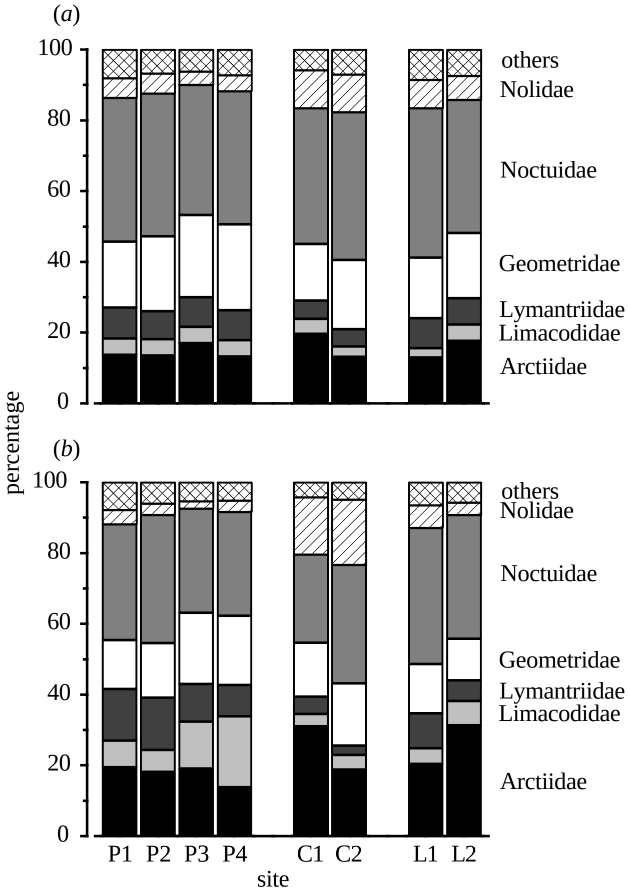

Figure 4. Proportions of different families at sites in primary forest understorey (P1–4), canopy (C1–2) and logged (L1–2) forest at Danum Valley: (*a*) species; (*b*) individuals.

This compares with an average of 18 species (5%) at the primary forest understorey sites and 28 species (7%) at the logged forest sites. There was considerably more family-level variation in abundance between sites (figure 4*b*). The proportion of Limacodidae within primary forest understorey sites ranged from 6% at P2 to 20% at P4, and averaged 4% and 6% of the canopy and logged sites, respectively. Nolidae were more abundant and Lymantriidae less abundant in the canopy relative to the other sites.

The most abundant species in each habitat (defined as those with a mean of ⩾ten individuals per site) are listed in table 3. Five species were abundant in all habitats (the arctiids *Amata prepuncta*, *Asura asaphes*, *Eugoa crassa* and lithosiine sp. 92, and the limacodid *Nirmides basalis*). In the canopy, 11 (61%) of the abundant species were only abundant in that habitat, compared to ten species (48%) in the primary understorey and three species (18%) in the logged forest. Out of those species which were abundant in two habitats, six were shared between primary forest understorey and logged forest, and three between the canopy and logged forest. None were shared between the primary forest understorey and canopy, reinforcing the impression of low similarity between these habitats.

(c) *Effects of logging*

To appraise the effects of logging on the moth community, two sets of species are of interest. First, those restricted to the primary forest (either the understorey or the canopy or both), being those which by definition appear not to persist in logged forest, and second, those species only found in logged forest which have invaded the system. This presence–absence criterion provides a conservative estimate of habitat specificity by not including those species which have only one or a few individuals in one habitat. Approximately 55% of species were restricted to the primary forest and 11% of species were restricted to logged forest (figure 5*a*). However, this includes species with only one individual which obviously can only have been recorded from one site. Considering species with at least five individuals, 21% were confined to primary forest, and less than 1% to logged forest (figure 5*b*), although as sampling effort in logged forest was approximately one-third of that in primary forest (see table 1), this result must be interpreted with some caution. In deciding the extent of habitat specificity, the choice of which minimum abundance, $N_{\min}$, to adopt as the criterion for inclusion of a species is of critical importance. A low $N_{\min}$ has the desirable property of including all or most species in the estimate, but is potentially subject to large sampling errors. A high $N_{\min}$ will be more statistically robust but only includes a small fraction of the species which may not represent the community as a whole and which is an inefficient use of data. In the present study, only 55 species (<5%) had more than 30 individuals, of which three, *Heringarosa cretacea* (Limacodidae), *Garudinia latana* (Arctiidae; Lithosiinae) and *Aiteta* sp.1 (Nolidae; Sarrothripinae), were restricted to primary forest.

The effect of the choice of $N_{\min}$ on apparent habitat specificity is illustrated in figure 6. There is a rapid decline in the number of species apparently restricted to primary forest as $N_{\min}$ increases, but the values are relatively stable around 10% as $N_{\min}$ ranges from six to 24 individuals. Drawing conclusions from those species with intermediate abundances reduces the problems of undue bias from either the rare or very common species. Species restricted to logged forest are mainly represented by

Table 3. *The most abundant (mean ≥ ten individuals per site) moth species in each habitat type at Danum, and the number of individuals of each*

(Note that sampling effort was approximately twice as great in the primary forest understorey.)

canopy	no.	primary understorey	no.	logged	no.
Amata prepuncta (Arctiidae)	106	*Nirmides basalis* (Limacodidae)	254	lithosiine sp. 92 (Arctiidae)	183
Asinduma exscripta (Nolidae)	93	*Hypomecis subdetractaria* (Geometridae)	170	*Amata prepuncta* (Arctiidae)	73
Hypochrosis binexata (Geometridae)	76	*Metaphaenia plagifera* (Noctuidae)	157	*Nirmides basalis* (Limacodidae)	69
Carea metaphaea (Nolidae)	52	*Hypena mandatalis* (Noctuidae)	149	*Hypochrosis binexata* (Geometridae)	59
Asura asaphes (Arctiidae)	50	*Amata prepuncta* (Arctiidae)	110	*Eugoa crassa* complex (Arctiidae)	59
Nirmides basalis (Limacodidae)	45	*Euproctis catala* (Lymantriidae)	106	*Asura asaphes* (Arctiidae)	49
Aiteta sp. 1 (Nolidae)	43	lithosiine sp. 92 (Arctiidae)	98	noctuid sp. 285 (Noctuidae)	49
Tathothripa continua (Nolidae)	42	*Heringarosa cretacea* (Limacodidae)	86	*Iambia lyricalis* (Noctuidae)	42
Eugoa crassa complex (Arctiidae)	39	*Redoa* sp. 4 (Lymantriidae)	82	*Redoa* sp. 4 (Lymantriidae)	41
Padenia duplicana (Arctiidae)	39	*Pseudalcis cinerascens* (Geometridae)	56	*Asura calamaria* (Arctiidae)	35
Ectropidia fimbripedata (Geometridae)	30	*Phazaca erosioides* (Uraniidae)	54	*Asura birivula* (Arctiidae)	32
lithosiine sp. 92 (Arctiidae)	29	*Asura asaphes* (Arctiidae)	54	*Hypena mandatalis* (Noctuidae)	26
Garudinia latana (Arctiidae)	29	*Spilosoma hosei* (Arctiidae)	54	*Cossus speidli* (Cossidae)	25
Parolulis olivescens (Noctuidae)	24	*Scopelodes pallivittata* (Limacodidae)	52	*Redoa* sp. 5 (Lymantriidae)	24
Lophoptera acuda (Noctuidae)	22	*Anticarsia creberrima* (Noctuidae)	50	*Metaphaenia plagifera* (Noctuidae)	23
Lophoptera pallibasis (Noctuidae)	22	*Medanella subterminalis* (Notodontidae)	49	*Hypomecis subdetractaria* (Geometridae)	23
Redoa sp. 5 (Lymantriidae)	21	*Euproctis* sp. 17 (Lymantriidae)	48	*Carea metaphaea* (Nolidae)	20
Hyposidra talaca (Geometridae)	21	noctuid sp. 285	47		
Thalassodes immissaria (Geometridae)	20	*Rhypotoses strigifimbria* (Lymantriidae)	46		
		Eugoa crassa complex (Arctiidae)	45		
		Asura calamaria (Arctiidae)	43		

singletons, and none are common (figure 6), with the most abundant, *Auchmothanes nothusalis* (Noctuidae; Herminiinae), represented by only six individuals. So this provides a conservative estimate of 10% of species of moths lost from primary forest at this site, but there is no evidence for these species having been replaced in logged forest.

4. DISCUSSION

There is typically little control for spatial heterogeneity in studies of the effects of forest management practices on biodiversity (Grieser Johns 1997). Within primary forest in Brunei, there was a difference in the assemblage of microlepidoptera from sites 1 km apart, but not in the Pyraloidea (Robinson & Tuck 1993). Density of primates (Grieser Johns & Grieser Johns 1995), and density and biomass of mousedeer (Heydon & Bulloh 1997), may vary more among primary forest sites than between primary and logged forest. This level of variability is echoed in the present study. While there has been work on vertical stratification in insect activity in tropical forests (e.g. Sutton *et al*. 1983; Hammond 1990; Kato *et al*. 1995; Wolda *et al*. 1998), this has rarely been incorporated into studies of disturbance (but see DeVries *et al*. 1997). This is a critical omission for two reasons. First, because the canopy fauna is a distinct assemblage, the diversity and species richness of the 'primary' forest will be seriously underestimated if sampling is purely ground-based. In this study, alpha diversity is 26% lower and species richness 12% lower in the understorey samples compared to the understorey and canopy combined. Although an explicit comparison of this difference is not possible from the published data, similar results are likely as there was significant turnover between canopy and ground faunas in Panamanian weevils (NESS = 0.884; Wolda *et al*. 1998), and Ecuadorian nymphalid butterflies (community similarity of species richness = 0.782; DeVries *et al*. 1997). Second, the logged forest fauna contains species more abundant in, or restricted to, the canopy. This will produce an inflated estimate of species richness and a distorted picture of the taxonomic composition in the logged forest relative to the primary forest understorey where these species have not been detected, or have been detected in reduced numbers (Davis & Sutton 1998). Holloway *et al*. (1992) reported *Hypochrosis binexata* (Geometridae) to be particularly abundant in logged forest at Danum. This result is repeated in the present study, but it is even more abundant in the canopy (table 3) while being scarce in the understorey (29 individuals collected from the four sites; data not shown). This result is not an isolated case as approximately 5% of species with more than five individuals were only found in the canopy or logged forest (figure 5*b*). A similar shift in distribution has been found for arboreal dung beetles at Danum (Davis & Sutton 1998) and in some birds, where three out of 16 species had significantly lower foraging height in logged forest (Lambert 1992), although the ability to detect such changes with ground-based sampling must be questionable. I would argue that any study of the effects of disturbance on arboreal or flying animals could be compromised by not including canopy sampling in the primary forest, or the disturbed forest if a high canopy persists.

There were no facilities for canopy access in the logged forest at Danum, so any 'canopy' component of the logged forest fauna may have been missed. I suggest that at this site, this error may be small, as the canopy of logged forest is considerably lower than primary forest (15 m compared to 45 m) and more open (10.7%

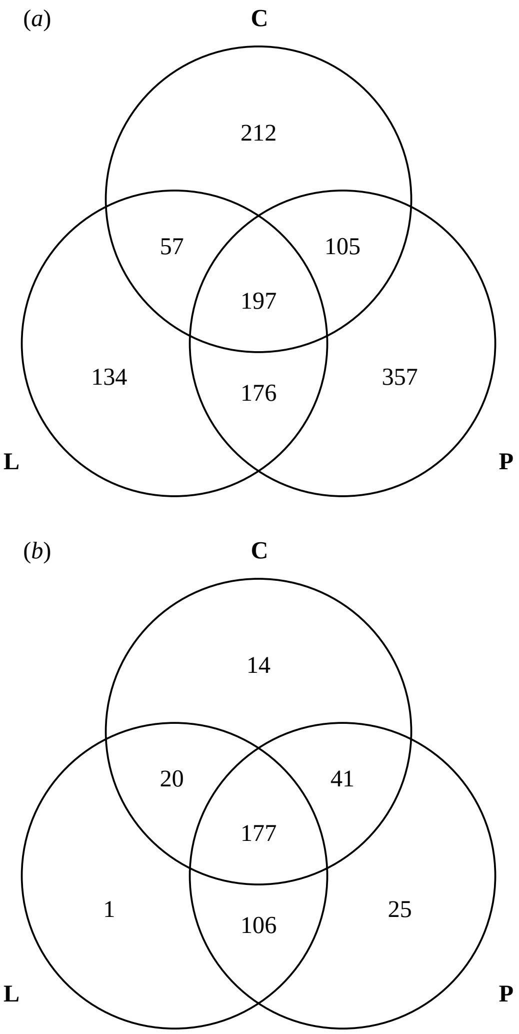

Figure 5. Species overlap among primary understorey (P), canopy (C) and logged (L) forest sites at Danum Valley: (*a*) all species; (*b*) species with ⩾five individuals.

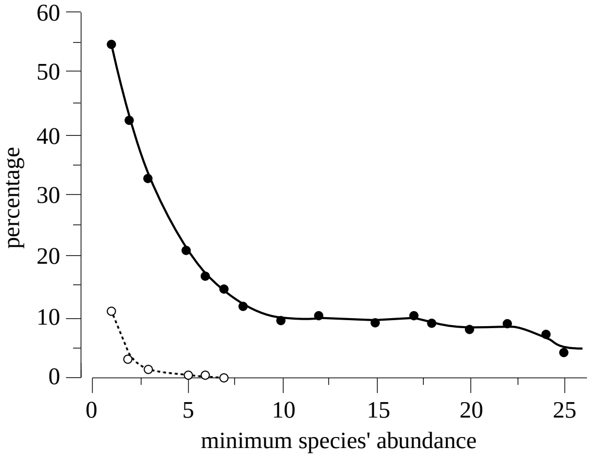

Figure 6. Percentage of species restricted to logged (L, open circles, dashed line) or primary forest understorey or canopy (P + C, filled circles, solid line) for different minimum species' abundance.

compared to 5.3%). As the effective trap radius of this type of light trap is 10–25 m (Muirhead-Thomson 1991), moths flying at these lower heights in more open vegetation are highly likely to enter light traps on the ground, and evidently do (figure 5). Nevertheless, a programme of sampling in the logged forest 'canopy' would be needed to rigorously test this, including sites adjacent to any remaining high forest.

The difference in rarefied species richness between logged forest and primary forest (understorey and canopy combined) is *ca.* 17% (table 1), and at least 10% of species are confined to primary forest over a range of species' abundances (figure 6). So two lines of evidence suggest a similar figure for the species' loss in logged forest at Danum Valley. While other studies on invertebrates have documented a reduction in diversity in disturbed forest in south-east Asia (eg. Chey *et al.* 1997; Hill *et al.* 1995; Holloway *et al.* 1992), I am not aware that the number of species lost has been explicitly quantified. Elsewhere, much work has concentrated on the persistence of species in forest fragments, where species richness generally declines (Turner 1996) and between 14 and 50% of abundant leaf-litter beetle species may be lost, depending on fragment size (Didham *et al.* 1998). The loss of at least 10% of species at Danum may represent a minimum for logged forest generally. Much of the biodiversity loss in logged forest comes not directly from the logging operation itself, but from the subsequent susceptibility of the forest to fire, or the encroachment of people who further clear the land for cattle ranching, fuel wood or agricultural crops (Grieser Johns 1997). None of this has occurred close to Danum. Furthermore, the logged forest sites were less than 4 km from a large block of primary forest (the DVCA), which may have acted initially as a refuge and later as a source for populations. Whether species losses would be greater further from a large area of primary forest remains to be seen. The persistence of birds in logged forest does not seem to be related to the distance from a large block of primary forest, but small refuge areas within logged forest are important (Grieser Johns 1996).

The total number of moth species at Danum was estimated to be at least 1850 species, based on samples taken within 9 km of the DVFC, and mainly within 4 km. This area does not include any gross changes in forest type, except that induced by logging, but there is no evidence that this caused any change in the species composition of the moth community. The total number of macrolepidoptera in Borneo is estimated to be around 4500 (Holloway 1987), of which about 30% are montane (Holloway *et al.* 1992). This leaves around 3100 species in the lowlands, of which Danum therefore has at least 60%. Some of the lowland species are undoubtedly restricted, via their larval host plants, to particular forest types, such as mangrove forest, peat swamp forest, or forest on limestone or ultrabasic rocks, but there are insufficient published data to estimate how many. It is likely to be a relatively small proportion (J. D. Holloway, personal communication), so a small area around DVFC may have over two-thirds of the general Bornean lowland fauna. Nevertheless, there are marked differences in community composition between closely separated sites (see table 2 and figure 4), and these differences are not correlated with their distance apart. This suggests that there is a relatively fine-grained mosaic of moth populations within the forest, although further sampling at a larger spatial scale would be needed to confirm this.

5. CONCLUSIONS

This study has demonstrated the necessity of encompassing the spatial heterogeneity of primary forest and, most importantly, including the canopy in any attempt to monitor the effects of disturbance on tropical forest communities. However, in cyclically logged forest, disturbance events are not limited to a single occasion. Most of the production forest in the Ulu Segama Forest Reserve, and Sabah generally, has now been logged once (Marsh 1995). To fully satisfy the criteria of sustainability, selective logging operations must preserve biodiversity over more than one cycle of logging activity (Bawa & Seidler 1998). For this to occur, the species composition of the logged forest must eventually approach that of primary forest, so it would be of considerable interest to know whether the 'lost' species returned as the forest regenerated following logging. The two alternatives to monitor recovery are to follow the same area of forest through time, which has been initiated in Tekam, Malaysia for birds and mammals, but which inevitably takes a long time (Grieser Johns 1997). Alternatively, different blocks of logged forest of known age since logging could be used, with space as a surrogate for time. The logged forest around Danum provides this opportunity, but there are formidable practical problems due to the variability of the forest, variation in logging intensity and the potentially confounding effect of distance from remaining areas of primary forest. This study has only considered forest logged five years previously, and so represents a snapshot in time, but it will provide a baseline set of data to monitor future changes in the moth community.

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