The response of some rain forest insect groups to logging and conversion to plantation

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SUMMARY

Data and analyses from pilot studies in the Danum area of Sabah, East Malaysia, and elsewhere in the Indo-Australian tropics are used to measure the effects of logging and other human disturbance, such as conversion to plantation, on insect diversity. The two insect groups studied have very different trophic requirements: moths, with floristically specific herbivory, and dung and carrion beetles, exploiting resources of much more uniform quality over different forest systems. Moths show significant loss of diversity and taxonomic quality with disturbance and conversion to plantation. The beetles show much less change in diversity and faunistic composition. The implications for conservation of biodiversity are discussed, and suggestions for further work are made.

1. INTRODUCTION

The threat to global biodiversity through clearance and other disturbance of tropical forests is currently under intensive discussion and the Royal Society's rain forest research programme developed to a large extent in response to this concern. Over half of global diversity in terms of numbers of species is represented by insects (see, for example, Holloway & Stork 1991), but few data are available that show the effects of forest disturbance and clearance on insect faunas. So far in the Royal Society's programme there has been little in the way of sustained entomological work, so the results here derive from a series of pilot studies in the Danum area of Sabah, East Malaysia, and from localities elsewhere in Borneo and the Indo-Australian tropics. They are therefore far from comprehensive.

We have sought to contrast two groups of insects with very different trophic requirements. Most moths are herbivores, their larvae defoliating living plants, although several groups are exceptions to this: detritivores, fungivores, algal browsers, stem and leaf miners, seed and flower feeders and a few predators. Moth herbivory is noted for its floristic specificity, so a general correlation in diversity between flora and moth fauna might be expected. Also, significant changes in floristic composition noted in natural succession and recovery after logging, or after conversion to plantation, are likely to be reflected by comparable changes in the composition of the moth fauna.

For our second group we have chosen dung and carrion beetles of the family Scarabaeidae. These are dependent on two resources that are of relatively uniform quality in different forest types yet may show variation in quantity. For example, the greater prevalence of foliage at ground level in logged forest may lead to a greater density of mammal herbivores. Major differences between the faunas of these beetles in disturbed and undisturbed forest and plantation forest will be less likely.

2. THE POTENTIAL FOR LOSS OF DIVERSITY IN BORNEAN LOWLAND FOREST INSECTS

Intensive surveys of tropical insect diversity are restricted to a very few tropical sites. The work of Project Wallace in northern Sulawesi (Knight & Holloway 1990) is probably the best example for the Indo-Australian tropics. Hence it is necessary to extrapolate from observations on key indicator groups to assess the potential for loss of insect diversity in the tropics through the activities of man. For the Indo-Australian tropics, moths are one of the best-studied groups. Quantified data from light-trap surveys are available for Malaysia, particularly the Bornean states, Sulawesi and Seram in Indonesia, high altitudes in Papua New Guinea, and for several Pacific archipelagos: Fiji, Vanuatu, New Caledonia, Norfolk Island (Robinson 1975; Hebert 1980; Holloway 1987, 1992; Holloway *et al.* 1990; Holloway & Barlow 1992; Holloway & Stork 1991).

These data show that Bornean moth diversity in natural forest at all altitudes exceeds that in all other areas except for the high-altitude New Guinea samples. In common with Sulawesi and Seram, there is a humped profile with altitude, with maximum diversity being encountered at altitudes between 600 m and 1000 m. Analysis of species associations over these altitude transects shows a sequence of associations replacing each other with altitude, but with some overlap between them. The lowland, lower montane and upper montane zones in the moths appear to correlate with floristic zonation, and the observed peak of diversity occurs at the upper extent of the lowland association and through the transition into the lower montane association. These profiles and patterns of zonation are discussed in detail in the references cited above.

It is evident from this that a major proportion of moth diversity resides in the lowland forest zone. The same is true of Bornean dung and carrion beetles (Hanski 1983; A. H. Kirk-Spriggs, personal observations) and probably for most other insect groups.

The moth species can be assigned to broad biogeographic categories (endemic, Sunda Shelf, wide Oriental, wide Indo-Australian and a few others), and then these categories can be cross-tabulated with the ecological associations just described, with the addition of an important open habitat category (Holloway *et al.* 1990). Taxonomic work on the Bornean moth fauna completed and in progress has enabled a total of about 1200 species to be tabulated in this manner (Holloway & Barlow 1992), and figure 1 shows the percentages of species assigned to each category. It can be seen that about 45% of the fauna is dependent on lowland forest, almost 30% of which is endemic or in the restricted Sundanian category. In general, vulnerability to extinction through habitat destruction ranges from high in the top left-hand corner of the matrix to low or negative (pest species) in the bottom right-hand corner.

This total sample can be subdivided into taxonomic groupings. In these the proportions of the various geographic–ecological categories vary widely, with some groups such as the Lasiocampidae, Limacodidae and some tribes of Geometridae with half or more of their species in the most vulnerable categories, and other such as the Sphingidae and trifine subfamilies of the Noctuidae with a high proportion of species in the more geographically widespread categories, with numbers of open habitat specialists including agricultural pests.

	Low	LMF	UMF	RS + S	LMF + UMF	Low + Mont.	Open
Endemic	9.43	1.54	7.76	1.15	1.58	2.30	0.13
Borneo + Wallacea	0.51	0.09	0.43	0.09	0.09	0.09	0.09
Sundaland	20.14	1.92	3.63		1.71	6.06	0.73
Sundaland + Wallacea	2.99	0.09	0.60		0.60	1.37	0.26
Himalaya + Sundaland	2.39	0.85	0.94		0.77	1.54	
Wide Oriental	6.19	0.64	2.05	0.26	1.32	3.07	1.07
Indo-Australian	3.28	0.38	1.02		0.60	4.01	4.27

Figure 1. Percentages of a sample of 1200 Bornean moth species falling within various habitat and geographic categories. Low = lowland forest, LMF = lower montane forest, UMF = upper montane forest. RS and S refer to higher altitude zones more or less exclusive to Gunung Kinabalu. From Holloway & Barlow (1992).

It is the effects on these more vulnerable higher taxonomic groups of logging and conversion to managed systems such as plantation that are of particular concern in the conservation of biodiversity.

3. THE EFFECTS OF FOREST DISTURBANCE AND CONVERSION

(*a*) *Moths*

There are even fewer quantified samples of moths from disturbed or managed systems in the Indo-Australian tropics than there are from natural habitats. Areas of field crops and mixed cash crop plantations have been sampled in Sulawesi (Holloway *et al.* 1990). A traditional shifting cultivation system has been surveyed in Seram (Holloway 1992; Holloway & Stork 1991). Observations in Borneo were virtually restricted to a single sample from regenerating (10 year) alluvial forest just outside the Gunung Mulu National Park (Holloway 1987) until the studies reported here were undertaken. Even these must be regarded very much as pilot observations.

(i) *Methods*

A.H. K-S. made three samples in the vicinity of the Danum Valley Field Centre (see Marsh & Greer, this symposium) in September and October 1987, by using a 125 W mercury vapour lamp as a source of illumination in front of a sheet. Collecting was from both sides of the sheet and the area immediately surrounding it. All 'macro-moths' (Cossoidea, Zygaenoidea, Bombycoidea, Noctuoidea, Geometroidea) were collected.

One sample was from within the undisturbed forest at E2 on the eastern ridge trail (Field Centre watershed area), in an area where the understorey is relatively clear and the canopy not entirely closed (five nights). Another was at the forest edge in the Centre clearing, with the trap overlooking the Sungai Palum Tambun (two nights). The third was made in an area of disturbed forest by the access road to the Centre and about 1 km from it (four nights). This area had been cleared about seven years previously, and extensive growth of vines, creepers and early stage successionals had already occurred.

C.V.K. made samples in four localities of plantation forest in Sabah during the period from May to July 1989 (Chey 1990). Three were of the legume, *Acacia mangium* Willd. and the fourth was of two species of pine.

The *Acacia* sites were at: (i) Telupid, with 9.07 hectares (ha)† planted in early 1984; the plantation had little undergrowth, mainly *Imperata cylindrica* (L.) Beauv., *Melastoma malabathricum* L., *Chromolaena odorata* (L.) R. M. King & H. Robinson and *Nephrolepis*

† 1 ha = 10^4 m^2

biserrata (Burm. 7.) Underw.; (ii) Mendolong, with 10 ha planted in late 1985; undergrowth was dense with all the above species and *Passiflora foetida* L.; and (iii) Sook, with 4.37 ha planted in May 1983 following the burning of a 1970s plantation; the undergrowth was moderate, with *I. cylindrica*, *M. malabathricum* and the ferns *Pteridium aquilinum* (L.) Kuhn and *Dicranopteris linearis* (Sw.) Schott.

The pine site was also at Sook, with the sample made on a road dividing plantations of *Pinus caribaea* Morelet (2.43 ha) and *Pinus oocarpa* Schiede (2.91 ha) planted in October 1972 and June 1973 respectively. The undergrowth was similar to that at the Sook *Acacia* site.

The Telupid and Mendolong plantations were surrounded by regenerating secondary forest, whereas that at Sook was surrounded in part by open habitat.

Collections were made over two nights at each site between 18 h 30 and 23 h 00, by using a 1.8 m square white sheet illuminated by 400 W Tungsram HGL1 bulb. All macrolepidoptera were collected except Sphingidae and Cossidae where the species are mostly highly mobile and unlikely therefore to be representative of the plantation fauna. All samples were sorted to species and identified through reference to the literature (Barlow 1982; Holloway 1983–1989; Kobes 1985) and to the collections of The Natural History Museum, London. Host-plant data for the species were collated from these sources and literature referred to therein.

The alpha statistic of Fisher *et al.* (1943) was used to calculate sample diversity for the total sample and for the two largest families: Noctuidae and Geometridae. This measure is preferred for its robustness and sample size independence (Robinson 1975; Taylor 1978; Wolda 1983; Holloway 1987; Barlow & Woiwod 1989). For similar reasons (see, for example, Holloway 1979, 1984; Holloway *et al.* 1990), the resemblance measure of Preston (1962) is preferred for comparison of samples in terms of faunal composition.

The observations from Danum can be placed within the context of a more extensive array of moth samples made in the Gunung Mulu National Park, Sarawak (Holloway 1984, 1987). These were made by using two different trapping systems. Only those samples made at lower elevations with a Robinson pattern moth trap with a mercury vapour lamp are discussed here, as they are the more comparable with the systems used in Sabah. The samples were, with two exceptions, made in undisturbed rain forest of various types. The exceptions are those from alluvial forest. One was made in what appeared to be primary forest, but local information suggested that much of the area had been farmed a century before (J. Proctor, personal communication). The other was in an area where forest had been regenerating for ten years on abandoned farmland.

(ii) *Results*

The alpha values for the complete samples are shown in figure 2. Those for the Mulu forest samples range between 230 and 320, with that from century-old alluvial forest at 280. Only the ten-year-old regenerating forest departs from this at about 130. The Danum samples all fall below the 200 level, but that from within the forest shows higher diversity than that from the forest edge, and both have significantly higher diversity than that of the sample from logged forest, which is at the level of the regenerating forest sample from the Mulu survey.

The samples from plantations at Mendolong and Telupid show diversity almost as high as that from the Danum forest edge sample, but those from Sook are lower (the *Pinus* sample was small so the 95% confidence limits are wide).

The diversity values for Noctuidae and Geometridae (figure 3) show similar, if less extreme, differences, although the values for Noctuidae from the plantations at Mendolong and Telupid are equivalent to, or higher than, those from the forest and forest edge at Danum. These plantations are located in the vicinity of secondary forest, and collation of the host-plants of the species recorded suggests that about half of them depend on plants not present in the plantation system. The samples may therefore contain a considerable component of the secondary forest fauna. This will be considered further below. It is a factor that must be assessed more rigorously in future studies.

The secondary forest sample at Danum, and to a lesser extent the forest edge sample, included very large numbers (274 and 97 respectively, compared with 18 in the understorey sample) of the ennomine geometrid *Hypochrosis binexata* Walker. Exclusion of this species leads to much higher geometrid diversity values for the edge and secondary Danum samples, although that from within the forest is little changed (open circles on figure 3). In the plantation samples the species was represented significantly only at Mendolong. With this adjustment, the plantation samples show generally lower geometrid diversity than do those from Danum. Geometridae are less mobile, and hence less influence would be expected from the secondary forest nearby.

The differences in diversity just described are accompanied by differences in faunal composition. In figure 4 the proportions of different moth families in the samples are illustrated. For consistency with the plantation samples, Sphingidae and Cossoidea are excluded, although both are more diverse in the edge and secondary Danum samples and in the Mulu alluvial samples. Macroglossine Sphingidae are generally specialists of disturbed and open habitats, and Cossidae mostly have larvae that bore in timber and hence respond to availability of dead trees and logs.

In the Mulu forest samples, including that from regenerating forest, proportions show no really significant differences. Representation of the minor groups (excluding Noctuidae, Geometridae, Arctiidae and Lymantriidae) ranges between 10% and 20%, averaging at 14%. All the Danum samples are comparable with those from Mulu. Amongst the plantation samples the range is from 5% to 7%.

In the Mendolong and Telupid samples, the proportion of Noctuidae is high and of Arctiidae and Lymantriidae low compared with the other samples, but the samples from Sook are more comparable. The

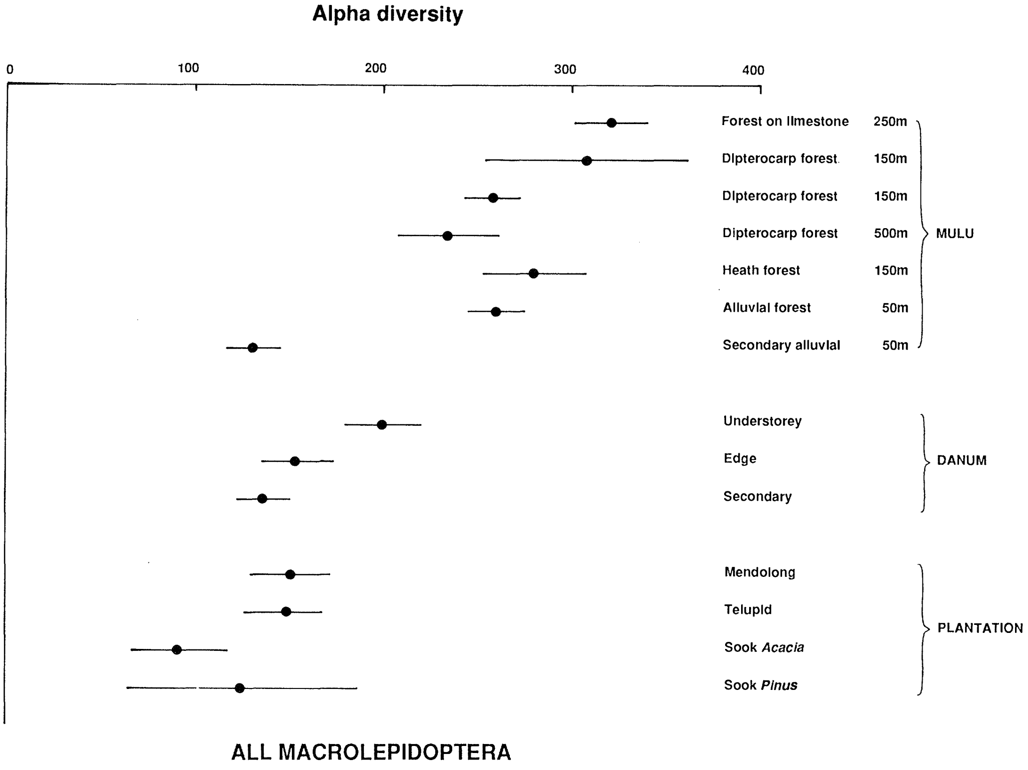

Figure 2. Alpha diversity values with 95% confidence limits (Fisher *et al.* 1943) obtained for samples of all macrolepidoptera from various Bornean forest types.

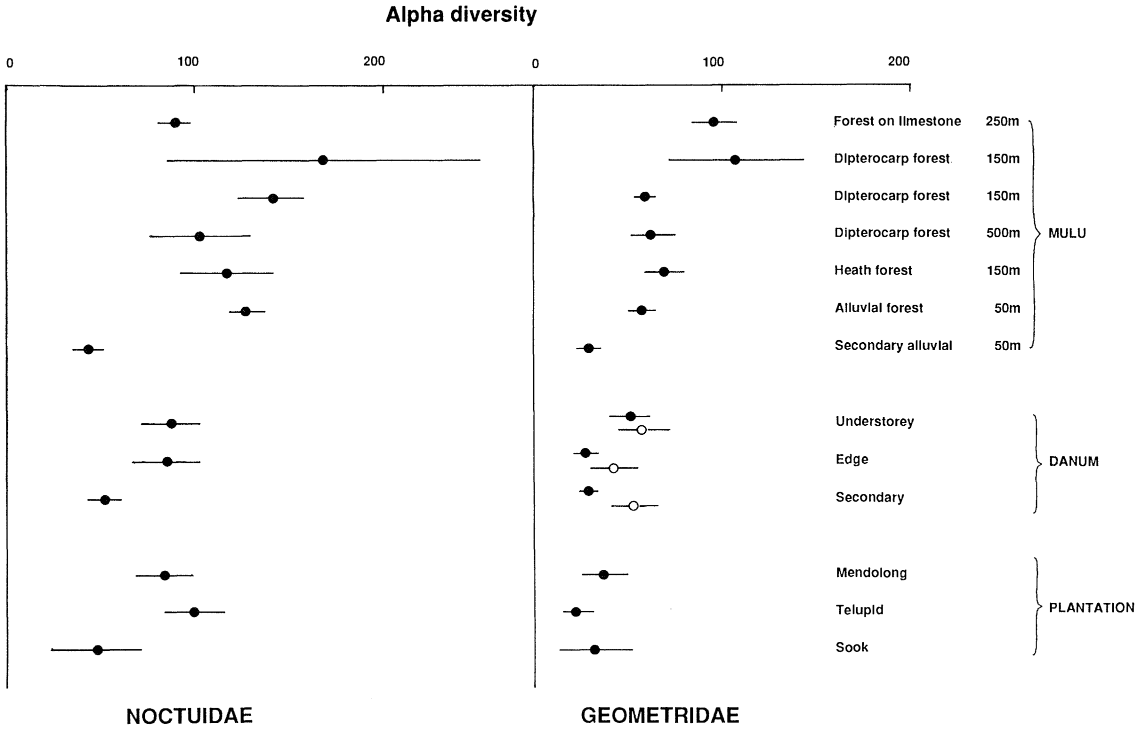

Figure 3. Alpha diversity values as for figure 2, but for samples of Noctuidae and Geometridae. The Sook plantation samples are pooled.

high diversity of Noctuidae at Mendolong and Telupid is apparent in a number of interesting sections of the family. The Stictopterinae and Euteliinae are diverse compared with their representation in the Danum samples, with eight species of each at Telupid, and 13 Stictopterinae and two Euteliinae at Mendolong. The two sections of Stictopterinae feed as larvae on Guttiferae (one section) and Euphorbiaceae and Dipterocarpaceae (the other section). The Euteliinae feed principally of Anacardiaceae, but with some

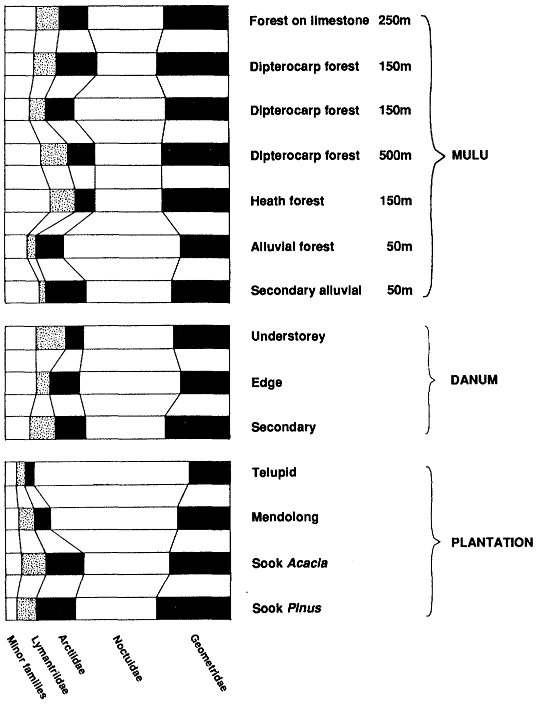

Figure 4. Proportions of different families in samples of macrolepidoptera from various Bornean forest types.

records from Burseraceae, Dipterocarpaceae and other families (Holloway 1983–1989, part 14). None of these families is represented in the plantations but may well occur in the neighbouring secondary forest (Euphorbiaceae tend to be abundant (Whitmore 1984)), hence the moths have probably flown into the plantation and augmented the intrinsic diversity. C.V.K. is currently investigating this effect on a transect from plantation into secondary forest.

The fern-feeding noctuid genus *Callopistria* is much more diverse in the Telupid (six species) and Mendolong (eight species) samples than in those from Danum or the Sook plantations. This may reflect the presence of *Nephrolepis*, a known host of the genus, in both plantations.

Species of open habitats, with herb-feeding larvae (mainly Gramineae, Compositae and Leguminosae, all represented in the plantations) (Holloway *et al.* 1990), are also most numerous at Telupid and Mendolong, such as members of the genera *Athetis*, *Chrysodeixis*, *Condica*, *Mocis* and allied genera, *Mythimna*, *Sesamia* and *Spodoptera*. These are virtually absent from the Danum samples except that from the forest edge which is, of course, adjacent to the major area of open habitat in the neighbourhood, the Field Centre clearing. This sample included three *Athetis bipuncta* and single specimens of *Chalciope mygdon*, *Condica illecta*, *Mythimna decisissima* and *Spodoptera pecten*. The legume-feeding *Mocis undata* was taken singly in the secondary forest sample.

Classifications of the three Danum and four plantation samples were derived from four data sets: for all macrolepidoptera and for three subsets, Noctuidae, Geometridae, and the remaining, minor families. Preston's resemblance equation was used to derive arrays of pairwise faunal dissimilarity values between all the samples. These were subjected to single-link cluster analysis to yield the dendrograms shown in figure 5. Linkage diagrams, showing dissimilarity values up to certain levels, are presented in figure 6.

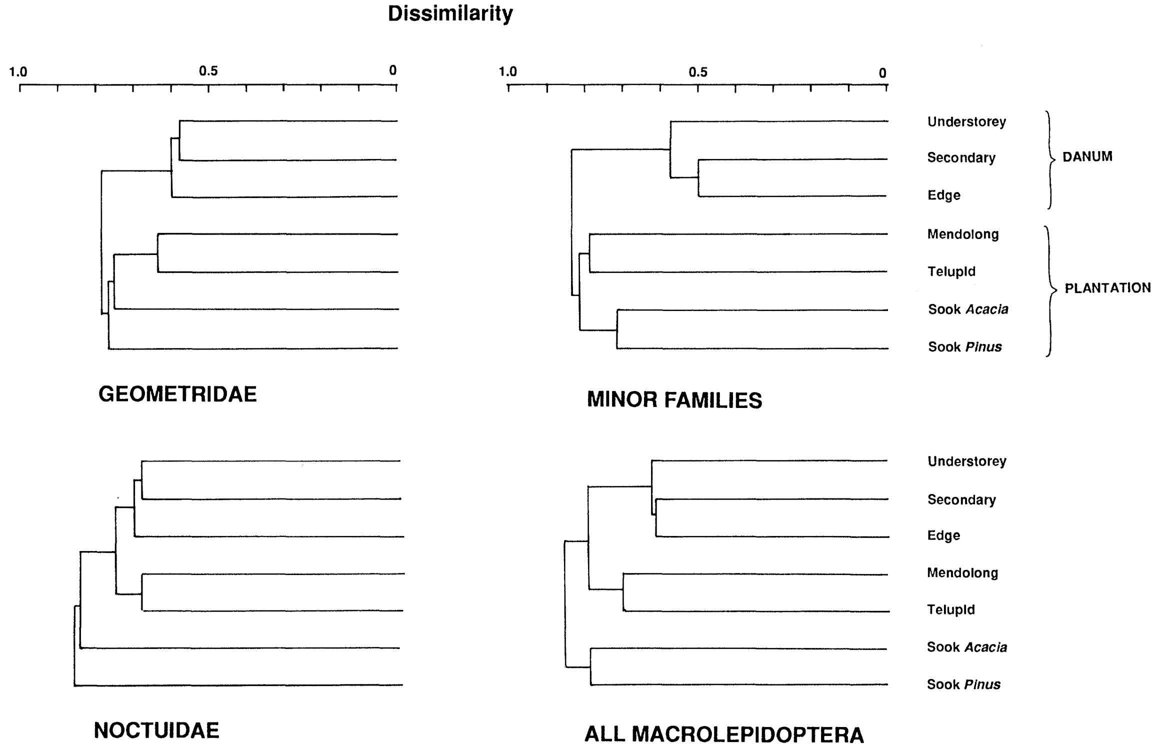

Figure 5. Dendrograms derived by single-link cluster analysis on Preston resemblance coefficients for samples of moths from various Bornean forest types.

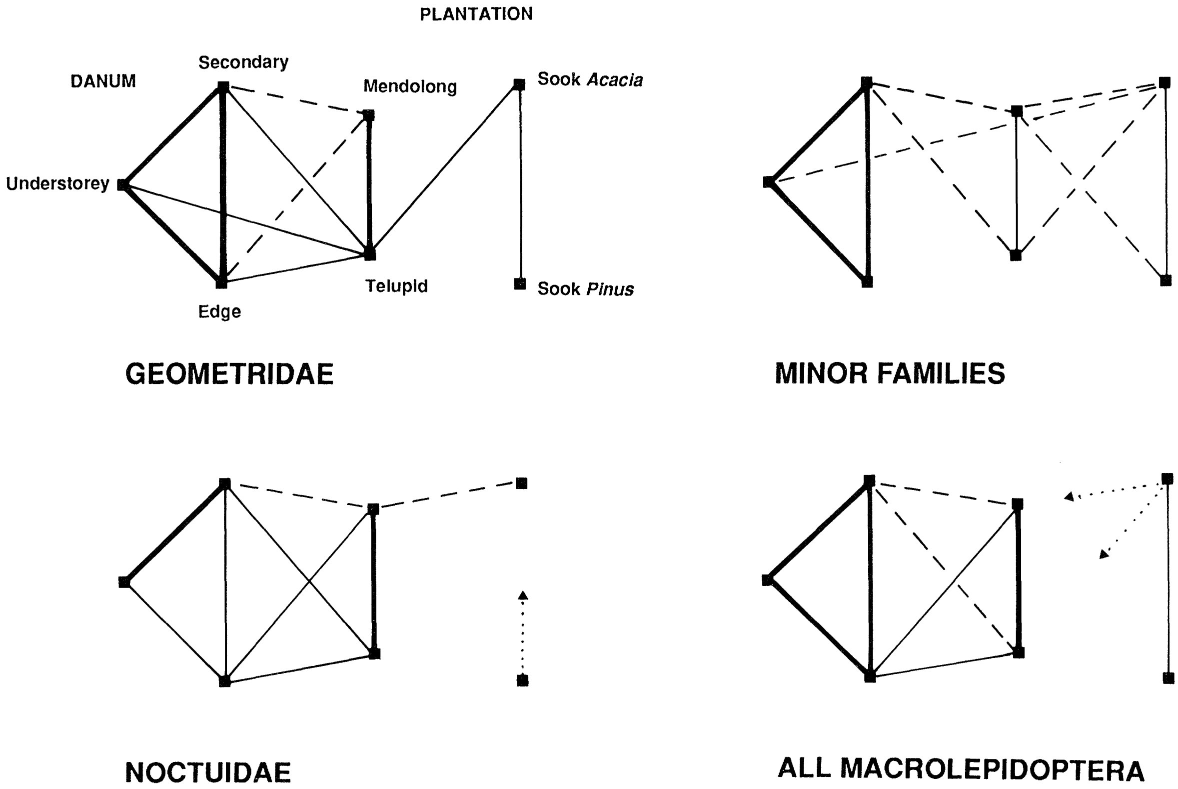

Figure 6. Linkage diagrams for the same data as in figure 5. Thick lines represent dissimilarities from 0 to 0.70, thin lines those from above 0.70 to 0.80, and broken lines those from above 0.80 to 0.85.

For all four data sets, the three Danum samples are grouped together in the cluster analysis, and the Mendolong and Telupid samples are paired. The two Sook samples are paired in the analysis for minor families and that for all macrolepidoptera. The four plantation samples are weakly grouped in the analyses for Geometridae and minor families, but the Mendolong–Telupid pair clusters with the Danum trio in the analysis for Noctuidae and all macrolepidoptera. The linkage diagrams show clearly the strong association of the Danum samples and the intermediate character of the Mendolong–Telupid pair. The contribution of the adjacent secondary forest to this intermediate character requires further investigation, but intrinsic similarities between Mendolong and Telupid are probably present also, e.g. with shared high diversity in the genus *Callopistria* mentioned above.

Chey (1990) did a similar classification for the plantation sites using data for all macrolepidoptera but segregating the two nights of samples for each site. The four Mendolong and Telupid samples were strongly grouped, and three out of four Sook samples formed a weaker group.

Apart from *Hypochrosis binexata* in the Danum samples, no species was highly abundant. Table 1 lists those species that showed strong association with the understorey sample or the secondary sample. Over half those more abundant in the secondary sample also featured strongly in the Mulu regenerating alluvial forest sample. Data on their host-plants are far from comprehensive, but feature dead wood, detritus, *Callicarpa*, *Ficus*, Compositae, Malvales, Myrtaceae and Sapindaceae. Larvae of *Creatonotos transiens* and *Tiracola plagiata* are polyphagous.

(iii) *Discussion*

The Mulu and Danum samples show clearly that there is a much lower moth diversity in the early stages of forest regeneration following clearance. This was also the case in Seram where samples were made at different stages in a shifting cultivation cycle (Holloway 1992; Holloway & Stork 1991). In all these instances, there was little change in the proportions of the different moth families.

The Seram data showed that, following clearance in the shifting cultivation cycle, a number of moth species became very abundant. These were not open habitat specialists but appeared to be forest gap specialists, mostly with arboreal feeding larvae and an intriguingly high representation of those groups noted to feed as adults from lachrymal secretions of large mammals or from carrion (Holloway 1992). These groups are not significantly represented in the list in table 1 of those species commoner in the secondary sample, although *Hypochrosis* is a genus that shows this habit generally.

As regeneration progresses in Seram, both the diversity and the faunal composition of the moth fauna progress towards the condition in pristine forest. We have no comparable data from the Bornean lowland forest, although the sequence of logging coupes at Danum over several decades offers an ideal situation from which to acquire them. We have no data on the changes in moth diversity and faunistics in

Table 1. *Moth species particularly strongly represented in the forest understorey sample or the secondary forest sample at Danum, and numbers of individuals and species in the total samples*

	understorey	forest edge	secondary
understorey			
Scopelodes albipalpalis (Limacodidae)	29	2	4
Setothosea asigna (Limacodidae)	27	2	3
Amata cinctelisa (Arctiidae)	11	1	0
Spilosoma hosei (Arctiidae)	13	2	5
Anticarsia creberrima (Noctuidae)	8	1	2
Nicevillea epiplemoides (Noctuidae)	7	0	0
Tamba dichroma (Noctuidae)	7	0	0
Tathothripa continua (Noctuidae)	10	0	1
Tanaorhinus rafflesii (Geometridae)	8	5	1
Maidania tetragonata (Geometridae)	16	0	1
secondary			
Xyleutes mineus (Cossidae)	0	0	7
Creatonotos transiens (Arctiidae)	0	5	7
Nyctemera muelleri (Arctiidae)	0	4	10
Simplicia rufa (Noctuidae)	1	29	14
Asota heliconia (Noctuidae)	2	5	12
Bocula microscala (Noctuidae)	2	6	8
Bocula tuhana (Noctuidae)	2	4	7
Carea sp. (Noctuidae)	0	0	8
Claterna cydonia (Noctuidae)	3	1	8
Episparis costistriga (Noctuidae)	1	7	28
Dipterygina vagivitta (Noctuidae)	2	7	14
Tiracola plagiata (Noctuidae)	0	0	15
Bracca georgiata (Geometridae)	3	12	23
Craspedosis arycandata (Geometridae)	1	4	7
Hypochrosis binexata (Geometridae)	18	97	274
Hypochrosis pyrrhophaeata (Geometridae)	0	7	14
total individuals	888	749	1020
total species	338	272	291

the period immediately following logging when there is an explosion of growth of pioneer species.

The pilot studies from plantation systems show that these support a much lower moth diversity, although the pattern was confused by inclusion of a component of secondary forest fauna from those plantations at Mendolong and Telupid that yielded relatively high diversity. The work in progress by C.V.K. should enable these components to be identified and segregated to yield a clearer impression of the ability of floristically impoverished plantations to support diversity in herbivorous insects.

The quality of diversity in purely secondary forests also requires analysis and comparison with those at Danum, where the selective logging process ensures that islands of primary forest persist in a matrix of regenerating forest.

The plantation forest samples saw a differential erosion of diversity in the smaller taxonomic groups, an erosion that proceeds further with conversion to open habitat, as seen in data from these systems in Sulawesi (Holloway 1987; Holloway *et al.* 1990). Ultimately the fauna of such systems becomes limited to an association of open habitat specialists of low diversity.

In open habitat associations most species are geographically very widespread, thus biogeographic diversity is also low. Many of the smaller taxonomic groups, e.g. the families in the Bombycoidea, are those identified as vulnerable through consisting of a high proportion of endemics or localized species of lowland forest. The noctuid species that we have suggested form a secondary forest component in the samples from Telupid and Mendolong are also of low biogeographic diversity, including a high proportion of widespread taxa with high ecological amplitude (Holloway & Barlow 1992), and hence are less vulnerable in conservation terms. Thus the process of logging, conversion to plantation and to simple agricultural systems, is accompanied by a loss of sample diversity in the moth fauna, of taxonomic diversity through the greater loss of more vulnerable groups, and of biogeographic diversity. It is therefore of great importance to ensure that procedures in natural logging cycles allow particularly the vulnerable groups to persist and recover. Again, a more extensive survey at Danum would enable this to be assessed.

(*b*) *Dung and carrion beetles*

The dung and carrion beetles sampled at Danum are all from the family Scarabaeidae, mostly of the subfamily Scarabaeinae but including *Phaeochroops* and *Phaeochridius* of the Hybosorinae. The larger Scarabaeinae, such as *Catharsius*, *Copris* and *Paragymnopleurus*, are mostly coprophages, but smaller ones, such as *Onthophagus* and *Phacosoma*, include both necrophages and coprophages, and the Hybosorinae are necrophages (Hanski 1987). Hanski & Cambefort (1991) have reviewed what is known of their natural history. They locate their resource by smell, and move upwind towards it. They appear to be highly competitive for the very localized resource represented by dung and carrion; once it is located, they feed from it and attempt to appropriate sufficient to enable them to breed. Hanski (1987) presented evidence to suggest that competitive exclusion is an important factor; there are indications of good ecological segregation and tight species packing. Seasonality of abundance in areas of the Indo-Australian tropics is weak (data from Sulawesi: Hanski & Krikken, 1991).

(i) *Methods*

Sampling was done by using pitfall traps baited with human dung and rotting fish. Traps were set in a transect, separated at a distance of 30 m, and emptied in most cases after four days and nights. Sets of samples were taken in undisturbed mixed dipterocarp forest in the conservation area near the Field Centre and in riparian forest facies in the nature trail area south of the Field Centre close to the Sungai Palum Tambun and S. Segama, and in similar forest types that had been selectively logged in 1981 adjacent to the Sungai Bole, 56 km west of Silam by the road to the Field Centre. The trapping data are set out in table 2. Unfortunately no comparable samples from plantations are available.

The data presented here are from three sources: Dr J. Krikken (National Museum of Natural History, Leiden), collected in 1987; Dr C. Malumphy, collected in 1986; A.H.K-S., collected in 1987. Taxonomic analysis has been by Dr J. Krikken, Dr J. A. J. M. Huijbregts and A.H.K-S.

Trap samples were pooled in four categories: primary and secondary dipterocarp, and primary and secondary riparian. Each category includes both dung and fish samples. These composite samples were assessed for diversity and for faunistic composition.

Hanski (1983) found that similar samples from Sarawak had relatively even distribution of abundance amongst the species compared with the log-series distribution, hence application of the alpha statistic of Fisher *et al.* (1943), based on the log-series, may not be entirely appropriate. Therefore rank/log. abundance plots for the four samples are also presented. The sample sizes (585–2229) and species numbers (31–41) here are very similar to those of Hanski (1983, 1987).

The sample sizes are of the same order as those for the Danum moth samples, but the species numbers involved are almost an order of magnitude less, with 20 species out of 56 occurring in all four samples. Therefore, as well as classifying the samples on presence or absence of species (binary data) using the Preston resemblance measure, further classifications were obtained using the fully quantified data with application of the Morisita index (Wolda 1981).

(ii) *Results*

Full data on the composition of the four samples are available from A.H. K-S. Two species of *Paragymnopleurus*, *P. striatus* and *P. maurus*, are excluded as they are easily confused, and it was not possible to achieve reliable segregation in all of the samples: they were field-counted as one in some of the samples that were later pooled. Including these, the total species taken was 58. So far over 80 species have been recorded from the Danum area as a whole, out of a current Bornean total (Hanski & Krikken 1991) of 120 species (which includes a montane component). Hanski & Cambefort (1991, p. 355) suggested there may be an upper limit of around 60 for locally co-occurring species, but the intensity of sampling at Danum has yielded a higher total.

Table 3 illustrates, for the samples under analysis, a number of clear instances of habitat preference: *Caccobius unicornis*, *Microcopris reflexus*, *Onthophagus mulleri*, *O. obscurior*, *O.* species (f) and *O.* species (j) favour riparian forest, although the last is known only from secondary riparian; *Copris agnus*, *Onthophagus ochromerus* (also in lower montane forest), *O. waterstradti* and *O. sarawacus* favour primary dipterocarp but *O. deliensis*, a fruit-feeding specialist (A. H. Kirk-Spriggs, unpublished data), and *O. pastillatus* prefer secondary dipterocarp, although the latter had also been found in lower montane forest up to 1030 m on Gunung

Table 2. *Pitfall trapping conducted in primary and secondary forest at the Danum Valley Field Centre and the Sungai Bole*

forest	altitude/m	dates of trapping	number of traps	number of trapping sites	trap nights	type of bait
secondary riparian	100–200	27.7–30.7	4	1	16	dung
secondary riparian	100–200	27.7–30.7	8	1	32	fish
primary riparian	100–200	18.7–21.7	4	1	16	dung
primary riparian	100–200 100	18.7–21.7 28.9–30.9	8	2	22	fish
secondary dipterocarp	100–200	19.1–23.1	8	1	40	dung
secondary dipterocarp	100–200	19.1–23.1	8	1	40	fish
primary dipterocarp	200–220	13.9–15.9	8	1	24	dung
primary dipterocarp	100–200	10.7–13.7	8	1	32	fish
totals			56		222	

Table 3. *Sample data for beetles that are important dominants or show clear habitat preference, together with numbers of species and individuals in the total samples*

	primary dipterocarp	primary riparian	secondary dipterocarp	secondary riparian
Caccobius unicornis	0	54	0	12
Microcopris reflexus	3	51	2	54
Onthophagus mulleri	5	39	10	69
Onthophagus obscurior	2	24	1	89
Onthophagus sp. (f)	0	10	0	5
Onthophagus sp. (j)	0	0	0	15
Copris agnus	18	0	0	0
Onthophagus ochromerus	10	0	1	0
Onthophagus waterstradti	31	0	2	3
Onthophagus sarawacus	42	1	0	0
Onthophagus deliensis	0	7	155	5
Onthophagus pastillatus	0	6	15	0
Catharsius molossus	29	73	1	0
Copris ramosiceps	29	73	1	0
Copris sinicus	13	6	1	3
Onthophagus dux	38	10	0	0
Paragymnopleurus sparsus	47	344	14	7
Sisyphus thoracicus	112	1122	71	75
Phaeochroops gilleti	39	50	23	1
total individuals	589	2229	585	605
total species	35	41	41	31

Danum (unpublished data); primary forest of either type is preferred by *Catharsius molossus*, *Copris ramosiceps*, *Copris sinicus*, *Onthophagus dux* and probably *Paragymnopleurus sparsus*. The letters for undescribed species do not correspond with those in Hanski (1983). The segregation of species between dipterocarp and riparian forest at Danum is reflected in Hanski's data from Sarawak, particularly for the riparian species in comparison with the alluvial forest fauna in Sarawak (I. Hanski, personal communication).

The alpha statistic (figure 7) shows little difference between the four samples. The rank/log. abundance plots (figure 8) are also very similar, but with indications of greater dominance in the primary riparian sample, *Sisyphus thoracicus* and *Paragymnopleurus sparsus* being the two most abundant species, as they are in the primary dipterocarp sample also (see table 3). Hanski (1987) referred to *Phaeochroops gilleti* as super-dominant in Sarawak alluvial and limestone forests, but in the Danum samples it is only moderately common (ranked 4 in primary dipterocarp and 10 in primary riparian).

The large number of species represented by one or two individuals in the secondary dipterocarp sample is no doubt a significant factor behind its high diversity. The shape of the rank/abundance plots is not the typical truncated sigmoid expected for a partial log-normal distribution. Indeed, the clumping of points in the secondary riparian sample and, to a lesser extent, in the secondary dipterocarp and primary riparian samples, is suggestive of the bimodality mentioned by Hanski (1987) for samples of saprophagous Staphylinidae from Sarawak, and by Hanski & Krikken (1991) for dung and carrion beetles in Borneo and Sulawesi.

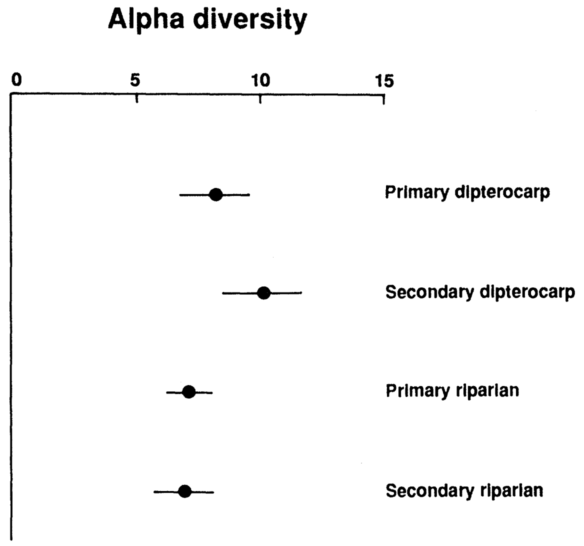

Figure 7. Alpha diversity values with 95% confidence limits (Fisher *et al.* 1943) obtained for samples of dung and carrion beetles from primary and secondary forest types at Danum.

Analysis of faunal similarities amongst the four samples by using the measure of Preston (figure 9:

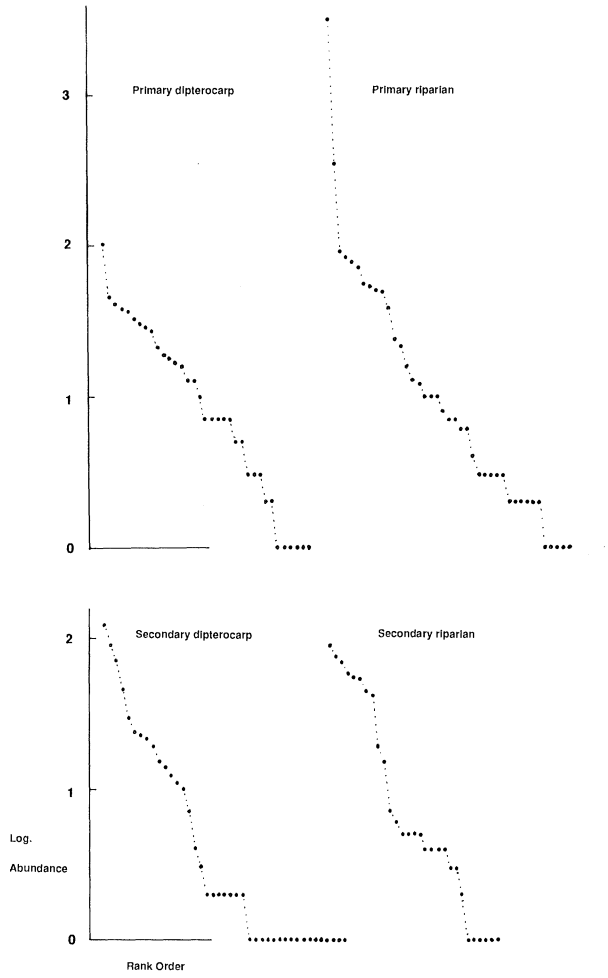

Figure 8. Rank/log. abundance plots for the same samples as in figure 7.

top) shows no strong segregation on grounds of either forest type or successional stage. The coefficients range between 0.287 and 0.395, whereas for the Danum moth data the lowest was in the region of 0.5, and the highest 0.739. Application of cluster analysis to Morisita coefficients for the full quantitative data (figure 9: bottom) reveals strong association of the primary forest samples. The strong dominance of *Sisyphus thoracicus* and *Paragymnopleurus sparsus* (ranked 1 and 2 in each case) together with moderate to strong representation of four other species favouring primary forest (see above) are major contributory factors. The secondary forest samples are much more dissimilar to each other and to the primary forest samples.

(iii) Discussion

The beetle data show far greater faunistic uniformity between primary and secondary forest types than is evident for moths, and no significant decline in alpha diversity that could be attributed to logging, although again the effects immediately following logging disturbance and in the first years of regeneration have yet to be measured. It could be said on the basis of these results that the effects of logging on dung and carrion beetle diversity are much more transient than the effects on moth diversity.

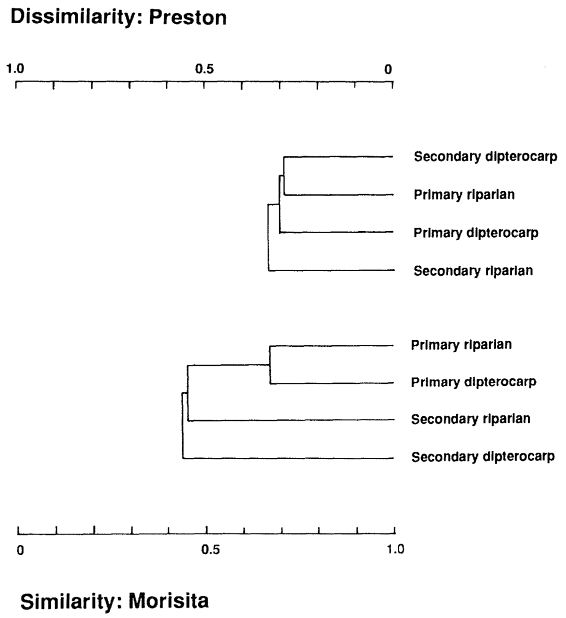

Figure 9. Dendrograms derived by single-link cluster analysis on Preston resemblance coefficients and Morisita coefficients for the four samples of dung and carrion beetles from Danum.

The rank/abundance curves and examination of the relative abundances of species in the samples suggest that differences between them, although smaller than for the moth samples, are nevertheless present, and both subtle and complex. Sample size did not permit assessment of any segregation on bait type, but this should be addressed in any future more extensive study.

The results are similar to those obtained by Nummelin & Hanski (1989) from the Kibale Forest in Uganda where the dung beetle faunas of virgin and selectively felled moist evergreen forest and 20 year conifer (*Pinus*, *Cupressus*) plantation at 1500 m were compared. No major differences were found in numbers of individuals and species in the first two forest types, but species richness was substantially reduced in the plantation forest (although total abundance was not).

4. CONCLUSIONS

These pilot samples show that the impact of logging and forest disturbance on the diversity of a major plant-feeding insect group is measurable and significant. Further changes occur on conversion to plantation. Effects on insects exploiting a more uniform resource base, such as dung or carrion, are much smaller, and will require a carefully controlled and more extensive programme of sampling to elucidate them. In both instances the systems appear to have spatial and temporal patterns that the few snapshots we have presented only begin to reveal.

Natural forest, logged forest and areas of plantation present a complex mosaic of habitats: successional phases, and physiography, including river corridors, are major features of forest undisturbed by man that may contribute to heterogeneity in the distribution of night-flying moths. In logged forest the proportions of these features are drastically changed and may only over decades or centuries converge on the previous natural state. In the natural forest, islands of regeneration, the gaps, occur in a matrix of maturing or mature forest. In logged forest such as at Danum, islands of relatively undisturbed forest occur in a matrix of regenerating vegetation. Plantations are often adjacent to other habitats: secondary forest, open wasteland or agricultural systems.

Both sampling methods rely on a bait, such as a light or a morsel of dung or carrion, the introduction of which will disturb to a degree the natural pattern of distribution of the target associations of species. Therefore, much care is needed to devise sampling programmes that will reveal natural pattern in forest ecosystems and assess seasonal patterns of abundance that occur even in continuously humid tropical areas.

The seven moth samples were relatively strategically sited: forest understorey, an edge between forest and a major clearing at a river corridor, a locality where major disturbance had occurred in the relatively recent past, plantations adjacent to secondary forest, and plantations adjacent to open wasteland. But the results show the need for a much greater array of samples to obtain a finer focus on the effects of habitat mosaics and of successional effects through a logging operation. The analyses here have been restricted to classification of samples (Q-mode), but a greater array of these will permit will permit associations of species with similar distributions amongst the samples to be recognized (R-mode classification) and correlated with different habitat types as indicators.

Such R-mode analyses would also be valuable applied to a greater spatial and temporal spread of beetle samples, including samples made sequentially through a logging operation. The rather atypical rank/abundance curves discussed here may arise through the co-occurrence in any one sample of two more or less ecologically independent associations of species, each of which has an intrinsically log-normal distribution of abundance. Patterns of interspecific aggregation in dung and carrion beetles are discussed in Hanski & Cambefort (1991).

Although dung and carrion beetle diversity at Danum is comparable with that recorded in the Gunung Mulu area of Sarawak by Hanski (1983), moth diversity in undisturbed forest appears to be very much lower (the understorey and edge samples in figures 2 and 3). Further sampling is needed from the Danum forest to test this observation for consistency, and to place the moth fauna supported at Danum within a wider Bornean context.

The moth data do support the trend of observations made previously: extensive forest disturbance reduces moth diversity; conversion to plantation and field crop systems leads to further reductions that may mostly be irreversible. The reduction of diversity is both in species richness and in taxonomic and biogeographic quality. Data from shifting cultivation systems in Seram suggest that the effects of forest disturbance on diversity can be reversible over time even when severe, a point supported by data from alluvial forest samples near Gunung Mulu and by data from Peninsular Malaysia (Holloway & Barlow 1992), provided sufficient fragments of untouched forest remain as reservoirs for recolonization. The environs of Danum provide ideal, almost experimental, conditions for studying this. For insects, the work has barely begun.

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REFERENCES

Barlow, H.S. 1982 *An introduction to the moths of South East Asia*. Kuala Lumpur: published by the author.

Barlow, H.S. & Woiwod, I.P. 1989 Moth diversity of a tropical forest in Peninsular Malaysia. *J. trop. Ecol.* **5**, 37–50.

Chey, V.K. 1990 A Study of the Moth Species found in Plantation Forests in Sabah. (87 pages.) Unpublished dissertation, Postgraduate Diploma in Applied Insect Taxonomy, University of Wales, Cardiff.

Fisher, R.A., Corbet, A.S. & Williams, C.B. 1943 The relation between the number of species and the number of individuals in a random sample of an animal population. *J. anim. Ecol.* **12**, 42–58.

Hanski, I. 1983 Distributional ecology and abundance of dung and carrion-feeding beetles (Scarabaeidae) in tropical rain forest in Sarawak, Borneo. *Acta zool. fenn.* **167**, 1–45.

Hanski, I. 1987 Dung beetles. In *Tropical rain forest ecosystems, biogeographical and ecological studies* (ed. H. Lieth & M. J. A. Werger) *Ecosystems of the World*, **14B**, 489–511.

Hanski, I. & Cambefort, Y. 1991 *Dung beetle ecology*. Princeton University Press.

Hanski, I. & Krikken, J. 1991 Dung beetles in tropical forests in South-east Asia. In *Dung beetle ecology* (ed. I. Hanski & Y. Cambefort), pp. 179–197. Princeton University Press.

Hebert, P.D.N. 1980 Moth communities in montane Papua New Guinea. *J. anim. Ecol.* **49**, 593–602.

Holloway, J.D. 1979 *A Survey of the Lepidoptera, biogeography and ecology of New Caledonia. Series Entomologica* 15. The Hague: W. Junk.

Holloway, J.D. 1983–1989 *The moths of Borneo*. Part 4 (1983) Notodontidae, *Malay. Nat. J.* **37**, 1–107. Part 14 (1985) Noctuidae (part), *Malay. Nat. J.* **38**, 157–317. Part 1 (1986), Key to families, Cossidae, Limacodidae etc., *Malay. Nat. J.* **40**, 1–166. Part 3 (1987), *Bombycoidea*. Kuala Lumpur: Southdene. Part 6 (1988), *Arctiidae* (part). Kuala Lumpur: Southdene. Part 12 (1989) Noctuidae (part), *Malay. Nat. J.* **42**, 57–226.

Holloway, J.D. 1984 The larger moths of Gunung Mulu National Park. In *Gunung Mulu National Park, Sarawak,* *Part 2* (ed. A. C. Jermy & K. P. Kavanagh), pp. 149–190. *Sarawak Mus. J.* **30**, Special Issue 2.

Holloway, J.D. 1987 Macrolepidoptera diversity in the Indo-Australian tropics: geographic biotopic and taxonomic variations. *Biol. J. Linn. Soc.* **30**, 325–341.

Holloway, J.D. 1992 Aspects of the biogeography and ecology of the Seram moth fauna. In *The natural history of Seram* (ed. J. Proctor & I. Edwards). (In the press.)

Holloway, J.D., Robinson, G.S. & Tuck, K.R. 1990 Zonation in the Lepidoptera of northern Sulawesi. *Insects and the rain forests of South-east Asia (Wallacea)* (ed. W. J. Knight & J. D. Holloway), pp. 153–166. London: Royal Entomological Society.

Holloway, J.D. & Stork, N.E. 1991 The dimensions of biodiversity: the use of invertebrates as indicators of man's impact. In *The biodiversity of microorganisms and invertebrates: its role in sustainable agriculture* (ed. D. L. Hawksworth). pp. 137–162. Wallingford: CAB International.

Holloway, J.D. & Barlow, H.S. 1992 Potential for loss of biodiversity in Malaysia, illustrated by the moth fauna. In *Pest management and the environment in 2000* (ed. H. S. Barlow & A. Aziz Kadir). CAB International and Agricultural Institute of Malaysia. (In the press.)

Knight, W.J. & Holloway, J.D. (ed.) 1990 *Insects and the rain forests of South-east Asia (Wallacea)*. (343 pages.) London: Royal Entomological Society.

Kobes, L.W.R. 1985 The Thyatiridae, Agaristidae, and Noctuidae (part 1: Pantheinae and Catocalinae) of Sumatra. *Heterocera Sumatrana*, **4**.

Nummelin, M. & Hanski, I. 1989 Dung beetles of the Kibale Forest, Uganda; comparison between virgin and managed forests. *J. trop. Ecol.* **5**, 349–352.

Preston, F.W. 1962 The canonical distribution of commonness and rarity. *Ecology* **43**, 185–215, 410–432.

Robinson, G.S. 1975 *Macrolepidoptera of Fiji and Rotuma, a taxonomic and geographic study*. Faringdon: E. W. Classey.

Taylor, L.R. 1978 Bates, Williams, Hutchinson – a variety of diversities. In *Diversity of insect faunas* (ed. L. A. Mound & N. Waloff). *Symp. R. ent. Soc. Lond.* **9**, 1–180.

Whitmore, T.C. 1984 *Tropical rain forests of the Far East*, 2nd edn. Oxford University Press.

Wolda, H. 1981 Similarity indices, sample size and diversity. *Oecologia, Berl.* **50**, 296–302.

Wolda, H. 1983 Diversity, diversity indices and tropical cockroaches. *Oecologia, Berl.* **58**, 290–298.