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Ecology of butterflies in natural and selectively logged forests of northern Borneo: the importance of habitat heterogeneity

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Summary

1. The impacts of habitat disturbance on biodiversity within tropical forests are an area of current concern but are poorly understood and difficult to predict. This is due in part to a poor understanding of how species respond to natural variation in environmental conditions within primary forest and how these conditions alter following anthropogenic disturbance. Within this context, the main aim of this study was to test the hypothesis that the gap and shade preferences of fruit-feeding butterflies in primary forest in northern Borneo can be used to predict species' responses to selective logging and thus explain changes in diversity and geographical distinctness in relation to habitat disturbance.

2. Overall, there was little difference in butterfly diversity between primary forest and forest that had been selectively logged 10–12 years previously. In contrast, there were marked differences in the composition of the butterfly assemblages in the two habitats, which were strongly associated with species' gap preferences and geographical distributions. In Satyrinae and Morphinae, those species with higher shade preferences and narrower geographical distributions were most adversely affected by logging, whereas cosmopolitan species with high light preferences benefited from logging. In Nymphalinae and Charaxinae the opposite was observed: those species with wider geographical distributions were adversely affected and those species with relatively restricted distributions were more common in logged forest.

3. These changes in butterfly assemblages were associated with changes in vegetation structure following selective logging, which resulted in much lower habitat heterogeneity with less dense shade and fewer open gaps in logged forest. Areas of dense shade, which were more common in unlogged forest, supported species of Satyrinae and Morphinae with restricted geographical distributions, whereas open gaps, which were also more common in unlogged forest, attracted widespread species of Nymphalinae and Charaxinae. These butterfly–habitat associations in primary forest explain the opposite responses of the two groups of butterflies to selective logging.

4. *Synthesis and applications.* This study highlights the need to sample at a sufficiently large spatial scale to account for impacts of disturbance on heterogeneity in forest environments. It also demonstrates how understanding the responses of species to natural variation in environmental conditions within undisturbed forest is crucial to interpreting responses of species to anthropogenic habitat modification. The results further indicate that selectively logged forests can make an important contribution to the conservation of tropical biodiversity, provided that they are managed in a way that maintains environmental heterogeneity.

Key-words: biodiversity, lepidoptera, Nymphalidae, rainforest, Sabah, selective logging.

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Introduction

Tropical rainforests are well known as centres of biodiversity (Wallace 1878; Richards 1952) and much interest has focused on the ecological processes responsible for generating and maintaining this diversity, with recent authors emphasizing the importance of natural disturbance and non-equilibrium dynamics, coupled with variations across environmental gradients generated by topographic and edaphic landscape features within forest (Huston 1994; Rosenzweig 1995; Hill *et al.* 2001). One of the major environmental gradients in tropical forests is the amount of light below the canopy, and this varies in relation to topographic features (e.g. from river edge to forest interior), from ground to canopy and in relation to gap dynamics. Gaps are formed by tree falls, and tropical forests naturally exist as dynamic mosaics of canopy gaps, areas of regeneration and mature forest with dense canopy cover (Whitmore 1991; Grieser Johns 1997). The potential role of light in determining plant assemblage structure and diversity has received much attention (Denslow 1987; Brokow & Busing 2000) but there have been few comparable studies of insects within undisturbed tropical forests: most studies have investigated changes in insect assemblages in relation to broad differences in light, such as gaps vs. dense shade (Spitzer *et al.* 1997; Feener & Schupp 1998), forest edge vs. interior (Brown & Hutchings 1997) and ground vs. canopy (DeVries, Walla & Greeney 1999; Hill *et al.* 2001), and few have considered impacts of finer-scale changes in light on species distribution along natural environmental gradients. Here we suggest that examining these relationships in primary forest will be an important prerequisite for understanding processes causing changes in distribution and diversity following anthropogenic disturbance (Kremen 1992; Davis *et al.* 2001).

Measures of local diversity are widely used to characterize species assemblages, but they give no information on species composition or conservation value (Hill *et al.* 1995; Lewis 2001). For example, canopy species and species found in forest gaps are generally mobile, opportunistic species with wide geographical distributions (Thomas 1991; Spitzer *et al.* 1997; Hill *et al.* 2001). Such species generally have low conservation value (Vane-Wright, Humphries & Williams 1991). Thus, understanding the relationship between shade preferences and geographical distributions of individual species is likely to be important for predicting impacts of anthropogenic forest disturbance on geographical distinctness and hence conservation value, but few studies have examined this relationship for species in undisturbed tropical forests.

Global diversity is currently estimated to be about 10 million species, of which > 60% of species are insects (Speight, Hunter & Watt 1999; Ødegaard 2000; Novotny *et al.* 2002). Responses of insects to anthropogenic disturbance of tropical forests are thus an area of current concern, but these responses are poorly understood and no clear consensus has emerged (for a recent review of Lepidoptera see Hamer & Hill 2000; Willott *et al.* 2000; Lewis 2001). This lack of consensus is due in part to differences in the spatial scale at which studies were carried out (Hamer & Hill 2000) and is compounded by a poor understanding of how species respond to natural variation in environmental conditions within primary forest and how these conditions alter following anthropogenic disturbance. For example, tropical butterflies differ in body morphology and habitat associations partly in relation to phylogeny. In butterflies, adult morphology has been related to flight ability (Chai & Srygley 1990; Dudley 1990; Srygley & Chai 1990; Hall & Willmott 2000). Within the Nymphalidae, members of the subfamilies Satyrinae and Morphinae have relatively broad wings, favouring slow agile flight, and are often encountered beneath the canopy in dense forest (Holloway 1984; Schulze & Fiedler 1998). In contrast, species in the subfamilies Nymphalinae and Charaxinae tend to have large, broad thoraces favouring rapid powerful flight, and are often encountered in more open areas (Hill *et al.* 2001; Schulze, Linsenmair & Fiedler 2001). Based on these and other morphological characters, the Satyrinae and Morphinae are regarded as being very closely related, forming a single clade, with the Nymphalinae and Charaxinae forming a separate grouping (along with the mainly neotropical Heliconiinae and Calinaginae) within the Nymphalidae (Ackery 1984; Parsons 1999). Species of Satyrinae and Morphinae might thus be expected to differ from species of Nymphalinae and Charaxinae in their responses to changes in the light regime within the forest, but this has not previously been examined.

Within south-east Asia the greatest impact of logging is on forests in the Malay archipelago, particularly the island of Borneo. Forests on Borneo are among the tallest tropical rainforests in the world (emergents can reach > 80 m in height) and are dominated numerically by tree species in the family Dipterocarpaceae. These are important timber species, and timber extraction rates on Borneo are among the highest globally (> 100 $m^3 h^{-1}$ in some cases; Collins, Sayer & Whitmore 1991). In the Malaysian state of Sabah (northern Borneo), most remaining forest is reserved as production forest and designated to be selectively logged at regular intervals of 30–60 years (Whitmore 1991). By the end of 2010, all remaining forest that is not within conservation areas is likely to have been selectively logged at least once, and there is increasing pressure on remaining areas of forest as timber resources run out. Borneo has a very rich flora and fauna (e.g. 265 of the 386 species of Dipterocarpaceae in the region of Malesia occur there; Newman, Burgess & Whitmore 1998) and butterfly assemblages on Borneo are diverse (*c.* 1000 species; Otsuka 1988), with many endemic species dependent on closed-canopy forest (Collins & Morris 1985; Sutton & Collins 1991). Changes in forest structure resulting from selective logging may thus be a particular threat to butterflies on Borneo.

In this study we tested the hypothesis that diversity of butterflies in primary forest is related to vegetation structure and canopy openness, and that this relationship differs between butterfly taxa in relation to phylogenetic differences in shade preferences. We examined how selective logging affects vegetation structure and tested the hypothesis that species' associations with light in primary forest can be used to predict responses to selective logging and thus explain changes in diversity and geographical distinctness in relation to habitat disturbance.

Materials and methods

STUDY SITE

Fieldwork took place within the Danum Valley Conservation Area (DVCA) and the Ulu Segama Forest Reserve, Sabah (5°N, 117°50′E; details of sites in Marsh & Greer 1992). The DVCA covers approximately 428 km^2 of unlogged lowland evergreen rainforest and is surrounded by extensive areas of production forest, most of which have been selectively logged. During the 1980s logging methods in the study area followed a modified uniform system (Whitmore 1984) in which all commercial stems $> 0{\cdot}6$ m diameter were removed using high lead cable and tractor extraction methods. Temperature (annual mean = 26·7 °C) and rainfall (annual mean = 2669 mm year^{-1}) at the study area are typical of the moist tropics (Walsh & Newbery 1999).

TRAPS

It is difficult to identify butterflies reliably when they are in flight in species-rich areas such as Borneo (Walpole & Sheldon 1999) and so we focused on the guild of fruit-feeding nymphalid butterflies that can be caught in traps baited with rotting fruit (this guild comprises approximately 75% of all nymphalid butterflies recorded on Borneo; Hill *et al.* 2001). In this study we used traps baited with rotting banana (for details of trap design see DeVries 1987; Daily & Ehrlich 1995). Two fresh bananas were placed in each trap on the day prior to the first sampling day, and were left in the trap for the rest of the sampling period; a fresh piece of banana was then added to each trap every second day. This ensured that all traps contained a mixture of fresh to well-rotted bait. During each sampling period traps were emptied daily, and all trapped butterflies were identified (following Otsuka 1988), marked with a felt-tipped pen and released. Individuals of the genera *Euthalia* and *Tanaecia* cannot be identified reliably in the field and were collected and identified in the laboratory using keys and figures in Corbert & Pendlebury 1992) and Otsuka (1988); where necessary, this included dissection of male genitalia.

MODES OF DATA ANALYSIS

Data collected in faunal surveys can be analysed in two complementary ways (Ribera *et al.* 2001; Davis *et al.* 2001): individual samples can be classified in terms of their faunal composition, for instance to compare species diversity among samples (Q-mode analysis), and individual species can be analysed according to their representation across samples, for instance to derive indices of association with particular environmental variables (R-mode analysis). Q-mode analysis has been used frequently to examine impacts of disturbance on species diversity in tropical forests, but few studies have used R-mode analysis to examine how individual species respond to environmental perturbation (Shahabuddin & Terborgh 1999; Davis *et al.* 2001; Hill *et al.* 2003). Given the contradictory results obtained from Q-mode analysis (Hamer & Hill 2000), R-mode analysis may provide an important tool for elucidating species' responses to disturbance. In this study we first used R-mode analysis to examine the light preferences of individual species in primary forest, and to relate these to species' geographical distributions and to responses of species to selective logging. We then used Q-mode analysis to examine the relationship between species diversity and vegetation structure in primary and logged forest. For R-mode analysis, we selected sites that differed markedly in terms of light regime; for Q-mode analysis, we selected sites that were, as far as possible, representative of the full range of forest structure and architecture within primary and logged forest.

R-MODE ANALYSIS

To examine light preferences of individual species in primary forest, traps were placed in forest gaps ($n = 12$ gaps) and under dense intact canopy ($n = 12$ shade locations) and hung 1–2 m from the ground. The forest gaps were formed by natural tree falls, were at least 10 × 10 m in size and received full sun at midday. Average canopy openness (measured using a spherical densiometer; Lemmon 1957) was 18% in gaps compared with < 1% in shade sites. We sampled butterflies in gaps and shade sites over four periods: 5 September–2 October 1998, 6 March–19 April 1999, 25 March–19 April 2000 and 18 December 2001–4 January 2002 (85 days in total). For each species, we calculated the proportion of individuals recorded in shade traps to indicate shade preference (value of 1 for species only in shade, value of 0 for species only in gaps). To reduce sampling error, we included only species where the total number of individuals sampled was ≥ 5 (this was more conservative than Davis *et al.* 2001 and Ribera *et al.* 2001, who each considered that $n \geq 2$ was sufficient for inclusion).

To examine impacts of selective logging on individual species of butterfly, we hung 80 traps at 100-m intervals along 8 km of transects in primary forest and forest selectively logged 10–12 years previously (40 traps in each habitat). Logged and unlogged forest were at similar altitudes within the same river catchment, and the maximum distance between traps in unlogged and logged forest was < 10 km. Thus there was likely to have been little β-diversity between habitats prior to logging. Transects were set up along straight lines on cardinal compass directions (N–S and E–W) irrespective of topography. We thus sampled a representative range of variation in forest structure within each habitat. In logged areas we avoided logging roads, which we considered to be non-forest habitats, but we included skid trails (formed by bulldozers pulling out logs) where transects crossed them. We sampled butterflies in primary and logged forest for 12 days per month for 12 months (October 1999–September 2000 inclusive) and we used the proportion of individuals of each species recorded in logged forest to indicate responses to logging (a value of 0 indicated species recorded only in unlogged forest and thus most adversely affected by logging; a value of 1 indicated species recorded only in logged forest, which were considered to have benefited most from logging). To ensure comparability of data sets, we included only those species that were included in the analysis of data from gap and shade traps ($n \geq 5$ in each case).

In order to relate light preferences and impacts of logging to species' geographical distributions, all species sampled in traps were ranked according to their geographical distribution using data from Tsukada (1982). The endemic species, *Mycalesis kina*, was assigned the highest rank (rank = 1) and the most widespread species, *Melanitis leda* (which occurs in the Oriental, African and Australasian regions), had the lowest rank (rank = 66). Species ranked 2–22 had distributions within Sundaland (Borneo, Sumatra, Java, West Malaysia and Palawan) and species ranked lower than 22 additionally occurred in other parts of the Oriental and/or Australasian regions (Appendix 1).

Q-MODE ANALYSIS

In order to relate the diversity of butterfly species to the habitat characteristics of the forest in which they occurred, we first examined the relationship between butterfly diversity and vegetation structure within primary forest, and we then compared diversity and vegetation structure between habitats.

VEGETATION STRUCTURE

In order to characterize the structure of the vegetation in primary and logged forest, the following data were recorded at each of the 80 sampling stations where traps were placed along transects: height, circumference at breast height, distance from station and identity (family Dipterocarpaceae or other) of the two nearest trees (circumference > 0·6 m) and saplings (circumference 0·1–0·6 m) in each of four quadrants centred at the station (eight trees plus eight saplings per station in total); height to the point of inversion (site of first major branch; Torquebiau 1986) of the two nearest trees in each quadrant; estimated vegetation cover (%) at ground, low (2 m above ground), understorey and canopy levels. Trees were identified with the assistance of staff from the Forest Research Centre, Sabah, using diagnostic features in Meijer & Wood (1964) and Newman, Burgess & Whitmore (1996, 1998). Girths were measured to the nearest 1 cm and distances to the nearest 10 cm with a tape measure. Tree and branch heights, to the nearest 2 m, were recorded as the means of at least four independent estimates taken by experienced recorders (Hill *et al*. 1995; Hamer *et al*. 1997) and calibrated against actual heights of a sample of trees measured using a clinometer. Vegetation covers, to the nearest 5%, were recorded as the means of at least four independent estimates; these varied among recorders by no more than 10%.

Table 1. Diversity of butterflies in primary and logged forest in northern Borneo in 1999–2000. Means in bold are significantly different at $P < 0.05$

	Nymphalinae and Charaxinae		Satyrinae and Morphinae	
	Mean	SE	Mean	SE
Simpson				
Primary	**6·25**	0·64	6·91	0·44
Logged	**5·22**	0·61	6·69	0·38
Margalef				
Primary	4·02	0·47	3·71	0·35
Logged	3·73	0·39	4·20	0·35

To examine the relationship between vegetation structure and species diversity in primary forest, vegetation measurements at the 40 sampling stations in primary forest were used to calculate 14 variables (Table 1), which were normalized where necessary (including arcsine transformation of percentages) and analysed by a principal components analysis (PCA; Hamer *et al*. 1997; Pearman 2002). This allowed ordination of differences among stations in vegetation structure, by generating a number of independent factors comprising sums of weighted variables, with each variable standardized (i.e. mean across all stations = 0, SD = 1). The relationship between vegetation factor scores and species diversity at each sampling station in primary forest was analysed using stepwise multiple regression. Weightings for each vegetation variable were then used to calculate factor scores for each of the 40 sampling stations in logged forest, to allow comparison of vegetation structure in the two habitats.

SPECIES DIVERSITY

We examined species diversity using Margalef's and Simpson's diversity indices (Magurran 1988). Margalef's index primarily measures species richness, whereas Simpson's index measures both richness and relative abundance and is equivalent to the probability of the next individual sampled being from a different species to the last individual (Hurlbert 1971). Bootstrap methods were used to calculate standard errors for each index

(Sokal & Rohlf 1995). In order to test for differences in diversity between primary and logged forest, pairwise randomization tests were carried out, based on 10 000 resamples of species abundance data, following Solow (1993).

Results

R-MODE ANALYSIS

Shade preferences and geographical distributions of butterflies in primary forest

Excluding recaptures, we sampled 1180 individuals of 53 species at 24 gap and shade sites (Appendix 1). The proportion of individuals of each species (where $n \geq 5$) occurring at shade sites was significantly higher in the Satyrinae and Morphinae (mean = 0·63, n = 14 species, SD = 0·20) than in the Nymphalinae and Charaxinae (mean = 0·39, n = 13 species, SD = 0·19; t-test using equal variance estimate with arcsine-transformed data; $t_{25} = 3{\cdot}0$, $P < 0{\cdot}01$).

Satyrinae and Morphinae had more restricted geographical distributions (median rank = 22·0, n = 35, interquartile range (IQR) ± 24·5) than Nymphalinae and Charaxinae (median rank = 44·5, n = 31, IQR ± 27·5; Mann–Whitney Z = 3·6, n = 27, $P < 0{\cdot}001$). Those species with greater shade preferences had significantly narrower geographical distributions (Fig. 1; Spearman correlation for species where $n \geq 5$, $r = -0{\cdot}72$; n = 27 species, $P < 0{\cdot}001$). This relationship was apparent within the Satyrinae and Morphinae ($r = -0{\cdot}65$, n = 14 species, $P = 0{\cdot}01$) and, less strongly, within the Nymphalinae and Charaxinae: species that were more common in shade traps had narrower geographical distributions than did species that were more common in gap traps (Mann–Whitney $Z = 2{\cdot}0$, n = 13, $P < 0{\cdot}05$).

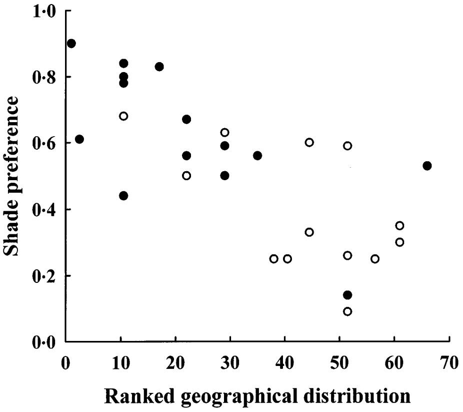

Fig. 1. The relationship between shade preference of butterflies and their ranked geographical distribution (solid circles, Satyrinae and Morphinae; open circles, Nymphalinae and Charaxinae). The highest-ranked species (rank 1) is endemic to Borneo; the lowest-ranked (66) is the most widespread species recorded during the study. See the Materials and methods for further details, and Appendix 1 for ranks of each species.

Impacts of logging on individual species

Excluding recaptures, we sampled 2064 individuals of 55 species at 40 stations on transects in primary forest, plus 1897 individuals of 56 species at 40 stations in logged forest (Appendix 1). For Satyrinae and Morphinae there was a significant negative relationship between shade preference and impact of logging (Spearman correlation; $r^S = -0{\cdot}74$, n = 14 species, $P < 0{\cdot}01$); those species with the strongest shade preference were the most adversely affected by logging. However, there was no relationship between shade preference and impact of logging on Nymphalinae and Charaxinae ($r^S = -0{\cdot}29$, n = 13 species, $P = 0{\cdot}34$).

For Satyrinae and Morphinae, there was a significant positive relationship between the impact of logging and ranked geographical distribution (Fig. 2; Spearman correlation; $r^S = 0{\cdot}63$, n = 14 species, $P = 0{\cdot}02$): those species with the widest geographical distributions were the most abundant in logged forest. For Nymphalinae and Charaxinae, there was a significant but opposite relationship (Fig. 2; $r^S = -0{\cdot}65$, $n = 13$, $P = 0{\cdot}02$): those species with the most restricted geographical distributions were the most abundant in logged forest.

Q-MODE ANALYSIS

Butterfly diversity in primary and logged forest

Across all species, there was no difference in diversity between primary and selectively logged forest ($P > 0{\cdot}3$ for Simpson's and Margalef's diversity indices). However, for Nymphalinae and Charaxinae Simpson's diversity index was significantly higher in unlogged forest than in logged forest (Table 1; pairwise randomization test based on 10 000 random samples; $\Delta = 1{\cdot}0$, $P = 0{\cdot}03$), although there was no difference between habitats in Margalef's index ($\Delta = 0{\cdot}3$, $P = 0{\cdot}5$). Thus logging primarily affected the relative abundances of

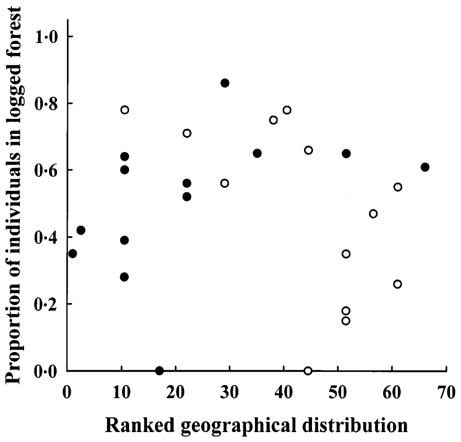

Fig. 2. The relationship between impact of selective logging on species and their ranked geographical distribution (solid circles, Satyrinae and Morphinae; open circles, Nymphalinae and Charaxinae).

Table 2. Contributions of different variables to two principal components of variation in vegetation structure. Variables making main contributions to each principal component are in bold

	Weighting	
Variable	PRIN1	PRIN2
Trees		
Mean height	0·19	**0·82**
Mean girth	−0·16	**0·81**
Density	**0·53**	**−0·49**
Proportion of dipterocarps	0·37	**0·77**
Proportion branching above	0·38	**0·46**
Saplings		
Mean height	**0·59**	0·15
Mean girth	0·05	0·12
Density	0·22	−0·05
Proportion of dipterocarps	**0·57**	0·27
Percentage cover		
Ground	**−0·84**	−0·09
Low	**−0·83**	−0·09
Understorey	**0·81**	−0·04
Canopy	**0·58**	0·31

species rather than species richness. For Satyrinae and Morphinae, there was no difference between habitats in either Simpson's or Margalef's diversity index (Table 1; $P > 0·1$ in both cases).

Vegetation structure and butterfly diversity in primary forest

PCA extracted two components of variation in primary forest (PRIN1 and PRIN2) that accounted for 32% and 18% of the variability in the vegetation data, respectively. The first factor increased with (in order from greatest to least importance) increasing vegetation cover in the canopy and understorey, decreasing vegetation cover at ground level and up to 2 m above the ground, increasing density of trees, increasing height but not girth of saplings and increasing proportion of diptercarps among saplings (Table 2). A high PRIN1 score thus represented dense forest with closely spaced trees, a closed canopy and a poorly developed field layer, with relatively spindly saplings comprising mainly dipterocarps. The PRIN2 score increased with increasing height and girth of trees, increasing proportion of dipterocarps and increasing height to the point of inversion (as a proportion of tree height; Table 2). Thus, PRIN1 primarily reflected density of forest whereas PRIN2 primarily represented sizes and architecture of trees.

Across all species, diversity of butterflies within primary forest was significantly and negatively related to vegetation density (PRIN1) but not tree size (PRIN2; stepwise multiple regression for Margalef's index, $F_{1,38} = 13·0$, $P = 0·001$; for Simpson's index, $F_{1,38} = 7·9$, $P = 0·01$). When Satyrinae and Morphinae were examined separately from Nymphalinae and Charaxinae, Margalef's index for Nymphalinae and Charaxinae was significantly and negatively related to both vegetation density (PRIN1) and tree size (PRIN2; $F_{2,37} = 10·6$, $P < 0·001$, $r^2 = 0·37$) according to the following equation:

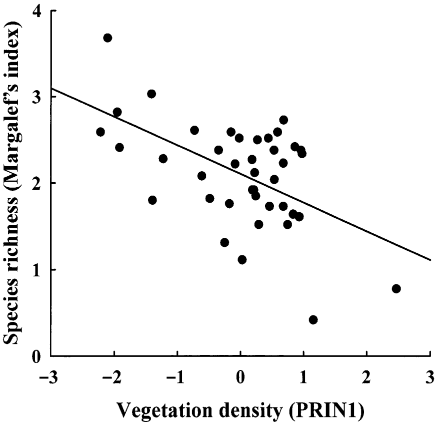

Fig. 3. Diversity of Nymphalinae and Charaxinae in relation to vegetation density and canopy openness. The independent variable is the major principal component of variation in vegetation structure, derived from a principal components analysis (see text and Table 2 for further details).

$$D_M = 2·10\ (\mathrm{SE} \pm 0·08) - 0·33\ (\mathrm{SE} \pm 0·08)\ \mathrm{PRIN1} - 0·16\ (\mathrm{SE} \pm 0·07)\ \mathrm{PRIN2}$$

PRIN1 accounted for 30% of the variation in Margalef's index (Fig. 3) and PRIN2 accounted for an additional 7%.

Simpson's diversity index (D_S) for Nymphalinae and Charaxinae was also negatively related to vegetation density, but not tree size ($F_{1,38} = 13·0$, $P = 0·001$, $r^2 = 0·26$). PRIN1 accounted for 26% of the variation in Simpson's index. In contrast, there was no relationship between species diversity of Satyrinae and Morphinae and either PRIN1 or PRIN2 scores ($P > 0·1$ in all cases).

Data from gap and shade traps showed similar patterns in relation to diversity and vegetation structure: species diversity of Nymphalinae and Charaxinae was significantly higher in gaps than in shade (Simpson's index; gap mean = 8·84, SE ± 1·26; shade mean = 5·18, SE ± 0·98; $\Delta = 3·65$, $P < 0·001$) but there was no difference for Satyrinae and Morphinae (gap mean = 8·22, SE ± 1·38; shade mean = 7·22, SE ± 0·85; $\Delta = 1·00$, $P = 0·24$).

Impacts of selective logging on forest structure

There was no difference between habitats in the mean score for PRIN1 (Table 3; t-test using unequal variance estimate; $t_{65·6} = 1·9$, $P = 0·1$). However, PRIN1 was much more variable in unlogged forest (Table 3; range = −11·1–9·3) than in logged forest (range = −6·1–4·1; Levene's test for equality of variances; $F_{1,78} = 4·0$, $P <$

Table 3. Individual variables plus two principal components of variation in vegetation structure in primary and selectively logged forest

Variable	Primary forest Mean	Primary forest SD	Selectively logged forest Mean	Selectively logged forest SD
Trees				
Mean height	42·2	5·9	37·6	6·1
Mean girth	134·3	35·8	117·5	29·6
Density	0·11	0·03	0·12	0·03
Proportion of dipterocarps	0·54	0·24	0·42	0·26
Proportion branching above	0·87	0·17	0·84	0·16
Saplings				
Mean height	8·6	2·0	9·2	2·1
Mean girth	23·4	4·0	23·0	3·9
Density	0·30	0·07	0·30	0·09
Proportion of dipterocarps	0·16	0·22	0·08	0·14
Percentage cover				
Ground	38·0	23·2	41·1	19·6
Low	56·4	24·5	63·3	19·5
Understorey	61·4	19·6	59·9	16·0
Canopy	39·4	20·7	15·1	11·4
PRIN1 (forest density)	0·70	4·21	–0·70	2·50
PRIN2 (tree size and architecture)	1·17	2·76	–1·17	2·36

0·05), indicating a significantly greater range of variation in vegetation density within unlogged forest.

PRIN2 was significantly higher in primary forest than in logged forest (Table 3; *t*-test using equal variance estimate; $t_{78} = 4·1$, $P < 0·001$), indicating larger, more widely spaced trees with a higher proportion of dipterocarps in primary forest. There was no difference between habitats in the variance in PRIN2 ($P = 0·4$).

Discussion

COLLECTION OF DATA

During the study we caught a total of 5141 individuals from 66 species, which represents > 80% of the fruit-feeding species that have been recorded at the study site and > 40% of the total number of species, across all families, recorded by Willott *et al.* (2000) at the same site over a 9-month sampling period. This species richness is similar to that recorded using similar methods at other sites in Sabah (Schulze & Fiedler 1998; Schulze, Linsenmair & Fiedler 2001). Although traps catch only one guild of butterflies, they avoid the problems of species identification that can be encountered using walk-and-count transect techniques in highly diverse regions (Walpole & Sheldon 1999).

There are no data on the distances over which traps attract butterflies or on the size of the area that traps sample. In this study, differences in the diversity of butterflies in traps 100 m apart indicate that distances over which species are attracted to traps may be relatively short. This is consistent with the results of other studies that also showed distinct butterfly assemblages in traps 50–100 m apart (Pinheiro & Ortiz 1992; Hill *et al.* 2001). However, the large number of individuals caught in traps in this study suggests that the area over which traps sample butterflies may be relatively large compared with other sampling techniques such as walk-and-count transects (Hamer & Hill 2000).

Observed differences in relative abundance among species could in part have reflected differences in attraction to traps (Davis & Sutton 1997; Hughes, Daily & Ehrlich 1998) but relatively long-term studies such as this one, which sampled for *c.* 13 000 trap days over a 28-month period, greatly reduce this problem (Hughes, Daily & Ehrlich 1998; Hill *et al.* 2001). Moreover, all traps at gap and shade sites were located in relatively close proximity to each other (within an area of < 20 ha), and so all these traps could in principle sample the same local assemblage of butterfly species. In a previous study at DVCA, fewer than 5% of individuals caught in traps escaped before the traps were sampled each day (Hill *et al.* 2001). Thus we are confident that differences in diversity between traps reflect differences in species' habitat preferences.

Multi-species comparisons, such as those used in this study, can be confounded by non-independence of data from closely related species (Harvey & Pagel 1991). When phylogenies are well known this problem can be avoided by analysis using independent contrasts, but this was not possible in this study because the phylogeny of south-east Asian butterflies is poorly resolved beyond the level of subfamily (Corbert & Pendlebury 1992; Parsons 1999). The 13 species of Nymphalinae and Charaxinae included in the R-mode analysis in this study were from 11 genera (Appendix 1) and the 14 species of Satyrinae and Morphinae were from only seven genera, but the largest genus (*Mycalesis*) included species with a wide range of geographical distribution, light preference and response to selective logging (Appendix 1). Thus we are confident that our analyses were not greatly confounded by pseudoreplication of data from closely related species, and that phylogenetic analysis qualitatively would not alter our conclusions.

EFFECTS OF LIGHT ON BUTTERFLIES

Many forest butterflies, particularly Satyrinae and Morphinae, are sensitive to changes in moisture availability and humidity (Schulze & Fiedler 1998; Hill 1999), and changes in canopy cover and light penetration may impact directly on butterfly distributions through microclimatic effects on adult and larval survival, as well as indirectly through effects on host-plant quality (Blau 1980). For all four subfamilies of Nymphalidae, those species with the greatest shade preferences also had the narrowest geographical distributions, indicating that gaps were exploited primarily by opportunistic species with widespread distributions, as was also found in previous studies (Thomas 1991; Spitzer *et al.* 1997; Hill *et al.* 2001).

In primary forest, species diversity of butterflies was higher at sites with a more open canopy. This supports other studies comparing disturbed and undisturbed habitats, which also showed that increased light was associated with increased butterfly diversity (Sparrow *et al.* 1994; Pinheiro & Ortiz 1992; Willott *et al.* 2000). This is also in agreement with the prediction that highest diversity should occur in situations of intermediate disturbance when both climax and pioneer species can coexist (Horn 1975; Connell 1978; Basset *et al.* 2001). The relationship with canopy openness was due primarily to Nymphalinae and Charaxinae (Fig. 3), which have a much stronger affinity than Satyrinae and Morphinae for gaps, associated with their much wider geographical distributions. Satyrinae and Morphinae do include some cosmopolitan species able to exploit gaps (*Melanitis leda*, *Mycalesis horsfieldi* and *Mycalesis orseis*; Appendix 1) but there was no relationship between canopy openness and diversity within this group. For Nymphalinae and Charaxinae there was also a small but independent effect of tree size and architecture on diversity, possibly indicating that, when the canopy was higher, there was less chance of sampling canopy species at ground level (DeVries, Walla & Greeney 1999; DeVries & Walla 2001; Hill *et al.* 2001). However, this effect was relatively small, accounting for only 7% of the variance in diversity, and of 54 species of Nymphalidae sampled by Hill *et al.* (2001) at the same study site only four species (7%) were sampled exclusively in the canopy.

IMPACTS OF SELECTIVE LOGGING ON VEGETATION STRUCTURE

The mean value for vegetation factor score 1, which primarily measured forest density and canopy openness, did not differ between habitats, in agreement with other studies investigating selective logging (Ganzhorn *et al.* 1990; Hill *et al.* 1995). However, in this study there was a significantly wider range of values in primary forest, due to a lower frequency of dense shade and of very open gaps in logged forest (Table 3). Loss of dense shade following logging presumably reflected a large reduction in tree basal area (typically > 50% reduction following selective logging on Borneo; Grieser Johns 1997). A lower frequency of very open gaps in logged forest probably occurred because natural canopy gaps in primary forest are relatively small compared with those caused by selective logging, and so persist for longer: natural gaps are often unsuitable for colonization by pioneer trees species and are usually dominated by slow-growing climax species that only slowly re-establish a canopy (Raiche & Gong 1990; Kennedy & Swaine 1992). In contrast, the more extensive open areas resulting from selective logging are rapidly invaded by pioneer tree species [primarily *Macaranga* spp. (Euphorbiaceae) on Borneo], which exhibit very rapid germination and growth after logging and quickly re-establish a canopy, although at much lower heights than canopies in primary forest (Grieser Johns 1997). Thus *Macaranga* species comprised an average of 26% of trees at stations in logged forest but were generally absent from stations in unlogged forest. Dead and dying standing trees, as well as large timber trees, are also generally removed by logging (Crome, More & Richards 1992; Grieser Johns 1997), which may further reduce the potential in logged forest for subsequent gap formation through natural tree falls and shedding of branches. Thus in this study there was much greater heterogeneity in forest structure within primary forest. This agrees with other studies that also recorded more homogeneous vegetation within forest after selective logging (Ganzhorn *et al.* 1990; Hill *et al.* 1995).

IMPACTS OF LOGGING ON BUTTERFLIES

There were marked differences in the faunal composition of butterfly assemblages in primary and logged forest, which were strongly associated with species' shade preferences and geographical distributions. In Satyrinae and Morphinae, those species with higher shade preferences, which also had narrower geographical distributions, were most adversely affected by logging, whereas cosmopolitan species with low shade preferences benefited from logging (Figs 1 and 2). In Nymphalinae and Charaxinae the opposite was observed: those species with the widest geographical distributions were most adversely affected by logging and those with relatively restricted distributions were more common in logged forest. Willott *et al.* (2000) found, using walk-and-count transects for all butterfly families, that there were fewer species with wide geographical distributions in logged forest. They suggested that this was because transects were less likely to record gap and canopy species in unlogged forest, yet our study has shown that gap and canopy species have wide geographical ranges (as also found by Hill *et al.* 2001) and so under-recording of gap and canopy species should lead to apparently narrower geographical ranges in unlogged forest, not logged forest as suggested by Willott *et al.* (2000). Thus a more likely explanation for the results in Willott *et al.* (2000), and in this study, is that gaps with greater canopy openness, which occurred more often in unlogged forest, attracted species with broad geographical distributions. Further data are required, however, to examine the relationships among morphology, gap preference and geographical distribution in non-Nymphalid butterflies.

Although there were marked differences in faunal composition, differences in species diversity between primary and logged forest were less marked. Primary forest had more gaps (Table 3) and diversity of Nymphalinae and Charaxinae, which were strongly associated with gaps, was higher in primary forest than in logged forest in terms of species evenness. For instance, the most abundant species (*Bassarona dunya*) comprised 231 of 618 individuals (37%) in logged forest but only 181 of 643 individuals (28%) in primary forest (Appendix 1). Diversity of Nymphalinae and Charaxinae in primary forest was also lower at sites with a higher canopy and larger trees (PRIN2), and this factor was significantly lower in logged forest than in primary forest (Table 3). There is some evidence that traps sample less efficiently in areas with higher canopies (DeVries & Walla 2001). Thus traps may have underestimated diversity of Nymphalinae and Charaxinae in unlogged forest compared with logged forest, and so butterfly diversity in unlogged forest in this study may have been higher than that reported. However, given that only 7% of species of Nymphalidae at the study site are confined to the canopy (see above), any such effect is likely to have been small. There was no impact of logging on diversity of Satyrinae and Morphinae because reductions in species with restricted geographical distributions were largely balanced by increases in wide-ranging species. This was in accord with the absence of any relationship with vegetation structure in primary forest for these species.

Previous studies have emphasized the importance of environmental heterogeneity for generating and maintaining species diversity in tropical forests (Huston 1994; Rosenzweig 1995), and our data indicate that important changes in butterfly assemblages were due largely to a loss of heterogeneity following selective logging. At the same study site, Willott *et al.* (2000) found a slightly higher diversity of butterflies, in terms of species evenness, in selectively logged forest, which was the opposite to that found here. This difference could have resulted in part from the inclusion, in the earlier study, of a wider range of butterfly taxa, which may also have shown individualistic responses to logging, as demonstrated here. Willott *et al.* (2000) also analysed their data at a small spatial scale, and Hamer & Hill (2000) found that small scales do not account for impacts of habitat disturbance on heterogeneity in vegetation structure, and so tend to overestimate diversity in disturbed forest, particularly in terms of species evenness. The difference in recorded impacts of logging in these two studies emphasizes the need to sample at a sufficiently large spatial scale to account for impacts of disturbance on heterogeneity in forest environments. The results of this study also emphasize the importance of understanding the responses of species to natural variation in environmental conditions within undisturbed forest, in order to interpret responses to anthropogenic habitat disturbance.

Degraded forest such as that produced by selective logging is often considered to have little value in terms of the conservation of biodiversity and, until recently, it was routinely included along with totally deforested areas in statistical analyses of rates of loss of forest (Myers 1989). In the current study, selective logging had a relatively minor impact on species diversity and this supports earlier studies in suggesting that selectively logged forest can in fact make an important contribution to the conservation of biodiversity (Johns 1992). However, there were important differences between habitats in faunal composition in the current study, which were strongly associated with a loss of environmental heterogeneity following selective logging. Thus future management to reduce impacts of logging on biodiversity should aim to preserve environmental heterogeneity as far as possible, for instance by retaining areas of undisturbed forest within production estates, by enhancing natural regeneration and by ensuring that, in addition to areas of dense shade, regenerating forest also contains open-canopy gaps free from invasive tree species that rapidly form dense canopies at relatively low heights. Most forested areas in the tropics are likely to be utilized in some way in the near future, and whilst the setting aside and active policing of large areas of intact forest would ensure the preservation of tropical biodiversity, this is not a viable option in most cases. Hence a more appropriate management strategy is probably to retain areas of intact forest in a matrix of sympathetically managed production forest. Indeed long-term trends in the conservation of tropical biodiversity are most likely to be affected not by the rates at which tropical forests are logged but by the extent to which forestry rules include provisions for maintaining environmental heterogeneity, the efficiency with which these rules are observed and the ability of foresters to protect the integrity of forest estates (Crome, More & Richards 1992; Grieser Johns 1997).

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References

Ackery, P.R. (1984) Systematic and faunistic studies on butterflies. *Biology of Butterflies* (eds R.I. Vane-Wright & P.R. Ackery), pp. 9–21. Academic Press, London, UK.

Basset, Y., Charles, E., Hammond, D.S. & Brown, V.K. (2001) Short-term effects of canopy openness on insect herbivores in a rain forest in Guyana. *Journal of Applied Ecology*, **38**, 1045–1058.

Blau, W.S. (1980) The effect of environmental disturbance on a tropical butterfly population. *Ecology*, **61**, 1005–1112.

Brokow, N. & Busing, R.T. (2000) Niche versus chance and tree diversity in forest gaps. *Trends in Ecology and Evolution*, **15**, 183–188.

Brown, K.S. & Hutchings, R.W. (1997) Disturbance, fragmentation and the dynamics of diversity in Amazonian forest butterflies. *Tropical Forest Remnants: Ecology, Management and Conservation* (eds W.F. Laurance & R.O. Bierregard), pp. 91–110. Chicago University Press, Chicago, IL.

Chai, P. & Srygley, R.B. (1990) Predation and the flight, morphology, and temperature of neotropical rain-forest butterflies. *American Naturalist*, **135**, 748–765.

Collins, N.M. & Morris, M.G. (1985) *Threatened Swallowtail Butterflies of the World*. International Union for the Conservation of Nature and Natural Resources, Gland, Sweden.

Collins, N.M., Sayer, J.A. & Whitmore, T.C. (1991) *The Conservation Atlas of Tropical Forests: Asia and the Pacific*. Macmillan, London, UK.

Connell, J.H. (1978) Diversity in rain forests and coral reefs. *Science*, **199**, 1302–1310.

Corbert, A.S. & Pendlebury, H.M. (1992) *The Butterflies of the Malay Archipelago*, 4th edn. Malayan Nature Society, Kuala Lumpur, Malaysia.

Crome, F.H.J., More, L.A. & Richards, G.C. (1992) A study of logging damage in upland rainforest in north Queensland. *Forest Ecology and Management*, **49**, 1–29.

Daily, G.C. & Ehrlich, P.R. (1995) Preservation of biodiversity in small rainforest patches: rapid evaluation using butterfly trapping. *Biodiversity and Conservation*, **4**, 35–55.

Davis, A.J. & Sutton, S.L. (1997) A dung beetle that feeds on fig: implications for the measurement of rarity. *Journal of Tropical Ecology*, **13**, 759–766.

Davis, A.J., Holloway, J.D., Huijbregts, H., Krikken, J., Kirk-Spriggs, A.H. & Sutton, S.L. (2001) Dung beetles as indicators of change in the forests of northern Borneo. *Journal of Applied Ecology*, **38**, 593–616.

Denslow, J.S. (1987) Tropical rainforest gaps and tree species diversity. *Annual Review of Ecology and Systematics*, **18**, 431–451.

DeVries, P.J. (1987) *The Butterflies of Costa Rica and Their Natural History. Vol. 1. Papilionidae, Pieridae and Nymphalidae*. Princeton University Press, Princeton, NJ.

DeVries, P.J. & Walla, T.R. (2001) Species diversity and community structure in neotropical fruit-feeding butterflies. *Biological Journal of the Linnean Society*, **74**, 1–15.

DeVries, P.J., Walla, T.R. & Greeney, H.F. (1999) Species diversity in spatial and temporal dimensions of fruit-feeding butterflies from two Ecuadorian rainforests. *Biological Journal of the Linnean Society*, **68**, 333–353.

Dudley, R. (1990) Biomechanics of flight in neotropical butterflies: morphometrics and kinematics. *Journal of Experimental Biology*, **150**, 37–53.

Feener, D.H. & Schupp, E.W. (1998) Effect of treefall gaps on the patchiness and species richness of Neotropical ant assemblages. *Oecologia*, **116**, 191–201.

Ganzhorn, J.U., Ganzhorn, A.W., Abraham, J.-P., Andriamanarivo, L. & Ramananjatovo, A. (1990) The impact of selective logging on forest structure and tenrec populations in western Madagascar. *Oecologia*, **84**, 126–133.

Grieser Johns, A.G. (1997) *Timber Production and Biodiversity Conservation in Tropical Rain Forests*. Cambridge University Press, Cambridge, UK.

Hall, J.P.W. & Willmott, K.R. (2000) Patterns of feeding behaviour in adult male riodinid butterflies and their relationship to morphology and ecology. *Biological Journal of the Linnean Society*, **69**, 1–23.

Hamer, K.C. & Hill, J.K. (2000) Scale-dependent consequences of habitat modification for species diversity in tropical forests. *Conservation Biology*, **14**, 1435–1440.

Hamer, K.C., Hill, J.K., Lace, L.A. & Langan, A.M. (1997) Ecological and biogeographical effects of forest disturbance on tropical butterflies of Sumba, Indonesia. *Journal of Biogeography*, **24**, 67–75.

Harvey, P.H. & Pagel, M.D. (1991) *The Comparative Method in Evolutionary Biology*. Oxford University Press, Oxford, UK.

Hill, J.K. (1999) Butterfly spatial distribution and habitat requirements in a tropical forest: impacts of selective logging. *Journal of Applied Ecology*, **36**, 564–574.

Hill, J.K., Hamer, K.C., Dawood, M.M., Tangah, J. & Chey, V.K. (2003) Interactive effects of rainfall and selective logging on a tropical forest butterfly in Sabah, Borneo. *Journal of Tropical Ecology*, **19**, 1–8.

Hill, J.K., Hamer, K.C., Lace, L.A. & Banham, W.M.T. (1995) Effects of selective logging on tropical butterflies on Buru, Indonesia. *Journal of Applied Ecology*, **32**, 454–460.

Hill, J.K., Hamer, K.C., Tangah, J. & Dawood, M. (2001) Ecology of tropical butterflies in rainforest gaps. *Oecologia*, **128**, 294–302.

Holloway, J.D. (1984) Notes on the butterflies of the Gunung Mulu National Park. *Sarawak Museum Journal*, **30** (Special Issue 2), 89–131.

Horn, H.S. (1975) Markovian properties of forest succession. *Ecology and Evolution of Communities* (eds M.L. Cody & J.M. Diamond), pp. 196–211. Harvard University Press, Cambridge, MA.

Hughes, J.B. & Daily, G.C. & Ehrlich, P.R. (1998) Use of fruit bait traps for monitoring of butterflies (Lepidoptera: Nymphalidae). *Revista de Biologia Tropical*, **46**, 697–704.

Hurlbert, S.H. (1971) The non-concept of species diversity: a critique and alternative parameters. *Ecology*, **52**, 577–586.

Huston, M.A. (1994) *Biological Diversity. The Coexistence of Species on Changing Landscapes*. Cambridge University Press, Cambridge, UK.

Johns, A.D. (1992) Species conservation in managed tropical forests. *Tropical Deforestation and Species Extinction* (eds T.C. Whitmore & J.A. Sayer), pp. 15–53. Chapman & Hall, London, UK.

Kennedy, D.N. & Swaine, M.D. (1992) Germination and growth of colonizing species in artificial gaps of different sizes in dipterocarp rain forest. *Tropical Rain Forest: Disturbance and Recovery* (eds A.G. Marshall & M.D. Swaine), pp. 357–366. The Royal Society, London, UK.

Kremen, C. (1992) Assessing the indicator properties of species assemblages for natural area monitoring. *Ecological Applications*, **2**, 203–217.

Lemmon, P.E. (1957) A new instrument for measuring forest overstorey density. *Journal of Forestry*, **55**, 667–669.

Lewis, O.T. (2001) Effect of experimental selective logging on tropical butterflies. *Conservation Biology*, **15**, 389–400.

Magurran, A.E. (1988) *Ecological Diversity and its Measurement*. Croom-Helm, London, UK.

Marsh, C.W. & Greer, A.G. (1992) Forest land-use in Sabah, Malaysia: an introduction to Danum Valley. *Philosophical Transactions of the Royal Society London Series B*, **335**, 331–339.

Meijer, W. & Wood, G.H.S. (1964) *Dipterocarps of Sabah (North Borneo)*. Sabah Forest Record No. 5. Forest Department, Sandakan, Sabah, Malaysia.

Myers, N. (1989) *Deforestation Rates in Tropical Countries and Their Climatic Implications*. Friends of the Earth, London, UK.

Newman, M.F., Burgess, P.F. & Whitmore, T.C. (1996) *Manuals of Dipterocarps for Foresters: Borneo Island Light Hardwoods*. Royal Botanical Gardens, Edinburgh, UK.

Newman, M.F., Burgess, P.F. & Whitmore, T.C. (1998) *Manuals of Dipterocarps for Foresters: Borneo Island Medium and Heavy Hardwoods*. Royal Botanical Gardens, Edinburgh, UK.

Novotny, V., Bassett, Y., Miller, S.E., Weiblen, G.D., Bremer, B., Cizek, L. & Drozd, P. (2002) Low host specificity of herbivorous insects in tropical forest. *Nature*, **416**, 841–844.

Ødegaard, F. (2000) How many species of arthropods? Erwin's estimate revised. *Biological Journal of the Linnean Society*, **71**, 583–597.

Otsuka, K. (1988) *Butterflies of Borneo*, Vol. 1. Tobishima Corporation, Tokyo, Japan.

Parsons, M. (1999) *The Butterflies of Papua New Guinea*. Academic Press, London, UK.

Pearman, P.B. (2002) The scale of community structure: habitat variation and avian guilds in tropical forest understorey. *Ecological Monographs*, **72**, 19–39.

Pinheiro, C.E.G. & Ortiz, J.V.C. (1992) Communities of fruit-feeding butterflies along a vegetation gradient in central Brazil. *Journal of Biogeography*, **19**, 505–511.

Raiche, J.W. & Gong, W.K. (1990) Effects of canopy opening on tree seed germination in a Malaysian dipterocarp forest. *Journal of Tropical Ecology*, **6**, 203–217.

Ribera, I., Dolédec, S., Downie, I.S. & Foster, G.N. (2001) Effect of land disturbance and stress on species traits of ground beetle assemblages. *Ecology*, **82**, 1112–1129.

Richards, P.W. (1952) *The Tropical Rain Forest*, 1st edn. Cambridge University Press, Cambridge, UK.

Rosenzweig, M.L. (1995) *Species Diversity in Space and Time*. Cambridge University Press, Cambridge, UK.

Schulze, C.H. & Fiedler, K. (1998) Habitat preference and flight activity of Morphinae butterflies in a Bornean rainforest, with a note on sound production by adult *Zeuxidia* (Lepidoptera: Nymphalidae). *Malay Naturalists' Journal*, **52**, 163–176.

Schulze, C.H., Linsenmair, K.E. & Fiedler, K. (2001) Understorey versus canopy – patterns of vertical stratification and diversity among Lepidoptera in a Bornean rainforest. *Plant Ecology*, **153**, 133–152.

Shahabuddin, G. & Terborgh, J.W. (1999) Frugivorous butterflies in Venezuelan forest fragments: abundance, diversity and the effects of isolation. *Journal of Tropical Ecology*, **15**, 703–722.

Sokal, R.R. & Rohlf, F.J. (1995) *Biometry*. W.H. Freeman Co., New York, NY.

Solow, A.R. (1993) A simple test for change in community structure. *Journal of Animal Ecology*, **62**, 191–193.

Sparrow, H., Sisk, T., Ehrlich, P. & Murphy, D. (1994) Techniques and guidelines for monitoring Neotropical butterflies. *Conservation Biology*, **8**, 800–809.

Speight, M.R., Hunter, M.D. & Watt, A.D. (1999) *Ecology of Insects. Concepts and Applications*. Blackwell Science, Oxford, UK.

Spitzer, K., Jaros, J., Havelka, J. & Leps, J. (1997) Effect of small-scale disturbance on butterfly communities of an Indochinese montane rainforest. *Biological Conservation*, **80**, 9–15.

Srygley, R.B. & Chai, P. (1990) Flight morphology of Neotropical butterflies: palatability and distribution of mass to the thorax and abdomen. *Oecologia*, **84**, 491–499.

Sutton, S.L. & Collins, N.M. (1991) Insects and tropical forest conservation. *The Conservation of Insects and their Habitats* (eds N.M. Collins & J.A. Thomas), pp. 405–422. Academic Press, London, UK.

Thomas, C.D. (1991) Habitat use and geographic ranges of butterflies from the wet lowlands of Costa Rica. *Biological Conservation*, **55**, 269–281.

Torquebiau, E.F. (1986) Mosaic patterns in Dipterocarp rain forest in Indonesia and their implications for practical forestry. *Journal of Tropical Ecology*, **2**, 301–325.

Tsukada, E. (1982) *Butterflies of the South East Asian Islands*, Vols 3–5. Plapac Company, Tokyo, Japan.

Vane-Wright, R.I., Humphries, C.J. & Williams, P.H. (1991) What to protect? Systematics and the agony of choice. *Biological Conservation*, **55**, 235–254.

Wallace, A.R. (1878) *Tropical Nature and Other Essays*. Macmillan, London, UK.

Walpole, M.J. & Sheldon, I. & R. (1999) Sampling butterflies in tropical rainforest: an evaluation of a transect walk method. *Biological Conservation*, **87**, 85–91.

Walsh, R.D.P. & Newbery, D.M. (1999) The ecoclimatology of Danum, Sabah, in the context of the world's rainforest regions, with particular reference to dry periods and their impact. *Philosophical Transactions of the Royal Society London Series B*, **354**, 1869–1883.

Whitmore, T.C. (1984) *Tropical Rain Forests of the Far East*, 2nd edn. Clarendon Press, Oxford, UK.

Whitmore, T.C. (1991) *An Introduction to Tropical Rain Forests*. Clarendon Press, Oxford, UK.

Willott, S.J., Lim, D.C., Compton, S.G. & Sutton, S.L. (2000) Effects of selective logging on the butterflies of a Bornean rainforest. *Conservation Biology*, **14**, 1055–1065.

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Appendix 1

Butterfly species sampled in fruit-baited traps according to trap location, with ranked scores for geographical distribution. The highest-ranked species (rank 1) is endemic to Borneo; the lowest-ranked (66) is the most widespread species recorded during the study.

	Trap location				
	Rank	Shade	Gap	Primary	Logged
Satyrinae					
Elymnias panthera Fabricius	22	0	1	1	2
E. dara Distant & Pryer	35	–	–	–	2
Melanitis leda L.	66	9	8	25	39
M. zitenius Herbst	58	–	–	3	1
Neorina lowii Doub.	22	123	60	225	287
Mycalesis anapita Moore	10·5	21	27	47	82
M. fusca Felder	35	1	–	1	5
M. patiana Eliot	2·5	23	15	14	10
M. kina Staudinger	1	19	2	74	39
M. dohertyi Elwes	10·5	18	5	66	26
M. horsfieldi Moore	29	10	10	1	6
M. maianeas Hewit.	10·5	42	8	96	144
M. oroatis Hewit.	17	92	19	383	1
M. orseis Hewit.	35	53	42	116	219
M. mineus L.	61	1	1	2	1
M. janardana Moore	35	2	2	–	6
Erites elegans Butler	10·5	1	3	7	12
E. argentina Butler	32	–	–	2	2
Ragadia makuta Horsfield	22	29	23	250	275
Ypthima pandocus Moore	22	–	–	–	1
Coelites epiminthia West.	35	–	1	–	–
Lethe dora Staudinger	2·5	–	–	1	–
Morphinae					
Faunis gracilis Butler	10·5	1	–	1	–
F. canens Hubner	47	1	–	–	2
F. kirata de Niceville	10·5	1	–	–	3
F. stomphax West.	10·5	2	–	3	1
Xanthotaenia busiris West.	22	–	–	8	4
Amathusia phiddippus L.	51·5	1	6	6	11
A. masina Fruhstorfer	4	–	1	–	–
Amathuxidia amythaon Doub.	51·5	2	0	7	4
Zeuxidia aurelius Cramer	10·5	4	1	20	13
Z. amethystus Butler	40·5	2	2	11	13
Z. doubdledayi West.	22	1	–	5	8
Thaumantis noureddin West.	10·5	1	2	1	3
Discophora necho Felder	29	10	7	45	57
Nymphalinae					
Cirrochroa emalea Guerin	44·5	4	–	16	2
Cupha erymanthis Drury	61	–	–	2	1
Paduca fasciata Felder	40·5	4	12	2	7
Terinos clarissa Boisduval	40·5	1	–	1	–
Kallima limborgii Moore	10·5	30	14	5	18
Rhinopalpa polynice Cram.	51·5	1	10	11	2
Neptis hylas L.	61	–	–	1	–
N. harita Moore	51·5	–	–	1	–
Athyma pravara Moore	51·5	–	1	2	2
A. reta Moore	44·5	–	–	1	1
Parthenos sylvia Cramer	65	–	–	–	1
Dophla evelina Stoll	61	21	39	45	16
Bassarona teuta Doub.	56·5	6	18	38	34
B. dunya Doub.	29	83	49	181	231
Lexias dirtea Fabricius	51·5	4	–	27	17
L. pardalis Moore	44·5	9	6	40	77
L. canescens Butler	10·5	2	–	10	3
Amnosia decora Doub.	22	3	3	9	22
Dichorragia nesimachus Doy.	61	3	7	5	6
Tanaecia aruna Felder	29	1	2	59	67
T. clathrata Vollenhoven	10·5	–	–	3	2

Appendix 1 *Continued*

	Trap location				
	Rank	Shade	Gap	Primary	Logged
T. pelea Fabric.	29	–	1	4	1
T. munda Fruh.	22	–	1	–	–
Euthalia monina Fabric.	56·5	–	1	1	4
E. iapis Godart	22	–	–	3	6
Charaxinae					
Prothoe franck Godart	51·5	41	29	154	84
Agatasa calydonia Hewit.	38	3	9	3	9
Polyura athamas Drury	64	–	1	–	1
P. jalysus Felder	40·5	–	1	–	–
Charaxes bernardus Fabricius	51·5	10	28	18	4
C. durnfordi Distant	44·5	2	4	1	–