

Impacts of rain forest fragmentation on butterflies in northern Borneo: species richness, turnover and the value of small fragments

S. BENEDICK,*† J. K. HILL,* N. MUSTAFFA,*† V. K. CHEY,‡ M. MARYATI,†
J. B. SEARLE,* M. SCHILTHUIZEN† and K. C. HAMER§

*Department of Biology, University of York, York YO10 5YW, UK; †Institute of Tropical Biology and Conservation, University Malaysia Sabah, Kota Kinabalu, Sabah, Malaysia; ‡Forest Research Centre, Sandakan, Sabah, Malaysia; §Earth Biosphere Institute and Faculty of Biological Sciences, University of Leeds, Leeds LS2 9JT, UK

Summary

1. Widespread and rapid losses of tropical rain forests have made understanding the responses of species to rain forest fragmentation an area of major concern. In this study we examined the impacts of habitat fragmentation on the species richness and faunal composition of butterflies in tropical rain forests in Sabah, Borneo. We analysed patterns of both α - and β -diversity to assess the relative importance of differences in patch size, isolation and vegetation structure on the diversity and similarity of species assemblages. We used additive partitioning to assess the relative contributions of intact forest and forest remnants to overall species richness at a landscape scale and we examined which traits of species best predicted their responses to fragmentation.

2. Species richness and diversity in rain forest remnants was significantly positively related to remnant size and significantly negatively related to isolation, in keeping with theories of island biogeography. Species assemblages at different sites were significantly nested, with those species most adversely affected by forest fragmentation having a narrow range of larval host-plants and, to a lesser extent, being large-bodied. No species endemic to Borneo was recorded in forest remnants smaller than 4000 ha, but even the smallest remnant (120 ha) supported species with geographical distributions confined within Sundaland (West Malaysia and the islands of the Sunda Shelf).

3. Although assemblages were significantly nested, they departed substantially from perfect nestedness, with some species recorded only or predominantly in small, relatively depauperate remnants. As a result there was substantial β -diversity among sites, which was related to variation in both fragment size and vegetation structure. At the landscape scale, diversity within sites was less than that between sites, and the majority of the diversity between sites was related to variation in fragment size.

4. *Synthesis and applications.* Substantial diversity was added to the assemblage of butterflies in Bornean rain forests by virtue of species differences among fragments, which were related mainly to differences in patch size and vegetation structure. The data reported indicate that, despite having lower species richness, relatively small and isolated remnants of rain forest make a substantial contribution to regional diversity. Small isolated forest remnants are generally accorded low conservation status and given little protection, with the result that they often disappear over time because of continued anthropogenic disturbance. The results of this study indicate that the conservation value of small remnants of forest, in particular their contribution to environmental heterogeneity, should not be overlooked.

Key-words: beta-diversity, biodiversity, extinction risk, landscape ecology, larval host-plants, nested subsets, species–area relationships

Journal of Applied Ecology (2006) **43**, 967–977
doi: 10.1111/j.1365-2664.2006.01209.x

Introduction

Throughout the world, previously extensive tracts of natural habitat now exist as isolated fragments scattered across inhospitable landscapes (Groombridge & Jenkins 2000). This is evident in tropical regions, where remnants of forest exist within agricultural and urban landscapes, resulting in the remaining forest patches supporting increasingly isolated populations of forest-dependent species (Brook, Sodhi & Ng 2003). Tropical rain forests support the majority of global biodiversity and contain large numbers of endemic species, and so understanding the impacts of forest fragmentation in these areas is crucial for the conservation of biodiversity (Turner 1996; Laurance & Bierregard 1997).

Species richness and persistence in forest remnants has primarily been related to patch size and isolation (Lovejoy *et al.* 1986; Soulé *et al.* 1988), echoing the classic equilibrium theory of island biogeography (MacArthur & Wilson 1967). Following fragmentation, however, forest remnants are almost invariably exposed to different scales of continuing human-induced disturbance, such as timber harvesting and removal of firewood (Hamer *et al.* 1997). Such habitat disturbance may have population- and community-level effects beyond the influences of patch area and isolation (Michalski & Peres 2005; Ewers & Didham 2006) but there are insufficient data to address this question.

Species in habitat patches frequently have nested distributions, in which those species present at depauperate sites are subsets of the species present at sites that are richer in species (Bolger, Alberts & Soulé 1991; Fleishman & MacNally 2002). This pattern may have important implications for the conservation value of forest remnants because, in a fragmented system perfectly nested by patch size, all species occur together in the largest patch and smaller patches make no additional contribution to total species richness (Patterson 1987; Berglund & Jonsson 2003). However, while statistically significant nestedness is common for species assemblages throughout the world (Atmar & Patterson 1995; Wright *et al.* 1998), perfect nestedness is very rare, and even the most depauperate sites may support species that do not occur elsewhere. Thus conservation management tools need to consider complementarity in addition to nestedness (Boecklen 1997). There are, however, currently few data to compare levels of nestedness and complementarity of species assemblages within fragmented landscapes (Peitinger, Bergamini & Schmid 2003; Fischer & Lindenmayer 2005). The widespread occurrence of nested species distributions highlights the fact that individual species differ in their responses to habitat fragmentation. Distinguishing the biological attributes of vulnerable and resistant species has been an important theme in conservation biology, and such traits are well-recorded for vertebrate species (Karr 1982; Laurance 1990; Kattan 1992; Lens *et al.* 2002). Few studies, however, have provided such information for invertebrates (Koh, Sodhi & Brook 2004a; Shahabuddin & Ponte 2005).

The Malaysian state of Sabah was originally almost entirely covered by rain forest, of which only 58% was remaining in 2001 (McMorrow & Talip 2001). Mechanization of timber extraction was developed in the 1950s, leading to rapid conversion of forest to other land uses, and many forest fragments probably became isolated at this time. These remnants now exist as differently sized patches surrounded by large areas of oil palm *Elais guineensis* Jacq. plantation and other forms of agriculture. Butterflies on Borneo are diverse (*c.* 1000 species; Otsuka 1988), with many endemic and restricted-range species that are dependent on closed-canopy forest and do not occur in oil palm or other crops. Fragmentation of rain forests may thus be a particular threat to butterflies on Borneo.

In this study we examined the impacts of habitat fragmentation on the species richness and faunal composition of butterflies in tropical rain forests in Sabah. We analysed patterns of both α - and β -diversity to assess the relative importance of differences in patch size, isolation and vegetation structure on the diversity and similarity of species assemblages. We quantified the nestedness of species assemblages in different fragments; we used additive partitioning (Lande 1996; Veech *et al.* 2002) to assess the relative contributions of intact forest and forest remnants to overall species richness at a landscape scale; and we examined which traits of species best predict their responses to fragmentation.

Materials and methods

Butterflies were sampled between November 2001 and August 2003 at 10 sites in Sabah, comprising two widely separated control sites within a single large area (*c.* 1 million ha) of contiguous forest and eight sites within forest remnants varying in size from 120 ha to 120 000 ha (Fig. 1). Sites all comprised lowland rain forest in eastern Sabah, to reduce any residual effects of β -diversity prior to fragmentation. Sites were chosen to span the entire range of sizes of remaining forest fragments across Sabah and, at the time of sampling, these were surrounded by an agricultural landscape containing mainly oil palm. Isolation of each fragment, measured in terms of the minimum distance to contiguous forest using a regional map of Sabah, varied from 6 km to 69 km (Fig. 1; area and isolation of each site are also given in Table 1).

We sampled fruit-feeding nymphalid butterflies with traps baited with rotting banana (for details of trap design see DeVries 1987). This guild comprises approximately 75% of all nymphalid butterflies recorded on Borneo (Hill *et al.* 2001). We hung 20 traps at 100-m intervals along 2 km of transects at each site, and sampled butterflies for 12 consecutive days on two occasions, covering both wet and dry seasons (to account for seasonal variation in species abundance; Hamer *et al.* 2005) at each site (4800 trap days in total). All traps were > 200 m within forest and so data were unlikely to have been influenced by edge effects, which do not extend beyond 100 m from the margins of rain forest fragments for

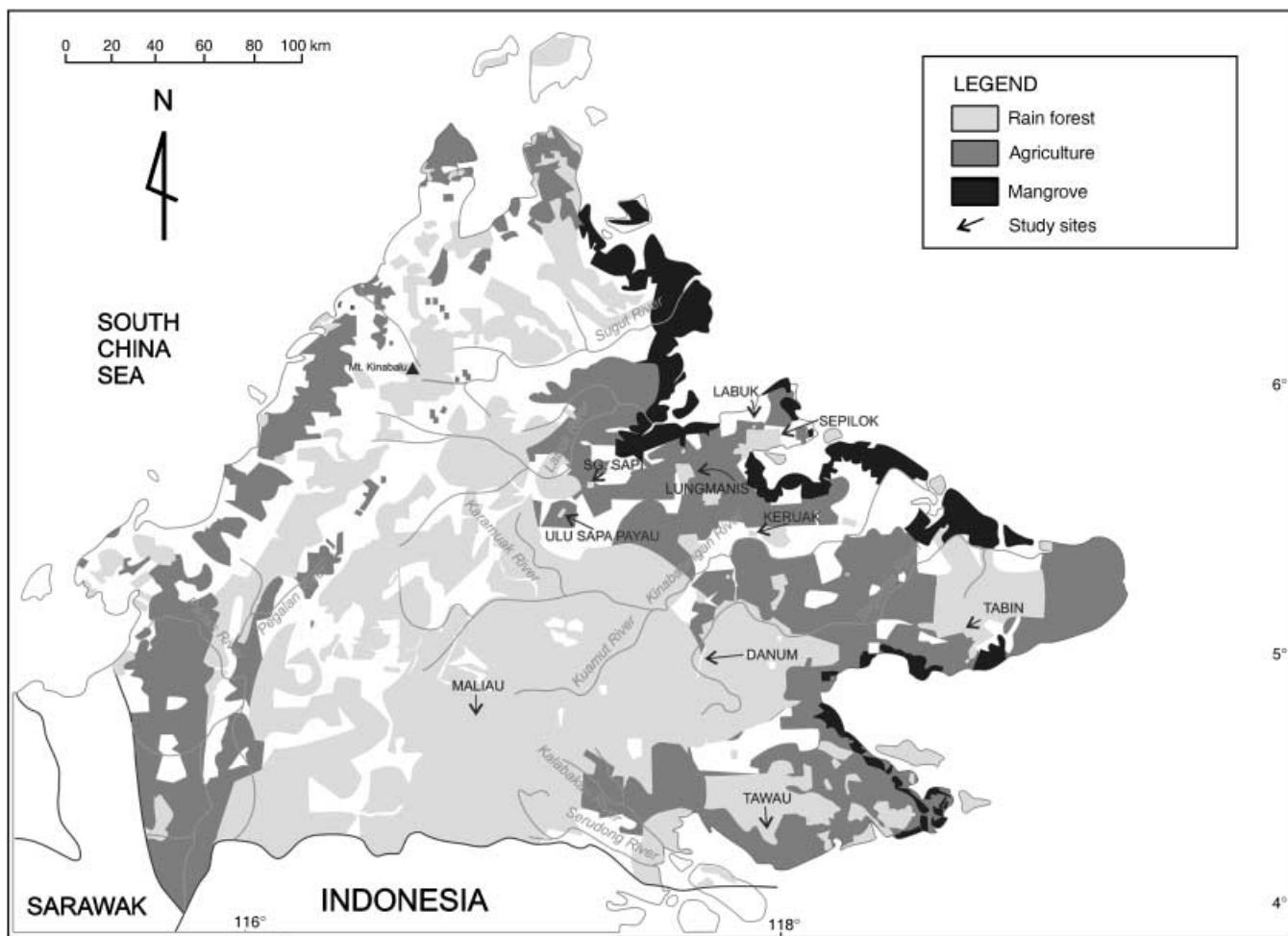


Fig. 1. Map of Sabah, Borneo, showing locations of study sites. Sizes of forest remnants: Tabin, 122 540 ha; Tawau, 91 590 ha; Sepilok, 4290 ha; Lungmannis, 3390 ha; Ulu Sapa Payau, 720 ha; Keruak, 640 ha; Sungai Sapi, 500 ha; Labuk, 120 ha.

plants or invertebrates (Didham 1997; Kapos *et al.* 1997). Bait was placed in traps on the day prior to the first sampling day, and was left in the trap for the rest of the sampling period. Fresh bait was added to each trap

every second day, thus ensuring that all traps contained a mixture ranging from fresh to well-rotted bait.

During each sampling period, traps were emptied daily and all trapped butterflies were identified where

Table 1. Area, isolation, vegetation characteristics and principal component of variation in vegetation structure in different-sized patches of lowland rain forest in Sabah, Borneo. Sites are listed in order of decreasing size: 1, Maliau; 2, Danum; 3, Tabin; 4, Tawau; 5, Sepilok; 6, Lungmannis; 7, Ulu Sapa Payau; 8, Keruak; 9, Sungai Sapi; 10, Labuk. See Fig. 1 for locations of sites within Sabah

Site	Log ₁₀ area (ha)	Isolation (km)	Trees				Vegetation cover (%)					
			Height		Density		Ground		Canopy		PRIN1	
			Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
1	6.00	–	42.5	8.5	4.00	0.00	36.3	19.4	77.5	14.8	2.09	0.54
2	6.00	–	32.8	9.3	4.00	0.00	40.0	21.8	36.6	18.0	0.86	0.71
3	5.09	56	21.1	6.4	2.45	1.15	67.8	21.0	42.5	17.9	–0.68	0.75
4	4.96	44	27.1	6.3	3.30	0.80	66.1	17.6	57.1	17.5	0.17	0.47
5	3.63	63	32.5	5.7	4.00	0.00	60.2	20.5	62.1	27.2	0.89	0.63
6	3.53	38	22.4	6.2	2.50	1.15	51.9	11.4	41.4	21.0	–0.28	0.77
7	2.86	6	21.7	6.4	3.05	1.05	75.0	19.6	40.0	19.8	–0.65	0.81
8	2.81	28	17.7	4.7	1.80	1.01	60.7	25.7	35.3	21.9	–1.02	0.76
9	2.70	25	17.9	6.9	2.35	1.23	63.3	26.7	60.2	26.7	–0.44	0.78
10	2.08	69	15.7	5.7	2.70	1.30	68.8	27.2	35.5	26.8	–0.94	0.92

possible in the field (following Otsuka 1988), marked with a felt-tipped pen and released. Individuals of the genera *Tanaecia* and *Euthalia* cannot be identified reliably in the field and were collected and identified in the laboratory using keys and figures in Corbet & Pendlebury (1992) and Otsuka (1988); where necessary, this included dissection of male genitalia. Data for each of the two sampling periods at each site were combined for analysis.

VEGETATION STRUCTURE

To characterize the structure of the vegetation at each site, the following data were collected at each of the 200 stations where traps were placed along transects: height of the two nearest trees (circumference > 0.6 m) within 30 m in each of four quadrats centred at the station (maximum of eight trees per station); number of quadrats with one or more trees within 30 m (maximum of four); estimated vegetation cover (%) at ground and canopy levels. Tree heights, to the nearest 2 m, were recorded as the means of at least two estimates taken by experienced recorders (Hamer *et al.* 2003) and calibrated against actual heights of a sample of trees measured with a clinometer. Vegetation cover, to the nearest 5%, was recorded as the mean of at least two independent estimates; these values generally varied among recorders by no more than 10%.

Vegetation measurements at the 200 sampling stations were normalized where necessary (i.e. arcsine transformation of percentages) and analysed by a principal components analysis (PCA; Pearman 2002; Hamer *et al.* 2003). This allowed ordination of differences among sites 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).

SPECIES RICHNESS AND TURNOVER

Obtaining complete inventories of species at each site was not possible and so, following Koh *et al.* (2002), we used a standardized sampling technique to determine species richness in terms of the number of species in a uniform sampling area. Species richness is highly sensitive to sample size and, even though sampling effort was standardized, sampling efficiency or total butterfly abundance may have varied across sites (Connor, Courtney & Yoder 2000). The numbers of species recorded at different sites could therefore have reflected the numbers of individuals sampled rather than the numbers of species inhabiting different patches. Hence as well as comparing species richness, we also examined species diversity using Margalef's index to account for variation in numbers of individuals sampled, following recommendations and formula in Magurran (1988); this index is largely independent of the underlying species abundance distributions. In addition we used a jack-knife estimate to assess the likely species pool

at each site, $S_{\max} \pm 1$ SE, from the number of species observed, S_{obs} , using the formula $S_{\max} = S_{\text{obs}} + a(n - 1/n)$ where n is the number of samples and a is the number of species in only one sample (Heltshel & Forrester 1983; Smith & van Belle 1984). To determine the stability of these estimates, we examined how S_{\max} changed with increasing sampling effort from 1 to 20 traps; each estimate of S_{\max} was the mean of 20 random selections from among the 20 traps sampled at each site, to remove sample order effects. We used stepwise multiple regression to relate each of our three estimates of species richness to patch area, isolation and vegetation structure.

To examine turnover of species, we calculated pairwise β -diversity between fragments, using Whittaker's index, $\beta_W = (S/\alpha) - 1$, where S is the total number of species at two sites and α is the average number of species per site. We then simultaneously related β -diversity to differences in patch size, distances between sites (measured from a regional map of Sabah) and differences in vegetation structure, using partial Mantel tests with 10 000 permutations (Manly 1997; Bonnet & Van de Peer 2002).

NESTEDNESS OF SPECIES ASSEMBLAGES AND PARTITIONING OF DIVERSITY

To determine whether or not species persistence and colonization patterns created nested species assemblages, we constructed a presence-absence matrix (1 = present, 0 = absent), where columns and rows represented species and sites, respectively. To reduce sampling error, we restricted this analysis to 48 species where the total number of individuals sampled ≥ 5 , following Hamer *et al.* (2003). 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. We then used a nestedness calculator (Atmar & Patterson 1995) to rank sites according to their species richness and species according to their ubiquity, and to quantify the nestedness of the resulting maximally packed matrix. The metric is described as a measure of heat disorder, calculated from the distribution of 'unexpected' species presences and absences within the matrix, and ranging from 0° (maximum order) to 100° (disorder).

To examine the contributions of different fragments to overall butterfly diversity, we used additive partitioning (Crist *et al.* 2003; Gering, Crist & Veech 2003) in which observed species richness and diversity were partitioned into positive, additive components within sites (α_i), between sites of similar sizes (β_i) and between sites of different sizes (β_s). This resulted in α and β diversity being expressed in the same units, allowing a direct assessment of their relative contributions to overall (γ) diversity.

DETERMINANTS OF SPECIES' RESPONSES TO FRAGMENTATION

To assess the importance of different traits in determining the responses of species to forest fragmentation, we

compared the population densities of species in contiguous forest and large forest remnants (> 90 000 ha; four sites in total, hereafter termed large sites) with those in small fragments (six sites < 5000 ha). Sampling effort was constant across sites and so we used the number of butterflies of a species sampled at each site as an index of population density. The percentage difference in density between large sites and small fragments was calculated for each of the 48 species with $n \geq 5$, as [(mean density in small fragments – mean density in large sites)/mean (density in small fragments + density in large sites)] \times 50 (modified from Shahabuddin & Ponte 2005). The resulting fragmentation response index (FRI) was negative for species with lower densities in small fragments and positive for species with lower densities in large sites, with a maximum range of –100 (species only in large sites) to +100 (species only in small fragments).

We used generalized linear models (GLMs) to examine how FRI of each species was related to the following traits, chosen a priori as potential correlates of responses to habitat fragmentation (Koh, Sodhi & Brook 2004a; Shahabuddin & Ponte 2005): (i) adult body size (forewing length measured to the nearest 0.1 mm with vernier callipers); (ii) larval host-plant specificity (narrow, all host-plants in single family; broad, exploits two or more families of host-plants; data for 38 species from Robinson *et al.* 2001); (iii) geographical distribution [endemic, occurs only Borneo; narrow, restricted to Sundaland (West Malaysia and islands of Sunda Shelf, comprising Borneo, Sumatra, Java, Bali and Palawan); moderate, restricted to Oriental region (bounded by Ethiopian region in west, Palaearctic region in north and Australasian region in east); wide, occurs beyond the Oriental region; from Tsukada 1982]. Larval host-plant specificity and geographical distribution were included in the model as fixed effects, with wing length as a covariate.

The lack of phylogenetic information for south-east Asian butterflies precluded the use of phylogenetic contrasts or related statistical techniques (Harvey & Pagel 1991) to control for phylogenetic non-independence. As an alternative, following Koh, Sodhi & Brook (2004a), we included subfamily as a fixed effect in our analysis. A single genus of Satyriinae (*Mycalesis*) was represented by 11 species (two endemic, seven with narrow distributions and two with moderate distributions; see Appendix S1 in the supplementary material). To avoid any phylogenetic bias at the level of genus, these species were conservatively condensed into three cases (one each with endemic, narrow and moderate distributions), using mean values for wing length and FRI (no species of *Mycalesis* exploited > 1 family of larval host-plants). The resulting data set contained 30 species from 23 genera (mean 1.3 species genus⁻¹) and so any phylogenetic non-independence at the level of genus was unlikely to have influenced our analysis. Results are presented for the condensed set of 30 species with $n \geq 5$; retaining separate information for all 11 species of *Mycalesis* did not qualitatively affect the results.

Results

VEGETATION STRUCTURE

PCA extracted a single component of variation (PRIN1) that accounted for 71% of variation in the vegetation data (Table 1). This factor increased with (in order from greatest to least importance) increasing canopy height, increasing density of trees, decreasing ground cover and increasing canopy cover (weightings of standardized variables were 0.98, 0.87, –0.76 and 0.75, respectively). A high PRIN1 score thus represented tall dense forest with a closed canopy and little ground vegetation. PRIN1 was significantly higher in contiguous protected forest (mean = 1.47, $n = 2$, $SD \pm 0.87$) than in forest remnants (mean = –0.37, $n = 8$, $SD \pm 0.63$; t -test using equal variance estimate; $t_8 = 3.5$, $P < 0.01$) but was not related to remnant size (Pearson correlation with \log_{10} area; $r = 0.41$, $n = 8$, $P = 0.3$).

SPECIES RICHNESS AND TURNOVER

Excluding recaptures, we sampled 6833 individuals of 84 species of butterfly across 10 forest sites. The number of species in forest remnants was significantly positively related to \log_{10} area and significantly negatively related to isolation (minimum distance to intact forest; stepwise multiple regression; $F_{2,5} = 24.0$, $P < 0.01$, $R^2 = 0.91$) according to the following equation: species richness = 4.86 (SE ± 0.79) \log_{10} area – 0.17 (SE ± 0.04) isolation + 19.38 (SE ± 2.96).

Patch area accounted for 54% of the variation in species richness, and isolation for an additional 37%. There was no relationship with vegetation structure (PRIN1).

Estimated total species richness, S_{\max} , increased with the number of traps sampled and was reasonably stable as final sampling effort was approached (Fig. 2). Comparison of final estimates of S_{\max} with numbers of species observed indicated that on average we detected 77% of the species present at each site (range = 69–84%). S_{\max}

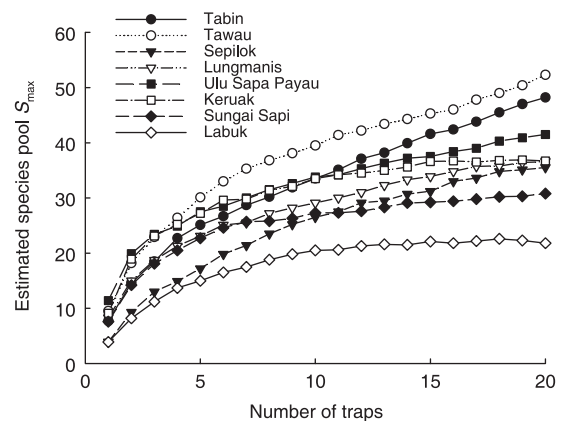


Fig. 2. Species accumulation curves showing changes in estimated size of species pool S_{\max} with increasing sampling effort for fruit-feeding butterflies in rain forest patches in Sabah, Borneo.

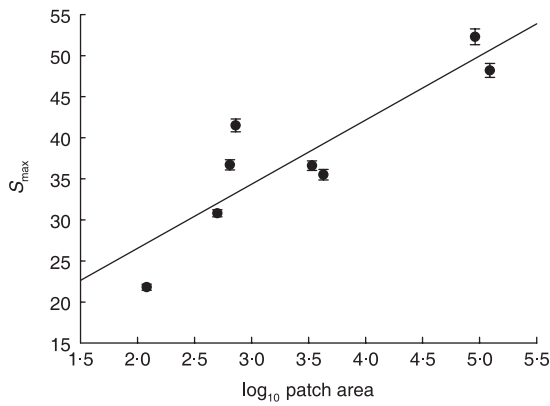


Fig. 3. Final estimated size of species pool $S_{max} \pm 1$ SE for fruit-feeding butterflies in rain forest patches in Sabah, Borneo, in relation to \log_{10} patch area.

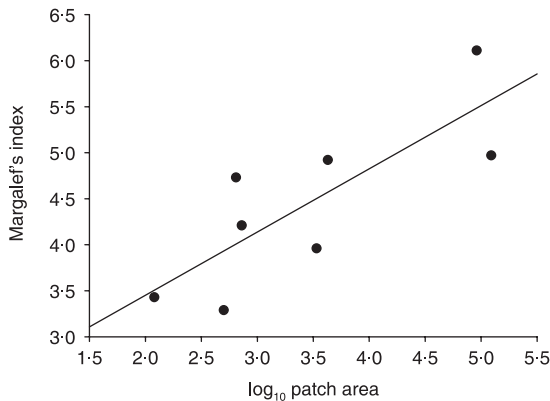


Fig. 4. Margalef's index of species richness for fruit-feeding butterflies in rain forest patches in Sabah, Borneo, in relation to \log_{10} patch area.

was significantly positively related to \log_{10} area and negatively related to isolation ($F_{2,5} = 35.9$, $P = 0.001$, $R^2 = 0.94$; Fig. 3) according to the following equation: $S_{max} = 8.61$ (SE ± 1.04) \log_{10} area $- 0.18$ (SE ± 0.05) isolation $+ 15.68$ (SE ± 3.89).

Patch area accounted for 78% of the variation in S_{max} and isolation for an additional 16%.

Table 2. Pairwise β -diversity of butterflies (below diagonal) and linear distances (km, above diagonal) between patches of lowland rain forest in Sabah, Borneo. Sites are listed in order of decreasing size: 1, Maliau; 2, Danum Valley; 3, Tabin; 4, Tawau; 5, Sepilok; 6, Lungmannis; 7, Ulu Sapa Payau; 8, Keruak; 9, Sungai Sapi; 10, Labuk. See Fig. 1 for locations of sites

Site	1	2	3	4	5	6	7	8	9	10
1		100	213	131	178	134	88	138	106	166
2	0.50		113	78	97	78	82	53	88	103
3	0.49	0.46		116	116	141	181	103	172	125
4	0.47	0.41	0.49		166	150	156	119	159	166
5	0.60	0.48	0.51	0.49		38	91	38	78	10
6	0.58	0.53	0.52	0.59	0.47		56	38	41	34
7	0.63	0.61	0.57	0.60	0.40	0.54		81	20	84
8	0.66	0.54	0.47	0.51	0.36	0.46	0.43		69	44
9	0.58	0.57	0.46	0.53	0.41	0.35	0.28	0.33		72
10	0.65	0.58	0.57	0.64	0.57	0.63	0.52	0.51	0.41	

Margalef's index of species diversity increased significantly with \log_{10} area (Fig. 4; $F_{1,6} = 11.0$, $P = 0.02$, $R^2 = 0.65$) but was not related to isolation or vegetation structure. Species richness and diversity in the largest forest remnants were no different to those in intact forest ($t_2 = 2.0$, $P = 0.2$; $t_2 = 2.7$, $P = 0.1$; $t_2 = 1.3$, $P = 0.3$; for number of species, S_{max} and Margalef's index, respectively).

Excluding species with < 5 individuals sampled, two species were recorded only in contiguous forest and 16 species only in forest remnants (see Appendix S1 in the supplementary material). β -diversity between sites, including contiguous forest, was positively correlated with difference in size (Table 2; partial Mantel test; $r = 0.52$, $P < 0.01$) and in PRIN1 score ($r = 0.39$, $P = 0.03$) but not with distance apart ($r = 0.20$, $P = 0.18$).

NESTEDNESS AND COMPLEMENTARITY OF SPECIES ASSEMBLAGES

The species occupancy data, excluding species with $n < 5$, filled 44% of the overall species-by-site matrix. Species assemblages were significantly nested: the mean temperature of 500 matrices drawn at random (57° , $SD \pm 5$) was significantly greater than that observed ($P = 0.01$), indicating that local extinction and colonization events were to some extent predictable across different species, from the most species-rich to the most depauperate site. None the less, the observed matrix temperature was high (46.0°), indicating a substantial departure from perfect nestedness (Fig. 5).

Additive partitioning of diversity data indicated that α -diversity within sites comprised 34% of total species richness and 47% of total species diversity (Margalef's index) across all sites. β -diversity between sites of similar size comprised 20% of species richness and diversity. β -diversity between sites of different size comprised 46% of species richness and 33% of species diversity (Fig. 6). Hence diversity within sites was less than that between sites, and the majority of the diversity between sites was related to variation in fragment size.

ECOLOGICAL DETERMINANTS OF RESPONSES TO FRAGMENTATION

There was a significant relationship between FRI and larval host-plant specificity (GLM; $F_{1,15} = 6.0$, $P = 0.02$), indicating that species with a single host-plant family were less abundant on average in small fragments (mean FRI = -24 , $n = 19$, $SD \pm 73$) whereas species with two or more families of host-plant were more abundant in small fragments (mean = 46 , $n = 11$, $SD \pm 52$). There was also a marginally significant effect of wing length ($F_{1,15} = 3.8$, $P = 0.06$), with a positive relationship, indicating a tendency for smaller species to be more abundant and larger species to be less abundant in small fragments. No other variables or interactions were significant ($P > 0.5$ in all cases). However, across all species with $n \geq 5$, there was a significant positive relationship between

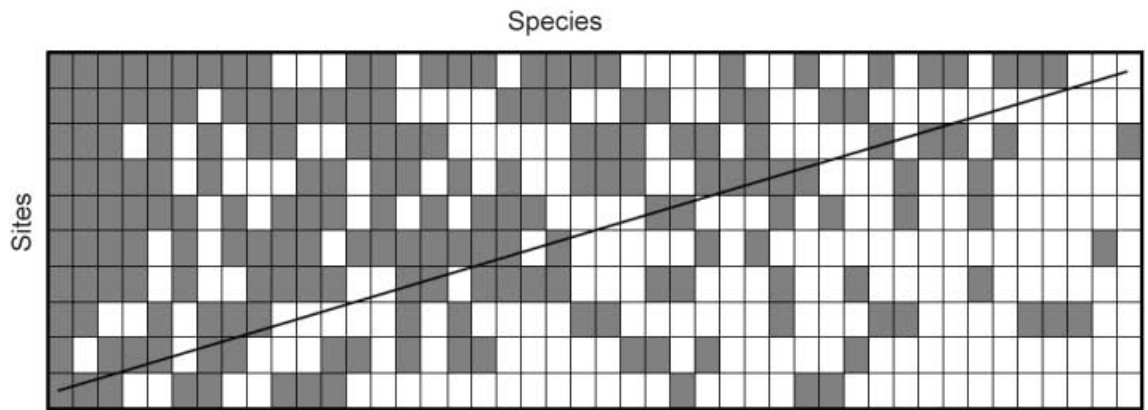


Fig. 5. Maximally ordered species presence–absence matrix for fruit-feeding butterflies in rain forest patches in Sabah, Borneo. Filled squares indicate presences, white squares indicate absences; five species present at all 10 sites have been compressed into a single column. In a perfectly nested matrix, all occupied sites would be above the diagonal line. Despite highly significant nestedness, there were a number of unexpected presences and absences, especially for uncommon species.

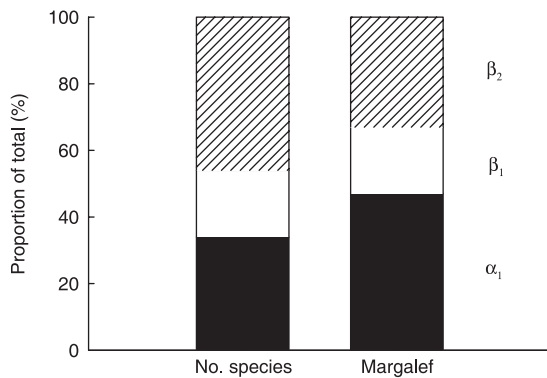


Fig. 6. Partitioning of species richness and diversity into separate components. α_1 (black bars), diversity within sites; β_1 (pale bars), diversity between sites of similar size; β_2 (grey bars), diversity between sites of different sizes.

geographical distribution and larval host-plant specificity (Spearman correlation; $r_s = 0.37$, $n = 48$, $P = 0.01$), suggesting that these two variables may have covaried in their relationship with FRI.

Discussion

COLLECTION OF DATA

During the study we caught a total of 6833 individuals from 84 species (see Appendix S1 in the supplementary material). This included 30 species in contiguous primary forest at Danum, which is 50% of the total number of fruit-feeding species recorded at this site from extensive sampling at both ground and canopy levels over a period of > 5 years (see appendices in Hill *et al.* 2001; Hamer *et al.* 2003; Dumbrell & Hill 2005; Hamer *et al.* 2006). These data suggest that about half the species present within intact forest were recorded in our study. Estimates of total species richness S_{\max} suggested that about three-quarters of the species present were observed during the study in both intact forest and forest remnants. Thus S_{\max} probably underestimated true species richness but did not appear to have been biased with respect to

fragment size. The probability of being sampled increases with population density, and so our data provide an assessment of variation in population densities in addition to permitting a comparison of species richness and turnover among sites. Analyses of nestedness and responses to fragmentation could have been affected by stochastic variation in sampling success but this problem was greatly reduced by restricting these analyses to species with $n \geq 5$ (Hamer *et al.* 2003). Although traps caught only one guild of butterflies, they avoided the problems of species identification that can be encountered using walk-and-count transect techniques in highly diverse regions (Walpole & Sheldon 1999).

ALPHA- AND BETA-DIVERSITY

Larger forest remnants had greater species richness in terms of the observed number of species, the estimated species pool S_{\max} and Margalef's index (Figs 3 and 4). More than half the individuals recorded at some sites were of a single species, *Amathusia phiddipus* (see Appendix S1 in the supplementary material). However, this did not bias our analysis; there was no relationship between \log_{10} fragment area and either the number of individuals recorded or the proportion of individuals comprising *A. phiddipus* (Pearson correlations following arcsine transformation of proportions, $r = -0.25$, $n = 8$, $P = 0.6$ and $r = -0.15$, $n = 8$, $P = 0.7$, respectively). Several authors have suggested that species–area relationships could be primarily a reflection of habitat diversity (Ricklefs & Lovette 1999; Fox & Fox 2000). Although all sites in our study comprised a single habitat, there could none the less have been greater variation in vegetation characteristics in larger remnants of forest. However, vegetation factor scores were equally variable in different remnants and there was no relationship between vegetation structure and species richness. Thus the observed pattern probably reflected patch size *per se* more than habitat diversity, as also found in other recent studies of tropical insects (Davies & Smith 1997; Peck, Wigfull & Nishida 1999; Koh *et al.* 2002).

Slopes of species–area relationships for habitat islands are generally lower than those for true islands, and this difference has been ascribed to the occasional immigration of individuals from source populations rescuing those at marginal ‘sink’ sites from extinction (Connor & McCoy 1979; Hanski 1999). In our study, there was a significant negative effect of isolation on the species richness of forest remnants, which suggests that there may have been occasional immigration into fragments across the surrounding matrix of oil palm and other crops. Several recent studies have stressed how variation in matrix characteristics can alter the effective isolation of habitat fragments for different species (Ricketts 2001; Dunford & Freemark 2005), and four of the species that we recorded in fragments were also recorded regularly in oil palm (*Elymnias esaea*, *Melanitis leda*, *Mycalesis mineus* and *Amathusia phiddipus*; Benedick 2005). However, most of the species that we sampled in remnants are confined to closed-canopy rain forest and do not normally occur in oil palm or other crops.

We recorded 45 species in forest remnants that were not sampled in contiguous forest. Of these, 31 species (marked with an asterisk in Appendix S1 in the supplementary material) have been recorded occasionally in small numbers during > 5 years of intensive sampling in contiguous forest at Danum. These species presumably occur only at low density in contiguous forest, and increased in density following fragmentation probably because they were able to exploit altered conditions (e.g. lower density of trees, lower, more open canopy and greater ground vegetation) in forest remnants. This notion is supported by the finding that β -diversity between sites was significantly related to the difference in vegetation structure. β -diversity could also to some extent have reflected differences in assemblages prior to fragmentation, although any such effect was probably small because all sites comprised lowland rain forest and β -diversity between sites was not related to distance apart.

Species assemblages were significantly nested but they none the less departed substantially from perfect nestedness, with some species found only or predominantly in small depauperate remnants (Fig. 5), as also found for forest butterflies on tropical islands (Shahabuddin & Terborgh 1999; Davidar, Yoganand & Ganesh 2002). As a result, diversity between sites was greater than that within sites. Moreover, the majority of the diversity between sites was related to variation in fragment size (Fig. 6). Thus fragments of different sizes made a valuable contribution to the landscape-scale species richness of tropical forest butterflies. We estimate that c. 25–50% of species present at each site were not detected during the study and, while these may have included some common species that seldom feed on fruit (Hamer *et al.* 2006), the majority of undetected species probably occurred at low density. Apparent departures from perfect nestedness can result from sampling error if species that occur at low density are recorded by chance at one site but not another. However, this problem was reduced by restricting the nestedness

analysis to species with $n \geq 5$. Moreover, species that occur at low density are also the least likely to be present at two or more locations (Cam *et al.* 2000) and so the true departure from perfect nestedness was probably greater than we recorded.

DETERMINANTS OF RESPONSES TO FRAGMENTATION

Responses of individual species to fragmentation were to some extent predictable from species' traits, which is consistent with the finding that species assemblages were significantly nested. The most important determinant of FRI in our study was larval host-plant specificity. This supports a similar finding for extinction-proneness of butterflies on tropical islands (Koh, Sodhi & Brook 2004a) and is consistent with the notion that species with narrow ecological niches are less able to adapt to rapid changes in environmental conditions, such as those associated with habitat loss and degradation (Purvis *et al.* 2000a; Koh, Sodhi & Brook 2004a). Species with a narrow range of host-plants are presumably more vulnerable to co-extinctions (Koh, Sodhi & Brook 2004b) in addition to being less able to exploit new opportunities arising from changes in plant assemblages following forest fragmentation.

In addition to host-plant specificity, there was also a weak, marginally significant effect of body size on FRI in our study, with larger species more adversely affected by rain forest fragmentation. Some previous studies have similarly found that increases in body size are associated with an increase in extinction risk in vertebrates (Bennett & Owens 1997; Purvis *et al.* 2000b) and in butterflies (Shahabuddin & Ponte 2005), possibly associated with greater resource requirements or a greater tendency to disperse away from habitat fragments in larger species. However, other studies found no relationship (for vertebrates, Foufopoulos & Ives 1999; Munoz-Duran 2002; for butterflies, Koh, Sodhi & Brook 2004a). Moreover, because body size is strongly correlated with a wide range of life-history traits, any relationship with body size is difficult to interpret.

We found no relationship between species' geographical distributions and FRI. However, a number of previous authors have suggested that species with narrow geographical distributions may be less able to adapt to changing environmental conditions within rain forests (Hill *et al.* 1995; Hamer *et al.* 1997; Hamer *et al.* 2003; Koh, Sodhi & Brook 2004a) and the absence of any additional effect of geographical distribution on FRI in our study was probably because of a significant positive relationship between geographical distribution and host-plant specificity.

IMPLICATIONS FOR CONSERVATION MANAGEMENT

Small isolated forest remnants were relatively species poor and showed the least similarity to intact forest. Moreover,

no endemic species were recorded in any remnants smaller than 4000 ha. These findings lend support to the common practice of targeting conservation strategies primarily around patch size and isolation. On the other hand, forest remnants supported relatively large populations of species found only at low density in intact forest, and diversity between sites of different size was up to half the total diversity across all sites. While there were no endemic species in small fragments, even the smallest remnants supported species with geographical distributions restricted within Sundaland. This may not have been true of fragments smaller than the ones we analysed, but our study encompassed the range of sizes of remaining forest fragments in Sabah and the smallest fragment we studied (120 ha) was not atypical of non-experimental forest fragment sizes elsewhere in the tropics. Small isolated forest remnants are generally accorded low conservation status and given little protection, with the result that they often disappear over time because of continued anthropogenic disturbance. The results of this study indicate that the importance of small remnants of forest, in particular their contribution to environmental heterogeneity (Benton, Vickery & Wilson 2003; Hamer *et al.* 2003; Fischer & Lindenmayer 2005), should not be overlooked.

Acknowledgements

We thank Yayasan Sabah (Forestry Division), Danum Valley Management Committee, the State Secretary (Internal Affairs and Research Office), Sabah Chief Minister's Department and the Economic Planning Unit of the Prime Minister's Department, Kuala Lumpur, for permission to conduct research in Sabah. We thank Glen Reynolds and Nasir bin Abdul Majid (Danum Valley Field Centre), Joseph Tangah (Forest Research Centre) and staff at Sabah Wildlife Department and Sabah Parks for logistical support, advice and assistance with collection of data. This paper is based on research carried out whilst the authors were participants in the Royal Society's South-east Asia Rainforest Research Programme and was supported by the UK government's Darwin Initiative (DEFRA).

References

- Atmar, W. & Patterson, D.B. (1995) *The Nestedness Temperature Calculator: A Visual Basic Program, Including 294 Presence–Absence Matrices*. AICS Research Incorporate and the Field Museum.
- Benedick, S. (2005) *Impacts of tropical forest fragmentation on fruit-feeding Nymphalid Butterflies in Sabah, Borneo*. Unpublished PhD Thesis. University Malaysia Sabah, Sabah, Malaysia.
- Bennett, P.M. & Owens, I.P.F. (1997) Variation in extinction risk among birds: chance or evolutionary predisposition? *Proceedings of the Royal Society of London Series B*, **264**, 401–408.
- Benton, T.G., Vickery, J.A. & Wilson, J.D. (2003) Farmland biodiversity: is habitat heterogeneity the key? *Trends in Ecology and Evolution*, **18**, 182–188.
- Berglund, H. & Jonsson, B.G. (2003) Nested plant and fungal

- communities; the importance of area and habitat quality in maximizing species capture in boreal old-growth forests. *Biological Conservation*, **112**, 319–328.
- Boecklen, W.J. (1997) Nestedness, biogeographic theory, and the design of nature reserves. *Oecologia*, **112**, 123–142.
- Bolger, D.T., Alberts, A.C. & Soulé, M.E. (1991) Occurrence patterns of bird species in habitat fragments: sampling, extinction, and nested species subsets. *American Naturalist*, **137**, 155–166.
- Bonnet, E. & Van de Peer, Y. (2002) Zt: a software tool for simple and partial Mantel tests. *Journal of Statistical Software*, **7**, 1–12.
- Brook, B.W., Sodhi, N.S. & Ng, P.K.L. (2003) Catastrophic extinctions follow deforestation in Singapore. *Nature*, **424**, 420–423.
- Cam, E., Nichols, J.D., Hines, J.E. & Sauer, J.R. (2000) Inferences about nested subsets structure when not all species are detected. *Oikos*, **91**, 428–434.
- Connor, E.F. & McCoy, E.D. (1979) The statistics and biology of the species–area relationship. *American Naturalist*, **113**, 791–833.
- Connor, E.F., Courtney, A.C. & Yoder, J.M. (2000) Individuals–area relationships: the relationship between animal population density and area. *Ecology*, **81**, 734–748.
- Corbet, A.S. & Pendlebury, H.M. (1992) *The Butterflies of the Malay Peninsula*, 4th edn. Malayan Nature Society, Kuala Lumpur, Malaysia.
- Crist, T.O., Veech, J.A., Gering, J.C. & Summerville, K.S. (2003) Partitioning species diversity across landscapes and regions: a hierarchical analysis of α , β and γ diversity. *American Naturalist*, **162**, 734–743.
- Davidar, P., Yoganad, K., Ganesh, T. & Devy, S. (2002) Distributions of forest birds and butterflies in the Andaman Islands, Bay of Bengal: nested patterns and processes. *Ecography*, **25**, 5–16.
- Davies, N. & Smith, D.S. (1997) Munroe revisited: a survey of West Indian butterfly faunas and their species–area relationship. *Global Ecology and Biogeography Letters*, **7**, 285–294.
- Davis, A.J., Holloway, J.D., Huijbrechts, 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.
- DeVries, P.J. (1987) *The Butterflies of Costa Rica and Their Natural History, Volume 1. Papilionidae, Pieridae and Nymphalidae*. Princeton University Press, Princeton, NJ.
- Didham, R.K. (1997) The influence of edge effects and forest fragmentation on leaf litter invertebrates in Central Amazonia. *Tropical Forest Remnants: Ecology, Management and Conservation of Fragmented Communities* (eds W.F. Laurance & R.O. Bierregaard), pp. 55–70. University of Chicago Press, Chicago, IL.
- Dumbrell, A.J. & Hill, J.K. (2005) Impacts of selective logging on ground and canopy assemblages of tropical forest butterflies: implications for sampling. *Biological Conservation*, **125**, 123–131.
- Dunford, W. & Freemark, K. (2005) Matrix matters: effects of surrounding land uses on forest birds near Ottawa, Canada. *Landscape Ecology*, **20**, 497–511.
- Ewers, R.M. & Didham, R.K. (2006) Confounding factors in the detection of species responses to habitat fragmentation. *Biological Reviews*, **81**, 117–142.
- Fischer, J. & Lindenmayer, D.B. (2005) Perfectly nested or significantly nested: an important difference for conservation management. *Oikos*, **109**, 485–494.
- Fleishman, E. & MacNally, R. (2002) Topographic determinants of faunal nestedness in Great Basin butterfly assemblages: applications to conservation planning. *Conservation Biology*, **16**, 422–429.
- Foufopoulos, J. & Ives, J.R. (1999) Reptile extinctions on land-bridge islands: life-history attributes and vulnerability to extinction. *American Naturalist*, **153**, 1–25.

- Fox, B.J. & Fox, M.D. (2000) Factors determining mammal species richness on habitat islands and isolates: habitat diversity, disturbance, species interactions and guild assembly rules. *Global Ecology and Biogeography*, **9**, 19–37.
- Gering, J.C., Crist, T.O. & Veech, J.A. (2003) Additive partitioning of species diversity across multiple spatial scales: implications for regional conservation of biodiversity. *Conservation Biology*, **17**, 488–499.
- Groombridge, B. & Jenkins, M.D. (2000) *Global Biodiversity: Earth's Living Resources in the 21st Century*. World Conservation Press, Cambridge, UK.
- Hamer, K.C., Hill, J.K., Benedick, S., Mustafa, N., Chey, V.K. & Mohamed, M. (2006) Diversity and ecology of carrion- and fruit-feeding butterflies in Bornean rainforest. *Journal of Tropical Ecology*, **22**, 25–33.
- Hamer, K.C., Hill, J.K., Benedick, S., Mustafa, N., Sherratt, T.N., Maryati, M. & Chey, V.K. (2003) Ecology of butterflies in natural and selectively logged forests of northern Borneo: the importance of habitat heterogeneity. *Journal of Applied Ecology*, **40**, 150–162.
- 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.
- Hamer, K.C., Hill, J.K., Mustafa, N., Benedick, S., Sherratt, T.N., Chey, V.K. & Maryati, M. (2005) Temporal variation in abundance and diversity of butterflies in Bornean rain forests: opposite impacts of logging recorded in different seasons. *Journal of Tropical Ecology*, **21**, 1–9.
- Hanski, I. (1999) *Metapopulation Ecology*. Oxford University Press, Oxford, UK.
- Harvey, P.H. & Pagel, M.D. (1991) *The Comparative Method in Evolutionary Biology*. Oxford University Press, Oxford, UK.
- Heltshe, J.F. & Forrester, N.E. (1983) Estimating species richness using the jackknife procedure. *Biometrics*, **39**, 1–11.
- 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.
- Kapos, V., Wandelli, E., Camargo, J.L. & Ganade, G. (1997) Edge-related changes in environment and plant responses due to forest fragmentation in Central Amazonia. *Tropical Forest Remnants: Ecology, Management and Conservation of Fragmented Communities* (eds W.F. Laurance & R.O. Bierregaard), pp. 33–44. University of Chicago Press, Chicago, IL.
- Karr, J.R. (1982) Avian extinction on Barro Colorado Island, Panama: a reassessment. *American Naturalist*, **119**, 220–239.
- Kattan, G.H. (1992) Rarity and vulnerability: the birds of Codillera Central of Columbia. *Conservation Biology*, **6**, 64–70.
- Koh, L.P., Sodhi, N.S. & Brook, B.W. (2004a) Ecological correlates of extinction proneness in tropical butterflies. *Conservation Biology*, **18**, 1571–1578.
- Koh, L.P., Sodhi, N.S. & Brook, B.W. (2004b) Co-extinctions of tropical butterflies and their host plants. *Biotropica*, **36**, 272–274.
- Koh, L.P., Sodhi, N.S., Tan, H.T.W. & Peh, K.S.-H. (2002) Factors affecting the distribution of vascular plants, spring-tails, butterflies and birds on small tropical islands. *Journal of Biogeography*, **29**, 93–108.
- Lande, R. (1996) Statistics and partitioning of species diversity, and similarity among multiple communities. *Oikos*, **76**, 5–13.
- Laurance, W.F. (1990) Comparative responses of five arboreal marsupials to tropical forest fragmentation. *Journal of Mammalogy*, **71**, 641–653.
- Laurance, W.F. & Bierregaard, R.O. (1997) *Tropical Forest Remnants: Ecology, Management and Conservation of Fragmented Communities*. University of Chicago Press, Chicago, IL.
- Lens, L., Van Dongen, S., Norris, K., Githiru, M. & Matthysen, E. (2002) Avian persistence in fragmented rainforest. *Science*, **298**, 1236–1238.
- Lovejoy, T.E., Bierregaard, R.O., Rylands, A.B., Malcolm, J.R., Quintela, C.E., Harper, L.H., Brown, K.S., Powell, A.H., Powell, G.V.N., Schubart, H.O. & Hays, M.B. (1986) Edge and other effects of isolation on Amazon forest fragments. *Conservation Biology: the Science of Scarcity and Diversity* (ed. M.E. Soulé), pp. 257–285. Sinauer, Sunderland, MA.
- MacArthur, R.H. & Wilson, E.O. (1967) *The Theory of Island Biogeography*. Princeton University Press, Princeton, NJ.
- McMorrow, J. & Talip, M.A. (2001) Decline of forest area in Sabah, Malaysia: relationship to state policies, land code and land capability. *Global Environmental Change*, **11**, 217–230.
- Magurran, A.E. (1988) *Ecological Diversity and its Measurement*. Croom-Helm, London, UK.
- Manly, B.F.J. (1997) *Randomization, Bootstrap and Monte Carlo Methods in Biology*, 2nd edn. Chapman & Hall, London, UK.
- Michalski, F. & Peres, C.A. (2005) Anthropogenic determinants of primate and carnivore local extinctions in a fragmented forest landscape of southern Amazonia. *Biological Conservation*, **124**, 383–396.
- Munoz-Duran, J. (2002) Correlates of speciation and extinction rates in the Carnivora. *Evolutionary Ecology Research*, **1**, 549–565.
- Otsuka, K. (1988) *Butterflies of Borneo, I*. Tobishima Corporation, Tokyo, Japan.
- Patterson, B.D. (1987) The principle of nested subsets and its implications for biological conservation. *Conservation Biology*, **1**, 323–334.
- Pearman, P.B. (2002) The scale of community structure: habitat variation and avian guilds in tropical forest understorey. *Ecological Monographs*, **72**, 19–39.
- Peck, S.B., Wigfull, P. & Nishida, G. (1999) Physical correlates of insular species diversity: the insects of the Hawaiian islands. *Annals of the Entomological Society of America*, **92**, 529–536.
- Peitinger, M., Bergamini, A. & Schmid, B. (2003) Species–area relationships and nestedness of four taxonomic groups in fragmented wetlands. *Basic and Applied Ecology*, **4**, 385–394.
- Purvis, A., Agapow, P.-M., Gittleman, J.L. & Mace, G.M. (2000a) Non-random extinction and the loss of evolutionary history. *Science*, **288**, 328–330.
- Purvis, A., Gittleman, J.L., Cowlshaw, G. & Mace, G.M. (2000b) Predicting extinction risk in declining species. *Proceedings of the Royal Society of London Series B*, **267**, 1947–1952.
- 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.
- Ricketts, T.H. (2001) The matrix matters: effective isolation in fragmented landscapes. *American Naturalist*, **158**, 87–99.
- Ricklefs, R.E. & Lovette, I.J. (1999) The roles of island area *per se* and habitat diversity in the species–area relationships of four Lesser Antillean faunal groups. *Journal of Animal Ecology*, **68**, 1142–1160.
- Robinson, G.S., Ackery, P.R., Kitching, I.J., Beccaloni, G.W. & Hernandez, L.M. (2001) *Hostplants of the Moth and Butterfly Caterpillars of the Oriental Region*. The Natural History Museum, London, UK.
- Shahabuddin, G. & Ponte, C.A. (2005) Frugivorous butterfly species in tropical forest fragments: correlates of vulnerability

- to extinction. *Biodiversity and Conservation*, **14**, 1137–1152.
- 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.
- Smith, E.P. & van Belle, G. (1984) Non-parametric estimation of species richness. *Biometrics*, **40**, 119–129.
- Soulé, M.E., Bolger, D.T., Alberts, A.C., Wright, J., Sorice, M. & Hills, S. (1988) Reconstructed dynamics of rapid extinctions of chaparral requiring birds in urban habitat islands. *Conservation Biology*, **2**, 75–92.
- Tsukada, E. (1982) *Butterflies of the South East Asian Islands. Volumes 3–5*. Plapac Company, Tokyo, Japan.
- Turner, I.M. (1996) Species loss in fragments of tropical rain forest: a review of the evidence. *Journal of Applied Ecology*, **33**, 200–209.
- Veech, J.A., Summerville, K.S., Crist, T.O. & Gering, J.C. (2002) The additive partitioning of diversity: recent revival of an old idea. *Oikos*, **99**, 3–9.
- Walpole, M.J. & Sheldon, I.R. (1999) Sampling butterflies in tropical rainforest: an evaluation of a transect walk method. *Biological Conservation*, **87**, 85–91.
- Wright, D.H., Patterson, B.D., Mikkelsen, G.M., Cutler, A. & Atmar, T. (1998) A comparative analysis of nested subset patterns of species composition. *Oecologia*, **113**, 1–20.

Received 28 October 2005; final copy received 23 May 2006

Editor: Rob Freckleton

Supplementary material

The following supplementary material is available as part of the online article (full text) from <http://www.blackwell-synergy.com>.

Appendix S1. Butterfly species sampled at each site.