

Butterfly species richness and community composition in forests affected by ENSO-induced burning and habitat isolation in Borneo

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Abstract: Landscape-scale studies of community traits such as species richness and community composition are sorely needed to explore the impact of large-scale disturbance events such as ENSO (El Niño Southern Oscillation)-induced burning and habitat isolation on rain-forest communities. Here we assess butterflies in continuous forest, in unburned isolates surrounded by burned forest and in burned forest, in addition to areas sampled before the most recent (1997/98) large-scale burn event in Borneo. Overall levels of species richness were significantly higher pre-ENSO and in continuous forest than in unburned isolates and burned forest. There was, however, some variation among butterfly families in these patterns, with no significant differences among habitats (continuous forest, isolates and burned forest) for the Hesperidae and significant differences for the other butterfly families. Patterns of community composition showed that similarity was greater between distant continuous forest and isolates than between either of these and burned forest. Since the unburned isolates were surrounded by the burned forest this indicates that the habitat (burned or unburned) overrides geographical differences. Dominant species that contributed substantially to differences among habitats were often completely absent from either burned or unburned forest. The combined patterns of species richness and community structure suggest that burning affects forest ecosystems by a replacement of dominant species while habitat isolation may affect areas by leading to the local extinction of rare species.

Key Words: El Niño Southern Oscillation, Hesperidae, Kalimantan, Lycaenidae, Nymphalidae

INTRODUCTION

The goal of this study was to ascertain the impact of burning and habitat isolation due to ENSO (El Niño Southern Oscillation)-induced fires on levels of butterfly species richness and community composition in Borneo. The 1997/98 ENSO event was the most severe and widespread in recorded history (Guilderson & Schrag 1998, Holmgren *et al.* 2001, Salafsky 1998, Timmermann *et al.* 1999), and there is evidence that such events are increasing in frequency and intensity (Holmgren *et al.* 2001). Fires occurred over more than 5.2 million ha of east Borneo during the 1997/98 event (Siegert *et al.* 2001). In Malaysian Borneo the 1997/98 ENSO event led to the decimation of a local wasp assemblage (Harrison 2000), and caused very high

tree mortality across different types of vegetation and over a large altitudinal range (Aiba & Kitayama 2002). Beyond these studies, however, very little is known about the response of Bornean rain-forest assemblages to severe ENSO events (Harrison 2000, Holmgren *et al.* 2001).

In the present study we assessed landscape-scale butterfly species richness across Borneo. Butterflies have been shown to be especially responsive to large-scale environmental phenomena. Pollard (1988, 1991), for instance, found a positive relationship between the increased overall abundance of butterflies and warm dry summers in England. Annual fluctuations and long-term trends at individual sites were closely synchronized with regional data so that in these local English populations, fluctuations were likely little influenced by local community interactions. Butterflies have, furthermore, been shown to be sensitive to global climate change (Dennis 1993); non-migratory European butterflies showed a significant response to climate

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Table 1. Landscapes sampled during the course of this study, and their location. Pre: Sampled before the 1997/98 ENSO event. Year of burning is the year in which the landscape burned. Note that the number of plots was substantially increased from pre- to post-ENSO. Eff: mean number of days spent per plot per landscape. Habitat: Con (continuous), Iso (isolate) and Bur (burned forest).

Name	Landscape	Plots	Eff (d)	n	Location	Habitat	Year of burning	Latitude	Longitude
Pre-Wanariset	B2	8	6	1333	East Borneo	97	1982/83	0°59'S	116°57'E
Pre-Berau	Be	3	6	507	North-east Borneo	97		2°04'N	117°19'E
Pre-Kayu Mas	C3	3	6	410	Central Borneo	97		1°16'S	112°24'E
Kayu Mas	C1	16	8	2841	Central Borneo	Con		1°17'S	112°22'E
Kayu Mas	C2	16	5	2200	Central Borneo	Con		1°20'S	112°20'E
Kayu Mas	C3	13	6	3147	Central Borneo	Con		1°16'S	112°24'E
Meratus	I1	16	7	3200	East Borneo	Iso		0°58'S	116°19'E
Sungai Wain	I2	16	6	3200	East Borneo	Iso		1°06'S	116°49'E
ITCI	I3	16	6	3200	East Borneo	Iso		0°57'S	116°21'E
Sungai Wain	B1	16	6	3200	East Borneo	Bur	1997/98	1°05'S	116°48'E
Wanariset	B2	18	5	3600	East Borneo	Bur	1982/83 and 1997/98	0°59'S	116°57'E
Km 30	B3	16	6	3200	East Borneo	Bur	Frequently	1°03'S	116°57'E

change by shifting their ranges (Parmesan *et al.* 1999). Butterflies are also often used as key indicators of disturbance and as surrogates for other taxa (Blair 1999, Fuller *et al.* 1998, Howard *et al.* 1998).

In addition to assessing the complete butterfly community we compared differences among butterfly families. Five major monophyletic butterfly families are recognized, namely Hesperidae, Papilionidae, Pieridae, Lycaenidae and Nymphalidae (de Jong *et al.* 1996). The Hesperidae are traditionally placed within their own superfamily, namely Hesperoidea, whereas the other four families are grouped in the superfamily Papilionoidea. Previous studies in butterflies and other taxa have shown that much of the variation in life history occurs among lineages, at or above, the level of families (Fiedler 1998, Owens & Bennett 1995). Papilionid and pierid butterflies, for example, are strongly associated with a small set of secondary plant classes and compounds that might restrain their ability to use a greater taxonomic range of plants (Fiedler 1998).

In the present study, we compared landscape-scale species richness among three habitat types differentially affected by the 1997/98 ENSO event: continuous forest, unburned isolates surrounded by burned forest and burned forest itself. We also considered samples taken before the event as representing a fourth, temporally defined sample. The following questions were addressed with this study: (1) Are there differences in large-scale species richness among habitat types? Is there a difference between areas sampled pre-ENSO and areas sampled post-ENSO? (2) Are the patterns of large-scale species richness congruent among butterfly families? (3) Does community composition differ among habitat types and is the pattern congruent across butterfly families? (4) Which species contribute most to differences in community composition among habitat types?

MATERIALS AND METHODS

Study area

All research took place in Indonesian Borneo (Table 1). Pre-ENSO (1997) we sampled landscapes in three widely separated areas: east Borneo (B2: Balikpapan–Samarinda region), central Borneo (C3: Sangai), and north-east Borneo (Be: Berau region). Post-ENSO, a total of nine landscapes were sampled in east and central Borneo. Each c. 450-ha landscape consisted of randomly assigned plots in a hierarchical sampling design. Post-ENSO three main disturbance classes were sampled (including resampling of the B2 and C3 landscapes): three landscapes in continuous forest, three in unburned forest isolates surrounded by burned forest, and three in the burned forest surrounding the unburned isolates.

The continuous forest landscapes (here designated C1, C2 and C3) were located in the province of Central Kalimantan in the large unburned central core of Borneo that was not affected by ENSO-induced fires. The unburned forest isolate landscapes (I1, I2 and I3) were located in the province of East Kalimantan, and were not directly affected by the 1997/98 ENSO event. The forest that surrounds these landscapes did burn during this event and contained our burned landscapes (B1, B2, B3).

All the continuous forest and unburned isolate landscapes had a similar vegetation structure, dominated by dipterocarp species as is typical for intact rain forest in Borneo (Kartawinata *et al.* 1981, van Nieuwstadt *et al.* 2001, Yamakura *et al.* 1986). The burned landscapes (B1, B2 and B3) were also originally covered by such dipterocarp forest (Kartawinata *et al.* 1981, van Nieuwstadt *et al.* 2001); B1 was burned for the first time during the 1997/98 ENSO event, B2 was partially burned first during the 1982/83 ENSO event and then again during the 1997/98 ENSO event, and B3 was located in

an area of slash-and-burn agriculture along km 30 of the Balikpapan to Samarinda highway. The unburned-isolate and burned landscapes were located in a large area of East Kalimantan ($5.2 \times 10^6 \text{ km}^2$) that changed from a habitat mosaic of natural forest with areas of secondary forest to an area dominated by secondary (burned) forest with only remnant unburned patches (the largest of which are the unburned isolates in this study; Siegert *et al.* 2001). The landscapes have been described in greater detail in Cleary (2003). Further detailed descriptions of the central Borneo research localities can be found in Asdak *et al.* (1998) and of the east Borneo research localities in Slik *et al.* (2002) and van Nieuwstadt *et al.* (2001).

Plot design and sampling

Sampling took place in 0.9-ha ($300 \times 30 \text{ m}$) plots assigned at random to grid cells on maps of each landscape. Each plot was located in the field with a compass and clinometer, and was geo-referenced with a handheld GPS device (Garmin 12 XL). The number of plots sampled and the average number of days spent per plot per landscape is shown in Table 1. On average we spent 6 d at a plot but this varied somewhat depending on weather conditions and ease of capture. Various plots in C1 and I1 were, for example, located on very steep slopes, which made collection particularly difficult and sampling time was increased in order to obtain a sufficient sample size. Because the best method for comparing actual species richness differences is to standardize by sample size (Willott 2001), plots were sampled until 200 individuals were taken where possible. Butterflies were sampled across the entire 0.9-ha plot. The total number of butterflies caught per landscape is given in Table 1. Sampling took place between 09h00 and 16h00, barring rain, using nets and with two people catching per plot. Voucher specimens of each species were preserved in silica gel, and deposited in the collection of the Zoological Museum of the University of Amsterdam. All individuals were identified to species using Maruyama & Otsuka (1991), Otsuka (1988), and Seki *et al.* (1991). In a few cases it was not possible to identify beyond a species-pair or species-group (e.g. *Allotinus leogoron* and *A. melos*). All these individuals were then considered to belong to the same species (*A. leogoron* in this case).

Analyses

Total rarefied species richness was assessed per landscape (pooling all plots; $n = 400$ individuals) using the Species Diversity option of the EcoSim program (Gotelli & Entsminger 2001) with 100 iterations and independent sampling of randomly chosen individuals from the total species pool in each landscape. Interpretations of

statistical significance among landscapes were based on the simulated 95% confidence intervals generated by EcoSim (Gotelli & Entsminger 2001, McCabe & Gotelli 2000). Since the species richness data were normally distributed (all $P > 0.05$ with a Kolmogorov–Smirnov d-test) we tested for differences among the four classes (continuous, isolates, burned and pre-ENSO) with a one-way ANOVA followed by a post hoc LSD test (using Statistica for Windows 1996). We present the actual uncorrected P-values for all tests. In addition to testing for differences in total species richness we also tested each family separately. Tests of families (Hesperiidae, Lycaenidae and Nymphalidae) were only performed on the post-ENSO dataset (so, among the three habitat types). The Papilionidae and Pieridae were not included because of very small sample sizes (especially in isolates) in these families. We tested for congruence in landscape species richness among families with a Pearson product-moment correlation (using Statistica for Windows 1996).

We tested for differences in community composition among habitats using data on species abundance per plot. A data matrix of pairwise comparisons among plots was composed using $\log_{10}(x + 1)$ transformed abundances with the program PRIMER (Clarke & Gorley 2001). Only plots with more than 10 individuals were included in the analyses. The data matrix consisted of pairwise comparisons among plots based on the Bray–Curtis similarity index. This index is frequently used in ecological work (Clarke & Gorley 2001, Ellingsen 2002).

Variation in community composition among habitats was subsequently tested for significance with an ANOSIM (analysis of similarity) using PRIMER. ANOSIM is roughly analogous to standard univariate ANOVA, and tests a priori defined groups against random groups in ordinate space. The R_{ANOSIM} statistic values, generated by ANOSIM in PRIMER, are a relative measure of separation of the a priori defined groups. A zero (0) indicates that there is no difference among groups, while a one (1) indicates that all samples within groups are more similar to one another than any samples from different groups (Clarke & Gorley 2001). In the results we present the ANOSIM in addition to a multidimensional scaling (MDS) ordination based on the same distance matrix. We tested for congruence in community similarity along the first two multidimensional axes between the Lycaenidae and Nymphalidae from the MDS with a Spearman Rank correlation (using Statistica for Windows 1996). We did not test for differences with the Hesperiidae because not all plots had a sufficient sample size for inclusion in the MDS analysis.

Finally we used SIMPER in PRIMER (Clarke & Gorley 2001) to explore the relative contribution of individual species to dissimilarity among habitats. In the results we present the average abundance and average contribution

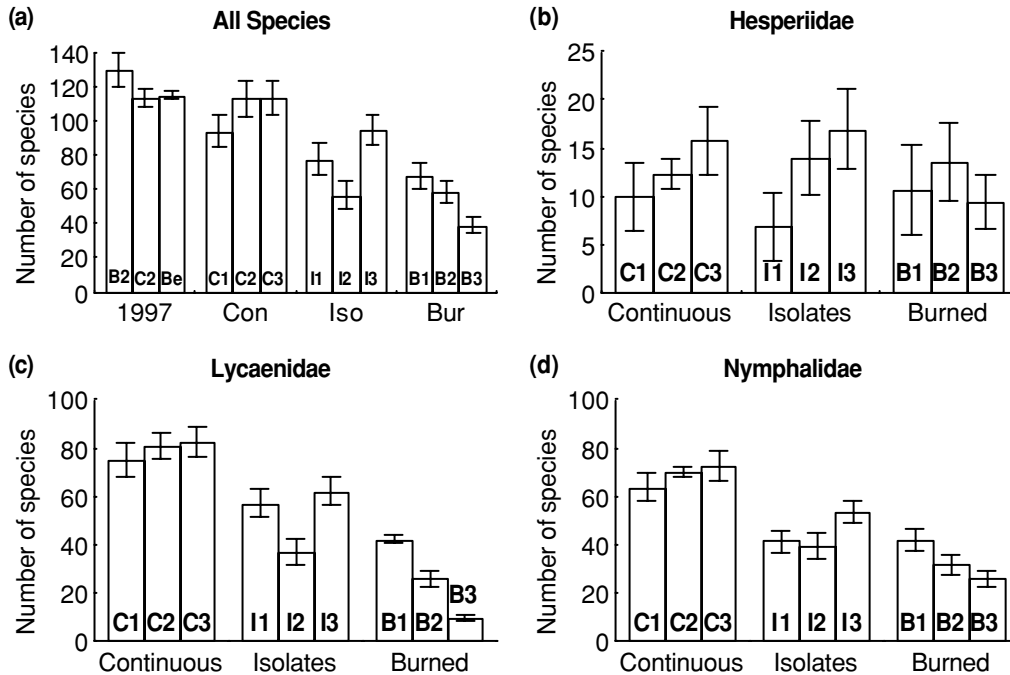


Figure 1. (a) Estimates of species richness (error bars are simulated 95% confidence intervals for a rarefied $n = 400$ individuals per landscape) of all butterfly species per landscape for three landscapes sampled pre-ENSO, three sampled in continuous forest (Con), three sampled in unburned isolates (Iso), and three sampled in burned forest (Bur). (b) Estimates of species richness for hesperids ($n = 60$ individuals per landscape). (c) Estimates of species richness for lycaenids ($n = 600$ individuals per landscape). (d) Estimates of species richness for nymphalids ($n = 600$ individuals per landscape).

of species to dissimilarity among habitats, measured using the Bray–Curtis (dis)-similarity index. The consistency of species in differentiating between habitats is, furthermore, indicated by the standard deviation of the dissimilarities presented in the results as the ratio of average dissimilarity divided by the standard deviation. A large ratio of average dissimilarity divided by the standard deviation indicates that a species contributes substantially and consistently to dissimilarity among habitats. Finally, we present the percentage of total dissimilarity that each species contributes and the cumulative percentage of the top five most discriminating species.

RESULTS

A total of 30 040 butterflies belonging to 522 species was sampled during the study. There was a significant difference ($F_{3,8} = 13.1$, $P = 0.002$) in total species richness among habitats (Figure 1a). Species richness was significantly higher in 1997 and in continuous forest than in isolates (LSD test; pre–iso: $P = 0.005$; con–iso: $P = 0.028$) and burned forest (LSD test; pre–bur: $P < 0.001$; con–bur: $P = 0.002$). There was no significant difference in species richness between 1997 and continuous forest (LSD test; $P = 0.302$) or between isolates and burned forest (LSD test; $P = 0.100$). If we

further divide our pre-ENSO plots to distinguish among landscapes, allowing temporally paired comparisons, then there was no significant temporal difference in species richness from pre- to post-ENSO at the central Borneo landscape (C3: $n = 400$ rarefied individuals: pre: 114.6 ± 2.2 species, post: 113.4 ± 10.2 species), but a dramatic loss of species at the east Borneo (Wanariset) landscape ($n = 1300$; pre: 211.1 ± 2.5 species, post: 86.6 ± 7.1 species).

Among families there were no significant differences among habitats post-ENSO in hesperid species richness (Figure 1b; $n = 60$ per landscape; $F_{2,6} = 0.141$, $P = 0.872$). Lycaenid species richness was significantly higher (Figure 1c; $n = 600$ individuals per landscape; $F_{2,6} = 13.8$, $P = 0.005$) in continuous forest than isolates (LSD test; $P = 0.036$) and burned forest (LSD test; $P = 0.002$) and significantly higher in isolates than burned forest (LSD test; $P = 0.043$). Nymphalid species richness was also significantly higher (Figure 1d; $n = 600$ per landscape; $F_{2,6} = 20.3$, $P = 0.002$) in continuous forest than isolates (LSD test; $P = 0.006$) and burned forest (LSD test; $P < 0.001$), but there was no significant difference between isolates and burned forest (LSD test; $P = 0.085$). Species richness was significantly correlated between lycaenids and nymphalids ($r = 0.965$, $P < 0.001$). Hesperid species richness was not significantly correlated with the other

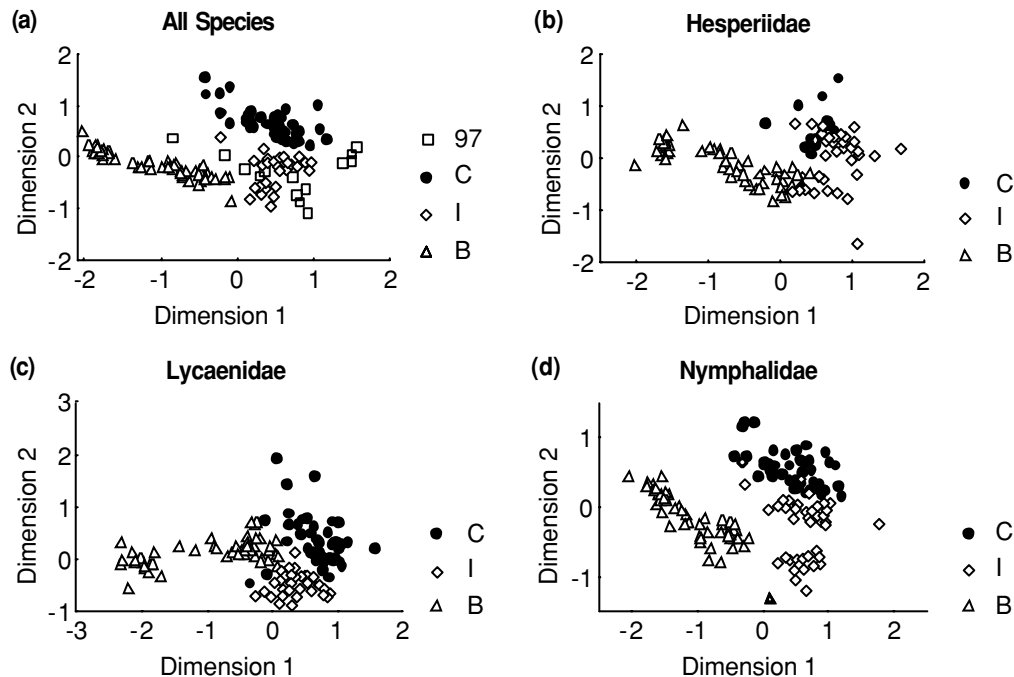


Figure 2. Results of the multidimensional scaling analysis for (a) all species, (b) hesperids, (c) lycaenids and (d) nymphalids. Only the first two axes are shown. 97: Pre-ENSO, C: continuous forest, I: isolates and B: burned forest.

families (lycaenids: $r = 0.444$, $P = 0.231$; nymphalids: $r = 0.376$, $P = 0.319$).

Community composition differed significantly ($P < 0.01$) in all comparisons between habitat types. For all species pre-ENSO, similarity was higher with continuous forest ($R_{ANOSIM} = 0.704$) and isolates ($R_{ANOSIM} = 0.635$) than with burned forest ($R_{ANOSIM} = 0.746$). Similarity was higher between continuous forest and isolates (all species: $R_{ANOSIM} = 0.680$; hesperids: $R_{ANOSIM} = 0.203$; lycaenids: $R_{ANOSIM} = 0.529$; nymphalids: $R_{ANOSIM} = 0.423$), than between continuous forest and burned forest (all species: $R_{ANOSIM} = 0.852$; hesperids: $R_{ANOSIM} = 0.612$; lycaenids: $R_{ANOSIM} = 0.538$; nymphalids: $R_{ANOSIM} = 0.884$) or between isolates and burned forest (all species: $R_{ANOSIM} = 0.787$; hesperids: $R_{ANOSIM} = 0.570$; lycaenids: $R_{ANOSIM} = 0.596$; nymphalids: $R_{ANOSIM} = 0.834$). The main gradients of community similarity (Figure 2) indicate a primary axis from burned forest to unburned forest along the first (horizontal) axis in the multidimensional scaling analysis and a secondary axis that separated the unburned isolates from the unburned continuous forest. The Lycaenidae and Nymphalidae had significantly congruent scores along the first (Dimension 1: $r = 0.789$, $P < 0.001$) and second (Dimension 2: $r = 0.264$, $P = 0.002$) axes of the MDS.

Table 2 lists the top five species that contributed most to dissimilarity among habitat types. Certain species that were present in all three habitat types such as the hesperid *Koruthailos rubecula* increased in abundance in burned

forest. Other species were, however, only abundant in a given habitat and completely absent from other habitats. Species such as *Potanthus omaha* and *Polytremis lubricans* were, for example, abundant in burned forest but absent from the nearby unburned isolates whereas the reverse was true with *Ancistroides gemmifer* that was restricted to unburned forest.

DISCUSSION

There was no significant difference in species richness between samples taken pre-ENSO and samples in continuous forest, suggesting that our more precise measures of community structure in continuous forest in Central Kalimantan are a good reflection of pre-ENSO forest butterfly species richness in the severely affected east. Post-ENSO species richness was significantly higher in continuous forest than the unburned isolates and burned forest. Patterns of species richness were furthermore significantly congruent across the families Lycaenidae and Nymphalidae but were not significantly related to species richness in the Hesperidae. In a broad-ranging analysis of the response of various invertebrate groups to disturbance in Africa, Lawton *et al.* (1998) found that no single animal group (e.g. birds, butterflies, nematodes) could serve as a good indicator taxon for the changes in the species richness of other groups. Butterfly families appear to show greater congruence, as might be

Table 2. Top five discriminating species for among-habitat comparisons of similarity. Dis: average dissimilarity, Comp: comparison, Ab: average abundance, SDis: species-specific contribution to average dissimilarity, Ratio: ratio of average species-specific contribution to dissimilarity divided by the standard deviation of contribution to dissimilarity among habitats, Co%: percentage of average dissimilarity due to species and Cu%: cumulative contribution of species to Dis. Note that 1 and 2 refer to comparisons of habitats. The habitats being compared and their designated number are given in the Comp column.

Family	Dis	Comp	Species	Ab 1	Ab 2	SDis	Ratio	Co%	Cu%
Hesperiidae	65.1	1.C-2.I	<i>Koruthaialos rubecula</i> (Plötz)	8.6	13.8	7.6	1.1	11.7	11.7
			<i>Ancistroides gemmifer</i> (Butler)	4.2	2.7	7.0	1.2	10.8	22.4
			<i>Ancistroides armatus</i> (Druce)	1.5	1.2	4.8	1.1	7.3	29.8
			<i>Celaenorrhinus ladana</i> (Butler)	1.3	0.4	4.4	1.2	6.8	36.5
			<i>Isma bononia</i> (Hewitson)	0.1	1.1	4.1	1.1	6.3	42.8
	84.5	1.C-2.B	<i>Koruthaialos rubecula</i> (Hewitson)	8.6	25.3	9.5	1.7	11.2	11.2
			<i>Ancistroides gemmifer</i>	4.2	0.0	7.9	1.8	9.3	20.6
			<i>Taractrocera ardonia</i>	1.1	9.5	7.5	1.1	8.8	29.4
			<i>Potanthus omaha</i> (Edwards)	0.0	4.2	5.3	1.2	6.2	35.6
			<i>Polytremis lubricans</i> (Herrich-Schäffer)	0.0	3.2	5.1	1.2	6.1	41.7
	81.7	1.I-2.B	<i>Koruthaialos rubecula</i>	13.8	25.3	8.6	1.4	10.5	10.5
			<i>Taractrocera ardonia</i>	0.0	9.5	7.1	1.1	8.6	19.1
			<i>Potanthus omaha</i>	0.0	4.2	5.1	1.2	6.2	25.3
			<i>Polytremis lubricans</i>	0.0	3.2	4.9	1.2	6.0	31.3
			<i>Ancistroides gemmifer</i>	2.7	0.0	4.5	1.0	5.6	36.9
Lycaenidae	75.2	1.C-2.I	<i>Allotinus leogoron</i> (Fruhstorfer)	1.5	14.3	3.9	1.5	5.1	5.1
			<i>Drupadia theda</i> (Felder)	3.1	20.2	3.6	1.5	4.8	10.0
			<i>Jamides pura</i> (Moore)	29.0	7.1	3.4	1.4	4.5	14.5
			<i>Allotinus unicolor</i> (C. and R. Felder)	1.2	9.8	3.0	1.4	4.0	18.5
			<i>Arhopala epimuta</i> (Moore)	2.2	9.5	2.9	1.4	3.9	22.4
	86.3	1.C-2.B	<i>Jamides pura</i>	29.0	11.3	5.3	1.2	6.2	6.2
			<i>Spindasis kutu</i>	0.0	8.4	4.1	0.9	4.8	11.0
			<i>Drupadia theda</i>	3.1	6.2	3.4	1.2	3.9	14.9
			<i>Abisara geza</i> (Fruhstorfer)	0.5	5.0	3.0	1.0	3.5	18.4
			<i>Paralaxita orphna</i> (Boisduval)	3.1	0.0	3.0	1.1	3.4	21.8
	83.2	1.I-2.B	<i>Allotinus leogoron</i>	14.3	0.9	5.2	1.5	6.3	6.3
			<i>Drupadia theda</i>	20.2	6.2	4.6	1.3	5.6	11.8
			<i>Arhopala epimuta</i>	9.5	0.7	4.5	1.8	5.4	17.2
			<i>Allotinus unicolor</i>	9.8	0.2	3.9	1.4	4.7	21.9
			<i>Jamides pura</i>	7.1	11.3	3.7	1.3	4.5	26.3
Nymphalidae	71.2	1.C-2.I	<i>Coelites eupythychioides</i> (Felder)	0.0	9.0	3.7	1.4	5.2	5.2
			<i>Ragadia makuta</i> (Horsfield)	15.0	11.0	3.4	1.3	4.8	10.0
			<i>Idea lynceus</i> (Drury)	4.7	2.6	2.4	1.4	3.4	13.4
			<i>Euthalia iapis</i> (Godart)	5.0	2.4	2.0	1.2	2.8	16.2
			<i>Xanthotaenia busiris</i> (Westwood)	1.1	3.4	2.0	1.3	2.8	19.0
	88.1	1.C-2.B	<i>Ragadia makuta</i>	15.0	0.0	4.9	1.8	5.6	5.6
			<i>Ypthima pandocus</i> (Moore)	0.4	18.5	4.6	1.8	5.2	10.8
			<i>Neptis hylas</i> (Linnaeus)	1.2	10.9	3.9	1.4	4.4	15.2
			<i>Idea lynceus</i>	4.7	0.0	3.4	2.2	3.8	19.0
			<i>Orsotriaena medus</i> (Wallengren)	0.1	7.9	3.3	1.2	3.8	22.8
	87.8	1.I-2.B	<i>Ypthima pandocus</i>	1.0	18.5	4.7	1.7	5.3	5.3
			<i>Neptis hylas</i>	0.0	10.9	4.6	1.5	5.3	10.6
			<i>Coelites eupythychioides</i>	9.0	0.2	3.9	1.3	4.5	15.0
			<i>Orsotriaena medus</i>	0.0	7.9	3.6	1.2	4.0	19.1
			<i>Ragadia makuta</i>	11.0	0.0	3.5	1.1	4.0	23.0

expected given their more restricted ecology. Our results suggest that large-scale studies of species richness across landscapes can be used to assess the impact of disturbance events on focal taxa. It is, however, important to assess areas of approximately equal size so as not to confound the impact of area sampled and disturbance.

Patterns of change in species composition were congruent across families, but this was predominantly related to a similar relationship to burning-induced disturbance along the first multidimensional scaling axis.

Along the second axis, which differentiated between the geographically distant isolates and continuous forest, congruence was weaker, suggesting that geographic factors play a secondary but discernable role in structuring butterfly communities.

In all families similarity was greater between the continuous forest and isolates than between both of these unburned forests and the burned forest despite the fact that the unburned isolates were embedded in the burned forest matrix. For Bornean butterflies habitat type (burned

versus unburned forest) therefore appeared to be a more important determinant of species composition than geography. This result is supported by the observations of Hughes *et al.* (2000), who found that montane hymenopteran and dipteran communities were differentiated by habitat type rather than geographic proximity.

This pattern can be further clarified if we consider the species that contributed most to differences among habitats. With the exception of *Coelites eupythychioides*, the species that differentiated between continuous forest and isolates were present in both habitats but differed in abundance. In comparisons between unburned and burned forest, however, discriminating species were often abundant in one habitat and completely absent from the other. In the hesperids, for example, three species (*Taractrocer a ardonia*, *Potanthus omaha* and *Polytremis lubricans*) were completely absent from the unburned isolates, and one (*Ancistroides gemmifer*) was completely absent from the burned forest. In the nymphalids, two species (*Neptis hylas* and *Orsotriaena medus*) were completely absent from the unburned isolates and one species (*Ragadia makuta*) was completely absent from the burned forest. These results emphasize the environmental differences between unburned and burned forest through their effect on abundant species. In contrast to these findings, Ricketts (2001) found that the majority of moth species in their sample from Central America seemed to use both native and agricultural (burned) landscapes surrounding large forest fragments, and moved frequently between the forest and agricultural landscape. Beck *et al.* (2002), however, found that geometrid moth species richness was significantly lower in areas of Borneo used for (slash-and-burn) agriculture than in natural forest, and the community composition of these areas differed substantially from the intact forest.

The relatively greater similarity in species composition between the isolates and continuous forest combined with the fact that overall species richness did not differ significantly between isolates and burned forest, indicates that rare species may have been disproportionately lost from these isolates. Previous studies have shown that rare species may be especially susceptible to local extinction following habitat isolation. During periods of rarity an intermittently rare species will have a greater risk of extinction due to demographic stochasticity (Ferriere & Cazelles 1999). In addition to habitat isolation, disturbance in general has been found to affect rare species – for example, bat species richness, number of rare bat species and diversity were negatively correlated with increasing disturbance over a very wide range of habitat types (Medellín *et al.* 2000). If such patterns are general, naturally rare species may require special conservation attention.

Rare species that occur in patchy habitats have, furthermore, been shown to have high migration

rates (Heino & Hanski 2001). Besides demographic stochasticity the tendency of rare species to disperse may affect local rates of extinction in isolated habitats. When suitable habitat is destroyed this reduces the upper dispersal threshold. Organisms that survive in a pristine but patchy habitat may go extinct in a partly destroyed landscape because their dispersal ability causes them to be lost in unsuitable habitat (Casagrandi & Gatto 1999). This loss may be related to deterioration of the matrix habitat, which causes an increase in migration mortality (Heino & Hanski 2001).

Previous studies on levels of species richness within a recently burned habitat-matrix in South America produced some conflicting patterns. Butterfly (and frog and small mammal) species richness was actually higher in isolates than in a similar area of continuous forest, whereas the species richness of ants and birds was significantly lower (Brown & Hutching 1997, Gascon *et al.* 1999). In the same area common species of beetle were significantly more likely than rare species to go extinct in small fragments of Amazonian rain forest (Didham *et al.* 1998). It may be that these burned areas were only moderately affected, leading to the now well-known phenomenon of higher species-richness in moderately disturbed landscapes. Important too is the fact that the isolates monitored in all these studies (Brown & Hutching 1997, Didham *et al.* 1998, Gascon *et al.* 1999) were surrounded by a burned habitat-matrix, but this burned habitat-matrix was in turn embedded in a much larger area of primary rain forest (Gascon *et al.* 1999). At a scale thus of hundreds of thousands of hectares, the main habitat-matrix component was actually primary rain forest. This is very different from our study in east Borneo where the isolates were embedded in a recently burned habitat matrix of millions of hectares. The negative effects of an adverse habitat matrix are, however, probably related to the degree and extent to which that habitat matrix has been altered (Ickes 2000). If this scale-dependence is an important contributor to the differences between our results and the South American patterns, then further questions demand scrutiny, including why butterflies respond positively to small-scale but negatively to large-scale disturbances (Cleary 2003).

If severe ENSO-induced burning and habitat isolation did indeed cause the overall low levels of species richness in post-ENSO east Borneo it is expected that community restoration will be very slow across the whole affected region because the zone of burning is now largely bounded by mountains and degraded areas (Siegert *et al.* 2001), both with very different species assemblages (Seki *et al.* 1991). This isolation will hinder re-introduction of locally extirpated species from any regional species pool. Preliminary analyses (Mooers & Cleary, unpubl. data) also suggest that extirpation has not been random across taxa: an important task for the future is to examine

which biological factors are correlated with the losses we document.

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