

Diversity and community composition of butterflies and odonates in an ENSO-induced fire affected habitat mosaic: a case study from East Kalimantan, Indonesia

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Little is known about the diversity of tropical animal communities in recently fire-affected environments. Here we assessed species richness, evenness, and community similarity of butterflies and odonates in landscapes located in unburned isolates and burned areas in a habitat mosaic that was severely affected by the 1997/98 ENSO (El Niño Southern Oscillation) event in east Kalimantan, Indonesian Borneo. In addition related community similarity to variation in geographic distance between sampling sites and the habitat/vegetation structure. Species richness and evenness differed significantly among landscapes but there was no congruence between both taxa. The species richness of butterflies was, for example, highest in sites located in a very large unburned isolate whereas odonate species richness was highest in sites located in a small unburned isolate and once-burned forest. We also found substantial variation in the habitat/vegetation structure among landscapes but this was mainly due to variation between unburned and burned landscapes and variation among burned landscapes.

Both distance and environment (habitat/vegetation) contributed substantially to explaining variation in the community similarity (beta diversity) of both taxa. The contribution of the environment was, however, mainly due to variation between unburned and burned landscapes, which contained very different assemblages of both taxa. Sites located in the burned forest contained assemblages that were intermediate between assemblages from sites in unburned forest and sites from a highly degraded slash-and-burn area indicating that the burned forest was probably recolonised by species from these disparate environments. We, furthermore, note that in contrast to species richness (alpha diversity) the patterns of community similarity (beta diversity) were highly congruent between both taxa. These results indicate that community-wide multivariate measures of beta diversity are more consistent among taxa and more reliable indicators of disturbance, such as ENSO-induced burning, than univariate measures.

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Relating patterns of biodiversity to spatial phenomena is becoming increasingly important in community ecology and related disciplines such as conservation biology (Spencer et al. 2002). The spatial arrangement of habitats can, for example, influence dispersal and thereby affect colonisation and extinction of species. Recently, Harte et al. (1999) and Hubbell (2001) have provided important theoretical insights into the relationship between species turnover and distance. If dispersal regulates community similarity then proximate plots will contain similar assemblages of species and in similar proportions, and this similarity will decline with distance as dispersal limitation sets in (Hubbell 2001). Alternatively, local environmental conditions may prevail because certain species depend on a given set of environmental conditions for survival. Both of these processes are likely to act in concert to determine patterns of community similarity within and among habitats. Partitioning ecological variation exhibited by communities into that explained by purely spatial and that explained by purely environmental phenomena is crucial to understanding the mechanisms behind patterns of biodiversity (Borcard et al. 1992, Condit et al. 2002, Duivenvoorden et al. 2002).

Tropical rainforests are important but threatened sources of biodiversity (so-called 'hotspots'; Myers et al. 2000). Under a frequent burn regime, however, these forests may be converted to non-forest habitat (Nepstad et al. 2001). A less frequent burn regime, such as that associated with periodic severe ENSO- (El Niño southern oscillation) induced droughts, may not cause permanent deforestation, but might have far-reaching consequences for normal ecosystem functioning in the affected forests (Laurance 1998, Nepstad et al. 1999, Curran and Leighton 2000, Holmgren et al. 2001); species assemblages may change, and important (key-stone) species may find the periodically burned forest unsuitable. The forest may also be transformed into a different (pioneer-dominated) transitional state, and maintained in that state by recurrent periodic fires.

Large-scale ENSO events can affect millions of hectares of rainforest. The 1997/98 ENSO event caused large-scale habitat inversions in Borneo, where still intact forest with patches of secondary forest transformed into a habitat matrix dominated by burned forest surrounding remnant unburned isolates (Siegert et al. 2001). Unfortunately, very little research has focused on the impact of ENSO-induced fire on tropical rainforest communities (Harrison 2000, Holmgren et al. 2001) despite the fact that tropical ENSO-induced burning is now considered one of the most critical threats to tropical forests (Laurance 2003). This is in marked contrast to studies in tropical marine environments, where severe ENSO events have been implicated in radical community restructuring, and even global ex-

tingtion (Glynn and De Weerd 1991, Nyström et al. 2000).

Research in this study took place within unburned forest isolate and burned forest landscapes in the Indonesian province of East Kalimantan. Prior to 1980 there were no recorded dry periods that lasted longer than two months. Since then the area has been affected by two major ENSO-induced droughts, viz. in 1982/83 and 1997/98. Both droughts were accompanied by large-scale fires, of which those in 1997/98 were by far the most severe and widespread that have ever been recorded in Borneo (Harrison 2000). In the research area we sampled six differentially disturbed landscapes: primary forest in a large (138 000 ha) unburned isolate (I1: 0° 58' S, 116° 19' E), primary forest in a small (3500 ha) unburned isolate (I2: 1° 06' S, 116° 49' E), logged forest in a large (138 000 ha) unburned isolate (I3: 0° 57' S, 116° 21' E), once-burned forest (B1: 1° 05' S, 116° 48' E) adjacent to the small primary isolate, twice-burned forest (B2: 0° 59' S, 116° 57' E), and an area dominated by slash-and-burn agriculture (B3: 1° 03' S, 116° 57' E).

Our research focused on two invertebrate taxa, namely butterflies (Lepidoptera: Papilionoidea and Hesperioidea) and odonates (Odonata: Zygoptera and Anisoptera). Both butterflies and odonates have been identified as important indicator organisms for assessing biodiversity, and for monitoring ecosystem responses to environmental perturbations (Dennis 1993, Fuller et al. 1998, Howard et al. 1998, Stewart and Samways 1998, Blair 1999, Parmesan et al. 1999, Sahlen and Ekestubbe 2001). The two taxa however, have very different life histories. Butterflies are predominantly phytophagous and non-aquatic (they use almost all major seed plant families and a few non-seed plants; Janz and Nylin 1998), whereas odonates are predators and have an obligate aquatic stage. The two groups therefore help us to test the generality of community response to measured environmental variables. A large study of tropical communities suggested that there is little congruence in the response of different taxa to disturbance (Lawton et al. 1998), and so more work is needed.

We consider the following questions:

- 1) Does butterfly and odonate species richness and evenness differ among landscapes?
- 2) Do landscapes differ significantly in habitat/vegetation structure and is this related to previous burns? Here we hypothesise that the magnitude of differences in habitat structure will be directly related to the number of burning events, and we expect a gradient from severely disturbed habitat in the slash-and-burn and twice-burned forest to the undisturbed structure of the primary forest.
- 3) Does community similarity differ significantly among landscapes and how is this related to spatial and environmental variation? Here we assess the

relative importance of spatial and environmental components in explaining variation in the community similarity of both taxa. We relate our findings to similar spatial studies with other taxa, in other biomes and consider the ramifications of our findings in the context of continued ENSO-induced burning in Borneo as well as elsewhere (Uhl and Kauffman 1990, Nepstad et al. 2001, Siegert et al. 2001, Laurance 2003).

- 4) Finally, are the spatial patterns of diversity congruent for butterflies and odonates? Here we compare patterns of species richness (alpha diversity) and community similarity (beta diversity) between butterflies and odonates.

Material and methods

Study area

Research on butterflies and odonates took place in and around the Balikpapan-Samarinda region of East Kalimantan, Indonesian Borneo from January–October 2000. The landscapes used in this study (including a map of all landscapes) are described in greater detail in Cleary (2003). In addition to sampling butterflies and odonates we measured a range of habitat/vegetation structure variables in all sites with a view to relating patterns of community composition in both taxa to their immediate environment. All six landscapes in unburned isolates (I1, I2, I3) and burned (B1, B2, B3) forest were located in the 5.2 million ha of East Kalimantan that changed from a habitat mosaic of forest with areas of secondary growth to an area dominated by secondary (burned) forest with only remnant unburned patches (Siegert et al. 2001). This type of very large-scale non-random distribution of disturbed areas in space opens the possibility that differences among habitats may be due to an unknown factor that is correlated with the extent of the studied disturbance (fire in this case) and its severity (Petraitis and Latham 1999).

Plot design and sampling

Sampling took place in all sites, which occupied a ca 0.9 ha area (along a 300 m transect demarcated with ironwood poles), assigned at random to a ca 450 ha landscape. Each site was located in the field with a compass and clinometer and then georeferenced with a handheld GPS device (Garmin 12XL, Garmin Ltd. Olathe Kansas). Per landscape, 16 sites were sampled (but 21 for B2). Butterflies and odonates were sampled along the entire transect, while habitat structure variables were sampled in single sub-plots of varying size (below). Butterflies and odonates were sampled when

encountered within ca 15 m on either side of the 300 m transect in each site. A transect was traversed repeatedly on foot from one end to the other at a steady pace, which was only broken to collect specimens. This procedure was repeated until at least 200 butterflies and 20 odonates were caught per site, thus avoiding very small samples which may yield unreliable similarity indices when comparing plots (Wolda 1981).

We measured 11 habitat/vegetation structure variables per 200-m² (10 × 20 m) sub-plot. A single sub-plot was assessed per transect. We measured the density (stems/plot including all woody plants taller than 130 cm) of the following:

- 1) small lianas (dbh < 1 cm; dbh is the diameter at breast height at ca 130 cm height)
- 2) large lianas (dbh > 1 cm)
- 3) bamboo lianas
- 4) palmae (palms and rattans)
- 5) saplings (dbh < 5 cm)
- 6) poles (5 cm < dbh < 10 cm)
- 7) trees (dbh > 10 cm) were measured in one 200-m² sub-plot per 0.9 ha plot
- 8) fern cover
- 9) grass cover
- 10) dicot herb cover
- 11) non-grasslike monocot herb cover

Cover was visually estimated in six cover classes (0%, 1–10%, 11–30%, 31–70%, 71–90%, and 91–100%) over one 8-m² sub-plot nested within the 200-m² sub-plot. Habitat structure variables were measured in all 16 sites in all landscapes except B2, in which it was measured in 14 of the 21 sites.

It is nearly impossible to accurately identify many Bornean butterflies and odonates on the wing (Walpole and Sheldon 1999). We therefore caught individuals with nets, and subsequently identified them in the field. After marking with an Edding 3000 marker, most of these were released. Although we always succeeded in collecting 200 butterflies per plot this was not always the case with the 20 odonates. Analyses of species richness therefore excluded plots where fewer than 20 odonates were sampled. Sampling took place between 9:00 am and 4:00 pm, except during rain, using nets and with two people catching per site. An average of 6.02 ± 0.61 days was spent sampling per site. The date of capture and location were noted for each individual. All butterflies were identified to species following Otsuka (1988), Maruyama and Otsuka (1991), and Seki et al. (1991). In a few cases it was not possible to identify beyond a species-pair or species-group (e.g. the butterflies *Allothinus leogoron* and *A. melos*). All such individuals were then considered to belong to the same species (*A. leogoron* in this case) because diagnostic characteristics could not be determined in the field (e.g. male genital

characters) or females could not be further identified unambiguously. Specimens from all butterfly and odonate species were preserved (using silica gel) and later rechecked in the Netherlands. Odonate works consulted include Lieftinck (1954) and Wilson (1995). Voucher specimens of all species have been deposited in the collection of the Zoological Museum of the University of Amsterdam.

Analyses

Species richness and evenness. Rarefied species richness and evenness (Pielou's J; Hayek and Buzas 1997) were assessed with the DIVERSE option of the program PRIMER (Clarke and Gorley 2001). First we tested for deviations from normality (using a Kolmogorov-Smirnov d-test) and homogeneity of variance (with a Levene's test) using Statistica for Windows (2003). Since we found no significant departure in both tests we subsequently tested for differences in mean species richness and evenness among landscapes with one-way ANOVAs on independent means (using Statistica for Windows 2003) with the landscape as the independent variable and rarefied species richness or evenness as the dependent variable, and a Bonferroni post hoc test to compare means across landscapes. Additionally total rarefied species richness across landscapes was assessed by pooling all individuals within a landscape using the 'Species Diversity' option of the EcoSim program (Gotelli and Entsminger 2001) with 100 iterations and independent sampling of randomly chosen individuals from the total species pool in each landscape. Interpretations of statistical significance of total species richness are based on the simulated 95% confidence intervals generated by EcoSim (McCabe and Gotelli 2000, Gotelli and Entsminger 2001).

Habitat structure. In the program PRIMER (Clarke and Gorley 2001) we used the 'Similarity' option under 'Data' to construct a triangular matrix of normalised Euclidean differences in vegetation structure between pairs of sites based on $\log_{10}(x+1)$ transformed habitat/vegetation structure variables. This matrix was then used for multidimensional scaling (MDS) ordination (using PRIMER). Multidimensional scaling has various advantages over other multivariate techniques for use in ecological studies; the results have been found to be robust under a wide range of conditions. MDS does not have stringent model assumptions, such as correspondence analysis, which assumes a unimodal response, and any similarity measure can be used for ordination (Beck et al. 2002). In order to assess the importance of individual habitat structure variables in generating differences between habitats, we additionally calculated correlation coefficients of individual habitat structure variables with the first and second dimensions obtained

with the MDS using a Pearson Product-Moment correlation (Statistica for Windows 2003).

Community similarity. We assessed community similarity among landscapes using the Bray-Curtis similarity coefficient, which is frequently used in ecological work (Clarke and Gorley 2001, Ellingsen 2002). Differences in similarity among landscapes are presented using an MDS ordination. In addition to the MDS we used the similarity percentages (SIMPER) routine in PRIMER (Clarke and Gorley 2001) to explore the relative contribution of individual species to dissimilarity among unburned and burned landscapes. In the results we present the average abundance and average contribution of species to dissimilarity among unburned and burned landscapes, measured using the Bray-Curtis (dis)similarity index. The consistency of species in differentiating between unburned and burned landscapes 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 unburned and burned landscapes.

Finally, we used matrix regression based on permutation tests (using the program PERMUTE! 3.4.9, Casgrain 2001) to assess the relationship between response matrices of community similarity (for butterflies and odonates) and a set of predictor matrices. The predictor matrices were obtained with the 'similarity' option under 'Data' in PRIMER. The input file consisted of raw environmental data or universal transmercator (UTM) coordinates for the spatial predictor matrix. First, we assessed univariate relationships between ($\log_{10}(x+1)$ transformed) response similarity matrices and predictor matrices of:

- 1) distance (\log_{10} transformed) between sites.
- 2) herb cover: normalised Euclidean difference between sites based on herb cover, grass cover, monocot and dicot herb cover.
- 3) liana abundance: normalised Euclidean difference between sites based on $\log_{10}(x+1)$ transformed small liana, large liana and bamboo liana abundance.
- 4) Palmae abundance: normalised Euclidean difference between sites based on $\log_{10}(x+1)$ transformed Palmae (palm and rattan) abundance.
- 5) tree abundance: normalised Euclidean difference between sites based on $\log_{10}(x+1)$ transformed sapling, pole and tree abundance.

In the program PERMUTE! the matrix permutation option was used with 999 permutations. For a full description of the use of matrix permutation tests in regression analyses see: <http://www.fas.umontreal.ca/>

biol/casgrain/en/labo/permute/index.html and Spencer et al. (2002) for the analogous use of mantel tests to assess relationships among distance matrices. An advantage of these tests is that no assumptions need be made about the distribution of data. Subsequently, in order to assess the degree to which variation in the response variables could be explained by the total set of predictor matrices, multiple forward matrix regression was applied. In PERMUTE! the matrix permutation option, 999 permutations, forward selection, and a Bonferroni-corrected p-to-enter level of 0.10 (the default) were used. For a description of the methodology consult <http://www.fas.umontreal.ca/biol/casgrain/en/labo/permute/index.htm>. The multiple matrix regression analysis resulted in partial regression coefficients and partial correlation coefficients that measured the effect of the various predictor matrices on the response matrix after controlling for all other independent predictor matrices (Spencer et al. 2002). Finally, multiple backward matrix regression was used to partition the total variation in community similarity into a purely environmental fraction, a spatially structured environmental fraction, and a purely spatial fraction. Borcard et al. (1992), Lobo et al. (2001) and Tuomisto et al. (2003) described the variance partitioning.

Results

Species richness and evenness

During this study we sampled 351 species of butterflies over 23,400 individuals and 72 species of odonates over

5,780 individuals. The species sampled and their abundance per landscape is presented in Appendix I for the butterflies and Appendix II for the odonates. Mean butterfly species richness ($F_{5,88} = 41.70$, $P < 0.001$) and evenness ($F_{5,88} = 4.59$, $P < 0.001$) differed significantly among landscapes (Fig. 1). Species richness and evenness were high in the landscapes located in the large unburned isolate (I1 and I3) but were lower in the burned landscapes, particularly in the slash-and-burn area (B3), but also in the small unburned isolate (I2). Mean odonate species richness ($F_{5,77} = 8.43$, $P < 0.001$) and evenness ($F_{5,77} = 9.39$, $P < 0.001$) also differed significantly among landscapes. In contrast to the butterflies, odonate species richness and evenness was highest in the once-burned landscape (B1) and the landscape in the small primary isolate (I2). Overall there was no significant relationship between butterfly and odonate species richness ($R = 0.124$, $P = 0.911$) or evenness ($R = -0.185$, $P = 0.095$).

Total butterfly species richness differed significantly (as indicated by the 95% confidence intervals in Fig. 2 and Table 1) among landscapes. Species richness was highest in I3 and declined in the order I1, B1, I2, B2 and finally B3. This result was largely consistent with the results obtained with mean species richness. Total odonate species richness also differed significantly among landscapes and was highest in I3, declining in the order I2, B1, I1, B2 and finally B3. This result was different to that obtained for mean species richness which was significantly higher in B1 than I3.

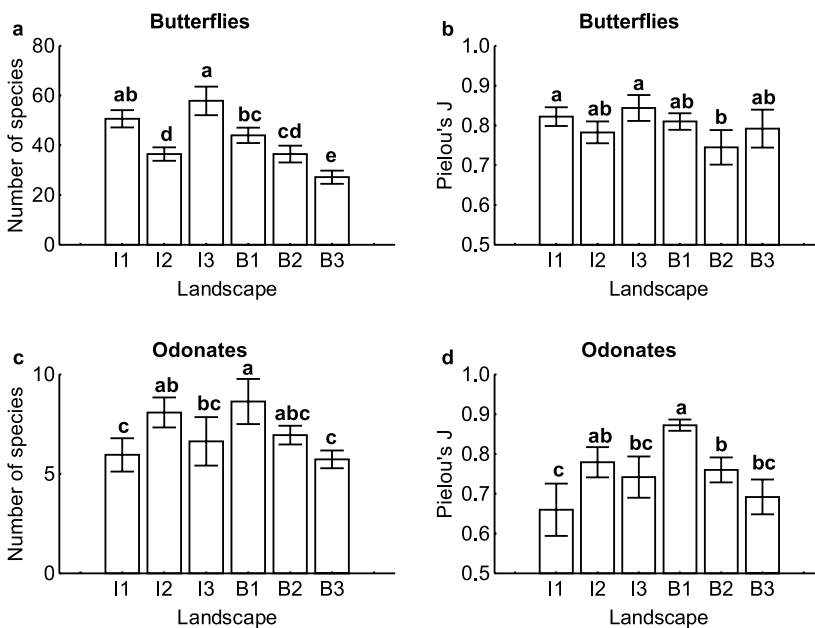


Fig. 1. Diversity indices for butterflies and odonates. Mean species richness (bars represent 95% confidence intervals) for (a) butterflies and (c) odonates. Mean evenness (bars represent 95% confidence intervals) for (b) butterflies and (d) odonates. Significance based on a Bonferroni post hoc test is indicated by a letter above the bars for each landscape. Means that differ significantly ($P < 0.05$) do not share any letter. I1: primary landscape in large unburned isolate, I2: primary landscape in small unburned isolate, I3: logged landscape in large unburned isolate, B1: once-burned forest, B2: twice-burned forest, B3: slash-and-burn area.

Table 1. Total rarefied and mean species richness of butterflies and odonates. For the 'total' values we assessed the species richness of butterflies at 2,800 individuals, and odonates at 350 individuals per landscape. For the 'mean' values we assessed the species richness of butterflies at 200 individuals per site, and odonates at 20 individuals per site. Means and 95% confidence intervals are shown. LaSc: landscape.

Taxon	LaSc	Total	Mean
Butterflies	I1	159.39 ± 5.13	50.63 ± 3.48
	I2	117.50 ± 4.70	36.40 ± 5.10
	I3	182.72 ± 5.11	57.88 ± 5.73
	B1	138.70 ± 4.50	44.00 ± 5.90
	B2	108.20 ± 5.00	35.40 ± 5.60
	B3	65.43 ± 2.16	27.19 ± 2.68
Odonates	I1	25.69 ± 4.39	5.95 ± 0.84
	I2	32.10 ± 3.70	8.10 ± 1.30
	I3	31.39 ± 3.83	6.64 ± 1.22
	B1	30.00 ± 1.90	8.60 ± 1.50
	B2	22.30 ± 3.60	6.90 ± 0.80
	B3	18.21 ± 4.39	5.73 ± 0.45

Habitat structure

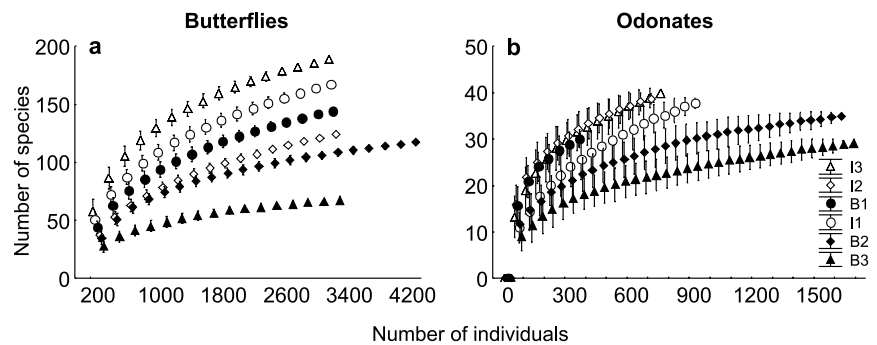
The multivariate assessment of habitat/vegetation structure variables showed that there was substantial variation in structure among landscapes (Fig. 3) but that this was largely attributable to variation between unburned and burned landscapes and to variation among the burned landscapes, particularly with relation to the slash-and-burn area (B3). There was a large amount of overlap of sites from different unburned landscapes indicating that variation in habitat/vegetation structure was more pronounced within than between unburned landscapes. The first dimension of Fig. 3c was positively correlated with sapling ($R = 0.54$), pole ($R = 0.57$) and tree ($R = 0.65$) abundance. The abundance of these variables thus declined from unburned forest to burned forest and was lowest in the slash-and-burn area. Dimension 2 was negatively related to the abundance of bamboo lianas ($R = -0.71$) and thus represents variation in the burned forest where certain sites were dominated by bamboo lianas which formed a mat and

greatly reduced grass and other herbaceous ground cover locally.

Community similarity

Both taxa showed a gradient in community similarity from sites in the unburned forest (I1, I2 and I3) to once-burned forest (B1), twice-burned forest (B2) and the slash-and-burn area (B3) along dimension 1, and from sites in the small unburned isolate (I2) to sites in the large unburned isolate (I1 and I3) along dimension 2 (Fig. 3). The 20 butterfly and odonate species that contributed most to the dissimilarity between unburned and burned landscapes are listed in Table 2. The clustering of sites from different landscapes is much more pronounced than in the habitat/vegetation analysis reflecting the importance of both distance (geographic locality) and environment in structuring the faunal assemblages. The importance of distance in structuring assemblages is reflected in the significantly negative relationship between distance and community similarity in both taxa (Fig. 4). There was also a highly significant association ($b = 0.829$, $R^2 = 0.687$, $P < 0.001$; Fig. 5) between the community similarities (beta diversity) of both taxa, in contrast to species richness (alpha diversity). This suggests that either taxa can function as significant predictor (indicator) of the spatial turnover of species in the other taxa. In both taxa distance was the most important explanatory variable and explained more than 50% of the variation in community similarity (Table 3). All predictor matrices were significantly related to butterfly and odonate community similarity (Table 3). For the butterflies the following variables were significant in a forward selection procedure of the multiple matrix regression: distance, tree abundance, herb cover, liana abundance and palmae abundance (Table 4). For odonates distance, tree abundance, palmae abundance and liana abundance were significant predictors of community similarity (Table 4). Overall the

Fig. 2. Species rarefaction curves of the number of species set out against the number of individuals sampled for (a) butterflies and (b) odonates. Symbols represent means at given abundance levels while the bars represent simulated 95% confidence intervals. Some confidence intervals are hidden behind the symbols. I1: primary landscape in large unburned isolate, I2: primary landscape in small unburned isolate, I3: logged landscape in large unburned isolate, B1: once-burned forest, B2: twice-burned forest, B3: slash-and-burn area.



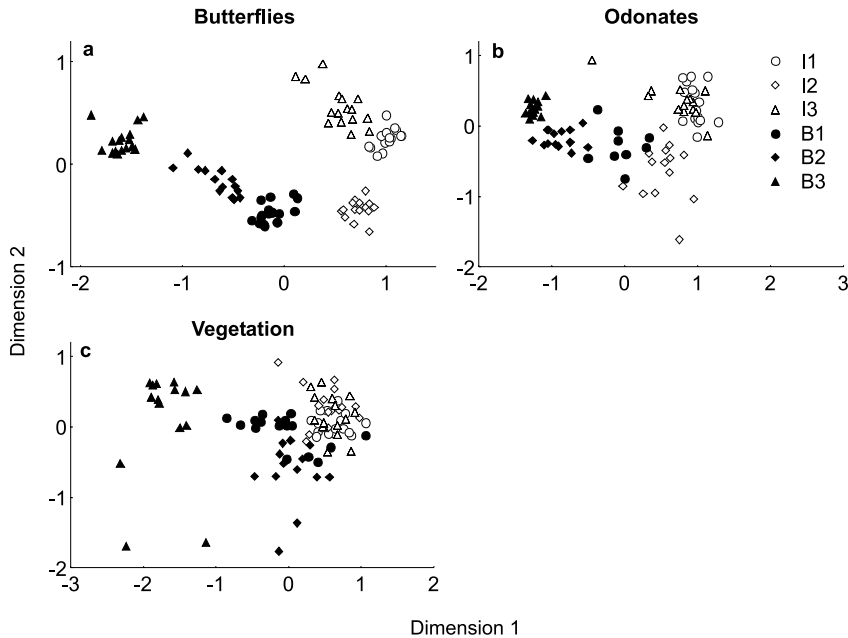


Fig. 3. Multidimensional scaling (MSD) ordination of (a) the butterfly community, (b) the odonate community, and (c) habitat/vegetation structure. Note the discrete nature (with no overlap among sites from different landscapes) of sites in the butterfly community compared to the same sites for which habitat structure was measured. Using Statistics for Windows 6.1. I1: primary landscape in large unburned isolate, I2: primary landscape in small unburned isolate, I3: logged landscape in large unburned isolate, B1: once-burned forest, B2: twice-burned forest, B3: slash-and-burn area.

environmental and distance predictor matrices explained 73.13% of variation in the community similarity of butterflies and 61.89% of variation in the community similarity of odonates. The purely spatial component explained the greatest amount of variation in both taxa (Table 5) followed by the spatially structured environmental and purely environmental components.

Discussion

Species richness and evenness

We chose to study three burned landscapes in detail and compare them with three unburned landscapes in the two largest remaining areas of unburned forest in the ca 5.2 million ha of rainforest that were directly affected by the 1997/98 ENSO event. We discuss how this study relates to and can be extrapolated to the global phenomena of forest loss as a result of ENSO-induced burning, noting that this type of extremely large-scale burning is not a purely natural phenomenon, but related to human land-use patterns (Cochrane 2001).

Mean and total rarefied butterfly species richness were higher in the landscapes located in the large unburned isolate and lower in the burned landscapes, particularly the slash-and-burn area, and in the small unburned isolate. Odonate species richness was, however, highest in B1, but total odonate species richness was highest in I3.

For butterflies, though, all landscapes contained 31–66% less butterfly species overall than obtained in the same area pre-ENSO (Cleary and Mooers 2004, Cleary

and Genner 2004). Because the B1 landscape had a higher species richness than the I2 landscape for butterflies and odonates, this single result might indicate that a single burn was in some way conducive to biodiversity (as might be predicted by the intermediate disturbance hypothesis; Connell 1978). An alternative explanation, however, is that the unburned isolate (I2) was itself heavily impacted by the 1997/98 ENSO event. Although speculative, this is consistent with the observation that all landscapes in the present study had substantially lower species richness levels than intact forest landscapes far-removed from the fires and from pre-ENSO levels of species richness from the same area (Cleary and Mooers 2004, Cleary and Genner 2004).

Spatial assessment of patterns of species richness, like our post-ENSO assessment, highlights a problem often encountered in environmental impact studies in that they are often initiated only after the disturbance event has taken place. Patterns of species richness and community composition are, for example, assessed across areas (disturbed and undisturbed) whereby it is assumed that differences between these areas are due to the disturbance. Ideally the impact assessment of disturbance would entail studying specific sites from an undisturbed state until a given period of time after disturbance. However, for most purposes this is impractical and spatial sampling is used as a substitute. If the entire mosaic of habitats is affected by a disturbance event, however, this assumption becomes unjustified. We suggest that ENSO-induced disturbance events might be a prime example of this.

Table 2. Top 20 discriminating species between unburned and burned landscapes. Mean Diss: mean dissimilarity, Unb: unburned, Bur: burned, Abun: mean abundance, Diss/SD: ratio of mean species-specific contribution to dissimilarity divided by the standard deviation of contribution to dissimilarity, Cont%: percentage of mean dissimilarity due to species and Cum%: cumulative contribution of species to Dis.

Taxon	Species	Abun Unb	Abun Bur	Mean Diss	Diss SD	Cont %	Cum %
Butterflies	<i>Ypthima pandocus</i>	0.98	19.79	1.99	1.69	2.33	2.33
	<i>Allotinus leogoron</i>	14.29	0.85	1.92	1.58	2.25	4.59
	<i>Neptis hylas</i>	0.00	11.70	1.85	1.60	2.17	6.75
	<i>Arhopala epimuta</i>	9.50	0.62	1.67	1.67	1.96	8.71
	<i>Coelites eupythychioides</i>	9.04	0.21	1.59	1.39	1.86	10.58
	<i>Drupadia theda</i>	20.21	6.51	1.58	1.47	1.86	12.43
	<i>Koruthaialos rubecula</i>	12.25	23.75	1.56	1.49	1.83	14.26
	<i>Allotinus unicolor</i>	9.77	0.23	1.48	1.32	1.74	16.00
	<i>Taractroera ardonia</i>	0.00	9.57	1.47	1.12	1.72	17.71
	<i>Orsotriaena medus</i>	0.00	7.94	1.46	1.32	1.71	19.42
	<i>Ragadia makuta</i>	11.02	0.00	1.45	1.13	1.69	21.12
	<i>Jamides pura</i>	7.12	11.23	1.34	1.36	1.57	22.68
	<i>Spindasis kutu</i>	0.06	8.13	1.31	1.06	1.54	24.22
	<i>Mycalies anapita</i>	4.62	3.38	1.21	1.63	1.41	25.63
	<i>Tanaecia aruna</i>	3.21	0.04	1.14	1.70	1.34	26.97
	<i>Jamides celeno</i>	2.62	4.94	1.11	1.09	1.29	28.26
	<i>Potanthus omaha</i>	0.02	4.38	1.06	1.09	1.25	29.51
	<i>Ideopsis vulgaris</i>	0.31	3.49	1.04	1.51	1.21	30.72
	<i>Paralaxita orphna</i>	4.00	0.00	1.01	1.12	1.18	31.90
	<i>Arhopala democritus</i>	2.62	0.00	0.99	1.64	1.16	33.06
Odonates	<i>Neurothemis fluctuans</i>	0.52	21.66	8.75	2.16	10.21	10.21
	<i>Vestalis amaryllis</i>	19.77	1.72	7.81	1.95	9.12	19.33
	<i>Coeliccia nigrahamata</i>	6.42	1.56	5.20	1.46	6.07	25.40
	<i>Orthetrum sabina</i>	0.19	8.88	5.14	1.33	6.00	31.40
	<i>Neurothemis terminata</i>	0.42	6.72	4.99	1.43	5.83	37.22
	<i>Ceragrion cerinorubellum</i>	0.10	5.46	4.39	1.20	5.12	42.35
	<i>Euphaea impar</i>	4.21	0.24	4.23	1.25	4.94	47.29
	<i>Rhyothemis phyllis</i>	0.17	5.22	3.63	0.96	4.24	51.52
	<i>Rhinocypha humeralis</i>	3.10	0.00	3.11	0.89	3.63	55.15
	<i>Orchithemis pulcherrima</i>	1.71	1.96	2.93	0.95	3.41	58.56
	<i>Diplacodes trivalis</i>	0.00	5.40	2.83	0.67	3.31	61.87
	<i>Prodasinera collaris</i>	0.25	1.60	2.35	0.84	2.75	64.62
	<i>Lyriothemis cleis</i>	1.00	0.10	1.85	1.01	2.16	66.78
	<i>Orthetrum chrysis</i>	0.29	1.04	1.72	0.89	2.00	68.78
	<i>Tyriobapta laidlawi</i>	0.92	0.20	1.68	0.80	1.96	70.74
	<i>Euphaea subcostalis</i>	1.65	0.02	1.62	0.63	1.89	72.63
	<i>Rhinocypha biseriata</i>	1.44	0.04	1.49	0.59	1.73	74.36
	<i>Rhyothemis obsolenscens</i>	0.02	1.06	1.26	0.55	1.47	75.83
	<i>Brachydiplax chalybea</i>	0.35	0.42	1.19	0.75	1.39	77.21
	<i>Tyriobapta torrida</i>	0.90	0.00	1.14	0.56	1.33	78.55

Large-scale environmental perturbations can affect both directly disturbed and undisturbed (or better indirectly disturbed) areas. Given that environmental repercussions from the 1997/98 ENSO event were felt in the entire region it is unlikely that the severe drought and noxious fumes from the fires had no impact on unburned isolates. Previously, Harrison (2000) found that the 1997/98 ENSO event resulted in community collapse and

species loss of mutualist fig wasps as a result of ENSO-related drought, even though the forest reserve (ca 6500 ha) in which they resided did not burn during the 1997/98 ENSO event. He also noted that the impact of the 1997/98 ENSO event was less severe in large isolates (> 50,000 ha) in agreement with this study. Additionally, Ricketts (2001) noted that if dispersal is reduced to varying degrees by the quality of the habitat-matrix then

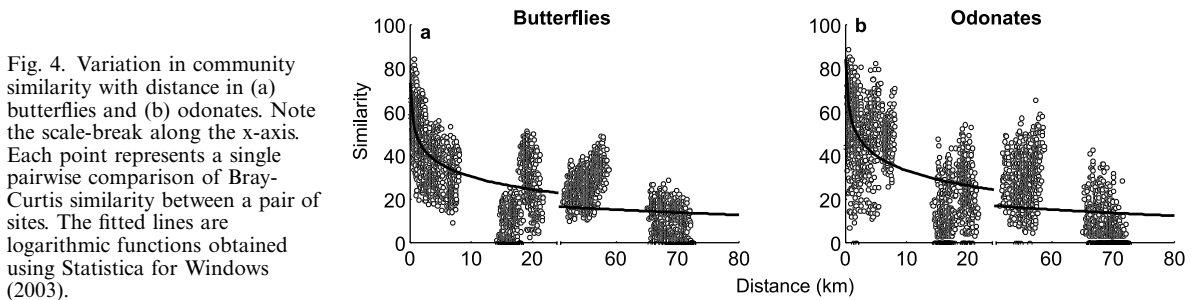


Fig. 4. Variation in community similarity with distance in (a) butterflies and (b) odonates. Note the scale-break along the x-axis. Each point represents a single pairwise comparison of Bray-Curtis similarity between a pair of sites. The fitted lines are logarithmic functions obtained using Statistica for Windows (2003).

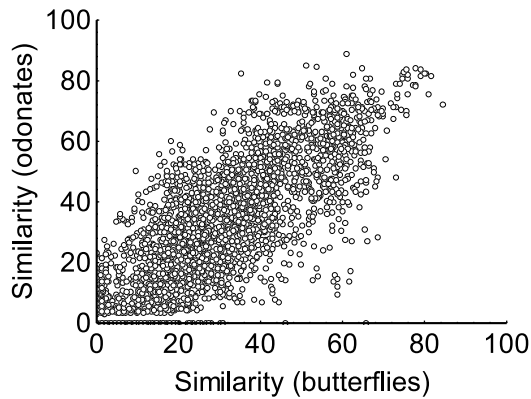


Fig. 5. Relationship between butterfly and odonate community similarity. Each point represents a single pairwise comparison of Bray-Curtis similarity between a pair of sites.

Table 3. Results of the univariate matrix regression analyses using Permute!

Taxon	Predictor	b	P	R ²
Butterflies	Distance	-0.721	0.001	0.520
	Cover	-0.412	0.001	0.169
	Lianas	-0.532	0.001	0.283
	Palmae	-0.110	0.001	0.012
	Trees	-0.603	0.001	0.363
Odonates	Distance	-0.728	0.001	0.531
	Cover	-0.246	0.001	0.061
	Lianas	-0.450	0.001	0.202
	Palmae	-0.183	0.001	0.034
	Trees	-0.458	0.001	0.209

Table 4. Results of the multiple forward matrix regression analyses using Permute! Predictors are shown in order of importance.

Taxon	Predictor	par. b	par. P	par. R ²
Butterflies	Distance	-0.721	0.001	0.520
	Trees	-0.447	0.001	0.187
	Herb cover	-0.131	0.001	0.013
	Lianas	-0.108	0.001	0.008
	Palmae	-0.057	0.001	0.003
Odonates	Distance	-0.728	0.001	0.531
	Trees	-0.279	0.001	0.072
	Palmae	-0.106	0.001	0.011
	Lianas	-0.088	0.001	0.005

Table 5. Results of the variance partitioning assessments based on results obtained with Permute!

Variance partitioning component	Butterflies	Odonates
Purely spatial	27.16	31.57
Spatially structured environmental	24.83	21.49
Purely environmental	21.14	8.83
Total explained	73.13	61.89
Unexplained	26.87	38.11

this should lead to lower species richness in isolated habitats.

Habitat structure

The landscapes differed substantially in structure, but there was relatively little difference among sites from different unburned landscapes. Most of the variation in vegetation structure was thus due to differences between sites from unburned and burned landscapes and sites from different burned landscapes. In the burned landscapes, for example, we observed prolific regeneration of pioneer trees in the twice-burned forest (B2), probably due to species that colonised the area after the burn of 1982/83 and saturated the seed bank. This would also explain the similar density of saplings in the unburned I2 (116.63 ± 42.84) and the twice-burned B2 (136.93 ± 53.32) compared to the once-burned B1 (46.44 ± 19.42). The lack of such a seed bank in B1 apparently could not inhibit massive colonization by ferns, probably, via long-distance wind-mediated spores. The dominant fern in this habitat was the cosmopolitan *Pteridium aquilinum* (Dennstaedtiaceae), or bracken, a species noted for colonising extremely perturbed acidic environments (Roberts and Gilliam 1995). When dense, the species is also known to exclude other plants. Indeed patches of this fern were prevalent in the Wanariset forest during pre-ENSO surveys, but have virtually disappeared since the 1997/98 forest fires (D. F. R. Cleary, pers. obs.). Recent disturbance history may thus be playing an important role in patterns of forest regeneration and local habitat structure.

Community similarity

Butterflies and odonates showed highly significant univariate relationships between community composition and locally measured habitat/vegetation structure variables. The importance of environmental variables in predicting the community similarity of butterflies and odonates may be largely attributable to substantial differences in the physical environment (e.g. vegetation structure) between unburned and burned forests, both of which housed very different assemblages. A substantial amount of variation in community similarity of both taxa was also related to the geographic distance between sampling sites suggesting that dispersal limitation is important for both taxa. Overall the combined environmental and distance predictor matrices explained 73.13% of variation in the community similarity of butterflies and 61.89% of variation in the community similarity of odonates.

Duivenvoorden (1995) found that distance and environment explained 16% of the variation in upland tree species composition of Columbian forests. A similar study of lowland terra firme forest tree species from

Central and South America based on data from Condit et al. (2002) showed that environmental and spatial factors could explain 41% of the observed variation in community similarity but only 7% was due to purely spatial variation (Duivenvoorden et al. 2002). Githaiga-Mwicigi et al. (2002) were able to explain 22.70% of the variation in bird community similarity in South Africa of which only 1.70% was due to purely spatial variation. Likewise, Magalhaes et al. (2002) studied two fish assemblages in Mira and Seixe Portugal and were able to explain 36.6% and 57.8% of the variation in the community similarity, respectively, of assemblages from both areas, but only 11.3% and 0.0% respectively was due to distance alone. The results of this study differs thus from these previous studies in the more pronounced importance of distance in structuring butterfly and odonate assemblages, suggesting that both taxa are strongly dispersal limited and thus perhaps less likely to occupy optimal environments. The pronounced distance-dependence exhibited by butterflies and odonates may, however, also be related to the recent burn event itself and higher dispersal-related mortality in the burned matrix. It is important, furthermore, to note that the still relatively important contribution of the environment to structuring the faunal assemblages in this study was predominantly related to the pronounced differences in habitat/vegetation structure between unburned and burned landscapes. When burned landscapes were excluded from the analyses then the contribution of the environmental variables became marginal (D. F. R. Cleary, unpubl.).

Unexplained variation was 26.87% for butterflies and 38.11% for odonates. Borcard et al. (1992) found that the amount of unexplained variation in selected taxa could be substantial (35–69%) and may be related to non-deterministic fluctuations, unmeasured environmental variables or spatial variation acting at a different (i.e. very local or very large) spatial scale or described by a more complex (e.g. polynomial) function. Other sources of unexplained variation may be related to large scale, unmeasured, environmental variables. Butterflies have, for example, been shown to be especially responsive to large-scale environmental phenomena (Pollard 1988, 1991, Dennis 1993, Parmesan et al. 1999).

In addition to the immediate effects of ENSO-induced drought and fire, one of the main longer-term impacts of burning is an opening of the canopy and shift in vegetation that results in pronounced microclimatic differences: temperatures are higher and humidity is lower than in continuous unburned forest (Holdsworth and Uhl 1997). This was also the case in the transition zone between the small unburned isolate (I2) and the once-burned forest (B1) where we measured a pronounced gradient in temperature, humidity, and light penetration between unburned and burned forest (D. F. R. Cleary, unpubl.). These variables also have a pro-

nounced edge effect and influence remnant areas of unburned forest in the burned habitat-matrix thereby altering the local microclimate (Laurance et al. 1997). Importantly, many butterfly species (especially satyrids) are known to be sensitive to changes in humidity and moisture availability (Hill 1999). In addition to species with pronounced preferences for either unburned (e.g. *Drupadia theda* and *Arhopala epimuta*) or burned areas (e.g. *Ypthima pandocus* and *Koruthailos rubecula*) there were also relatively abundant species that were completely restricted to unburned (e.g. *Ragadia makuta* and *Paralaxita orphna*) or burned areas (e.g. *Neptis hylas* and *Taractrocera ardonia*) thereby emphasising the magnitude of the environmental gradient between unburned and burned forest.

The burned forests (B1 and B2) still, however, had substantial networks of unburned forest that traversed the burned vegetation. The area occupied by these unburned networks was estimated at 10.6% (B1) and 8.1% (B2) of the total area (K. A. O. Eichhorn, unpubl.). These unburned networks were primarily found along the flood plain, and contained vegetation, dominated by dipterocarps, that was similar to that of unburned forest (D. F. R. Cleary and K. A. O. Eichhorn, pers. obs.). Like the burned forest in B1, most of the burned forest in B2 was heavily damaged by the fires, but in contrast to B1, a dense secondary forest has since developed, mainly consisting of pioneer trees in the genera *Trema* (Ulmaceae), *Mallotus*, and *Macaranga* (both Euphorbiaceae). Sites located in these networks had habitat structures that were similar to that of unburned forest. The faunal composition of these sites, however, differed substantially from that in primary forest. In addition to abiotic edge effects, these may also be severely affected by biotic edge effects such as increased competition or predation from species in the burned habitat-matrix making them less attractive to primary forest species and easily invaded by pioneer species from the burned forest. These areas are, furthermore, susceptible to generalist predators, such as *Orthetrum sabina*, a large dragonfly that we observed preying on butterflies, and other odonates in the burned matrix (D. F. R. Cleary, pers. obs.). No individuals of this species were observed in the contiguous primary forest landscapes (I1 and I3), but the species was present in the logged I3.

In the butterfly community, reduction in similarity between unburned and burned sites suggests that the burned habitat-matrix is inhospitable to unburned forest species and may additionally limit dispersal. This dispersal limitation may be behavioural or physiological because of differences in microenvironment characteristics of burned versus unburned forest, or may be because active dispersers simply die in the burned forest. It is difficult at this stage to differentiate between these two alternative hypotheses. Ricketts (2001), though, noted that although the quality of the habitat-matrix

affected movement between sites, the composition of site boundaries did not (with only a single exception) influence the rate at which butterflies exited sites. As in Ricketts (2001) study we often observed butterflies such as various *Arhopala* spp. readily crossing boundaries between unburned and burned forest (from I2 to B1), but we failed to record most of these species in the more distant B2 landscape, and they were very rare in B1. Before the fires (1997), we recorded 42 species (372 individuals) of *Arhopala* in B2 (over 1333 butterflies collected) (Cleary and Mooers 2004). After the fires (2000, this study) we only recorded 2 species (2 individuals over 3600 butterflies collected). This suggests that they either return to unburned forest, or die in the burned habitat-matrix.

Dispersal limitation may also be responsible for the reduced levels of species richness in B2. In this scenario, primary forest species succeed in (temporarily) colonising the proximate B1, but fail to reach B2. This seems to be the case for both butterflies and odonates. The higher species richness of butterflies in the B1 than the I2 landscape may thus be due to a mixing of faunas from the two very different pools (unburned and burned areas).

Previous studies have shown that the impact of an altered habitat-matrix can have widely variable effects on different taxa. In a study of birds, frogs, small mammals, and ants, Gascon et al. (1999) found that these taxa had varying responses to habitat isolation, and an important component of this response was how the various taxa used the intervening habitat-matrix (regrowth following burning) that surrounded remnant isolates of undisturbed habitat. Many species of frogs and small mammals were able to use the intervening habitat-matrix and even entered primary isolates thereby augmenting the species richness of these areas relative to a similar area of continuous forest. However, a large number of bird and ant species were lost in isolates relative to continuous primary forest. Ricketts et al. (2001) found that the majority of moth species in an area of Costa Rica also seemed to use both native and agricultural landscapes surrounding large forest fragments, and moved frequently between both habitat types.

In the odonate community less variation was explained overall by the set of environmental and spatial predictor matrices. This may primarily be related to the lower number of odonates collected per site compared to butterflies, resulting in less accurate estimates of community similarity. Across all sites, though distance was slightly more important in explaining the reduction in similarity in odonates than butterflies. This may be due to odonates using unburned forest networks in the burned habitat-matrix and more effectively spreading into the proximate burned forest (B1) than butterflies. The unburned networks, contained most of the swamps and streams where odonates spend much of their larval,

pupal, and often adult life. Odonates may, in fact, be pre-adapted to the use of these 'corridors' throughout the burned forests whereas butterflies may experience their habitat at a greater spatial scale and not make optimum use of the unburned areas for dispersal.

Use of the unburned networks in the burned forest may explain the almost identical odonate diversities and greater similarity in community composition between the proximate I2 and B1 landscapes, in contrast to the butterflies where the distant B1 and B2 landscapes were more similar (Fig. 4b). Dispersal limitation may, however, have prevented odonates from recolonising the more distant B2 area, at least within the time scales of this study (two years after the 1997/98 ENSO event). Having shown that both butterflies and odonates exhibit significant variation in both species richness and community similarity across landscapes, and that a large proportion of this variation can be explained by a reduction in similarity between unburned and burned areas, we now turn to how this relates to the global phenomenon of ENSO-induced burning.

Fully addressing the much larger phenomenon of ENSO-induced disturbance should, however, entail a series of such studies over a much larger geographical scale and amount of taxa. These studies can be subsequently integrated into meta-analysis type studies in order to test general hypotheses. Oksanen (2001) reviewed this approach to similar large-scale phenomena and issues such as the 'opportunity cost' between scale of assessment and the related issue of 'pseudoreplications'. Like Oksanen (2001) we believe that the appropriate scale of assessment, especially when dealing with large-scale phenomena such as landscape patterns in fire affected habitat must have priority over replication. Because of the spatial nature of ENSO-induced disturbance in our particular research setting we chose to assess six large landscapes representing different habitats under the assumption that they are representative of the impact of ENSO-induced burning in our area. Recent studies in the Neotropics (reviewed by Laurance 2003) have shown that ENSO-induced burning can be highly destructive, despite the fact that the fires themselves are often unimpressive. In the Amazon ENSO-induced burning led to very high tree and liana mortality and dramatically affected forest bird communities. Disturbance-sensitive species and habitat specialists were particularly affected. Unfortunately, there appears to be too few similar studies especially in the Asian tropics, addressing this issue, except in general terms, and most of these focus on remote sensing techniques (Nepstad et al. 1999, Siegert et al. 2001). Although these studies provide important insights into the spatial extent of ENSO-induced burning we also need to focus on the actual communities that are effected by these fires and address local and eventually global impacts on important phenomena such as species richness and community

similarity (Tilman 1999). In the present study the fact that burned forests contained assemblages intermediate between the unburned forests and the severely degraded slash-and-burn area indicates that the burned forest has been recolonised from these two very different sources. While potentially creating relatively new and unique assemblages of butterflies and odonates, burning is not necessarily conducive to maintaining global biodiversity, especially in light of the fact that Bornean endemics were completely absent from the burned forest (Cleary and Genner 2004).

An important result of the present study is the observation that while there was no relationship between butterfly and odonate species richness (alpha diversity) in line with previous studies (Howard et al. 1998, Lawton et al. 1998), the spatial turnover (beta diversity) of both taxa was highly congruent. Importantly, studies of turnover diversity are potentially far more interesting ecologically than studies of sample species richness, or estimates of total species richness of an area (Gray 2000). We also suggest that much more emphasis should be placed on studying beta diversity than at the present in which studies of alpha diversity or species richness are dominant. In the future, we expect the greatest insights in patterns of biodiversity to come from studying patterns of biodiversity at different scales and assessing the scales at which most communities perceive their environment. Modelling and remote sensing may also make significant contributions to this endeavour, but large-scale field assessments of natural animal and plant communities must remain the central focal point.

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Appendix I. Alphabetical list of butterfly species and number of individuals collected per landscape. I1: primary landscape in large unburned isolate, I2: primary landscape in small unburned isolate, I3: logged landscape in large unburned isolate, B1: once-burned forest, B2: twice-burned forest, B3: slash-and-burn area.

Species	Family	I1	I2	I3	B1	B2	B3
<i>Abisara geza</i> Fruhstorfer	Lycaenidae	9	11	3	186	70	0
<i>Abisara savitri</i> C. & R. Felder	Lycaenidae	4	0	5	0	0	0
<i>Acerbas duris</i> Evans	Hesperiidae	0	0	2	0	0	0
<i>Agatasa calydonia</i> Hewitson	Nymphalidae	0	0	1	0	0	0
<i>Allotinus apries</i> Fruhstorfer	Lycaenidae	1	0	21	0	0	0
<i>Allotinus borneensis</i> Moulton	Lycaenidae	1	0	0	1	0	0
<i>Allotinus corbeti</i> Eliot	Lycaenidae	2	10	22	0	1	0
<i>Allotinus davidis</i> Eliot	Lycaenidae	0	2	0	1	1	0
<i>Allotinus fabius</i> Distant & Pryer	Lycaenidae	0	0	1	0	0	0
<i>Allotinus leogoron</i> Fruhstorfer	Lycaenidae	52	470	164	32	13	0
<i>Allotinus strigatus</i> Moulton	Lycaenidae	0	1	1	0	0	0
<i>Allotinus subviolaceus</i> C. & R. Felder	Lycaenidae	0	0	73	0	0	0
<i>Allotinus unicolor</i> C. & R. Felder	Lycaenidae	9	132	328	8	4	0
<i>Amathusia ochraceofusca</i> Honrath	Nymphalidae	0	0	0	0	1	6
<i>Amathuxidia amythaon</i> Doubleday	Nymphalidae	0	0	1	0	0	0
<i>Ancistroides armatus</i> Druce	Hesperiidae	29	0	19	0	0	0
<i>Ancistroides gemmifer</i> Butler	Hesperiidae	65	0	48	0	0	0
<i>Ancistroides nigrita</i> Latreille	Hesperiidae	31	0	26	4	0	0
<i>Anosia genutia</i> Cramer	Nymphalidae	0	0	0	17	20	3
<i>Anosia melanippus</i> Cramer	Nymphalidae	0	0	0	68	51	21
<i>Anthene emolus</i> Godart	Lycaenidae	0	0	12	0	1	0
<i>Appias lycinda</i> Cramer	Pieridae	1	0	0	0	0	0
<i>Araotes lapithis</i> Moore	Lycaenidae	0	2	1	0	0	0
<i>Arhopala abseus</i> Hewitson	Lycaenidae	6	0	3	0	1	0
<i>Arhopala achelous</i> Hewitson	Lycaenidae	0	0	5	0	0	0
<i>Arhopala aedias</i> Hewitson	Lycaenidae	0	1	0	0	0	0
<i>Arhopala aenigma</i> Eliot	Lycaenidae	0	2	0	0	0	0
<i>Arhopala agesias</i> Hewitson	Lycaenidae	4	0	1	0	0	0
<i>Arhopala agesilaus</i> Staudinger	Lycaenidae	1	4	0	0	0	0
<i>Arhopala agrata</i> de Nicéville	Lycaenidae	1	1	0	0	0	0
<i>Arhopala alaconia</i> Hewitson	Lycaenidae	2	4	1	2	0	0
<i>Arhopala ammon</i> Hewitson	Lycaenidae	0	0	0	1	0	0
<i>Arhopala amphimuta</i> Felder	Lycaenidae	0	2	0	0	0	0
<i>Arhopala anthelus</i> Westwood	Lycaenidae	3	3	0	1	0	0
<i>Arhopala antimuta</i> Felder	Lycaenidae	2	3	11	0	0	0
<i>Arhopala ariel</i> Doherty	Lycaenidae	0	4	0	0	0	0
<i>Arhopala aroa</i> Hewitson	Lycaenidae	1	0	0	0	0	0
<i>Arhopala arvina</i> Hewitson	Lycaenidae	0	11	1	1	0	0
<i>Arhopala athada</i> Staudinger	Lycaenidae	0	0	1	0	0	0
<i>Arhopala atosia</i> Hewitson	Lycaenidae	12	11	6	2	0	0
<i>Arhopala aurea</i> Hewitson	Lycaenidae	6	0	19	0	0	0
<i>Arhopala avatha</i> de Nicéville	Lycaenidae	1	1	0	0	0	0
<i>Arhopala avathina</i> Corbet	Lycaenidae	0	1	1	0	0	0
<i>Arhopala baluensis</i> Bethune-Baker	Lycaenidae	0	1	0	0	0	0
<i>Arhopala borneensis</i> Hewitson	Lycaenidae	21	0	5	0	0	0
<i>Arhopala buddha</i> Bethune-Baker	Lycaenidae	0	2	0	3	0	0
<i>Arhopala corinda</i> Hewitson	Lycaenidae	0	0	0	0	1	0
<i>Arhopala democritus</i> Fabricius	Lycaenidae	53	43	30	0	0	0
<i>Arhopala denta</i> Evans	Lycaenidae	0	1	0	0	0	0
<i>Arhopala elopura</i> Druce	Lycaenidae	9	81	2	14	0	0
<i>Arhopala epimuta</i> Moore	Lycaenidae	57	259	140	33	0	0
<i>Arhopala eumolphus</i> Cramer	Lycaenidae	0	0	2	0	0	0
<i>Arhopala evansi</i> Corbet	Lycaenidae	0	1	3	1	0	0
<i>Arhopala fulla</i> Corbet	Lycaenidae	2	1	3	0	0	0
<i>Arhopala horsfieldi</i> Pagenstecher	Lycaenidae	0	1	0	1	0	0
<i>Arhopala hypomuta</i> Hewitson	Lycaenidae	42	6	13	0	0	0
<i>Arhopala kinabala</i> Druce	Lycaenidae	10	0	3	0	0	0
<i>Arhopala labuana</i> Bethune-Baker	Lycaenidae	3	1	0	1	0	0
<i>Arhopala major</i> Staudinger	Lycaenidae	3	1	44	2	0	0
<i>Arhopala metamuta</i> Hewitson	Lycaenidae	1	0	2	0	0	0
<i>Arhopala moolaiana</i> Moore	Lycaenidae	1	32	0	3	0	0
<i>Arhopala moorei</i> Bethune-Baker	Lycaenidae	39	60	12	10	0	0
<i>Arhopala norda</i> Evans	Lycaenidae	1	40	7	8	0	0

Species	Family	I1	I2	I3	B1	B2	B3
<i>Arhopala normani</i> Eliot	Lycaenidae	2	0	0	0	0	0
<i>Arhopala phanda</i> Corbet	Lycaenidae	7	2	1	1	0	0
<i>Arhopala pseudocentaurus</i> Doubleday	Lycaenidae	1	0	0	0	0	0
<i>Arhopala pseudomuta</i> Staudinger	Lycaenidae	10	21	3	6	0	0
<i>Arhopala silhetensis</i> Hewitson	Lycaenidae	2	1	2	0	0	0
<i>Arhopala similis</i> Druce	Lycaenidae	19	0	10	0	0	0
<i>Arhopala sintanga</i> Corbet	Lycaenidae	0	7	0	0	0	0
<i>Arhopala zambra</i> Swinhoe	Lycaenidae	4	0	4	0	0	0
<i>Athyma asura</i> Moore	Nymphalidae	0	0	0	7	0	0
<i>Athyma kanwa</i> Moore	Nymphalidae	8	15	52	160	53	0
<i>Athyma laryma</i> Doubleday	Nymphalidae	0	0	1	0	0	0
<i>Athyma nefte</i> Cramer	Nymphalidae	1	0	22	24	36	1
<i>Athyma pravara</i> Moore	Nymphalidae	4	1	30	62	21	0
<i>Athyma reta</i> Moore	Nymphalidae	1	0	4	11	2	0
<i>Athyma selenophora</i> Kollar	Nymphalidae	1	0	0	2	1	0
<i>Baoris oceia</i> Hewitson	Hesperiidae	0	0	0	4	1	0
<i>Bullis elioti</i> Corbet	Lycaenidae	1	0	0	1	0	0
<i>Caleta elna</i> Hewitson	Lycaenidae	7	5	11	4	0	0
<i>Callenya lenya</i> Evans	Lycaenidae	0	0	1	0	0	0
<i>Caltoris bromus</i> Leech	Hesperiidae	0	0	0	2	0	1
<i>Caltoris brunnea</i> Snellen	Hesperiidae	0	0	0	0	17	6
<i>Caltoris cormasa</i> Hewitson	Hesperiidae	0	0	0	0	1	2
<i>Caltoris malaya</i> Evans	Hesperiidae	1	2	0	0	6	0
<i>Caltoris philippina</i> Herrich-Schäffer	Hesperiidae	0	0	0	0	1	0
<i>Caltoris plebeia</i> de Nicéville	Hesperiidae	1	0	0	2	1	2
<i>Capila phanaeus</i> Hewitson	Hesperiidae	6	0	12	3	2	0
<i>Catopsilia pomona</i> Fabricius	Pieridae	0	0	1	0	0	0
<i>Catopsilia pyranthe</i> Linnaeus	Pieridae	0	0	0	0	0	2
<i>Catopyrops ancyra</i> Toxopeus	Lycaenidae	0	0	10	2	17	4
<i>Celaenorrhinus ficulnea</i> Hewitson	Hesperiidae	17	0	0	0	0	0
<i>Celaenorrhinus ladana</i> Butler	Hesperiidae	10	0	8	0	0	0
<i>Celastrina lavendularis</i> Moore	Lycaenidae	0	0	2	0	0	0
<i>Cethosia hypsea</i> Doubleday	Nymphalidae	0	1	0	25	3	0
<i>Charaxes bernardus</i> Fabricius	Nymphalidae	26	15	8	10	2	0
<i>Charaxes solon</i> Fabricius	Nymphalidae	0	1	0	0	0	0
<i>Chersonesia intermedia</i> Martin	Nymphalidae	8	0	2	0	0	0
<i>Chersonesia peraka</i> Distant	Nymphalidae	7	0	2	0	0	0
<i>Chersonesia rahria</i> Moore	Nymphalidae	3	0	4	0	0	0
<i>Chilasa paradoxa</i> Zinken	Papilionidae	0	0	0	1	0	0
<i>Choaspes plateni</i> Staudinger	Hesperiidae	1	0	0	0	0	0
<i>Cirrochroa emalea</i> Guérin	Nymphalidae	3	0	8	0	0	0
<i>Cirrochroa satallita</i> Butler	Nymphalidae	0	2	5	1	0	0
<i>Coelites epiminthia</i> Westwood	Nymphalidae	12	17	0	4	0	0
<i>Coelites eupythychioides</i> Felder	Nymphalidae	67	343	24	4	7	0
<i>Cupha erymanthis</i> Drury	Nymphalidae	9	2	13	3	1	0
<i>Curetis felderi</i> Distant	Lycaenidae	0	1	1	0	0	0
<i>Curetis tagalica</i> Felder	Lycaenidae	0	0	19	0	0	0
<i>Darpa striata</i> Druce	Hesperiidae	2	2	7	0	0	0
<i>Deudorix staudingeri</i> Druce	Lycaenidae	0	0	0	1	0	1
<i>Discophora necho</i> Felder	Nymphalidae	0	0	0	1	6	18
<i>Dolpha evelina</i> Stoll	Nymphalidae	1	3	2	2	0	0
<i>Drupadia ravindra</i> Horsfield	Lycaenidae	10	2	58	0	0	0
<i>Drupadia theda</i> Felder	Lycaenidae	581	175	214	96	249	0
<i>Eetion elia</i> Hewitson	Hesperiidae	0	0	0	0	3	0
<i>Eliotia jalindra</i> Horsfield	Lycaenidae	0	0	0	1	0	0
<i>Elymnias harteri</i> Honrath	Nymphalidae	0	0	0	0	0	1
<i>Elymnias hypermnestra</i> Linnaeus	Nymphalidae	0	0	0	0	0	67
<i>Elymnias nesaea</i> Linnaeus	Nymphalidae	1	0	11	3	0	6
<i>Elymnias panthera</i> Fabricius	Nymphalidae	0	0	1	2	3	1
<i>Elymnias penanga</i> Westwood	Nymphalidae	1	1	0	0	0	0
<i>Erionota sybirta</i> Hewitson	Hesperiidae	0	0	0	1	0	0
<i>Erionota thrax</i> Linnaeus	Hesperiidae	0	0	0	0	0	25
<i>Erites argentina</i> Butler	Nymphalidae	2	1	1	0	0	0
<i>Erites elegans</i> Butler	Nymphalidae	18	12	3	24	0	0
<i>Euchrysops cnejus</i> Fabricius	Lycaenidae	1	0	0	0	0	91

Species	Family	I1	I2	I3	B1	B2	B3
<i>Eulaceura osteria</i> Westwood	Nymphalidae	5	27	5	31	1	0
<i>Euploea algea</i> Godart	Nymphalidae	0	0	0	1	0	0
<i>Euploea crameri</i> Lucas	Nymphalidae	0	0	0	1	1	1
<i>Euploea diocletianus</i> Fabricius	Nymphalidae	1	0	2	0	0	0
<i>Euploea eyndhovii</i> Godart	Nymphalidae	0	0	2	1	0	0
<i>Euploea mulciber</i> Cramer	Nymphalidae	1	0	6	19	10	2
<i>Euploea phaenareta</i> Schaller	Nymphalidae	0	1	0	0	0	0
<i>Eurema ada</i> Distant & Pryer	Pieridae	0	0	0	0	0	1
<i>Eurema blanda</i> Boisduval	Pieridae	0	0	1	2	0	3
<i>Eurema hecabe</i> Linnaeus	Pieridae	0	0	0	3	20	98
<i>Eurema nicevillei</i> Horsfield	Pieridae	0	1	0	55	0	0
<i>Eurema sari</i> Horsfield	Pieridae	0	32	1	103	79	4
<i>Eurema simulatrix</i> Semper	Pieridae	0	0	0	0	2	0
<i>Eurema tominia</i> Vollenhoven	Pieridae	0	2	0	33	0	0
<i>Euthalia aconthea</i> Cramer	Nymphalidae	0	1	0	0	0	2
<i>Euthalia alpheda</i> Godart	Nymphalidae	0	0	0	0	0	2
<i>Euthalia godartii</i> Gray	Nymphalidae	0	2	0	1	0	0
<i>Euthalia iapis</i> Godart	Nymphalidae	55	26	35	0	0	0
<i>Euthalia monina</i> Fabricius	Nymphalidae	10	18	28	15	2	0
<i>Faunis kirata</i> de Nicéville	Nymphalidae	1	0	0	0	0	0
<i>Faunis stomphax</i> Westwood	Nymphalidae	49	97	10	63	70	0
<i>Flos anniella</i> Hewitson	Lycaenidae	0	0	22	1	0	0
<i>Flos apidanus</i> Cramer	Lycaenidae	0	0	1	2	0	0
<i>Gandaca harina</i> Horsfield	Pieridae	1	0	2	0	0	0
<i>Gangara thyrus</i> Fabricius	Hesperiidae	1	0	0	0	0	0
<i>Graphium agamemnon</i> Linnaeus	Papilionidae	2	1	4	15	2	1
<i>Graphium antiphates</i> Cramer	Papilionidae	0	0	0	0	1	0
<i>Graphium delesserti</i> Guérin	Papilionidae	1	0	0	3	0	0
<i>Graphium ramaceus</i> Westwood	Papilionidae	0	0	0	1	0	0
<i>Graphium sarpedon</i> Linnaeus	Papilionidae	0	0	1	3	0	0
<i>Halpe insignis</i> Distant	Hesperiidae	0	0	0	0	10	0
<i>Halpe ormenes</i> Plötz	Hesperiidae	0	0	1	13	27	0
<i>Hasora quadripunctata</i> Mabille	Hesperiidae	0	0	0	0	2	0
<i>Hasora schoenherr</i> Latreille	Hesperiidae	0	1	1	0	0	0
<i>Hasora taminatus</i> Hübner	Hesperiidae	0	0	0	0	1	0
<i>Hidari irava</i> Moore	Hesperiidae	0	6	0	3	2	4
<i>Hyarotis adrastus</i> Moore	Hesperiidae	0	0	0	3	0	0
<i>Hyarotis iadera</i> de Nicéville	Hesperiidae	0	0	1	3	1	0
<i>Hypolimnas anomala</i> Wallace	Nymphalidae	0	0	0	1	3	0
<i>Hypolimnas bolina</i> Linnaeus	Nymphalidae	0	0	0	0	0	1
<i>Hypolimnas misippus</i> Linnaeus	Nymphalidae	0	0	0	0	0	4
<i>Hypolycaena merguia</i> Doherty	Lycaenidae	6	0	0	0	0	0
<i>Hypolycaena othona</i> Hewitson	Lycaenidae	2	0	0	0	0	0
<i>Iambrix stellifer</i> Butler	Hesperiidae	1	0	4	0	41	0
<i>Idea lynceus</i> Drury	Nymphalidae	34	0	91	1	0	0
<i>Ideopsis vulgaris</i> Butler	Nymphalidae	0	1	14	113	48	24
<i>Ionolyce hellicon</i> Felder	Lycaenidae	0	0	0	2	0	0
<i>Iraota distanti</i> Staudinger	Lycaenidae	1	0	0	0	0	0
<i>Isma bononia</i> Hewitson	Hesperiidae	15	19	13	20	0	0
<i>Isma iapis</i> de Nicéville	Hesperiidae	0	0	1	0	0	0
<i>Isma protoctlea</i> Herrich-Schäffer	Hesperiidae	2	0	0	0	0	0
<i>Isma umbrosa</i> Elwes & Edwards	Hesperiidae	2	0	0	0	0	0
<i>Jacoona anasuja</i> C. & R. Felder	Lycaenidae	0	0	3	0	0	0
<i>Jamides alecto</i> Felder	Lycaenidae	0	0	2	0	0	0
<i>Jamides bochus</i> Stoll	Lycaenidae	1	0	0	0	0	0
<i>Jamides caeruleus</i> Druce	Lycaenidae	1	0	0	0	0	0
<i>Jamides celeno</i> Cramer	Lycaenidae	1	0	125	13	156	93
<i>Jamides philatus</i> Snellen	Lycaenidae	3	0	0	0	0	0
<i>Jamides puloensis</i> Tite	Lycaenidae	1	0	2	0	0	0
<i>Jamides pura</i> Moore	Lycaenidae	36	255	51	132	463	0
<i>Jamides talinga</i> Kheil	Lycaenidae	0	0	26	0	0	0
<i>Jamides virgulatus</i> Druce	Lycaenidae	1	0	6	0	0	0
<i>Junonia atlites</i> Linnaeus	Nymphalidae	0	0	0	0	2	68
<i>Junonia iphita</i> Cramer	Nymphalidae	0	0	0	0	0	10
<i>Junonia oritya</i> Linnaeus	Nymphalidae	0	0	0	0	0	34

Species	Family	I1	I2	I3	B1	B2	B3
<i>Koruthaialos rubecula</i> Plötz	Hesperiidae	139	386	63	569	690	0
<i>Lampides boeticus</i> Linnaeus	Lycaenidae	0	0	0	0	5	81
<i>Laringa castelnaui</i> Felder	Nymphalidae	0	0	1	0	0	0
<i>Lasippa heliodore</i> Fabricius	Nymphalidae	1	0	1	0	0	0
<i>Lasippa monata</i> Weyenbergh	Nymphalidae	1	1	1	0	0	0
<i>Lasippa tiga</i> Moore	Nymphalidae	8	10	5	62	0	0
<i>Lasippa viraja</i> Moore	Nymphalidae	0	0	1	0	0	0
<i>Laxita thuisto</i> Hewitson	Lycaenidae	2	0	2	0	0	0
<i>Lebadea martha</i> Fabricius	Nymphalidae	8	1	3	0	0	0
<i>Leptosia nina</i> Hübner	Pieridae	0	0	0	0	3	0
<i>Lexias dirtea</i> Fabricius	Nymphalidae	0	2	0	1	0	1
<i>Lexias pardalis</i> Moore	Nymphalidae	8	22	0	25	9	6
<i>Logania distantis</i> Semper	Lycaenidae	36	0	13	0	0	0
<i>Logania malayica</i> Distant	Lycaenidae	14	0	4	0	0	0
<i>Logania marmorata</i> Moore	Lycaenidae	0	0	2	2	0	0
<i>Logania regina</i> Druce	Lycaenidae	0	0	1	0	0	0
<i>Losaria neptunus</i> Guérin	Papilionidae	6	0	5	0	0	0
<i>Lotongus avesta</i> Hewitson	Hesperiidae	0	0	1	0	0	0
<i>Lotongus calathus</i> Hewitson	Hesperiidae	2	2	2	1	0	0
<i>Lycaenopsis haraldus</i> C. & R. Felder	Lycaenidae	25	0	42	0	0	0
<i>Matapa aria</i> Moore	Hesperiidae	2	0	0	4	0	0
<i>Matapa druna</i> Moore	Hesperiidae	2	3	1	0	1	0
<i>Megisba malaya</i> Horsfield	Lycaenidae	0	0	0	0	4	0
<i>Melanitis leda</i> Linnaeus	Nymphalidae	0	0	1	0	1	5
<i>Milletus biggsii</i> Distant	Lycaenidae	0	1	1	1	12	0
<i>Milletus drucei</i> Semper	Lycaenidae	0	0	0	0	1	0
<i>Milletus gallus</i> de Nicéville	Lycaenidae	0	0	0	0	1	0
<i>Milletus gopara</i> de Nicéville	Lycaenidae	7	16	12	5	57	0
<i>Milletus symethus</i> Cramer	Lycaenidae	0	0	0	0	38	0
<i>Moduza procris</i> Cramer	Nymphalidae	2	0	20	71	5	5
<i>Mycalesis anapita</i> Moore	Nymphalidae	71	33	118	179	0	0
<i>Mycalesis fusca</i> Felder	Nymphalidae	0	0	0	1	0	0
<i>Mycalesis horsfieldi</i> Moore	Nymphalidae	0	0	2	7	20	74
<i>Mycalesis janardana</i> Moore	Nymphalidae	0	0	2	0	0	0
<i>Mycalesis maianae</i> Hewitson	Nymphalidae	1	0	0	0	0	0
<i>Mycalesis mineus</i> Linnaeus	Nymphalidae	0	0	0	0	0	57
<i>Mycalesis orseis</i> Hewitson	Nymphalidae	33	0	25	0	0	0
<i>Mycalesis pattiana</i> Eliot	Nymphalidae	47	13	15	0	0	0
<i>Mycalesis perseus</i> Fabricius	Nymphalidae	0	0	0	0	0	180
<i>Mycalesis thyateira</i> Fruhstorfer	Nymphalidae	142	0	32	0	0	0
<i>Nacaduba asaga</i> Fruhstorfer	Lycaenidae	2	0	0	0	0	0
<i>Nacaduba berenice</i> Herrich-Schäffer	Lycaenidae	0	0	48	8	84	1
<i>Nacaduba beroe</i> Felder	Lycaenidae	0	1	32	8	13	0
<i>Nacaduba caularia</i> Felder	Lycaenidae	0	0	1	1	14	0
<i>Nacaduba hermus</i> Felder	Lycaenidae	13	5	5	0	0	0
<i>Nacaduba kurawa</i> Moore	Lycaenidae	2	0	3	1	15	0
<i>Nacaduba normani</i> Eliot	Lycaenidae	0	0	20	0	24	0
<i>Nacaduba solta</i> Eliot	Lycaenidae	3	0	4	0	0	0
<i>Neopithecopis zalmora</i> Butler	Lycaenidae	3	0	0	0	0	0
<i>Neptis duryodana</i> Moore	Nymphalidae	0	0	0	1	0	0
<i>Neptis hylas</i> Linnaeus	Nymphalidae	0	0	0	14	384	222
<i>Neptis ilira</i> Kheil	Nymphalidae	0	1	1	0	0	0
<i>Neptis leucoporus</i> Fruhstorfer	Nymphalidae	1	11	3	26	6	0
<i>Neptis magadha</i> Felder	Nymphalidae	0	0	2	3	0	0
<i>Neptis nata</i> Moore	Nymphalidae	0	2	0	0	0	0
<i>Notocrypta clavata</i> Staudinger	Hesperiidae	0	0	4	7	12	0
<i>Notocrypta curvifascia</i> C. & R. Felder	Hesperiidae	0	0	1	0	0	0
<i>Notocrypta paralysos</i> Wood-Mason & de Nicéville	Hesperiidae	0	0	0	3	6	0
<i>Notocrypta pria</i> Druce	Hesperiidae	21	0	39	0	0	0
<i>Odontoptilum pygela</i> Hewitson	Hesperiidae	0	0	4	0	0	0
<i>Oerane microthyrus</i> Mabille	Hesperiidae	9	0	13	0	0	0
<i>Oriens gola</i> Moore	Hesperiidae	0	0	0	0	2	2
<i>Orsotriaena medus</i> Wallengren	Nymphalidae	0	0	0	20	97	304
<i>Pandita sinope</i> Moore	Nymphalidae	0	0	0	21	4	9
<i>Pantoporia aurelia</i> Staudinger	Nymphalidae	1	1	2	0	0	0

Appendix I (Continued)

Species	Family	I1	I2	I3	B1	B2	B3
<i>Pantoporia dingdinga</i> Butler	Nymphalidae	0	0	0	1	0	0
<i>Pantoporia paraka</i> Butler	Nymphalidae	0	2	0	3	2	0
<i>Papilio demoleus</i> Linnaeus	Papilionidae	0	0	0	0	0	3
<i>Papilio demolion</i> Cramer	Papilionidae	1	1	4	0	0	0
<i>Papilio memnon</i> Linnaeus	Papilionidae	6	0	0	0	0	14
<i>Papilio nephelus</i> Boisduval	Papilionidae	3	0	9	0	0	0
<i>Papilio polytes</i> Linnaeus	Papilionidae	0	0	0	0	0	3
<i>Paralaxita damajanti</i> Felder	Lycaenidae	4	0	0	0	0	0
<i>Paralaxita orphna</i> Boisduval	Lycaenidae	151	0	41	0	0	0
<i>Paralaxita telesia</i> Hewitson	Lycaenidae	30	0	12	0	0	0
<i>Parantica agleoides</i> Felder	Nymphalidae	0	0	0	1	30	58
<i>Parantica aspasia</i> Fabricius	Nymphalidae	0	1	11	23	22	0
<i>Parnara apostata</i> Snellen	Hesperiidae	0	0	0	0	6	10
<i>Parnara naso</i> Fabricius	Hesperiidae	0	0	0	0	0	2
<i>Parthenos sylvia</i> Cramer	Nymphalidae	0	0	0	0	1	0
<i>Pelopidas agna</i> Moore	Hesperiidae	0	0	0	0	3	19
<i>Pelopidas conjunctus</i> Herrich-Schäffer	Hesperiidae	0	0	0	0	1	1
<i>Pelopidas mathias</i> Fabricius	Hesperiidae	0	0	1	0	0	0
<i>Pemara pugnans</i> de Nicéville	Hesperiidae	0	0	0	2	29	0
<i>Petrelaea dana</i> de Nicéville	Lycaenidae	1	0	0	0	0	0
<i>Pirdana distanti</i> Staudinger	Hesperiidae	2	0	2	0	0	0
<i>Plastingia naga</i> de Nicéville	Hesperiidae	0	3	0	2	1	0
<i>Plastingia pelsonia</i> Fruhstorfer	Hesperiidae	1	6	0	5	8	0
<i>Plautella cossaea</i> de Nicéville	Lycaenidae	0	0	1	0	0	0
<i>Polytremis lubricans</i> Herrich-Schäffer	Hesperiidae	0	0	0	16	29	117
<i>Polyura athamas</i> Drury	Nymphalidae	0	0	2	0	0	0
<i>Polyura delphis</i> Doubleday	Nymphalidae	1	0	0	0	0	0
<i>Polyura schreiber</i> Godart	Nymphalidae	0	1	0	0	0	0
<i>Poritia sumatrae</i> Felder	Lycaenidae	1	0	0	0	0	0
<i>Potanthus ganda</i> Fruhstorfer	Hesperiidae	0	0	2	11	34	36
<i>Potanthus omaha</i> Edwards	Hesperiidae	0	0	1	11	87	134
<i>Potanthus trachala</i> Mabille	Hesperiidae	0	0	2	3	24	69
<i>Pratapa icetoides</i> Elwes	Lycaenidae	3	0	0	0	0	0
<i>Prosotas aluta</i> Druce	Lycaenidae	0	0	0	0	12	0
<i>Prosotas dubiosa</i> Semper	Lycaenidae	0	0	0	1	0	0
<i>Prosotas gracilis</i> Röber	Lycaenidae	0	0	0	0	5	0
<i>Prosotas nora</i> Felder	Lycaenidae	1	0	8	6	13	2
<i>Prothoe franck</i> Godart	Nymphalidae	3	25	8	4	0	0
<i>Pseudokerana fulgur</i> de Nicéville	Hesperiidae	1	0	0	0	0	0
<i>Psolos fuligo</i> Staudinger	Hesperiidae	4	0	6	7	7	0
<i>Pyronaura callineura</i> C & R. Felder	Hesperiidae	0	0	0	0	1	0
<i>Pyronaura helena</i> Butler	Hesperiidae	0	4	0	0	0	0
<i>Pyronaura latoia</i> Hewitson	Hesperiidae	1	4	0	0	0	0
<i>Pyronaura niasana</i> Fruhstorfer	Hesperiidae	0	3	0	1	0	0
<i>Quedara monteithi</i> Wood-Mason & de Nicéville	Hesperiidae	0	0	0	4	11	0
<i>Ragadia makuta</i> Horsfield	Nymphalidae	397	0	132	0	0	0
<i>Rapala dienece</i> Hewitson	Lycaenidae	0	0	0	0	7	0
<i>Rapala manea</i> Hewitson	Lycaenidae	0	0	0	0	1	0
<i>Rapala pheretima</i> Hewitson	Lycaenidae	0	0	1	0	0	1
<i>Ritra aurea</i> Druce	Lycaenidae	0	8	0	0	0	0
<i>Salanoemia fuscicornis</i> Elwes & Edwards	Hesperiidae	0	1	0	1	0	0
<i>Salanoemia sala</i> Hewitson	Hesperiidae	0	0	1	0	2	0
<i>Salanoemia similis</i> Elwes & Edwards	Hesperiidae	3	2	0	15	15	0
<i>Salanoemia tavoyana</i> Evans	Hesperiidae	0	0	0	4	1	0
<i>Saletara panda</i> Butler	Pieridae	0	0	0	0	19	0
<i>Simiskina phalia</i> Hewitson	Lycaenidae	0	1	0	0	0	0
<i>Simiskina pharyge</i> Hewitson	Lycaenidae	0	1	1	0	0	0
<i>Simiskina philura</i> Druce	Lycaenidae	0	2	0	0	0	0
<i>Sinthusa privata</i> Fruhstorfer	Lycaenidae	0	0	12	0	0	0
<i>Sithon nedymond</i> Cramer	Lycaenidae	3	6	1	0	0	0
<i>Spalgis epius</i> Westwood	Lycaenidae	0	0	6	0	0	0
<i>Spindasis kutu</i> Corbet	Lycaenidae	0	0	3	0	143	288
<i>Suastus everyx</i> Mabille	Hesperiidae	0	1	0	1	0	0
<i>Surenbra vivarna</i> Horsfield	Lycaenidae	1	0	1	0	0	0
<i>Tagiades gana</i> Moore	Hesperiidae	1	1	1	2	0	0

Appendix I (Continued)

Species	Family	I1	I2	I3	B1	B2	B3
<i>Tagiades japetus</i> Stoll	Hesperiidae	0	1	0	1	3	0
<i>Tajuria isaeus</i> Hewitson	Lycaenidae	0	0	1	0	3	0
<i>Tanaecia aruna</i> Felder	Nymphalidae	55	72	27	2	0	0
<i>Tanaecia clathrata</i> Vollenhoven	Nymphalidae	6	14	6	2	1	0
<i>Tanaecia munda</i> Fruhstorfer	Nymphalidae	48	52	6	4	8	0
<i>Tanaecia orphne</i> Butler	Nymphalidae	24	1	7	0	0	0
<i>Tanaecia pelea</i> Fabricius	Nymphalidae	1	2	0	0	0	0
<i>Taractrocera ardonia</i> Hewitson	Hesperiidae	0	0	0	1	156	350
<i>Taxila haquimus</i> Fabricius	Lycaenidae	5	0	1	0	0	0
<i>Telicota besta</i> Evans	Hesperiidae	0	0	0	1	19	108
<i>Terinos clarissa</i> Boisduval	Nymphalidae	11	4	9	2	0	0
<i>Terinos terpander</i> Hewitson	Nymphalidae	0	96	0	113	1	0
<i>Thamala marciana</i> Hewitson	Lycaenidae	0	14	0	9	0	0
<i>Thaumantis odona</i> Godart	Nymphalidae	89	24	17	1	1	0
<i>Trogonoptera brookiana</i> Wallace	Papilionidae	0	0	1	0	0	0
<i>Troides amphrysus</i> Cramer	Papilionidae	1	0	3	0	0	0
<i>Vindula dejone</i> Erichson	Nymphalidae	1	0	1	0	0	0
<i>Xanthotaenia busiris</i> Westwood	Nymphalidae	117	0	48	0	0	0
<i>Ypthima fasciata</i> Hewitson	Nymphalidae	18	0	82	0	0	0
<i>Ypthima pandocus</i> Moore	Nymphalidae	1	3	43	370	441	238
<i>Zela elioti</i> Evans	Hesperiidae	0	0	0	1	4	0
<i>Zela zenon</i> de Nicéville	Hesperiidae	0	0	0	1	0	0
<i>Zemeros emesoides</i> Felder	Lycaenidae	11	0	50	0	0	0
<i>Zemeros flegyas</i> Cramer	Lycaenidae	3	0	6	0	0	0
<i>Zeuxidia amethystus</i> Butler	Nymphalidae	1	4	0	0	0	0
<i>Zeuxidia doubledayi</i> Westwood	Nymphalidae	0	1	0	0	0	0
<i>Zizina otis</i> Fabricius	Lycaenidae	0	0	0	0	0	190
<i>Zographetus doxus</i> Eliot	Hesperiidae	2	0	4	0	0	0

Appendix II. Alphabetical list of odonate species and number of individuals collected per landscape. I1: primary landscape in large unburned isolate, I2: primary landscape in small unburned isolate, I3: logged landscape in large unburned isolate, B1: once-burned forest, B2: twice-burned forest, B3: slash-and-burn area.

Species	Family	I1	I2	I3	B1	B2	B3
<i>Aciagrion borneense</i> Ris	Coenagrionidae	0	0	0	0	0	1
<i>Aciagrion</i> sp1	Coenagrionidae	0	0	0	0	0	2
<i>Acisoma panorpoides</i> Rambur	Libellulidae	0	0	0	0	0	1
<i>Agriocnemis femina</i> Rambur	Coenagrionidae	0	0	0	0	0	7
<i>Agriocnemis pygmaea</i> Rambur	Coenagrionidae	0	0	0	0	0	1
<i>Agriocnemis rubescens</i> Selys	Coenagrionidae	0	6	0	11	1	1
<i>Agriocnemis</i> sp1	Coenagrionidae	0	0	0	0	0	1
<i>Agrionoptera insignis</i> Rambur	Libellulidae	0	0	1	0	0	0
<i>Amphicnemis remiger</i> Laidlaw	Coenagrionidae	1	25	0	3	0	0
<i>Archibasis melanocyana</i> Selys	Coenagrionidae	0	1	0	0	0	0
<i>Archibasis viola</i> Liefstinck	Coenagrionidae	1	19	1	5	3	0
<i>Brachydiplax chalybea</i> Brauer	Libellulidae	0	15	2	1	7	13
<i>Brachydiplax farinosa</i> Krüger	Libellulidae	0	3	0	0	0	0
<i>Brachygonia oculata</i> Brauer	Libellulidae	0	3	0	0	1	0
<i>Camasinea gigantea</i> Brauer	Libellulidae	0	0	7	0	0	0
<i>Ceriagrion cerinorubellum</i> Brauer	Coenagrionidae	0	5	0	3	186	84
<i>Coelliccia arcuata</i> Liefstinck	Platycnemididae	7	0	2	0	0	0
<i>Coelliccia nigrahmata</i> Laidlaw	Platycnemididae	85	145	78	21	57	0
<i>Copera vittata</i> Selys	Platycnemididae	1	21	1	10	8	1
<i>Cratilla lineata</i> Brauer	Libellulidae	0	0	7	0	0	0
<i>Cratilla metallica</i> Brauer	Libellulidae	3	5	3	0	0	0
<i>Devadatta</i> sp1	Amphipterygidae	0	2	0	0	0	0
<i>Diplacodes trinitalis</i> Rambur	Libellulidae	0	0	0	0	3	267
<i>Dysphaea dimidiata</i> Selys	Euphaeidae	4	0	0	0	0	0
<i>Elatoneura analis</i> Selys	Protoneuridae	0	3	0	1	0	0
<i>Euphaea impar</i> Selys	Euphaeidae	90	14	98	9	3	0
<i>Euphaea subcostalis</i> Selys	Euphaeidae	65	0	14	1	0	0
<i>Euphaea tricolor</i> Selys	Euphaeidae	2	0	2	0	0	0
<i>Gomphidae</i> sp1	Gomphidae	0	0	1	0	0	0
<i>Gomphidia maclachlani</i> Selys	Gomphidae	3	0	0	0	0	0
<i>Gynacantha dohrni</i> Krüger	Aeschnidae	1	2	0	0	2	0
<i>Heliaeschna idae</i> Brauer	Aeschnidae	0	1	0	1	0	0
<i>Hemicordulia</i> sp	Cordulidae	1	0	0	0	0	0
<i>Hydrobasileus croceus</i> Brauer	Libellulidae	1	1	0	0	3	0
<i>Ictinogomphus decoratus</i> Selys	Gomphidae	0	0	0	0	2	0
<i>Idionyx</i> sp	Cordulidae	1	0	11	0	0	0
<i>Indaeschna grubaueri</i> Förster	Aeschnidae	0	0	1	0	0	0
<i>Ischnura senegalensis</i> Rambur	Coenagrionidae	0	0	0	0	0	16
<i>Lathrecista asiatica</i> Fabricius	Libellulidae	0	1	2	2	0	0
<i>Leptogomphus cf coomansi</i> Laidlaw	Gomphidae	1	0	2	0	0	0
<i>Libellago hyalina</i> Selys	Chlorocyphidae	0	7	0	0	9	7
<i>Lyriothemis biappendiculata</i> Selys	Libellulidae	5	17	1	0	6	0
<i>Lyriothemis cleis</i> Brauer	Libellulidae	12	22	14	5	0	0
<i>Macromia cineta</i> Rambur	Cordulidae	0	1	0	0	0	2
<i>Megalogomphus icterops</i> Martin	Gomphidae	1	0	0	0	0	0
<i>Microgomphus chelifera</i> Selys	Gomphidae	1	0	1	0	0	0
<i>Mortonagrion alyone</i> Laidlaw	Coenagrionidae	0	0	0	0	1	0
<i>Mortonagrion forficulatum</i> Liefstinck	Coenagrionidae	0	1	0	0	0	0
<i>Namophya pygmaea</i> Rambur	Libellulidae	0	0	0	6	1	7
<i>Nesoxenia lineata</i> Selys	Libellulidae	0	0	0	2	0	0
<i>Nesoxenia sexlineata</i> Selys	Libellulidae	0	1	0	0	0	0
<i>Neurobasis</i> sp	Calopterygidae	18	0	0	0	0	0
<i>Neurothemis fluctuans</i> Fabricius	Libellulidae	1	17	7	85	401	597
<i>Neurothemis ramburii?</i> Kaup in Brauer	Libellulidae	0	0	1	0	0	0
<i>Neurothemis terminata</i> Ris	Libellulidae	1	2	17	10	168	158
<i>Onychargia atrocyana</i> Selys	Coenagrionidae	0	0	0	0	17	3
<i>Orchithemis pulcherrima</i> Brauer	Libellulidae	1	81	0	26	72	0
<i>Orolestes wallacei</i> Kirby	Lestidae	0	1	4	0	0	0
<i>Orthetrum chrysis</i> Selys	Libellulidae	6	0	8	11	22	19
<i>Orthetrum glaucum</i> Brauer	Libellulidae	0	0	19	0	5	0
<i>Orthetrum pruinosum</i> Burmeister	Libellulidae	3	0	6	0	0	1
<i>Orthetrum sabina</i> Drury	Libellulidae	0	0	9	17	54	373
<i>Orthetrum testaceum</i> Burmeister	Libellulidae	1	0	6	1	4	6

Appendix II (Continued)

Species	Family	I1	I2	I3	B1	B2	B3
<i>Pantala flavescens</i> Fabricius	Libellulidae	0	0	0	0	0	9
<i>Platylestes heterostylus</i> Lieftinck	Lestidae	0	1	0	0	0	0
<i>Platystictidae</i> sp1	Platystictidae	2	0	0	0	0	0
<i>Podolestes orientalis</i> Selys	Megapodagrionidae	0	8	0	4	0	0
<i>Prodasinera collaris</i> Selys	Protoneuridae	0	12	0	48	32	0
<i>Prodasinera hyperythra</i> Selys	Protoneuridae	7	5	5	1	1	0
<i>Pseudagrion microcephalum</i> Rambur	Coenagrionidae	0	0	0	0	1	6
<i>Rhinagrion borneense</i> Selys	Megapodagrionidae	2	0	1	0	0	0
<i>Rhinocypha biseriata</i> Selys	Chlorocyphidae	62	0	7	0	2	0
<i>Rhinocypha cucullata</i> Selys	Chlorocyphidae	1	0	0	0	0	0
<i>Rhinocypha humeralis</i> Selys	Chlorocyphidae	58	0	91	0	0	0
<i>Rhyothemis obsolescens</i> Kirby	Libellulidae	0	1	0	4	49	0
<i>Rhyothemis phyllis</i> Sulzer	Libellulidae	0	0	8	6	207	48
<i>Sundacypha petiolata</i> Selys	Chlorocyphidae	0	11	0	1	0	0
<i>Teinobasis rajah</i> Laidlaw	Coenagrionidae	0	2	0	0	0	0
<i>Tetracanthagyna plagiata</i> Waterhouse	Aeschnidae	0	2	0	3	0	0
<i>Tetrathemis flavescens</i> Kirby	Libellulidae	0	0	1	0	0	0
<i>Tholymis tillarga</i> Fabricius	Libellulidae	0	0	1	0	0	16
<i>Tramea</i> sp	Libellulidae	0	0	0	0	0	2
<i>Trithemis aurora</i> Burmeister	Libellulidae	2	0	0	0	0	0
<i>Tyriobapta laidlawi</i> Ris	Libellulidae	6	34	4	10	0	0
<i>Tyriobapta torrida</i> Kirby	Libellulidae	2	38	3	0	0	0
<i>Ureothemis signata</i> Rambur	Libellulidae	0	0	0	0	3	1
<i>Vestalis amaryllis</i> Lieftinck	Calopterygidae	450	187	312	86	0	0
<i>Vestalis atropa</i> Lieftinck	Calopterygidae	7	0	1	1	0	0
<i>Zyxomma petiolatum</i> Rambur	Libellulidae	0	0	0	0	4	1