Biodiversity and environmental change in the rainforests of Borneo

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Scale-dependent impact of ENSO-induced disturbance and logging on the diversity and community composition of Bornean butterflies

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ENSO-(El Niño Southern Oscillation) induced burning and logging have already affected the majority of lowland rainforest in Borneo and other tropical regions. Here the scale-related impact of both forms of disturbance on the species richness and community composition of an important indicator community, namely, butterflies (more than 470 species over more than 28,000 individuals sampled) is addressed using small (0.9 ha) plots nested within large (450 ha) landscapes. The landscapes were located in three disturbance classes: 1) continuous forest, 2) unburned isolates surrounded by burned forest, and 3) burned forest. Within the unburned disturbance classes (1 and 2) landscape-plots were established in primary and logged forest.

Overall species richness was significantly lower in burned forest than continuous forest. Species richness in the isolates was intermediate. The difference was more pronounced at the large spatial scale (landscape-plots) than at the smaller spatial scale (0.9 ha plots). In contrast to species richness, there was no significant difference in either dominance or evenness among disturbance classes, although there was considerable variation within disturbance classes. Contrary to burning, logging led to an increase in species richness although the effect here was more pronounced at the smaller spatial scale.

We additionally assessed levels of abundance and species richness from butterfly guilds (based on larval host-plant use). Within disturbance classes herb and tree specialist abundance was higher in primary forest but species richness was higher in logged forest. Generalist abundance and species richness was higher in logged forest.

Among disturbance classes tree specialist abundance and species richness was significantly lower in burned forest than continuous forest and herb specialist abundance (but not species richness) was significantly higher. The largest difference in species richness was, however, in the generalist guild; there were significantly fewer species in burned forest and isolates than in continuous forest. Our results with guilds indicate that a response to one form of disturbance (logging) provides very little insight into responses from other disturbance forms such as ENSO-induced burning.

As the global climate becomes more conducive to severe ENSO events, the probability increases that a fire-affected landscape will become the dominant matrix with dire consequences for extant biodiversity. Most of Borneo has been logged or will be in the near future. Logged areas can maintain high levels of biodiversity, but are also more susceptible and conducive to burning and other forms of disturbance over a large spatial extent. Protecting extant levels of biodiversity in Borneo’s extensive logged forests should be seen as a conservation priority.
Introduction

ENSO-(El Niño Southern Oscillation) induced forest fires and logging are the two most important forms of disturbance in the highly diverse rainforests of insular Southeast Asia, an area of very high conservation value (Myers et al., 2000). In this area, commercial logging is generally a recent activity and subject to minimal regulation as well as continuous threat from encroachment and illegal logging activities (Uhl and Kauffman, 1990). In the research area Indonesian Borneo, logging is by far the single most important type of land-use (Siegert et al., 2001). Extensive areas of pristine and logged forest have, however, already been affected by ENSO- (El Niño Southern Oscillation) induced disturbance (Siegert et al., 2001; Fig. 1). A severe ENSO-event can cause an extreme drought that induces trees to lose their leaves and makes the drought-affected forest highly susceptible to forest fires (Nepstad et al., 1998). The 1997/98 ENSO event was the most severe and widespread in recorded history (Harrison 2000; Nyström et al., 2000; Siegert et al., 2001), and there is evidence that such events are increasing in frequency (Holmgren et al., 2001; Tudhope et al. 2001).

Both forms of disturbance (logging and ENSO-induced fires) have been implicated with species loss, but despite the profusion of studies on especially logging, and to a much lesser extent ENSO-induced disturbance, no consistent pattern emerges (Cannon et al. 1998; Danielsen and Heegaard, 1995; Lewis, 2001; Malcolm and Ray, 2000; Thiollay, 1997; Willott et al., 2000). The large variation in the scale of assessment and methodology used in such studies makes any generalization about the impact of both disturbance forms dubious at best. Furthermore, and importantly, the impact of disturbance on species richness may be scale-dependent (Hamer and Hill, 2000). At small spatial scales, for example, there has been a lot of observed variance in community structure. Studies in the most diverse ecosystems, coral reefs and tropical rainforests, have shown that enlarging the spatial scale of study leads to highly consistent patterns in community structure. The high variability observed within sites thus declines, often dramatically, as larger areas are sampled; variability is generally lowest at intermediate scales of 1- to 100-Kms (Pandolfi, 2002). Sampling within this range should thus alleviate problems with variability and ensure that the area sampled is representative of both natural and disturbance-induced habitat heterogeneity.

Additionally, local-scale data may not be appropriate for inferring effects of large-scale conditions (Gutzwiller and Barrow, 2002 and refs therein). Small-scale studies, for example, that studied ecological phenomena in isolation from the larger landscape-context proved successful in elucidating ecological phenomena such as competition, mutualism, predation, and disease, but proved much less successful in identifying causes for the spatial and temporal variation in the abundance, distribution, and richness of species and their communities (Brown et al., 2001).

Unfortunately it is not as easy to replicate landscapes or very large plots, as it is to replicate smaller plots. Choosing for a large-scale perspective will automatically entail a loss of statistical power in standard statistical tests as fewer plots can be sampled. The lack of replication power may, however, be compensated when predictions of change are dramatic enough to make any otherwise spontaneous changes in the system of negligible importance (Oksanen, 2001). Simulated confidence intervals (e.g. via bootstraps or permutations) provide an additional source of statistical comparison that does not depend on strict replication (Gotelli and Colwell, 2001).

In this study the impact of logging and ENSO-induced disturbance on butterfly species richness and community structure is assessed by comparing species richness in both unburned fragments surrounded by burned forest and the burned forest itself with continuous forest that has remained unaffected by ENSO-induced disturbance. To this end, butterflies were assessed using randomly assigned plots within landscapes. Each landscape was
approximately 450 ha and the total number of butterflies sampled per landscape varied from 2200 to 3600 individuals. During the course of this study more than 28 000 individuals belonging to 478 species of butterflies were sampled.

A total of nine landscapes (landscape-plots) were sampled post-ENSO (after the 1997/98 ENSO event). Three of the landscape were located in large unburned isolates (3 500 - 138 000 ha) and were completely surrounded by forest that burned during the 1997/98 ENSO event (Fig. 1). Three were sampled in the burned forest surrounding these isolates. These two disturbance classes were located in an area of eastern Borneo that has been intensively studied both pre- and post-ENSO and where vegetational shifts as a result of the 1997/98 ENSO event have been documented with both satellite images and ground truthing (Siebert et al. 2001). Finally, three landscapes were sampled in an area of continuous forest. This area is located at a considerable distance from the eastern Borneo isolates and burned forest landscape-plots (Fig. 1), and represents one of the few large remaining expanses of lowland, unburned and continuous forest in Kalimantan. In order to assess the impact of logging, three of the landscapes, one in an isolate (I3) and two in the continuous forest (C2 and C3), were located in areas that have been commercially logged. The other three unburned landscape-plots were in areas of primary forest, one in the continuous forest (C1), and two in isolates (I1 and I2).

In order to assess the impact of ENSO-induced disturbance and logging on butterflies we quantified patterns of butterfly species richness and community composition within and among disturbance classes. Butterflies have been identified as key environmental indicators (Blair, 1999; Dennis, 1993; Fuller et al., 1998; Howard et al., 1998; Parmesan et al., 1999; Spitzer et al., 1997). The life histories of butterfly species in Borneo are also reasonably well known (Fiedler 1991, Suguru and Haruo, 1997; Suguru and Haruo, 2000). We therefore grouped species into larval feeding guilds in order to test if species differed in their communal response (overall abundance and species richness) to logging and ENSO-induced disturbance based on larval feeding preferences.

The questions addressed with this study are:

1) Are the biodiversity indices (i.e. species richness, dominance, and evenness) correlated?
2) What impact does logging have on species richness, dominance, and evenness of butterflies?
3) What impact does ENSO-induced disturbance have on these biodiversity indices?
4) Does the scale of assessment influence the degree of change in species richness?
5) Is there a difference in guild species richness and abundance among disturbance classes and among logged, primary, and burned forest?
6) Does species composition differ among disturbance classes, and among logged, primary, and burned forest?

Materials and Methods

A. Site descriptions

All landscape-plots (Fig. 1) were situated within zero and two degrees latitude and 112 and 118 degrees longitude in Indonesian Borneo. All research took place in the provinces of
East and Central Kalimantan, Indonesian Borneo. These include landscapes in east Borneo (Balikpapan-Samarinda region) and central Borneo (in the large Kayu Mas concession). Post-ENSO a total of nine landscapes (450 ha) were sampled, each consisting of randomly assigned plots in a hierarchical sampling design over three main disturbance classes. Three landscapes were sampled in continuous forest, three in unburned forest isolates surrounded by burned forest, and three in the burned forest surrounding the unburned isolates.

Fig. 1. Maps of the study area. a) Borneo showing burned areas (shaded), 200 m contour, and the study areas, b) isolates and burned forest, and c) continuous forest. Acronyms as described in the Materials and Methods section. Data was provided by Florian Siegert, and includes satellite and ground referenced data from August 1997 - May 1998 and additional data was downloaded from the NASA website which provided information on the fires in western Indo-Malaysia from July 1997 until December 1997. Note that most of the lowland area of Kalimantan (Indonesian Borneo) has been affected by fire.

The continuous forest landscapes (here designated C1, C2, and C3) are located in the province of Central Kalimantan in the large unburned central core of Borneo that has not yet been affected by ENSO-induced fires (Fig. 1). C1 is primary forest, C2 was previously logged in 1989/90, and C3 was previously logged in 1993/94. The unburned forest isolate landscapes (I1, I2, and I3) are located in the province of East Kalimantan, and were not directly affected by the 1997/98 ENSO event, but are completely surrounded by forest that burned during this event. The I1 (primary) and I3 (logged in 1993/94) landscapes are located in a 108 000 ha isolate located in parts of the ITCI and adjacent BFI concessions (see Hoffmann et al., 1999 for a description of these concessions) and includes the Gunung Meratus Protected Forest Reserve (ca. 30000 ha). The I2 landscape is located in a 3500 ha unburned primary isolate that is all that remained post-ENSO of the Sungai Wain Nature Reserve (originally 10000 ha).

All the continuous forest and unburned isolate landscapes had similar vegetation. All the unburned landscapes were also dominated by dipterocarp species as is typical for intact
lowland dipterocarp rainforest in Borneo (Yamakura et al., 1986). The burned landscapes (B1, B2, and B3) are located in the province of East Kalimantan and surround the unburned forest isolates. B1 was burned for the first time during the 1997/98 ENSO event and is located in the burned part of the Sungai Wain Nature Reserve. B2 was partially burned during the 1982/83 ENSO event and again during the 1997/98 ENSO event and is located in the Wanariset Samboja Research Forest. B3 is located in an area of slash and burn agriculture along Km 30 of the Balikpapan to Samarinda highway and here the forest is frequently burned (probably on average every two years, Kauffman et al., 1998).

The unburned isolate and burned landscapes are located in a large area of East Kalimantan (5.22 million ha) 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 burned landscapes were similar in having relatively low tree densities. Tree densities per 200-m² subplots, nested with the sample plots varied from a mean per landscape of 0.13 ± 0.34 to 4.56 ± 4.15 in the burned forest compared to 7.19 ± 2.59 to 11.94 ± 5.05 in the unburned forest (DFRC unpublished data). Dominant vegetation types were grasses in B3 (especially *Imperata cylindrica* or alang alang), ferns in B1 (especially the cosmopolitan *Pteridium aquilinum*, Dennstaedtiaceae, or bracken) and euphorb pioneer trees (especially *Macaranga* spp.) in B2. The burned areas, though, had substantial networks of unburned forest that traversed the otherwise burned vegetation. In B1 and B2 the area occupied by these unburned networks was estimated at 10.6% (B1) and 8.1% (B2) of the total area (K. Eichhorn, unpublished data). These unburned networks were primarily found along the flood plain, and contained vegetation dominated by dipterocarps, similar to that of the contiguous unburned forest in the continuous forest and unburned isolate landscapes. Locations of the landscapes and the area of Borneo affected by the 1997/98 ENSO event are shown in Fig. 1. 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. (2001) and Van Nieuwstadt et al. (2001).

### B. Plot design and sampling

Landscapes in the continuous forest were sampled in 1998, and landscapes in the isolates and burned forest were sampled in 2000. Sampling took place in 0.9 ha plots (a 300 x 30 metre strip that was demarcated with ironwood poles) assigned at random to a 450 ha area of each habitat type (primary, logged or burned forest) within a disturbance class. Each plot was located in the field with a compass and clinometer, and then georeferenced with a handheld GPS device (Garmin 12XL).

Butterflies were sampled when encountered within the boundaries of each plot. A plot was traversed repeatedly on foot from one end of the plot to the other at a steady pace, which was only underbroken to collect specimens. This procedure was repeated until at least 200 butterflies were collected. We wanted to avoid small samples, which may yield unreliable similarity indices when comparing plots (Wolda, 1981).

It is very difficult, if not impossible to accurately identify most Bornean butterflies on the wing (Walpole and Sheldon, 1999). We therefore caught all encountered individuals with nets, and subsequently identified them in the field. Most individuals were marked and subsequently released in order to avoid multiple observations of the same individual. Because of the minimum sample size, sometimes-adverse weather conditions, and local variations in abundance, the number of days spent at each plot varied (mean and standard deviation: 6.16 ± 0.83 days). Sampling took place between 9:00 and 16:00 hours, except during rain, using standard nets and with two people catching per plot. The date of capture and location were
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noted for each individual. All butterflies were identified to species following Maruyama and 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., the butterflies *Allotinus 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. All individuals encountered (butterflies and skippers) were collected. Voucher specimens from all butterfly species were preserved (using silica gel) and later rechecked in the Netherlands. These have been deposited in the Zoological Museum of the University of Amsterdam.

**Butterfly Functional Groups:** Janz and Nylin (1998) found that plant growth form is a more conservative aspect of host association than plant phylogeny. This suggests that factors such as habitat and community structure play an important role in forming patterns of butterfly-host plant association. The butterflies sampled during this study were grouped into four distinct functional groups based on the plant form on which they feed. They include:

1) generalists: feed on plants used by at least two of the following guilds
2) herb specialists: feed on monocot and/or dicot herbs, and/or other herb-like plants (e.g., lycophytes)
3) liana specialists: feed on monocot and/or dicot lianas (vines)
4) tree specialists: feed on woody monocots and/or dicot shrubs and/or trees

Host-plant use assessment was based on literature (Corbet and Pendlebury, 1992; Maruyama and Otsuka, 1991; Seki et al., 1991; Suguru and Haruo, 1997; Suguru and Haruo, 2000), Internet databases (http://www.funet.fi/pub/sci/bio/life/warp/food-plants-a.html), and personal observations. For some species, no life history data was available. These species were then assigned to the functional group of their closest known relative. Species that do not feed on plants (predators, e.g. *Milletus* spp.) were not included in the guild assessments.

**C Analyses**

Because of differing sample sizes in the landscapes, rarefaction analysis was used with the Species Diversity option of the EcoSim program (Gotelli and Entsminger, 2001) using 100 iterations and independent sampling of randomly chosen individuals from the total species pool in each landscape. Results are presented using N=2200 individuals/landscape for large-scale species richness, dominance, and evenness. Large-scale species richness is the total rarefied number of species (N = 2200) in the entire 450 ha landscape-plot. Dominance is the relative abundance of the most common species in each landscape-plot, and is a useful index of resource monopolisation by a superior competitor (Gotelli and Entsminger, 2001). Hurlbert's (1971) probability of an interspecific encounter (PIE), which describes the probability that two individuals chosen at random from a pooled sample are from different species, was used as an index of evenness in each landscape-plot. In addition to large-scale species richness, small-scale species richness was also calculated, which is the mean number of species per 0.9 ha plot. Simulated confidence intervals were obtained for large-scale species richness, evenness, and dominance with EcoSim (Gotelli and Entsminger, 2001; McCabe and Gotelli, 2000). Confidence intervals for small-scale species richness were calculated using the mean and standard deviation of the 0.9 ha plots in each landscape-plot. Interpretations of statistical significance within disturbance classes are based on the confidence intervals.

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Overall variation among disturbance classes was additionally tested with a one-way ANOVAs and Scheffé post hoc tests (Statistica for Windows, 1996). Here, disturbance class with three levels (continuous, isolates, or burned) was the independent variable and either small-scale species richness, large-scale species richness, dominance, evenness, or guild species richness and relative abundance (for generalists, herb specialists, liana specialists and tree specialists separately) was used as the dependent variable. Variation in the overall community composition among disturbance classes, and among primary, logged, and burned forest was tested for significance using ANOSIM (non-parametric analysis of similarities) with the package PRIMER (Clarke and Gorley, 2001). ANOSIM is roughly analogous to standard univariate ANOVAs, and tests the variance within and among a priori defined groups in ordinate space. A Bray-Curtis similarity matrix (Bray and Curtis, 1957) was used for across-plot comparisons. The R_{ANOSIM} statistic values are an absolute measure of how separated the a priori defined groups are. A zero (0) indicates that there is no difference among groups, while a one (1) indicates that all samples (here plots) within groups are more similar to one another than any samples from different groups (Clarke and Gorley, 2001). The results of the ANOSIM are presented in addition to a multidimensional scaling ordination based on the same similarity matrix. Two one-way ANOSIMs were used to test for significant differences among disturbance classes, and among logged, primary, and burned forest.

**Results**

Overall small- and large-scale species richness was strongly correlated ($r = 0.943$, $p < 0.001$, $n = 9$). Both had weak, but significant correlations with evenness (small-scale species richness with evenness: $r = 0.784$, $p = 0.012$, $n = 9$; large-scale species richness with evenness: $r = 0.753$, $p = 0.019$, $n = 9$). There was no significant correlation between dominance and the other biodiversity indices.

Logging in both the continuous forest and forest isolates was associated with significant increases (using the confidence intervals) in species richness relative to proximate primary forest (Fig. 2). Small-scale species richness in logged landscapes was on average 14 - 26% higher than in proximate primary forest (here C1 is compared with C2 and C3, and I1 is compared with 13). Large-scale richness was, however, only 5 - 16% higher.

Among disturbance classes there was no significant difference in small-scale species richness, although the difference borders significance ($F_{2.6} = 4.815$, $p = 0.057$). There was, however, a significant difference in large-scale species richness ($F_{2.6} = 13.363$, $p = 0.006$). Despite the strong correlation between small-scale and large-scale species richness, there were differences in the impact of disturbance. At the small scale, species richness in unburned isolates and the burned forest was 17% (isolates) and 39% (burned) lower than in the continuous forest, while at the large scale, species richness in unburned isolates and the burned forest was 33% (isolates) and 54% (burned) lower than in the continuous forest.

There was no significant difference in dominance or evenness among disturbance classes (dominance: $F_{2.6} = 0.143$, $p = 0.869$; evenness: $F_{2.6} = 2.466$, $p = 0.165$), although there was considerable variation within disturbance classes. With the exception of C2 in the continuous forest, dominance was higher in primary than logged forest, and higher in once- and twice-burned forest than in frequently burned forest. Evenness was higher in logged forest than primary forest and higher in frequently burned forest than once- and twice-burned forest.

Generalist guild abundance was significantly higher in continuous and burned forest than in unburned isolates ($F_{2.6} = 18.524$, $p = 0.003$; Fig. 3a). Generalist large-scale species richness was significantly higher in the continuous forest than in the isolates and burned
Within disturbance classes herb specialist abundance was higher in primary forest (significantly so in isolates), but species richness was significantly higher in logged forest. Liana specialist abundance ($F_{2, 6} = 4.977, p = 0.053$) and species richness ($F_{2, 6} = 5.857, p = 0.039$; Scheffé test > 0.05) did not differ significantly among disturbance classes. Within disturbance classes liana specialist abundance was significantly higher in logged forest, but species richness did not differ significantly between primary and logged forest. Tree specialist abundance was significantly higher in the continuous forest and isolates than in the burned forest ($F_{2, 6} = 16.528, p = 0.004$), but species richness was significantly higher in continuous forest than burned forest ($F_{2, 6} = 6.042, p = 0.036$). Within disturbance classes tree specialist abundance was higher in logged forest and significantly higher in recently logged forest (C3) in the continuous disturbance class. Tree specialists species richness was, however, significantly higher in logged than primary forest.

In the burned disturbance class there was a significant drop in abundance of woody feeders (liana and tree specialists) from once-burned (B1) to multiple-burned forest (B2 and B3).
Generalist abundance was highest in twice-burned (B2) forest while herb specialists abundance was highest in frequently burned forest (B3).

![Graphs showing relative abundance of generalists, herb specialists, liana specialists, and tree specialists across different forest conditions.](image)

Fig. 3. Relative abundance (error bars are 95% confidence intervals) of a) generalists, b) herb specialists, c) liana specialists and d) tree specialists per landscape. Acronyms are described in Materials and Methods section.

Generalist and tree specialist species richness declined significantly from once- to twice- and frequently-burned forest. Herb specialist species richness peaked significantly in the twice-burned forest and liana specialist species richness was almost equal in once- and twice-burned forest, but significantly lower in frequently burned forest. Additional interesting results include the pronounced low levels of species richness for the small unburned isolate (I2); this is especially the case for the generalist and herb specialist guilds where levels are even lower than the surrounding burned forest.

In line with the shifts in guild abundance and species richness community composition differed significantly among logged, primary, and burned forest (global $\text{RANOSIM} = 0.634$, $p < 0.001$; Fig. 5). Similarity was higher between logged and primary forest than between either of these and burned forest (primary with logged: $\text{RANOSIM} = 0.299$; primary with burned: $\text{RANOSIM} = 0.760$, $p < 0.001$; logged with burned: $\text{RANOSIM} = 0.777$, $p < 0.001$). Although all disturbance classes differed significantly from one another (global $\text{RANOSIM} = 0.754$, $p < 0.001$), there was a higher similarity between the continuous forest and the isolates than between both of these and the burned forest despite the fact that the isolates are geographically embedded within the burned forest (Fig. 5: Continuous with isolates $\text{RANOSIM} = 0.679$, $p < 0.001$; continuous with burned: $\text{RANOSIM} = 0.840$, $p < 0.001$; isolates with burned: $\text{RANOSIM} = 0.776$, $p < 0.001$). Note also that the similarity between burned forest and the other disturbance classes declines with multiple burning (Fig. 5). There is also more variation in the continuous forest and the burned forest compared to the isolates and more
variation in logged forest plots where some are indistinguishable from primary forest while others have a very different composition as indicated by the separation along the horizontal axis of Fig. 5.

Fig. 4. Large-scale rarefied species richness (N = 2200) of a) generalists, b) herb specialists, c) liana specialists and d) tree specialists per landscape and among disturbance classes. Acronyms are described in Materials and Methods section.

Discussion

Ecological patterns and processes are scale dependent, and observations at one spatial scale often do not apply to other scales. This has important consequences in conservation biology for the relation between management decisions (landscape scale) and standard research (small plots) (Andersen 1999). Hamer and Hill (2000), for instance, found that as scale decreased the probability of a positive effect (i.e., higher species richness) of disturbance on diversity increased. A non-uniform spatial distribution of species, for example as a result of logging, can cause density estimates to be highly biased when assessed from a small spatial scale (Robinson et al. 2000). In a study of corals local species richness in small quadrates was much more sensitive to local variables such as depth and habitat and insensitive to regional richness. Large quadrates, however, were sensitive to regional species richness (Karlson and Cornell, 2002). The spatial scale of assessment also had a strong effect on estimates of species richness and density in a study of birds in Central and South America (Robinson et al., 2000).
Fig. 5. Multidimensional scaling analysis of the community composition of butterflies. The stress (a measurement of the goodness of fit) is 0.14, indicating an acceptable fit (Clarke and Gorley, 2001). In the figure, circles (○) indicate primary forest plots, triangles logged forest plots (△), crosses once-burned plots (●), and crosses (+) multiply burned plots. Open circles and triangles indicate continuous forest, black circles and triangles isolates. Con-Pri: continuous primary, Con-Log: continuous logged, Iso-Pri: isolates primary, Iso-Log: isolates logged, Bur-Once: once-burned forest, Bur-Mult: twice- and frequently-burned forest.

Although in this study species richness at small and large scales was generally correlated, there were differences. Small-scale species richness in logged forests, within disturbance classes, was on average 14 - 24% higher than in proximate primary forest. The large-scale species richness of logged forest was, however, only 5 - 16% higher, similar to what was found in Hamer and Hill’s (2000) study. Contrastingly, among disturbance classes, small-scale species richness in unburned isolates surrounded by burned forest and the burned forest itself was on average respectively 17% and 39% lower than continuous forest. Large-scale species richness in unburned isolates surrounded by burned forest and the burned forest itself was on average respectively 33% and 54% lower than in continuous forest.

Assessment at a large spatial scale may lack the statistical power of small replicated plots, but probably gives a more biologically meaningful estimate of changes in species richness. This entails that logging may raise local species richness throughout a logging concession, possibly due to the road network which facilitates the movement of pioneer and edge species (Bennett, 2000; Laurance et al., 2001; Malcolm and Ray, 2000), but will not have a marked effect at the larger spatial scale because it is the same set of pioneers which can be found throughout the concession. ENSO-induced burning on the other hand is more pronounced at the larger spatial scale indicating that a substantial proportion of rare or patchy species have disappeared as a result of this type of disturbance.

The impact of direct burning under a severe ENSO event is highlighted by the greater similarity between the distant continuous forest and unburned isolates than between the unburned isolates and the proximate, surrounding burned forest. Burning clearly has a radical effect on species composition and multiple burns appear to exacerbate this affect. There was also a much higher degree of similarity between primary and logged forests than between either of these and burned forests.
The response of other biodiversity measures to disturbance was somewhat counterintuitive. One would expect, for example, evenness to decline with disturbance, and dominance to increase (Mackey and Currie, 2000). In this study, however, both measures did not differ significantly among disturbance classes but there was considerable variation within disturbance classes. Evenness was even higher in the frequently burned forest than in proximate areas of primary forest (Fig. 2). Evenness was also higher in logged than primary forest.

Caswell (1976) showed that communities in more stable pristine environments tend to be less diverse and exhibit greater degrees of dominance than early or mid-succession communities or communities in disturbed habitats. Various mechanisms can be used to explain the increased dominance of pristine environments. In climax situations dominant species, for example, may be able to competitively exclude rare species that were able to survive previously due to past disturbances (Caswell, 1976).

The case of the frequently burned forest is interesting since this landscape had relatively high evenness but very low species richness. Since the frequently burned forest was clearly strongly affected by disturbance one would expect that it might only contain a nested subset of individuals from surrounding lesser-disturbed habitats. These would have dispersed into the frequently burned forest from the surrounding forest leading to expectations of high evenness, low dominance, low abundance, and low species richness as observed. The species assemblage would then consist of the more dispersive element of lesser-disturbed surrounding habitats. This, however, was not the case and the frequently-burned forest, in fact, had the most unique fauna composed of species with a generally very large global distribution (e.g. Lampides boeticus that is also known in Europe) that were highly abundant in the frequently burned forest and very rare or usually completely absent from the other lesser disturbed landscapes. Under frequent burning thus, it appears that an impoverished community of globally widespread butterflies can exist with low species richness, but high evenness and very little relationship with the unburned forest.

The impact of logging on biotic diversity is equivocal. Logging has been shown to have negative (Danielsen and Heegaard, 1995; Thiollay, 1992; Thiollay, 1997), positive (Malcolm and Ray, 2000; Whitmore, 1997), or no effect on species richness (Cannon et al., 1998; Johns, 1992; Lewis, 2001; Pearman, 1997; Vasconcelos et al., 2000; Willott et al., 2000).

The present study indicates that if logging is performed in such a way that it does not increase the probability of forest fire, areas of logged forest provide an important habitat for biodiversity. Logged landscapes, however, have been found to be more susceptible to fires than primary forest (Holdsworth and Uhl, 1997; Siegert et al., 2001). ENSO-induced burning, as opposed to logging, had a negative effect on levels of species richness in directly burned forests and isolates surrounded by burned forest (Fig. 2). Critically, the influence of the ENSO-event extended from previously disturbed areas that are prone to fire (Siegert et al., 2001) into very large unburned fragments (up to 138 000 ha in Borneo).

The impact of ENSO-induced disturbance on butterfly guilds was surprising. Among the disturbance classes the lower tree specialist and higher herb specialist abundance in burned forest may indeed be expected. The lower abundance of generalists in the isolates is, however, more difficult to explain.

Among specialist guilds there were only minor shifts in species richness. Herb specialist and liana specialist species richness did not vary significantly among disturbance classes and there was only a small, but significant, difference in tree specialist richness between continuous forest and burned forest. The largest drop in species richness, however, was in the generalist guild. Species richness was significantly lower in both the isolates and burned forest than in the continuous forest.
Our results within disturbance classes, when we compare primary and logged forest, were what one would expect based on the known impact of logging on vegetation composition. The abundance (but not species richness) of liana specialists was higher in logged forest. Logged forests can have twice the liana density of primary forests (Schnitzer and Bongers, 2002) but the floristic composition of lianas in logged and primary forest may not differ. Laurance et al. (2001) found that although forest edges significantly altered liana abundance they did not alter floristic composition. Likewise Gardette (1998) found no significant difference in species richness between primary and logged forest.

In contrast to liana specialists herb specialist and tree specialist species richness is higher in logged forest but abundance is higher in primary forest. This is probably related to the increase in habitat heterogeneity, including colonisation of logged forest by otherwise rare pioneers (e.g. *Macaranga*; Heydon and Bulloh, 1997). An increase in habitat heterogeneity or diversity due to, among other things, the intermediate level of disturbance related to logging should lead to an increase in species (Connell, 1978; Rozenzweig, 1995). For generalist species, species richness and abundance was higher in logged forest.

In another study (Cleary et al., in prep) we demonstrated that generalist abundance was negatively correlated with tree density, suggesting a possible association with gaps. Gaps often contain unique assemblages of forest butterflies (Hill et al., 2001), and the inherently patchy nature of gap microhabitats (Brokaw and Busing, 2000) may make it possible for generalist species to maintain populations on ephemeral resources that disappear and reappear as gaps close and are established elsewhere. As trees are replaced by logging-gaps this may benefit generalist/gap species that replace tree specialist species. Under this scenario it might be expected that logging, by increasing the density of gaps (Holdsworth and Uhl, 1997, Whitmore, 1997) may benefit generalists; our data support this since logged areas harboured more species of generalists and a greater abundance compared to proximate primary forest. Although generalist abundance was relatively high in burned forests, generalist species richness was significantly lower in both burned forest and isolates than in the continuous forest. Loss of generalist species may be related to loss of habitat, as forest and associated gaps are replaced by burned forest. It may also be related to population dynamics of generalist species, which tend to be somewhat better dispersers than specialists (Parsons, 1998; Scheiner, 1998). Destruction of suitable habitat reduces upper dispersal thresholds (Casagrandi and Gatto, 1999). Thus, organisms with high dispersal abilities that survive in a pristine, but patchy habitat may become extinct in a partially destroyed landscape, because their high dispersal ability causes them to be lost to unsuitable habitat (Casagrandi and Gatto, 1999). In this sense, behaviour at a smaller spatial scale related to gap dynamics may actually drive species loss, but only when large-scale processes alter the macro-habitat.

Another factor that may have influenced results of this study is isolate size. It is noteworthy that the landscape in the smallest isolate (12), had the lowest species richness of herb specialists and generalists of all nine landscapes, and fewer liana specialist and tree specialist species than all the other unburned landscape plots. Similarly, Harrison (2000) showed that species richness of mutualist fig wasps declined substantially in a 6 500 ha reserve surrounded by secondary scrub in northern Borneo following the 1997/98 ENSO event. He further observed that the impact of the 1997/98 ENSO event was much more pronounced in smaller isolates than in locations with significant areas of intact forest (> 50 000 ha). Here species richness was indeed substantially higher in the landscapes located in the large isolate (11 and 13; > 100 000 ha). Taken in their conglomerate, however, overall levels of species richness in the small and large isolates were lower than in continuous forest indicating that loss of diversity may even occur in very large isolates.
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The large spatial scale of the ENSO-induced fires combined with the severe and widespread drought makes this form of disturbance both severe and unpredictable. The losses associated with these fires are probably not solely due to fires themselves, but rather the combination of intense drought and fires. These fires can be partly attributed to greater fire susceptibility of disturbed forests and the increased density of man-made ignition sources (Woods, 1989). Fires in association with ENSO events have been described for East Kalimantan as early as 1914, but until recently these were small in scale. This has been attributed to the normally high resistance of undisturbed primary forest to burning, and the lack of ignition sources in such forests (Siegert et al., 2001). The greatest threat of logging is probably not therefore due to the impact of logging itself on rainforest communities but because logging increases the probability of future fires under severe ENSO-induced drought.

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