

# Burning and logging differentially affect endemic vs. widely distributed butterfly species in Borneo

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## ABSTRACT

We assess the differential impact of logging and ENSO (El Niño Southern Oscillation)-induced disturbance on the relative butterfly abundance and species richness of range-restricted and widespread species within the island of Borneo. Relative abundance and species richness were assessed using rarefaction and species accumulation curves in unburned isolates surrounded by burned forest, the burned forest itself, and continuous forest unaffected by ENSO-induced disturbance in addition to logged and unlogged landscapes in unburned forest. The relative abundance of endemics was significantly higher in unlogged forest than logged forest and significantly higher in unburned forest than burned forest. Rarefied species richness of range categories was similar (Bornean endemics) or higher (other categories) in selectively logged than unlogged forest. In contrast, rarefied species richness of range-restricted species was highest in continuous forest, intermediate in unburned isolates, and lowest in burned forest. Only two individuals of a single Bornean endemic species were found in all the burned forest. Although species richness was higher in all range categories in continuous forest than in unburned isolates and in burned forest, the difference was most pronounced for range-restricted species. Logging and ENSO-induced fires thus have contrasting effects on range-restricted species. While both increase the relative abundance of widely distributed species at the expense of range-restricted species, only ENSO-induced disturbance lowers the rarefied number of restricted range species. Our research highlights the threat that severe ENSO events pose to geographically restricted classes of biodiversity.

## Keywords

Abundance, El Niño, disturbance, endemism, extirpation, fire.

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## INTRODUCTION

Previous studies have shown that range-restricted (endemic) species are sensitive to disturbance (Hill *et al.*, 1995, 2001; Spitzer *et al.*, 1997; Willott *et al.*, 2000; Collar *et al.*, 2001; Lehtonen *et al.*, 2001; Lewis, 2001; Trainor, 2002; Cleary & Genner, 2004; Koh *et al.*, 2004; Charrette *et al.* in press). Endemics are of particular concern because local extirpation may lead to global extinction. Endemics are often largely restricted to unmodified habitats and are less able to utilize human-modified habitats than widely distributed species (Thomas, 1991; Lewis *et al.*, 1998). Natural habitat loss will therefore affect endemic species disproportionately and homogenize faunas globally as local endemics are extirpated (Thomas, 1991).

Several reasons have been postulated for the sensitivity of endemics to disturbance, e.g. smaller perturbations occur more frequently than larger ones and can affect the complete range of geographically restricted species (Malamud *et al.*, 1998). There is

also a tendency for local abundance and global range to be positively correlated (Brown, 1984; Gaston & Lawton, 1990; Kouki & Häyrynen, 1991; Gaston *et al.*, 1997; Quinn *et al.*, 1997) that would make endemics rare and therefore more vulnerable to extirpation as a result of disturbance (Bolger *et al.*, 1991; Newmark, 1991; Spiller *et al.*, 1998; Barlow *et al.*, 2002; Henle *et al.*, 2004). Other attributes of endemic species that may make them more susceptible to disturbance are their propensity to be more specialized than widely distributed species (Henle *et al.*, 2004; Charrette *et al.* in press) and preference of pristine habitat (for butterflies, see Leps & Spitzer, 1990; Spitzer *et al.*, 1993; Lewis *et al.*, 1998; Hill *et al.*, 2001; but see also Wood & Gillman, 1998).

The impact of human-induced habitat disturbance on tropical rainforests is an issue of major concern (Andersen, 1999; Summerville & Crist, 2002), particularly in South-East Asia, which harbours among the most diverse and most threatened rainforests in the world (Harrison, 2000; Myers *et al.*, 2000; Jepson *et al.*, 2001; Sodhi *et al.*, 2004). South-East Asia has one of

the highest global concentrations of endemic species (Myers *et al.*, 2000) but also has a very high rate of deforestation and may lose up to 25% of its total biodiversity by the next century (Brook *et al.*, 2003; Sodhi *et al.*, 2004). As elsewhere in the tropics, the rainforests of South-East Asia, and Borneo in particular, which is the second largest tropical island in the world, have been logged to supply the international demand for timber. In addition to being a conservation concern in its own right (Putz *et al.*, 2001), logging synergistically affects the probability of large-scale forest fires, particularly during increasingly frequent and severe ENSO (El Niño Southern Oscillation) events (Timmerman *et al.*, 1999; Holmgren *et al.*, 2001; Siegert *et al.*, 2001; Tudhope *et al.*, 2001). These 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 events on tropical rainforest communities (Harrison, 2000; Holmgren *et al.*, 2001), despite the fact that ENSO-induced burning is now considered one of the most critical threats to tropical forests (Laurance, 2003).

Butterflies are probably the best-known invertebrate taxon, with an estimated 20,000 species worldwide and a prominent place in conservation programs and biodiversity assessments (Stork *et al.*, 2003). There are almost 1000 species of butterflies in Borneo, of which 98 are endemic to Borneo and surrounding satellite islands (Otsuka, 1988; Maruyama & Otsuka, 1991; Seki *et al.*, 1991). Butterflies have been previously identified as important bioindicators for assessing biodiversity and monitoring ecosystem responses to environmental perturbations (Howard *et al.*, 1998; Parmesan *et al.*, 1999; Grill & Cleary, 2003; Cleary, 2004). Butterfly communities are also under continuing threat and have, when reliable baseline data are available, shown marked declines in distribution and richness (Warren *et al.*, 1997; Maes & van Dyck, 2001; Thomas *et al.*, 2004).

In this study we compare the impact of logging and ENSO-induced disturbance on species richness and relative abundance of butterflies in four range categories: (1) endemic to Borneo, (2) endemic to Sundaland, (3) species with a moderate distribution (i.e. restricted to the oriental region), and (4) species with a wide distribution in unburned isolates surrounded by burned forest, the burned forest itself, and continuous forest that has remained unaffected by ENSO-induced disturbance. In order to assess the impact of logging, landscapes (study areas) in the two unburned habitat classes (continuous forest and isolates) were located in both primary unlogged and commercially logged forest. Each landscape was approximately 450 ha. Within landscapes, butterflies were sampled within 0.9 ha sample sites.

## METHODS

### Study site and sampling

Site descriptions and sampling methods are described in detail in Cleary (2003). Three habitat classes were considered: unburned

continuous forest (C), unburned isolates surrounded by burned forest (I), and burned forest (B). Within each habitat class, we sampled three 450-ha landscapes (study areas) with varying histories (logged vs. unlogged in both C and I, and burned once vs. burned > 1 time in B). We describe patterns for the individual landscapes as well as test for differences among habitat classes and histories.

All continuous forest landscapes were located in the province of Central Kalimantan, within the Kayu Mas concession, in the large unburned central core of Borneo that has not yet been affected by ENSO-induced fires. Unburned isolate landscapes were located in the province of East Kalimantan, and did not burn during the 1997/98 ENSO event, but were completely surrounded by forest that did burn during this event. I1 and I3 were located in a 108,000-ha isolate located in part of the ITCI (International Timber Concessions Indonesia) and adjacent BFI (Balikpapan Forest Industries) concessions and including the Gunung Meratus Protected Forest Reserve. I2 was located in a 3500-ha unburned isolate that was all that remained of the Sungai Wain Nature Reserve. The burned landscapes were located in the province of East Kalimantan and surrounded the unburned forest isolates. B1 was located in the burned part of the Sungai Wain Protected Forest, B2 in the Wanariset Samboja Research Forest, and B3 in an area of frequently burned slash-and-burn agriculture along km 30 of the Balikpapan to Samarinda highway. Both continuous forest and isolates contained primary unlogged forest (C1, I1, and I2) and logged forest (C2, C3, and I3). Logging in the continuous forest and isolate landscapes was selective, with a cutting cycle of 35 years, extracting mainly dipterocarp tree species. Logging intensities varied due to local variation in commercial tree stocking with between five and 20 trees extracted per hectare (Slik, 2004). Logging had a pronounced impact on the vegetation structure in both continuous habitats and in isolates. In the continuous forest habitat, for example, logged forest contained more non-woody and small-woody lianas, mesophyll-sized leaf litter, ferns, and fallen dead wood compared to unlogged forest, which was characterized by abundant tall poles and saplings, trees, microphyll-sized leaf litter, and greater crown depth and height (Cleary *et al.*, 2005).

Burned forest included a landscape affected by one burn event (B1: burned 1997/98), a landscape affected by two burn events (B2: burned 1982/83 and 1997/98), and a landscape (B3) in an area dominated by slash-and-burn agriculture. Pioneer tree density in previously unburned (B1) forest was much lower than in previously burned (B2) forest (Slik *et al.*, 2002; Slik & Eichhorn, 2003). This in turn probably influenced the much higher prevalence of herbs such as ferns and gingers in the forest understorey of the once-burned forest. In B3, grass (particularly *Imperata cylindrica*) was the dominant vegetation, but this varied depending on local conditions. In swampy areas, for example, *Scleria* spp. were dominant and there was some sparse shrub and tree growth (e.g. *Melastoma malabathricum*, *Piper aduncum*, and *Lantana camera*) in addition to locally planted fruit trees (e.g. rambutan *Nephelium lappaceum*). The bamboo *Dinochloa scandens* also formed dense mats in some areas. Continuous forest was sampled from July to October 1998, while isolates and burned

forest were sampled from February to September 2000. Each 450-ha landscape contained between 11 and 21 sample sites. Butterflies were sampled when encountered within *c.* 15 m on either side of a 300-m transect in each sample site. The transect was traversed repeatedly on foot from one end to the other at a steady pace. Two hundred butterflies were sampled at each sample site.

Individuals were caught with nets, and subsequently identified in the field. Most of these individuals were marked and subsequently released in order to avoid multiple observations of the same individual. Sampling took place between 9:00 and 16:00 h, except during rain. The date of capture and location were noted for each individual. Voucher specimens of each species were conserved in silica gel and later deposited in the collection of the Zoological Museum of the University of Amsterdam. All individuals were identified to species; species names follow 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 because diagnostic characteristics could not be determined in the field (e.g. male genital characters) or females could not be further identified unambiguously. For the geographical distribution, each species was placed in one of four range categories: (1) endemic to the island of Borneo; (2) endemic to the Sundaland region (i.e. Malaysia, Southern Thailand, Sumatra, Java, Borneo, and satellite islands); (3) found in Sundaland and surrounding biogeographical regions (Indo-Burma, Wallacea and/or, the Philippines, 'moderate'); (4) Sundaland and extending into more distant biogeographical regions (e.g. Australia, Africa, Europe; 'wide ranging'). Note that Sundaland is surrounded by three distinct biogeographical regions/hotspots, Wallacea to the east, the Philippines to the north-east, and the Indo-Burma region to the north; each of these contains distinct and threatened faunal communities (Myers *et al.*, 2000). For Sundaic endemics, we included species recorded in southern Thailand and/or Myanmar, i.e. around the isthmus of Kra but otherwise restricted to Sundaland. We compiled our geographical distribution data from Otsuka (1988), Maruyama and Otsuka (1991), Seki *et al.* (1991), and Igarashi and Fukada (1997, 2000). A list of the species sampled is available upon request to the first author.

### Analyses of relative abundance and species richness

Because of differing sample sizes in the landscapes (due to the different number of sample sites per landscape), rarefaction analysis was used with the Species Diversity option of the ECOSIM program (Gotelli & Entsminger, 2001) using 1000 iterations and independent sampling of randomly chosen individuals from the total species pool in each landscape. Results are presented using species accumulation curves for the entire 450-ha landscape for (1) Bornean endemics, (2) Sundaic endemics, (3) species with a moderate distribution, and (4) species with a wide distribution. Simulated 95% confidence intervals were obtained for species richness with ECOSIM (McCabe & Gotelli, 2000; Gotelli & Entsminger, 2001). Interpretations of statistical significance among landscapes are based on the confidence intervals (*sensu* McCabe & Gotelli, 2000).

Differences in relative abundance and species richness among habitat classes and between unlogged and logged forest were tested for significance with one-way ANOVAS followed by Fisher LSD post-hoc tests using STATISTICA 6.1 (Statsoft, Tulsa, OK, USA). Here, habitat class with three levels (continuous, isolates, or burned) was the independent variable and species richness or relative abundance the dependent variable. Unfortunately we could not use the site-level data for assessments of species richness due to low sample sizes, in particular, of the endemics. Sample sizes need to be sufficient to distinguish between different patterns of species richness because rarefaction curves tend to converge at low abundances (Gotelli & Colwell, 2001). For species richness analyses, the sample site data are therefore pooled and landscapes are used as samples. For the abundance data, where we can pool species into range categories, we can use the sample site as our observation. However, because we collected 200 butterflies per sample site, we have only relative abundances. We therefore only report statistical tests for endemics (Bornean and Sundaic endemics combined).

## RESULTS

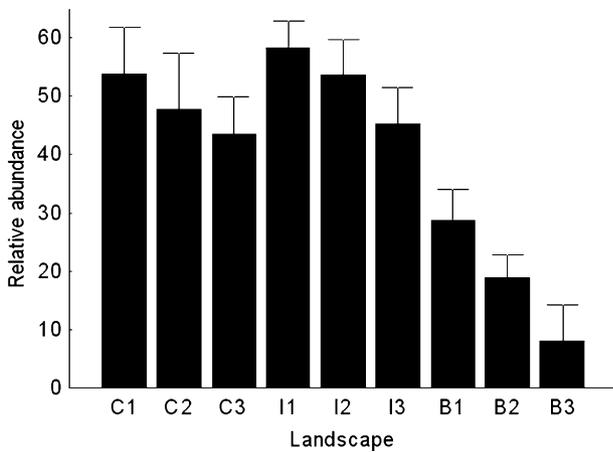
### Relative abundance

The relative abundance of (Bornean plus Sundaic) endemics ( $F_{1,89} = 16.048$ ,  $P < 0.001$ ) was significantly higher in unlogged ( $55.3 \pm 3.4$ ) than logged ( $45.2 \pm 3.6$ ) forest. In parallel with the patterns for logging, the mean relative abundance of endemics was significantly higher ( $F_{2,141} = 104.886$ ,  $P < 0.001$ ) in continuous forest ( $48.4 \pm 3.9$ ) and in unburned isolates ( $52.4 \pm 3.7$ ) than in burned forest ( $18.6 \pm 3.5$ ) (Fig. 1). Bornean endemics in particular were extremely rare in the burned forest. Only two individuals of the Bornean endemic *Miletus cellarius* were found across all the burned forest landscapes over a total of 10,600 observations of individuals from all range classes. As a result, the relative abundances of the species in the wider range categories were higher in the burned forest landscapes.

### Species richness

We recorded a total of 477 butterfly species ( $n = 28,789$  individuals), including 27 Bornean endemics ( $n = 658$  individuals), 153 Sundaic endemics ( $n = 10,512$  individuals), 186 species with a moderate distribution ( $n = 12,050$  individuals), and 113 species with a wide distribution ( $n = 5569$  individuals) (Table 1). Pooled species richness was, by far, highest in continuous forest (347 species) despite the lowest sampling effort (8589 individuals, Table 1). Species richness was also substantially higher in unburned isolates (271 species) than burned forest (203 species).

Mean species richness of Bornean endemics ( $n = 50$  individuals) was significantly higher ( $F_{1,3} = 21.33$ ,  $P = 0.019$ ) in continuous forest ( $9.4 \pm 0.8$  species) than in unburned isolates ( $4.7 \pm 1.6$  species). Only a single Bornean endemic species was found in burned forest and only in B2. Mean species richness of Sundaic endemics ( $n = 250$  individuals) was significantly higher



**Figure 1** Mean relative abundance (bars are  $\pm 95\%$  confidence intervals, using sample sites) of (Bornean plus Sundaic) endemics in each landscape. Note that the mean relative abundance of endemics is  $> 50\%$  in unlogged forest (C1, I1, I2), between 40% and 50% in logged forest (C2, C3, I3) and less than 30% in burned forest (B1, B2, B3). Endemic abundance, furthermore, declines steeply with additional burn events.

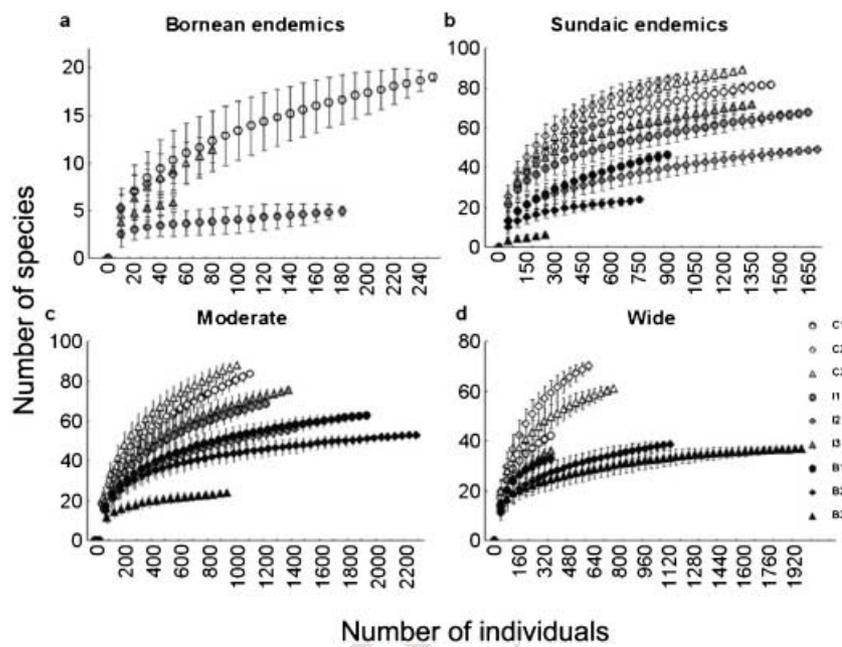
( $F_{2,6} = 11.800, P = 0.008$ ) in continuous forest ( $51.4 \pm 4.3$  species;  $P = 0.003$ ) and in unburned isolates ( $36.6 \pm 10.1$  species;  $P = 0.032$ ) than in burned forest ( $16.8 \pm 10.4$  species), but was marginally non-significantly different between continuous forest and isolates ( $P = 0.083$ ). Mean species richness of species with a moderate distribution ( $n = 750$  individuals) was significantly higher ( $F_{2,6} = 11.041, P = 0.010$ ) in continuous forest ( $74.3 \pm 4.9$  species) than in burned forest ( $37.5 \pm 13.2$  species;  $P = 0.004$ ), but was marginally non-significantly different between continuous

forest and isolates ( $56.0 \pm 8.9$  species;  $P = 0.062$ ) and isolates and burned forest ( $P = 0.057$ ). Mean species richness of species with a wide distribution ( $n = 120$  individuals) was marginally non-significantly different among landscapes ( $F_{2,5} = 5.087, P = 0.062$ ); richness was  $32.8 \pm 4.0$  species in continuous forest,  $24.4 \pm 0.2$  species in unburned isolates, and  $21.9 \pm 5.6$  species in burned forest. Note that in the ANOVA's comparing species richness, we had limited power due to low sample size per habitat class ( $n = 3$ ) and low sample sizes of certain landscapes, which further limited the actual differences due to convergence of accumulation curves at low abundances. The species accumulation curves of all continuous forest landscapes were, furthermore, invariably higher than accumulation curves in unburned isolates and burned forest. There were no significant differences in the species richness of Bornean endemics ( $F_{1,3} = 0.135, P = 0.738$ ), Sundaic endemics ( $F_{1,4} = 3.689, P = 0.128$ ), and species with a moderate ( $F_{1,4} = 1.853, P = 0.245$ ) or wide ( $F_{1,3} = 0.921, P = 0.408$ ) distribution between unlogged and logged forest. Note, however, that this can be attributed to the larger difference in species richness between continuous forest and forest isolates for these range categories. If we look within habitat classes, the species accumulation curves were invariably significantly higher in logged than unlogged forest based on the simulated 95% confidence intervals.

Although species richness was lower in unburned isolates and burned forest than continuous forest for all range classes, the difference was most pronounced for the range-restricted categories. For example, there were 2.0 times as many Bornean endemics, 1.4 times as many Sundaic endemics, and 1.3 times as many species with a moderate and wide distribution in continuous forest than in unburned isolates. Likewise there were 24.0 times as many Bornean endemics (24 species vs. 1 species), 3.0 times as

**Table 1** Summary data for each landscape. EB, Bornean endemics; ES, Sundaic endemics; M, species with a moderate distribution; W, species with a wide distribution; T, total species pool. Rarefied species richness was calculated for 50 individuals (EB), 250 individuals (ES), 750 individuals (M), and 120 individuals (W). Numbers in italics are the number of observed species for landscapes where fewer than  $n = 57$  individuals (EB) and  $n = 120$  individuals (W) were sampled. Con, total for continuous forest; Iso, total for unburned isolates; Bur, total for burned forest

Landscape	Species richness					Rarefied species richness				Number of individuals				
	EB	ES	M	W	T	EB	ES	M	W	EB	ES	M	W	T
C1	19	82	84	42	227	10.3	47.1	71.9	28.6	251	1472	1113	363	3199
C2	9	86	72	47	214	8.8	55.6	71.1	36.7	57	994	782	365	2198
C3	12	89	89	61	251	9.2	51.5	79.9	33.3	89	1302	1033	768	3192
I1	5	68	69	25	167	3.5	39.3	58.8	24.5	187	1680	1207	126	3200
I2	6	49	56	15	126	6.0	25.4	46.1	15.0	13	1707	1408	72	3200
I3	6	72	76	36	190	5.8	45.1	63.1	24.2	59	1387	1392	362	3200
B1	0	47	63	33	143	0.0	26.8	48.5	28.3	0	922	1915	363	3200
B2	1	24	53	39	117	1.0	17.6	41.2	18.6	2	792	2251	1155	4200
B3	0	6	24	37	67	0.0	5.9	22.9	18.6	0	256	949	1995	3200
Con	24	121	129	73	347					397	3768	2928	1496	8589
Iso	11	99	111	50	271					259	4774	4007	560	9600
Bur	1	53	83	66	203					2	1970	5115	3513	10600
Total	27	152	184	113	477					658	10512	12050	5569	28789



**7** Figure 2 Species accumulation curves (bars are simulated  $\pm$  95% confidence intervals) of (a) Bornean endemics (b) Sundaic endemics (c) species with a moderate distribution and (d) species with a wide distribution. Symbols represent samples from different landscapes.

many Sundaic endemics, 2.0 times as many species with a moderate distribution, and 1.5 times as many species with a wide distribution in continuous forest than in burned forest.

## DISCUSSION

### Effect of logging

One of the main effects of logging was a marked reduction in the relative abundance of range-restricted (Bornean and Sundaic endemic) species vs. species with broader distributions (Table 1). One of the principal differences between logged and primary forest is the frequency and size of canopy openings (gaps) (Thiollay, 1997; Nepstad *et al.*, 1998; Chappell *et al.*, 2001; Schnitzer & Bongers, 2002). In northern, Brown *et al.*, 2001) noted that butterfly species in gaps had morphologies adapted for fast flight. The presence of these mobile species (who are often also widespread) in the gaps suggests that disturbances that modify the canopy may cause a general increase in widespread species at the expense of range-restricted species (Hill *et al.*, 2001). Indeed, butterflies caught mainly in shaded patches of tropical rainforests had more restricted ranges than species caught mainly in gaps (Spitzer *et al.*, 1997; Hill *et al.*, 2001). Hill *et al.* (2001) suggest that losses of restricted range species are probably due to changes in light penetration that affect microclimatic variables such as temperature and humidity that are known to affect many butterfly species.

Despite logging lowering the relative abundance of Bornean and Sundaic endemics, we detected no adverse affect on species richness. The species richness of Bornean endemics was similar in logged and unlogged forest and that of Sundaic endemics even higher in the logged forest. Within habitat classes, the species accumulation curves of Sundaic endemics in logged forest were

invariably higher than in unlogged forest. Species richness was also much reduced in the small unburned isolate I2, indicating that isolate size also played a role in lowering species richness.

The lack of difference in the richness of range-restricted species is somewhat in contrast to other studies (Hill *et al.*, 1995, 2001; Spitzer *et al.*, 1997; Lewis, 2001; Fermon *et al.*, 2005). These studies found that, even though species richness may be higher in disturbed forest, this is often due to an influx of pioneer species that usually have wide global distributions. In a comparison of disturbed and undisturbed hill forest in Sulawesi, species richness was highest in disturbed forest, but the abundance and diversity of endemic butterflies were highest in undisturbed forest (Fermon *et al.*, 2005). In the present study, however, it seems logged forest provided habitat of sufficient quality for a less abundant but still diverse endemic fauna and that selectively logged forests should therefore be considered for higher conservation priority. It is important to keep in mind that the secondary effects of logging are often much worse than the primary effects, by facilitating an influx of hunters, ranchers, and slash-and-burn farmers (Laurance, 2000). In particular, logging leads to a significant increase in total fuel mass (Uhl & Kauffman, 1990). On Borneo both logging and ENSO-induced fires have affected rainforests (Jepson *et al.*, 2001; Putz *et al.*, 2001; Siegert *et al.*, 2001), and there is evidence that these factors have interacted compounding effects. For example, logging causes drought-resistant forests to become susceptible to fires by opening the canopy, increasing the fuel load and drying the forest interior (Nepstad *et al.*, 1998). Little is known of long-term impacts of logging and fires on rainforest communities (Harrison, 2000; Holmgren *et al.*, 2001); the short-term effects are drastic (see, e.g. below). Measures can, however, be taken to mitigate the susceptibility of logged forest to burning (Holdsworth & Uhl, 1997) and encroachment (Kursar & Grauel, 2002).

### Effect of ENSO-induced disturbance

In the present study, Bornean endemic richness and abundance were highest in continuous forest, intermediate in forest isolates, and lowest (only a single Bornean endemic species was recorded) in burned forest. Although the continuous forest, isolates, and burned forest were sampled in different years, they were all sampled after the 1997/98 ENSO event. Studies of temporal variation in a single unburned isolate landscape (I2) and two burned forest landscapes (B1 and B2) also showed that these areas increased their species richness from 1998 to 2000, following very low richness levels immediately after the drought and fires (Cleary & Genner, 2004). We also do not expect there to have been any fluctuations in the richness of the continuous forest due to the lack of any severe perturbations. In general, species richness is expected to change very little in the absence of severe perturbations (Brown *et al.*, 2001).

The results here show that the consequences of a severe ENSO event in Borneo can cause potentially catastrophic ecological changes, especially if the loss of butterfly species is reflected in other taxa, which is likely (Brown, 1998; Brook *et al.*, 2003; Cleary *et al.*, 2004). In Costa Rica, for example, biogeographical regions and zones of endemism of butterflies corresponded well with those of vegetation and vertebrates (Thomas, 1991). In Sulawesi, Schulze *et al.* (2004) also found species richness of most taxonomic groups to be significantly correlated across a gradient from near-primary to secondary forest. Taxa included trees, understorey plants, birds, butterflies, and dung beetles. Butterflies have, furthermore, been shown to be important flagship taxa for invertebrate conservation (New *et al.*, 1995). It is probable that many taxa will be adversely affected by increasing habitat disturbance and that range-restricted taxa in particular will suffer losses due to their strong association with unmodified habitat (Thomas, 1991; Lewis *et al.*, 1998; Lehtonen *et al.*, 2001). Koh *et al.* (2004), for example, found that range-restricted butterflies were three times more likely to become extinct in Singapore than were cosmopolitan butterflies. The lack of extinctions in widely spread species may be due to their ability to exploit a wide range of ecological niches (Jones *et al.*, 2001; Harcourt *et al.*, 2002). Significantly, our results across differentially disturbed areas of Borneo closely mirror temporal variation in species richness before and after the 1997/98 ENSO event in East Kalimantan Borneo, where range restriction and generalism proved to be significant predictors of species loss and return (Charrette *et al.* in press). Tropical deforestation following burning will therefore affect endemic species disproportionately and homogenize faunas globally as local endemics are extirpated, something that already appears to be well underway in Indonesian Borneo.

Our results confirm the threat posed by ENSO-induced fires for extant biodiversity in Borneo and elsewhere (e.g. the Amazon; Barlow *et al.* 2002; Laurance, 2003). Importantly, ENSO events are increasing in frequency, severity, and geographical scale (Tudhope *et al.*, 2001; see also Timmerman *et al.*, 1999; Holmgren *et al.*, 2001). Future events may therefore be even worse than the 1997/98 ENSO event, which was the worst in

recorded history and broke the record of the previous 1982/83 event. The severe loss of species in ENSO affected areas suggests that an increase in the scale and frequency of this type of disturbance might increase the probability that temporary extirpation will lead to global extinction for restricted-range butterfly species in the tropics. If our range categories for butterflies are indicators of other taxa, this would have relevance for conservation interventions, perhaps particularly for species not yet so rare as to be deemed 'at risk' using conventional measures.

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