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Cleary, D.F.R.

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Chapter 10

Assessing levels of butterfly species richness in Borneo using species rarefaction curves

Daniel F. R. Cleary, Arne Ø. Mooers, Timothy J. B. Boyle, and Steph B. J. Menken

Community variability is expected to be lowest at intermediate (landscape-scale) spatial scales, but unfortunately few studies assess communities at these spatial scales. Landscape-scale studies of community traits, such as species richness, are sorely needed to explore the impact of large-scale disturbance events such as ENSO (El Niño Southern Oscillation) induced burning and habitat isolation on rainforest communities. An important means of generating data for such assessments is to sample landscapes of similar size using randomised plots. Comparisons among landscapes can then be made with the use of rarefaction curves.

In the present study species richness estimates from individual-based rarefaction curves were assessed across 450 ha landscapes. Three landscapes were sampled before the 1997/98 ENSO event and nine landscapes were sampled after this event in burned and unburned forest. The results show a lack of change in species richness in an area unaffected by the 1997/98 ENSO event and a significant loss of species in an area directly affected by the 1997/98 ENSO event. Post-ENSO results across the nine landscapes suggest that the 1997/98 ENSO event was much more widespread, affecting a range of burned habitats in addition to small and large unburned isolates now surrounded by burned forest. Our results validate the use of large-scale methods to compare community traits such as species richness.
Introduction

The scale of study can affect the detection of relationships between habitat and species diversity (Pearman, 2002). Small-scale studies 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). At small spatial scales community structure seems to show greater than expected variance (Pandolfi, 2002). Studies in the most diverse ecosystems, coral reefs, and tropical rainforests, for example, have shown that enlarging the spatial scale of study leads to highly consistent patterns in community structure. The high variability observed within sites declines, often dramatically, as larger areas (landscapes) are sampled (Pandolfi, 2002).

Despite this the majority of studies that relate species richness to factors such as disturbance occur on small to very small spatial scales, generally less than one hectare (Summerville and Crist, 2002 and refs therein). Importantly many of these studies (mentioned in Summerville and Crist, 2002) failed to find an effect of disturbances, such as logging, on diversity and the mixed success of studies in relating habitat structure to faunal diversity has often been related to an inappropriate scale of assessment (Williams et al., 2002). Although, very large-scale historical and regional processes are often impossible to duplicate experimentally we can use comparative studies, statistical analyses of patterns, and natural experiments to compensate for this (Ricklefs, 1987; Pearman, 2002). Here comparisons are made using rarefied species curves. Species accumulation or the analogous rarefaction curves are an ‘essential component’ of studies that compare levels of species richness among sites (Willott, 2001) and the best method of comparing the actual level of species richness is to use the number of individuals as the measure of sampling effort (Willott, 2001).

The goal of this study is to ascertain the impact of ENSO-induced disturbance on landscape-scale levels of butterfly species richness. The 1997/98 ENSO event was the most severe and widespread in recorded history (Guilderson and Schrag, 1998; Holmgren et al. 2001; Salašky 1998; Timmermann et al., 1999), and there is evidence that such events are increasing in frequency and intensity (Holmgren et al., 2001). Two previous studies in Malaysian Borneo showed that the 1997/98 ENSO event was more severe than any previous events. Besides decimating a local wasp assemblage (Harrison, 2000), the event caused very high mortality across different types of vegetation and over a large altitudinal range (Aiba and Kitayama, 2002). Outside of these studies, however, very little is known about the response of rainforest assemblages to severe ENSO events (Harrison, 2000; Holmgren, 2001).

Butterflies have been shown to be especially responsive to large-scale environmental phenomena. Pollard (1988, 1991), for instance, found a positive relationship between the increased numbers of butterflies and warm dry summers in England. In general, annual fluctuations and long-term trends at individual sites were closely synchronised with regional data so that in these local populations, fluctuations were likely little influenced by local community interactions. Butterflies have further been shown to be sensitive to global climate change (Dennis, 1993); non-migratory European butterflies showed a significant response to climate change by shifting their ranges (Parmesan et al., 1999). Butterflies are also often used as key indicators of disturbance and as surrogates for other taxa (Blair, 1999; Fuller et al., 1998; Howard et al., 1998).
Temporally (pre- and post-ENSO) we compared landscape-scale species richness in two areas, unaffected (central Borneo) and severely affected (east Borneo), by the 1997/98 ENSO event. Fires occurred over more than 5.2 million ha. of east Borneo (Siebert et al., 2001). We also have data from northeast Borneo that allows us to assess pre-ENSO levels of species richness there. Spatially, species richness was assessed post-ENSO in primary and logged continuous forest and forest isolates surrounded by burned forest, and in differentially disturbed burned forest. Elsewhere, Willott et al. (2000) and Lewis (2001) have demonstrated in Borneo and Central America that butterfly small-scale species richness was similar in logged and primary forest and that there was little effect of logging on assemblage composition. Here we assess species richness in logged and proximate primary forest at landscape scales to see if this also holds at the larger spatial scale.

In addition to sampling two landscapes (here a landscape is defined as a ca. 450 ha of primary or disturbed forest) pre- and post-ENSO in central and east Borneo we sampled nine additional landscapes post-ENSO in differentially affected locations. These nine landscapes included three in central Borneo and six in east Borneo. In east Borneo forest was sampled forest that had been directly affected by the 1997/98 ENSO event and burned, and previously continuous unburned forest that was now isolated due to ENSO-induced burning. In central Borneo landscapes were sampled in primary and logged forest imbedded in a continuous unburned forest matrix.

Although we had no pre-ENSO data in east Borneo from areas that did not burn, we assume that levels of richness censused at large spatial (landscape) scales would be similar across the then continuous forest. In east Borneo three of the six areas we sampled pre- and post-ENSO were also proximate (The most distant plots were less than 22 Km apart) and these areas all had similar pre-fire vegetation, topographical characteristics, soil type, and rainfall, and highly diverse mixed dipterocarp forest (Kartawinata et al., 1981; van Nieuwstadt et al., 2001), which is the dominant forest type in Borneo, covered both reserves. Importantly two of these areas burned during the 1997/98 ENSO event but one moderately-sized isolate (3 500) remained unscathed.

With this study we tested the following hypotheses on the impact of ENSO-induced burning on species richness:

1) From pre- to post-ENSO we expect no significant difference in species richness in the unaffected central Borneo area and a loss of species at the ENSO-affected east Borneo area.

2) Overall species richness is expected to be highest in continuous forest, intermediate in unburned isolates and lowest in the burned forest. In the unburned isolates species richness is expected to be higher in the larger isolate.

Materials and Methods

Study area and disturbance classes

All research took place in Indonesian Borneo (Table 1) in the provinces of East and Central Kalimantan. Pre-ENSO (1997) we sampled in three landscapes in widely separated areas of Borneo. These include landscapes in east Borneo (Balikpapan-Samarinda region), central Borneo (in the large Kayu Mas concession), and northeast Borneo (Berau region). Post-ENSO a total of nine landscapes (450 ha) were sampled. Each landscape consisted of randomly assigned plots in
a hierarchical sampling design. Post-ENSO three main disturbance classes were sampled; three landscapes in continuous forest, three in unburned forest isolates surrounded by burned forest, and three in the burned forest surrounding the unburned isolates.

Table 1. Landscapes sampled during the course of this study, and their location, type and time of disturbance, and landuse. Pre: Sampled before the 1997/98 ENSO event. Time of disturbance is the year in which the major disturbance took place (logging or burning).

<table>
<thead>
<tr>
<th>Name</th>
<th>Landscape</th>
<th>Location</th>
<th>Class</th>
<th>Landuse</th>
<th>Time of disturbance</th>
<th>Latitude</th>
<th>Longitude</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pre-B2</td>
<td>East Borneo</td>
<td>Continuous</td>
<td>Burned</td>
<td></td>
<td>1982/83</td>
<td>0 59 S</td>
<td>116 57 E</td>
</tr>
<tr>
<td>Pre-Be</td>
<td>Northeast Borneo</td>
<td>Continuous</td>
<td>Logged</td>
<td></td>
<td>1994/95</td>
<td>2 04 N</td>
<td>117 19 E</td>
</tr>
<tr>
<td>Pre-C3</td>
<td>Central Borneo</td>
<td>Continuous</td>
<td>Logged</td>
<td></td>
<td>1993/94</td>
<td>1 16 S</td>
<td>112 24 E</td>
</tr>
<tr>
<td>Kayu Mas</td>
<td>C1 Central Borneo</td>
<td>Continuous</td>
<td>Primary</td>
<td></td>
<td>-</td>
<td>1 17 S</td>
<td>112 22 E</td>
</tr>
<tr>
<td>Kayu Mas</td>
<td>C2 Central Borneo</td>
<td>Continuous</td>
<td>Logged</td>
<td></td>
<td>1989/90</td>
<td>1 20 S</td>
<td>112 20 E</td>
</tr>
<tr>
<td>Kayu Mas</td>
<td>C3 Central Borneo</td>
<td>Continuous</td>
<td>Logged</td>
<td></td>
<td>1993/94</td>
<td>1 16 S</td>
<td>112 24 E</td>
</tr>
<tr>
<td>Meratus</td>
<td>I1 East Borneo</td>
<td>Isolate</td>
<td>Primary</td>
<td></td>
<td>-</td>
<td>0 58 S</td>
<td>116 19 E</td>
</tr>
<tr>
<td>Sungai Wain</td>
<td>I2 East Borneo</td>
<td>Isolate</td>
<td>Primary</td>
<td></td>
<td>-</td>
<td>1 06 S</td>
<td>116 49 E</td>
</tr>
<tr>
<td>Sungai Wain</td>
<td>B1 East Borneo</td>
<td>Burned</td>
<td>Burned</td>
<td></td>
<td>1997/98</td>
<td>1 05 S</td>
<td>116 48 E</td>
</tr>
<tr>
<td>Wanariset</td>
<td>B2 East Borneo</td>
<td>Burned</td>
<td>Burned</td>
<td>1982/83 and 1997/98</td>
<td>0 59 S</td>
<td>116 57 E</td>
<td></td>
</tr>
<tr>
<td>Km 30</td>
<td>B3 East Borneo</td>
<td>Burned</td>
<td>Burned</td>
<td>Frequently</td>
<td>1 03 S</td>
<td>116 57 E</td>
<td></td>
</tr>
</tbody>
</table>

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. 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) landscapes are located in a 108,000 ha isolate that overlaps the ITCI and BFI concessions (see Hoffmann et al., 1999 for a description of these concessions) and includes the Gunung Meratus protected forest (ca. 30,000 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.

All the continuous forest and unburned isolate landscapes had a similar vegetation structure, dominated by dipterocarp species as is typical for intact 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. The unburned isolate and burned landscape-plots are located in a large area of East Kalimantan (5.2 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). All landscapes are described in greater detail in chapter 8. 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).

Plot design and scale

Sampling took place in 0.9 ha (300 x 30 metre) plots assigned at random to grid cells on maps of each landscape. Each plot was located in the field with a compass and clinometer, and was georeferenced with a handheld GPS device (Garmin 12 XL). An average (± standard deviation) of 13 ± 5 plots were sampled per landscape. Butterflies were sampled across the entire 0.9 ha plot. The total number of butterflies caught per landscape is given in Table 1. The mean (± standard deviation) number of days spent sampling per plot was 6.2 ± 0.8 days. Sampling took place between 9:00 and 16:00 hours, barring rain, using standard nets and with two people catching per plot. A detailed description of the sampling methodology can be found in Chapter 8. Voucher specimens of each species were conserved in silica gel, and deposited in the collection of the Zoological Museum of the University of Amsterdam. All individuals were identified to species using Maruyama 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., Alolitus leogoron and A. melos). All these individuals were then considered to belong to the same species (A. leogoron in this case).

Analyses

Total rarefied species richness was assessed per landscape (pooling all plots) 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 are based on the simulated 95% confidence intervals generated by EcoSim (McCabe and Gotelli, 2000; Gotelli and Entsminger, 2001).

Results

A total of 30,040 butterflies belonging to 522 species were sampled during the study.

No significant difference in species richness was found between the two logged landscapes in central (N = 400; 114.6 ± 2.2 species; significance is based on confidence intervals) and northeast Borneo (N = 400; 113.7 ± 5.2). The previously burned landscape in east Borneo (pre-B2) had significantly higher species richness (N = 400; 129.7 ± 10.2 species), and the highest overall species richness (Fig. 1a and Table 2).

From pre- to post-ENSO there was no significant difference at the central Borneo landscape (N = 400; pre: 114.6 ± 2.2 species, post: 113.4 ± 10.2 species). In contrast to this, a dramatic loss of species was recorded at the east Borneo (Wanariset) landscape (N = 1300; pre: 211.1 ± 2.5
species, post: 86.6 ± 7.1 species). Comparison of the species richness in the (now burned) landscape B2 (Wanariset) sampled before and then two years after the 1997/98 ENSO event highlights the magnitude of the decline (Fig. 1a and Table 2): species richness in this landscape dropped to 41% of the pre-ENSO value. Even this underestimates community collapse, as only 30% of the pre-ENSO species were resampled post-ENSO (over the entire sample of 3600 individuals): the other species are most likely, immigrants associated with, and newly arrived from, proximate disturbed areas.

![Species accumulation curves](image)

**Fig. 1.** Species accumulation curves of butterfly assemblages that were assessed at approximately equally sized landscapes a) pre- and post-ENSO and b) post-ENSO. Symbols indicate mean values per landscape per abundance level. • - continuous pre-ENSO, ○ - continuous post-ENSO, ▲ - burned pre-ENSO, △ - burned post-ENSO, + - Berau pre-ENSO, 0 - isolate post-ENSO. Error bars are 95% confidence intervals. For a description of acronyms see material and methods section. Pre-BE: Berau landscape in northeast Borneo.

Post-ENSO, we recorded significantly lower levels of species richness in burned forest in east Borneo compared to continuous forest in central Borneo (Figure 3b). All burned landscapes had significantly lower levels of species richness than all continuous landscapes (N = 1300; range continuous: 152.2-184.7, range burned: 54.3-107.0). All landscapes in forest isolates, even in the very large 108 000 ha isolate (12 and 13), also had significantly lower levels of species richness than the continuous forest landscapes (N = 1300; range isolates: 89.3-145.0). Species richness of the landscapes in the large 108000 ha isolate was significantly higher (N = 2800; I1: 159.4 ± 5.1, I3: 182.7 ± 5.1) than that of the landscape in the 3500 ha isolate (N = 2800; I2: 117.5 ± 4.7). Species richness of the landscape in the small isolate was even lower than in the landscape in the once-burned forest (N = 2800; B1: 138 ± 4.5). Logged landscapes (C2 and C3 > C1 and I3 > I1: Fig 1b) also had significantly higher levels of species richness than primary landscapes.

**Discussion**

Both of our hypotheses were validated by this study. Species richness did not change in central Borneo that was unaffected by ENSO-induced disturbance, but dropped dramatically in east Borneo that was severely affected by ENSO-induced disturbance. Post-ENSO species richness was also higher in continuous forest than burned forest and intermediate in the unburned isolates. Logged forest, however, had significantly higher species richness than primary forest
indicating that the intermediate type of disturbance caused by logging seems to augment butterfly species richness.

Importantly, all three areas sampled pre-ENSO were previously disturbed (by logging or a previous burn), but were still (in 1997) located in an area dominated by largely intact and continuous (primary or logged but not burned) lowland dipterocarp forest (Siegert et al., 2001). These forests were all dominated by the typical dipterocarp species (e.g., Shorea spp.) that are much sought after by logging companies. This can explain the relatively high species richness of the pre-ENSO (Wanariset: B2) landscape in east Borneo. Although it had been affected by the less severe (Harrison 2000) 1982/83 ENSO event, it was still imbedded in a largely intact habitat-matrix. The large Bukit Suharto National Forest (> 70 000 ha) abutted the pre-ENSO (Wanariset) forest to the north, and the still largely intact Inhutani concession and contiguous Sungai Wain Protected forest to the south. Substantial patches of unburned forest were also found within the pre-ENSO (Wanariset) landscape (Slik et al., 2001). During the forest fires an estimated 93% (67100 ha of 71900 ha) of the Bukit Suharto National forest burned. An estimated 93% of the Inhutani concession (16300 ha of 17500 ha) also burned, and 65% of the Sungai Wain Protected Forest burned (Hoffmann et al., 1999). Species of butterflies that completely disappeared from the pre-ENSO landscape (Wanariset) and the proximate once-burned (B1) and primary (I2) forests include Ragadia makuta and Paralaxita telesia. These species are normally abundant in primary lowland dipterocarp forest in Borneo (Hill, 1999; D. F. R. Cleary, pers. Obs.), but especially R. makuta has been shown to be sensitive to drought (Hill, 1999).

Table 2. Mean and 95% confidence intervals for landscapes at three different abundance levels. N = total number of butterflies sampled at a given landscape. The letters refer to significant differences (based on the 95% confidence intervals) in species richness at given abundance levels.

<table>
<thead>
<tr>
<th>Name</th>
<th>Landscape</th>
<th>N=400*</th>
<th>N=1300*</th>
<th>N=2800*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pre-B2</td>
<td>1333</td>
<td>129.7± 10.2 a</td>
<td>211.1± 2.5 a</td>
<td></td>
</tr>
<tr>
<td>Pre-Be</td>
<td>507</td>
<td>113.7± 5.2 b</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pre-C3</td>
<td>410</td>
<td>114.6± 2.2 b</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Kayu Mas C1</td>
<td>2841</td>
<td>94.0± 9.2 c</td>
<td>152.2± 9.7 c</td>
<td>198.0± 1.9 b</td>
</tr>
<tr>
<td>Kayu Mas C2</td>
<td>2200</td>
<td>112.8± 10.2 b</td>
<td>180.2± 7.9 b</td>
<td></td>
</tr>
<tr>
<td>Kayu Mas C3</td>
<td>3147</td>
<td>113.4± 10.2 b</td>
<td>184.7± 9.7 b</td>
<td>242.9± 2.2 a</td>
</tr>
<tr>
<td>Meratus I1</td>
<td>3200</td>
<td>77.7± 9.0 d</td>
<td>123.0± 9.5 d</td>
<td>159.4± 5.1 d</td>
</tr>
<tr>
<td>Sungai Wain I2</td>
<td>3200</td>
<td>56.4± 8.3 f</td>
<td>89.3± 7.6 f</td>
<td>117.5± 4.7 f</td>
</tr>
<tr>
<td>ITCI I3</td>
<td>3200</td>
<td>94.7± 9.0 c</td>
<td>145.0± 8.1 c</td>
<td>182.7± 5.1 c</td>
</tr>
<tr>
<td>Sungai Wain B1</td>
<td>3200</td>
<td>67.3± 7.5 e</td>
<td>107.0± 8.1 e</td>
<td>138.7± 4.5 e</td>
</tr>
<tr>
<td>Wanariset B2</td>
<td>3600</td>
<td>58.8± 6.5 f</td>
<td>86.6± 7.1 f</td>
<td>108.2± 5.0 g</td>
</tr>
<tr>
<td>Km 30</td>
<td>3200</td>
<td>39.1± 5.0 g</td>
<td>54.3± 5.2 g</td>
<td>65.4± 2.2 h</td>
</tr>
</tbody>
</table>

* ± 95% confidence intervals
Though ENSO-events have previously been associated with species loss in coral reefs (Glynn and de Weerdt, 1991) and in a single small community of fig wasps (Harrison, 2000), the results presented here from Borneo are the first to document a degree of loss at this magnitude - in excess of 100 species - at landscape scale (Table 2) for an important indicator community. More importantly, the impact of the ENSO-event has not only affected burned areas, but appears to have affected moderately sized (3500 ha) and large (138000 ha) unburned isolates.

Previous studies of a recently burned habitat-matrix on levels of species richness had mixed results in South America. Species richness of frogs and small mammals, for example, was actually higher in isolates than in a similar area of continuous forest whereas species richness of ants and birds was significantly lower (Gascon et al., 1999). The negative effects of an adverse habitat-matrix are, however, probably related to the degree and extent to which that habitat-matrix has been altered (Ickes, 2000). Although in the Gascon et al. (1999) study, isolates were surrounded by a burned habitat-matrix, this burned habitat-matrix was in turn imbedded in a much larger area of primary rainforest (Gascon et al., 1999). At a scale thus of hundreds of thousands of hectares, the main habitat-matrix component was actually primary rain forest. This is very different from our study in east Borneo where the isolates were imbedded in a recently burned habitat matrix of millions of hectares.

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

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References

Chapter 10


