



## Impacts of forest gaps on butterfly diversity in a Bornean peat-swamp forest

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### ABSTRACT

Forest degradation is leading to widespread negative impacts on biodiversity in South-east Asia. Tropical peat-swamp forests are one South-east Asian habitat in which insect communities, and the impacts of forest degradation on them, are poorly understood. To address this information deficit, we investigated the impacts of forest gaps on fruit-feeding butterflies in the Sabangau peat-swamp forest, Central Kalimantan, Indonesia. Fruit-baited traps were used to monitor butterflies for 3 months during the 2009 dry season. A network of 34 traps ( $n_{\text{gap}} = 17$ ,  $n_{\text{shade}} = 17$ ) was assembled in a grid covering a 35 ha area. A total of 445 capture events were recorded, comprising 384 individuals from 8 species and 2 additional species complexes classified to genera. On an inter-site scale, canopy traps captured higher species richness than understory traps; however, understory traps captured higher diversity within each site. Species richness was positively correlated with percent canopy cover and comparisons of diversity indices support these findings. Coupled with results demonstrating morphological differences in thorax volume and forewing length between species caught in closed-canopy traps vs. those in gaps, this indicates that forest degradation has a profound effect on butterfly communities in this habitat, with more generalist species being favored in disturbed conditions. Further studies are necessary to better understand the influences of macro-habitat quality and seasonal variations on butterfly diversity and community composition in South-east Asian peat-swamp forests.

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### Introduction

As part of the Sundaland biodiversity hotspot, Borneo is home to some of the most complex and diverse forest ecosystems on Earth (Myers et al., 2000; Sodhi et al., 2004). Within Borneo, tropical peat-swamp forests are a particularly important habitat type, due to their expansive coverage in the lowlands and important populations of many threatened species (Morrogh-Bernard et al., 2003; Posa et al., 2011). Unfortunately, however, the rate of peat-swamp forest loss and degradation on Borneo is also very high, as a result of selective logging, fire, and conversion to plantations (Harrison et al., 2009; Miettinen and Liew, 2010). This, plus the need for biodiversity conservation and REDD+ (Reduced Emissions from Deforestation and Degradation, CCBA, 2008) projects to demonstrate positive biodiversity impacts makes studies investigating and monitoring the impacts of such

disturbance on forest biodiversity a conservation priority (Gardner, 2010; Harrison and Husson, 2011; Harrison et al., 2012).

Terrestrial arthropods are sensitive to environmental impacts and the use of specific terrestrial arthropod taxa or guilds as “indicator” assemblages can be advantageous, and oftentimes more rapid and reliable than vertebrates or plants, for assessing the impact of conservation management on biodiversity (Kremen, 1992; Kremen et al., 1993). Butterflies are particularly responsive to light gaps caused by natural and anthropogenic disturbances, and the Nymphalidae are widely considered to be good indicators of forest disturbance when systematically sampled with fruit-bait trapping methods (Daily and Ehrlich, 1995; Spitzer et al., 1997; Lewis, 2000; Hill et al., 2001; Schulze et al., 2004). Many butterfly studies have been conducted throughout the tropics using fruit-baited traps, providing great insight into butterfly ecology and methods for rapid assessment of communities (DeVries, 1987; Daily and Ehrlich, 1995; Spitzer et al., 1997; Lewis, 2000; Hill et al., 2001; Schulze et al., 2004). Although such studies provide results reflective of an ecosystem's current status, many tropical forests worldwide are in constant disequilibrium due to ongoing human disturbance and degradation. Continued monitoring of biodiversity is therefore crucial to accurately document the impacts of habitat degradation on biological communities (Lindenmayer and

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Likens, 2009). On Borneo, approximately 75% of nymphalids are fruit feeding (Hill et al., 2001) and Houlihan et al. (2012) report a similar percentage (79%) of nymphalids that feed on fruit in Sabangau. Thus, we consider that surveying this guild provides a good representation of Nymphalidae diversity.

In light of the information gaps described above, the aims of this study were to (1) assess butterfly diversity in a peat-swamp forest; (2) identify species habitat preferences and their relation to morphological adaptations and phylogeny; and, moreover, (3) identify the impacts of forest gaps on peat-swamp forest butterflies. In so doing, we also aim to generate results of use for informing the development of ecological monitoring systems for nymphalid butterflies in tropical peat-swamp forests.

## Materials and methods

### Study site

Fieldwork took place as part of the Orangutan Tropical Peatland Project (OuTrop) multi-disciplinary research program, conducted in collaboration with CIMTROP at the Natural Laboratory of Peat-Swamp Forest (NLPSF), Sabangau, Central Kalimantan, Indonesia. This site is located 20 km southwest of the city of Palangka Raya at 2° 20' 42" south and 114° 2' 11" east, on the site of the former Setia Alam logging concession and in the upper reaches of the Sabangau River (Fig. 1). The Sabangau Forest covers an area of 5780 km<sup>2</sup> between the Katingan River to the west and the Kahayan River to the east, making it the largest remaining expanse of lowland rainforest in Kalimantan (Cheyne and MacDonald, 2011). Illegal logging in the area stopped in 2004 (Husson et al., 2007) and no timber extraction occurred during the course of this study. The forest is a mixture of primary and

secondary growth, consisting of evergreen forest, which under natural conditions is flooded for the majority of the year (Page et al., 1999). All trapping for this study was conducted in the mixed-swamp forest habitat sub-type, in which forest productivity is intermediate and closed-canopy height averages 15–25 m (Page et al., 1999).

### Traps

Studying habitat preferences in tropical forest butterflies can be difficult because of the dense vegetation and high canopy. Although canopy height in a peat-swamp forest is low relative to other lowland rainforest types in the region (Page et al., 1999), identification of canopy Lepidoptera from the forest floor remains difficult. Fruit-baited traps provide a systematic means of surveying fruit-feeding butterflies, especially from heights that cannot be easily reached by hand nets, and allow for meaningful comparison of distribution and abundance of species from various sites (Hughes et al., 1998). The traps used for the study were constructed according to standard specifications and designs (DeVries, 1987; Daily and Ehrlich, 1995).

A network of 34 traps, divided evenly between forest gaps ( $n=17$ ) and closed-canopy/"shade" ( $n=17$ ), was set up in a grid covering an area of 35 ha. Gap sites were small-scale (100 m<sup>2</sup> to 250 m<sup>2</sup>) and created by natural and anthropogenic tree-falls. Traps were separated into pairs, creating 16 sites ( $n_{\text{gap}}=8$ ,  $n_{\text{shade}}=8$ ), each with one understory trap ( $1.7 \pm 0.7$  m), and one canopy trap ( $8.3 \pm 5$  m). Due to the odd number of traps used in each condition, the remaining two traps were set at equal heights (2.0 m) and were split between gap and shade. Abundances were corrected for sampling effort by dividing the number of captures from each habitat by the number of traps. Understory traps were tied to a rope and positioned by placing the rope over a low tree branch. Canopy traps were set with the use of a slingshot to launch a

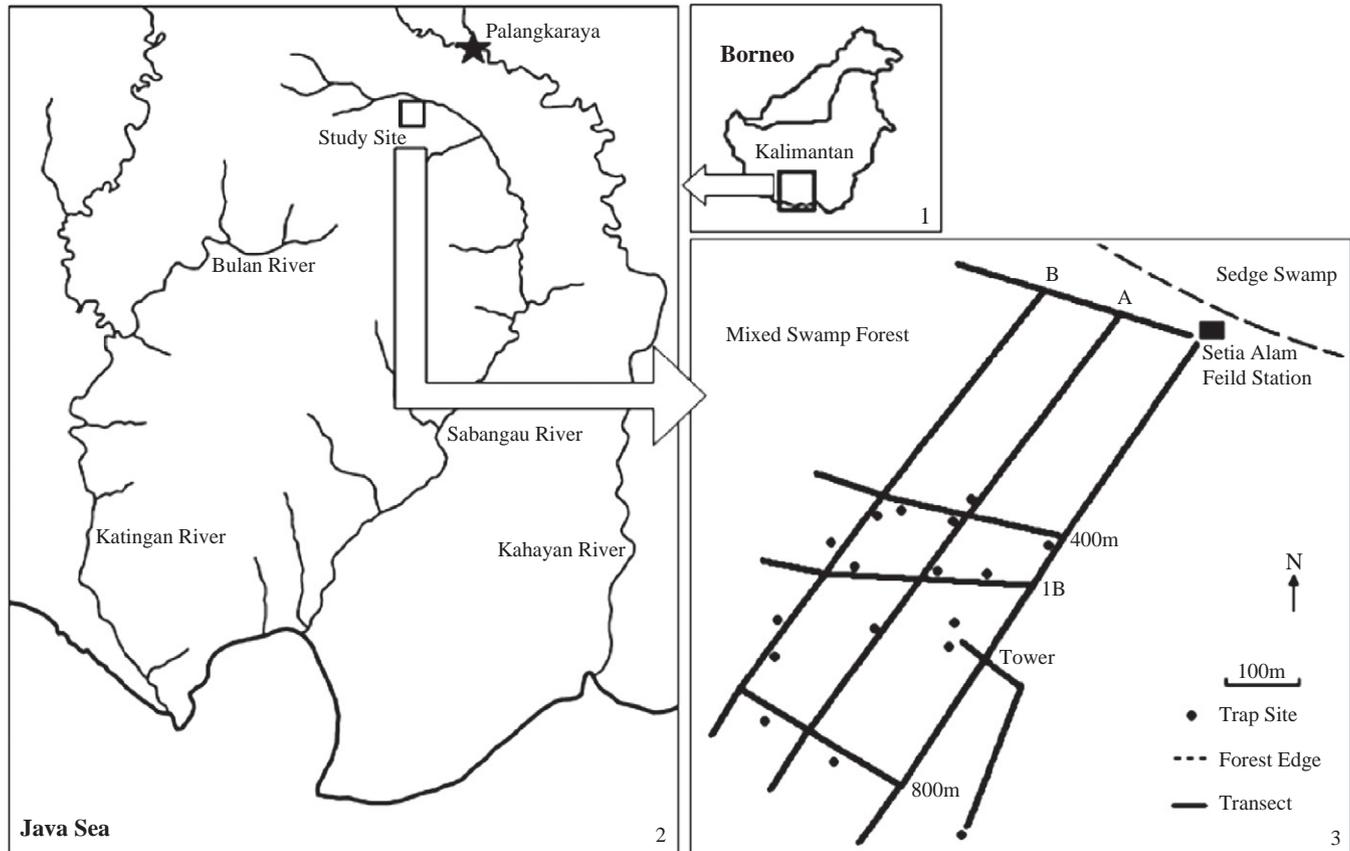


Fig. 1. Map of the island of Borneo (1), showing the location of the Natural Laboratory of Peat-swamp Forest, Sabangau, Central Kalimantan, Indonesia (2), and the study site, including trap locations (3). Understory and canopy traps were positioned in each location (see Methods for details).

metal fishing weight, attached to fishing line, over branches in the canopy. A rope was then tied to the fishing line, pulled over the branch, and tied to secure canopy traps. Traps were baited with a blend of fermenting bananas, sugar, and alcohol, which was kept consistent throughout the course of the study.

### Monitoring

Traps were monitored from 5 July to 10 September 2009. Two routes, each approximately 3.5 km long, were created to check half of the traps in one day. One route would be checked on day one, and the second route would be checked the following day; on day three, two teams would cover both routes. On average, each trap was therefore checked on two out of every three days. Freshly fermenting bait was added each time a trap was checked, preventing the bait from over-drying and replenishing bait occasionally washed out by rains or consumed by small mammals (mostly squirrels) and primates, including Bornean orangutans (*Pongo pygmaeus wurmbii*) and troops of pig-tailed macaques (*Macaca nemestrina*). Traps were checked between 0800 and 1200 h.

Butterflies from each trap were removed and identified following Otsuka (2001). Individuals of the genera *Tanaecia* and *Euthalia* were reliably identified to genus, but further classification to species was not attempted because laboratory analysis of genitalia is required for accurate identification (Hill et al., 2001). The forewing length and thorax dimensions of each individual were measured using calipers and recorded prior to releasing the butterfly. All individuals were uniquely marked with a black felt-tip pen on the forewing or hindwing. Recapture rates were recorded to calculate the probability that individuals of each species would display a preference when returning to a trap after initial capture, because of the trap's height or canopy cover, and to test previous hypotheses suggesting that frugivorous butterflies may (Hughes et al., 1998), or may not (Hill et al., 2001; Marini-Filho and Martins, 2001) become “trap happy.”

### Community diversity and statistics

Due to the different abundances in each assemblage, expected species accumulation curves with 95% confidence intervals were constructed using the Mao Tau estimator of sample-based rarefaction and rescaled by individuals to provide a direct comparison of species richness in canopy cover and height classifications (Randomizations = 50; Bootstrapped 200 times) (Magurran, 2004; Barlow et al., 2007; Colwell, 2011). Undersampling was suspected in assemblages with non-asymptotic species accumulation curves. To address potential biases related to undersampling, Shannon's entropy ( $e^{Hbc}$ ) was calculated to provide a bias-controlled comparison of the effective number of species (Beck and Schwanghart, 2010; Beck et al., 2011). These statistics were calculated using EstimateS (Version 8.2.0) (Colwell, 2011). Two-tailed T-tests were calculated to determine differences in species preference between understory and canopy traps within each site (paired), as well as between shade and gap habitats (independent).

To better understand the relationship between forest degradation and Nymphalidae diversity, traps were allocated to three categories according to percent canopy cover (<70, 70–84.9 and 85–100%), which was measured using a densitometer, and abundances were corrected for sampling effort (see *Traps* above). Differences between species richness in the three canopy cover categories were assessed using a Kruskal–Wallis test. Renkonen's (Proportional) Similarity Index (P) accounts for relative abundances and therefore provides a comprehensive explanation of  $\beta$  diversity while avoiding potential biases associated with indices that exclusively analyze presence/absence data (Balmer, 2002). Renkonen's Similarity Index was calculated to compare  $\beta$  diversity in understory vs. canopy traps and shade vs. gap traps, where a value of 1 signifies completely

proportionate abundances and a value of 0 signifies that zero species are shared between communities (Balmer, 2002).

## Results

Traps were monitored over 43 days, totaling 986 trap days. A total of 445 capture events were recorded, including 384 individuals (Table 1) from at least eleven species (individuals of *Tanaecia* and *Euthalia* were only identified to genus – see *Methods*). Although classification to genus was used for *Tanaecia* and *Euthalia*, we were able to confirm the presence of *Tanaecia clathrata* Vollenhoven, *Tanaecia munda* Fruhstorfer, and *Euthalia kanda* Moore following the conclusion of fieldwork through careful morphological analyses in the laboratory (Houlihan et al., 2012). A total of 50 individuals were recaptured, representing 11.2% of the individuals recorded. Recapture rates were low ( $10.9\% \pm 8.5\%$ ) in all species and repeated captures of single individuals were uncommon (recaptures: 1st: 50, 2nd: 10, and 3rd: 1), suggesting that butterflies in this forest do not become “trap happy.”

### Community diversity

Paired two-tailed T-tests revealed significantly higher butterfly species richness in understory traps than in canopy traps at the same sampling sites; however, macro-habitat inter-site species richness comparisons calculated using Shannon's Entropy ( $e^{Hbc}$ ) revealed higher overall true diversity in canopy traps (Table 1). Mao Tau expected species accumulation curves for understory and canopy traps were asymptotic, signifying sufficient sampling efforts (Fig. 2A). Despite recording approximately half as many individuals as the understory traps, canopy traps were visited by one more species (*Charaxes solon*). Although only five *C. solon* individuals were recorded in total, observed richness for canopy traps including 95% confidence intervals exceeded the 95% confidence interval of the expected species richness of understory traps, indicating a significant difference in species richness between understory and canopy trap communities (Fig. 2A). Renkonen's Similarity Index was calculated to compare the proportion of shared species and abundance between habitats (Table 1), which revealed that understory and canopy communities exhibited the greatest dissimilarity of all micro-habitat comparisons.

Expected species richness was higher in gap traps according to sample-based Mao Tau rarefaction curves, but observed richness for both habitats fell within the 95% confidence interval for shade trap richness and therefore differences were not considered significant (Fig. 2B). Similarity was relatively high between shade and gap habitats, supporting the lack of differences between expected species richness in these habitats (Table 1). Although differences in expected species richness were not significant, the effective number of species ( $e^{Hbc}$ ) was higher in shade sites and differences between these habitats calculated with independent two-tailed T-tests were significant (Table 1).

Traps in high canopy cover sites captured the greatest number of individuals and the asymptotic behavior of expected species accumulation curves for medium and high canopy cover traps indicated that the sampling effort was sufficient (Fig. 2C). Mao Tau curves overlapped between medium and high canopy cover and thus differences were not significant (Fig. 2C). Proportional similarity was greatest between sites of medium and high canopy cover, and declined when these traps were compared with the proportional abundance of low canopy cover traps (Table 1). The low abundance of butterflies captured in low canopy cover traps provided reason to suspect undersampling and thus, additional captures were necessary in low canopy cover trap sites to reach an adequate stopping point. Due to this suspected undersampling, Shannon's entropy ( $e^{Hbc}$ ) was calculated to provide a bias-controlled comparison of the effective number of species for each of the three canopy cover classifications. Using this, there was a positive correlation between percent canopy cover and the effective number of species ( $r =$

**Table 1**  
Differences in captures between understory vs. canopy traps, shade vs. gap sites, and canopy cover classifications show species habitat preferences and community diversity. The Charaxinae were the only subfamily lacking significant habitat preferences. Figures for vertical stratification and canopy cover represent the number of captures (mean  $\pm$  SD) of each species per trap. Two-tailed T-tests were calculated to determine differences in species preference between understory and canopy traps within each site (paired), as well as between shade and gap habitats (independent). Differences between species richness in the three canopy cover categories were assessed using a Kruskal–Wallis test. Significant differences between populations are shown in bold where  $p < 0.05$ .

Subfamily	Species	Total captures	Understory	Canopy	P	Shade	Gap	P	100%–85%	84.9%–70%	<70%	P	Relative species abundance (%)
Charaxinae	<i>Agatasa calydonia</i>	39	0.76 $\pm$ 1.03	1.47 $\pm$ 1.84	0.158	1.16 $\pm$ 1.50	2.50 $\pm$ 1.58	0.866	1.16 $\pm$ 1.50	1.00 $\pm$ 1.63	1.20 $\pm$ 1.64	0.891	8.8
	<i>Charaxes bernardus</i>	98	2.35 $\pm$ 2.64	2.82 $\pm$ 4.13	0.583	2.32 $\pm$ 3.43	2.93 $\pm$ 3.50	0.607	2.90 $\pm$ 3.91	2.90 $\pm$ 3.10	0.80 $\pm$ 1.10	0.341	22
	<i>Charaxes solon</i>	5	0.00 $\pm$ 0.00	0.29 $\pm$ 0.85	0.172	0.00 $\pm$ 0.00	0.33 $\pm$ 0.90	0.159	0.00 $\pm$ 0.00	0.30 $\pm$ 0.95	0.40 $\pm$ 0.89	0.771	1.1
	<i>Polyura hebe</i>	6	0.18 $\pm$ 0.39	0.18 $\pm$ 0.39	1.000	0.11 $\pm$ 0.32	0.27 $\pm$ 0.46	0.261	0.16 $\pm$ 0.38	0.30 $\pm$ 0.48	0.00 $\pm$ 0.00	0.631	1.3
	<i>Dophla evelina</i>	34	0.94 $\pm$ 1.03	0.94 $\pm$ 1.14	1.000	1.11 $\pm$ 1.05	0.73 $\pm$ 1.10	0.324	1.32 $\pm$ 1.20	0.60 $\pm$ 0.70	0.20 $\pm$ 0.45	<b>0.050</b>	7.6
Limenitidinae	<i>Euthalia</i> spp.	26	0.94 $\pm$ 1.03	0.53 $\pm$ 0.94	0.129	1.05 $\pm$ 1.03	0.33 $\pm$ 0.85	<b>0.034</b>	1.00 $\pm$ 1.00	0.60 $\pm$ 1.08	0.00 $\pm$ 0.00	0.087	5.8
	<i>Lexias pardalis</i>	9	0.47 $\pm$ 0.80	0.06 $\pm$ 0.24	<b>0.049</b>	0.42 $\pm$ 0.77	0.07 $\pm$ 0.26	0.071	0.37 $\pm$ 0.76	0.10 $\pm$ 0.32	0.20 $\pm$ 0.45	0.760	2.0
	<i>Tanaecia</i> spp.	156	6.71 $\pm$ 6.21	2.24 $\pm$ 1.79	<b>0.008</b>	4.79 $\pm$ 5.40	4.07 $\pm$ 1.27	0.679	5.05 $\pm$ 5.37	4.00 $\pm$ 5.03	3.20 $\pm$ 4.32	0.499	35.1
Morphinae	<i>Zeuxidia aurelius</i>	26	1.35 $\pm$ 1.27	0.18 $\pm$ 0.39	<b>0.002</b>	1.26 $\pm$ 1.24	0.13 $\pm$ 0.35	<b>0.001</b>	1.05 $\pm$ 1.08	0.50 $\pm$ 1.27	0.20 $\pm$ 0.45	0.154	5.8
	<i>Melanitis leda</i>	46	1.88 $\pm$ 1.62	0.71 $\pm$ 0.92	<b>0.022</b>	1.84 $\pm$ 1.54	0.60 $\pm$ 0.70	<b>0.007</b>	1.74 $\pm$ 1.60	0.80 $\pm$ 1.03	0.60 $\pm$ 0.90	0.141	10.3
Satyrinae	Mean species richness by traps	5.29 $\pm$ 1.69	3.88 $\pm$ 1.69	<b>0.005</b>	5.32 $\pm$ 1.34	3.53 $\pm$ 1.77	<b>0.002</b>	5.42 $\pm$ 1.35	3.90 $\pm$ 1.91	2.80 $\pm$ 1.30	<b>0.008</b>		
	Shannon's Entropy ( $e^{H'}$ )		Two-tailed T test: $t = 3.22$ , $df = 16$	Canopy = 6.25		Two-tailed T test: $t = 3.54$ , $df = 25.72$	Kruskal–Wallis Test: $H = 9.78$ , $df = 2$		High = 6.48	Med. = 6.15	Low = 4.55		
	Renkonen's Similarity Index		Understory = 5.88	Canopy = 0.657		Shade/Gap = 0.773	High/Low = 0.757		High/Med = 0.861	Med/Low = 0.757	High/Low = 0.723		

0.579,  $n = 34$ ,  $p < 0.001$ ), and overall differences tested between canopy cover classifications with the Kruskal–Wallis Test were significant (Table 1).

### Habitat preferences and morphology

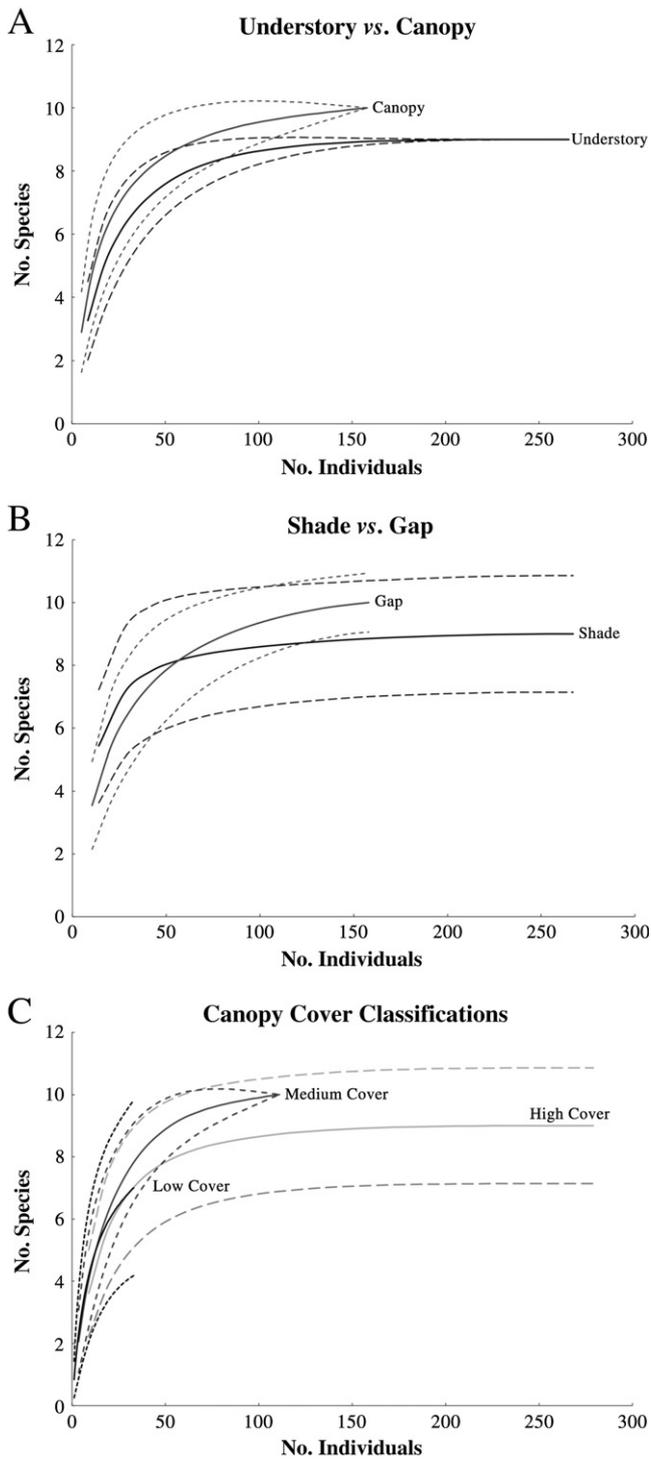
Differences between habitats were significant for some species (Table 1), and the five species with the lowest thorax volume relative to forewing length had a preference for understory and/or shade and high canopy cover sites (Table 2). *Lexias pardalis* (Moore), *Melanitis leda* (Linnaeus), *Tanaecia* spp., and *Zeuxidia aurelius* (Cramer) all showed a preference for understory traps. *M. leda* and *Z. aurelius* also preferred shade traps to gap traps, as did *Euthalia* spp. *Dophla evelina* (Stoll) was the only species to show any preference with respect to canopy cover classifications, which was significantly more abundant in the most intact forest (85–100%). Only one species (*Lexias pardalis*) had similar habitat preferences but a large thorax volume to forewing length ratio. The Charaxinae subfamily was the only subfamily to lack species with significant habitat preferences (Table 1) and these species comprised four of the five largest thorax volumes relative to forewing length (Table 2). *Charaxes solon* was only captured in canopy traps and gap sites, and was therefore suspected to prefer these habitats, however more captures of this species were necessary to test the significance of this preference.

## Discussion

### Habitat preference and flight morphology

The dry season peat-swamp forest butterfly community in Sabangau displayed micro-habitat preferences based on vertical stratification and percentage canopy cover, supporting previous work concerning gap ecology of tropical butterflies (Spitzer et al., 1997; Hill et al., 2001; Hamer et al., 2003; Dumbrell and Hill, 2005; Fermon et al., 2005). These preferences are important to understand in order to fully comprehend seasonal variations and predict future changes in the community composition of degraded (and degrading/regenerating) ecosystems. Four of the ten species captured preferred the understory during this dry season study and four preferred shade/high canopy cover to gap sites. The latter may have particular utility as indicators of high forest quality.

As in previous similar studies (e.g. Spitzer et al., 1997; Hill et al., 2001; Schulze et al., 2001; Hamer et al., 2003; Fermon et al., 2005), the species captured here exhibited morphologies (thorax volume and forewing length) that favored the micro-habitat in which they were prevalent. Large thorax volumes combined with comparatively shorter forewing lengths in the Charaxinae are commonly associated with stronger flight investment that allows easier navigation in less-dense forest, explaining their greater abundance with increased height and disturbance (Hill et al., 2001; Hamer et al., 2003; Fermon et al., 2005). These butterflies are also largely opportunistic feeders and should not therefore be expected to reside exclusively in specific micro-habitat types. Such adaptive morphologies shared through the species' phylogeny permit flight across greater distances, and these distances may fluctuate with regard to various fruiting events. For this reason, opportunistic foragers are frequently referred to as generalists. Further, low canopy height in the mixed-swamp forest may provide easier access to canopy fruit for opportunistic feeders. This may be compounded by the vertical distribution of fruits in the canopy, which can on occasion be found lodged or over-ripened at various heights in trees during fruiting phenology studies (MEH, pers. obs.). Potentially, this could allow overflying butterflies to feed from the upper reaches of the canopy rather than having to descend to the forest floor to feed on fallen, rotting fruit. This foraging behavior is similar to that of nectar-feeding Lepidoptera that are often most abundant in the canopy (Spitzer et al., 1993; Schulze et al., 2001). The influence of this effect is likely to vary seasonally, as the fruits of different



**Fig. 2.** Individual-based expected species accumulation (Mao Tau) curves with 95% confidence intervals (dotted lines) in understory and canopy traps (A), shade and gap traps (B) and classifications of low, medium, and high canopy cover (C). Differences in accumulation curves were only significant between understory and canopy traps. Significant differences were determined where observed richness of one classification, including 95% confidence intervals, exceeded the 95% confidence interval of the expected species richness in the other classification(s).

tree species show different propensities for over-ripening in the canopy vs. dropping to the forest floor, and the frequency of high winds and rain that could dislodge canopy fruits varies. However, fruit-feeding butterflies are most abundant and diverse in some forest canopies, especially in parts of the Neotropics (DeVries, 1988), where greater epiphytic growth reduces the proportion of fruit that falls to the understory

(Schulze et al., 2001). Schulze et al. (2001) report similar vertical distribution of nymphalids in dipterocarp forests of Sabah, Borneo. Although taller dipterocarp forests provide a more dramatic division between the understory and canopy – Schulze et al. (2001) reported a maximum forest canopy height of roughly 55 m – our data support the hypothesis that niche separation on this basis still exists in peat-swamp forests with an average canopy height less than half as tall (Page et al., 1999).

Meanwhile, the subfamilies displaying preferences for shade and/or understory habitats were those with relatively long forewings in comparison to thorax volumes (Limenitidinae, Morphinae, and Satyrinae). These species are larger and less agile targets for insectivorous birds and this predatory dilemma likely further restricts large-winged fruit-feeding butterflies from the open canopy (Schulze et al., 2001). *Lexias pardalis* was a morphological exception to this trend, but behaved similarly to other members of the Limenitidinae subfamily. It is likely that seasonal variations and habitat differences between peat-swamp forest and other forest types in which *L. pardalis* has been studied account for this altered foraging behavior. Despite its morphology, which indicates potential for more opportunistic foraging like that of the Charaxinae, monitoring studies currently underway in Sabangau (Houlihan et al., unpublished data) and the species' phylogeny support the present data on the understory preference of *L. pardalis*.

#### Butterfly monitoring in South-east Asian peat-swamp forests

Butterfly studies in South-east Asian, and particularly Bornean, peat-swamp forests are in great need of attention. The overwhelming majority of studies focusing on Bornean butterflies have been conducted in the dryland dipterocarp forests of Sabah (Hill, 1999; Willott et al., 2000; Hamer et al., 2003; Dumbrell and Hill, 2005; Benedick et al., 2006; Hamer et al., 2006) and to a much lesser degree, East and Central Kalimantan (Cleary, 2004; Cleary and Genner, 2006; Cleary et al., 2009; Cheyne et al., 2012). Dipterocarp forests differ greatly in species composition and diversity from the peat-swamp forests of southern Kalimantan where this study was conducted. For example, Paoli et al. (2010) found that the Fisher's alpha diversity of woody plants in peat-swamp forests was less than a quarter of those on mineral soils; bat species richness was approximately 2/3 in peat swamps, with densities less than half; and densities of vertebrate species were generally lower, and frequently 50% or more lower, in peat swamps. Similar to our study, Sutrisno (2005) reported lower moth diversity in Sabangau than in secondary dipterocarp rain forests. In this context, the relatively low number of butterfly species captured in this study is not surprising, and further studies should investigate the correlation between host plant diversity and invertebrate species richness within peat-swamp forests. It should therefore be noted that our data represent preliminary documentation of the forest's overall butterfly diversity, showing a heavy bias towards dry season butterfly communities attracted to fruit-baited traps.

The task of understanding the impacts of human disturbance on forest butterflies is complicated, owing to naturally occurring and anthropogenically induced micro-habitats, and seemingly drastic seasonal variations. Comparisons with previous Nymphalidae surveys in Sabangau (Brady, 2004) provide insight into these complexities. Brady (2004) recorded remarkably different community composition, based on species rankings and abundances. Importantly, Brady's (2004) study was conducted at the onset of the rainy season, as opposed to ours in the middle of the dry season. We believe that this potential seasonal influence is more likely to be the cause of seasonality than undersampling; despite Sabangau's proximity to the equator, the timing of the onsets of the different seasons and the actual rainfall in these seasons can vary widely between years (Harrison et al., 2010). Basset et al. (1998) mention the concerns associated with rapid assessments conducted during one season of the year, which may overlook specialist species with more drastic seasonal preferences than the generalists that appear abundant year-round. Year-round

**Table 2**  
Habitat preferences – species are listed in order of thorax volume to forewing length ratios. Measurements of thorax length and diameter were used to calculate the cylindrical volume of each species' thorax. Significant habitat preferences are indicated for each species (✓). \*Species preference inferred based on presence/absence data, but not significant due to low abundance.

Species	Understory	Canopy	Shade	Gap	85–100%	70–84.9%	<70%	Thorax volume Forewing length
<i>Melanitis leda</i>	✓		✓					1.63
<i>Tanaecia</i> sp.	✓							1.97
<i>Dophla evelina</i>					✓			4.09
<i>Zeuxidia aurelius</i>	✓							4.29
<i>Euthalia</i> sp.			✓					4.54
<i>Agatasa calydonia</i>								6.08
<i>Polyura hebe</i>								7.49
<i>Charaxes solon</i> *		✓						8.80
<i>Lexias pardalis</i>	✓		✓		✓			11.21
<i>Charaxes bernardus</i>								11.90

studies are therefore needed to reveal seasonal differences in butterfly species communities and the implications of these for assessing differences in captures between studies conducted at different times of year. Three more species were trapped in the early rainy season of 2004 (Brady, 2004) than in the dry season of 2009 (this study): *Athyma kanwa*, *Charaxes borneensis* and *Prothoe franck*. However, one of these species, *P. franck*, was recorded in September 2009, early in the wet season and after the conclusion of trapping for this study, and another, *C. borneensis*, has been abundant in surveys in subsequent years (Houlihan et al., 2012, PRH, unpublished data). Additionally, Brady's (2004) trap sites were located in closer proximity to the forest edge and, hence, her results are more likely to be influenced by edge effects. Monitoring studies subsequent to this one have since expanded the number of species recorded in Sabangau (Houlihan et al., 2012). Additional studies are needed to assess changes in the peat-swamp forest butterfly community in response to changes in the nature and intensity of human activities, including both threats and conservation management actions, on a larger spatial scale.

## Conclusion

Composition of the resident butterfly communities in degraded or regenerating forest will fluctuate according to the species that are better adapted for the current level of disturbance. The decline in diversity from intact (relatively closed canopy) to disturbed (relatively open canopy) forest documented in this study indicates that the deteriorating state of Borneo's peat-swamp forests will result in a transition in nymphalid butterfly community structure and a decline in diversity, which is consistent with similar studies conducted on a larger spatial scale (Hill and Hamer, 2004; Koh, 2007). Further habitat degradation in Borneo's peat-swamp forest and resultant declines in forest quality are therefore expected to lead to shifts in relative abundance and diversity of butterfly communities, including increased populations of more generalist species, and decreased populations of more specialized shade and understory species.

Our study demonstrates that rapid assessments of butterfly communities can be conducted in peat-swamp forests in order to gain an understanding of the impacts of forest disturbance in a relatively short time period. Potential seasonal differences in captures between this and the one previous comparable study in the area (Brady, 2004) appear likely, indicating a need for studies in peat-swamp forest to investigate the influences of seasonal variability on butterfly community structure. Finally, while our study indicates that nymphalid butterflies respond to changes in micro-habitat (i.e., small-scale canopy gaps), specific relationships between variables describing macro-habitat quality, butterfly diversity, and community composition have yet to be adequately determined (though some progress has been made towards this end, Brady, 2006). The authors are currently addressing these information deficits through ongoing studies in Sabangau.

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