

TROPICAL BUTTERFLY COMMUNITIES ON LAND-BRIDGE ISLANDS IN PENINSULAR MALAYSIA

Ding Li Yong

*Nature Society (Singapore), 510 Geylang Road, #02-05, The Sunflower, Singapore 389466
Department of Biological Sciences, National University of Singapore, 14 Science Drive 4, Singapore 117543
Email: zoothera@yahoo.com*

David J. Lohman

*Department of Biology, The City College of New York, The City University of New York
Convent Avenue at 138th Street, New York, NY 10031, USA
Department of Biological Sciences, National University of Singapore, 14 Science Drive 4, Singapore 117543*

Cheong Weei Gan

*Nature Society (Singapore)
510 Geylang Road, #02-05, The Sunflower, Singapore 389466*

Lan Qie

*Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences
Menglun, Yunnan 666303, China*

Susan Lee-Hong Lim

*Institute of Biology, University of Malaya
50603 Kuala Lumpur, Malaysia*

ABSTRACT. — We sampled and compared butterfly diversity on six land-bridge islands and two comparable control sites in forest on the mainland in Lake Kenyir, northern peninsular Malaysia, from Jun.2007 to Jan.2008 using 123 line transects. We recorded a total of 131 species in five families, three-quarters of which were Nymphalidae and Lycaenidae; nine additional species were observed moving between sampling sites. Butterfly assemblages on the smallest islands included species that tended to be smaller in size, less forest-dependant, and were generally more wide-ranging compared to assemblages on large islands and control sites. We supplemented transect sampling with specimens from fruit-baited traps, which caught butterflies on mainland but not island sites. Notably, although control sites and large islands were more species-rich, species assemblages differed greatly among sites, suggesting that butterfly communities were not only weakly nested, but also spatially variable within a small landscape. Effective conservation of intact forest butterfly communities needs to take into consideration high between-site β -diversity arising from habitat heterogeneity even at small spatial scales.

KEYWORDS. — Beta diversity, conservation, fragmentation, land-bridge islands, matrix, species assemblage, tropical butterflies

INTRODUCTION

Tropical evergreen forests are increasingly lost and degraded throughout Southeast Asia at the highest relative rates across the tropics (Sodhi et al., 2010) due largely to logging (Lambert & Collar, 2002) and agricultural expansion (Koh & Wilcove, 2008) at the expense of one of the richest and most endemic global biodiversity regions (Sodhi et al., 2010). A key outcome of forest loss and degradation is the formation of a patchwork-like landscape of habitat

fragments (Wright, 2005), which is a major conservation concern worldwide due to the significant loss of biodiversity following fragmentation. While effects of ‘contemporary’ forest fragmentation on tropical biodiversity, particularly vertebrates (e.g., Chiarello, 1999; Stouffer et al., 2006) and to a lesser extent, insects (e.g., Didham et al., 1996), have received considerable scientific attention, less well-studied is habitat fragmentation caused by inundation of forested landscapes by damming, and which can result in the formation of numerous, forested land-bridge islands in the resulting

reservoir (Diamond, 2001). Land-bridge islands are ideal settings for studying fragmentation impacts on biodiversity because the water matrix cannot be utilised by terrestrial species. In contrast, terrestrial forest fragments are usually surrounded by potentially inhabitable vegetation-mosaic matrix that confounds study of fragmentation effects.

On land-bridge islands, dispersal of most insular fauna is effectively limited, with drastic ecological ramifications. For example, Terborgh et al. (1997) demonstrated that major ecosystem modifications on land-bridge islands in Lago Guri, Venezuela occurred when large-bodied vertebrates and entire trophic guilds became locally extirpated. Similarly, studies of insular mammal communities by Lynam & Billick (1998) after the creation of the Chiew Larn reservoir in peninsular Thailand documented faunal relaxation and subsequent collapse of native mammalian communities on land-bridge islands while disturbance-tolerant species persisted.

Studies of tropical insect responses to fragmentation are relatively limited, even though many insects are susceptible to fragmentation effects (Didham et al., 1996), including butterflies. Even fewer empirical studies have attempted to quantify habitat fragmentation impacts on tropical butterfly communities, and most studies are Neotropical (e.g., Shahabuddin & Terborgh, 1999; Ramos, 2000; Horner-Devine et al., 2003) with a few in Southeast Asia (e.g., Benedick et al., 2006). Studies examining tropical butterfly communities across differential spatial scales and biogeographic realms have demonstrated varied, sometimes even contradicting, responses to forest fragmentation (Koh, 2007). For example, Shahabuddin & Terborgh (1999) inventoried frugivorous butterflies on land-bridge islands in Lago Guri and found isolation to be important in determining diversity and abundance on islands close to colonising sources, while fragments far from colonising sources had lower densities, even though species richness and composition showed no clear patterns. Similarly, Benedick et al. (2006) showed that butterfly species richness and diversity in forest fragments in north Borneo are positively correlated with fragment size and negatively correlated with fragment isolation. Large-bodied species, species with narrow larval host plant ranges, and species with small geographical ranges were more adversely impacted. In contrast, Vedderler et al. (2005) found that forest fragment isolation in Sulawesi had no significant effect on richness; only a few species were affected. Likewise, Leidner et al.'s (2010) study of butterflies across multiple forest fragments in central Amazon over 11 years did not find significant changes in abundance and richness, but instead noted greater temporal variability in butterfly communities.

Unlike community studies, single-species studies can account for species-specific persistence patterns that may otherwise be masked. Moreover, many fragmentation studies on tropical butterfly faunas tend to emphasize area effects while neglecting habitat heterogeneity-associated dynamics, which play an important role in shaping butterfly communities after fragmentation (Thomas & Harrison, 1992; Hamer et al., 2003). Indeed, as shown in Koh et al. (2004), host plant

specificity of larvae and habitat specialisation of adults best explained differences in extinction risk of many Southeast Asian butterflies, highlighting that habitat characteristics at fine spatial scales are important in influencing which species occur and can persist long term. For instance, the single-species study of the nymphalid *Hamadryas februa* on land-bridge islands in Lago Guri by Shahabuddin et al. (2000) found its densities correlated with higher larval host plant densities, demonstrating that habitat heterogeneity and dispersal ability are both important for understanding its persistence patterns in fragments. Likewise, poor dispersal ability besides habitat heterogeneity in the forest nymphalid *Ragadia makuta* in Borneo render it more vulnerable to effects of forest disturbance (Hill, 1999), reducing its chances of survival in fragmented landscapes.

To date, there are few diversity studies or inventories of butterfly communities anywhere in peninsular Malaysia despite an exceptionally rich butterfly fauna of over 1000 species (Corbet & Pendlebury, 1992), and none conducted in forest fragments on land-bridge islands, an increasingly common landscape feature due to widespread damming (e.g., Lake Temenggor, Pedu) (Yeap et al., 2007). We systematically sampled butterfly communities on six land-bridge islands and two comparable control (mainland) sites over a one-year period to generate species inventories and address two key research questions: 1) How does a non-forest matrix (i.e., open water) shape assemblages of butterflies on forested islands over short timescales? 2) To what extent do specific species traits influence occurrence on forest islands? We also highlight ecological implications for butterfly conservation in the rapidly disappearing lowland dipterocarp forests of Sundaic Southeast Asia.

MATERIAL AND METHODS

Site description. — Our study was carried out in Lake Kenyir (5°00'N, 102°48'E), a large man-made lake in the northeastern state of Terengganu in peninsular Malaysia, which was formed by damming the upper tributaries of the Terengganu River (Fig. 1). A more detailed account of the vegetation and logging history of lowland forest in the area is described in Yong et al. (2011). Eight study sites were chosen using topographic maps in Google Earth and from carrying out onsite surveys prior to sampling. Of the eight sites, six are islands of different areas, which are grouped into three area classes, while two are control sites on the mainland that are contiguous with the forest that extends into the northeastern sector of the Taman Negara National Park (ca. 434,000 ha). Islands were grouped into 'large islands', with area of >100 ha (Jelatang, Jerangau), 'medium islands' with area of 20–50 ha (Kuala Laban), and 'small islands', with area <20 ha (Latak, Petelot, Yazid). All six islands sampled are topographically similar because they were formerly hilltops or ridges, and covered with tall lowland dipterocarp forest with similar logging histories.

Butterfly sampling. — We sampled the butterfly community using the line transect technique at all eight study sites (Basset

Table 1. Measurements of island size, isolation, richness, and diversity. Richness/transect is mean \pm SD. Proportion detected is calculated from the mean of six estimators.

Site Parameters	Control sites		Large islands		Medium islands		Small islands	
	ML1	ML2	Jelatang	Jerangau	K. Laban	Latak	Yazid	Petelot
Area (km ²)	4340	4340	1.276	1.194	0.352	0.079	0.052	0.011
Perimeter (km)	—	—	19.105	7.153	3.658	1.535	2.515	0.523
P/A ratio	—	—	14.97	5.991	10.39	19.43	48.37	47.55
Distance from nearest landmass (km)	—	—	0.117	0.305	0.084	0.500	0.305	0.292
Isolation (km)	—	—	0.889	0.222	0.389	0.611	0.625	1.625
Number of transects	30	26	22	15	13	7	6	6
Mean richness/transect	1.97 \pm 0.26	4.65 \pm 0.56	2.43 \pm 0.33	2.21 \pm 0.42	2.23 \pm 0.30	1.14 \pm 0.40	1.50 \pm 0.56	1.33 \pm 0.49
Shannon-Weiner index	3.62	4.10	3.26	2.96	3.02	1.59	2.10	1.67
Observed sp. richness	43	75	38	24	24	7	9	7
Observed abundance	66	149	65	40	33	21	11	11
ACE	61.56	84.17	83.53	29.2	26.71	7.58	11.56	7.75
Chao1	53.55	83.34	60.46	27.51	24.02	7.14	9.98	8.35
Chao2	71.4	108.88	68.8	36.45	122.46	9.41	12.76	8.7
Jack1	55.29	95.56	49.17	30.96	24.95	9.15	12.24	8.95
Bootstrap	48.98	84.81	43.57	27.46	24.39	8.02	10.53	7.98
MMmeans	117.49	178.29	95.87	57.31	28.66	19.29	28.75	18.08
Proportion detected	64.07	71.01	58.32	69.16	60.62	69.13	63.23	70.47

et al., 2011, 2012). Between 11 Jun.2007 – 18 Feb.2008, four cycles of butterfly sampling were conducted at all eight sites and spread over June, August, October and February. Butterfly sampling over all cycles was carried out by DLY to minimise observer sampling bias. Sampling transects of 100 m length were randomly marked out in the eight sites, ranging from six on the smallest site to 30 on the mainland controls for a total of 123 transects (Table 1). Following Posa & Sodhi (2006), entry points for transects were spaced at least 100 m along the forest edge to minimise dependence. Our sampling did not take into account edge effects and transects started at the points of entry into the forest islands. This modification in transect design was made because many butterflies occurred at the edges, and not including this microhabitat may overlook a significant fraction of local diversity. Furthermore, many

forest butterfly species are more detectable in forest fringes than in closed canopy forest.

Although our sampling was constrained by steep topography—especially on the island sites—we marked straight line transects which were parallel to each other where possible. During sampling, the surveyor walked for 10 m along the transect at a constant pace and then paused for 1-min intervals to visually search for butterflies. Any butterfly observed within 5 m on either side of the transect and within 5 m off the ground was recorded, following the sampling protocol of Koh et al. (2002) and Posa & Sodhi (2006). While this sampling method detects most understorey and many of the middle-storey butterflies, we acknowledge that many canopy-dwelling species may be overlooked. Although most of the larger butterfly species could be easily identified, many nondescript or small-bodied nymphalids, hesperiids, and similar-looking lycaenids of a few genera (e.g., *Arhopala*, *Allotinus*) could not be reliably identified on sight. As such, voucher specimens were collected using a two-foot long insect sweep net and brought back for identification in the laboratory using identification keys and photographs in Corbet & Pendlebury (1992) and Ek-Amnuay (2006). Specimens were subsequently vouchered at the Zoological Reference Collection (ZRC), Raffles Museum of Biodiversity Research, National University of Singapore, Singapore.

Supplementary sampling.— We also conducted supplementary sampling of frugivorous butterflies, specifically large understorey nymphalids, using fruit-baited traps as many species (e.g., *Amathuxidia*, *Zeuxidia* sp.) are often difficult to detect visually due to their secretive habits (Corbet & Pendlebury, 1992). A single, flat bottom cone trap (bioquip.

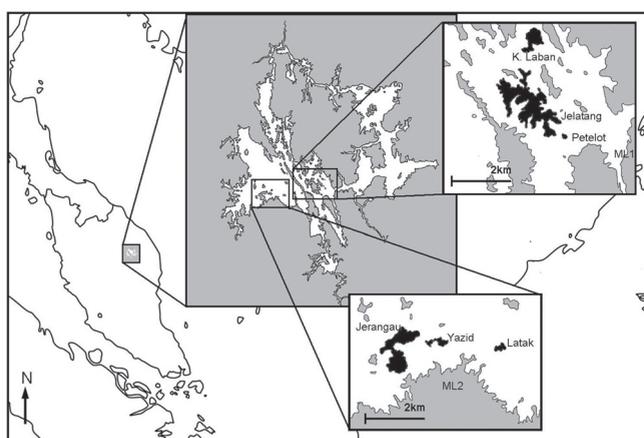


Fig. 1. Map of Lake Kenyir, peninsular Malaysia showing the two main study areas with the locations of the island and mainland (ML) study sites (inset).

com) baited with approximately 50 g of rotting bananas was hung about 1 m above the ground and left overnight, at two points each at one mainland site (ML1) and one island site (Jelatang), before being checked and emptied. Both sampling points were located at least 100 m from the point of entry to minimise edge effects. Due to the limited trap effort, we regard comparisons based on these trap data as suggestive. More intensive re-sampling must be carried out to determine occurrence patterns and densities of frugivorous butterflies across the study sites. We also recorded species that were observed flying over water, which we were able to observe when moving between sampling sites. While we were unable to identify every species encountered, especially distant individuals, most of the larger butterflies observed this way could be readily identified.

Analyses. — We plotted species rarefaction curves based on smoothed species accumulation against individuals sampled for all eight study sites to assess completeness and intensity of sampling efforts using EstimateS (Version 8.2, R. K. Colwell, <http://purl.oclc.org/estimates>). The use of species rarefaction curves not only allows for a standardised and robust comparison of diversity across our sampling sites, but allows estimating of sampling completeness (Gotelli & Colwell, 2001). We used the six non-parametric estimates of species richness recommended by Walther & Moore (2005) as that with least bias and are most accurate: Chao1, Chao2, Jack1, ACE, MMmeans, and Bootstrap.

We compared butterfly assemblage composition in our study sites by performing Sørensen (Bray–Curtis) cluster analysis using a presence-absence matrix of all species sampled. This was carried out using the PC-ORD 2.0 software (MjM

Software, Gleneden Beach, Oregon, USA). Information on three key species traits: forest dependence (forest dependant, non-forest dependant), restricted geographical range (i.e., widespread Oriental species, Southeast Asia restricted species, Sundaland endemics, Malay peninsula endemics), and body size (size estimates are from published photographic plates of known scale and were classified as: large bodied, medium bodied, small bodied) were compiled from Corbet & Pendlebury (1992) and Inayoshi (2011) to test whether butterfly assemblages varied significantly among sites. Due to our small sample size, we performed simple univariate analysis on species assemblages with specific species-distribution traits (forest-dependence, restricted range) pooled across sampling sites (e.g., control sites ($N = 2$), large islands ($N = 2$), small islands ($N = 3$)) classes using the Yates-corrected Chi-square test, and Kruskal-Wallis ANOVA to test for differences in mean body sizes across sites. All statistical computation was carried out using the Minitab 15 Statistical Software (2008).

RESULTS

We sampled 396 individuals of 131 species of butterflies in all five butterfly families (Table 1). Species richness varied from 75 species at ML2, to a mere seven species on the smallest land-bridge island, Petelot. Amongst the six land-bridge islands, Jelatang supported the richest assemblage of butterflies, with 38 observed species, while the three small islands each supported fewer than 10 species. While species rarefaction curves for many of the sites appeared to be approaching asymptotes, indicating relatively complete sampling efforts (Fig. 2), the curve for ML2 continued to

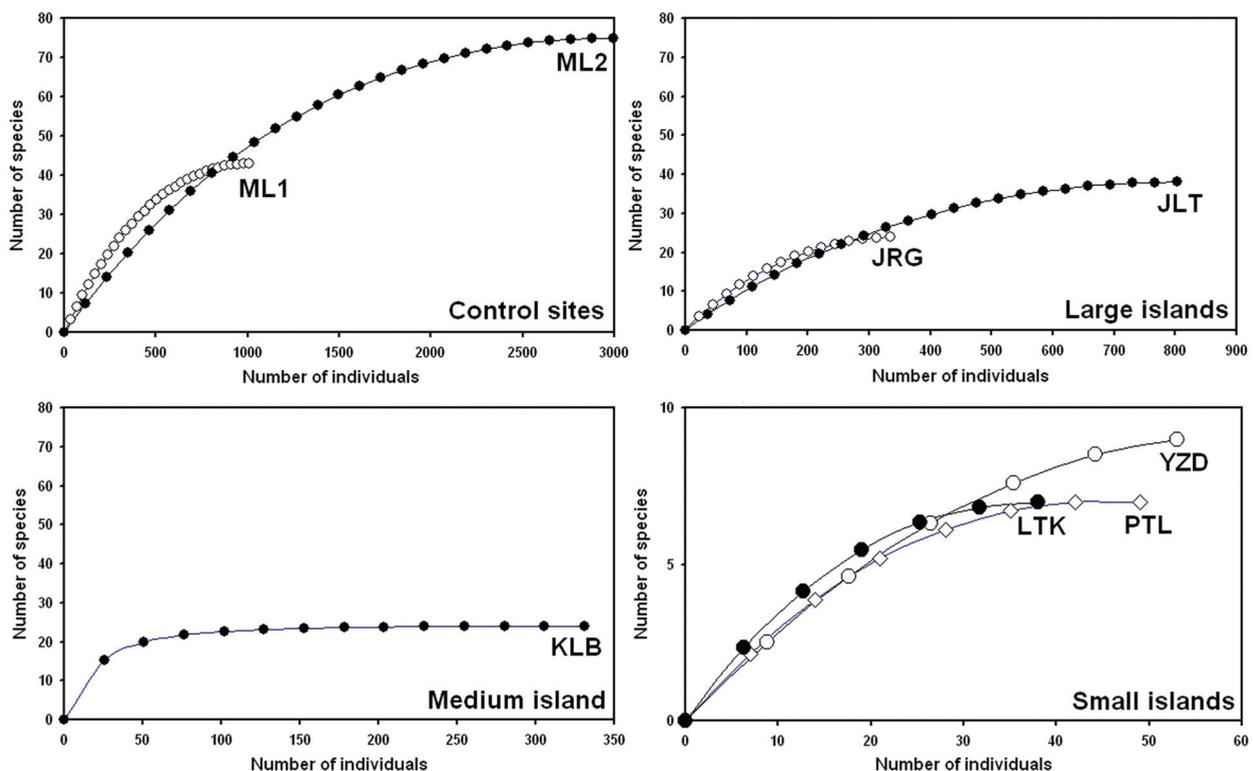


Fig. 2. Species accumulation curves for butterflies (rescaled to number of individuals) at six islands and two mainland sites (JLT: Jelatang, JRG: Jerangau, KLB: Kuala Laban, YZD: Yazid, LTK: Latak, PTL: Petelot).

increase despite nearly 30 transects, indicating that it likely supports the richest butterfly assemblage. Using the mean of six diversity estimators, 58–71% of all butterfly species present were detected by our sampling efforts in our eight study sites.

Butterfly assemblages at both mainland control sites were considerably different. Each mainland site was more similar to its nearest large island site (Fig. 3) than to the other mainland site. For example, the butterfly assemblage of ML1 was most similar to Jelatang while ML2's assemblage was most similar to adjacent Jerangau. Of the three smallest islands, two of them (i.e., Petelot and Latak) are comparatively more isolated than other islands, and were more similar to each other in their respective butterfly assemblages than any of the other sites.

At all sites, nymphalid species were most common, followed by lycaenids (Fig. 4). Both families dominated butterfly assemblages at all sites in terms of species richness and abundance, although diversity was depressed on the three smallest islands, which also exhibited simpler, more uneven communities (Table 1, Fig. 4). Interestingly, all of the smallest islands supported species that were neither found in larger islands nor on the mainland. Nymphalids were especially species rich (36 species) at ML2, which may be linked to greater habitat heterogeneity as indicated by an abundance of forest clearings there.

As island area decreased, overall species richness in Nymphalidae and Lycaenidae also steadily declined, and both families were poorly represented on the three smallest islands (Fig. 4). On the other hand, papilionid butterflies appeared to show no clear pattern in occurrence across the sites, including even on the smallest islands, and may be a result of better dispersal ability, which is supported by our opportunistic observations of at least three species of papilionid butterflies flying over open water (e.g., *Pathysa antiphates*).

Our comparisons of butterfly assemblages based on three species traits showed no significant patterns (Fig. 5). However, butterflies on small islands were generally less forest-dependant and had smaller geographical ranges

(Sundaland endemics); large islands and mainland sites had more forest-dependent species. The small islands supported only nine forest dependant species (ca. 44% of the assemblage on these islands), whereas 57 species at the mainland sites constituted 60% of this butterfly assemblage. Similarly, the three small islands supported only three Sundaland endemics combined compared to 12 species on the two large islands, which comprised more than 20% of the butterfly assemblage.

Finally, our supplementary sampling using baited fruit traps found two additional species that were not detected in our transects: the nymphalids *Neorina lowii* and *Dophla evelina*. In total, six species of large-bodied butterflies were caught in fruit traps at both sampling points at ML1 (Appendix 2). In contrast, no butterflies were collected from the traps placed at two points on the large island, Jelatang, suggesting a locally depauperate frugivorous butterfly assemblage.

DISCUSSION

The very few empirical studies of butterfly communities in peninsular Malaysia indicate the poor knowledge of butterfly diversity patterns in response to landscape modification or degradation. This is of major conservation concern given the rapid loss and fragmentation of existing lowland dipterocarp forests in peninsular Malaysia for other land uses, especially oil palm agriculture (Lambert & Collar, 2002). Our study in Lake Kenyir, a large area of logged and pristine lowland dipterocarp forest, recorded 131 species at six insular and two mainland sites, plus at least nine additional species seen in flight over water (e.g., *Euploea mulciber*, *Terinos atlita*). This is comparable to other lowland sites surveyed in peninsular Malaysia such as Endau Rompin National Park, where over 230 butterfly species have been recorded over a much larger contiguous area (Tan et al., 1992) and over a longer sampling period. Mean species richness on ML1 was relatively low and averaged only 1.97 species per transect; many species detected were represented by single individuals. This contrasts with ML2, which supports a more species-rich butterfly assemblage with 4.65 species recorded per transect, possibly a result of greater habitat heterogeneity offered by numerous open forest clearings.

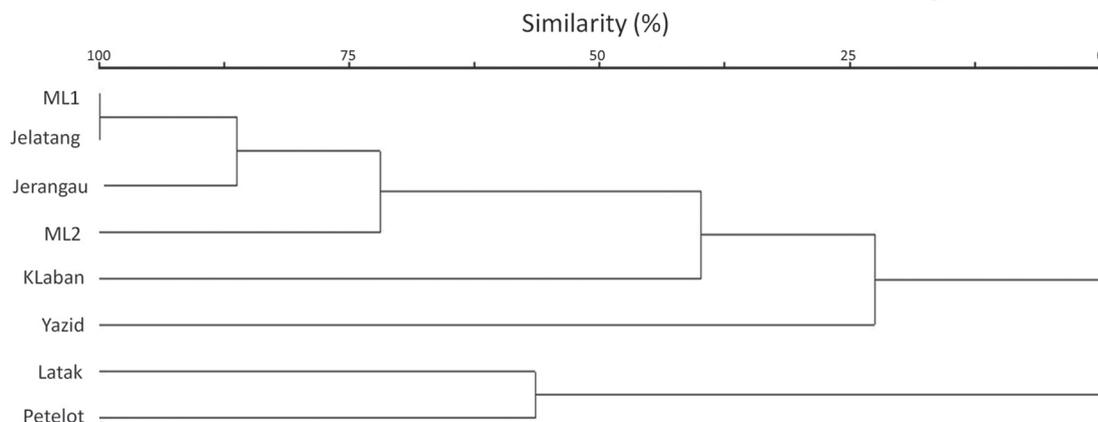


Fig. 3. Dendrogram showing degree of similarity in butterfly species richness among sites based on a cluster analysis of Bray-Curtis similarity indices using presence-absence data.

When species assemblages among the study sites were compared using Bray-Curtis cluster analysis, sites in similar area-classes supported notably dissimilar assemblages of butterflies, suggesting weakly nested patterns. For instance, both control sites supported comparatively different assemblages although their forests are essentially contiguous. On the other hand, their respective species assemblages appeared more similar to their nearest large islands. ML1 supported a butterfly assemblage more similar to Jelatang than to ML2 (Fig. 3), which is likely due to similarities in specific microhabitat characteristics, and among-site dispersal. Among the three small island sites sampled, their butterfly assemblages were more similar to each other, but did not support a subset of species that occurred on the larger islands or control sites, suggesting that microhabitats preferred by some species may be patchily distributed across the larger landscape. For example, multiple individuals ($N = 4$) of *Arhopala epimuta* were detected on transects clustered on a single island, Petelot, and none of the larger islands or control sites. This may be because its host plant is rare and patchily distributed, such that site occupancy of that species is restricted by the presence of suitable microhabitats for its host. Because most butterflies are oligophagous, their occurrences may also be limited by occurrences of suitable host plants. In addition, many lycaenids, including miletines and *Arhopala* butterflies, are known to show very specific myrmecophilous relationships and thus their occurrences in fragments depends on the occurrences of certain ant species (Megens, 2002; Pierce, et al., 2002; Lohman & Samarita, 2009).

Among the butterfly species recorded, not all are equally able to persist in fragmented landscapes. Koh (2007) analysed a large dataset of Southeast Asian butterflies in relation to various species-specific traits and found that larval host-plant specificity, habitat specialisation, and geographic distribution were among the best determinants of local extinction risk. The importance of these factors is underscored by empirical studies elsewhere in the tropics (e.g., Shahabuddin et al., 2000). Our study examined three species traits that are easily scored using current natural history literature (e.g., Inayoshi,

2011), and which were found to be significant in other studies (e.g., Koh & Sodhi, 2004; Koh, 2007). Although we did not find significant differences in the proportions of Sundaland endemics or forest-dependant species across sites, possibly due to incomplete sampling, we noted these species to be consistently poorly represented in assemblages on the smallest islands, indicating that they are likely most vulnerable to the effects of habitat fragmentation. Forest species are especially at risk because reduced habitat heterogeneity due to loss of microhabitats in forest fragments means that they are less likely to persist, and thus suffer local extinctions. Furthermore, many forest butterflies that occur strictly in the understorey (e.g., *Paralaxita damajanti*) are small-bodied and have short wings, limiting their ability to disperse from fragments once suitable surrounding habitat is lost and converted to a non-forest matrix.

Due to our short sampling period and methodology, we may have failed to detect a number of forest species, many which are small-bodied, inconspicuous (e.g., lycaenids, hesperiids), or canopy dwelling, biasing our study towards the more conspicuous, large-bodied, or colourful species that frequent forest understories. Furthermore, because it is difficult to distinguish transient and breeding species at

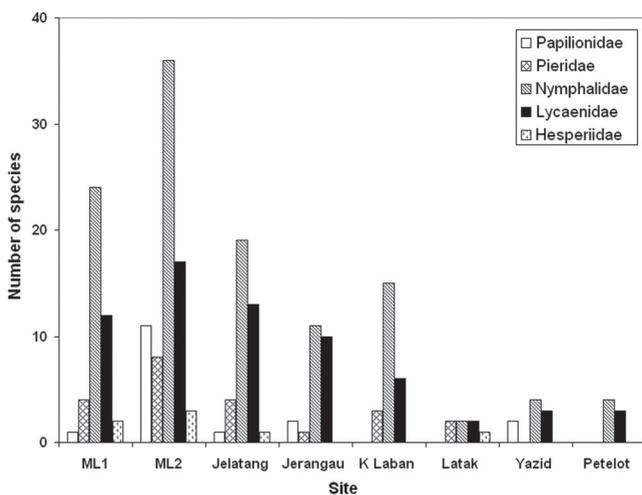


Fig. 4. Differences in species richness for individual butterfly families across all eight sampling sites.

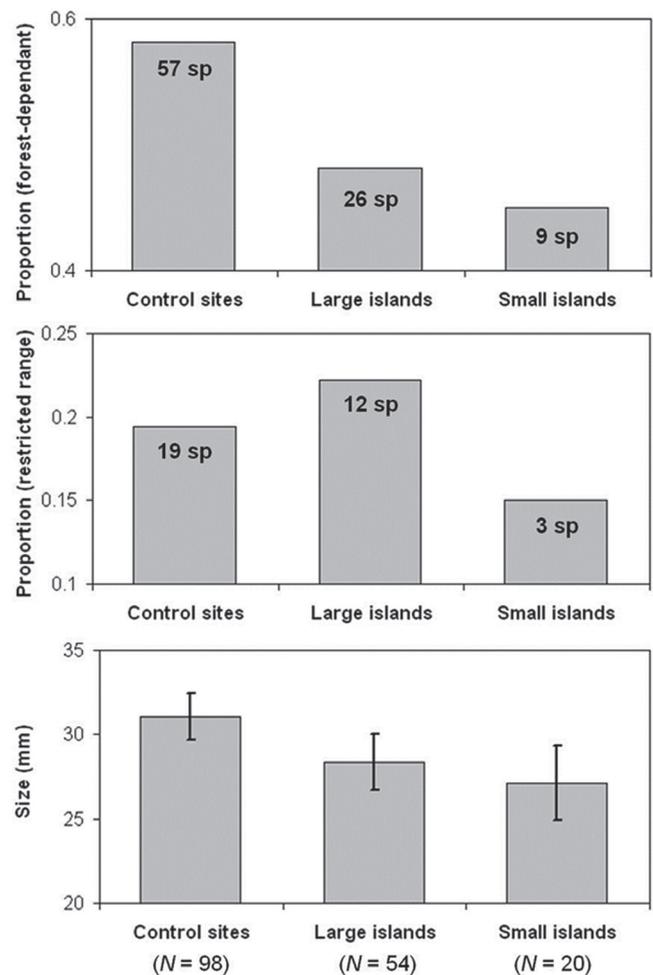


Fig. 5. Bar charts comparing pooled diversity across site classes based on three key ecological characters described in Koh (2007): forest-dependancy ($P = 0.61$, Yates-corrected $\chi^2 = 0.958$), restricted range (Sunda endemic) ($P = 0.81$, Yates-corrected $\chi^2 = 0.402$), and body size ($P = 0.29$, $df = 2$, Kruskal-Wallis $H = 1.234$).

the studies sites, our study may have inadvertently included transient individuals that are not part of the resident (breeding) butterfly assemblages, confounding richness estimation for some sites. Large-bodied and long-winged species, especially papilionids and pierids, are more vagile than other butterflies and can easily travel across a non-forest matrix as indicated by our observations of a number of individuals flying across open water, and are possibly more resilient to the effects of fragmentation. Furthermore, given the diverse and often species-specific ecological traits of many butterflies (Koh et al., 2004), community diversity studies, including ours, may mask responses of individual butterfly species or guilds. Studies examining (meta)population persistence patterns of specific guilds or single forest species, like Hill (1999) and Shahabuddin et al. (2000) are currently few, but is necessary to identify species-specific responses and persistence patterns across a larger fragmented landscape, as are studies that examine how community changes could disrupt ecosystem functioning (Didham et al., 1996). Particularly important to improve understanding of persistence patterns would be studies that address dispersal ability and patch occupancies across a larger landscape (Benedick et al., 2006; Leidner & Haddad, 2011).

Nevertheless, despite these methodological shortcomings, our study indicates how butterfly communities in Southeast Asia, specifically peninsular Malaysia, would respond as rapid land-use change driven by agricultural expansion and commercial logging continue to fragment formerly contiguous tropical lowland forests. Our results suggest that butterflies with narrow geographical ranges that depend on forests are less likely to occur in small isolated patches of forests. On the other hand, despite lower species richness and increased assemblage unevenness, small forest patches can support species not found in larger patches, if species-specific microhabitats and host plant(s) are available. These results have implications for butterfly conservation and the designation of reserves to protect tropical butterfly populations.

ACKNOWLEDGEMENTS

We thank the Economic Planning Unit (Malaysia) for providing the permits (UPE: 40/200/19/1539) to conduct this study. Ding Li Yong especially thanks Lian Pin Koh for advice and for providing some of the butterfly ecological data used in our study, Yusuke Takanami for help in species identification and Marzuki for assistance in the field, especially in cutting transects and collecting voucher specimens. We are also grateful to two anonymous reviewers whose comments improved the manuscript. Our study was supported by the National University of Singapore Grant No. R-154-000-331-122. David Lohman was also supported by DEB-1120380 from the U.S. National Science Foundation. This study is dedicated to the late Navjot S. Sodhi who conceived the study, and advised all the authors throughout the course of the fieldwork.

LITERATURE CITED

- Basset, Y., R. Eastwood, L. Sam, D. J. Lohman, V. Novotny, T. Treuer, S. E. Miller, G. D. Weiblen, N. E. Pierce, S. Bunyavejchewin, W. Sakchoowong, P. Kongnoo & M. A. Osorio-Arenas, 2011. Comparison of rainforest butterfly assemblages across three biogeographical regions using standardized protocols. *Journal of Research on the Lepidoptera*, **44**: 17–28.
- Basset, Y., R. Eastwood, L. Sam, D. J. Lohman, V. Novotny, T. Treuer, S. E. Miller, G. D. Weiblen, N. E. Pierce, S. Bunyavejchewin, W. Sakchoowong, P. Kongnoo & M. A. Osorio-Arenas, 2012. Cross-continental comparisons of butterfly assemblages in rainforests: Implications for biological monitoring. *Insect Conservation and Diversity*, in press.
- Benedick, S., J. K. Hill, N. Mustaffa, V. K. Chey, M. Maryati, J. B. Searle, M. Schilthuizen & K. C. Hamer, 2006. Impact of rainforest fragmentation on butterflies in northern Borneo: Species richness, turnover, and the value of small fragments. *Journal of Applied Ecology*, **43**: 967–977.
- Corbet, A. S. & H. M. Pendlebury, 1992. *The Butterflies of the Malay Peninsula. Fourth Edition*. Malayan Nature Society, Kuala Lumpur. 600 pp.
- Diamond, J., 2001. Dammed experiments! *Science*, **294**: 1847–1848.
- Didham, R. K., J. Ghazoul., N. E. Stork & A. J. Davis, 1996. Insects in fragmented forests: A functional approach. *Trends in Ecology and Evolution*, **11**: 255–260.
- Ek-Amnuay, P., 2006. *Butterflies of Thailand. First Edition*. Amarin Printing and Publishing Ltd Co, Bangkok. 849 pp.
- Gotelli, N. J. & R. K. Colwell, 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*, **4**: 379–391.
- Hamer, K. C., J. K. Hill., S. Benedick., N. Mustaffa, T. N. Sherratt., M. Maryati & V. K. Chey, 2003. Ecology of butterflies in natural and selectively logged forests of northern Borneo: The importance of habitat heterogeneity. *Journal of Applied Ecology*, **40**: 150–162.
- Hill, J. K., 1999. Butterfly spatial distribution and habitat requirements in a tropical forest: Impact of selective logging. *Journal of Applied Ecology*, **36**: 564–572.
- Horner-Devine, M. C., G. C. Daily., P. R. Ehrlich & B. L. Boggs, 2003. Countryside biogeography of tropical butterflies. *Conservation Biology*, **17**: 168–177.
- Inayoshi, Y., 2011. *A Checklist of Butterflies in Indo-China, Chiefly from Thailand, Laos and Vietnam*. www.yutaka.it-n.jp/. (Accessed 10 Mar.2012).
- Koh, L. P., 2007. Impacts of land use change in South-east Asian forest butterflies: A review. *Journal of Applied Ecology*, **44**: 703–713.
- Koh, L. P. & N. S. Sodhi, 2004. Importance of reserves, fragments, and park for butterfly conservation in a tropical urban landscape. *Ecological Applications*, **14**: 1695–1708.
- Koh, L. P. & D. S. Wilcove, 2008. Is oil palm agriculture destroying tropical biodiversity? *Conservation Letters*, **1**: 60–64.
- Koh, L. P., N. S. Sodhi., H. T. W. Tan & K. S-H. Peh, 2002. Factors affecting the distribution of vascular plants, springtails, butterflies and birds on small tropical islands. *Journal of Biogeography*, **29**: 93–108.
- Koh, L. P., N. S. Sodhi & B. W. Brook, 2004. Ecological correlates of extinction proneness in tropical butterflies. *Conservation Biology*, **18**: 1571–1578.

- Lambert, F. R. & N. J. Collar, 2002. The future for Sundaic lowland forest birds: Long-term effects of commercial logging and fragmentation. *Forktail*, **18**: 127–146.
- Leidner, A. K. & N. M. Haddad, 2011. Combining measures of dispersal to identify conservation strategies in fragmented landscape. *Conservation Biology*, **25**: 1022–1031.
- Leidner, A. K., N. M. Haddad & T. E. Lovejoy, 2010. Does tropical forest fragmentation increase long-term variability of butterfly communities? *PLoS ONE*, **5**(3): e9534.
- Lohman, D. J. & V. U. Samarita, 2009. The biology of carnivorous butterfly larvae (Lepidoptera: Lycaenidae: Miletinae: Miletini) and their ant-tended hemipteran prey in Thailand and the Philippines. *Journal of Natural History*, **43**: 569–581.
- Lynam, A. J. & I. Billick, 1998. Differential responses of small mammals to forest fragmentation in Thailand. *Biological Conservation*, **91**: 191–200.
- Megens, H-J. 2002. *Understanding the Diversity of the Speciose Tropical Butterfly Genus Arhopala*. Nationaal Natuurhistorisch Museum, Naturalis, Leiden. 151 pp.
- Minitab 15 Statistical Software, 2008. [Computer software]. Minitab, Inc., State College, PA. www.minitab.com.
- Pierce, N. E., M. R. Braby, A. Heath, D. J. Lohman, J. Mathew, D. B. Rand & M. A. Travassos, 2002. The ecology and evolution of interactions between lycaenid butterflies and ants. *Annual Review of Entomology*, **47**: 733–771.
- Posa, M. R. C. & N. S. Sodhi, 2006. Effects of anthropogenic land use on birds and butterflies in Subic Bay, Philippines. *Biological Conservation*, **129**: 256–270.
- Ramos, F. A., 2000. Nymphalid butterfly communities in an Amazonian forest fragment. *Journal of Research on the Lepidoptera*, **35**: 29–31.
- Shahabuddin, G. & J. W. Terborgh, 1999. Frugivorous butterflies in Venezuela forest fragments: Abundance, diversity and the effects of isolation. *Journal of Tropical Ecology*, **15**: 703–722.
- Shahabuddin, G., G. A. Herzner, C. R. Aponte & M. D. C. Gomez, 2000. Persistence of a frugivorous butterfly species in Venezuelan forest fragments: The role of movement and habitat quality. *Biodiversity and Conservation*, **9**: 1623–1641.
- Sodhi, N. S., M. R. C. Posa, T. M. Lee, D. Bickford, L. P. Koh & B. W. Brook, 2010. The state and conservation of Southeast Asian biodiversity. *Biodiversity and Conservation*, **19**: 317–328.
- Stouffer, P. C., R. O. Bierregaard, C. Strong & T. E. Lovejoy, 2006. Long-term landscape change and bird abundance in Amazonian rainforest fragments. *Conservation Biology*, **20**: 1212–1223.
- Tan, M. W., L. G. Kirton & C. G. Kirton, 1992. Composition and distribution of butterflies in Rompin-Endau, especially Sungai Kinchin and its vicinity. In: Yap, S. K. & S. W. Lee (eds.), *Proceedings of the International Conference on Tropical Biodiversity*. Malaysian Nature Society, Kuala Lumpur. Pp. 193–212.
- Terborgh, J., L. Lopez, J. Tello, D. Yu & A. R. Bruni, 1997. Transitory states in relaxing ecosystems of landbridge islands. In: Laurance, W. F. & R. O. Bierregaard (eds.), *Tropical Forest Remnants, Ecology, Management and Conservation of Fragmented Communities*. University of Chicago Press, Chicago. Pp. 256–274.
- Thomas, C. D. & S. Harrison, 1992. Spatial dynamics of a patchily-distributed butterfly species. *Journal of Animal Ecology*, **61**: 437–446.
- Veddeler, D., C. H. Schulze, I. Steffan-Dewenter, D. Buchori & T. Tscharnke, 2005. The contribution of tropical secondary forest fragments to the conservation of fruit-feeding butterflies: effects of isolation and age. *Biodiversity and Conservation*, **14**: 3577–3592.
- Vu, L. V. & C. Q. Vu, 2011. Diversity pattern of butterfly communities (Lepidoptera, Papilionoidea) in different habitat types in a tropical rain forest of Southern Vietnam. *ISRN Zoology*, **2011**: Article 818545, 8 pp. doi: 10.540/2011/818545.
- Walther, B. A. & J. L. Moore, 2005. The concept of bias, precision and accuracy, and their use in testing the performance of species richness estimators, with a literature review of estimator performance. *Ecography*, **28**: 815–829.
- Wright, S. J., 2005. Tropical forests in a changing environment. *Trends in Ecology and Evolution*, **20**: 553–559.
- Yeap, C. A., A. C. Sebastian & G. W. H. Davison, 2007. *Directory of Important Bird Areas in Malaysia: Key Sites for Conservation*. Malaysian Nature Society, Kuala Lumpur. 330 pp.
- Yong, D. L., L. Qie., N. S. Sodhi., L. P. Koh., K. S-H. Peh., T. M. Lee., H. C. Lim & S. L-H. Lim, 2011. Do insectivorous birds communities decline on land-bridge forest islands in peninsular Malaysia? *Journal of Tropical Ecology*, **27**: 1–14.

Appendix 1. List of butterfly species detected at each sampling site with species trait information. L = large, M = medium, S = small, A = Southeast Asia restricted species, O = Oriental, S = Sundaland endemics, F = forest dependant, N = non-forest dependant.

Species									Body size	Geographic range	Forest dependence
	ML1	ML2	Jelatang	Jerangau	K. Laban	Latak	Yazid	Petelot			
Papilionidae (12 spp.)											
<i>Graphium agamemnon</i>		+					+		L	O	N
<i>Graphium eurypylus</i>		+							L	O	F
<i>Graphium evemon</i>		+							M	A	F
<i>Pachliopta aristolochiae</i>				+					L	A	N
<i>Pachliopta neptunus</i>		+	+						L	S	N
<i>Papilio demolion</i>		+							L	O	N
<i>Papilio memnon</i>		+							L	O	N
<i>Papilio nephelus</i>		+							L	O	F
<i>Pathysa antiphates</i>		+							L	A	F
<i>Pathysa delessertii</i>	+	+					+		L	S	F
<i>Pathysa macareus</i>		+							L	O	F
<i>Pathysa ramaceus</i>		+		+					L	A	F
Pieridae (12 spp.)											
<i>Appias indra</i>		+							M	A	N
<i>Appias nero</i>		+	+		+				M	O	F
<i>Catopsilia pomona</i>	+		+						M	O	F
<i>Cepora iudith</i>		+							M	O	F
<i>Dercas verhuelli</i>	+			+					M	O	F
<i>Eurema andersoni</i>	+								S	A	F
<i>Eurema hecabe</i>		+					+		S	O	N
<i>Eurema sari</i>	+	+					+		S	A	F
<i>Eurema tilaha</i>					+				M	S	F
<i>Gandaca harina</i>		+	+		+				M	O	N
<i>Prioneris philonome</i>		+							M	O	N
<i>Saletara liberia</i>		+							M	A	N
Nymphalidae (67 spp.)											
<i>Amathuxia perakana</i>			+						L	S	F
<i>Amathuxidia amythaon</i>	+								L	O	F
<i>Bassarona dunya</i>	+	+							M	A	F
<i>Bassarona teuta</i>	+	+							M	A	F
<i>Charaxes durnfordi</i>		+							L	O	F
<i>Cirrochroa emalea</i>		+	+						M	A	N
<i>Cirrochroa orissa</i>		+	+	+	+		+		M	S	N
<i>Cupha erymantis</i>							+	+	M	A	N
<i>Danaus genutia</i>			+						L	O	N
<i>Danaus melanippus</i>		+							L	A	N
<i>Discophora sondaica</i>								+	M	A	N
<i>Dophla evelina</i>	+								L	O	F
<i>Elymnias casiphone</i>			+						L	A	F
<i>Elymnias panthera</i>				+					M	S	F
<i>Euploea eyndhovii</i>		+	+		+		+		L	A	F
<i>Euploea mulciber</i>		+	+	+					L	A	N
<i>Euploea radamanthus</i>		+							M	A	N
<i>Euploea tulliolus</i>		+							M	O	F
<i>Euthalia monina</i>		+		+	+				M	O	N
<i>Faunis canens</i>			+		+		+		M	A	N
<i>Herona sumatrana</i>					+				M	S	F

Appendix 1. Cont'd.

Species									Body size	Geographic range	Forest dependence
	ML1	ML2	Jelatang	Jerangau	K. Laban	Latak	Yazid	Petelot			
<i>Hypolimnas anomala</i>		+							M	O	F
<i>Hypolimnas bolina</i>	+	+	+						L	O	N
<i>Idea hypermnestra</i>		+							L	S	F
<i>Idea stollii</i>		+							L	A	F
<i>Ideopsis gaura</i>		+							L	S	F
<i>Ideopsis similis</i>		+							M	O	N
<i>Ideopsis vulgaris</i>								+	M	A	N
<i>Kallima limborgii</i>					+				M	S	F
<i>Lexia pardalis</i>	+	+	+		+				L	A	N
<i>Lexias canescens</i>	+	+							M	S	F
<i>Lexias cyanipardus</i>	+		+						L	A	F
<i>Melanitis phedima</i>	+	+	+	+					M	O	N
<i>Melanocyza faunula</i>	+								L	A	F
<i>Moduza procris</i>	+								M	O	N
<i>Mycalesis fusca</i>				+					S	S	F
<i>Mycalesis horsfieldi</i>		+							M	A	N
<i>Mycalesis intermedia</i>	+	+	+	+				+	M	O	N
<i>Mycalesis maianeas</i>		+							M	S	F
<i>Mycalesis mineus</i>			+						M	A	N
<i>Mycalesis orseis</i>	+	+			+	+			M	A	F
<i>Mycalesis perseoides</i>		+							M	A	N
<i>Mycalesis perseus</i>	+		+						M	A	N
<i>Neorina lowii</i>	+								L	S	F
<i>Neptis clinia</i>		+							M	A	F
<i>Neptis hylas</i>		+							M	O	N
<i>Neptis leucoporos</i>					+		+		M	A	F
<i>Neptis miah</i>					+				M	A	F
<i>Orsotriaena medus</i>	+								M	O	N
<i>Pantoporia aurelia</i>					+				S	A	F
<i>Pantoporia hordonia</i>			+						M	O	N
<i>Prothoe franck</i>					+				M	O	F
<i>Ragadia makuta</i>	+								M	S	F
<i>Tanaecia aruna</i>	+	+		+	+				M	S	F
<i>Tanaecia godartii</i>	+								M	A	F
<i>Tanaecia iapis</i>	+		+						M	A	F
<i>Tanaecia julii</i>		+							M	O	F
<i>Tanaecia palguna</i>		+							M	A	F
<i>Thaumantis odona</i>		+			+				L	S	F
<i>Thauria aliris</i>		+							L	A	F
<i>Vindula dejone</i>			+						M	O	F
<i>Xanthotaenia busiris</i>	+			+	+				M	A	F
<i>Ypthima baldus</i>		+		+					S	A	N
<i>Ypthima horsfieldi</i>	+	+	+						M	S	N
<i>Ypthima huebneri</i>		+							S	A	N
<i>Ypthima pandocus</i>	+	+	+						M	A	N
<i>Zeuxidia amethystus</i>	+			+					L	A	F
Lycaenidae (33 spp.)											
<i>Abisara savitri</i>								+	M	A	F
<i>Allotinus borneensis</i>	+								S	S	F

Appendix 1. Cont'd.

Species	ML1	ML2	Jelatang	Jerangau	K. Laban	Latak	Yazid	Petelot	Body size	Geographic range	Forest dependence
<i>Allotinus horsfieldi</i>	+	+		+	+				M	S	N
<i>Allotinus substrigosus</i>	+								S	A	F
<i>Allotinus unicolor</i>	+		+	+		+	+	+	S	A	N
<i>Anthene emolus</i>		+	+						S	O	N
<i>Arhopala azinis</i>	+								S	S	F
<i>Arhopala democritus</i>		+		+					S	A	F
<i>Arhopala epimuta</i>								+	M	A	F
<i>Caleta roxus</i>		+							S	O	F
<i>Cheritra freja</i>		+			+				S	A	F
<i>Drupadia ravindra</i>	+	+		+	+				S	A	N
<i>Eooxylides tharis</i>	+	+							S	A	F
<i>Jamides celeno</i>	+	+	+	+			+		S	O	N
<i>Jamides elpis</i>	+	+	+						S	A	F
<i>Jamides malaccanus</i>		+							S	S	F
<i>Logania malayica</i>		+							S	A	N
<i>Mantoides gama</i>			+						S	A	F
<i>Nacaduba kurava</i>		+					+		S	O	N
<i>Nacaduba subperusia</i>		+		+					S	A	N
<i>Neopitheops zalmora</i>			+						S	O	F
<i>Paralaxita damajanti</i>	+	+	+		+				S	S	F
<i>Paralaxita telesia</i>		+		+					S	A	F
<i>Prosotas nora</i>	+			+					S	O	N
<i>Rapala iarbus</i>			+						S	A	N
<i>Rapala pheretima</i>	+								S	A	N
<i>Stiboges nymphidia</i>		+							S	O	F
<i>Surendra florimel</i>					+				S	S	F
<i>Tajuria dominus</i>			+						S	S	N
<i>Taxila haquinus</i>			+	+					M	O	F
<i>Thamala marciana</i>			+						S	A	F
<i>Ticherra acte</i>			+						S	O	F
<i>Zemeros emeisoides</i>			+		+			+	S	S	F
Hesperiidae (7 spp.)											
<i>Ancistroides nigrita</i>						+			M	A	F
<i>Caltoris cormasa</i>			+						S	A	F
<i>Celaenorrhinus asmara</i>		+							S	A	F
<i>Pelopidas agra</i>	+								S	O	N
<i>Psolo fuligo</i>		+							S	A	N
<i>Tagiades calligana</i>	+								S	S	F
<i>Tagiatus japetus</i>		+							S	O	N

Appendix 2. List of butterfly species that were sampled from fruit-baited traps or were opportunistically observed over water.

Species	Number of individuals
Species caught in baited traps	
<i>Bassarona dunya</i>	3
<i>Dophla evelina</i> *	1
<i>Neorina lowii</i> *	1
<i>Amathuxidia amythaon</i>	1
<i>Zeuxidia amethystus</i>	2
<i>Ragadia makuta</i>	1
Species observed in flight over water	
<i>Graphium agamemnon</i>	1
<i>Pathysa antiphates</i>	1
<i>Pachliopta aristolochiae</i>	1
<i>Eurema sari</i>	1
<i>Eurema hecabe</i>	1
<i>Euploea camaralzaman</i> *	1
<i>Euploea tulliolus</i>	1
<i>Euploea mulciber</i>	2
<i>Terinos atlita</i>	1
<i>Junonia atlities</i> *	1

*Denotes a species not recorded from any transect