EFFECTS OF VERTICAL GRADIENT ON THE DIVERSITY AND ABUNDANCE OF NYMPHALIDAE IN A BORNEAN RAINFOREST

Saurin Gintoron Christharina*, Idris Muhamad Ikhwan & Abang Fatimah
Pusat Pengajian Pra-Universiti,
Universiti Malaysia Sarawak, 94300,
Kota Samarahan, Sarawak, Malaysia.
*Corresponding author: *sgchristharina@unimas.my*

ABSTRACT

The forest canopy is known to harbour high insect diversity, yet descriptive studies that simultaneously measure species richness on both ground and canopy strata are not common. The Nymphalidae are abundant in the canopy and their distribution across the vertical dimension contributes to tropical diversity. A comprehensive study of the vertical distribution of nymphalids in four forest habitats in the Kubah lowland mixed-dipterocarp forest: primary, secondary, heath forest and forest edge were conducted. Forty baited traps were installed at both ground and canopy levels and sampled over a six-month period. The preference of the nymphalids for the lower stratum was significant for abundance, diversity, and common species such as *Bassarona dunya*. Observed pattern could be due to the distribution of available adult resources and larval hostplants. Being practically ‘sun-lovers’, highest diversity of nymphalids at the canopy level was recorded at the forest edge (H’ = 2.525). Meanwhile, more microhabitats are offered at the lower level in secondary forest and thus supporting the most diverse nymphalids here (H’ = 3.020). Vertical study of nymphalids provides knowledge and fluctuation patterns of its diversity and thus more similar study is suggested to be conducted in the future.

Keywords: Borneo, diversity, Nymphalidae, vertical distribution

ABSTRAK

Kanopi hutan dikenalpasti mempunyai kepelbagaian serangga yang tinggi, namun kajian deskriptif yang mengukur kekayaan spesies di aras tanah dan strata kanopi secara serentak adalah jarang dijalankan. Nymphalidae banyak terdapat di kanopi pokok dan taburannya yang melintasi dimensi menegak telah menyumbang kepada kepelbagaian tropika. Kajian komprehensif ke atas taburan menegak nymphalid di empat habitat hutan di hutan dipterokap tanah rendah Kubah: primer, sekunder, hutan kerangas dan pinggir hutan telah dijalankan. Empat puluh perangkap umpan dipasang di aras tanah dan kanopi dalam tempoh tempoh enam bulan. Pemilihan nymphalid pada stratum bawah adalah signifikan bagi kelimpahan, kepelbagaian, dan spesies umum seperti *Bassarona dunya*. Corak penemuan ini mungkin disebabkan oleh ketersediaan sumber makanan kupu-kupu dewasa yang ada dan tanaman perumah bagi larva. Kepelbagaian kupu-kupu pemakan buah tertinggi direkodkan di strata kanopi pinggir hutan (H '= 2.525) yang berkemungkinan disebabkan oleh sifat kupu-kupu yang menggemari sinar matahari. Sementara itu, lebih banyak habitat mikro ditawarkan di aras tanah di hutan sekunder dan dengan itu menyokong rekod spesies yang paling pelbagai di sini (H ’= 3.020). Kajian menegak nymphalid memberikan pengetahuan dan corak turun naik mengenai kepelbagaiannya dan oleh itu kajian yang lebih kurang sama dicadangkan untuk dilakukan pada masa akan datang.

Katakunci: Borneo, kelimpahan, Nymphalidae, taburan menegak

INTRODUCTION

The vast diversity in the tropical rainforest is related with the enormous communities of flora and fauna found from the tree crown to the forest floor. The stratification between the upper and lower strata is in fact a significant factor which characterises the tropical diversity (Basset et al. 2015; Davis et al. 2011; Devries et al. 2012; Nakamura et al. 2017; Whitworth et al. 2016). Vertical patterns are one of the crucial variables that need to be considered in order to understand the community characteristics of any particular habitat (Davis et al. 2011; Nakamura et al. 2017; Whitworth et al. 2016). Being recognised as a major characteristic of intact rainforest ecosystem, the vertical approach has become one of the greatest concerns among the conservationists (Davis et al. 2011; Devries et al. 2012; Nakamura et al. 2017).

Some of the previous studies that emphasised on the vertical stratification of nymphalid butterflies, and overall entomofauna in the tropical rainforest includes Brant et al. (2016), Gintoron and Abang (2014; 2021), Skarped (2014), and Widhiono (2015). Various types of forest habitats in the tropical region could sustain different and unique nymphalids’ communities, and thus require more scientific studies. The vast diversity in the tropical rainforest is also contributed by natural disturbances such as fallen trees which affects the complexity of vegetation structure (Brant et al. 2016; Pardonnet 2010; Skarped 2014). Irregularities in forest structure are common and forest gaps can also form for example caused by natural tree death (Muscolo et al. 2014; Pardonnet 2010; Terborgh et al. 2020).

The microclimates formed by those gaps influence the species that survive and create more unique microhabitats that increase the biodiversity of both flora and fauna in the forest (Egbe et al. 2012; He et al. 2012; Muscolo et al. 2014; Roznik et al. 2015). Fluctuation in climatic conditions such as the availability of water (rainfall) also affect the assemblage of plants and arthropods (Araujo et al. 2020; Gupta et al. 2019; Houlihan et al. 2013; Kumar et al. 2016; Widhiono 2015). For example, satyrine butterflies are sensitive to any fluctuations in humidity, especially those in the lowland rainforest (Gintoron & Abang 2014; Pertiwi et al. 2020; Widhiono 2015). Seasonal timing affects the nymphalids diversity (Araujo et al. 2020; Ojianwuna 2015) though in the tropics it is characterised by the indefinite dry and wet seasons. Rainfall is one of the variables that impacts the nymphalids diversity. For example, during heavy rainfall, higher mortality rate of the pupa was recorded (Araujo et al. 2020; Comay et al. 2021; Gintoron & Abang 2021) and fungus infection to the adult nymphalids (Beck et al. 2006). The main purpose in investigating the vertical distribution in a particular area is to understand the processes in terms of the species composition of the overall communities in the multi-layered forest. The segregation of both upper and lower strata to understand the vertical characteristics of the fruit-feeding butterflies is important and thus should be studied at the same time. The vertical stratification of the Nymphalidae was investigated in four different habitat types within Kubah lowland mixed-dipterocarp forest. Effects of rainfall on to the vertical stratification of the nymphalids were also observed.

MATERIALS AND METHODS

Study Area

Our study site was Kubah National Park (N 1°36'48.43", E 110°11'51.59") located in the Kuching Division, Sarawak, Malaysia (Figure 1). The study area consisted mainly of mixed dipterocarp forest, heath forest, and secondary forests (Hazebroek & Abang 2000). the sampling was conducted along four trails (Waterfall Trail, Rayu Trail, Summit Trail and Belian Trail) that were representatives of the different habitats within the park (Figure 2). Swampy areas and small jungle streams are found at the Waterfall Trail, and damp areas were also observed along the Summit Trail. Local fruit trees were found at Belian Trail, while wild durian can also be seen at the Waterfall Trail.

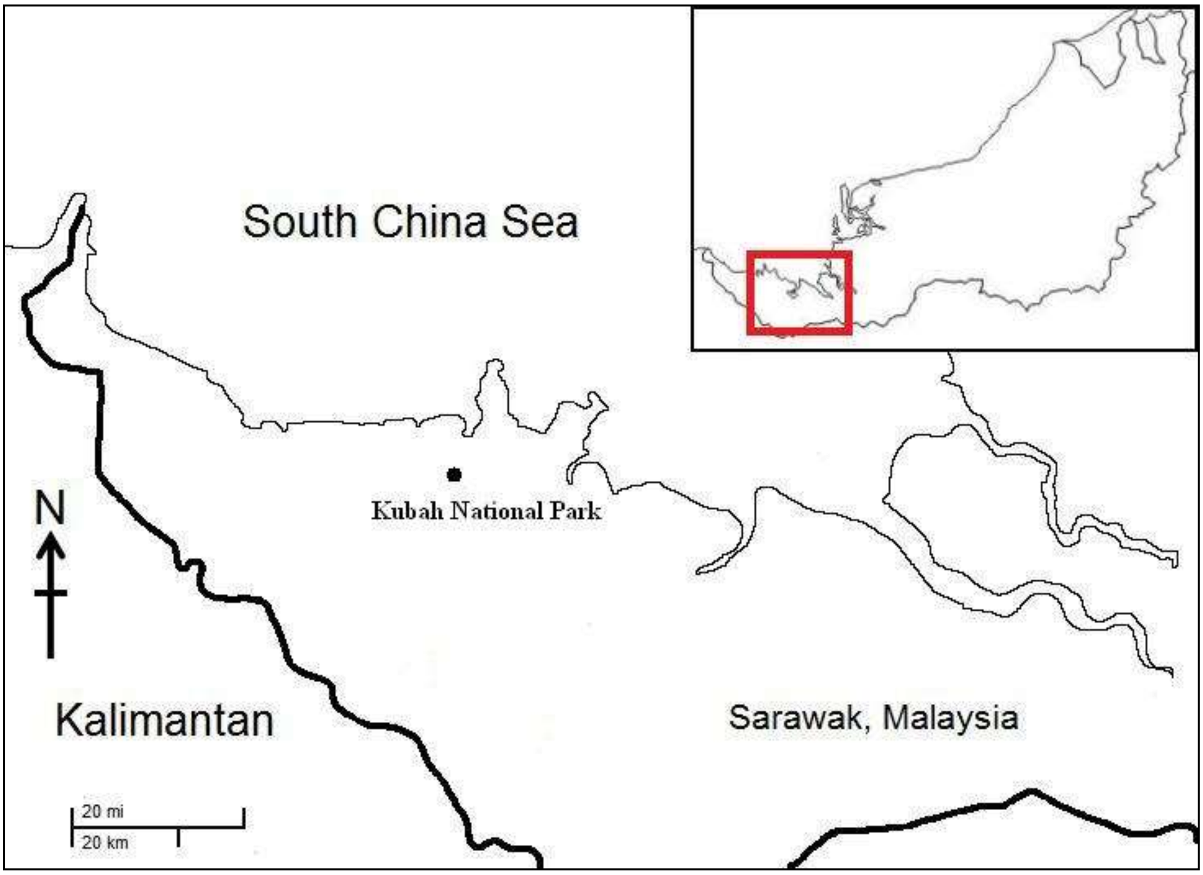


Figure 1. Study area which is in Kubah National Park, Sarawak, in southern part of Malaysian Borneo

(Source: Modified after Google Map 2011)

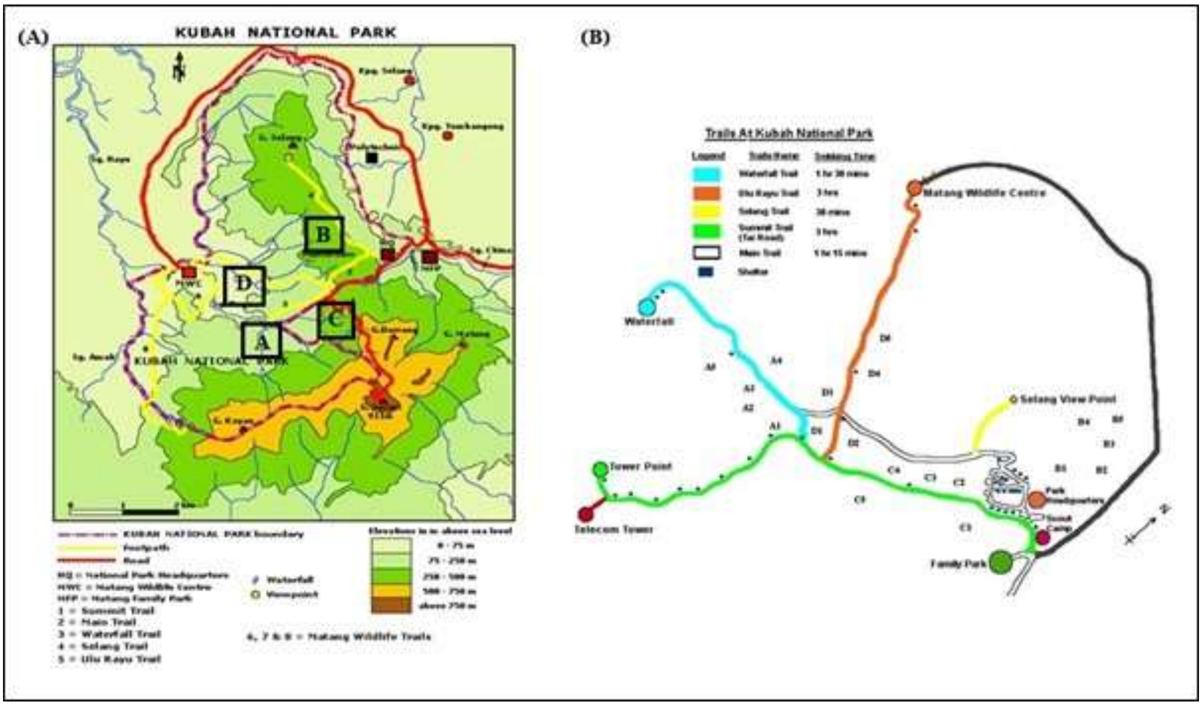


Figure 2. (A) Study site in Kubah National Park, Sarawak with four sampling areas; A. Primary Forest, B. Secondary Forest, C. Forest edge, D. Heath Forest; (B) Numbers designate individual replicate sampling units which represents one canopy and one ground level trap (Note: Map is not up to scale)

(Source: Hazebroek & Abang 2000).

Data Collection and Species Identification

Five replicates (sampling unit trees) were established within each forest habitat. In each replicate, one ground level trap was hung between 1 and 1.5 m above the ground, whereas the canopy baited traps were positioned between 21 and 27 m above the ground. This provided a total of ten baited-traps in each forest habitat – five canopy, and five ground level, and a total of 40 traps overall. The traps were set-up by using the Single-Rope Technique and as the traps were suspended from thin nylon ropes run over the branches, they could be adjusted to the proper height.

Traps were baited with pineapples which were placed on the day prior to the sampling interval and replenished with fresh one on the subsequent trapping days. All 40 traps were baited and sampled daily for 14 consecutive days per month and then collected. The field sampling was conducted from 13th May 2009 to 17th November 2009 with baited traps (ripe pineapple) maintained for 14 days every month except October 2009 and resulted in total of 3360 samples effort (2 traps (canopy, ground level) x 5 trees per trail (habitat type) x 4 trails x 84 sampling days).

Species Identification

Specimens collected, preserved and were identified up to species level following Otsuka (1988) and Tsukada (1991) using a stereomicroscope.

Statistical Analysis

Conventional biodiversity indices were produced with EstimateS program version 8.2 (Colwell 2006) and compared between vertical strata using unpaired t-tests. The correlations between numbers of individuals trapped with trap heights were analysed with Spearman correlation test. All analyses were performed with PAST version 1.96 (Hammer et al. 2001) and MINITAB Release 13.20 statistical software.

RESULTS

Overall Diversity and Abundance of the Nymphalids in Both Ground and Canopy Stratum

A total of 665 nymphalids sorted to 49 species within four subfamilies were collected from Kubah National Park, over 84 days of field sampling. The proportion of overall species abundance was significantly higher at the ground level (all subfamilies pooled together) than the canopy (Mann-Whitney: $P < 0.05$). Species abundance distribution ranged from 11 species representing singletons to one species with 93 individuals (*Bassarona dunya*) (Figure 3). Among the 20 most abundant nymphalid species sampled, 11 showed significant vertical stratification and were mostly trapped at the ground level (Table 1). The total abundance of ground specimens were seven times more than the canopy specimens, and almost doubled in total species as well (Table 2) (Mann-Whitney: $P < 0.05$).

Table 1. Vertical distribution for 20 most abundant (n ≥ 20) fruit-feeding butterflies' species (Lepidoptera: Nymphalidae), pooled across the four forest habitats and 84-days of sampling, in Kubah National Park, Sarawak

Taxon	**Individual Abundance**			***P*-value**
	Ground	**Canopy**	**Total**	
Amathuxidia amythaon ottomana Butler 1869*	46	3	49	< 0.05
Bassarona dunya monara Fruh 1913*	93	0	93	< 0.05
Bassarona teuta bellata Distant 1886	48	24	72	ns
Lexias dirtea chalcenoides Fruh 1913*	19	1	20	< 0.05
Lexias pardalis dirteana Corbet 1941*	26	1	27	< 0.05
Melanitis leda leda Linnaeus 1758	14	8	22	ns
Melanitis zitenius rufinus Fruh 1908	11	3	14	ns
Mycalesis fusca adustata Fruh 1906	9	2	11	ns
Mycalesis kina Staudinger 1892*	17	3	20	< 0.05
Mycalesis maianeas kadasan Aoki & Uemura 1982*	9	1	10	< 0.05
Mycalesis mnasicles mnasicles Hewitson 1864*	18	3	21	< 0.05
Mycalesis orseis borneensis Fruh 1906	13	3	16	ns
Neorina lowii lowii Doubleday 1849*	20	1	21	< 0.05
Prothoe franckii borneensis Fruh 1913*	24	1	25	< 0.05
Ragadia makuta umbrata Fruh 1911*	37	1	38	< 0.05
Tanaecia aruna aparasa Vollenhoeven 1862	11	1	12	ns
Tanaecia clathrata coerulescens Vollenhoeven 1862*	23	3	26	< 0.05
Zeuxidia amethystus wallacei C. & R. Felder 1867	42	3	45	ns
Zeuxidia aurelius euthycrite Fruh 1911	24	1	25	ns
Zeuxidia doubledayi horsefieldii C. & R. Felder 1867	27	4	31	ns

Species with asterisks (*) depart significantly ($P < 0.05$) between forest strata (ns = not significant)

Table 2. Total number of individuals and species (Lepidoptera: Nymphalidae) sampled in 40 baited traps (20 at the ground level, 20 at the canopy level) over the 84 days of sampling, in Kubah National Park, Sarawak

	Ground	**Canopy**
Individuals	581	84
Species	44	29
Singletons	9	16
Doubletons	7	1
Species excluding singletons and doubletons	28	12

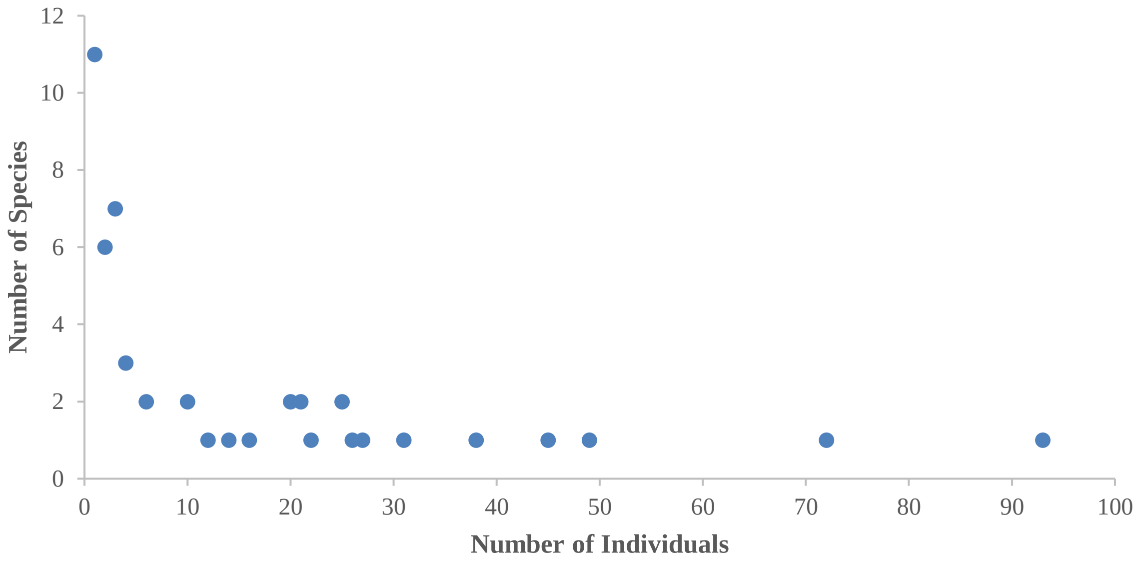
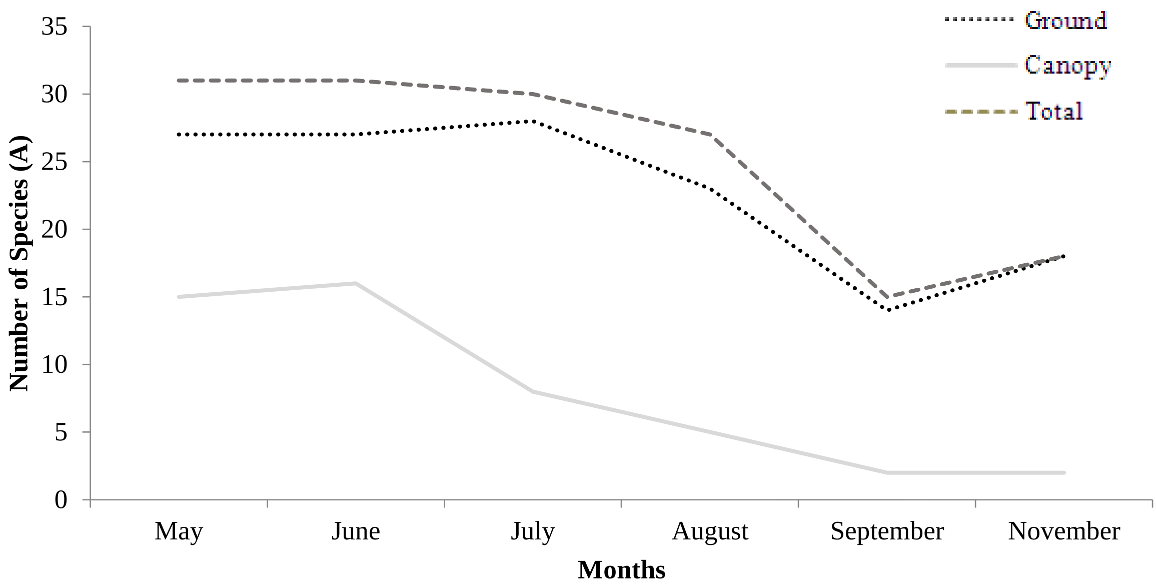


Figure 3. Species abundance distribution ranged from 11 species representing singletons to one species with 93 individuals throughout the six months of sampling, in Kubah National Park, Sarawak

Nymphalid species diversity was significantly greater in the ground traps than the canopy traps (Diversity *t*-test; t = 3.3322, df = 99.368, $P < 0.05$). Within subfamilies, Nymphalinae was more diverse at the ground than the canopy level (Diversity *t*-test: t = 3.3162, df = 47.801, $P < 0.05$), but there was no significant difference in diversity between strata in the Satyrinae (Diversity *t*-test; t = 1.9421, df = 34.549, P = 0.06), Morphinae (Diversity *t*-test: t = 0.983, df = 17.08, P = 0.339) or Charaxinae (Diversity *t*-test: t = -0.837, df = 7.987, P = 0.427).

Vertical Diversity and Patterns of the Nymphalids Across Six Monthly Replicates and Four Forest Habitats

Species richness of Nymphalidae peaked in June in canopy traps and then declined in subsequent sampling periods, whereas in ground traps it peaked in July, decline in August and September, and increased again in November (Figure 4A). Abundance of nymphalids in both canopy and ground traps peaked in June and then decreased in subsequent months until November, when it increased in ground traps (Figure 4B). In July 2009, nymphalid species richness increased in ground traps and decreased in canopy traps. There were significant differences in nymphalid abundance among these six sampling occasions, (Kruskal-Wallis: H = 26.04, Hc = 29.61, $P < 0.05$). Species abundance was lowest in September and November 2009, which also coincides with the rainy period (Figure 5).



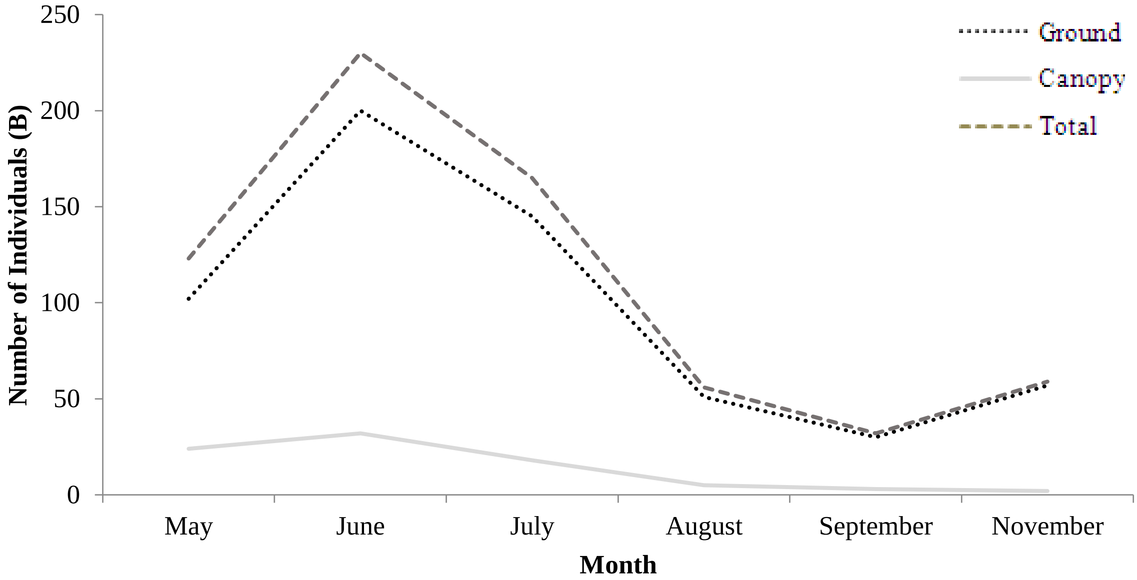


Figure 4. Total species richness (A) as well as abundance (B) for the fruit-feeding butterflies (Lepidoptera: Nymphalidae) in each stratum throughout the six months of sampling, in Kubah National Park, Sarawak

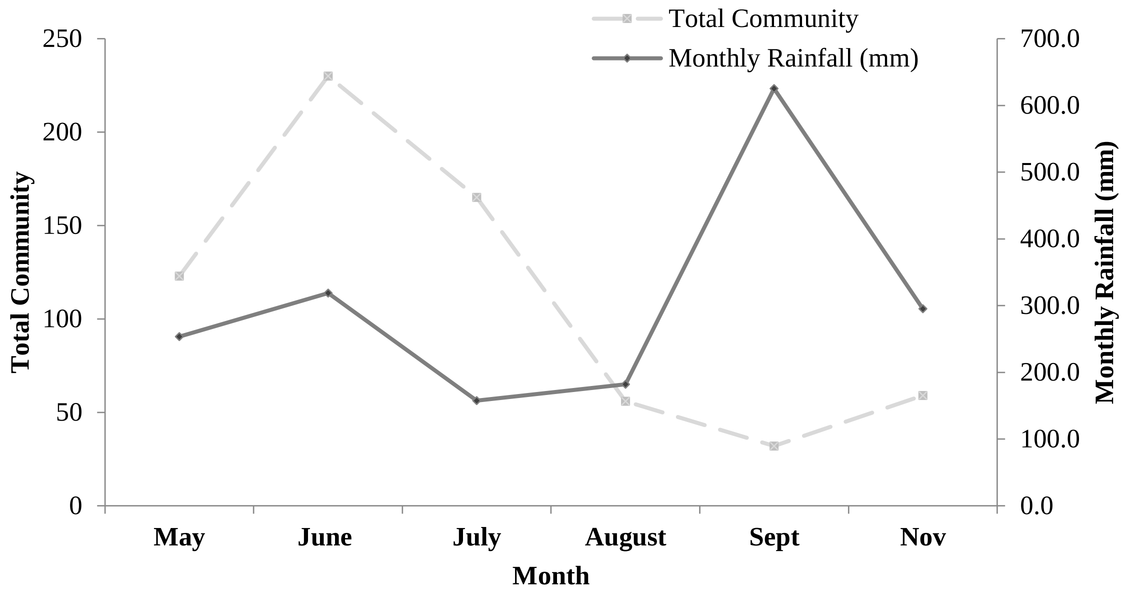


Figure 5. Temporal variations in the total community of fruit-feeding butterflies (Lepidoptera: Nymphalidae) throughout the six sampling occasions in Kubah National Park, Sarawak

All 11 nymphalid species which significantly inhibited certain stratum showed preference to the ground level (Table 1). When analysed for species diversity, the lower strata of the secondary forest showed the highest index value (H'=3.020) (Table 3). On the other hand, for the upper strata, forest edge (H'= 2.525) attains the most diverse assemblages of canopy fliers. Only one of the four baited nymphalid subfamilies showed a significant correlation between the number of individuals sampled and trap height, which was the Satyrinae (Spearman: rs = 0.642, n = 185, P = 0.007) (Table 4). Within this subfamily, a trend was observed which revealed a decrease in abundance at the canopy stratum, specifically for *Mycalesis kina*, *M. mnasicles*, *Neorina lowii* and *Ragadia makuta*. There was no significant correlation between the species number and trap height of any nymphalid subfamilies in this study (Spearman: P > 0.05 in all cases).

Nearly half of the total nymphalid species recorded at the ground level (except for heath forest) was sampled in all three forest habitats: primary, secondary and forest edge (Figure 6 (A)). Six nymphalid species were recorded as unique to the lower strata of the secondary forest and forest edge respectively. Meanwhile, there were only two singletons; *Charaxes durnfordi* and *Phalanta alcippe*, which were unique to the primary forest. On the other hand, 35% of the total species listed at the canopy was unique to the forest edge, which includes two singletons: *Tanaecia pelea* and *M. horsefieldii*, and one of the most abundant Charaxinae nymphalids in this study, *Prothoe franckii* (Figure 6 (B)).

Table 3. Species richness, abundance, and diversity of the fruit-feeding butterflies (Lepidoptera: Nymphalidae) in vertical dimension, for all four forest habitats in Kubah National Park, Sarawak

	Primary			**Secondary**			**Edge**			**Heath**		
	Ground	**Canopy**	**Total**	**Ground**	**Canopy**	**Total**	**Ground**	**Canopy**	**Total**	**Ground**	**Canopy**	**Total**
Number of Species	24	11	26	30	7	32	31	16	37	25	13	29
Number of Unique Species	2	0	2	4	1	5	5	4	7	3	2	4
Individuals	138	15	153	117	16	133	164	25	189	162	28	190
Shannon-Weiner (H')	2.728	2.342	2.799	3.020	1.629	3.033	2.872	2.525	2.991	2.824	2.145	2.893
Simpson's Diversity (D)	0.914	0.898	0.921	0.936	0.742	0.933	0.914	0.893	0.923	0.925	0.824	0.930
Margalef	4.661	3.789	4.970	6.090	2.264	6.339	5.883	4.660	6.677	4.717	3.601	5.336

Table 4. Spearman rank correlation between fruit-feeding butterflies' (Lepidoptera: Nymphalidae) abundance and species richness with trap heights in Kubah National Park, Sarawak

	Ground	**Canopy**	**Total**	***rs***	***P*-value**
Abundance					
Charaxinae	28	5	33	0.316	ns
Morphinae	147	13	160	0.691	ns
Nymphalinae	248	39	287	0.059	ns
Satyrinae*	158	27	185	0.642	< 0.05
Species Number					
Charaxinae	3	3	4	0.333	ns
Morphinae	8	5	8	0.395	ns
Nymphalinae	18	10	21	-0.428	ns
Satyrinae	15	11	16	-0.174	ns

Subfamilies with asterisks depart significantly ($P < 0.05$) between forest strata (ns = not significant)

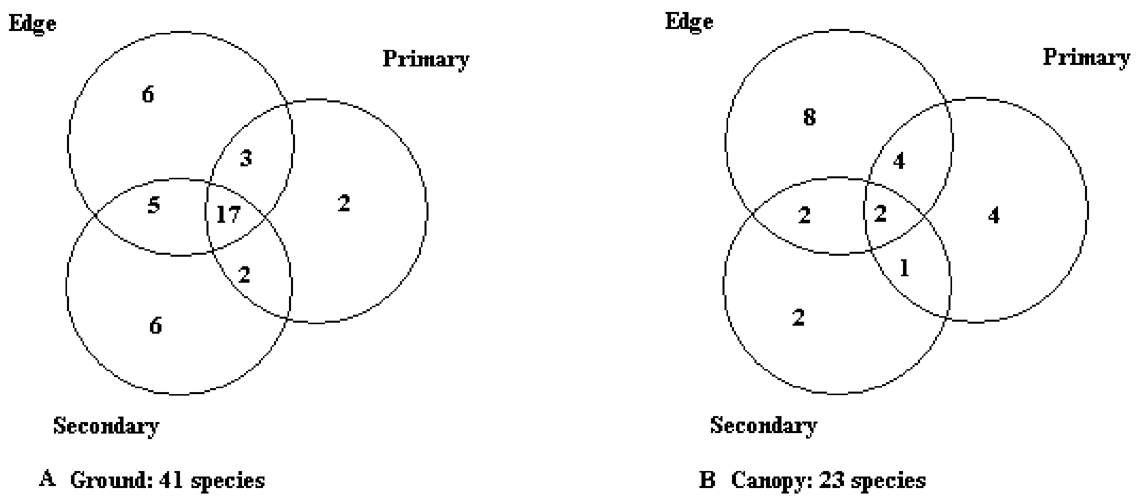


Figure 6. Species overlap among primary, secondary and forest edge (heath forest was omitted for better clarity) of fruit-feeding butterflies (Lepidoptera: Nymphalidae) in Kubah National Park, Sarawak; (A) ground and (B) canopy

DISCUSSION

Overall Diversity and Abundance of the Nymphalids in Both Ground and Canopy Strata

The difference in terms of abundance and species diversity of the nymphalids between the ground and canopy layer has been documented previously such as in the Peruvian Amazon (Whitworth et al. 2016), Bolivia (Skarped 2014), and Borneo (Gintoron & Abang 2021). Almost 90% of the nymphalid species listed in the present study were sampled at the ground level in contrast to some previous studies which observed either no vertical pattern (Schulze et al. 2001; Stork & Grimbacher 2006), or a more diverse array of nymphalids at the forest canopy (Nakamura et al. 2017). Similar finding of higher nymphalid assemblages in the lower stratum was also observed by Skarped (2014), Widhiono (2015) and Whitworth et al. (2016), who suggested that this might be due to plentiful food resources for adult's butterflies in the lower stratum. It is documented that the availability of specific resources for adults strongly influenced the species occurrence pattern and thus play important role in determining overall abundance as well as diversity (Davis et al. 2011; Gintoron & Abang 2021; Widhiono 2015). For example, rotting fruits are usually found at the forest floor and with the strong smell, it could attract the fruit-feeding butterflies.

Bassarona dunya was the most abundant nymphalid species in this study, and all 93 specimens were collected from the ground level. According to Hamer et al. (2003), the Nymphalinae butterflies are highly associated with gaps. Forest gap allows more light penetration, and this creates unique microhabitat that in turn increase species diversity (Egbe et al. 2012). In the present study site, the canopy cover was not even due to fallen trees and the mixture of smaller trees. This allows more gaps at the lower stratum and attracts more *B. dunya* and other Nymphalinae butterflies, in general, at this habitat.

In the present study, the tree crowns sustained higher proportion of singletons when compared with the lower strata. Being subjected to harsh microclimatic conditions (Kenzo et al. 2015) at this higher stratum, the dispersion of the canopy nymphalids could take place. Essentially, this could be possibly caused by the high wind velocities at this stratum height, and consequently these few rare in abundance nymphalids were sampled here (Pertiwi et al. 2020).

Vertical population Fluctuations of the Nymphalids in Six Monthly Replicates and in Different Forest Habitats

In the present study, a vertical pattern of the nymphalids was observed throughout the six-month sampling, which revealed the decreasing total number of species as well as individuals with the heavy rainfall for overall total community. In general, rainfall distribution is proven to influence the invertebrates (Araujo et al. 2020; Comay et al. 2021; Houlihan et al. 2013; Lourenço et al. 2020; Ojianwuna 2015) and presently, the trends were evident regardless of the stratum height. Heavy rainfall could affect the availability of food resources of the insects including nymphalids, and thus rarely observed during rainy days (Araujo et al. 2020; Comay et al. 2021; Gintoron & Abang 2021).

Apart from that, with the humidity associated with the rainfall, adult nymphalids could also be fatally susceptible to fungus infection (Beck et al. 2006). Furthermore, heavy rainfall is considered to affect the larval and pupal survival, which can cause the increase in mortality rate (Fermon et al. 2000; Hill et al. 2003). Widhiono (2015) and Pertiwi et al. (2020) also suggested that the butterflies of Satyrinae and Morphinae especially are sensitive to changes in humidity.

Vertical stratification of nymphalids community in a particular habitat is usually related with the vegetation types and forest status (Gupta et al. 2019; Martins et al. 2017; Widhiono 2015). In general, species richness of the entomofauna is observed to be positively related with the plants' diversity (Idris et al. 2021; Pertiwi et al. 2020; Widhiono 2015). Butterflies for instance is host-specific, and thus related with the distribution of their larval food-plants (Arya et al. 2014; Gintoron & Abang 2014; 2021; Ojianwuna 2015; Skarped 2014; Widhiono 2015). Furthermore, the occurrence of different species including vertical stratification pattern is determined by the local conditions and differences in food supply (Davis et al. 2011).

Most of the nymphalids sampled at the ground level were recorded at the secondary forest. The high diversity of nymphalids in this forest habitat may relate to the existing natural and intermediate disturbance (Loaiza et al. 2017; Pardonnet 2010). Belian Trail was previously farmed by the locals years ago and now that it is included as protected area, this secondary forest is characterised with the mixture of smaller trees and local fruit trees as well as less developed canopy structures. Widhiono (2015) suggested that natural or artificial disturbances could affect the vertical pattern of butterflies. Fallen trees or forest gaps caused irregularities in forest structure (Brant et al. 2016), and thus offer a variety of habitats and food resources that can accommodate a diverse group of butterflies (Pardonne 2010; Skarped 2014).

Light penetrability is also proven to influence the distribution of the nymphalids (Pardonnet 2010; Pertiwi et al. 2020). The amount of light at the ground level was almost similar between these three forest areas. However, at the forest canopy, the light penetrability was not uniform, as it depends on the tree crowns respectively. This will affect the occurrence of nymphalids, as being an ectothermic, this guild of butterflies needs the solar radiation to elevate their body temperature (Pertiwi et al. 2020). According to Didham and Ewers (2014), there was a significant interaction between vertical height and distance from forest edge for all microclimate variables, which is decreasing in magnitude from edge to interior at the canopy level. Perhaps the unique microclimatic factors such as temperature and light penetrability at the tree crown of the forest edge are favoured by the nymphalids (Pertiwi et al. 2020)

In terms of species diversity, the occurrence of more than half nymphalid species at the ground level of secondary forest could be due to the decreased canopy cover and more forest gaps (Egbe et al. 2012; Muscolo et al. 2014). A few of these abundant ground-based nymphalids were *B. dunya* which was documented to have heliophobia (Fermon et al. 2000) and *R. makuta*, a satyrine butterfly which is categorised as poor fliers and thus abundantly inhabiting this stratum (Corbet & Pendlebury 1992; Hill et al. 2003). In the primary forest however, due to the closed canopy most of the monocotyledonous food plants are restricted to the lower forest layer. This caused the satyrine butterflies which exclusively feed on this type of plant to be abundant at this level (Widhiono 2015).

Conversely, highest diversity at the forest canopy was observed at both forest edge as well as primary forest. With the high variation of microclimate at the forest canopy, diverse array of nymphalids is predicted in this stratum (Fermon et al. 2000; Basset et al. 2003). Moreover, with the closed canopy at the primary forest, most of the canopy nymphalids would be seldom at the lower strata as there was no presence of forest gaps to be confused as the canopy (Fermon et al. 2003).

CONCLUSION

The preference of the nymphalids assemblages to the lower stratum has been clearly observed in the current study. This vertical stratification was similarly present when tested for abundance and species diversity. Apart from being determined by the availability of adult resources, larval hostplants and avoidance from predator had probably influenced their vertical patterns. Rainfall could possibly affect the pupal survival and thus leads to the declining number and richness of the nymphalids, regardless of the strata heights. Apart from that, significant species abundance and richness of these nymphalids at the ground level were also observed in all four forest habitats. Distinctive nymphalids' communities along the vertical gradient were also revealed which possibly contributed by the microclimatic parameters such as light availability.

In order to conduct a better vertical survey for the nymphalids in the future, a few modifications should be made to the research sampling. In relation to the forest habitats, respective sites should at least be one km apart to compare the specific vertical patterns acquired by the nymphalids. Apart from that, environmental variables such as percentage of canopy cover and trees density should also be documented so that any relationships between the vegetation types with the vertical distribution of nymphalids could be studied. Lastly, mark-recapture could also be conducted to investigate more on the movement and confinement of the nymphalids, as well as their lifespan.

ACKNOWLEDGEMENTS

The authors would like to thank everyone who helped throughout the completion of this research especially Irene Christianus, Jailani Mortada, Raymond Atet and Wahap Marni. We also thank the UNIMAS Insect Reference Collection of Faculty Resource Science and Technology and the staff of Kubah National Park, Sarawak. Thank you to Sarawak Forestry Corporation for granting permission to conduct this research in Kubah National Park (Permit No. NCCD.907.4 (IV) – 20 and 21, Park Permit No: 22/2009 and 23/2009). This study was supported financially by UNIMAS Zamalah Postgraduate Scholarship.

REFERENCES

Araujo, E. da C., Martins, L.P., Duarte, M. & Azevedo, G.G. 2020. Temporal distribution of fruit-feeding butterflies (Lepidoptera, Nymphalidae) in the eastern extreme of the Amazon region. *Acta Amazonica* 50: 12–23.

Arya, M.K., Dayakrishna, & Chaudary, R. 2014. Species richness and diversity of Butterflies in and around Kumaun University, Nainital, Uttarakhand, India. *Journal of Entomology and Nematology* 2(3): 153–159.

Basset, Y., Novotny, V., Miller, S.E. & Kitching, R.L. 2003. Methodological Advances and Limitations in Canopy Entomology. In. Basset, Y., Novotny, V., Miller, S.E. & Kitching, R.L. (eds.). *Arthropods of Tropical Forests. Spatio-temporal Dynamics and Resource Use in the Canopy*, pp. 7-16. Cambridge: Cambridge University Press.

Basset, Y., Cizek, L., Cuénoud, P., Didham, R.K., Novotny, V., Ødegaard, F., Roslin, T., Tishechkin, A.K., Schmidl, J., Winchester, N.N., Roubik, D.W., Aberlenc, H.P., Bail, J., Barrios, H., Bridle, J.R., Castaño-Meneses, G., Corbara, B., Curletti, G., Duarte Da Rocha, W., De Bakker, D., Delabie, J.H.C., Dejean, A., Fagan, L.L., Floren, A., Kitching, R.L., Medianero, E., Gama De Oliveira, E., Orivel, J., Pollet, M., Rapp, M., Ribeiro, S.P., Roisin, Y., Schmidt, J.B., Sorensen, L., Lewinsohn, T.M. & Leponce, M. 2015. Arthropod distribution in a tropical rainforest: Tackling a four dimensional puzzle. *PLoS ONE 10*(12): e0144110.

Beck, J., Mandel, F. & Peer, M. 2006. Geometrid Moth (Lepidoptera: Geometridae) in Borneo: How Homogeneous Are Assemblages from a 'Uniform' Lowland Primary Forest? *Journal of the Zoological Society Wallacea* 2: 44-53.

Brant, H.L., Ewers, R.M., Vythilingam, I., Drakeley, C., Benedick, S., & Mumford, J.D. 2016. Vertical stratification of adult mosquitoes (Diptera: Culicidae) within a tropical rainforest in Sabah, Malaysia. *Malaria Journal 15*(1): 370.

Colwell, R.K. 2006 *EstimateS:* Statistical Estimation of Species Richness and Shared Species from Samples (Version 8.20). USA: University of Connecticut.

Comay, O., Yehuda, O.B., Schwartz-Tzachor, R. & Benyamini, D. 2021. Environmental controls on butterfly occurrence and species richness in Israel: The importance of temperature over rainfall. *Ecology and Evolution* 11: 12035–12050.

Corbet, A.S. & Pendlebury, H.M. 1992. *The Butterflies of the Malay Peninsula*. Kuala Lumpur: Malayan Nature Society.

Davis, A.J., Sutton, S.L. & Brendell, M.J.D. 2011. Vertical distribution of beetles in a tropical rainforest in Sulawesi: the role of the canopy in contributing to biodiversity. *Sepilok Bulletin* 13 & 14: 59–83.

Devries, P.J., Alexander, L.G., Chacon, I.A. & Fordyce, J.A. 2012. Similarity and difference among rainforest fruit-feeding butterfly communities in Central and South America. *Journal Of Animal Ecology* 81: 472–482.

Didham, R.K. & Ewers, R.M. 2014. Edge effects disrupt vertical stratification of microclimate in a temperate forest canopy. *Pacific Science* 68(4): 493–508.

Egbe, E.A., Chuyong, G.B., Fonge, B.A. & Namuene, K.S. 2012. Forest disturbance and natural regeneration in an African rainforest at Korup National Park, Cameroon. *International Journal of Biodiversity and Conservation* 4(11): 377–384.

Fermon, H., Waltert, M. & Mühlenberg, M. 2003. Movement and Vertical stratification of fruit-feeding butterflies in a managed West African Rainforest. *Journal of Insect Conservation* 7: 7-19.

Fermon, H., Waltert, M., Larsen, T.B., Dall'Asta, U. & Mühlenberg, M. 2000. Effects of forest management on diversity and abundance of fruit-feeding Nymphalid butterflies in South-Eastern Côte d'Ivoire. *Journal of Insect Conservation* 4: 173-189.

Gintoron, C.S. & Abang, F. 2014. Composition of Fruit-Feeding Butterflies (Lepidoptera: Nymphalidae) in a Peat Swamp Forest, Kota Samarahan, Sarawak. *Serangga*, *19*(1), 1-17.

Gintoron, C.S. & Abang, F. 2021. Temporal diversity of the Nymphalids in Kubah National Park, Sarawak, Malaysia. *Tropical Natural History* 21(2): 285-298.

Gupta, H., Tiwari, C. & Diwakar, S. 2019. Butterfly diversity and effect of temperature and humidity gradients on butterfly assemblages in a sub-tropical urban landscape. *Tropical Ecology* 60(1): 150–158.

Hamer, K.C., Hill, J.K., Benedick, S., Mustaffa, N., Sherratt, T.N., Maryati, M. & Chey, V.K. 2003. Ecology of butterflies in natural and selectively logged forests of Northern Borneo : The Importance of habitat heterogeneity. *Journal of Applied Ecology* 40(1): 150-162.

Hammer, Ø., Harper, D.A.T. & Ryan, P.D. 2001. *PAST:* Paleontological Statistics Software Package for Education and Data Analysis (Version 1.96).
https://past.en.lo4d.com/windows [1 January 2010]

Hazebroek, H.A. & Abang Morshidi, A.K. 2000. *National Parks of Sarawak*. Sabah: Natural History Publications (Borneo), Kota Kinabalu.

He, Z., Liu, J., Wu, C., Zheng, S., Hong, W., Su, S. & Wu, C. 2012. Effects of forest gaps on some microclimate variables in Castanopsis kawakamii natural Forest. *Journal of Mountain Science* 9: 706-714.

Hill, J.K., Hamer, K.C., Dawood, M.M., Tangah, J., Chey, V.K. 2003. Rainfall but not selective logging affect changes in abundance of a tropical forest butterfly in Sabah, Borneo. *Journal of Tropical Ecology* 19: 35-42.

Houlihan, P.R., Harrison, M.E. & Cheyne, S.M. 2013. Impacts of forest gaps on butterfly diversity in a Bornean peat-swamp forest. *Journal of Asia-Pacific Entomology 16*(1): 67-73.

Idris, M.I., Ruslan, I.M., Gintoron, C.S. & Ghazali, R.I. 2021. Diversity of macromoths (Lepidoptera: Heterocera) in Perlis State Park, Kedawi Region, Malaysia: New Distributional record of noctuid. *Serangga* 26(2): 82-96.

Kenzo, T., Inoue, Y., Yoshimura, M., Yamashita, M., Tanaka-Oda, A. & Ichie, T. 2015. Height-related changes in leaf photosynthetic traits in diverse Bornean tropical rain forest trees. *Oecologia* 177: 191-202.

Kumar, P., Devi, R. & Mattu, V.K. 2016. Diversity and abundance of butterfly fauna (Insecta: Lepidoptera) of Subalpine area of Chanshal Valley of District Shimla (Himachal Pradesh). *Journal of Entomology and Zoology Studies* 4(4): 243-247.

Loaiza, J.R., Dutari, L.C., Rovira, J.R., Sanjur, O.I., Laporta, G.Z., Pecor, J., Foley, D.H., Eastwood, G., Kramer, L.D., Radtke, M. & Pongsiri, M. 2017. Disturbance and mosquito diversity in the lowland tropical rainforest of central Panama OPEN. *Scientific Reports* 7(7248): 1-13.

Lourenço, G.M., Luna, P., Guevara, R., Dáttilo, W., Freitas, A.V.L. & Ribeiro, S.P. 2020. Temporal shifts in butterfly diversity: responses to natural and anthropic forest transitions. *Journal of Insect Conservation* 24: 353-363.

Martins, L.P., Araujo Junior, E. da C., Martins, A.R.P., Duarte, M. & Azevedo, G.G. 2017. Species diversity and community structure of fruit-feeding butterflies (Lepidoptera: Nymphalidae) in an Eastern Amazonian forest. *Papeis Avulsos de Zoologia* 57(38): 481–489.

Muscolo, A., Bagnato, S., Sidari, M. & Mercurio, R. 2014. A review of the roles of forest canopy gaps. *Journal of Forestry Research* 25(4): 725–736.

Nakamura, A., Kitching, R.L., Cao, M., Creedy, T.J., Fayle, T.M., Freiberg, M., Hewitt, C.N., Itioka, T., Koh, L.P., Ma, K., Malhi, Y., Mitchell, A., Novotny, V., Ozanne, C.M.P., Song, L., Wang, H. & Ashton, L.A. 2017. Forests and their canopies: Achievements and horizons in canopy science. *Trends in Ecology and Evolution* 32(6): 438-451.

Ojianwuna, C.C. 2015. Climatic variables as factors affecting diversity and abundance of butterflies in Okomu National Park, Edo State, Nigeria. *Journal of Natural Sciences Research* 5(2): 70-76.

Otsuka, K. 1988. *Butterflies of Borneo*. Tokyo: Tobishima Corporation.

Pardonnet, S. 2010. *Effect of tree-fall gaps on fruit-feeding Nymphalidae assemblages in a Peruvian rainforest*. Sweden: Linköpings Universitet.

Pertiwi, R.A.P., Sugiyarto, Budiharjo, A. & Nayasilana, I.N. 2020. Diversity of butterflies (Lepidoptera) in Mount Bromo Forest area with special purpose (Fasp), Karanganyar, Central Jawa. *Zoo Indonesia* 29(2): 166-176.

Roznik, E.A., Sapsford, S.J., Pike, D.A., Schwarzkopf, L. & Alford, R.A. 2015. Natural disturbance reduces disease risk in endangered rainforest frog populations OPEN. *Scientific Reports 5*(13472): 1-11.

Schulze, C.H., Linsenmair, K.E. & Fiedler, K. 2001. Understorey versus canopy-patterns of vertical stratification and diversity among lepidoptera in a Bornean Rainforest. *Plant Ecology* 153: 133-152.

Skarped, L. 2014. Vertical stratification and species composition of Nymphalidae butterfly assemblages in tree-fall gaps and understory in Madidi National. Bachelor's thesis, Linköping University, Sweden.

Stork, N.E., & Grimbacher, P.S. 2006. Beetle Assemblages from an Australian Tropical Rainforest show that the canopy and the ground strata contribute equally to biodiversity. *Proceedings of the Royal Society B*, 273: 1969-1975.

Terborgh, J., Huanca Nuñez, N., Feeley, K. & Beck, H. 2020. Gaps present a trade-off between dispersal and establishment that nourishes species diversity. *Ecology* 101(5): e02996.

Tsukada, E. 1991. *Butterflies of the South-East Asian Islands Vol V: Nymphalidae (II)*. Tokyo: Azumino Butterflies Research Institute

Whitworth, A., Villacampa, J., Brown, A., Pillco Huarcaya, R., Downie, R. & Macleod, R. 2016. Past human disturbance effects upon biodiversity are greatest in the canopy; A case study on rainforest butterflies. *PLoS ONE* 11(3): 1-20.

Widhiono, I. 2015. Diversity of butterflies in four different forest types in Mount Slamet, Central Java, Indonesia. *Biodiversitas* 16(2): 196-204.