The effect of habitat type and month on variation in community structure of fruit and frugivorous *Lepidoptera* in a tropical lowland forest landscape

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I certify that all material in this thesis which is not my own work has been identified and that any material that has previously been submitted and approved for the award of a degree by this or any other University has been acknowledged.

Eleanor
Signature: ……………………………………

Abstract

Tropical rainforests are one of the most diverse biomes on the planet and provide vital ecological services, including climate regulation through carbon sequestration. Borneo has incredibly high biodiversity that is under threat due to anthropogenic pressure, which leads to widespread deforestation due to mining, logging and the conversion of land to plantations. Protecting this biodiversity, as well as documenting and monitoring it to inform conservation strategies, are of great priority. This study centres on the unprotected Rungan Forest Landscape in Central Kalimantan Province, Indonesian Borneo. This lowland forest is a mosaic of different habitats, including peat swamp forests (Low Pole), the sandy soil heath forest (Kerangas) and a transitional forest between the two (Mixed Swamp). Peatlands are relatively well studied and are known to be a key habitat for critically endangered species such as orangutans (*Pongo pygmaeus*) as well as storing large quantities of carbon. Lowland Kerangas habitats, on the other hand are less well studied and, unlike peat forest, are currently not represented in any protected areas, despite its potential to harbour a rich and unique biodiversity. High heterogeneity in the Rungan landscape is hypothesised to allow it to support higher biodiversity than expected from peat swamp or Kerangas by itself, due to habitat complementarity, but this has not yet been tested. Here, I investigate this by studying spatial and temporal variation in the community of frugivorous *Lepidoptera* and their fruit resources. Using ground fruit surveys and baited *Lepidoptera* traps, 17 plots of three different habitats (Kerangas, Mixed Swamp and Low Pole) were surveyed monthly for five consecutive months between April and August 2019. In chapter 2 I use this data to test whether there are significant differences in frugivorous *Lepidoptera* abundance, richness and diversity between the habitat types and months and whether this correlates with variation in fruit abundance, richness and diversity. I show that there are significant differences in: fruit abundance and diversity; butterfly abundance; and moth abundance and species richness. I also show that there was no correlation between *Lepidoptera* abundance, richness and diversity with fruit abundance, richness and diversity. In chapter 3 I use the same data set to test whether species composition of *Lepidoptera* and fruit differs between the habitats. Secondly, I test whether similarity in *Lepidoptera* species composition among sample sites correlates with similarity in fruit species composition among sample sites. Thirdly, I test for spatial correlation in species composition regardless of habitat. I show that species composition of *Lepidoptera* and fruit differs between the habitats and has a correlation between them. Finally I show there is spatial correlation within the study. Temporal variation in abundance, richness and diversity over the five study months indicates that further study is required to identify the drivers of this, for example seasonality, which may lead to asynchrony in resource availability among the habitats, providing a further source of complementarity. Further, it is noted that among *Lepidoptera*, the results are not always consistent between moths and butterflies and this raises questions about assumptions underlaying the use of ‘indicator taxa’, such as butterflies. Using this study as a baseline for community structures across several habitats and months, future surveys will be able to quickly detect any changes due to any external pressures like mining or fragmentation due to logging. Being able to quickly identify the effect of such threats on community structures can help guide protection measures. Together, the results indicate that the heterogeneous landscape could be leading to greater overall species diversity of the region, and therefore the principal of habitat complementarity stresses that all the habitats within the mosaic of the Rungan landscape should be protected.

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Chapter 1: General Introduction and Research Methods

1.1 Introduction

1.1.1 Loss of rainforests and biodiversity

Tropical rainforests only cover around 12% of the worlds ice-free terrestrial surface, yet support over two thirds of all terrestrial species (Barlow et al. 2018). It has been well documented that tropical rainforests are one of the most diverse biomes on the planet (Wilson 1992; Mayer and Primm 1997; Myers et al. 2000; Carvalho et al. 2014; Barlow et al. 2018; França et al. 2020) and support many endemic and endangered species (Morrogh-Bernard 2003; Beck and Chey 2008; Raes et al. 2009). As well as having a high diversity of flora and fauna, rainforests can provide fundamental human resources like timber, food and medicinal plants for local communities (Balick and Mendelsohn 1992; Peluso 1992). On a global scale, tropical rainforests provide critical ecological services such as climate regulation through carbon sequestration, which influences the exchange of greenhouse gases between terrestrial environments and atmospheric environments (Alamgir et al. 2016; Fu et al. 2018). In fact, conserving tropical rainforests is thought to be one of the most effective ways to mitigate against the current threats of global warming (IPCC 2007; Harrison 2013). Despite scientific recognition of the importance of these ecosystems and the known negative impacts to biodiversity (Bawa and Seidler 1998), increasing pressures from anthropogenic development has, and is continuing to cause large scale deforestation (Geist and Lambin 2001; Curran 2004; Lohani et al. 2020). It has been shown that 30% of Borneo's rainforests were destroyed between 1973 and 2012 (Gaveau et al. 2014). This is alarming, as maintaining high biodiversity is vital to ecosystem functioning and ultimately the provision of ecological services vital to human life, which has high economic value (Gamfeldt et al. 2008).

Biodiversity is also an essential component of ecosystem multifunctionality, whereby species contribute different functions due to their unique physical and behavioural characteristics (Lohbeck et al. 2016). Alongside this, habitat loss can lead to various species becoming extinct, which could potentially trigger ecological cascades of further extinctions if keystone species are lost (Mills et al. 1993; Brook et al. 2008). However, this forest loss, despite seeming a major threat, is still prevalent to this day and Cushman et al. (2017) has predicted that these high rates of forest loss will continue. Borneo has had one of the highest rates of forest loss globally (Cushman et al. 2017), despite its status as a biodiversity hotspot (Myers et al. 2000; Mittermeier et al. 2005). By 2012 only 12% of the lowland forests remained intact (Gaveau et al. 2014). This deforestation is mainly owed to human pressures such as mining, logging and the conversion of forest to plantations for products like palm oil (Carlson et al. 2012; Curran et al. 2004; Wilcove 2013; Abood 2014). Due to limited knowledge on the full extent of future forest loss and the response of species inhabiting these areas, immediate surveys are critical to determine the biodiversity present and the best areas to conserve to maintain high biodiversity. This has never been more prevalent as, not long after the study period of the current study, unprecedented forest fires were documented throughout Southeast Asia, including Borneo. Increasing frequencies of extreme climatic events alongside ongoing threats of habitat loss are known to threaten biodiversity and ecosystem functioning by altering fundamental biological processes (Lamarre et al. 2020).

1.1.2 Introduction to lowland forest habitat types

Indonesian Borneo’s lowland forests are dominated by peat swamps and in Southeast Asia the impacts of forest loss in tropical peat swamps are poorly understood (Houlihan et al. 2013). Tropical peatland is one of the most threatened peatland habitats despite it being the most biodiverse of all peatland environments (Page et al. 2006; Yule 2010; Turetsky et al. 2015). Peat itself is defined as ‘organic matter derived from vegetation having 25% or less inorganic matter on a dry basis’, while peatlands are ‘wetland ecosystems that are characterised by the accumulation of organic matter, which is produced and deposited at a greater rate than it is decomposed, leading to the formation of peat’ and therefore these landscapes are usually supported by a high-water table (Paavilainen and Päivänen 1995). Fire and the conversion of land to plantations are some of the threats that lead to deforestation in these lowland forest landscapes (Harrison et al. 2009). Tropical peatlands are vital for many reasons including, but not limited to, fire and flood prevention, carbon sequestration, cultural significance and the provision of resources for local communities (Page & Rieley 1998, Page et al. 2011, MoEF 2018, Harrison and Rieley 2018). It has been reported that 33% of bird species and 45% of mammal species recorded in tropical peat swamp forests have a near threatened or higher IUCN Red List status, reinforcing the notion that peatland forests are an important area to focus conservation efforts (Posa et al. 2011). There have been few in depth studies of biodiversity in peatland forests and of those, many focus on more charismatic species such as orangutans (*Pongo pygmaeus*). Therefore, there is a need to further investigate biodiversity in peat-based habitats in order to construct and implement appropriate protective measures (Harrison and Rieley. 2018). Also, within Indonesian Borneo’s lowland forests, tropical heath forests are even more understudied than lowland peat forests (Maimunah et al. 2019). Tropical heath forests are characterised by ‘a dominant sand layer with a thin organic horizon on top’ and due to nutrient poor sandy soil, has previously been considered to be a low diversity habitat (Maimunah et al. 2019). However, increasingly more studies are finding that heath forests in Central Kalimantan contain high biodiversity with important endemic fauna and flora and thus should be considered more of a conservation priority (Morrogh-Bernard et al. 2003, Maimunah et al. 2019). Borneo’s lowland forests are a mosaic of heath forests and peat swamp forests, which make it an interesting region to investigate the effects of habitat type on biodiversity.

1.1.3 Biodiversity and Habitat Complementarity

Research that aids in the protection of biodiversity could be one of the potential solutions to the threat of deforestation and biodiversity loss. Conservation could focus on understanding and protecting habitats with the highest biodiversity to mitigate against local extinctions and population declines (Mokany et al. 2020). There are many factors that affect the biodiversity of a region, otherwise known as gamma diversity (Whittaker 1972). Firstly, diversity of the region is split into alpha and beta diversities respectively, alpha being the diversity found at a specific locality whilst beta diversity is the change of diversity between two localities (Whittaker 1960; Arellano and Halffter 2003). Therefore, as each locality can have different diversities, it is important to investigate the influence of a heterogeneous habitat landscape on diversity. If a landscape has various habitats within a region, it has been suggested that there will be more available niches leading to a heterogenous landscape being able to potentially support a higher diversity when compared to a homogenous landscape (Kerr and Packer 1997; Benton et al. 2003; Hill et al. 2003). Like many landscapes around the world, there are many different habitat types within a rainforest (Andrew et al. 2020; Vu and Vu 2001), suggesting that rainforests generally have high heterogeneity that could lead to high biodiversity. The diversity of an area could also be affected by the abundance of species and their movements across different habitats throughout the annual cycle. Consequently, various factors of species community structure are important to investigate to comprehend the strategies required to conserve the highest proportion of diversity in a particular area. The habitat complementarity principle is a well-established conservation tool that aims to protect the highest possible diversity within an area (Williams and Manne 2001). Habitat complementarity is present when a network or mosaic of various habitat types support different and complementary compositions of species (Justus and Sarkar 2002; Dunlop 2013). There has always been great importance placed on understanding the ecological processes within an area in order to be able to effectively conserve and protect it. Therefore, without an understanding on the effects of ecological factors like habitat type, seasonality, drivers of populations, and variation in patterns of species composition on the overall biodiversity of an area, it is unlikely that an effective conservation strategy can be actioned to develop and preserve biodiversity or prevent potential extinction cascades.

1.2.4 Introduction to the study

Within Borneo, between the Rungan and Kayayan rivers, lies the Rungan Landscape, a stretch of 140,000 hectares of relatively intact, but so far unprotected, forest (Harrison et al. 2010), see Figure 1b. This area has yet to be the focus of any formal conservation efforts but is of great ecological interest due to its high biodiversity and population densities of endangered species, such as orangutans, which is surprising for the low productivity of the sandy-soil forests found within the landscape (Morrogh-Bernard et al. 2003). The Rungan landscape is of high value not only because of the high abundance of protected ulin (Borneo ironwood, *Eusideroxylon zwageri*) trees, but also because it hosts a range of species like clouded leopards (*Neofelis nebulosa*) and rhinoceros hornbills (*Buceros rhinoceros*), which are at risk of extinction (Harrison et al. 2010). This highlights the importance of conserving this landscape in order to protect these at-risk species and the overall high biodiversity of the Rungan. This landscape has high heterogeneity and previous studies have found this could be the reason for the high diversity found in this landscape despite it previously being regarded as comprising of poor-quality habitats (Morrogh-Bernard et al. 2003). The landscape contains habitats such as peat swamp forests (Low Pole), sandy soil heath forests (Kerangas) and transitional forests between the two (Mixed Swamp). Peatlands are relatively well studied and are known to be a key habitat for critically endangered species such as orangutans as well as storing large quantities of carbon (Morrogh-Bernard et al. 2003; Page et al. 2011; Harrison and Rieley 2018). Lowland Kerangas habitats, on the other hand, are less well studied and, unlike peat forests, are currently not represented in any protected areas, despite the potential for these habitats to harbour rich and unique biodiversity (Morrogh-Bernard et al. 2003; Maimunah et al. 2019). It is therefore hypothesised that the high heterogeneity of the Rungan landscape allows it to support higher biodiversity than expected from Low Pole, Kerangas or Mixed Swamp habitats independently, due to habitat complementarity, but this has not yet been tested. While there have been some studies within this area that have started to investigate the biodiversity and key species that inhabit the Rungan, there are currently no studies that have investigated the effect of fruit availability and habitat variation on the species structure of *Lepidoptera*. Here, I investigate this by studying the spatial and temporal variation in frugivorous *Lepidoptera* communities and their fruit resources. Identifying the effects of habitat type and month on *Lepidoptera* community structure could enable identification of how other, potentially critically endangered, species could be impacted by biodiversity loss and/or other anthropogenic influences by using *Lepidoptera* as bioindicators. Furthermore, it would lead to a good basis of understanding of community ecology in the forest to help advise future protection and conservation strategies. Borneo Nature Foundation (BNF) have completed baseline biodiversity surveys in this area and one of their primary goals align with the aims of the research project: ‘To understand how and why forest biodiversity varies over space and time, in response to both natural events and, particularly, human activities (monitoring)’ (Borneo Nature Foundation 2021). Therefore, the aim of the current study is to create a baseline dataset of frugivorous *Lepidoptera* and fruit compositions and community structures to enable future surveys to monitor any changes to species compositions or community structures in response to biodiversity loss and/or other anthropogenic influences.

1.1.5 Study System

1.1.5.1 Fruit

When looking at a rainforest ecosystem it is important to consider phenology and the variation of important resources like fruit in a landscape. Phenology is the study of periodic flora and fauna life cycle events that include the fruiting of trees (Harrison et al. 2016). Fruit is an important element of a rainforest’s ecosystem and fleshy fruit in particular is an integral diet component of many fauna (Lashley at al. 2014). Therefore, it is vital to understand the factors that drive these events as it could influence other species within the ecosystem. Furthermore, it could also impact future surveying and the ecological understanding of an area. For example, if fruiting variations are disregarded, it would be difficult to rule out that the variation in species community structure is driven by fruit. However, even if fruit is investigated, without understanding the variation in fruiting events over time an important element could be missed which could affect how species structure is viewed within an area. This is particularly important as the timing of fruiting is not always consistent and could be influenced by variables such as climatic seasonality, in particular precipitation (Hamann 2004; Cannon 2007). Fruits produced by trees are vital to support not only the tree itself via reproductive events, but also a vast array of species that may rely on trees for nutrition and survival (Harrison 2005; Newbury et al. 2006; Sánchez et al. 2012). Various fruit feeding species may base their movements on the distribution of fruiting trees (Caillaud et al. 2010) and fruit availability has been shown to influence insects, tropical birds and frugivorous bats (O'Donnell and Dilks 1994; Herrera et al. 2005; Sánchez et al. 2012; Basset et al. 2021). It is also important to consider that high habitat heterogeneity in an area may provide fruit at different times within the year, either because they are dominated by different tree species that fruit in different seasons and/or because the same tree species may fruit at different times of the year in different habitats due to variation in abiotic conditions (Harrison et al. 2007). Therefore, there is a need to understand how habitat complementarity, temporal variation, the movement of species and the drivers of population sizes could impact species composition within an area. Yet, understanding the influence of temporal variation brings a distinct set of challenges to future forest restoration. This is due to the unpredictability of the synchronised flowering and consequent mass fruiting of many forest trees in Borneo (Kettle et al. 2010). With this in mind, this survey in the Rungan is the first survey in the landscape to study fruit and its links to frugivorous *Lepidoptera* between different habitat types.

1.1.5.2 *Lepidoptera*

Lepidoptera, like all insects, play a vital role in many ecosystem processes such as herbivory, pollination, seed predation and the provision of nutrients to other organisms within the ecosystem (Janzen 1987; Bond 1994; Tangah et al. 2004). This highlights the importance of *Lepidoptera* within an ecosystem and the need to conserve and protect them against threats such as habitat loss. In addition, an abundance of surveys use *Lepidoptera*, such as butterflies, as bioindicators to represent potential patterns across other taxa within the same environment (Molleman et al. 2006; Kerr et al. 2008; Bonebrake et al. 2010; Whitworth et al. 2018). Surveying all taxa within a landscape is both time consuming and costly, so the use of *Lepidoptera* as indicators provides a quick and cost-effective way of determining the response of ecosystems to various environmental and ecological variables (Porath and Aranda 2020). This in turn helps accelerate basic biodiversity research which aids in advising future conservation and management strategies within an area (Hairah et al. 2018). *Lepidoptera* have often been used to infer the community structure and responses of other species within an ecosystem to disturbance (Howard et al. 1998; Lawton et al. 1998). They are also useful indicators to understand the effects of temporal variation, habitat type and habitat change on species due to their short life cycles allowing them to respond quickly to environmental change (Bonebrake et al. 2010). *Lepidoptera* are therefore an ideal candidate to infer the diversity of an area as generally if their diversity is high it can be assumed that overall diversity, across multiple taxa, is also high (Kitching et al. 2002; Summerville et al. 2004). However, environmental factors that control phenology and temporal variation in tropical insect communities are poorly understood. This needs to be addressed to ensure researchers can predict and mitigate against the potential consequences of these influences, for example climate change, on tropical insect communities to assess their long-term persistence (Valtonen et al. 2013). Frugivorous *Lepidoptera*, like *Nymphalidae*, are easily surveyed by using traps with fruit bait (Daily and Ehrlich 1995; DeVries and Walla 2001; Houlihan et al. 2010, Sousa et al. 2019). The current study aims to evaluate the drivers of frugivorous *Lepidoptera* populations by investigating the influence of adult food availability. It is important to note that the larvae of *Lepidoptera* depend on host plants, which is important to keep in consideration throughout the study as larval host plants have been found to drive some species of *Lepidoptera* (Braschler and Hill 2007; Tiple et al. 2011; Forister et al 2015). Previous evaluation on indicators in the tropics showed that only a few taxonomic groups can be effective predictors of others, this included trees for fruit and fruit feeding butterflies with an 83% explanation (Schulze et al. 2004). To successfully prioritise areas for conservation, there needs to be sufficient information on the diversity of species in threatened habitats, as well as open access to these resources. It is imperative that quicker ways to estimate the condition of selected habitats are developed, such as the selection of indicator taxa, use of rapid biodiversity assessments based on morphospecies, and analysis of community structure (Kerr et al. 2008). If fruit does influence frugivorous *Lepidoptera* patterns, then surveys of fruit could be used to indicate the potential presence of *Lepidoptera* species and perhaps overall habitat quality (Bonebrake et al. 2010). Focusing on one group, such as fruit, that involves less invasive and complicated methods and equipment could be one way of creating more immediate and effective biodiversity assessments to aid conservation strategies.

1.1.6 Study Aims

This study aims to gain a deeper understanding of fruit and *Lepidoptera* patterns in a heterogeneous landscape in Borneo, to address a key knowledge gap of frugivorous *Lepidoptera* and fruit patterns in the Rungan landscape. The habitats that will be the focus of this study include Low Pole, a peat swamp habitat, Kerangas, a heath habitat and Mixed Swamp characterised as a transitional habitat between Low Pole and Kerangas. Knowledge of the effects of this mosaic of habitats on fruit and frugivorous *Lepidoptera* over time could aid in future conservation management strategies by providing a proven indicator that responds rapidly to habitat change. This would create a foundation for ongoing research and develop an accessible method of assessing biodiversity for local communities and research bodies to enable continuous monitoring. It is also important to understand the ecological drivers of populations, like *Lepidoptera,* as this could enable a better understanding on the conservation methods that will aid in the protection of biodiversity, including species at risk of extinction. This study will be the first of its kind in the Rungan Landscape and will consider the effect of habitat type and temporal variation on fruit and frugivorous *Lepidoptera* community structures in a heterogenous landscape. This will therefore highlight factors that potentially explain their adjacency to other endangered species.

To help further understand this topic, three questions will be asked in each chapter. For chapter 2, the first two questions asked are: How does fruit and *Lepidoptera* abundance, richness and diversity change over months and between habitats? These questions will allow future research to further explore the patterns and correlations of fruit and frugivorous *Lepidoptera* diversity across different habitats and months. Investigating how temporal patterns vary between habitats could help ecologists and conservationists understand whether habitat complementarity is at play in the diverse landscape and if this could potentially support a more biodiverse community of fruit and *Lepidoptera*. Since the study focuses on frugivorous *Lepidoptera*, it could be assumed that fruit abundance, richness and diversity could drive *Lepidoptera* abundance as these insects mainly feed on fermented fruits (Sousa et al. 2019). Therefore, the third question will ask whether *Lepidoptera* match patterns of those observed in fruit, specifically abundance, richness and diversity? However, it is important to also consider how the composition of fruit and *Lepidoptera* are impacted by habitats, as even if habitats all have similar species diversity, richness and abundance, they may include different composition of species. This could impact how we view diversity within the landscape as if each habitat supports different species, then the overall gamma diversity will be higher (Whittaker 1972). Therefore, in chapter 3 the first question is: does habitat type influence species composition? Question 2 starts to link *Lepidoptera* and fruit together to investigate whether fruit composition is correlated with *Lepidoptera* composition. Question 2: Is similarity in fruit composition correlated positively with similarity in *Lepidoptera* composition? Finally Question 3 asks whether closer geographical plots affects similarity in species composition? This tests for spatial correlation in species composition regardless of habitat. Ultimately, the aim of the study is to gain understanding of the effect of habitat type and temporal variation on community structure of frugivorous *Lepidoptera* and fruit in a tropical forest landscape and how this could inform future conservation strategies. If the heterogenous landscape shows indications of habitat complementarity this could highlight the importance of protecting and conserving all habitats within the Rungan landscape.

1.2 Research Methods

1.2.1 Study Site

This study was carried out in the Mungku Baru Education forest, also known as Kawasan Hutan Dengan Tujuan Khusus (KHDTK) in Indonesian. This is a 4,910 hectare plot in the Rungan Landscape (Figure 1b) which is located in the south of Borneo, Indonesia (Figure 1a). The Rungan Landscape itself is a stretch of 140,000 hectares of mixed forest habitats between the Kahayan and Rungan rivers. Managing the education forest, the access transects and base camp within it is the University Muhammadiyah Palangka Raya. This study site comprises of a mosaic of habitats that is dominated by peat and heath forest types (Figure 1c). The focus of this study includes three habitats: Kerangas, a sandy soil heath forest (Figure 2a); Low Pole, a peatland forest (Figure 2b) and Mixed Swamp a transitional forest between Kerangas and Low Pole (Figure 2c). Habitat type was determined through ground truthing surveys previously carried out in the landscape and through personal observations. Kerangas tends to have low tree species diversity that is dominated by *Syzygium sp* and *Semecarpus sp* (KHDTK Report 2016-2017), with a generally porous white sand as the majority of the soil structure. Kerangas is typically dry underfoot with no large pools of water and can have a very thin layer of peat (Figure 2a). Low Pole on the other hand is identified as having a permanent presence of large pools of water, typically seen as channels through the habitat (Figure 2b). The canopy in Low pole is typically a lot lower than the other two habitats and Low Pole tends to dominate the study site despite it being less prominent within the wider landscape (Figure 1b). Finally, Mixed Swamp tends to be classified as a transitional habitat between Low Pole and Kerangas, with a range of canopy hights and an irregular peat distribution (Figure 2c).

1a)


CAMBODIA
Phnom Penh
Ho Chi Minh
Andaman Sea
Gulf of Thailand
SPRATLY ISLANDS
Mindoro
Palawan
MALAYSIA
Kota Bharu
Kuala Lumpur
BRUNEI
Bandar Seri Begawan
Celebes Sea
Borneo
Sumatra
Sulawesi
Pontianak
Java Sea
Jakarta
INDONESIA
Indian Ocean
Flores Sea
Banda Sea
Dili
TIMOR LESTE
Timor Sea

1b)


Indonesia
Rungan

1c)

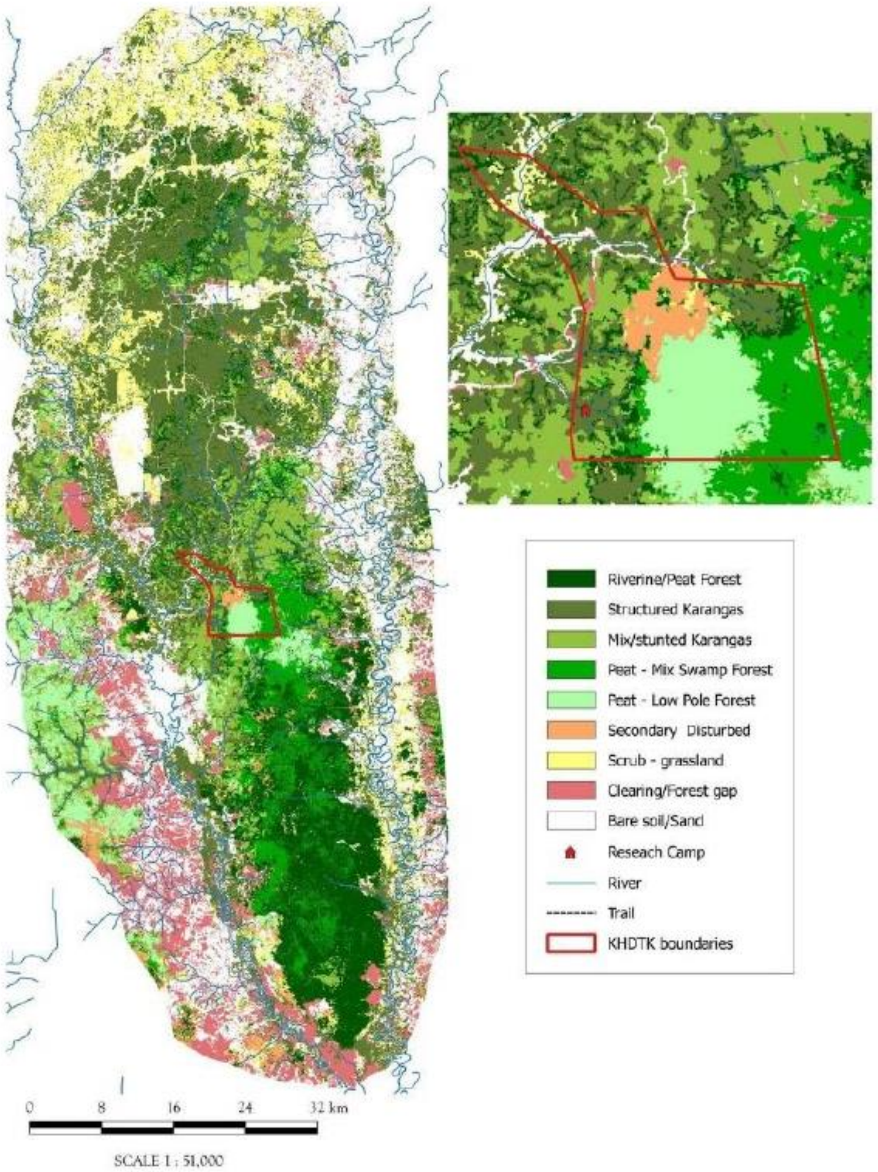


Figure 1: Map of a) the island of Borneo and the surrounding Indonesian and Malaysian islands (Image from Borneo Eco Tours), b) the islands of the archipelago of Indonesia (top left corner of the diagram), with the island of Indonesian Borneo highlighted in lighter green. The central focus on the image is the Indonesian region of the island of Borneo. The research sites of Borneo Nature Foundation (BNF) are highlighted in white with the Rungan Landscape indicated by the red pin. Image from BNF website. And c) The topograohy of the Rungan Landscape. Colours represent the different habitats and landscape. The red outline marks the boundaries of the Mungku Baru Education Forest. Map provided by BNF.

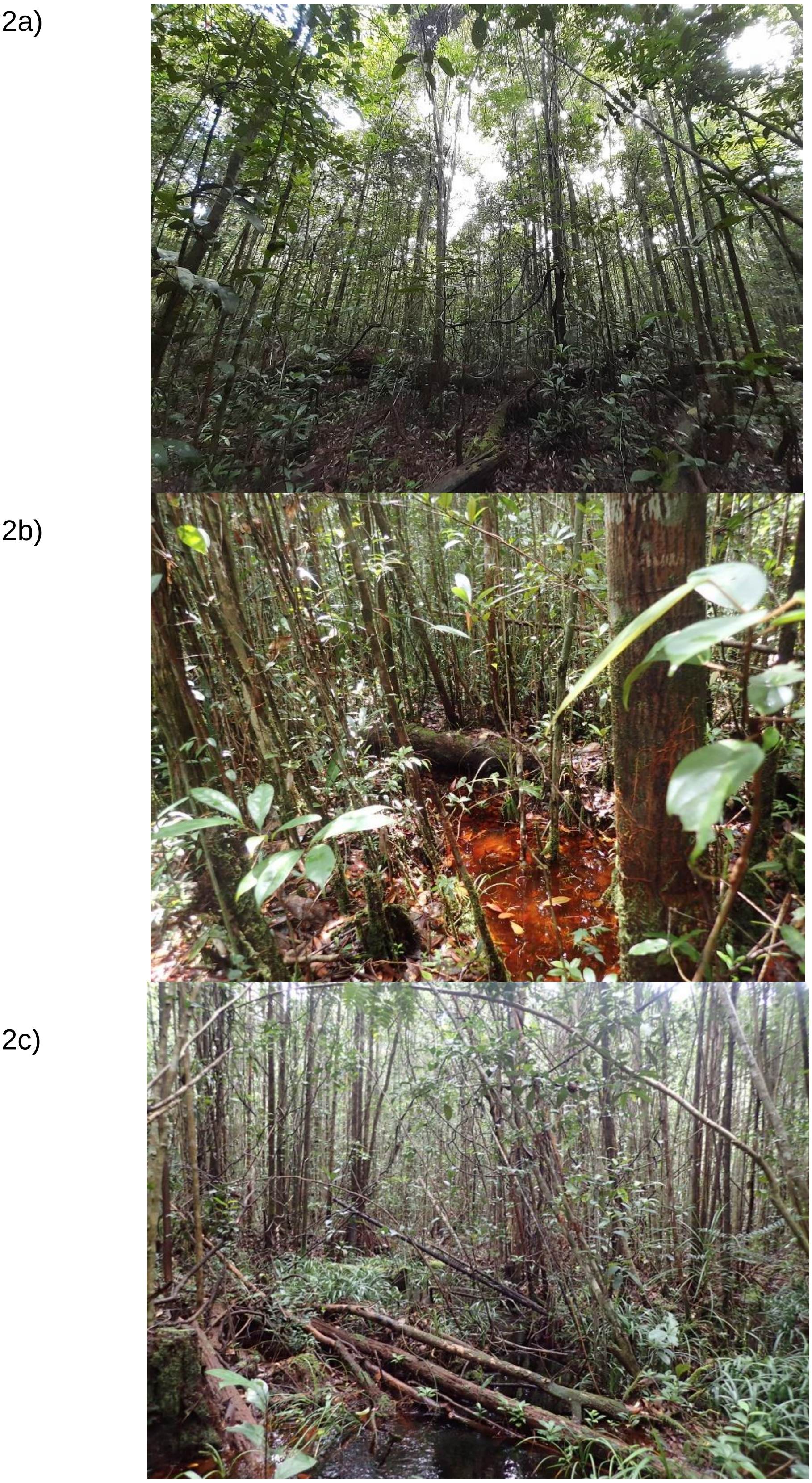


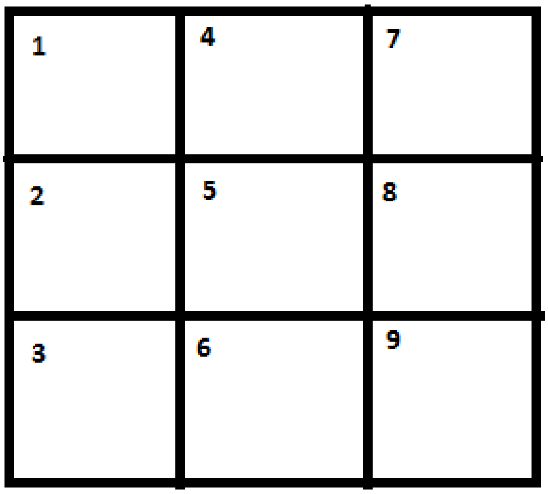
Figure 2: Photos of a) Kerangas habitat, b) Low Pole Habitat and c) Mixed Swamp habitat.

1.2.2 Data Collection

1.2.2.1 Choosing Plots

Thirty-two 30m x 30m plots have previously been established across the study site by the Borneo Nature Foundation (BNF) who work in collaboration with Universitas Muhammadiyah Palangkaraya to manage the site. The plots are continuously managed, so those used for this survey were chosen from these existing plots to ensure repeatability for future surveys. It was imperative to sample plots of the three different habitats (Kerangas, Mixed Swamp and Low Pole) during the same days with as many repeats as possible. Therefore, six plots of Kerangas, six plots of Mixed Swamp and five plots of Low Pole were chosen to be surveyed (17 plots in total) over the course of a month, see Figure 4 for plot location and appendix V for latitude and longitude of plots. Only five plots of Low Pole were chosen as it was not logistically feasible to include a sixth during this survey period. Plots were chosen as far apart from each other as logistically possible in order to reduce spatial autocorrelation (Kerr et al. 2008), see appendix VI for the distance between plots. The average distance between plots was 1445m with the minimum distance at 299m and the maximum distance at 3136m. The same 17 plots were surveyed every month in order to investigate how pattens of fruit and *Lepidoptera* changed during this time period (Figure 4). Within each month, six plots (five for Low Pole) were surveyed per week, (Figure 4). Week one surveyed the plots K1, K2, MS1, MS2, LP1 and LP2, with the letter corresponding to the habitat type (K= Kerangas, MS=Mixed Swamp and LP=Low Pole) and the number differentiating between different plots within the same habitat. Week two surveyed K3, K4, MS3, MS4, LP3, LP4 and week three K5, K6, MS5, MS6 and LP5 (Figure 4).

The 30m x 30m plots were further divided into nine subplots for ease of orientation within the plot when carrying out the fruit and *Lepidoptera* surveys (Figure 3). Subplot 1 always started in the North-West.



1	4	7
2	5	8
3	6	9

Figure 3: Diagram of the 30m x 30m plots and how it was divided into nine subplots. Subplot 1 always started in the North-West.

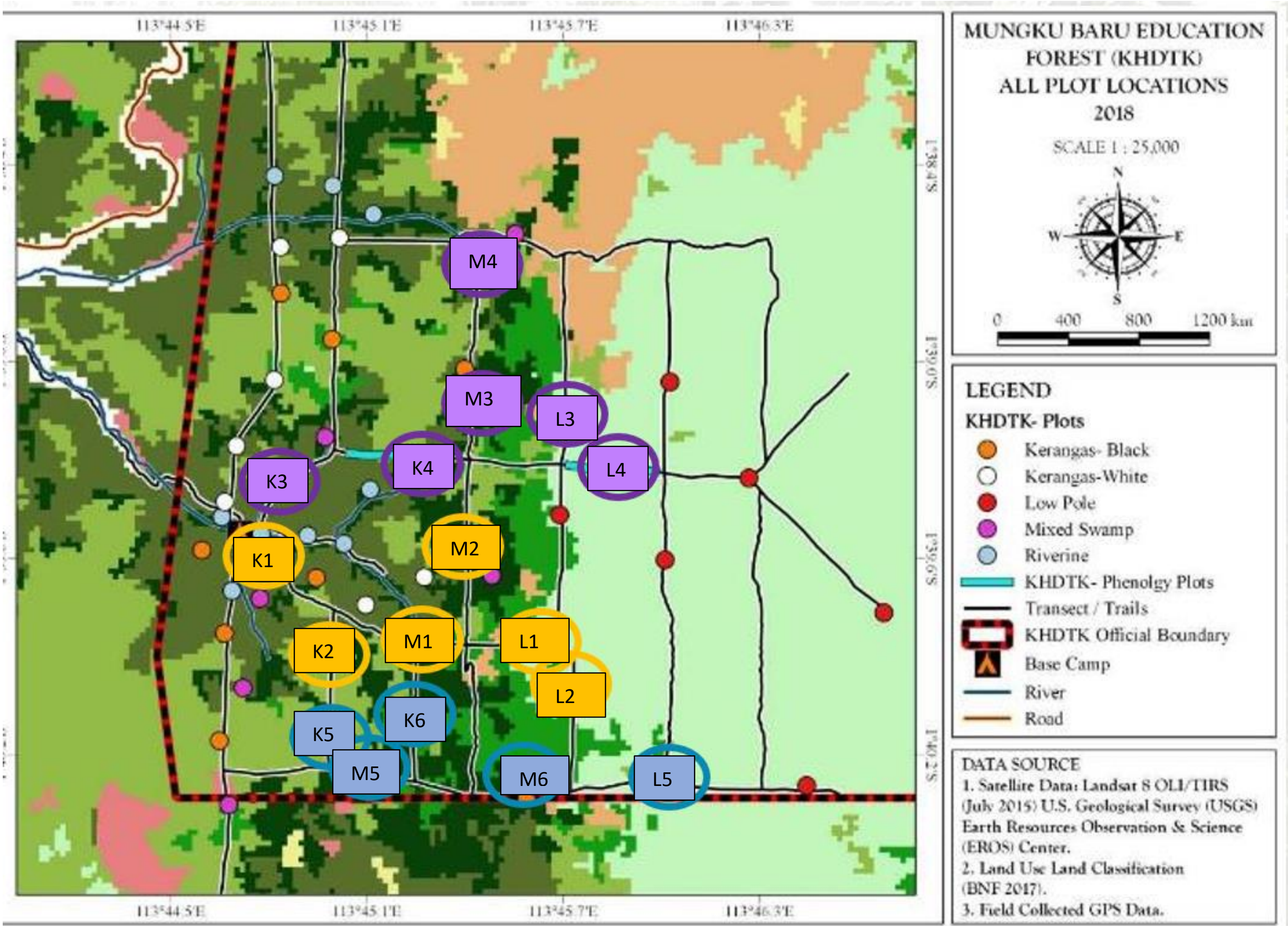


Figure 4: A map of the Mungku Baru Education Forest. Black lines represent transects and coloured boxes represent the plots used. The colour represents which week of the month each plot was surveyed with yellow: week one, purple: week two and blue: week three. Within each box, plots were given a code with the letters representing the habitat type and numbers differentiating between plots of the same habitat (K=Kerangas, MS= Mixed Swamp and LP= Low Pole).

1.2.2.2 Fruit Data Collection

The entirety of each plot was surveyed for fallen fruit every month. All six plots were surveyed within the same day at the start of each week to ensure conditions were the same. Ground fruit surveys were chosen over canopy surveys and fruit nets due to ground surveys being able to accurately estimate fruit biomass (Lashley et al. 2014) and represent the fruit present across the whole plot while being feasible to conduct alongside *Lepidoptera* surveys. Each survey would start in subplot 1 (Figure 3) with the research team of three members 5m apart walking slowly through every subplot in a straight line, scanning the ground 2.5m either side to look for fruit. Once fruit was spotted, either rotting or ripe, it was identified to a morpho code and the number of each code found in the plot was tallied and totalled. Every time a new fruit was found it was assigned a number and added to an ID guide of morpho codes. The first five individuals found of a new fruit would be measured (width and length with callipers), photographed, described, and added to a morpho code identification guide. This guide was then used for the remaining surveys in order to identify and classify fruit as the same, see appendix I. Fruit were assigned codes based on their appearance and so fruit that looked different would be given different codes, see example in Figure 5a and Figure 5b. If fruit looked extremely similar to others they would be cut in half to further help differentiate them (Figure 5a). Fruits were identified to morpho codes rather than species as the high diversity of fruit meant that it would have been difficult to classify them in the field to species level. To increase the reliability of the data one person classified and checked that the fruit was assigned the correct morpho code in each plot.

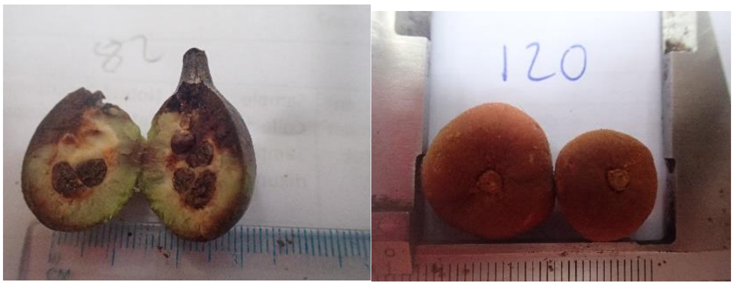

5a) 5b)

Figure 5: Image examples of a) morpho code 82 fruit cut in half to help with future identification, and b) morpho code 120, fruit were measured to help with future identification. A ruler is included for size reference and callipers were used for measuring. Fruit would be measured individually.

1.2.2.3 Lepidoptera Data Collection

18 large black Blendon *Lepidoptera* traps were set out each week to trap butterflies and moths. In each plot surveyed three butterfly traps were set up in a diagonal across the plot with at least 10m distance between them. Each trap, see Figure 6, was 40cm in diameter and 90cm tall with a rimmed plate suspended 2 inches from the bottom of the net. Each net was tied to a suitable branch, so it hung suspended 1m off the ground to the plate. A vertical zip along the side of the net allowed for *Lepidoptera* to be released. The traps were set out at the start of each week and left out for a total of five days. The number of days was determined by preliminary surveys, where after day five there was no increase seen in the number of individuals captured. After the five days traps were relocated to another set of six forestry plots and again after a further five days to another set of six forestry plots (following the weekly plan of plots described in section 1.2.2.2). This was then repeated monthly. Each trap was baited in order to attract butterflies and moths to the trap. 20 small bananas, 1tbsp sugar and 2 cups of local grape wine were mixed before leaving for the survey and was evenly spread between each of the 18 traps

and topped up daily as needed. This bait is known to be an olfactory attraction for butterflies which draws them to the nets to aid in trapping (Hughes et al. 1998). The nets were checked and bait refreshed each day within the five trapping days. Every 24 hours when the traps where checked each *Lepidoptera* individual within the net would be counted and identified. Butterflies were identified to species level by using a guide provided by BNF. The forewing and body length of butterflies were measured, with callipers. as well as their wings marked with a marker pen to identify whether the same individual revisited traps. Any marked butterflies in traps were subsequently recorded as a recapture. Any new species of butterfly found within the traps that were not previously mentioned in the BNF ID guide were measured, photographed and given a temporary code name and were then added into a separate ID guide created for this study, see appendix lll. Moths were treated similarly to butterflies when found in traps but were counted and identified to a morpho code rather than to species level. Moths have not previously been identified to species level within the survey area and so morpho codes were the most appropriate to use in a field setting with no ID guide. Each new moth found within the trap would be measured, photographed, and given its own individual code, see appendix ll. Moths were not marked due to the fragility of their wings.

Each ID guide that was created by the survey include code names, pictures, measurements, and descriptions of key visual features, see appendices l, ll and lll for code names and pictures.

Figure 6: Image of a large black Blendon butterfly trap used in the study baited with a mixture of bananas, sugar and local wine.

Chapter 2: How species diversity, richness and abundance changes over the months in the three habitats.

2.1 Abstract

Tropical lowland forest habitats are declining due to anthropogenic pressures such as the conversion of pristine rainforest to palm oil monocultures and natural events like forest fires. There is an immediate need to understand how species community structures are distributed within an intact forest landscape, like the Rungan Landscape, over time so that future surveys can efficiently identify any changes to community structure due to these pressures. This study centres on the unprotected Rungan Forest Landscape in Central Kalimantan Province, Indonesian Borneo. This lowland forest is a mosaic of different habitats, including the sandy soil heath forest known as Kerangas, a peatland forest known as Low Pole and a transitional habitat between the two called Mixed Swamp. High heterogeneity in the Rungan landscape is hypothesised to allow it to support higher biodiversity than expected from the habitats independently, due to habitat complementarity, but this has not yet been tested. Here, I investigate this by studying spatial and temporal variation in the community of frugivorous *Lepidoptera* and their fruit resources. Using ground fruit surveys and baited *Lepidoptera* traps, 17 plots of three different habitats were surveyed monthly for five consecutive months from April to August 2019. In chapter 2 I use this data to test whether there are significant differences in frugivorous *Lepidoptera* abundance, richness and diversity between the habitat types and months, and whether this correlates with variation in fruit abundance, richness and diversity. I show that: fruit abundance was influenced by an interaction between habitat and month; fruit diversity was influenced by habitat; fruit richness was not affected by habitat or month; butterfly abundance was influenced by month; butterfly

richness was not explained by either habitat or month; moth abundance and species richness were both influenced by habitat type and by month; and *Lepidoptera* diversity, both butterflies and moths, were not influenced by either month or habitat. I also show that there was no correlation between *Lepidoptera* abundance, richness and diversity with fruit abundance, richness and diversity. Temporal variation in abundance, richness and diversity over the five study months indicates that further study, with longer survey periods, is required to investigate the effect of seasonality, which may lead to asynchrony in resource availability among the habitats, providing a further source of complementarity. Further, it is noted that among *Lepidoptera*, the results are not always consistent between moths and butterflies and this raises questions about assumptions underlying the use of 'indicator taxa', such as butterflies. Finally, fruit abundance, richness and diversity were not found to drive frugivorous *Lepidoptera* abundance, richness or diversity and it is hypothesised that it is the caterpillar's food source, rather than adult food sources, that could be influencing *Lepidoptera* community structure. Therefore, further research that encompasses the whole of *Lepidoptera*'s life cycle would be needed to answer this knowledge gap in the Rungan Landscape. Together, the results overall indicate that the heterogeneous landscape could be leading to greater overall species diversity of the region, and therefore the principal of habitat complementarity stresses that all the habitats within the mosaic of the Rungan landscape should be protected.

2.2 Introduction

Lowland forest habitats in Indonesian Borneo are declining due to anthropogenic pressures such as the conversion of pristine rainforest to palm oil monocultures and natural events like forest fires and climate change (Geist and Lambin 2001; Curran 2004; Lohani et al. 2020). Lowland forests in Indonesian Borneo include peat swamp habitats (Low Pole), heath habitats (Kerangas) and transitional habitats between Low Pole and Kerangas (Mixed Swamp). Peat swamp habitats are vital globally for carbon sequestration and along with Kerangas, are important for local resources, income and culture (Page and Rieley 1998; Page et al. 2011; MoEF 2018; Harrison and Rieley 2018). Therefore, with the growing loss of lowland forests in Indonesian Borneo there is an important and immediate need to understand the biodiversity present within the landscape and if certain areas and/or habitats should be a priority for conservation efforts. In order to assess an area, baseline studies that investigate species diversity, richness and abundance within a landscape can be conducted. Having a baseline is important as when paired with future monitoring, any future changes to community structures due to future anthropogenic pressure can be detected more readily which can inform management of an area. The conservation of areas is expensive (Curran et al. 2004) and so surveys and management plans need to be assessed as quickly and as cost effectively as possible (Harrison et al. 2012). Focus on the quality of habitats and the biodiversity within these habitats could be a way to prioritise places to protect, as if all species depend on only one habitat type it could be argued that this habitat is an area of priority for conservation efforts. Using *Lepidoptera* as bioindicators for indices of community structure could also be a way to assess an area in a quick and cost effective way (Harrison et al. 2012). *Lepidoptera*, such as butterflies, are ideal bioindicators due to their short life spans which can show quick responses to environmental change (Bonebrake et al. 2010). Therefore, understanding how *Lepidoptera* patterns are affected by habitat and month would enable a preliminary understanding on how best to conserve heterogeneous forest landscapes, such as the Rungan, found in Borneo. However, mechanisms that structure tropical communities like moths and butterflies are still under-studied and poorly understood (Delabye et al. 2020). Droughts caused by El Nino are thought to drive the ecology of Bornean rainforests as they trigger synchronous fruiting events across Borneo which in turn causes faunal reproduction that sustains many populations (Curran et al. 2004). This suggests that fruiting could drive many populations of species and therefore it is vital to understand how or if fruit are driving population dynamics within an area. Phenology is the study of periodic flora and fauna life cycle events that include the fruiting of trees (Harrison et al. 2016). Phenology has previously been described as a ‘key adaptive trait in shaping species distribution’ (Chuine 2020). Therefore, monitoring phenology, such as the timing of tree fruiting, is vital to understand the distribution of *Lepidoptera* in this study site. It is also possible that if the forest is disturbed through human activities like logging that cause deforestation, then fruit production could change quickly in forest succession. This means that having a baseline of the fruits produced through various months in undisturbed habitat could help ecologists understand how certain activities affect the fruit produced in an area in future studies. Pairing fruiting patterns with information on how fruit feeding species, like *Lepidoptera*, may change due to fruit structure changes, would help identify whether a change or decrease in fruit abundance, richness and/or diversity would affect fruit feeding species within the forest. This would subsequently help ecologists to have a better understanding of shifts in wildlife quality (Lashley et al. 2014).

This study focuses on the Rungan Landscape, a majority Low Pole, Kerangas and Mixed Swamp lowland forest, within Central Kalimantan Province, Indonesian Borneo, Figure 1b. The study was carried out in the Mungku Baru Education forest, also known as Kawasan Hutan Dengan Tujuan Khusu (KHDTK), within the Rungan Landscape. Research in the Rungan landscape has not previously incorporated a multiple month survey focused on the effects of habitat type and month on fruit and frugivorous *Lepidoptera*. There is little information readily available about the drivers of *Lepidoptera* populations in this landscape and therefore it will be interesting to investigate whether fruit and *Lepidoptera* have similar patterns. For chapter 2, the first question asked is: How does fruit abundance, richness and diversity change over months and between habitats? This study hypothesises that fruit abundance, richness and diversity will change over months and between habitats and that there will be variation in temporal patterns between habitats. This prediction is due to the theory of habitat complementarity, which describes how different habitats provide resources over different periods of time to avoid competition with other species (Dunlop 2013), which in turn supports species that feed on these resources. The second question asked is similar to the first but looks at how *Lepidoptera* species abundance, richness and diversity will change between habitats and over months. I hypothesised that *Lepidoptera* abundance, richness and diversity change over space and time following the assumption that the resource they feed upon, fruit, will also be changing over space and time. In order to see if there is a direct relationship between fruit and fruit feeding *Lepidoptera*, another question asked is whether *Lepidoptera* match patterns of those observed in fruit. It is assumed here that fruit drives the community structure of adult fruit feeding *Lepidoptera* so it is hypothesised that *Lepidoptera* will match patterns demonstrated in fruit. However, it is not known for certain that fruit is a main driver of *Lepidoptera* patterns as their larval stage or the regions climatic variation may also be influencing adult *Lepidoptera* patterns, so fruit will be treated as a response variable in analysis rather than an explanatory variable.

2.3 Methods

For survey site, data collection and assigning morpho codes see section 1.2 Research Methods.

2.3.1 Hypothesis testing

All statistical tests and the creation of plots were carried out in R (R Core Team 2021). Shannon's diversity index was calculated using the formula:

$$\text{Shannon- Wiener Index } H' = -\sum\left[\left(\frac{n\mathrm{i}}{N}\right) \times \ln\left(\frac{n\mathrm{i}}{N}\right)\right]$$

Key: ni = Number of individuals of each species, N= Total no. of individuals for the site and ln= Log.

Shannon's diversity index was used over other diversity indices because it accounts for both species richness and evenness. Shannon's diversity index was calculated from abundance data for each plot. Species richness was defined as the count of species or morpho codes identified in each plot. Abundance was defined as the count of each individual caught or fruit counted within the different plots. Estimates of expected species richness were calculated using functions relating to the Chao method (Chao 1984; Chao and Chiu 2016) in the 'fossil' package of R (R Core Team 2021).

To investigate the effectiveness of sampling effort across habitat types and the ability of samples in the study to be representative of the populations present, species rarefaction curves were created using the 'vegan' package of R (R Core Team 2021).

To check the hypothesises of questions 1 and 2: Fruit and *Lepidoptera* abundance, richness and diversity will change over months and between different habitats, mixed effect models were created using the lme4 package of R studio (R Core Team 2021). Plot was included as a random effect due to repeated measures in each plot nested within each habitat type. Diagnostics were checked for all models to ensure homogeneity of variances, normality, linearity and to identify any outliers. Likelihood ratio tests were used to test the significance between models using the ‘anova’ function in the ‘stats’ package of R studio(R Core Team 2021). A post hoc Tukey multiple pairwise-comparison was undertaken on mixed effect models that were significantly different from the null to determine which specific group pairs were significantly different using the package ‘emmeans’ in R studio (R Core Team 2021).

Hypothesis 3: *Lepidoptera* will match the patterns in fruit, was tested through Spearman’s rank correlation. The raw data was also plotted and a positive rho value indicates a positive relationship between variables. The variables tested were *Lepidoptera* abundance and fruit abundance, *Lepidoptera* diversity and fruit diversity as well as *Lepidoptera* species richness and fruit species richness. To take a cautious approach, correlation was chosen over regression as it was not known for certain that *Lepidoptera* populations were driven by fruit and instead both may be influenced by an alternative driver.

2.4 Results

The timeframe of the survey between April and August 2019 had 75 trapping days in total, in which 11,475 fruit, 4,539 moth and 744 butterfly individuals were recorded. Within these, 166 fruit, 83 moth and 25 butterfly species or morpho codes were identified and described. It is important to note that April and May are within what are considered the ‘wet’ season and June, July and August are within what are known as the ‘dry’ season. The fruit recorded most consistently (mode) over the five months was Code 3 (Lutan) which was recorded during each month of the survey and was found in all habitat sites. However, the most abundant fruit recorded was Code 73 (Jumbu-Jumbu) with a total of 3114 individuals recorded. Code 8 was the most abundant moth recorded over the six months and habitats with a total of 83 individuals. Within the butterfly species identified *Lexias pardalis* had the highest numbers recorded at 172 individuals, however the genus *Tanacia* was overall the most abundant genus with 242 individuals described. There were 12 species of butterfly that had not previously been identified or listed in the last published report of the research site (KHDTK Report 2016-2017), Table 1.

Table 1: List of butterflies not previously identified in the Rungan Landscape.

Latin name
Lexias canescens
Lexias cyanipardus
Polyura hebe
Faunis stomphax
Thaumantis noureddin
Amathusia phidippus
Zeuxidia orange
Zeuxidia blue
Tanacia godartii
Coelites euptychioides euptychioides
Tanaecia iapis
Thaumantis odana cyclops

These butterflies (Table 1 and Table 2) were identified either using ID guides provided by BNF or temporarily via google searches. *Zeuxidia orange* and *Zeuxidia blue* have not yet been identified to species level, with orange and blue used as a placeholder to aid in the differentiation of the two butterflies until they have been identified to species level. See Appendix lll for photos of the new butterflies identified in the Rungan Landscape and appendix IV for all butterflies identified within the study. Table 2 lists all species of butterfly identified throughout the study and their abundance in each of the three habitats, there are a few rare species where only one individual of that species was recorded in the survey, for example, *Thaumantis noureddin* and *Polyura hebe.*

Table 2: List of butterflies and their abundance in each habitat and overall.

	Abundance (number of individuals) found in each habitat across the study period			
Species of Butterfly	**Kerangas**	**Mixed Swamp**	**Low Pole**	**All habitats**
Agatasa calydonia	3	1	1	5
Amathusia phidippus	0	1	0	1
Charaxes bernardus	5	10	9	24
Charaxes borneensis	1	0	0	1
Charaxes solon	0	0	1	1
Dophla evelina	7	5	8	20
Euthalia monina	1	0	0	1
Faunis stomphax	1	3	2	6
Lexias canescens	4	1	9	14
Lexias cyanipardus	0	0	1	1
Lexias pardalis	59	45	69	173
Melantis leda	27	6	5	38
Mycalesis pitana/patiana/anapita	24	19	3	46
Coelites euptychioides euptychioides	6	15	1	22
Polyura hebe	1	0	0	1
Prothoe franck	23	23	8	54
Tanaecia clathrata	44	19	24	87
Tanaecia godartii	9	3	3	15
Tanaecia iapis	6	3	0	9
Tanaecia munda	83	32	25	140
Thaumantis noureddin	0	0	1	1
Zeuxidia aurelius	2	6	2	10
Zeuxidia blue	11	7	3	21
Zeuxidia doubledayii	2	5	1	8
Zeuxidia orange	11	13	2	26
Thaumantis odana cyclops	0	1	0	1

The habitat in which the highest number of fruit morpho codes were recorded over the survey period was Mixed Swamp with 73 codes found. Low Pole had the highest fruit abundance with a total of 5692 individual fruit recorded within the habitat over the five months. For butterflies and moths individually the highest number of species identified, and the highest number of individuals recorded (abundance) was within Kerangas. 21 butterfly species were identified, and 334 individual butterflies were recorded in the Kerangas habitat, Table 3. On the other hand, 63 moth morpho codes and 2127 individual moths were recorded in Kerangas, Table 3.

Table 3: Total number of species in their respective habitat type and study group as well as the total abundance of individuals in each study group recorded in the habitat types. Third column contains the Chao species richness estimate.

Study group	Habitat	Total abundance	Total number of Species	Chao Species Richness estimate
Fruit	Kerangas	4028	65	94
	Mixed Swamp	1658	73	95
	Low Pole	5692	27	34
Butterfly	Kerangas	334	21	22
	Mixed Swamp	217	19	22
	Low Pole	179	19	21
Moth	Kerangas	2127	63	70
	Mixed Swamp	1527	56	99
	Low Pole	940	55	109

Rarefaction curves:

All curves on the three rarefaction curves, Figure 7 start to plateau suggesting that a high proportion of the total number of species of fruit and *Lepidoptera* within these habitats were sampled. Butterflies and moths had similar curves, while fruit had more drastically different curves for the different habitats, Figure 7 and Table 3 includes the Chao species richness estimates for each of the habitats and study group, which is reflected in the rarefaction curves. Chao species richness estimates the asymptote of the rarefaction curves, or the species of richness that would be expected if sampling continued. Richness and Chao species estimates were mostly similar for butterflies, suggesting that out of the three study groups butterfly sampling was the most effective.

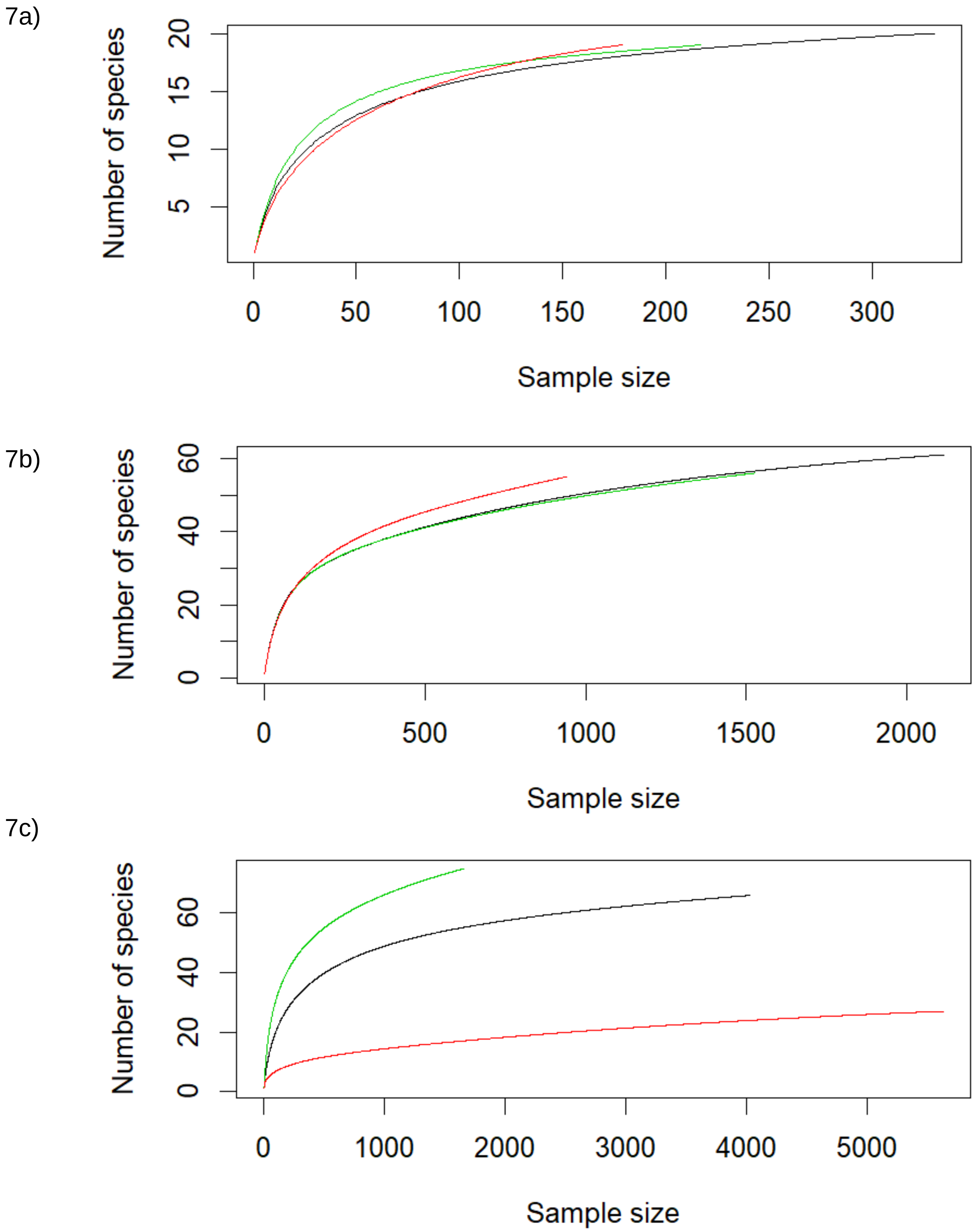


Figure 7: Rarefaction curves for a) butterfly b) moth c) fruit. Red=Low Pole, Black =Kerangas, Green = Mixed Swamp.

2.4.1 Question 1: How does fruit abundance, richness and diversity change over months and between habitats?

Fruit Abundance

The best model using model simplification incorporated habitat and month as explanatory variables and was significantly different from the null model (Likelihood Ratio Test: $\chi 2(10) = 51.6$, $P < 0.001$). The relationship between fruit abundance and habitat was influenced by an interaction with month (Likelihood Ratio Test: $\chi 2(8) = 1941.1$, $P < 0.001$). There was an interaction between month and habitat for fruit abundance, therefore temporal patterns do vary between habitats. The abundance of fruit found in Low Pole during June seems to be the most consistently significantly different from all other habitats and against the different months (Table 4), Figure 8, shows that the fruit abundance in Low Pole in June is higher than the other two habitats. The average abundance of fruit in Low Pole starts low in April and May but increases significantly in June (Table 4, Figure 8). The average abundance of fruit in Low Pole then decreases in July and August (Table 4, Figure 8). This pattern is not followed in Kerangas and Mixed Swamp further showing that there is temporal variation between habitats (Figure 8). The Tukey test output, see Table 4, shows the month and habitat pairs that are significantly different from each other, see appendix VII for full output of Tukey test.

Table 4: Output from a multiple pairwise Tukey Test that investigated which habitat-month combinations are statistically different from abundance fruit data in different habitats and months.

Pairwise differences of Month, Habitat	**P Value**
April Kerangas – June LowPole	0.0192
August Kerangas – June LowPole	0.0008
July Kerangas – June LowPole	0.0003
June Kerangas – June LowPole	0.0002
May Kerangas – June LowPole	0.0053
April LowPole – June LowPole	0.0001
August LowPole – June LowPole	0.0025
July LowPole – June MixedSwamp	0.0499
June LowPole – May LowPole	0.0001
June LowPole – April MixedSwamp	<0.0001
June LowPole – August MixedSwamp	<0.0001
June LowPole – July MixedSwamp	<0.0001
June LowPole – June MixedSwamp	<0.0001
June LowPole – May MixedSwamp	<0.0001

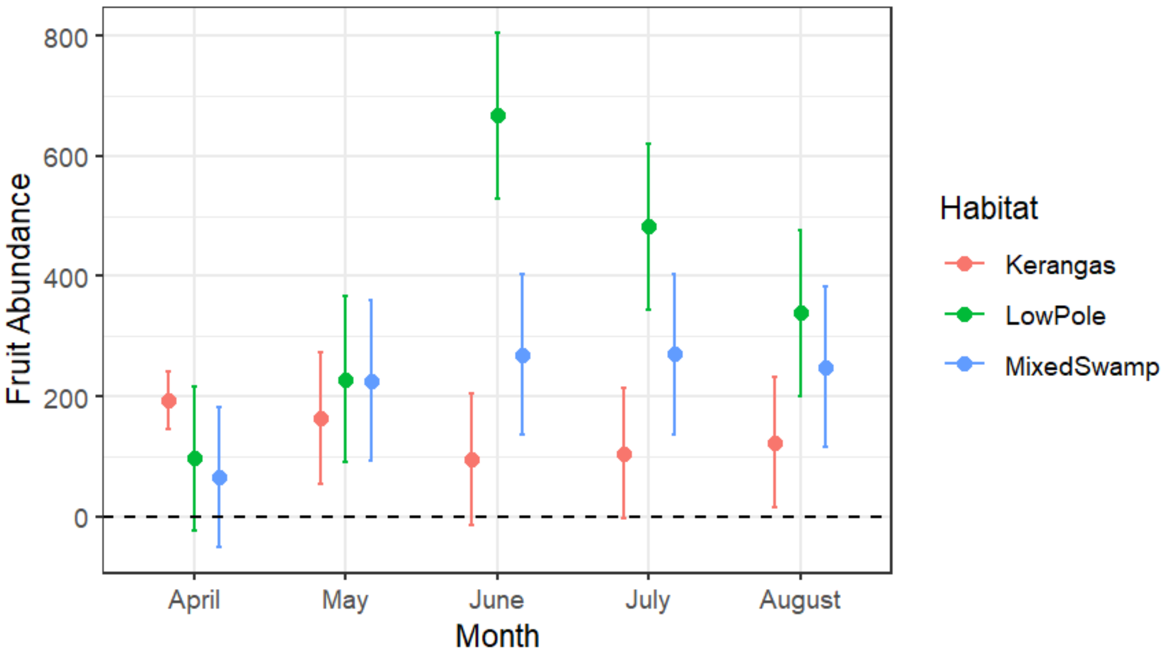


Figure 8: Total fruit abundance in Kerangas (red), Low Pole (green) and Mixed Swamp (red) across the five consecutive months (April to August). The middle point represents the prediction of fruit abundance from the mixed models with the lines either side of the point representing standard error.

Fruit Diversity

The best model using model simplification incorporated habitat as the explanatory variable and was significantly different from the null model (Likelihood Ratio Test: $\chi 2(2) = 12.8$, $P < 0.01$). This suggests that fruit diversity does not change significantly with month. Species diversity does however change significantly with habitat with Kerangas having the highest species diversity and Low pole the lowest, Figure 9. See appendix VII for Tukey test on fruit diversity, only Low Pole–Mixed Swamp are statistically significantly different with a p value of 0.0041.

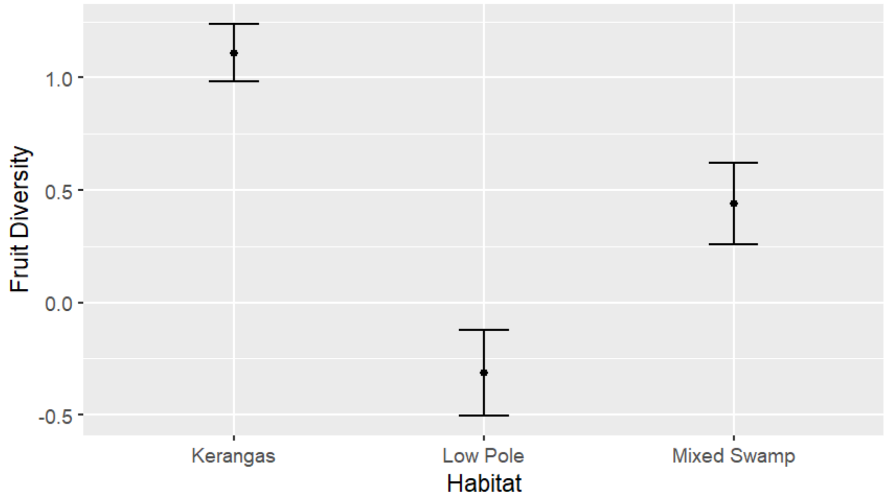


Figure 9: Fruit species diversity, calculated by Shannon's diversity index, across the three habitats Kerangas, Low Pole and Mixed Swamp. The whiskers from the point represent standard error.

Fruit Species Richness

The best model using model simplification incorporated habitat as an explanatory variable but was not significantly different from the null model (Likelihood Ratio Test: $\chi2(2) = 5.81$, P=0.055).

2.4.2 Question 2: How does *Lepidoptera* abundance and species diversity change over months and between habitats?

Butterfly and Moth Abundance

For butterfly Abundance the best model using model simplification incorporated month as the explanatory variable and was significantly different from the null model (Likelihood Ratio Test: $\chi2(4) = 14.4$, $P < 0.01$). This suggests that butterfly abundance does not significantly change between the different habitats, but does vary over the months, Figure 10. April has the highest abundance of butterflies, which subsequently declines significantly in the following month of May, then from

June to August, the abundance of butterflies subtly increases, Figure 10. See Appendix VII for Tukey test on butterfly abundance. There were two multiple pairwise combinations that were significantly different from the rest, August-May with a p value of 0.0042 and August-June with a p value of 0.0449.

For moths, the best model using model simplification incorporated habitat and month as explanatory variables and was significantly different from the null model (Likelihood Ratio Test: $\chi 2(6) = 64.4$, $P < 0.001$). There was no significant interaction between these variables (Likelihood Ratio Test: $\chi 2(8) = 5.2$, $P = 0.739$). Kerangas had the highest number of moths found in each habitat, as shown in Figure 11, compared to Low Pole and Mixed Swamp, with the highest number of moths found in Kerangas in June compared to the lowest number of moths found in Low Pole in April. See Appendix VII for full Tukey test output on moth abundance; there are 41 pair combinations that are statistically different from each other.

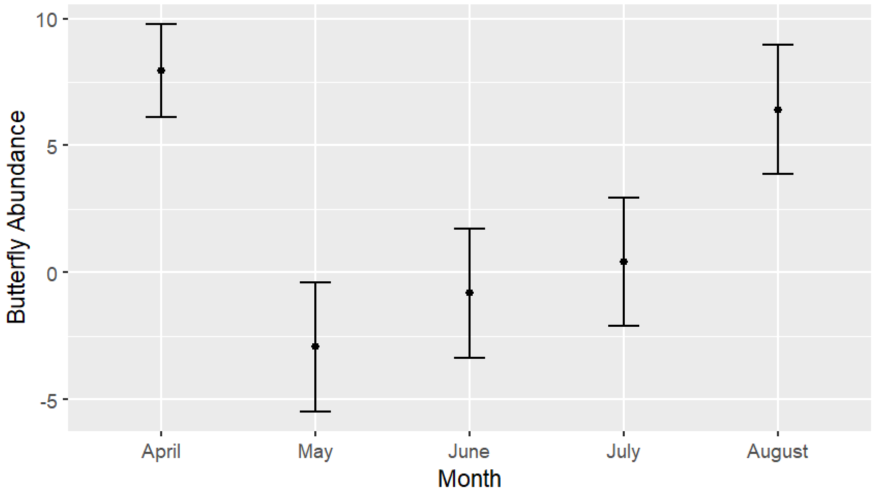


Figure 10: Butterfly abundance across the five months April to August. Points represent the predictions of butterfly abundance and the whiskers, standard error.

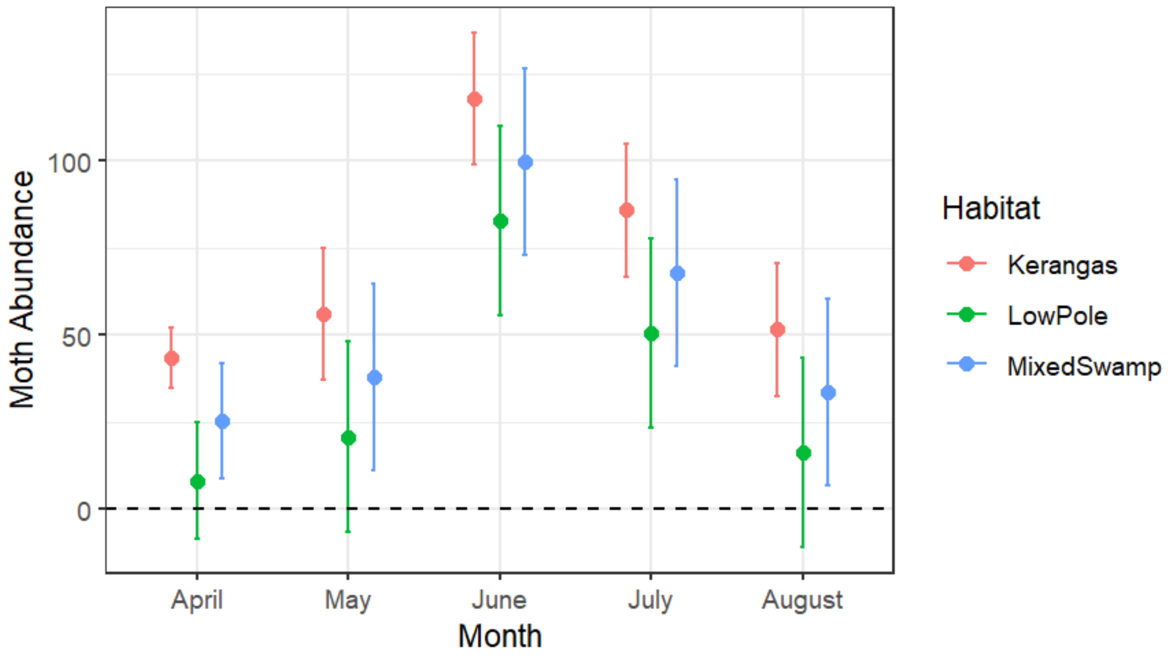


Figure 11: Moth Abundance across the five months April to August with Habitat coloured separately: Red = Kerangas, Green = Low Pole, Blue = Mixed Swamp. Whiskers from the points represent standard error and the points themselves are species richness predictions.

Butterfly and Moth Diversity

For butterflies the model incorporating habitat as an explanatory variable was not significantly different to the null model (Likelihood Ratio Test: $\chi 2(2) = 3.1$, $P = 0.216$). Similarly, the model incorporating month as an explanatory variable was not significantly different to the null model (Likelihood Ratio Test: $\chi 2(4) = 6.2$, $P = 0.184$). For moths the model incorporating habitat as an explanatory variable was not significantly different to the null model (Likelihood Ratio Test: $\chi 2(2) = 1.3$, $P = 0.513$). Similarly, the model incorporating month as an explanatory variable was not significantly different to the null model (Likelihood Ratio Test: $\chi 2(4) = 9.0$, $P = 0.061$). This suggests that *Lepidoptera* diversity does not change over months or habitats.

Butterfly and Moth Richness

The best model using model simplification for butterflies incorporated habitat as the explanatory variable but was not significantly different from the null model (Likelihood Ratio Test: $\chi2(2) = 4.908$, P= 0.086).

For moths the best model using model simplification incorporated habitat and month as explanatory variables (Figure 12) and was significantly different from the null (Likelihood Ratio Test: $\chi2(6) = 42.01$, $P < 0.01$). There was no significant interaction between these variables (Likelihood Ratio Test: $\chi2(8) = 8.598$, P = 0.377). See Appendix VII for full Tukey test output on moth richness; there are 24 significantly different month-habitat combinations.

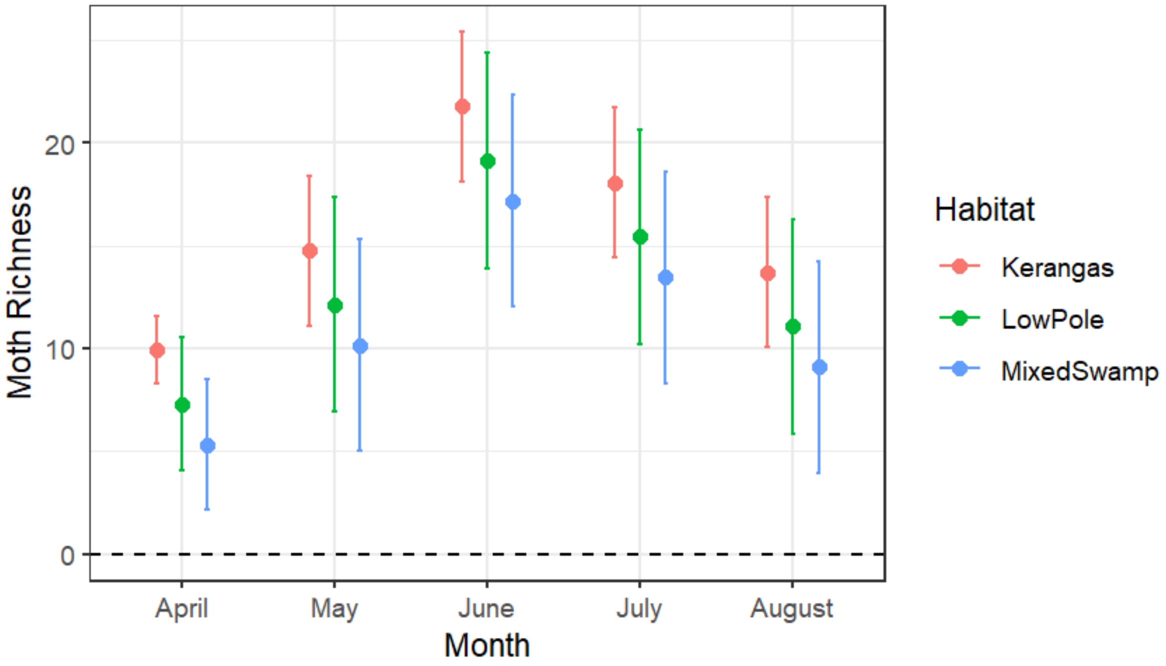
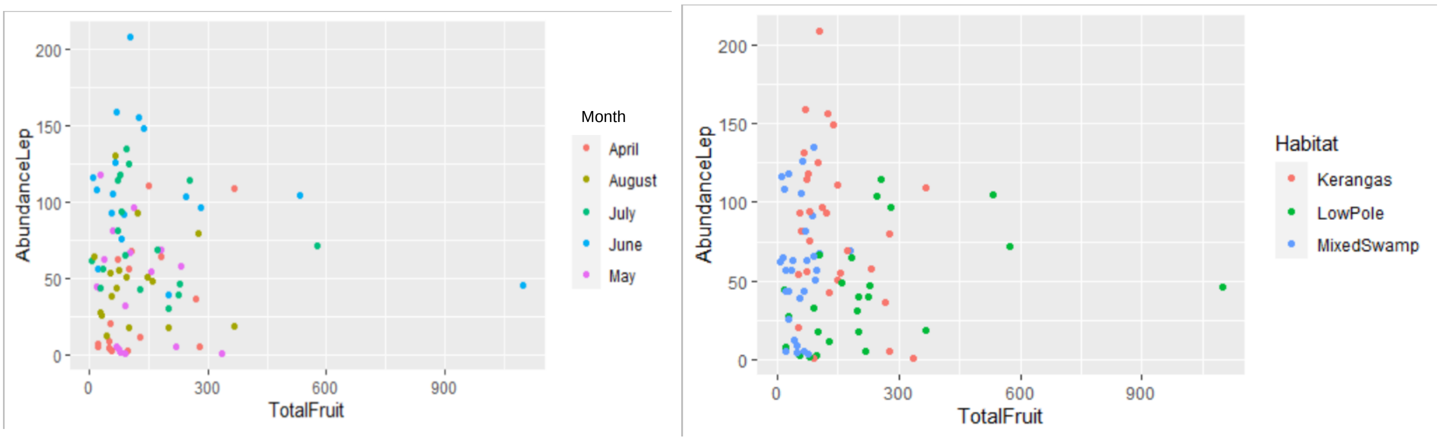


Figure 12: Moth species Richness across the five months (April to August) with Habitat coloured separately: Red = Kerangas, Green = Low Pole, Blue = Mixed Swamp. Whiskers from the points represent standard error and the points themselves are species richness predictions.

2.4.3 Question 3: Does *Lepidoptera* match the patterns observed in fruit?

There was no significant correlation between butterfly abundance and fruit abundance (Spearman's rank correlation: rho= 0.03, P= 0.765) or with moth abundance and fruit abundance (Spearman's rank correlation: rho= 0.06, P=0.591), Figure 17a, Figure 17b. There was also no significant correlation between butterfly species diversity and fruit species diversity (Spearman's rank correlation: rho= 0.10, P= 0.358) or moth diversity and fruit diversity (Spearman's rank correlation: rho= -0.01, P=0.902), Figure 18a, Figure 18b. There was also no relationship between fruit richness and butterfly richness (Spearman's rank correlation: rho= 0.44, P=0.689) or between fruit richness and moth richness (Spearman's rank correlation: rho= 0.13, P=0.254), Figures 19a &19b.

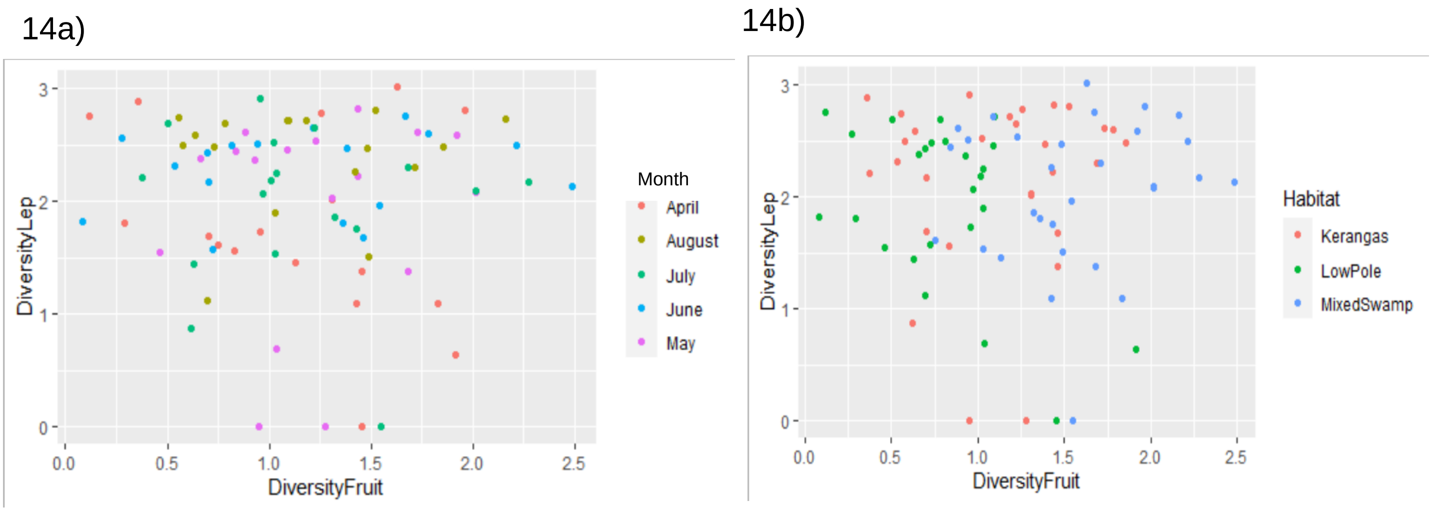
Only *Lepidoptera* data, and moth data for species richness, was plotted as individually butterflies and moths showed similar patterns, with no correlation. All outliers were confirmed to be real data points and not data input error.



13a)

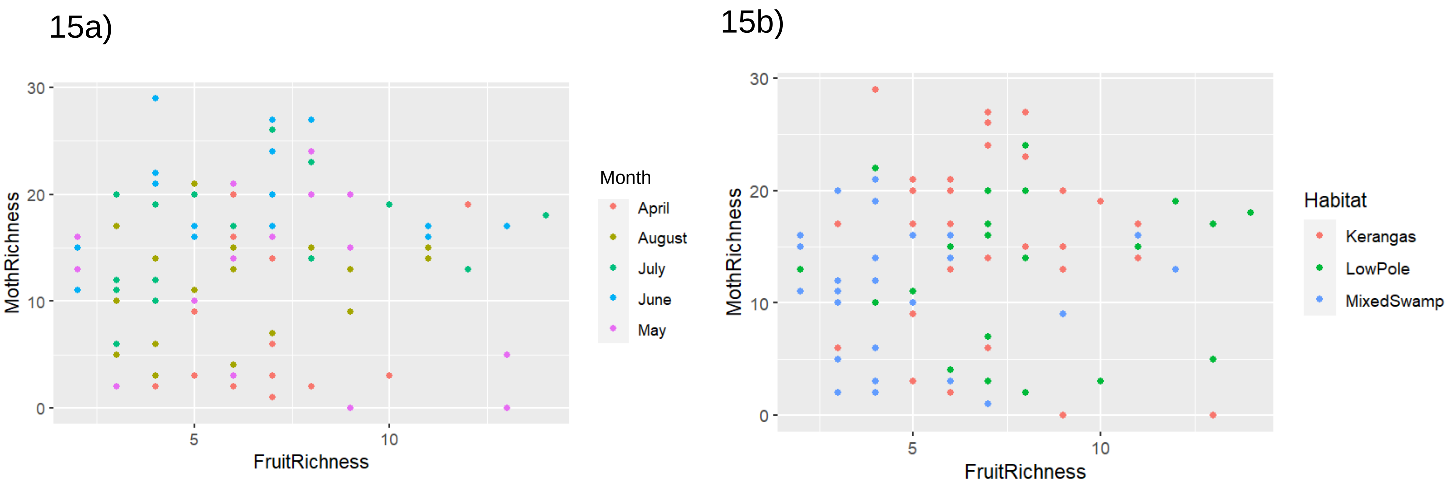
13b)

Figure 13a & b: Plot between *Lepidoptera* abundance (total number of butterflies and moths found in each plot) on the y-axis and total fruit on the x-axis, the total number of fruit counted in each plot. For 13a each point represents a plot and are colour coded depending on the month they are in. Red = April, Gold = August, Green = July, Blue = June and Pink = May. For 13b plots are colour coded depending on the habitat they are in with Red = Kerangas, Green = Low Pole and Blue = Mixed Swamp.


14a)

14b)

Figure 14a&b: Plot between *Lepidoptera* species diversity on the y-axis and fruit diversity on the x-axis, Shannon Weiner's Diversity index was used for both variables. For 14a each point represents a plot and they are colour coded into which month the point refers to. Red = April, Gold = August, Green = July, Blue = June and Pink = May. For 14b each point represents a plot and they are colour coded into which month the point refers to. Red = Kerangas, Green = Low Pole and Blue = Mixed Swamp.


15a)

15b)

Figure 15a&b: Plot between moth species richness on the y-axis and fruit species richness on the x-axis. For 15a each point represents a plot and they are colour coded into which month the point refers to. Red = April, Gold = August, Green = July, Blue = June and Pink = May. For 15b each point represents a plot and they are colour coded into which month the point refers to. Red = Kerangas, Green = Low Pole and Blue = Mixed Swamp.

2.5 Discussion

There were 12 species of butterfly that had not previously been identified and listed in the last published report of the research site (KHDTK Report 2016-2017), Table 1. The fact that butterflies identified in the current survey were not previously listed highlights that there are a higher number of butterfly species undescribed in the area. The new moths and detailed morpho code fruit and moth morpho code ID guides from this study further expand and add to the baseline of the species that cohabit the KHDTK study site in the Rungan landscape. These factors stress that the Rungan landscape is important to conserve and continuously monitor in order to understand the full extent of species found within the area. This will enable ecologists to identify any changes to species structure due to natural events or human activities. Having a baseline of species is important to understand the ecology of an area and to help focus conservation strategies (Martins 2017). Therefore, this baseline created by the current study aids in further monitoring of the area to provide appropriate conservation strategies that protect biodiversity and at-risk species.

Species rarefaction curves for the three study groups were beginning to plateau suggesting that there was a high proportion of the number of species recorded in each habitat, Figure 7. However, the Chao species richness estimates were greater than the species richness calculated in the current study. Because Chao species richness estimates predict the number of species that would have been found if there was increased sampling effort, if the survey had included more trapping days then more species in each group would have been found. The fact that more species would have been identified if sampling continued will be kept in mind during discussion of results. Since the curves were starting to plateau, there is more confidence a good number of species were represented in this study.

Question 1: How does fruit abundance, richness, and diversity change over months and between habitats?

Fruit Abundance

The results of this study suggests that fruit abundance was affected by an interaction between month and habitat, Figure 8. Considering the interaction found between month and habitat for fruit abundance this shows that temporal patterns do vary between habitats which could support the theory of habitat complementarity within this landscape. This would suggest each individual habitat is complementing each other in terms of fruit abundance being higher in different habitats in different times of the year, which would potentially support a higher diversity of species (Dunlop 2013). Low Pole collectively had the highest abundance of fruit recorded (5692 individuals), Kerangas the second highest (4028 individuals) and Mixed Swamp had the lowest (1658 individuals), Table 3. However, Low Pole was dominated by two morpho codes 73 (Jumbu jumbu) and 12 (Tumih). This could be one of the interactions seen between month and habitat as in June the abundance of Low Pole increased dramatically compared to the other two habitats (Figure 8), which could be when Jumbu Jumbu and Tumih were fruiting. Trees can produce a different volume of fruit depending on the size of the fruit, Jumbu Jumbu and Tumih are relatively small, see appendix I, and so this could be why higher numbers of these species were found (Lee 1988). This suggests it could be more important to focus on the diversity of fruit and the timing of fruiting due to fruiting of trees potentially skewing results. It also suggests that it would be useful to take the size of the fruit into account as while there may be a lower abundance of one species, the total mass of that species compared to a small fruit with high abundance could be the same.

Fruit Diversity

Fruit diversity was found to not have temporal variation between habitats and was only found to be influenced by habitat and not month, Figure 9. This could be due to the fact that ground fruit surveys include rotting fruit and so due to decaying time, fruit of different species could have been counted in surveys within a particular month even if they fruited within a previous month. Therefore, to fully grasp fruiting patterns canopy surveys may be more accurate as they will only include trees that are actively fruiting (Zhang and Wang 2009). However, it has been found in other surveys that ground fruit surveys are relatively accurate in describing the diversity, richness and abundance of an area (Lashley et al. 2014) and so we can be relatively confident that the ground surveys have represented the diversity, richness and abundance of fruit in the KHDTK study site but have potentially not fully grasped the effect of month due to the nature of the survey. Habitat was, however shown to be significantly different for fruit diversity with Kerangas having the highest diversity and Low Pole the lowest, Figure 9. Since Low Pole had the highest overall abundance yet lowest diversity, this further supports the idea that a few species were dominating abundance values. Kerangas could possibly have a higher species diversity as the ground is less flooded in these habitats compared to Mixed Swamp and Low Pole and therefore perhaps meaning a higher number of species can survive in this habitat. It is also possible that due to less flooding ground fruit surveys were easier to complete in Kerangas.

Fruit Richness

Fruit richness, whilst affected slightly by habitat was not significantly predicted by explanatory variables so habitat and month do not appear to influence fruit richness in this landscape. Fruit richness was not affected by month or habitat even though diversity was affected by habitat, which could be due to the influence of abundance which is included within diversity indices. Species richness of fruit however, while similar for Kerangas and Mixed Swamp with a Chao species estimate of 94 and 95 respectively was lower for Low pole with a species richness estimate of 34, Table 3, potentially suggesting that only a few specialist species can survive in the flooded peatland. Further studies investigating and identifying the species of trees could help explain the differences of fruit within the landscape.

Conclusions

Each habitat had either the highest abundance, diversity or richness: the highest number of fruit morpho codes that were recorded over the survey period was within Mixed Swamp with 81 codes found; Low Pole had the highest fruit abundance with a total of 5692 fruit recorded within the habitat over the five months; and Kerangas had the highest diversity of fruit, Table 3. This could suggest that each habitat should be protected rather than focusing conservation efforts on one habitat as each habitat was found to have a highest factor of community structure. The results of the study show fruit species abundance is affected by month and habitat while diversity is only affected by habitat and fruit richness by neither. Therefore, the study can only truly accept the hypothesis that fruit abundance will be affected by habitat type and month. We can partially accept the hypothesis for fruit diversity and must reject the hypothesis for fruit species richness. It is important to first note that this survey was only over a five-month long period and other studies that discuss the temporal variation of fruits stress the importance of surveying fruit across a whole year (Molleman et al. 2006; Harrison et al. 2010; Grøtan et al. 2012). Therefore, to truly understand the patterns of fruit in a heterogenous landscape surveys would need to encompass the whole year to grasp the ecology of the area. Future surveys would also be urged to collect temperature and precipitation data in order to investigate if temporal variation relates to climatic variation across the year.

Question 2: How does *Lepidoptera* abundance, richness and diversity change over months and between habitats?

Lepidoptera Abundance

Butterfly abundance was only affected by month and not habitat (Figure 10) while moth abundance was affected by both habitat and month individually (Figure 11), but there was no interaction between these explanatory variables. Unlike fruit, there was no significant difference in butterfly abundance between each habitat suggesting that habitat itself does not impact butterfly abundance. This could be due to their ability to move through habitats within the mosaic landscape as they tend to have large home ranges (Marchant et al. 2015). Median daily movements of butterflies within a peat swamp forest in Borneo has been found to be approximately 200-250m and can frequently move distances of 1km between plots (Marchant et al. 2015). In this study butterfly abundance was found to be influenced by month which is supported by a study in Brazil, which found that butterfly abundance was strongly influenced by temporal variation, in particular precipitation levels were thought to drive butterfly abundance (Nobre et al. 2012). Of course, caution needs to be applied when comparing the studies of frugivorous *Lepidoptera* in different regions as there will be different species of butterflies and plant communities which respond differently to habitat type and month. Precipitation and other climatic factors were not measured within this study but the wet season in Borneo ends in May and with the beginning of the dry season starting in June. There was a significant difference in the abundance of butterflies found in each month. There were significantly more butterflies found in August than any other months. This could be due to the area moving into the dry season with decreased precipitation levels and perhaps a temperature change, which have been shown previously to affect butterfly compositions (Mustaffa 2001; Basset et al. 2012; Santos et al. 2019). Butterflies are sensitive to temperature and their performance and activity levels are related to environmental temperature (Santos et al. 2019). Less rain observed in August during the dry season of the study could have resulted in butterflies being more active within the canopy and so our study caught more either because there where higher abundances of butterfly present or they were more likely to get caught as they were more active with less precipitation. There is also potential that at the end of the survey butterflies became ‘trap happy’ (Marchant et al. 2015), where butterflies can learn that there is a constant source of food and therefore specifically seek out traps. Further data analyses and proper mark catch recapture procedures would need to be followed in further surveys in order to comfortably rule this out. In light of this, the study recommends that for further surveys identifying and monitoring butterflies in the KHDTK study site in the Rungan landscape, climatic data like rainfall and temperature are collected to further inform what could be driving butterfly abundance over month as butterflies are highly climate dependent (Mustaffa 2001; Santos et al. 2019).

In contrast to butterflies, the greatest abundance of moths was found in June, with abundance levels decreasing towards August. Either moths do not become as trap happy as butterflies or other factors such as precipitation and temperature may have a different effect on moth abundance than butterflies. Moth abundance was found to be influenced by month and habitat, Figure 11. The higher number of moths found in Kerangas over Low Pole could show a habitat preference of Kerangas. If this is the case, this could be due to the specific conditions of Kerangas habitat being preferable or there could be more fruit they prefer in Kerangas and therefore, further studies could investigate specific fruit that may drive moth species. Moth species have been found to be dependent on plant diversity (Delabye et al. 2020), which could be due to there being more food resources or an increase in available niches. Since there was no correlation between fruit diversity and moth diversity found within this study, it could be suggested that it is the larval stage of moths influenced by plant diversity. Another hypothesis is that a moth’s host plant in their larval stage could be found within the Kerangas habitat and so higher numbers would be found there. Little literature is available on the relationship between tropical moths and their larval food source but it is well documented that the caterpillar of butterflies is dependent on their specialised host plant for a food source (Forister et al. 2015). Although in this current study it is interesting that this pattern described in moths was not found in butterflies, further investigation into both butterfly and moth host plants during their larval stage should accompany future *Lepidoptera* surveys in order to fully understand what drives their abundance in certain habitats.

Lepidoptera Diversity

Butterfly and moth diversity were both similar where habitat and month did not explain any patterns found in the diversity. Together there was little variation in

Lepidoptera diversity over month and between habitats and with no interaction between month and habitat seen for either groups it could be said that there is no temporal variation in butterfly or moth diversity between habitats. This suggests that *Lepidoptera* diversity is driven by different external factors rather than habitat type or month.

Lepidoptera Richness

While butterfly richness was found to be affected by habitat it was not significant and so could be stated that habitat and month do not affect patterns in butterfly richness. On the other hand, moth richness patterns were explained by both habitat and month, with no interaction between the two explanatory variables, Figure 12. Butterflies and moths had the highest number of species in the Kerangas habitat over the whole survey period, although not significantly higher than the other habitats for butterflies. This could be due to a more open canopy as; butterfly and moth communities have been found to depend on 'forest openness' (Delabye et al. 2020). Although it is important to note that moths and butterflies do tend to respond in different directions to openness as butterflies like open sunny areas while moths prefer darker areas (Sparks et al. 1996; Merckx et al. 2003; Slade et al. 2013). Plant diversity has also been shown to influence moth community structure so Kerangas could have a plant diversity that moths rely on (Delabye et al. 2020). This could be attributed to the fact that Kerangas is less flooded than the other habitats and so more foodplants could be available for fruit feeding moths in their adult or larval stage, perhaps more important in their larval stage due to being less mobile than their adult stage. Further studies could focus on what specific plant diversity moths utilise within a landscape. It is important to note that Delabye et al. (2020) survey took place within the rainforests of Mount Cameroon and so the communities within the peat swamp forests of Borneo may be influenced differently. Additionally, the results of this current study showed that the highest number of species for fruit found in the survey was in Mixed Swamp. This habitat is characterised as a transitional habitat between Kerangas and Low Pole and therefore could have a higher number of tree species that subsequently produce the higher number of fruit species observed within the habitat. It is important to add that it may not be fruit specifically that could be driving *Lepidoptera* but the overall increase in tree species that *Lepidoptera* may use in their life cycle.

Species richness was very similar for butterflies with the Chao species estimates for all three habitats lying between 21 and 22, which potentially supports the idea that butterflies are highly mobile species, and this is why a similar number of species are found in each habitat. Although further investigation into the species composition of butterflies will reveal if these are different species. Moth species richness, on the other hand, had greater variation with Low Pole only having a Chao estimate of 34 and Kerangas and Mixed Swamp having estimates of 94 and 95 respectively. This could suggest that moths may have a stronger preference for habitat type over butterflies. Butterfly species richness was not significantly affected by month or habitat, whilst moth species richness was affected by both month and habitat. This could indicate that moths in this particular landscape are more easily affected by external factors like month and habitat while other factors, like climate could be affecting butterflies that were not recorded in the study. Further surveys could investigate why moths are more likely to be influenced by month and habitat.

Conclusions

The hypotheses for question 2 can be partially accepted and rejected. The hypothesis of habitat and month affecting patterns in *Lepidoptera* can be fully accepted for only moth abundance and species richness. The hypothesis can be partially accepted for butterfly abundance as only month is affecting the patterns found in this study. Finally, the hypothesis must be rejected for butterfly diversity, species richness and moth diversity as neither factor can explain patterns found. The difference found between abundance, richness and diversity of moths and butterflies as adults could be due to their fundamental differences. The majority of adult moths are most active during the night whereas butterflies are active during the day and utilise sunny spots for behavioural thermoregulation (Barton et al. 2014). Since moths are less influenced by solar radiation perhaps this is why we see differences in moth and butterfly abundance as potentially moths are less likely to be driven by the same abiotic factors as butterflies when flying at night. This highlights that moths and butterflies can be influenced very differently by habitat type and month and future surveys could be advised to be cautious using butterflies as a proxy for moth patterns, or other taxa within the landscape. Other studies have found that while butterflies are normally a good indicator, they may not be able to accurately represent all other groups (Schulze et al. 2004). Kerr et al. (2008) suggested that butterflies can be used to predict *Hymenoptera* species richness, so this is still a highly debated topic. Therefore, research suggests that butterflies can be used to predict specific factors but should not be assumed to accurately predict the complete community structures of other taxa. Using preliminary surveys, like this one, butterfly and moth patterns can be assessed to discover if butterflies can be used as bioindicators for moths in future surveys, to be more cost effective. This suggests that including multiple taxa in a preliminary study to evaluate if a certain group, like butterflies, can be used as indicators to inform future surveys would be beneficial in order to efficiently complete future surveys within an area. Again, like fruit, it is important to note that this current study was only collecting data over five consecutive months and other surveys have found that multiple year surveys are needed in order to truly evaluate the effect of month and habitat on frugivorous butterflies (Sanos et al. 2019; Araujo et al. 2020). In order to fully understand the ecology of a landscape, this study suggests a multi-taxon preliminary survey with climatic data collection should be undertaken to understand the specific drivers that are causing the effects of habitat type and month shown in this survey. This would also allow more specific surveys to be undertaken to show how these factors affect each taxon individually.

Q3: Do *Lepidoptera* patterns match those in fruit?

All correlations comparing fruit with *Lepidoptera* were not significant indicating that in relation to this study, there is no relationship between fruit abundance, diversity and richness and *Lepidoptera* abundance, diversity and richness. Therefore, *Lepidoptera* do not match the patterns found in fruit and going one step further it could be stated that these factors of fruit (abundance, diversity and richness) are not driving *Lepidoptera* community structure. It could also be assumed that there are different external factors driving both fruit and *Lepidoptera* as the patterns do not match. Further investigation into the specific species of each group and their individual patterns is needed to see if there are any groups of fruit that specific frugivorous *Lepidoptera* are following, as some species of *Lepidoptera* are specialists and may only be following one specific fruit and the analysis in this study did not take this into account. Further investigation into the specific species found within the landscape and which species are dominating and therefore increasing abundance values are needed. This is because as diversity stays relatively the same, the abundance fluctuates which suggests that there could be a few specific species responsible for the high abundance found in certain months. Other studies have found that there is often a dominant species in surveys which could be due to them being generalist species and thus thrive across broader conditions that month and habitat differences cause (Santos et al. 2019). Another potential reason that no relationship was found between fruit and *Lepidoptera* in this question is that this study only reflects the adult stage of *Lepidoptera*'s lifecycle, and so could be missing how other stages in *Lepidoptera*'s lifecycles could be affecting the patterns found within *Lepidoptera*. It could be vital to also consider that *Lepidoptera* have a larval stage as well which could affect the adult stage as studies have found that in some species of *Lepidoptera* the larval stage does influence the distribution of adults (Mustaffa 2001; Altermatt and Pearse 2011; Holloway et al. 2013). Therefore, conservation implications need to be aware of the host plant and the food source of the larvae or other pressures that could affect the larvae, predators for example. It may be worth monitoring or factoring in the larval stage when investigating what affects the adult *Lepidoptera* in future surveys in order to truly grasp what could be affecting abundance, diversity and richness of *Lepidoptera*.

Another potential reason that no relationship was found is that this survey was only five months long and potentially did not capture the full effect of month and habitat type in fruit and *Lepidoptera*, as often fruit and *Lepidoptera* can have annual or biannual patterns (Molleman et al. 2006). The need for long term surveying of butterfly communities to fully understand butterfly ecology and accurately assess biodiversity in an area has been expressed many times (DeVries et al. 2008). However, quick surveys are often required to efficiently and cost effectively survey an area that is in need of perhaps urgent protection. Short term surveys can lead to inaccurate estimations of species abundance, richness and diversity therefore this five-month long survey may not have been long enough to truly capture the diversity, richness and abundance of *Lepidoptera* populations in this landscape. It is vital that accurate estimations of an area's biodiversity are calculated as poor estimations could lead to uninformed conservation management and potentially even miss the importance of an area leading it to go unprotected. Therefore, it is stressed that long term studies need to be carried out in the Rungan Landscape, to fully understand any temporal patterns in the distribution of *Lepidoptera* species structure. Overall, the hypothesis of this question must be rejected as the patterns of *Lepidoptera* discussed in the chapter do not match those of fruit.

Chapter 3: How habitat affects the composition of fruit and *Lepidoptera* species

3.1 Abstract

Tropical rainforests support a wide range of species including many that are endangered. Protecting highly biodiverse areas, such as tropical rainforests, is of great importance as biodiversity loss can lead to population declines and local extinctions. This can be particularly ecologically harmful if key species that provide vital ecosystem services are lost. This study centres on a lowland rainforest landscape, the Rungan Landscape located in central Kalimantan, Indonesia. This landscape contains many distinct habitats, but this study focuses on three: Kerangas, a sandy soil habitat; Low Pole, a peat swamp-based habitat; and Mixed Swamp, a transitional habitat between Kerangas and Low Pole. To understand how a highly heterogenous landscape affects species compositions of fruit and *Lepidoptera*, three questions were evaluated. Firstly, does habitat affect species composition? Secondly, is similarity in fruit composition correlated positively with similarity in *Lepidoptera* composition? And thirdly while testing for spatial correlation in species composition, do closer geographical plots affect similarity in species composition? Habitat was found to affect species composition of fruit and *Lepidoptera*, and Multi-Dimensional Scaling (MDS) visualized this with little to no overlap of species composition between habitats. Therefore, highly heterogeneous landscapes could be leading to a larger overall species diversity of the region. This means that all habitats within the mosaic of the Rungan landscape should be protected according to the use of the habitat complementarity principle. Similarity in fruit species composition was correlated positively with similarity in *Lepidoptera* species composition which suggests that specific assemblages of fruit affects the distribution of assemblages of *Lepidoptera*. Finally, plots that were less

geographically distant were more similar in their species composition, regardless of habitat. This highlights the fact that spatial autocorrelation between the plots may have influenced the results of this study due to the low distance between plots. This study acts as a baseline for future studies to further investigate community composition over time and therefore efficiently identify changes to the composition of species as a result of external anthropogenic pressures, such as forest fires or fragmentation due to logging. Furthermore, continuing research into how fruit composition drives *Lepidoptera* composition will assure more attention is given to this topic. This will ensure fruit and *Lepidoptera* are equally surveyed and protected in future conservation management strategies.

3.2 Introduction

The increasing frequency of extreme climatic events and ongoing habitat loss experienced worldwide is known to threaten biodiversity and ecosystem functioning by altering fundamental biological processes (Lamarre et al. 2020). Borneo has an incredibly diverse range of fauna and flora and thus has been identified as a major ‘evolutionary hotspot’ (Bruyan et al. 2014) that is a focus of conservation efforts to protect biodiversity. Evaluating the response of ecosystems to external threats requires continuous long-term monitoring to identify changes over time. However, this requires knowledge on how species are assembled within a landscape, which first needs to be documented. The distribution and patterns of species are influenced by their response to environmental variables, and it is a key objective of many ecology studies to understand this response and the possible drivers (Gaston 2000; Molina-Martinez et al. 2013). Therefore, evaluating the effects of habitat on species composition could be a good start in investigating the assemblage of species in largely undocumented landscapes. Establishing drivers of the general patterns of organisms across a landscape can help reduce population declines and local extinction by prioritising conservation focus. This is especially prevalent with predictions that climate change could lead to local extinctions in tropical ecosystems that are highly diverse (Molina-Martinez et al. 2013). While focus, in Borneo, has previously been in mountainous areas there will be more focus on lowland tropical areas like the Rungan due to the high biodiversity found within the region (Harrison et al. 2010). This study centres on the Rungan Landscape within Central Kalimantan province, Indonesia, which comprises of a mosaic landscape with many different habitat types, from peat land to sandy soil habitats. The study was carried out in the Mungku Baru Education forest, also known as Kawasan Hutan Dengan Tujuan Khusu (KHDTK), within the Rungan Landscape. Generally studies on Lepidoptera in Borneo have previously focused on how vertical stratification affects community composition (Molleman et al. 2006) and how habitat fragmentation from anthropogenic influences affects the composition of *Lepidoptera* species (Melo et al. 2019). However, there is a lack of information on intact habitats within the same landscape with no varying altitude or human pressures, such as the Rungan Landscape. Therefore, to investigate the assemblage of species in this largely undocumented landscape, the effect of habitat type on the composition of frugivorous *Lepidoptera* species and their fruit resources was undertaken. From completing one of the first surveys to look at the potential link of fruit and *Lepidoptera* species composition in the Rungan landscape any further changes to the environment and its effect on fruit and *Lepidoptera* species can be quickly and efficiently monitored. However, when looking at the response of fruit and *Lepidoptera* species to external drivers, it is important to understand the habitat complementarity principle; that in order to protect the highest biodiversity in a landscape a network of habitats that have complementary species assemblages should be protected (Justus and Sarkar 2002; Dunlop 2013). This is especially prevalent in heterogenous landscapes, like the Rungan Landscape, where the established mosaic of habitats may lead to higher biodiversity than a homogenous landscape. This is due to multiple habitats likely having a higher availability of niches available to support a higher diversity of species. It is also important to investigate how the distance between survey plots could influence results and distributions. If the distance between survey plots is too small, then spatial autocorrelation may violate the assumptions of many statistical tests (Koenig 1999).

The Rungan landscape has three distinct habitats that are the focus of this survey: Kerangas, Mixed Swamp and Low Pole. These habitats were assessed to see if they influence the species composition of fruit and *Lepidoptera*. To survey *Lepidoptera* effectively, traps baited with fruit were used to draw in frugivorous *Lepidoptera*. To understand whether frugivorous *Lepidoptera* distributions are driven by habitat or the composition of fruit within each habitat, composition comparisons were undertaken to increase understanding on the influence of habitat type on community composition. It is important to consider how the composition of fruit and *Lepidoptera* species are impacted by habitat, as even if habitats all have similar species diversity and abundance, they might have different species compositions which would increase the biodiversity of the area (Dunlop 2013). Therefore, in chapter 3 the first question of does habitat affect species composition is asked, with the hypothesis that different habitats have a different composition of species. This is due to different habitats generally supporting different populations (Dunlop 2013). Question 2 starts to link *Lepidoptera* and fruit together to see if fruit composition is potentially affecting *Lepidoptera* composition. Question 2: Is similarity in fruit composition correlated positively with similarity in *Lepidoptera* composition? This study hypothesises that similarity in fruit composition will be correlated positively with *Lepidoptera* composition due to the assumption that different *Lepidoptera* will have preferences for certain fruit. Question 3 asks does geographical distance between plots affect similarity in species composition? It is important to note that there is a possibility that due to spatial autocorrelation survey areas that are closer together may have more similar species which could potentially impact results (Koenig 1999). It is also interesting to investigate whether habitat or distance has more of an impact on species composition as this could comment on the dispersal of the study groups between close by plots. Therefore, it is hypothesised that plots closer together will have more similar species composition regardless of habitat.

3.3 Methods

For survey site, data collection and creating morpho codes see section 1.2 Research Methods.

3.3.1 Hypothesis testing

All statistical tests, creation of matrices and plots were carried out using the ‘vegan’ and ‘Mass’ packages of R (R Core Team, 2021). Within *Lepidoptera*, butterfly and moth data were separated and tested individually due to the high number of moths potentially skewing the results in favour of moth patterns. Data from all the months were compiled to identify how the composition of species were affected by habitat. To check the hypothesis of question 1: Habitats will differ in species composition, a square matrix of pairwise Bray-Curtis dissimilarities among the plots was created for *Lepidoptera* and a Jaccard matrix for fruit. The dissimilarity matrices show how dissimilar the species of two plots are. The Bray-Curtis and Jaccard matrices were then ranked to carry out an analysis of dissimilarity (ANOSIM) statistical test.

ANOSIM tests whether within-habitat dissimilarities of pairwise plot comparisons are smaller than between-habitat ones, in other words, to see if species compositions are more similar within the same habitat types than between different habitat types. Dendrograms were also created to show how the similarity of compositions in plots cluster as well as creating a Multi – Dimensional Scaling (MDS) of the matrices to visualise any overlap of species between different habitats; the MDS plots were two dimensional. The Jaccard method was used for fruit as the fruit rarefaction curve, Figure 11, highlighted that there was a possibility that one species of tree could be in a plot fruiting and dominating the abundance data. The Jaccard method uses binary presence/absence data to prevent rarer species being masked by more dominant/common species. The Bray-Curtis method uses abundance data to compare the evenness of species.

Hypothesis for question 2: similarity in fruit composition will be correlated positively with similarity in *Lepidoptera* composition, was investigated by performing a Spearman's Rank Mantel Test on the Bray-Curtis and Jaccard dissimilarity matrices of fruit and *Lepidoptera*. This highlights whether there is a similar species composition of *Lepidoptera* as fruit. Again, butterflies and moths were separated and tested separately against fruit in order to show differences of butterflies that may be overshadowed by moths.

Hypothesis for question 3: plots closer together will have more similar species compositions irrespective of habitat, was investigated by running a Spearman's Mantel test on the Bray-Curtis and Jaccard dissimilarity matrices of fruits, butterflies and moths with a matrix of geographical distances among the plots. The distance matrix was created in R (R Core Team, 2021) from the latitude and longitude points of each of the plots, see appendix V. Package 'geosphere' calculated the Haversine distance, the distance between two points on a sphere (Sinnot 1984), which became the distance matrix, see appendix VI. The distance between plots could influence results, spatial autocorrelation, and so it is important to test whether the distance between plots could be affecting the results.

3.4 Results

3.4.1 Question 1: Does habitat affect species composition?

Fruit

The ANOSIM test on the Jaccard matrix highlighted that fruit species within plots of the same habitat were significantly more similar than fruit in plots of different habitats (R= 0.849, P=0.001). The dendrogram shows how plots cluster together with more similar plots grouping together, Figure 16a. Low Pole has grouped completely separately from Mixed Swamp and Kerangas on the left side of Figure 16a. It is interesting to note that plots spatially closer (Figure 4, Appendix VI) are grouped together for example LP1 and LP2 and again with LP3 and LP4. Mixed swamp and Kerangas are more randomly spread out on the dendrogram than Low Pole plots with K3 being shown as separate from the other Kerangas plots.

The MDS plots of the Bray Curtis dissimilarity matrix visualises the species composition overlap between the different habitats and plots (Figure 17a). As supported by the dendrogram, Low Pole (LP plots) are clustered separately on the left side of the while Mixed Swamp and Kerangas have a small overlap (the ends of the branches are mixed between K and MS across the right side of the Figure), highlighting that Mixed Swamp and Kerangas share some similar fruit species. Running the above methods on each individual month shows varying differing overlap between Kerangas and Mixed Swamp with Low Pole staying separate.

Moths

The ANOSIM test on the Bray-Curtis matrix (R = 0.348, P = 0.003) highlighted that moth morpho codes within plots of the same habitat were significantly more similar than moths in plots of different habitats, although there was more overlap in species composition of moths than there was with fruit, as indicated by the lower R value. The dendrogram shows less clusters than fruit with different habitats interspersed with others (Figure 16a). Low Pole still stays mainly separate on the left side of Figure 16a however, LP5 is clustered with Mixed Swamp and Kerangas plots in the middle of the Figure. The moth MDS plot (Figure 17b) shows a higher degree of overlap than fruit (Figure 16b), showing that the species compositions are more overlapped sharing similar species across the habitats.

Butterflies

With the most overlap out of fruits, butterflies and moths the ANOSIM test (R = 0.169, P= 0.019) on the Bray-Curtis matrix showed that plots of butterfly compositions were statistically more similar to those plots in the same habitat than in other habitats. The dendrogram (Figure 16c) and MDS plots (Figure 17c) show overlap between the species compositions of each habitat.

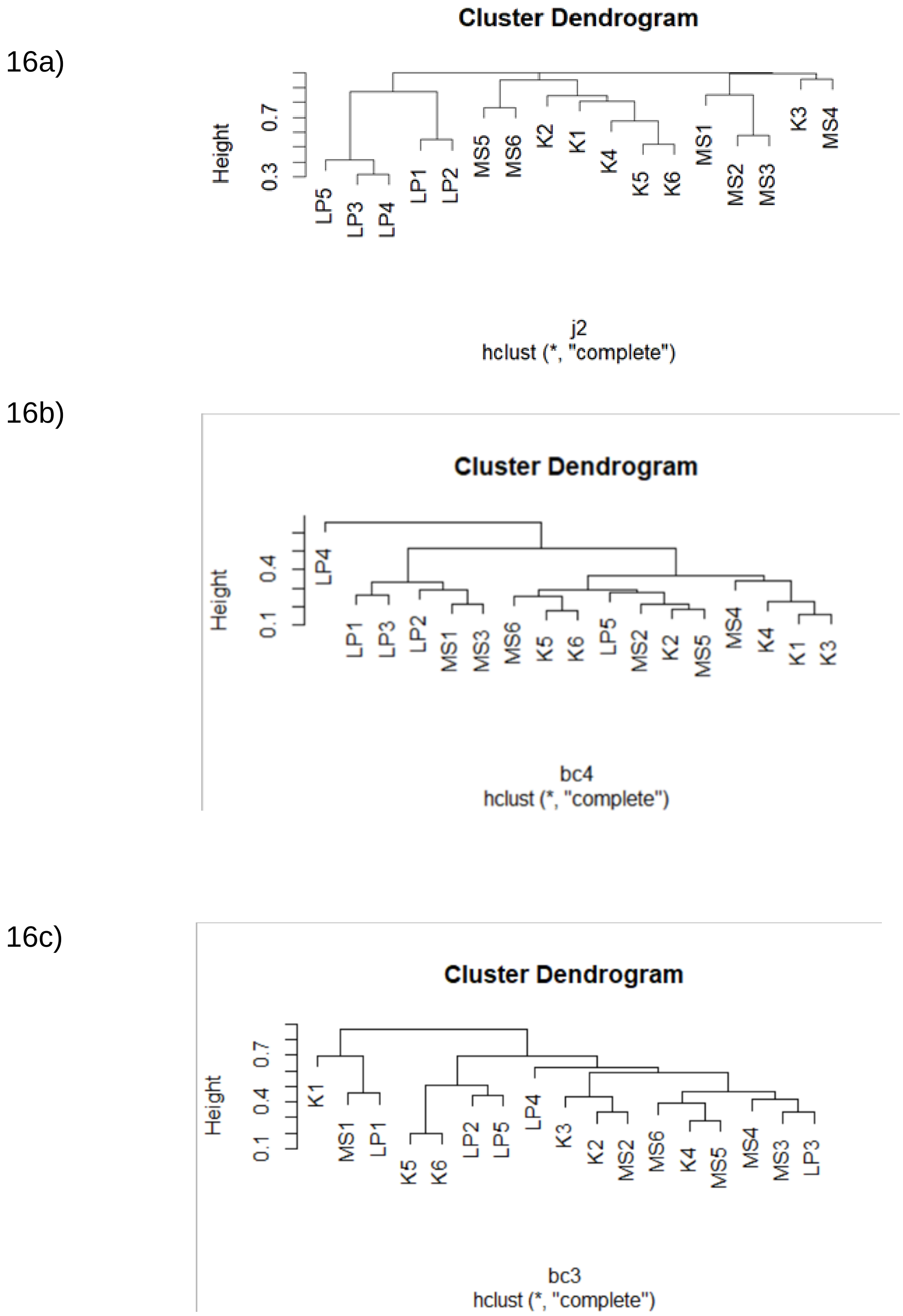
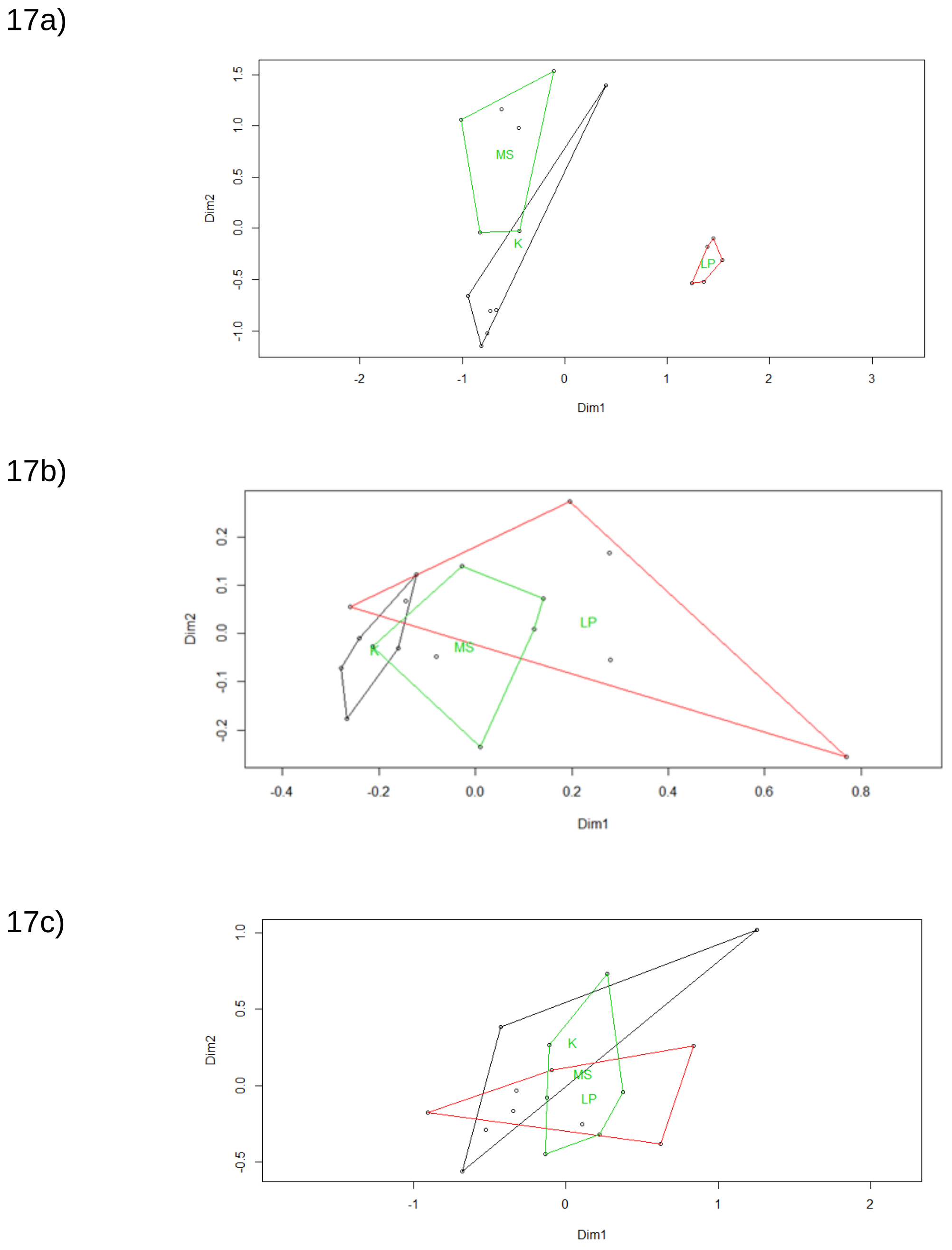


Figure 16: Dendrograms of the Jaccard dissimilarity matrix for a) fruit and dendrograms of the Bray-Curtis dissimilarity index of b) moth species c) butterfly species. Each label at the end of the branch represents an individual plot/repetition. Key: LP = Low Pole, MS = Mixed Swamp, K = Kerangas and each number represents a repetition.


17a)

17b)

17c)

Figure 17: 2D multidimensional scaling of analyses (MDS) of dissimilarity on a Jaccard matrix for a) fruit morpho codes and 2D MDS of dissimilarity on a Bray-Curtis dissimilarity index of b) moth morpho codes c) butterfly species. Habitat key: MS = Mixed Swamp, K = Kerangas and LP = Low Pole. Each point represents a plot and the lines join up every plot from the same habitat to show how composition of species overlap. Colour key: Green = Mixed Swamp, Black = Kerangas and Red = Low pole

3.4.2 Question 2: Is similarity in fruit composition correlated positively with *Lepidoptera* composition?

The Bray-Curtis dissimilarity matrices of fruit composition against butterfly composition, tested with a Mantel test, showed that fruit and butterfly composition were positively correlated (R = 0.191, P = 0.038) suggesting that plots that are more similar in terms of their fruit composition are also more similar in terms of their butterfly composition. The correlation between fruit and moths was also positively correlated and significant (R = 0.304, P = 0.004) highlighting that plots of fruit and moths group similarly in terms of their composition.

3.4.3 Question 3: Does distance between plots have an impact on species composition?

The Bray-Curtis matrix of fruit composition against the Haversine distance matrix, tested with a Mantel test, shows that fruit composition and distance were positively and significantly correlated (R = 0.337, P = 0.002). The positive correlation between butterflies and distance was also significant (R = 0.069, P = 0.011). Furthermore, the Bray-Curtis matrix of moth composition against the distance matrix shows that moth composition and distance are also positively correlated (R = 0.280, P=0.010). These results suggest that geographically closer plots were more similar in their species composition than plots further apart, irrespective of habitat. The design of the study was to ensure, when possible, that plots geographically closer together were not of the same habitat, and since habitat was not specifically accounted for in the statistical analyses it was generalised that the results of this question was not influenced by habitat. Therefore, overall, spatial correlation is likely affecting these results. The map, Figure 4, is used for ease to see how close plots are together, see appendix VI for the distance matrix.

3.5 Discussion

The results of the study indicate that habitat does affect species composition of fruit, moths and butterflies. It also suggests that fruit species composition could be influencing *Lepidoptera* species composition and finally, that there was spatial autocorrelation between plots, with geographically closer plots having more similar species compositions than more distant plots.

Question 1: Does habitat affect species composition?

Fruit

Habitat was found to affect species composition in each of the study groups and therefore the study can accept the hypothesis that habitat type influences species composition. Habitat seems to have the largest effect on the species composition of fruit, compared to *Lepidoptera*, with nearly no overlap between fruit species found in each habitat, Figure 17c. It is likely that this is due to tree composition as variation in tree species between habitats would subsequently produce different fruit. However, this could not be determined in this study as the scientific names of trees are not yet known in this area and so trees were not factored into data collection. It is also possible that tree composition was similar between habitats and the composition of fruit was instead influenced by tree species fruiting in different habitats during the study period. Tree species do not always produce fruit regularly and even rarer mass fruiting of many forest trees in Borneo is unpredictable (Kettle et al. 2010). Therefore, a longer study period, perhaps spanning over two years, may be more suitable to greater understand how fruit composition is dispersed and affected by a heterogenous habitat landscape across the year.

Lepidoptera

Habitat type was found to affect both moth and butterfly composition, Figure 17b and 17c. Although there was big overlap of the MDS plots for butterflies, the ANOSIM test found that the composition of *Lepidoptera* was more similar in plots within the same habitat compared to plots within different habitats. This could be due to *Lepidoptera* being specialists to the niches present within a specific habitat. It could also be due to some butterflies having small home ranges, although this is unlikely as some *Nymphalidae* butterflies have been reported to frequently move distances up to 2km between sampling plots (Marchant et al. 2015). This movement of butterflies could be why butterflies show the most overlap in species composition than fruit and moths as they could be more likely to move between habitat types. However, since butterfly composition is more similar within the same habitat than in other habitats, it could show that butterflies still have a habitat preference but will fly between habitats. It could also be likely that plant diversity of the habitat is driving *Lepidoptera* distribution, which is supported by Delabye et al. (2020). The species of moths and butterflies could vary between habitats due to a variety of reasons. For example, the specific ecological and environmental conditions of a habitat could meet their needs, an example being the fact that a habitat may possess the correct larval host plant, food source for adult *Lepidoptera* or canopy structure (Valtonen et al. 2013; Beirao et al. 2017). The distribution of some species of butterflies in particular are known to be positively influenced by the open nature of canopies in some habitat types, with a preference to more open canopies (Santos et al. 2019). Studies have also found that the spatial composition of *Lepidoptera* can vary due to temperature change or seasonality (Devries and Walla 2001). Therefore, further studies should investigate how the composition of fruit and *Lepidoptera* change throughout the annual cycle and identify the abiotic factors within an environment, such as temperature, that influence this spatial variation. Furthermore, future studies could focus on the specific beta diversity turn over and how this aids in increasing the biodiversity of a region, as in some areas it is the turnover that is the main source of variation in beta diversity (Checa et al. 2013; Pereira et al. 2017). The more dissimilar two plots are in species assemblage the higher the beta diversity of the two plots and therefore higher overall gamma diversity in the region. Again, it is stressed that multiple habitats within a landscape will have higher biodiversity than a landscape monopolised by one habitat, which is shown through the low overlap of species composition between habitats as seen in Figure 17 (Williams et al. 2006). A previous study found that species composition is affected by habitat type, fragment area and distance between sampling plots (Melo et al. 2019) and that to effectively conserve butterfly communities, the protection of a connected and heterogenous landscape is needed. Evidence suggests that butterfly communities are not randomly structured, and their distribution depends heavily on local and landscape effects (Pereira et al. 2017). We can assume a similar effect on moths due to species composition also being more similar within habitat types. The larval host of *Lepidoptera* could explain why there are different compositions in different habitats. Similarities between adult and larval feeding have been observed in *Lepidoptera* (Altermatt and Pearse 2011) and therefore both butterflies and moths could be found within specific habitats that host their larval food source. This could explain the correlation between fruit species composition and *Lepidoptera* composition. Future surveys could explore the relationship between the larval food source and the adult food source within the Rungan to see if this is a driver of *Lepidoptera* distribution.

Conclusions

Since each habitat contained fruit and *Lepidoptera* that were not present within the other habitats studied, conserving all habitats should be a priority over one habitat that might seem more biodiverse. This highlights the habitat complementarity principle, that habitats within a landscape will complement each other and individual habitat species compositions will combine to increase the overall number of species within a landscape. Thus, when choosing areas to conserve the habitat complementarity principle should be considered to ensure the highest number of species possible is protected (Williams and Manne 2001).

Question 2: Is similarity in fruit composition correlated positively with *Lepidoptera* composition?

There is a relationship between fruit composition and *Lepidoptera* composition as similarity in fruit composition correlated positively with *Lepidoptera* composition. Or in other terms, the two species assemblages cluster in similar ways, see dendrograms in section 3.4.1. This suggests that fruit composition may drive the composition of *Lepidoptera* within a habitat. This could be due to the fact that there are certain fruits that the adult *Lepidoptera* feed off of, or that the larval host feeds off and the adults do not disperse and stay feeding on the same fruit, or on other fruits, within the habitat (Altermatt and Pearse 2011). It is also possible there is an alternate factor that could be driving both fruit and *Lepidoptera*, such as habitat condition. Further surveys potentially manipulating the fruit present in an area could further investigate whether fruit is the main driver of *Lepidoptera* populations over other factors.

Question 3: Does distance between plots have an impact on species composition?

The mantal tests on the fruit Jaccard dissimilarity matrix and the *Lepidoptera*'s Bray-Curtis dissimilarity matrices against the Haversine distance matrix were all statistically significant. This shows that plots that are geographically closer were more similar in their species composition, regardless of habitat. This suggests that distance between plots has an effect on species composition. For butterflies, this could be because they are highly mobile and can easily fly through various close habitats, even if they do not contain suitable resources. *Nymphalid* butterflies have been found to disperse from 500m to 870m (Marini-Filho and Martins 2010) and within highly heterogenous habitats there is likely to be movement through habitats to access preferred habitat. While distances between plots in this study were on average 1445m apart, the shortest distance between plots was only 299m, which is well within *Nymphalid* butterflies flying range, appendix VI for more information on the distances between plots. Therefore, butterflies and moths could have similar compositions to closer plots, irrespective of habitat, due to being able to be mobile throughout the landscape. It could also be argued that fruit similarity in closer plots could be due to the dispersal of seeds to nearby plots leading to similar species of trees also being similar in nearby plots. In addition, because ground fruit surveys were used the similarity between close by plots could also be from animal dispersers moving fruit between plots or potentially when the ground is flooded fruit could float to another habitat with large connected flooded areas. Canopy fruit surveys in future studies would be able to mitigate this dispersal possibility. However, the consistent results of similarity between close geographical plots could also show that all three study groups showed spatial correlation between plots, therefore spatial correlation needs to be considered when discussing results. Spatial correlation occurs when ‘values of a variable sampled at nearby locations are more similar than those sampled at locations more distant from each other’ (Liebhold and Sharov 1998). Spatial correlation within study data may lead to statistical tests becoming invalid as it would violate the assumption that each plot is independent (Koeing 1999). In a study by Swengel and Swengel (2005) it was found that sites less than 3km apart had the strongest spatial correlation and this decreased with increasing distance between sites. This highlights the importance of surveying plots that are as geographically distant from other plots as logistically possible to ensure the most accurate representation of the species present within a landscape. Within this study plots were placed as far apart as logistically possible, but it is important to note that spatial autocorrelation between plots could be affecting the results. Unfortunately, while some plots were over 3000m apart, a few plots were at low as 299m apart, see Appendix VI. This means that in the survey, plots were potentially not spread out enough. Therefore, in future surveys, if possible, it would be important to survey plots with greater geographical distance between them. However, this study had been designed so plots near each other would most often be different habitats. Therefore, we can be more confident that results in this study are due to habitat type rather than spatial autocorrelation. Although this must be done with caution as overall, there is some spatial correlation within this study and so there must be caution when interpreting results. Furthermore, even if there was no spatial autocorrelation between plots the fact that distance could have more of an influence on fruit and *Lepidoptera* species assemblage means focusing on one small area to survey may miss potentially vital species. This could potentially misinform any future conservation strategies and could lead to the less suitable habitats receiving protection or mitigation against anthropogenic influences over more suitable habitats.

Chapter 4: General Discussion and Recommendations

There were 12 species of butterfly that had not previously been identified and listed in the last published report of the research site (KHDTK Report 2016-2017), Table 1. The fact that butterflies identified in the current survey were not previously listed suggests that there is a high number of butterfly species undescribed in the area. The new moths and detailed fruit and moth morpho code ID guides from this study further expand and add to the baseline of what species cohabit the KHDTK study site in the Rungan landscape. These factors stress that the Rungan landscape is an important area to conserve and continuously monitor in order to fully understand the extent and response of species found within the area. This baseline can aid in further monitoring of the area to aid in the conservation of species. Any shifts or loss of species due to natural events or human activities will therefore be easier to identify. Having a baseline of species is important to understand the ecology of an area and to help focus conservation strategies. The results of this study complete the aims to investigate how habitat type and month affects community structure of fruit and frugivorous *Lepidoptera* in a tropical landscape. Through the results, a deeper understanding of fruit and *Lepidoptera* patterns in the heterogeneous KHDTK study site in the Rungan Landscape, Indonesian Borneo, is gained and the knowledge gap of spatial and temporal variation in the community of frugivorous *Lepidoptera* and their fruit resources has been addressed. Understanding how the mosaic of habitats between months affects fruit and *Lepidoptera* community structure, and composition can aid in future conservation management strategies. The results show that a mosaic habitat landscape increases overall diversity in the area and through habitat complementarity habitats, provide different resources at different times which increases the number of species a landscape can support. Therefore, it is important to focus conservation management strategies that aim on protecting all habitats within a mosaic landscape and not just one habitat that is thought to be more biodiverse, which would result in the highest amount of biodiversity maintained and protected. It is also important to understand the ecological drivers of populations like *Lepidoptera* to identify the drivers of their distribution and composition.

The main results are as follows: Fruit abundance is influenced by an interaction between habitat and month, reflecting that temporal patterns do vary between habitats. Fruit diversity is influenced by habitat but not by month while fruit richness is not affected by habitat or month. Butterfly abundance is influenced by month but not by habitat while butterfly species richness is not explained by either habitat or month. Moth abundance and species richness are both influenced by habitat type and by month but there is no interaction and so there is no variation in temporal patterns between habitats. *Lepidoptera* diversity, both butterflies and moths, are not influenced by either month or habitat. The results highlight that fruit, butterflies and moths are all influenced by habitat type and month differently. Fruit abundance in particular shows that that habitat complementarity is in play, in this landscape, with certain trees producing higher abundance of fruit in certain habitats across the different months. Another explanation could be that one or two tree species in each habitat had a period of fruiting in different months, for example Code 73: Jumbu-Jumbu in August dominated the abundance totals of the habitat Low Pole but was not seen in any other months or habitats. This suggests that fruiting occurs in different months for different species in the Rungan Landscape and future surveys encompassing at least two years should be carried out to truly understand fruiting patterns and be able to properly document the total fruiting events of the species in this landscape. The results of the study also suggest that fruit abundance, richness and diversity are not drivers of *Lepidoptera* abundance, richness or diversity. However, fruit composition could be a driver of *Lepidoptera* species composition. This could be due to there being a very specific fruit that a *Lepidoptera* feeds on and this fruit is not reflected by an increase in abundance, richness or diversity. In other terms, *Lepidoptera* may feed on one or two fruit within a habitat that are not reflected by other highly abundant fruit species. Further research is needed to determine whether this is the case and should investigate the specific fruits adult *Lepidoptera* species are feeding on within the landscape. The results of the study also indicate that habitat type does affect the composition of fruit, moth and butterfly species, with species composition being more similar within habitat type than between different habitat types. This highlights that each study group has preferences for certain habitats, although the slight overlap for *Lepidoptera* between habitats show that they are potentially using multiple habitats. The use of multiple habitats by *Lepidoptera* supports the habitat complementarity principle that the landscape is providing resources at different times in different areas in order to support a higher overall biodiversity. Dunlop (2013) suggested that the complementarity principle is the most effective conservation method regarding protecting diversity and a large number of species from climate change. Therefore, the mosaic of habitats in the Rungan Landscape should all be protected to not disrupt the habitat complementarity effect and keep the overall diversity of the Rungan Landscape high. The final main results look into spatial autocorrelation between the plots and it was discovered that plots that were geographically closer together were more similar in their species compositions, irrespective of their habitat. This shows that there was some spatial autocorrelation between plots. However, the study was designed to ensure, as much as possible, that plots next to each other were different habitat types, so we can still be confident that the effect of habitat found within this study is significant. Although, it is important to apply caution when discussing the results and future studies should ensure that plots are spaced further apart.

There are limitations to any study, and these are discussed below:

The full diversity of the area has perhaps not been fully described for *Lepidoptera* communities as previous studies in tropical rainforests have found that short term sampling solely in the understory can lead to inaccurate estimates of *Lepidoptera* populations (Molleman et al. 2006). Previous studies have confirmed that investigating vertical stratification will reveal higher biodiversity with significant numbers of species found separately in the canopy to the understory (DeVries and Walla 2001; Tangah et al. 2004), stressing that to fully understand diversity of a landscape the vertical stratification of tropical rainforests should be taken into account to ensure biodiversity is not underestimated. However, recaptured butterflies between traps in the understory and canopy included in the studies described by Tangah et al. (2004) suggest that species are confined to certain heights. Therefore, this study can confidently say it has examined community compositions of *Lepidoptera* in the understory and perhaps future surveys could incorporate higher canopy traps to more accurately describe the full diversity and composition of *Lepidoptera* within various habitats in this tropical forest landscape. For the purpose of this study to understand whether habitat type and month affects community structure, it was deemed appropriate to focus survey effort on more plot repeats of the same habitat rather than incorporating canopy traps to fully grasp how habitat type affects populations. Furthermore, in preliminary surveys of this study canopy traps in this area were found to be less reliable with higher escape rates of the study species before identification was possible, which was due to the time needed to lower traps. Therefore, it is also implied that if future studies choose to use traps in the canopy, that they devise a method to ensure trapped species cannot escape the net as it is lowered. Another limitation to consider is not incorporating the influence of other nearby habitats as Fermon et al. (2005) through comparative studies has stressed the importance of incorporating the influences from nearby habitat patches in the surrounding landscape mosaic as this could affect community composition, i.e. considering the scale at which sampling is carried out. Since the KHDTK study site is surrounded by further mosaic of similar habitat types it is determined that the influence of the wider scale of the region has already been considered. Although not all habitat types or sub habitat types were evaluated in this survey and so there could be unknown influence on results from another habitat or a sub habitat of one of the habitats surveyed. Therefore, future surveys could be more thorough and investigate all habitat and sub habitat types. For the purpose of this baseline survey, the three main habitat types have been surveyed and deemed appropriate to answer the questions posed by this project.

Survey method limitations include the possibility that traps were not left out for long enough, this study set out traps for periods of five days at a time, while others used longer ranging time frames from seven to eleven days (Purwanto et al. 2015). The species rarefaction curves for each of the study species were beginning to plateau, Figure 7, which suggests that a high proportion of species were recorded in the time frame. If the traps were left for longer, the Chao species estimates show that more species would have been found in each of the habitats. However, preliminary surveys carried out in the month of March before the survey determined only five days were needed to capture a good representation of the *Nymphalidae* and fruit feeding moth populations and the fact that the species rarefaction curves start to plateau help corroborate this. There was also a possibility that spatial autocorrelation affected results as plots that were closer together had more similar species, which could be due to plots within the survey site being too close together. Logistically, it would be hard to space these plots any further apart, but it does stress the need for future surveys to place plots geographically further apart if possible to avoid skewed results. Overall, it has already been discussed that perhaps a five month study is too short to fully capture the effect of temporal variation on fruit and *Lepidoptera* species compositions and community structures as previous studies have found longer cycles and variation across many years (Molleman et al. 2006; Harrison et al. 2010; Grøtan et al. 2012).

Within this project, *Lepidoptera* have been used as a general indicator for how other taxa in the environment may respond to habitat and month as it is well documented that *Lepidoptera*, especially butterflies, make great bioindicators and are often used in studies as such (Kerr et al. 2008; Bonebrake et al. 2010; Whitworth et al. 2018). However, the disparity between the results of butterflies and moths within this study, especially for factors like abundance and species richness, highlight that potentially butterflies are not the best indicator of moth patterns and vice versa in this area and therefore, potentially will not be able to confidently indicate how other taxa would respond to external factors. There are studies that agree that *Lepidoptera*, like butterflies and moths, cannot truly be a good indicator for other taxa due to different morphological adaptions of each taxon influencing the response of species (Schulze et al. 2004). A study also investigating how frugivorous moth and butterfly communities differ in response to habitat structure highlighted that even though the two groups are closely related, they did also differ in their responses (Delabye et al. 2020). Therefore, the generalisation that butterflies can be used as an indicator for moths should be taken with caution. Single taxon studies are perhaps not able to fully act as indicators for other groups, even similarly related groups. Therefore, this stresses the need for multi taxon surveys to fully understand how each taxon reacts to habitat type and temporal variation if the aim of future studies is to understand an overview of taxa within a landscape. In light of this, results from this study can only be related to the specific study group and *Lepidoptera* results will not be used to make comments of other taxon within the Rungan landscape. In other studies, trees are found to be a good predictor for fruit feeding butterflies in Schulze et al. (2004), but throughout the paper it is stressed that very few taxonomic groups are good predictors for others. It has however also been discovered that *Lepidoptera* can be used to predict *Hymenoptera* populations (Kerr et al. 2008), again suggesting that *Lepidoptera* in certain cases can be used as indicators reasonably for other taxa. This conflicting literature suggests that using *Lepidoptera* as general bioindicators needs to be decided with caution and on a case-by-case basis, depending on the taxa present and the studies aims. For this project’s aims of a quick and effective community structure survey linking frugivorous *Lepidoptera* with fruit, it is appropriate but perhaps should not be used to suggest how other taxa may react to month and habitat type.

In this study, only fruit species composition, the specific fruit assemblages, among the different habitat types seems to drive *Lepidoptera* composition, specific *Lepidoptera* species assemblages, it could be determined that fruit could be used as an indicator for *Lepidoptera* species composition but cannot be used as an indicator for measures such as diversity, richness and abundances of *Lepidoptera*. This will only be true after a more in-depth investigation to what specific fruit morpho code or set of morpho codes the *Lepidoptera* are specifically feeding on, or using in some way. Therefore, future research could potentially focus on attack surveys to see which specific fruits in the landscape the *Lepidoptera* feed from, a recommended survey would loosely follow Ctvrtecka et al. (2016) where they determined which qualities of the fruit influenced the probability that fruit would be attacked by an insect frugivore. Phenology, overall, has previously been described as a ‘key adaptive trait in shaping species distribution’ and that in changing climate conditions it is an adaptive trait prone to evolve rapidly (Chuine 2020). Therefore, it is key to monitor phenology, such as timing of fruiting, to understand in a broader context how climate change could affect species distribution across specific landscapes. With continued monitoring of fruiting and research investigating the response of *Lepidoptera* to changing pressures these surveys could guide conservation management practices in the Rungan landscape.

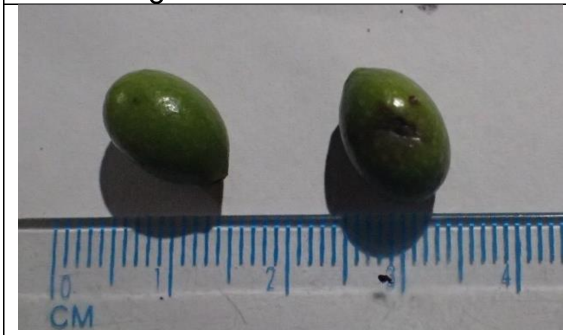
The overall recommendation of this study is that future conservation management strategies in the Rungan landscape should focus on protecting all habitats within the mosaic landscape, rather than just one high quality habitat type in order to protect the effect of habitat complementarity in the landscape. This is supported by the fact that not one individual habitat in this study was shown to be more vital to fruit or *Lepidoptera* species community structure than another. This will keep the overall diversity of the region high, as different habitats support different species composition. The reason to aim for promoting continuation of high biodiversity is to decrease possibility for any population declines or local extinctions (Gaston 2000) and to ensure that no key species are lost that could lead to further declines in essential ecological processes, or cause cascades of population declines across taxa that rely on these key species (Molina-Martinez et al. 2013). In terms of ecological monitoring, it is important to be able to observe these communities after natural events like fires or fragmentation due to pressures such as logging or mining (Gaveau et al. 2014). Having this baseline survey of an intact rainforest landscape will help show how future communities are affected by these pressures and guide any further conservation that might be needed. Since this survey was undertaken, Borneo rainforests have had a major forest fire event, similar to the one in 2015 (Latifah et al. 2019). It would be interesting to complete a similar survey again to see whether species composition has been affected in the aftermath of these forest fires. Generally, the composition of *Lepidoptera* communities tends to change between specialist to generalist species, after a forest fire (Houlihan et al. 2013; Cleary and Genner 2004) and overall *Lepidoptera* diversity decreases, favouring more generalist species that utilise the new open canopy (Cleary 2003; Cleary and Genner 2004). This again highlights the importance of this survey as a foundation to help aid future surveys to determine the influences of such events on community structure. This survey, along with support from the wider literature, shows that patterns of fruiting and *Lepidoptera* cannot be successfully surveyed in a five-month period. It is therefore recommended that longer-term studies are undertaken to further understand the influence of habitat type and month on fruit and *Lepidoptera* community structure and potentially further support the findings of this study. Since fruit abundance, richness and diversity are not found to be drivers of *Lepidoptera* abundance, richness or diversity in this study, future surveys could instead investigate variables such as precipitation, temperature and larval host plants to aid in the understanding of extrinsic drivers that influence the abundance and diversity of *Lepidoptera* in this landscape. The overall conclusion of this study, in the KHDTK study site, is frugivorous *Lepidoptera,* and their fruit resources are mostly influenced by habitat type and that the heterogeneous landscape could be leading to greater overall species diversity of the region, and therefore the principal of habitat complementarity stresses that all the habitats within the mosaic of the Rungan landscape should be protected.

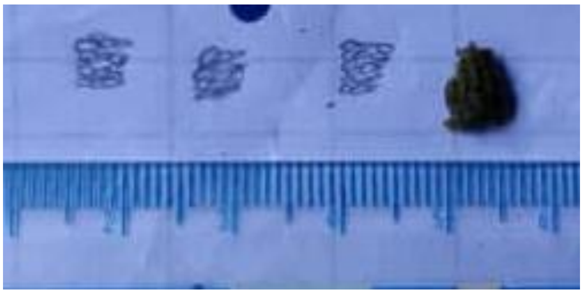
Appendix I: Morpho Code Fruit ID Guide

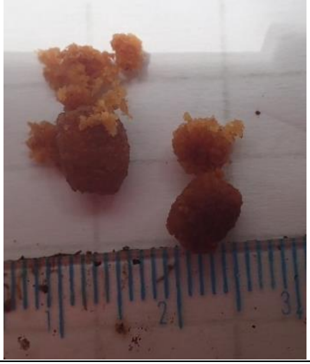
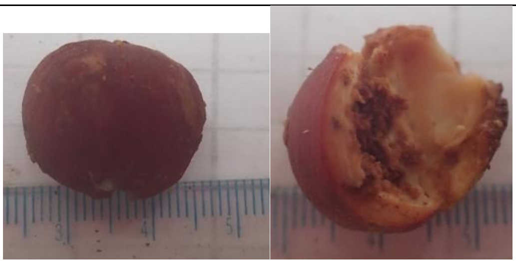
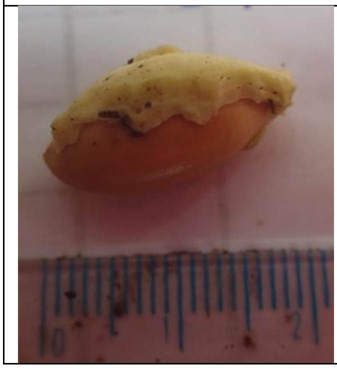
Further photos, written descriptions from the field and average width and length of the fruit are available for future surveys

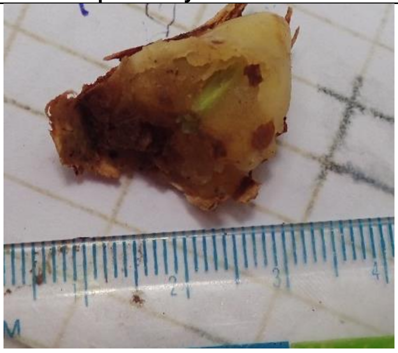
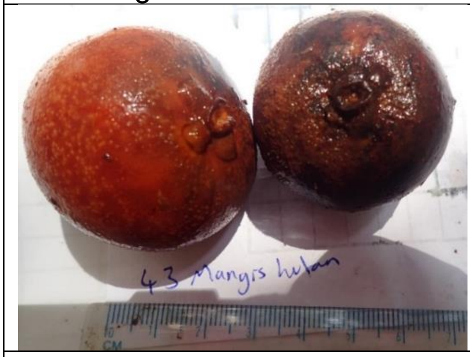
1: Kapurnaga laut	2:Jinjit
	
3: Lutan	4: Pilou
	
5: Kumpang	6: Ehang Samtou
	
7: Sartak nyaring	8: Gantalang
	

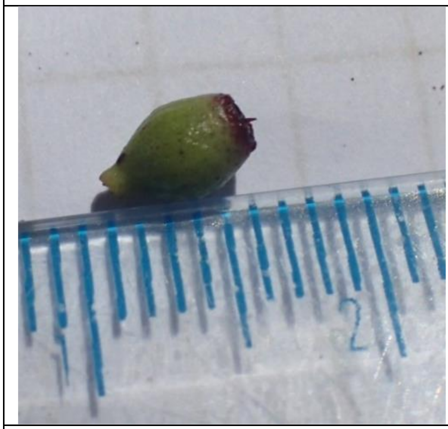
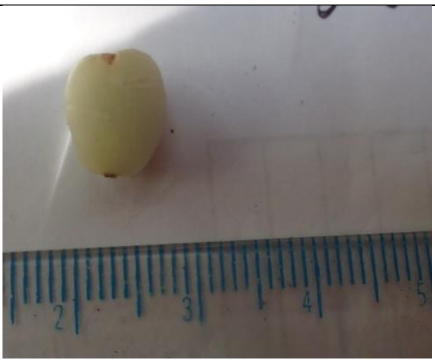
9: Myatu gagas	10 : Tabunter dan kechil/ Gorinia
	
11: Lutan when small	12: Tumih comb retocorpus rutundatus
	
13: Flower	14: Lapak
	
15	16: Bintah
N/A	

17	18: Jambu-jambu
N/A	
19: Little green	20: Mahalilis
	
21	22
	
23: Katiau	24: Little pink
	

25: Fagaceae	26: Little Orange
	
27: Longish	28: Bright Bitty Green
	
29	30
	
31	32
	

33	34
	
35	36: Lunkuk
	
37	38
	
39	40
	

41: Tabulous bumung	42: Keput bajuku
	
43: Mangis hutan	44
	
45	46: Lintit myamuk
	
47	48: Sasundur
N/A	

49	50
	
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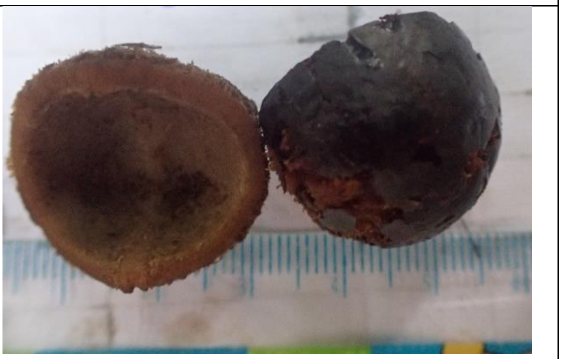
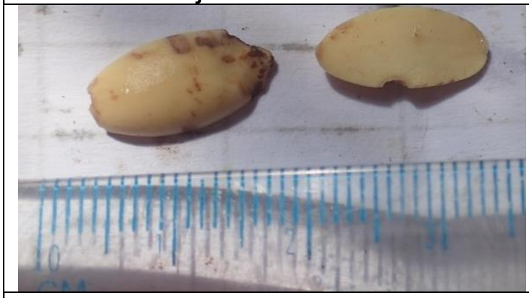
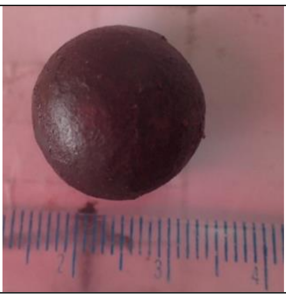
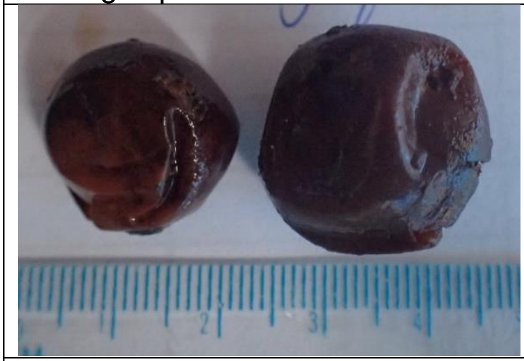
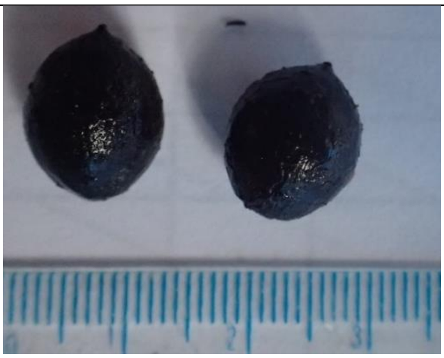
	
53: Katiau biji	54
	
55: Smaller pink	56: Black with stalk
	

57	58: Panpaning
	
59: Big Squish	60
	
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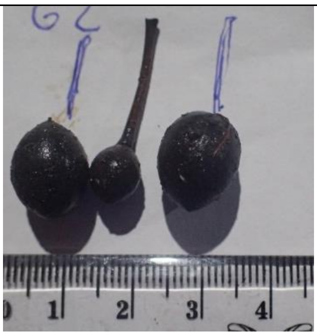
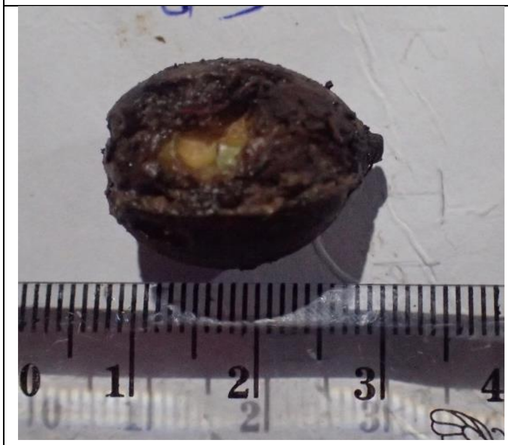
	
63	64: Tagaron
	

65	66: Oyang
	
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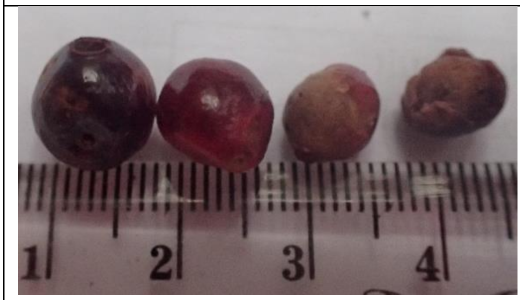	
75: Nonang	76
	
77: Karipak	78
	
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83: Lutan	84
	
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	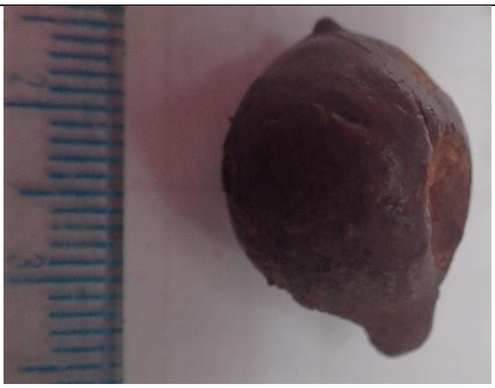
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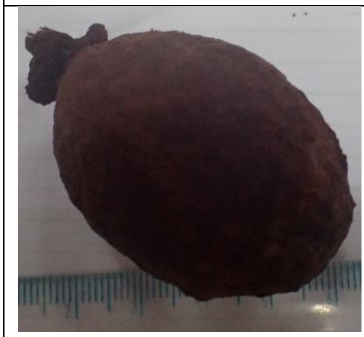	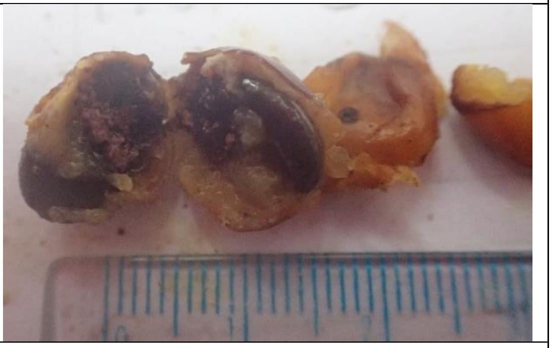
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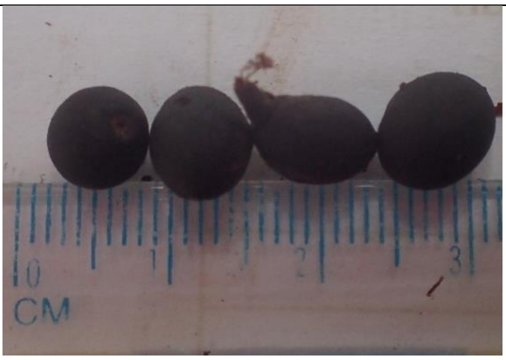
98: Katiau Kayu	99
	
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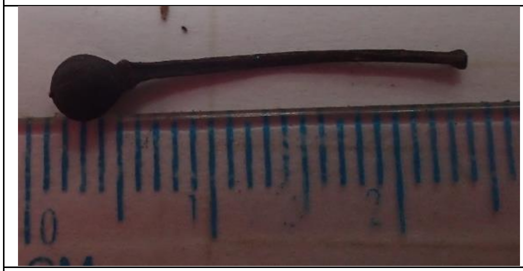
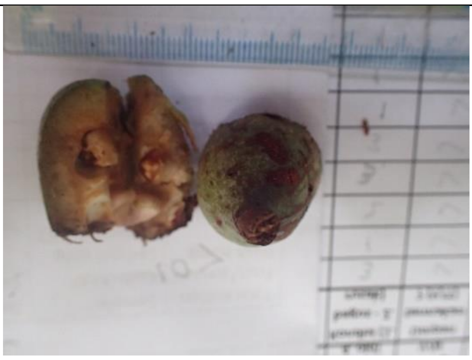
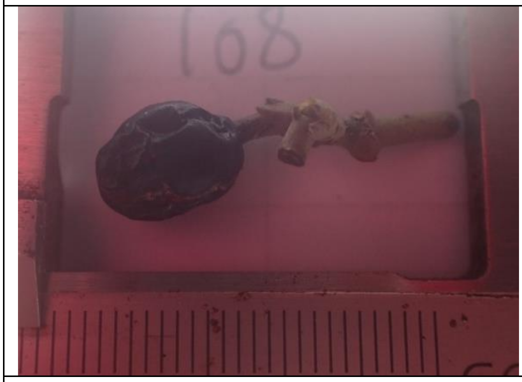
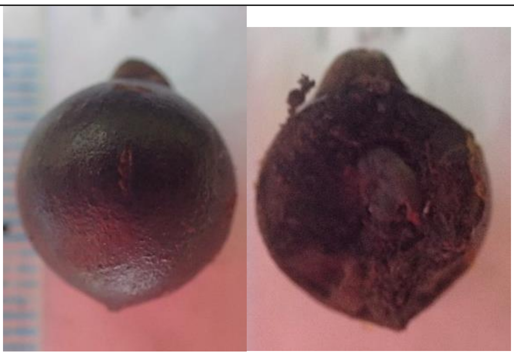
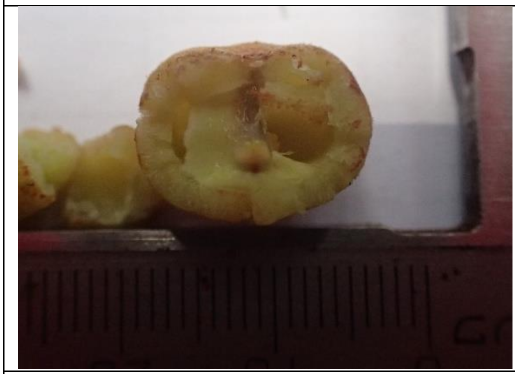
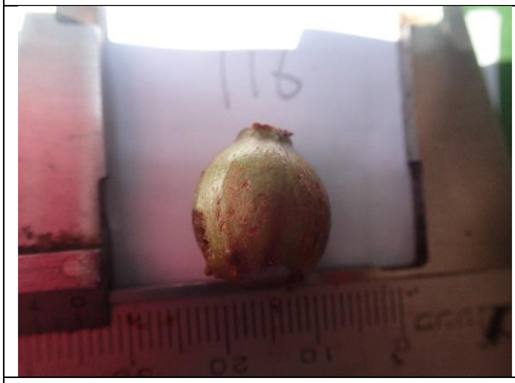
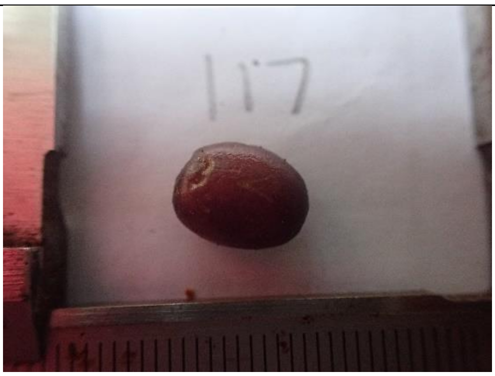
	
102	103
	
104	105
	

106	107
	
108	109
	
110 Big Pilau	111
	
112	113: Tagarun
	

114: Gandis	115: Kumpang
	
116: Putat	117
	
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Appendix II: Moth Morpho Code Guide

Further photos, written descriptions from the field and average body and wing lengths are available for future surveys

*morpho codes 1-17 described by BNF Guide

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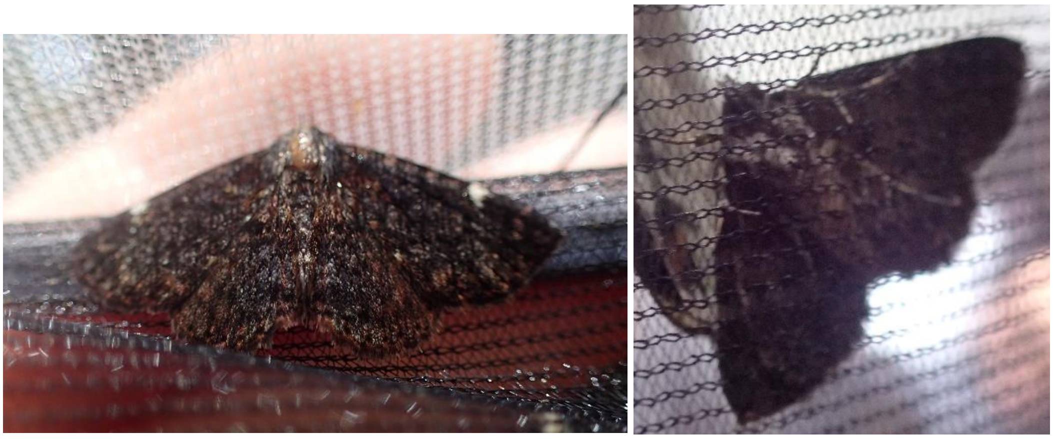

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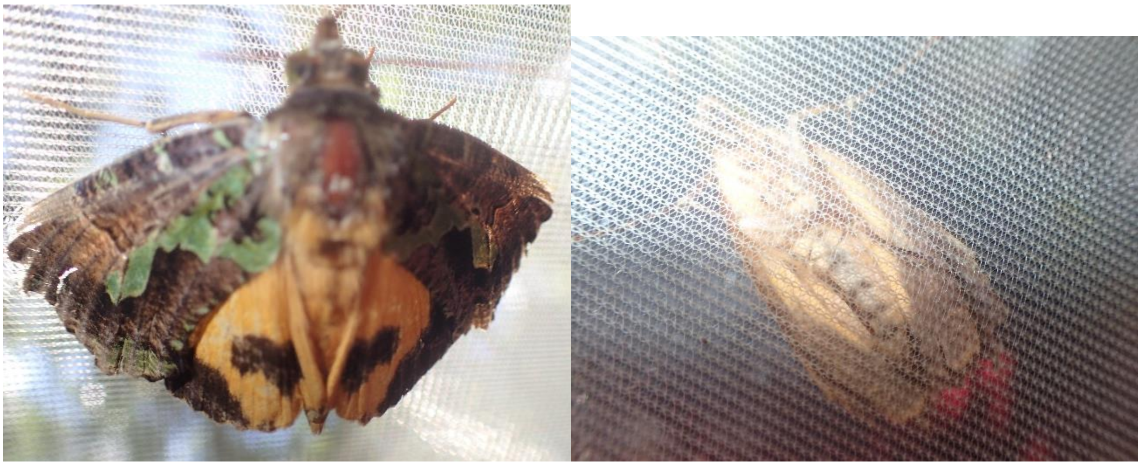

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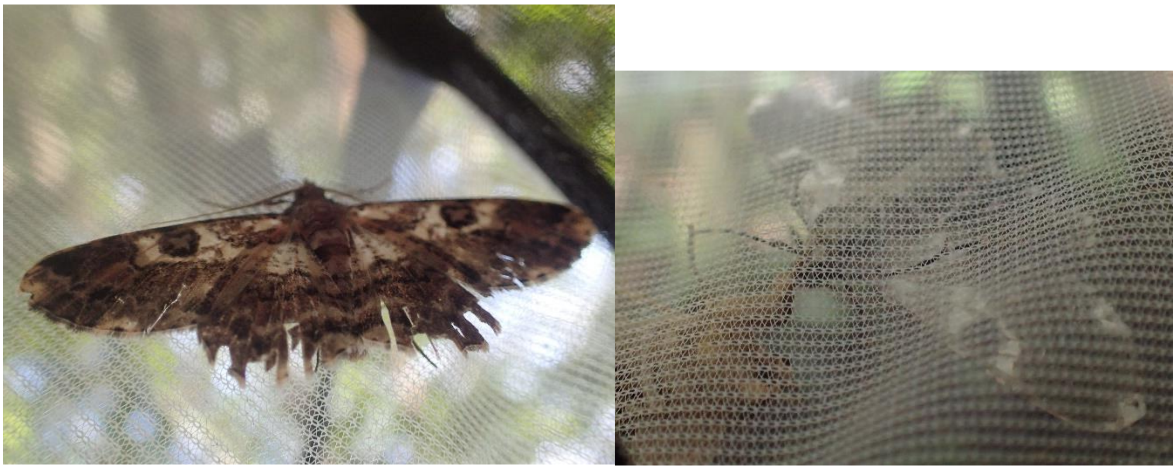

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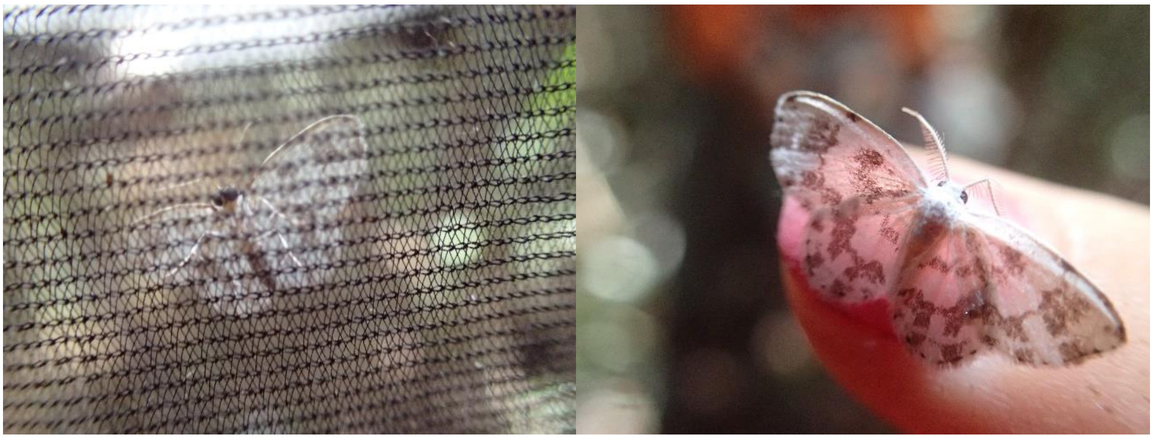

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Appendix lll: New Butterfly ID guide

List of butterflies not previously identified in the Rungan Landscape- Visual written descriptions and average wing and body length available for each species

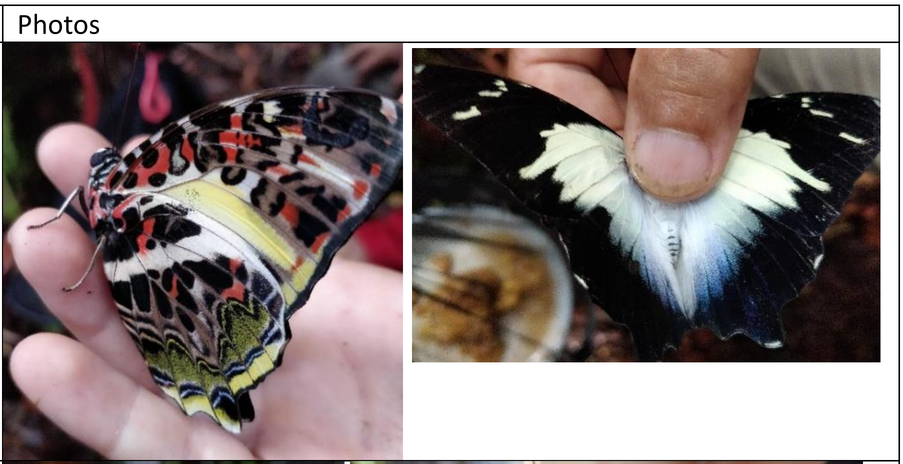
Latin name	**Photos**
Lexias canescens	Male  Female 
Lexias cyanipardus	Male  Female 
Polyura hebe	 
Faunis stomphax	 

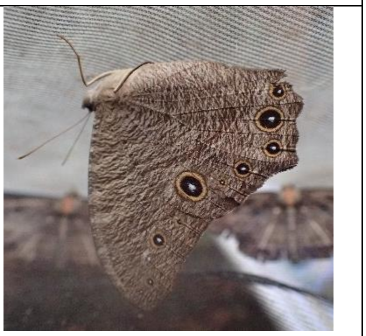
Thaumantis noureddin	
Amathusia phidippus	
*Zeuxidia orange**	
*Zeuxidia blue**	

Tanacia godartii	 
Coelites euptychioides *euptychioides*	
Tanaecia iapis	
Thaumantis odana *cyclops*	

Appendix IV: Butterfly ID guide of butterflies

List of butterflies identified in this survey that have previously been identified and listed in the KHDTK Report 2016-2017. Visual written descriptions and average wing and body length available for each species

Latin name	Photos
Agatasa calydonia	
Charaxes bernardus	
Charaxes borneensis	
Charaxes solon	N/A
Dophla evelina	
Euthalia monina	N/A

Lexias pardalis	 
Melantis leda	 
Mycalesis pitana/patiana/anapita	
Prothoe franck	 

Tanaecia clathrata	  Male Female
Tanaecia munda	 
Zeuxidia aurelius	 
Zeuxidia doubledayii	 

Appendix VI: Latitude and Longitude of plots

Key:

K = Kerangas

MS = Mixed Swamp

LP = Low Pole

Numbers: To differentiate between plots of the same habitat

Plot name in Study	Number of BNF plot	Latitude	Longitude
K1	40	-1.6599	113.747
K2	46	-1.6651	113.75
K3	24	-1.6561	113.747
K4	9	-1.6548	113.755
K5	53	-1.6693	113.75
K6	15	-1.6686	113.754
MS1	50	-1.6646	113.754
MS2	38	-1.6609	113.758
MS3	42	-1.6522	113.757
MS4	31	-1.6448	113.758
MS5	13	-1.6711	113.752
MS6	48	-1.6716	113.761
LP1	41	-1.6644	113.761
LP2	33	-1.6667	113.763
LP3	43	-1.6528	113.762
LP4	5	-1.6554	113.765
LP5	17	-1.6715	113.767

Appendix V: Distance matrix of plots using Haversine Distance

This is the distance matrix with the plots as the column and row titles, values are in metres. The letters represent the habitat the plot is in and the numbers distinguish between different plots.

Key:

K = Kerangas

MS = Mixed Swamp

LP = Low Pole

	K1	K2	K3	K4	K5	K6	MS1	MS2	MS3	MS4	MS5	MS6	LP1	LP2	LP3	LP4
K2	668															
K3	423	1056														
K4	1055	1274	901													
K5	1098	467	1506	1707												
K6	1242	591	1594	1540	451											
MS1	938	448	1225	1096	686	445										
MS2	1229	1005	1335	756	1291	965	606									
MS3	1404	1633	1194	365	2056	1855	1420	974								
MS4	2079	2428	1755	1162	2868	2686	2248	1792	831							
MS5	1365	704	1760	1844	299	356	757	1317	2176	3002						
MS6	2030	1421	2324	1985	1250	847	1101	1237	2204	3001	1002					
LP1	1636	1226	1811	1260	1340	908	779	513	1429	2207	1248	801				
LP2	1934	1457	2135	1596	1475	1023	1028	852	1746	2500	1318	589	339			
LP3	1846	1912	1709	810	2270	1971	1586	1005	560	995	2321	2095	1296	1551		
LP4	2064	1987	2004	1114	2275	1912	1595	990	958	1413	2268	1857	1096	1277	441	
LP5	2572	2021	2809	2288	1907	1482	1637	1547	2419	3136	1669	667	1034	695	2154	1806

Appendix VII: Multiple pairwise Tukey test output

K= Kerangas, MS= Mixed Swamp, LP= Low Pole

Bold = significant

Fruit abundance

	April K	May K	June K	July K	August K	April MS	May MS	June MS	July MS	August MS	April LP	May LP	June LP	July LP
May Kerangas	1.0000		0.9979	0.9996	1.0000									
June Kerangas	0.9439			1.0000	1.0000									
July Kerangas	0.9750				1.0000									
August Kerangas	0.9971				1.0000									
April Mixed Swamp	0.8568	0.9806	1.0000	1.0000	0.9999									
May Mixed Swamp	0.8702	0.9838	1.0000	1.0000	1.0000	1.0000								
June Mixed Swamp	0.6538	0.8986	1.0000	0.9998	0.9970	1.0000	1.0000							
July Mixed Swamp	0.7526	0.9464	1.0000	1.0000	0.9993	1.0000	1.0000	1.0000	1.0000					
August Mixed Swamp	0.7282	0.9359	1.0000	1.0000	0.9989	1.0000	1.0000	1.0000						
April Low Pole	0.9885	0.9998	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000				
May Low Pole	0.9927	0.9999	1.0000	1.0000	1.0000	1.0000	1.0000	0.9999	1.0000	1.0000	1.0000			
June Low Pole	0.0192	**0.0053**	**0.0002**	**0.0003**	**0.0008**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**0.0001**	**0.0001**		
July Low Pole	0.9812	0.8686	0.2724	0.3461	0.5128	0.1139	0.1217	**0.0499**	0.0729	0.0662	0.1843	0.9773	0.3627	
August Low Pole	1.0000	1.0000	0.9991	0.9998	1.0000	1.0000	0.9808	0.8947	0.9420	0.9315	0.9984	0.9992	**0.0025**	0.8451

Butterfly Abundance

	April	May	June	July
May	0.7746			
June	0.9975	0.919		
July	0.9998	0.6795	0.9883	
August	0.0976	**0.0042**	**0.0449**	0.1389

Moth Abundance

	April K	May K	June K	July K	August K	April MS	May MS	June MS	July MS	August MS	April LP	May LP	June LP	July LP
May Kerangas	0.9960		**<0.0001**	0.2380	1.0000									
June Kerangas	**<0.0001**			0.1524	**<0.0001**									
July Kerangas	**0.0098**				0.0914									
August Kerangas	1.0000													
April Mixed Swamp	0.6015	0.5556	**<0.0001**	**0.0015**	0.7815									
May Mixed Swamp	1.0000	0.6015	**<0.001**	**0.0327**	0.9991	0.9960								
June Mixed Swamp	**0.0043**	0.0763	0.6015	0.9989	**0.0303**	**<0.0001**	**<0.0001**							
July Mixed Swamp	0.8564	0.9998	**0.0201**	0.6015	0.9948	**0.0098**	0.2380	0.1524						
August Mixed Swamp	1.0000	0.9168	**<0.0001**	**0.0119**	0.6015	1.0000	1.0000	**<0.0001**	0.0914					
April Low Pole	**0.0332**	**0.0413**	**<0.0001**	**<0.0001**	0.0984	0.7272	0.6348	**<0.0001**	**0.0027**	0.8395				
May Low Pole	0.9242	**0.0332**	**<0.0001**	**0.0007**	0.5804	1.0000	0.7272	**<0.0001**	**0.0487**	0.9997	0.9960			
June Low Pole	0.1960	0.7801	**0.0332**	1.0000	0.5588	**0.0046**	**0.0750**	0.7272	0.9981	**0.0305**	**<0.0001**	**<0.0001**		
July Low Pole	1.0000	1.0000	**0.0004**	**0.0332**	1.0000	0.8371	0.9997	**0.0309**	0.7272	0.9923	**0.0098**	0.2380	0.1524	
August Low Pole	0.7694	0.1887	**<0.0001**	**0.0002**	**0.0332**	1.0000	0.9464	**<0.0001**	**0.0189**	0.7272	1.0000	1.0000	**<0.0001**	0.0914

Moth Species Richness

	April K	May K	June K	July K	August K	April MS	May MS	June MS	July MS	August MS	April LP	May LP	June LP	July LP
May Kerangas	0.5107		0.0523	0.9395	1.0000									
June Kerangas	**<.0001**			0.8640	**0.0111**									
July Kerangas	**0.0101**				0.6751									
August Kerangas	0.8501													
April Mixed Swamp	0.2371	**0.0249**	**<0.0001**	**0.0003**	0.0795									
May Mixed Swamp	1.0000	0.2371	**0.0015**	0.1216	0.9825	0.5107								
June Mixed Swamp	0.2272	0.9997	0.2371	1.0000	0.9858	**<0.0001**	0.0523							
July Mixed Swamp	0.9835	1.0000	0.0844	0.2371	1.0000	**0.0101**	0.9395	0.8640						
August Mixed Swamp	1.0000	0.6171	**0.0003**	**0.0425**	0.2371	0.8501	1.0000	**0.0111**	0.6751					
April Low Pole	0.9110	0.2102	**<0.0001**	**0.0063**	0.4435		0.9981	**0.0199**	0.5098	1.0000	0.9894			
May Low Pole	0.9999	0.9110	**0.0243**	0.5712	1.0000	0.3457	0.9894	0.8009	1.0000	0.9966	0.5107			
June Low Pole	**0.0399**	0.9189	0.9110	1.0000	0.7066	**0.0001**	0.0507	0.9894	0.6411	**0.0154**	**<0.001**	0.0523		
July Low Pole	0.6913	1.0000	0.4590	0.9110	1.0000	**0.0144**	0.7480	1.0000	0.9894	0.4642	**0.0101**	0.9395	0.8640	
August Low Pole	1.0000	0.9782	**0.0068**	0.3015	0.9110	0.6251	1.0000	0.5258	0.9997	0.9894	0.8501	1.0000	**0.0111**	0.6751

Bibliography

Abood, S.A., Huay Lee, J.S., Burivalova, Z., Garcia-Ulloa, J. and Kog, L.P. (2014) Relative Contributions of the Logging, Fiber, Oil Palm, and Mining Industries to Forest Loss in Indonesia, *Conservation Letters*, *8*(1): 58-67.

Alamgir, M., Turton, S.M., Macgregor, C.J. and Pert, P.L., 2016. Assessing regulating and provisioning ecosystem services in a contrasting tropical forest landscape. *Ecological Indicators*, *64*, pp.319-334.

Altermatt, F. and Pearse, I.S., 2011. Similarity and specialization of the larval versus adult diet of European butterflies and moths. *The American Naturalist*, *178*(3), pp.372-382.

Andrew, E.E., Ndah, N.R., Bechem, E. and Lucha, C.F.B., 2020. Soil Physico-chemical Properties at Different Habitat Types in Disturbed and Undisturbed Sites of the Takamanda Rainforest, Cameroon. International Journal of Plant & Soil Science, pp.1-17.

Araujo, P.F., Freitas, A.V.L., Goncalves, G.A.D.S. and Ribeiro, D.B., 2021. Vertical stratification on a small scale: the distribution of fruit-feeding butterflies in a semi-deciduous Atlantic forest in Brazil. *Studies on Neotropical Fauna and Environment*, *56*(1), pp.10-39.

Arellano, L. and Halffter, G., 2003. Gamma diversity: derived from and a determinant of alpha diversity and beta diversity. An analysis of three tropical landscapes. Acta Zoológica Mexicana, (90), pp.27-76.

Balick, M.J. and Mendelsohn, R. (1992) Assessing the economic value of traditional medicines from tropical rain forests. *Conservation biology*, *6*(1): 128-130.

Barton, M., Porter, W. and Kearney, M., 2014. Behavioural thermoregulation and the relative roles of convection and radiation in a basking butterfly. *Journal of Thermal Biology*, *41*, pp.65-71.

Basset, Y., Eastwood, R., Sam, L., Lohman, D.J., Novotny, V., Treuer, T., Miller, S.E., Weiblen, G.D., Pierce, N.E., Bunyavejchewin, S. and Sakchoowong, W., 2013. Cross-continental comparisons of butterfly assemblages in tropical rainforests: implications for biological monitoring. *Insect Conservation and Diversity*, *6*(3), pp.223-233.

Basset, Y., Jorge, L.R., Butterill, P.T., Lamarre, G.P., Dahl, C., Ctvrtecka, R., Gripenberg, S., Lewis, O.T., Barrios, H., Brown, J.W. and Bunyavejchewin, S., 2021. Host specificity and interaction networks of insects feeding on seeds and fruits in tropical rainforests. Oikos.

Beck, J. and Chey, V.K. (2008) Explaining the elevational diversity pattern of geometrid moths from Borneo: a test of five hypotheses. *Journal of Biogeography*, *35*(8): 1452-1464.

Beirão, M.V., Neves, F.S., Penz, C.M., DeVries, P.J. and Fernandes, G.W., 2017. High butterfly beta diversity between Brazilian cerrado and cerrado–caatinga transition zones. *Journal of Insect Conservation*, *21*(5), pp.849-860.

Bonebrake, T.C., Ponisio, L.C., Boggs, C.L., Ehrlich, P.R. (2010) More than just indicators: A review of tropical butterfly ecology and conservation. *Biological Conservation, 143*(8): 1831-1841.

Borneo Nature Foundation (2021) Borneo Nature Foundation [Online] Accessed on 22/08/2021 from: https://www.borneonaturefoundation.org/

Braschler, B. and Hill, J.K., 2007. Role of larval host plants in the climate-driven range expansion of the butterfly Polygonia c-album. *Journal of Animal Ecology*, *76*(3), pp.415-423.

Brook, B.W., Sodhi, N.S. and Bradshaw, C.J. (2008) Synergies among extinction drivers under global change. *Trends in ecology & evolution*, *23*(8): 453-460.

Carlson, K.M., Curran, L.M., Asner, G.P., Pittman, A.M., Trigg, S.N. and Adeney, J.M. (2013) Carbon emissions from forest conversion by Kalimantan oil palm plantations. *Nature Climate Change*, *3*(3): 283.

Carvalho, G.R., De Bruyn, M., Stelbrink, B., Morley, R.J., Hall, R., Cannon, C.H., van den Bergh, G., Meijaard, E., Metcalfe, I., Boitani, L. and Maiorano, L. (2014) Borneo and Indochina are major evolutionary hotspots for Southeast Asian biodiversity. *Systematic Biology*, *63*(6): 879-901.

Chao, A., 1984. Nonparametric estimation of the number of classes in a population. Scandinavian Journal of statistics, pp.265-270.

Chao, A. and Chiu, C.H., 2016. Species richness: estimation and comparison. Wiley StatsRef: statistics reference online,*1*, p.26.

Cleary, D.F. and Genner, M.J. (2004) Changes in rain forest butterfly diversity following major ENSO-induced fires in Borneo. *Global Ecology and Biogeography*, *13*(2): 129-140.

Curran, L.M., Trigg, S.N., McDonald, A.K., Astiani, D., Hardiono, Y.M., Siregar, P., Caniago, I. and Kasischke, E. (2004) Lowland forest loss in protected areas of Indonesian Borneo. *Science*, *303*(5660): 1000-1003.

Cushman, S.A., Macdonald, E.A., Landguth, E.L., Malhi, Y. and Macdonald, D.W. (2017). Multiple-scale prediction of forest loss risk across Borneo. *Landscape Ecology*, *32*(8): 1581-1598.

Ctvrtecka, R., Sam, K., Miller, S.E., Weiblen, G.D. and Novotny, V., 2016. Fruit sizes and the structure of frugivorous communities in a New Guinea lowland rainforest. *Austral Ecology*, *41*(3), pp.228-237.

Daily, G.C. and Ehrlich, P.R. (1995) Preservation of biodiversity in small rainforest patches: rapid evaluations using butterfly trapping. *Biodiversity & Conservation*, *4*(1): 35-55.

De Bruyn, M., Stelbrink, B., Morley, R.J., Hall, R., Carvalho, G.R., Cannon, C.H., van den Bergh, G., Meijaard, E., Metcalfe, I., Boitani, L. and Maiorano, L., 2014. Borneo and Indochina are major evolutionary hotspots for Southeast Asian biodiversity. *Systematic Biology*, *63*(6), pp.879-901.Caillaud et al. 2010

Delabye, S., Maicher, V., Sáfián, S., Doležal, J., Altman, J., Janeček, Š., Kobe, I.N., Murkwe, M., Šebek, P. and Tropek, R., 2021. Butterfly and moth communities differ in their response to habitat structure in rainforests of Mount Cameroon. *Biotropica*, *53*(2), pp.567-580.

DeVries, P.J. and Walla, T.R. (2001) Species diversity and community structure in neotropical fruit-feeding butterflies. *Biological journal of the Linnean Society*, *74*(1): 1-15.

Dunlop, M. (2013) Biodiversity: Strategy conservation. *Nature Climate Change*, *3*(1): 1019–1020.

Fermon, H., Waltert, M., Vane-Wright, R.I. and Mühlenberg, M., 2005. Forest use and vertical stratification in fruit-feeding butterflies of Sulawesi, Indonesia: impacts for conservation. *Biodiversity & Conservation*, *14*(2), pp.333-350.

Fernanda Checa, M., Barragán, A., Rodríguez, J. and Christman, M., 2009, January. Temporal abundance patterns of butterfly communities (*Lepidoptera*: *Nymphalidae*) in the Ecuadorian Amazonia and their relationship with climate. In Annales de la *Société entomologique de France*, 45(4), pp. 470-486). Taylor & Francis Group.

Fu, Z., Gerken, T., Bromley, G., Araújo, A., Bonal, D., Burban, B., Ficklin, D., Fuentes, J.D., Goulden, M., Hirano, T. and Kosugi, Y., 2018. The surface-atmosphere exchange of carbon dioxide in tropical rainforests: Sensitivity to environmental drivers and flux measurement methodology. *Agricultural and Forest Meteorology*, *263*, pp.292-307.

Gamfeldt, L., Hillebrand, H. and Jonsson, P.R., 2008. Multiple functions increase the importance of biodiversity for overall ecosystem functioning. *Ecology, 89*(5), pp.1223-1231.

Gaston, K.J., 2000. Global patterns in biodiversity. *Nature*, *405*(6783), pp.220-227.

Gaveau, D.L.A., Sloan, S., Molidena, E., Yaen, H., Sheil, D., Abram, N.K., Ancrenaz, M., Nasi, R., Quinones, M., Wielaard, N. and Meijaard, E. (2014) Four Decades of Forest Persistence, Clearance and Logging on Borneo. *PLoS ONE*, *9*(7): 115-120.

Geist, H.J. and Lambin, E.F., 2001. What drives tropical deforestation. LUCC Report series, *4*, p.116.

Grøtan, V., Lande, R., Engen, S., Sæther, B.E. and DeVries, P.J., 2012. Seasonal cycles of species diversity and similarity in a tropical butterfly community. *Journal of Animal Ecology*, *81*(3), pp.714-723.

Hairah, U., Tejawati, A., Budiman, E. and Agus, F., 2017, October. Borneo biodiversity: Exploring endemic tree species and wood characteristics. In *2017 3rd International Conference on Science in Information Technology (ICSITech)*, pp. 435-440. IEEE.

Hamann, A., 2004. Flowering and fruiting phenology of a Philippine submontane rain forest: climatic factors as proximate and ultimate causes. *Journal of Ecology, 92*(1), pp.24-31.

Harrison, M., Hendri, D.M., Krisno, J., Cheyne, S.M. and Husson, S.J., 2010. Biodiversity of the mungku baru ulin forest, Central Kalimantan, Indonesia. *Report produced by the Orangutan Tropical Peatland Project for International Animal Rescue. Palangka Raya, Indonesia.: Orangutan Tropical Peatland Project*.

Harrison, M.E., Cheyne, S.M., Husson, S.J., Jeffers, K.A., Smallcombe, J.V. and Ehlers Smith, D.A., 2012. Preliminary Assessment of the Biodiversity and Conservation Value of the Bawan Forest, Central Kalimantan, Indonesia. Orangutan *Tropical Peatland Project Report*. Palangka Raya, Indonesia.

Harrison, M.E., Hendri, Dragiewicz, M.L., Cheyne, S.M., Krisno and Husson, S.J., 2010. Biodiversity of the Mungku Baru Ulin Forest, Central Kalimantan, Indonesia. Report produced by the Orangutan Tropical Peatland Project for International Animal Rescue and local government, Palangka Raya, Indonesia.

Harrison, R.D., 2005. Figs and the diversity of tropical rainforests. Bioscience, *55(*12), pp.1053-1064.

Harrison, M.E., Marchant, N.C. and Husson, S.J., 2012. Ecological monitoring to support conservation in Kalimantan’s forests: concepts and design.

Harrison, M.E. and Rieley, J.O., 2018. Tropical peatland biodiversity and conservation in Southeast Asia. *Foreword Mires and Peat, 22*, pp.1-7.

Herrera M, L.G., Hobson, K.A., Hernández C, P. and Rodríguez G, M., 2005. Quantifying differential responses to fruit abundance by two rainforest birds using long-term isotopic monitoring. *The Auk, 122*(3), pp.783-792.

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

Houlihan, P.R., Harrison., M.E. and 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.

Howard, P.C., Viskanic, P., Davenport, T.R., Kigenyi, F.W., Baltzer, M., Dickinson, C.J., Lwanga, J.S., Matthews, R.A. and Balmford, A. (1998) Complementarity and the use of indicator groups for reserve selection in Uganda. *Nature*, *394*(6692): 472

Hughes, J.B., Daily, G.C., and Ehrlich, P.R. (1998) Use of fruit bait traps for monitoring of butterflies (*Lepidoptera*: *Nymphalidae*). *Revista de biología tropical*, *46*(3): 697-704.

Janzen, D.H., 1987. Insect diversity of a Costa Rican dry forest: why keep it, and how?. *Biological Journal of the Linnean Society*, *30*(4), pp.343-356.

Justus, J. and Sarkar, S. (2002) The principle of complementarity in the design of reserve networks to conserve biodiversity: a preliminary history. *Journal of Biosciences*, *27*(4): 421-435.

Kerr, J.T. and Packer, L. (1997) Habitat heterogeneity as a determinant of mammal species richness in high-energy regions. *Nature*, *385*(6613): 252.

Kerr, J.T., Sugar, A. and Packer, L., 2000. Indicator taxa, rapid biodiversity assessment, and nestedness in an endangered ecosystem. *Conservation biology*, *14*(6), pp.1726-1734.

Kettle, C.J., Ghazoul, J., Ashton, P., Cannon, C.H., Chong, L., Diway, B., Faridah, E., Harrison, R., Hector, A., Hollingsworth, P. and Koh, L.P., 2011. Seeing the fruit for the trees in Borneo. *Conservation Letters*, *4*(3), pp.184-191.

KHDTK Report 2016-2017

Kitching, R.L., Orr, A.G., Thalib, L., Mitchell, H., Hopkins, M.S. and Graham, A.W. (2000) Moth assemblages as indicators of environmental quality in remnants of upland Australian rain forest. *Journal of applied Ecology*, *37*(2): 284-297.

Koenig, W.D., 1999. Spatial autocorrelation of ecological phenomena. *Trends in Ecology & Evolution*, *14*(1), pp.22-26.

Lamarre, G.P., Fayle, T.M., Segar, S.T., Laird-Hopkins, B.C., Nakamura, A., Souto-Vilarós, D., Watanabe, S. and Basset, Y., 2020. Monitoring tropical insects in the 21st century. *Advances in Ecological Research*, *62*, pp.295-330.

Lashley, M.A., Thompson, J.R., Chitwood, M.C., DePerno, C.S. and Moorman, C.E., 2014. Evaluation of methods to estimate understory fruit biomass. *PloS one*, *9*(5), p.e96898.

Latifah, A.L., Shabrina, A., Wahyuni, I.N. and Sadikin, R., 2019, October. Evaluation of Random Forest model for forest fire prediction based on climatology over Borneo. In *2019 International Conference on Computer, Control, Informatics and its Applications (IC3INA)* (pp. 4-8). IEEE.

Lee, T.D., 1988. Patterns of fruit and seed production. *Plant reproductive ecology: patterns and strategies*, pp.179-202.

Liebhold, A.M. and Sharov, A.A., 2020. Testing for correlation in the presence of spatial autocorrelation in insect count data. In *Population and community ecology for insect management and conservation*, pp. 111-118. CRC Press.

Lohani, S., Dilts, T.E., Weisberg, P.J., Null, S.E. and Hogan, Z.S., 2020. Rapidly accelerating deforestation in Cambodia's Mekong River Basin: A comparative analysis of spatial patterns and drivers. *Water, 12*(8), p.2191.

Lohbeck, M., Bongers, F., Martinez-Ramos, M. and Poorter, L., 2016. The importance of biodiversity and dominance for multiple ecosystem functions in a human-modified tropical landscape. *Ecology, 97*(10), pp.2772-2779.

Marchant, N.C., Purwanto, A., Harsanto, F.A., Boyd, N.S., Harrison, M.E. and Houlihan, P.R., 2015. 'Random-flight'dispersal in tropical fruit-feeding butterflies? High mobility, long lifespans and no home ranges. *Ecological Entomology*, *40*(6), pp.696-706.

Maimunah, S., Capilla, B.R. and Harrison, M.E., 2019, May. Tree diversity and forest composition of a Bornean heath forest, Indonesia. In IOP Conference Series: *Earth and Environmental Science,* IOP Publishing. *270*(1), p. 012028

Marini-Filho, O.J. and Martins, R.P., 2010. Nymphalid butterfly dispersal among forest fragments at Serra da Canastra National Park, Brazil. *Journal of Insect Conservation*, *14*(4), pp.401-411.

Martini, I.P., Cortizas, A.M. and Chesworth, W. eds., 2007. Peatlands: evolution and records of environmental and climate changes. *Elsevier*. Amsterdam, pp. 145–172

Martins, L.P., ARAUJO, E.D.C., Martins, A.R.P., Duarte, M. and Azevedo, G.G., 2017. Species diversity and community structure of fruit-feeding butterflies (*Lepidoptera*: *Nymphalidae*) in an eastern Amazonian forest. *Papéis Avulsos de Zoologia*, *57*, pp.481-489.

Mayer A.L. and Pimm S.L. (1997) Tropical rainforests: Diversity begets diversity. *Current Biology*. *7*(7): 430-432.

Melo, D.H.A., Filgueiras, B.K.C., Iserhard, C.A., Iannuzzi, L., Freitas, A.V.L. and Leal, I.R., 2019. Effect of habitat loss and fragmentation on fruit-feeding butterflies in the Brazilian Atlantic Forest. *Canadian journal of zoology*, *97*(7), pp.588-596.

Merckx, T., Dyck, H.V., Karlsson, B. and Leimar, O., 2003. The evolution of movements and behaviour at boundaries in different landscapes: a common arena experiment with butterflies. Proceedings of the Royal Society of London. Series B: *Biological Sciences*, *270*(1526), pp.1815-1821.

Mills, L.S., Soulé, M.E. and Doak, D.F. (1993) The keystone-species concept in ecology and conservation. *BioScience*, *43*(4): 219-224.

Mittermeier, R.A., Myers, N., Mittermeier, C.G. and Robles Gil, P., 1999. Hotspots: Earth's biologically richest and most endangered terrestrial ecoregions. CEMEX, SA, Agrupación Sierra Madre, SC.

MoEF., 2018. Managing Peatlands to Cope with Climate Change: Indonesia's Experience. Ministry of Environment and Forestry, Jakarta, Indonesia, pp. 30

Mokany, K., Ferrier, S., Harwood, T.D., Ware, C., Di Marco, M., Grantham, H.S., Venter, O., Hoskins, A.J. and Watson, J.E., 2020. Reconciling global priorities for conserving biodiversity habitat. *Proceedings of the National Academy of Sciences, 117*(18), pp.9906-9911.

Molina-Martínez, A., León-Cortés, J.L. and Regan, H.M., 2013. Climatic and geometric constraints as driving factors of butterfly species richness along a Neotropical elevational gradient. *Journal of insect conservation*, *17*(6), pp.1169-1180.

Molleman, F., Kop, A., Brakefield, P.M. and Zwaan, B.J., 2006. Vertical and temporal patterns of biodiversity of fruit-feeding butterflies in a tropical forest in Uganda. *Biodiversity & Conservation*, *15*(1), pp.107-121.

Morrogh-Bernard, H.C., Husson, S.J., Page, S.E. and Rieley, J.O. (2003) Population status of the Bornean orang-utan (Pongo pygmaeus) in the Sebangau peat swamp forest, Central Kalimantan, Indonesia*. Biological Conservation, 110*(1): 141-152.

Mustaffa.,N 2001 Temporal variation in fruit-feeding forest butterfly communities in Sabah, Borneo.: Masters thesis

Myers, N., Mittermeier, R. A., Mittermeier, C. G., Da Fonseca, G. A. and J. Kent (2000) Biodiversity hotspots for conservation priorities. *Nature*, *403*(6772): 853-858.

Newbery, D.M., Chuyong, G.B. and Zimmermann, L., 2006. Mast fruiting of large ectomycorrhizal African rain forest trees: importance of dry season intensity, and the resource-limitation hypothesis. *New Phytologist, 170*(3), pp.561-579.

Nobre, C.E.B., Iannuzzi, L. and Schlindwein, C., 2012. Seasonality of fruit-feeding butterflies (*Lepidoptera*, *Nymphalidae*) in a Brazilian semiarid area. *International Scholarly Research Notices*.

O'Donnell, C.F. and Dilks, P.J., 1994. Foods and foraging of forest birds in temperate rainforest, South Westland, New Zealand. *New Zealand journal of ecology*, pp.87-107.

Paavilainen, E. and Päivänen, J., 1995. Peatland forestry: ecology and principles (Vol. 111). Springer Science & Business Media.

Page, S.E., Rieley, J.O. and Wüst, R., 2006. Lowland tropical peatlands of Southeast Asia. *Developments in earth surface processes*, *9*, pp.145-172.

Page, S.E., Rieley, J.O. and Banks, C.J., 2011. Global and regional importance of the tropical peatland carbon pool. *Global change biology, 17*(2), pp.798-818.

Peluso, N.L., 1992. The political ecology of extraction and extractive reserves in East Kalimantan, Indonesia. *Development and change*, *23*(4), pp.49-74.

Pereira, G.C.N., Coelho, M.S., Beirao, M.D.V., Braga, R.F. and Fernandes, G.W., 2017. Diversity of fruit-feeding butterflies in a mountaintop archipelago of rainforest. *Plos One*, *12*(6), p.e0180007.

Porath, I.A.T. and Aranda, R., 2020. Frugivorous butterflies (*Lepidoptera Nymphalidae*) as a habitat quality indicator in Cerrado urban fragment. *EntomoBrasilis*, *13*, p.6.

Purwanto, A., Harsanto, F.A., Marchant, N.C., Houlihan, P.R., Ross, K., Tremlett, C. and Harrison, M.E., 2015. Good practice guidelines: Butterfly canopy trapping.

Raes, N., Roos, M.C., Slik, J.W., Van Loon, E.E. and Steege, H.T. (2009) Botanical richness and endemicity patterns of Borneo derived from species distribution models. *Ecography*, *32*(1): 180-192.

Sánchez, M.S., Carrizo, L.V., Giannini, N.P. and Barquez, R.M., 2012. Seasonal patterns in the diet of frugivorous bats in the subtropical rainforests of Argentina. Mammalia, *76*(3), pp.269-275.

Santos, A.D.C., Sales, P.C.L., Ribeiro, D.B. and Silva, P.R.R., 2020. Habitat conversion affects beta diversity in frugivorous butterfly assemblages. *Studies on Neotropical Fauna and Environment*, *55*(3), pp.180-192.

Schulze, C.H., Waltert, M., Kessler, P.J., Pitopang, R., Veddeler, D., Mühlenberg, M., Gradstein, S.R., Leuschner, C., Steffan-Dewenter, I. and Tscharntke, T., 2004. Biodiversity indicator groups of tropical land-use systems: comparing plants, birds, and insects. *Ecological applications*, *14*(5), pp.1321-1333.

Sinnott, R.W., 1984. Virtues of the Haversine. *Sky and telescope*, *68*(2), p.158.

Slade, E.M., Merckx, T., Riutta, T., Bebber, D.P., Redhead, D., Riordan, P. and Macdonald, D.W., 2013. Life-history traits and landscape characteristics predict macro-moth responses to forest fragmentation. *Ecology*, *94*(7), pp.1519-1530.

Sousa, W.O.D., Sousa, L.E., da Silva, F.R., Santos, W.I. and Aranda, R., 2019. Composition and structure of the frugivorous butterfly community (*Lepidoptera*: *Nymphalidae*) at the Serra Azul State Park (PESA), Mato Grosso, Brazil. *Zoologia (Curitiba)*, *36*.

Sparks, T.H., Greatorex-Davies, J.N., Mountford, J.O., Hall, M.L. and Marrs, R.H., 1996. The effects of shade on the plant communities of rides in plantation woodland

and implications for butterfly conservation. *Forest Ecology and Management*, *80*(1-3), pp.197-207.

Summerville, K.S., Ritter, L.M. and Crist, T.O. (2004) Forest moth taxa as indicators of *Lepidoptera*n richness and habitat disturbance: a preliminary assessment. *Biological Conservation*, *116*(1): 9-18.

Tangah, J., Hill, J.K., Hamer, K.C. and Dawood, M.M., 2004. Vertical distribution of fruit-feeding butterflies in Sabah, Borneo. *Sepilok Bulletin*, *1*(17), pp.17-27.

Tiple, A.D., Khurad, A.M. and Dennis, R.L., 2011. Butterfly larval host plant use in a tropical urban context: Life history associations, herbivory, and landscape factors. *Journal of Insect Science*, *11*(1), p.65.

Turetsky, M.R., Benscoter, B., Page, S., Rein, G., Van Der Werf, G.R. and Watts, A., 2015. Global vulnerability of peatlands to fire and carbon loss. *Nature Geoscience*, *8*(1), pp.11-14.

Valtonen, A., Molleman, F., Chapman, C.A., Carey, J.R., Ayres, M.P. and Roininen, H., 2013. Tropical phenology: Bi-annual rhythms and interannual variation in an Afrotropical butterfly assemblage. *Ecosphere*, *4*(3), pp.1-28.

Vane-Wright, R.I., Humphries, C.J. and Williams, P.H. (1991) What to protect?—Systematics and the agony of choice. *Biological conservation*, *55*(3): 235-254.

Vu, L.V. and Quang Vu, C., 2011. Diversity pattern of butterfly communities (*Lepidoptera*, Papilionoidae) in different habitat types in a tropical rain forest of Southern Vietnam. International Scholarly Research Notices, 2011.

Whittaker, R.H., 1972. Evolution and measurement of species diversity. *Taxon, 21*(2-3), pp.213-251.

Whitworth, A., Huarcaya, R.P., Mercado, H.G., Braunholtz, L.D. and MacLeod, R., 2018. Food for thought. Rainforest carrion-feeding butterflies are more sensitive indicators of disturbance history than fruit feeders. *Biological Conservation*, *217*, pp.383-390.

Wilcove, D.S., Giam, X., Edwards, D.P., Fisher, B. and Koh, L.P. (2014) Navjot's nightmare revisited: Logging, agriculture, and biodiversity in Southeast Asia. *Trends in Ecology & Evolution, 28*(9): 531–540.

Williams, P.H and Manne, L. (2001) 'Complementarity', in Levin, S.A. (ed.) *Encyclopedia of Biodiversity.* Oxford, UK*:* Academic Press: 192-200. Williams et al. 2006

Willott, S.J., 1999. The effects of selective logging on the distribution of moths in a Bornean rainforest. In *Changes And Disturbance In Tropical Rainforest In South-East Asia*, pp. 59-66.

Yule, C.M., 2010. Loss of biodiversity and ecosystem functioning in Indo-Malayan peat swamp forests. *Biodiversity and conservation*, *19*(2), pp.393-409.

Zhang, S.Y. and Wang, L.X., 1995. Comparison of three fruit census methods in French Guiana. *Journal of Tropical Ecology*, *11*(2), pp.281-294.