Impacts of selective logging on tropical butterflies in Sabah, Malaysia

Joseph Tangah

Impacts of Selective Logging on Tropical Butterflies in Sabah, Malaysia

M.Sc. thesis submitted

to

University of Durham

Department of Biological Sciences

by

Joseph Tangah

2000

Declaration

The candidate confirms that the work submitted is his own and that appropriate credit has been given where reference has been made to the work of others.

Copyright ©

Impacts of Selective Logging on Tropical Butterflies in Sabah, Malaysia

M.Sc. thesis submitted by Joseph Tangah, 2000

ABSTRACT

This study investigated the impacts of selective logging on tropical butterflies in the lowland dipterocarp rainforest of Sabah (Malaysia, Borneo). Walk and point-count transect methods were used to survey butterflies in unlogged forest and forest that had been selectively logged 10–11 years previously. The study focused on butterflies in the sub-families satyrinae and morphinae (Nymphalidae) and the family Riodinidae. A total of 1825 adult butterflies was recorded from 34 species at 80 observation stations on 8km transects repeated four times per month for a period of one year (March 1999–February 2000). Most of the butterfly species that were present in the unlogged forest were also present in logged forest. There was little difference in numbers of individuals or numbers of species recorded in logged and unlogged forest. However Shannon-Wiener and Simpson's diversity indices (species evenness) were significantly higher in unlogged forest than the logged forest, although there was no difference in Margalef's index (species richness). These results show that selective logging affected species evenness of tropical butterflies more than species richness. Vegetation structure in logged forest was significantly different from that in unlogged forest >10 years after logging. However changes in vegetation structure were only weakly related to butterfly diversity. There was no strong evidence that selective logging contributed to the loss of butterfly species with more restricted geographical distributions. Seasonal effects in terms of monthly rainfall did not relate to seasonal changes in diversity of butterflies, but there was a relationship with sunshine. Fruit-baited traps were used to investigate vertical stratification of butterflies in unlogged forest from ground to canopy levels. A total of 542 individuals from 40 species were captured in traps. Low-level (2m) traps caught species with more restricted distributions than medium-level (20m) or high-level (40m) traps (31, 19 and 12 species repectively). Adult longevity showed that individuals could survive up to 164 days. Movement of butterflies between traps at different heights was relatively low. Data from traps confirmed that species of satyrinae can be recorded reliably using ground-based transect techniques.

ACKNOWLEDGEMENTS

First and foremost I would like to express my gratitude to my supervisors, Dr Keith C. Hamer, Dr Jane K. Hill, and Dr Tom N. Sherratt, for their invaluable guidance throughout my MSc studies. Their expertise, knowledge, dedication and know-how in the field made the project a great pleasure. I would also like to thank the Darwin Initiative (DETR), UK and Sabah Forestry Department, for their financial support. I also thank the Danum Valley Management Committee (DVMC) for allowing me to carry out studies in the conservation areas. This is Project No. DV158. This work was carried out while I was a participant in the Royal Society's South East Asia Rainforest Research Programme.

It is my pleasure to thank the following personal for their help and support in one way or another: The Director of Forestry Department of Sabah, Mr. Daniel K.S. Khiong, the Head of Forest Research Centre Sandakan, Dr. Sining Unchi, Mr. Pilis Malim (senior forestry officer), Dr. Chey Vun Khen (research advisor), Dr. Arthur Y.C. Chung, Mr. Jaffirin J. Lapongan, Mr. Robert C. Ong and Mr. John Baptist Sugau. Friends and colleagues, particularly Mr. Aning Amat, Glen Renyolds (Senior Scientists), Maria Ajik, Jupiri Titin, Dr. Lee, Dr. Noreen, J.Kulip, J.Josue, A.M.Ricky, Hamzah Tangki, Mahadimenakbar M.Dawood, Suzan Benedick, Nazirah Mustafa, Wong Siew Tee, Y.Zamrie, N.Reuben, T.P.Joan, G.Petol, Ubaldus, T.E.Chen, Momin, Willie, R.D.Melvin, J.Larenus, BBO, Tarman, Kelly, Mary, Fauziah, K.L.Poon and all who know me, thank you for your kind friendship and help. I also thank the staff of Conservation Section (Sepilok Arboretum), in particular Soinin Satman, Anselm & Poungga for field assistance in the Sepilok Arboretum, and S.Dewol & L.Madani for plant identification. Dr. Arthur Y.C. Chung is appreciated for his statistical advice and comments.

For my mother (Mdm. Tinuim Sabiat), mother in-law (Mdm. Kok Kui Yin), brothers (Jooh, Lawrence, Paul & Mohd. Rafein Ipin) and sisters (Joleh & Jelly) thank you for your strong support and understanding. Especially for my wife Chia Fui Ree, thank you for your love, support, caring and for being with me.

TABLE OF CONTENTS

List of figures

List of tables

Chapter 1 General Introduction

1.1 Tropical Rainforest

Tropical rainforest is a complex community and is probably the most diverse terrestrial ecosystem on earth, with the greatest numbers of co-existing plant and animal species (Whitmore 1984; Marshall 1992). The term 'tropical rainforest' was first described by A.F.W. Schimper in 1898, as "evergreen, different in character, at least 30 m high, rich in thick-stemmed or woody lianas as well as herbaceous epiphytes" (Schimper 1903). There are two major kinds of tropical humid forest, tropical rainforest and monsoon forest (Collins *et al.* 1991). Rainforests occur in per-humid climates where rainfall occurs throughout the year, although it may not be uniformly distributed. Rainfall in these areas averages 100mm or more per month, although there may be drier periods in certain months (Whitmore 1984). Tropical monsoon forest occurs where there are long dry seasons, usually with more than three months with less than 60mm rainfall (Collins *et al.* 1991).

Globally, there are three major regions of tropical rainforest; South American rainforest covers the largest area, followed by Southeast Asian rainforest, and African rainforest. South American rainforest covers an area of approximately four million km^2 concentrated around the Amazon and Orinoco river basins. Indo–Malayan rainforest occurs in the eastern tropics (SE Asia and NE Australia) and covers approximately 2.8 million km^2 (Davis *et al.* 1995). The smallest tropical rainforest area is the African rainforest with approximately 1.8 million km^2, mainly centred in the Zaire basin of central Africa. Temperature in these regions is invariably above 18°C, even during the coldest months, with the exception of some tropical montane forest (Whitmore 1990). Average temperatures are usually between 25°C and 28°C. There is a strong influence of the surrounding seas on total rainfall received in these rainforests (Whitmore 1984). SE Asia is more influenced by the surrounding oceans (Indian Ocean to the West and South, and the Pacific Ocean to the North–East) compared with the two rainforest blocks of Western Africa and South America. In this respect, the tropical rainforest of SE Asia receives more uniformly distributed (on a monthly basis) and higher rainfall compared with other areas (Whitmore 1984; 1990). The most arid climates in the Indo-Malayan rainforest are confined to parts of central Burma and Australia.

There are various forest formations within tropical rainforest and monsoon forest depending on local conditions of soil, topography, climate and groundwater (Collins *et al.* 1991). Forest formations differ from one another in physiognomy (forest structure), and floristic composition (Whitmore 1990). The existing tropical rainforest formations in SE Asia are lowland mixed-dipterocarp forest, peat swamp and freshwater swamp forest, heath forest, ultramafic forest, limestone forest, montane forest, mangrove forest, and beach forest. In Borneo, at least eight major forest formations are recognised (Whitmore 1984,1990; Ashton 1995). These are:- littoral forest (sandy and rocky beach, and mangrove vegetation), peat swamp and freshwater swamp forest, lowland and hill mixed dipterocarp forest, forest on limestone hills, forest on ultramafic soils, lower montane forest, upper montane forest, and subalpine woodland. Depending on the topography, altitude and soil types of a particular locality, there may be a wide range of variation in term of species richness within each type of these forest formations (Whitmore 1990).

Borneo is the third largest island in the world and covers a total land area of approximately 740,000km^2 within the latitudes of 7°15'N–5°45'S and longitudes 119°15'E–109°15'E. Tropical rainforest on Borneo is shared by three countries; Malaysia (States of Sabah –73,710km^2 and Sarawak –124,499km^2), Indonesia (Kalimantan –534,490km^2), and Brunei –5765 km^2 (Collins *et al.* 1991). This study was conducted in Sabah (4°05'N–7°15'N latitude; 115°05'E–119°30'E longitude) located at the Northern tip of Borneo (Tangah & Wong 1995).

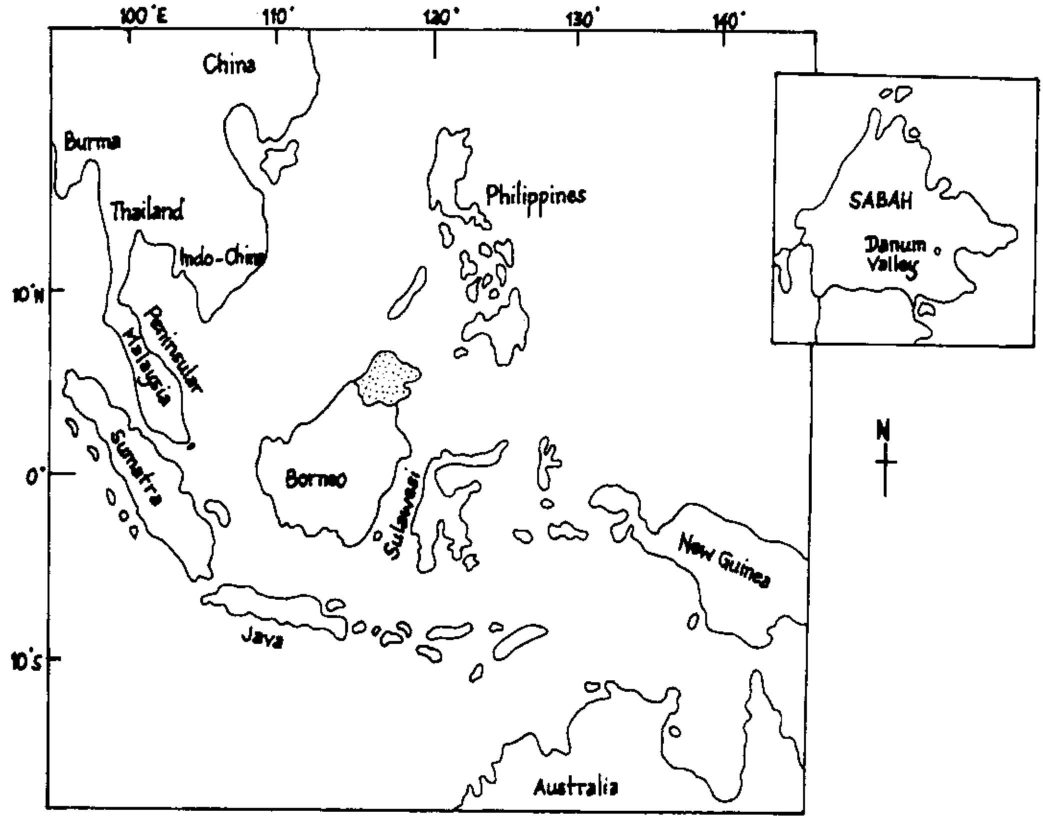


Figure 1.1: Map of South East Asia; insert: State of Sabah, Malaysia.

1.2 Biodiversity

Biodiversity can be defined as the variety and variability of plant and animal species (IUCN/UNEP/WWF 1991). It refers to the range of biological differences within the living world. Biodiversity is usually defined in terms of species, genes and ecosystems, corresponding to three fundamental and hierarchically-related levels of biological organisation (Groombridge 1992). There are three different scales of biodiversity, namely alpha (α), beta (β) and gamma (γ) diversity (Heywood & Watson 1995). Alpha diversity is the local diversity of a given sample representing a community regarded as homogenous (Whittaker 1977). Beta diversity is a measure of between-area diversity, which represents the variability in species composition among local sites. Gamma diversity is regional diversity because it is refers to overall diversity within a large region (Cornell 1985). It is the product of alpha- and beta-diversity (Whittaker 1960, 1972; Harrison *et al.* 1992; Hutson 1994; Mawdsley 1994), that is:

$$\gamma = \alpha \times \beta$$

where γ = regional species richness, α = local species richness and β = beta diversity.

Although it is difficult to quantify the economic value of biodiversity, the genetic variation within species, the variety of species, and the existence of diverse and productive ecosystems are undoubtedly of economic importance (IUCN/UNEP/WWF 1991). One important aspect of biological diversity may be the conservation and preservation of biological ecosystems to meet needs which are as yet unforeseen (Evans 1976). Biological diversity comprises species richness and species evenness (Begon *et al.* 1996). The more species there are and the more nearly even their abundance the greater the diversity (Pielou 1975). However higher species diversity does not necessarily entail more endemic species compared with lower species diversity (Spellerberg 1991).

1.3 Biodiversity in tropical rainforests

Tropical rainforest is probably the richest terrestrial ecosystem ever to have existed (Marshall 1992). Although it covers only 6% of the earth's total land area, it contains approximately half of the world's animal and plant species, including 70–75% of all known arthropods (Mabberley 1983). Borneo covers less than 0.2% of earth's land surface, yet it contains 5% of all known birds and mammals (MacKinnon *et al.* 1996). This region also contains one of the richest tropical rainforest habitats (Whitmore 1990). For example, the flora of this region is estimated to comprise 25,000 species of flowering plants which is about 4–9% of the world's flora (Whitmore 1984). Within the state of Sabah rainforests are typically diverse, with some 10,000 species of flowering plants, 449 species of birds, 189 species of mammals, 89 species of amphibians and a large number of other plant and animal species (Rajaratnam 1997; Andau 1998). Sabah's rainforests contain 174 (65%) of 267 species of dipterocarps found in Borneo, more than half of all Bornean rhododendrons and pitcher plant species, and perhaps as many as 1,500 of approximately 2,000 Bornean orchids (Wong 1992).

May (1990) estimated more than 750,000 insect species while Hammond (1992) suggested 950,000 species globally of which over half are in tropical forests (Wilson 1988). In Borneo, there are more than 900 butterfly species (Otsuka 1988), and 8,500 species of moths (Robinson & Tuck 1993). In Sabah there are approximately 103 species of termites (Thapa 1981), whilst, more than half of the 1,711 beetle morphospecies collected are not known taxonomically (Chung 1999). This high diversity corresponds with high levels of endemism (Holloway 1987).

The occurrence of high diversity of plants and animals in Borneo may be attributed to the conducive paleoclimates during the Tertiary (2–65 million years ago) and Quaternary (up to 2 million years ago) periods (Morley & Flenley 1987), coupled with the availability of diverse types of natural habitats (ranging from mangrove and other coastal habitats to the highest mountain between continental Asia and Papua New Guinea) resulting from recent geological history (Whitmore 1984, 1990; Ashton 1995). Although tropical rainforests are diverse in species richness, they are among the most threatened of all habitats because of exploitation of forest for timber and development (Whitmore 1984; Wilson 1988).

1.4 Forest disturbance

Throughout SE Asia, much forested land area is either being fragmented or converted to other land uses such as agriculture, human settlement, recreation, amenity or industry (McNeely *et al.* 1995). Cultivation and logging have been practiced for centuries, but have increased dramatically in the twentieth century (Collins 1990). However, data on effects of this forest disturbance on insect communities are still lacking (Hill *et al.* 1995; Hamer *et al.* 1997; Hill 1999). Clear felling and conversion of forested land areas to agriculture normally leads to a decrease in insect diversity (Holloway 1987; Holloway, Kirk-Spriggs & Chey 1992). However, less severe disturbance may have only a small effect on species richness (Wolda 1987) or may increase diversity of insects (Blau 1980; Janzen 1987; Raguso & Llorente-Bousquets 1990; Wood & Gillman 1998). Selective commercial logging has been shown to affect insect diversity, in particular affecting species with more restricted geographical distributions, and thus greater conservation value (Hill *et al.* 1995; Hill 1999).

Selective commercial logging of timbers in SE Asia has led to major destruction of forested land areas, probably due to the limited implementation of silvicultural management systems designed to ensure sustained yields (Poore *et al.* 1989; Collins *et al.* 1991). In this system, all commercial timber trees (on Borneo, mainly dipterocarps, *Dryobalanops* spp., *Shorea* spp., *Parashorea* spp., and *Dipterocarpus* spp.) with a diameter at breast height (DBH) greater than 60cm are harvested in a single operation (Poore *et al.* 1989). Normally the extraction rates of selective logging are relatively high in Sabah *i.e.* about 8–15 trees per hectare (Marsh & Greer 1992; Pinard & Cropper 2000). However, although relatively few trees are taken, associated damage can be severe with up to 80% of remaining trees damaged (Lambert 1992). A major impact of selective logging is the destruction of canopy, and subsequent invasion of logged areas by dense re-growth of pioneer trees such as *Macaranga* spp.

Selective logging also causes the removal of topsoil at timber collection areas (log landings where logs are debarked, stored and loaded on to trucks for removal) and skid trails (trails used by bulldozers and other heavy machinery to extract logs). This continuous disturbance of topsoil results in soil compaction and causes removal of soil nutrients which retards the recovery of vegetation (Nussbaum *et al.* 1995; Pinard & Putz 1996). Besides forest floor and canopy disturbance, selective logging also increases the risk of fire due to a combination of drier conditions, increased presence of dead wood and greater access by people, who accidentally or deliberately start forest fires (Beaman *et al.* 1985; Payne 1996).

The continuous destruction of tropical rainforests in SE Asia may contribute to the extinction of many invertebrate species (New 1991), and the most affected groups of insect are likely to be the endemic and highly specialist species (Hill *et al.* 1995; Spitzer *et al.* 1997; Hamer *et al.* 1997). In 1953 more than 86% of Sabah (then British North Borneo) was covered by forest (Collins 1990), but by 1992, only about 45% (approximately 33,486km^2) remained covered by natural forest (Sabah Forest Department 1992). However, most of these forested areas have been selectively logged, and the unlogged forests within the commercial production forest reserves in Sabah decreased by 90% from 1970 to 1995 (Sabah State Government 1998). These figures show that the tropical rainforest is depleting at a rapid rate. With the exception of protected forests (approximately 342,216ha or about 9.5% of the total forest reserves in Sabah), all forested areas on Sabah may be selectively logged within the next decade.

Thus, there is an urgent need to understand the impacts of forest disturbance on the flora and fauna of these areas.

1.5 Impacts of forest disturbance on insects

It is estimated that over half of global diversity in terms of the number of species is represented by insects (Stork 1991), and probably Lepidoptera form a rich component of the tropical rainforest insects. Insects are the most diverse fauna on earth, and respond to disturbance more rapidly than other fauna, and butterflies in particular are extremely sensitive to environmental changes resulting from disturbance (Janzen 1987; Kremen *et al.* 1993). Comparative studies have been conducted in Sabah on various invertebrate groups (Burghouts *et al.* 1992), butterflies (Lim 1996; Hill 1999), moths (Holloway *et al.* 1992; Chey 1994), dung beetles (Davis 1993), termites (Eggleton *et al.* 1997), ants (Chung & Maryati 1993, 1996) and Coleoptera (Chung 1999), and these generally concluded a decrease in species diversity following forest disturbance. Table 1.1 summarizes results of studies investigating impacts of different kinds of forest disturbance on insects in Sabah.

Table 1.1: Type of forest disturbances and their effects on insect groups in Sabah.

Insect group	Type of disturbance	Effect	Reference
Ants	Selective logging	decrease in species richness	Chung & Maryati (1996)
Beetles	Selective logging	decrease in species diversity	Davis (1993)
Beetles	Conversion to oil palm plantations	decrease in species diversity	Chung (1999)
Butterflies	Selective logging	decrease in species abundance	Hill (1999)
Butterflies	Selective logging	no effect on species diversity	Willott *et al.* (2000)
Moths	Conversion to agriculture	decrease in species diversity	Holloway *et al.* (1992)
Moths	Forest plantations	decrease in diversity	Chey *et al.* (1997)
Termites	Selective logging	decrease in species diversity	Eggleton *et al.* (1997)
Invertebrates	Selective logging	decrease in diversity	Burghouts *et al.* (1992)

1.6 Butterflies in tropical rainforests

Butterflies are ideal for the type of study described here because they are comparatively easy to sample (Holloway 1984; New 1991; Sparrow *et al.* 1994) and their taxonomy is well known (Spitzer *et al.* 1997; DeVries *et al.* 1997). Therefore, the study of butterfly assemblages in unlogged and selectively logged forest may be useful to investigate the impacts of forest disturbance. Several studies have investigated effects of forest disturbance on tropical butterflies, such as the effects of selective logging (Hill *et al.* 1995; Hill 1999; Willott *et al.* 2000), effects of small-scale disturbance (Bowman *et al.* 1990; Spitzer *et al.* 1997; Wood & Gillman 1998) and the effects of forest fragmentation (Daily & Ehrlich 1995).

In general, these studies recorded a loss of species following disturbance, in particular among those species with restricted distributions (Spitzer *et al.* 1993; Hill *et al.* 1995; Hamer *et al.* 1997). However, more data are still needed especially data on the effects of forest disturbance on foodplants and habitat requirements of butterflies (Hill 1999). To date, a total of 938 butterfly species has been recorded for Borneo (Otsuka 1988; Maruyama & Otsuka 1991; Seki *et al.* 1991; Hauser *et al.* 1997), which is approximately 7% of the world fauna of around 13,000 species (Corbet & Pendlebury 1992). This indicates that the Bornean rainforest is an area of high diversity of butterflies.

This study concentrates on two groups of butterfly; Nymphalidae (subfamilies Satyrinae and Morphinae) and Riodinidae. These groups were chosen because they are well known taxonomically, are relatively easy to identify in flight and can be reliably surveyed from the ground. These groups also contain many species which are forest or shade dependent and are thus likely to be affected by forest disturbance which opens up the canopy (Holloway 1984).

This thesis describes the effects of selective logging on tropical rainforest butterfly assemblages. The study areas include logged forest which was selectively logged in 1988/89, approximately >10 years prior to this study, and unlogged forest within the largest Protection Forest Reserve-Class I (approximately 428km^2) in Sabah, Malaysia. Chapter 2 describes the methodology and data analysis used in this study. Chapter 3 describes the impacts of selective logging on vegetation structure and butterfly diversity in selectively logged and unlogged forest. This chapter discusses species diversity of butterflies in relation to vegetation structure, and describes the use of several diversity indices in measuring species diversity. Chapter 4 describes the biogeographical effects of logging on tropical rainforest butterflies. Chapter 5 describes the seasonal changes in butterfly assemblages in unlogged and selectively logged forest. Chapter 6 describes the vertical distribution of fruit-feeding butterflies using fruit-baited traps at three different heights (low-2m; medium-20m; and high-40m). Finally, Chapter 7 discusses the findings of this study and suggests some recommendations for future studies of tropical rainforests butterflies.

Chapter 2 General Methodology

2.1 Study sites

The study site was located at Danum Valley Conservation Area (DVCA) which is a Class I (Protection) Forest Reserve covering approximately 428 km^2 of undisturbed forest and surrounded by the Ulu Segama Commercial Forest Reserve (203, 808 ha). It is situated approximately 80 km west of Lahad Datu, Sabah, Malaysia at 5°01'N; 117°47'E (details of site in Marsh & Greer 1992).

The study was carried out in two different forest areas, unlogged and selectively logged lowland mixed-dipterocarp forest. The two study areas share the same general topographic features, with altitudes ranging from about 150m to 230m a.s.l. The logging technique used was conventional selective logging where timber trees above 0.6m diameter at breast height (dbh) were cut in a single operation (Poore *et al.* 1989). Trees of less than 0.6m dbh were retained as seed-bearing trees and for subsequent rotation crops. The logged forest was selectively logged in 1988 and 1989, and the volume of extraction for coupes 1988 and 1989 was 2262.7m^3 ha and 2728.2m^3 ha respectively (Costa & Karolus 1995). Although only about 7–10% of trees were taken per hectare, associated damage was severe (Lambert 1992), as heavy machinery was used where bulldozers and tractors used skid trails (networks of bulldozer paths) to extract logs, and at the log landings (timber collections or log yarding areas) where logs were debarked, stored and loaded on to trucks for removal (see Chapter 1). The study area receives average mean annual rainfall of 2822mm with a mean annual temperature of 26.7°C (Marsh & Greer 1992; Walsh 1996).

2.2 Butterfly survey methods

Prior to the study, I spent three months familiarising myself with the butterfly fauna of the area. Most of the species under investigation can be identified in flight or when perched on vegetation. However some species cannot easily be identified on the wing and I attempted to catch those individuals when possible. Nevertheless, in two cases, species could not be separated in flight (*Mycalesis anapita* and *M. patiana*) and these cases were combined for analysis. Individuals that were not seen clearly were recorded as unidentified. Voucher specimens were taken during the study and these specimens will be kept in the entomology collection of the Forest Research Centre, Sandakan.

The species richness, abundance and evenness of butterflies in the two habitats (unlogged and selectively logged forest) were assessed by surveying species along trails and paths. Two transects were set up in each of the two habitats (four transects in total) and each transect had 20 observation stations (total of 80 stations in the study). Location of the study area is shown in Figure 2.1.

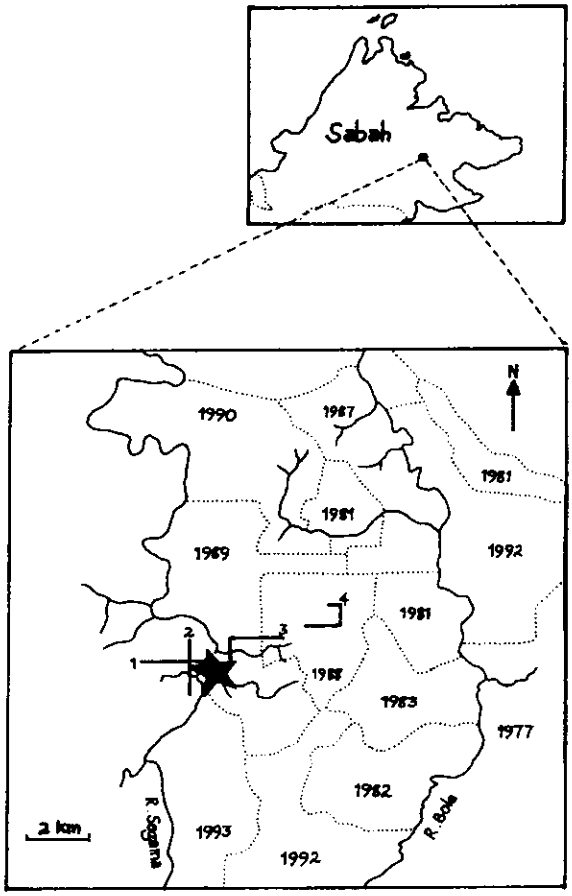


Figure 2.1: Location of study areas (after Hill 1999), transects 3 & 4 located in selectively logged forest and transects 1 & 2 in unlogged forest. Year refers to year of logging. All areas west of Segama River lie within unlogged forest (DVCA). Star indicates the location of the Danum Valley Field Centre.

Each observation station was 100m apart and the total length of each transect was 2km (total of 8km). Butterflies were recorded on transects by using walk and point-count methods (Hill *et al.* 1995; Hamer *et al.* 1997; Hill 1999). Surveys were carried out four times a month, by two observers (myself and M. Dawood) on each transect (2 repeats per observer) from March 1999 - February 2000. Following Hamer *et al.* (1997), data were then summed for the four repeats each month. Total numbers of butterflies recorded at each station include all butterflies seen within 5m of the path, while the recorder walked at a constant pace of approximately 1.2km per hour between stations.

Butterflies seen within in 10m radius of each station during a 5 minutes period were also recorded.

2.3 Measuring vegetation structure

In order to relate any changes in butterfly diversity to changes in vegetation structure following logging, a total of seventy-seven measurements from 14 variables were recorded at every station (see Chapter 3). These data were then analysed using a principal component analysis (PCA) to produce a small number of independent factors from a large group of closely correlated variables, and relate these factors to butterfly diversity. In addition, daily rainfall and sunshine data throughout the study period were obtained from the meteorological station at Danum Valley Field Centre.

2.4 Fruit-baited traps

The vertical distribution of fruit-feeding butterflies was investigated using a tree platform constructed around a *Shorea johorensis* tree in primary forest approximately 1km from the field station. Two butterfly traps were fixed at 40m (high-traps); two at 20m (medium-traps) and two at 2m (low-traps). The design of the butterfly traps is shown in Figure 2.2.

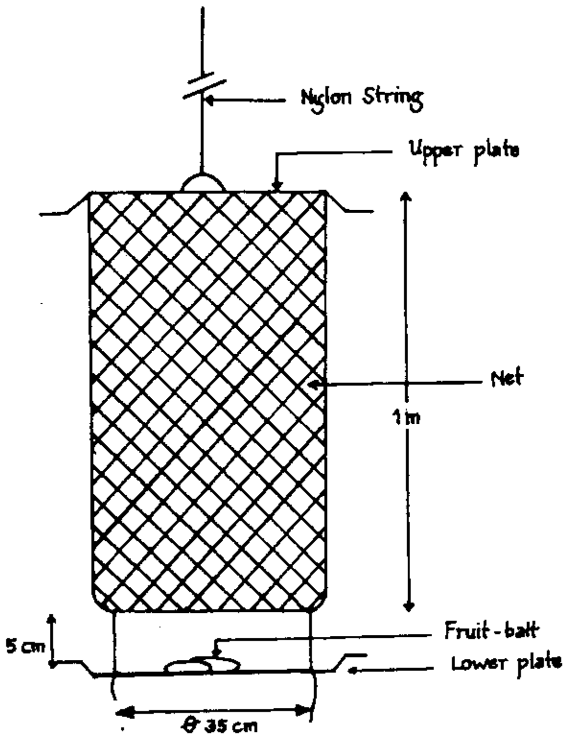


Figure 2.2: A butterfly trap.

Traps were deployed for 14 days continuously every month (March 1999 - February 2000). Two bananas were put on the lower plate of the traps on the first day of the trapping period and fresh fruit was then added every second day. Occasionally, the fruit became too dry or was taken, and on these occasions it was replaced with fresh banana. Data collections were carried out each day at 16.00–18.00h. All butterflies captured were marked on the underside of the forewing with a permanent coloured marker according to height of capture (green for 40m, blue for 20m and red for 2m). Butterflies recaptured at a different height from where they were originally caught were given an additional mark for that height. Large butterflies were individually numbered, whereas the small ones were marked with a dot. Specimens for unidentified species such as *Tanaecia* spp. and *Euthalia* spp. were taken for subsequent identification in the laboratory.

2.5 Statistical Analyses

Statistical analysis and data manipulations were carried out using Microsoft Excel, Statistics Package for Social Sciences (SPSS) version 6.1 for Windows, and a computer program on "Species Richness and Diversity" (Henderson & Seaby 1998 version 2). All data were tested for normality (using Kolmogorov-Smirnov one-sample tests) before applying parametric statistics. Non-normal data were either transformed (including arc-sine transformation for percentages) or analysed non-parametrically. Species diversity was calculated using an array of non-parametric indices that took account of both species richness and species evenness.

Chapter 3 Impact of selective logging on vegetation structure and diversity of tropical rainforest butterflies

3.1 Introduction

Selective logging at Danum Valley follows methods described in detail in Chapter 1, where all commercial timber trees (on Borneo, mostly dipterocarps) with a diameter at breast height (dbh) greater than 60cm are harvested in a single operation. Selective logging can have a number of different impacts on the forest depending partly on timber volume extracted, the harvesting system used (in this case conventional selective logging), the extent of damage to residual trees (such as small trees, saplings and seedlings), and also damage to the soil (Pinard & Cropper 2000). For example, bulldozers and other heavy machinery used during the logging operation can remove the topsoil particularly along skid trails and log landings (see Chapter 1), and also damage a large portion of remaining vegetation structure when saplings and other non-timber trees are indirectly smashed or hit by falling logs (Nussbaum *et al.* 1995). Apart from generating logging debris, selective logging also causes the removal of topsoil which through erosion can reduce the nutrient content of the soil (Nussbaum 1995; Pinard *et al.* 2000). Continuous disturbance of topsoil by machinery results in soil compaction, and retards the recovery of the vegetation (Pinard & Putz 1996). Therefore, forest disturbance due to selective logging can cause major changes in vegetation structure and the forest environment (Sayer & Whitmore 1991).

The disturbance caused by commercial selective logging can affect numerous aspects of forest structure, such as species composition and microclimate (e.g light penetration to the forest floor, humidity and temperature; Lovejoy *et al.* 1986). It is likely that changes in vegetation structure caused by forest disturbance will affect plant species composition in the logged areas, through changes in canopy cover due to removal of large timber trees. This in turn is likely to increase the abundance of pioneer trees which become established in disturbed areas after logging (Corner 1988; Whitmore 1991). Changes in canopy cover are thought to be the main factor determining the amount of sunlight penetrating to the forest floor. Thus, the formation of gaps and loss of canopy cover following commercial logging may allow invasion by a wide range of plant species such as weeds and lianas which may dominate logged areas for many years (Fox 1976; Chai & Udarbe 1977). Vegetation structure is therefore an important factor to measure in order to quantify the degree of forest disturbance in logged areas, and to compare logged and unlogged forest (Newbery *et al.* 1996). Vegetation structure is likely to be an important factor to butterflies because it is likely to affect the availability of adult and larval resources (Owen 1971; Corbet & Pendlebury 1992; Kooi *et al.* 1996). In addition butterflies are known to be sensitive to local weather, light intensity and humidity in both temperate and tropical regions (Watt *et al.* 1968; Owen *et al.* 1972; Ehrlich *et al.* 1972; Weiss *et al.* 1987; Pollard & Yates 1993). Therefore changes in vegetation structure may also directly influence species composition of butterflies (Owen 1971; Ehrlich & Raven 1964).

Conversion to agriculture and clear felling generally results in decreased insect diversity (Holloway *et al.* 1992) but impacts of less severe habitat modification are less clear (Wolda 1983; Barlow & Woiwod 1989; Eggleton *et al.* 1996; Hill 1999). There are a growing number of studies describing effects of forest disturbance on butterfly communities. These studies have shown different results with both decreased and increased diversity of butterflies in response to disturbance (*e.g.* Raguso & Llorente-Bousquets 1990; Bowman *et al.* 1990; Kremen 1992; Hill *et al.* 1995; Spitzer *et al.* 1993, 1997; Hamer *et al.* 1997; DeVries *et al.* 1997, 1999; Lewis *et al.* 1998; Lawton *et al.* 1998; Wood & Gillman 1998; Hill 1999; Willott *et al.* 2000). The aims of this chapter are as follows;

- To measure vegetation structure in unlogged and selectively logged forest.
- To measure butterfly diversity in unlogged and selectively logged forest over a period of one complete year.
- To relate changes in butterfly diversity to changes in forest structure.

3.2 Materials and methods

3.2.1 Vegetation data

Transects were established in unlogged and selectively logged forest (total length 8km). The logged area had been selectively logged >10 years ago, in 1989 (coupe 89) and 1988 (coupe 88). Observation stations were marked at 100m intervals along each transect (80 stations in total) and vegetation structure was measured at all stations. Each station was divided into 4 quadrants and the 2 nearest large (> 0.6m girth at breast height (GBH)) and small (>0.1m GBH) trees were measured in each quadrant, up to a maximum distance of 30m from the station. The total number of trees, circumference at breast height, point of inversion (whether the first major branch was above or below the mid height of the tree; Torquebiau, 1986), height of trees, type of trees (dipterocarps/non-dipterocarps or *Macaranga* spp.), and distance from the station of each of the trees was recorded. Estimated vegetation cover (%) at ground ($\leq$2m), mid-level (2–5m), understorey (5–20m) and canopy (>20m) was recorded by two independent observers and the mean value was used. Total vegetation density at each station was also measured using a spherical densiometer (a concave mirror with an engraved grid and held horizontally; Lemmon 1957). Four densiometer measurements were taken by 2 independent observers at each station facing north, south, east and west. These data were used to quantify canopy openness (gaps) where the mean value of the two recorders was used. All these measurements (summarised in Table 3.1) were used to calculate 14 variables which were normalized using arc-sine transformation of percentages and $\log_{10}$ transformation, and analysed by a principal components analysis (Norusis 1990). Principal component analysis (PCA) is a data reduction procedure used to analyse variables that are highly correlated. The aim of the PCA was to produce a small number of independent factors from a large group of closely correlated variables and to allow ordination of stations with respect to these factors.

Table 3.1: List of measurements taken during the study.

Variables	Measurement	Precision
Vegetation density /canopy openness (measurement of total vegetation cover of the station)	Spherical densiometer (measured by 2 observers)	1%
Canopy cover (>20m)	Estimated by 2 independent observers	5%
Understorey cover (5–20m)	Estimated by 2 independent observers	5%
Mid-level cover (<5m)	Estimated by 2 independent observers	5%
Ground cover (≤ 2m)	Estimated by 2 independent observers	5%
8 large trees (>0.6m GBH) (2 per-quarter)		
type	Dipterocarp/non-dipterocarp/ *Macaranga* spp.	
point of inversion	Above/below mid part	
girth	Measuring tape	1cm
height	Estimated by two observers	5m
distance from station	Measuring tape	10cm
8 small trees (>0.1m GBH) (2 per-quarter)		
type	Dipterocarp/non-dipterocarp/ *Macaranga* spp.	
girth	Measuring tape	1cm
height	Estimated by two observers	5m
distance from station	Measuring tape	10cm

3.2.2 Butterfly data

Butterflies were surveyed in unlogged and selectively logged forest over one year (March 1999 to February 2000). Survey techniques followed transect methods used by Pollard (1977) in temperate forest and the walk and point-count transect methods used by Hill *et al.* (1995), Hamer *et al.* (1997) and Hill (1999) in tropical rainforest. Butterflies were recorded up to 5m either side of the path while a single observer was walking at a constant rate between stations, and for 5 minutes at each station. Two transects were set up in unlogged forest (Transect 1(T1)-west trail; Transect 2(T2)-rhino trail) and two transects in selectively logged forest (Transect 3(T3)-coupe 89; Transect 4(T4)-coupe 88). All transects were walked by two observers (myself and M.Dawood) twice every month. Two groups of butterflies were studied; Nymphalidae (subfamilies Satyrinae and Morphinae) and Riodinidae. These groups were chosen because they contain many species which are forest or shade dependent (Corbet & Pendlebury 1992), and can be reliably surveyed from the ground. In addition, these groups are well known taxonomically, and they are relatively easy to identify in flight. Apart from these groups, *Idea stolli* (Danainae) was included in this study because this species is also common in closed-canopy forest.

3.2.3 Data analysis

Data for butterflies were analysed using a computer program "Species Richness and Diversity" (Henderson & Seaby 1998 version 2). Pairwise randomization tests based on 10,000 random samples (Solow 1993) were carried out to test for significant differences in species richness and evenness. Goodness of fit tests were also carried out to assess whether species abundance distributions of butterflies in logged and unlogged forest best fitted a log-normal or log-series distribution. This analysis used chi-square tests to compare observed distributions of species with those predicted from log series and log normal models. Following Magurran (1988) I used Shannon-Wiener (H'), Margalef's and Simpson's indices of diversity.

Shannon-Wiener index

The Shannon-Wiener index (H') is an estimate of species diversity which incorporates richness and evenness into a single measure.

$$H' = -\Sigma p_i \ln p_i$$

where, p_i is the proportion of individuals found in the i^{th} species.

Margalef's index

The Margalef index is an estimate of species richness.

$$D = (S - 1)/ \ln N \quad \text{where,}$$

S = species number

N = total number of individuals in the sample.

Simpson's index

Simpson's index is a measure of species evenness.

$$D = 1/C \quad \text{where}$$

$$C = \Sigma p_i^2, \quad \text{and} \quad p_i^2 = (N_i / N_T)^2$$

Spearman Correlation Coefficients were used to test whether there was any relationship between butterfly diversity and vegetation structure (PCA factor scores), in selectively logged and unlogged forest and on different transects.

3.3 Results

3.3.1 Vegetation structure in unlogged and selectively logged forest

A total of seventy-seven measurements of fourteen variables (Table 3.1) were taken at each observation station in unlogged (see Plate 1) and selectively logged forest (see Plate 2). These variables were used to measure vegetation structure at both sites. Table 3.2 shows mean values for each variable at both sites.

Table 3.2: Mean scores for fourteen variables relating to vegetation structure in unlogged and selectively logged forest. Normalized where appropriate by arc-sine transformation with number of cases =80. Means were compared using t-tests, and asterisks denote significant differences at 5% (*), 1% (**) and 0.1% (***) levels.

Variables	Unlogged forest (40 cases)		Logged forest (40 cases)	
	Mean	Sd	Mean	Sd
Point of inversion	1.18	0.37	1.05	0.36
Proportion of large dipterocarps*	0.63	0.38	0.46	0.31
Proportion of small dipterocarps*	0.18	0.29	0.08	0.15
% Canopy openness	0.03	0.04	0.03	0.03
% Canopy cover (above 20m)***	0.41	0.17	0.15	0.12
% Understorey cover (5–20m)	0.68	0.24	0.66	0.20
% Mid-level cover (2–5m)*	0.61	0.19	0.70	0.19
% Ground cover (≤2m)	0.40	0.23	0.45	0.29
Proportion of large *Macaranga* spp.***	0	0	0.26	0.33
Proportion of small *Macaranga* spp.**	0	0	0.12	0.23
Girth of large trees (>0.6m)*	134.28	35.77	117.52	29.55
Girth of small trees (>0.1m)	23.44	4.03	23.02	3.87
Height of large trees***	32.18	4.87	27.57	5.10
Height of small trees**	8.57	2.04	9.81	1.89
Number of large trees	7.82	0.59	7.98	0.16
Distance to large trees*	0.10	0.03	0.12	0.03
Distance to small trees	0.29	0.07	0.30	0.09
Factor 1 ***	0.51	0.77	-0.51	0.95
Factor 2	-0.08	1.08	0.08	0.92
Factor 3	-0.007	0.87	0.007	1.13

Plate 1: View of unlogged forest in the study sites, mostly dominated by dipterocarp.

Plate 2: Logged forest in the study sites, mostly dominated by pioneer trees such as, *Macaranga* spp.

3.3.2 Principal components analyses (PCA)

The PCA extracted five factors from 14 vegetation variables, which accounted for 66.6% of the variability in the data set. Factors 4 and 5 explained only 13% of the variance and so were excluded from further analysis: the remaining analyses consider only factors 1, 2 and 3 (Table 3.3).

Table 3.3: Factors from PCA of vegetation structure. The percentage of variance explained by each factor (eigenvalue > 1) is shown.

Factor	Eigenvalue	Percentage of variance	Cummulative percentage
1	4.35	25.6	25.6
2	2.71	15.9	41.5
3	2.06	12.1	53.7
4	1.19	7.0	60.7
5	1.01	6.0	66.6

Factor 1 accounted for 25.6% of the variance in the data, and increased with increasing canopy cover, girth and height of large trees and proportion of large dipterocarps, and with decreasing distance to large trees and decreasing proportion of *Macaranga* spp. Therefore a high score for factor 1 could be considered to represent a vegetation structure characteristic of primary or undisturbed forest (Table 3.4). Factor 2 accounted for a further 15.9% of the variability of the data set and increased with increasing understorey cover and height of small trees, and decreasing mid-level cover. Therefore a high score for factor 2 indicated a vegetation structure characteristic of secondary or regenerating forest (Table 3.4). Factor 3 accounted for a further 12.1% of the variance in the data set and was characteristic of forest with low vegetation density (*i.e.* large percentage of gaps) and a high density of small trees, particularly *Macaranga* spp. This vegetation structure is characteristic of heavily disturbed forest (Table 3.4). There was a significant difference between logged and unlogged forest in Factor 1 (Table 3.2; t-test, t=0.1, df=1, P=0.001). However there was no significant difference between logged and unlogged in either Factor 2 or Factor 3 (P>0.05 in both cases).

Table 3.4: Factor weightings from PCA.

Variables	Factor 1	Factor 2	Factor 3
Point of inversion	0.42	0.38	0.02
Proportion of large dipterocarps	0.73	0.16	-0.09
Proportion of small dipterocarps	0.11	0.12	0.03
Canopy openness	-0.04	-0.31	0.69
Canopy cover	0.65	0.25	-0.26
Understorey cover	0.00	0.68	-0.29
Mid-level cover	-0.10	-0.65	-0.09
Ground cover	-0.42	-0.35	0.54
Proportion of large *Macaranga* spp	-0.72	0.17	0.33
Proportion of small *Macaranga* spp	-0.42	0.34	0.58
Girth of large trees	0.80	-0.09	0.11
Girth of small trees	0.11	0.44	0.51
Height of large trees	0.84	0.08	-0.19
Height of small trees	-0.12	0.74	-0.05
Number of large trees	-0.06	0.20	-0.02
Distance to large trees	-0.52	0.25	-0.28
Distance to small trees	0.07	-0.01	-0.76

3.3.3 Species abundance of butterflies in unlogged and selectively logged forest

A total of 1825 individuals of 34 species were recorded during the study of which 902 individuals were recorded in unlogged forest and 923 in selectively logged forest. Ten individuals (1% of the total) were unidentified due to poor sightings and were not included in further analyses. Two butterfly species that are difficult to separate in flight (*Mycalesis anapita* and *M. patiana*) were combined for the analysis. Over the study period, 29 species were recorded in unlogged forest and 30 species in logged forest (Table 3.5).

In unlogged forest, the highest numbers of individuals recorded (>50) were *Ragadia makuta* (367 individuals), *Mycalesis anapita/patiana* (93), *Idea stolli* (85), *Ypthima fasciata* (67) and *Paralaxita orphna* (52). In selectively logged forest, four species recorded >50 individuals; *Ragadia makuta* (439), *Ypthima fasciata* (85), *Idea stolli* (82) and *Xanthotaenia busiris* (85). The numerically dominant species in all transects was *Ragadia makuta* with Transect 3 (62%) recording the highest percentage, followed by Transect 2 (42%), Transect 1 (40%) and 30% in Transect 4 (Table 3.5).

Rank abundance plots for butterflies in unlogged and selectively logged forest are shown in Figure 3.1. Both unlogged and selectively logged forest were dominated numerically by *Ragadia makuta* which made up of >40% of total individuals in both habitats. Figure 3.2 shows species accumulation curves in unlogged and selectively logged forest on a monthly basis.

Table 3.5: Butterflies sampled in unlogged (UL) and selectively logged (L) forest. Data are shown separately for the four transects (T1 & T2 in unlogged forest, T3 & T4 in logged forest).

	T1	T2	UL (T1 &T2)	T3	T4	L (T3 &T4)	Total (UL & L)
Nymphalidae							
Danainae							
Idea stolli Fruh.	33	52	85	35	47	82	167
Morphinae							
Faunis canens Fruh.	13	7	20	15	7	22	42
Faunis kirata De Nic.	1	0	1	1	0	1	2
Faunis stomphax West.	3	1	4	3	0	3	7
Xanthotaenia busiris Stich.	13	20	33	30	26	56	89
Amathusia phiddipus Linn.	0	0	0	0	1	1	1
Zeuxidia amethystus C&R Fel.	0	1	1	0	0	0	1
Thaumantis odona Fruh.	2	4	6	10	4	14	20
Thaumantis nouredin Fruh.	1	0	1	0	0	0	1
Satyrinae							
Melanitis leda Linn.	0	1	1	0	1	1	2
Neorina lowii Doubl.	3	12	15	3	6	9	24
Lethe chandica Stau.	0	0	0	1	0	1	1
Mycalesis anapita/patiana	27	66	93	19	23	42	135
Mycalesis fusca Fruh.	0	0	0	0	1	1	1
Mycalesis kina Stau.	1	4	5	0	0	0	5
Mycalesis dohertyii Fruh.	4	5	9	4	0	4	13
Mycalesis horsfieldi Fruh.	1	4	5	0	0	0	5
Mycalesis orseis Fruh.	2	5	7	5	2	7	14
Mycalesis maianeas A. & U.	3	2	5	6	19	25	30
Mycalesis oroatis Hew.	13	13	26	3	4	7	33
Erites argentina Butl.	15	14	29	14	14	28	57
Erites elegans Butl.	7	8	15	8	13	21	36
Ragadia makuta Fruh.	136	231	367	320	119	439	806
Ypthima baldus Fruh.	6	12	18	2	7	9	27
Ypthima fasciata Hew.	31	36	67	8	77	85	152
Ypthima pandocus Fruh.	0	1	1	0	2	2	3
Riodinidae							
Zemeros flegyas Fruh.	0	1	1	0	1	1	2
Zemeros emesoides Fruh.	1	5	6	3	3	6	12
Abisara geza Fruh.	0	0	0	0	2	2	2
Abisara kausambi Benn.	0	0	0	1	0	1	1
Paralaxita damajanti De Nic.	6	5	11	3	2	5	16
Paralaxita telesia Fruh.	8	5	13	6	5	11	24
Paralaxita orphna Boisd.	12	40	52	17	13	30	82
Taxila haquinus Fruh.	1	0	1	0	1	1	2
Unidentified	2	2	4	4	2	6	10
Number of species	25	26	29	23	25	30	34
Total number of individuals	345	557	902	521	402	923	1825

Figure 3.1: Proportional abundance plot in unlogged (open bars) and selectively logged (closed bars) forest.

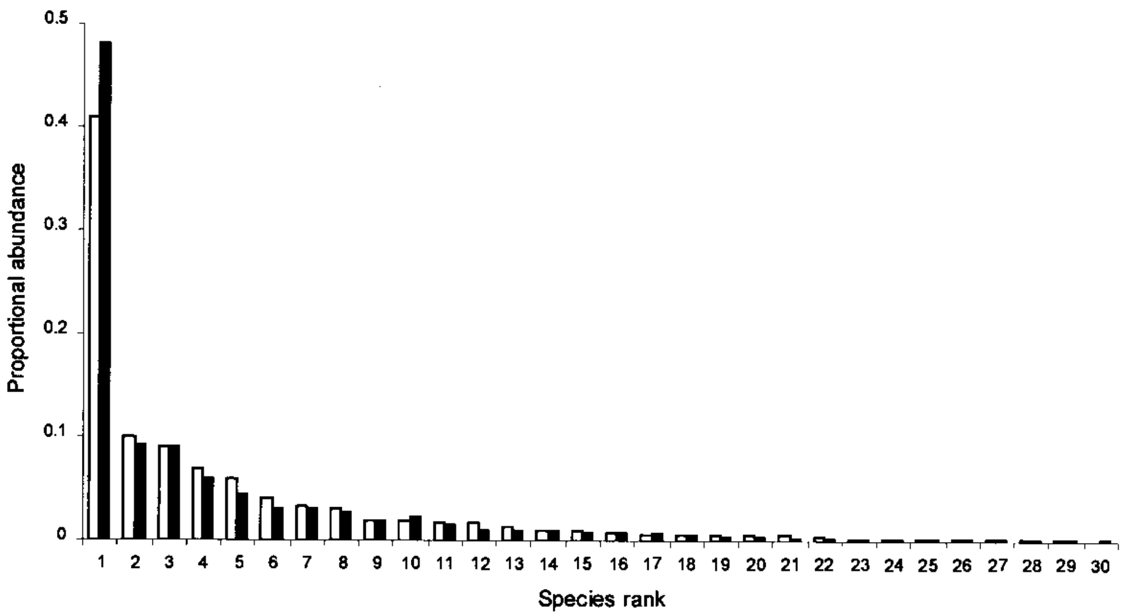
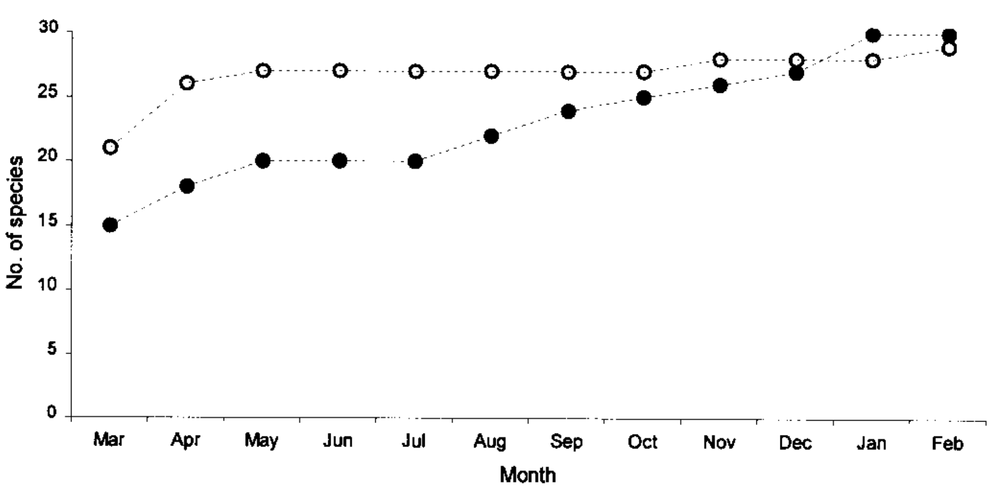


Figure 3.2: Species accumulation curves in unlogged forest (-o-) and selectively logged forest (-•-).



3.3.4 Species diversity in unlogged and selectively logged forest

Table 3.6 shows Shannon, Simpson and Margalef diversity indices in unlogged and selectively logged forest, plus goodness of fit for log-series and log-normal distributions. Butterfly assemblages in unlogged and selectively logged forest were not significantly different from either log-series or log-normal distributions (P>0.5 in all cases). Shannon's and Simpson's indices showed significantly higher species diversity in unlogged forest compared to logged forest (delta=-0.18, P=0.01 and delta=1.06, P=0.004 respectively), but there was no difference in species richness (Margalef's index, delta=-0.14, P=0.76).

Table 3.6: Species diversity of butterflies in unlogged and logged forest. Indices with asterisks are significantly different (* P<0.05; ** P<0.01).

	Unlogged forest	Logged forest
Number of species	29	30
Number of individuals	899	916
Shannon Wiener index (H')*	2.25	2.07
Standard error (SE)	0.01	0.01
Simpson index**	4.98	3.92
SE	0.58	0.44
Margalef index	4.12	4.25
SE	0.38	0.38
Fit to log series	Yes Chi-square = 7.03 df = 8 P = 0.53	Yes Chi-square = 3.94 df = 8 P = 0.86
Fit to log normal	Yes Chi-square = 4.96 df = 8 P = 0.76	Yes Chi-square = 3.20 df = 8 P = 0.92

I also examined differences in species diversity among transects. Shannon-Wiener H' and Simpson D were significantly lower on Transect 3 (logged forest) than elsewhere and Simpson D was significantly higher on Transect 4 (logged forest) than elsewhere. There were no significant differences among transects in Margalef's index (P>0.1 in all cases).

Table 3.7: Diversity indices for each transects. Index values for each measure followed by different letters are significantly different (P<0.05).

Measurement	Transect 1	Transect 2	Transect 3	Transect 4
Number of species	25	26	23	25
Number of individuals	343	556	517	399
Shannon Wiener index	2.28 **a**	2.20 **a**	1.67 **b**	2.33 **a**
SE	0.14	0.12	0.14	0.13
Simpson index	5.32 **ac**	4.78 **a**	2.53 **b**	6.62 **c**
SE	0.97	0.66	0.31	0.90
Margalef index	4.11 **a**	3.96 **a**	3.52 **a**	4.00 **a**
SE	0.44	0.33	0.33	0.43

3.3.5 Relationship between butterfly diversity and vegetation structure

I used Spearman correlations to investigate relationships between diversity of butterflies and vegetation structure (PCA-Factors 1–3). Species evenness (Simpson D) and species diversity (Shannon-Wiener) were negatively correlated with Factor 1 in selectively logged forest (Simpson: r_s=-0.35, P=0.03; Shannon: r_s=-0.37, P=0.02). However both these relationships were quite weak (Figure 3.3 and 3.4) and there were no other significant correlations with vegetation structure (P>0.05 in all cases).

Figure 3.3: Species richness (Simpson index) relationship with vegetation structure (PCA - Factor 1) in selectively logged forest.

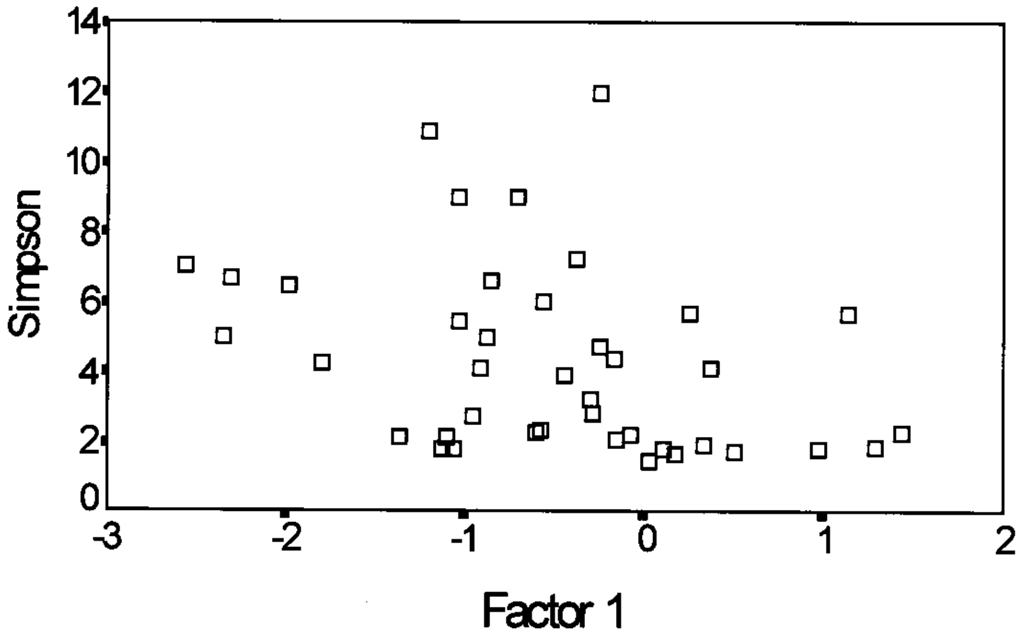
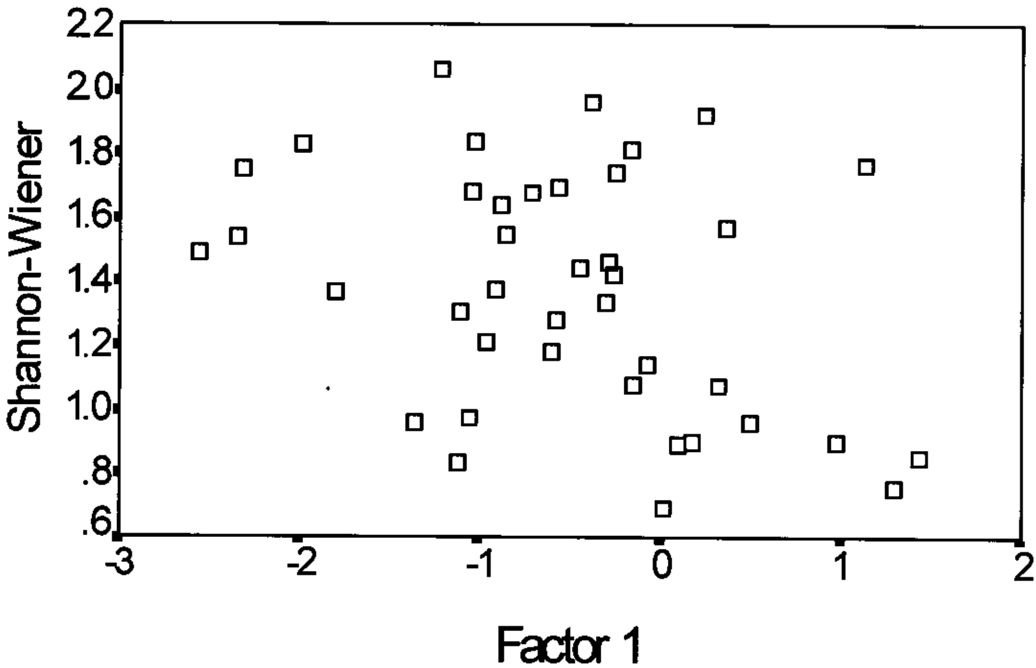


Figure 3.4: Species diversity (Shannon-Wiener) relationship with vegetation structure (PCA - Factor 1) in selectively logged forest.



3. 4 Discussion

3.4.1 Collection of data

Walk and point count methods were used to survey butterflies in logged and unlogged forest (Hill *et al.* 1995; Hamer *et al.* 1997; Hill 1999). The use of this method in tropical forests has been criticized because of difficulties in species identification (Walpole & Sheldon 1999). To avoid this problem, I restricted the study to groups of butterflies that can be reliably recorded from the ground. I also spent three months familiarizing myself with these butterflies before starting fieldwork. In this study, only 10 individuals (<1%) were unidentified from the total of 1825 individuals sampled. A total of 384km was walked on transects and time spent sampling was approximately 770 hours (10.00–14.00h on each transect) over a full year (to minimize seasonal effects; DeVries *et al.* 1997; Willot *et al.* 2000). Thus this method resulted in a large and reliable dataset for comparison between study sites. Some Satyrid butterflies (e.g. *Melanitis leda*) would not have been observed during this sampling because they are crepuscular species (active only during dawn and dusk; Corbet & Pendlebury 1992). Nevertheless, this is a relatively small number of species and their omission is unlikely to have had a significant effect on the study.

3.4.2 Impacts of selective logging on vegetation structure

The measurement of vegetation structure was carried out in unlogged and selectively logged forest in order to quantify the degree of forest disturbance in the selectively logged area (see Hill 1999). This is also because forest disturbance might affect the availability of resources to butterflies (Owen 1971). Fourteen variables (see Table 3.1) relating to vegetation structure were measured for this study. All measurement was taken as accurately as possible, and estimates of forest cover and heights of tree taken by two independent observers were generally in close agreement (5–10% of each other). In addition a densiometer measure for vegetation cover was also taken by two independent observers to estimate the total vegetation density for all stations.

Comparison of vegetation structure in unlogged and selectively logged forest showed significant differences in vegetation structure >10 years after logging. Unlogged forest typically had larger and taller trees (mostly dominated by dipterocarps) with greater canopy cover (Whitmore 1990). Previous studies by Nussbaum *et al.* (1995) on growth of indigenous trees, and by Pinard *et al.* (2000) on effect of logging on dipterocarp forest, both showed that the impacts of selective logging on vegetation structure are still evident >6 years after logging. The occurrence of a low density of trees, low vegetation cover at canopy and understorey levels, high vegetation cover at low level and a high proportion of trees with points of inversion in the lower half of the trunk, are all characteristics of disturbed forest (Oldemann 1983; Torquebiau 1986; Hill *et al.* 1995; Hamer *et al.* 1997; Hill 1999) and were characteristic of selectively logged forest in this study. The logged forest generally had lower canopy cover and included a high proportion (25%) of large trees of pioneer species such as those in the genus *Macaranga*. Similar changes following logging have been found elsewhere (Fox 1976; Chai & Udarbe 1977; Nussbaum *et al.* 1995; Pinard & Cropper 2000; Willott *et al.* 2000).

3.4.3 Impacts of selective logging on butterfly assemblages

The Shannon-Wiener index (which incorporates richness and eveness into a single measure) and Simpson's index (species evenness) both indicated that species diversity was significantly higher in unlogged forest than in selectively logged forest (Table 3.6). This result is in agreement with a number of others studies on insects showing decreases in species diversity in response to selective logging (e.g. Collins 1980; Wong 1986; Holloway 1987; Holloway *et al.* 1992; Davis 1993; Chey 1994; Hill *et al.* 1995; Chung & Maryati 1996; Chey *et al.* 1997; Eggleton *et al.* 1997; Spitzer *et al.* 1997; Lewis *et al.* 1998). However there were no differences found in this study in the number of species, and Margalef's index (species richness) also showed no significant difference between habitats. Thus the main impact of logging was on species evenness rather than species richness. Comparison among transects showed that Transect 3, in logged forest, had the lowest diversity and Transect 4, also in logged forest, had the highest. This may be attributed to the degree of forest disturbance and topography among transects in the logged forest (Marsh & Greer 1992; Hill 1999). Transect 3 passed through a river catchment containing areas of less severely logged forest (Douglas *et al.* 1992), whereas Transect 4 was in a more heavily disturbed area of forest, as indicated by vegetation structure.

The results of this study contrast with some other studies where forest disturbance resulted in an increase in species diversity of butterflies (Lovejoy *et al.* 1986; Janzen 1987; Raguso & Llorente-Bousquets 1990; Spitzer *et al.* 1993; DeVries *et al.* 1997; Wood & Gillman 1998) and with some other studies which suggested that there was no difference in species diversity between undisturbed and moderately disturbed forest (Wolda 1987; Willott *et al.* 2000). Hamer & Hill (2000) found that the recorded impacts of disturbance on diversity are heavily dependent on the spatial scale at which data are collected and analysed. The results of the current study support the idea that whilst disturbance may increase diversity over small spatial scales, diversity at large scales is decreased by disturbance.

In this study species abundance (Table 3.6) fitted both log-series and log-normal distributions in both logged and unlogged forest. However in unlogged forest, abundance fitted the log-normal distribution much better than the log-series. This may be because the unlogged forest consists of a relatively complex assembly of species (May 1981; Hill & Hamer 1998). This was also shown by two recent studies in selectively logged and unlogged rainforest elsewhere (Hill *et al.* 1995; Hamer *et al.* 1997). However in the current study the species abundance distribution of butterflies in selectively logged forest also fitted a log-normal distribution (Table 3.6). These result suggest that selectively logged areas in this study may be approaching similar conditions to those in unlogged forest, provided that there is no further disturbance (Willott *et al.* 2000). However the potential effects of further selective logging are not known (Pinard *et al.* 2000).

3.4.4 Relationship between vegetation structure and butterfly diversity

Shannon-Wiener and Simpson's index were negatively correlated with Factor 1 in logged forest (Figure 3.3 & 3.4). Although the relationship was weak, it suggests that in logged forest, butterfly diversity at a small spatial scale increased with increasing disturbance to the vegetation, as indicated by a low score for Factor 1. This agrees with the scale-dependent relationship between disturbance and diversity proposed by Hamer & Hill (2000). The lack of a relationship in unlogged forest probably reflected the smaller range of values for Factor 1 in that habitat (Table 3.2; variance=0.59 in unlogged forest, variance=0.90 in logged forest).

Chapter 4 Biogeographical effects of logging on rainforest butterflies

4.1 Introduction

The Malesian Archipelago is located within the Oriental region, and stretches from Sumatra in the west to the Bismarck islands (off the north-east coast of New Guinea) in the east (Figure 4.1). It consists of three faunal sub-regions, Sundaland, Wallacea and the Australasian region (Cox & Moore 2000). The Malaysian state of Sabah is located at the northern tip of the island of Borneo, in the biogeographic region of Sundaland, comprising Sumatra, Peninsular Malaysia, Java, Borneo and their surrounding islets, which are connected by shallow seas (Otsuka 1988; Cox & Moore 2000).

During the late Pliocene and Quaternary, falling ocean levels exposed land connections between these major islands and the Asian continent. The formation of these land-bridges (which were last breached approximately 10,000 years ago) may explain why the flora and fauna of the Sundaland islands have much in common (Inger 1966; Whitmore 1984; Morley & Flenley 1987; Ashton 1995). For example, out of 358 species of resident land birds in Borneo, 306 (85%) are shared with Sumatra and 297 (83%) with Peninsular Malaysia. In contrast, Sulawesi (to the east of Borneo), although very close to Borneo (approximately 100 km), is not part of Sundaland and had no land-bridge connections, and is separated by deep ocean and has only 63 (26%) bird species in common (MacKinnon *et al.* 1996). Similarly for butterflies, out of 336 species recorded for Borneo, 209 (62%) are shared with Sumatra whilst only 4 (1%) occur in Sulawesi (Otsuka 1988).

The pattern and duration of land connections have had other effects on the present distribution of species and the occurrence of localized endemic forms in Sundaland (Morley & Flenley 1987). There are a large number of butterfly species that are endemic to Borneo and thus have high conservation value. It is important to investigate the geographical distribution of species and also their responses to forest disturbance such as selective logging (Hill *et al.* 1995).

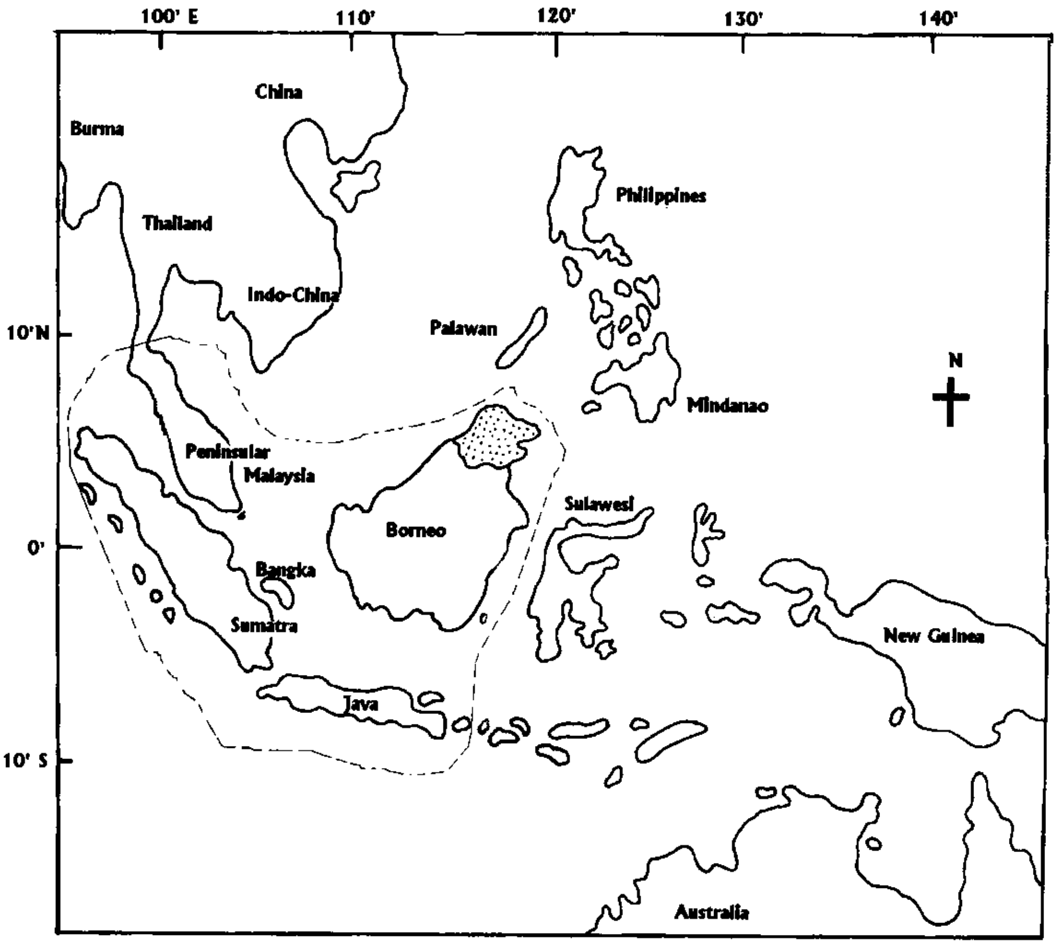


Figure 4.1: Map of South East Asia; dashed line shows the extent of the Sundaland region.

The geographical ranges of butterfly species are closely related to their life-history characteristics, and many endemic species are very specialised (Thomas 1991). In addition, specialized species are generally restricted to dense forest habitats (Thomas & Mallorie 1985; Hamer *et al.* 1997; Spitzer *et al.* 1997; Lewis *et al.* 1998). This suggests that forest disturbance such as selective logging that opens up the canopy (see Chapter 3), may affect butterfly species with narrow geographical ranges (Thomas 1991; Spitzer *et al.* 1993; Hill *et al.* 1995; Hamer *et al.* 1997; Spitzer *et al.* 1997; Hill 1999). Recent studies by Hill *et al.* (1995) and Hamer *et al.* (1997), show that selective logging results in the lost of species with narrow geographical ranges. Although species loss and extinction is a natural process (Darwin 1859), it is occurring at a rapid rate particularly in tropical rainforests, probably because of the rapid loss of natural habitats (Sayer & Whitmore 1990; Collins *et al.* 1991; Chapin *et al.* 2000). Furthermore, tropical rainforests are very diverse ecosystems with large numbers of rare species, many of which are likely to be threatened with extinction (Janzen 1987; DeVries *et al.* 1997). The aim of this chapter is to investigate impacts of selective logging on butterflies in the context of their biogeographical distribution.

4.2 Materials and methods

Butterflies was surveyed along four transects in unlogged and selectively logged forests (total length 8km). Butterflies were surveyed at 80 observation stations along these transects. All transects was surveyed twice by 2 recorders (myself and M.Dawood) each month (total of 4 repeats per month) using methods described by Hill *et al.* (1995), Hamer *et al.* (1997) and Hill (1999) in tropical rainforest (see Chapter 2 and Chapter 3). All adults butterflies of the subfamilies Satyrinae, Morphinae, Riodinidae, and *Idea stolli* was recorded within a 10m radius of each station and 5m either side of the path between stations.

Geographical ranges and distribution records of butterflies follow Otsuka (1988). The study was carried out for twelve months and monthly data were combined for analysis. Each species was ranked according to its geographical distribution (see Hill *et al.* 1995; Hamer *et al.* 1997). Species endemic to Borneo *i.e. Mycalesis kina*, were given the highest rank (ranked 1), and widespread species such as *Melanitis leda*, the lowest rank (ranked 34). No attempt was made to split species with very similar ranges (e.g. species confined to Sundaland) and these were allocated tied ranks. Table 4.1 gives distributions of all species recorded during the study, and their ranks.

Habitat preferences in relation to rank were then assessed in terms of the site where each species attained highest density (Hill *et al.* 1995; Hamer *et al.* 1997; Willott *et al.* 2000). Butterfly species with the same density at both sites were excluded from the biogeographical analysis (see Hill *et al.* 1995). Non-parametric tests, Mann-Whitney Z-test and Kruskal-Wallis one-way analysis of variance (ANOVA) were used to test whether there was any significant difference in biogeographical distribution between butterflies in logged and unlogged forest.

4.3 Results

4.3.1 Biogeographical distribution of rainforest butterflies

Altogether, 1825 individual butterflies from 34 species were recorded (see chapter 3). One hundred and thirty-five individuals (7%) of *Mycalesis anapita* and *M. patiana* could not be separated due to difficulties in identifying them in flight and were combined for the analysis. However their biogeographical distributions are almost identical and they have the same biogeographical rank (rank 2). Ten individuals (<1%) were unidentified due to poor sightings, and were excluded from the biogeographical analysis. There were approximately equal numbers of unidentified individuals in logged and unlogged habitats, therefore their exclusion from the analysis was unlikely to affect the results.

Table 4.1: Butterfly species recorded on transects, with habitats (1-unlogged; 2-selectively logged), and ranked scores for geographical distribution.

	Distribution of species	Habitats	Rank
Nymphalidae			
Danainae			
Idea stolli	Java, PEN, SUM	1, 2	11
Morphinae			
Faunis canens	SDL, THA	1, 2	18
Faunis kirata	PEN, SUM	1, 2	2
Faunis stomphax	SUM, PAL	1, 2	2
Xanthotaenia busiris	PEN, SUM, THA	1, 2	18
Amathusia phiddipus	BUR, THA, IDCH, PEN, PHI, SUL	2	28
Zeuxidia amethystus	PEN, SUM, PAL, MIN, BUR, THA	1	23
Thaumantis odona	PEN, SUM, Java	1, 2	11
Thaumantis nouredin	PEN, SUM	1	2
Satyrinae			
Melanitis leda	Oriental region, Australia, Africa	1, 2	34
Neorina lowii	PEN, SUM, PAL	1, 2	11
Lethe chandica	SUM, Java, PEN, PAL, PHI, S China, N India, Taiwan	2	32
Mycalesis anapita/patinana	PEN, SUM	1, 2	2
Mycalesis fusca	PEN, SUM, Java	2	11
Mycalesis kina	Endemic to Borneo	1	1
Mycalesis dohertyii	PEN, SUM	1, 2	2
Mycalesis horsfieldi	SUM, Java, PAL, Bali, SUL	1	28
Mycalesis orseis	PEN, SUM, PAL, BUR, THA	1, 2	18
Mycalesis maianeas	PEN, SUM	1, 2	2
Mycalesis oroatis	PEN, SUM, Java	1, 2	11
Erites argentina	PEN, SUM, Java	1, 2	11
Erites elegans	PEN, SUM	1, 2	2
Ragadia makuta	PEN, SUM, Java	1, 2	11
Ypthima baldus	SDL	1, 2	18
Ypthima fasciata	PEN, SUM	1, 2	2
Ypthima pandocus	Java, SUM, PEN, PAL, MIN	1, 2	23
Riodinidae			
Zemeros flegyas	PEN, SUM, Java, Sikim, S China, BUR, THA, IDCH, PHI, SUL	1, 2	33
Zemeros emesoides	PEN, SUM	1, 2	2
Abisara geza	PEN, SUM, PAL, Java	2	18
Abisara kausambi	Java, PEN, SUM, SUL, PAL	2	28
Paralaxita damajanti	PEN, SUM, BUR, THA	1, 2	23
Paralaxita telesia	PEN, SUM, BUR, THA	1, 2	23
Paralaxita orphna	PEN, SUM, BUR, THA	1, 2	23
Taxila haquinus	N India, BUR, THA, PEN, SUM, Java, PAL	1, 2	28

The underlined habitat has the highest density of butterflies. Classification and distribution follows Otsuka (1988). SDL, Sundaland (includes Sumatra, Peninsular Malaysia, Java, Borneo); SUM, Sumatra; PEN, Peninsular Malaysia; Java,; PAL, Palawan; THA, Thailand; SUL, Sulawesi; PHI, Philippines; MIN, Mindanao; IDCH, Indo-China; BUR, Burma.

There was no significant difference in biogeographical distributions of butterfly assemblages in unlogged and selectively logged forest (unlogged, median rank=11, number of cases=15; selectively logged, median rank=18, number of cases=12; Mann-Whitney Z-test; Z=-0.75, P>0.46). There was also no significant difference in biogeographical distribution among transects (Kruskal-Wallis one-way ANOVA of ranks; chi-square=3.27, number of cases=26, P>0.35).

Four species occurred only in unlogged forest from a total of 34 species. These were the endemic species *Mycalesis kina* (ranked 1, total individuals (N)=5), plus *Mycalesis horsfieldi* (ranked 28, N=5), *Thaumantis nouredin* (ranked 2, N=1), and *Zeuxidia amethystus* (ranked 23, N=1). Five species occurred only in selectively logged forest; *Amathusia phiddipus* (ranked 28, N=1), *Lethe chandica* (ranked 32, N=1), *Mycalesis fusca* (ranked 11, N=1), *Abisara geza* (ranked 18, N=2) and *Abisara kausambi* (ranked 28, N=1), whilst twenty-five species occurred in both habitats (Table 4.1).

In this study 22 of the 34 species recorded on transects (>60%) were restricted to Sundaland (rank 11 or higher in Table 4.1). Eight of these species occurred at highest density in unlogged forest, whilst seven occurred at highest density in the logged forest. Two of these species occurred only in unlogged forest (*Mycalesis kina* and *Thaumantis nouredin*), and two only in logged forest (*Abisara geza* and *Mycalesis fusca*).

4.4 Discussion

The abundances of species may be described in terms of their geographical ranges, habitat types, and population density within habitats as well as by species richness (Spitzer *et al.* 1993). Measures of species diversity give no information on the composition of the fauna, or its conservation value. In disturbed habitats, species generally have widespread distribution and broad habitat requirements (Holloway *et al.* 1992). Usually species that are sensitive to environmental changes are those with restricted geographical distribution that occur only in a very limited number of habitats (Thomas & Mallorie 1985; Thomas 1991; Spitzer *et al.* 1993; Hill *et al.* 1995; Hamer *et al.* 1997; Spitzer *et al.* 1997; DeVries *et al.* 1997; Lewis *et al.* 1998). Most common species are usually widespread and able to disperse in disturbed habitat (Spitzer *et al.* 1993) unlike the rare species (Hill *et al.* 1995; Spitzer *et al.* 1997).

In this study the biogeographical distribution of butterflies did not differ between unlogged and logged forest habitats. However, the mean rank for biogeographical distribution in unlogged forest was slightly lower (although not statistically) than in logged forest, suggesting that biogeographical distributions of butterflies in unlogged forest showed a trend of more restricted distributions than in the logged forest. For example, one species that is endemic to Borneo (*Mycalesis kina*) was only recorded in the unlogged site, suggesting that endemic species may tend to be lost in disturbed environments (Lewis *et al.* 1998; Gaston 2000). Therefore, this result may suggest that the probability of losing endemic species is greater in disturbed forests than in undisturbed forests (Spitzer *et al.* 1997). This may be because endemic species have highly specialised habitat requirements (Thomas 1991; Spitzer *et al.* 1993; Hill *et al.* 1995; Hamer *et al.* 1997). The vulnerablility of endemic species to habitat disturbance is of great concern given that these species have high conservation value (Hill *et al.* 1995; Spitzer *et al.* 1997; Lewis *et al.* 1998). Several studies have shown that generalist species with widespread distributions occur more frequently in disturbed habitat (Thomas 1991; Spitzer *et al.* 1993, 1997; Hill *et al.* 1995; Hamer *et al.* 1997).

However, it should be stressed that this study showed no significant difference in biogeographical distribution between sites or among transects. This may be because most of the species recorded (>60%) are confined to Sundaland region and therefore have narrow geographical ranges.

In summary, the biogeographical distribution of understorey forest butterfly assemblages generally was not affected by selective logging. However further studies should investigate if this is also the case for other groups of butterflies in other tropical regions.

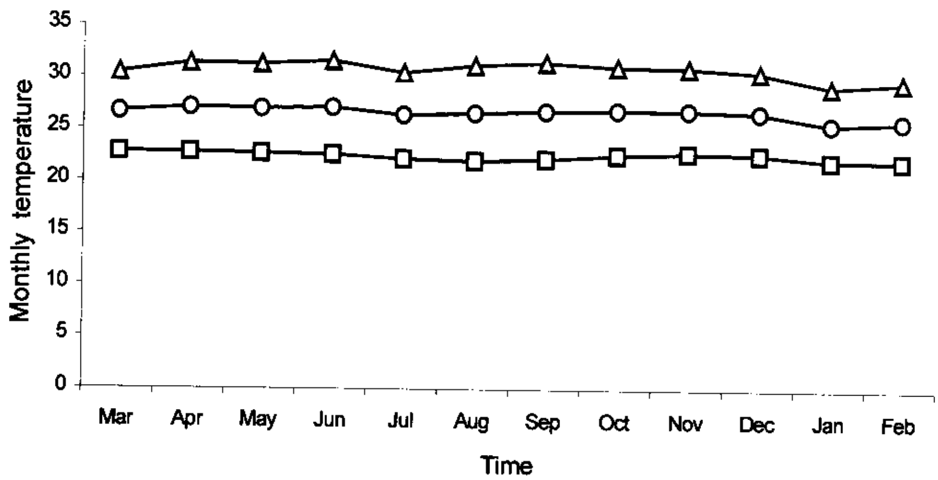
Chapter 5 Seasonal changes in diversity of tropical butterflies

5.1 Introduction

The responses of insects to seasonal changes have received much attention, particularly in temperate regions (Dennis 1993; Speight *et al.* 1999). Insects are sensitive to changes in temperature and photoperiod (Pollard & Yates 1993) and many species enter diapause or migrate to avoid unsuitable periods (Dennis 1993). By contrast, tropical regions are considered to be less seasonal and do not experience marked changes in either photoperiod or temperature. For example Figure 5.1 shows mean, maximum and minimum temperature at the study site from March 1999 to February 2000, showing little variation in temperature (highest =27.0°C and the lowest =25.5°C). Photoperiods at the study site are also relatively constant throughout the year, 12 hours of sunlight and 12 hours of dark periods (12L: 12D).

In contrast to temperature and light, many tropical areas show marked changes in rainfall, particularly those parts of the tropics (e.g. Amazon and Australian rainforest) with distinct wet and dry seasons (Janzen 1987, Braby 1995). Even tropical regions that are generally considered to be aseasonal (such as Borneo) can experience significant changes in rainfall, for example droughts associated with El Nino-Southern Oscillation (ENSO) events (Walsh 1996).

Figure 5.1: Mean (-o-), maximum (-△-), and minimum (-□-) of monthly temperature recorded at DVFC from March 1999 – February 2000



There is evidence that some tropical butterflies are highly seasonal with adults present for only a short period of the year (Owen 1983). There are several studies showing an increase in species abundance of butterflies during the wet season (Owen 1971; Braby 1995), although some species increase during the dry season (Emmel & Leck 1970; Jones & Rienks 1987). There are also studies showing that some changes in butterfly abundance are not related to either wet or dry seasons (e.g. Owen & Chanter 1972; Braby 1993). In tropical areas where rainfall is generally uniform throughout the year, seasonality of Lepidoptera may be less obvious (Herbert 1980). However, there is still a lack of information on seasonal changes in butterflies, particularly in aseasonal tropical areas, and most studies are conducted only over a short period of time (Spitzer *et al.* 1993; Hill *et al.* 1995; Hamer *et al.* 1997).

Butterflies are sensitive to sunshine (Dennis 1993; Pollard & Yates 1993) and in tropical regions many adults butterflies are only active during sunny conditions (Corbet & Pendlebury 1992). Therefore changes in sunshine may also affect tropical butterfly abundance, although this has not been investigated. The aims of this study are as follows;

- To investigate seasonal changes in diversity and abundance of tropical butterflies.
- To relate changes on total rainfall to changes in sunshine hours on a monthly basis.
- To relate changes in total monthly rainfall and monthly sunshine to changes in butterfly diversity.

5.2 Materials and methods

Few butterflies are active during poor weather conditions and therefore no observations were carried out on rainy days or in bad weather (e.g. Hill *et al.* 1995; Hill 1999). Butterfly surveys were carried out only during good weather. Survey were carried out on four transects (total length 8km) in selectively logged (Transect 3 & 4) and in unlogged forest (Transect 1 & 2). All transects were surveyed twice by two recorders (myself and M. Dawood) each month (total of four transects per month). Butterflies were surveyed at 80 observation stations along the transects. In this study all adults butterflies in the groups of Satyrinae, Morphinae, Riodinidae and *Idea stolli* were recorded within a 10m radius of each station and also 5m either side of the path between stations (see Chapter 2). Data for monthly rainfall and sunshine from December 1998 to February 2000 were obtained from a meteorological station at the Danum Valley Field Centre (DVFC).

Data on rainfall and sunshine were calculated as the total rainfall (mm) and total sunshine (hours) each month. These data were used to compute eight variables; monthly rainfall and sunshine in month of survey, rainfall and sunshine in the previous month, rainfall and sunshine in the previous 2 months, and also rainfall and sunshine 3 months before the survey. These time periods were chosen in order to cover the life span of adult butterflies seen on surveys and also the development time of larvae giving rise to adults and seen during the period of survey.

Multiple stepwise regression analysis was used to find out whether there was any relationship between any of the climate variables and butterfly diversity. Correlations were carried out to investigate whether there were any relationships among the climate variables. Following recommendation by Magurran (1988) the Shannon-Wiener index was chosen for measurement of species diversity recorded on transects because this measurement incorporates both species richness and species evenness into a single measure (see Chapter 3 for formula of Shannon-Wiener index).

5.3 Results

5.3.1 Monthly rainfall, sunshine, number of species and individuals

Figure 5.2 shows total monthly rainfall recorded at DVFC from December 1998 until February 2000. Total monthly rainfall during the study period from March 1999 to February 2000 was 3334 mm, with a total of 254 rain days and 112 days with no rain. The highest rainfall during the study period was recorded in January 2000 (489.4mm) and the lowest in September 1999 (144.8mm). Rainfall during the study period was typically high and was similar to rainfall at the site since 1986 and this was typical of wet equatorial conditions (Marsh & Greer 1992; Walsh 1996). Compared with rainfall, monthly sunshine showed less variation during the study period; March 1999 had the lowest sunshine (89.1hours) and July the highest (183.8 hours). Figure 5.3 shows monthly sunshine recorded at DVFC from December 1998 until February 2000.

Figure 5.4 shows the number of butterfly species and individuals recorded each month in unlogged and selectively logged forest. In unlogged forest, the number of species recorded each month varied from 9 to 29, and in logged forest varied from 11 to 17 species. The number of individuals recorded varied from 50 to 111 and 52 to 134 in unlogged and logged forest, respectively.

Figure 5.2: Monthly total rainfall (mm) recorded at DVFC during the study.

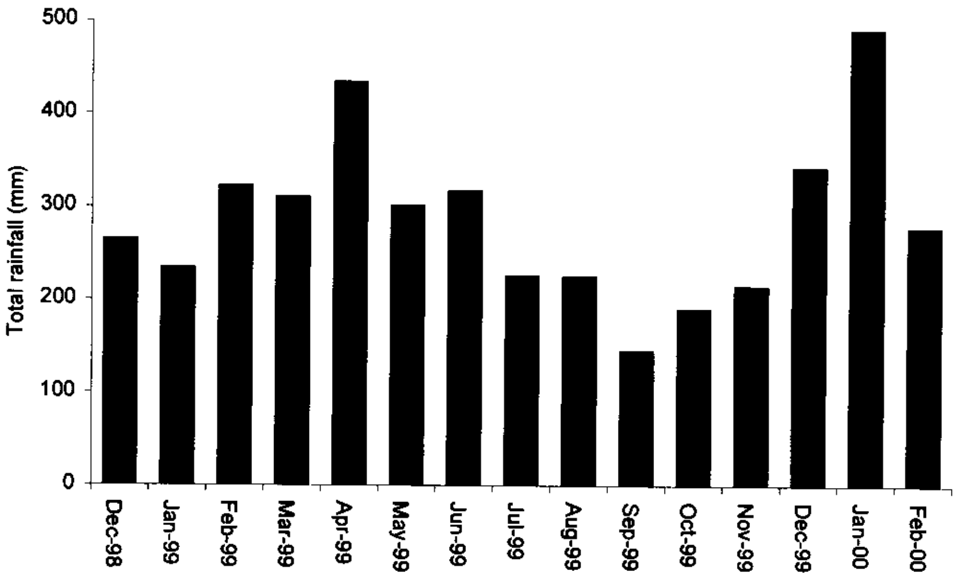


Figure 5.3: Monthly total sunshine (hours) recorded at DVFC during the study.

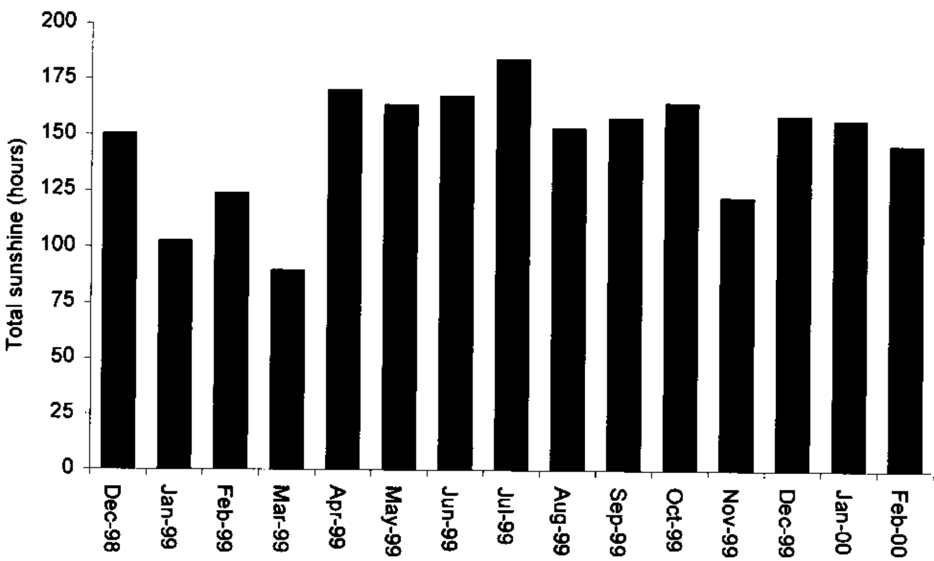
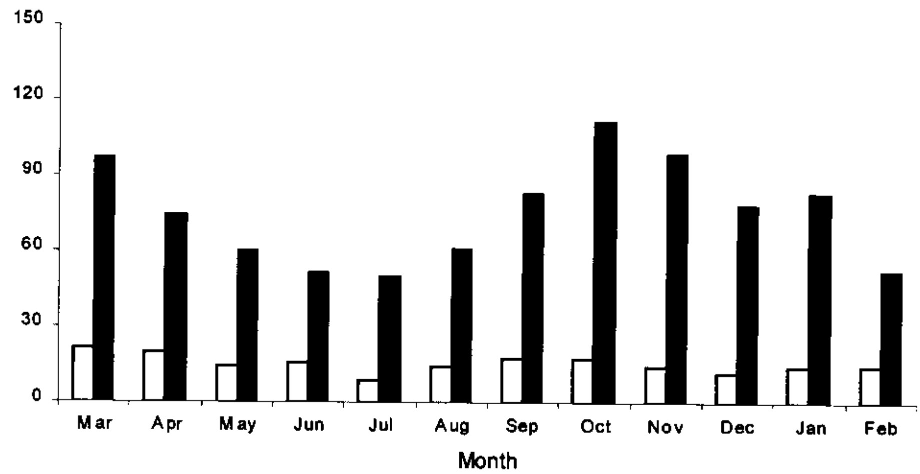
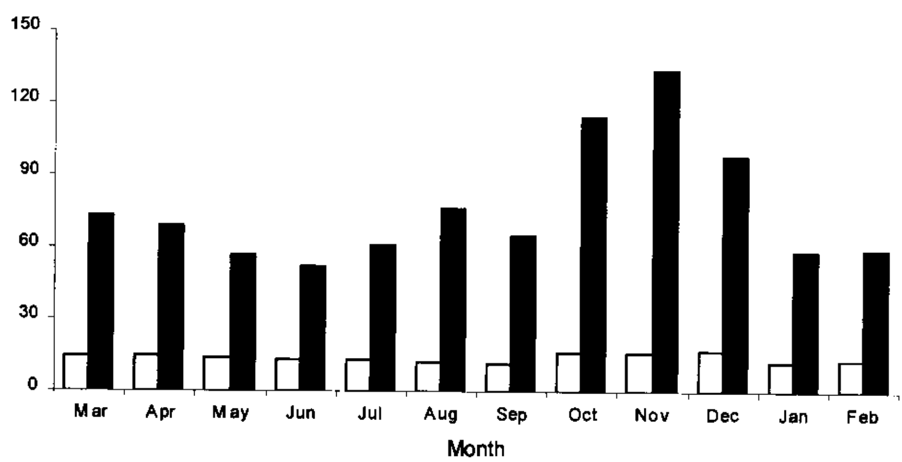


Figure 5.4: Number of species (open bars) and individuals (closed bars) recorded per month in, a.) unlogged forest, b.) selectively logged forest.

a.)



b.)



5.3.2 Seasonal effects

In this study there was no significant correlation between total monthly rainfall and sunshine hours in either the month of study, or 1, 2, or 3 months previously ($P>0.05$ in all cases).

Species diversity in selectively logged and unlogged forest was measured using the Shannon-Wiener index. The relationship between species diversity and monthly total rainfall at the study area was investigated using stepwise multiple regression. Of the climate variables investigated, sunshine two and three months before the study were significantly and negatively related to species diversity. The relationship was very similar in both sites (unlogged, $r^2 = 0.56$, $F_{2,9} = 23.87$, $P=0.0003$; logged, $r^2=0.73$, $F_{2,9} = 11.91$, $P=0.003$) and is described by the following equations;

unlogged forest,

$$\text{diversity} = -0.63\ \text{SUN2}\ (\text{SE}=0.0063) - 0.46\ \text{SUN3}\ (\text{SE}=0.0018) + 3.47\ (\text{SE}=0.333)$$

logged forest,

$$\text{diversity} = -0.63\ \text{SUN2}\ (\text{SE}=0.0007) - 0.55\ \text{SUN3}\ (\text{SE}=0.0007) + 2.58\ (\text{SE}=0.128)$$

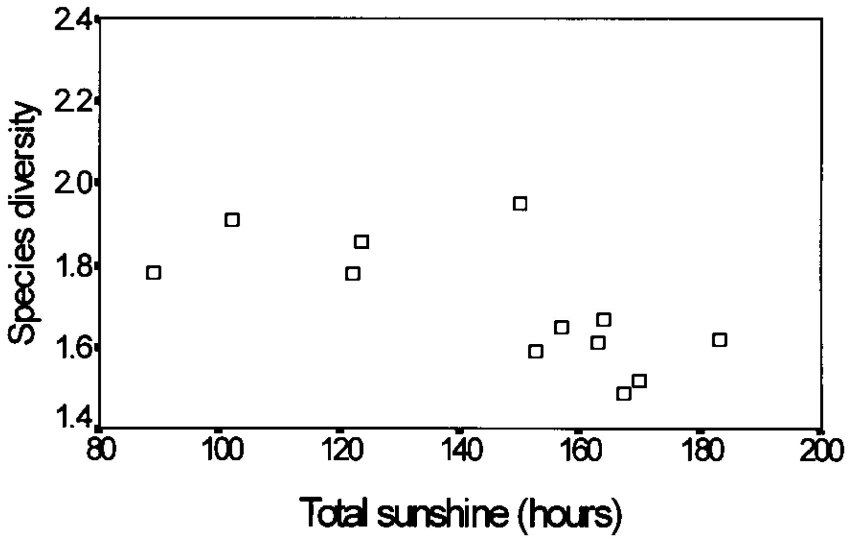
where, SUN2= sunshine hours 2 months previously, and

SUN3= sunshine hours 3 months previously

The relationships between species diversity and monthly sunshine two and three months before the survey in unlogged and selectively logged forest are shown in Figure 5.5 and 5.6 respectively. There were no other significant correlations between species diversity and any other of the variables.

Figure 5.5: Species diversity (measured by Shannon index) versus sunshine three months previously in unlogged and selectively logged forest.

a.) Unlogged forest.



b.) Selectively logged forest.

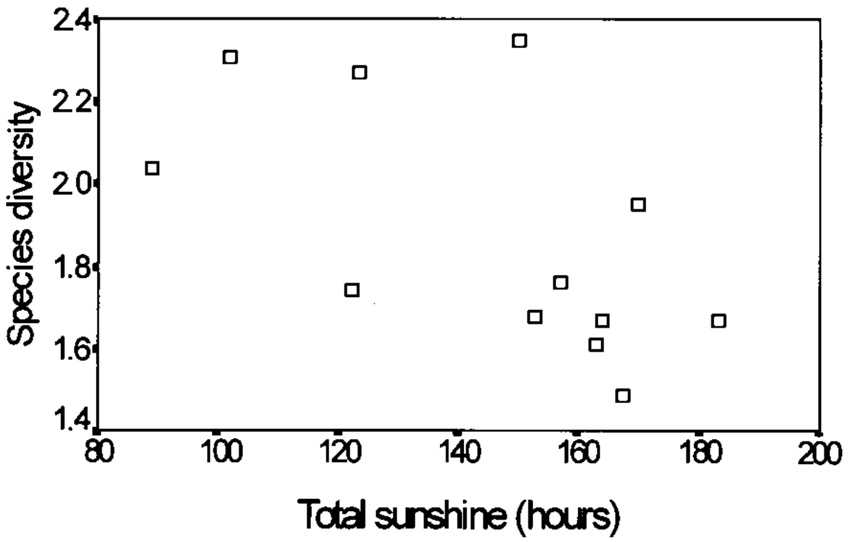
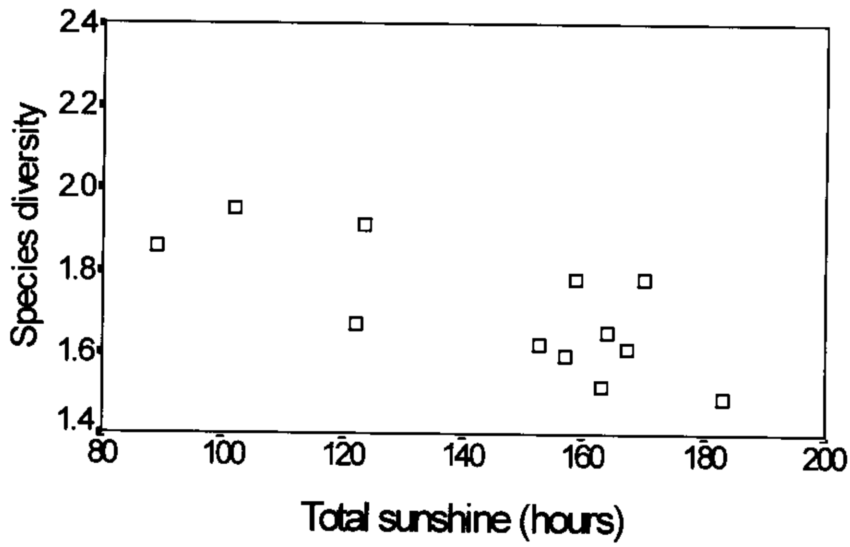
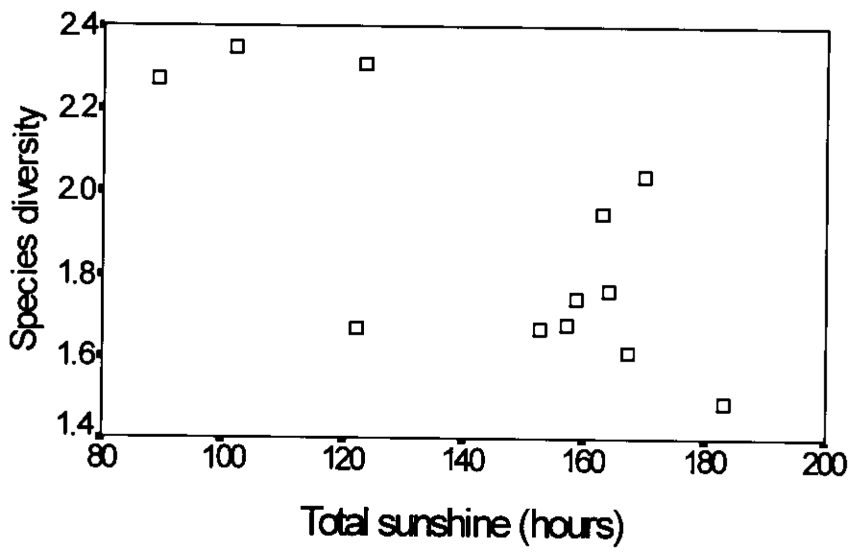


Figure 5.6: Species diversity (measured by Shannon index) versus sunshine two months previously in unlogged and selectively logged forest.

a.) Unlogged forest



b.) Selectively logged forest



5.4 Discussion

5.4 1 Seasonal effects on tropical butterflies

Several studies have shown that butterflies are sensitive to climate (Dennis 1993) and this has been shown to affect the abundance of butterflies, particularly the satyrinae (Braby 1995). In temperate regions, butterflies are sensitive to temperature and photoperiod and undergo extended periods during winter when they are inactive and enter diapause (Pollard & Yates 1993; Dennis 1993). Studies in the temperate regions also show that butterflies are sensitive to rainfall and also decline during droughts (Dennis 1993; Sutcliffe *et al.* 1997).

In the tropics rainfall and sunshine are generally more important to butterflies particularly in the equatorial tropical forests where temperature and photoperiod are relatively constant all year round (Otsuka 1988). There are some studies suggesting that seasonal changes in rainfall may influence butterfly assemblages (Braby 1995; Roskam & Brakefield 1999), particularly in areas showing marked wet and dry seasons. However in those part of the tropics where wet and dry periods are not marked (aseasonal), data are lacking (Hill 1999; Willott *et al.* 2000). In this study, there were changes in abundance from month to month but the number of species observed remained relatively constant.

5.4.2 Relationship between rainfall and butterflies

This study showed that rainfall was not significantly correlated to butterfly diversity. This contrasts with other studies showing that tropical butterflies are affected by rainfall (Braby 1995; Kooi *et al.* 1996; Hill 1999). However these studies were carried out during marked droughts or in the seasonal tropics.

Hill (1999) showed that there were significant effects of rainfall on the abundance of the satyrid butterfly *Ragadia makuta* during and after prolonged drought associated with the ENSO event in 1997. This was probably because larval host-plant quality decreased during drought conditions. Widespread and prolonged drought may also increase the risk of fire due to a combination of drier conditions, increased presence of leaf litter and dead wood on the forest floor (Payne 1996).

5.4.3 Relationship between sunshine and butterflies

In this study sunshine two and three months before the study showed significant negative correlations with diversity of butterflies. This result suggests that sunshine two and three months previously may have adversely affected larval host-plant quality through its effects on local microclimates, particularly humidity. Increased sunshine may also have adversely affected the reproductive behaviour of shade-dependent butterflies.

There are other variables (for instance life-history characteristics such as presence of dormancy and mortality rate) that might influence seasonal changes in the diversity of butterflies in the tropics, and this has not been investigated. These might explain the relatively low r^2 values in this study.

Chapter 6 Vertical distribution of fruit-feeding butterflies

6.1 Introduction

Insects are an important group for studying the patterns of biological diversification in tropical rainforests (DeVries *et al.* 1997). This is because more than half of all described species on earth are insects (Groombridge 1992). Globally the destruction of tropical rainforests is occurring at a rapid rate (Collins *et al.* 1991) therefore, the measurement of species diversity is urgently needed in order to understand tropical communities and their conservation value (Holloway *et al.* 1992; DeVries *et al.* 1997; Spitzer *et al.* 1997). Insects contribute a major role in many tropical rainforest ecosystem processes such as pollination, decomposition, nutrient cycling, seed predation, parasitism, and herbivory (Janzen 1987; Bond 1994).

Light is important in determining the distribution of many forest insects and many insects including butterflies are vertically stratified from the ground to the canopy (Davis & Sutton 1998). Some studies have suggested that there is a distinctive canopy fauna and that ground-based surveys miss a substantial component of forest biodiversity (Hughes *et al.* 1998; Davis & Sutton 1998). Several studies investigating vertical stratification in butterflies have demonstrated a distinctive canopy fauna compared with understorey, probably due to differences in the light environment in the canopy compared with the understorey (DeVries *et al.* 1997, 1999; Beck & Schulze in press). However, studies on butterflies in the canopy are still lacking, particularly in SE Asian rainforest (Schulze *et al.* in press).

In this study I used fruit-baited traps to sample butterflies in the canopy. This is a method that allows easy access to the canopy (Barker & Sutton 1997). Butterflies can be split into 2 guilds depending on whether adults feed on fruit or nectar. Fruit-baited traps sample species of butterfly that feed on rotting fruit; these species generally belong to the family Nymphalidae. Approximately 75% of nymphalid species recorded in Sabah feed on fruit. As far as I am aware, there are no studies on fruit-feeding butterflies investigating butterfly diversity at different heights above the ground for one full year in lowland dipterocarp rainforest in SE Asia. The results of this study will provide baseline data on fruit-feeding butterflies in undisturbed tropical rainforest of Sabah.

The aims of this study were as follows;

- To investigate the vertical distribution of fruit-feeding butterflies in primary rainforest.
- To investigate the biogeographical distribution of fruit-feeding butterflies at different heights above the ground.
- To investigate the longevity of fruit-feeding butterflies.
- To investigate if ground-based surveys can reliably survey satyrinae and morphinae butterflies, or whether there are significant numbers of these species restricted to the canopy.

6.2 Materials and methods

6.2.1 Study site

The study site was located within unlogged lowland primary forest approximately 1km from the Danum Valley Field Centre. Six traps were fixed at three levels (40m-high level, 2 traps; 20m-medium level, 2 traps; 2m-low level, 2 traps) from tree platforms around an emergent *Shorea johorensis* tree. The low and medium level traps were under dense canopy cover, whereas the high-level traps were within the canopy and received higher levels of sunlight (estimated at 70-85% canopy openness). Sunlight penetration at ground level was minimal (<10%).

6.2.2 Sampling of butterflies

Butterfly traps were operated every month for 14 days each month, from March 1999 until February 2000 (12 months). Traps were baited with two fresh bananas on the first day of trapping and were re-baited every second day with a small piece of fresh banana. This ensured that all traps contained a mixture of fresh and well-rotten bait. Traps were emptied each day between 16.00 and 18.00 hours.

All butterflies were individually marked on the underside of the forewing with felt-tipped pen according to trap location. For large butterflies (e.g. *Kallima limborgi, Bassarona dunya, Neorina lowii, Prothoe franckii*), each individual was marked with a unique number. All marked butterflies were then released back into the population unharmed. *Euthalia* spp and *Tanaecia* spp can only be identified from male genitalia

(Otsuka 1988) and were not identified to species in this study. These were excluded from the analyses. All other fruit feeding butterflies that were captured (and recaptured) were identified to species level, following Otsuka (1988).

6.2.3 Analysis of data

Species diversity of fruit feeding butterflies was calculated using the Shannon-Wiener index, and Margalef's and Simpson's indices following recommendations by Magurran (1988). The Shannon index incorporates measures of species richness and evenness into a single measure, Simpson's index measures species evenness, and Margalef's index measures species richness. Longevity of fruit-feeding butterflies was investigated for the most abundant species which had been individually marked (*Bassarona dunya*, *Kallima limborgi*, and *Neorina lowii*).

6.2.4 Ranking methods

The biogeographical distribution of butterflies at low-, medium- and high-levels was assessed in terms of the goegraphical distributions of species. To achieve this, all species were ranked according to geographical distribution (Otsuka 1988). Species endemic to Borneo (e.g. *Mycalesis kina* and *Stibochiona schoenbergi*) were given the highest rank (ranked 1), and widespread species such as *Melanitis leda*, the lowest ranked (ranked 40). No attempt was made to split species with very similar ranges (e.g. Sundaland species) and these were allocated tied ranks.

Height preferences of fruit feeding butterflies in relation to rank were assessed in terms of the location where each species attained highest density. Butterfly species with the same density at any of the three levels were excluded from the biogeographical analysis. I used Kruskal-Wallis one-way ANOVA to test whether there was any significant difference in biogeographical distribution of fruit-feeding butterflies between levels in terms of rank.

6.3 Results

6.3.1 Species assemblages of fruit-feeding butterflies

A total of 542 individuals from 40 species were recorded during the one year trapping period (total of 1008 trap days). Only 8% of total individuals captured were unidentified and these are unlikely to have affected the results.

In this study 17 species were recorded only at low-level (total individuals=107), whereas 4 species were recorded only at medium-level and four species only at high-level (12 and 4 individuals respectively). Thirty-one species were more common at low traps whereas twenty-three species were more common in medium and high traps. Table 6.1 shows the number of species trapped at different heights, and their relative abundance.

Table 6.1: Number of individuals butterflies (Nymphalidae) captured and recaptured (shown in brackets) in traps at three different heights (2m-low; 20m-medium; 40m-high).

	Low	Medium	High	Total
Satyrinae				
Neorina lowii Doubl.	68 (126)	1 (1)	0	69 (127)
Coelites epiminthia West.	0	1	0	1
Elymnias dara Dist.	0	0	3	3
Ragadia makuta Fruh.	62	0	0	62
Melanitis leda Linn.	22 (5)	20 (5)	13 (1)	55 (11)
Mycalesis anapita Fruh.	3	1	0	4
Mycalesis dohertyii Fruh.	2	0	0	2
Mycalesis horsfieldi Fruh.	0	1	1	2
Mycalesis kina Stau.	4 (2)	0	0	4 (2)
Mycalesis maianeas A. & U.	5	0	0	5
Mycalesis orseis Fruh.	14 (5)	0	0	14 (5)
Mycalesis patiana Eli.	6 (4)	1	0	7 (4)
Morphinae				
Amathusia phiddipus Linn.	1 (1)	4 (1)	2	7 (2)
Amathusia masina Fruh.	0	0	1	1
Amathuxidia amythaon Butl.	0	1	0	1
Zeuxidia aurelius Fruh.	1 (1)	0	0	1 (1)
Xanthotaenia busiris Stich.	1	0	0	1
Discophora necho C. & R. Fel.	3	0	0	3
Faunis canens Fruh.	1	0	0	1
Faunis stomphax West.	2 (1)	0	0	2 (1)
Nymphalinae				
Cirrochroa tyche Fruh.	1	0	0	1
Cupha erymanthis Dru.	1	0	0	1
Bassarona dunya Fruh.	73 (331)	4 (1)	0	77 (332)
Bassarona teuta Dist.	7 (6)	12 (11)	3 (1)	22 (18)
Amnosia decora Fruh.	3 (1)	0	0	3 (1)
Kallima limborgi Moo.	30 (50)	3	0	33 (50)
Parthenos sylvia Stau.	0	1	0	1
Dophla evelina Fruh.	30 (18)	26 (16)	2 (1)	58 (35)
Dichoraggia nesimachus Fruh.	2	5 (1)	0 (1)	7 (2)
Lexias canescens Butl.	2	0	0	2
Paduca fasciata C. & R. Fel.	1	0	0	1
Terinos clarissa Fruh.	2	0	0	2
Stibochiona schoenbergi Hon.	2	0	0	2
Rhinopalpa polynice Fruh.	1	2	0	3
Charaxinae				
Prothoe franckii Fruh.	38 (22)	14 (2)	1	53 (24)
Polyura athamas Roth. & J.	0	0	3	3
Charaxes bernardus Butl.	0	1	7	8
Charaxes solon Butl.	0	0	5	5
Charaxes durnfordi Roth.	5	4	0	9
Agatasa calydonia Fruh.	2	4	0	6
Number of individuals captured	395	106	41	542
Number of recaptures	(573)	(38)	(4)	(615)

6.3.2 Diversity of fruit-feeding butterflies

Table 6.2 shows diversity indices for Shannon-Wiener index, Simpson's and Margalef's indices at each level. Pairwise comparisons using randomization tests based on 10,000 random samples (Solow 1993), showed that there were no significant differences in species diversity between any of the levels (P>0.05 in all cases).

Table 6.2: Species diversity of fruit-feeding butterflies at three different heights.

	Low-level (2m)	Medium-level (20m)	High-level (40m)
Number of species	28	19	11
Number of individuals	395	106	41
Shannon-Wiener index, H'	2.51	2.34	2.06
95% Confidence interval	0.22	0.38	0.14
Simpson's index	8.87	7.81	6.83
95% Confidence interval	1.92	3.75	5.37
Margalef's index	5.02	3.87	2.69
95% Confidence interval	1.00	1.07	0.81

6.3.3 Movement of fruit-feeding butterflies between traps at different heights

From 542 individuals captured in traps during the study, there were 615 recaptures (Table 6.1). Few individuals were recaptured moving between traps at different heights, but the greatest number was of individuals moving between low traps and medium traps (Table 6.3).

Table 6.3: Recapture rates among low-, medium-, and high-level traps.

	Low	Mid	High
Mid	40 (6.5%)	0	0
High	2 (0.3%)	5 (0.8%)	0

6.3.4 Biogeographical distribution of fruit-feeding butterflies

The biogeographical distribution of fruit-feeding butterflies at each location was compared using Kruskal-Wallis one-way ANOVA (Table 6.4). There was a significant difference in biogeographical distribution of fruit-feeding butterflies at different heights above the ground (Kruskal-Wallis chi-square= 6.93, n=39, $P<0.05$). Butterflies trapped most commonly at low level had the most restricted biogeographical distributions (median rank=15, number of species=27) and butterflies at high high level the least restricted (median rank=32, number of species=5). Butterflies trapped most commonly at medium-level had intermediate values (median rank=26, number of species=7). Two endemic species recorded in the study were only recorded at the low-level traps; *Mycalesis kina* Stau. (see Plate 3) and *Stibochiona schoenbergi* Hon. Of the 40 species sampled, 23 species were restricted to the Sundaland region and seventeen species had widespread distribution (occurring outside the Sundaland region). Table 6.4 shows that 15 of the 23 species with distributions restricted to Sundaland were confined to low-level traps.

Plate 3: *Mycalesis kina* Stau., endemic to Borneo. This species was recorded along transects and also caught in fruit-baited traps.

Table 6.4: Butterfly species recorded in traps at three different heights (1-low level, 2m; 2-medium level, 20 m; and 3-high level, 40m) and ranked scores for geographical distribution. Underlined levels show the highest abundance.

	Distribution	Level	Rank
Satyrinae			
Coelites epiminthia West.	THA, PEN, SUM, Java	2	15
Melanitis leda Linn.	Oriental, Australia, Africa	1, 2, 3	40
Elymnias dara Dist.	THA, PEN, SUM, Java	3	15
Mycalesis anapita Fruh.	PEN, SUM	1, 2	3
Mycalesis dohertyii Fruh.	PEN, SUM	1	3
Mycalesis horsfieldi Fruh.	SUM, Java, PAL, Bali, SUL	2, 3	25
Mycalesis kina Staudinger	Endemic to Borneo	1	1
Mycalesis maianeas A. & U.	PEN, SUM	1	3
Mycalesis orseis Fruh.	PEN, SUM, PAL, BUR, THA	1	15
Mycalesis patiana Eliot	PEN	1, 2	3
Neorina lowii Doub.	PEN, SUM, PAL	1, 2	3
Ragadia makuta Fruh.	PEN, SUM, Java	1	3
Morphinae			
Amathusia masina Fruh.	PEN, Bangka	3	3
Amathusia phiddipus Linn.	SDL, BUR, THA, IDCH, PEN, PHI, SUL	1, 2, 3	25
Amathuxidia amythaon Butl.	Oriental, N India, Java, Mindanao	2	32
Discophora necho C & R Fel.	PEN, SUM, Java, PAL, THA	1	15
Faunis canens Fruh.	SDL, IDCH, THA	1	15
Faunis stomphax West.	SUM, PAL	1	3
Xanthotaenia busiris Stich.	PEN, SUM, THA	1	15
Zeuxidia aurelius Fruh.	PEN, SUM, THA	1	15
Nymphalinae			
Bassarona dunya Fruh.	PEN, SUM, Java, PAL	1, 2	3
Bassarona teuta Dist.	Assam, BUR, THA, PEN, SUM, Jave	1, 2, 3	27
Cirrochroa tyche Fruh.	PHI, PEN, Assam, IDCH	1	27
Cupha erymanthis Drury	IDCH, PEN, Java, SUM, S India, BUR, THA, S China	1	32
Rhinopalpa polynice Fruh.	India, BUR, THA, PEN, SUM, Java, PHI, SUL	1, 2	27
Amnosia decora Fruh.	PEN, SUM, Java	1	3
Dichoraggia nesimachus Fruh.	N India, S China, IDCH, THA, PEN, SUM, Java, PHI	1, 2	32
Dophla evelina Fruh.	Sri Lanka, India, BUR, THA, PEN, SUM, Java, SUL	1, 2, 3	27
Kallima limborgi Moore	PEN, SUM	1, 2	3
Lexias canescens Butl.	PEN, SUM	1	3
Paduca fasciata C. & R. Fel.	PEN, THA, SUM, Java	1	15
Parthenos sylvia Stau.	S India, SDL, New Guinea, Solomon	2	32
Stibochiona schoenbergi Hon.	Endemic to Borneo	1	1
Terinos clarissa Fruh.	PEN, SUM, Java, PAL, PHI	1	15
Charaxinae			
Prothoe franckii Fruh.	N India, BUR, THA, PEN, SUM, Java, PHI	1, 2, 3	32
Polyura athamas Roth. & J.	Nepal, India, BUR, THA, S China, IDCH, PEN, SUM, Java, PHI, SUL	3	32
Agatasa calydonia Fruh.	BUR, THA, PEN, SUM, Java, PHI	1, 2	24
Charaxes bernardus Butl.	India, BUR, S China, IDCH, THA, PEN	2, 3	32
Charaxes solon Butl.	Oriental region except Java	3	32
Charaxes durnfordi Roth.	Assam, BUR, THA, PEN, SUM, Java	1, 2	27

(note: For details of place names and map of the Sundaland region, see Chapter 4).

6.3.5 Adult longevity of fruit-feeding butterflies

The three most commonly caught species of fruit-feeding butterflies were used to investigate adult longevity. These species were *Bassarona dunya* (total caught=77), *Neorina lowii* (total caught=69), and *Kallima limborgi* (total caught=33). The total number of recaptures for each species was 54, 46, and 12 individuals, respectively. Figure 6.1 shows adult longevity of each species in terms of the number of days over which species were recaptured. *Kallima limborgi* recorded the greatest longevity (maximum of 164 days) whereas *Bassarona dunya* (see Plate 4) and *Neorina lowii* (Plate 5) recorded a maximum of 60 and 24 days respectively (see Figure 6.1).

Plate 4: *Bassarona dunya* Fruh., a frequent visitor to fruit-baited traps.

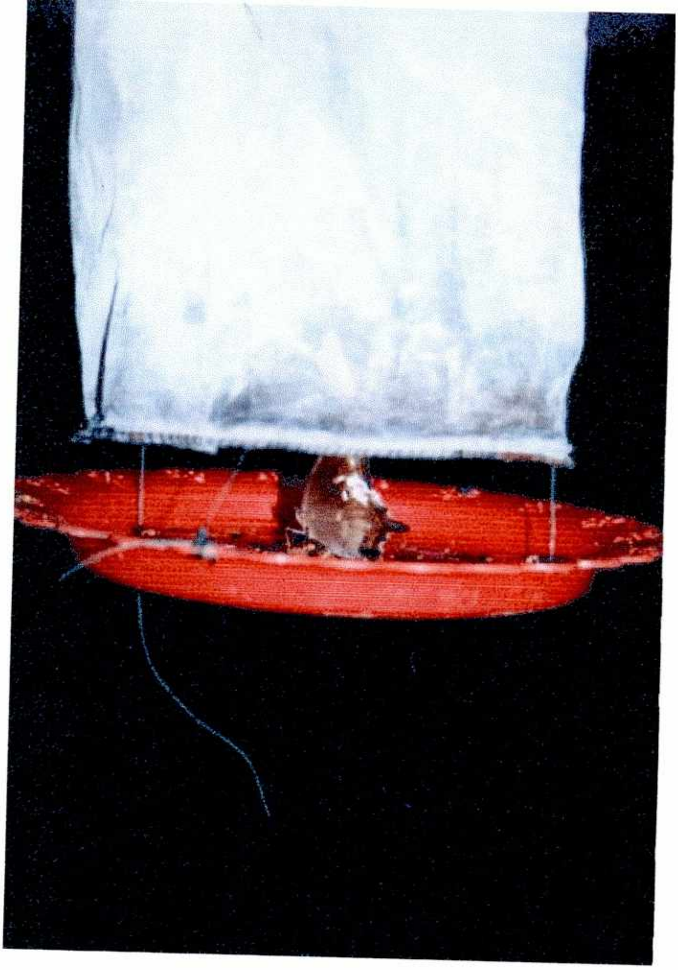
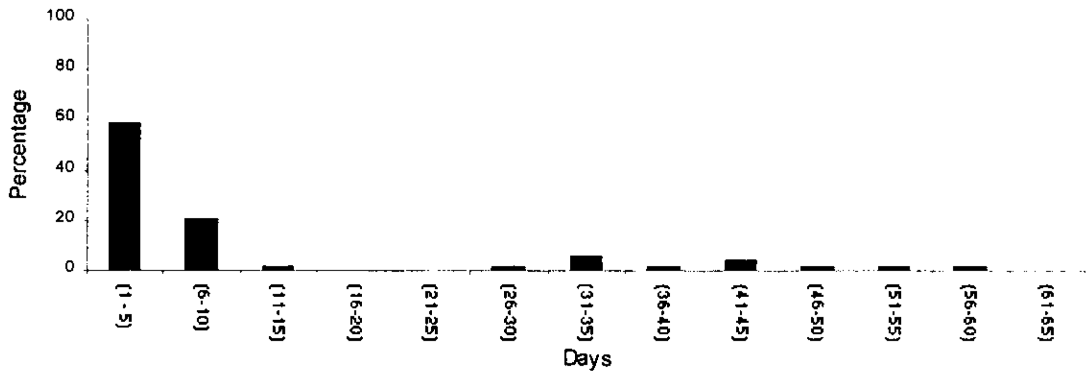


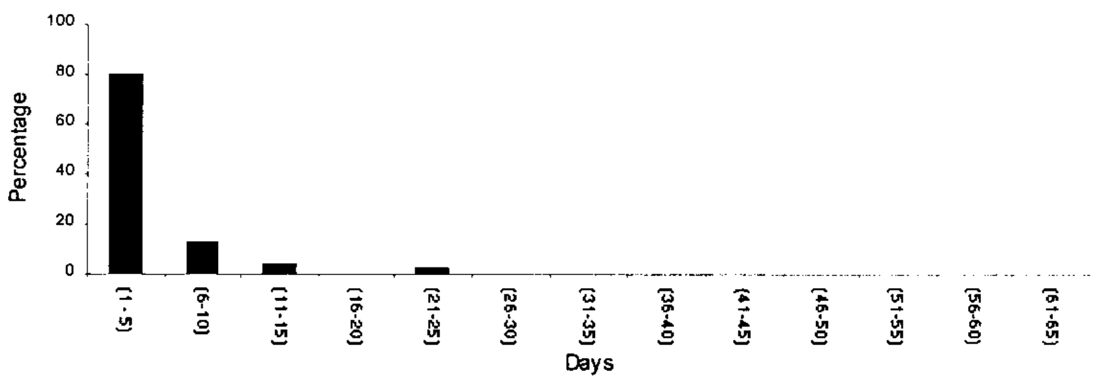
Plate 5: *Neorina lowii* Doub., feeding on fruit in a trap.

Figure 6.1: Longevity of fruit-feeding butterflies based on percentage of marked individuals recaptured over different time periods; **a.**) *Bassarona dunya*, **b.**) *Neorina lowii*, **c.**) *Kallima limborgi*.

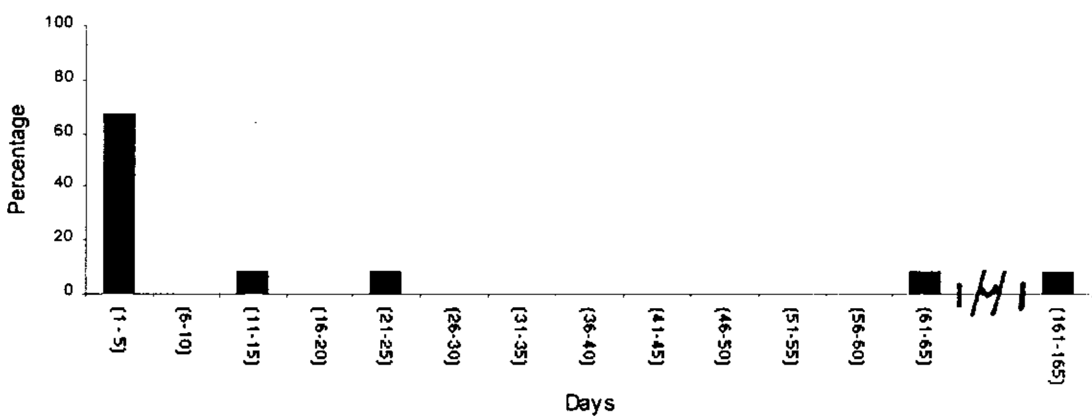
a.)



b.)



c.)



6.4 Discussion

6.4.1 Collection of data

Investigation of the vertical distribution of butterflies is important for studying butterfly diversity in tropical rainforest (e.g. Wolda 1983; DeVries 1988). Access to the canopy is a major problem in surveying butterflies in the canopy, which cannot be done by walk and count transects. This problem was partially overcome by using trapping methods. However, fruit traps only trap the guild of butterflies that are attracted to rotting fruit. Moreover there is no information concerning the distances over which species are attracted to traps, or if different species are attracted differently to traps. Trapping methods reduce the problems of identification in the field because all individuals are captured and more easily identified. Thus fruit-baited traps are the most suitable technique to sample butterflies in the canopy.

6.4.2 Vertical distribution of fruit feeding butterflies

Some studies have suggested that ground-based surveys will miss a large component of diversity that is confined to the canopy (DeVries *et al.*1997). In this study, of 14 species recorded on transects, 13 were caught in low level traps (Tables 3.5 and 6.4). However six species of satyrinae and morphinae were caught in traps but not recorded on transects, and four of these were caught above ground level. These data indicate that whilst ground-based transect techniques can survey satyrinae and morphinae butterflies fairly reliably, they are likely to miss a component of the fauna that does not occur at ground level. Species caught in low level traps but not seen on transects may have been crepuscular (Corbet & Pendlebury 1992), and these species will also be under-recorded using walk and point-count transects.

This study showed that low-level traps caught species with more restricted distributions than either medium- or high-level traps. This result suggests that butterflies at ground level contain many specialised species with more restricted geographical distributions, and therefore higher conservation value (Thomas 1991; Hill *et al.* 1995; Spitzer *et al.* 1997; Lewis *et al.* 1998).

Other studies of fruit-feeding butterflies have shown higher diversity at ground level, compared with the canopy (Hughes *et al.* 1998). This may be because rotting fruit generally fall to the ground. In this study, 17 of 40 of species (43%) were recorded only in the low-level traps. However, nine species (23%) were recorded only in intermediate or in high-level traps (e.g. *Elymnias dara*, *Polyura athamas* and *Charaxes solon*; Table 6.4) indicating that some fruit may normally rot *in situ* or may often get trapped in the upper branches.

6.4.3 Adult longevity of fruit-feeding butterflies

In this study, *Kallima limborgi* recorded the greatest longevity with a maximum of 164 days (approximately five and a half months). *Bassarona dunya* recorded the second highest longevity with a maximum of 60 days (eight and a half weeks), and *Neorina lowii* recorded a slightly lower longevity at 24 days (three and a half weeks). The results shown here may be used as preliminary information on longevity of fruit-feeding butterflies in Sabah. Further studies are needed in order to obtain more comprehensive information on fruit feeding butterflies in tropical rainforest.

Other studies on longevity of fruit-feeding Nymphalids in highland dipterocarp forest of Sabah (Beck & Schulze, in press) showed that some butterflies may live up to six weeks. In neotropical rainforest, a pollen-feeding butterfly *Heliconius* sp (Heliconiinae) recorded up to six months longevity (Dunlap-Pianka *et al.* 1977). In temperate regions, adult longevity of some butterflies may be similarly long but only in species where adults are inactive during the winter (Pollard & Yates 1993). In temperate species where adults do not enter diapause, adult longevity is generally only 1–2 weeks (Thomas & Hanski 1997; Thomas *et al.* 1998).

6.4.4 Movement of butterflies

In this study, movements of recaptured butterflies between traps at different heights were minimal. This indicates that species are confined only to certain heights. This vertical stratification may be maintained by adult resources or other factors such as distribution of larval host plants (Beccaloni 1997) or predation (Schulze *et al.* in press). Results from this study show that fruit-traps are a good method for sampling in the canopy. There are few long-term studies such as this, that have sampled in the canopy.

More research is needed to investigate if habitat disturbance will affects patterns of vertical distribution (Davis & Sutton 1998).

Chapter 7 General Discussion

7.1 Impacts of selective logging on butterflies

Tropical rainforests are one of the most diverse ecosystems on earth (Whitmore 1984, 1990; Speight *et al.* 1999). However forests are being lost at an increasingly rapid rate and understanding the impacts of habitat loss and/or modification on forest biota is of great concern for conservationists (Collins *et al.* 1991). Tropical insects are particularly diverse and contribute significantly to the maintenance and stability of tropical rainforest ecosystems through their roles in pollination, decomposition, nutrient cycling, seed predation and dispersal, etc. The complexity of tropical rainforest ecosystems and their response to forest disturbance were discussed in detail in Chapter 1. Among tropical insects, butterflies have been relatively well studied and their taxonomy is well known (Corbet & Pendlebury 1992) and so this group was chosen for this study which investigated the impacts of forest disturbance on butterflies in tropical regions.

In Chapter 2, the need for developing a standardized methodology for monitoring butterfly assemblages was highlighted. I used a transect method modified from methods used in temperate regions (Pollard 1977) and surveyed butterflies by using walk and point-count transect methods. Four transects of 2km length each (total of 8km) were established along existing paths and trails in unlogged and forest that had been selectively logged 10–11 years previously. By covering a long distance, these transects represented a wide variety of habitats (e.g. different terrains, undulating topography, streams, river catchment areas, etc.) found within the study areas. Thus the study included areas with different vegetation structure and most probably sampled areas which differed in the availability of resources for adult and larval butterflies.

The main objective of this study was to investigate the impacts of habitat disturbance on tropical butterflies in Sabah by comparing the species richness and diversity of shade-dependent forest butterflies in selectively logged and unlogged forest (Chapter 3). In order to investigate species diversity in different habitats alpha diversity indices (Shannon-Wiener index, Simpson D and Margalef D) were calculated and these showed that unlogged forest was more diverse than the logged forest in terms of species evenness. However there was no difference between habitats in species richness. Results from this study agree with previous studies indicating that species diversity of butterflies decreased in response to moderate forest disturbance (Bowman et al. 1990; Raguso & Llorente-Bousquets 1990; Daily & Ehrlich 1995; Hill *et al.* 1995). However other studies reveal that moderate disrurbance *increases* species diversity (e.g. Kremen 1992, Pinhiero & Ortiz 1992; Spitzer *et al.* 1993, 1997; Hamer *et al.* 1997; Lawton *et al.* 1998; Lewis *et al.* 1998; Wood & Gillman 1998), whilst other studies show no effects (Willott *et al.* 2000). It is not yet clear why different studies report qualitatively different results. This may be due to different studies being carried out in different region or using different techniques, or due to differences in the degree of disturbance being investigated. One other possibility that has received little attention is that differences in results obtained may be a result of the spatial scale over which studies were carried out. Studies carried out over small spatial scales appear more likely to report a significant increase in diversity in response to disturbance (Hamer & Hill 2000). This was indicated in my study by the relationship between diversity and vegetation structure at each station in logged forest (Figure 3.3 and 3.4) and needs further investigation.

The biogeographical distribution of species in different habitats was investigated in order to examine the species composition of butterflies and its conservation value, and this was discussed in Chapter 4. This study showed that endemic species and species with restricted geographical distributions were equally abundant in logged and unlogged forest. This differs from other studies which have reported that endemic species are more vulnerable to habitat disturbance (Spitzer *et al.* 1993, 1997; Hill *et al.* 1995, Hamer *et al.* 1997). However, these studies sampled the entire local butterfly community while my study focused only on understorey species which generally have relatively restricted distributions. For example, >65% of species recorded in this study have distributions that are restricted to the Sundaland region. Given that there was no difference in species richness between unlogged and logged sites in this study, this may also explain why there was no evidence for species with restricted distribution being more vulnerable to disturbance.

Another aspect of this study was to investigate seasonal changes in butterflies in relation to rainfall and sunshine (Chapter 5). Other studies have shown that seasonal changes in the species composition of butterflies in rainforests are not that great (Orr & Haeuser 1996). In this study there was no strong relationship between butterfly diversity and rainfall during the year's study. However there was a negative relationship between the amount of sunshine two and three months before the study and butterfly diversity. This indicated that higher diversity of butterflies corresponded with lower levels of sunshine during larval development. There is little information on larval development rates or larval habitat requirements for any tropical butterfly (Corbet & Pendlebury 1992; Fiedler 1998). However, the amount of sunshine may affect local microclimates, particularly humidity, and this may affect larval host plant quality. Decreased host plant quality may affect larval survival, as has been shown in temperate butterflies (Pollard & Yates 1993). More information is needed on larval development rates of tropical butterflies and on the importance of changes in local climates on butterfly mortality.

This study showed no effects of rainfall on butterfly diversity. Rainfall during the study was typical for the study area and although there was some variation from month to month, the variation was not that great compared with areas within the seasonal tropics (Braby 1995). However, droughts are occasionally recorded at the study site, associated with El Nino events (Walsh 1996) and these droughts have been shown to affect butterfly abundance (Hill 1999).

7.2 Selective commercial logging and vegetation structure

The results presented in Chapter 3, showed that there was a significant difference in vegetation structure between unlogged and logged forest, showing that the effects of forest disturbance from selective logging were still evident >10 years after logging. The unlogged forest was dominated by large trees (generally dipterocarp species) which were tall and produced greater canopy cover than in logged forest. The logged forest was more dominated by pioneer trees such as *Macaranga* spp. Although there were differences in vegetation structure between logged and unlogged habitats, butterfly diversity was not strongly related to any of the vegetation variables measured in the study. This may have been because the impacts of selective logging were not that great compared with other types of disturbance such as clear felling and conversion of forest areas to agriculture. In addition, the study sites in logged forest were less than 10km from a large area of protected, undisturbed forest (Danum Valley Conservation Area; DVCA). Although there are no data on dispersal rates for any tropical species, it is possible that butterfly assemblages in the logged areas were supplemented by individuals from the undisturbed forest. This would increase the diversity of logged areas. The conservation value of selectively logged forest may be greater if it includes, or is close to, areas of undisturbed forest.

7.3 Vertical stratification of fruit-feeding butterflies

Chapter 6 investigated the vertical stratification of butterflies in unlogged forest. This was to investigate if the ground-based transects used in this study reliably sampled understorey species. Other studies have suggested that ground-based studies may underestimate diversity because they do not include canopy species (DeVries *et al.* 1999; Willott 1999). I used fruit-baited traps to gain access to the canopy fauna and to investigate butterfly assemblages at different heights in terms of diversity and geographical ranges. I also investigated adult longevity. Fruit-baited traps sample only nymphalid butterflies whose adults feed on rotting fruit.

In this study butterflies occurring close to the ground (2m) had more restricted geographical distributions than those at the heights of 20m and 40m from the ground. Generally there was no significant difference in species diversity (measured by Shannon-Wiener), species evenness (measured by Simpson's index), and species richness (measured by Margalef's index) of fruit feeding butterflies among the three different heights, although slightly more species were trapped in ground level traps (31 species) than in upper level traps (23 species).

In this study, vertical stratification was investigated only in unlogged forest. However the investigation of vertical stratification of fruit-feeding butterflies in logged forest would also be interesting. Comparison with data from undisturbed forest might give more comprehensive information and help understand the effects of habitat disturbance on tropical rainforest butterflies. There is no information on the distances over which butterflies are attracted to traps or if some species are more attracted to traps than others (Hughes *et al.* 1998). This would provide scope for further investigation in the future.

Trapping data confirmed that understorey butterflies can be recorded fairly reliably from ground-based surveys, although there was evidence for some species of satyrinae and morphinae being confined to the canopy.

7.4 Conservation of insect diversity in Sabah

Butterflies are probably one of the best known groups of insects because of their colourful appearance and relatively large size. They are relatively easy to sample, thus making them an ideal candidate for the study of species diversity in tropical rainforests (DeVries *et al.* 1997). Probably the most appropriate way of deciding whether or not conservation measures are needed for a particular insect species or group is to monitor species abundance and distribution (Speight *et al.* 1999). Conservation of habitats and maintaining species diversity within these areas is likely to be the best strategy in dealing with species loss and species extinction in the depleting SE Asian rainforest.

In order to promote the conservation of insect faunas there is a need to implement insect diversity policies in tropical regions. There is a need for better protection of insects, particularly those with higher conservation value such as endemic butterflies. Although this is not an easy task, cooperation among researchers, policy-makers and the general public, as well as collaborations with international organisations in promoting conservation of insects of high conservation value, will be important for conservation of insect biodiversity in the near future. The legislation on protection of invertebrates is still uncertain in Sabah, as the Wildlife Conservation Enactment of Sabah (see Andau 1998) is still new. This enactment mainly covers vertebrates and to some extent endangered species of orchids in Sabah. The protection of invertebrates such as insects and in particular butterflies is still in question. A further revision of this legislation will enhance the chances of greater protection of insect fauna including butterfly communities in tropical rainforest of Sabah.

In this study there was evidence that some elements of the butterfly fauna were affected by selective logging, although the effects were not that great. Given that the timber industry is a major revenue income for the state of Sabah (Sabah State Government 1998) it is likely that commercial selective logging will continue. In the near future, all areas of production forest in Sabah will have been selectively logged once. Forests are due to be selectively logged on a rotation cycle of 35–60 years (Whitmore 1984, 1990). It is anticipated that the second rotation of logging in Sabah could contribute to a significant decrease in butterflies. Hence, there is an urgent need to monitor and conserve sufficient habitats within forest reserves to allow the protection of the large numbers of flora and fauna dependent on forest. Conversion of forested land areas to other land uses such as plantations and agriculture should be discouraged, because this will almost certainly contribute to a major loss of biodiversity (Holloway *et al.* 1992).

We have no choice but to protect the forest environment as much as we can for the benefit of the present generation and future generations to come. As a saying goes, this rainforest is not inherited from our ancestors but merely borrowed from our great-grandchildren. Although this is a very simple statement, we are depending on it; the dignity of human life is more meaningful than all the sophisticated rules and regulations of the day.

References

Andau, M. (1998) Biodiversity in the context of Sabah's wildlife. Paper presented at the State Level Seminar on National Policy on Biological Diversity in Kota Kinabalu, Sabah, Malaysia, 6 August, 1998.

Ashton, P.S. (1995) In E.Soepadmo and Wong, K.M. (eds.): *Tree Flora of Sabah and Sarawak.* **1,** xliii–li.

Barker, M.G. & Sutton, S.L. (1997) Low-tech methods for forest canopy access. *Biotropica*, **29**, 243–247.

Barlow, H.S. & Woiwod, I.P. (1989) Moth diversity of a tropical forest in Peninsular Malaysia. *Journal of Tropical Ecology*, **5**, 37–50.

Beaman, R.S., Beaman, J.H., Marsh, C. & Woods, P. (1985) Drought and forest fires in Sabah in 1983. *Sabah Society Journal*, **8,** 10–30.

Beccaloni, G.W. (1997) Vertical stratification of itomiine butterfly (Nymphalidae: Ithomiinae) mimicry complexes: the relationship between adult flight and larval host-plant height. *Biological Journal of the Linnean Society*, **62,** 313–341.

Beck, J. & Schulze, C.H. (in press) Diversity of fruit-feeding butterflies (Nymphalidae) along a gradient of tropical rainforest succession in Borneo with some remarks on the problem of 'pseudoreplicates'. *Transactions of the lepidopterological Society of Japan.*

Begon, M., Harper, J.L. & Townsend, C.R. (1996). *Ecology: Individuals, Populations and Communities.* 3rd. edition, reprinted in 1997. Blackwell, Oxford, 1068 p.

Bond, W.J. (1994) Do mutualisms matter? Assessing the impact of pollinator and disperser disruption on plant extinction. *Philosophical Transactions of the Royal Society of London B*, **344,** 83–90.

Bowman, D.M.J.S, Woinarski, J.C.Z., Sands, D.P.A., Wells, A. & McShane, V.J. (1990) Slash-and-burn agriculture in the wet coastal lowlands of Papua New Guinea: response of birds, butterflies and reptiles. *Journal of Biogeography*, **17**, 227–239.

Braby, M.F. (1993) Early stages, biology and taxonomic status of Tisiphone helena (Olliff) (Lepidoptera: Nymphalidae, Satyrinae). *Journal of the Australian Entomological Society*, **32**, 273-282.

Braby, M.F. (1995) Seasonal changes in relative abundance and spatial distribution of Australian lowland tropical satyrinae butterflies. *Australian Journal of Zoology*, **43**, 209–229.

Burghouts, T., Ernsting, G., Korthals, G. & Vries, T.D. (1992) Litterfall, leaf litter decomposition and litter invertebrates in primary and selectively logged diptercocarp forest in Sabah, Malaysia. *Philosophical Transactions of the Royal Society of London, Series B*, **335**, 407–416.

Chai, D.N.P. & Udarbe, M.P. (1977) The effectiveness of current silvicultural practice in Sabah. *Malaysian Forester*, **40**, 27–35.

Chapin, F.S.III, Zavaleta, E.S., Eviner, V.T., Naylor, R.L., Vitousek, P.M., Reynold, H.L., Hooper, D.U., Lavorel, S., Sala, O.E., Hobbie, S.E., Mack, M.C., & Diaz, S. (2000) Review article: Consequences of changing biodiversity. *Nature*, **405**, 234–242.

Chey, V.K. (1994) Comparison of biodiversity between plantation and natural forests in Sabah using moths as indicators. Unpublished Phd. thesis, University of Oxford.

Chey, V.K., Holloway, J.D. & Speight, M.R. (1997) Diversity of moths in forest plantations and natural forests in Sabah. *Bulletin of Entomological Research*, **87**, 371–385.

Chung, A.Y.C. & Maryati, M. (1993) The organisation and some ecological aspects of the giant forest ant, *Camponotus gigas*. *Sabah Society Journal* **10**, 41–55.

Chung, A.Y.C. & Maryati, M. (1996) A comparative study of the ant fauna in a primary and secondary forest in Sabah, Malaysia. In D.S. Edwards, W.E. Booth & S.C.Choy (eds.), *Tropical rainforest research–current issues.* Kluwer Academic Publishers, London. pp. 357–366

Chung, A.Y.C. (1999) The diversity of Coleoptera assemblages in different habitat types in Sabah , Malaysia with special reference to herbivory. Unpublished Phd. thesis, University of Oxford.

Collins, N.M. (1980) The effect of logging on termite (Isoptera) diversity and decomposition processes in lowland dipterocarp forests. In J.I. Furtado (ed.), Tropical ecology and development. *Proceedings of the 5th International Symposium of Tropical Ecology.* International Society of Tropical Ecology, Kuala Lumpur.

Collins, N.M. (ed.). (1990) *The Last Rain Forests.* Mitchell Beazley, London.

Collins, N.M., Sayer, J.A. & Whitmore, T.C. (1991) *The Conservation Atlas of Tropical Forests-Asia and the Pacific.* (IUCN) Macmillan Press, London.

Corbet, A.S. & Pendlebury, H.M. (1992) *The Butterflies of the Malay Peninsula* (4th edition), Malayan Nature Society, Kuala Lumpur.

Cornell, H.V. (1985) Local and regional richness of cynipine gall wasps on California oaks. *Ecology*, **66**, 1247–1260.

Corner, E.J. (1988) *Wayside Tree of Malaya.* 3rd edn. United Selangor Press, Kuala Lumpur, Malaysia.

Costa, P.M. & Karolus, A. (1995) Timber Extraction Volumes (1970–1991), Ulu Segama Forest Reserve. *Innoprise Corporation Internal Reports.*

Cox, C.B. & Moore, P.D. (2000) *Biogeography-an ecological and evolutionary approach.* 6th edition, Alden Press Oxford.

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

Darwin, C. (1859) *On the origin of species by means of natural selection.* Murray, London 1859.

Davis, A.J., (1993) The Ecology and Behaviour of Rainforest Dung Beetles in Northern Borneo. Unpublished Phd. thesis, University of Leeds.

Davis, A.J. & Sutton, S.L. (1998) The effects of rainforest canopy loss on arboreal dung beetles in Borneo: implications for the measurement of biodiversity in derived tropical ecosystems. *Diversity Distributions*, **4,** 167–173.

Davis, S.D., Heywood, V.H. & Hamilton, A.C. (eds) (1995) *Centres of plant diversity: volume 2 – Asia, Australasia and the Pacific.* WWF & IUCN.

Dennis, R.H.L. (1993) *Butterflies and climate change.* Manchester University Press, Manchester, U.K., 302p.

DeVries, P.J. (1988) Stratification of fruit-feeding nymphalid butterflies in a Costa Rican rainforest. *Journal of Research on the Lepidoptera,* **26**, 98–108.

DeVries, P.J., Murray, D. & Lande, R. (1997) Species diversity in vertical, horizontal, and temporal dimensions of a fruit-feeding butterfly community in an Ecuadorian rainforest. *Biological Journal of the Linnean Society,* **62**, 343–364.

DeVries, P.J., Walla, T.R. & Greeney, H.F. (1999) Species diversity in spatial and temporal dimensions of fruit-feeding butterflies from two Ecuadorian rainforests. *Biological Journal of the Linnean Society*, **68**, 333–353.

Douglas, I., Spencer, T. Greer, A., Bidin, K, Sinun, W. & Wong, W.M. (1992) The impact of selective commercial logging on stream hydrology, chemistry and sediment loads in the Ulu Segama rainforest, Sabah, Malaysia. *Philosophical Transactions of the Royal Society of London, Series B*, **335**, 397–406.

Dunlap-Pianka, H., Boggs, C.L., & Gilbert, L.E. (1977) Ovarian dynamics in Heliconiiane butterflies: Programmed senescence versus eternal youth. *Science* **197**, 487–490.

Ehrlich, P.R. & Raven, P.H. (1964) Butterflies and plants: a study in coevolution. *Evolution*, **18**, 586–608.

Ehrlich, P.R., Breedlove, D.E., Brussard, P.F. & Sharp, M.A. (1972) Weather and the regulation of subapline populations. *Ecology*, **53**, 243–247.

Eggleton, P., Bignell, D.E., Sands, W.A., Mawdsley, N.A., Lawton, J.H., Wood, T.G. & Bignell, N.C. (1996) The diversity, abundance and biomass of termites under differing levels of disturbance in the Mbalmayo Forest Reserve, southern Cameroon. *Philosophical Transaction of the Royal Society of London, Series B*, **351**, 51–68.

Eggleton, P., Homathevi, R., Jeeva, D., Jones, D.T., Davies, R.G., & Maryati, M. (1997) The species richness and composition of Termites (Isoptera) in primary and regenerating lowland dipterocarp forest in Sabah, East Malaysia. *Ecotropica* **3**, 119–128.

Emmel, T.C. & Leck, C.F. (1970) Seasonal changes in organisation of tropical rainforest butterfly populations in Panama. *Journal of Research on the Lepidoptera*, **8**, 133–152.

Evans, G.C. (1976) A sack of uncut diamonds: the study of ecosystems and the future resources of mankind. *Journal of Ecology*, **64**, 1–39.

Fiedler, K. (1998) Diet breadth and host plant diversity of tropical- vs temperate- zone herbivores: South-East Asian and West Palaearctic butterflies as a study. *Ecological Entomology*, **23**, 285–297.

Fox, J.E.D. (1976) Constraints on the natural regeneration of tropical moist forest. *Forest Ecology and Management*, **1**, 37–65.

Gaston, K.J. (2000) Review article: Global patterns in biodiversity. *Nature,* **405**, 220–227.

Groombridge, B. (1992) In B. Groombridge (ed.) *Global biodiversity - status of the earth's living resources.* WCMC, Chapman & Hall, London.

Hamer, K.C. & Hill, J.K. (2000) Scale-dependent effects of habitat modification for species diversity in tropical forests. *Conservation Biology*, in press.

Hamer, K.C., J.K. Hill., L.A. Lace, & M. Langhan. (1997) Ecological and biogeographic effects of disturbance on tropical forest butterflies of Sumba, Indonesia. *Journal of Biogeography*, **24**, 67–75.

Hammond, P.M. (1992) Species inventory. In B. Groombridge (ed.), *Global biodiversity - status of the earth's living resources.* WCMC, Chapman & Hall, London. pp. 17–39.

Harrison, S., Ross, S.J., & Lawton, J.H. (1992) Beta diversity on geographic gradients in Britain. *Journal of Animal Ecology*, **62**, 151–158.

Hauser, C.L., Schulze, C.H. & Fiedler, K. (1997) The butterfly species (Insecta: Lepoidoptera: Rhopalocera) of Kinabalu Park, Sabah. *The Raffles Bulletin of Zoology*, **45(2),** 281–304.

Henderson, P.A. & Seaby, R.M.H. (1998) *Species and richness diversity program*, Version 2. Oxford University, London.

Herbert, P.D.N. (1980) Moth communities in montane Papua New Guinea. *Journal of Animal Ecology,* **49**, 593–602.

Heywood, V.H. & Watson, R.T. (eds.). (1995) *Global biodiversity assessment.* UNEP, Cambridge University Press, Cambridge.

Hill, J.K. (1999) Butterfly spatial distribution and habitat requirements in a tropical forest: impacts of selective logging. *Journal of Applied Ecology,* **36**, 564–572.

Hill, J.K. & Hamer, K.C. (1998) Using species abundance models as indicators of habitat disturbance in tropical forests. *Journal of Applied Ecology*, **36**, 564–572.

Hill, J.K., Hamer, K.C., Lace, L.A. & Banham, W.M.T. (1995) Effects of selective logging on tropical forest butterflies on Buru, Indonesia. *Journal of Applied Ecology*, **32**, 454–460.

Holloway, J.D. (1984) Notes on the butterflies of the Gunung Mulu National Park. *Sarawak Museum Journal*, **30**, 89–131.

Holloway, J.D. (1987) Macrolepidoptera diversity in the Indo-Australian tropics: geographic, biotopic and taxonomic variations. *Biological Journal of the Linnean Society*, **30**, 32–341.

Holloway, J.D. and Barlow, H.S. (1983) The role of taxonomy, reference works and insect collections in tropical ecology. *Antenna* **7**, 50–53.

Holloway, J.D., Kirk-Spriggs, A.H. & Chey, V.K. (1992) The response of some rain forest insect groups to logging and conversion to plantation. *Philosophical Transactions of the Royal Society of London, Series B*, **335**, 425–436.

Hughes, J.B., Daily, G.C., & Ehrlich, P.R. (1998) Use of fruit bait traps for monitoring of butterflies (Lepidoptera: Nymphalidae), *Revista De Biologia Tropical*, **46(3)**, 697–704.

Hutson, M.A. (1994) *Biological diversity - the coexistence of species on changing landscapes*. Cambridge University Press, Cambridge.

Inger, R.F. (1966) The systematics and zoogeography of the amphibia of Borneo. *Fieldiana Zoology* **52**, 1–402.

IUCN/UNEP/WWF. (1991) *Caring for the Earth: A Strategy for Sustainable Living.* IUCN, Gland, Switzerland, 228p.

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

Jones, R.E. & Rienks, J. (1987) Reproductive seasonality in the tropical genus Eurema (Lepidoptera: Pieridae). *Biotropica*, **19**, 7–16.

Kremen, C. (1992) Assessing the indicator properties of species assemblages for natural areas monitoring. *Ecological Applications*. **2**, 203–217.

Kremen, C., Colwell, R.K., Erwin, T.L., Murphy, D.D., Noss, R.F. & Sanjayan, M.A. (1993) Terrestrial arthropod assemblages: their use in conservation planning. *Conservation Biology*, **7**, 796–808.

Kooi, R.E., Brakefield, P.M., & Rossie W.E.M (1996) Effects of food plant on phenotypic plasticity in the tropical butterfly *Bicyclus anynana*. *Entomologia Experientia et Applicata*, **80**, 149–151.

Lambert, F.R. (1992) The consequences of selective logging for Bornean lowland forest birds. *Philosophical Transactions of the Royal Society of London, Series B*, **335**, 443–457.

Lawton, J.H., Bignell, D.E., Bolton, B., *et al.* (1998) Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest. *Nature*, **391**, 72–76.

Lemmon, P.E., (1957) A new instrument for measuring forest overstory density. *Journal of Forestry* **55**, 667–669.

Lewis, O.T., Wilson, R.J. & Harper, M.C. (1998) Endemic butterflies on Grande Comore: habitat preferences and conservation priorities. *Biological Conservation*, **85**, 113–121.

Lim, D.C.E. (1996) The responses of butterflies to logging of rainforest in Sabah (Malaysia). Unpublished Msc. thesis, University of Leeds.

Lovejoy, T.E., Bierregaard, R.O., Rylands, A.B., Malcolm, J.R., Quintela, C.E., Harper, L.H., Brown Jr., K.S., Powell, A.H., Powell, G.V.N., Schubert, H.O.R., Hays, M.B. (1986) Edge and other effects of isolation on Amazonian forest fragments. In: Soute M.E., ed. *Conservation Biology: The Science of scarcity and diversity.* Sunderland, M.A.: Sinauer, 376–325.

Magurran, A.E. (1988) *Ecological diversity and its measurement.* Princeton University Press, London.

Mabberley, D.J. (1983) *Tropical rain forest ecology.* Glasgow & London: Blackie & Sons Ltd.

MacKinnon, K., Gusti Hatta, Hakimah Halim and Arthur Mengalik. (1996) *The ecology of Kalimantan Indonesian Borneo.* The Ecology of Indonesia Series. Vol. III. Periplus Editions.

Marsh, C.W. & Greer, A.G. (1992) Forest land-use in Sabah, Malaysia: an introduction to Danum Valley. *Philosophical Transactions of the Royal Society of London, Series B,* **335**, 331–339.

Marshall, A.G. (1992) The Royal Society's South-east Asian rainforest research programme: an introduction. *Philosophical Transactions of the Royal Society of London, Series B,* **335**, 327–330.

Maruyama, K. & Otsuka, K. (1991) *Butterflies of Borneo.* Vol. 2, No. 2. Tobishima Corporation, Tokyo.

Mawdsley, N.A. (1994) Community structure of Coleoptera assemblage in a Bornean tropical forest. Ph.D. thesis, University of London.

May, R.M. (1981) Patterns in multi-species communities. In *Theoretical Ecology. Principles and Applications* (ed. by R.M. May). pp. 197–227, 2nd edition, Blackwell Scientific Publication, Oxford.

May, R.M. (1988) How many species are there on earth? *Science*, 241, 18–24.

May, R.M. (1990) How many species? *Philosophical Transactions of the Royal Society London B*, **330**, 293–304.

McNeely, J.A., Gadgil, M., Leveque, C., Padoch, C. & Redford, K. (1995) Human influences on biodiversity. In V.H. Heywood & R.T. Watson (eds.), *Global biodiversity assessment.* UNEP, Cambridge University Press, Cambridge. pp. 711–822.

Morley, R.J. & Flenly, J.R. (1987) Late cainozoic vegetation and environmental changes in the Malay Archipelago. In T.C. Whitmore (ed.). *Biogeographical evolution of the Malay Archipelago*. Clarendon Press, Oxford. pp. 50–59.

New, T.R., (1991) *Butterfly Conservation.* Oxford University Press, Australia.

Newbery, D.McC., Campbell, E.J.F., Proctor, J. & Still, M.J. (1996) Primary lowland dipterocarp forest at Danum Valley, Sabah, Malaysia. Species composition and patterns in the understorey. *Vegetation*, **122**, 193–220.

Norusis, M.J. (1990) *SPSS/PC + Professional Statistics.* SPSS Inc. Chicago, IL, USA.

Nussbaum, R.E. (1995) The effect of selective logging of tropical rainforest on soil properties, and implications for forest recovery in Sabah, Malaysia. Unpublished Phd thesis, University of Exeter, United Kingdom.

Nussbaum, R.E., Anderson, J., & Spencer, T. (1995) Factors limiting the growth of indigenous tree seedlings planted on degraded rainforest soils in Sabah, Malaysia. *Forest Ecology and Management*, **74**, 149–159.

Oldeman, R.A.A (1983) Tropical rain forest; architecture, silvigenesis and diversity. *Tropical rain forest: ecology and management* (eds. S.L. Sutton, T.C.Whitmore and A.C. Chadwick), pp 139–150. Blackwell Scientific Publications, Oxford.

Orr, A.G. & Haeuser, C.L. (1996) Temporal and spatial patterns of butterfly diversity in a lowland tropical rainforest. In D.S. Edwards, W.E. Booth, & S.C. Choy (eds.) *Tropical Rainforest Research–Current Issues*, Kluwer Acadamic Publishers, Netherlands. pp. 125–138.

Otsuka, K. (1988) *Butterflies of Borneo*. Vol. 1. Tobishima Corporation, Tokyo.

Owen, D.F. (1971) Species diversity in butterflies in a tropical garden. *Biological Conservation.* **3(3)**, 191–198.

Owen, D.F. (1983) The abundance and biomass of forest animals. *Ecosystems of the World*, Vol. 14A (ed. F.B.Golley), pp. 93 –100. Elsevier, Amsterdam.

Owen, D.F. & Chanter, D.O. (1972) Species diversity and seasonal abundance in Charaxes butterflies (Nymphalidae). *Journal of Entomology.* **46**, 135–143.

Owen, D.F., Owen, J. & Chanter, D.O. (1972) Seasonal changes in relative abundance and estimates of species diversity in a family of tropical butterflies. *Oikos*, **23**, 200–205.

Payne, J. (1996) Conservation Of Natural Diversity: Problems, Strategies and Implications. (In) Kugan, F. & Kollert, W. (eds.) Forest Sector Coordination Towards Sustainable Development. *Proceedings of the Seminar, 4 September 1996*, Forestry Department Sabah.

Pielou, E. C. (1975) *Ecological diversity.* Wiley, New York.

Pinard, M.A. & Cropper, W.P. (2000) Simulated effects of logging on carbon storage in dipterocarp forest. *Journal of Applied Ecology*, **37**, 267–283.

Pinard, M.A. & Putz, F.E. (1996) Retaining forest biomass by reducing logging damage. *Biotropica,* **28**, 278–295.

Pinard, M.A., Barker, M.G. & Tay, J. (2000) Soil disturbance resulting from bulldozer-yarding of logs and post-logging forest recovery on skid trails in Sabah, Malaysia. *Forest Ecology and Management*, in press.

Pinhiero, C.E.G. & Ortiz, J.V.C. (1992) Communitie of fruit-feeding butterflies along a vegetation gradient in central Brazil. *Journal of Biogeography*, **19**, 505–511.

Pollard, E. (1977) A method for assessing changes in abundance of butterflies. *Biological Conservation*, **12**, 115–131.

Pollard, E. & Yates, T.J. (1993) *Monitoring butterflies for ecology and conservation.* Chapman & Hall, London.

Poore, D., Burgess, P.F., Palmer, J., Rietbergen, S & Synnott, T. (1989) *No timber without Trees.* Earthscan Publications, London, 209 p.

Raguso, R.A. & Llorente-Bousquets, J. (1990) The butterflies (Lepidoptera) of the Tuxtlas Mts., Veracruz, Mexico, Revisited: Species-Richness and habitat disturbance. *Journal of Research on the Lepidoptera*, **29**, 105–133

Robinson, G.S. and Tuck, K.R. (1993) Diversity and faunistics of small moths (Microlepidoptera) in Bornean Rainforest. *Ecological Entomology* **18**, 385–393.

Roskam, J.C. & Brakefield, P.M. (1999) Seasonal polyphenism in Bicyclus (Lepidoptera: Satyrinae) butterflies: different climates need different cues. *Biological Journal of the Linnean Society*, **66,** 345–356.

Sabah Forest Department. (1992) (Untitled) Map of Sabah, showing Natural & Plantation Forests.

Sabah State Government. (1998) *Forestry in Sabah: Status, Policy and Action.* Corporate Communication Department, Yayasan Sabah.

Sayer, J.A. & Whitmore, T.C. (1991) Tropical moist forests: Destruction and species extinction. *Biological Conservation*, **55**, 199–213.

Schimper, A.F.W. (1898) *Pflanzengeogrphie auf physiologischer grundlage.* Gustav-Fischer, Jena.

Schimper, A.F.W. (1903) *Plant geography upon a physiological basis* (Transl. W.R. Fisher, P. Groom & I.B. Balfour). Oxford University Press, Oxford.

Schulze, C.H., Linsenmair, K.D. & Fiedler, K. (in press) Understorey versus canopy– Patterns of vertical stratification and diversity among Lepidoptera in a Bornean rainforest. *Plant Ecology*.

Seki, Y., Takanami, Y., & Otsuka, K. (1991) *Butterflies of Borneo*. Vol. 2, No.1 Tobishima Corporation, Tokyo.

Solow, A.R. (1993) A simple test for change in community structure. *Journal of Animal Ecology*, **62**, 191–193.

Sparrow, H., Sisk, T., Ehrlich, P. & Murphy, D. (1994) Techniques and guidelines for monitoring Neotropical butterflies. *Conservation Biology*, **8,** 800–809.

Spellerberg, I.F. (1991) *Monitoring ecological change*. Cambridge University Press, London.

Speight, M.R., Hunter,M.D. & Watt, A.D. (1999) *Ecology of insects; concepts and applications*. Blackwell Science Ltd. London.

Spitzer, K., Novotny, V., Tooner, M., Leps, J., (1993) Habitat preferences, distribution and seasonality of the butterflies (Lepidoptera, Papilionoidea) in a montane tropical rainforest, Vietnam. *Journal of Biogeography*, **20**, 109–121.

Spitzer, K., Jaros, J., Havelka, J. & Leps, J. (1997) Effect of small-scale disturbance on butterfly communities of an Indochinese montane rainforest. *Biological Conservation*, **80**, 9–15.

Stork, N.E. (1991) The composition of the arthropod fauna of Bornean lowland rainforest trees. *Journal of Tropical Ecology*, **7**, 161–180.

Sutcliffe, O.L., Thomas, C.D., Yates, T.J. & Greatorex-Davies, J.N. (1997) Correlated extinctions, colonizations and population fluctuations in a highly connected ringlet butterfly metapopulation. *Oecologia*, **109**, 235–241.

Tangah, J. & K.M. Wong (1995) *A Sabah Gazetteer*. Forestry Dept. Sabah & FRIM.

Thapa, R.S. (1981) *Termites of Sabah.* Sabah Forest Record No. 12. Sabah Forestry Department Sabah.

Thomas, C.D. (1991) Habitat use and geographic ranges of butterflies from the wet lowlands of Costa Rica. *Biological Conservation*, **55**, 269–281.

Thomas, C.D. & Hanski, I. (1997) *Butterfly metapopulation. Metapopulation biology, Ecology, Genetics, and Evolution* (eds I. Hanski & M. Gilpin), pp. 359–386, Academic Press, London, UK.

Thomas, C.D., Jordana, D., Lewis, O.T., Hill. J.K., Sutcliffe, O.L. & Thomas, J.A. (1998) Butterfly distributional pattems, processes and conservation. pp 107 –138. In *Conservation in a changing World* (eds. G.M. Mace, A. Balmford & J.R. Ginsberg). Cambridge University Press.

Thomas, C.D. & Mallorie, H.C. (1985) Rarity, species richness and conservation: butterflies of the Atlas mountains in Morocco. *Biological Conservation*, **33**, 95–117.

Torquebiau, E.F. (1986) Mosaic pattems in dipterocarp rainforest in Indonesia and their implications for practical forestry. *Journal of Tropical Ecology*, **2**, 302–325.

Walpole, M.J. & Sheldon, I.R. (1999) Sampling butterflies in tropical rainforest: an evaluation of transect walk method. *Biological Conservation*, **87**, 85–91.

Walsh, R.P.D. (1996) Drought frequency changes in Sabah and adjacent parts of northern Bomeo since the late nineteenth century and possible implications for tropical forest dynamics. *Journal of Tropical Ecology*, **12**, 385–407.

Watt, W.B., Chew, F.S., Snyder, L.R.G., Watt, A.G. & Rothschild, D.E. (1968) Population structure of pierid butterflies, I. Numbers and movements of some montane *Colias* species. *Oecologia*, **27**, 1–22.

Weiss, S.B., White, R.R., Murphy, D.D. & Ehrlich, P.R. (1987) Growth and dispersal of larvae of the checkerspot butterfly *Euphydryas editha. Oikos*, **50,** 161–166.

Whittaker, R.H. (1960) Vegetation of the Siskiyon Mountains , Oregan and California. *Ecological Monographs* **30**, 279–338.

Whittaker, R.H. (1972) Evolution and measurement of species diversity. *Taxon*, **21**, 213–251.

Whittaker, R.H. (1977) Evolution of species diversity in land communities. *Evolutionary Biology* **10**, 1–67.

Whitmore, T.C. (1984) *Tropical Rain Forests of the Far East.* 2nd Edition, reprinted 1985. Oxford University Press, Oxford, 352 p.

Whitmore, T.C. (1990) *An introduction to Tropical Rain Forests.* Clarendon Press: Oxford, 226 pp.

Whitmore, T.C. (1991) Tropical rainforest dynamics and it implications for management. In *Rainforest regeneration and management* (eds. A. Gomez-Pompa, T.C. Whitmore & M. Hadley), pp. 67–89. Paris: UNESCO.

Willott, S.J. (1999) The effects of selective logging on the distribution of moths in a Bornean rainforest. *Philosophical Transactions of the Royal Society of London Series B*, 354, 1783–1790.

Willott, S.J., Lim, D.C., Compton, S.G., & Sutton, L.S. (2000) Effects of selective logging on the butterflies of a Bornean rainforest. *Conservation Biology*, **14**, 1–12.

Wilson, E.O., (1988) *The current state of biodiversity.* E.O. Wilson (ed.). Biodiversity, pp 3–18. National Academy Press.

Wolda, H (1983) Diversity, diversity indices and tropical cockroaches. *Oecologia*, **58**, 290–298.

Wolda, H. (1987) Altitude, habitat and tropical insect diversity. *Biological Journal of the Linnean Society*, **30**, 313–323.

Wolda, H. (1988), Insect seasonality: why? *Annual Review of Ecology and Systematics*, **19,** 1–18.

Wong, K.M. (1992) Rafflesia and diversity of flora in Sabah, Borneo. In *Proceeding of the Malaysian Ecological Symposium*, Kuala Lumpur, Malaysia.

Wong, M. (1986) Trophic organisation of understory birds in a Malaysian dipterocarp forest. *Auk* **103**, 100–116.

Wood, B. & Gillman, M.P. (1998) The effects of disturbance on forest butterflies using two methods of sampling in Trinidad. *Biodiversity and Conservation*, **7(5)**, 597–616.