Temporal variation in fruit-feeding forest butterfly communities in Sabah, Borneo.

Mustaffa, Nazirah

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TEMPORAL VARIATION IN FRUIT-FEEDING FOREST BUTTERFLY COMMUNITIES IN SABAH, BORNEO.

NAZIRAH MUSTAFFA

PRESENTED IN CANDIDATURE FOR THE DEGREE OF

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DECLARATION

No part of this thesis has been previously submitted for a degree of this or any other university. All works is the author's own except where indicated.

Temporal Variation in Fruit-Feeding Forest Butterfly Communities in Sabah, Borneo.

M. Sc. thesis submitted by Nazirah Mustaffa, 2001.

Abstract

This study investigated temporal variation in fruit-feeding butterfly communities in Sabah, Borneo. Fruit-baited traps were used to sample butterflies in primary forest and forest that had been selectively logged 11-12 years previously in 1988 and 1989. Traps were hung 1-2m from the ground along four transects in primary and logged forest (8 km in total). Traps were operated for 12 days each month for a year (October 1999 to September 2000). This study focused on Nymphalid species whose adults feed on rotting fruit. A total of 3996 individuals from 63 species were recorded during the study. Rates of species accumulation were slightly higher in logged forest than in primary forest, but there was no difference between habitats in species diversity over the whole year. However, whereas diversity was generally higher in primary forest during March-July, it was higher in logged forest during August-February, resulting in a significant habitat by time-of-year interaction for two separate diversity indices. β diversity (species turnover) also showed opposite differences between habitats at different times of year. These results have important implications for the reliability of short-term studies that do not sample over the course of an entire year. Effects of three environmental factors (sunshine, rainfall and fruit availability) on butterfly diversity were investigated. Rainfall had a significant positive effect on species evenness (Simpson's index) and abundance of *P. franck*. Rainfall may have acted via its effects on adult survival as well as via indirect effects on larval host plant quality.

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Nazirah Mustaffa
University of Durham
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TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

CHAPTER 1

Introduction

1.1 Tropical rain forest

Tropical forests occur in a belt circling the world between latitudes 23.5°N and 23.5°S. There are two major kinds of tropical forests; rain forest which is aseasonal and monsoon forest which has well-defined wet and dry seasons. The combination of these two types of forest is often referred to as tropical moist forest (Collins *et al.* 1991). Tropical rain forest occurs in humid climates where rainfall is relatively evenly distributed throughout the year. Generally, annual rainfall is more than 2000 mm (Collins, 1990) with no regular dry season and no month with rainfall less than 60 mm, or a dry season of only one or a few months' duration (Jacobs, 1988). The maximum temperature seldom exceeds 34°C with mean temperatures of around 20°C even in the coolest months of the year (Jacobs, 1988).

Tropical rain forest is characterised by evergreen woody vegetation, forming a thick canopy. The dense canopy prevents a view of the ground from above the trees. The canopy is usually 30m to 50m from the ground. The crowns of the very highest trees, which are termed emergent, protrude above the canopy and can reach up to 70m high. Many trees are buttressed at their base and these buttresses can be greater than 10 cm thick and several square metres in area. In association with the trees, many other types of vegetation such as lianas, vines and other woody climbers are also characteristic of tropical rain forest. Tropical rain forests also contain many extraordinary forms of plants including parasitic pitcher plants *Nepenthes spp.* and rafflesias *Rafflesia spp.* The richness of plant species in tropical rain forest is far higher than any other terrestrial ecosystems in the world. For example, in a single hectare of primary rain forest, there are seldom fewer than 40 (often over 100) trees species over 10 cm in diameter at breast height, whereas in the richest temperate forest such as mixed mesophytic forest of China and Southeastern North America, the number of species per hectare is only 20 to 30 (Richards, 1996).

Within rain forests, there are various forest formations which vary floristically from place to place depending upon local conditions such as soil, topography, climate and ground water. These formations are classified into several major types which are lowland rain forest, montane rain forest and coastal swamp forest (Collins *et al.* 1991). The demarcation line between lowland rain forests and montane rain forests commonly occurs at altitudes of approximately 1000m, with a temperature decrease on the average of about 0.6 deg C per 100m increase in elevation (Jacobs, 1988).

1.2 Biodiversity in tropical rain forests

A large fraction of the earth's biological diversity ~~lives~~ occurs in forests or depends on forests, especially tropical forests. Covering only 6% of the earth's surface, tropical rain forests contain about 50% of global species richness (Terborgh, 1992). In biogeographic terms, most species diversity increases greatly with declining latitude, although this is not uniform across all groups of organisms. There are many explanations for high diversity in tropical regions. Fossil evidence indicates that tropical forests have been present since the Cretaceous (Richards, 1996) and thus there has been a very long stable period for speciation to take place. Tropical regions generally have high net primary productivity (Mahli & Grace, 2000) and high humidity means that many different vegetation growth forms can exist beneath the canopy (Huston, 1994). Low nutrient levels in the soil (UNESCO/UNEP/FAO, 1978) also mean that in most cases no one species can dominate the plant community. This means that there are abundant niches for herbivores to occupy. In tropical regions, fruit and nectar are available all year allowing co-evolution between plants and animal species specialising on these resources (Sutton & Collins, 1991). Short generation times and low dispersal rates in tropical regions may also result in high speciation rates. However, a simple concise answer to the remarkable richness of living species in tropical rain forests has not, and may not be achieved (Gaston, 2000).

Tropical rain forests contain a wide range of animal groups comprising many different taxa. Insects comprise the major proportion of global species richness, and are mostly found in tropical rain forest (Erwin, 1982; Stork & Gaston, 1990). For instance, a survey carried out on 1,753 beetle species in collections of the British Natural History Museum (about half of the beetle species currently described in the world), showed that 946 species were from tropical countries, 625 were from temperate countries and 182 from countries with temperate and tropical regions (e.g Australia) (Stork, 1997). This suggests that tropical forests are housing over half of all beetle species. In other groups, the proportion is even higher. For example, birds and mammals are about twice as diverse in the tropics as in temperate regions (Raven, 1985). It is estimated that of 2,600 species of birds, about 30% depend on tropical forests for some part of their life cycle (Diamond, 1985).

1.3 Tropical rain forests of Sabah

Sabah is a State of Malaysia, situated in the northern part of Borneo. The State covers a land area of 73,371 km^2 which is about 10% of the island of Borneo (Marsh & Greer, 1992). Sabah is divided by a mountain chain running north-south known as the Crocker Range which splits the state into a larger eastern half and a smaller western half (Shuttleworth, 1981). Lowland tropical rain forest covers the land from sea level up to 1,000 m where it is replaced by montane rain forest. The rain forest of Sabah is believed to be one of the oldest rain forests in the world (Chey *et al.* 1997). Forests in Sabah, particularly in the eastern half of the state, are extremely rich in large trees in the Family Dipterocarpaceae. Sabah has at least 180 species in this family (Marsh & Greer, 1992). Originally, all of Sabah was covered by forest, of which 36,000 km^2 (50%) was estimated to be remaining in 1985 (Collins *et al.* 1991).

Sabah is a rich region of flora and fauna with high diversity in many insect groups, including butterflies. The Danum Valley area, where this study was carried out, supports approximately one quarter of the entire butterfly fauna of Borneo and this proportion is likely to rise with further sampling (Lim, 1996). A total of 235 species of butterfly from 112 genera have been recorded at the study site. Lycaenidae and Nymphalidae represented the largest numbers of both species and genera. A large proportion (73%) of the 235 species currently recorded at Danum Valley have distributions restricted to Sundaland (the region comprising West Malaysia, Sumatra, Java, Borneo and Palawan) and are not found outside South-east Asia. Endemic species represent about 5% of all species in the area, and most of these species are dependent on forest habitats (Corbet & Pendlebury, 1992). However, there have been no specific ecological studies carried out on these endemic species. The area around the Mount Kinabalu region is the main centre of butterfly diversity in Borneo. More than 340 species have been recorded from Kinabalu National Park (Othsuka, 1996) and most of the 50 endemic species recorded on Borneo have been found in this region (Otsuka, 1988). This may reflect the uniqueness and high diversity of vegetation at high altitude in this area.

1.4 Deforestation and degradation of tropical rain forests

Globally, the total area presently covered by tropical rain forests is estimated at 12 million km^2, which accounts for nearly a third of the world's forest (covering roughly 30 million km^2) (Park, 1992). The major tropical rain forests are found in three areas which are Central and South America (50%), Western Equatorial Africa (18%) and Southeast Asia (25% of the world total) (Park, 1992). In most tropical countries where they occur, rain forests provide a valuable asset, for example, dipterocarp trees from rain forests of Southeast Asia contain many commercially valuable timber species.

Annually, 4 to 5 million hectares of tropical closed forests are logged, of which 20% and 10% are logged in Asia and Latin America, respectively (Sharma, 1992). Other causes of deforestation include shifting cultivation, conversion to permanent agriculture, cattle rearing and fuelwood gathering (Ooi, 1993). Lowland forests experience the most damage and clearance because they are easily accessible (Collins, 1990).

By contrast to clear felling, selective logging is a technique which removes only commercially valuable timber trees (generally 12 to 15 trees per hectare in Southeast

Asia; Johns, 1988). In this technique, only a limited number of trees more than 0.6m diameter at breast height (DBH) are removed. However, selective logging causes a number of different impacts to the forest. During tree felling, when a large tree with a wide crown is felled, it can break and fall against a number of neighbouring stems. Thus extensive areas of forest can be severely damaged, particularly in forests which contain many vines and woody climbers. When tree crowns are interconnected by woody climbers, the tree being felled can pull neighbouring trees with it, thereby breaking or uprooting them (Marn & Jonkers, 1981).

Marn & Jonkers (1981) suggested that under well-planned and supervised harvesting operations, employing directional felling does far less damage to the residual stand, and can reduce the number of tree lost by up to 33%. This compares with conventional selective logging which can destroy 40% of the residual forest and can kill almost half of the young growing stock (Marn & Jonkers, 1981). However, in 1988, a report by the International Tropical Timber Organisation concluded that the total area of tropical moist forests managed sustainably for timber production was only 0.125% (Sharma, 1992). The least damaging techniques for removing timber from forest are the use of balloons, helicopters and aerial cables to remove timber. However, these methods may be impractical in remote tropical locations or may not be economically viable (Sharma, 1992).

Other impacts of logging are due to the compaction of soil as timbers are extracted from the forest. Tropical rain forest soils are poor in nutrients compared with temperate forests (UNESCO/UNEP/FAO, 1978), and nutrient contents of soils are further reduced following logging due to increased water runoff and leaching of bare soils (Douglas *et al.* 1992; Sinun *et al.* 1992). Degradation of soil quality can severely inhibit the development of young trees and soil compaction following logging can limit the recruitment of pioneer trees (Pinard *et al.* 1996). After trees are extracted from the forest, formation of different sizes of canopy gaps allows different amounts of sunlight to penetrate through the forest's canopy. This can affect regeneration as seedlings of many forest species are shade-adapted and are scorched by strong sunlight (Brown & Press, 1992).

Indirect effects of logging also include the opening up of forest areas to subsistence farmers. A high proportion of logged-over forests later becomes cropland or is converted to other land uses.

1.5 Selective logging in Sabah

In 1986, 60.1% of Sabah's land area was lowland forest (Marsh & Greer, 1992). Although Sabah is still heavily forested by regional standards, there remains relatively little undisturbed lowland dipterocarp forest (Marsh & Greer, 1992). In recent decades, the main cause of forest disturbance in Sabah has been the timber industry (Marsh & Greer, 1992). Yayasan Sabah (YS; Sabah Foundation) has a large concession of commercial forest estate in Sabah which generates important revenue for the State from the sale of timber. The mission of YS is to improve the livelihood of Sabahan people by funding activities principally in the fields of education, welfare and income generation. In 1970, Yayasan Sabah was allocated 854, 700 ha of timber land and in 1984, this area was expanded and consolidated into a single block of 972, 804 ha. The new concession area also contains some areas which are protected and will remain unlogged. The two largest designated Conservation Areas ~~an~~ are Danum Valley (43,800 ha) and Maliau Basin (58,840 ha).

During the period from 1952 to the mid 1960's, commercial forests in Sabah were managed by an area control system in which annual coupes were issued to logging companies (Udarbe & Chai, 1992). The concession area was divided into 100 annual coupes and concessions to log these coupes were sold to logging companies for a single logging cycle. Following selective logging, areas were left to regenerate, and in theory in Sabah, they will be logged on a 35-60 year cycle (Collins *et al.* 1991). Commercial timber trees are felled by chain saw. Conventional logging methods include the removal of logs by tractor skidding and highlead yarding. In tractor skidding, logs are dragged from the stumps to the roadside with one end raised above the ground. In flat to undulating terrain, the skid trails are laid out in a herringbone formation. In hilly terrain, the main skid trail is usually laid out to favour downhill skidding towards the landing whenever possible. On rainy days, wet skid trails become very muddy and after repeated passes become difficult to negotiate. Consequently, the operator often excavates a new skid trail or fills up the muddy trail with top soil from nearby undisturbed ground and so causes additional damage. Even in dry conditions, tractors can cause severe damage to non-commercial trees and compaction of the soil during the extraction of logs.

In highlead methods, logs are dragged to a central yarding area using a lead from a mobile tower. Logs can be dragged both uphill and downhill, although the latter results in extensive damage to surrounding areas as logs tend to roll. Although highlead yarding causes less soil compaction than extraction by tractor, it causes much more destruction to the surrounding vegetation . Because of the damaged it caused, highlead extraction methods have not been used in Sabah since 1996.

Another significant cause of forest loss has been shifting cultivation which is estimated to affect about 15% of Sabah's land area (Marsh & Greer, 1992).

1.6 Consequences of tropical forest disturbance

In any examination of the linkages between large-scale anthropogenic disturbance of tropical rain forest and species extinction it is necessary to draw a distinction between forest degradation and deforestation. Degradation as result of, for example, selective logging may lead to a deterioration of natural habitats but is unlikely to lead to widespread species extinction except when the specialised habitats are destroyed. By contrast, habitat destruction will have the effect of creating 'islands' of remaining rain forest in a 'sea' of cleared land. As proposed by the theory of island biogeography (MacArthur & Wilson, 1967), if 90% of an area is destroyed and the remaining 10% is preserved as a habitat island, this island will initially support most of the original area's species, but this is more species than it can support at equilibrium. As a result, some species will become extinct until a new equilibrium is reached, which is expected to be about half of the original number of species. Both the rate of extinction and the survival prospects of individual species depend on the area of rain forest that remains and its relative isolation.

Theoretical studies predict that diversity should initially increase but then decline in the most severely disturbed areas ~~nonlinear changes~~ in species diversity with increasing disturbance. This theory has been termed the 'intermediate disturbance hypothesis' (Connell, 1978) and predicts that diversity should initially ~~increase~~ with increasing disturbance but then ~~decline~~ in the most severely disturbed ~~areas~~. Termite species richness in Southern Cameroon was found to be greatest in old secondary and young plantation forest, followed by near primary forest and lowest in the two severely disturbed forests (Eggleton *et al.* 1995) and this supports the intermediate disturbance hypothesis that intermediate levels of disturbance may increase species richness (Connell, 1978). However, few other studies have explicitly tested this hypothesis in tropical regions.

Some ~~Many~~ of the species found in tropical forests occur only in the small area where they evolved. Such endemic species are especially vulnerable because of their localized distribution. Between 40% and 60% of tropical species in some countries are endemic (Sharma, 1992). The destruction of even relatively small areas of forest can therefore eliminate entire species. During the last 20th century ~~At present~~, an estimated 10,000 species were ~~are~~ extinguished each year because of tropical deforestation (Wilson, 1988). Many of the remaining threatened species may have economic value as important sources of food, medicine, genetic material for crop hybridization and other marketable products (Sharma, 1992).

Several studies have investigated the consequences of forest disturbance on insects. Insects are believed to be particularly vulnerable to disturbance of forest habitats because of their close interdependency with plants. Some studies show that logging and other forms of disturbance have a significant effect on the diversity of major plant-feeding insect groups. For example, Hill (1999) found that 8-9 years after logging, differences in vegetation structure were still evident and butterfly distribution and abundance were lower in the most severely disturbed areas. The pattern of decreasing species richness has been shown in moths as the forest becomes more disturbed and fragmented (Holloway *et al.* 1992).

Regional (γ) diversity is made up of local (α) diversity and beta (β) diversity, which measures species turnover from place to place, or over time. Most studies investigating patterns of diversity in tropical regions have focused on changes in α diversity, and β diversity has rarely been considered (Mawdsley, 1996). Few studies have been carried out over sufficient time periods to investigate temporal changes in species turnover, or a large enough spatial scale to investigate spatial turnover in species. However, in highly diverse areas such as tropical regions, it is likely that β diversity will be an important component of overall diversity (Huston, 1994). Despite this, the effect of habitat disturbance on β diversity has not been adequately studied in tropical regions.

1.7 Forest disturbance and butterflies

Butterflies have been suggested as potential ecological indicators of the impacts of habitat disturbance on ecosystems (Kremen, 1992: Beccaloni & Gaston, 1995; Schulze & Fiedler, 1998; Wood & Gillman, 1998). On a practical basis, butterflies are better known taxonomically (in comparison to other taxa) and can in many areas be reliably identified in the field (Kremen, 1992) and are easy to sample (Beccaloni & Gaston, 1995). Moreover, adult butterflies are relatively large, mostly diurnal and can be visually censused by a skilled observer (Pollard, 1977). On biological grounds, coevolution between butterflies and their larval host-plants in some cases has led to high butterfly-plant specificity (Ehrlich & Raven, 1964). Butterflies interact with plants both as larval herbivores and possibly as adult pollinators, potentially influencing plant population dynamics in both interactions (Kremen, 1992). These characteristics of butterflies have made tropical butterflies a popular group for investigation (Hill *et al.* 1995; Hamer *et al.* 1997; Spitzer *et al.* 1997; Lewis *et al.* 1998; Wood & Gillman, 1998; Hamer & Hill, 2000; Hill *et al.* in press).

Tropical butterfly communities in Southeast Asia are highly diverse, for example, 40% of swallowtails are endemic to Indonesia (Collins & Morris, 1985). In view of global destruction of tropical forests, it is thus important to understand the effects of environmental changes on butterfly faunas. Studies on butterflies have reported both increased and decreased diversity in response to habitat disturbance (review in Hamer & Hill, 2000). Differences in results obtained may have been due to several factors, such as degree of disturbance, area of study, method of sampling, but no clear concensus has emerged. However, most studies indicate that endemic species and species with more restricted geographical distribution are most vulnerable to disturbance (Hill *et al.* 1995; Hamer *et al.* 1997; Spitzer *et al.* 1997). In Sabah, consequences of logging for butterflies may be largely indirect because there are no records that butterfly larvae feed on dipterocarps (Corbet & Pendlebury, 1992). Moreover, dipterocarp trees have tiny flowers which are unlikely to provide resources used by butterflies (Willot *et al.* 2000). However, logging causes a reduction in canopy cover, incident damage to other tree species which are utilised as hosts or provide nectar, and increased growth of pioneer trees, herbs and grasses. Thus data are needed to describe the impacts of selective logging on butterflies in Sabah.

1.8 Seasonality and variation in tropical butterflies

Seasonality in tropical butterflies has been investigated in West Africa, Central America, East Africa and Southeast Asia (Braby, 1995). Tropical butterflies, like many other tropical insects (Wolda, 1978), exhibit seasonal and annual variations in abundance particularly in those areas with marked wet and dry periods (Braby, 1995; De Vries *et al.* 1997; Kunte, 1997). Factors likely to influence the patterns of abundance and seasonality in tropical butterflies are life-history characteristics such as developmental rates, longevity and reproductive rates (Owen, 1971), abiotic and biotic factors such as temperature, rainfall, parasitism and predation (Owen, 1971), dispersal and migration rates (Shahabudin *et al.* 2000) and phenology of larval food sources (Braby, 1995). Even in tropical areas that are considered to be aseasonal, these factors are likely to vary over time, but have rarely been studied.

Among butterflies, several studies have reported that many species increase in abundance during the wet season (Owen, 1971; De Vries *et al.* 1997; Spitzer 1993). By contrast to temperate regions, where temperature is the most important factor influencing the seasons, rainfall is probably the most important factor influencing temporal changes in the tropics. For example, rainfall affected the abundance of tropical Satyrinae in Australia through its effect on the availability and quality of larval food (Braby, 1995). Hill (1999) reported that a severe El Niño Southern Oscillation drought had a significant effect on the abundance and distribution of the satyrine *Ragadia* *makuta*. Corresponding to changes in rainfall, *R. makuta* was nearly three times more abundant in the year after the drought and was more widely distributed. Thus environmental changes are likely to affect butterfly diversity, but this has rarely been considered in those parts of the tropics that are generally considered to be aseasonal, such as Borneo.

Tropical butterfly communities consist of two major adult feeding guilds. One guild is composed of species that obtain the majority of their adult nutritional requirements from flower nectar and the second guild is composed of many of the Nymphalidae whose adults gain virtually of all their nutritional requirements by feeding on rotting fruit (Corbet & Pendlebury, 1992; Wood & [illegible]). Approximately 75% of nymphalid species recorded on Borneo feed on fruit juices (Hill *et al.* in press). In this study, I used fruit-baited traps to study fruit-feeding nymphalid forest butterflies in Sabah, Borneo.

1.9 Aims of the study

In this study, I investigated temporal changes in butterfly communities in primary and selectively logged forest in Sabah, Borneo. In Chapter 2, I describe the methods used in the 12-month study and describe the study area. In Chapter 3, I investigate seasonal changes in α diversity in primary and logged forest and examine whether or not patterns of temporal change are similar in primary and logged forest. I also investigate impacts of rainfall, sunshine and fruit availability on butterfly diversity. In Chapter 4, I describe patterns of β diversity in primary and logged forest, and I investigate whether or not these patterns are similar in primary and logged forest. In Chapter 5, I focus on three particularly abundant species and investigate temporal variation in their abundance in more detail. The overall results of this study and their implications for butterfly conservation in Borneo are discussed in Chapter 6.

CHAPTER 2

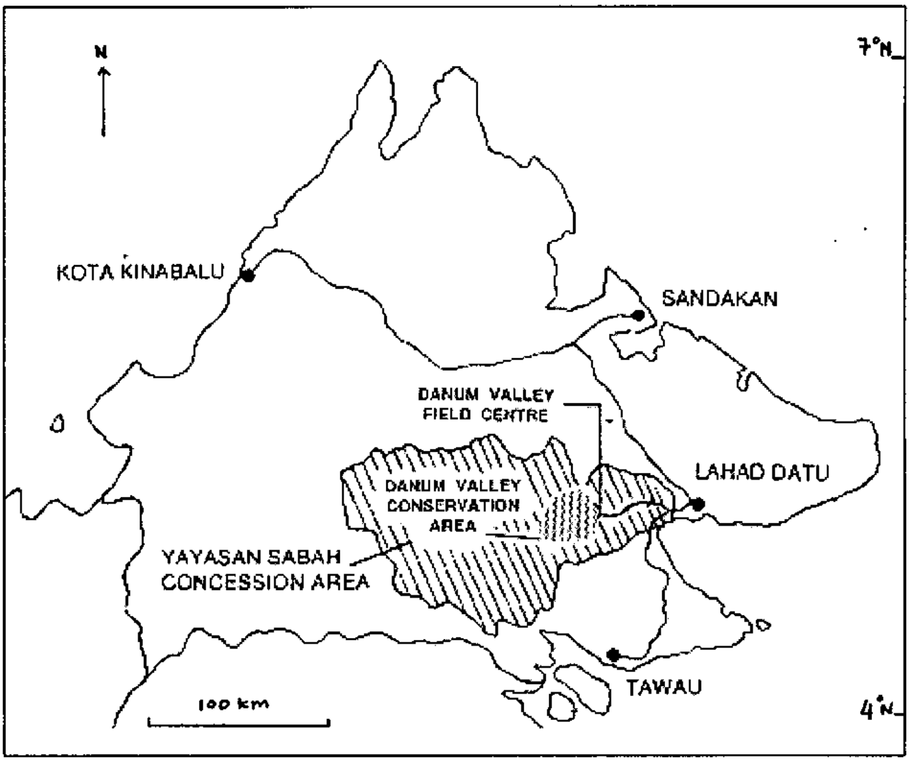
General methods

2.1 Study area

This study was carried out within the Danum Valley Conservation Area (DVCA) and in areas of production forest adjacent to DVCA, in the Malaysian state of Sabah (north Borneo) (Figure 2.1). DVCA covers 43,800 ha of intact lowland rain forest. It is the largest area of pristine rain forest remaining in Sabah. Most of DVCA is lowland, evergreen dipterocarp forest which comprises about 91% of the Conservation Area and the remaining area is classified as lower montane forest (Marsh & Greer, 1992). Species of the family Dipterocarpaceae make up approximately 88% of the total volume of large trees in DVCA (Marsh & Greer, 1992). The area is remarkably rich in flora and fauna and in 1986, the area was gazetted as a Class 1 Protected Area, resulting in DVCA becoming a permanent conservation area.

Adjacent to DVCA, lies a timber concession area (9,728 km^2) which belongs to Yayasan Sabah (the Sabah Foundation). This area is divided into logging coupes from which timber has been extracted since the 1960s (Marshall, 1992). In 1958, an American-owned company called Kennedy Bay Sdn. Bhd. acquired the rights to log 40,000 ha. In 1966, this company was bought by Weyerhauser Corporation, who obtained further timber concessions in 1970. Since 1970, the intensity of timber extraction has averaged 118 m^3 ha^{-1} but this has varied considerably between coupes (range 73-166 m^3 ha^{-1}) (Marsh & Greer, 1992). Conventional tractor logging methods were used on moderate terrain, while cable yarding or highlead techniques were used on the steeper slopes.

Figure 2.1: Location of the study area (Danum Valley Conservation Area; DVCA).



In 1984, a Memorandum of Understanding (MoU) was signed between the Sabah Forestry Deparment, Sabah Foundation and Universiti Kebangsaan Malaysia (now Universiti Malaysia Sabah) for the planning of the Danum Valley Rain Forest Research and Training Programme. A supplementary agreement between these bodies and the Royal Society (UK) provided a framework for collaborative involvement by British scientists. In 1986, a field centre was built to the east of DVCA to provide facilities for the researchers (Marsh & Greer, 1992).

Annual rainfall recorded at DVFC from 1985-1998 averaged 2669 mm ranging from 3294 mm in 1995 to only 1918 mm (460 mm below that of any previous year on record) in 1997, the year associated with a severe El Niño-Southern Oscillation (ENSO) event (Walsh & Newbery, 1999). Monthly means range from 119.5 mm in April to 302 mm in January and October. Rainfall is generally lowest in March to April. Danum Valley experiences intermediate levels of rainfall between the drier coast of Borneo and the wetter regions of south-western Sabah, Sarawak, and western and central Kalimantan. Rain falls on average on 218 days per year.

Temperature and relative humidity at Danum Valley are typical of equatorial rainforest locations. Monthly mean temperature range is only 1.9 deg C around an annual mean of 26.7°C, and the mean daily range also varies little through the year (range = 8.4 deg C). Temperatures rarely exceed 34°C; higher temperatures are generally recorded during prolonged dry spells, and the highest temperature of 36.3°C was recorded in April 1998 during the 1997-98 ENSO event.

2.2 Location of study sites

During the study period from October 1999 to September 2000, data were collected from four study sites. Two of the sites were located in undisturbed primary forest and the other two were in the timber concession area at sites that had been selectively logged. Two transects were set up along existing paths and trails within DVCA (Transect 1 and Transect 2). In the concession area, transects were set up in Coupe 1988 (Transect 3) and Coupe 1989 (Transect 4) (Figure 2.2). Each of the four transects consisted of 20 observation stations at 100 m intervals (total of 80 stations, total transect length 8 km). Two transects were sampled each month (T1 and T3, or T2 and T4), one in primary forest and one in logged forests. Pairs of transects sampled were alternated each month, resulting in each transect being sampled six times over the 12-month study period (Table 2.1).

Coupe 1988 was logged in 1988 by a logging company (Silam Forest Products; SFI), using tractor and highlead methods (Costa & Karolus, 1992). This coupe is situated about 6 km from DVFC. The total area logged in this coupe was about 2,263 ha and about 170,000 m^3 of timber (75 $m^3 ha^{-1}$) was extracted. Coupe 1989 was logged in 1989 by SFI. It is located about 1 km from DVFC. Tractor and highlead techniques were also used in this coupe. The total area logged in this coupe was about 1957 ha which produced about 210,000 m^3 (107 $m^3 ha^{-1}$) of timber (Costa & Karolus, 1992).

Figure 2.2: Location of study sites (primary forest = transects 1 and 2, logged forest = transects 3 and 4). Location of DVFC is shown by the asterisk. Boundaries of logging coupes (and year of logging) and are shown by dotted lines. All areas to the west of the River Segama are primary forest (DVCA).

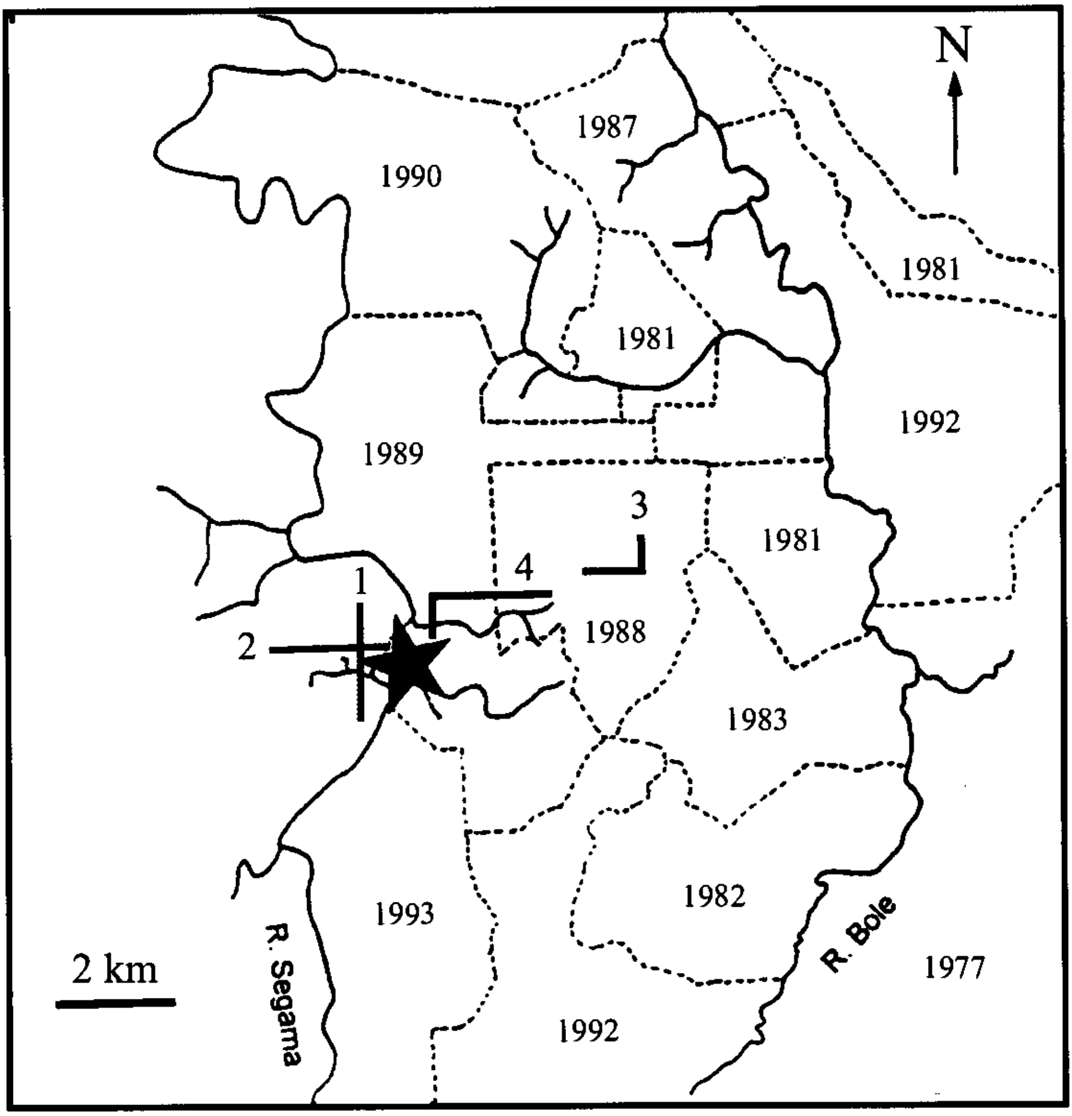


Table 2.1: Study sites sampled each month.

	Study sites	
Sampling month	Undisturbed forest	Disturbed forest
October 1999	Transect 1	Transect 3
November 1999	Transect 2	Transect 4
December 1999	Transect 1	Transect 3
January 2000	Transect 2	Transect 4
February 2000	Transect 1	Transect 3
March 2000	Transect 2	Transect 4
April 2000	Transect 1	Transect 3
May 2000	Transect 2	Transect 4
June 2000	Transect 1	Transect 3
July 2000	Transect 2	Transect 4
August 2000	Transect 1	Transect 3
September 2000	Transect 2	Transect 4

2.3 Materials and methods

Butterflies were sampled using fruit-baited traps. The trap design consisted of a 1 m cylindrical tube of nylon netting sewn onto two wire loops. The bottom of the tube was open for the butterflies to fly into the trap and the top was closed to prevent the butterflies from escaping. The top of the trap was covered by a plastic tray to shelter any trapped butterflies from rain (Figure 2.3). Mashed rotting banana was placed on another plastic tray which was hung about 10 cm below the netting. In order to increase the chance of butterflies being trapped, the bait was placed on a platform approximately 10 cm above the base of the trap.

Butterflies were sampled over a 12-month period from October 1999 until September 2000. Each month, traps were checked each day over a period of 12 days. Traps were checked by two people. Each trap was baited with one fresh banana on the first day of the 12-day sampling period, and a fresh banana was added every second day. This ensured that all traps contained a mixture of fresh to well-rotten banana. Occassionally, baits were removed (eaten by squirrels, macaques, monkeys, etc.), on these occassions traps were baited with fresh banana the next day. On three occasions during the study, a total of 22 traps were destroyed by elephants. In these cases, traps were repaired and replaced as quickly as possible and trapping continued until all traps had been sampled for 12 days. Traps were emptied every day during the sampling periods, between 10.00 and 14.00 hours.

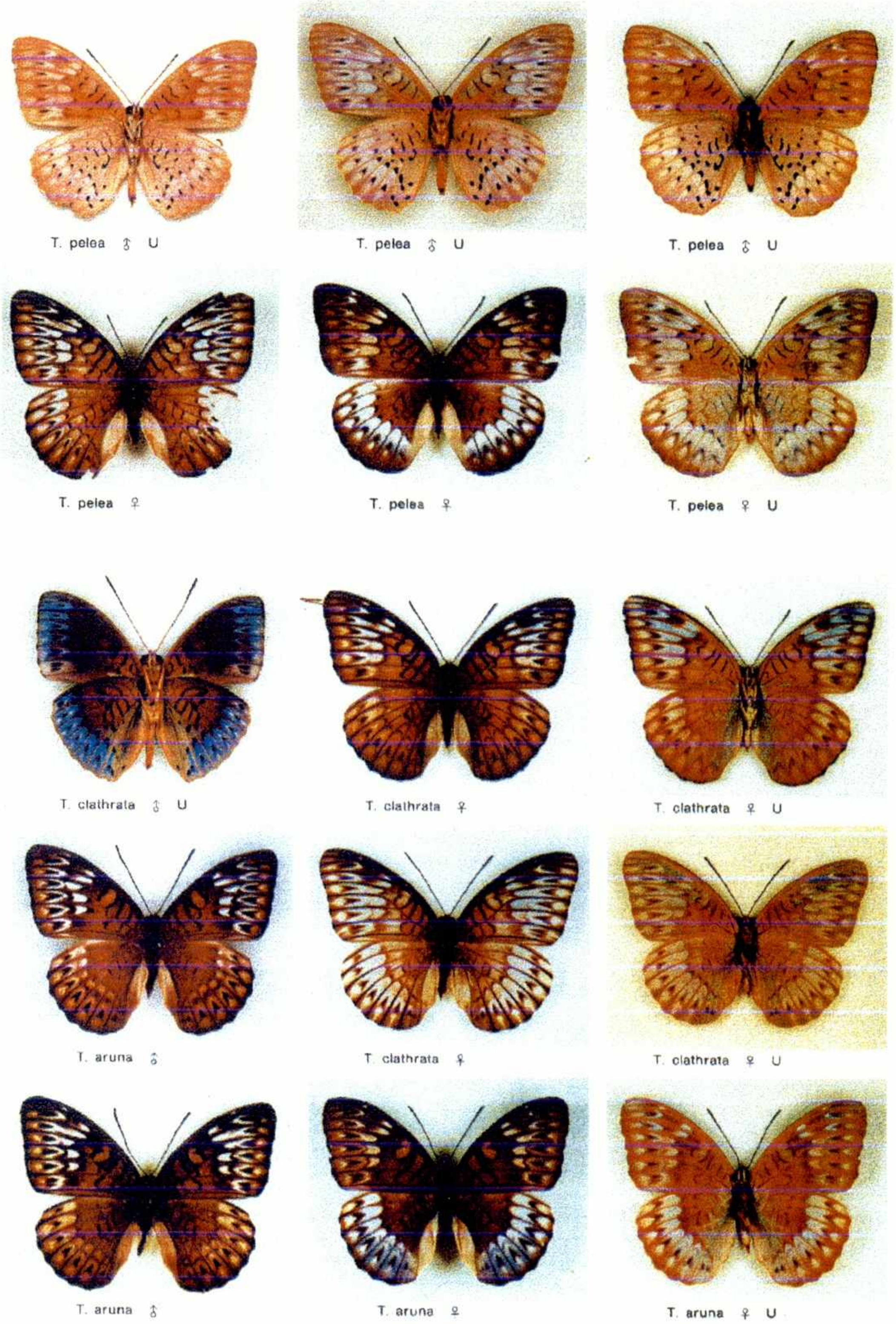
Figure 2.3: Butterfly trap.

All butterflies that were trapped were identified and their sex determined. All adults were marked with felt-tipped pen and released. Large butterflies were marked with a unique number on the underside of their left hindwing. Smaller butterflies (e.g *Mycalesis spp.*) which were too small to put a number on, were marked with a small spot on the underside of their left hindwing according to the transect they were captured on. By these markings, recaptured butterflies could be separated from new individuals. Butterflies that could not be identified in the field were taken as specimens for subsequent identification in the lab.

Identification of butterflies species was based on Otsuka (1988) and Corbet & Pendlebury (1992). Species of the genera *Euthalia* and *Tanaecia* are difficult to identify from wing patterns (Figure 2.4). For these species identification was confirmed by dissecting out the male genitalia (Corbet & Pendlebury, 1992).

In order to investigate the importance of fruit availability for butterfly diversity, the availability of fruit was measured prior to each 12-day sampling each month. An area of 10 m radius around the trapping station was divided into four quadrants. Each quadrant was systematically searched for fallen and rotting fruit for 2 minutes. Fruit phenology data were used as a measure of fruit availability in terms of the proportion of trapping stations with fruit. Climate data (monthly rainfall and sunshine) during the study period were obtained from a metereological station at DVFC.

Figure 2.4: Butterflies of the genus *Tanaecia*. Figures show adult uppersides unless indicated by 'U' = underside. These species are very similar to species of *Euthalia* and cannot be identified by wing colour patterns.
Figure reproduced from Otsuka, 1988.



T. pelea ♂ U
T. pelea ♂ U
T. pelea ♂ U
T. pelea ♀
T. pelea ♀
T. pelea ♀ U
T. clathrata ♂ U
T. clathrata ♀
T. clathrata ♀ U
T. aruna ♂
T. clathrata ♀
T. clathrata ♀ U
T. aruna ♂
T. aruna ♀
T. aruna ♀ U

2.4 Statistical analyses

Statistical analyses were carried out using SPSS and diversity indices were measured using the computer program 'Species Richness and Diversity' (Henderson & Seaby, 1998).

CHAPTER 3

Temporal variation in butterfly diversity

3.1 Introduction

Insects are known to be sensitive to environmental changes such as temperature and photoperiod (Dennis, 1993) and all insects can be considered to be poikilotherms (their body temperature varies with that of the surroundings; Speight *et al.* 1999). Butterflies, like other insects, are dependent on environmental conditions for growth, development and survival (Dennis, 1993).

In temperate regions, temperature and photoperiod are the two main factors affecting butterfly growth and activity. For example, temperature affects butterflies through their flight activity (Dennis, 1993; Pollard & Yates, 1993). Flight muscles of butterflies require a relatively small range of temperature (28°C - 38°C) for efficient contraction (Shreeve, 1992), and so, warm conditions are important for activity and to find food, mates and for females to find suitable sites for egg-laying (Shreeve, 1992). Some studies on temperate butterflies showed that some species did not lay eggs when temperatures were below 16°C and egg-laying increased steadily within the range 16°C - 24°C (Warren, 1992). All temperate species migrate or enter diapause or become dormant during the winter (Warren, 1992). Photoperiod is important for temperate insects as an indicator to determine the timing of reproduction and development (Speight *et al.* 1999).

By contrast, tropical regions exhibit little variation in temperature or photoperiod throughout the year compared with the temperate regions. The maximum temperature seldom exceeds 34°C with mean temperatures of around 20°C even in the coolest months (Jacobs, 1988). Photoperiod is more or less constant with 12 hours light and 12 hours dark. Variation in sunshine hours may be important for many aspects of tropical forest butterfly behaviour. De Vries (1988) noted that different species of butterflies usually fly in particular heights within any habitat and that changes in light intensities can act as barriers between habitats. Therefore, sunshine may affect butterflies through variation in the amount of sunlight penetrating the canopy to the forest floor (Lovejoy *et al.* 1986). In tropical forests, variation in sunlight penetrating the canopy is related to gap formation which can be caused by natural disturbance (e.g natural treefalls) (Feener Jr. & Schupp, 1998) and also by human disturbance such as timber extraction (Spitzer *et al.* 1997).

Tropical regions experience high variation in rainfall throughout the year. In some parts of the tropics, dry and wet seasons are very pronounced (seasonal tropics), but in other parts, rainfall is more or less evenly distributed throughout the year with no marked wet and dry season (aseasonal tropics) (Collins *et. al.* 1991). In spite of generally little variation in rainfall, extreme climatic factors such as droughts associated with El Niño-Southern Oscillation (ENSO) events do occasionally occur in some parts of the aseasonal tropics such as Borneo (Walsh, 1996).

Rainfall has been suggested to be an important factor influencing seasonality in tropical butterflies. Studies in the seasonal tropics revealed that some butterfly species increased in abundance during the dry season and declined with the first wet-season rains (Braby, 1995) while other species decreased during the dry season and increased in the rainy season (De Vries *et al.* 1997).

Rainfall may influence butterfly species richness and abundance in several ways. Butterflies are directly dependent on plants for larval and adult food resources (Spitzer *et al.* 1993) and there is increasing evidence that rainfall may affect butterflies through its impacts on the availability and quality of larval food resources (Spitzer *et al.* 1993; Braby, 1995; Kunte, 1997). Braby (1995) found that patterns of seasonality in *Mycalesis spp.* were related to variation in rainfall and its effects on larval host plant (grass) moisture content.

Temporal changes in butterfly diversity have received little attention in the aseasonal tropics. Studies by Orr & Haeuser (1996) in the rainforest of Brunei found that there was little evidence of any seasonal pattern in butterfly diversity and abundance. However, both high monthly rainfall and a severe drought event associated with an ENSO event which affected Borneo in 1997-98 significantly reduced the abundance and distribution of a satyrid butterfly *Ragadia makuta* (Hill, 1999). It is not known how much temporal variation there is in species richness and abundance in Sabah, or whether any such variation differs between disturbed and undisturbed forest. The latter could have important consequences for comparisons of species diversity in different forest habitats, particularly from studies that do not span an entire year.

This study investigated temporal changes in fruit-feeding butterfly diversity over a 12-month sampling period. Changes in butterfly diversity were examined on a monthly basis in undisturbed primary forest and forest that had been selectively logged 11-12 years previously. In addition, seven environmental variables were included in the study in order to understand how different environmental factors affected butterfly communities in primary and logged forest. These variables included total rainfall, sunshine and proportion of trapping stations with rotting fruit each month, which were expected to affect adults directly. Four other variables investigated were total rainfall one, two, three and four months prior to study, which were expected to influence adult butterfly diversity through effects on larval and pupal stages.

The aims of this chapter are:

1. To investigate temporal variation in butterfly diversity (species richness and evenness) in primary forest and logged forest over the course of one year.
2. To investigate effects of rainfall, sunshine and adult food availability on temporal changes in butterfly diversity in primary and logged forest.

3.2 Materials and methods

3.2.1 Butterfly data

Butterflies were sampled using fruit-baited traps on four transects in primary and logged forest around DVCA, Sabah. Two of the transects were in undisturbed primary forest and the other two were located in forest selectively logged in 1988 and 1989. Each transect consisted of 20 trapping stations at 100m intervals (total of 80 stations, 8 km of transect). In each month, two transects were sampled (total of 40 trapping stations per month) one in primary forest and one in logged forest. Sampling alternated between pairs of transects from month to month (see Chapter 2 for details).

3.2.2 Environmental variables

Prior to each month's sampling, the number of stations where fallen fruit occurred was recorded in order to measure the proportion of trapping stations with fruit. This was done by dividing each station into quadrants within a 10m radius of the station and searching for fallen fruit for two minutes in each quadrant. Total rainfall (mm) from June 1999 to September 2000 and total sunshine (hours) from October 1999 to September 2000 were obtained from a metereological station at Danum Valley Field Centre (DVFC). Table 3.1 shows the environmental variables included in this study.

Table 3.1: Environmental variables included in this study.

Total rainfall (mm) in each month of sampling.

Total rainfall (mm) one month prior to sampling.

Total rainfall (mm) two months prior to sampling.

Total rainfall (mm) three months prior to sampling.

Total rainfall (mm) four months prior to sampling.

Total amount of sunshine (hours) in the month of sampling.

Proportion of trapping stations with fruit in the month of sampling.

3.2.3 Data analysis

3.2.3.1 Species accumulation

All analyses were based only on individuals and excluded recaptures. Species accumulation curves in primary and logged forest were determined by 20 random shuffles of the data to smooth out the effects of sample order. Differences in the rate of species accumulation in primary and logged forest were tested by ANCOVA of $\log_{10}$-transformed data.

3.2.3.2 Butterfly diversity

Based on recommendations by Magurran (1988), the following diversity measurements were used:

The Shannon-Wiener index (H)

This index incorporates species richness and evenness into a single measure.

$$H = -\sum p_i \ln p_i$$

where p_i = proportion of the individuals found in the ith species

Margalef's index (D_M)

This index is used to estimate species richness.

$$D_M = (S - 1) / \ln N$$

where S = species number

and N = total number of individuals in the sample.

Simpson's index (D_S)

This index is used to measure species evenness.

$$D_S = \frac{\sum (n_i (n_i - 1))}{(N (N-1))}$$

where n_i = the number of individuals in the $_i$th species and, N = the total number of individuals

The reciprocal form of Simpson's index is adopted ($1 / D_S$) so that the index increases with increasing diversity.

T-tests were used to compare diversity between habitats over the entire study period. Pearson's correlation tests were carried out to investigate any relationship between patterns of temporal fluctuation in diversity in primary and logged forest.

3.2.3.3 Effects of environmental changes on butterfly diversity

Prior to analysis, all environmental variable data were tested for normality and data based on proportions (~~e.g. fruit abundance~~) were arc-sine transformed. In this study, all data were normally distributed. Pearson's correlation tests were carried out to investigate inter-relationships among the environmental variables. Multiple stepwise regression was then used to investigate effects of seven environmental variables on butterfly diversity.

3.3 Results

3.3.1 Species accumulation

A total of 3996 individuals from 63 butterflies species was recorded during the study, of which 2065 individuals of 54 species were recorded in primary forest and 1931 individuals of 56 species were recorded in logged forest (Table 3.2). The number of species and individual butterflies recorded each month in primary forest and logged forest are shown in Figure 3.1 and Figure 3.2, respectively.

Table 3.2: List of species trapped in primary and logged forest. (+) indicates species presence and (-) indicates species absence.

Species	Primary forest	Logged forest
Melanitis leda	+	+
Melanitis zitenius	+	+
Elymnias panthera	+	+
Elymnias dara	–	+
Neorina lowii	+	+
Xanthotaenia busiris	+	+
Mycalesis anapita	+	+
Mycalesis fusca	+	+
Mycalesis kina	+	+
Mycalesis dohertyi	+	+
Mycalesis orseis	+	+
Mycalesis maianeas	+	+
Mycalesis horsfieldi	+	+
Mycalesis oroatis	+	–
Mycalesis patiana	+	+
Mycalesis mineus	+	+
Mycalesis janadarna	–	+
Erites elegans	+	+
Erites argentina	+	+
Ragadia makuta	+	+
Ypthima pandocus	–	+
Paduca fasciata	+	+
Faunis stomphax	+	+
Faunis kirata	–	+
Faunis gracilis	+	–
Faunis canens	–	+
Amathusia phidippus	+	+
Amathuxidia amythaon	+	+
Zeuxidia aurelius	+	+
Zeuxidia amethystus	+	+
Zeuxidia doubledayi	+	+

Discophora necho	+	+
Thaumantis nouredin	+	+
Charaxes bernadus	+	+
Charaxes durnfordi	+	–
Cupha erymanthis	+	+
Terinos clarissa	+	–
Rhinopalpa polynice	+	+
Athyma reta	+	+
Athyma pravara	+	+
Moduza procis	–	+
Parthenos sylvia	–	+
Bassarona dunya	+	+
Bassarona teuta	+	+
Lexias pardalis	+	+
Lexias dirtea	+	+
Lexias canescens	+	+
Amnosia decora	+	+
Dischorragia nesimachus	+	+
Prothoe franck	+	+
Polyura athamas	–	+
Cirrochroa emalea	+	+
Dophla evelina	+	+
Kalima limborgi	+	+
Agatasa calydonia	+	+
Neptis hylas	+	–
Neptis harita	+	–
Lethe dora	+	–
Tanaecia aruna	+	+
Tanaecia clathrata	+	+
Tanaecia pelea	+	+
Euthalia monina	–	+
Euthalia iapis.	+	+

Figure 3.1: Number of butterfly species in primary and logged forest each month.

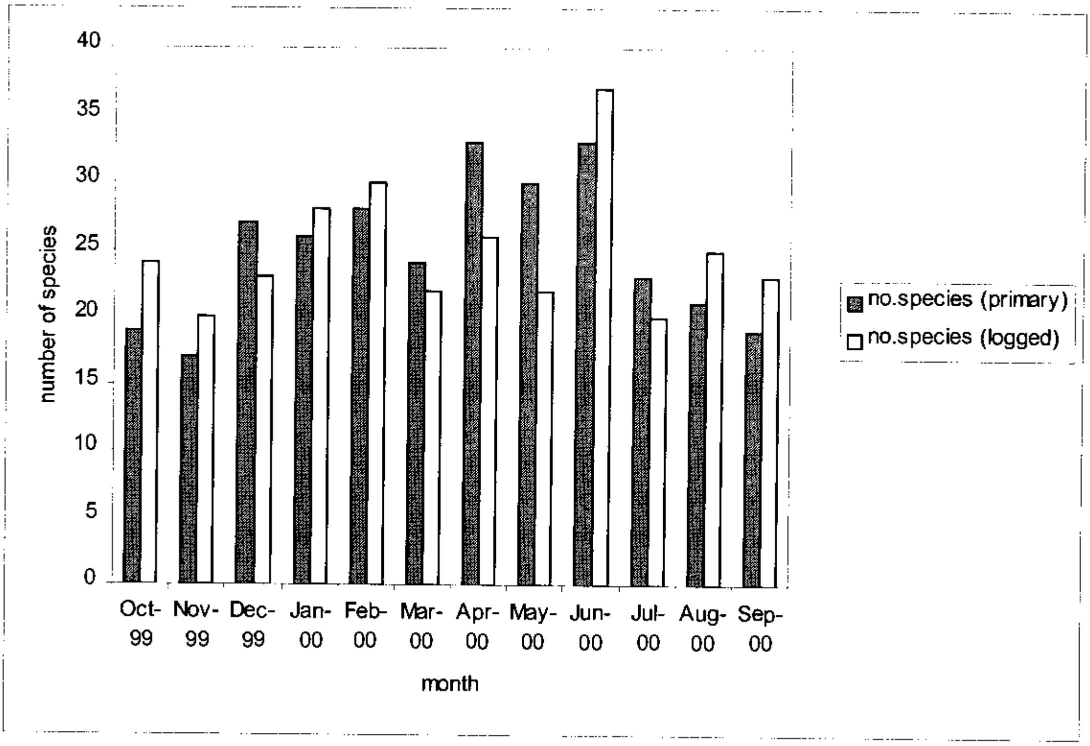


Figure 3.2: Number of individuals in primary and logged forest each month.

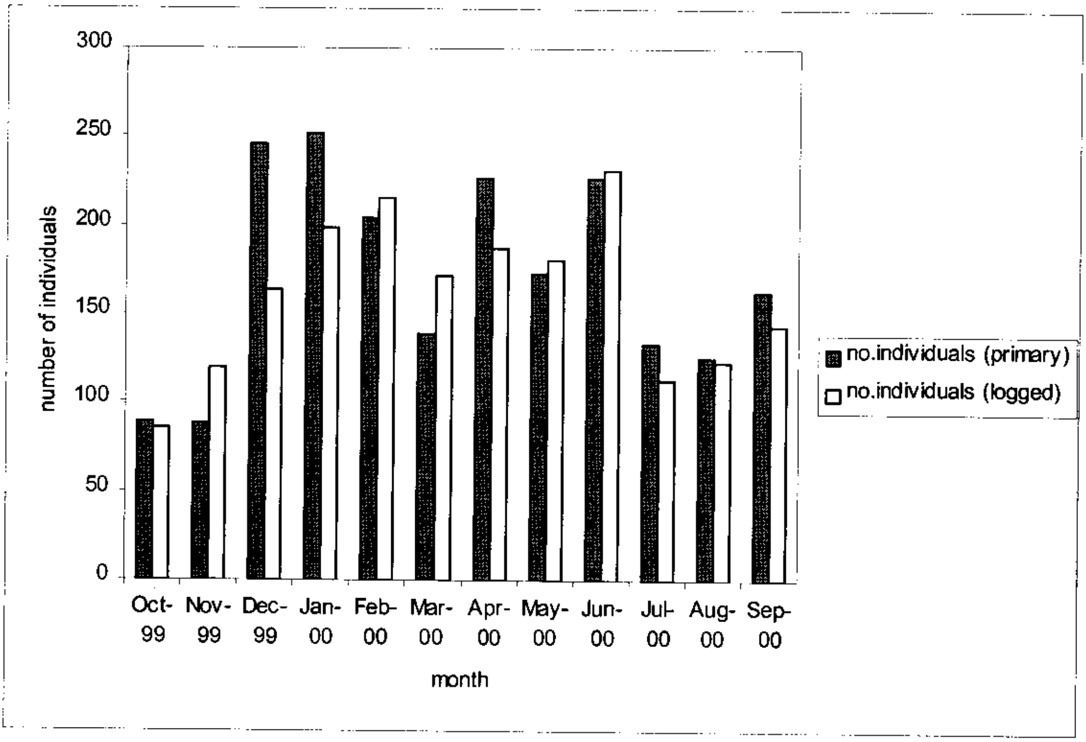
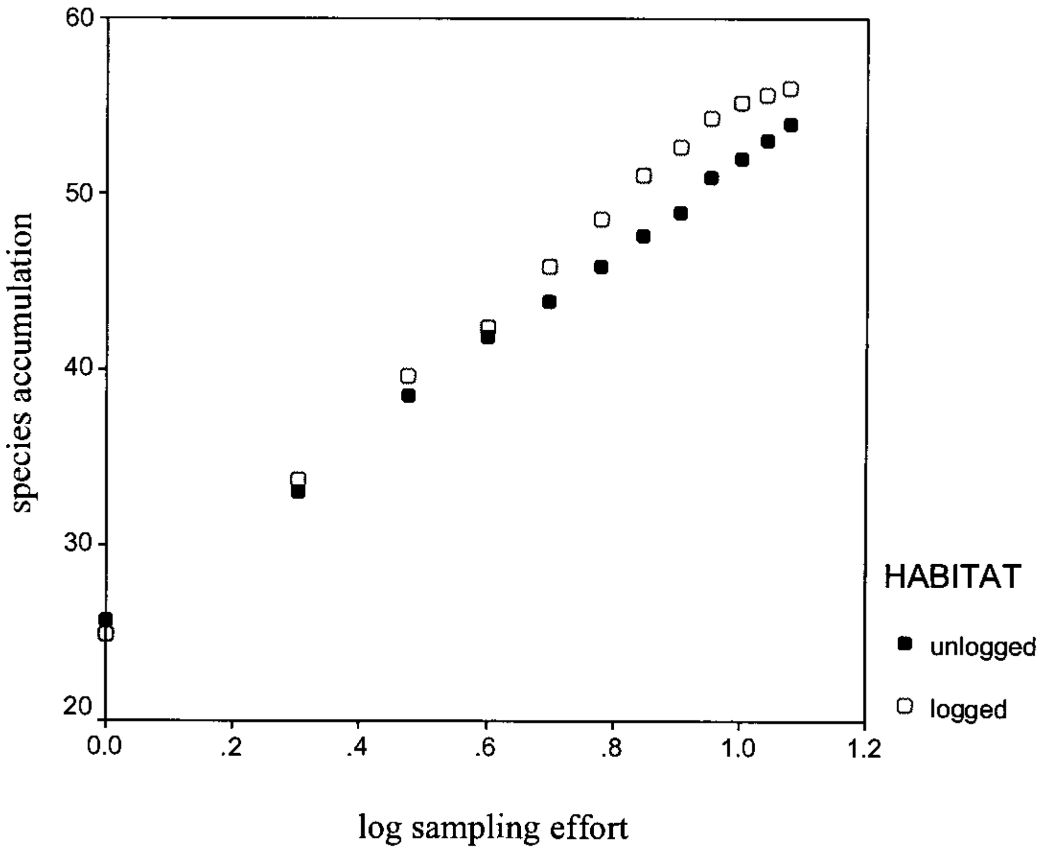


Figure 3.3 shows species accumulation curves in primary and logged forest. The result from the ANCOVA indicated that the rate of species accumulation was significantly faster in logged forest than primary forest (ANCOVA: species * time interaction $F_{1,2}$ = 32.44, $P < 0.001$; logged forest, slope = 29.93 (SE=0.59), primary forest, slope = 26.25 (SE=0.27).

Figure 3.3: Species accumulation in primary and logged forest (semi-log plot).



However, there was no difference between habitats in species diversity (Shannon-Wiener, Simpson or Margalef) over the whole year (t-test; Shannon, t = 0.52, df = 22, P = 0.50, primary mean = 2.58, SE = 0.07, logged mean = 2.53, SE = 0.06; Simpson, t = 0.61, df =22, P = 0.55, primary mean = 10.07, SE = 0.84, logged mean = 9.43, SE =

0.63; Margalef, t = -0.19, df = 22, P = 0.85, primary mean = 4.68, SE = 0.24, logged mean = 4.74, SE = 0.22).

3.3.2 Temporal variation in butterfly diversity in primary and logged forest

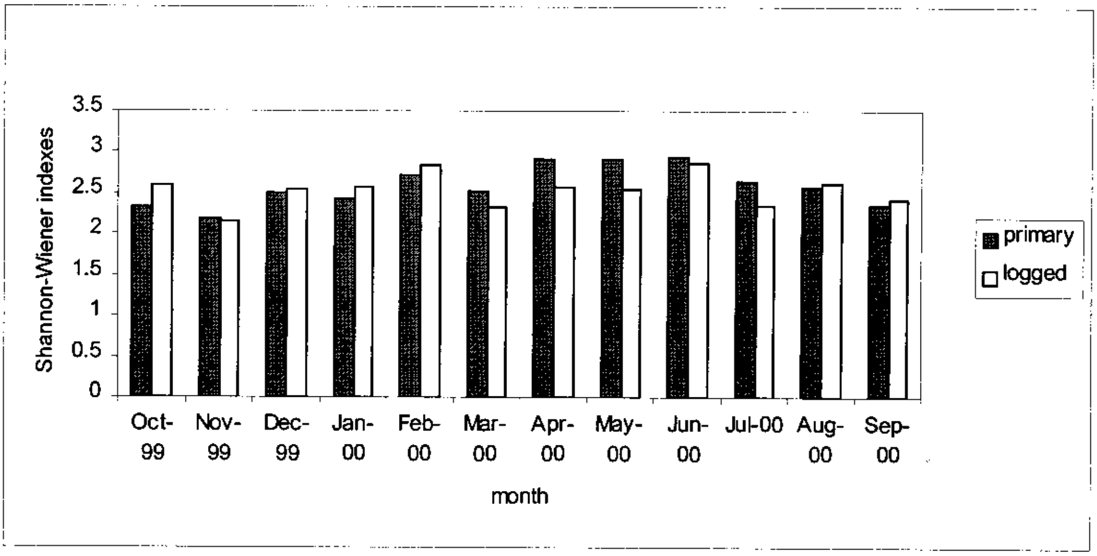
Generally, the three diversity indices (Shannon-Wiener H, Simpson's D_S and Margalef's D_M) showed a similar pattern of monthly variation to each other in primary and logged forest. In primary forest, diversity generally was higher in April, May and June, and low in November. In logged forest, all diversity indices were higher in February and June and lower in November (Figure 3.4).

Monthly Shannon-Wiener diversity indices in both primary and logged forest habitats showed relatively little variation during the study period (primary forest; range = 2.19 – 2.94, logged forest; range = 2.26-2.87). Simpson's diversity index (species evenness) showed greater variation from month to month in both habitats (primary forest; range = 6.24 – 15.04, logged forest; range = 5.22 – 13.09). Margalef's diversity index (species richness) also showed variation from to month in both habitats (primary forest; range = 3.54 – 5.63, logged forest; range = 3.98 – 6.61).

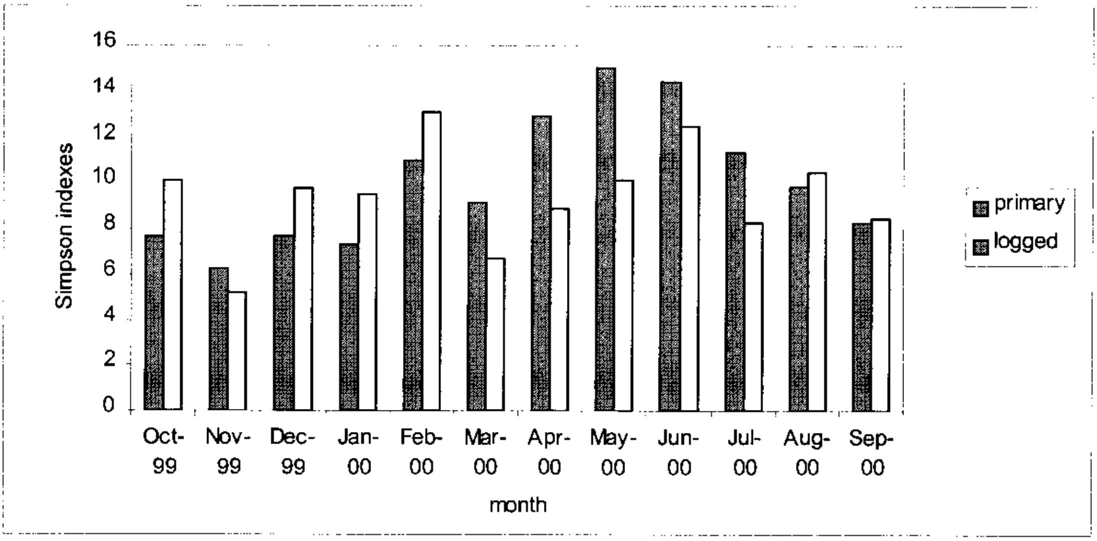
There was weak evidence that temporal patterns of butterfly diversity as measured by Shannon-Wiener were positively correlated in primary and logged forest (Pearson's correlation; r = 0.58, n = 12, P = 0.05) indicating that butterfly diversity in the two habitats fluctuated in synchrony to some extent from month to month. However, no significant correlation was found for other indices (Pearson's correlation, P> 0.05 in both cases). Moreover, for all three indices, the difference between habitats varied across the year. In each case, species diversity was higher in primary forest in all months (Shannon-Wiener and Simpson) or all but one month (Margelef) from March to July. Conversely, species diversity according to all three indices was higher in logged forest in all but one month from August to February (Figure 3.4). In a 2-way ANOVA of diversity by habitat and time-of-year (March to July versus August to February) there was a significant habitat by time-of-year interaction for Shannon ($F_{1,20} = 4.89$, $P = 0.039$) and Simpson ($F_{1,20} = 6.42$, $P = 0.02$) and a marginal result for Margalef ($F_{1,20} = 3.71$, $P = 0.068$).

Figure 3.4: Butterfly diversity in primary and logged forest.

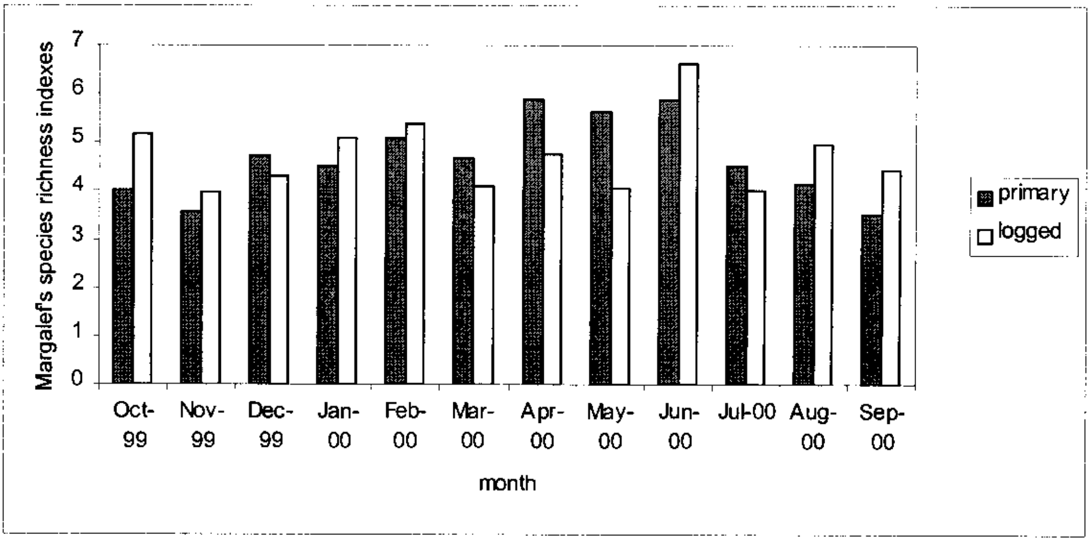
(a) Shannon-Wiener index



(b) Simpson's index (species evenness)



(c) Margalef's index (species richness)



3.3.3 Effects of environmental variables on temporal variation in butterfly diversity

Total monthly rainfall and monthly proportion of trapping stations with fruit was negatively correlated (Pearson's correlation: r = - 0.42, P = 0.04). However, none of the other six environmental variables (total monthly rainfall, total rainfall previous one month, two months, three months or four months, or total monthly sunshine) were correlated with any other variable (Pearson's correlation, P > 0.28 in all cases). Therefore, results in this analysis were unlikely to be confounded by inter-relationships among variables except for the relationship between monthly total rainfall and proportion of trapping stations with fruit.

Total monthly rainfall (mm) from June 1999 to September 2000 is shown in Figure 3.5. Total rainfall during the trapping period from October 1999 to September 2000 was 3339 mm, which was slightly higher than a five year mean (2795 mm) recorded at DVFC between 1986 and 1990 (Douglas *et al.* 1992). However, there was similar variation in monthly rainfall during the study period compared with monthly rainfall recorded at DVFC over a thirteen-year period (1985-1998) which ranged from 120 mm to 302 mm (Walsh & Newbery, 1999). In this study, the highest rainfall was recorded in January 2000 (489 mm). This was a unusually high and was associated with an extensive flood at DVFC. The lowest rainfall was in September 2000 (178 mm).

Total monthly sunshine (hours) from October 1999 to September 2000 is shown in Figure 3.6. There was relatively little variation in sunshine during the study period, but the highest sunshine was recorded in September 2000 (188 hours) and the lowest was in November 1999 (122 hours).

The proportion of trapping stations where fallen fruit was recorded in primary and logged forests during the study period (October 1999 to September 2000) is shown in Figure 3.7. Overall there was high variation in fruit abundance during the study but little variation between habitats (primary forest range = 0 – 31% of the stations; logged forest range: 0 – 26%). The patterns of fruit abundance in the two habitats were not correlated (Pearson's correlation with arcsine-transformed, $r = 0.19$, $n = 12$, $P > 0.05$).

Figure 3.5: Monthly total rainfall (mm) recorded at DVFC each month from June 1999 to September 2000.

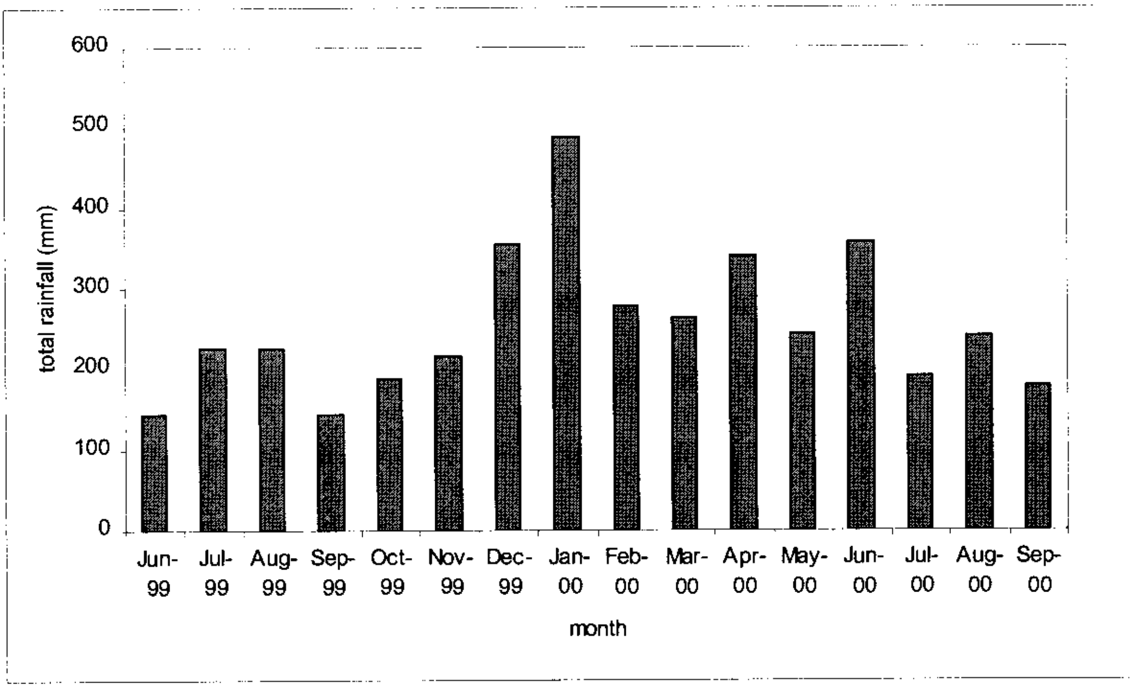


Figure 3.6: Monthly total sunshine (hours) recorded at DVFC during the study period.

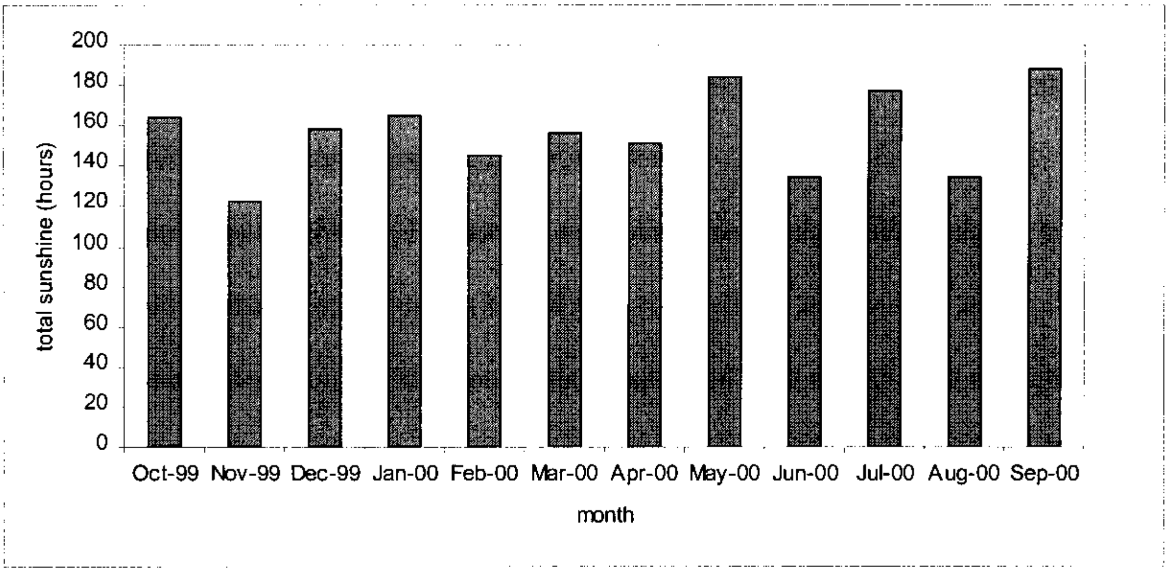
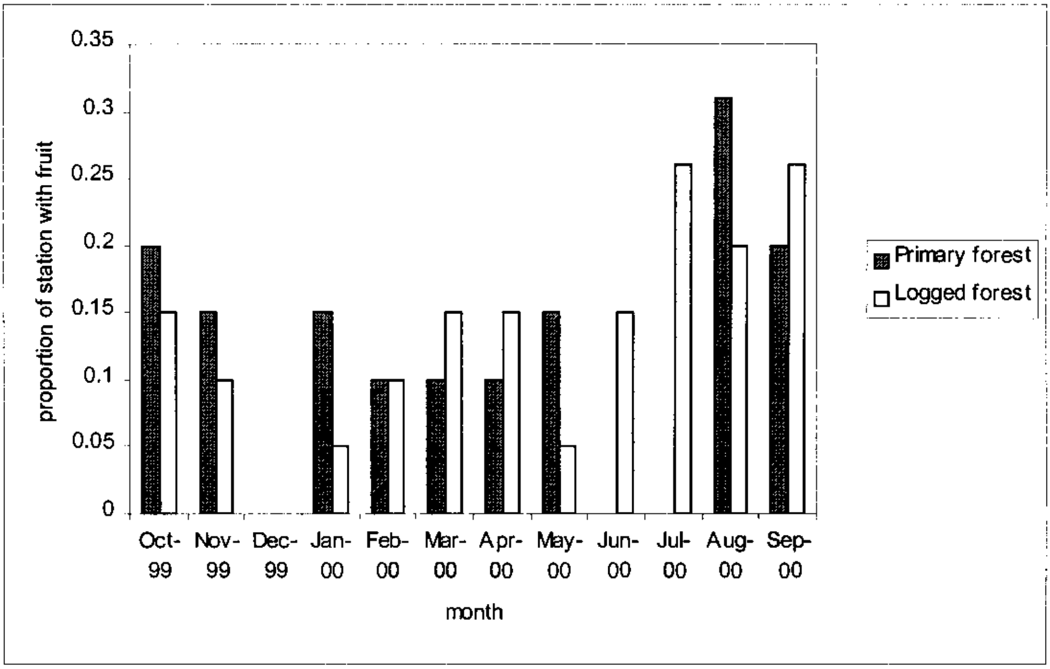


Figure 3.7: Proportion of trapping stations with fruit in primary and logged forest.



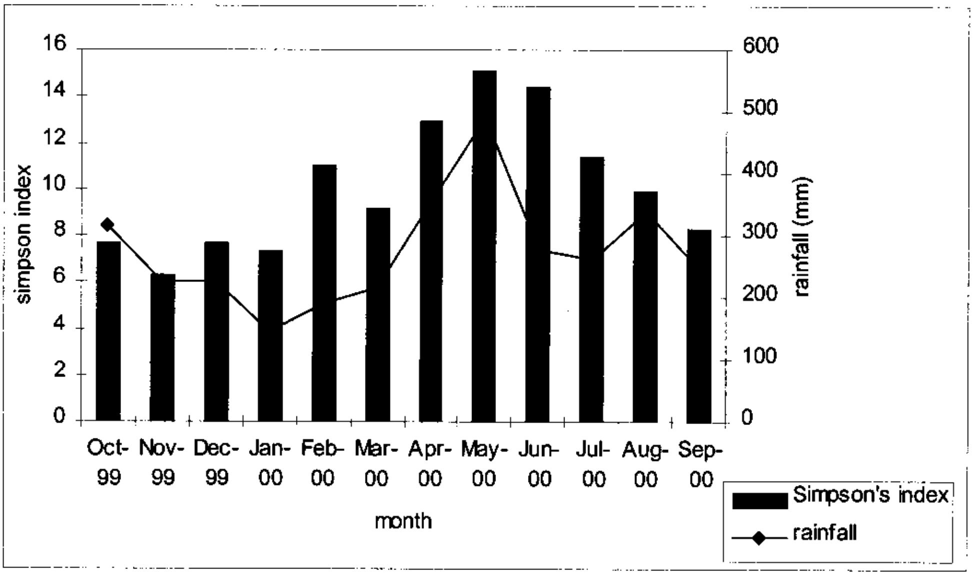
Stepwise multiple regression showed that in primary forest there was a significant positive relationship between Simpson's diversity index and rainfall four months and one month before the sampling period (Figure 3.8; $R^2 = 0.67$, $F_{2,9} = 9.07$, $P = 0.007$). The relationship is described by the following equation:

> Simpson diversity = 0.024 (rainfall 4 month's previously) (SE = 0.01) + 0.0016 (rainfall 1 month previously) (SE = 0.01) – 0.67 (SE = 2.66).

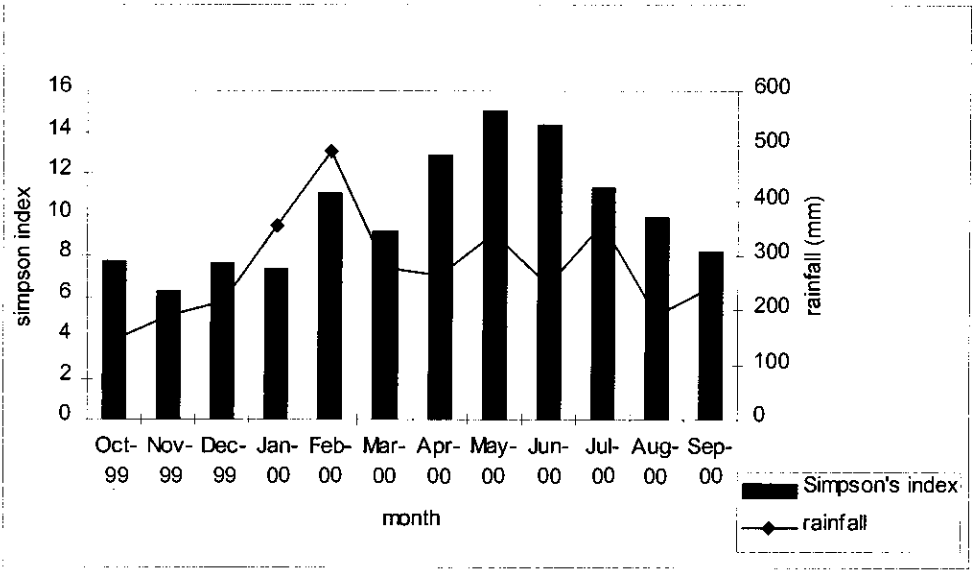
Rainfall four months and one month previously explained 42% and 25 % respectively of the monthly variation in species evenness in primary forest. There were no significant relationships between any of the other diversity measures and any of the environmental variables, either in primary or logged forest ($P > 0.05$ in all cases).

Figure 3.8: Relationship between rainfall and Simpson's diversity index in primary forest.

(a) Relationship between total rainfall four months before sampling and diversity.



(b) Relationship between total rainfall one month before sampling and diversity.



3.4 Discussion

3.4.1 Butterfly species accumulation

This study sampled over a period of 12 months, resulting in a total of 5760 trap days, which is one of the longest studies monitoring butterfly diversity in the tropics. As a consequence, a relatively large sample size was obtained. Sample sizes have important effects on comparative diversity estimates because rare species are likely to be absent from small samples (DeVries *et al.* 1997). Therefore small sample sizes can be unreliable in assessing diversity, particularly in a region with high diversity such as Borneo.

This study showed that the rate of species accumulation was significantly faster in logged forest compared with primary forest (Figure 3.3), reflecting slightly higher total species richness in logged forest (56 species) than in primary forest (54 species).

However, there was no difference between habitats in any of the three diversity indices over the whole year.

3.4.2 Temporal variation in diversity

In view of the current concern on the impacts of tropical forest disturbance and global climate changes on species diversity, there is a need for long-term monitoring in order to understand how these impacts affect temporal changes in butterfly diversity. Most studies investigating tropical butterfly diversity have been carried out over relatively short-time periods (generally less than six months) (e.g Beccaloni & Gaston, 1995; Spitzer *et al.* 1997; Wood & Gillman, 1998; Beck & Schulze, 2000). Short-term studies may miss valuable information concerning temporal changes in diversity and if these changes differ between habitats in terms of the size or pattern of fluctuations, then short-term studies may provide unreliable results (De Vries *et al.* 1997).

Tropical butterflies are known to exhibit seasonal fluctuations in diversity and abundance (Braby, 1995, De Vries *et al.* 1997), but these studies have been confined to the seasonal tropics where changes in rainfall are very marked. This study has revealed that even in the aseasonal tropics where rainfall is more or less evenly distributed throughout the year, there were changes in butterfly diversity across the year. In primary forest, butterfly diversity generally was higher in April, May and June, and lower in November while in logged forest, butterfly diversity generally was higher in February and June and lower in November. These patterns were observed in all diversity indices measured (Figure 3.4). This result was in contrast to a study by Orr & Haeuser (1996) which found no trends in temporal patterns of butterfly diversity in Brunei, where there was less temporal variations in rainfall than in Sabah (Chapter 1).

In this study, butterfly diversity was higher in primary forest during March-July but higher in logged forest during August-February. Thus short-term studies lasting less than six months could have found opposite effects of logging on diversity at different times of the year. Moreover, over the course of an entire year, these differences between habitats evenned out, so that there was no marked effect of logging on overall species richness. This might explain why Willot *et al.* (2000) found no effect of logging on butterfly diversity in the study area.

3.4.3 Effects of environmental variables on temporal changes in butterfly diversity

In this study, butterfly species evenness (Simpson's index) in primary forest was positively related to rainfall four months and one month before sampling. Other studies have found that temporal patterns of butterfly abundance and diversity were also affected by rainfall, through its effects on the availability and quality of larval food plants (Braby, 1995; Spitzer *et al.* 1993; Kunte, 1997). Wolda (1978) recorded that seasonal fluctuations in tropical insect abundance were positively related with rainfall through leaf production. This may suggest that effects of rainfall on butterfly species evenness in this study were due to indirect effects on the availability and quality of larval food plants. However, in this study effects of rainfall on butterfly species evenness were only observed in primary forest.

This study showed that variation in sunshine hours did not affect butterfly diversity. Other studies have shown that increased canopy openness in logged forest can affect butterfly diversity through changes in microclimates (Spitzer *et al.* 1997), however, there was little variation in total sunshine hours during the study period and this may not have been sufficient to affect butterfly diversity in either habitat.

In this study, availability of rotting fruit did not affect fruit-feeding nymphalid butterfly diversity even though adults of this guild gain their nutritional requirements by feeding on juices of fruits. However, little is known about the relationship between butterflies diversity and fruit availability (Owen, 1971). Forests in the study area are dominated by trees of the Dipterocarpaceae (Marsh & Greer, 1992), which do not produce fleshy fruits. This means that food resources for fruit-feeding butterflies must include other plant groups. A study on frugivorous mammals (ungulates) in the study area found no differences in either the overall fruit resources or fruit availability between primary and logged forest. However, a 17-month survey of fruiting trees in 2 ha of primary and 12-year old logged forest showed that there was evidence of marked temporal variation of fruiting in both forest types (Heydon & Bulloh, 1997). Fig trees were found to be keystone food resources for many tropical frugivores (Heydon & Bulloh, 1997; Davis & Sutton, 1997). This finding may suggest that fruit-feeding butterflies in tropical forest also depend on figs as an important adult food resource, but this needs further investigation.

In this study, there was negative correlation between rainfall and fruit availability and thus positive effects of rainfall on species evenness may have been confounded by availability of fruits. A negative relationship between species evenness and fruit availability would support the notion of higher species evenness in unproductive ecosystems (Huston, 1994). It is also possible that the efficiency of traps may be affected by the availability of fruit in the surrounding forest. This has not been considered in previous studies and requires further investigation.

CHAPTER 4

Beta diversity of butterfly species in primary and logged forest

4.1 Introduction

Regional diversity (γ diversity) can be partitioned into separate components of species richness and evenness (α diversity) and species turnover (β diversity). Throughout the ecological literature, patterns of α diversity have been very well studied, while β diversity has been far less studied (Whittaker, 1960; Harrison *et al.* 1992). As pointed out by Süssenbech & Fiedler (1999), biodiversity research is not only concerned with adequate measures of richness of communities (α diversity), but also with discriminating between communities, which is β diversity.

β diversity measures the degree of turnover of species composition and the similarity (or difference) of habitats or samples in terms of the species found in them (Magurran, 1988). The measure of β diversity can be applied spatially by measuring diversity along environmental gradients, and also temporally by measuring diversity over time (Wilson & Shmida, 1984). Most attempts to measure β diversity are in relation to spatial scale (e.g Harrison *et al.* 1992; Kunte *et al.* 1999). Attempts to measure β diversity over time are very few because changes in conditions over time are thought to occur relatively slowly compared with changes in the spatial dimension (Hengevald, 1996).

In spatial dimensions, β diversity measured among taxa is expected to be higher in poorer dispersers and in species with restricted ranges. Within taxa, β diversity is expected to increase with increasing environmental dissimilarity between sites and also the distance between sites (Harrison *et al.* 1992). Orr & Hauser (1996) suggested that spatial β diversity is probably a less important component of total diversity in butterflies compared with poorly dispersing groups such as Coleoptera and Microlepidoptera, but there are few studies investigating this topic (DeVries *et al.* 1997; De Vries *et al.* 1999). However, Pinheiro & Ortiz (1992) found marked changes in butterfly species turnover along vegetation gradients, indicating that β diversity is an important component of tropical diversity in butterflies.

There have been few studies on β diversity over time in tropical regions. However, even in the aseasonal tropics where changes in rainfall are not very marked, some species of butterflies are unlikely to be present throughout the year. Moreover, patterns of β diversity may differ in relation to habitat disturbance and this may affect investigation of the impacts of habitat disturbance, but this has not been studied.

The aims of this chapter are:

1. To investigate changes in β diversity between primary and logged forest.
2. To investigate temporal changes in β diversity ~~form~~ from month to month in primary and logged forest over a 12-month period.

4.2 Materials and methods

4.2.1 Butterfly data

Butterflies were sampled using fruit-baited traps along four transects in primary and logged forest. Two transects were in primary forest and two transects were in forest selectively logged in 1988 and 1989. Each transect consisted of 20 traps which were placed at 100 m intervals (total of 20 traps per transect, transect length 2 km). Two transects were sampled each month, one in primary forest and one in logged forest. Pairs of transects sampled were alternated each month (see Chapter 2).

4.2.2 Data analysis

All analyses were based on the number of individuals trapped and excluded recaptures. β diversity from month to month was calculated using Whittaker's index (β_w) (Magurran, 1988) which is:

$$\beta_w = (S/a) - 1$$

where S = the total number of species in two [illegible] ~~samples~~

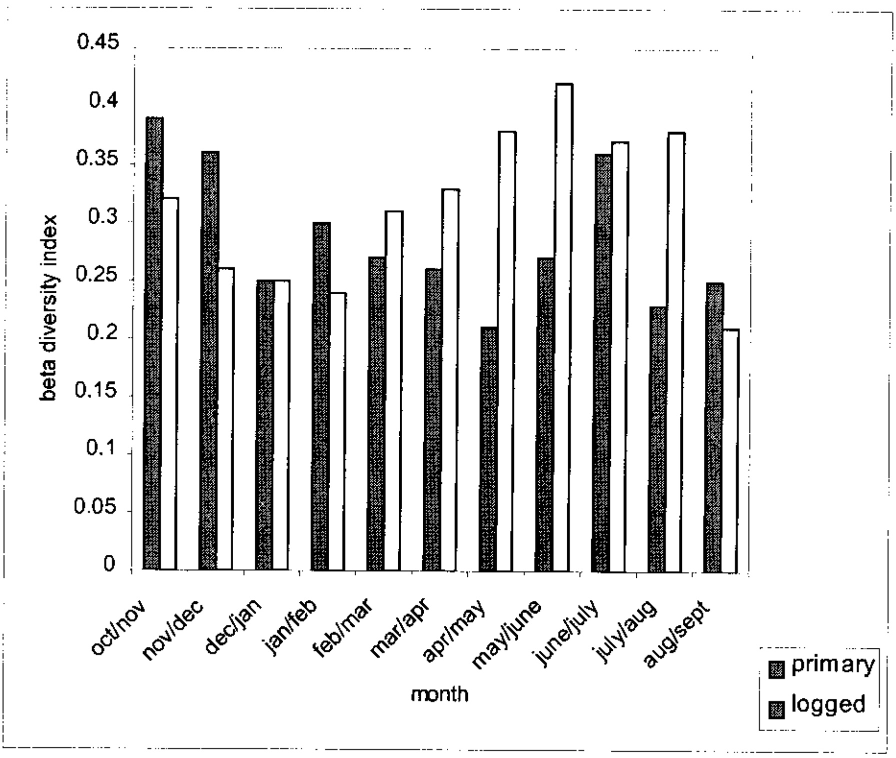
and, a = the average of the number of species in the two [illegible] samples.

Spearman's rank correlation was used to investigate whether patterns of monthly changes in β diversity were similar in primary and logged forest. T-tests were used to investigate differences in mean values of monthly changes in β diversity between primary and logged forest.

4.3 Results

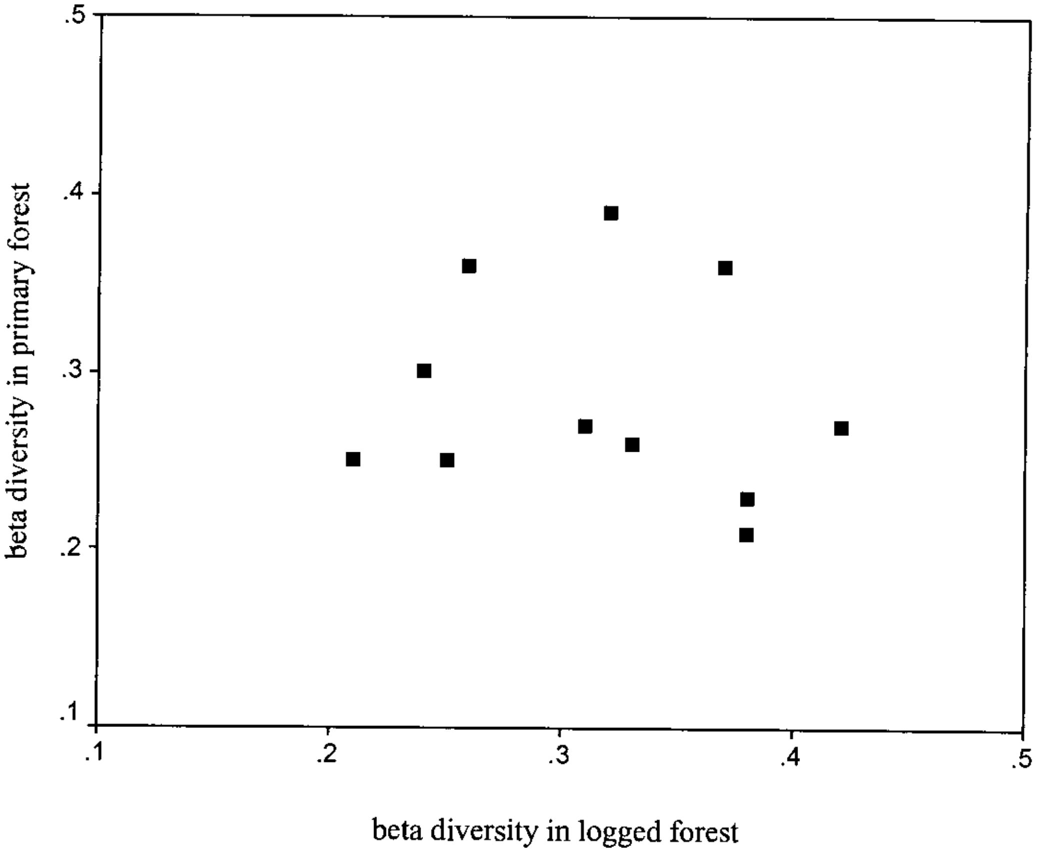
There was little difference between primary and logged forest in the range of β diversity values recorded (primary forest, range = 0.21 - 0.39; logged forest, range = 0.21 – 0.42) during the study period (Figure 4.1) and no significant difference between mean β diversity in primary and logged forest (t-test; t = -1.07, df = 20, P = 0.30; primary forest, mean = 0.29, SD = 0.06, logged forest, mean = 0.32, SD = 0.07). However, this masked the fact that β diversity between months was consistently higher in logged forest during February-August and in primary forest during August- February (Figure 4.1)

Figure 4.1: Beta diversity between months (Whittaker's index) in primary and logged forest.



There was no correlation between β diversity in primary and logged forest (r = -0.17, n =11, P = 0.62; Figure 4.2), which confirmed that the pattern of turnover of species from month to month was different in the two habitats.

Figure 4.2: Relationship between patterns of temporal beta diversity in primary and logged forest.



4.4 Discussion

4.4.1 β diversity across space

One important point in assessing similarities or differences between habitats in terms of species composition is to investigate the pattern of species turnover within and between habitats (Price, 1975; Price, 1997). Several studies have shown that natural forest habitats tend to have higher β diversity compared with altered vegetation types such as cerrado (savanna-like vegetation) (Pinheiro & Ortiz, 1992) and parkland (a variety of cultivated and naturalized plants) (Kunte *et al.* 1999).

During this study, a wide range of fruit-feeding butterfly species was sampled, and among these were species with wide geographical distributions such as *Melanitis leda* and species endemic to Borneo, such as *Mycalesis kina* (based on biogeographical distributions in Otsuka, 1988; Corbet & Pendlebury, 1992) which were sampled in both primary and logged forest. This suggests that butterfly resources and breeding habitats may have been equally available in primary and logged forest leading to similarity in patterns of spatial β diversity in the two habitat, although this was not tested here.

4.4.2 β diversity across time

β diversity was higher in primary forest in the first few months of sampling, and then logged forest had higher β diversity until close to the end of the study (Figure 4.1). Thus as with α diversity (Chapter 3), studies lasting only a few months may have obtained a false impression of differences in β diversity between habitats.

Higher β diversity in primary forest could have resulted from a greater proportion of small, poorly-dispersive species with relatively short adult lifespans (Hill *et al.* in press). Conversely, widespread migratory species may be better able to colonise disturbed forests with more open canopies and higher light levels. These species usually appear on an irregular basis, and may have led to higher β diversity in logged forest in some months. This requires further study.

CHAPTER 5

Temporal changes in abundance of fruit-feeding butterflies (*Neorina lowii*, *Bassarona dunya* and *Prothoe franck*

5.1 Introduction

Temporal changes in butterfly species abundance are well documented from temperate regions (Warren, 1992; Pollard & Yates, 1992; Pollard & Eversham, 1995) in association with marked changes in temperature and photoperiod during the year (Tauber *et al.* 1986; Dennis, 1993). As discussed in Chapter 3, tropical regions exhibit less variation in temperature and photoperiod throughout the year compared with temperate regions, but effects of several environmental factors such as rainfall, and resource availability (e.g adult and larval food) are likely to influence temporal variation in tropical butterfly species abundance. In Borneo, sub-annual variation in the distribution and abundance of the satyrid butterfly *Ragadia makuta* was closely related to changes in rainfall, probably through its impacts on larval growth and survival (Dawood, 2000). Further data are now needed to investigate temporal variation in the distribution and abundance of other species.

Recent studies have shown that habitat modification may severely affect butterfly abundance and distribution in both temperate (Hanski & Gilpin, 1991) and tropical regions (Brown & Hutchings, 1997). In tropical forests, habitat modification such as selective logging may have a marked effect on microclimatic conditions such as temperature and light intensity at ground level within the forest. This could modify the effects of temporal variation in climate, so that temporal variation in the distribution and abundance of particular species of butterfly may differ between disturbed and undisturbed forest. This in turn could have a marked effect on comparisons between habitats, particularly if such comparisons are carried out over less than a year. However, to my knowledge, no previous study has investigated this problem.

The butterfly community at Danum Valley is highly diverse (as discussed in Chapter 1), but few species are sufficiently abundant for this type of study. Three locally common species, *Neorina lowii* Doubleday (Subfamiliy: Satyrinae), *Bassarona dunya* Fruhstorfer (Subfamily: Nymphalinae) and *Prothoe franck* Fruhstorfer (Subfamily: Charaxinae) were selected for studying changes in abundance in primary and logged forest over the course of one year. Species in the subfamily Satyrinae are mostly medium-sized butterflies with weak flight, that frequent shady conditions near the ground, and *N. lowii* is the largest sampled representative of this subfamily. This species is confined to dense forest (Corbet & Pendlebury, 1992). Most species in the subfamily Nymphalinae have wider geographical ranges. They are generally larger than the Satyrinae, and they usually have strong and rapid flight (Corbet & Pendlebury, 1992; Hill *et al.* in press). Subfamily Charaxinae consists of large and robust butterflies, many of which fly above the canopy (Hill *et al.* in press).

Adults of the three species studied in this chapter all gain their nutritional requirements by feeding on rotting fruit. The larvae of *P. franck* are known to feed on *Friesodielsia cuneiformis* (Family: Anonnaceae) whereas the larval host-plants of the other two species are unknown (Corbet & Pendlebury, 1992). Based on Otsuka (1988) and Corbet & Pendlebury (1992), *P. franck* is distributed in Sundaland (comprising of West Malaysia, Sumatra, Java, Borneo and Palawan), Thailand and the Philippines, while the distributions of *B. dunya* and *N. lowii* are restricted to Sundaland. Thus all the three species are of fairly high conservation value.

In this study, all environmental variables considered in Chapter 3 were included to investigate their effects on butterfly abundance. The variables were total rainfall (during each month of sampling and one to four months prior to sampling), total sunshine during each month of sampling and total proportion of trapping stations with fruit during each month of sampling. As discussed in Chapter 3, total rainfall, total sunshine and proportion of trapping stations with fallen fruit during the month of sampling were considered likely to affect adult butterflies, while rainfall one to four months prior to the sampling period were considered likely to affect larvae and pupae.

The aims of this chapter are:

1. To investigate temporal changes in the abundance of *N. lowii*, *B. dunya* and *P. franck* in primary and logged forest over the course of one year.
2. To investigate whether or not temporal variation in the abundance of *N. lowii*, *B. dunya and P. franck* is similar in primary and logged forest.
3. To investigate the effects of rainfall, sunshine and adult food availability on temporal fluctuations in abundance of the three study species in primary and logged forest.

5.2 Materials and methods

5.2.1 Butterfly data

Butterfly data were collected using fruit-baited traps. Four transects were used in this study, of which two were in primary forest and two were in forest that had been selectively logged 11-12 years prior to the study period (in 1988 and 1989). Each transect was 2 km long with traps placed every 100 m (20 traps per transect). Each month two transects were studied, one transect in primary forest and one in logged forest (see Chapter 2 for details). Traps were operated for 12 days (total 480 trap days per month) for 12 months (October 1999 to September 2000). All adults of the selected species (*N. lowii*, *B. dunya* and *P.franck*) which were trapped were marked with a unique number on the underside of the left hindwing and then realesed.

5.2.2 Environmental variables

Total rainfall (mm) for each month from June 1999 to September 2000 and monthly sunshine (hours) from October 1999 to September 2000 were obtained from a metereological station at Danum Valley Field Centre (DVFC). Immediately prior to each month's sampling, the number of trapping stations with fruits was recorded. This was done by dividing an area of 10 m radius around each trapping station into four quadrants. Every quadrant was searched for fallen fruit for two minutes (see Chapter 2 for details). All environmental variables included in this study are listed in Table 5.1.

Table 5.1: Environmental variables included in this study.

Total rainfall (mm) in each month of sampling.

Total rainfall (mm) one month prior to sampling.

Total rainfall (mm) two months prior to sampling.

Total rainfall (mm) three months prior to sampling.

Total rainfall (mm) four months prior to sampling.

Total sunshine (hours) in the month of sampling.

Proportion of trapping stations with fruit in the month of sampling.

5.2.3 Statistical analysis

All analyses are based on the number of individuals of each of the three species trapped each month (October 1999 to September 2000) and exclude any recaptures. Pearson's correlation tests were carried out to investigate patterns of relative abundance of *N. lowi*, *B. dunya* and *P. franck* in primary and logged forest.

All environmental variables were tested for normality and, where necessary, transformed to normality if possible. Data that were based on proportions were arc-sine transformed prior to analysis. In this analysis, all environmental variable were normally distributed and Pearson's correlation tests were carried out to investigate inter-relationships among the environmental variables included in this study. Multiple forward stepwise regression was carried out to investigate effects of seven environmental factors on relative abundance of each species in the two habitats.

5.3 Results

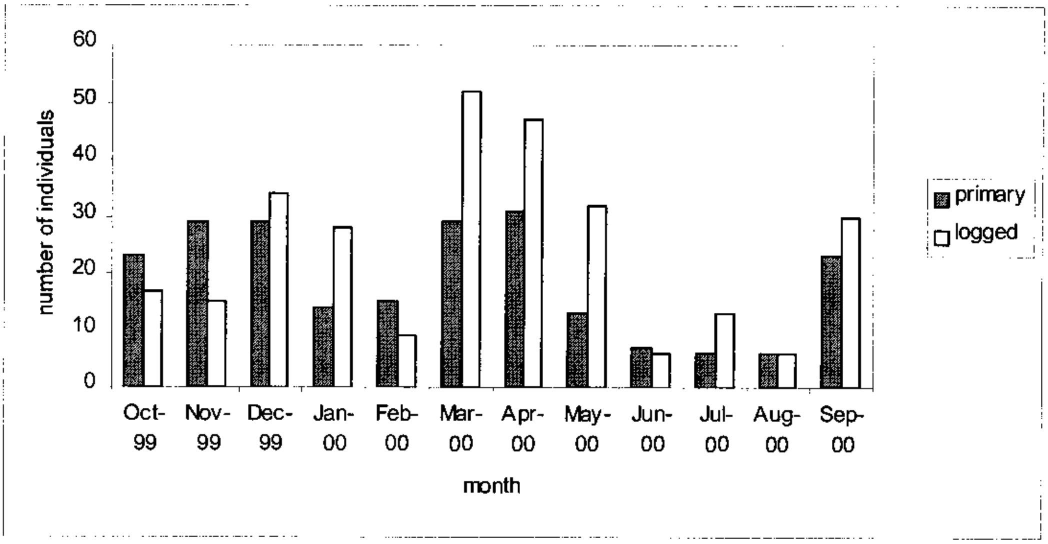
5.3.1 Temporal changes in butterfly abundance in primary and logged forest

A total of 514 individuals of *N. lowii*, 413 of *B. dunya* and 238 of *P. franck* were recorded during the study period. Figure 5.1 shows the number of individuals of each species recorded each month in primary forest and logged forest. Generally, the three study species showed three different patterns of temporal abundance. *B. dunya* was more abundant in logged forest than primary forest each month. In contrast, *P. franck* was higher in abundance in primary forest than in primary forest each month, while *N. lowii* was commoner in primary forest in October and November but commoner in logged forest in most other months.

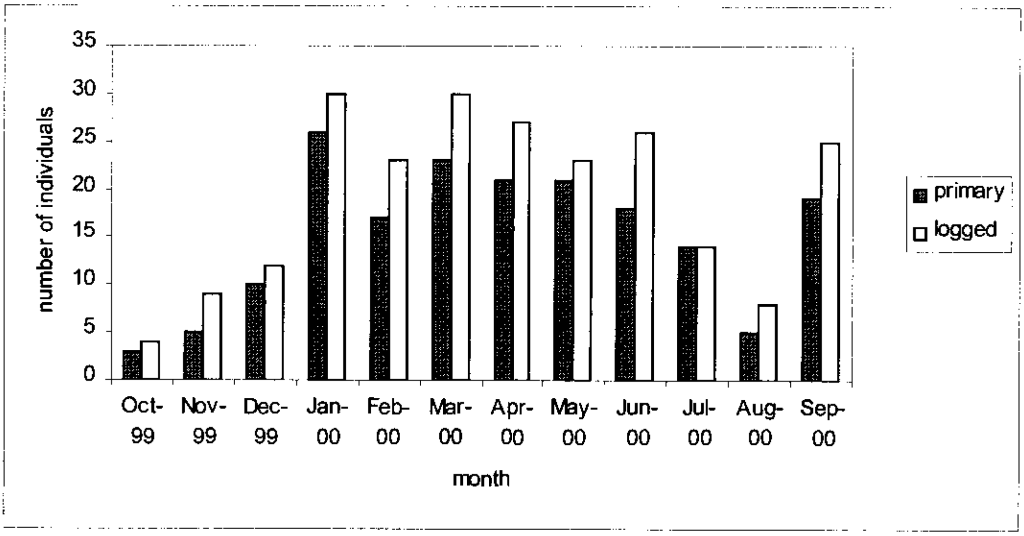
There was a significant positive correlation between monthly abundances of all three study species in primary and logged forest (Figure 5.2-5.4; *N. lowii*: $r = 0.69$, $n = 12$, $P < 0.05$; *B. dunya*: $r = 0.97$, $n = 12$, $P < 0.01$; *P. franck*: $r = 0.74$, $n = 12$, $P < 0.01$).

Figure 5.1: The number of individuals of *N. lowii, B. dunya* and *P. franck* trapped each month in primary and logged forest.

(a) *N. lowii*



(b) *B. dunya*



(c) *P. franck*

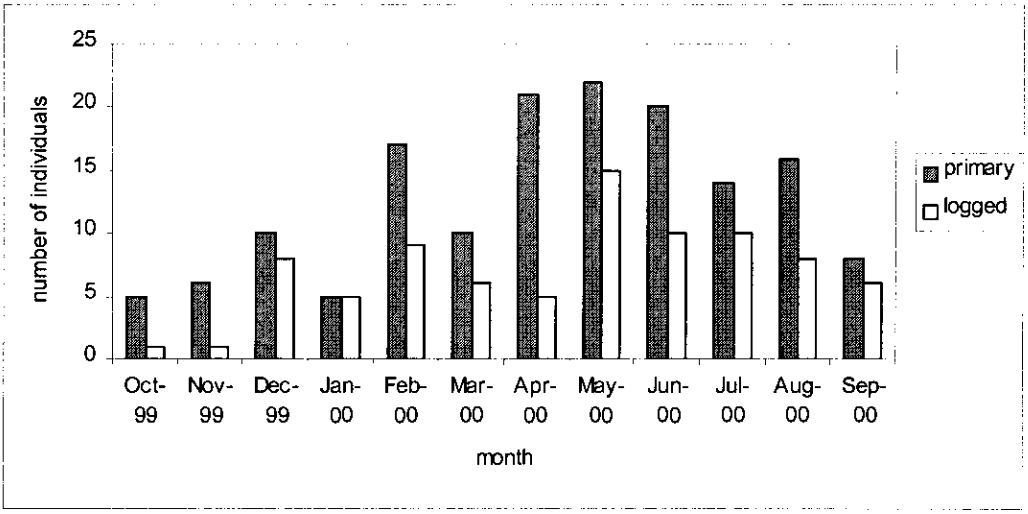

25
20
15
10
5
0
number of individuals
Oct-99
Nov-99
Dec-99
Jan-00
Feb-00
Mar-00
Apr-00
May-00
Jun-00
Jul-00
Aug-00
Sep-00
month
▨ primary
☐ logged

Figure 5.2: Relationship between monthly abundance of *N. lowii* in primary and logged forest.

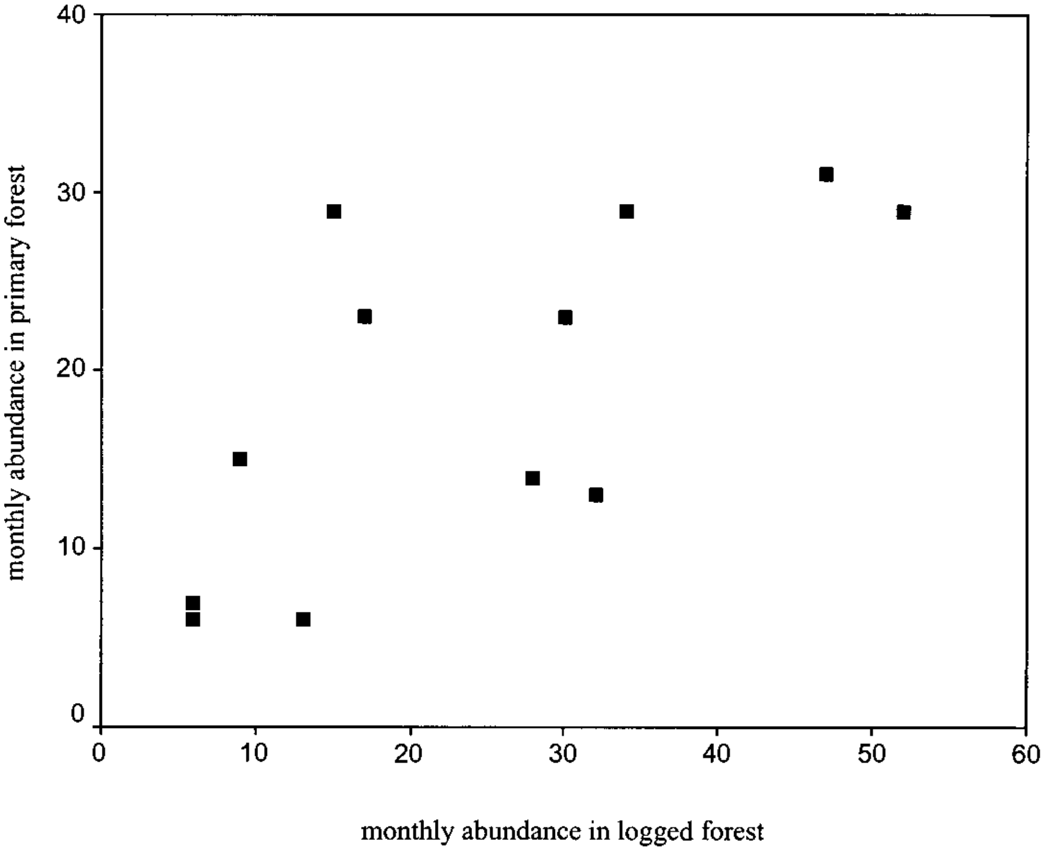


Figure 5.3: Relationship between monthly abundance of *B. dunya* in primary and logged forest.

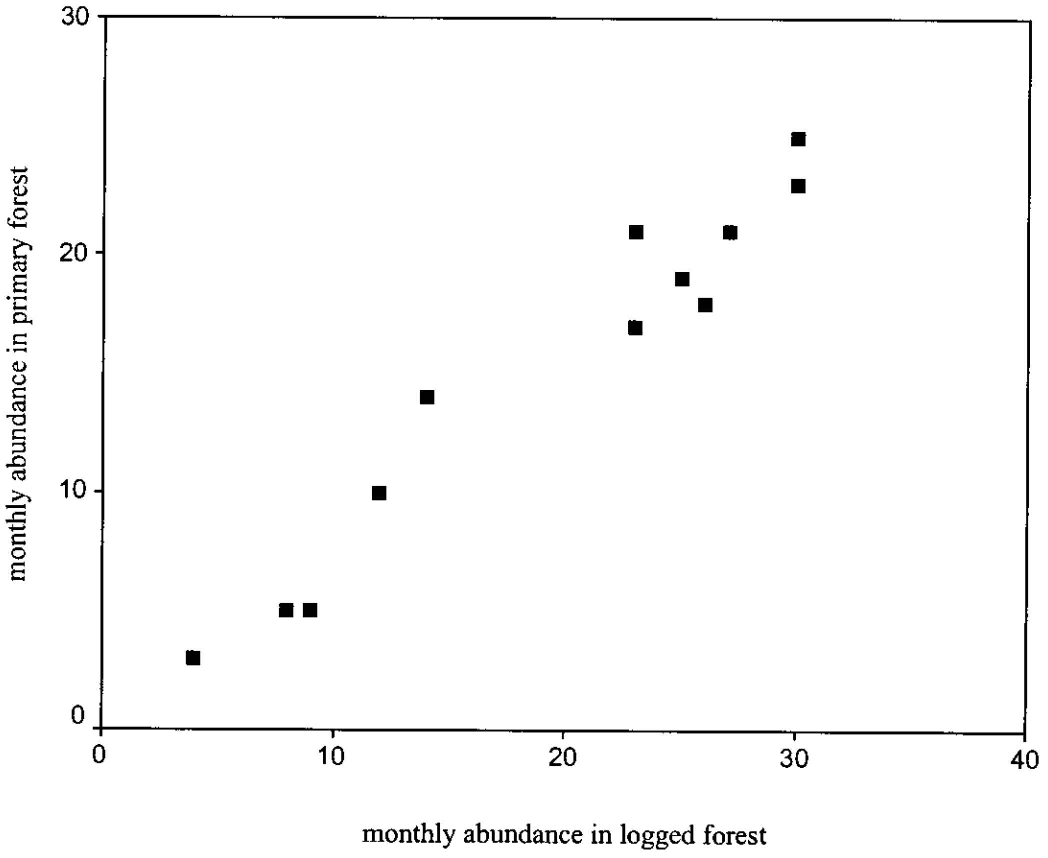
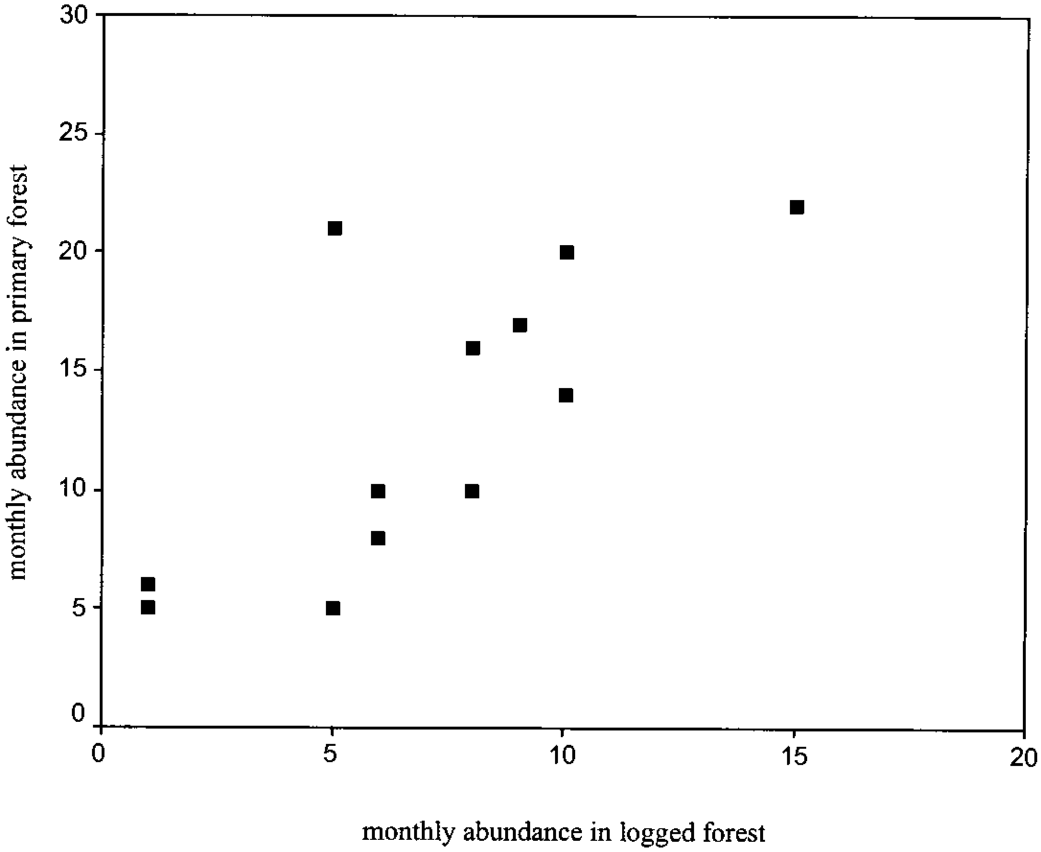


Figure 5.4: Relationship between monthly abundance of *P. franck* in primary and logged forest.



5.3.2 Effects of environmental variables on species abundance in primary and logged forest

Monthly rainfall and monthly proportion of trapping stations with fruit were negatively correlated (Pearson's correlation: $r = -0.42$, $P = 0.04$). However there were no correlations among any other environmental variables ($P > 0.28$ in all cases). Therefore, any significant environmental effect on butterfly abundance was unlikely to be confounded by any inter-relationships among variables, except in the case of a relationship between monthly rainfall and proportion of trapping stations with fruit.

Since monthly variation in the abundance of each species was correlated in primary and logged forest (see above), data for the two habitats were combined for analysis of relationships with environmental variables. The stepwise multiple regression showed that rainfall four months and one month prior to sampling were positively and independently related to the abundance of *P. franck* each month (combining data in primary and logged forest; $R^2 = 0.68$, $F_{2,9} = 9.65$, $P < 0.01$). The relationship is described by the equation below:

> *P. franck* abundance = 0.075 (rainfall four months previously) (SE = 0.02) + 0.059 (rainfall in previous month) (SE = 0.02) – 16.764 (SE = 8.55).

Rainfall four months and one month previously explained 35% and 33% respectively of the monthly variation in abundance of *P. franck* (Figure 5.5 and 5.6). None of these environmental variables explained any of the monthly variation in either of the other two species ($P>0.1$ in all cases).

Figure 5.5: Relationship between number of *P. franck* trapped each month and total rainfall four months previously.

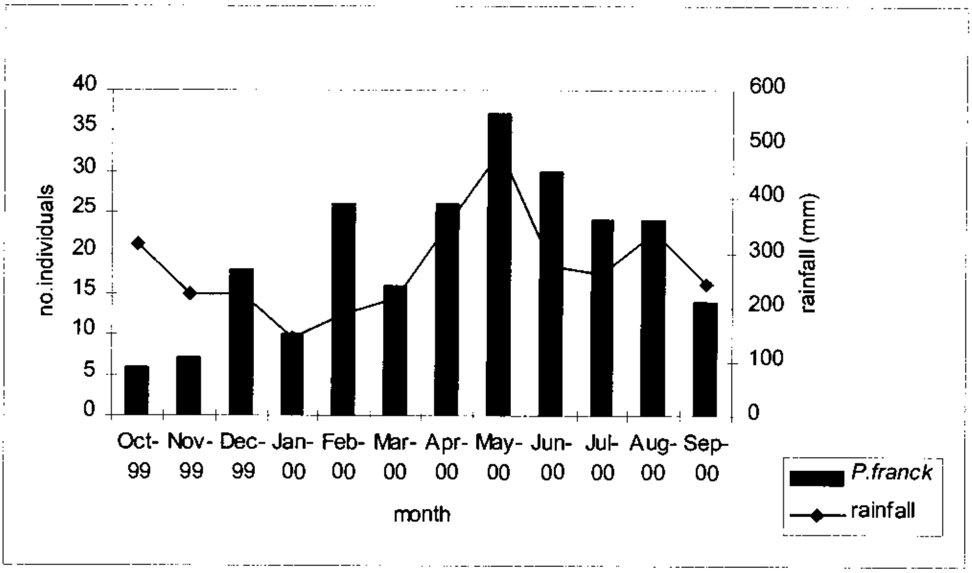
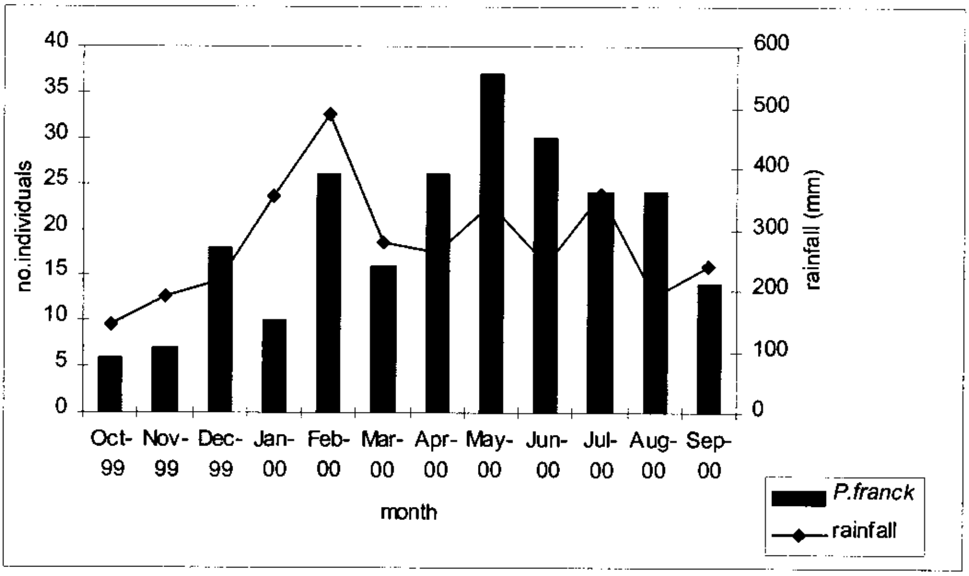


Figure 5.6: Relationship between number of *P. franck* trapped each month and rainfall one month previously.



5.4 Discussion

5.4.1 Temporal changes in species abundance in primary and logged forest

This study showed that butterfly species abundance fluctuated in synchrony in primary and logged forest habitats, suggesting that butterfly population dynamics were changing similarly in the undisturbed and disturbed habitats. *P. franck*, *B. dunya* and *N. lowii* are relatively large in size, and so individual adults may be able to disperse over a wide area. The close proximity between primary and logged sites in this study (approximately 1 km to 6 km; Figure 2.2) may thus have allowed adults to move between the two habitats, therefore reducing any differences between habitats. In support of this notion, one individual *B. dunya* trapped by primary forest was subsequently recaptured in logged forest. Similarly, Shahabudin *et al.* (2000) recorded a frugivorous nymphalid butterfly (*Hamadryas februa*) able to disperse 2.7 km over water, which supports the idea that fruit-feeding butterfly species have relatively high dispersal ability. However, this needs further investigation for other species.

In addition to butterflies moving between habitats, butterfly species abundance in primary and logged forest may have been controlled by the same environmental conditions, with species responding similarly in the two habitats. Hanski and Woiwood (1993) found that synchronous variation in populations of temperate moths and aphids was due to their sensitivity to weather conditions. Similarly Sutcliffe *et al.* (1996) found that populations of butterflies in the UK fluctuated synchronously over wide areas. Even though these studies were carried out in temperate regions, they indicate that sensitivity to changes in environmental conditions may lead to coupled changes in butterfly populations in different habitats. The results of my study indicate that a similar pattern may occur in tropical forests.

5.4.2 Effects of environmental changes on butterfly species abundance

Rainfall four months and one month prior to sampling had independent positive effects on the abundance of *P. franck* and together these two variables accounted for 68 % of the variation in *P. franck* abundance. This may indicate that rainfall influenced abundance both during the larval and pupal stages and the adult stage. On Barro Colorado Island, Panama, a major leaf flush occurred at the beginning of the rainy season, with very little production during the latter part of the rainy season and during the dry season (Wolda, 1978). Plants have evolved may defence mechanisms against herbivory and mature leaves are often higher in toxins with low nutrient contents. Young leaves, by contrast, are often low in toxins and have higher nutrient contents than mature leaves (Feeny, 1970). Fodgen (1972) found that the seasonal cycle of caterpillars and orthopteroid insects was well correlated with that of leaf production. Therefore, in this study, increased growth of young leaves in months with high rainfall may explain the observed effects of rainfall on *P. franck* abundance. Braby (1995) similarly found that increased abundance of *Mycalesis spp.* was related to rainfall and grass moisture content, and therefore larval food availability and quality.

Adult longevity of *P. franck* is unknown (Corbet & Pendlebury, 1992), but in this study, individual butterflies were recaptured at intervals greater than one month. It is therefore possible that rainfall in the month prior to sampling affected adult longevity, possibly through effects of increased humidity (Braby, 1995).

This study revealed that variation in rainfall was an important factor affecting the abundance of *P. franck*, but not the other two species studied. Therefore, it is probable that different butterfly species respond in different ways to variation in climate. For fruit-feeding butterflies, larval host plant quality may be as important in determining overall abundance as the availability of adult food resources. Further data are now required to examine the impacts of rainfall on host-plant quality and larval survival and development more directly.

CHAPTER 6

General Discussion

6.1 Sampling techniques

In this study, fruit-baited traps were used to sample butterflies. These have also been used in many other butterfly studies in the tropics (e.g. De Vries *et al.* 1997; Shahabudin & Terborgh, 1999; Beck & Schulze, 2000; Hill *et al.* in press). Traps are a good method for several reasons. Firstly, some butterfly species in subfamilies Morphinae (Schulze & Fiedler, 1998) and Satyrinae (Corbet & Pendlebury, 1992), are crepuscular and are unlikely to be recorded by walk-and-count techniques, which generally sample only during sunny weather in the middle of the day (Sparrow *et al.* 1994). Secondly, traps operate continuously and so usually sample more butterflies in total. Thirdly, traps allow identification of species that are impossible to identify in flight (Walpole & Sheldon, 1998).

There are, however, some drawbacks to using traps. Firstly, during this study, traps gradually deteriorated due to exposure to weather and often needed to be mended. Secondly, traps attracted other animals including frugivorous mammals such as squirrels and monkeys. Baits were sometimes eaten or removed by these animals and needed to be replaced from time to time. In addition, Asian elephants *Elephas maximus*, destroyed a total of 22 traps over three different occasions during the study. Thirdly, fruit-baited traps rely on attracting individuals into traps for sampling. There is little information on how butterflies respond to traps or whether traps sample all species equally efficiently and this needs more study. However most studies indicate that traps operate similarly in different habitats (Hughes *et al.* 1998) and so comparisons of butterfly communities in different habitats are likely to be reliable. In addition, traps only sample the guild of fruit-feeding butterfly species. Although this group comprises

75% of Nymphalidae, it is not representative of all butterfly families, and a combination of different sampling techniques would be required to study a wide range of species.

6.2 Temporal variation in diversity

In Chapter 3, patterns of species accumulation were investigated in primary and logged forest. Over a study period of 5760 trap days, I recorded a total of 3996 individuals from 63 species. In primary forest, 2065 individuals of 54 species were recorded, while in logged forest, 1931 individuals from 56 species were recorded. Rates of species accumulation were faster in logged forest compared with primary forest but the difference in rates between two habitats was not that great. As discussed in Chapter 3, several factors may have caused the difference in accumulation rates. A total of two more species was recorded in logged forest compared with primary forest and therefore accumulation rates would be expected to be slightly higher in logged forest. Effects of sampling even over long periods may by chance result in more species being recorded in one habitat than another, especially in an area of high butterfly diversity such as the study area; the observed small difference in species richness could therefore simply reflect sampling error. Seasonality in butterfly species may also cause differences between habitats if species appear as adults at different times in logged and primary forest. However, the long period over which this study was carried out means that this was unlikely to have been a problem. Overall, there was little difference in species richness between habitats in this study, which agrees with other studies in the area which sampled butterflies using walk and point-count transects (Tangah, 2000; Dawood, 2000; Willot *et al.* 2000).

During this study, a total of 15 new species was added to the current list of species recorded at DVFC but no species new to Borneo were recorded (based on Lim, 1996). In comparison with other taxa, butterflies are very well studied in Borneo and nearly all species have been described (Otsuka, 1988; Corbet & Pendlebury, 1992).

Temporal changes in butterfly diversity are widely observed in the seasonal tropics, associated with marked variation in rainfall (e.g Raguso & Llorento-Bousqutes, 1990; Spitzer *et al.*, 1993; Braby, 1995; De Vries *et al.*, 1997). Results from this study revealed that even in the aseasonal tropics, where rainfall is more evenly distributed throughout the year, temporal changes in butterfly diversity were observed in relation to rainfall. Long-term studies such as this are important for studying temporal patterns of diversity in the aseasonal tropics, particularly when the studies involve comparison of patterns among habitats.

Results from Chapter 3 showed that patterns of temporal changes in α diversity of butterflies were different in primary and logged forest. According to three different indices of diversity, primary forest was more diverse for five consecutive months, then logged forest was more diverse for most of the remaining seven months. As a result, there was no systematic difference in diversity between habitats over the course of an entire year. Chapter 4 showed a similar pattern with respect to β diversity. These results have clear implications for the reliability of short-term studies that do not sample over the course of an entire year.

In Chapter 5, temporal patterns of species abundance were investigated in more detail in three species from three different subfamilies (Nymphalinae: *Bassaroma dunya*; Satyrinae: *Neorina lowii*; Charaxinae: *Prothoe franck*). Temporal changes in abundance of these species were positively correlated between primary and logged forest showing that in contrast to species diversity, abundances of each of these three species fluctuated in synchrony between the two habitats.

6.3 Effects of environmental factors on butterfly diversity and abundance

Some studies have suggested that indirect effects of weather on insect growth and survival through effects on host plant quality may be as important as direct effects (Wolda, 1978; Wolda, 1988). Weather may influence the level of stress in the host plant, which in turn may alter its nutritional quality, chemical defenses or digestibility (Wolda, 1978; Martinat, 1987). In this study, both species evenness and the abundance of *P. franck* were related to rainfall four months and one month prior to sampling whilst the availability of fruit within the forest was negatively related to rainfall. Thus changes in species evenness plus abundance of *P. franck* may have been due to indirect effects on availability and quality of adult and larval food resources, as suggested by other studies (Owen, 1971; Braby, 1995; Spitzer *et al.* 1993; De Vries *et al.* 1997; Hill *et al.* in prep).

6.4 Future work

To my knowledge, this is the first study to investigate temporal changes in butterfly diversity over the course of an entire year, and more studies are needed to see if these results are representative of other taxa in other regions. In term of butterfly conservation, this study indicates that moderately disturbed forest areas may provide important resources for many species and may allow even vulnerable species such as those with restricted geographical ranges to persist. Given the increased loss of forest areas in tropical regions (Collins *et al.* 1991), these moderately disturbed areas will become more and more important for the persistence of forest-dependent species. Therefore, decisions on timber harvesting systems should be considered carefully. If forests are repeatedly logged, resulting in more severely disturbed habitats, this may have a more profound effect on species richness (Holloway *et al.* 1992; Spitzer *et al.* 1993; Hill *et al.* 1995; Spitzer *et al.* 1997; Chey *et al.* 1997). [illegible] ~~In the~~ near future, all production forest in Sabah will have been logged and areas will start to be logged for the second time. Studies are needed to investigate the consequences of repeated habitat disturbance on forest-dependent species.

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