Impacts of selective logging on tropical-forest butterflies of Borneo

Thesis submitted by

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For examination for the degree of Doctor of Philosophy

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February 2006

"All things by immortal power,
Near or far,
Hiddenly
To each other linked are,
That they canst not stir a flower
Without the troubling of a star."

From 'The Mistress of Vision' by Francis Thompson (1897).

A poem about spatial non-independence?

Abstract

Commercial, selective logging is a major cause of habitat disturbance in Southeast Asian rainforests, yet despite much research there is little consensus on the impacts of disturbance on biodiversity. I used fruit-baited traps to sample Nymphalid butterflies from primary forest and forest selectively logged 15 years previously in Danum Valley, Sabah (Malaysian Borneo) for a 10-month period between April 2003 and December 2004. I sampled 1280 individuals from 61 species from 30 traps along 2 km linear transects and 2244 individuals from 62 species from 25 traps on $\approx$80 ha square grids in primary and selectively-logged forest. I found that long term (5-month) and large spatial-scale (transects $\geq$ 1.6 km) samples were needed in order to detect a significant decline in diversity following disturbance. I showed that sampling canopy fauna was important for producing species inventories but not for detecting changes in species conservation value between habitats. I found higher α and β diversity in primary forest compared with selectively-logged forest. Differences in α diversity between habitats were dependent on the spatial scale at which data were analysed because α diversity increased with spatial scale at a significantly faster rate in primary forest compared with selectively-logged forest. This reflected higher vegetation heterogeneity in primary forest compared with selectively-logged forest. Measures of α diversity were spatially autocorrelated in primary forest, and β diversity between samples was distance-dependent in primary forest, but not in selectively-logged forest. These spatial patterns of α and β diversity reflected patterns of vegetation structure. Selectively-logged forest contained species with higher light tolerance and some evidence suggested wider geographical ranges and thus, lower conservation value than primary forest. I conclude that as spatial patterns of diversity change following disturbance, conservationists need to be aware that the placement of their traps and the spatial scale of their study may largely predetermine their results.

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Acknowledgments

First and foremost, I would like to thank my supervisor Dr. Jane K. Hill (University of York, U.K.) for her continued guidance and advice while I was studying for my Ph.D. and the Natural Environment Research Council for funding. I would also like to thank my Malaysian collaborators Dr. Chey Vun Khen (Forest Research Centre, Sabah) and Prof. Dr. Maryati Mohamed (University of Malaysia, Sabah) for supporting my research in Sabah.

I would like to express my gratitude to the Economic Planning Unit of the Prime Minister's Department, Putra Jaya (Malaysia) and the Sabah Chief Minister's Department for permission to conduct research in Sabah, Malaysia. I would like to thank Yayasan Sabah (Forestry Division) and the Danum Valley Management Committee for permission to conduct research in the Danum Valley Conservation Area and surrounding Ulu Segama Forest Reserve.

I would like to thank all the staff and scientists at the Danum Valley Field Centre (DVFC). I would especially like to thank Glen Reynolds for logistic support and advice while I was at the DVFC. A special thank you goes to Glen Reynolds for continued permission to use the Royal Societies' vehicles, even though I occasionally might have driven a little quickly. I would like to thank all the Royal Societies' Research Assistants (RAs) at the DVFC who assisted me in the field, especially Nasir Majid and Johnny Larenus for help collecting butterflies. I would also like to thank Jamil Hanapi, Philip Uluk and all the RAs from the Malua forest reserve for help clearing trails. I would like to thank Mike Bernardus for helping me identify many of Borneo's native flora and fauna and his help coaching me on the badminton court. A massive thank you goes to the kitchen staff at the DVFC for keeping me so well fed during my field-work. To all my other friends at the DVFC thank you for your support and friendship during my stay.

I would like to thank my colleagues Suzan Benedick, Nazirah Mustaffa, Edgar Turner and Robi Bagchi for support in Danum. I would also like to thank Nick Dawnay for making a truly fantastic field assistant in Danum. To all my colleagues in York, especially Helen Edwards, Hannah Lewis, Carolyn Jewell, Sally Fraser, Mike Gray and Clare Hughes and my training committee members, Calvin Dytham and Richard Law, thank you for your help and support throughout my Ph.D.

A final thanks goes to my family and especially to Fiona Buckley for supporting me through the duration of my Ph.D.

Declaration

I declare that the work contained within this thesis is the result of my own work and was written entirely by myself.

Chapter 3 contains data that were originally collected by Suzan Benedick and Nasirah Mustaffa (Benedick, 2001; Mustaffa, 2001). These data were re-analysed for this thesis and all results and conclusions were of my own work. Nick Dawnay helped with the collection of trapping efficiency data used in Chapter 3.

Chapter 4 was in part published as:

Dumbrell, A.J., Hill, J. K. 2005. Impacts of selective logging on canopy and ground assemblages of tropical-forest butterflies: Implications for sampling. *Biological conservation* **125**, 123 – 131

The title illustration and plates 1.1 and 1.2 were photographed by and included with permission from Frank Mallard. Plate 5.1 contains two photographs; *Bassarona dunya* photographed by Frank Mallard and *Mycalesis orseis* was photographed by Suzan Bendick and reproduced with permission from Benedick (2005). Plate 2.2 was photographed and included with permission from Jane Hill. Plate 7.1 was photographed and included with permission from Edgar Turner.

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2005

Chapter 1 General Introduction

1.1 BIODIVERSITY

1.1.1 Biodiversity

The word biodiversity is a contraction of the words 'Biological Diversity' or 'Biotic Diversity' and is used as a synonym for the variety of life (Gaston, 1996). The term biodiversity was first used in scientific literature in the early 1980s, initially by Lovejoy (1980a, 1980b) and Norse & McManus (1980) (Harper and Hawksworth, 1994). However, the term was not widely used until Wilson (1988) published 'BioDiversity' (Harper & Hawksworth, 1994). "Biodiversity is the genetic, taxonomic and ecosystem variety in living organisms of a given area, environment, ecosystem or the whole planet" (McAllister, 1991). It can be divided into genetic, organismal and ecological diversity (Harper and Hawksworth, 1994). Genetic diversity is defined as the variety of genes within a species, organismal diversity is the variety of species within a community, and ecological diversity is the variety of biomes within a geographic area (Harper and Hawksworth, 1994).

Much ecological research has focused on describing and quantifying biodiversity (*e.g.* May, 1988, 1990; Reid, 1998; Purvis and Hector, 2000; Orme *et al.*, 2005). However, globally much biodiversity remains poorly studied and further research is needed to examine patterns of biodiversity (Williams *et al.*, 1997a, 1997b, 1997c) especially in remote habitats; for example, tropical rainforests. The majority of biodiversity research focuses on organismal diversity, which is often simply termed 'diversity'.

1.1.2 Quantifying diversity

The total diversity of an area (γ) can be divided into α diversity and β diversity, either as the sum of α and β diversity (MacArthur *et al.*, 1966; Lande, 1996; Veech *et al.*, 2002) or as the product of these two measures (Whittaker, 1960, 1972). α diversity is the number and relative abundance of species within a sample whereas β diversity is the change in species composition between samples (Magurran, 1988; 2004). Numerous methods have been proposed for quantifying α and β diversity (see Magurran, 1988; 2004).

The simplest measure of α diversity is a measure of species richness (Lande, 1996). This is the number of species in a community and is based on presence or absence data and does not take into account the relative abundance of different species (Lande, 1996).

However, more quantitative indices of α diversity are generally used and these combine species richness and relative abundance into a single measure (*e.g.* Simpson, 1949; Peet, 1974; Clifford and Stephenson, 1975; May, 1975; Whittaker, 1977). In general, the most reliable measures of α diversity are nonparametric, statistically robust and applicable to any sample irrespective of underlying species abundance distributions (Lande, 1996).

Measures of β diversity can be divided into qualitative and quantitative metrics (Magurran, 2004). Qualitative measures of β diversity describe changes in species composition in terms of presence and absence of species. These are normally based on a ratio of the percentage similarity of species between samples (Whittaker, 1960; Cody, 1975; Wilson and Schmida, 1984; Veech *et al.*, 2002). Quantitative measures of β diversity incorporate an additional measure of change in relative abundance of species between samples and these are considered statistically more robust than qualitative measures (Wolda, 1981; Magurran, 2004).

1.1.3 Global biodiversity

Much ecological research has focused on describing and quantifying global species diversity (*e.g.* Erwin, 1982; May, 1988; Stork 1988, 1993; Wilson, 2000; Species, 2000). Currently, there are approximately 1.5 – 1.8 million named species (Wilson, 2000) and estimates of total global biodiversity are often much higher ranging from 5 – 50 million species (Bartlett *et al.*, 1999). However, many studies examining global diversity rely on extrapolating estimates from relative well-studied taxa and usually ignore more obscure organisms. Thus, more quantitative studies are needed for a more reliable estimate of global species richness (May, 1988, 1992).

It is generally considered that more than 60% of global biodiversity is represented by insects (Groombridge, 1992; Speight *et al.*, 1999; Ødegaard, 2000). The most species-rich order of insects is the Coleoptera (beetles) followed by the Hymenoptera (social insects and wasps), Diptera (true flies) and Lepidoptera (moths and butterflies) (Groombridge, 1992; Speight *et al.*, 1999). These four orders of insect account for > 0.6 million named species (May, 1988). In addition to a disproportionately higher contribution to global biodiversity than any other taxon, insects play important roles in ecosystem processes and functioning (Speight *et al.*, 1999; Samways, 2005). It has been suggested that insects are keystone organisms in ecosystem processes (Samways, 2005). This means that the contribution of an insect species to ecosystem functioning is disproportionately large

relative to its abundance (Samways, 2005). Although the concept of insects as keystone species has met with some debate, insects are generally considered a highly important taxon within an ecosystem (Speight *et al.*, 1999; Samways, 2005). For example, insects occupy important roles across trophic levels as pollinators, herbivores, prey, predators, parasitoids and as parasite vectors (Speight *et al.*, 1999; Samways, 2005). Insects also play important roles as ecosystem engineers, modifying soils and decomposing organic matter (Samways, 2005).

Insects like much of global biodiversity (Orme *et al.*, 2005) are under threat from human-induced environmental changes (Samways, 2005). Thus, due to their high diversity and importance in ecosystem functioning, understanding the impact of environmental change on insect species is of great current concern (Samways, 2005). However, although research is accumulating, the response of insect species to environmental changes is poorly understood (Samways, 2005), especially in tropical regions (Lawton *et al.*, 1998). Therefore, examining the impacts of environmental change on insect species within the tropics merits further study.

1.1.4 Biodiversity hotspots

Describing global patterns of biodiversity is a central theme in ecology (Williams *et al.*, 1997c; Reid, 1998; Olson *et al.*, 2001). Previous research has shown biodiversity to be unevenly distributed across the globe and in general, biodiversity is highest in tropical regions (Myers *et al.*, 2000; Olson *et al.*, 2001; Orme *et al.*, 2005). This has led conservationists interested in preserving biodiversity to highlight the need to prioritise conservation strategies around global "biodiversity hotspots" (Prendergast *et al.*, 1993; Reid, 1998; Myers *et al.*, 2000; Orme *et al.*, 2005). The majority of biodiversity hotspots are located in tropical regions and include areas of high species richness, high levels of endemism and highly-threatened habitats (Orme *et al.*, 2005). In general, biodiversity hotspots are idiosyncratic ($\geq 80\%$ of all biodiversity hotspots) with very few ($\approx 2.5\%$) incorporating high species richness, high endemism and highly-threatened habitats (Orme *et al.*, 2005). The Sundaland region, in Southeast Asia, is one recognised biodiversity hotspot (Myers *et al.*, 2000). The Sundaland region incorporates, the Malay peninsular and island chains along the Sunda Shelf (Sumatra, Java, Borneo and Palawan) and includes the political regions of Malaysia, Singapore, Brunei and Indonesia (Myers *et al.*, 2000).

1.1.5 Sundaland biogeography

Following the separation of the Gondwanaland super-continent, the Asian continental plate began to move towards it current location and by the Latest Cretaceous ($\approx$69.4 million years ago) most of the Sundaland region was entering its current position (McLoughlin, 2001). During the Cenozoic period, glacial episodes caused episodic changes in sea level and much of the Sundaland region was either isolated during inter-glacial periods or connected during glacial periods (Wilson and Moss, 1999). The episodic covering and uncovering of the Sundaland region continued until approximately 10,000 years ago when the sea reached modern levels and the Sunda Islands have remained isolated since (Meijaard and Van der Zon, 2003). During glacial periods, low sea levels resulted in land bridges connecting the islands along the Sunda shelf. This allowed southern range expansion of North-Asian species into Sundaland and biotic migrations between previously isolated islands (Sodhi *et al.*, 2004). In contrast, during inter-glacial periods high sea levels produced rainforest refugia on isolated mountain tops. This allowed the persistence of rainforest species during the inter-glacial periods and also provided conditions ideal for speciation (Cox and Moore, 2000). Thus, the Sunda Islands contain a mix of endemic species following speciation caused by vicariant events during inter-glacial periods, species with ranges restricted to Sundaland from biotic migrations during glacial periods, and widespread species which arrived during glacial periods from mainland Asia (Sodhi *et al.*, 2004). For example, there are approximately 328 species of mammal in Sundaland of which 115 species are endemic (35%) whereas on Borneo, the largest Sunda island, 44 of the 150 species of mammal (29%) are endemic (Myers *et al.*, 2000). This illustrates the high levels of endemism across Sundaland and the mixture of endemics and restricted-range species on the Sunda Islands.

Due to its geological and biogeographical history, location and stable tropical climate Sundaland includes some of the most species-rich habitats on Earth with relatively high levels of endemism (Sodhi *et al.*, 2004; Orme *et al.*, 2005). However, Sundaland is also one of the most threatened biodiversity hotspots (Sodhi *et al.*, 2004; Orme *et al.*, 2005). The biggest threat to Sundaland biodiversity comes from the logging industry (Curran *et al.*, 2004; Sodhi *et al.*, 2004; Wright, 2005) and associated knock-on effects such as increased risk from forest fires in recently-logged forests (Holdsworth and Uhl, 1997; Siegert *et al.*, 2001). Thus, it is of great current interest to assess the impacts of logging on

biodiversity and to provide reliable information for conservation efforts attempting to preserve Sundaland biodiversity (Curran *et al.*, 2004).

1.2 Global Biodiversity Patterns

1.2.1 Latitudinal gradients in species richness

One of the few general rules in ecology is that species richness increases with a decrease in latitude (Hillebrand, 2004). There are however, a few noticeable exceptions to this rule. For example, grasses (Whittaker *et al.*, 2001), Ichneumonid parasitoids (Owen and Owen, 1974; Rathcke and Price, 1976; Janzen, 1981; Sime and Brower, 1998), sawflies (Kouki *et al.*, 1994) and some species of Marine mollusc (Valdovinos *et al.*, 2003) show a decrease in species richness towards the equator.

The latitudinal gradient in species richness is arguably the oldest and most famous ecological pattern described (Hawkins, 2001). Although most authors cite seminal work by Wallace, (1853, 1878), Darwin (1859) and Bates (1862) as initially describing the tropics as being more diverse than temperate regions, naturalists attempted to describe and explain the latitudinal gradient in species richness far earlier (Hawkins, 2001). Citing Otté and Bohn (1850), Hawkins (2001) suggested that Alexander von Humboldt first described the latitudinal gradient in species richness in 1807. In addition, von Humboldt attempted to explain the gradient, proposing that warm, stable, tropical climates can support a greater variety of life forms (Hawkins, 2001).

Modern research has proposed more than 30 hypotheses explaining the latitudinal gradient in species richness (Hawkins, 2001). Many review articles have discussed the relative scientific merit of each of these hypotheses (Fischer, 1960; Pianka, 1966; Rohde, 1992; Waide *et al.*, 1999; Gaston, 2000; Willig *et al.*, 2003). However, little agreement has been reached over the most likely causal mechanisms driving the latitudinal gradient in species richness. The reasons why many hypotheses are not widely accepted include a lack of empirical evidence and that some arguments are circular (Rohde, 1992). Although many hypotheses have been dismissed (see Rohde, 1992), some hypotheses are more widely regarded than others. For example: the species richness-energy hypothesis (Currie, 1991; Rohde, 1992; Roy, *et al.*, 1998; Gaston, 2000), climate-speciation hypothesis (Fischer, 1960; Rohde, 1978a, 1978b, 1992; Bromham and Cardillio, 2003), the geographic-area model (Terborgh, 1973; Rosenzwieg, 1992, 1995; Chown and Gaston, 2000; Willig *et al.*,

2003), and the intermediate disturbance hypothesis (Connell, 1978; Sheil and Burslem, 2003).

1.2.2 Species richness-energy hypothesis

One important factor regulating the number of species an area can support is the amount of "ambient available ('usable') environmental energy" (Gaston, 2000). The species richness-energy hypothesis suggests that greater species richness is expected at lower latitudes due to increased available energy towards equatorial regions (Currie, 1991). This is a broad hypothesis under which many more specific explanations for high tropical diversity exist; for example, climatic stability, environmental stability, environmental predictably, aseasonality and environmental harshness (Willig *et al.*, 2003).

Due to the shape of the Earth, equatorial areas receive higher solar radiation compared with areas at high latitudes. This high level of available energy enables tropical regions to support greater biomass than temperate regions (Gaston, 2000). Greater biomass in turn allows more individual organisms to coexist and can support more species at viable population levels (Gaston, 2000). In addition to receiving relatively high solar radiation, equatorial regions receive solar radiation at an approximately constant rate throughout the year. This produces stable, predictable, aseasonal environments which favour organism's thermal optima (Willig *et al.*, 2003). Thus, tropical regions are thermally and climatically more favourable environments than are temperate regions making it physiologically easier for species to persist (Willig *et al.*, 2003).

The species richness-energy hypothesis is supported by empirical evidence from both terrestrial (Currie, 1991) and marine species (Roy *et al.*, 1998) that show increased species richness with increased ambient environmental energy. For example, Currie (1991) showed that species richness of a range of taxa (trees, birds, mammals, reptiles and amphibians) was correlated with potential evapotranspiration (PET). PET is a direct measure of ambient environmental energy and is negatively correlated with latitude (Currie, 1991). Thus, an increase in ambient environmental energy (PET) with a decrease in latitude may be responsible for increased species richness (Currie, 1991).

1.2.3 Climate-speciation hypothesis

The species richness-energy hypothesis provides a mechanism for why so many species coexist within tropical regions. However, it does little to explain how so many species

became to be present within the tropics. The climate-speciation hypothesis suggests a mechanism for why tropical regions have greater species richness by proposing higher rates of speciation in tropical regions compared to temperate areas (Rohde, 1992; Bromham and Cardillo, 2003). The climate-speciation hypothesis is inseparably linked to the species richness-energy hypothesis as the driving mechanism for both hypotheses is higher solar radiation in tropical regions (Willig *et al.*, 2003). The climate-speciation hypothesis suggests that climatic conditions in tropical areas favour higher rates of speciation compared with higher latitudes. Rohde (1992) suggested two causal pathways that explain how climatic conditions in tropical regions cause high levels of speciation.

The first causal pathway suggests that increased solar radiation at lower latitudes causes higher mutation rates in an organism's DNA compared with organisms at high latitudes (Bromham and Cardillo, 2003). Thus, tropical species may rapidly accumulate genetic variation due to the mutagenic effect of solar radiation on DNA. This may cause rapid reproductive isolation when populations become geographically isolated and thus, increase the likelihood of allopatric speciation (Bromham and Cardillo, 2003). The second causal pathway suggests that favourable climate conditions at lower latitudes promote shorter generation times of tropical organisms compared with temperate organisms (Bromham and Cardillo, 2003). This is because higher mean temperatures throughout the year increase individual growth rates and shorten generation times (Fischer, 1960; Bromham and Cardillo, 2003). This mechanism promotes high levels of speciation as shorter generation time increases the speed at which selection operates (Bromham and Cardillo, 2003).

There are few data available to support the climate-speciation hypothesis (Bromham and Cardillo, 2003). This may be due to limitations in molecular techniques associated with assessing accumulation of genetic variation within species (Bromham and Cardillo, 2003). However, research is accumulating in support of the climate-speciation hypothesis (Davies *et al.*, 2004; Cardillio *et al.*, 2005). For example, Davies *et al.* (2004) showed faster rates of genetic mutation in angiosperms with increased environmental energy. Davies *et al.* (2004) examined molecular evolution rates (accumulated genetic variation) across a range of nuclear ribosomal (rDNA) and protein coding (DNA) genes and showed increased molecular evolution with environmental energy. This demonstrated the first direct link between an organism's molecular evolution rates and environmental energy using a robust molecular analysis (Davies *et al.*, 2004).

1.2.4 Geographic-area model

Complementing the climate-speciation hypothesis, the geographic-area model suggests an additional causal pathway that may promote high speciation and thus, high species richness in tropical regions (Rosenzwieg, 1995; Chown and Gaston, 2000). The geographic-area model was originally proposed by Terborgh (1973) and more recently has been developed by Rosenzweig (1995) (Willig *et al.*, 2003). The fundamental concept of this hypothesis is that due to the shape of the Earth the tropics cover a larger surface area than any other climatically-similar biome. This allows more species to coexist (due to species-area relationships) and an increased probability of speciation events occurring (Chown and Gaston, 2000).

The geographic-area model makes three main assumptions about why a geographically large, climatically-similar area might result in high speciation rates (Chown and Gaston, 2000). Firstly, it assumes the geographic ranges of tropical species are larger than those of temperate species as they can persist across larger climatically-similar areas. Secondly, it assumes there is an increased likelihood of allopatric speciation of species with large geographic ranges because of an increased chance of vicariance. Finally, it assumes that species with relatively large ranges sizes are buffered against wide spread catastrophes and thus, unlikely to become extinct (Chown and Gaston, 2000). The majority of these assumptions are difficult to test and rely on tropical species having large ranges (Chown and Gaston, 2000). This is in contrast to existing research that suggests species range size in positively correlated with latitude (*i.e.* tropical species have small geographic ranges; Rapoport, 1975, 1982; Stevens, 1989). However, this model does highlight the high probability of allopathic speciation in some tropical species. This will occur if the limiting resource for a species' distribution is climate or habitat. Thus, in tropical species with widespread distributions high allopathic speciation may occur due to increased vicariance. Therefore, the geographic-area model provides a possible mechanism for increased species richness in some tropical organisms.

1.2.5 Intermediate disturbance hypothesis

The intermediate disturbance hypothesis (IDH) suggests that diversity of tropical tree species is highest at intermediate levels of disturbance which allow both pioneer and climax species to coexist (Connell, 1978; Sheil and Burslem, 2003). The mechanism behind the IDH suggests that patterns of natural disturbance produce a mosaic of gaps and old growth

areas within tropical forests. Newly-formed gaps (*e.g.* tree falls) are rapidly colonised by fast-growing pioneer species that efficiently utilise available resources. These provide shade which allows the establishment of shade-tolerant species which eventually succeed their predecessors (Sheil and Burslem, 2003). Therefore, this process of succession following natural disturbance events allows the coexistence of both pioneer and climax species and thus promotes high tropical diversity. In addition, the repeated occurrence of natural disturbance events causes tropical forests to be in a perpetual state of succession (*i.e.* governed by non-equilibrium dynamics). This avoids competitive exclusion by reducing the chance of a superior competitor dominating tropical-forest communities (Connell, 1978). The IDH addresses how natural disturbance may promote high tropical diversity. What is less clear however, is how human induced disturbance affects tropical diversity.

1.3 Tropical Rainforests

1.3.1 History of Tropical forests

The tropics are located between the tropic of Cancer (23.5° N) and the tropic of Capricorn (23.5 °S). Tropical rainforests can potentially cover the majority of available land around the equator within this region (Whitmore, 1998). However, at higher latitudes close to the tropics of Cancer and Capricorn, dry forests, shrubby grassland and savannas also exist (Richards, 1996). Originally, large portions of terrestrial habitats in the tropics were covered by tropical rainforests. However, due to increased logging pressures and shifting agricultural practice forest cover is currently much less (Whitmore, 1998). Tropical forests are some of the oldest terrestrial habitats on Earth (Richards, 1996). Fossil evidence suggests tropical forests similar to today's existed during the Tertiary period (approximately 65 million years ago) and most likely came into existence even earlier during the Cretaceous (Richards, 1996). For example, fossils of *Macaranga* spp. (Euphobiaceae) and *Parashorea* spp. (Dipterocarpaceae), two currently abundant genera of trees in Bornean rainforests (Newbery *et al.*, 1992; Burghouts *et al.*, 1994), were shown to have originated from the Middle Eocene (Richards, 1996).

Fossil evidence shows angiosperms evolved in the tropics at the beginning of the Cretaceous approximately 136 million years ago (Richards, 1996). The first angiosperms were relatively small-shrubby 'treelets' that were most likely adapted to living in disturbed

habitats. During the middle of the Cretaceous period early angiosperms were becoming able to compete with the dominate tree form of the Mesozoic, the conifers (Richards, 1996). By the Late Cretaceous (≈65 million years ago), broad-leaved dicotyledonous trees had replaced the conifers as the dominant tall-tree species in tropical forests. This resulted in tropical forests similar to modern tropical forests where conifers are almost entirely absent (Richards, 1996).

1.3.2 Tropical rainforest climate

Tropical rainforests have wet, humid, hot climates with little or no dry season (Walsh, 1996a). Tropical rainforest climates are defined as having high annual rainfall (≥1700 mm $year^{-1}$) and lacking a pronounced dry season or having a short dry season (≤4 months) with less than 100 mm of rainfall (Walsh, 1996a). Mean monthly temperatures (≥18 °C) in tropical rainforests are relatively constant throughout the year (Walsh, 1996a). However, climate does vary across tropical rainforest areas and differences in rainfall between tropical regions result in climatically different tropical rainforest types. For example, tropical rainforest climates can be broadly separated into Superwet (rainfall ≥3000 mm $year^{-1}$), Wet (≥ 2000 mm $year^{-1}$) and Wet-Seasonal (≥ 1700 mm $year^{-1}$) forests. The majority of tropical forests have Wet and Wet-Seasonal climates. Wet tropical rainforests tend to be located close to the equator and Wet-Seasonal forests are found at higher latitudes (Walsh, 1996a). There is little monthly or annual variation in temperature in tropical rainforest regions and typical mean annual temperatures within tropical forests range from 24 – 28 °C (Walsh, 1996a). However, there are differences in temperature between tropical regions and temperature generally decreases with distance from the equator (Walsh, 1996a). In addition to relatively constant temperatures, tropical rainforests have a constant, relatively high level of humidity. Typically, absolute humidity (≥ 20 mmHg) is around 80% saturation during the day and between 95 – 100% saturation during the night (Walsh, 1996a). The relatively stable, aseasonal climate throughout the year has probably been a key factor in the evolution and maintenance of tropical forest ecosystems (Richards, 1996).

1.3.3 Tropical rainforest ecology

Tropical rainforests cover approximately 8,300,000 km^2 of the Earth's surface and can be broadly split into three areas, Neotropical (Central and South America), Malesian (Central

and Southeast Asia) and African rainforests (Whitmore, 1998). Neotropical rainforests cover the largest area (4×10^6 km^2) followed by Malesian (2.5×10^6 km^2) and African (1.8×10^6 km^2) rainforests (Whitmore, 1998). Within the Wet Tropics, the majority of rainforest is tropical lowland ($\leq$1200 m a.s.l.) evergreen rainforest (Whitmore, 1998).

Plate 1.1 Example of tropical lowland evergreen rainforest in Danum Valley in Sabah, Malaysian Borneo. Lowland evergreen rainforest is structurally complex with a relatively high (30 – 40 m) canopy.

Lowland evergreen rainforest is characterised by a high diversity of tall (> 45 m) broad-leaved trees (Plate 1.1), often with distinct buttresses to aid support. Cauliflory and ramiflory are common in rainforest trees and many trees are also covered by epiphytes and woody climbers (*e.g.* Lianas) which are often abundant throughout the forest (Whitmore, 1998). Tropical rainforests exist in a continuous cycle of growth; large mature trees collapse forming open gaps (gap-phase) which are quickly colonised by light-loving pioneer species that provide shade and allow climax species to establish (building-phase). Eventually climax species succeed pioneer species producing a closed canopy mature forest (mature-phase). This process results in a mosaic of gap-phase, building-phase and mature-phase forest (Whitmore, 1998). Thus, tree species in tropical rainforests can be split broadly into two ecological groups, climax and pioneer species. Seedlings of climax species require shade under a closed canopy to geminate whereas pioneer species require high levels of

light to establish as seedlings (Whitmore, 1998). The continual growth cycles of tropical rainforests produce distinct vertical layers of vegetation cover. All overstorey vegetation cover in tropical rainforests is often referred to as the canopy (Whitmore, 1998). However, the rainforest canopy can be subdivided into different vertical strata depending on the age and ecology (climax or pioneer) of tree species. For example, in Malesian rainforests emergent climax species *e.g. Koompassia excelsa* are relatively tall (60 – 90 m) with crowns producing a high canopy (Plate 1.2). More dominant climax species *e.g. Shorea* spp. are shorter (30 – 40 m) and produce a medium-height canopy (Plate 1.1). At lower vertical levels, fast growing pioneer species *e.g. Acacia mangium* produce an even lower (20 – 25 m) canopy (Whitmore, 1998). Thus tropical rainforests are highly heterogeneous environments comprised of a mosaic of gaps and mature growth forest with distinct vertical strata. The heterogeneous nature of tropical rainforests probably promotes high tropical diversity by partitioning environmental resources and producing many unique environmental niches (Tews *et al.*, 2004).

Plate 1.2 Example of a relatively tall climax-tree species, *Koompassia excelsa,* at Danum Valley in Sabah, Malaysian Borneo.

A defining ecological feature of tropical rainforests is high species richness (Richards, 1996; Whitmore, 1998). Approximately 1.1×10^6 km^2 of Malesian rainforest ($\approx$ 45 %) is located within the political regions of Malaysia and Indonesia (Sodhi *et al.*, 2004). Records of species richness in Malaysian rainforests suggest over 15,500 species of vascular plant (23% endemic), 198 species of amphibian (35% endemic), 379 species of reptile (19% endemic), 254 species of bird (17% endemic) and 300 species of mammal (0% endemic) exist in the region (Sodhi *et al.*, 2004). Species richness is even higher in Indonesian rainforests which support 29,375 species of vascular plant (60% endemic), 278

species of amphibian (41% endemic), 745 species of reptile (41% endemic), 929 species of bird (44% endemic) and 515 species of mammal (0% endemic) (Sodhi *et al.*, 2004). In addition to the ecological significance of rainforests as areas which support high species richness, rainforests also play important roles in global atmospheric and carbon cycles. Rainforests act as a source of atmospheric oxygen and sinks of atmospheric carbon dioxide (Malhi, 2002; Clark, 2004a). Tropical forests act as oxygen sources releasing oxygen into the atmosphere via photosynthesis and approximately 50% of global photosynthesis occurs in forest ecosystems (Malhi, 2002). Tropical forests act as global carbon sinks and account for 32 – 36% of global carbon net primary production (NPP), fixing atmospheric carbon (CO_2) as organic matter (Clarke, 2004a, 2004b). However, tropical forests are increasingly under threat from human-induced disturbance (Curran *et al.*, 2004; Sodhi *et al.*, 2004; Asner *et al.*, 2004a, 2005; Wright, 2005). Thus, it is of great current importance to understand the ecological impacts of human-induced disturbance on tropical forests.

1.4 Tropical Forest Disturbance

1.4.1 Current threats to tropical rainforests

Human populations in tropical countries are continuing to grow and will increase by approximately two billion people in the next 25 years (Wright, 2005). Thus, growing human populations are placing increasing pressure on remaining tropical forests and their associated resources (Wright, 2005). The main anthropogenic threats to tropical rainforest ecosystems are conversion of forest to agricultural land and timber extraction for the logging industry (Sodhi *et al.*, 2004; Wright, 2005). Originally, post-glacial tropical rainforests covered an area of approximately 20×10^6 km^2 globally (Grieser Johns, 1997). However, due to intensive deforestation from 1960 – 1980 only 52% of original rainforest land cover remained by 1980. This reduced further during the 1980s and by 1990 globally tropical rainforests covered an area of only approximately 10×10^6 km^2 (Grieser Johns, 1997). Current estimates of global rainforest land cover vary (Wright, 2005), but are likely to account 8.3×10^6 km^2 of global land cover (Whitmore, 1998). Conversion of rainforest to agricultural land is the main reason of forest clearance (Whitmore, 1998). This practice is likely to increase as human populations expand (Whitmore, 1998). The conversion of rainforest to agricultural land usually results in the removal of all tree species and the loss of forest-dependant species. This is the most invasive of all threats to tropical rainforests

and if agricultural land is abandoned it is likely to take several centuries before structurally-complex, species-rich forest is restored (Whitmore, 1998). In contrast, selective timber extraction by the logging industry is less invasive.

1.4.2 Selective logging

Commercial selective logging refers to a method of timber extraction used by logging industries across the globe. Selective logging involves the cutting of a limited number of commercial tree species and the removal of timber to offsite saw mills (Asner *et al.*, 2005). In general, selective logging is considered a moderate form of habitat disturbance in tropical forests. This is primarily because selective logging usually leaves a forest rich in primary tree species which can return to structurally complex, mature forest within a century (Whitmore, 1998). However, this is not uniformly accepted and some studies suggest relatively long periods of time may be needed for selectively-logged forest to recover (Sodhi *et al.*, 2004).

Criteria for selective timber extraction vary globally. However, most extracted timber has to meet species (*i.e.* commercially viable) and size (minimum girth) requirements (Whitmore, 1998). In addition, some selective-logging protocols inhibit the removal of timber from riparian forests and steep slopes. Felled trees are extracted from forested-concession areas to roadside log-landing sites where timber is loaded onto trucks that deliver timber to saw mills (Plate 1.3). A range of techniques are available for extracting timber (yarding) once trees have been felled (Putz *et al.*, 2001). These include; aerial yarding, high-lead (cable) yarding and ground-based yarding techniques. Aerial yarding is the least invasive of all timber extraction methods and deploys the use of helicopters or skylines from cranes to extract timber (Putz *et al.*, 2001). High-lead and ground-based yarding both involve the haulage of timber through the forest and are consequently more invasive techniques than aerial yarding (Putz *et al.*, 2001). High-lead yarding involves skidding logs across the ground using overhead cables that originate from log-landing sites. Ground-based yarding skids logs across the forest behind tractors, articulated skidders or bulldozers (Putz *et al.*, 2001).

Plate 1.3 Truck delivering timber from roadside log-landing sites to timber saw mills. The truck contains selectively-logged timber from the Yayasan Sabah Concession in Sabah, Malaysian Borneo.

The intensity of selective logging varies across tropical regions (Putz *et al.*, 2001; Achard *et al.*, 2002; Sodhi *et al.*, 2004; Asner *et al.*, 2005). Malesian rainforests have the highest average timber harvest intensity (33 m^3 ha^{-1}) followed by African (13 m^3 ha^{-1}) and Neotropical (8 m^3 ha^{-1}) rainforests (Whitmore, 1998). The intensity of timber extraction largely determines the extent of habitat disturbance produced and the time it takes for forests to recover (Whitmore, 1998). However, even relatively high intensities of selective logging are consider a moderate form of tropical forest disturbance compared with clear felling. Timber extraction by selective logging unavoidably alters forest structure (Putz *et al.*, 2001). Initially, logging opens up the forest canopy and disturbs the natural growth cycles of the forest (Putz *et al.*, 2001). Over time, selectively-logged forest regains canopy cover but it is often lower and less dense (Whitmore, 1998). In addition to changes in forest architecture, timber yarding leaves permanent skid trails made of compacted soil that reduce tree growth (Putz *et al.*, 2001). Increasing human populations will place increasing pressure on remaining forests resources (Wright, 2005). Much remaining rainforest is under threat and will be converted to agricultural areas and plantation forest or to secondary disturbed forest following selective logging (Achard *et al.*, 2002; Curran *et al.*, 2004). Thus, selectively-logged forests will become increasingly important in the conservation of

tropical biodiversity as it becomes the last remaining habitat for many species. It is therefore of great importance to understand the impacts of selective logging on the diversity of tropical forest communities.

1.5 Thesis Objectives

1.5.1 Thesis rationale

Insects are globally the most diverse class of organism and play important roles in maintaining biodiversity and ecosystem functioning (Speight *et al.*, 1999). However, insect biodiversity in under constant pressure from human-induced environmental changes (Samways, 2005). Lepidoptera are the fourth most species-rich order of insect, comprising an estimated 110,000 described species (Speight *et al.*, 1999). Two sub-orders of Lepidoptera exist, the Rhopalocera (butterflies) and the Heterocera (moths), of which butterflies comprise approximately 10% of all extant Lepidoptera species (Corbet and Pendlebury, 1992). Butterflies rely on specific host plant(s) as larvae and as adults are highly sensitive to environmental gradients in temperature, light and humidity (Sparrow *et al.*, 1994). Thus, the persistence of butterflies is inseparably linked to the health of an ecosystem (Sparrow *et al.*, 1994).

There are approximately 936 described species of butterfly (10% endemic) on Borneo (Otsuka, 1996). However, Borneo's remaining rainforest are under increasing threat from the logging industry (Curran *et al.*, 2004; Sodhi *et al.*, 2004). In general, total deforestation and conversion of rainforest to agricultural land reduces diversity (Holloway *et al.*, 1992). However, the response of insects, notably butterflies, to more moderate forms of habitat disturbance, such as selective logging, is less clear (Hamer and Hill, 2000). Selective logging is a major threat to biodiversity in Southeast Asia, with timber extraction rates among the highest globally (Sodhi *et al.*, 2004). Thus, it is of great importance to understand the impact of selective logging on biodiversity. In an ever-degraded landscape reliable information about the impact of moderate habitat disturbance on biodiversity will become increasingly important in addressing conservation issues. Thus, the overall aim of this thesis is to provide a better understanding of the impact of habitat disturbance on butterfly diversity.

1.5.2 Thesis objectives and format

- ✧ In Chapter 2, I describe the study sites and explain the general materials and methods used throughout this thesis.

- ✧ In Chapter 3, I investigate how differences in sampling effort affect the perceived response of butterfly diversity to selective logging. In addition, I examine the efficiency and reliability of fruit-baited traps as a method for sampling tropical-forest butterflies.

- ✧ In Chapter 4, I investigate how sampling from both ground and canopy strata affect the perceived response of butterfly diversity to selective logging. I also examine how sampling from both ground and canopy strata affect the perceived conservation value of habitats in terms of species geographic range sizes.

- ✧ In Chapter 5, I investigate the relationship between butterfly α diversity and spatial scale in primary and selectively-logged forests. Using geostatistical techniques, I examine spatial autocorrelation in α diversity in primary and selectively-logged forests. I investigate how selective logging alters rainforest vegetation structure and examine spatial autocorrelation in vegetation data. I use vegetation data to help explain patterns of butterfly α diversity in primary and selectively-logged forests.

- ✧ In Chapter 6, I investigate the impact of selective logging on butterfly β diversity. I examine spatial patterns of β diversity in primary and selectively-logged forest and relate these to spatial patterns in vegetation structure. I use ordination methods to examine the relationship between vegetation structure and butterfly species composition in different habitats and examine the ecology and morphology of butterflies in primary and selectively-logged forests.

- ✧ In Chapter 7, I discuss the findings from previous chapters in relation to one another and in relation to existing and future research. I highlight areas of possible future research and discuss the implications of my findings for future conservation studies.

Chapter 2 General Materials and Methods

2.1 Study Site

2.1.1 Introduction

Fieldwork was conducted from April to July 2003, from January to May 2004 and from October to December 2004 at the Danum Valley Field Centre (DVFC) and the surrounding Ulu Segama Forest Reserve (USFR) in Sabah, Malaysian Borneo (Figure 2.1; 5° N, 117° 5' E).

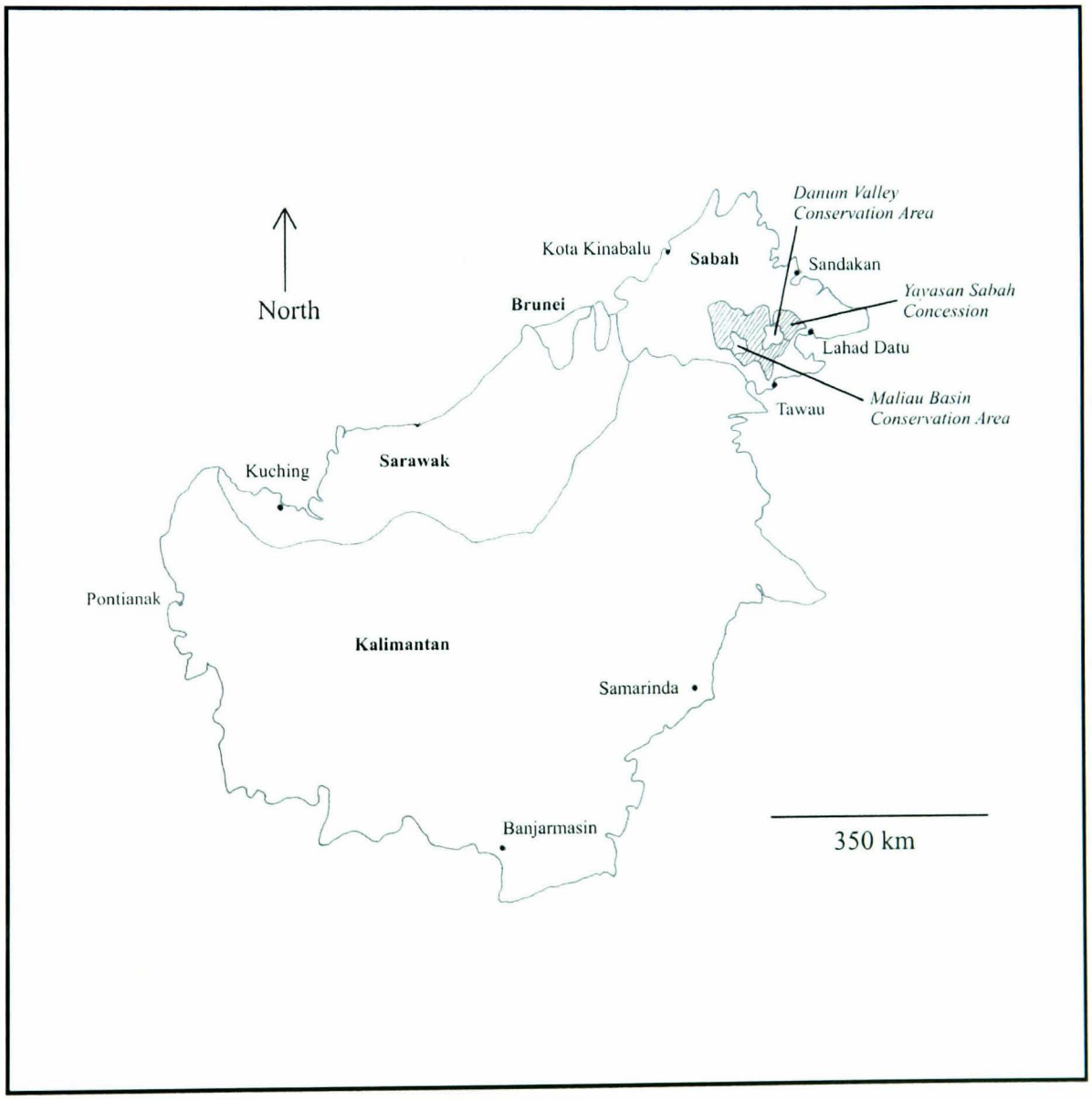


Figure 2.1 Map of Borneo (5° N, 117° 5' E), the Danum Valley Conservation Area is highlighted and shown inside the Yayasan Sabah concession which contains the Ulu Segama Forest Reserve.

2.1.2 Sabah, north Borneo

The Malaysian state of Sabah is situated in the northeast tip of the island of Borneo (Figure 2.1) and makes up one of the political regions of Borneo along with the other Malaysian State of Sarawak, the Sultanate of Brunei and the Indonesian State of Kalimantan. Sabah covers approximately a 10^{th} of the total land area of Borneo (≈7,337,100 ha). Sabah is the third most populated of all the Malaysian States with approximately 2.6 million people and has the second largest mean annual-growth rate at around 4% $year^{-1}$ (Department of Statistics Malaysia, 2001). Sabah has an estimated population density of 35 persons km^{-2}, which is still relatively low compared with other countries within the Asian tropics such as Thailand (113 persons km^{-2}) and Indonesia (103 persons km^{-2}) (McMorrow and Talip, 2001). Sabah's land cover is a mix of agricultural crops, forest and urban areas. The majority of urban towns are situated along Sabah's coast with the rainforest in the interior surrounded by agricultural areas (Figure 2.2).

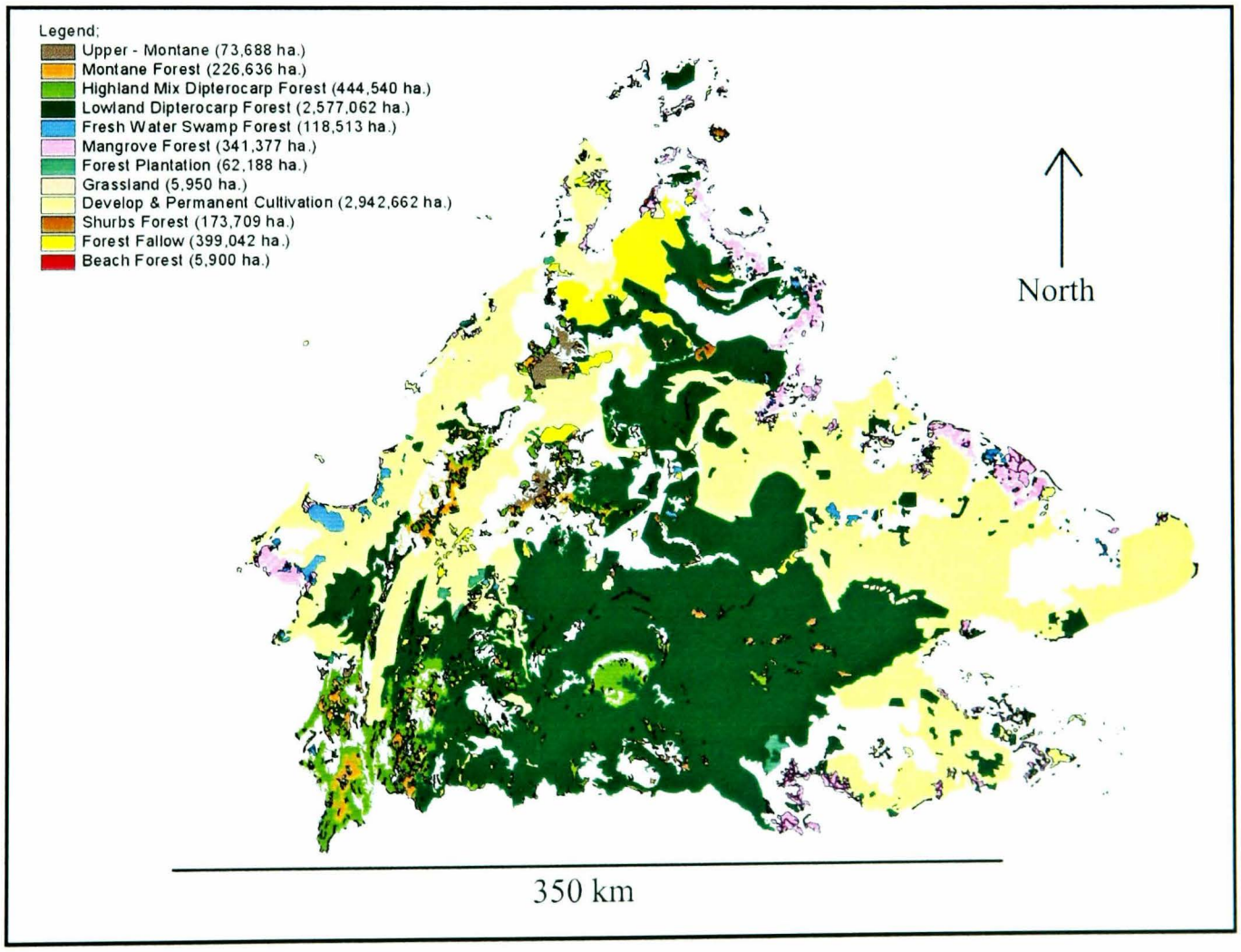


Figure 2.2 1997 land-cover map of Sabah reproduced from the Sabah Forestry Department (2005). Land cover in Sabah is a mix of agricultural crops, forest and urban areas.

Permanent forest reserves within Sabah currently account for approximately 49% (3,594,520 ha) of total land cover (Figure 2.3; Sabah Forestry Department, 2005). A large proportion of Sabah's forests are contained within commercial production forest reserves (Table 2.1; McMorrow and Talip, 2001). However, it is likely that a further 10% of total land cover (733,700 ha) is comprised of forests that are not contained within permanent forest reserves (Figure 2.3; McMorrow and Talip, 2001).

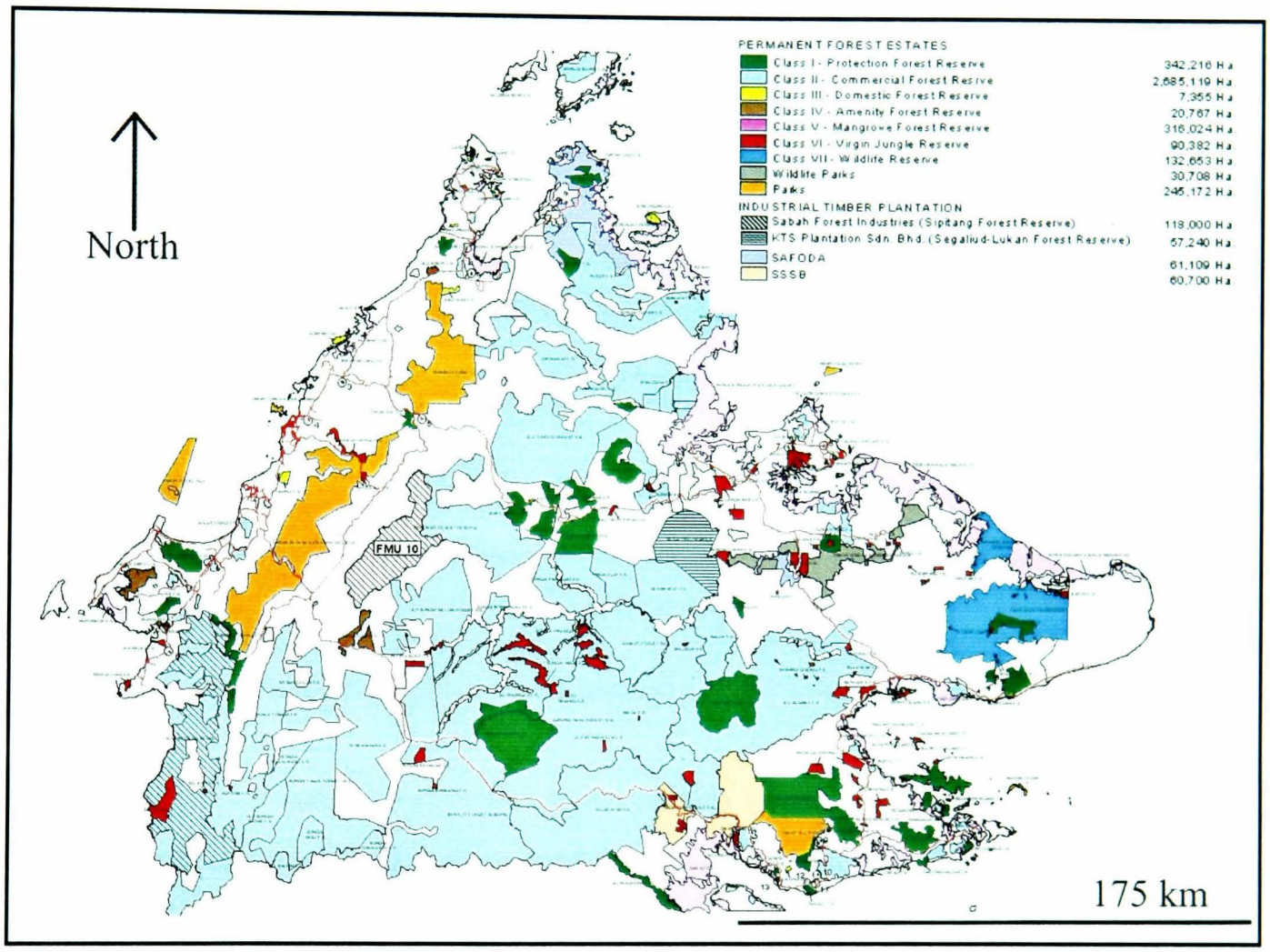


Figure 2.3 Forest-reserve land-cover map of Sabah. Class I to Class VII forest types are highlighted. Areas shown in white contain agricultural land and forest not contained within permanent forest reserves (Sabah Forestry Department, 2005).

Sabah's forested areas are split into six functional types (Table 2.1). Originally almost all of Sabah would have been covered by a mixture of lowland dipterocarp, montane, swamp and mangrove forests (McMorrow and Talip, 2001). However, due to deforestation forest cover at present is far less.

Class	Type	Function	Area (ha)	% Total land cover
I	Protection Forest Reserve	Safeguarding of water supply, Soil fertility and environmental quality	283,376	3.8
II	Commercial Forest Reserve	Timber and forest products supply for state revenue	2,743,959	37.2
III	Domestic Forest Reserve	Timber and forest products supply for local population	7,355	0.1
IV	Amenity Forest Reserve	Recreation, education, research and protection of flora and fauna	20,767	0.3
V	Mangrove Forest Reserve	Supply of mangrove timber and protection of marine life	316,024	4.3
VI	Virgin jungle Reserve	Research and conservation	90,366	1.2
VII	Wildlife Reserve	Protection of wildlife	132,653	1.8
	Total		3,594,520	48.8

Table 2.1 Function and area (ha) of forest reserves in Sabah, from McMorrow and Talip (2001). Figures are from a 1996 survey of forest cover and land use (McMorrow and Talip, 2001).

During the period 1890 – 1930, large areas of Sabah's forests were logged by the British North Borneo Company, which felled trees for timber and converted areas of forest to tobacco and rubber plantations (John, 1974; Cleary, 1992; McMorrow and Talip, 2001). This reduced the total forested land cover to 86% by 1953. With continued logging and conversion to agricultural land (supervised by Sabah's Forest Department) by 1981 only 68% of total land cover was forest (FAO, 1981). Forested land cover fell steadily to 63% by 1984 (Collins *et al.*, 1991). Although over the past 20 years the logging industry has decreased the intensity of its operations, it still remains a vital component to Sabah economy and timber production accounted for 28 – 30% of Sabah's total annual revenue in 2000 (Forest Research Centre, 2005). However, not all of Sabah's remaining forested areas

are reserved for production forest (Table 2.1) and 536,708 ha (7.3% total land cover) of forest is located within protected areas. The total land cover of fully protected areas is split between Protection Forest Reserve (Class I), Virgin Jungle Reserve (Class VI) and Wildlife Reserve (Class VII) forest types (Table 2.1). Due to the high biodiversity value of much of Borneo, a total of 15 parks or reserves under the management of Sabah Parks, the Sabah Wildlife Department and Yayasan Sabah (the Sabah Foundation) have been created (Table 2.2; Figure 2.3). Yayasan Sabah is responsible for the two largest conservation areas, Danum Valley and Maliau Basin (Table 2.2; Figure 2.3).

Authority	Protected areas	Total Area (ha) protected
Sabah Parks	6	265,794
Sabah Wildlife Department	7	170,150
Yayasan Sabah	2	
Danum Valley Conservation Area		43,800
Maliau Basin Conservation Area		56,964
Total	15	536,708

Table 2.2 Total area (ha) of protected forest reserves in Sabah managed by Sabah Parks, the Sabah Wildlife Department and Yayasan Sabah.

A substantial area of Sabah's total land cover is covered by agricultural areas (Figure 2.2) which cover approximately 17% (1,255,361 ha) of total land cover (Department of Agriculture, Sabah, 2005). The main industrial agricultural crop is oil palm, *Elaeis guineensis*, which covers approximately 15% of total land cover (1,076,775 ha) or 85% of the total agricultural land cover (Department of Agriculture, Sabah, 2005). The remaining agricultural land cover (15%) is split between other industrial agricultural crops (*e.g.* coffee, rice and tea) and between fruit, vegetable and spice crops (Department of Agriculture, Sabah, 2005). Although total agricultural cover has only increased by approximately 55,000 ha between the years 2000 and 2003, oil palm cover has increased by approximately 100,000 ha, representing a shift in agricultural practices (Department of Agriculture, Sabah, 2005). Oil palm is the most economically important agricultural crop in Sabah and provides approximately 30% of the states total annual revenue from exports

(Institute for Development Studies, Sabah, 2005). Thus, the timber industry and oil palm production estates account for the majority of the land cover use in Sabah and provide ≥ 60% of the State's total annual revenue.

2.1.3 Yayasan Sabah Concession and the Ulu Segama Forest Reserve (USFR)

The Yayasan Sabah (the Sabah Foundation) Forest Concession is an area of forest (972,804 ha) located in the southeast of Sabah (Figure 2.1). The majority of this area is reserved for timber production and selectively logged in yearly logging coupes or contains plantation forest (*e.g. Acacia mangium*). However, approximately 20% of the land within the Yayasan Sabah Forest Concession is scheduled to remain unlogged, including two conservation areas, Danum Valley and Maliau Basin, which cover 43,800 ha and 39,000 ha respectively (Table 2.3; Marsh and Greer, 1992).

Forest type	Area (ha)
Conservation areas	
Danum Valley	43,800
Maliau Basin	39,000
Virgin jungle reserves	1,705
Unworkable areas	97,280
Road side reserves	500
Riparian Reserves	4,000
Water Catchments	5,550
Total	191,835

Table 2.3 Total area of forest that is scheduled to remain unlogged in the Yayasan Sabah Concession from Marsh and Greer (1992). Forest that is not reserved for logging is split between conservation areas and other forest reserves.

The Ulu Segama Forest Reserve (USFR) is contained within the Yayasan Sabah Forest Concession and is classed as a Class II Commercial Forest Reserve (Table 2.1). The Danum Valley Conservation Area is adjacent to the Ulu Segama Forest Reserve and has Class I Protection Forest Reserve Status (Table 2.1). Logging in the USFR started in 1958 under direction of the American company Kennedy Bay Sdn. Bhd., which later went on to form a

joint venture with Yayasan Sabah forming Pacific Hardwoods Sdn Bhd., which has taken over logging operation since the 1970s (Marsh and Greer, 1992). Between 1970 and 1991 selective logging removed all trees ≥60 cm diameter at breast height (DBH) in this area (Innoprise, 1992). All areas within the USFR were selectively logged, the exceptions being slopes of ≥20° inclination and riparian reserves, defined as areas within 20 m of a major river. The Ulu Segama Forest Reserve was separated into yearly logging coupes of an average area of 2672 ha (*SE* 177) and each logging coupe was subdivided into smaller logging setups of approximately 20 – 50 ha (Innoprise, 1992). Logging was conducted for one year in each coupe and then left to regenerate while the other coupes were logged in turn. Timber extraction from the Ulu Segama Forest Reserve was carried out using tractor yarding and high lead cable yarding, (see Chapter 1; Innoprise, 1992). Logging took all commercially viable stems; the main timber types within this area are comprised of White Seraya (*Parashorea* spp.), Red Seraya (*Shorea* spp.), Yellow Seraya (*Shorea* spp.), Kapur (*Drybalanops lanceolata*), Keruing (*Dipterocarpus* spp.) and Selangan Batu (*Shorea* spp.) all of which are from the family Dipterocarpacea (Innoprise, 1992). This resulted in a total extraction volume of 6,080,017 m^3 of timber between 1970 and 1991 from this area (Figure 2.4).

The area of selectively-logged forest investigated in this study was located within the 1988 logging coupe (Coupe 88) which is approximately 7 km away from the boundary of the Danum Valley Conservation Area. Coupe 88 was logged by Silam Forest Products Sdn. Bhd., a subsidiary of Pacific Hardwoods Sdn. Bhd. Coupe 88 was subdivided into 75 logging setups which ranged in area from between 108 to 12 ha. A mixture of high lead and tractor yarding extraction methods (19 setups used high lead, 56 used tractor) were used in the separate logging setups in the 1988 logging coupe. 168,761 m^3 of timber was extracted over the 2263 ha area from the 75 logging setups at an average extraction intensity of 74.58 (*SE* 5.5) m^3 ha^{-1} (Figure 2.5). Selective logging in Coupe 88 resulted in a mosaic of different disturbance intensity caused by different timber extraction methods used and the different logging intensities in each setup (Marsh and Greer, 1992). Thus, areas of selectively-logged forest investigated in this study incorporated a range of logging setups. However, one uniform feature of selectively-logged forest in Coupe 88 is that all commercially viable trees (timber species ≥60 cm DBH) of the family Dipterocarpeacea were removed (Innoprise, 1992).

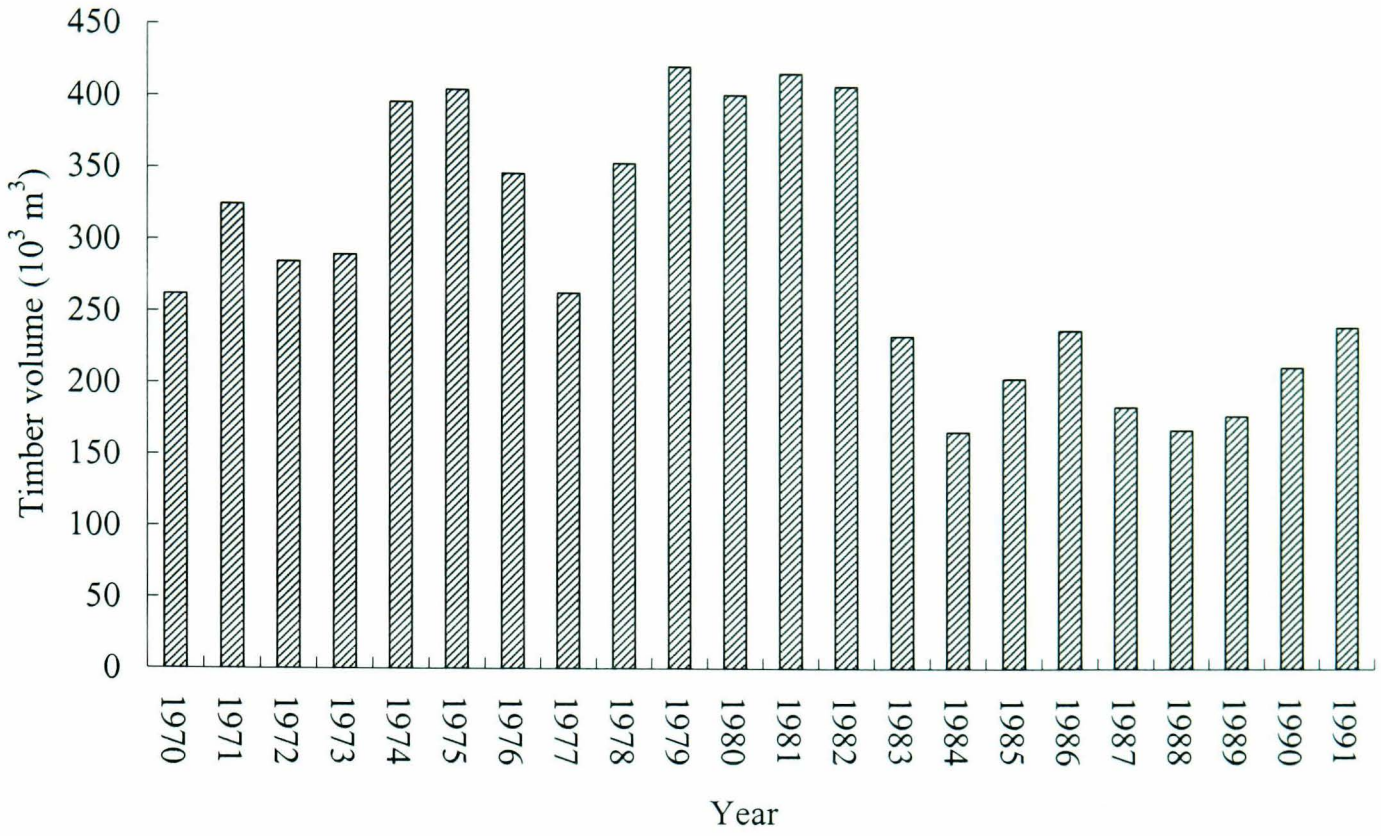


Figure 2.4 Yearly timber-extraction volumes from Ulu Segama Forest Reserve (Innoprise, 1992). A total of 6,080,017 m^3 of timber was extracted from 1970 to 1991.

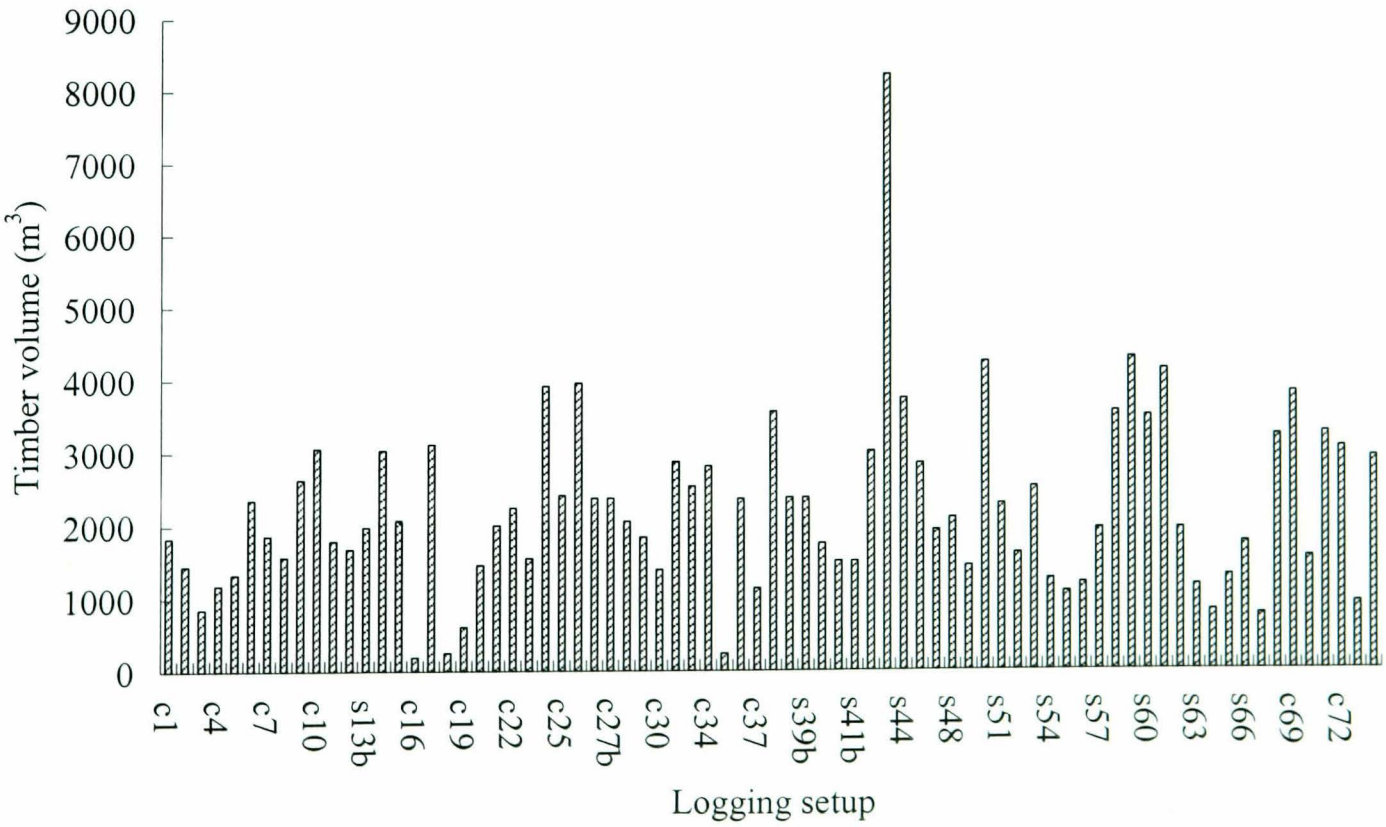


Figure 2.5 Total timber volume (m^3) removed from each of the 75 logging setups inside the 1988 logging coupe. A total of 168,761 m^3 of timber was extracted (Innoprise, 1992).

2.1.4 Danum Valley Conservation Area and Danum Valley Field Centre

The Danum Valley Conservation Area (DVCA) covers 42,800 ha of primary, lowland-dipterocarp rainforest. The conservation area is surrounded on its eastern and southern boundaries by the Segama River and by the Danum River to the north. The Danum Valley Field Centre (DVFC) is located just outside the conservation area on the eastern banks of the Segama River and this area is *ca*. 170 m above sea level (Plate 2.1).

Plate 2.1 The Danum Valley Field Centre, located outside the Danum Valley Conservation Area on the eastern banks of the Segama River. The boundary of the Danum Valley Conservation Area is located on the adjacent, western bank of the Segama River.

2.1.4.1 Dipterocarp forest in the Danum Valley Conservation Area

The majority of forest within the Danum Valley Conservation Area is comprised of lowland mixed dipterocarp forest (Figure 2.6). Taking the conventional altitudinal limit for lowland forest of 760 m a.s.l., 91% of the conservation area can be considered to be lowland forest (Marsh and Greer, 1992). Trees of the family Dipterocarpaceae make up 88% (Sabah Forestry Department, 2005) of the total volume of large trees within the conservation area and are dominant throughout the conservation area except for areas of small-crowned, dense montane forest around Mt. Danum (Figure 2.6).

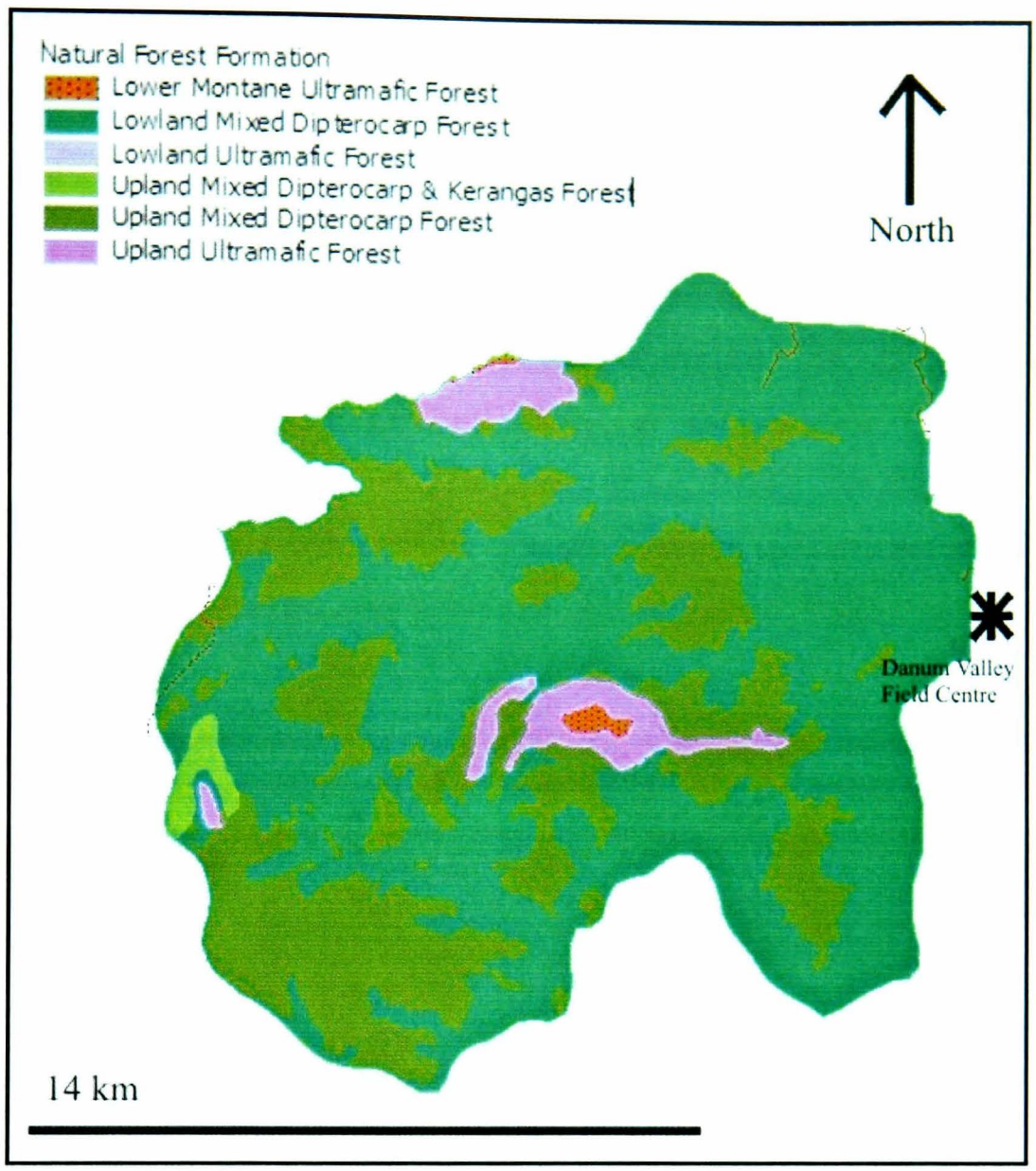


Figure 2.6 Vegetation cover map of the Danum Valley Conservation Area from Sabah Forestry Department (2005). The majority of the DVCA (≈91%) is comprised of lowland mixed dipterocarp forest.

Newbery *et al.*, (1992) set up two semi-permanent 4 ha plots close to the Danum Valley Field Centre. Data from these plots described 511 tree species from 164 genera and 59 families, with 388 and 387 tree species present in the two plots respectively, indicating high species turnover even over the small spatial scale sampled. The mean tree density in these plots was 2248 tree ha^{-1} and 470 tree ha^{-1} for trees classed as ≥10 cm DBH and ≥30 cm DBH respectively. 10 cm DBH is used as the lower bound for trees (*i.e.* trees < 10 cm DBH are saplings) in forestry studies as it incorporates all trees producing canopy/overstorey cover and emergent trees (Newbery *et al.*, 1992). The density of pioneer tree species was significantly lower with only 70 trees ha^{-1} and 18 trees ha^{-1} for the ≥10 cm DBH and ≥30 cm DBH size classes respectively, indicating the presence of well established mature-

growth forest (Newbery *et al.*, 1992). Newbery *et al.*, (1992) showed that the majority of tree species present were represented by fewer than five individuals (51% n ≤5) and a large proportion of trees species were represented by only one individual (31% n = 1). This in addition to still rising species accumulation curves for trees of all size classes (≥10 cm, ≥ 30 cm and ≥100 cm DBH) indicated high species richness in the DVCA. The four most species-rich families were shown to be the Lauraceae (83 species, 11 genera), Euphorbiaceae (51 species, 17 genera), Meliaceae (36 species 7 genera) and the Dipterocarpaceae (30 species 6 genera) (Newbery *et al.*, 1992). The four families of trees that structurally dominate the conservation area and have the largest basal area (m^2 ha^{-1}) are the Dipterocarpaceae, Euphorbiaceae, Lauraceae and Mytaceae (Table 2.4).

Family	Size class (cm DBH)		
	≥10	≥30	≥100
Dipterocarpaceae	13.42	13.10	11.87
Euphorbiaceae	3.12	1.84	0.17
Lauraceae	1.78	1.49	0.94
Mytaceae	1.34	1.19	0.64
Olacaceae	1.23	1.19	0.97
Meliaceae	1.19	0.95	0.22
Fagaceae	1.00	0.94	0.50
Annonaceae	0.91	0.57	0.02
Leguminosae	0.84	0.68	0.61
Sapotaceae	0.82	0.70	0.30
Tiliaceae	0.68	0.61	0.13
Burseraceae	0.51	0.44	0.23
Lecythidaceae	0.43	0.41	0.06
Verbenaceae	0.27	0.26	0.20
Thymelaeaceae	0.27	0.23	0.13
Xanthophyllaceae	0.21	0.15	0.01
Melastomataceae	0.17	0.12	0.04

Table 2.4 Mean basal area (m^2 ha^{-1}) of tree families in the Danum Valley Conservation Area (Newbery *et al.*, 1992).

Plant families with the greatest density of trees (tree ha^{-1}) in the conservation area are the Euphobiaceae, Dipterocarpaceae, Annonaceae and the Lauraceae (Table 2.5) although trees of the family Dipterocarpaceae have by far the greatest density of trees ≥100 cm DBH representing 42.8% of these large trees (Newbery *et al.*, 1992).

Family	Size class (cm DBH)		
	≥10	≥30	≥100
Euphorbiaceae	619.00	97.00	1.30
Dipterocarpaceae	210.00	76.00	27.10
Annonaceae	172.00	29.00	0.30
Lauraceae	152.00	32.00	4.50
Meliaceae	142.00	35.00	1.80
Mytaceae	92.00	27.00	3.80
Leguminosae	79.00	5.00	1.60
Rubiaceae	74.00	4.00	0.00
Myrsinaceae	74.00	6.00	0.00
Sapotaceae	70.00	17.00	2.40
Tiliaceae	49.00	21.00	1.10
Fagaceae	45.00	20.00	3.20
Burseraceae	42.00	12.00	1.50
Flacourtiaceae	39.00	5.00	0.00
Xanthophyllaceae	34.00	7.00	0.10
Olacaceae	33.00	10.00	5.30

Table 2.5 Mean density (tree ha^{-1}) of tree families in the Danum Valley Conservation Area (Newbery *et al.*, 1992).

The Danum Valley Conservation Area is dominated by tree species of Dipterocarpaceae and Euphorbiaceae and this is typical of lowland Dipterocarp forest throughout Borneo, with 22% and 12% of all trees species on Borneo belonging to these two families respectively (Silik *et al.*, 2003). The Danum Valley Conservation Area along with the Sepilok Forest Reserve fall into the eastern Sabah cluster of forest type on Borneo. The distinction of this forest type from the rest of Borneo is due to the slightly more pronounced seasonal climate affected by the northeast monsoon (Silik *et al.*, 2003). More detailed analysis of the tree species composition carried out by Fox (1970) suggested that the majority of the Danum Valley Conservation Area is comprised of Type A, *Parashorea malaanon*, forest (Marsh and Greer, 1992). Again this type of forest predominates over much of eastern Sabah (Silik *et al.*, 2003). The dominant species of this forest type in the DVCA are *Parashorea malaanon*, *Shorea johorenis*, *S. leprosula*, *S. superba* on flatter areas of the conservation area with the species: *S. atrinervosa*, *S. faguetiana*, *S. gibbosa* and *S. superba* dominant on the ridges (Sabah Forestry Department, 2005). This again is typical of the rest of Borneo with 12% of all trees species from the genera *Shorea* (Silik *et al.*,

2003). The majority of the DVCA falls within the types of forest described here, there is some exception around the mountainous areas and approximately 10% of the conservation area is montane forest characterized by small-crowned trees *e.g. Dacrydium* spp. (Marsh and Greer, 1992).

2.1.4.2 Climate

Northern Borneo has a typically wet tropical climate which is controlled by the Indo-Australian monsoon system (Walsh, 1996b). Borneo has high monthly rainfall throughout the year, but the monsoon system leads to periods of heavier rainfall during the northeast monsoon (November – March) and the southwest monsoon (June – July) periods. Borneo has a generally constant climate from year to year. However, Borneo's climate is affected by El Niño-Southern Oscillation (ENSO) events. Mild ENSO events occur on a 3 – 4 year cycle and severe ENSO events are never less than 6 – 7 years apart (Walsh, 1996b). ENSO events lead to extreme drought conditions in eastern Borneo and tend to start between March and May and continue for over a year (Walsh, 1996b). The most recent ENSO events occurred in 1982 – 83 (Walsh, 1996b), 1986 – 87, 1991 – 94 and 1997 – 98 (Walsh and Newbery, 1999), with the 1982 – 83 and the 1997 – 98 ENSO events being particular severe (Walsh and Newbery, 1999).

The Danum Valley Conservation Area has climate typical of Borneo (Walsh and Newbery, 1999) and although generally considered aseasonal, does have slightly wetter months associated with the northeast and southwest monsoons (Marsh and Greer, 1992). The meteorological field station at the DVFC recorded a mean annual rainfall of 2826 mm $year^{-1}$ over a 19-year period from 1986 – 2004 (Figure 2.7). This makes DVCA slightly drier than most northern parts of Sabah (1982 – 1988, 3051 mm $year^{-1}$) but slightly wetter than the east (1960 – 1983 2062 mm $year^{-1}$) (Marsh and Greer, 1992). Generally April, July and August are drier months in DVCA and October, December and January are wetter months with intermediate values for the other months (Figure 2.8). The study months in which field work was conducted had rainfall typical of those months. Fieldwork incorporated wetter (January, September, November and December 2004) and drier months (February, March and April 2004 and January 2005) and rainfall during these months was typical of their monthly averages (Figure 2.8).

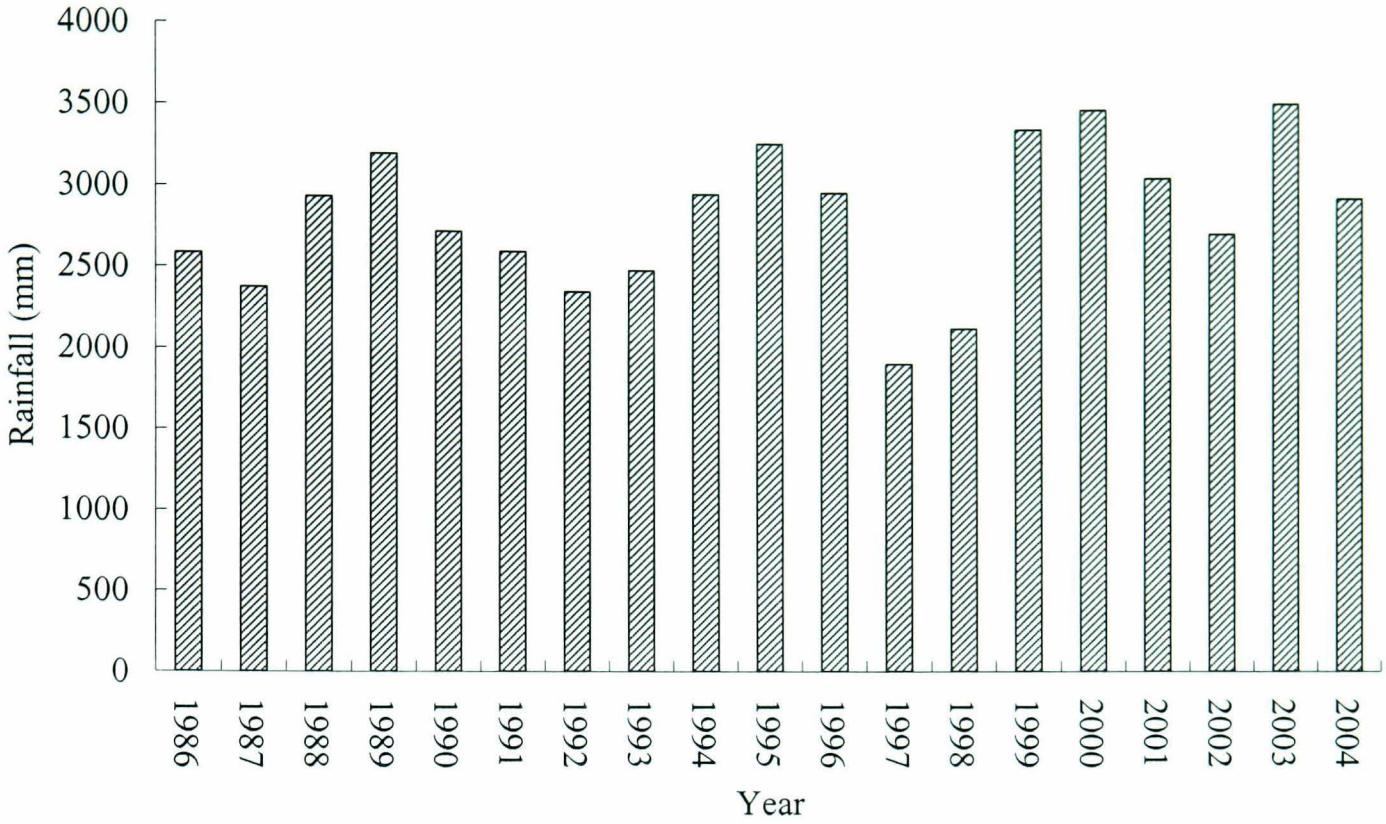


Figure 2.7 Annual rainfall recorded at the Danum Valley Field Centre from 1986 – 2004.

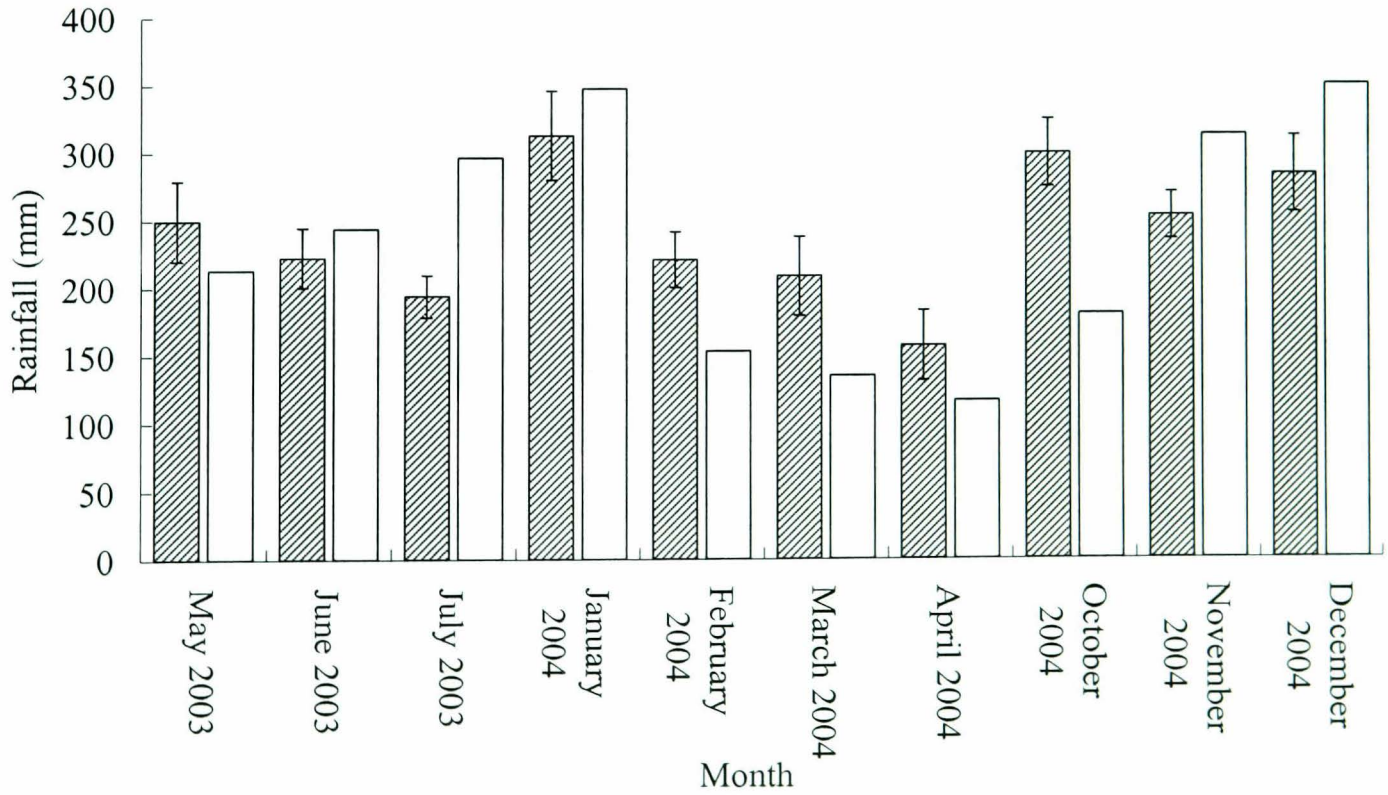


Figure 2.8 Total rainfall recorded during field-work months (open bars) compared with mean (± SE) monthly rainfall (shaded bars) recorded at the Danum Valley Field Centre.

The temperature measured by the DVFC metrological station is typical of the wet tropics (Walsh and Newbery, 1992). The mean minimum and maximum temperatures are 31.1° C and 22.5° C respectively with an annual mean of 26.8° C (September 1985 – June 2003). As with most tropical regions there is little variation around the mean temperature with monthly average varying by 29.2° C – 31.8° C around the mean annual maximum temperature and varying by 22.2° C – 23.0° C around the mean annual minimum temperature. This leads to stable monthly and yearly temperature with little variance and can generally be considered constant with only a 2° C change between wetter and drier months' maximum temperatures.

Relative humidity reaches saturation around 08:00 hours (annual mean = 95.3%) and has decreased by 14:00 hours (annual mean = 78.3%; September 1985 – June 2003). Again there is little variation of relative humidity around the annual mean each month at both 08:00 hours (varying by 89.9 – 6.7%) and at 14:00 hours (varying by 73.7 – 83.2%) giving a relatively constant morning and afternoon relative humidity. The placement of the meteorological station adjacent to the DVFC must be taken into consideration when interpreting both temperature and relative humidity. The meteorological station is in a large clearing adjacent to the Segama River and as of such the temperature inside the forest tends to be slightly cooler and relative humidity tends to stay nearer saturation throughout the day (Marsh and Greer, 1992).

2.2 Butterfly Sampling

The identification of butterflies in flight in highly diverse areas such as Borneo is problematic (Walpole and Sheldon, 1999). Walpole and Sheldon (1999) showed that using standard walk and count methods (Pollard, 1977) less than 50% of individuals recorded could be identified to species level. To avoid these problems I used fruit-baited traps (Plate 2.2) to sample butterfly species in primary and selectively-logged forest (for details of trap design see DeVries, 1987; Daily and Ehrlich, 1995; Sutherland, 1996). Fruit-baited traps sample the fruit-feeding guild of Nymphalid butterflies which represents approximately 75% of all Nymphalid species present on Borneo (Hamer *et al.*, 2003).

Plate 2.2 Fruit-baited trap. Traps are baited with banana on the yellow pot which attracts fruit-feeding Nymphalid butterflies. Butterflies fly inside the green netting where they remain until being sampled.

Butterflies were sampled in primary and selectively-logged forests in, and around the Danum Valley Conservation Area using two arrangements of traps. The first arrangement sampled along a 2 km transect and included canopy traps, the second sampled across a square grid and sampled over a ≈80 ha area. This is described in more detail below.

2.2.1 Transect and canopy sampling

Butterflies were trapped along two 2-km transects, one in primary forest and the other in forest selectively logged in 1988 (Figure 2.9). Traps were hung at ground level approximately 2 m above the ground (hereafter termed ground-level) every 100 m along transects (n = 40 ground-level traps in total). Canopy-level traps were hung directly above ground-level traps every 200 m (n = 20 canopy traps) and were lowered to ground level for sampling. Canopy traps were hung above every other ground trap. Canopy traps were set up

by first firing a fishing line over a suitable tree branch using a bow and arrow. The fishing line was then used to reel up suitably thick rope and canopy traps were attached to these ropes and were then reeled up into the canopy to the appropriate height. Canopy traps were hung at similar heights in the two habitats (primary forest, mean height of traps = 27.2 m *SE* = 1.39; selectively-logged forest, mean height = 26.3 m *SE* = 0.67; *t*-test comparing heights; $t_{19} = 0.74$, $p > 0.1$).

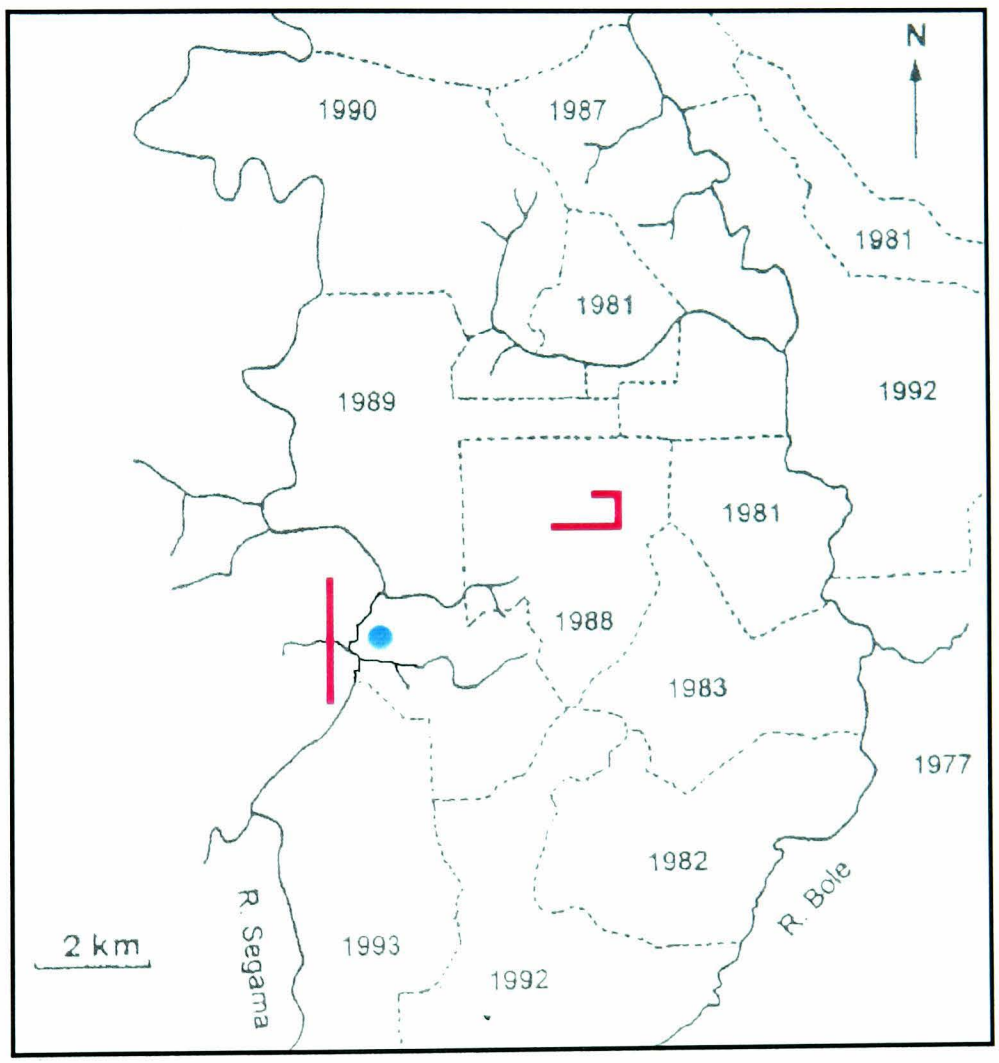


Figure 2.9 Location of transects. The blue cycle represents the Danum Valley Filed Centre, the dashed lines indicate boundaries between logging coupes (with logging dates) and solid lines show location of rivers. The area west of the Segama River is the Danum Valley Conservation Area. One transect is located in primary forest the other in forest selectively logged in 1988. Map from Hill (1999).

2.2.2 Grid sampling

Butterflies were sampled on two 80 ha grids, one inside primary forest and the other in forest selectively logged in 1988. Traps were hung every 200 m inside the grid in a 5 by 5 trap arrangement (Figure 2.10). All traps (n = 50) were hung at approximately 2 m above ground level.

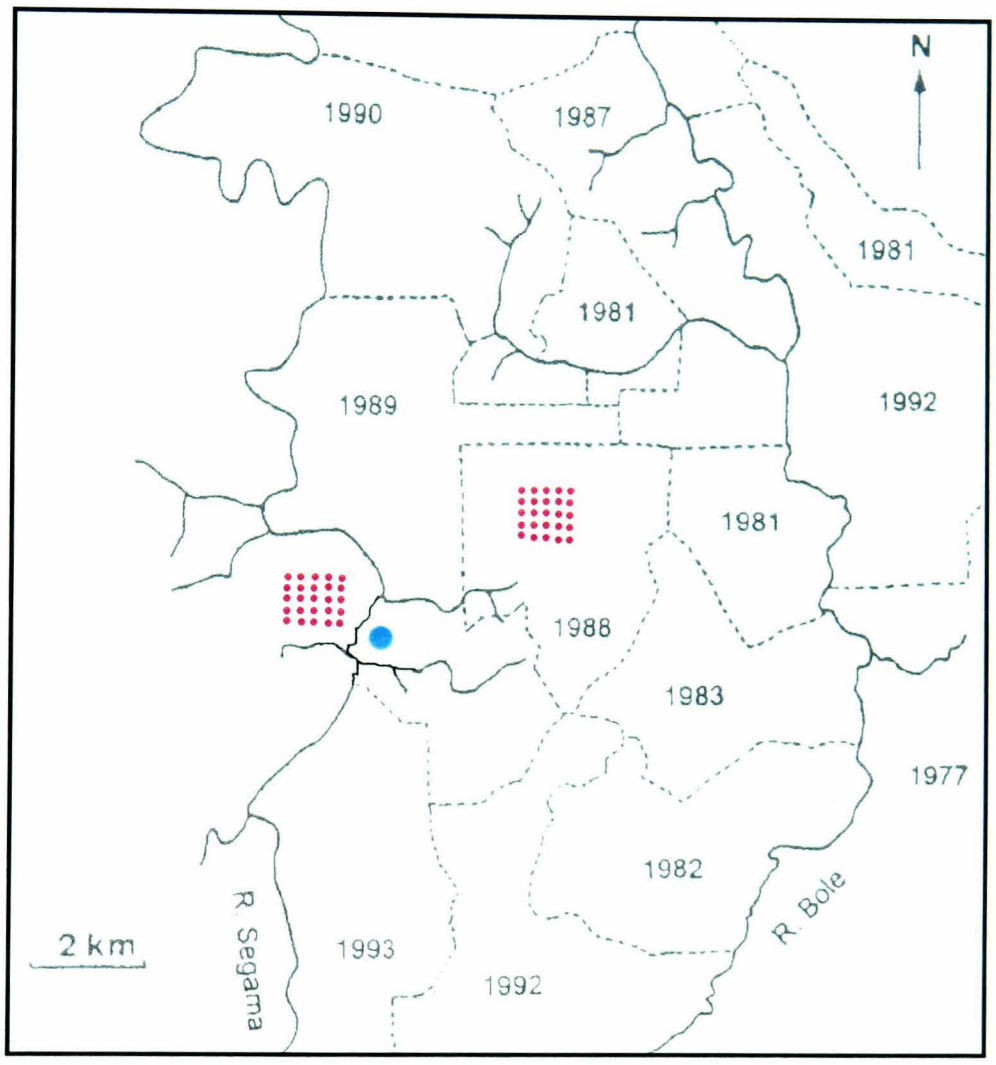


Figure 2.10 Location of grids. Traps (red cycles) are arranged in a 5 by 5 grid. The blue cycle represents the Danum Valley Field Centre, the dashed lines indicate boundaries between logging coupes (with logging dates) and solid lines show location of rivers. The area west of the Segama River is the Danum Valley Conservation Area. One grid is located in primary forest the other in forest selectively logged in 1988. Map from Hill (1999).

2.2.3 Sampling protocols

Butterfly sampling followed the same methods irrespective of whether sampling was conducted along transects (Figure 2.9; Chapter 4) or on grids (Figure 2.10; Chapters 5 and 6). I sampled butterflies along transects during May and July 2003 and from January to

February 2004. Sampling on the grids was conducted during June 2003, from March to April 2004 and from October to December 2004. All traps were baited with fresh banana prior to the first day of sampling and an additional piece of banana was added daily. This ensured a mix of fresh and well-rotted fruit. Sampling was conducted for 12 days each month in each habitat. Traps were checked daily between 10 am and 2 pm. All butterflies caught were identified, marked with a felt-tipped pen and released at ground level irrespective of whether they were caught in the canopy or at ground level. Recaptured individuals were excluded from diversity analyses. Any butterflies that could not be reliably identified in the field (*e.g. Euthalia* spp. and *Tanaecia* spp.) were collected and identified in the laboratory following Otsuka (1988) and Corbet and Pendlebury (1992).

2.3 Butterfly Ecological Traits and Flight Morphology

To investigate the impacts of selective logging on butterfly species with different ecological traits I assigned values to species which described their ecologies in terms of their geographical distribution, light environment preferences and larval host plant choice.

2.3.1 Geographic range

I ranked all butterfly species in terms of their geographical distributions (following Hamer *et al.*, 2003). The endemic species, *Mycalesis kina*, *M. amoena*, *Tanaecia orphane* and *Thauria aliris* shared the highest rank (rank = 1), and the most widespread species, *Melanitis leda*, (which occurs through the African, Oriental and Australasian regions) was assigned the lowest rank (rank = 62. Species with distributions restricted to Sundaland (Borneo, Sumatra, Java, West Malaysia and Palawan) were ranked 3-18 (Appendix 2, 3). Species that had geographical distributions which also included the Oriental and Australasian regions were ranked 19-61. Differences between habitats in geographical distributions of species were investigated using Mann-Whitney U tests.

2.3.2 Light environment preference

I assigned all species a light-index value which described their light environment preference. Species light preference was calculated in terms of the proportional abundance of individuals ($n \geq 10$) for each species that were caught in gaps *versus* shade traps from Hill *et al.*, 2001 and Hamer *et al.*, 2003. Thus species with light index value of close to 1

were highly light tolerant and only present in gaps *e.g. Rhinopalpa poynice* ($L = 0.909$) and species with low light-index values were relatively light intolerant *e.g. Mycalesis kina* ($L = 0.095$). Differences in species light preference indices between habitats were investigated using *t*-tests; data were arc-sine transformed before analysis.

2.3.3 Larval host plant specificity

All butterfly species were ranked according to their larval host plant specificity. Information on larval host plant choice was gathered from Robinson *et al.*, (2001) and Suguru and Haruo (1997, 2000). Butterflies were ranked according to number of different host plant families they could feed from. Specialist feeders were given the highest rank (rank = 1) with highly polyphagous, generalist, butterfly species that fed on a wide range of plant families given the lowest rank (rank = 9). The majority of species (66% of all species) for which data were available shared the highest rank of 1 and only a single species *Charaxes bernardus* was ranked 9. Differences between butterfly species larval host plant specificity between habitats were investigated using Mann-Whitney U tests.

2.3.4 Flight morphology

All trapped butterflies were measured to an accuracy of 0.1 mm using Vernier callipers. Measurements of thorax length and width, abdomen length and width, and forewing wing length (wing base to apex) and width (minimum distance between tornus and costa) were recorded (Figure 2.11). These measurements when used to derive four variables; thorax and abdomen volumes (length $\times$ width^2), thorax shape (width / length) and forewing wing shape (wing length / breadth). In butterflies thorax mass, thorax width and wing span are all positively correlated to flight speed (Chai and Srygley, 1990; Dudley, 1990; Srygley and Chai, 1990). In contrast relative abdomen mass which contains all the reproductive organs is negatively correlated to flight speed (Srygley and Chai, 1990). Thus, thorax and wing measurements are likely to represent relative investment in flight while abdomen measurements are likely to reflect investment in reproduction. All variables were $\log_{10}$ transformed prior to analysis. Only species for which at least 10 individuals were measured for each sex were included in analysis and mean values were calculated for males and females of each species. All variables except wing shape were allometrically related to body length (measured as thorax length + abdomen length). To account for this allometry, data were analysed using ANCOVA with body length as a covariate and sex and sub-family

(Satyrinae, Morphinae, Nymphalinae, Charaxinae) as factors. All analyses were weighted by sample size.

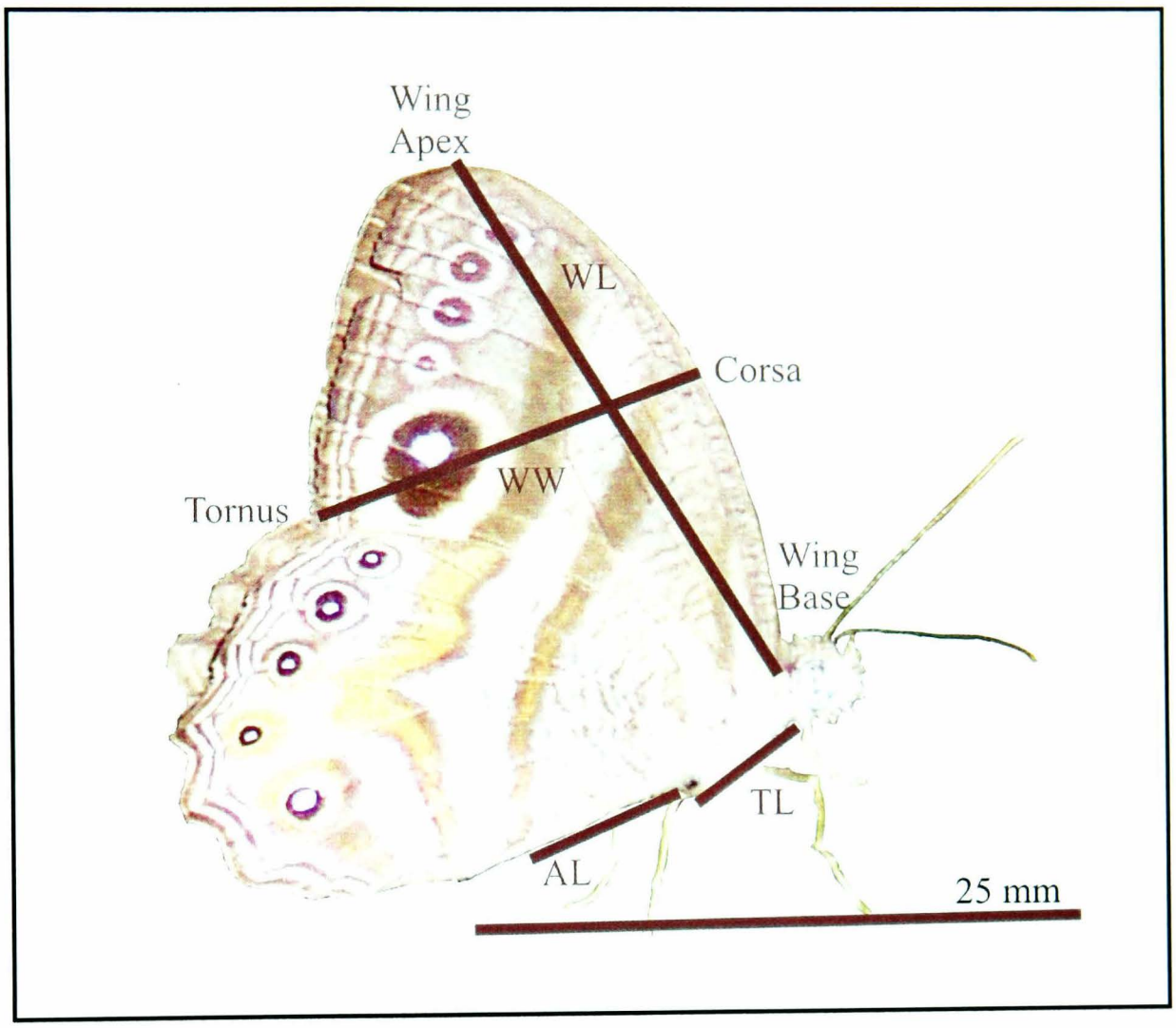


Figure 2.11 Morphology measurements taken from sampled butterflies. *Erites argentina* (Family: Nymphalidae; sub-family, Satyrinae) is shown. Thorax length (TL) and abdomen length (AL) were measured. Thorax and abdomen width were also measured at the widest point. Forewing wing length (WL) was measured between the base and apex and forewing width (WW) was the minimum distance between tornus and costa.

2.4 Diversity Analysis

To investigate the impact of selective logging on butterfly diversity I calculated three diversity indices, Shannon-Wiener (Equation 2.1), Margalef (Equation 2.2) and Simpson (Equation 2.3) indices, following recommendations by Magurran (1988; 2004). For Simpson's index the reciprocal ($1/D$) was used so that an increase in the value of Simpson's index represented an increase in species evenness.

$$H' = -\sum_{i=1}^{Sobs} P_i \ln P_i$$

Equation 2.1

P_i is the proportion of individuals in the ith species and thus, $P_i = \frac{n_i}{N}$ were n_i is the number of individuals in species i and N is the total number of individuals recorded.

$$D_{Mg} = \frac{S-1}{\ln N}$$

Equation 2.2

S is the total number of species recorded and N the total number of individuals recorded.

$$D = \sum_{i=1}^{S} \frac{n_i(n_i - 1)}{N(N-1)}$$

Equation 2.3

n_i is the number of individuals in species i and N is the total number of individuals.

The Shannon-Wiener index (Equation 2.1) is a measure of α diversity and incorporates both species richness and evenness. This index is based on information theory and assumes that all individuals are randomly sampled from an infinitely large community and that samples contain all species from that community. As a measure of α diversity the Shannon-Wiener index is disproportionably influenced by rare species (Magurran, 1988; 2004; Pielou, 1975). Margalef's index (Equation 2.2) is primarily a measure of species richness (Clifford and Stephenson, 1975). Although Margalef's index incorporates the number of individuals recorded and therefore constrains for sample size, it is still influenced by the size of sample recorded (Magurran, 1988; 2004). When using this index to compare between different samples, care must be taken when interpreting data if one sample contains disproportional more individuals than another. Simpson's index (Equation 2.3) is primarily a measure of species evenness (Simpson, 1949). Simpson's index is considered a robust measure of α diversity and captures the variance of the underlying species abundance distribution.

However Simpson's index is subject to being heavily biased by the most abundant species (Magurran, 1988; 2004).

Bootstrapping methods were applied to diversity indices allowing computation of standard errors and confidence intervals (Sokal and Rohlf, 1995). The bootstrap is a technique for obtaining standard errors and confidence limits for a statistic with a single sample. Here the statistic is the diversity index of a sample. The value for the diversity index, D, is computed for a sample of n species. Using a random replacement method of n within the sample, D is recomputed n times. This gives variance around the original diversity index and can be used to calculate standard errors and confidence limits.

To compare diversity indices between samples, pairwise randomization tests were carried out based on 10,000 resamples of species abundance data following Solow (1993). The randomization test works by first calculating the difference between samples (sample 1 – sample 2). Then combing the species abundance data from two original samples into a single data set and randomly partitioning it into to two separate subsets. The diversity index is then recalculated for each subset and the difference recorded. This is repeated 10,000 times. Assuming that under the null hypothesis there is no difference in community structure between original samples the partitioning of the total data into subsets are equally likely. Thus an alpha value (p) can be calculated as the proportion of subset partitions that results in a difference between samples greater than the original difference between samples.

2.5 Vegetation Data

To assess the structural composition of the vegetation in primary and selectively-logged forest, each trapping station was divided into four quadrants centred on the trap, and the following variables were recorded in each quadrant within a 30 m radius of the trap: height, girth at breast height, point of inversion (whether the first major branch was above or below the mid-point of the tree; Torquebiau, 1986), distance from trap, and identity (family Dipterocarpaceae, pioneer *Macaranga spp.*, or other) of the two trees (> 0.6 m girth) nearest to the trap (n = 8 trees per station; n = 160 trees per transect; n = 200 trees per grid). The distance from the trap, girth at breast height, and identity (family Dipterocarpaceae, *Macaranga spp.* or other) of the nearest two saplings (0.1 - 0.6 m girth) were also recorded in each quadrant (n = 8 saplings per station). In each quadrant, the percentage cover of

ground, low level (> 2 m from ground height) and understorey vegetation were estimated within a 10 m radius of the trap. A single estimate of percentage canopy cover was taken within a 10 m radius of the trap. Overhead vegetation cover was also estimated from four readings, facing each major compass direction, using a densiometer (Lemmon, 1957). Trees were identified by staff from DVFC. Distances and tree girths were measured to the nearest 1 cm using a tape measure, tree height was estimated to the nearest 2 m and cover to the nearest 5% by AJD. These data were used to derive 17 vegetation variables which were normalised where necessary (including arcsine transformation of proportions) prior to analysis. These variables were then analysed by principal component analysis (PCA; Hamer *et al.*, 1997, 2003).

Principal component analysis is a form of multivariate statistic that transforms multivariate data, where many of the variables are correlated, into fewer independent variables that describe the underlying variance within the data (Quinn and Keough, 2002). PCA makes the assumption that the underlying data are continuous and normally distributed. In the simplest sense principal component analysis will take two or more variables that are correlated and find the line of best fit between them and this will generate the first principal component axis or eigenvector. A second axis is generated by fitting a second line perpendicular to the first and thus generating the second eigenvector. This process occurs in multidimensional space and each dimension is used for each additional variable and the lines fitted are formed by weighting each variable according to the amount of variance it explains within the data (Quinn and Keough, 2002). Each eigenvector is then described in terms of the weighting of the variables describing it. Thus each sample can then be scored along the eigenvector by the proportion of each variable recorded for that sample. Principal component analysis will continue to extract eigenvectors until all the underlying variance within the data are explained. Therefore each eigenvector is given an eigenvalue that describes the proportion of the variance within the data it explains and thus eigenvalues decrease with each additional eigenvector extracted (Quinn and Keough, 2002).

Chapter 3 Using fruit-baited traps to monitor tropical butterfly diversity in primary and disturbed habitats

3.1 Abstract

Tropical rainforests are increasingly under threat from anthropogenic disturbance such as logging and shifting agriculture practices. Thus, much research has focused on monitoring the impacts of habitat disturbance on diversity. Within the tropics the fruit-feeding guild of Nymphalid butterflies are increasingly being used to monitor diversity in primary and disturbed habitats. This involves trapping butterflies using fruit-baited traps. However, few data are available on the best sampling protocols to follow when using fruit-baited traps. In this chapter I addressed a series of questions about sampling using fruit-baited traps and examined how differences in sampling protocols affected the perceived response of butterfly diversity to selective logging. I re-analysed existing data to examine how the length of time spent sampling and the spatial resolution of sampling influenced the perceived response of butterfly diversity to selective logging. I compared diversity between primary and selectively-logged forest over a range of sampling periods (1 – 6 months). I found that data from at least five 1-month samples were needed to detect a significant difference in diversity following selective logging. However, these five 1-month samples were spread across a 10-month period. This suggested that the length of study period as well as the number of samples were important in detecting a significant difference in diversity between habitats. I compared diversity between primary and selectively-logged forest at a range of spatial scales (0.4 – 2.0 km). I found that data from at least a 1.6 km transect were needed to detect a significant difference in diversity following selective logging. This study highlighted the need to sample over a relatively long time span and over a relatively large spatial scale in order to detect a change in butterfly diversity following selective logging when using fruit-baited traps. In addition, I investigated the best time of day to empty fruit-baited traps and how efficient traps are at retaining butterflies. I found significantly more individuals entered traps between 8.00 – 9.00 am than at any other time of day. I found that 70% of these individuals remained within traps for the next five hours. Thus, I conclude that sampling daily between 9.00 am – 2.00 pm is the most efficient method of sampling using fruit-baited traps.

3.2 INTRODUCTION

3.2.1 Habitat disturbance and biodiversity

Globally there are approximately 1.5 – 1.8 million named species (Wilson, 2000). However, estimates of total global biodiversity are often much higher ranging from 5 – 50 million species (Bartlett *et al.*, 1999). More than half of these species are represented by insects (Stork, 1993). Thus, it is of major concern to understand how insect species respond to habitat disturbance. Within tropical regions a major form of habitat disturbance comes from the logging industry (Asner *et al.*, 2005). Globally large portions of remaining tropical forests are contained within timber concessions and reserved for selective logging (Nepstad *et al.*, 1999; Curran *et al.*, 2004; Asner *et al.*, 2004, 2005). Consequently much research has focused on examining the impacts of selective logging on insect species (*e.g.* Davis *et al.*, 2001; Lewis, 2001; Widodo *et al.*, 2004). However, even in frequently-studied taxa, such as Lepidoptera, there is little agreement on the most appropriate methods of sampling these species within tropical rainforests.

3.2.2 Butterflies as diversity indicators

It has been suggested that butterflies are possibly the best group of species for assessing terrestrial insect diversity (Kremen, 1992; Caldas and Robbins, 2003). Thus, butterflies have been widely used to quantify changes in diversity and for establishing conservation priorities following disturbance (Kremen, 1992; Sparrow *et al.*, 1994; Kerr *et al.*, 2000). There are numerous criteria that butterflies satisfy which make them an ideal taxon for monitoring diversity following habitat disturbance (McGeoch, 1998). For example, an estimated 90% of butterfly species have been described and butterfly biology and taxonomy are well known (Caldas and Robbins, 2003). In addition butterflies are abundant and occur in a range of habitats from disturbed to pristine areas (Caldas and Robbins, 2003). There are reliable field keys to identify butterflies and identification is relatively straightforward even in highly diverse tropical regions (DeVries, 1987; Otsuka, 1988, 1991; Corbet and Pendlebury, 1992). Butterflies are highly sensitive to small-scale changes in environmental conditions such as relative humidity, light levels and temperature (Sparrow *et al.*, 1994). In addition, butterflies depend on specific host plants as larvae. Thus, butterflies respond quickly to changes in environmental conditions and changes in host plant abundance caused by habitat disturbance (Sparrow *et al.*, 1994). Finally, butterflies species are often brightly

coloured, highly conspicuous and provoke high public interest making them ideal flagship species for conservation studies. The suitability of butterfly species for monitoring diversity has produced many studies that examine the impacts of selective logging on tropical butterfly diversity (*e.g.* Hill *et al.*, 1995; Hamer *et al.*, 1997, 2003; Willott *et al.*, 2000; Lewis, 2001).

3.2.3 Monitoring butterfly diversity

Within temperate regions standard monitoring protocols have been established for monitoring butterflies (Pollard, 1977, 1979; Pollard and Yates, 1993). Standard transect methods involve counting the number of individuals of particular butterfly species along 5 m wide transects that are walked by a recorder at a constant rate (Pollard and Yates, 1993). Although the standard transect method is primarily used for monitoring changes in abundance of individual butterfly species across different sites or over time (Pollard and Yates, 1993), it can be adapted to record the relative abundance of all butterfly species observed by the recorder (Ausden, 1996). This method has been used successfully to monitor butterfly diversity within temperate regions (*e.g.* Blair and Launer, 1997; Huntzinger, 2003; Maes *et al.*, 2003; Croxton *et al.*, 2005). However, within tropical forests the identification of species in flight is problematic (Walpole and Sheldon, 1999). This is primarily due to low light levels within the forest understorey making it difficult to spot many small, fast-flying species (*e.g.* species of Lycaenidae) (Walpole and Sheldon, 1999). In addition, tropical forests are highly species rich, containing many species of butterfly that are difficult to differentiate from congenerics. For example, in Borneo, *Chersonesia* spp., *Euthalia* spp. and *Tanaecia* spp. are difficult to identify from wing colour patterns (Otsuka, 1988). In addition, butterfly mimicry complexes are well documented in the tropics (Beccaloni, 1997; Joron and Mallet, 1998; Willmott and Mallet, 2004) and this makes differentiation between species in flight difficult (Walpole and Sheldon, 1999). This means studies using standard transect methods in tropical forests often need to include hand netting during sampling (Caldas and Robbins, 2003) or to spend additional time building a species inventory before sampling (Hill *et al.*, 1995). The use of fruit-baited traps largely overcomes these identification problems (DeVries, 1987; Daily and Ehrlich, 1995). Consequently fruit-baited traps are used in a growing number of studies investigating patterns of tropical butterfly diversity within tropical forests (DeVries, 1988; DeVries and Walla, 2001) and in studies investigating changes in butterfly diversity following

disturbance (DeVries *et al.*, 1997, 1999a; Wood and Gillman, 1998; Hamer *et al.*, 2003; Dumbrell and Hill, 2005).

3.2.4 Using fruit-baited traps to monitor tropical butterfly diversity

Data on the efficiency and most appropriate methods of sampling tropical butterflies using fruit-baited traps are accumulating (Hughes *et al.*, 1998; Wood and Gillman, 1998; Dumbrell and Hill, 2005). However, there is little uniformity in the sampling methods used between studies when using fruit-baited traps to investigate the impacts of habitat disturbance on tropical butterflies. This makes it difficult to draw general conclusions about the impact of habitat disturbance on tropical butterflies from published studies. For example, the amount of time spent sampling varies greatly among studies ranging from as few as 320 trap days (Wood and Gillman, 1998) to as many as ≈13,000 trap days (Hamer *et al.*, 2003). In addition to differences between studies in the number of days traps are sampled, the time period over which sampling is conducted varies among studies. For example, Pinheiro and Ortiz (1992) and Wood and Gillman (1998) both sampled over a similar number of trap days, these were 336 and 320 trap days respectively. However, Pinheiro and Ortiz (1992) sampled over a 12-month period sampling traps for two days each month, whereas Wood and Gillman (1998) sampled traps every day for one month.

3.2.5 Temporal sampling effort

Often tropical insect species show temporal fluctuations in abundance between wet and dry seasons (DeVries *et al.*, 1997; Novotny and Basset, 1998; Wagner, 2001). However, in areas such as Borneo, which are generally considered aseasonal (Walsh and Newbery, 1999) fluctuations in insect abundance may be less pronounced. However, Hill *et al.* (2003) and Hamer *et al.* (2005) showed tropical butterfly abundance in Borneo to be affected by relatively small monthly variation in rainfall. Further to this, butterfly species sampled using fruit-baited traps from primary and selectively-logged forest showed a different relationship between butterfly abundance and rainfall (Hamer *et al.*, 2005). Primary forest species tended to increase in abundance and diversity during the drier part of the year. However species in selectively-logged forest showed little variation in abundance with rainfall (Hamer *et al.*, 2005). Thus, primary forest is likely to be perceived as more diverse if sampling is conducted during drier months (Hamer *et al.*, 2005). This indicates that sampling should be conducted during both wetter and drier months and highlights the need

to spread sampling across a long time span, for example sampling every other month for a year rather than sampling six months consecutively. However, there are few data that address how differences in sampling effort over time affect perceived patterns of butterfly diversity.

Ecologists have long recognised the relationship between time and observed species numbers, the species time relationship (STR; Preston, 1960). The STR shows an increase in the observed numbers of species with an increase in time spent sampling (Preston, 1960). However, conservationists are increasingly relying on rapid, short-term monitoring protocols to assess insect diversity in primary and disturbed habitats (Jones and Eggleton, 2000; Kitching *et al.*, 2001). This is primarily due to a lack of resources available to conservationists which prohibit the use of long-term, extensive surveys (Balmford *et al.*, 2003). However, as long as STR patterns do not vary across habitats reliable comparative analysis can be conducted from rapid diversity assessment even if the STR has yet to asymptote (Magurran, 2004). However, the length of time over which sampling should be conducted tends to be an arbitrary decision based on funding and resources available. Mac Nally *et al.* (2004) examined whether the relationship between plant and butterfly diversity observed over a long-term data set was still observed with reduced temporal sampling effort. In their study, Mac Nally *et al.* (2004) showed that similar conclusions about associations between butterflies and plants were made regardless of sampling effort. This indicates that relatively short-term sampling can produce robust estimates of butterfly diversity. Thus, using fruit-baited traps may produce reliable estimates of butterfly diversity in primary and disturbed habitats from relatively short-term studies as long as sampling includes wetter and drier months (Hamer *et al.*, 2005) and STR patterns do not vary across habitats (Magurran, 2004). However, this has yet to be investigated.

3.2.6 Spatial sampling effort

It is increasingly evident that the perceived response of diversity to disturbance is dependent upon the spatial resolution at which sampling is conducted (Hamer and Hill, 2000; Cleary, 2003; Kaiser, 2003; Hill and Hamer, 2004; Ribas *et al.*, 2005). Hamer and Hill (2000) and Hill and Hamer (2004) reviewed previous studies that investigated the impact of habitat disturbance on tropical butterfly species. In these reviews Hamer and Hill (2000) and Hill and Hamer (2004) showed that studies reporting increased diversity were generally conducted at small (<1 ha) spatial scales whereas those reporting decreased

diversity or no change following habitat disturbance were conducted at large (> 3 ha) spatial scales. Hamer and Hill (2000) and Hill and Hamer (2004) reviewed 26 studies that investigated the impact of habitat disturbance on Lepidoptera, nine of these studies used fruit-baited traps. One of the nine studies that used fruit-baited traps (Pinherio and Ortiz, 1992) was conducted over a small spatial scale, the rest sampled at a relatively large spatial scale. This is primarily because fruit-baited traps are assumed to sample over a 100 m radius, thus it is assumed that a single trap will sample 3.16 ha (Hamer and Hill, 2000). Approximately half of the studies that used fruit-baited traps reported a decrease in diversity following habitat disturbance whereas the others reported no effect of habitat disturbance on butterfly diversity (Hamer and Hill 2000; Hill and Hamer, 2004). Studies that reported no effect of habitat disturbance on butterfly diversity tended to be conduct a smaller spatial resolution to those that reported decreased diversity following habitat disturbance (Hill and Hamer, 2004). However, it is unclear at what spatial resolution a difference in diversity following habitat disturbance would be detected when using fruit-baited traps to monitor tropical butterflies.

3.2.7 Trap efficiency

The efficiency of sampling using fruit-baited traps depends largely on the ability of traps to retain butterflies before being emptied each day. Few data are available on the best time of day to sample fruit-baited traps or how efficient traps are at retaining butterflies once captured. Studies in the Neotropics suggest that the time of day has a significant effect on trapping efficiency (Hughes *et al.*, 1998). Hughes *et al.* (1998) showed that the number of individuals captured by fruit-baited traps was significantly higher between 10.00 am and 5.00 pm than in periods before or after these times. This reflected the diurnal nature of the species captured (Hughes *et al.*, 1998). In general, most studies sample between 9.00 am and 2.00 pm (Pinherio and Ortiz, 1992; Hill *et al.*, 2001; Dumbrell and Hill, 2005). This is because this probably coincides with periods of peak flight activity in tropical butterflies (Hill *et al.*, 1995). However, there are few data available on the most appropriate time to sample during the day. In addition, it is unclear how long butterflies remain within the traps once captured. It has been suggested that butterflies that enter the traps tend to remain there until the traps are emptied and only a small proportion of individuals (< 5%) are lost prior to traps being emptied (Hill *et al.*, 2001). However, there is little empirical evidence to support this. Detailed information on how efficient traps are and what time of day to sample

are needed to enable conservationists to partition their resources in a way that maximises their sampling efficiency. This in turn may give a more robust estimate of diversity.

3.2.8 Chapter objectives

In this chapter,

1. I re-analyse existing data and provide new data that investigate using fruit-baited traps to monitor the impacts of habitat disturbance on tropical butterfly diversity.

2. I investigate how temporal and spatial sampling effort influences the perceived response of butterfly diversity to selective logging.

3. I examine what time of day the majority of individual butterflies typically enter fruit-baited traps.

4. I investigate the efficiency of fruit-baited traps in retaining butterflies once captured and calculate the length of time butterflies typically remain within the traps.

5. I use the results to make recommendations for future conservation studies on how to sample tropical butterflies using fruit-baited traps.

3.3 Materials and Methods

A brief recap of the general methods used in this chapter follows. For detailed information on the study site, butterfly sampling methods and analysis see Chapter 2 General Materials and Methods.

3.3.1 Study site

Fieldwork was conducted from October 1999 – September 2000 and from April – May 2004 at the Danum Valley Field Centre (DVFC) and surrounding Ulu Segama Forest Reserve (USFR) in Sabah, Malaysian Borneo (5°N, 117°5'E). Sampling during this study was conducted within primary forest adjacent to DVFC and within forest that was selectively-logged in 1989 using high lead and tractor extraction methods, where all commercially viable stems > 60 cm diameter at breast high were removed. Logging extraction data from 1989 indicate that approximately 180,000 m^3 of timber was extracted (Innoprise, 1992).

3.3.2 Sampling effort

All butterfly data analysed within this section (3.3.2 Sampling effort) were collected by Suzan Benedick and Nasirah Mustaffa (Benedick, 2001; Mustaffa, 2001). The following section, *3.3.2.1 Butterfly sampling*, outlines the methods used by S. Benedick and N. Mustaffa to collected butterfly data.

3.3.2.1 Butterfly sampling

Fieldwork was conducted from October 1999 – September 2000. Butterflies were trapped along two 2-km transects, one in primary forest (the same transect as in Chapter 4) and the other in forest selectively-logged in 1989 (see Figure 2.9 in Chapter 2 for location of 1989 logging coupe). Fruit-baited traps were hung approximately 2 m above ground level every 100 m along each transect. All traps were baited with fresh banana prior to the first day of sampling and an additional piece of banana was added daily. This ensured a mixture of fresh and well rotted fruit. Each sampling period lasted for 12 days per month with sampling each month alternating between primary and selectively-logged forest sites. Six one-month samples were collected in each habitat (Table 3.1). Typically September – February are wetter months and March – August are drier months (Hamer *et al.*, 2005), thus sampling incorporated an equal number of wetter and drier months in each habitat. Traps

were checked daily between 09:30 and 13:00 hours. All butterflies caught were identified to species level (following Otsuka, 1988), marked with a felt-tipped pen and released. All recaptured butterflies were excluded from subsequent analysis. Any butterflies that could not be identified in the field (*e.g. Tanaecia* spp. and *Euthalia* spp.) were collected and identified in the laboratory following keys and figures in Corbet and Pendlebury (1992), this included dissection of male genitalia where necessary.

Primary forest		Selectively-logged forest
October 1999	--------	November 1999
December 1999	--------	January 2000
February 2000	--------	March 2000
April 2000	--------	May 2000
June 2000	--------	July 2000
August 2000	--------	September 2000

Table 3.1 Location of sampling during the 12-month study, 6-months data were collected in primary and selectively-logged forest. The dashed line indicates adjacent pairs of months between habitats. Comparison of diversity data between habitats were always between adjacent months.

3.3.2.2 Diversity analysis

Species accumulation curves were computed using rarefaction for data from primary and selectively-logged forest. To investigate whether the species accumulation rates were similar in each habitat, data were $\log_{10}$-transformed and the slopes of the species accumulation curves were compared using ANCOVA. I calculated three indices of α diversity, Shannon-Wiener, Margalef (species richness) and Simpson (species evenness), for both primary and selectively-logged forests following Magurran (2004). I used bootstrapping methods to calculate confidence intervals for each index (Sokal and Rohlf, 1995) and compared indices between habitats using *pairwise* randomization tests based on 10,000 re-samples of species abundance data, following Solow (1993). Analysis of butterfly diversity was conducted using the computer programs PISCES and EstimateS.

3.3.2.3 Temporal sampling effort

To investigate how the duration of sampling affects the perceived response of butterfly species to selective logging I analysed diversity data over a range of time spans. Butterfly diversity was compared between primary and selectively-logged forest combining data across the 12-month study (Table 3.1, primary forest combing 1 – 6 month samples; selectively-logged forest combing 1 – 6 month samples). Data were then sub-divided into 1-month samples from primary and selectively-logged forest. Each 1-month sample from primary forest was paired with the adjacent 1-month sample from selectively-logged forest (Table 3.1) and butterfly diversity was compared between habitats using pairwise randomization tests based on 10,000 re-samples of species abundance data, following Solow (1993). This gave six comparisons of diversity between primary and selectively-logged forest. Data from two pairs of 1-month samples (paired between primary and selectively-logged forest) were then combined. This was then repeated for every possible combination of two pairs of one-month samples from primary and selectively-logged forest. This allowed diversity to be compared between habitats using two-month's data. This procedure was then repeated comparing diversity between habitats combining 3, 4 and 5-month's data.

3.3.2.4 Spatial sampling effort

To investigate how the spatial resolution of a study affects the perceived response of butterfly species to selective logging I analysed diversity data over a range of spatial scales (0.4 – 2.0 km). First, data were combined across the twelve month study (Table 3.1). Data were initially collected from two 2-km transects (one in primary forest, one in selectively-logged forest). Data were then subdivided into five 0.4 km samples. Each 0.4 km sample from primary forest was paired with the same 0.4 km sample from selectively-logged forest (*i.e.* the first 400 m on each transect were paired then the second) and butterfly diversity was compared between habitats using pairwise randomization tests based on 10,000 re-samples of species abundance data, following Solow (1993). This gave five comparisons of diversity between primary and selectively-logged forest. Data from two pairs of 0.4 km samples (paired between primary and selectively-logged forest) were then combined. This was then repeated for every possible combination of two pairs of 0.4 km samples from primary and selectively-logged forest. This allowed diversity to be compared between

habitats using data from 0.8 km transects. This procedure was then repeated comparing diversity between habitats using data from 1.2 km and 1.6 km transects.

3.3.3 Trap efficiency

3.3.3.1 Butterfly sampling

I conducted fieldwork from April – May 2004. Butterflies were trapped along one 500 m transect in primary forest adjacent to DVFC. Fruit-baited traps (n = 5) were hung approximately 2 m above ground level every 100 m of the 500 m transect. Traps were baited with fresh banana prior to sampling and an additional piece of banana was added daily at 8 am. All traps were checked hourly between 8 am – 5 pm everyday for 12 days. All butterflies caught were identified, marked with a felt pen and placed back into the trap. The time of day each individual was first captured and time spent in the trap were recorded.

3.3.3.2 Sampling time

To investigate what time of day individuals entered the traps, data were combined across the 12-day study period for each of the five traps. Differences in the mean number of individuals recorded in traps at each hourly sample were investigated using a Kruskal-Wallis test. To examine which hourly sample contained most individuals *post hoc* comparisons between pairs of hourly samples were investigated using Mann-Whitney U tests.

3.3.3.3 Trap efficiency

The reliability of sampling using fruit-baited traps depends primarily on the efficiency of the traps to retain butterflies before a recorder can sample them. To investigate how efficient fruit-baited trap are at retaining individuals once captured, data were combined across the 12-day study and across the 5 traps. The length of time individuals spent in traps was plotted as the cumulative proportion of individuals remaining in the trap over time.

3.4 RESULTS

3.4.1 Butterfly diversity in primary and selectively-logged forest

Excluding recaptures, a total of 2039 individuals from 58 species of fruit-feeding Nymphalid (Family: Nymphalidae; sub-families, Satyrinae, Morphinae, Nymphalinae, Charaxinae) butterfly were trapped over the 12-month study period (1999 – 2000). 1102 individuals from 54 species were trapped in primary forest and 937 individuals from 44 species were trapped in selectively-logged forest (Appendix 1).

3.4.1.1 Species accumulation curves

Inspection of species accumulation curves (Figure 3.1) showed species accumulation had begun to asymptote in both primary and selectively-logged forests. Thus, further time spent sampling may have added only a few additional data and would be unlikely to qualitatively affect the results (Figure 3.1). Therefore any comparisons between habitats are likely to be robust and unlikely to be the result of differences in sampling efficiency between traps in primary and selectively-logged forest. Species accumulation estimates using rarefaction showed primary forest had greater species richness than selectively-logged forest (Figure 3.1). There was no significant difference in species accumulation rates between primary and selectively-logged forest (Figure 3.1, ANCOVA of rarefied species richness in primary and selectively-logged forest with sampling effort as a covariate, habitat by sampling effort interaction, $F_{1,8} = 2.28, p = 0.17$).

3.4.1.2 α diversity

Primary forest was significantly more diverse than selectively-logged forest when data from the entire 12-month study period were combined (6-month primary forest, 6-month selectively-logged forest) for analysis using Shannon-Wiener's and Simpson's indices (Table 3.2; pairwise randomisation test, Shannon-Wiener index $\delta = 0.24$, $p < 0.0001$; Simpson's index, $\delta = 1.96$, $p = 0.004$). However, there was no difference in diversity between habitats when measured using Margalef's index (Table 3.2; pairwise randomisation test, $\delta = 0.71, p = 0.25$).

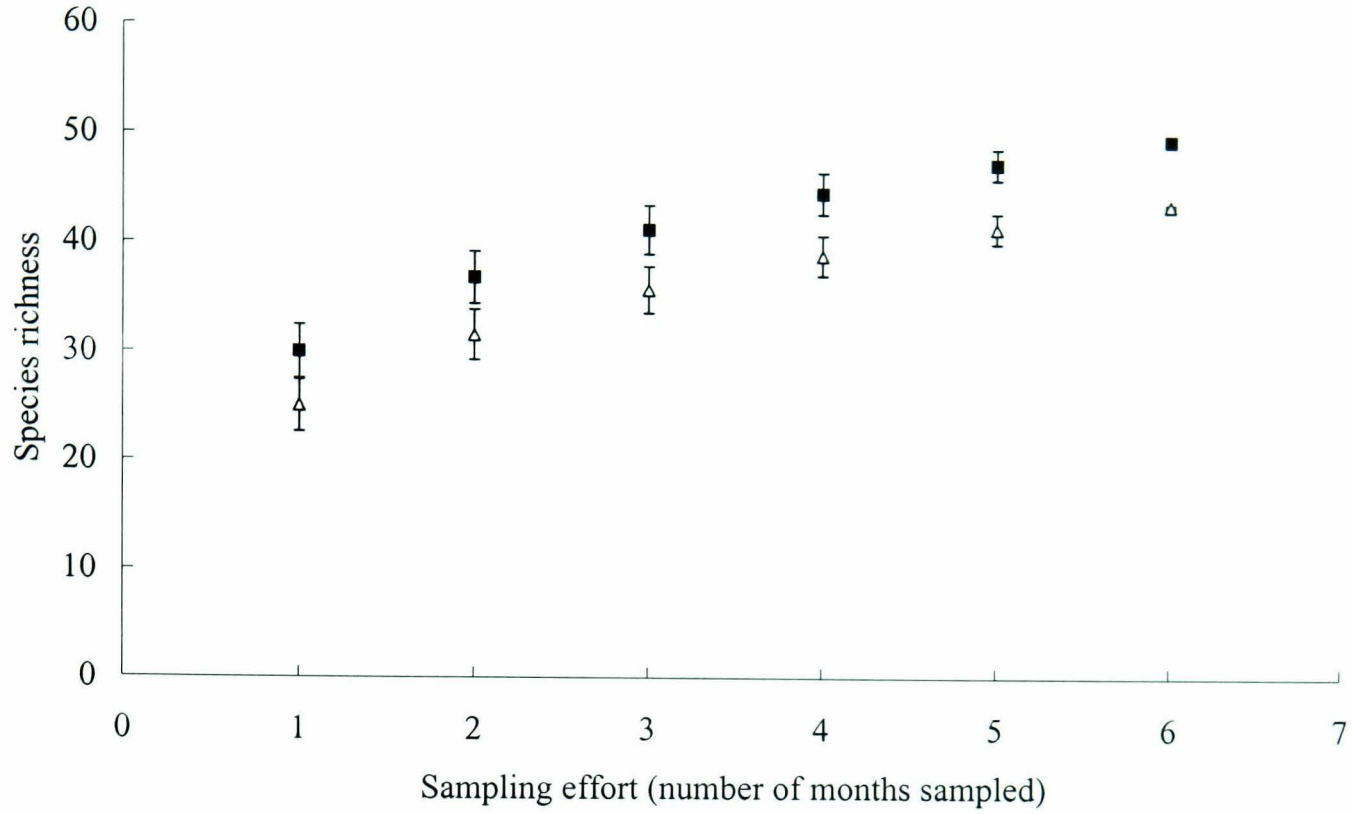


Figure 3.1 Species accumulation curves in primary (squares) and selectively-logged (triangles) forest. Data points show estimated species richness (± SE) using rarefaction. There was no significant difference in the rates of species accumulation between habitats.

	Primary forest		Selectively-logged forest	
No. of species	50		44	
No. of individuals	1102		937	
Shannon-Wiener	**2.90**	(0.14)	**2.67**	(0.16)
Simpson	**11.42**	(2.29)	**9.46**	(1.47)
Margalef	7.00	(1.14)	6.28	(1.03)

Table 3.2 Species richness, abundance and diversity of Nymphalid butterflies sampled over 12 months (6 months in primary forest and 6 months in selectively-logged forest). Diversity indices are shown with 95% confidence intervals in brackets. Values highlighted in bold are significantly different between habitats at the 5% level.

3.4.2 Detecting a difference in diversity between primary and selectively-logged forest

Sampling effort can be broadly split into temporal effort (how long to sample for) and spatial effort (what distance to sample over). In order to examine what sampling effort is required to detect a significant difference in diversity between primary and selectively-logged forest, data were analysed from a range of sampling extensities.

3.4.2.1 Temporal sampling effort

The probability of detecting a significant difference in diversity between primary and selectively-logged forest increased with increasing number of months sampled (Table 3.3, Spearman correlation of the probability of detecting a significant difference in diversity between habitats and the number of months sampled, Simpson's index, $r = 0.89$, $p = 0.018$; Shannon-Wiener index, $r = 0.95$, $p = 0.003$). There was a 100% probability of detecting a significant difference in diversity between primary and selectively-logged forest after 5 months when diversity was measured using Shannon-Wiener index (Table 3.3). When diversity was measured using Simpson's index, the probability of detecting a significant difference in diversity between habitats did not reach 100% until 6 months of sampling (Table 3.3). However, the probability of detecting a significant difference in diversity between habitats was approaching 100% after 5 months of sampling (Table 3.3). Thus, 5 months sampling effort produces sufficient data to detect a significant difference in diversity between primary and selectively-logged forest when investigating the impacts of selective logging on butterfly diversity using fruit-baited traps.

Simpson's index				
Months sampled	Replicates	Decrease	Increase	No Change
1	6	0.17	0	0.83
2	15	0.20	0	0.80
3	20	0.30	0	0.70
4	15	0.33	0	0.67
5	6	0.83	0	0.17
6	1	1.00	0	0.00
Shannon-Wiener index				
Months sampled	Replicates	Decrease	Increase	No Change
1	6	0.17	0	0.83
2	15	0.33	0	0.67
3	20	0.55	0	0.45
4	15	0.66	0	0.34
5	6	1.00	0	0.00
6	1	1.00	0	0.00

Table 3.3 Probability of detecting a significant difference in the diversity of Nymphalid butterflies between primary and selectively-logged forest using fruit-baited traps over a range of sampling time spans. Diversity is measured using Simpson's and Shannon-Wiener's indices. 5 months sampling effort produced sufficient data to detect a significant difference in diversity between primary and selectively-logged forest.

3.4.2.2 Spatial sampling effort

The probability of detecting a significant difference in diversity between primary and selectively-logged forest increased with increasing transect length (Table 3.4, Spearman correlation of the probability of detecting a significant difference in diversity between habitats and transect length, Simpson's index, $r = 0.96$, $p = 0.005$; Shannon-Wiener index, $r = 0.96$, $p = 0.005$). There was a 100% probability of detecting a significant difference in diversity between primary and selectively-logged forest when butterflies were sampled from a 1.6 km transect with diversity measured by Simpson's and Shannon-Weiner's indices (Table 3.4). Thus sampling from a 1.6 km transect produces sufficient data to detect a significant difference in diversity between primary and selectively-logged forest when investigating the impacts of selective logging on butterfly diversity using fruit-baited traps.

Simpson's index				
Transect length (km)	Replicates	Decrease	Increase	No Change
0.40	5	0.20	0	0.80
0.80	10	0.30	0	0.70
1.20	10	0.50	0	0.50
1.60	5	1.00	0	0.00
2.00	1	1.00	0	0.00
Shannon-Wiener index				
Transect length (km)	Replicates	Decrease	Increase	No Change
0.40	5	0.00	0	1.00
0.80	10	0.40	0	0.60
1.20	10	0.50	0	0.50
1.60	5	1.00	0	0.00
2.00	1	1.00	0	0.00

Table 3.4 Probability of detecting a significant difference in the diversity of Nymphalid butterflies between primary and selectively-logged forest using fruit-baited traps over a range of spatial resolutions. Diversity is measured using Simpson's and Shannon-Wiener's indices. Sampling from a 1.6 km transect produced sufficient data to detect a significant difference in diversity between primary and selectively-logged forest.

3.4.3 Efficiency of fruit-baited traps in retaining Nymphalid butterflies

In order to examine the efficiency of fruit-baited traps in retaining captured butterflies and to investigate what the most appropriate time of day and frequency of sampling from fruit-baited taps is data from an intensive 12-day study were analysed.

Excluding recaptures, a total of 62 individuals from 19 species of fruit-feeding Nymphalid (Family: Nymphalidae; sub-families, Satyrinae, Morphinae, Nymphalinae, Charaxinae) butterfly were trapped over the 12-day study period (2004). During the 12-day study, 160 capture events were recorded. A capture event was when an individual was first caught in the trap or when an individual subsequently returned to a trap after previously leaving.

3.4.3.1 Sampling time

Butterflies were sampled from five fruit-baited traps between 8:00 am and 5:00 pm. Between 5 pm and 6 pm, all captured butterflies remaining in the trap escaped. The number of individuals recorded in the traps was significantly different between sampling times (Figure 3.2, Kruskal-Wallis test, $H_{9.0} = 24.05$, $p = 0.004$). There were significantly more new individuals captured at 9.00 am than at any other time of day (paired Mann-Whitney U tests $Z = -2.31 - -2.63$, p 0.02 – 0.008). This suggests that a large proportion (38%) of new daily captures is recorded at 9.00 am, indicating most butterflies entered the traps between 8.00 am and 9.00 am (Figure 3.2). A further 12% of new captures were recorded at 10.00 am, indicating that ≈50% of all new captures occurred before 11.00 am (Figure 3.2).

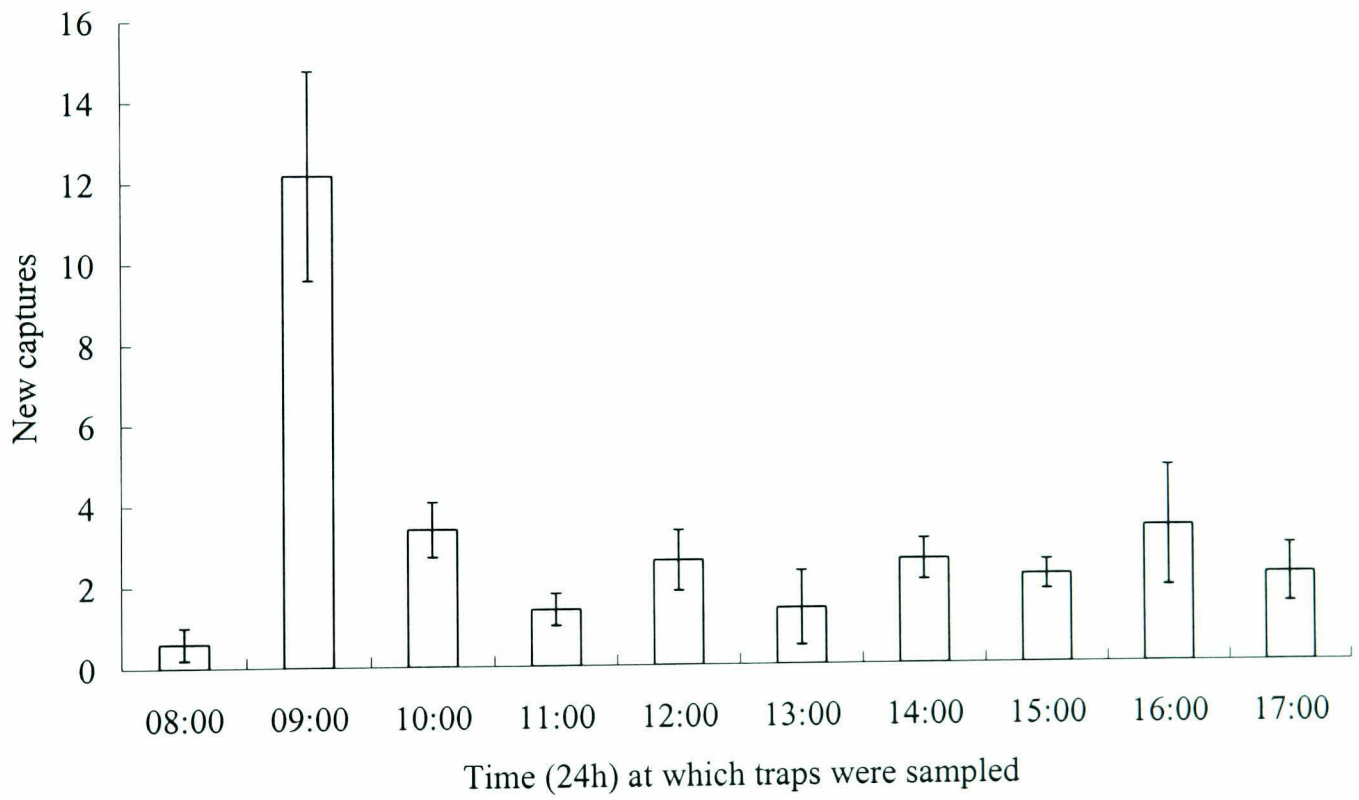


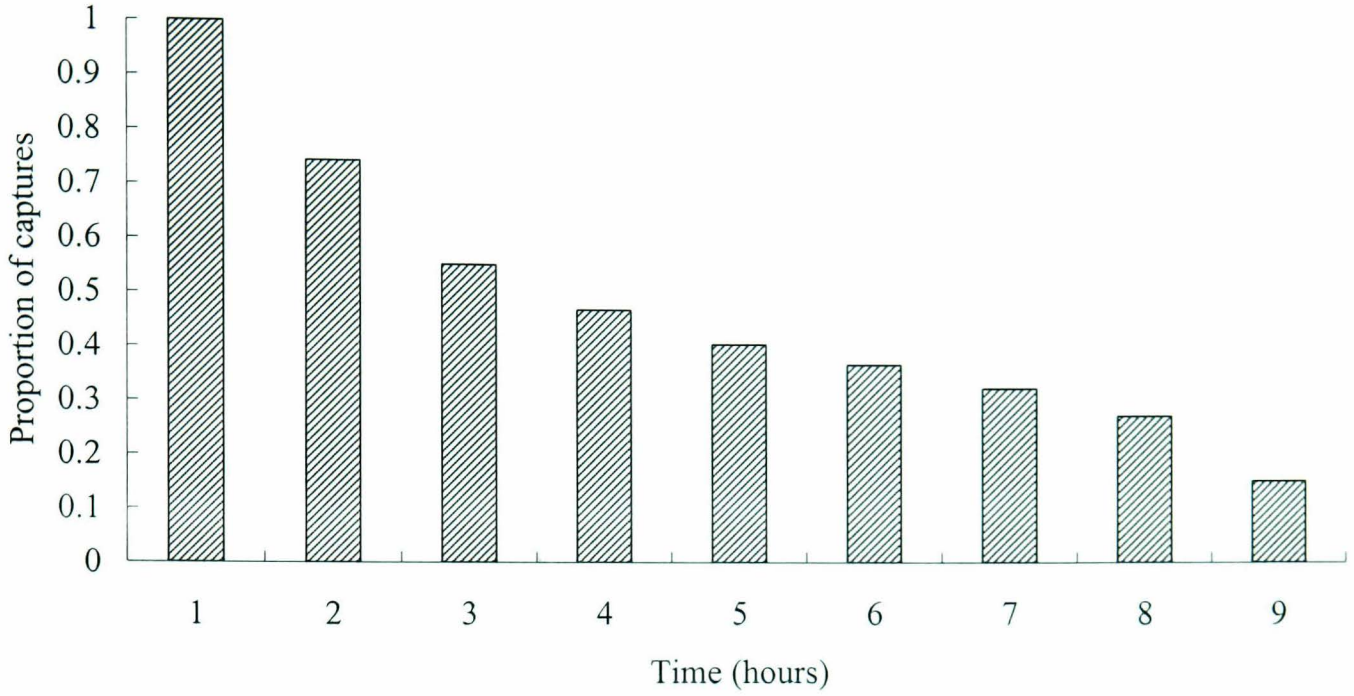
Figure 3.2 Mean (± SE) captures of butterflies recorded in 5 fruit-baited traps between 8.00 am and 5.00 pm, ≈50% of all captures occurred before 11.00 am. Significantly more captures were recorded at 9.00 am than in any other hourly sample.

3.4.3.2 Trap efficiency

The reliability of sampling with fruit-baited traps depends largely on the efficiency of a trap to retain butterflies before being sampled. Half (50%) of all captured butterflies remained in the trap for four hours after initially being trapped (Figure 3.3). However, as all captured

butterflies left before 6.00 pm butterflies caught in the afternoon remained in the traps for less time than those caught in the morning. Approximately 50% of butterflies that entered the trap between 8.00 and 9.00 am remained within the trap until 5.00 pm (Figure 3.3). More than 70% of butterflies that entered the trap between 8.00 and 9.00 am remained within the trap for at least five hours (Figure 3.3). Thus if traps are sampled between 9.00 am and 2.00 pm at least 50% of all captures are recorded.

A



B

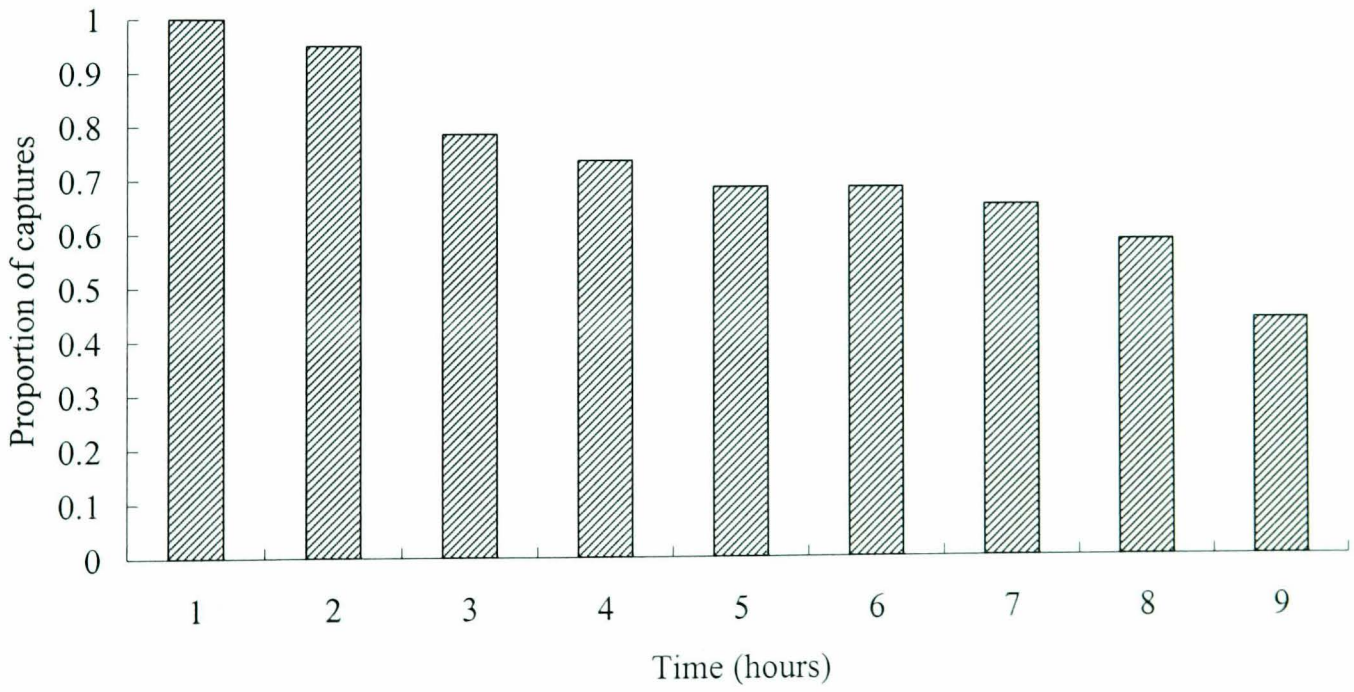


Figure 3.3 Proportion of captured butterflies that remain within a fruit-baited trap over time. The majority of butterflies remained within the trap for at least five hours after capture (A). > 70% of individuals caught between 8.00 – 9.00 am remained for five hours (B).

3.5 DISCUSSION

3.5.1 Sampling effort

Primary forest was significantly more diverse than forest selectively-logged 12 years previously when measured using Shannon-Wiener's and Simpson's indices combining data across all traps and months (12 months total; primary forest 6 months, selectively-logged forest 6 months). However, there was no difference in diversity between habitats when measured using Margalef's index. Subsequently there was no significant difference in diversity between habitats measured by Margalef's index when data were analysed from fewer months or over small spatial resolution.

3.5.1.1 Temporal sampling effort

At least five 1-month samples were needed in order to detect a significant change in diversity between primary and selectively-logged forest. As STR patterns were not significantly different between habitats, primary forest had greater species richness than selectively-logged forest at all sampling efforts considered. However, there was no significant difference in diversity between habitats when data were analysed from fewer than five 1-month samples. This most likely reflects the large sample size needed for diversity indices to give a robust estimate of diversity (Magurran, 2004). Mac Nally *et al.* (2004) showed that similar conclusions about associations between butterfly and plant diversity were made regardless of sampling effort. Mac Nally *et al.* (2004) suggested that patterns of butterfly diversity in temperate regions can be examined even with greatly reduced sampling effort. In contrast, my results show relatively large periods of time are needed to examine patterns of tropical butterfly diversity and only a slight reduction ($\geq$ 33%) in sampling effort produces qualitatively different results. This is probably because, although tropical butterfly communities are highly species rich, few species are present in relatively large numbers (Hill, 1999). Thus as diversity indices require a relatively large sample size (numbers of individuals and species) to be calculated accurately, relatively long-term studies are required to produce sufficient data to calculate robust estimates of diversity (Magurran, 2004).

The five 1-month samples required to detect a significant difference in diversity between habitats were sampled over a 10 month study period alternating between habitats each month. Thus it is unclear as to whether qualitatively similar results would be observed

from five consecutive 1-month samples, or whether sampling needs to be spread across a 10-month period. Further data are needed to address this.

3.5.1.2 Spatial sampling effort

Data collected from at least a 1.6 km transect were needed in order to detect a significant difference in diversity between primary and selectively-logged forest. This result was similar to the analysis of diversity data, as a small reduction (≥40%) in sampling effort produced qualitatively different results.

In this study, even at the smallest spatial resolution analysed (0.4 km) the traps sampled over a relatively large spatial scale (≈3.2 ha assuming each trap had a 100 m sampling radius). Hamer and Hill (2000) and Hill and Hamer (2004) showed that decreased diversity or no effect on diversity following habitat disturbance would be expected in large scale (≥3.1 ha) studies. Thus my results agree with Hamer and Hill (2000) and Hill and Hamer (2004), as I reported no effect of selective logging when data were analysed at smaller spatial scales (≈3.2 ha), but I reported decreased diversity following selective logging when data were analysed at a larger spatial resolution (≥13 ha). Hill and Hamer (2004) suggested that habitat disturbance results in a more homogenous vegetation structure and that this would reduce faunal β diversity between samples, subsequently reducing overall habitat diversity. In contrast, primary forest has a very heterogeneous vegetation structure and thus high β diversity between samples. Therefore if butterflies are sampled over a relatively large spatial scale primary forest will be significantly more diverse than disturbed habitats due to higher within-habitat β diversity (Hill and Hamer, 2004). Thus, one possible explanation for the results of this study is that a relatively large spatial scale is needed to account for the impacts of habitat disturbance on forest heterogeneity (Hamer *et al.*, 2003). Thus, a significant decrease in diversity is more likely to be reported when data are analysed at a large spatial scale (≥13 ha). However, there is another possible explanation for the results of this study. When analysed at small spatial resolution data from fewer traps were used and subsequently the sample size is reduced. In a similar way to how reduced sampling time affects the perceived response of diversity to habitat disturbance, a reduction in spatial sampling effort may also lead to reduced power in analysis. It is therefore unclear as to whether these results are purely caused by reduced sample sizes or if a minimum 1.6 km transect is needed to account for the impacts of habitat disturbance on forest heterogeneity. This requires further study.

Species area relationships (SAR) and species time relationships (STR) interact (Adler and Lauenroth, 2003). When sampling is conducted at small spatial scales the slope of the STR is steep but at large spatial scales the slope of the STR is shallow (Adler and Lauenroth, 2003). A similar relationship was shown with SAR with a shallow gradient when sampling covers a long time span but a steep gradient when sampling covers a short time span. Thus reduced time spent sampling will result in a smaller sample size unless sampling covers a greater spatial scale and *vice versa*. What is unclear in this study is whether five 1-month samples are sufficient to detect a significant difference in diversity following selective logging if measured along a 1.6 km transect.

3.5.2 Efficiency of fruit-baited traps

Significantly more butterflies were trapped between 8.00 – 9.00 am than at any other time during the day. Approximately 40% of all captures entered the traps between 8.00 – 9.00 am. The remaining 60% of daily captures were distributed relatively equally over the rest of the day. All captured butterflies were observed leaving the traps before 6 pm each day. This study agrees with previous studies from the Neotropics that suggest that the majority of butterflies enter fruit-baited traps in the late morning to midday and from midday to early afternoon (Hughes *et al.*, 1998). This most likely reflects the diurnal nature of fruit-feeding Nymphalids (Hughes *et al.*, 1998). Hughes *et al.* (1998) recommended that butterflies should be sampled from the traps every two days, suggesting that few data would be lost compared to checking daily. However, results from this study showed that all captured butterflies leave the traps at dusk each day. In addition, individuals did not return to the same trap the following morning and some individuals were not recorded again. However, due to small sample size this could not be tested statistically. Thus, I suggest sampling daily is most efficient and is necessary to account for daily escape of butterflies from the traps at dusk. This is in contrast Hughes *et al.*'s (1998) suggestion that sampling every two days produces qualitatively similar data compared with sampling daily.

My results suggest that fruit-baited traps are efficient at retaining captured butterflies until being sampled. The majority (> 70%) of butterflies that entered the traps between 8.00 – 9.00 am remained there for at least five hours. Thus, sampling between 9.00 am – 2.00 pm will record the majority of daily captures. Most previous studies have emptied traps daily between 9.00 am – 2.00 pm (*e.g.* Wood and Gillman, 1998; Lewis, 2001; Hamer *et al.*, 2003; Dumbrell and Hill, 2005). Results from this study indicate that

this sampling method is most efficient at sampling the majority of butterflies attracted to fruit-baited traps.

3.5.3 Implications for the design of future conservation studies

Conservationists increasingly have to make difficult decisions about setting conservation priorities of species and habitats. Often conservationists rely on rapid, short-term monitoring protocols to assess insect diversity in primary and disturbed habitats (Jones and Eggleton, 2000; Kitching *et al.*, 2001). However, resources vary greatly between studies and geographic locations (Balmford *et al.*, 2003). Consequently there is little agreement about appropriate monitoring protocol for tropical insects. Here I showed that using fruit-baited traps are a reliable and efficient method for sampling tropical butterflies. This study highlighted that relatively long-term studies, conducted at a relatively large spatial resolution are needed to give a robust estimate of diversity changes following habitat disturbance. However, conservationists need to be aware that the perceived response of diversity to selective logging is dependent upon the sampling effort used. Based on the results of this study I conclude that fruit-baited traps can provide a useful tool for monitoring tropical butterfly diversity.

Chapter 4 Impacts of selective logging on ground and canopy assemblages of tropical-forest butterflies: implications for sampling

4.1 ABSTRACT

Commercial selective logging is a major form of habitat disturbance in Southeast Asian rainforests. However, despite growing research into the impacts of selective logging on faunal diversity there is little agreement on the most appropriate methods for sampling tropical species, making it difficult to draw conclusions from published studies. For example, many studies have used butterflies to assess impacts of selective logging but sampling has been conducted at ground level and the canopy fauna has often been ignored. In this chapter, I investigated the impacts of selective logging on ground and canopy fruit-feeding butterfly assemblages. Butterflies were sampled using fruit-baited traps in the canopy (≈25 m above ground level) and at ground level (≈2 m high). Analysis of data combined from canopy and ground level traps showed significantly lower diversity following selective logging. However, this result was not observed when data from only ground level traps were analysed. Primary forest was shown to support a butterfly assemblage comprised of species with significantly more restricted geographical ranges, and thus higher conservation value, compared with selectively-logged forest. This result was observed regardless of whether or not data were included from canopy traps. I confirmed results from previous studies and showed that tropical butterfly assemblages are vertically stratified through the forest strata. In addition, I showed that selective logging did not breakdown this pattern of vertical stratification and that both primary and selectively-logged forest had distinct canopy assemblages. However, selective logging caused a loss of canopy species. Canopy assemblages were shown to contain geographically wide-spread species with low conservation value, whereas ground assemblages contained more endemic species with higher conservation value. I conclude that sampling in the canopy is crucial when building species inventories, but of less importance when determining the impacts of selective logging on restricted-range species.

This chapter is re-written from Dumbrell and Hill (2005).

4.2 INTRODUCTION

4.2.1 Species diversity in tropical forest canopies

Tropical forest canopies are known to support a highly diverse fauna (Erwin, 1982; Stork, 1988; Nadkarni and Longino, 1990; Lowman and Moffett, 1993), often containing species only found in the canopy (Stork, 1991; Francis, 1994; Ozanne *et al.*, 2003; Sørensen, 2003). Estimates of global species richness suggest tropical forest canopies contain approximately 40% of all extant species (Rodgers and Kitching 1998; Novotny *et al.*, 2002; Ozanne *et al.*, 2003). This has led to a growing body of literature attempting to quantify species richness in tropical forest canopies (*e.g.* Erwin, 1982; Stork, 1991; Russell-Smith and Stork, 1994, 1995; Guilbert, 1998; Novotny *et al.*, 2002; Srinivasa *et al.*, 2004). For example, Stork (1991) sampled *ca* 24,000 individuals from ≥3000 species of arthropods from the canopy of just ten trees in Borneo. In contrast, Basset (1999) working in Guyana sampled only from saplings and recorded *ca* 9000 individuals from *ca* 250 species. These studies are not directly comparable due to differences in sampling location, techniques and intensities. However, the overwhelming difference in species richness between the two studies highlights the highly species-rich nature of tropical forest canopies. More recent work has shown that estimates of canopy species richness maybe even higher when samples are included from within canopy epiphytes (Ellwood *et al.*, 2002; Stuntz *et al.*, 2002; Ellwood and Foster 2004). These studies not only illustrated the high species diversity of tropical forest canopies, but also highlighted potential microhabitats within the canopy that may support a greater abundance of species than previously recorded (Ellwood *et al.*, 2002; Stuntz *et al.*, 2002; Ellwood and Foster 2004).

The high level of species richness in tropical forest canopies led to dramatic revisions of estimates of global insect species richness (Erwin, 1982). Erwin (1982), using insecticidal fogging techniques, sampled canopy insects in Panama from the tree *Luehea seemannii*. Working only on Coleoptera, Erwin (1982) suggested that global species richness estimates should approximate 30 million species. Erwin (1982) extrapolated this figure by first estimating the proportion of canopy Coleoptera that specialised in feeding only on *Luehea seemannii* and assuming other tree species were host to a similar proportion of specialists. Once the number of specialist Coleoptera is known, an approximate of other specialist insect species can be estimated (assuming 40% of insects are Coleopterans) and this can be multiplied by total global tree species richness (Erwin, 1982). Erwin's (1982)

estimation of global insect richness has subsequently met with much criticism (Stork 1988, 1993, 1994; May, 1990; Novotny *et al.*, 2002). Critiques of Erwin's (1982) estimate generally suggest that although the calculations used reflect an accurate method of estimating global insect richness, more conservative estimates of the degree of host plant specificity and the proportion of insect species represented in the Coleoptera should be used (Novotny *et al.*, 2002). Nonetheless, Erwin's (1982) estimate highlights the high faunal species richness and highly-specialised nature of species present in tropical canopies. Further to this, Erwin (1982) also highlighted the possibilities of sampling from within the rainforest canopy, a habitat often out of reach to most naturalists (Lowman and Wittman, 1996; Godfray *et al.*, 1999).

4.2.2 Vertical stratification in tropical rainforests

It is estimated that approximately 20 – 25% of invertebrate species are unique to the canopy (Sørensen, 2003). In addition, about 10% of vascular plants are epiphytic species also unique to the canopy (Ozanne *et al.*, 2003). This results in distinct species assemblages within the canopy that are often independent of species assemblages within the low-level forest strata. This pattern of vertical stratification is shown in a number of taxa including mammals (Francis, 1994), insects (Schulze *et al.*, 2001), arachnids (Russell-Smith and Stork, 1994, 1995), birds (Walther, 2002a, 2002b) and plants (Baker and Wilson, 2000). Generally, the availability of food within the forest ground and canopy strata causes patterns of vertical stratification in birds, mammals and some invertebrate groups (Karr, 1980; Francis, 1994; Russell-Smith and Stork, 1994, 1995). For example, within Neotropical bird communities frugivores are more abundant in the forest canopy, reflecting the availability of fruit (Karr, 1980).

For the Lepidoptera, it is known that light plays an important role in determining the distribution of butterflies from the ground to canopy levels within the tropical forest (*e.g.* DeVries, 1988; DeVries *et al.*, 1997; Hill *et al.*, 2001, Schulze *et al.*, 2001). Lepidoptera have distinct understorey and canopy assemblages; vertical stratification of these assemblages is thought to be caused by differences in species' light preferences within their immediate environment (DeVries, 1988; Burd, 1994; Beccaloni, 1997; DeVries *et al.*, 1997, 1999a; Schulze & Fiedler, 1998; Hill *et al.*, 2001, Schulze *et. al.*, 2001). Light levels are highest within the forest canopy and decrease towards ground level. Consequently, many ground butterfly species prefer a darker light environment with light-loving species

more abundant in the forest canopy (Hill *et al.*, 2001). Apart from differences in light levels, females of some species of ithomiine (Nymphalidae: Ithomiinae) butterflies fly at different heights due to larval host plant availability and males fly at similar heights to locate females (Beccaloni, 1997). Many species of the predominantly Neotropical Ithomiinae form distinct Müllerian mimicry complexes and differences in larval host plant height produce vertical stratification of 'mimicry rings' caused by butterflies flying at a similar height to the location of their larval host plants (Beccaloni, 1997; DeVries *et al.*, 1999b; Willmott and Mallet, 2004; Joron, 2005).

Vertical stratification of butterfly communities has produced canopy and ground assemblages that contain species with different ecological and morphological characters. For example, canopy Nymphalids have previously been shown to have morphologies associated with relatively high investment in flight (DeVries 1988; Hill *et al.*, 2001; Schulze *et al.*, 2001). Canopy species with morphologies associated with faster more powerful flight are better adapted to avoid insectivorous aerial-hawking birds which are more abundant within the canopy (Schulze *et al.*, 2001). In addition, wind speed is often higher in the canopy and this could select for species that are stronger fliers (Schulze *et al.*, 2001). In contrast, species located closer to the ground may be adapted for slower more manoeuvrable flight which aids movement thought the dense vegetation of the forest understorey (Schulze *et al.*, 2001).

4.2.3 Tropical forest disturbance and canopy species

Tropical rainforests are increasingly under threat from anthropogenic disturbance such as logging and shifting agricultural practices (Collins *et al.*, 1991). It is therefore of great current concern to understand the ecological consequences of this habitat disturbance on tropical forest species and ecosystems (Curran *et al.*, 2004). There is little agreement on the most appropriate methods for sampling species, even in well-studied taxa such as Lepidoptera. There is some information on the efficiency of different sampling methods for butterflies (Wood and Gillman, 1998; Walpole and Sheldon, 1999; Caldas and Robbins, 2003). Studies tend to investigate appropriate protocols for a single type of survey technique *e.g.* 'Pollard Transects' (Walpole and Sheldon, 1999; Caldas and Robbins, 2003), or compare between two sampling techniques *e.g.* fruit baited traps *versus* walk and count transects (Wood and Gillman, 1998). However, there is little information on best-practice for other issues relating to sampling protocols within forest habitats. Few data are available

on the appropriate placement of traps or transects within a habitat type, or whether sampling should include the canopy, and how different sampling methods may affect the perceived response of butterflies to habitat disturbance.

Data collected from the rainforest canopy have rarely been included in studies comparing the diversity of Lepidoptera in primary and disturbed habitats, the exceptions being Wood and Gillman (1998) and Fermon *et al.*, (2005). There has been one study that compared between primary forest fauna, disturbed forest fauna and primary forest canopy fauna (Willott, 1999), but in general few data are available on the effects of selective logging on canopy faunas. Selective logging reduces canopy cover and height, removing areas of dense canopy and producing large open gaps (Ganzhorn *et al.*, 1990; Burghouts *et al.*, 1994; Cannon *et al.*, 1994; Okuda *et al.*, 2003; Asner *et al.*, 2003). This change in forest structure is likely to alter the amount of light penetrating the forest and may lead to disruption in the vertical stratification of Lepidoptera species (Willott, 1999). Thus, previous studies have suggested that canopy butterfly species may be recorded at ground level in selectively-logged forest due to increased light levels (Willott *et al.*, 2000; Hill *et al.*, 2001). This in turn could affect estimates of diversity based solely on ground-level surveys and subsequently affect recorded differences between primary and selectively-logged habitats when data from the canopy are excluded. However, data are lacking on whether failure to sample in the canopy qualitatively affects reported response of diversity to habitat disturbance. Given the logistic difficulties of canopy sampling, such information would be valuable for designing future sampling protocols.

4.2.4 Conservation value of tropical-forest butterflies

Comparative studies between primary and disturbed habitats tend to focus on α diversity. Point diversity measures are useful in comparing habitats in terms of differences in species richness and abundance. However, they give little information on the composition of the fauna in either habitat or their respective conservation values (Hill *et al.*, 1995; Hamer *et al.*, 1997; Willott *et al.*, 2000; Hamer *et al.*, 2003). When assessing the impacts of habitat disturbance, change in the conservation value of fauna within a habitat is often more important to conservation strategies than change in α diversity (Vane-Wright *et al.*, 1991). A widely-used predicator of species' conservation value is species' geographical range size, with locally endemic species having the highest conservation value (Vane-Wright *et al.*, 1991; Hill *et al.*, 1995; Hamer *et al.*, 1997; Willott *et al.*, 2000; Hamer *et al.*, 2003). This is

because local extinctions of endemic species have an increased probability of resulting in global extinction, whereas species with broad geographical ranges are less likely to become globally extinct even when local extinctions follow habitat disturbance. Thus, emphasis has shifted from quantifying changes in α diversity following selective logging to also examining changes in faunal conservation values assessed in terms of species' geographical range size (Hill *et al.*, 1995; Hamer *et al.*, 1997; Willott *et al.*, 2000; Hamer *et al.*, 2003). However, few data are available on whether inclusion of data from canopy samples would qualitatively affect estimates of the conservation value of assemblages following habitat disturbance.

4.2.5 Chapter objectives

In this Chapter,

1. I test the hypothesis that sampling from both canopy and ground levels is important for determining the impacts of habitat disturbance.

2. I investigate how the inclusion of diversity data from canopy traps affects the perceived response of tropical-forest butterflies to disturbance.

3. I investigate how the inclusion of data on geographical ranges of species from canopy traps affects the perceived conservation value of disturbed habitats

4. I test the hypothesis that selective logging causes a breakdown in the vertical stratification of tropical-forest butterflies by examining β diversity of butterflies between ground and canopy traps.

4.3. MATERIALS AND METHODS

A brief recap of the general methods used in this chapter follows. For detailed information on the study site and butterfly sampling methods see Chapter 2 General Materials and Methods.

4.3.1 Study site

Fieldwork was conducted during May and July 2003 and from January to February 2004 at the Danum Valley Field Centre (DVFC) and surrounding Ulu Segama Forest Reserve (USFR) in Sabah, Malaysian Borneo (5°N, 117°5'E). Sampling during this study was conducted within primary forest adjacent to DVFC and within forest that was selectively-logged in 1988 using high lead and tractor extraction methods, where all commercially viable stems > 60 cm diameter at breast high were removed. Logging extraction data from 1988 indicate that approximately 170,000 m^3 of timber was extracted from an area of approximately 2300 ha (Innoprise, 1992).

4.3.2 Butterfly sampling

Butterflies were trapped along two 2-km transects, one in primary forest and the other in forest selectively-logged in 1988. Traps were hung at ground level approximately 2 m above the ground (hereafter termed ground-level) every 100 m along transects (n = 40 ground-level traps in total). Canopy-level traps were hung directly above ground-level traps every 200 m (n = 20 canopy traps) and were lowered to ground level for sampling. Canopy traps were hung above every other ground trap. Canopy traps were set up by first firing a fishing line over a suitable tree branch using a bow and arrow. The fishing line was then used to reel up suitably thick rope and canopy traps were attached to these ropes and were then reeled up into the canopy to the appropriate height. Canopy traps were hung at similar heights in the two habitats (primary forest, mean height of traps = 27.2 m SE = 1.39; selectively-logged forest, mean height = 26.3 m SE = 0.67; t-test comparing heights; t_{18} = 0.74, $p > 0.1$).

All traps were baited with a piece of banana prior to the first day of sampling and an additional piece of banana was added daily. This ensured a mix of fresh and well-rotted fruit. Sampling was conducted for 12 days each month in each habitat over the four-month study period (48 days in total in each habitat). Traps were checked daily between 10 am and 2 pm. All butterflies caught were identified to species level, marked with a felt pen and

released at ground level irrespective of whether they were caught in the canopy or at ground level. Recaptures were excluded from diversity analyses. Recapture data were used to examine dispersal of individuals between traps.

4.3.3 Butterfly diversity

Species accumulation curves were computed using rarefaction for ground and canopy traps in primary and selectively-logged forest. I calculated three diversity indices; Shannon-Wiener, Margalef (species richness) and Simpson (species evenness) for both primary-forest and selectively-logged-forest habitats following Magurran (2004). I used bootstrapping methods to calculate confidence intervals for each index (Sokal and Rohlf, 1995). Following Solow (1993), I compared diversity indices between habitats using pairwise randomization tests based on 10,000 re-samples of species abundance data. Species turnover between canopy and ground-level assemblages was investigated using Whittaker's qualitative index of β diversity, following methods in Magurran (2004). Analysis of butterfly diversity was conducted using the computer programs PISCES and EstimateS.

4.3.4 Geographical distribution of butterfly species

I ranked all butterfly species in terms of their geographical distributions (following Hamer *et al.*, 2003). The endemic species *Mycalesis kina* and *Mycalesis amoena* shared the highest rank (rank = 1). The geographically most widespread species *Melanitis leda* (which occurs through the African, Oriental and Australasian regions) was assigned the lowest rank (rank = 61). Species with distributions restricted to areas of Sundaland (Borneo, Sumatra, Java, West Malaysia and Palawan) were ranked 3-18. Species that had geographical distributions which also included the Oriental and Australasian regions were ranked 19-61 (Appendix 2). Differences between habitats in geographical distribution of species were investigated using Mann-Whitney U tests.

4.4 RESULTS

4.4.1 Butterfly diversity in primary and selectively-logged forest

Excluding recaptures, a total of 1280 individuals from 61 species of fruit-feeding Nymphalid (Family: Nymphalidae; sub-families, Satyrinae, Morphinae, Nymphalinae, Charaxinae) butterfly were trapped over the 4-month study period. 674 individuals from 58 species were trapped in primary forest and 606 individuals from 44 species were trapped in selectively-logged forest (Appendix 2).

4.4.1.1 Species accumulation curves

Inspection of species accumulation curves (Figure 4.1) showed that species accumulation rates appeared to have reached asymptotes in selectively-logged forest in both ground and canopy traps as well as in canopy traps in primary forest, whereas the species accumulation curve in ground traps in primary forest was still rising at the end of the study period. Primary forest is reported to be more diverse, thus any further data collection would be unlikely to qualitatively affect these results.

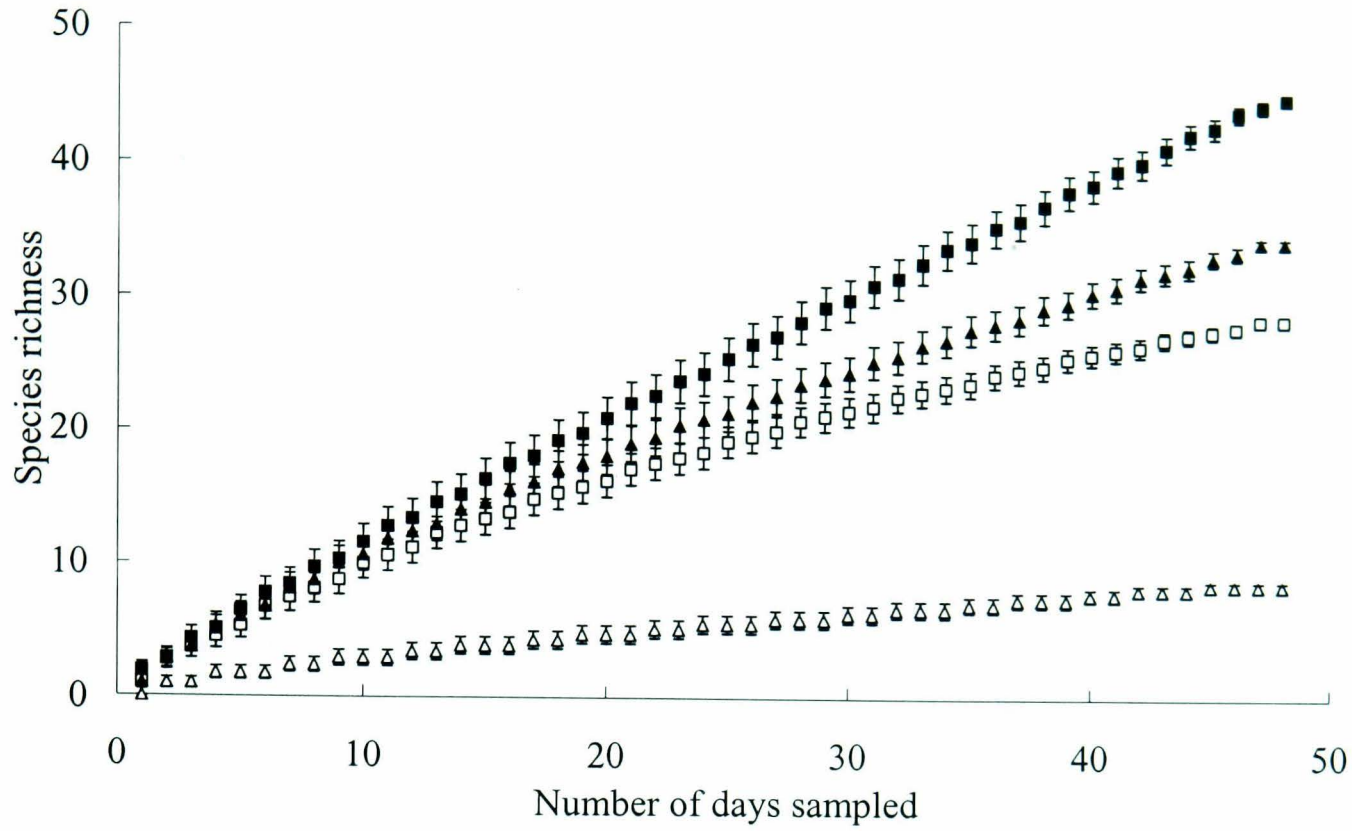


Figure 4.1 Species accumulation curves in primary (squares) and selectively-logged (triangles) forest in ground-level (solid symbols) and canopy (open symbols) traps. Data points show estimated species richness (+ SE) using rarefaction.

4.4.1.2 α diversity

Primary forest was significantly more diverse than selectively-logged forest when data from ground and canopy traps were combined for analysis (Table 4.1; pairwise randomisation tests; Shannon-Wiener's index, $\delta = 0.26$, $p < 0.001$; Margalef's index, $\delta = 2.04$, $p < 0.001$; Simpson's index was approaching significance, $\delta = 2.55$, $p = 0.06$). However, there was no difference in diversity between habitats when only ground level data were analysed (Table 4.1; Shannon-Wiener's index, $\delta = 0.11$, $p = 0.1$; Margalef's index, $\delta = 0.58$, $p = 0.3$; Simpson's index, $\delta = 0.84$, $p = 0.5$).

These results were qualitatively the same regardless of whether data were analysed per transect (as above) or per trap (Table 4.2; *t*-test assuming unequal variance; combined canopy and ground data analysed per trap, Shannon-Wiener's $t_{39.06} = 2.38$, $p = 0.02$, Margalef $t_{43.30} = 2.35$, p = 0.02, Simpson, $t_{56.33} = 1.30$, $p = 0.2$; ground-level data only, Shannon-Wiener $t_{35.19} = 0.35$, $p = 0.35$, Margalef $t_{36.67} = 0.97$, $p = 0.34$, Simpson, $t_{31.67} = 0.27$, $p = 0.79$).

	Habitat								
	Primary forest					Selectively-logged forest			
	Ground		Canopy		Total	Ground		Canopy		Total	
Species present	47		29		58	43		9		44	
Unique species	29		11		17	35		1		3	
Individuals	613		61		674	587		19		606	
Shannon-Wiener	3.01	(0.18)	**3.04**	(0.48)	**3.2**	(0.18)	2.9	(0.18)	**1.73**	(0.97)	**2.93**	(0.18)
Margalef	7.17	(1.09)	**6.81**	(1.70)	**8.75**	(1.23)	6.59	(1.10)	**2.72**	(1.36)	**6.71**	(1.25)
Simpson	12.7	(2.94)	19.1	(12.88)	14.9	(3.50)	11.8	(2.79)	4.38	(6.56)	12.4	(2.79)

Table 4.1 Species richness, abundance and diversity of Nymphalid butterflies from primary and selectively-logged forest in ground and canopy traps. Diversity indices are shown with 95% confidence intervals. 'Total' = data combined from both canopy and ground level traps. 'Unique species' are those present only at ground or canopy levels in a particular habitat ('ground', 'canopy') or unique to a particular habitat ('total'). Values shown in bold are significantly different between habitats at the 5% level.

	Habitat								
	Primary forest						Selectively-logged forest		
	Ground		Canopy		Total		Ground	Canopy	Total
Shannon-Wiener	2.27	(0.05)	**1.57**	(0.09)	**2.04**	(0.07)	2.20 (0.06)	**0.37** (0.16)	**1.59** (0.17)
Margalef	3.58	(0.14)	**2.36**	(0.11)	**3.18**	(0.14)	3.37 (0.17)	**0.55** (0.25)	**2.43** (0.28)
Simpson	10.2	(0.73)	8.75	(2.41)	9.74	(0.92)	10.6 (1.17)	2.40 (0.91)	7.88 (1.10)

Table 4.2 Diversity of Nymphalid butterflies in primary and selectively-logged forest. In contrast to Table 4.1, data were analysed per trap. Mean trap diversity (± SE) is shown. 'Total' = data combined from both canopy and ground level traps. 'Unique species' are those present only at ground or canopy levels in a particular habitat ('ground', 'canopy') or unique to a particular habitat ('total'). Values shown in bold are significantly different between habitats at the 5% level.

4.4.1.3 β diversity

Whittaker's index showed that β diversity between ground and canopy was higher in logged forest (Table 4.3; $\beta w = 0.69$) than in primary forest ($\beta w = 0.53$). This was primarily due to loss of canopy species in logged forest, as shown by the much lower α diversity of canopy faunas in logged forest (Table 4.1, 4.2). Low α diversity in the canopy in logged forest explains why analyses based on combined data from ground and canopy level traps revealed significantly lower diversity in logged forest. This was evident despite higher β diversity between canopy and ground-level traps in logged forest compared with primary forest. In contrast analyses based on data from ground-level traps showed no significant difference in diversity between habitats. The strong effect of whether or not canopy data were included in comparisons of diversity between habitats was also evident in the finding that ground level traps were more similar between habitats (Table 4.3; $\beta w = 0.18$) than were canopy traps (Table 4.3; $\beta w = 0.63$).

	Primary ground	Primary canopy	Logged ground	Logged canopy
Primary ground	-			
Primary canopy	0.53			
Logged ground	0.18	0.53	-	
Logged canopy	0.71	0.63	0.69	-

Table 4.3 β diversity measures of butterfly assemblages between habitats (primary *versus* logged forest) and locations (ground *versus* canopy). Whittaker's qualitative index is shown. A higher value shows a greater turnover of species between sites/locations.

4.4.2 Butterfly recapture rates and movement between traps

A total of 206 recaptures were recorded during the 4-month study period. 119 recaptures were in primary forest and 87 recaptures were in selectively-logged forest. The greatest recapture rate (recaptures/all capture events) was between traps at ground level within the primary forest (Table 4.4). Recapture rates between traps at ground level were also high within selectively-logged forest (Table 4.4). There were no movements of individuals detected between primary and selectively-logged forest. A single individual originally caught in the canopy in selectively-logged forest was recaptured in the same trap in the

canopy the following day (Table 4.4). No individuals were detected moving between ground and canopy traps in either primary or selectively-logged forest (Table 4.4). A lack of movement between ground and canopy traps confirms evidence for distinct ground and canopy assemblages in primary and selectively-logged forest.

	Primary forest		Selectively-logged forest	
	Ground	Canopy	Ground	Canopy
Capture events	732	61	673	20
Recaptures	119	0	86	1
Recapture rate	0.16	0.00	0.13	0.05

Table 4.4 Total captures, recaptures and recapture rates of butterflies in ground and canopy traps in primary and selectively-logged forest

4.4.3 Geographical distributions of butterflies in primary and selectively-logged forest

Primary forest contained species with significantly narrower geographical ranges regardless of whether or not data from canopy traps were included for analysis (Table 4.5; combining data for canopy and ground traps, primary forest median rank = 21.5, n = 674, IQR = 18.5; logged forest median rank = 29.0, n = 606, IQR = 17.5; Mann-Whitney U test; Z = -4.174, $p < 0.001$; analysing data for only ground-level traps, Mann-Whitney U-test; Z = -4.81, $p < 0.001$). In contrast to analysis of butterfly diversity between primary and selectively-logged forest, inclusion of canopy data did not qualitatively affect the results when comparing butterfly geographical ranges between habitats. Compared with ground-level, canopy assemblages in both primary and logged forest comprised species with widespread geographical distributions (Table 4.5; primary forest, median rank of canopy species = 47.5, IQR = 32.5; logged forest, median rank of canopy species = 53.0, IQR = 5.5).

Habitat	Trap level					
	Ground		Canopy		Total	
Primary forest	**21.50**	(18.50)	47.50	(32.50)	**21.50**	(18.50)
Selectively-logged forest	**29.00**	(13.00)	53.00	(5.50)	**29.00**	(17.50)

Table 4.5 Median geographical rank (+IQR) of butterflies in primary and selectively-logged forest. 'Total' = data combined from both canopy and ground level traps. Values shown in bold are significantly different between habitats at the 5% level

4.5 DISCUSSION

4.5.1 Data collection

During the study, I caught a total of 61 species of fruit-feeding Nymphalid butterfly. Excluding species I caught exclusively in the canopy, this represents approximately 74% of Nymphalid butterfly species recorded at the same study site by Hamer *et al.* (2003) who sampled only at ground level, but for a longer time span. I caught a single species (*Elymnias panthera*) exclusively in the canopy that was also recorded by Hamer *et al.* (2003) at ground level. However, the other species caught exclusively in the canopy were not recorded by Hamer *et al.* (2003), even though they sampled for a longer period (12 months compared with four months in this study). This indicates that even if sampling in this study had been conducted for longer, it is unlikely that these canopy species would have been recorded at ground level. I also recorded four species in ground level traps that were not recorded by Hamer *et al.* (2003), which highlights the long time period of sampling necessary for producing complete inventories of species in tropical regions. Figure 4.1 indicates that the species accumulation curve was still rising in ground-level traps in primary forest. However, given that primary forest was reported to be more diverse in this study, any extra sampling that detected additional species in primary forest would be unlikely to qualitatively affect the results.

The traps used in this study sampled only fruit-feeding Nymphalid butterflies but did allow sampling in the canopy. There are few data on the efficiency of fruit-baited traps in attracting and retaining species (see Chapter 3), but any differences are likely to vary among species rather than between habitats or locations and are therefore unlikely to affect conclusions. Previous studies have suggested that relatively long-term studies, like this one which sampled for 2880 trap days, greatly reduce any problems associated with differences in species' capture and escape rates (Hughes *et al.*, 1998). In addition, although the study area is aseasonal there is variation in rainfall and I sampled during both wetter and drier months in order to take account of any temporal fluctuations in butterfly abundance caused by differences in rainfall (Hill *et al.*, 2003), which are known to affect estimates of diversity (Hamer *et al.*, 2005).

4.5.2 Impacts of selective logging on species diversity and composition

Combining data from ground and canopy traps showed primary forest to be significantly more diverse than selectively-logged forest. However, this difference was not evident if data from only ground traps were analysed. Many of the species recorded within the primary forest canopy were unique to the canopy of primary forest (11 species). Although four of these species had been recorded at the same study site in ground-based surveys (Hamer *et al.*, 2003), the canopy in primary forest contained a relatively high proportion of unique species. This confirms previous studies which suggest that the canopy of tropical forests contains species only found in the canopy (Erwin, 1982; Stork, 1988, 1991; Nadkarni and Longino, 1990; Lowman and Moffett, 1993; Francis, 1994; Ozanne *et al.*, 2003; Sørensen, 2003). However, in contrast to studies on other taxa, I found the fruit-feeding guild of Nymphalid butterflies do not have highly diverse canopy assemblages. This may reflect the low availably of rotting fruit within the rainforest canopy as rotting fruit is probably more abundant on the ground (Schulze *et al.*, 2001).

Previous studies have pointed out the lack of consensus in the reported impacts of disturbance on Lepidoptera diversity (Hamer and Hill, 2000; Hill and Hamer, 2004). The reported impact of disturbance depends principally on the spatial scale at which the study is conducted. Lepidoptera studies sampling over large spatial scales were more likely to report decreased diversity following disturbance. In contrast, studies conducted over a small spatial scale are more likely to report increased diversity following selective logging (Hamer and Hill, 2000; Hill and Hamer, 2004). These spatial scale effects have been explained in terms of changes in habitat heterogeneity following disturbance and its associated impacts on relationships between α diversity of butterflies at each sampling location and β diversity between sampling locations (Chapters 5 and 6). Here decreased diversity was reported following selective logging when data from canopy traps are included. What is not clear about the implications of including canopy samples is whether the increase in the number of traps and subsequent increase in sample area was important regardless of the position of these traps, or whether selective logging reduces habitat heterogeneity on a vertical dimensions as well as a horizontal plane. Gaining access to the canopy and gathering information on vegetation structure through the forest strata from the ground to the canopy is logistically difficult. However, as many species show distinct patterns of vertical stratification (Francis, 1994; Russell-Smith and Stork, 1994; Baker and Wilson, 2000; Schulze *et al.*, 2001; Walther, 2002a, 2002b), such information would be

highly valuable in helping to understand the impacts of habitat modification on tropical forest diversity and this area of research warrants further study.

Primary forest was shown to contain more species with restricted geographical ranges and thus had a relatively high conservation value compared with selectively-logged forest (this will be discussed in greater detail in Chapter 6). However in contrast to the analysis of diversity data, the inclusion of data from canopy traps did not qualitatively affect the results. This suggests that inclusion of canopy data is important for building species inventories and comparing diversity between habitats but of less importance when assessing the conservation value of selectively-logged forest.

4.5.3 Vertical stratification of tropical butterfly assemblages

β diversity indices confirmed vertical stratification of butterfly assemblages and revealed a distinctive canopy fauna in both habitats. This was supported by species' recapture rates which showed no vertical movement of butterflies between ground and canopy traps in either habitat. Previous studies have suggested that butterfly species from the canopy may be recorded at ground level following selective logging (Willott *et al.*, 2000; Hill *et al.*, 2001; Hamer *et al.*, 2003). It has been suggested that a reduction in canopy height and canopy cover following selective logging may allow light-loving canopy species access to lower forest levels. In this study analysis of vegetation data (see Chapter 5) showed a reduction in canopy height and canopy cover following selective-logging, this supports previous findings (Burghouts *et al.*, 1994; Cannon *et al.*, 1994; Okuda *et al.*, 2003; Asner *et al.*, 2003). However, selective logging in this study resulted in the loss of canopy species and there was no evidence for canopy species being more likely to be sampled at ground level in selectively-logged forest sites (Willott *et al.*, 2000; Hill *et al.*, 2001; Hamer *et al.*, 2003). Thus, selective-logging did not apparently result in a breakdown of the vertical stratification of butterfly assemblages and both primary and selectively-logged habitats had distinct canopy assemblages.

4.5.4 Implications for design of future conservation studies

Conservationists increasingly have to make difficult decisions about setting conservation priorities for species and habitats. Generally, faunal composition of communities is considered a more useful measure of conservation value than are measures of community diversity (Vane-Wright *et al.*, 1991). For example, if two communities are equally diverse

yet one of these communities contains a higher proportion of endemics, whose local extinction has a higher probability of resulting in global extinction, then this community has the higher conservation value (Vane-Wright *et al.*, 1991). Here I showed that for Nymphalid butterflies, sampling from the canopy gave little additional information on responses of restricted-range species to habitat disturbance beyond that obtained from ground-level traps. However, the inclusion of canopy traps qualitatively affected the perceived response of butterfly diversity to selective logging. The guild of Nymphalid butterflies studied here feed on rotting fruit (Hamer *et al.*, 2006) which is likely to be more abundant on the forest floor (Schulze *et al.*, 2001). Consequently high Nymphalid diversity may be expected at ground level reflecting the presence of adult food sources. However, species with different resources requirements may show different results to those reported here and this merits further study.

Differences in results for the responses of restricted range species and diversity following disturbance when data from canopy traps are included highlights the need for careful planning of surveys. Often when undertaking conservation surveys, funding, manpower and time are limited and careful allocation of resources is needed (Balmford *et al.*, 2003). If the assessment of a community's response to disturbance relies on analysis of diversity then data from the forest canopy may be crucial for producing reliable species inventories. However, if conservationists are more interested in understanding the response of restricted-range species to disturbance then ground based surveys are sufficient. Thus the choice of sampling design and location of sampling points clearly depends on the aims of the research project. However, for research investigating the impacts of selective logging on diversity, conservationists need to be aware that the placement of their traps and the spatial scale of their study may largely pre-determine their results.

Chapter 5 Impacts of selective logging on spatial patterns of α diversity of tropical-forest butterflies

5.1 ABSTRACT

Understanding the ecological impacts of selective logging is of great current concern. Yet, despite growing research, little consensus has been reached as to whether selective logging causes an increase or decrease in diversity. Large-scale studies tend to report a decrease in diversity, whereas small-scale studies report an increase following habitat disturbance. Here I examined the underlying ecological mechanisms that may be responsible for this lack of consensus. I investigated α diversity in butterflies, using Shannon-Wiener's, Simpson's and Margalef's indices in primary and selectively-logged forests at a range of spatial scales (3.16 – 80 ha). I showed that differences in α diversity between habitats are dependent on the spatial scale at which data are analysed. I found diversity increased with spatial scale at a significantly faster rate in primary forest than in selectively-logged forest. I used measures of vegetation structure to explain differences in the relationships between spatial scale and butterfly diversity between habitats. The significantly faster rate that butterfly diversity increased with spatial scale in primary forest reflected higher habitat heterogeneity in primary forest. I examined the spatial distribution of butterfly α diversity in primary and selectively-logged forest using geostatistical techniques. Semivariogram analysis revealed that α diversity between samples was spatially autocorrelated in primary forest over short distances, but samples separated by $\geq$345.4 m were independent of each other. This was in contrast to selectively-logged forest where α diversity was not spatially autocorrelated. Patterns of spatial autocorrelation of butterfly diversity reflected patterns of spatial autocorrelation in canopy cover of primary and selectively-logged forests, but not patterns of spatial autocorrelation in measures of vegetation that were extracted by PCA. The main factor extracted by PCA described habitats primarily by differences in tree ecologies (*i.e.* climax *versus* pioneer species). Thus, changes in the spatial patterns of canopy cover following selective logging were more important in determining the spatial distribution of butterfly α diversity than changes in tree composition between habitats. This study highlighted the need for future conservation studies to examine the spatial component of diversity data and for conservationists to be aware that the impacts of disturbance reported at a single spatial scale may not be representative of all spatial scales.

5.2 INTRODUCTION

5.2.1 α diversity

The description and understanding of patterns in diversity is a central theme in ecological research (Rosenzweig, 1995; Gaston, 1996; Magurran, 1988, 2004). For example, a large portion of ecological literature is devoted to describing and explaining the latitudinal gradient in species richness (Fischer, 1960; Pianka, 1966; Rohde, 1992; Willig *et al.*, 2003) and recent research has shifted focus to describing spatial patterns of diversity (*e.g.* He *et al.*, 1996; Selmi and Boulinier, 2001; Lucky *et al.*, 2002). Diversity generally refers to species richness or species evenness at a site and this can be described as α diversity. The regional diversity of an area (γ) can be subdivided into two component parts, α and β diversity (Whittaker, 1960; 1972). α diversity refers to the number and relative abundance of species at any site within the region and β diversity (see Chapter 6) refers to species turnover between sites within a region. Although γ diversity can be partitioned into components of α diversity and β diversity, the majority of ecological research describing patterns of diversity focuses primarily on α diversity (Lennon *et al.*, 2001).

5.2.2 Tropical diversity and habitat heterogeneity

Tropical rainforests have long been recognised as areas of exceptionally high diversity (Wallace, 1878). Although much research has attempted to explain high tropical diversity, little consensus has been reached as to what processes produce and maintain high diversity within tropical rainforests (Fischer, 1960; Pianka, 1966; Rohde, 1992; Willig *et al.*, 2003). A well-documented predictor of α diversity, which is highly supported as a possible explanation for high tropical diversity, is habitat heterogeneity (Pianka, 1966; Kotler and Brown, 1988; Rhode, 1992; Rosenzweig, 1995; Tews *et al.*, 2004).

Within a community, species can coexist by interspecific partitioning of limiting resources such as food and microhabitat availability (Shorrocks *et al.*, 1984). In a more heterogeneous environment, higher species diversity is expected as more environmental niches containing these limited resources are created (Tews *et al.*, 2004). Thus species may evolve novel ways to exploit environmental resources and this in turn may lead to high species diversity within heterogeneous environments (Tews *et al.*, 2004).

5.2.3 Tropical forest disturbance and α diversity

Tropical rainforests are increasingly under threat from anthropogenic disturbance such as logging and shifting agricultural practices (Collins *et al.*, 1991). Currently Southeast Asia has the highest rate of deforestation of any major tropical region (Sodhi *et al.*, 2004). It is estimated that Southeast Asian rainforests could lose 75% of their original land cover within the next hundred years (Sodhi *et al.*, 2004). In addition, it is estimated that within the same time frame rainforests within Southeast Asia could lose $\approx 42\%$ of their biodiversity, of which a high proportion is endemic to the region (Sodhi *et al.*, 2004). It is therefore of great current concern to understand the ecological consequences of this habitat disturbance on tropical forest ecosystems (Curran *et al.*, 2004). Reduced diversity is generally reported following severe habitat disturbance, such as clear-felling and the conversion of tropical forests to grassland (Holloway *et al.*, 1992). However, the impacts of moderate habitat disturbance, such as selective logging, on diversity are less clear. Commercial selective logging represents a major threat to tropical forest ecosystems, with large portions of the world's tropical rainforest contained within logging concessions that are selectively-logged on a regular cycle (Whitmore, 1991; Nepstad *et al.*, 1999; Asner *et al.*, 2004a, 2005). This has lead to a growing body of literature investigating the ecological impacts of selective logging on species diversity. However, there is little consensus on the reported impacts of selective logging on species diversity (Hamer and Hill, 2000; Hill and Hamer, 2004). This is true even in relatively well-studied taxa like Lepidoptera and birds where approximately equal numbers of studies reported increased and decreased diversity after logging (for full reviews see Hamer and Hill, 2000; Hill and Hamer, 2004).

Hamer and Hill (2000) and Hill and Hamer (2004), showed these results were heavily scale dependent. Lepidoptera studies reporting increased diversity were generally conducted at small (<1 ha) spatial scales whereas those reporting decreased diversity were conducted at large (> 3 ha) spatial scales (Hamer and Hill, 2000). These effects of spatial scale on reported impacts of selective logging on diversity have been explained in terms of changes in vegetation structure following disturbance and its associated impacts on the relationship between α diversity of butterflies at each sampling location and species turnover (β diversity) between sampling locations. Selective logging has been shown to result in more homogenous vegetation structure compared with primary forest (Ganzhorn *et al.*, 1990; Burghouts *et al.*, 1994; Hamer *et al.*, 2003; Okuda *et al.*, 2003; Dumbrell and Hill, 2005) and so decreased diversity would be expected in selectively-logged forest when

measured on large (> 3 ha) spatial scales due to the reduction in β diversity in more homogenous habitats (Hill and Hamer, 2004). However, increased diversity would be expected in logged forest when measured at small (< 1 ha) spatial scales due to the opening up of closed-canopy forest in selectively-logged habitats which creates novel opportunities for species not found in primary forest (Hill and Hamer, 2004).

Measures of vegetation structure are often positively spatially autocorrelated within heterogeneous habitats due to the patchy distribution of vegetation types (Lichstein *et al.*, 2002; Dungan *et al.*, 2002), but data are lacking on whether spatial autocorrelation is also evident within the more homogenous habitats that follow selective logging. As habitat heterogeneity is a predictor of butterfly diversity (Hamer *et al.*, 2003), changes in the spatial autocorrelation of vegetation measures following selective logging may result in similar changes in the spatial distribution of α diversity, but this has yet to be investigated.

5.2.4 Spatial autocorrelation of ecological data

Where ecological data are positively spatially autocorrelated, values from samples taken at relatively small distances apart will be more similar than those separated by larger distances (Legendre, 1993; Koenig, 1999; Englund and Cooper, 2003; Blackburn, 2004). Positive spatial autocorrelation will be observed, with the similarity of values between sampling points decreasing with the distance between samples, until a distance is reached at which samples are independent. Studying the spatial component of ecological data is important for two main reasons; firstly, in the presence of spatial autocorrelation data are no longer independent and thus violate assumptions of most standard statistical tests (Legendre, 1993; Lennon, 2000; Diniz-Filho *et al.*, 2003), and secondly, describing spatial patterns in data can help explain the ecological processes generating them (Speight *et al.*, 1998; Diniz-Filho *et al.*, 2003; Thogmartin *et al.*, 2004; Blackburn, 2004).

5.2.4.1 Spatial autocorrelated data violates the assumptions of standard statistical tests

Spatial autocorrelation in ecological data increases the chance of Type 1 statistical errors in data analysis (Legendre, 1993; Lennon, 2000; Diniz-Filho *et al.*, 2003). When analysing spatially autocorrelated data using standard statistical techniques (*e.g.* ANOVA, correlation and regression), standard errors are often underestimated and so increasing the chance of a significant difference or significant relationship between factors, and the erroneous rejection of the null hypothesis (Legendre, 1993; Lennon, 2000; Diniz-Filho *et al.*, 2003).

In addition, Lennon (2000) suggested that the increased likelihood of a significant relationship (Type 1 error using regression analysis) between explanatory and response variables would produce "red-herrings". These "red-herrings" would be explanatory variables that have been accepted as causal because their statistical significance is greater (*i.e.* smaller *p* values) than the real causal variable (Lennon, 2000). However, more recent research has suggested that although evidence for spatial autocorrelation should be examined in order to reduce Type 1 errors it does not lead to a bias in false associations between explanatory and response variables that hide true causal associations (Diniz-Filho *et al.*, 2003). Diniz-Filho *et al.* (2003) compared results from a spatially generalised least squares regression (GLS, controlling for spatial autocorrelation) with those of an ordinary least squares (OLS) regression showing that they were highly correlated and thus, similar explanatory and response variables would be suggested. However, using OLS regression standard errors maybe underestimated causing predicator variables to appear more significantly related to response variables than those using GLS, but the associations between explanatory and response variables are the same using both methods, and thus standard OLS regression avoids false associations (Diniz-Filho *et al.*, 2003). In addition, Diniz-Filho *et al.* (2003) suggested that although Lennon (2000) is statistically correct, the interpretation of results is often not ecologically or biologically meaningful. Therefore significant statistical associations are not the same as meaningful biological or ecological relationships.

5.2.4.2 Inferring underlying ecological process from spatially autocorrelated data

Apart from examining spatial autocorrelation in ecological data in order to avoid misinterpreting statistical analyses, understanding spatial patterns in data can help explain the underlying processes that generate them and answer specific ecological questions. There is more than one way in which examining the spatial autocorrelation of ecological data can help explain underlying processes. Firstly, examining the spatial pattern in both explanatory and predictor variables can help infer associations between the two based on the similarity of their spatial distribution (Diniz-Filho *et al.*, 2003). For example, Loescher *et al.* (2002) showed rain through-fall volume (the amount of precipitation penetrating the forest canopy) within a tropical forest was spatially autocorrelated up to a range of 45 m. This distance was associated with the spatial distribution of canopy gaps and dense canopy cover caused by large trees. Thus, Loescher *et al.* (2002) concluded that the spatial

autocorrelation of rain through-fall volumes was caused by the spatial distribution of canopy cover and canopy gaps. Secondly, assumptions about the spatial distribution of data can be made to answer specific hypotheses. He *et al.* (1996) tested the hypothesis that tropical rainforests are non-equilibrium communities by examining whether data on tree species diversity were spatially autocorrelated. If a community is in equilibrium, the distribution of diversity values is expected to show a clear and consistent spatial pattern. In an equilibrium community species coexist by interspecific partitioning of limiting resources such as food and microhabitat availability. These limiting resources are in turn patchily distributed and lead to a spatial pattern in the distribution of species within an equilibrium community. In contrast to equilibrium communities, non-equilibrium communities are unpredictable in terms of their compositional structure due to high stochastic effects, and this leads to a lack of clear and consistent spatial structure (He *et al.*, 1996). Although He *et al.* (1996) showed diversity data to be spatially autocorrelated, this pattern was not consistent among diversity measures and so they concluded that tropical forest trees are non-equilibrium communities. In addition to answering specific ecological questions, examining spatial autocorrelation in ecological data allows more reliable extrapolation of data when mapping ecological factors, such as maps of insect pest outbreaks (Speight *et al.*, 1998), geographical distribution of organisms (Thogmartin *et al.*, 2004), and predictive maps of human disease epidemiology (Munasinghe and Morris, 1996).

5.2.5 Using geostatistics to examine spatial autocorrelation in ecological data

Many methods have been suggested for studying spatial patterns in ecological data (for recent reviews see; Dale *et al.*, 2002; Perry *et al.*, 2002). One of these methods, collectively referred to as geostatistics, has been widely used for a long time to understand the spatial distribution of geological data and has only recently made a transition to ecological studies (*e.g.* He *et al.*, 1996; Speight *et al.*, 1998; Nicotra *et al.*, 1999; Bebber *et al.*, 2002; Scheller and Mladenoff, 2002; Wagner *et al.*, 2005). Geostatistical techniques use the estimation of a semivariogram to detect spatial autocorrelation in data. A semivariogram is a statistic that assesses the average decrease in similarity between values of variables from pairs of sampling points as distance increases between sampling points (Olea, 1999). This statistic can be applied to ecological data where distances between sampling locations are known. Examples of its application include being used to examine spatial patterns in insect

abundances (Speight *et al.*, 1998) and investigating the spatial distribution of tropical forest gaps and their impacts on seedling growth dynamics (Bebber *et al.*, 2002).

Speight *et al.*, (1998) examined the spatial distribution of horse chestnut scale (*Pulvinaria regalis*; Homoptera: Coccidae) on host trees in an urban environment. They showed abundance of horse chestnut scale to be spatially autocorrelated along a single direction which was attributed to wind speed and direction through the urban environment (Speight *et al.*, 1998). In their study, Speight *et al.*, (1998) showed geostatistical techniques could be successfully employed to examine ecological data and to identify spatial autocorrelation where present. Speight *et al.*'s (1998) study highlighted the strength of geostatistical techniques in two ways. Firstly, by incorporating both standard and geostatistical techniques they avoided Type 1 statistical error. Secondly, by quantifying patterns of spatial autocorrelation they could attribute observed abundance-distribution patterns to underlying causal mechanisms, in this case wind speed and direction (Speight *et al.*, 1998). Thus, geostatistics can be successfully used to address the two main reasons for examining spatial autocorrelation in ecological data.

5.2.6 Impacts of selective logging on the spatial autocorrelation of ecological data

Spatial patterns in the distribution of butterfly α diversity and measures of vegetation structure have rarely been examined within both primary and selectively-logged tropical forests. As selective logging may produce a more homogenous vegetation structure compared with primary forest, it may also affect patterns of spatial autocorrelation of vegetation structure. This in turn may affect the spatial distribution of butterfly α diversity, but few data are available to address this. Understanding the underlying spatial distribution of these data is of great importance to conservationists and ecologists working on the impacts of selective logging. Conservationists increasingly have to make difficult decisions about setting conservation priorities for habitats in an ever-degraded landscape. Thus for conservationists, understanding the underlying spatial pattern in diversity data may help avoid Type 1 statistical errors and allow a more reliable assessment of the impact of habitat disturbance on α diversity. In addition, describing spatial patterns in α diversity and how these change following habitat disturbance may help ecologists understand the underlying mechanisms that regulate the distribution of diversity within tropical rainforests.

5.2.7 Chapter objectives

In this chapter,

1. I investigate the impacts of selective logging on butterfly α diversity and examine how the perceived response of diversity to disturbance is affected by the spatial scale of analysis.

2. I examine the relationship between species α diversity and spatial scale in primary and selectively-logged forest. I test the hypothesis that α diversity increases with spatial scale at a significantly faster rate in primary forest compared with selectively-logged forest.

3. I investigate the impacts of selective logging on vegetation structure using principal component analysis. I use the analysis of vegetation data to examine the relationship between species diversity and spatial scale in primary and selectively-logged forests.

4. Using geostatistics, I examine the spatial distribution of α diversity in primary and selectively-logged forest. I compare the patterns of spatial autocorrelation of α diversity in primary and selectively-logged forest. I test the hypothesis that selective logging reduces the spatial autocorrelation of α diversity.

5. I also use geostatistical techniques to examine the spatial distribution of measures of vegetation structure and canopy cover in primary and selectively-logged forest and relate patterns of spatial autocorrelation in vegetation data to patterns of spatial autocorrelation in α diversity in both habitats.

5.3 MATERIALS AND METHODS

A brief recap of the general methods used in this chapter follows. For detailed information on the study site, butterfly sampling methods and the analysis and collection of vegetation data see Chapter 2 General Materials and Methods.

5.3.1 Study site

Fieldwork was conducted during June 2003, from March to April 2004 and from October to December 2004 at the Danum Valley Field Centre (DVFC) and surrounding Ulu Segama Forest Reserve (USFR) in Sabah, Malaysian Borneo (5°N, 117°5'E). Sampling during this study was conducted within primary forest adjacent to DVFC and within forest that was selectively-logged in 1988 using high lead and tractor extraction methods, where all commercially viable stems > 60 cm diameter at breast high were removed. Logging extraction data from 1988 indicate that approximately 170,000 m^3 of timber was extracted from an area of approximately 2300 ha (Innoprise, 1992).

5.3.2 Butterfly sampling

Butterflies were trapped within two grids that were set up to sample a ≈80 ha area, one grid in primary forest and the other in forest selectively-logged in 1988. 25 traps were hung approximately 2 m above the ground every 200 m in a 5 by 5 trap arrangement (see Figure 2.10 in Chapter 2 General Materials and Methods).

This sampling strategy allows data to be analysed at a range of spatial scales. Many spatial patterns in ecological data show signs of anisotropy or directionality (Peterson and Parker, 1998), for example ecological data may be spatial autocorrelated along an environmental or latitudinal gradient (*e.g.* Speight *et al.*, 1998; Diniz-Filho *et al.*, 2003). Arranging traps in a grid format allows spatial patterns in data to be analysed multi-directionally to account for anisotropy.

All traps were baited with a piece of banana prior to the first day of sampling and an additional piece of banana was added daily. This ensured a mix of fresh and well-rotted fruit. Sampling was conducted for 12 days each month in each habitat over the six-month study period (72 days in total in each habitat). Traps were checked daily between 10 am and 2 pm. All butterflies caught were identified to species level, marked with a felt pen and released. Recaptures were excluded from any analysis of diversity. Recapture data were used to examine dispersal of butterflies in primary and selectively-logged forest.

5.3.3 Butterfly diversity

Species accumulation curves were computed using rarefaction for data from primary and selectively-logged forest. I calculated three indices of α diversity, Shannon-Wiener, Margalef (species richness) and Simpson (species evenness), for both primary and selectively-logged forests following methods in Magurran (2004). I used bootstrapping methods to calculate confidence intervals for each index (Sokal and Rohlf, 1995) and compared indices between habitats using pairwise randomization tests based on 10,000 re-samples of species abundance data, following Solow (1993). Analysis of butterfly diversity was conducted using the computer programs PISCES and EstimateS.

Diversity indices (Shannon-Wiener, Simpson and Margalef) were used to examine the relationship between spatial scale and diversity in primary and selectively-logged forests. Diversity indices were calculated at a range of spatial scales (3.16 – 80 ha). Firstly, diversity indices were calculated for a single trap selected at random. As traps were placed every 200 m, I assumed individual traps sampled over a radius of 100 m in each direction and thus over a 3.16 ha area. A second trap was then selected at random and diversity was re-calculated combining data from both traps. This process was continued by adding an additional trap selected at random and recalculating diversity values until all traps had been included. This process was then randomised 50 times to remove any effect of trap order on diversity. Confidence intervals were computed using bootstrapping techniques for each value of diversity at all spatial scales (Sokal and Rohlf, 1995). This method produced α diversity values at increasing spatial scales from 3.16 – 80 ha by continually including one trapping station that sampled across 3.16 ha in each increment.

Linear regression was used to examine the relationship between α diversity and spatial scale ($\log_{10}$ transformed) in primary and selectively-logged forests. Diversity – area plots based on double log transformations best describe communities in equilibrium (He *et al.*, 1996). However, as tropical rainforest are generally not considered at equilibrium, single log plots are more appropriate in describing these communities (He *et al.*, 1996). Thus single log plots were used to describe the relationship between α diversity and spatial scale in primary and selectively-logged forests.

In order to examine the impacts of selective logging on the relationship between α diversity and spatial scale, I used analysis of covariance (ANCOVA) to compare the slopes of the relationship between diversity and spatial scale in primary and selectively-logged forest. Although ANCOVA assumes samples are independent, here each diversity sample is

dependent on the previous sample. This may lead to a greater likelihood of a Type 1 error and significance levels close to $\alpha = 0.05$ should be accepted with caution. However, the use of ANCOVA remains the only suitable test for comparisons of regression slopes and has been used in previous studies on similar data (*e.g.* Hamer and Hill, 2000).

5.3.4 Vegetation data

To assess the structural composition of the vegetation in primary and selectively-logged forest, each trapping station was divided into four quadrants centred on the trap. The following variables were recorded in each quadrant within a 30 m radius of the trap: height, girth at breast height, point of inversion (whether the first major branch was above or below the mid-point of the tree; Torquebiau, 1986), distance from trap, and identity (family Dipterocarpaceae, pioneer *Macaranga* spp., or other) of the two trees (> 0.6 m girth) nearest to the trap (n = 8 trees per station). The distance from the trap, girth at breast height, and identity (family Dipterocarpaceae, *Macaranga* spp. or other) of the nearest two saplings (0.1 - 0.6 m girth) were also recorded in each quadrant (n = 8 saplings per station). In each quadrant, the percentage cover of ground, low level (> 2 m from ground height) and understorey vegetation were estimated within a 10 m radius of the trap. A single estimate of percentage canopy cover was taken within a 10 m radius of the trap. Overstorey vegetation cover was also estimated from four readings, facing each major compass direction, using a densiometer (Lemmon, 1957). These data were used to derive 17 vegetation variables which were normalised where necessary (including arcsine transformation of proportions) prior to analysis. These variables were then analysed by principal component analysis (PCA; Hamer *et al.*, 1997, 2003).

5.3.5 Geostatistical analysis of spatial autocorrelation in diversity and vegetation data

Geostatistics use the estimation of a semivariogram to detect spatial autocorrelation in data. The semivariogram calculates the average decrease in similarity between pairs of sampling points as the spatial distance between pairs of sampling points (lag distance) increases (Olea, 1999). Therefore, if data are positively spatially autocorrelated pairs of sampling points close together will be more similar than pairs of sampling points further apart and the semivariogram will give relatively small values at small lag distances and relatively large values at large lag distances (Figure 5.1).

The semivariogram can be described in terms of its component parts (Figure 5.1). The nugget is the amount of variation attributed to error or any spatial autocorrelation shown at distances smaller than the smallest lag distance between a pair of sampling points (Figure 5.1). The sill is the amount of variation described by spatial autocorrelation. The sum of the values of the sill and nugget are equal to the overall variance within the data and therefore the sill can be expressed as the percentage of the overall variance of the data that shows spatial autocorrelation (Figure 5.1). The range is the minimum lag distance between sampling pairs at which semivariogram values reach the overall data variance (Figure 5.1). All sampling pairs separated by a distance greater than the range are considered independent; any sampling pairs separated by a distance less than the range are spatially autocorrelated (Olea, 1999).

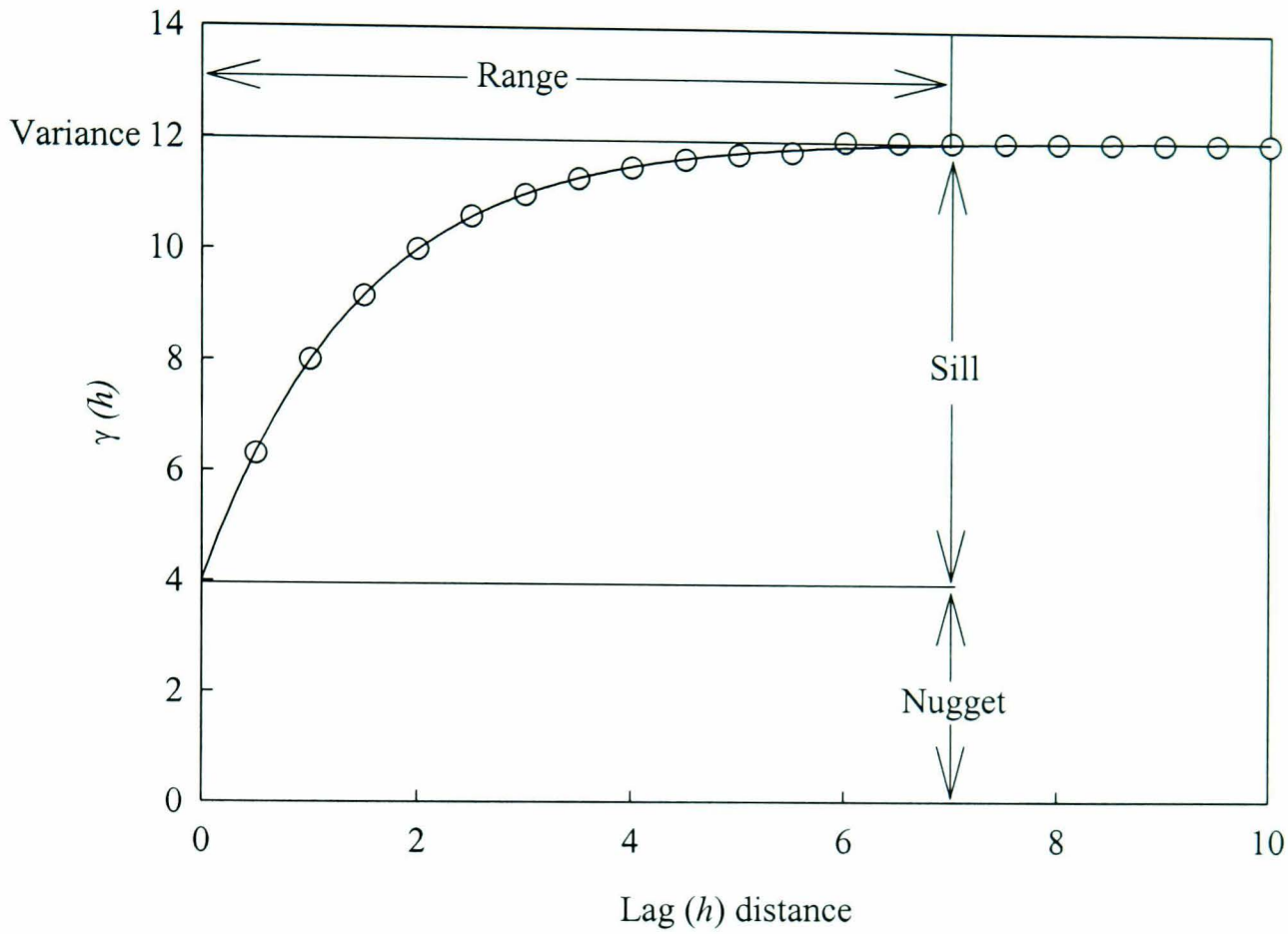


Figure 5.1 Illustration of a semivariogram with its component features. γ is the semivariogram value, or mean difference, between pairs of samples separated by a distance or lag, h. The nugget is the amount of variation attributed to error or spatial autocorrelation between samples separated by a lag smaller than the lowest lag considered. The sill shows the amount of variation explained by spatial autocorrelation. The range is the maximum distance (lag) between samples at which samples are no longer spatially autocorrelated.

Computation of the semivariogram follows Equation 5.1, where γ (the semivariogram value) is the mean difference between pairs of sampling locations x_i and $x_i + h$, separated by a lag distance h (Olea, 1999). All semivariograms were computed using the Prevar2D and Vario2D programs of the geostatistical package Variowin 2.2 (Pannatier, 1996) as well as being checked manually.

$$\gamma(h) = \frac{\sum_{i=1}^{N(h)} [z(x_i) - z(x_i + h)]^2}{2N(h)}$$

Equation 5.1

Once a semivariogram has been calculated it can be fitted to a model describing the distribution of semivariogram values at increasing lag distances, these models then give values for the component parts, nugget, sill and range, of the semivariogram (Equation 5.2, 5.3, 5.4).

In order to investigate the impacts of selective logging on the spatial autocorrelation of butterfly α diversity, semivariograms were used to examine the spatial distribution of α diversity in primary and selectively-logged forest. Semivariograms were calculated for diversity data from values of Simpson, Shannon-Wiener and Margalef indices at each sampling point (trapping station) in primary and selectively-logged forest following Equation 5.1. In order to examine the impacts of selective logging on the spatial autocorrelation of vegetation structure semivariograms were computed following Equation 5.1 for measures of vegetation structure based on PCA scores. In order to test the hypothesis that reduced habitat heterogeneity following selective logging may affect patterns of spatial autocorrelation in vegetation measures I computed semivariograms following Equation 5.1 for canopy cover in primary and selectively-logged forest, as this vegetation measure showed the greatest reduction in heterogeneity following selective logging. Patterns of spatial autocorrelation in vegetation data were then related to patterns of spatial autocorrelation of butterfly α diversity in primary and selectively-logged forest.

Examination of the semivariograms showed whether or not data were spatially autocorrelated. Where semivariograms showed no spatial autocorrelation, the semivariogram value for the smallest lag distance was equal to or greater than the overall variance; this is described as the pure nugget effect (Olea, 1999). Where semivariograms showed data to be spatially autocorrelated, the distributions of semivariogram values were modelled using the Model program of the Variowin 2.2 package (Pannatier, 1996). All semivariograms that showed data to be spatially autocorrelated were tested against the following models to give values for the nugget, sill and range:

$$\gamma(h) = c\left\{1 - \exp\left(-\frac{h}{r}\right)\right\}$$

Equation 5.2

$$\gamma(h) = c\left\{1 - \exp\left(-\frac{h^2}{r^2}\right)\right\}$$

Equation 5.3

$$\gamma(h) = \alpha h^{\beta}$$

Equation 5.4

Equations 5.2 and 5.3 represent a negative exponential and Gaussian model of the distribution of semivariogram values respectively where c is the sill and r the range, the nugget is then calculated as the difference between the overall data variance and the sill, c. Equation 5.4 shows a power increase model where α is the variation and β the curvature of the power function line. A power increase model best describes the distribution of semivariogram values where the spatial autocorrelation within the data has not reached its range. Thus the power function cannot describe the semivariogram in terms of its nugget, sill or range but shows continuous spatial autocorrelation within the data. The accuracy of a model in describing the distribution of semivariogram values was assessed using the Indicative Goodness of Fit (IGF) function of the Model program of the Variowin 2.2 package (Pannatier, 1996). The IGF function is a statistic based on a least squares estimator that determines the goodness of fit of a semivariogram model to the distribution of the data with a degree of statistical significance and is defined by Equation 5.5. Where N is the number of directional semivariograms, $n(k)$ is the number of lags relative to semivariogram k, $D(k)$ is the maximum distance relative to semivariogram k, $P(i)$ is the number of pairs of lag i of semivariogram k, $\gamma(i)$ is the experimental measure of spatial continuity for lag i, $\hat{\gamma}(i)$ is the modelled measure of spatial continuity for $d(i)$, and σ^2 is the variance of the data for the semivariogram (Pannatier, 1996).

$$IGF = \frac{1}{N}\sum_{k=1}^{N}\sum_{i=0}^{n(k)} \frac{P(i)}{\sum_{j=0}^{n(k)} P(j)} \cdot \frac{D(k)}{d(i)} \cdot \left[\frac{\gamma(i) - \hat{\gamma}(i)}{\sigma^2}\right]^2$$

Equation 5.5

The closer the IGF value is to zero the better the fit of the suggested model to the distribution of the data. As with standard statistics, a significance level of IGF = 0.05 is usually adopted (Pannatier, 1996).

The z-test (Equation 5.7; Kabrick *et al.*, 1997) was used to test for significant differences in semivariogram values to overall data variance (significant levels of $z \geq 1.7$, p

≤ 0.05; $z \geq 2.4$, p ≤ 0.01; $z \geq 3.1$, p ≤ 0.001 were used) following Bebber *et al.*, (2002). This allowed the computation of the range (the lag distance between sampling pairs at which data are no longer spatially autocorrelated) with a degree of statistical accuracy. Thus the point at which values are no longer spatially autocorrelated can be statistically verified.

$$\mathrm{var}[2\gamma(h)] \approx \frac{2[2\gamma(h)]^2}{N(h)}$$

Equation 5.6

$$z(h) = \frac{2\gamma_1(h) - 2\gamma_2(h)}{\sqrt{\mathrm{var}_1 + \mathrm{var}_2}}$$

Equation 5.7

The z statistic was manually calculated following Equation 5.7 where the variance of the semivariogram values was estimated by Equation 5.6 where N is the number of pairs of samples (Kabrick *et al.*, 1997; Bebber *et al.*, 2002).

5.3.6 Butterfly dispersal

Any differences in the distribution of α diversity within primary and selectively-logged forest may be a direct consequence of selective logging on α diversity or as an indirect effect of selective logging on butterfly behaviour. One potential change in butterfly behaviour is their dispersal in relation to habitat disturbance. For example, increased dispersal may lead to a reduction in β diversity between traps and subsequently higher α diversity within each trap. To investigate the impacts of selective logging on butterfly dispersal, recapture data were analysed for two of the most abundant butterfly species, a relatively large species, *Bassarona dunya* (Plate 5.1; mean wing length, ♀ = 50.8 mm, SE = 0.81, n = 31; ♂ = 43.4 mm, SE = 0.22, n = 49), from the sub-family Nymphalinae and a relatively small species, *Mycalesis orseis* (Plate 5.1; mean wing length, ♀ = 24.3 mm, SE = 0.32, n = 37; ♂ = 22.9 mm, SE = 0.23, n = 54) from the subfamily Satyrinae. Flight speed in butterflies is positively correlated with wing span (Dudley, 1990) and so the choice of species probably covered a range of dispersal capabilities. Recapture data were totalled across the entire 10 month study period, using data collected along transects (Chapter 4.0) and within grids (Chapters 5.0, 6.0). The transects and grids in each habitat were close to each other and so butterflies released from one site were often recaptured while sampling

another. For each individual recaptured, the maximum distance moved between traps was calculated from all recapture events. Recapture data were pooled across both sexes as previous studies have shown no significant difference in dispersal between sexes for these tropical species (Benedick, 2001). These data were then plotted as the cumulative proportion of individuals that travelled a given distance. Data were $\log_{10}$ transformed and regression analysis was used to fit data to an inverse power function (Equation 5.8) that described the distribution of dispersal distances for each species in each habitat.

$$I = CD^{-n}$$

Equation 5.8

Where I is the probability of an individual moving a certain distance, D (m) where C and n are scaling constants. Many equations have been suggested to describe the distribution of dispersal distances. The inverse power function is widely used and predicts more long distance dispersal than other functions *e.g.* negative exponential (Schwartz, 1993). I used ANCOVA to examine differences in the relationship between dispersal and distance in primary and selectively-logged forest for each species.

Plate 5.1 An example of the two species of Nymphalid butterfly *Bassarona dunya* (left) and *Mycalesis orseis* (right). *B. dunya* (sub-family: Nymphalinae) is a relatively large species (mean wing length, ♀ = 50.8 mm, SE = 0.81; ♂ = 43.4 mm, SE = 0.22) which prefers areas of dense shade within closed canopy forest. *M. orseis* (sub-family: Satyrinae) is a relatively small species (mean wing length, ♀ = 24.3 mm, SE = 0.32; ♂ = 22.9 mm, SE = 0.23) which prefers more open areas of forest.

5.4 RESULTS

5.4.1 Butterfly diversity in primary and selectively-logged forest

Excluding recaptures, a total of 2244 individuals from 62 species of fruit-feeding Nymphalid (Family: Nymphalidae; sub-families, Satyrinae, Morphinae, Nymphalinae, Charaxinae) butterfly were trapped over the 6 month study period. 1150 individuals from 56 species were trapped in primary forest and 1094 individuals from 51 species were trapped in selectively-logged forest (Appendix 3).

5.4.1.1 Species accumulation curves

Inspection of species accumulation curves (Figure 5.2) showed that species accumulation rates appeared to have reached asymptotes in primary and selectively-logged forests. Thus further time spent sampling may have added only few additional data and would be unlikely to have qualitatively affected the results. Therefore comparisons between habitats are valid and any differences are unlikely to be a result of differences in sampling efficiency between traps in primary and selectively-logged forest. In addition, there was no difference between primary and selectively-logged forest in mean number of individuals recorded per trap (mean trap abundance, primary = 46.00, (SE = 3.42); logged = 43.76, (SE = 3.30); *t*-test assuming unequal variance, $t_{47.94} = 0.471$, $p = 0.64$). Therefore further comparisons between habitats, based on differences between pairs of traps within habitats, are unlikely to be biased by differences in sample sizes between habitats.

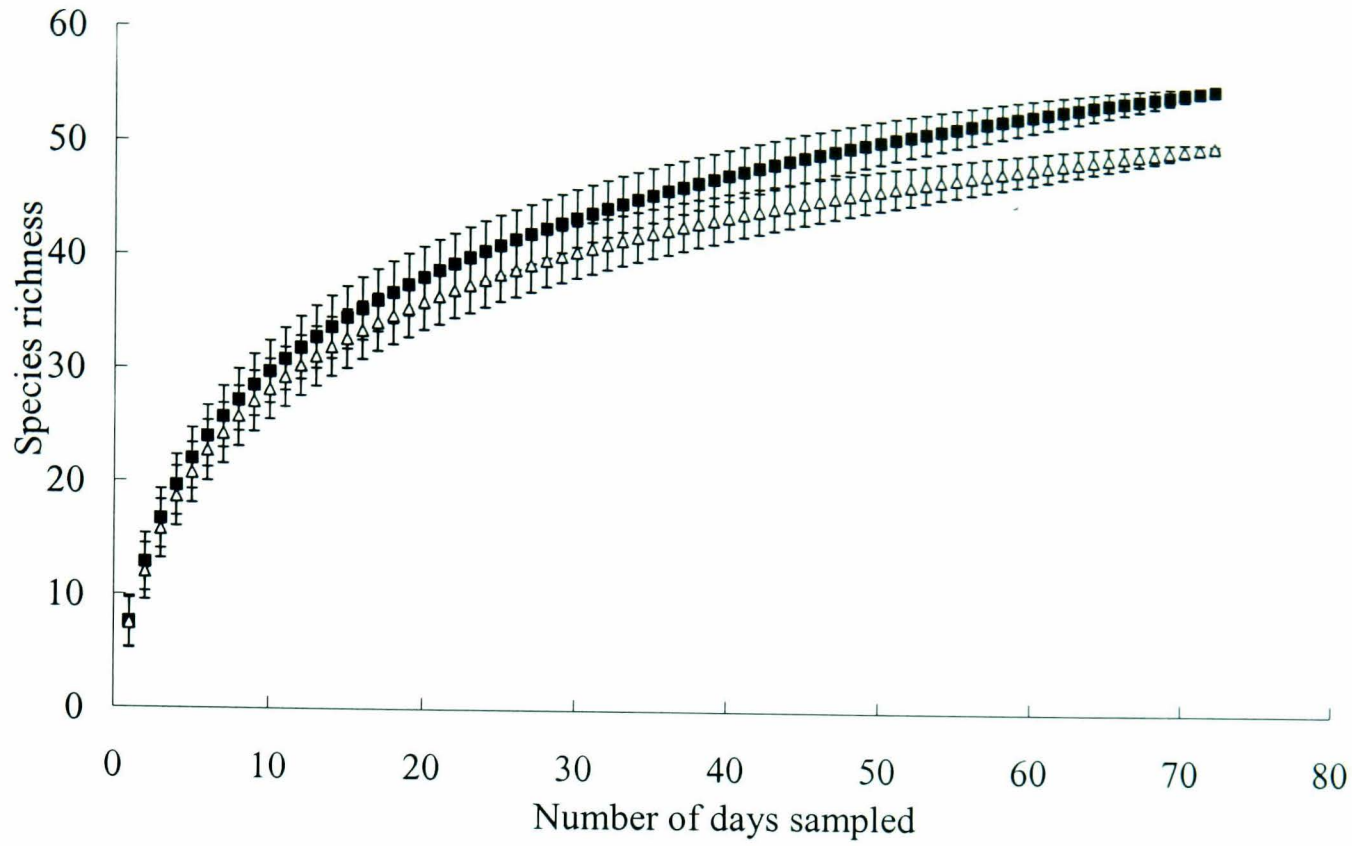


Figure 5.2 Species accumulation curves of Nymphalid butterflies in primary (squares) and selectively-logged (triangles) forest. Data points show estimated species richness (± SE) using rarefaction.

5.4.1.2 α diversity

Primary forest was significantly more diverse than selectively-logged forest measured using the Shannon-Wiener diversity index (Table 5.1; combining data from 25 traps; pairwise randomization test, $\delta = 0.093$, $p < 0.05$) and Simpson's index was approaching significance (Table 5.1; Simpson's index, $\delta = 1.55$, $p = 0.056$). This is in contrast to results from Chapter 4 that showed that canopy samples were needed to detect a change in diversity following selective logging (this will be discussed in detail in Chapter 7 General Discussion). There was no significant difference in diversity between habitats using Margalef's diversity index (Table 5.1; Margalef's index, $\delta = 0.66$, $p = 0.16$).

These results were qualitatively different depending on whether data were analysed per grid (as above) or per trap. When data were analysed per trap there was no difference between habitats (Table 5.2; *t*-test assuming unequal variance; Shannon-Wiener, $t_{47.77} = 0.99$, $p = 0.33$; Simpson's, $t_{46.93} = 0.098$, $p = 0.922$, Margalef's, $t_{47.81} = 1.196$, $p = 0.24$). This suggests that perceived impacts of selective logging may be scale dependent, with

analysis of data per trap (small scale) differing qualitatively from analyses of data per grid (large scale).

	Primary forest		Selectively-logged forest	
No. of species per grid	56		51	
No. of individuals per grid	1150		1094	
Shannon-Wiener	**3.09**	(0.07)	**3.00**	(0.08)
Simpson	14.98	(1.06)	13.43	(1.07)
Margalef	7.80	(0.57)	7.15	(0.05)

Table 5.1 Species richness, abundance, and diversity of Nymphalid butterflies sampled from 25 fruit-baited traps in primary and selectively-logged forest. Diversity indices are shown with 95% confidence intervals, values in bold are significantly different between habitats when data are combined across all 25 traps. Values for Simpson's index (underlined) were approaching a significant difference ($p = 0.056$) between habitats.

	Primary forest		Selectively-logged forest	
No. of species per trap	14.64	(0.72)	13.44	(0.68)
No. of individuals per trap	46.00	(3.42)	43.76	(3.30)
Shannon-Wiener	2.28	(0.06)	2.20	(0.06)
Simpson	9.25	(0.60)	9.16	(0.70)
Margalef	3.59	(0.16)	3.33	(0.15)

Table 5.2 Mean per trap, species richness, abundance, and diversity of Nymphalid butterflies in primary and selectively-logged forest. All values are shown with standard errors. There was no significant difference in species richness, abundance, or diversity of Nymphalid butterflies between primary and selectively-logged forest when data were analysed per trap.

5.4.2 Relationships between spatial scale and butterfly α diversity in primary and selectively-logged forest

There was a significant positive linear relationship between species richness and spatial scale in both primary and selectively-logged forest (Figure 5.3, Table 5.3; primary forest, $F_{1,23} = 2827.94$, $p < 0.001$; selectively-logged forest, $F_{1,23} = 17318.73$, $p < 0.001$). There was also a significant positive linear relationship between butterfly α diversity and spatial scale in both primary and selectively-logged forest for all three diversity indices (Figure 5.3; Table 5.3; Margalef's index; primary forest, $F_{1,23} = 4059.99$, $p < 0.001$; selectively-logged forest, $F_{1,23} = 2471.10$, $p < 0.001$; Simpson's index, primary forest, $F_{1,23} = 876.12$, $p < 0.001$; selectively-logged forest, $F_{1,23} = 107.60$, $p < 0.001$; Shannon-Wiener's index, primary forest, $F_{1,23} = 340.14$, $p < 0.001$; selectively-logged forest, $F_{1,23} = 154.33$, $p < 0.001$).

	Primary forest			Selectively-logged forest		
	R^2	Gradient		R^2	Gradient	
Species richness	0.99	30.30	(0.57)	0.99	27.19	(0.21)
Margalef	0.99	3.00	(0.05)	0.99	2.62	(0.05)
Simpson	0.97	3.66	(0.12)	0.82	2.48	(0.20)
Shannon-Wiener	0.94	0.46	(0.03)	0.87	0.456	(0.04)

Table 5.3 R^2 and gradient values for the slopes of the relationship between α diversity, measured by Margalef's, Simpson's and Shannon-Wiener's indices, and spatial scale in primary and selectively-logged forest. Estimated gradient values are shown with standard errors.

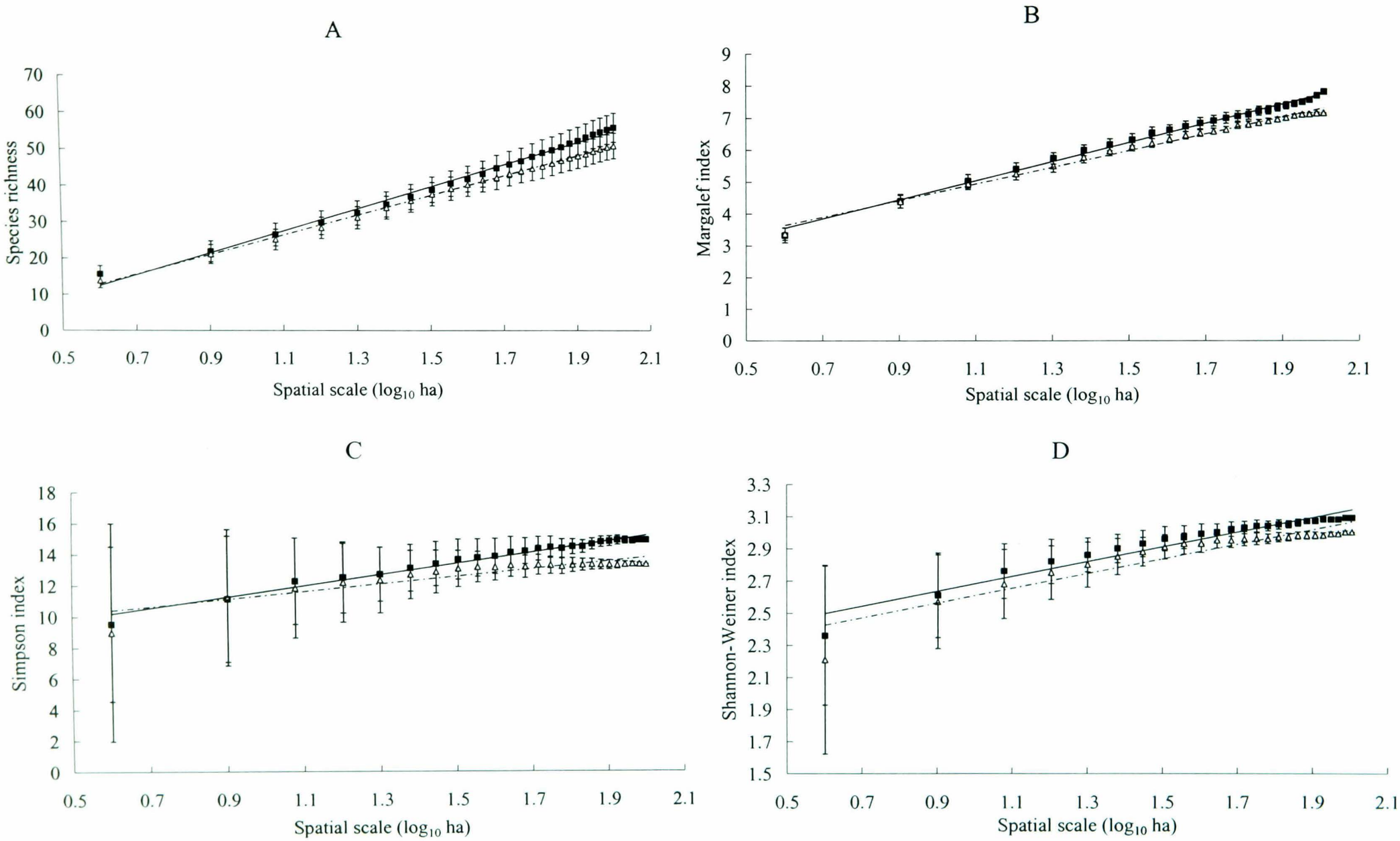


Figure 5.3 Relationship between spatial scale and species richness (A), Margalef's index (B), Simpson's index (C), and Shannon-Wiener's index (D) in primary (squares and solid line) and selectively-logged (triangles and dashed line) forest. Error bars show 95% confidence intervals.

In order to examine the impacts of selective logging on the relationship between α diversity and spatial scale the slopes of the regression lines (Table 5.3) were compared between habitats. This showed that species richness, Margalef's and Simpson's indices increased at a significantly faster rate in primary forest than in selectively-logged forest (Figure 5.3; ANCOVA of species richness in primary and selectively-logged forest with spatial scale as a covariate, habitat by spatial scale interaction $F_{1,46} = 8995.79$, $p < 0.001$; Margalef index, $F_{1,46} = 29.58$, $p < 0.001$; Simpson's index, $F_{1,46} = 19.01$, $p < 0.001$). This result was not observed when α diversity was measured using the Shannon-Wiener index (Figure 5.3; Shannon-Wiener index, $F_{1,46} = 0.004$, $p = 0.950$).

5.4.3 Effect of selective logging on vegetation structure

To assess the structural composition of the vegetation in primary and selectively-logged forest 17 vegetation variables were recorded at each trapping station. Primary forest had significantly taller, larger trees and higher overstorey, ground and canopy cover (Table 5.4; t-test assuming unequal variance; tree height, $t_{36.73} = 6.92$, $p < 0.001$; tree girth, $t_{38.81} = 2.67$, $p = 0.01$; overstorey cover, $t_{34.61} = -2.35$, $p = 0.024$; ground cover, $t_{47.60} = 2.74$, $p = 0.01$; canopy cover $t_{26.36} = 4.99$, $p < 0.001$). Primary forest had a significantly higher proportion of Dipterocarp trees and saplings and a significantly lower proportion of trees and saplings of the pioneer genus *Macaranga* (Table 5.4; Dipterocarp trees, $t_{46.44} = 9.87$, $p < 0.001$; Dipterocarp saplings, $t_{45.65} = 5.38$, $p < 0.001$; *Macaranga* spp. trees, $t_{24.00} = -7.39$, $p < 0.001$; *Macaranga* spp. saplings, $t_{24.00} = -3.35$, $p < 0.001$). Measures of tree height, tree girth and canopy cover had significantly greater variance in primary forest than selectively-logged forest indicating more heterogeneous vegetation structure in primary forest (Table 5.4; Levene's test for equality of variances, tree height, $F_{1,48} = 7.51$, $p = 0.009$; tree girth, $F_{1,48} = 9.80$, $p = 0.003$; canopy cover, $F_{1,48} = 41.42$, $p < 0.001$). The proportion of *Macaranga* spp. trees and saplings had significantly greater variance in selectively-logged forest than primary forest (Table 5.4; Levene's test for equality of variances, *Macaranga* spp. trees $F_{1,48} = 31.07$, $p < 0.001$; *Macaranga* spp. saplings, $F_{1,48} = 33.91$, $p < 0.001$). There was no significant difference the variance of any other vegetation measures between primary and selectively-logged forests.

	Primary forest		Selectively-logged forest	
Variable	Mean	SE	Mean	SE
Trees				
Number of trees	7.76	0.12	7.72	0.14
Proportion branching above mid point	0.83	0.03	0.78	0.06
Mean height (m) ***	27.80	0.89	20.80	0.47
Mean girth (m)**	1.55	0.12	1.18	0.07
Mean density	84.34	12.77	71.20	8.41
Proportion of Dipterocarps***	0.63	0.03	0.16	0.03
Proportion of *Macaranga* spp. ***	0.00	0.00	0.48	0.05
Saplings				
Number of saplings	8.00	0.00	8.00	0.00
Mean girth (m)	0.20	0.01	0.20	0.01
Mean density	3.80	0.29	3.91	0.44
Proportion of Dipterocarps***	0.57	0.03	0.27	0.04
Proportion of *Macaranga* spp. **	0.00	0.00	0.11	0.03
Percentage covers				
Densiometer*	87.80	0.56	84.71	1.17
Ground**	39.10	2.97	27.80	2.76
Low level (2m)	45.50	2.34	43.10	2.72
Understorey	45.50	2.31	44.30	2.98
Canopy ***	25.80	4.36	2.80	1.04
PCA factors				
Principal component 1 (PRIN1) ***	0.87	0.07	-0.87	0.12
Principal component 2 (PRIN2)	-0.04	0.20	0.04	0.21

Table 5.4 Mean values of vegetation variables plus the first two principal component scores of vegetation structure in primary and selectively-logged forest. Mean values are shown with their standard errors. Asterisks denote significant differences between habitats using *t*-tests.

Principal components analysis extracted two main components from the 17 vegetation variables (PRIN1 and PRIN2) that explained 27% and 15% of the variation within the vegetation data, respectively (Table 5.5). The first principal component factor (PRIN1) increased, in order of importance, with a decrease in the proportion of *Macaranga* spp. trees and an increase in the proportion of Dipterocarp trees and Dipterocarp saplings, mean tree height and percentage canopy cover, it decreased with an increase in the proportion of *Macaranga* spp. saplings (Table 5.5). The second factor, PRIN2, increased in order of importance, with a decrease in percentage low level cover and increased with the number of trees present and percentage understorey cover (Table 5.5). Thus a high PRIN1 score describes a forest structure that contains tall trees with a well-devolved crown from the family Dipterocarpaceae, with very few pioneer trees. PRIN2 score primarily described changes in vegetation cover, with a high score describing a relatively dense understorey cover. Therefore PRIN1 can be considered a measure of an undisturbed primary forest as a high PRIN1 score reflects the presence of climax tree species with few pioneer species and a well developed canopy. PRIN2 is principally a measure of lower strata vegetation cover. Primary forest had a significantly higher PRIN1 score than selectively-logged forest (Table 5.4; *t*-test comparing between habitats; $t_{48} = 12.64$, $p < 0.001$). However, there was no difference in PRIN2 scores between habitats (Table 5.4; *t*-test; $t_{48} = -0.29$, $p = 0.78$).

Variable	Weighting PRIN1	PRIN2
Trees		
Number of trees	-0.02	**0.85**
Proportion branching above mid point	0.04	0.04
Mean height	**0.65**	-0.08
Mean girth	0.26	-0.19
Mean density	0.01	0.30
Proportion of Dipterocarps	**0.84**	0.09
Proportion of *Macaranga* spp.	**-0.85**	0.19
Saplings		
Mean girth	0.02	0.01
Mean density	-0.18	0.10
Proportion of Dipterocarps	**0.75**	0.23
Proportion of *Macaranga* spp.	**-0.60**	0.20
Covers		
Densiometer	-0.49	0.13
Ground	0.26	-0.22
Low level (2m)	0.04	**-0.89**
Understorey	0.20	**0.76**
Canopy	**0.65**	0.12

Table 5.5 Contributions of 17 vegetation variables to the first two principal component factors that explained 27% and 15% of the variation within the vegetation data, respectively. Variables making the main contribution to each principal component are shown in bold.

5.4.4 Impacts of selective logging on the spatial distribution of α diversity

In order to examine the impacts of selective logging on the spatial distribution of α diversity values, semivariograms were calculated for α diversity in primary and selectively-logged forest. Semivariogram values, γ, were calculated for all three diversity indices (Margelf, Simpson and Shannon-Wiener) based on the average difference between pairs of sampling points (traps) at all possible distances, h, that separated samples.

Examination of the semivariogram for data from Simpson's index showed diversity to be positively autocorrelated in primary forest but not in selectively-logged forest (Figure 5.4). Semivariogram values for logged forest indicated data from traps were independent at all lag distances considered, with the semivariogram value at the smallest lag distance being greater than the overall data set variance (Figure 5.4; logged γ_1 (h = 237 m) = 11.50; logged overall data γ = 10.9). When semivariogram values at short lag distances are equal to, or greater than the overall variance, the data exhibit a pure nugget effect. As the nugget, n, is higher than the overall variance the data can not be modelled in terms of their component parts. Thus Simpson's index in logged forest could not be fitted to any model suggested. Therefore the distribution of α diversity values in selectively-logged forest were not spatially autocorrelated (Figure 5.4).

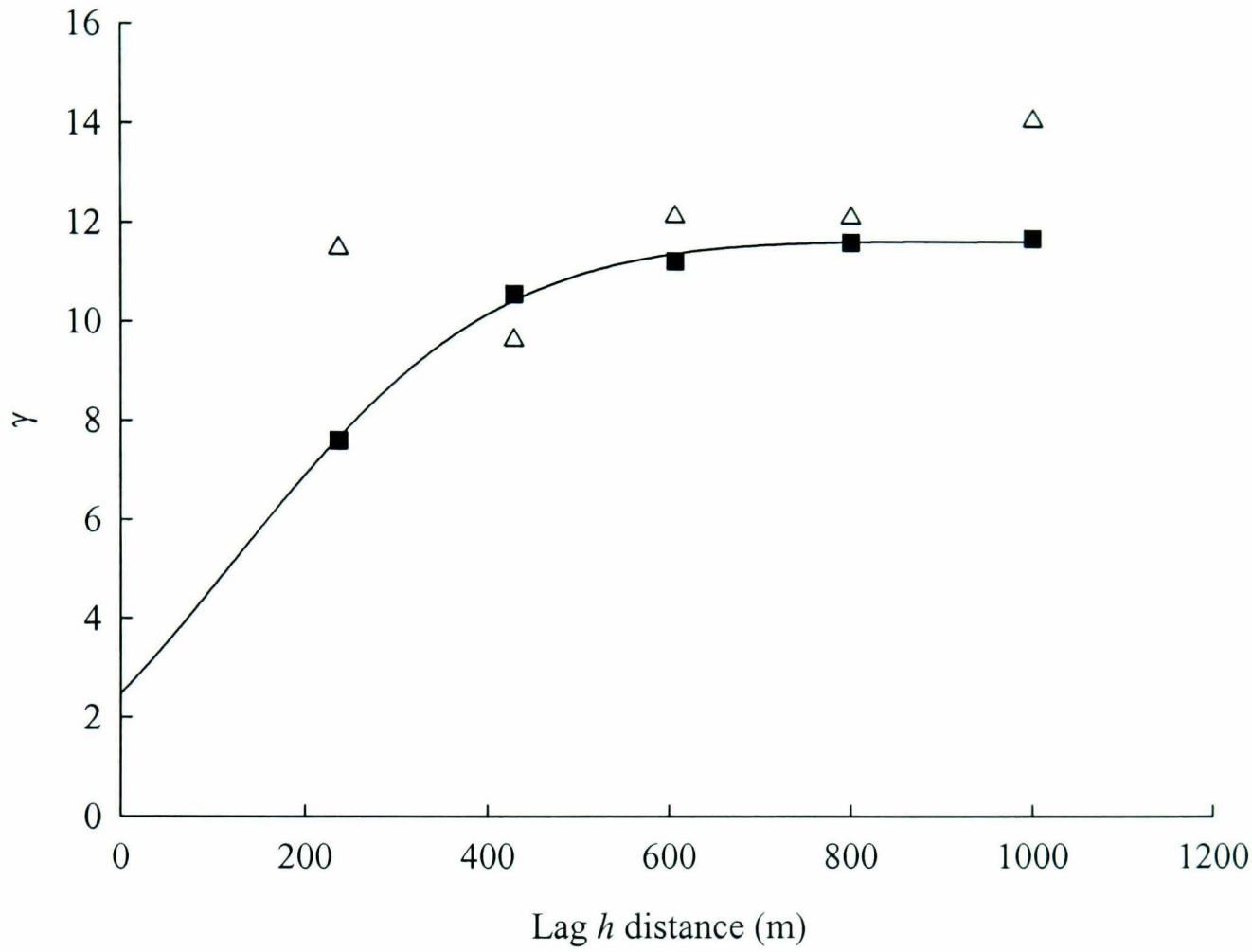


Figure 5.4 Semivariogram of Simpson's index in primary (squares) and selectively-logged forest (triangles). Line shows fit of semivariogram values to a Gaussian model (Equation 5.3) in primary forest.

The distribution of semivariogram values for Simpson's index in primary forest was shown to fit the Gaussian model best (Figure 5.4; indicative goodness of fit, IGF = 0.0007) and produced the following values; nugget = 2.49, sill = 8.93 and range = 345.4. The high proportion of the variance explained by the sill (78%) suggests that Simpson's index in primary forest was strongly positively spatially autocorrelated between pairs of sampling points separated by distances smaller than the range (345.4 m). The *z*-test confirmed Simpson's index to be significantly spatially autocorrelated in primary forest between sampling points separated by small lag distances up to the range, 345.4 m ($h = 237$, $z > 3.10$, $p < 0.001$; $h = 429$, $z < 1.7$, $p > 0.05$).

Semivariogram values for the other diversity indices (Margalef and Shannon-Weiner) analysed were all shown to exhibit a pure nugget effect in both primary and selectively-logged forest. Thus these values were independent at all spatial scales considered and no further analysis of spatial autocorrelation was attempted.

I also computed semivariograms based on the average difference in vegetation principal component scores (PRIN1 and PRIN2) between pairs of trapping stations in both habitats. Examination of semivariograms of principal component scores showed PRIN1 to be positively spatially autocorrelated in both primary and selectively-logged forest (Figure 5.5). The distribution of semivariogram values for PRIN1 was shown to fit an exponential model (Equation 5.2) best in both primary and selectively-logged forest (primary forest, IGF = 0.0004; selectively-logged forest, IGF = 0.0007) and produced the following values; primary forest, nugget = 0.00, sill = 0.14, range = 326.93; selectively-logged forest, nugget = 0.13, sill = 0.20, range = 362.30. The high proportion of variance explained by the sill in both habitats (primary forest = 100%; selectively-logged forest = 61%) suggest that PRIN1 was strongly positively autocorrelated at distances smaller than the range (primary forest = 326.93 m; selectively-logged forest = 362.30 m) within primary and selectively-logged forest. This was confirmed by the z-test that showed PRIN1 to be significantly, positively spatially autocorrelated between samples separated by smaller lag distances than the range (primary forest = 326.93 m; selectively-logged forest = 362.30 m) within primary and selectively-logged forest ($h = 237, z > 3.10, p < 0.001$; $h = 429, z < 1.7, p > 0.05$).

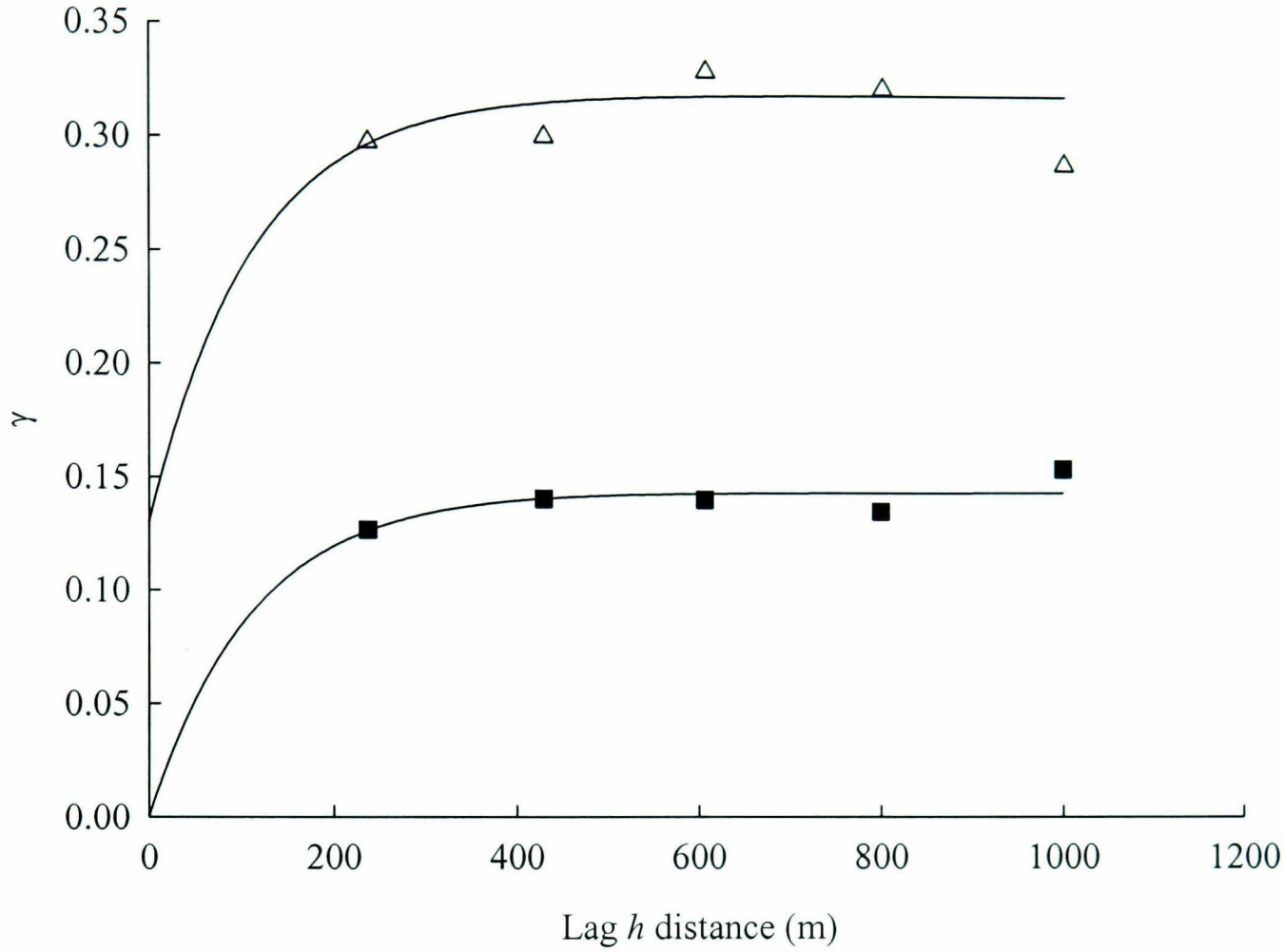


Figure 5.5 Semivariogram of the first vegetation principal component score (PRIN1) in primary (squares) and selectively-logged forest (triangles). Line shows fit of semivariogram values to an exponential model (Equation 5.2) in both habitats.

In contrast to the spatial distribution of PRIN1, examination of semivariograms of PRIN2 showed PRIN2 to be positively spatially autocorrelated in primary forest but not in selectively-logged forest (Figure 5.6). Semivariogram values for PRIN2 in logged forest indicated data from trapping stations were independent at all lag distances considered. The semivariogram value at the smallest lag distance was greater than the overall data set variance (Figure 5.6; γ_1 (h = 237 m) = 1.04; logged overall data γ = 0.89). Due to this pure nugget effect PRIN2 values in logged forest could not be fitted to any model suggested. Therefore the distribution of PRIN2 values in selectively-logged forest was not spatially autocorrelated (Figure 5.6).

The distribution of semivariogram values for PRIN2 in primary forest was shown to fit the power model best (Figure 5.6; IGF = 0.0004). Using the power model (Equation 5.4) produced the following values; nugget = 0.41, power = 1.05. As the semivariogram values

for PRIN2 fitted the power function best the range at which sampling points became independent could not be estimated. This is because the power model will fit semivariograms if values are significantly spatially autocorrelated beyond a range greater than the maximum distance that separates recorded samples (z-test of primary forest PRIN2 values, $h = 1200$, $z > 3.10$, $p < 0.001$). This indicates PRIN2 is spatially autocorrelated in primary forest over a greater spatial scale than sampled here.

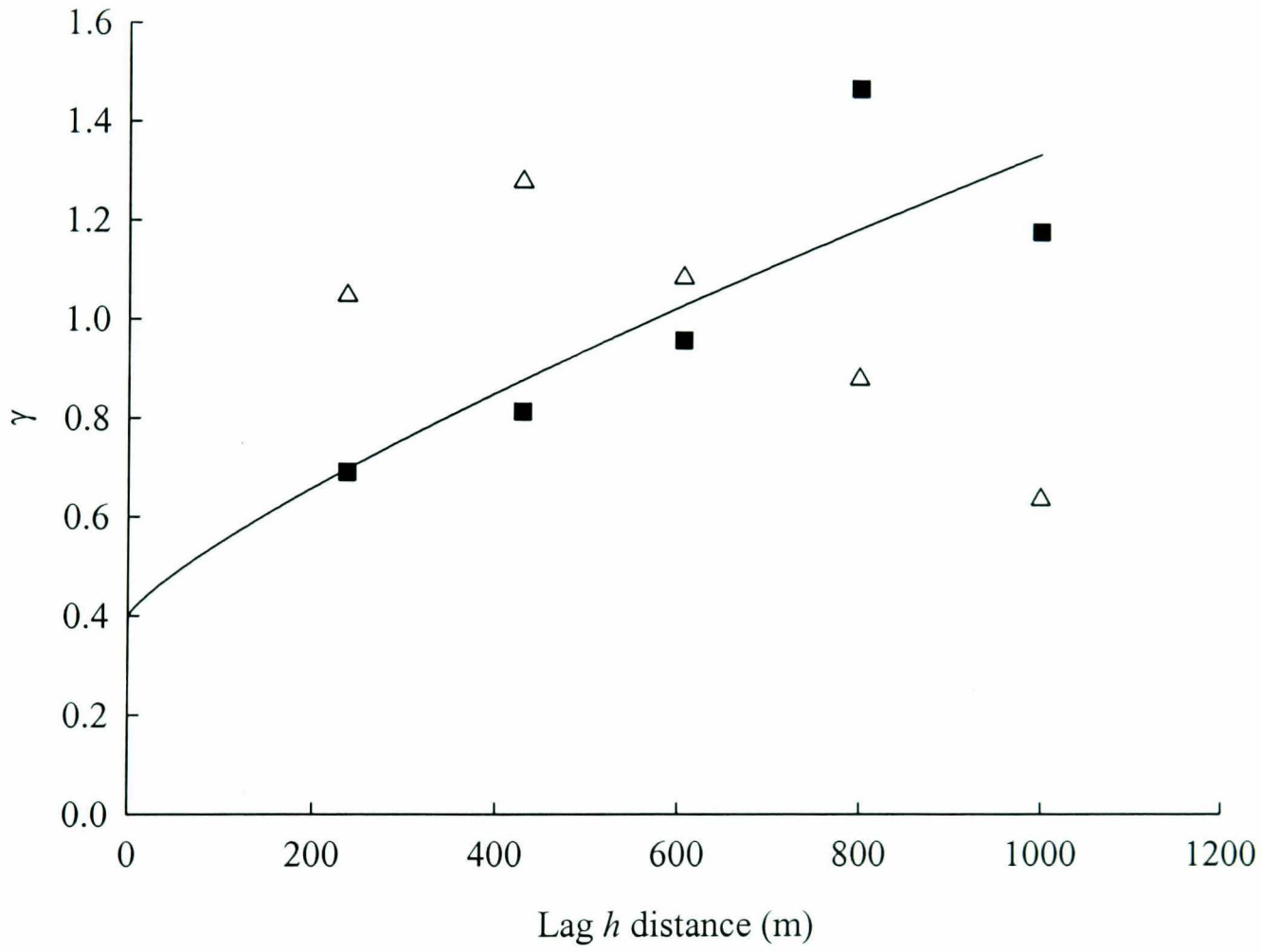


Figure 5.6 Semivariogram of the second vegetation principal component score (PRIN2) in primary (squares) and selectively-logged forest (triangles). Line shows fit of semivariogram values to a power function model (Equation 5.4) in primary forest.

In order to test the hypothesis that reduced habitat heterogeneity following selective logging affects patterns of spatial autocorrelation in vegetation measures, I also computed semivariograms for canopy cover in primary and selectively-logged forest (this vegetation measure showed the most significant reduction in heterogeneity following selective logging). Examination of the semivariograms showed canopy cover to be positively

spatially autocorrelated in primary forest but not in selectively-logged forest (Figure 5.7). Semivariogram values for logged forest indicated canopy cover data were independent at all lag distances considered, with the semivariogram value at the smallest lag distance being greater than the overall data set variance (Figure 5.7; logged γ_1 (h = 237 m) = 22.6; logged overall data γ= 20.9).

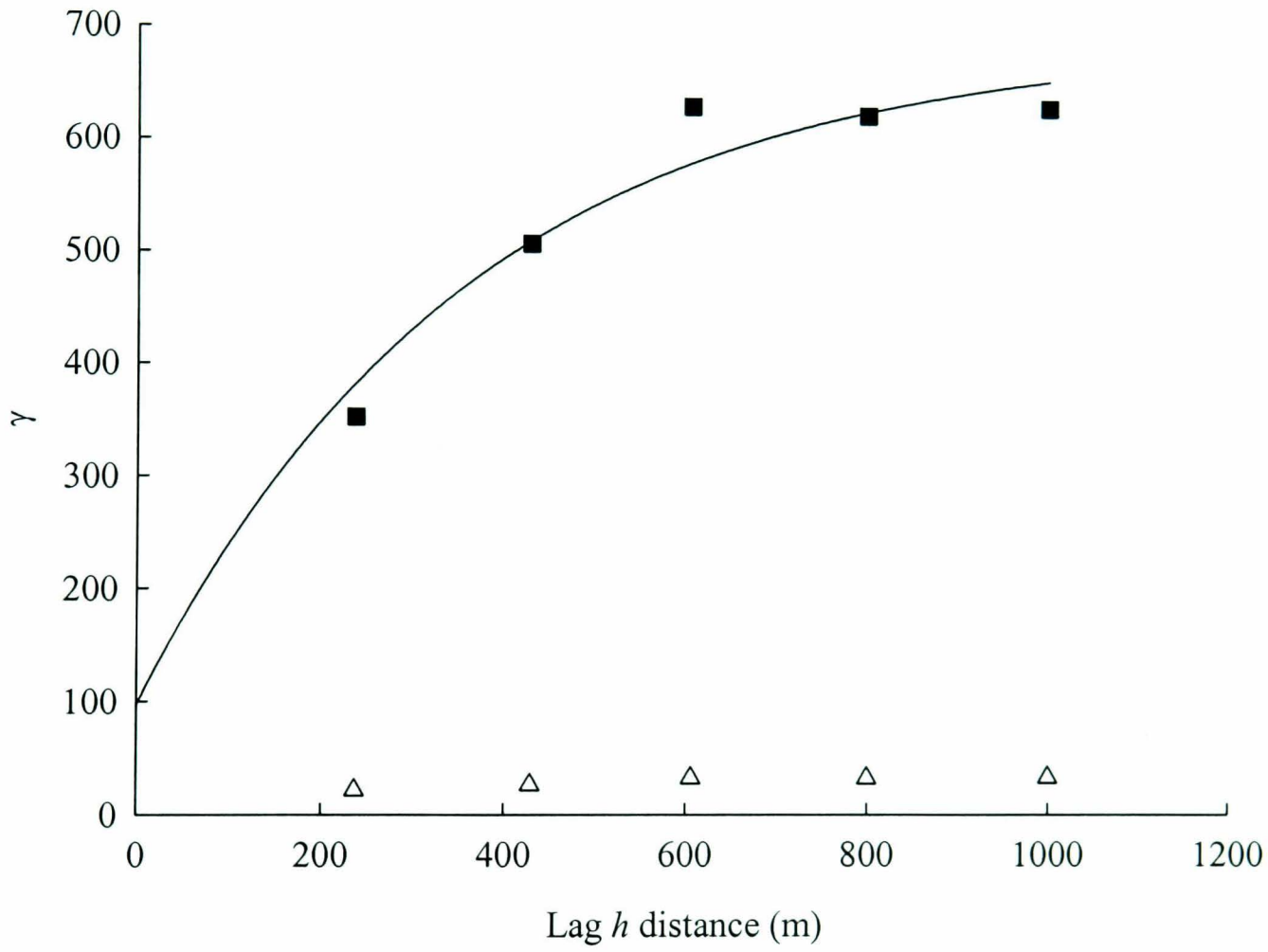


Figure 5.7 Semivariogram of canopy cover in primary (squares) and selectively-logged forest (triangles). Line shows fit of semivariogram values to a Gaussian model (Equation 5.3) in primary forest.

The distribution of semivariogram values for canopy cover in primary forest was shown to fit the Gaussian model best (Figure 5.7; indicative goodness of fit, IGF = 0.01) and produced the following values; nugget = 106, sill = 354 and range = 409.5. The high proportion of the variance explained by the sill (77%) suggests that canopy cover in primary forest was strongly positively spatially autocorrelated between pairs of sampling points separated by distances smaller than the range (409.5 m). The z-test confirmed canopy cover to be significantly spatially autocorrelated in primary forest between

sampling points separated by small lag distances up to the range, 409.5 m (h = 237, z > 3.10, $p < 0.001$; h = 429, $z < 1.7$, $p > 0.05$).

5.4.5 Butterfly dispersal in primary and selectively-logged forest

A total of 396 recaptures were recorded during the entire 10 month study, 221 recaptures in primary forest and 175 recaptures in selectively-logged forest. Overall, recapture rates of all species (recaptures/total capture events) were similar in primary and selectively-logged habitats (primary = 0.11; logged = 0.10). Individuals of *Bassarona dunya* were recaptured 36 times in primary forest and 36 times in selectively-logged forest. Individuals of *Mycalesis orseis* were recaptured 32 times in primary forest and 36 times in selectively-logged forest.

Data from Figure 5.8 and Figure 5.9 were double-log transformed and fitted to an inverse power function. Regression analysis showed that the distribution of dispersal distances for both *B. dunya* and *M. orseis* fitted an inverse power function in both habitats (*B. dunya* primary forest, $R^2 = 0.921$, $F_{1,24} = 279.47$, $p < 0.001$; selectively-logged forest, $R^2 = 0.897$, $F_{1,24} = 208.50$, $p < 0.001$; *M. orseis* primary forest, $R^2 = 0.757$, $F_{1,24} = 12.44$, $p < 0.05$; selectively-logged forest $R^2 = 0.721$, $F_{1,24} = 10.34$, $p < 0.05$). There was no significant difference between primary and selectively-logged forest in the slopes of the relationship that described the distribution of dispersal distances for either *B. dunya* or *M. orseis* (Figure 5.8, 5.9; ANCOVA of *B. dunya* dispersal in primary and logged forest with distance as a covariate, distance by habitat interaction, $F_{1,46} = 0.123$, $p = 0.728$; *M. orseis*, $F_{1,6} = 0.567$, $p = 0.48$).

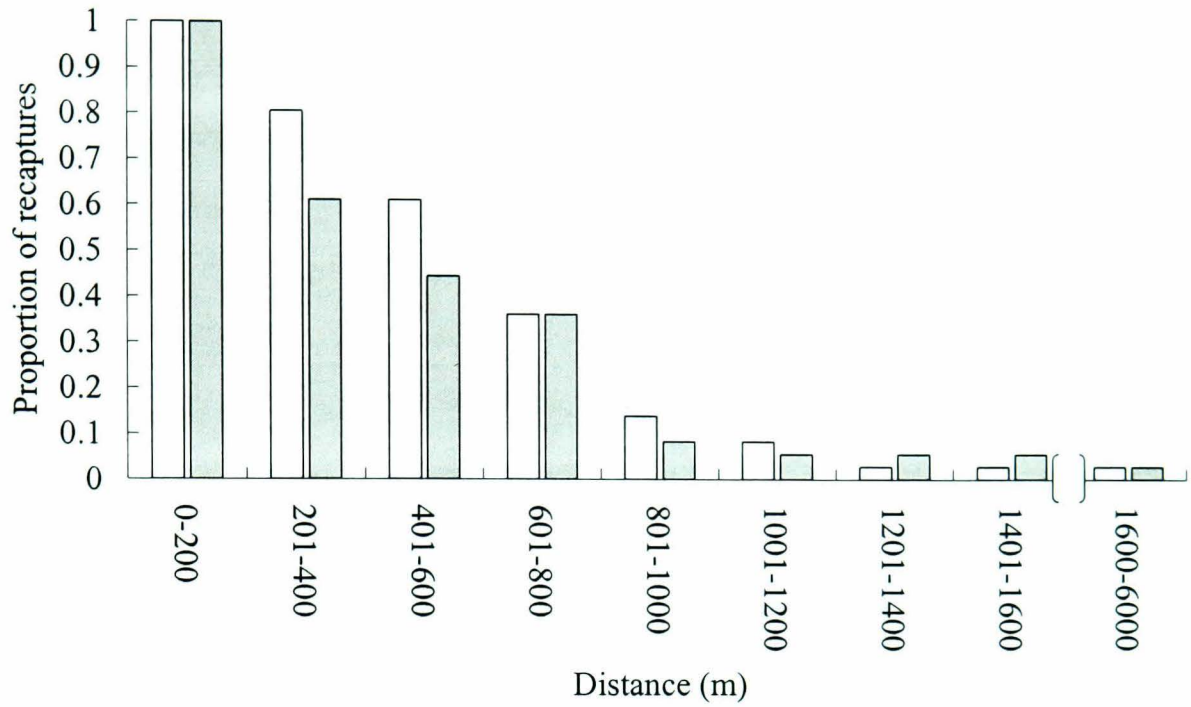


Figure 5.8 Frequency of recaptures of *Bassarona dunya* with increasing distance in primary (closed bars) and selectively-logged (open bars) forest

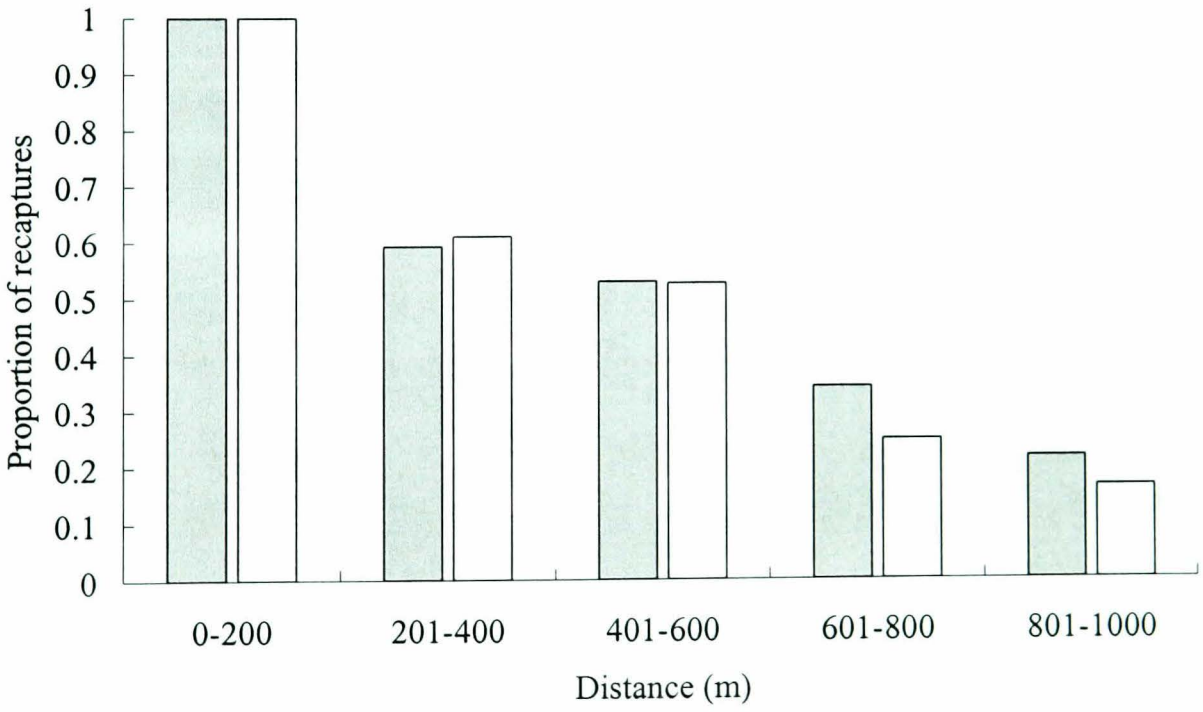


Figure 5.9 Frequency of recaptures of *Mycalesis orseis* with increasing distance in primary (closed bars) and selectively-logged (open bars) forest.

5.5 DISCUSSION

5.5.1 Data collection

During the six month study, I recorded a total of 62 species of fruit-feeding Nymphalid butterfly. This represents approximately 75% of the fruit-feeding Nymphalids recorded at this study site (Willott *et al.*, 2000; Hamer *et al.*, 2003; Dumbrell and Hill, 2005). This level of species richness is quantitatively similar to results from other studies at different sites in Sabah that have used similar sampling methods (Schulze and Fiedler, 1998; Schulze *et al.*, 2001). I recorded eight additional species, including two endemics *Mycalesis amoena* and *Thauria aliris* compared with Hamer *et al.* (2003) who also conducted field work at the same study site using similar trapping methods. Hamer *et al.* (2003) conducted their study for 12 months and highlighted the need for long-term studies when compiling species inventories and comparing diversity between primary and disturbed habitats. Hamer *et al.* (2003) recorded a further 11 species that were not present in my study. Thus there was some species turnover between studies. In this study species accumulation curves had begun to asymptote in both primary and selectively-logged forest (Figure 5.2). Thus although additional sampling would have produced a more complete species inventory, further sampling effort was unlikely to qualitatively affect comparisons between habitats.

In this study, I used fruit-baited traps which only sample the fruit-feeding guild of Nymphalid butterflies. Although, this restricts the sampling to only one guild from one family of butterfly, it allows a reliable, repeatable sampling technique within different areas of the forest and in different habitats (Walpole and Sheldon, 1999). There is little information on the efficiency of fruit-baited traps in attracting and retaining species (but see Chapter 3). However, it is likely that any differences in the trap's efficiency at capturing and retaining butterflies are likely to vary between species rather than between habitats and thus conclusions based on trap data are likely to be robust. In addition, it has been suggested in previous studies that relatively long-term sampling such as conducted here, which sampled for 3600 trap-days, greatly reduces any problems associated with differences in species' capture and escape rates from traps (Hughes *et al.*, 1998).

The study site at which sampling was conducted is generally considered aseasonal with relatively constant monthly rainfall throughout the year (Walsh and Newbury, 1999). However, there is some variation in rainfall caused by the northerly monsoon in the South China Seas (Walsh, 1996b). This variation in rainfall is known to cause temporal variation

in butterfly abundances (Hill *et al.*, 2003), which in turn effect estimates of diversity and comparisons between habitats (Hamer *et al.*, 2005). To account for temporal variation in butterfly abundances I made sure to sample in both drier and wetter months across the year.

5.5.2 Impacts of selective logging on butterfly α diversity

The results showed that primary forest was significantly more diverse than selectively-logged forest when measured using the Shannon-Wiener index. In addition Simpson's index was approaching significance ($p = 0.056$), thus supporting results from the analysis of the Shannon-Wiener index. These results were in contrast to results from Chapter 4. In Chapter 4, I showed sampling from the canopy was needed in order to detect a significant change in diversity following selective logging. However, in this chapter I reported a change in diversity following selective logging based solely on ground-level traps. The lack of consensus between chapters 4 and 5 may reflect difference in the spatial scale of sampling using transect (Chapter 4) and grid methods (Chapter 5) and this will be discussed in full in Chapter 7 (General Discussion). Results of diversity analysis in this Chapter were qualitatively different depending on whether data were analysed per trap or per grid. Primary forest was significantly more diverse when analysis combined data from all traps across the grid (as described above). However, when data were analysed per trap, comparing mean trap diversity between habitats, no significant change in diversity was observed following selectively logging. This suggests that the perceived impacts of selective logging are scale dependent. Hamer and Hill (2000) and Hill and Hamer (2004) suggested that increased diversity in selectively-logged habitats would be expected when measured at small spatial scales (≤ 1 ha) but a decrease in diversity or no change in diversity is expected at large spatial scales (≥ 3 ha). In this study, decreased diversity was reported following selective logging when measured on a large spatial scale (≈ 80 ha). However, no change in diversity was reported when measured at a smaller spatial scale (≈ 3 ha), but this was still at a scale classified as 'large' by Hamer and Hill (2000) and Hill and Hamer (2004). Thus I confirm predictions that a decrease in diversity, or no change in diversity, is expected when butterfly data are analysed at relatively large spatial scales.

A growing body of literature has highlighted the importance of spatial scale when measuring diversity (Hamer and Hill, 2000; Lawes and Eeley, 2000; Cleary, 2003; Kaiser, 2003; Hill and Hamer, 2004; Ribas *et al.*, 2005; Rahbek, 2005). A recurring theme in ecological literature is that measures of diversity at small scales are not necessarily

representative of measures of diversity at larger spatial scales (Rahbek, 2005). Thus ecologists monitoring diversity need to be aware that diversity measured at a single spatial scale may not be representative of all spatial scales. Perhaps more importantly, conservationists need to be aware that the perceived response of diversity to disturbance is largely dependent upon the spatial scale at which studies are conducted (Hamer and Hill, 2000; Cleary, 2003; Kaiser, 2003; Hill and Hamer, 2004; Ribas *et al.*, 2005). In this chapter, I showed that reported changes in diversity following selective logging are dependent upon the spatial of the study with qualitatively different results from analyses of data at different spatial scales. Therefore future studies need to consider that results obtained at a single spatial scale may not be representative of all spatial scales and further effort may be required to examine the effects of disturbance across a range of spatial scales.

5.5.3 Effects of spatial scale and habitat heterogeneity on α diversity

Species richness and diversity, measured by the Shannon-Wiener, Margalef and Simpson indices, were significantly positively related to spatial scale in both primary and selectively-logged forests. These relationships increased at a significantly faster rate in primary forest compared with selectively-logged forest. Previous research has suggested that changes in the species-area relationship following selective logging may reflect changes in the pattern and scale of habitat heterogeneity in tropical forests (Hill and Hamer, 2004). As a general rule the greater the habitat heterogeneity of an area the greater the species diversity within that area (Rosenzweig, 1995). Consequently species-area patterns reflect habitat heterogeneity, with a steeper relationship between species and area in more heterogeneous environments compared with homogenous environments (Rosenzweig, 1995). Thus the reduction in the rate at which species diversity increases with spatial scale following selective logging shown here most likely reflects a reduction in habitat heterogeneity in selectively-logged forests (Hamer and Hill, 2000).

Habitat heterogeneity plays a key role in promoting diversity (He *et al.*, 1996; Kerr *et al.*, 2001; van Rensburg *et al.*, 2002; Hamer *et al.*, 2003; Tews *et al.*, 2004) and an increase in habitat heterogeneity in tropical regions may explain high diversity in the tropics (Pianka, 1966; Kotler and Brown, 1988; Rhode, 1992). Analysis of vegetation data showed the variance of some vegetation variables to be higher in primary forest compared with selectively-logged forest, indicating a more heterogeneous forest structure in primary forest. Primary forest had a significantly greater range of canopy cover values, tree heights

and tree sizes (Table 5.5). This supports previous studies that show a reduction in habitat heterogeneity following selective logging (Ganzhorn *et al.*, 1990; Burghouts *et al.*, 1994; Okuda *et al.*, 2003; Hamer *et al.*, 2003; Dumbrell and Hill, 2005). Vegetation structure probably becomes more homogenous following selective logging because the initial impact of selective logging dramatically opens up the forest canopy. This results in rapid colonisation by invasive pioneer species such as *Macaranga* spp. (Burghouts *et al.*, 1994). In this study, approximately half of all tree species recorded in selectively-logged forest were from the genus *Macaranga*. Thus the dominance of a single tree genus in selectively-logged forest was probably responsible for the more homogenous forest structure (shown by a reduction in the variance of measures for canopy cover, tree height and tree size) and a significant reduction in canopy height and canopy cover reflecting the physiology of *Macaranga* species. However, what is less clear, concerning the impact of disturbance on α diversity in relation to habitat heterogeneity is the response of α diversity to disturbance measured at much larger spatial scales than those considered here. At a very large spatial scale selectively logging may result in a mosaic of habitat types ranging from log-landing sites to fragments of primary forest along riparian reserves (Hamer and Hill, 2000). This might lead to higher species diversity at the landscape scale due to higher β diversity between areas differing in disturbance intensity and this deserves further study (Hamer and Hill, 2000).

5.5.4 Impacts of selective logging on vegetation structure

There were significant differences in vegetation structure between primary and selectively-logged forest 15 years after logging. Primary forest contained significantly taller and larger trees (girth at breast height) and had higher percentage ground, canopy and overstorey vegetation covers (Table 5.4). There was a significantly higher proportion of Dipterocarp trees and saplings in primary forest and species of the pioneer genus *Macaranga* were not present (Table 5.4). This agrees with previous findings (Burghouts *et al.*, 1994; Cannon *et al.*, 1994; Okuda *et al.*, 2003; Asner *et al.*, 2003).

The first principal component factor (PRIN1) extracted from vegetation data was significantly higher in primary forest than in selectively-logged forest. PRIN1 increased in order of importance, with a decrease in the proportion of *Macaranga* spp. trees and increase in the proportion of Dipterocarp trees and saplings, mean tree height and percentage canopy cover, it decreased with an increase in the proportion of *Macaranga* spp. saplings (Table

5.5). Thus PRIN1 primarily described vegetation in terms of tree species ecologies with a high PRIN1 score indicating a high proportion of climax species and a low PRIN1 score indicating a high proportion of pioneer species. Therefore, PCA showed primary forest in Danum Valley is typical of mature growth Dipterocarp forest, containing relatively large, tall trees with a dense canopy cover and a high proportion of Dipterocarp species and relatively few invasive pioneer species (Burghouts *et al.*, 1994; Okuda *et al.*, 2003). PCA analysis supported the analysis of individual vegetation variables and confirmed previous findings on the impact of selective logging on vegetation structure (Burghouts *et al.*, 1994; Cannon *et al.*, 1994; Okuda *et al.*, 2003; Asner *et al.*, 2003, 2004b).

5.5.4 Patterns of spatial autocorrelation in primary and selectively-logged forest

Results from geostatistical analyses showed that values of butterfly α diversity as measured by Simpson's index were positively spatially autocorrelated in primary forest. This spatial autocorrelation was evident up to a distance of $\approx$350 m between sampling points. In contrast, α diversity in selectively-logged forest showed no spatial autocorrelation. Analysis of butterfly dispersal data showed no change in dispersal patterns of butterflies following selective logging, suggesting that observed changes in the spatial patterns of α diversity were more likely to be a direct impact of habitat disturbance on α diversity and not due to changes in butterfly behaviour. Geostatistical analysis of vegetation data (PRIN1 and PRIN2) revealed patterns of spatial autocorrelation in vegetation measures in both habitats. The first principal component (PRIN1) of the vegetation data had a similar pattern of spatial autocorrelation in primary forest to that in selectively-logged forest. This spatial autocorrelation was evident up to a distance of $\approx$325 m in primary forest and $\approx$360 m in selectively-logged forest. The second principal component (PRIN2) of the vegetation data was spatially autocorrelated in primary forest but not in selectively-logged forest. This spatial autocorrelation was evident across all the distances (200 – 1135 m) separating samples. Thus, selective logging does not cause a change in patterns of spatial autocorrelation in measures of vegetation that reflect the ecologies of tree species (PRIN1). However, geostatistical analysis of percentage canopy covers revealed differences in patterns of spatial autocorrelation between habitats. Canopy cover was spatially autocorrelated up to a distance of $\approx$406 m between sampling points in primary forest, but was not spatially autocorrelated in selectively-logged forest. Thus, the observed reduction

in canopy heterogeneity in selectively-logged forest also resulted in a change in the spatial autocorrelation of canopy cover following selective logging.

A possible explanation for observed patterns of spatial autocorrelation in ecological data is that it reflects spatial autocorrelation in a limiting environmental resource (Koenig, 1999). Light is the limiting abiotic factor that determines the distribution of tropical butterfly species throughout the forest (Hill *et al.*, 2001; Schulze *et al.*, 2001; DeVries, 1988). Estimates of canopy cover reflect the amount of light penetrating through the vertical layers of the forest (Costa and Magnusson, 2002; Koukoulas and Blackburn, 2004). The results from this study showed patterns of spatial autocorrelation in butterfly α diversity reflected patterns of spatial autocorrelation in canopy cover in primary and selectively-logged habitats. Thus, changes in the patterns of spatial autocorrelation of butterfly α diversity are probably caused by changes in the patterns of spatial autocorrelation of light penetration. Therefore a more homogeneous light environment following selective logging results in a more spatially homogenous distribution of butterfly α diversity.

Previous studies have shown canopy cover to be spatially autocorrelated in primary forest (Clark *et al.*, 1996; Nicotra *et al.*, 1999) and have suggested that patterns of spatial autocorrelation in light penetrating the canopy change following selective logging (Bebber *et al.*, 2002). However, previous research has looked either at patterns of spatial autocorrelation of canopy covers in primary (Clark *et al.*, 1996; Nicotra *et al.*, 1999) or selectively-logged (Bebber *et al.*, 2002) forest. Here I examined spatial autocorrelation in canopy cover in both habitats and showed a change in the spatial autocorrelation of canopy cover following selective logging. This confirms predictions made by Bebber *et al.* (2002) who only looked at spatial patterns in selectively-logged forest and made no direct comparisons with primary forest. Few data are available on patterns of spatial autocorrelation of vegetation measures in primary and selectively-logged forests. Here I show vegetation structure (PRIN1) to be spatially autocorrelated in both habitats. This highlights the need for future study to examine the spatial component of vegetation data to avoid erroneous statistical analysis (Legendre, 1993).

In this study only Simpson's index was spatially autocorrelated in primary forest whereas Shannon-Wiener and Margalef's indices were not. There are a number of possible explanations for this lack of consensus among diversity indices. Semivariograms of α diversity measured by Shannon-Wiener and Margalef's indices showed a pure nugget

effect. This means that the semivariogram value at the lowest lag distance was greater than the overall variance. A pure nugget effect may be observed if an insufficient number of samples have been measured (Olea, 1999). This is because the variance in the average difference between samples at the lowest lag distance maybe over estimated due to a small number of possible *pairwise* comparisons between samples (Olea, 1999). Another possible explanation for the observed nugget effect is that values for Shannon-Wiener and Margalef's indices are spatially autocorrelated between samples separated by smaller distances than were considered (Olea, 1999). However, the number of samples used here were sufficient to show spatial autocorrelation in values of Simpson's index in primary forest. In addition this spatial autocorrelation was detected up to a range greater than the minimum distance separating samples. Thus it is likely that the pure nugget effect shown by Shannon-Wiener and Margalef's indices indicates their values were not spatially autocorrelated in primary forest. Therefore it is most likely that the results shown here reflect differences between indices. Simpson's index is disproportional biased by the most abundant species whereas Shannon-Wiener and Margalef's indices are biased by rare species (Magurran, 2004). Thus the spatial autocorrelation in butterfly α diversity within primary forest is most likely driven by species abundance patterns rather than species richness patterns. This is in agreement with previous studies that have suggested species abundance patterns are spatially autocorrelated for most species (Legendre, 1993).

5.5.5 Implications for future conservation studies

Measures of α diversity are widely used to assess the impacts of habitat disturbance in highly diverse environments such as tropical rainforests (Hill and Hamer, 2004). Conservationists are beginning to recognise that only using measures of α diversity may not be sufficient to gauge the impacts of habitat disturbance and that a measurement of species composition should also be included (Vane-Wright, 1991; Hamer *et al.*, 2003; Dumbrell and Hill, 2005). However, due to limited recourses available to many conservationists (Balmford *et al.*, 2003) and the relative ease at which α diversity can be measured, it remains a widely-used tool for assessing the impacts of habitat disturbance (Hill and Hamer, 2004). In the presence of spatial autocorrelation within α diversity data, careful choice of sampling methods and statistical analysis are required when assessing the impacts of habitat disturbance. Conservationists need to be aware that when assessing the impacts of habitat disturbance on α diversity, examining the spatial component of the data is of

prime importance to avoid statistically unreliable results. Thus, future studies should examine whether diversity data are spatially autocorrelated before conducting any further analysis. In the light of spatial autocorrelation being reported in most ecological data (Legendre, 1993) a vast array of statistical techniques has been proposed that examine data that are spatially autocorrelated (Gittleman and Luh, 1992; Dutilleul, 1993a, 1993b; Legendre, 1993; Cerioli, 1997; Perry *et al.*, 2002; Keitt *et al.*, 2002; Legendre *et al.*, 2002; Lichstein *et al.*, 2002). For example, randomisation tests (Solow, 1993), adjusted model ANOVAs (Bartlett, 1978), Monte Carlo permutation techniques (Legendre *et al.*, 1990; Legendre, 1993; see Sokal and Rohlf, 1995), modified *t*-tests (Dutilleul, 1993a; Legendre *et al.*, 2002) and Mantel tests of dissimilarity (Legendre, 1993) are all statistically robust techniques that can examine spatially autocorrelated data.

Butterflies are widely used to quantify changes in diversity and for establishing conservation priorities following disturbance (Kremen, 1992; Sparrow *et al.*, 1994; Kerr *et al.*, 2000). Within tropical regions, fruit-baited traps provide a robust and efficient method of sampling tropical-forest butterflies (see Chapter 3.0; DeVries, 1987; Daily and Ehrlich, 1995). However, future monitoring schemes that assess the impact of habitat disturbance on fruit-feeding butterfly diversity need to be aware that data from traps placed less than ≈350 m apart are not independent. In addition, the perceived response of diversity to habitat disturbance is dependent upon the spatial scale of sampling. Thus, when designing future sampling protocols, conservationists should consider that the placement of the traps within the forest and the spatial scale of sampling can affect the perceived response of butterfly diversity to disturbance.

Chapter 6 Impacts of selective logging on β diversity and composition of tropical forest butterfly assemblages

6.1 ABSTRACT

Understanding the ecological impacts of habitat disturbance on tropical forest diversity is of great current concern. However, the majority of studies have focused on α diversity and the impacts of habitat disturbance on species turnover (β diversity) have largely been ignored. In this chapter, I use fruit-baited traps to examine patterns of butterfly β diversity in primary forest and forest selectively-logged 15 years previously. I found significantly higher β diversity between traps in primary forest than in selectively-logged forest. Mantel tests revealed that β diversity was positively correlated with geographic distance between samples in primary forest but not in selectively-logged forest. This reflected patterns of vegetation structure, where similarity of vegetation structure decreased with increasing geographic distance between sites in primary forest but not in selectively-logged forest. Thus, patterns of butterfly β diversity between habitats mirrored those of vegetation structure. Canonical correspondence analysis revealed that changes in butterfly species composition following selective logging were associated with changes in vegetation structure. Species that were most adversely affected by selective logging preferred closed-canopy climax forest whereas those less adversely affected preferred more shrubby pioneer forest. Further to this, I examined how species with different ecological traits responded to selective logging. I showed that primary forest contained significantly more species with a lower light tolerance than selectively-logged forest. I found no significant difference between habitats in species' geographical distributions, species' morphologies or larval host plant specificity. This study highlighted the need for information on species' ecologies and habitat preferences when interpreting diversity patterns in primary and selectively-logged forest.

6.2 INTRODUCTION

6.2.1 Faunal surveys in ecological research

Faunal surveys provide the backbone of much ecological research. Typically faunal surveys are recorded as species abundance data, recording the abundance of each species sampled at each sampling site (Magurran, 1988; 2004). Data from faunal surveys have been used to investigate many ecological patterns. For example, to describe and understand the latitudinal gradient in species richness (Rohde, 1992; Willig *et al.*, 2003), to investigate spatial patterns of diversity (Carroll and Pearson 1998a, 1998b; Nummelin and Zilihona, 2004) and to investigate the impacts of habitat disturbance (Sekercioglu, 2002; Clarke *et al.*, 2005; Dumbrell and Hill, 2005). Data collected in faunal surveys can be analysed in two complementary ways, using Q-mode and R-mode analysis (Davis *et al.*, 2001; Ribera *et al.*, 2001; Hamer *et al.*, 2003). Q-mode analysis describes samples by their species composition, for example by calculating diversity indices. R-mode analysis focuses on describing samples by the presence of individual species, for example by explaining the presence of individual species in relation to species' ecologies or a species' association with a particular environmental variable (Davis *et al.*, 2001; Hamer *et al.*, 2003). Much recent research has used data from faunal surveys to examine the impacts of habitat disturbance in tropical rainforests (Sekercioglu, 2002; Clarke *et al.*, 2005; Dumbrell and Hill, 2005). The majority of these studies have used Q-mode analysis (*e.g.* Dumbrell and Hill, 2005) or used R-mode analysis to examine the impact of habitat disturbance in relation to individual species (*e.g.* Spitzer *et al.*, 1997). However, few studies have used both Q-mode and R-mode analysis together to investigate the impacts of habitat disturbance (Hamer *et al.*, 2003).

6.2.2 Q-Mode analysis

6.2.2.1 Additive partitioning of diversity

The total species diversity of an area or regional diversity (γ diversity) can be partitioned into α diversity and β diversity (Whittaker, 1960, 1972). α diversity is the species diversity of the samples within the region and β diversity is the species turnover or change in species composition between samples (Whittaker, 1960, 1972). Historically γ diversity was considered the product of α and β diversity (Whittaker, 1960). However, more recent

research has suggested diversity can be additively partitioned and that γ diversity is the sum of α and β diversity (Lande, 1996). Additive partitioning of diversity can examine the relative contributions of α diversity and β diversity within a region to the overall γ diversity (Lande, 1996). Some recent studies have used this method to examine patterns of α, β and γ diversity (*e.g.* DeVries and Walla, 2001; Gering *et al.*, 2003; Stendera and Johnson, 2005). However, the majority of ecological research describing patterns of diversity focus primarily on α diversity (Lennon *et al.*, 2001). For example, describing the island species-area relationship (MacArthur and Wilson, 1967) or the latitudinal diversity gradient (Gaston, 2000; Willig *et al.*, 2003). Consequently far less research has focused on β diversity (Lennon *et al.*, 2001).

6.2.2.2 β diversity

β diversity is a measure of species turnover between samples and increases with a decrease in the similarity of species composition between samples (Magurran, 1988, 2004). Thus, the greater the difference in species composition between two samples the higher the β diversity. β diversity can be assessed either spatially or temporally by examining species turnover between samples separated by space or time (Rosenzweig, 1995). The majority of recent ecological research on β diversity has focused on spatial patterns of β diversity and have generally focused on describing β diversity along an environmental gradient, for example, along altitudinal (Novotny and Weiblen, 2005), latitudinal (Rodriguez and Arita, 2004) or environmental disturbance gradients (Fiedler and Schulze, 2004). Temporal studies in β diversity have focused either on long-term trends in β diversity, for example over geological time (Brenchley *et al.*, 2001), or smaller temporal-scale studies investigating seasonal patterns in β diversity (Romanuk and Kolasa, 2001). Previous studies have suggested that increased β diversity is caused by an increase in environmental dissimilarity between samples (Harrison *et al.*, 1992; Balvanera *et al.*, 2002). Thus, the spatial distribution of environmental variables such as temperature, light availability and rainfall across a geographic region may affect the distribution of species and consequently β diversity within the region (Harrison *et al.*, 1992). This relationship between the environmental similarity of sites and β diversity is not restricted to temperate terrestrial organisms and has been shown in tropical mammal species (Williams *et al.*, 2002), freshwater cichlid fish species (Genner *et al.*, 2004) and within the marine environment (Clarke and Lidgard, 2000).

6.2.2.3 Latitudinal gradient and β diversity

Tropical areas have long been known for their high biodiversity compared with temperate regions (Wallace, 1878). This latitudinal gradient in species richness is among the most highly documented, yet least understood of ecological patterns (Gaston, 2000). Although numerous studies have proposed underlying mechanisms that drive this pattern (*e.g.* Pianka, 1966; Currie, 1991; Rohde, 1992, 1997, 1998; Rosenzweig, 1995; Gaston, 2000; Koleff and Gaston, 2001; Koleff *et al.*, 2003), little agreement has been reached as to what the most important theory or theories are. However, one significant contributor to high regional diversity in the tropics is thought to be the higher rate of species turnover (β diversity) at lower latitudes, which is associated with the high levels of endemism present in the tropical regions (Koleff *et al.*, 2003). Increased β diversity at lower latitudes has been shown for a number of taxa including birds (Blackburn and Gaston, 1996a, 1996b; Koleff and Gaston, 2001), some mammal groups (Stevens and Willig, 2002) and some plant taxa (Mourelle and Ezcurra, 1997). In addition, Harrison *et al.* (1992) also suggested that high β diversity is recorded over much smaller spatial scales in tropical regions compared with temperate regions. Comparing β diversity in British and Hawaiian bird species Harrison *et al.* (1992) suggested that β diversity was $\approx$10 times higher in tropical bird species than in temperate bird species. This higher rate of β diversity in tropical species was observed over a range of distances (10 – 335 km) considerably smaller than the range of distances (50 – 850 km) over which β diversity was measured in temperate regions (Harrison *et al.*, 1992). Thus, the high level of β diversity in tropical forests observed at the local scale is a key factor in promoting high species diversity at the regional scale (Kolef *et al.*, 2003). However, despite the importance of local β diversity in promoting regional diversity in the tropics, relatively few studies have focused on patterns of β diversity compared with patterns of α diversity in tropical regions (Balvanera *et al.*, 2002; Condit *et al.*, 2002). In addition, few data are available on how β diversity changes with both environmental heterogeneity and spatial scale in tropical forests (Balvanera *et al.*, 2002). Further to this, what data are available generally focus on the flora, and the fauna is largely overlooked (Balvanera *et al.*, 2002; Condit *et al.*, 2002; Duivenvoorden *et al.*, 2002a, 2002b).

6.2.2.4 Tropical forest disturbance and β diversity

Due to rapid deforestation and shifting agricultural practices the total area covered by tropical rainforests is decreasing (Collins *et al.*, 1991; Curran *et al.*, 2004; Sodhi *et al.*,

2004; Asner *et al.*, 2005). It is therefore of great current concern to understand the ecological consequences of this habitat disturbance on tropical forest ecosystems (Curran *et al.*, 2004). In Southeast Asia, the major threat to remaining forests comes from the logging industry and a large portion of remaining forests are contained within selective logging concessions (Sodhi *et al.*, 2004). This has led to a growing body of literature investigating the ecological impacts of selective logging on α diversity. However, there is little consensus on the reported impacts of selective logging on α diversity (Hamer and Hill, 2000; Hill and Hamer, 2004). Chapter 5 showed that reported responses of butterfly α diversity to selective logging are scale dependent. These effects of spatial scale have been explained in terms of changes in vegetation structure following disturbance and its associated impacts on the relationship between α diversity of butterflies at each sampling location and species turnover (β diversity) between sampling locations (Hill and Hamer, 2004). However, the impacts of selective logging on butterfly β diversity have rarely been examined. Willott (1999) showed greater β diversity of moths within habitats than between habitats and that β diversity was similarly high within primary and selectively-logged forest. This suggested that selective logging had little impact on β diversity, but Willott (1999) analysed only two samples from selectively-logged forest and four from primary forest, thus drawing robust conclusions may be difficult due to low sample sizes.

Balvanera *et al.* (2002) showed β diversity of tropical forest tree species to increase with environmental heterogeneity and also with spatial scale between samples (Balvanera *et al.*, 2002). Thus any reduction in environmental heterogeneity following selective logging may affect β diversity between samples (Hill and Hamer, 2004) and these effects may be dependent on the spatial scale at which β diversity is measured (Balvanera *et al.*, 2002). However, the impacts of selective logging on butterfly β diversity have yet to be examined within the ecological literature.

6.2.3 R-Mode analysis

6.2.3.1 Butterfly ecologies and conservation

Measures of diversity are widely used to assess impacts of habitat disturbance and reliably quantify changes in butterfly species richness and abundance following disturbance (*e.g.* Hill *et al.*, 1995; DeVries *et al.*, 1997; Wood and Gillman 1998; Lewis *et al.*, 2001; Hamer *et al.*, 2003). However, diversity measures give little information on how individual species

respond to disturbance and how this may lead to a change in species composition and thus the conservation value of a habitat (Lewis, 2001; Hamer *et al.*, 2003). It is important to assess which species are adversely affected by habitat disturbance and the ecological traits associated with vulnerability (Koh *et al.*, 2004). This information can then be used to design reliable future conservation strategies and determine the conservation value of disturbed habitats (Vane-Wright *et al.*, 1991; Koh *et al.*, 2004). Consequently, recent research has suggested that to complement analysis of diversity, a measure of how individual species respond to habitat disturbance should also be incorporated (Hamer *et al.*, 2003). Previous studies on a range of taxa have shown that specialist species are more adversely affected by disturbance than generalists (Barnett and Brandon Jones, 1997; King *et al.*, 1998; Magura *et al.*, 2004; Summerville *et al.*, 2005). In tropical butterflies, it has been suggested that endemic species with restricted geographical ranges are the most adversely affected by habitat disturbance (Hill *et al.*, 1995; Hamer *et al.*, 1997; Lewis *et al.*, 1998; Hamer *et al.*, 2003; Horner-Devine *et al.*, 2003; Dumbrell and Hill, 2005). In addition, it has been proposed that specialist species with restricted habitat requirements (Koh *et al.*, 2004; Shahabuddin and Ponte, 2005) are most vulnerable to habitat loss. However, it is less clear how butterfly species with specialist ecologies respond to moderate habitat disturbance such as selective logging.

6.2.3.2 Butterfly geographical distributions

Species' range size is positively correlated with latitude, thus tropical species have more restricted ranges than temperate species (Rapoport, 1975, 1982; Stevens, 1989). This explains why tropical forests support a high proportion of endemics. Borneo and many other islands along the Sunda Shelf contain many endemic species and are consequently recognised as biodiversity hotspots (Orme *et al.*, 2005). On Borneo, approximately 10% of all butterfly species are endemic (Otsuka, 1998). Endemic species with restricted geographical distributions have a higher conservation value compared with species with broad geographical distributions (Vane-Wright *et al.*, 1991). This is because endemic species are at increased risk of global extinction if they become locally extinct following habitat disturbance. It is therefore important to understand how species with restricted geographical ranges respond to moderate habitat disturbance such as selective logging. In general, endemic species and species with restricted geographical distributions are more adversely affected following selective logging compared with species with broader

geographical distributions (Holloway *et al.*, 1992; Spitzer *et al.*, 1993; Hamer *et al.*, 2003; Dumbrell and Hill, 2005). However, there is no consensus on this and some studies have reported an increase, or no change, in the number of species with restricted geographical distributions in selectively-logged forest (Willott *et al.*, 2000; Lewis 2001). Thus further data are needed to examine the impact of selective logging on restricted-range species.

6.2.3.3 Butterfly shade preference

The amount of light penetrating the canopy produces an abiotic environmental gradient within tropical forests. This gradient ranges from areas of dense shade under well developed canopies to areas of high light levels in forest gaps (Whitmore, 1998). Forest gaps are formed by natural tree falls and consequently tropical forests exist as a dynamic mosaic of gaps, regenerating forest and mature forest (Whitmore, 1998). Light plays an important role in determining the distribution of butterflies within the forest (DeVries, 1988; Burd, 1994; Beccaloni, 1997; DeVries *et al.*, 1997, 1999a; Schulze & Fiedler, 1998; Hill *et al.*, 2001, Schulze *et. al.*, 2001) and many butterfly species are dependent on closed canopy, densely shaded areas within tropical forests (Hill *et al.*, 2001; Hamer *et al.*, 2003). Selective logging leads to a reduction in canopy height and canopy cover (Burghouts *et al.*, 1994; Cannon *et al.*, 1994; Okuda *et al.*, 2003; Asner *et al.*, 2003). Consequently, selectively-logged forest has fewer areas of dense shade and fewer areas of large tree fall gaps, but a generally more uniform and brighter light environment compared with primary forest. Thus, butterfly species that are closed-canopy forest specialist or large-gap specialists are more likely to be adversely affected by selective logging than are generalist species (Hill *et al.*, 2001; Hamer *et al.*, 2003).

6.2.3.4 Larval host plant specificity

The presence of suitable larval habitat (*e.g.* abundance of larval host plants and suitable habitat cover) has been suggested to be the main predictor of the presence of butterfly species (Thomas *et al.*, 2001). Thus, any change in individual species abundance following habitat disturbance may reflect changes in the suitability of disturbed habitats for supporting butterfly larva. In support of this, it has been shown that butterfly species with highly specific larval host plant preferences have a high probability of local population declines following severe habitat disturbance (Koh *et al.*, 2004). This is primarily due to the loss of larval host plants following habitat disturbance (Koh *et al.*, 2004). However, it is

less clear how butterfly species with specific larval host plant preferences respond to moderate habitat disturbance such as selective logging (Willott *et al.*, 2000; Cleary *et al.*, 2005). Willott *et al.* (2000) suggested that changes in butterfly species abundances following selective logging in Sabah were not a direct result of loss in larval host plants. This was because selective logging in Sabah primarily removes trees from the family Dipterocarpaceae and it was suggested that few butterfly larva feed on Dipterocarp species (Willott *et al.*, 2000). Thus, any changes in butterfly species abundances were related to how butterflies responded to changes in the physical environment (Willott *et al.*, 2000). However, more recent catalogues of larval host plant associations show some Nymphalid larvae feed from Dipterocarp species, for example *Euthalia monina* whose larval host plant is *Shorea robusta* (Robinson *et al.*, 2001). In contrast to Willott *et al* (2000), Cleary *et al.* (2005) suggested that changes in butterfly species abundances following selective logging were largely predetermined by their larval host plant specificity. Cleary *et al.* (2005) investigated the impact of selective logging on four butterfly larval feeding guilds, liana, herb and tree specialists and generalists. They showed that generalist species and species whose larva were herb specialists increased in richness and liana specialists increased in abundance following selective logging (Cleary *et al.*, 2005). However, there was no clear consensus on the impacts of selective logging across the larval feeding guilds considered (Cleary *et al.*, 2005). Thus further data are needed to investigate the impacts of selective logging on specialist and generalist butterfly species.

6.2.3.5 Butterfly dispersal

In insects it is assumed that there is an evolutionary trade off between dispersal and reproduction (Zera and Denno, 1997). Consequently insects invest developmentally in morphologies associated with either increased dispersal ability or increased fecundity (Zera and Denno, 1997). In butterflies thoracic mass is positively correlated with flight speed (Dempster *et al.*, 1976; Marden, 1987; Chai and Srygley, 1990; Dudley, 1990; Dudley and Srygley, 1994). This is because the thorax of butterflies primarily contains muscles used for flight. Thus, butterfly species with relatively larger thorax masses may be able to sustain more prolonged periods of flight and thus have better dispersal ability (Dudley and Srygley, 1994; Berwaerts *et al.*, 2002). In contrast, butterfly species with relatively large abdomens may be less well adapted for fast flight, as abdomen mass is negatively correlated with flight speed (Srygley and Chai, 1990). As the reproductive organs of butterflies are located

in the abdomen, species with relatively large abdomens have a higher developmental investment in reproduction (Srygley and Chai, 1990; Hill *et al.*, 1999). Species with morphologies associated with increased dispersal ability may be favoured in disturbed or un-predictable habitats (Bowler and Benton, 2005). This is because resources may be limited (*e.g.* larval host plant availability) and species that can disperse within a habitat to high quality patches of resources will be less adversely affected (Bowler and Benton, 2005). Thus following selective logging, butterfly species with increased dispersal ability may be less adversely affected than poorer dispersers. However, there are few data available to address this.

6.2.4 Chapter objectives

In this chapter,

1. I investigate the impacts of selective logging on tropical-forest butterflies using Q-mode and R-mode analyses.

2. I examine patterns of butterfly β diversity in primary and selectively-logged forests. I investigate the relationships between β diversity and spatial scale in primary and selectively-logged forests and test the hypothesis that β diversity increases with spatial scale at a significantly faster rate in primary forest compared with selectively-logged forest.

3. I investigate the relationships between change in vegetation structure and spatial scale in primary and selectively-logged forest. I relate spatial patterns in vegetation structure to spatial patterns in butterfly β diversity in primary and selectively-logged forests.

4. I examine the impacts of selective logging on butterfly community composition using detrended correspondence analysis and canonical correspondence analysis. I use these ordination techniques to relate vegetation structure to butterfly species composition.

5. I test the hypothesis that primary forest contains more restricted range species with high larval host plant specificity and low light tolerance compared with selectively-logged forest.

6. I compare the flight morphology of butterflies between primary and selectively-logged forests and test the hypothesis that selectively-logged forest contains more species with morphologies associated with increased dispersal ability.

6.3 Materials and Methods

A brief recap of the general methods used in this chapter follows, for detailed information on the study site, butterfly sampling methods and the analysis and collection of vegetation data see Chapter 2 General Materials and Methods.

6.3.1 Study site

Fieldwork was conducted during June 2003, from March to April 2004 and from October to December 2004 at the Danum Valley Field Centre (DVFC) and surrounding Ulu Segama Forest Reserve (USFR) in Sabah, Malaysian Borneo (5°N, 117°5'E). Sampling during this study was conducted within primary forest adjacent to DVFC and within forest that was selectively-logged in 1988 using high lead and tractor extraction methods, where all commercially viable stems > 60 cm diameter at breast high were removed. Logging extraction data from 1988 indicate that approximately 170,000 m^3 of timber was extracted from an area of approximately 2300 ha (Innoprise, 1992).

6.3.2 Butterfly sampling

Butterflies were trapped within two grids that were set up to sample a ≈80 ha area, one grid in primary forest and the other in forest selectively-logged in 1988. 25 traps were hung approximately 2 m above the ground every 200 m in a 5 by 5 trap arrangement (see Figure 2.10 in Chapter 2 General Materials and Methods).

This sampling strategy allows data to be analysed at a range of spatial scales. In addition arranging traps in a grid format allows spatial patterns in data to be analysed multi-directionally to account for anisotropy.

All traps were baited with a piece of banana prior to the first day of sampling and an additional piece of banana was added daily. This ensured a mix of fresh and well-rotted fruit. Sampling was conducted for 12 days each month in each habitat over the six-month study period (72 days in total in each habitat). Traps were checked daily between 10 am and 2 pm. All butterflies caught were identified to species level, marked with a felt pen and released. Recaptures were excluded from any analysis of diversity.

6.3.3 Q-Mode analysis

6.3.3.1 Additive partitioning of butterfly diversity

Total diversity (γ) can be additively partitioned into its component parts, α and β diversity. γ diversity is the sum of the mean α diversity of samples and the total β diversity between samples, where the α diversity of samples and total diversity (γ) are measured as species richness or by a diversity index (Lande, 1996). I used additive partitioning of diversity to examine the relative contribution of α and β diversity to overall γ diversity in primary and selectively-logged forests. α and γ diversity were measured as either species richness, Shannon-Wiener or Simpson's indices and β diversity was calculated as γ diversity minus α diversity following recommendations by Lande (1996). Any measure of diversity can be used in partitioning analysis as long as it is concave. This means that the total diversity of a set of samples is greater than, or equal to, the mean diversity within samples. Simpson's index is only concave when expressed as 1-*D* (Lande, 1996). Thus, I use 1-*D* for Simpson's index instead of the reciprocal that is used elsewhere in this thesis (see Chapter 2 General Materials and Methods).

6.3.3.2 Butterfly diversity

Following recommendations by Magurran (2004), β diversity was calculated using Morisita-Horn (Equation 6.1) and Jaccard's (Equation 6.2) similarity indices. Data were calculated for each pairwise combination of traps in primary (n = 300) and selectively-logged forest (n = 300). The choice of similarity indices gave one quantitative (Morisita-Horn) and one qualitative (Jaccard's) index, thus allowing assessment of the importance of the relative abundance of each species to measures of β diversity. All indices are quoted such that an increase in value represents an increase in β diversity, this was achieved by subtracting the value of the similarity indices from 1 (Magurran, 2004).

$$C_{MH} = \frac{2\sum(a_i \cdot b_i)}{\left[\left(\frac{\sum a_i^2}{N_a^2}\right)+\left(\frac{\sum b_i^2}{N_b^2}\right)\right]\times(N_a \cdot N_b)}$$

Equation 6.1

The Moristia-Horn index is shown in Equation 6.1, where N_a and N_b are the total number of individuals in site *A* and *B* respectively, with a_i and b_i being the number of individuals in the *i*th species in sites *A* and *B*, respectively.

$$C_J = \frac{a}{a+b+c}$$

Equation 6.2

Jaccard's index is shown in Equation 6.2, where *a* is the total number of species present in both samples and *b* and *c* are the number of species present only in sample one and two, respectively. Analysis of butterfly diversity was conducted using the computer programs PISCES and EstimateS.

Relationships between β diversity and distance (spatial scale) between samples in primary and selectively-logged forest were examined using Mantel tests. Significance levels of the Mantel coefficient were computed using 10,000 re-samples of the data following Sokal and Rohlf (1995). Analysis of covariance (ANCOVA) was used to compare the slopes of the relationships between β diversity and geographic distance in primary and selectively-logged forest, weighted by the number of combinations of traps for each distance. ANCOVA assumes samples are independent, but in this analysis data from the same trap are used more than once and are therefore no longer independent. This may lead to a greater likelihood of a Type 1 error and significance levels around $\alpha = 0.05$ should be accepted with caution. However, the use of ANCOVA remains the only suitable test for comparisons of the slopes and has been used in previous studies on similar data (*e.g.* Hamer and Hill, 2000).

6.3.3.4 Vegetation data

To assess the structural composition of the vegetation in primary and selectively-logged forest I used vegetation data analysed by principal component analysis presented in Chapter 5. Summary data from this principal component analysis are also included in this chapter. To investigate how change in vegetation structure between samples may affect β diversity in primary and selectively-logged forest, I examined how differences in vegetation structure between sites changed with increasing distance between sites using Mantel tests.

Significance levels of the Mantel coefficient were computed using 10,000 re-samples of the data following Sokal and Rohlf (1995).

6.3.4 R-Mode analysis

6.3.4.1 Species composition in primary and selectively-logged forest

To examine the impact of selective logging on butterfly species composition, species abundance data were analyzed using detrended correspondence analysis (DCA) and canonical correspondence analysis (CCA) ordination methods. Ordination methods are a class of multivariate statistics that group samples in terms of their species composition (DCA) and describe relationships between species composition and those environmental variables which best discriminate between samples (CCA). From these analyses I examined which vegetation variables were most important in describing butterfly species composition within and between habitats.

6.3.4.2 Detrended correspondence analysis (DCA)

Detrended correspondence analysis assumes a unimodal response of species to environmental data. DCA does not attempt to directly relate the species composition of each sample to any underlying environmental variable, but scores each sample along an eigenvector, or axis, based solely on its species composition (Jongman *et al.*, 1995). The first eigenvector represents the environmental gradient explaining the majority of the variation within the data. Further eigenvectors are computed until all the variation within the data is explained, with each subsequent eigenvector explaining a smaller additional proportion of the variability not explained by previous eigenvectors (Jongman *et al.*, 1995). From this analysis, scores for each sample along the first two eigenvectors can be correlated with environmental variables and thus it is possible to examine which environmental variables best explain changes in the composition of species among samples.

Here I use DCA to group sample sites (trapping stations) from both primary and selectively-logged forest by species composition. The eigenvector scores of each sample site are plotted on a two-dimensional graph of the first eigenvector/axis against the second. The degree of separation between sample sites along each axis represents β diversity between sites.

6.3.4.3 Canonical correspondence analysis (CCA)

As with DCA, canonical correspondence analysis also assumes a unimodal response of species to environmental data. However, unlike DCA, CCA directly relates the species composition of each sample to known environmental variables. CCA computes scores for each sample in a similar manner to DCA by separating each sample according to species composition and giving them an eigenvector score. However, when DCA separates sites it relies on a theoretical environmental variable that explains the variation in species composition between samples and this is used to maximize differences between samples along the eigenvector. By contrast, CCA scores are separated along the eigenvectors in relation to measured environmental variables. Environmental variables are incorporated in a linear combination that best separates samples in terms of species composition (Jongman *et al.*, 1995). This method not only gives sample scores derived in relation to species composition, but also gives each species a score according to the environmental variables which best describe its presence in a sample.

I used CCA to separate samples by the relationship between species composition and vegetation variables measured at that site. The first two principal component factor scores from analysis of the vegetation data (Chapter 5) were used in the CCA to examine the relationship between species composition and vegetation structure. Principal component analysis reduced a large number of correlated vegetation variables (n = 17) down into two independent variables (factor scores) describing the vegetation of each sample (Jongman *et al.*, 1995). The significance of each vegetation variable (extracted principal component score) in contributing to the species – environment relationship was assessed using a distribution free Monte Carlo randomization test (Sokal and Rohlf, 1995). Ordination analysis was conducted using the computer package Canoco 4.5.

6.3.4.4 Ecology of butterfly species in primary and selectively-logged forests

Generalist species are likely to have a broader range of larval host plants, greater preference for areas of high light availability (Hill *et al.*, 2001) and broader geographic ranges (Vane-Wright *et al.*, 1991) compared with more specialist species. To compare the ecological traits of primary and selectively-logged forest butterfly species each butterfly species included in the analysis was included only once as either a primary or selectively-logged forest species. Butterfly data from Chapters 4, 5 and 6 were combined across habitats and any butterfly species with fewer than 10 individuals recorded was omitted from further

analysis. Species were considered a predominantly primary forest species if ≥51 % of their total captures (primary forest and selectively-logged forest captures combined) were recorded in primary forest and species were consider a selectively-logged forest species if ≤ 50 % of their total captures were recorded in primary forest (Appendix 2, 3 and 4).

I ranked all butterfly species sampled in terms of their geographical distributions (following Hamer *et al.*, 2003). The endemic species, *Mycalesis kina* and *Mycalesis amoena* shared the highest rank (rank = 1). The geographically most widespread species *Melanitis leda* (which occurs through the African, Oriental and Australasian regions) was assigned the lowest rank (rank = 62). Species with distributions restricted to Sundaland (Borneo, Sumatra, Java, West Malaysia and Palawan) were ranked 3-20. Species that had geographical distributions which also included the Oriental and Australasian regions were ranked 21-62 (Appendix 3). Differences between habitats in geographical distribution of species were investigated using Mann-Whitney U tests.

Species' light preference was calculated in terms of the proportional abundance of individuals for each species that were reported to be caught in forest gap *versus* shade traps by Hill *et al.*, 2001 and Hamer *et al.*, 2003. Thus species with light index value of close to 1 were highly light tolerant and only present in gaps *e.g. Rhinopalpa poynice* (L = 0.909) and species with low light index values were relatively light intolerant *e.g. Mycalesis kina* (L = 0.095). Differences in species light preference indices between habitats were investigated using *t*-tests; data were arc-sine transformed prior to analysis.

All butterfly species were ranked according to their larval host plant specificity. Information on larval host plant choice was gathered from Robinson *et al.*, (2001) and Suguru and Haruo (1997, 2000). Butterflies were ranked according to the number of different host plant families they could feed from. Specialist feeders were given the highest rank (rank = 1) with highly polyphagous, generalist species that fed on a wide range of plant families given the lowest rank (rank = 9). The majority of species (66% of all species) for which data were available shared the highest rank of 1 and only a single species *Charaxes bernardus* was ranked 9. Differences between butterfly species larval host plant specificity between habitats were investigated using Mann-Whitney U tests.

6.3.4.5 Flight morphology of butterfly species in primary and selectively-logged forests

Butterfly flight morphology can be considered an indirect measure of dispersal ability with butterfly species whose morphologies are associated with prolonged periods of flight

considered to have greater dispersal abilities. The flight morphology of butterflies species recorded predominantly in primary forests was compared with those recorded predominantly in selectively-logged forest in a similar way to comparisons of ecological traits. All trapped butterflies were measured to an accuracy of 0.1 mm using Vernier callipers. Measurements of thorax length and width, abdomen length and width, and forewing wing length (wing base to apex) and width (minimum distance between tornus and costa) were recorded (see Figure 2.11 in Chapter 2 General Materials and Methods). These measurements when used to derive four variables; thorax and abdomen volumes (length × width^2), thorax shape (width / length) and forewing wing shape (wing length / breadth). In butterflies thorax mass, thorax width and wing span are all positively correlated to flight speed (Chai and Srygley, 1990; Dudley, 1990; Srygley and Chai, 1990). In contrast, relative abdomen mass which contains all the reproductive organs is negatively correlated to flight speed (Srygley and Chai, 1990). Thus, thorax and wing measurements are likely to represent relative investment in flight while abdomen measurements are likely to reflect investment in reproduction. All variables were $\log_{10}$ transformed prior to analysis. Only species for which at least 10 individuals were measured for each sex were included in analysis and mean values were calculated for males and females of each species. All variables except wing shape were allometrically related to body length (measured as thorax length + abdomen length). To account for this allometry, data were analysed using ANCOVA with body length as a covariate and sex and sub-family (Satyrinae, Morphinae, Nymphalinae and Charaxinae) as factors. All analyses were weighted by sample size.

6.4 RESULTS

6.4.1 Q-Mode analysis

6.4.1.1 Additive partitioning of butterfly diversity

To investigate diversity within habitats, γ diversity in primary and selectively-logged forests was additively partitioned in into its respective α and β diversity components. α diversity of traps (Simpson's and Shannon-Wiener's index) within primary and selectively-logged forest made the highest contribution to each habitats' γ diversity (Figure 6.1). However, β diversity between traps was relatively high and comprised approximately a third of total (γ) species diversity (Shannon-Wiener index) and species evenness (Simpson's index) in both habitats. β diversity between traps comprised $\approx$70% of total (γ) species richness in primary and selectively-logged forest (Figure 6.1). Thus β diversity within both primary and selectively-logged habitats made a large contribution to overall habitat γ diversity.

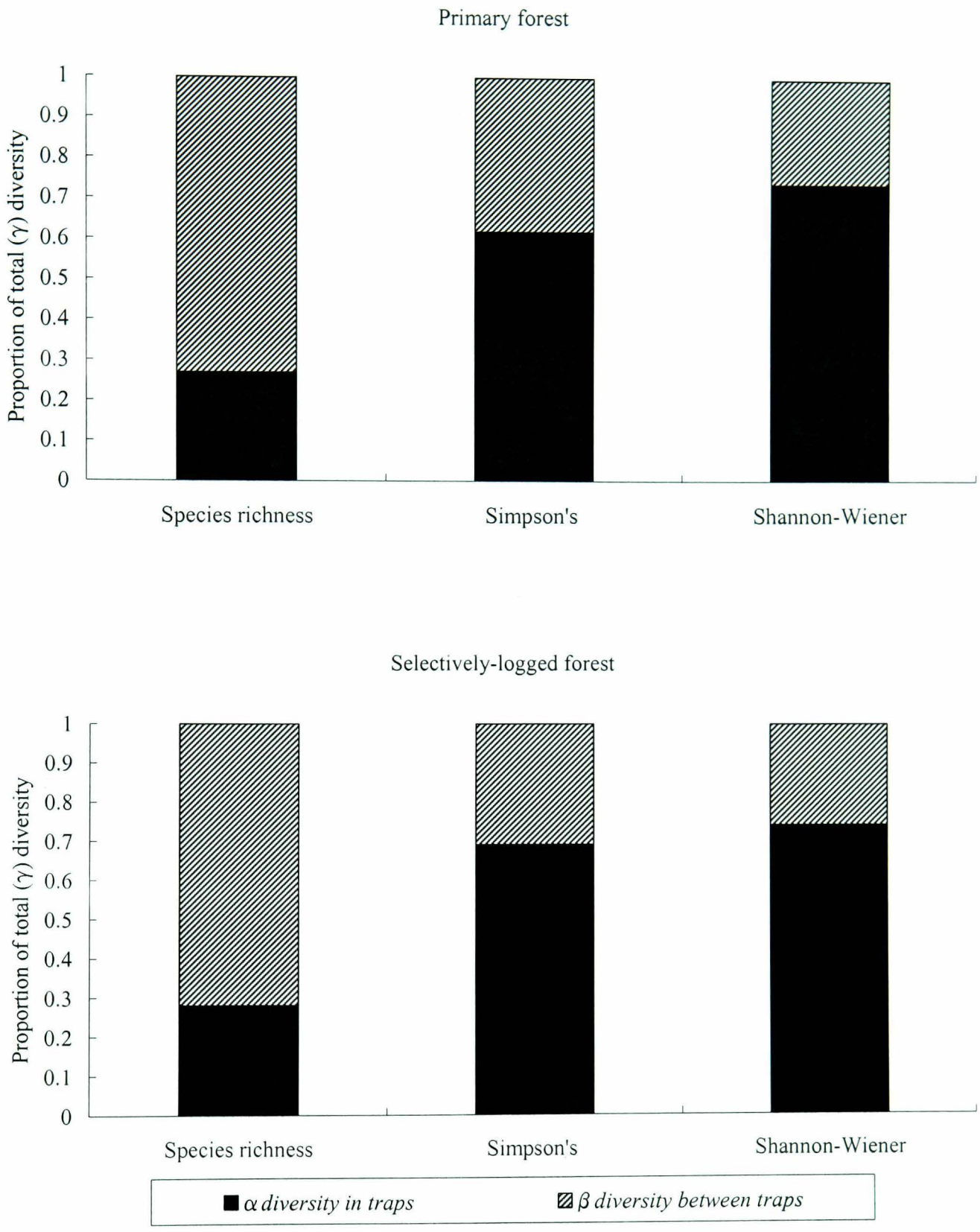


Figure 6.1 Additive partitioning of γ diversity in primary and selectively-logged forest, measured by Simpson's and Shannon-Wiener indices and species richness into α diversity in traps and β diversity between traps.

6.4.1.1 β diversity of butterflies in primary and selectively-logged forest

β diversity indices were used to examine the impact of selective logging on butterfly β diversity. Primary forest had significantly higher within-habitat β diversity than selectively-logged forest as measured by Morisita-Horn and Jaccard's indices (Table 6.1; *t*-test, Morisita-Horn index $t_{598} = 2.87, p = 0.004$; Jaccard's index, $t_{598} = 2.11, p = 0.035$).

	Primary forest		Selectively-logged forest	
Morisita-Horn	0.54	(0.01)	0.50	(0.01)
Jaccard	0.35	(0.01)	0.33	(0.01)

Table 6.1 Mean β diversity (± SE) between traps measured by Morisita-Horn and Jaccard's indices within primary and selectively-logged forest. β diversity was significantly higher in primary forest as measured by both indices.

Mantel tests showed that β diversity measured by Morisita-Horn's index was positively correlated with geographical distance between traps in primary forest but not in selectively-logged forest (Figure 6.2; Mantel test, using 10,000 randomisations; primary forest, $r = 0.23, p = 0.001$; selectively-logged forest, $r = 0.04, p = 0.3$). The rate at which β diversity increased with distance was significantly greater in primary forest than selectively-logged forest (Figure 6.2; ANCOVA of Morisita-Horn's index in primary and selectively-logged forest with distance as a covariate, habitat by distance interaction; $F_{1,24} = 8.39, p < 0.01$).

In contrast to analysis of β diversity measured by Morisita-Horn's index, there was no evidence that β diversity was related to distance between traps in either primary forest or selectively-logged forest using Jaccard's index (Figure 6.2; Mantel test, using 10,000 randomisations; primary forest, $r = 0.07, p = 0.11$; logged forest, $r = 0.01, p = 0.43$). Thus, there was no significant difference in the rate at which β diversity increased with distance between primary and selectively-logged forest (Figure 6.2; ANCOVA of Jaccard's index in primary and selectively-logged forest with distance as a covariate, habitat by distance interaction; $F_{1,24} = 0.61, p = 0.44$). However, Jaccard's index is a qualitative index of β diversity and thus does not take into account relative species abundance. Due to this, qualitative indices are often unsatisfactory when trying to assess β diversity and quantitative indices are generally considered more robust (Magurran, 2004).

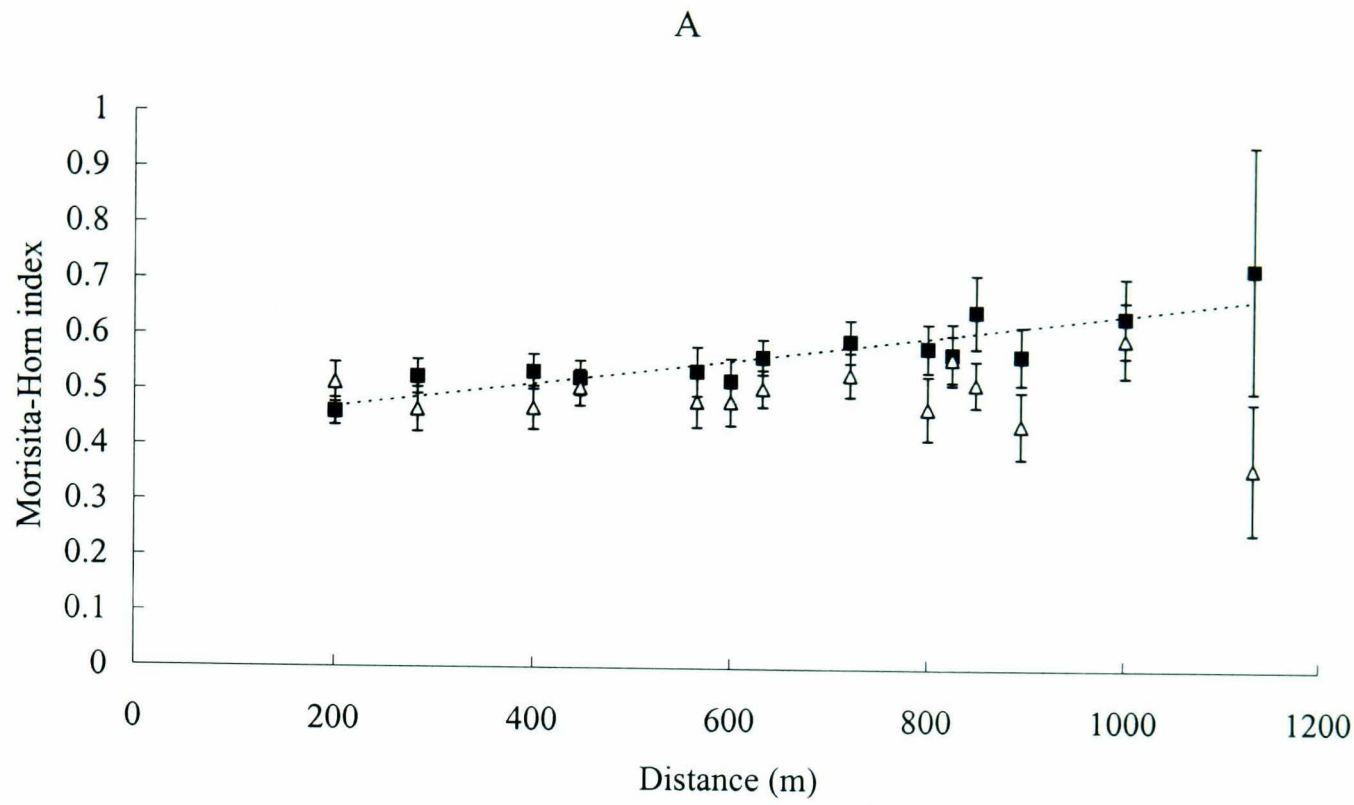


Figure 6.2 Mean butterfly β diversity (± SE) between traps in primary forest (squares) and selectively-logged forest (triangles) in relation to distance between traps. β diversity is measured by Morisita-Horn (A) and Jaccard's (B) indices. The dashed line (A) indicates a significant relationship (using Mantel tests) in primary forest.

6.4.1.3 Impact of selective logging on vegetation structure

Vegetation data were collected for 17 variables (no. of trees and saplings, point of inversion, mean height, girth and density of trees, mean girth and density of saplings, proportion of Dipterocarp trees and saplings, proportion of *Macaranga* spp. trees and saplings and percentage canopy, overstorey, understorey, low-level and ground covers) that were analysed by principal component analysis. Principal components analysis extracted two main components (PRIN1 and PRIN2) that explained 27% and 15% of the variation within the vegetation data respectively (Chapter 5.0). The first factor, PRIN1, increased with an increase in the proportion of Dipterocarp trees and saplings, mean tree height and percentage canopy cover. It decreased with an increase in the proportion of *Macaranga* spp. trees and saplings (Table 6.2). The second factor, PRIN2, increased with an increase in the number of trees present and percentage understorey cover, and it decreased with an increase in percentage low-level cover (Table 6.2). Primary forest had a significantly higher PRIN1 score than selectively-logged forest (primary forest, mean = 0.87, SE = 0.07; Selectively-logged forest, mean = -0.87, SE = 0.12; *t*-test comparing between habitats; t_{48} = 12.64, $p < 0.001$). However, there was no different in the PRIN2 between habitats (primary forest, mean = -0.04, SE = 0.20; Selectively-logged forest, mean = 0.04, SE = 0.21; *t*-test; t_{48} = -0.29, $p = 0.78$).

	Weighting	
Variable	PRIN1	PRIN2
Proportion of Dipterocarp trees	**0.84**	0.09
Proportion of Dipterocarp saplings	**0.75**	0.23
Mean height	**0.65**	-0.08
Canopy	**0.65**	0.12
Proportion of *Macaranga* spp. trees	**-0.85**	0.19
Proportion of *Macaranga* spp. saplings	**-0.60**	0.20
Understorey	0.20	**0.76**
Low level (2m)	0.04	**-0.89**
Number of trees	-0.02	**0.85**

Table 6.2 Relative contribution of different vegetation variables to the first two principal component scores of variation in vegetation data extracted using PCA analysis. Variables that make the most important contributions to factor scores are highlighted in bold.

Mantel tests were used to examine the relationship between vegetation PCA scores and geographic distance between samples. There was no relationship between pairwise differences in PRIN1 and geographic distance in either primary or selectively-logged forest (Figure 6.3; Mantel test, using 10,000 randomisations; primary forest, $r = 0.02$, $p = 0.42$; selectively-logged forest, $r = 0.09$, $p = 0.19$). However, pairwise differences between samples in PRIN2 were correlated with geographic distance between samples in primary forest but not in selectively-logged forest (Figure 6.3; Mantel test, using 10,000 randomisations; primary forest, $r = 0.18$, $p = 0.03$, selectively-logged forest, $r = 0.08$, $p = 0.22$). Thus the observed relationship between increasing butterfly β diversity and distance in primary forest may reflect patterns in vegetation PRIN2 scores.

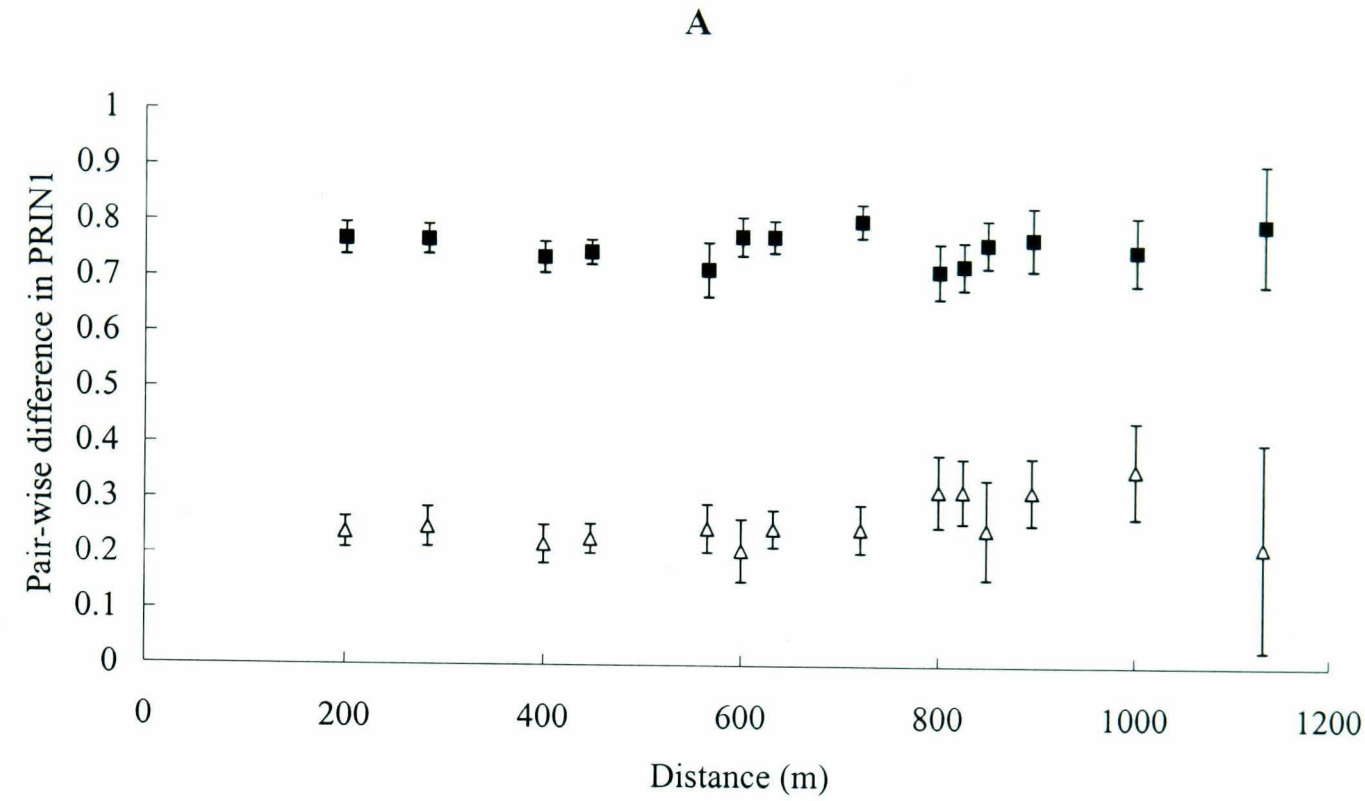


Figure 6.3 Mean difference (± SE) between traps in the PCA scores, PRIN1 (A) and PRIN2 (B), extracted from vegetation data in primary forest (squares) and selectively-logged forest (triangles) in relation to distance between traps. The dashed line (B) indicates a significant relationship (using Mantel tests) in primary forest.

6.4.2 R-Mode analysis

6.4.2.1 Butterfly community composition in primary and selectively-logged forest

Ordination techniques were used to assess the impacts of selective logging on species composition. Indirect ordination (DCA) of the species abundance data from sites in primary and selectively-logged forest showed distinct patterns of species composition in the two habitats (Figure 6.4) The first ordination axis (DCA1) explained 11.5% of the variation within the species abundance data and the second axis (DCA2) a further 6%. Sites in primary forest had significantly different DCA1 scores compared with sites in selectively-logged forest (Figure 6.4; primary forest mean DCA1 score = 0.81 (SE = 0.1); selectively-logged forest mean DCA1 score = 1.25 (SE = 0.11); *t*-test assuming unequal variance; $t_{47.60}$ = -3.09, p = 0.003). However, there was no difference in DCA2 scores between primary and selectively-logged forest (Figure 6.4; primary forest mean DCA2 score = 1.0 (SE = 0.1); selectively-logged forest mean DCA2 score = 1.21 (SE = 0.07) *t*-test assuming unequal variance; $t_{45.38}$ = -1.78, p = 0.082). Therefore not only is there a significant decrease in butterfly diversity following selective logging (Chapters 5 and 6), but also a significant change in species composition.

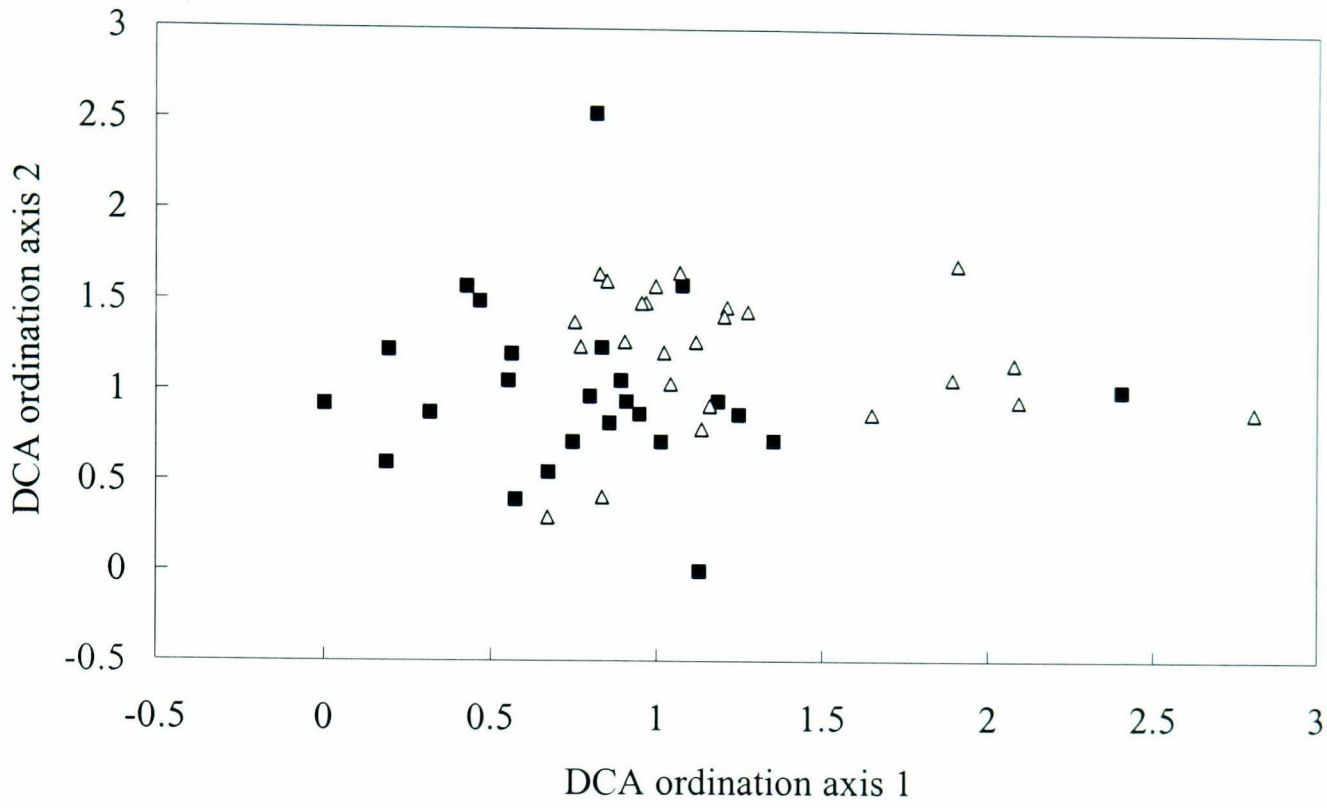


Figure 6.4 Indirect ordination plot, using detrended correspondence analysis (DCA), of butterfly species abundance data from sites in primary (squares) and selectively-logged (triangles) forest. DCA ordination axis 1 scores are significantly different between habitats indicating distinct species assemblages in primary and selectively-logged forests.

Constrained ordination (CCA) was used to investigate which vegetation variables (PCA factor scores) best described the presence of species at trap sites within primary and selectively-logged forest. The first axis explained 68.9% of the variation in the species vegetation relationship and the second axis explained a further 31.1% of the variation in the species vegetation relationship (Figure 6.5). Both vegetation variables PRIN1 and PRIN2 were significantly related to species composition and thus change in vegetation explained change in species composition (Monte Carlo permutation test of the relationship between vegetation and species composition, PRIN1, $F = 3.19$, $p < 0.001$; PRIN2, $F = 1.61$, $p = 0.026$). The first ordination axis increased with an increase in PRIN1 and the second ordination axis increased with a decrease in PRIN2 (Table 6.3).

	Weighting	
Vegetation variable	CCA ordination axis one	CCA ordination axis two
PRIN1	**0.80**	0.18
PRIN2	0.15	**-0.73**

Table 6.3 Relative contribution of the two main vegetation scores extracted by PCA to the first two axes of a direct ordination (CCA) of species abundance data. Variables that make the main contributions to each axis that explain the relationship between species composition and vegetation are highlighted in bold.

Species with a high score along the first ordination axis preferred closed canopy, undisturbed primary forest, as described by PRIN1 (Figure 6.5). In contrast, species with a low score along the first ordination axis preferred secondary forest dominated by a relatively high proportion of pioneer tree species, reflecting a low PRIN1 score. Species' distributions along the second ordination axis reflect species' preferences for understorey and low-level vegetation cover as described by PRIN2. Thus, the difference in species composition between habitats (Figure 6.5) can be described by changes in PRIN1 and PRIN2 scores between primary and selectively-logged forest.

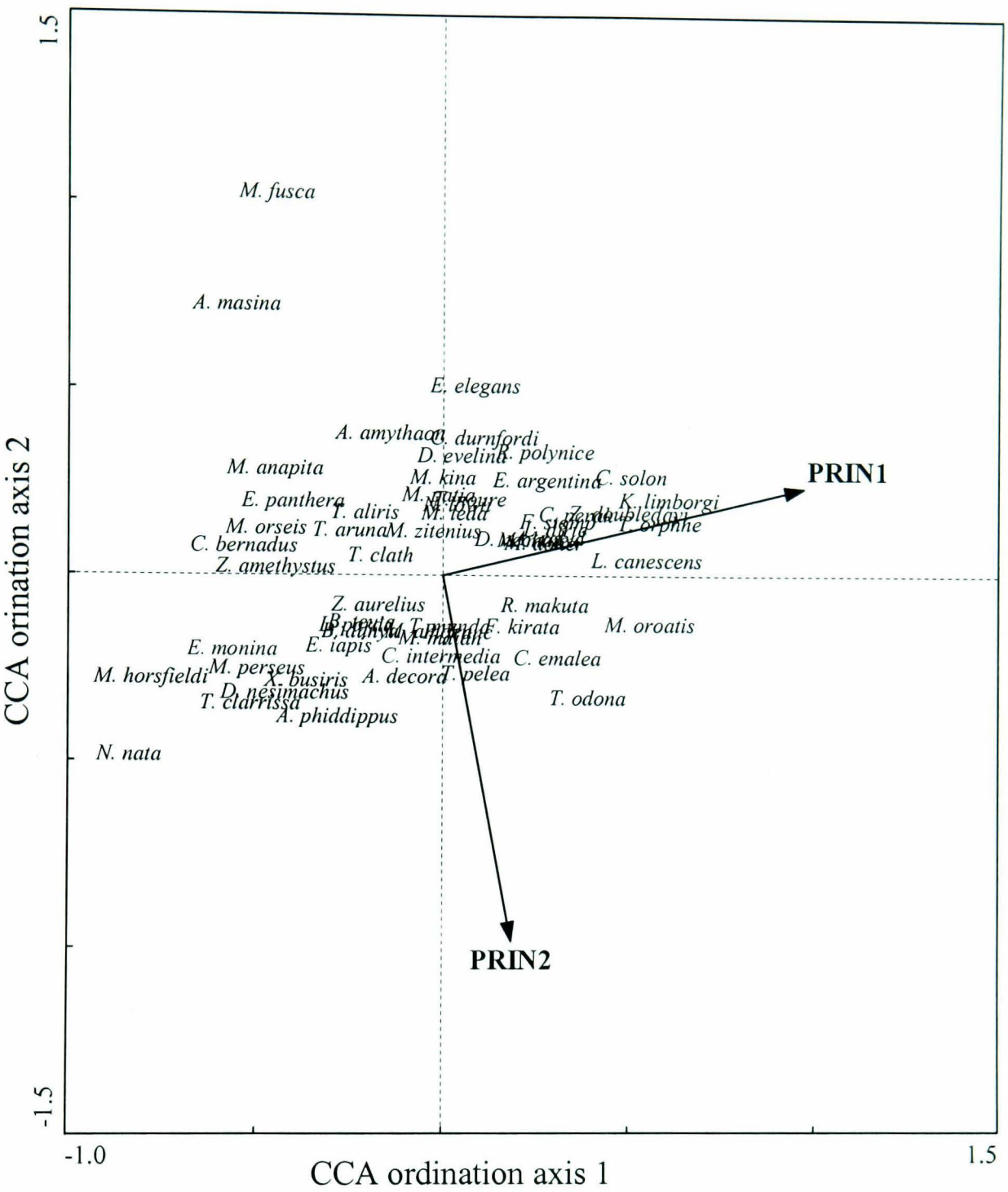


Figure 6.5 Direct ordination plot, using canonical correspondence analysis (CCA), of butterfly species abundance data in relation to the first two vegetation variables extracted by PCA. The first CCA axis explains 68.9% of the relationship between species composition and vegetation, the second axis explains a further 31.1%. Both vegetation variables PRIN1 and PRIN2 are significantly related to species composition.

6.4.2.2 Ecology of butterflies in primary and selectively-logged forest

Butterfly species were assigned a habitat preference based on the proportional abundance of individuals caught in primary or selectively-logged forests. Butterfly ecological traits were compared between primary and selectively-logged forest species.

Data on species light preference for 43 of the 62 species recorded were extracted from Hamer *et al.* (2003) and Hill *et al.* (2001). Butterfly species in selectively-logged forest had significantly lower preference for areas of dense shade compared to species from primary forest (Table 6.4; primary forest species mean = 0.41, n = 24, SE = 0.09; selectively-logged forest species mean = 0.79, n = 19, SE = 0.12; t-test assuming unequal variance, $t_{31.74} = 3.16$ $p = 0.003$).

All butterfly species caught in primary and selectively-logged forest were ranked according to their geographical distributions. There was no significant difference between primary and selectively-logged forest species in the extent of their geographical distributions (Table 6.4; primary forest species median rank = 29.0, n = 17, IQR = 38.5; selectively-logged forest species median rank = 29.0, n = 19, IQR = 33; Mann-Whitney U test; $Z = -0.5$, $p = 0.64$).

Data on larval host plant preference for 49 of the 62 species recorded were extracted from Robinson *et al.* (2001) and Suguru and Haruo (1997, 2000). There was no significant difference between primary and selectively-logged forest species in their larval host plant specificity (Table 6.4; primary forest species median rank = 1.0, n = 26, IQR = 1.5; logged forest species median rank = 1.0, n = 23, IQR = 1.5; Mann-Whitney U test; $Z = -0.19$, $p = 0.85$).

	Primary forest		Selectively-logged forest	
Light preference	**0.41**	(0.09)	**0.79**	(0.12)
Geographical rank	29.00	(38.50)	29.00	(33.00)
Host plant specificity	1.00	(1.50)	1.00	(1.50)

Table 6.4 Median (+ IQR) host plant specificity, geographical rank and mean (± SE) light preference of Nymphalid butterflies in primary and selectively-logged forest. Values highlighted in bold are significantly different between habitats at the 5% level.

6.4.2.3 Flight morphology of butterflies in primary and selectively-logged forest

Morphological data were collected for 31 species of fruit-feeding Nymphalid butterfly. 16 species were more abundant in primary forest and 15 species were more abundant in selectively-logged forest. There were significant differences between male and female butterflies in the allometric relationship between thorax shape and body length (ANCOVA of thorax shape with sex and sub-family as factors and body length as a covariate, weighted by sample size; sex by body length interaction, $F_{1,49} = 11.71$, $p < 0.001$). Thus comparisons between habitats were conducted separately for each sex. There was no significant difference in thorax volume between habitats for either males or females (ANCOVA of thorax volume with habitat and sub-family as a factors and body length as a covariate, weighted by sample size, habitat by sub-family interaction, males, $F_{2,19} = 0.71$, $p = 0.51$; females, $F_{2,19} = 0.51$, $p = 0.61$). There was also no significant difference between habitats in thorax shape (males, $F_{2,19} = 0.57$, $p = 0.57$; females $F_{2,19} = 1.63$, $p = 0.22$), abdomen volume (males, $F_{2,19} = 1.99$, $p = 0.16$; females $F_{2,19} = 0.17$, $p = 0.85$) and wing shape (2-way ANOVA of wing shape with habitat and sub-family as a factors, weighted by sample size, habitat by sub-family interaction, males, $F_{2,24} = 0.13$, $p = 0.88$; females, $F_{2,24} = 1.86$, $p = 0.18$).

6.5 Discussion

6.5.1 Q-Mode analysis

6.5.1.1 Impacts of selective logging on butterfly β diversity

Additive partitioning of diversity revealed that β diversity made a relatively higher contribution to total diversity (γ) in primary forest compared with selectively-logged forest, indicating that selective-logging had a negative impact on butterfly β diversity. Morisita-Horn and Jaccard's indices confirmed this, and revealed significantly higher β diversity in primary forest compared with selectively-logged forest. Thus, one of the impacts of selective logging on tropical-forest butterflies is a reduction in within-habitat β diversity. This may explain why significantly higher α diversity was reported in primary forest compared with selectively-logged forest (Chapter 5). Previous studies have suggested that increased β diversity is caused by a decrease in environmental similarity between samples (Harrison *et al.*, 1992; Balvanera *et al.*, 2002). Analysis of vegetation data (Chapter 5) showed the variance of some vegetation variables to be significantly higher in primary forest compared with selectively-logged forest. This indicates a greater range of vegetation structure in primary forest and thus, a decrease in the similarity of vegetation characteristics between samples. Therefore, difference between primary and selectively-logged forest in within-habitat β diversity most likely reflected differences between samples in vegetation structure in each habitat.

Results from this chapter disagree with those of Willott (1999) who suggested that selective logging did not cause a significant change in within-habitat β diversity. However, Willott (1999) investigated the impacts of selective logging on moth diversity and results presented in this study focus on butterfly diversity. Thus, difference between the reported impacts of selective logging on β diversity may reflect difference between species. Previous research has shown the impacts of habitat modification on α diversity are not necessarily reflected across a range of species (Lawton *et al.*, 1998). However, few data are available on how habitat modification affects β diversity across species and further research is needed to address this. In addition, Willott (1999) drew conclusions about patterns of β diversity from only two samples from selectively-logged forest and four from primary forest. Thus, Willott's (1999) analysis of β diversity lacks power due to small sample size

and also, may not have sampled a sufficiently large area to account for the impacts of selective logging on habitat heterogeneity.

6.5.1.2 Spatial patterns of β diversity and vegetation structure

β diversity was significantly positively correlated with increasing geographic distance between samples in primary forest but not in selectively-logged forest. Differences in spatial patterns of butterfly β diversity between habitats may be explained by differences between habitats in within-habitat spatial patterns in vegetation structure (Balvanera *et al.*, 2002) or by differences between habitats in the dispersal of the studied organisms (Cadotte and Fukami, 2005). For example, high dispersal may be favoured in disturbed habitats (Bowler and Benton, 2005) and this may lead to reduced β diversity between traps in selectively-logged forest. In this study there was no significant difference in flight morphology between butterfly species in primary and selectively-logged forests, indicating that butterfly species from primary and selectively-logged forest have similar dispersal capabilities. In addition, direct measures of dispersal from analysis of recapture data showed no significant change in dispersal capabilities of butterfly species between habitats (Chapter 5). Thus, changes in spatial patterns of butterfly β diversity are most likely explained by changes in spatial patterns of vegetation structure and not by changes in butterfly dispersal following selective logging. Differences in butterfly β diversity between samples reflected differences in vegetation structure measured by PRIN2 (which reflected understorey and low-level vegetation covers) which increases with distance between samples. This is supported by canonical correspondence analysis which shows butterfly species composition to be significantly related to PRIN2 scores from each sample.

In Chapter 5, I showed that differences in butterfly α diversity between primary and selectively-logged forest were dependent on the spatial scale of sampling. It has been suggested that primary forest has greater α diversity compared to selectively-logged forest when analysed at a large spatial scale because of a reduction in β diversity between samples following selective logging and that this is not evident when analysed at a small spatial scale (Hill and Hamer, 2004). Results from this study provide evidence to support this suggestion and show β diversity to be distance dependent in primary forest but not in selectively-logged forest. Thus, α diversity is expected to be significantly higher in primary forest than selectively-logged forest (Chapter 5), when analysed at a large spatial scale reflecting greater β diversity between samples in primary forest (Figure 6.2). However, β

diversity between samples separated by relatively short distances is similar in both habitats (Figure 6.2). Thus, no difference in α diversity is expected when measured on the small spatial scales (Chapter 5).

One significant contributor to high regional diversity in the tropics is thought to be a higher rate of species turnover (β diversity) at lower latitudes, which is associated with the high levels of endemism present in the tropical regions (Koleff *et al.*, 2003). Using an adapted version of Whittaker's (1960) β diversity measure Harrison *et al.* (1992) showed butterfly β diversity to have a value of $\beta_W = 3.6$ across a transect running West-East across Britain. Following Harrison *et al.*'s (1992) methods, primary-forest butterfly β diversity in this study is over 3 times higher ($\beta_W = 11.77$) than British butterfly diversity. Harrison *et al.* (1992) analysed butterfly data from a 400 km transect compared to the 80 ha sample from primary forest. Thus results from this study loosely support the suggestion of higher β diversity within the tropics compared to temperate regions. In addition as β diversity was higher over a smaller range of distance this indicates a higher rate of species turnover (β diversity) at lower latitudes (Harrison *et al.*, 1992; Koleff *et al.*, 2003). However, results showed selective logging significantly reduced butterfly β diversity. This may have implications for maintaining high tropical biodiversity. Thus, careful management of logging concessions is needed to maintain high levels of β diversity in selectively-logged forest.

6.5.2 R-Mode analysis

6.5.2.1 Butterfly species composition in primary and selectively-logged forests

Detrended correspondence analysis revealed significant differences in faunal composition between sites in primary and selectively-logged forests. Canonical correspondence analysis showed these were significantly related to vegetation structure. The majority of the variation ($\approx$70%) in the relationship between species composition and vegetation structure was explained by the first ordination axis and the remaining variation ($\approx$30%) by the second ordination axis. Ordination axes were significantly related to PRIN1 and PRIN2 scores from each sample. Thus, species with a high positive score along the first ordination axis preferred closed-canopy forest typical of undisturbed primary forest. In contrast, species with a negative score along the first ordination axis preferred secondary forest dominated by a high proportion of *Macaranga* tree species. As *Macaranga* spp. is an

invasive secondary forest pioneer (Burghouts *et al.*, 1994) and is rarely recorded in primary forest it can be assumed that species with a negative score along the first ordination axis prefer selectively-logged forest. Thus the significant difference in species composition between sites in primary and selectively-logged forest reflects significant differences in vegetation between habitats.

6.5.2.2 Ecology and morphology of butterflies in primary and selectively-logged forests

Primary forest contained species with significantly lower light tolerance. However, there was no significant difference in geographic range sizes and the larval host plant specificity of species between primary and selectively-logged forest. Analysis of morphological data revealed there was no significant difference in flight morphology between butterfly species in primary and selectively-logged forests. This indicated that butterfly species from primary and selectively-logged forest have similar dispersal capabilities supporting findings from dispersal analysis in Chapter 5.

Previous studies have suggested that Lepidoptera species with restricted geographic ranges are more adversely affected by selective logging than species with broad geographic distributions (Hill *et al.*, 1995; Hamer *et al.*, 1997; Lewis *et al.*, 1998; Hamer *et al.*, 2003: Horner-Devine *et al.*, 2003; Dumbrell and Hill, 2005). However, there is no clear consensus on this (Willott *et al.*, 2000; Lewis, 2001). Results from this study suggest there is little impact of selective logging on species with restricted geographical distributions. In addition when data from Chapter 4 were analysed on a per-species basis instead of a per-individual basis (Chapter 4) similar results were observed (ground-level species; primary forest species median rank = 29.0, n = 17, IQR = 39; selectively-logged forest species median rank = 29.0, n = 19, IQR = 29.5; Mann-Whitney U test; Z = -0.5, p = 0.64). This adds further evidence that selective logging has a minimal impact on restricted range species. However, only 36 species from the 62 recorded were included in the analysis. This has implications for drawing conclusions about the impact of selective logging on restricted range species as many rare species not included in this analysis were endemic or had restricted geographical ranges. For example, the endemic species *Tanaecia orphne* was recorded only in primary forest (Appendix 3). Loss of endemic species is a major threat to global biodiversity (Orme *et al.*, 2005) and there is some evidence here to indicate that selective logging results in the loss of endemic and restricted range species (Appendix 3).

However, not all endemic species were adversely affected by selective logging and the endemic species *M. kina* and *Thauria aliris* were present in selectively-logged forest.

Light plays an important role in determining the distribution of butterflies within tropical forests (DeVries, 1988; Burd, 1994; Beccaloni, 1997; DeVries *et al.*, 1997, 1999; Schulze & Fiedler, 1998; Hill *et al.*, 2001, Schulze *et. al.*, 2001). Primary forest contained species with a preference for more densely shaded areas compared with selectively-logged forest. This reflected changes in vegetation structure between habitats as primary forest had significantly greater canopy cover (Chapter 5) and thus was darker than selectively-logged forest. Ordination analysis revealed that species composition of sites was significantly related to vegetation structure which reflects the light environment of the forest. Thus, differences in the light environment within, and between, habitats are most likely responsible for the distribution of butterfly species (Hill *et al.*, 2001, Schulze *et. al.*, 2001). Chapter 5 showed that selective logging resulted in a more homogenous light environment, as shown by significantly lower variance in measures of canopy cover and a spatially more homogenous distribution of canopy covers. Consequently, reduced β diversity in selectively-logged forest may reflect reduced variance in the light environment following selective logging as species which prefer densely shaded areas and large tree fall gaps in primary forest are no longer present (Hamer *et al.*, 2003).

Previous studies have suggested that butterfly species with specific larval host plant requirements are more prone to extinction (Shahabuddin and Terbough, 1999; Shahabuddin *et al.*, 2000; Koh *et al.*, 2004). This is because they require a single larval host plant to survive and can no longer persist in an area once this has been removed (Thomas *et al.*, 2001). Here I showed no difference in larval host plant specificity between habitats. This may be because although many species of butterfly recorded required a specific larval host plant family, these plants were not adversely affected by selective logging. For example, *Mycalesis* spp. have larvae that are Gramineae specialists (Robinson *et al.*, 2001) which is generally unaffected by selective logging (Sawadogo *et al.*, 2005). However, in this study, analysis of larval host plant specificity focused on host plant families reflecting available published data. This produced little variance within the data and consequently the statistics lacked power. Thus, further data are required on the impact of selective logging on species with specialist feeding requirements.

6.5.3 Conservation implications

Globally, selective logging is an increasing threat to large portions of remaining tropical forests (Nepstad *et al.*, 1999; Asner *et al.*, 2005). For selective logging to be sustainable in the tropics, both careful management of timber resources and conservation of biodiversity is needed (Pearce *et al.*, 2003). Results from this study showed reduced butterfly β diversity was observed following selective logging. A reduction in β diversity reflected the absence of some endemic and restricted-range species and species with a preference for closed-canopy forest following selective logging. Thus, to increase the biodiversity value of selectively-logged forest, management of logging concessions should aim to maximise β diversity by reducing the impacts of selective logging on environmental heterogeneity. This might be achieved by including areas of undisturbed forest within logging concessions and by enhancing natural regeneration in selectively-logged forest (Hamer *et al.*, 2003). In addition, management of selectively-logged areas should aim to increase areas of dense shade and reduce rapidly-colonising pioneer species from dominating large tree-fall gaps (Hamer *et al.*, 2003). This would help to produce a relatively heterogeneous light environment that could support species with a range of light preferences, thus maximising β diversity. As timber resources become ever depleted remaining primary forest may increasingly be used to meet demand from the logging industry (Curran *et al.*, 2004). Thus, careful management of current logging concession may become increasingly important in preserving tropical biodiversity as demand for timber continues to increase.

Chapter 7 General Discussion

7.1 Thesis Objectives

A large portion of global biodiversity is represented by, and located within, tropical rainforests (Myers *et al.*, 2000; Olson *et al.*, 2001; Orme *et al.*, 2005). However, as human populations in the tropics continue to grow tropical biodiversity is placed under increasing threat from anthropogenic disturbance (Wright, 2005). For example, in Southeast Asia, forests are under increasing threat from the logging industry and much remaining forest is reserved within commercial selective-logging concessions (Sodhi *et al.*, 2004). Thus, it is of great current concern to understand the impact of selective logging on diversity (Curran *et al.*, 2004).

Insects account for the majority of global biodiversity (> 60% of species richness) and play important roles in maintaining biodiversity and ecosystem functioning (Speight *et al.*, 1999). In complement with other taxa, insect diversity is highest within the tropics (Speight *et al.*, 1999). Thus, it is important to understand how insects respond to habitat disturbance within tropical forests (Samways, 2005). Due to their sensitivity to local environmental gradients and specific larval host plant requirements, butterflies are often used to assess the impacts of habitat disturbance on insect diversity (Sparrow *et al.*, 1994). In general, severe forms of disturbance, such as deforestation and conversion of rainforest to agricultural land, reduce insect diversity (Holloway *et al.*, 1992). However, the response of insects, notably butterflies, to moderate forms of habitat disturbance such as selective logging is less clear (Hamer and Hill, 2000).

In an ever degraded landscape, reliable information about the impact of moderate habitat disturbance on biodiversity will become increasingly important in addressing conservation issues. Thus, the overall objective of this thesis was to provide a better understanding of the impact of habitat disturbance on butterfly diversity.

7.2 Summary of Thesis Findings

7.2.1 Chapter 3 summary

In Chapter 3, existing data were re-analysed to examine how the length of time spent sampling and the spatial resolution of sampling influenced the perceived response of

butterfly diversity to selective logging. In addition, new data were collected and analysed to investigate the efficiency of sampling tropical-forest butterflies using fruit-baited traps. Results from Chapter 3 showed that relatively long-term studies conducted at relatively large spatial scales were needed to detect changes in diversity following selective logging. This most likely reflected the large sample sizes needed for diversity indices to give a robust estimate of diversity (Magurran, 2004) and the relatively large spatial scale of sampling needed to account for the impacts of habitat disturbance on vegetation heterogeneity (Hamer *et al.*, 2003). Chapter 3 showed that fruit-baited traps are efficient at retaining captured butterflies and that emptying traps daily between 9.00 am – 2.00 pm records the majority of captures.

7.2.2 Chapter 4 summary

In Chapter 4, I investigated the impacts of selective logging on ground and canopy butterfly assemblages. Results from Chapter 4 showed that inclusion of canopy samples was needed in order to detect a significant difference in diversity between primary and selectively-logged forest. However, when assessing the impact of selective logging on restricted range species (*i.e.* species' conservation value) whether or not data from canopy samples were included in analysis did not qualitatively affect results and showed significantly lower conservation value of selectively-logged forest. Further to this, results from Chapter 4 showed that primary and selectively-logged forests contained distinct canopy assemblages and that selective logging did not cause a breakdown in the vertical stratification of butterfly assemblages. Overall, results from Chapter 4 indicated that selective logging caused a loss of canopy species but that these species were of relatively low conservation value.

7.2.3 Chapter 5 summary

In Chapter 5, I investigated the impacts of selective logging on butterfly α diversity and the relationships between α diversity and spatial scale in primary and selectively-logged forests. I also examined the impacts of selective logging on vegetation structure and examined patterns of spatial autocorrelation of butterfly α diversity and vegetation structure in primary and selectively-logged forests. Results from Chapter 5 showed that primary forest had significantly higher α diversity than selectively-logged forest. However, these results were dependent on the spatial scale of analysis (large spatial scale reported

decreased diversity following selective logging but small spatial scale reported no change in diversity). This was because the relationships between species richness and diversity increased at a significantly faster rate in primary forest than in selectively-logged forest. Analysis of vegetation data showed that selective logging caused a significant reduction in the variance of some vegetation variables and this indicated a reduction in habitat heterogeneity. Thus, the reduction in the rate at which species diversity increased with spatial scale following selective logging probably reflected a reduction in habitat heterogeneity in selectively-logged forests. Butterfly α diversity was spatially autocorrelated up to a range of 350 m in primary forest. In contrast, α diversity in selectively-logged forest showed no spatial autocorrelation. Patterns of spatial autocorrelation of butterfly α diversity reflected patterns of spatial autocorrelation in canopy cover which was spatially autocorrelated up to a distance of $\approx$406 m between sampling points in primary forest, but was not spatially autocorrelated in selectively-logged forest. This chapter highlighted the need for careful planning of future conservation studies to avoid misleading results associated with the spatial scale of analysis and the increased likelihood of Type 1 statistical errors when dealing with spatially autocorrelated data.

7.2.4 Chapter 6 summary

In Chapter 6, I investigated the impacts of selective-logging on butterfly β diversity and the relationships between β diversity and spatial scale in primary and selectively-logged forests. I also examined the relationships between vegetation structure and species composition in primary and selectively-logged forest. Finally, I investigated the impacts of selective logging on butterfly species with different ecological traits and morphologies. Results from Chapter 6 showed that primary forest had significantly higher β diversity than selectively-logged forest. β diversity was positively correlated with increasing geographic distance between samples in primary forest but not in selectively-logged forest and this reflected patterns of vegetation structure. Species composition was significantly related to vegetation structure and changes in vegetation structure following selective logging resulted in significant changes in butterfly species composition. Primary forest contained significantly more species with preferences for low-light levels within closed-canopy forest, but there was no significant difference between habitats in the geographic range sizes of species or the number of species with restricted larval host plant requirements. There was also no difference in the adult flight morphology of species in primary and

selectively-logged forests indicating no difference in the dispersal abilities of butterflies between habitats. Changes in patterns of β diversity between habitats reflected species ecologies and their response to changes in vegetation structure and light environment. This chapter highlighted the need for information on species' ecologies and habitat preferences when interpreting diversity patterns in primary and selectively-logged forest.

7.3 Butterfly Sampling

7.3.1 Data collection

During the 10-month study, I recorded a total of 3524 individuals from 72 species of fruit-feeding Nymphalid butterfly (data from Chapters 4, 5 and 6 combined). This represents > 90% of the fruit-feeding Nymphalids previously recorded at this study site (Willott *et al.*, 2000; Hamer *et al.*, 2003). In addition, I recorded 15 previously un-recorded species, including thee endemics (*e.g. Thauria aliris*) and seven species restricted to the canopy (*e.g. Euthalia djata*) compared with Hamer *et al.* (2003) who also conducted field work at the same study site using similar trapping methods. This level of species richness is quantitatively similar to results from other studies at different sites in Sabah that have used similar sampling methods (Schulze and Fiedler, 1998; Schulze *et al.*, 2001).

7.3.2 Sampling methods

Butterfly data analysed in Chapters 4, 5 and 6 were collected using two different sampling methods. Data were collected from fruit-baited traps along transects (including canopy traps) (Chapter 4) and from traps distributed over grids (Chapters 5 and 6). Both methods sampled for relatively long periods of time spanning an 18-month time period (May 2003 – December 2004). In addition, traps sampled over a relatively large area on both transects ($\approx$ 24 ha) and grids ($\approx$80 ha). Thus data were probably collected over a sufficiently long time span and large spatial scale as to give robust estimates of changes in diversity following selective logging (Chapter 3). Butterfly data used in this thesis (Chapters 4, 5 and 6) were collected from fruit-baited traps that were emptied between 10.00 am – 2.00 pm daily. Results from Chapter 3 suggested that this was an efficient sampling protocol and that butterfly data collected in this thesis (Chapter 4, 5 and 6) are likely to include the majority of fruit-feeding Nymphalid butterflies that entered the traps during the study period (Chapter 3). Although fruit-baited traps only sample a single feeding guild of butterfly, they

avoid problems associated with species identification in highly diverse regions and allow a reliable, repeatable sampling technique within different areas of the forest and in different habitats (Walpole and Sheldon, 1999). In addition, using fruit-baited traps allowed sampling to be conducted in the forest canopy (Chapter 4) and this would not have been possible using standard walk and count transect techniques. Results from Chapter 4 showed that canopy samples were necessary to build species inventories and necessary in providing a robust estimate of change in diversity following selective logging. There is some evidence to suggest that fruit-feeding butterfly diversity is highly correlated with overall butterfly diversity (Horner-Devine *et al.*, 2003). Thus the long time span, large spatial scale and sampling methods used in this study are likely to give a robust estimate of changes in fruit-feeding butterfly diversity following selective logging (Chapter 3 and 4) and are likely to represent changes in overall butterfly diversity (Horner-Devine *et al.*, 2003). Species' attraction to baited traps can vary even within feeding guilds (Davis and Sutton, 1997) and fruit feeding butterflies have been shown to be attracted to carrion as well as fruit (Hamer *et al.*, 2006). However, differences between species' attraction to traps are unlikely to vary between habitats and thus unlikely to affect reported changes in diversity following selective logging.

7.3.3 Sampling area

There are few data on the distance over which traps attract butterflies and on the area over which traps sample (Hamer *et al.*, 2003). Previous studies have suggested that traps attract butterflies over relatively short distances (50 – 100 m), as traps separated by distances of 50 – 100 m had distinct butterfly assemblages (Pinheiro and Ortiz, 1992; Hill *et al.*, 2001; Hamer *et al.*, 2003). Results from DCA in Chapter 6 showed distinct butterfly assemblages in traps placed ≥200 m apart in primary and selectively-logged forests. However, analysis of β diversity between traps indicated approximately 50% similarity in trap assemblages placed 200 m apart. This indicated that traps might sample butterflies over a distance closer to 200 m compared with the short distances over which traps are likely to attract butterflies (Pinheiro and Ortiz, 1992; Hill *et al.*, 2001; Hamer *et al.*, 2003). Thus, it is likely that traps sample over much larger areas than the distances over which butterflies may be initially attracted to traps. Results from Chapter 5 confirm this and showed diversity samples were not independent between traps separated by ≤345 m in primary forest and therefore are likely to sample diversity over a radius close to 350 m. In addition, traps sample large

numbers of individuals which indicates a large sample area (Hamer *et al.*, 2003). Thus, fruit-baited traps provide a way of sampling butterfly diversity over a relatively large spatial scale (radius of 200-350 m per trap). This provides an efficient way of sampling butterfly diversity over a large spatial scale by reducing the number of man-hours needed to cover a similar spatial scale using standard walk and count techniques.

7.4 Habitat Heterogeneity

7.4.1 Selective logging reduces environmental heterogeneity

Analysis of vegetation data in Chapter 5 showed a more heterogeneous forest structure in primary forest compared with selectively-logged forest and supported previous studies that showed a reduction in habitat heterogeneity following selective logging (Ganzhorn *et al.*, 1990; Burghouts *et al.*, 1994; Hill, 1999; Okuda *et al.*, 2003; Hamer *et al.*, 2003; Dumbrell and Hill, 2005). In this study, selective-logging resulted in a reduction in habitat heterogeneity by primarily reducing canopy heterogeneity (Plate 7.1; primary forest had significantly greater variance in canopy cover, tree heights and tree sizes). Measures of vegetation structure are often positively spatially autocorrelated within heterogeneous habitats (Lichstein *et al.*, 2002; Dungan *et al.*, 2002) but, what was not clear previously was what impact this reduction in habitat heterogeneity following selective logging would have on spatial patterns of canopy cover. In Chapter 5, I showed canopy cover was spatially autocorrelated in primary forest but, not in selectively-logged forest reflecting a reduction in habitat heterogeneity following selective logging. Estimates of canopy cover reflect the amount of light penetrating through the vertical layers of the forest (Costa and Magnusson, 2002; Koukoulas and Blackburn, 2004) and thus, selective logging caused a spatially more homogenous light environment compared with primary forest. Changes in the spatial distribution of light in the forest following selective logging were associated with changes in the distribution of butterfly species, reflecting species' light preferences (Chapter 6). Analysis of β diversity between traps indicated that this resulted in a spatially more uniform distribution of butterfly diversity as β diversity was distant-dependent in primary forest but not in selectively-logged forest (Chapter 6). Thus, changes in butterfly diversity following selective logging probably followed species' responses to a spatially more uniform light environment. Light is an important abiotic factor that determines the distribution of many tropical-forest species. For example, vascular epiphytes (Cardelus *et al.*, 2006) and insects

including the Coleoptera, Orthoptera (Barbosa *et al.*, 2005) and Lepidoptera (DeVries *et al.*, 1997; Hill *et al.*, 2001). In this study, selective logging changed the forest light environment and this was most likely the primary cause of changes in the spatial distribution of butterfly diversity (Chapter 5 and 6).

Plate 7.1 Aerial view of primary (top) and selectively-logged (bottom) forest canopies in Danum Valley. Primary forest had significantly greater variance in canopy cover, tree heights and tree sizes.

7.4.2 Habitat heterogeneity from ground to canopy

Results from Chapter 4 suggested that another impact of selective logging may be a reduction in habitat heterogeneity vertically from ground to canopy strata. This was consistent with the results of diversity analysis in Chapter 4 which showed that the incorporation of canopy traps increased estimates of diversity in primary forest but had little effect in selectively-logged forest. Assessing whether selective logging reduces habitat heterogeneity vertically as well as horizontally is logistically difficult. However, recent advances in remote sensing techniques have allowed the characterisation of vertical-vegetation structure in tropical forests using aerial large-footprint light detection and ranging (lidar) remote sensors (Drake *et al.*, 2002a, 2002b; Drake *et al.*, 2003). Lidar equipment, mounted from an aircraft or satellite, emits a pulse of laser energy (near-infrared wavelength for vegetation mapping) through the forest canopy towards the ground. Lidar sensors then record the incident pulse (returning pulse) that has interacted with vegetation (*e.g.* canopy leaves, branches and lianas) and ground surfaces where it is reflected back to the sensor (Drake *et al.*, 2002a). These build a picture of the complexity of the vegetation structure through the forest strata. Lidar estimates of above-ground biomass from ground to canopy strata have greater variance in primary forest indicating greater vertical habitat heterogeneity in primary forest compared with secondary or agroforestry plots. The secondary forest plots studied by Drake *et al.* (2002b) were a mixture of moderately disturbed, semi-deforested and selectively-logged areas (Nicotra *et al.*, 1999). This may indicate that the moderate disturbance caused by selective logging in the Ulu Segama Forest Reserve in this study could also result in a reduction in habitat heterogeneity vertically as well as horizontally.

7.5 Spatial Scale

Results from Chapter 5 showed that differences in diversity between primary and selectively-logged forest were dependent on the spatial scale of analysis. This was apparently because the relationships between species richness and diversity increased at a significantly faster rate in primary forest than in selectively-logged forest reflecting greater habitat heterogeneity in primary forest. Previous studies have suggested that decreased diversity following selective logging will be reported when the spatial scale of analysis is large enough to account for the impacts of disturbance on habitat heterogeneity (Hamer and

Hill, 2000; Hill and Hamer 2004). Thus, large-scale studies tend to report no change or decreased diversity following selective logging whereas small-scale studies are more likely to report increased diversity following selective logging (Hamer and Hill, 2000; Hill and Hamer 2004). The change between large-scale studies reporting no difference in diversity and those reporting decreased diversity probably reflects an increase in spatial scale between studies (Chapter 3).

Results from Chapter 5 were in contrast to results from Chapter 4. In Chapter 4, I showed that canopy samples were needed in order to detect a significant decrease in diversity following selective logging. However, in Chapter 5, I reported a decrease in diversity following selective logging based solely on ground-level traps. This contrast in results between chapters may be explained by differences in the spatial scale of sampling in each investigation. In Chapter 4, I sampled butterflies at ground level using 20 fruit-baited traps placed every 100 m and sampled 10 traps in the canopy placed every 200 m along 2 km transects in primary and selectively-logged forest. In Chapter 5, 25 fruit-baited traps placed ≥200 m apart across a square grid were used to sample butterflies in primary and selectively-logged forest. Assuming traps sampled over a similar area in both habitats and at both heights (ground *versus* canopy traps), data from Chapter 4 were analysed at a smaller spatial scale than were data from Chapter 5 when only data from ground traps (Chapter 4, $n = 20$; Chapter 5, $n = 25$) were analysed but sampled a larger area when canopy trap data were included (Chapter 4, $n = 30$; Chapter 5, $n = 25$). Results from Chapter 5 showed that selective logging reduced habitat heterogeneity and results from Chapter 3 indicated that the probability of recording a decline in diversity following disturbance increased when the spatial scale of analysis was large enough to account for the impacts of disturbance on habitat heterogeneity. Thus, the difference in the spatial scale of analysis at ground level between Chapters 4 and 5 may explain why decreased diversity was reported in selectively-logged forest in Chapter 5 but not in Chapter 4. However, what is less clear, is whether the extra 10 traps used to sample the canopy in Chapter 4 were important in detecting a decrease in diversity following disturbance because they increased the spatial scale of the study or because the sampled canopy species that are not recorded at ground level.

7.6 Impacts of Selective Logging Across Taxa

7.6.1 Butterfly diversity may not reflect the diversity of other taxa

This thesis focused on the impacts of selective logging on butterfly diversity and generally reported a decrease in diversity following selective logging. However, previous research has suggested that the response of diversity to habitat disturbance measured by a single taxon is not necessarily representative across taxa (Lawton *et al.*, 1998; Perfecto *et al.*, 2003) and there has been little progress in finding a single indicator taxon to use in assessing the impact of disturbance on diversity (McGeoch, 1998). For example, in contrast to results presented here, previous research has shown that selective logging did not effect the diversity of Microchiropteran bats (Clarke *et al.*, 2005), insects (ants, Dunn, 2004; Widodo *et al.*, 2004; dung beetles, Scheffler, 2005), amphibians (Fredericksen and Fredericksen, 2004) and birds (Dunn, 2004). There are two likely explanations for the contrast in results across taxa. Firstly, differences between taxa may reflect differences in species ecologies (Lawton *et al.*, 1998) and secondly, differences between taxa may reflect differences in the methods and spatial scale of sampling (Hill and Hamer, 2004).

7.6.2 Differences across taxa reflects species ecologies

In this study, changes in butterfly diversity following selective logging were related to changes in spatial patterns of vegetation structure (Chapter 6) and environmental heterogeneity in estimates of canopy cover (Chapter 5). Both of these measures probably reflected the amount of light penetrating through the vertical layers of the forest (Costa and Magnusson, 2002; Koukoulas and Blackburn, 2004). Light is the major abiotic factor in determining the distribution of butterflies through the forest (*e.g.* DeVries, 1988; DeVries *et al.*, 1997; Hill *et al.*, 2001, Schulze *et al.*, 2001). Thus, changes in butterfly diversity following selective logging probably reflected species responses to changes in light environment (Chapters 5 and 6). Differences in light environment within the forest play an important role in determining the distribution of many tropical forest species. For example, tree seedlings have specific light requirements and will only grow in areas with certain light levels (Balderrama and Chazdon, 2005; Bazzaz and Pickett, 1980). This in turn affects herbivorous insects (Barbosa *et al.*, 2005) and some species of birds are also dependent on plants with specific light requirement (Altshuler, 2003). In addition, the distribution of other non-Lepidopteran insect species is also dependent on local forest light environment

(Perfecto and Vandermeer, 1996). Selective logging causes a change in the spatial distribution of light and reduces variability of light environments within the forest (Chapter 5). Therefore, species with specific light requirements may be more affected by selective logging than species' whose distribution through the forest is not limited by light levels. Thus, although changes in butterfly diversity following habitat disturbance may not reflect changes in diversity across all taxa (Lawton *et al.*, 1998), it is likely that it is representative of change in diversity of taxa with similar light requirements. Lawton *et al.* (1998) showed changes in the diversity of butterflies were correlated with changes in the diversity of canopy ants following disturbance but not with changes in leaf-litter ant diversity. This may be because canopy ants are more sensitive to changes in light environment, similar to butterflies, than are leaf-litter ants, because leaf-litter cover does not significantly change following selective logging (Vasconcelos *et al.*, 2000) but canopy cover does (Chapter 5). Thus, measures of the response of butterfly diversity to disturbance are likely to be indicative of the response of diversity of taxa with similar ecologies and indicative of changes in the environmental and ecological condition of tropical forests (McGeoch, 1998). However, this has yet to be tested and making future cross-taxa comparisons of the response of diversity of species with similar ecologies is likely to reveal significant correlations.

7.6.3 Differences across taxa reflect the spatial scale of sampling

Estimates of changes in butterfly diversity following disturbance were shown to be dependant on the spatial scale of sampling (Chapter 5). This reflected the impact of disturbance on environmental heterogeneity within the forest (Chapter 5). The response of bird (Hill and Hamer, 2004), marine invertebrate (Kaiser, 2003) and cricket (Ribas *et al.*, 2005) diversity to habitat disturbance showed a similar scale-dependent response which reflected the impact of habitat disturbance on environmental heterogeneity. Thus, the difference in the response of diversity to disturbance across taxa (Lawton *et al.*, 1998) may reflect differences in the spatial scale of sampling (Hill and Hamer, 2004). When monitoring the impacts of selective logging on fruit-feeding butterfly diversity, sampling over a relatively large spatial scale (transect $\geq$1.6 km) is required to collect sufficient data to give a robust estimate of diversity (Chapter 3). In other taxa sufficient data for a robust estimate of diversity may be gained from sampling a much smaller spatial scale. For example, Jones and Eggleton (2000) showed that sufficient data for a reliable estimate of

termite diversity can be gathered from 100 m transects. These differences in the sample area needed to give a robust estimate of diversity most likely reflect the size and mobility of the studied taxa. As some taxa are sampled over relatively small spatial scales and others over large scales differences in the reported response of diversity to habitat disturbance between taxa may be confounded by the spatial scale of sampling. This does not necessarily mean all taxa should be sampled at the same spatial scale but it does highlight the need to sample over a sufficiently large spatial scale to account difference across taxa in how species respond to the impact of selective logging on habitat heterogeneity (Hill and Hamer, 2004). However, what may be more important when investigating impacts of disturbance on diversity is examining how differences in the spatial scale of analysis affect the perceived response of diversity to disturbance across taxa and future studies should consider examining diversity at a range of spatial scales.

7.7 Conservation and Future Research

7.7.1 Conservation implications

Continued human population growth is placing increasing pressure on remaining forest resources and demand for timber is continuing to grow (Wright, 2005). Within the next few decades, most remaining rainforest that is not reserved within protected areas is likely to be logged (Achard *et al.*, 2002; Sodhi *et al.*, 2004; Asner *et al.*, 2005). However, as timber resources become ever depleted remaining primary forest may increasingly be used to meet demand from the logging industry (Curran *et al.*, 2004). Thus, it is important that conservationists act promptly to protect the future of tropical biodiversity as it is likely that even protected areas of primary forest will reduce in size to meet timber demand (Curran *et al.*, 2004). For example, in Kalimantan (Indonesian Borneo) protected forest areas have been logged to meet demand from the timber trade (Curran *et al.*, 2004). However, in Sabah protected forests reserves are under greater legal protection and are likely to remain unlogged. DVCA (the study site) is a Class 1 Protection Forest Reserve (see Chapter 2) and is under full protection by Sabah's State Assembly. Therefore, it is likely that the DVCA will remain as primary rainforest for the foreseeable future. Thus, future conservation efforts in Sabah should probably focus on the remaining areas of forest reserved for selective logging and on areas of already selectively-logged forest as primary rainforest reserves are effectively protected.

Selective logging caused a decrease in diversity (Chapters 4, 5 and 6) and significantly changed the species composition of butterfly assemblages (Chapters 4 and 6). Nevertheless, selectively-logged forest did contain distinct butterfly assemblages both in the forest understorey (Chapter 6) and canopy (Chapter 4). Thus, selectively-logged forest can play an important role in conserving biodiversity. As revenue from timber production continues to decrease (Sabah Forestry Department, 2001), areas of selectively-logged forest may be threatened by conversion to oil palm plantations (Sodhi *et al.*, 2004) which dramatically reduces diversity (Chung *et al.*, 2000; Sodhi *et al.*, 2004) and conserving selectively-logged forest may become increasingly important. In light of the economic crisis in Southeast Asia during the late 1990s large areas of logged forest in Sabah were converted to oil palm estates (McMorrow and Talip, 2001). This provided a 'cash crop' which quickly generated revenue for the State (McMorrow and Talip, 2001). Previously however, maximising revenue from agricultural crops relied on expanding agricultural land by further forest clearance and only recently has agricultural policy shifted to encourage farming permanent agricultural land using modern intense farming techniques (McMorrow and Talip, 2001). Two competing solutions have been proposed to maximise diversity in agricultural landscapes. This can be achieved by either 'wildlife-friendly farming' which is at relatively low intensity over a large area and promotes diversity on farmland or by 'land sparing' which uses high-intensity farming in a smaller area thus reducing the demand for farmland and promoting diversity by preserving surrounding natural habitats (Green *et al.*, 2005). In tropical regions, high-yield farming has caused 'land sparing' to occur by decreasing the rate of conversion to farmland and producing lower deforestation rates and has helped conserve diversity by persevering larger areas of natural habitat (Green *et al.*, 2005). Thus, using high-yield farming (land sparing) on existing agricultural land in Sabah may meet the requirements of Sabah Agricultural Department who plan to accelerate agricultural and rural development by increasing agricultural efficiency (McMorrow and Talip, 2001) but might also protect areas of selectively-logged forest by meeting agricultural yield targets without the need for further forest conversion (Green *et al.*, 2005). However, the protection of selectively-logged forest reserves will still largely rely on their continued economic viability. In Sabah, areas of forest reserved for selective logging need to provide long-term sources of forest products, and thus revenue, to protect them from conversion to agriculture (McMorrow and Talip, 2001; Pearce *et al.*, 2003). Logging areas of primary forest using less invasive logging techniques will enhance natural regeneration

and help promote a sustainable source of timber by increasing forest regeneration (Forshed *et al.*, 2006). Various methods for less invasive timber harvesting have been suggested; for example, supervised logging (SL; Forshed *et al.*, 2006) and reduced impact logging (RIL; Pinard and Putz, 1996; Pinard *et al.*, 1995, 2000). Studies have shown that SL, which uses pre-marked skid trials and directional felling to minimise the indirect impacts of selective logging on the surrounding vegetation structure, produced a forest with high numbers of dipterocarp seedlings and few damaged large trees (Forshed *et al.*, 2006). RIL techniques also aim to minimise skid trail damage by implementing felling, skidding and harvesting restrictions and RIL techniques have been shown to leave a forest structure with high levels of canopy cover and more dipterocarp saplings compared with conventional techniques (Pinard *et al.*, 2000). Both SL and RIL techniques increase the future yield of production forests (Pinard *et al.*, 2000; Forshed *et al.*, 2006), thus producing an economic incentive to keep these forests rather than convert them to agricultural land. In addition, both SL and RIL techniques produced a greater range of vegetation structure compared with conventional logging techniques (Pinard *et al.*, 2000; Forshed *et al.*, 2006). This helps maintain high habitat heterogeneity which in turn will promote higher butterfly diversity (Chapter 5 and 6). Maximising future timber yields when re-logging areas of forest originally logged using conventional techniques may be less straight forward and covering the costs to the timber company of completely protecting areas of selectively-logged forest by intensely logging other areas might be a viable option. In addition, using SL and RIL techniques to re-log areas that have regenerated will most likely produce sustainable harvests of timber and thus provide a financial incentive to protect areas of selectively-logged forest. In conclusion, selectively-logged forest can play an important role in protecting Sabah's biodiversity and can support distinct butterfly assemblages (Chapter 6). However, future management of logging concession must aim to maximise vegetation heterogeneity and thus diversity (Chapter 5 and 6) as well as producing a sustainable yield of timber. Thus, the future conservation of biodiversity in Sabah will rely on producing a landscape comprised of a mosaic of completely protected areas of primary forest, areas of selectively-logged forest protected by their continued commercial value and areas of intensely farmed oil palm estates that produce high yields reducing the incentive to encroach further on areas of production forest.

7.7.2 Future work

Selective-logging has been shown to reduce environmental heterogeneity (Chapter 5; Ganzhorn *et al.*, 1990; Burghouts *et al.*, 1994; Hill, 1999; Dumbrell and Hill, 2005). This in turn causes a reduction in β diversity between samples and a reduction in habitat α diversity following selective logging (Chapters 5 and 6). However, most research has focused on the impacts of habitat disturbance on environmental heterogeneity at ground level and few data are available on whether selective logging reduces habitat heterogeneity vertically as well as horizontally. Assessing habitat heterogeneity vertically as well as horizontally is logistically difficult. However, recent advances in remote-sensing techniques have allowed the characterisation of vertical structure in tropical forests (Drake *et al.*, 2002a, 2002b; Drake *et al.*, 2003). Thus, further research should focus on assessing the impacts of selective logging from ground to canopy as well as between ground-level sites.

The study site at which sampling was conducted in this thesis is generally considered aseasonal with relatively constant rainfall throughout the year (Walsh and Newbury, 1999). However, there is some variation in rainfall caused by the northerly monsoon in the South China Seas (Walsh, 1996b) which is known to result in temporal variation in butterfly abundances (Hill *et al.*, 2003). This can affect estimates of diversity change following selective logging as butterfly abundances apparently respond to rainfall in opposite ways in primary and selectively-logged habitats (Hamer *et al.*, 2005). Climate change is generally considered a minor threat to tropical biodiversity compared with land use changes (Sala *et al.*, 2000). However, climate models predict an increase in monsoon intensity over Southeast Asia (Coppola and Giorgi, 2005) and an increase in the variance of rainfall at equatorial locations (Dore, 2005). Thus, it is likely that butterfly abundances may change following altered patterns in precipitation. What is less clear however, is whether the response of butterfly diversity to climate change may interact with the response of butterfly diversity to land-use changes such as selective-logging. This warrants further study and recording baseline data and understanding patterns of butterfly β diversity between years and between months may become increasingly important for the future conservation of tropical diversity. In addition to changes in precipitation patterns, global patterns of climate change are likely to increase the severity and frequency of El Niño-Southern Oscillation (ENSO) events (Holmgren *et al.*, 2001; Dore, 2005). In Borneo, ENSO events cause widespread droughts (Walsh, 1996b) and areas of logged forest may be increasingly prone to fire during ENSO events (Siegert *et al.*, 2001). The response of forest

butterflies on Borneo to recent ENSO events has been reasonably well documented and butterfly abundance tends to decrease during ENSO events (Hill *et al.*, 2003; Cleary and Grill, 2004; Cleary and Genner, 2004; Cleary and Mooers, 2004; Cleary *et al.*, 2004). However, these ENSO effects are relatively short lived (Hill *et al.*, 2003) but, the long term impacts of increased ENSO frequency and severity on tropical diversity warrants further study.

Results from Chapter 5 showed that the reported impacts of selective logging on diversity were dependent on the spatial scale at which data were analysed. This supports the suggestion that differences between studies investigating the impacts of selective logging on diversity are caused by difference between studies in the spatial scale of sampling (Hamer and Hill, 2000; Hill and Hamer, 2004). However, in addition to difference between studies in the spatial scale of sampling it is likely that the logging intensity also varies. Therefore, differences in the reported response of diversity to selective logging between studies may be confounded not only by differences in the spatial scale of sampling but also by differences in the intensity of logging operations. For example, the spatial scale of sampling needed to account for the impact of low intensity logging may be larger than the spatial scale of sampling needed to account for the impact of high intensity logging. Thus, further research is needed into how differences in logging intensity may affect diversity and studies that investigate impacts of selective logging intensity, whilst accounting for spatial scale are required.

The majority of research on the impacts of selective logging on butterfly diversity has compared primary forest and forest that has been selectively logged only once (Hill *et al.*, 1995; Hamer *et al.*, 1997; Willott *et al.*, 2000; Lewis, 2001; Hamer *et al.*, 2003: Dumbrell and Hill, 2005). However, with increasing human population density there is an ever increasing demand for forest resources and forests that have already been selectively-logged may be re-logged (Wright, 2005). In Malaysia, production rainforest is to be selectively logged on a 35-year cycle (Whitmore, 1991) but, it is not clear how repeated logging of forests affects diversity. This is a key question that needs to be addressed and will allow foresters and conservationists to implement clear management plans that not only provide sustainable timber harvest but also maximise tropical biodiversity.

APPENDIX 1

Data analysed in Chapter 3. Numbers of butterflies from each species sampled in primary and selectively-logged forests over a 12-month period between October 1999 and September 2000. Data were originally collected by Benedick (2001) and Mustaffa (2001). Butterfly nomenclature follows Otsuka (1988).

	Habitat		Total
	Primary forest	Selectively-logged forest	
Satyrinae			
Elyminas panthera Fabricius	1	0	1
E. dara Distant and Pryer	0	1	1
Melanitis leda L.	14	18	32
M. zitenius Herbst	1	1	2
Neorina lowii Doub.	112	166	278
M. anapita Moore	46	20	66
M. fusca Felder	0	3	3
M. patiana Eliot	7	4	11
M. kina Staudinger	30	16	46
M. dohertyi Elwes	29	12	41
M. horsfieldi Moore	1	0	1
M. maianeas Hewit.	41	74	115
M. oroatis Hewit.	235	1	236
M. orseis Hewit.	84	108	192
M. mineus L.	2	0	2
M. janardana Moore	0	1	1
Erites elegans Butler	7	4	11
E. argentina Butler	0	1	1
Ragadia makuta Horsfield	98	166	264
Lethe dora Staudinger	1	0	1
Morphinae			
Faunis gracilis Butler	1	0	1
F. canens Hubner	0	2	2
F. stomphax West.	3	0	3
Xanthotaenia busiris West.	7	3	10
Amathusia phidippus L.	3	3	6
Amathuxidia amythaon Doub.	3	2	5
Zeuxidia aurelius Cramer	9	5	14
Z. amethystus Butler	6	7	13
Z. doubledayi West.	0	1	1
Thaumantis noureddin West.	1	0	1
Discophora necho Felder	22	29	51

APPENDIX 1 CONTINUED

	Habitat		Total
	Primary forest	Selectively-logged forest	
Nymphalinae			
Cirrochroa emalea Guerin	15	0	15
Cupha erymanthis Drury	2	0	2
Paduca fasciata Felder	1	3	4
Terinos clarissa Boisduval	1	0	1
Kallima limborgii Moore	1	11	12
Rhinopalpa polynice Cram.	11	1	12
Neptis hylas L.	1	0	1
N. harita Moore	1	0	1
Athyma pravara Moore	2	0	2
A. reta Moore	1	0	1
Parthenos sylvia Cramer	0	1	1
Dophla evelina Stoll	26	9	35
Bassarona teuta Doub	18	18	36
B. dunya Doub.	78	125	203
Lexias dirtea Fabricius	18	8	26
L. pardalis Moore	25	27	52
L. canescens Butler	8	1	9
Amnosia decora Doub.	4	9	13
Dichorragia nesimachus Doy.	3	3	6
Tanaecia aruna Felder	21	21	42
T. clathrata Vollenhoven	0	1	1
T. pelea Fabric.	2	1	3
E. iapis Godart	2	2	4
E. monina Fabric.	1	1	2
Charaxinae			
Prothoe franck Godart	86	42	128
Agatasa calydonia Hewit	2	4	6
Charaxes bernardus Fabricius	8	1	9

APPENDIX 2

Data analysed in Chapter 4. Numbers of butterflies from each species sampled in primary and selectively-logged forests at canopy and ground levels. Species are ranked according to geographical distribution, species endemic to Borneo have the highest rank (rank = 1); the lowest ranked species (rank = 61) is the most widespread recorded during this study. Butterfly nomenclature follows Otsuka (1988).

	Rank	Habitat and trap height				Total
		Primary forest		Selectively-logged forest		
		ground	canopy	ground	canopy	
Satyrinae						
Elyminas panthera Fabricius	21.5	0	2	0	0	2
E. dara Distant and Pryer	34.5	0	1	1	0	2
E. harterti Shelf.	4	0	3	0	0	3
Melanitis leda L.	61	13	4	9	3	29
M. zitenius Herbst	55	5	0	5	0	10
Neorina lowii Doub.	21.5	60	0	26	0	86
Mycalesis amoena Druce	1.5	1	0	1	0	2
M. anapita Moore	9.5	17	3	4	0	24
M. fusca Felder	34.5	3	0	1	0	4
M. patiana Eliot	3	1	1	0	0	2
M. kina Staudinger	1.5	16	0	8	0	24
M. dohertyi Elwes	9.5	13	0	22	0	35
M. horsfieldi Moore	29	7	0	1	1	9
M. maianeas Hewit.	9.5	21	0	40	0	61
M. oroatis Hewit.	16	100	0	0	0	100
M. orseis Hewit.	34.5	46	0	89	0	135
M. perseus Butler	60	1	0	1	0	2
M. mineus L.	58	4	0	2	0	6
Erites elegans Butler	9.5	6	1	5	0	12
E. argentina Butler	32	13	0	0	0	13
Ragadia makuta Horsfield	21.5	94	0	104	0	198
Coelites epiminthia West	34.5	1	0	0	0	1
Morphinae						
Faunis stomphax West.	9.5	4	0	1	0	5
Xanthotaenia busiris West.	21.5	2	0	2	0	4
Amathusia phidippus L.	47.5	0	0	4	0	4
Amathuxidia amythaon Doub.	47.5	4	0	1	0	5
Zeuxidia aurelius Cramer	9.5	6	1	11	0	18
Z. amethystus Butler	39	4	0	7	0	11
Thaumantis noureddin West.	9.5	1	0	0	0	1
T. odona Fruhstorfer	26	1	0	1	0	2
Discophora necho Felder	29	14	1	14	1	30

APPENDIX 2 CONTINUED

	Rank	Habitat and trap height				Total
		Primary forest		Selectively-logged forest		
		ground	canopy	ground	canopy	
Nymphalinae						
Paduca fasciata Felder	39	2	1	0	0	3
Terinos clarissa Boisduval	39	1	0	0	0	1
Kallima limborgii Moore	9.5	0	0	1	0	1
Chersonesia intermedia Martin	15	0	0	1	0	1
Rhinopalpa polynice Cram.	47.5	1	1	0	0	2
Parthenos sylvia Cramer	59	1	0	0	0	1
Dophla evelina Stoll	57	10	3	11	0	24
Bassarona teuta Doub	53	7	8	10	9	34
B. dunya Doub.	29	52	0	66	1	119
Lexias dirtea Fabricius	47.5	12	0	21	0	33
L. pardalis Moore	42	16	1	34	0	51
L. canescens Butler	9.5	3	0	3	0	6
Amnosia decora Doub.	21.5	2	0	11	0	13
Dichorragia nesimachus Doy.	56	0	1	1	0	2
Moduza procris Fruhstorfer	51.5	0	1	0	0	1
Lebadea martha Fruhstorfer	51.5	0	1	0	0	1
Tanaecia aruna Felder	29	5	2	7	0	14
T. clathrata Vollenhoven	9.5	7	2	10	1	20
T. pelea Fabric.	29	4	2	5	0	11
T. munda Fruh	21.5	3	1	10	0	14
Euthalia godarti Butler	17	0	1	0	0	1
E. iapis Godart	21.5	4	3	1	0	8
E. monina Fabric.	54	0	10	2	1	13
E. djata Distant	42	0	1	0	0	1
Charaxinae						
Prothoe franck Godart	47.5	18	1	31	1	51
Agatasa calydonia Hewit	37	2	0	1	0	3
Charaxes bernardus Fabricius	47.5	4	2	0	1	7
C. solon Butler	44	0	1	0	0	1
C. durnfordi Distant	42	1	0	1	0	2
C. harmodius Rothschild	21.5	0	1	0	0	1

APPENDIX 3

Data analysed in Chapters 5 and 6. Numbers of butterflies from each species sampled in primary and selectively-logged forests. Species are ranked according to geographical distribution (G. Rank), light preference (Light) and host plant specificity (H-P Rank). Butterfly nomenclature follows Otsuka (1988).

	G.Rank	Light	H-P Rank	Habitat		Total
				Primary forest	Selectively-logged forest	
Satyrinae						
Elyminas panthera Fabricius	20	1.000	2	2	4	6
E. dara Distant and Pryer	35			1	0	1
Melanitis leda L.	62	0.470	2	13	9	22
M. zitenius Herbst	56		1	3	3	6
Neorina lowii Doub.	20	0.328	1	126	92	218
Mycalesis amoena Druce	1			2	1	3
M. anapita Moore	7	0.563	1	31	49	80
M. fusca Felder	35	0.000		0	1	1
M. patiana Eliot	5	0.395	1	11	7	18
M. kina Staudinger	1	0.095		14	9	23
M. dohertyi Elwes	7	0.217		27	22	49
M. horsfieldi Moore	29	0.500	1	2	21	23
M. maianeas Hewit.	7	0.160	1	53	105	158
M. oroatis Hewit.	19	0.171	1	141	2	143
M. orseis Hewit.	35	0.440	1	76	136	212
M. perseus Butler	61		1	10	16	26
M. mineus L.	60	0.500	1	14	6	20
M. janardana Moore	35	0.500		1	0	1
Erites elegans Butler	7	0.750	1	12	2	14
E. argentina Butler	34		1	8	5	13
Ragadia makuta Horsfield	20	0.442	1	142	86	228
Morphinae						
Faunis stomphax West.	7	0.000	1	4	1	5
F. kirata Hubner	7	0.000		2	1	3
Xanthotaenia busiris West.	20		1	1	5	6
Thauria aliris West.	1		1	1	1	2
Amathusia phidippus L.	48	0.857	2	0	2	2
A. masina Fruhstorfer	6	1.000	1	0	2	2
Amathuxidia amythaon Doub.	48	0.000		1	1	2
Zeuxidia aurelius Cramer	7	0.200	1	13	17	30
Z. amethystus Butler	40	0.500	1	2	7	9
Z. doubledayi West.	20	0.000	1	2	0	2
Thaumantis noureddin West.	7	0.660		2	1	3
T. odona Fruhstorfer	28			3	0	3
Discophora necho Felder	29	0.412	1	37	29	66

APPENDIX 3 CONTINUED

	G.Rank	Light	H-P Rank	Habitat		Total
				Primary forest	Selectively-logged forest	
Nymphalinae						
Cirrochroa emalea Guerin	44	0.000	1	2	0	2
Paduca fasciata Felder	40	0.750		5	8	13
Terinos clarissa Boisduval	40	0.000	1	0	1	1
Kallima limborgii Moore	7	0.318	1	1	0	1
Chersonesia intermedia Martin	18		1	1	2	3
C. peraka Martin	44		1	2	0	2
Rhinopalpa polynice Cram.	48	0.909	2	5	0	5
Neptis nata L.	58		1	0	2	2
Dophla evelina Stoll	58	0.650	4	26	6	32
Bassarona teuta Doub	54	0.750		34	43	77
B. dunya Doub.	29	0.371		104	171	275
Lexias dirtea Fabricius	48	0.000	3	55	11	66
L. pardalis Moore	44	0.400	2	35	71	106
L. canescens Butler	7	0.000	3	3	0	3
Amnosia decora Doub.	20	0.500	1	5	16	21
Dichorragia nesimachus Doy.	57	0.700	2	0	6	6
Tanaecia aruna Felder	29	0.667	1	2	2	4
T. clathrata Vollenhoven	7		1	16	24	40
T. pelea Fabric.	29	1.000	1	7	4	11
T. munda Fruh	20	1.000	1	25	32	57
T. orphane Fabric.	1		1	1	0	1
Euthalia. iapis Godart	20		2	3	5	8
E. monina Fabric.	55	1.000	4	1	3	4
Charaxinae						
Prothoe franck Godart	48	0.414	1	51	36	87
Agatasa calydonia Hewit	39	0.750	1	3	1	4
Charaxes bernardus Fabricius	47	0.737	9	3	6	9
C. solon Butler	48		3	1	0	1
C. durnfordi Distant	43	0.667	0	2	1	3

APPENDIX 4

Distribution of butterfly species in primary and selectively logged forest from data in Appendices 1, 2 and 3. Numbers show which habitat species were most abundant in from data from Appendices 1, 2 and 3. Only butterfly species recorded in all three samples were included Butterfly nomenclature follows Otsuka (1988).

	Habitat		
	Primary forest	Selectively-logged forest	Equall numbers in both habiats
Satyrinae			
Elyminas panthera Fabricius	1,2	3	
E. dara Distant and Pryer	3	1	2
Melanitis leda L.	2,3	1	
M. zitenius Herbst			1,2,3
Neorina lowii Doub.	2,3	1	
M. anapita Moore	2,1	3	
M. patiana Eliot	1,2,3		
M. kina Staudinger	1,2,3		
M. dohertyi Elwes	1,3	2	
M. horsfieldi Moore	1,2	3	
M. maianeas Hewit.		1,2,3	
M. oroatis Hewit.	1,2,3		
M. orseis Hewit.		1,2,3	
M. mineus L.	1,2,3		
Erites elegans Butler	1,2,3		
E. argentina Butler	2,3		
Ragadia makuta Horsfield	3	1,2	
Morphinae			
Faunis stomphax West.	1,2,3		
Xanthotaenia busiris West.	1	3	2
Amathusia phidippus L.		2,3	1
Amathuxidia amythaon Doub.	1,2		3
Zeuxidia aurelius Cramer	1	2,3	
Z. amethystus Butler		1,2,3	
Thaumantis noureddin West.	1,2,3		
Discophora necho Felder	3	1	2

	Habitat		
	Primary forest	Selectively-logged forest	Equall numbers in both habiats
Nymphalinae			
Terinos clarissa Boisduval	1,2	3	
Kallima limborgii Moore	3	1,2	
Rhinopalpa polynice Cram.	1,2,3		
Dophla evelina Stoll	1,2,3		
Bassarona teuta Doub	2,3	1	
B. dunya Doub.		1,2,3	
Lexias dirtea Fabricius	1,3	2	
L. pardalis Moore		1,2,3	
L. canescens Butler	1,3		2
Amnosia decora Doub.		1,2,3	
Dichorragia nesimachus Doy.		3	1,2
Tanaecia aruna Felder			1,2,3
T. clathrata Vollenhoven		1,2,3	
T. pelea Fabric.	1,2,3		
Euthalia. iapis Godart	2	3	1
E. monina Fabric.	2	3	1
Charaxinae			
Prothoe franck Godart	1,3	2	
Agatasa calydonia Hewit	2,3	1	
Charaxes bernardus Fabricius	1,2	3	

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