Moths and Mountains: Diversity, Altitude and Latitude

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Submitted in fulfilment of the requirements of the degree of
Doctor of Philosophy

February 2013
Synopsis

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Moths and mountains: diversity, altitude and latitude

Moth assemblages have been widely used to examine patterns of beta-diversity in forest ecosystems. This thesis aims to expand and test the generality of results obtained as part of the IBISCA-Queensland Project (Investigating Biodiversity of Soil and Canopy Arthropods-Qld) which examined patterns of diversity in a large sub-set of night-flying moths along an altitudinal gradient in subtropical rainforest. The permanent IBISCA-Qld transect, located in Lamington National Park (NP), in south-east Queensland, Australia, spans altitudes from 300 to 1100 meters above sea level (m a.s.l.) within continuous rainforest. Along this transect, moth assemblages showed strong altitudinal stratification. A number of species were restricted to the Nothofagus moorei dominated cloud forest around 1100m a.s.l., and may be the most threatened by climatic change. The IBISCA-Qld Project produced a set of moth species that could be included within a predictor set of taxa that may be useful for future monitoring of the impact of global warming on forest biodiversity.

The IBISCA-Qld study was predicated on the idea that a range of adjacent climates along a single altitudinal gradient can be taken as a surrogate for larger scale climatic changes which occur along latitudinal gradients. This thesis expands on the IBISCA-Qld Project by establishing a latitudinal network of analogous altitudinal transects, in Australia and south-west China (tropical, subtropical and sub-alpine temperate forests), allowing inter-continental comparisons on the generality of altitudinal patterns of diversity.
The aims of this PhD research are to:

1. Assess the richness and assemblage structure of moths along a series of altitudinal gradients within rainforest, along the east coast of Australia and south-west China,
2. examine the differences in assemblage turnover at different taxonomic resolutions across altitude and latitude,
3. identify which species are most important in driving altitudinal and latitudinal changes in assemblage structure and which may be useful as indicator species for climate change monitoring,
4. investigate the degree to which moth fauna are vertically stratified, across altitude and latitude.

Lepidoptera were sampled along altitudinal gradients at, Mt Lewis NP (tropical) and Border Ranges NP (sub-tropical) in Australia, and in Mengla (tropical), Ailao Shan (sub-tropical) and Lijiang (temperate) sites in Yunnan Provence, China. In total, 118,035 individual moths were collected and identified as part of this research. Here, I present the results in a series of papers, each focusing on different aspects of the diversity and distribution of this key group of insect herbivores.
STATEMENT OF ORIGINALITY

I certify that this thesis is my original work and has not previously been submitted for a degree or diploma in any university. To the best of my knowledge and belief, the thesis contains no material previously published or written by another person except where due reference is made in the thesis itself.

__________________________________________
Louise Ashton
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Acknowledgements

I would like to thank and acknowledge the traditional custodians of the land on which this research was conducted – The Githabul people at Border Ranges National Park, NSW, the Mingunburri, Wangerriburri and Bundjalung groups of Lamington National Park, Queensland, and the Kuku Yalanji, traditional owners of the Mossman area, including Mt Lewis, in north Queensland.

During the course of this PhD I have been very fortunate to work in an exceptional research group, I have received support and encouragement from my friends and family, and had the privilege of working in the rainforests of Australia, China and Borneo, always with an excellent team of researchers who help each other out. There are many people who helped me in all stages of this research. My partner Paul always encouraged me and didn’t mind too much when I was in the bush for months at a time; thank you Paul for your patience and support. Thank you to my parents Geraldine and Bob Ashton who have always been behind me and my sister Siân who has always been positive and kind. I am grateful to Professor Roger Kitching, for running a first year field course in Borneo, in which I developed a passion for rainforest ecology and learnt how to be a natural historian. Roger has given me many opportunities to participate in international research projects, working with top ecologists in some of the most beautiful rainforest in the world, for which I am deeply grateful. Thank you to my supervisor Dr Chris Burwell, who gave me honest advice and in-depth feedback at all stages of my research. Thank you to my third supervisor James McBroom for statistical help and encouragement. I am grateful to Aki Nakamura, who ran the China trip, and who has helped me with statistics and writing, and is always fun to be around in the field. It has been a privilege to work with Bill McDonald, John Hunter and Stephanie Horton who identified trees on the Border Ranges and Mt Lewis plots, a huge amount of work they conducted in their own time, for which I am thankful. Thank you to Jude Buckman, who has edited my work, always in an encouraging and positive way.
John Grey assisted me in the field for 3, month long field sessions; thank you for being so generous with your time and your hard work, and for encouraging me to get a bike so I may be as fit as you when I’m 65.

The Mt Lewis section of this project would not have been possible without Sarah Maunsell, Casey Hall and Christy Harvey who were invaluable in the field and lab. I am very appreciative of all the help Kyran Staunton has given and for advice and encouragement, and help with the Mt Lewis transect. The Queensland Museum was also generous in enabling me to access its collections.

This project has been kindly supported by Griffith School of Environment, The Environmental Futures Centre, Queensland-Chinese Academy of Science Biotechnology Funding and Conservation Volunteers Australia. The Investigating Biodiversity of Soil and Canopy Arthropods (IBISCA) Queensland data incorporated into this study was supported by the State of Queensland for Smart State Funding, Griffith University, Queensland Museum, Global Canopy Programme, NRM Queensland (SEQ Catchments) and the Queensland National Parks Association.
Preface

Taxonomic support for selected insect groups was aided by Ted Edwards, at the Australian National Insect Collection (ANIC).

Several sections of this thesis have been published, or are in preparation for publication. Papers presented here are my original work, produced in collaboration with co-authors, who contributed to the papers presented here by (in some cases) editing, assisting in data collection and analysis. All co-authors are listed at the beginning of each Chapter.

Papers published during the course of this research higher degree


¹ These authors contributed equally.
Papers presented at conferences during the course of this research higher degree

Symposium presentations


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Chapter 1

Introduction

This dissertation describes studies carried out along altitudinal and latitudinal gradients within forests in Australia and Asia. A major group of herbivores, the moths, have been used to develop an understanding of the community dynamics of forest diversity and their responses, both spatial and temporal, to synoptic climate. This has been done against a background of anticipated anthropogenic climate change predicted to occur over the next several decades. In spite of this highly topical and apposite underpinning, this remains, nevertheless a study which attempts to measure and understand the way diversity changes in space and time. As such it shares relevance and theoretical underpinnings with other studies of spatial and temporal variation in ecological diversity whether driven by climate, vegetation, environmental degradation, or any of the other factors which produce environmental heterogeneity.

Understanding the driving forces that shape biodiversity is imperative if we are to make informed management decisions in a time of rapid ecological change. Much of the world’s biodiversity is held in tropical rainforests, which cover only 7% of the world’s land surface, and are estimated to hold half the world’s biodiversity (Myers 1984, Wilson 1988). Many tropical rainforests are at risk of rapid diversity loss, driven by anthropogenic forces including land clearing and climate change, which has lead to fragmentation and habitat loss (Mittermeier et al. 1998, Sodhi et al. 2010, Corlett 2012).

This thesis examines six altitudinal transects – three in eastern Queensland (Qld), Australia and three in Yunnan province, south-western China. In Australia, a permanent altitudinal transect was established in Lamington National Park (NP), south east Qld (data collected before the commencement of this PhD, by Prof. Roger Kitching and Louise Ashton as part of the IBISCA-Qld project – see below). We then established an analogous altitudinal transect
in the same bioregion at Border Ranges NP, north-east New South Wales (NSW) (28.4°S), approximately 20 kilometres (km) from the Lamington transect. We established this transect in an area with many of the same characteristics as the Lamington transect, the key difference between the two being aspect – sites were placed on south-westerly facing slopes in Border Ranges NP, and north-easterly facing slopes in Lamington NP. Aspect is an important factor shaping plant community structure, especially in subtropical rainforests, as southerly slopes can receive less than 10 hours of sunlight in winter (Laidlaw et al. 2011). Through studying transects that are closely related geographically and with similar floristic and faunistic communities, we can investigate generality of altitudinal stratification in this region, and the importance of a key environmental factor - aspect.

Through establishing three permanent survey transects in China, and three in Australia, intercontinental comparisons can be made. There are several scales in which we can examine factors influencing the distribution of biota (in this instance, moths). Firstly, the local scale (e.g. each of our altitudinal gradients) is influenced by local environmental factors such as temperature, moisture and the effects of microhabitats. Secondly, at the regional scale (encompassed in our latitudinal gradients in Australia and China), where the patterns of diversity we find may also be influenced by regional climate and biogeographical history. Thirdly, we may be able to make statements about inter-continental variation in assemblage structure, and comment on how different forests types across these two continents shift with altitude.

The work reported here was carried out either consequential upon, or as an integral part, of two major larger projects.

*The IBISCA Queensland Project*

The IBISCA (Investigating the Biodiversity of Soil and Canopy Arthropods) Queensland Project was a collaborative, international project aimed at studying
the distributions of a range of arthropod groups along an altitudinal gradient. This gradient was located in continuous subtropical rainforest, at Lamington NP, south east Qld, Australia and the study was conducted between 2006 and 2008 (Kitching et al. 2011). Over 55 scientists from 14 countries participated, each contributing expertise in their specialised taxa. This study was predicated on the idea that adjacent altitudinal bands can be used as a surrogate for changes in climate; along the altitudinal gradient, a 200 metres above sea level (m a.s.l.) increase in altitude corresponded to an average drop of 1.5°C (Strong et al. 2011). This project identified a ‘predictor set’ (Kitching et al. 2000) of different arthropods (including moths) that are sensitive to climate, and have the potential to be used to monitor distribution shifts with future climate warming.

Moths were a major target group during the IBISCA-Qld project, a total of 11 379 individual moths were sampled in two sampling seasons (October 2006 and March 2007). Assemblages of moths collected along the IBISCA-Qld transect showed strong altitudinal zonation (Ashton et al. 2011, see Appendix 1, page 272) and patterns of altitudinal zonation varied among different moth families (Ashton et al. In preparation). In addition, a predictor set of altitudinally restricted moth species was identified, for future monitoring of climate driven shifts in distribution. The question that arose from the IBISCA-Qld Project, and that has led to the development of the current research, is how do altitudinal patterns observed at the local scale (a single transect in subtropical rainforest at Lamington NP, Qld, Australia) vary across regions, forest types and biogeographic regions? Is the strong altitudinal stratification of moth assemblages observed in the subtropical rainforest in south-east Qld (Ashton et al 2011) the same at other latitudes in Australia? Are the local processes producing similarly stratified moth assemblages, or will regional factors produce different patterns?

Through examining altitudinal distributions of moth assemblages at different latitudes and forest types, we can put the Lamington results into a wider
context. This study aims to examine a series of moth assemblages across altitudinal and latitudinal gradients in order to examine patterns in diversity by examining rainforest moth assemblage structure at both the regional and local scales. We seek to establish comprehensive baseline distribution data, across multiple altitudinal gradients. Additionally, we will identify predictor sets of species for each location, which are altitudinally restricted and can be used to monitor future distribution shifts.

The Mt Lewis Transect

In addition to the work carried out as part of these two major projects an additional tropical transect was established at Mt Lewis in far northern Queensland. Our tropical Australian altitudinal transect is located at Mount Lewis National Park (NP)(16.3º S), in the Wet Tropics of north Qld. Our sites coincided with those in use by Professor Stephen Williams and his group from James Cook University (Williams et al. 2003). This transect allowed us to investigate the distributions of plants and herbivores in a tropical forest, again expanding on the generality of the Lamington results, in an area with a different biogeographical history, at a different latitude and with a warmer climate. Aspect may not be an important factor closer to the equator, as both north and south facing slopes will receive similar amounts of sunlight.

QCAS – Queensland/Chinese Academy of Science Joint Biotechnology Project

Asian rainforests are under threat, covering a smaller land surface than African and Neotropical rainforests, while at the same time being cleared at a higher rate (Laurance 1999). China, with one of the largest populations in the world, has a suite of environmental issues associated with its rapid development and large population, including pollution, deforestation and species loss (Liu and Diamond 2005). Throughout the duration of this research, we have had the opportunity to collaborate with the Chinese Academy of Sciences, exploring the biodiversity of arthropods across three altitudinal gradients located at different
latitudes within Yunnan Province in south-western China. Very little work on the life history, ecology and distributions of forest arthropods has been carried out in China. Our research in Yunnan, China, is a continuation of the IBISCA-Qld project, and the additional Australian altitudinal study sites established since. Fieldwork was carried out in July 2011 at Ailao Shan (subtropical rainforest – 24.5°N), July 2012 at Mengla (tropical rainforest – 21.5°N), and August 2013 at Lijiang (sub-alpine temperate forest - 27°N).

Aims of research

Collecting extensive data of a key herbivore group across environmental gradients will allow us to explore ecological themes including distributions of species richness and beta diversity (across latitude and altitude), the vertical stratification of assemblages (across latitude and altitude), the relationship between herbivores and vegetation assemblages across gradients, and to what extent these ecological patterns differ for families within the Lepidoptera with contrasting life histories.

Over the course of the next century climate change may well exceed the resilience of many species to adapt in situ. This study establishes baseline data for three altitudinal transects along the eastern coast of Australia, and an analogous set of altitudinal transects in mainland China, which can be used in future studies to document shifts in the moth fauna. Macrolepidoptera have been collected, identified and analysed in order to identify species that are most sensitive to altitudinal change. Potentially useful species for monitoring distribution shifts will be proposed.

The aims of this PhD research are to:

(i) Assess the richness and assemblage structure of moths along a series of altitudinal gradients within rainforest, along the east coast of Australia.
(2) Examine the differences in assemblage turnover at different taxonomic resolutions across altitude and latitude.

(3) Investigate the vertical stratification of moth species richness and assemblage structure, across altitude, latitude and forest type.

(4) Examine and compare the patterns of altitudinal and latitudinal shift in moth assemblages in Australia with those found in mainland China.

(5) Identify which species are most important in driving altitudinal and latitudinal changes in assemblage structure and which may be useful as indicator species for monitoring distribution shifts in Australia and China.

**Structure of thesis**

This thesis aims to analyse the distribution of moths across these different ecological gradients. This research has involved extensive field and laboratory work, collecting and identifying many thousands of moth specimens and species, in different forest types and climate, across altitude and latitude, and on different continents. To achieve this aim this dissertation will employ the following structure, in the format of a series of scientific papers:

Chapter 1 – A general introduction gives the background, justification and major aims of this research.

Chapter 2 – This provides an overview of the ecological theory, and relevant literature associated with the study of diversity across gradients.

Chapter 3 – “Altitudinal stratification of macrolepidoptera diversity change with latitude”, focuses on the patterns of turnover with altitude found in
subtropical and tropical Australian rainforest. Vegetation shifts across altitude are also examined, as a major biotic factor determining the distribution of moth assemblages.

Chapter 4 – “Rainforest moths and altitude: family to family differences in subtropical rainforests”, investigates family and sub-family patterns of moth diversity across several altitudinal gradients. The results describe differences between the observed patterns of family and sub-family differences, which are then put into the context of life history information. Moth families that are sensitive to altitude and can be targeted for future monitoring of climate change shifts are discussed.

Chapter 5 – “Vertical stratification of rainforest moths across altitude, latitude and continents”, examines the degree to which moth assemblages are compartmentalised vertically. This chapter addresses the following questions: (1) Are night-flying Lepidoptera vertically stratified at the assemblage level across forest types, and are there altitudinal or latitudinal patterns in vertical stratification? And (2) is the canopy more species rich than the understory and does this change with increasing altitude or latitude? Life history information, where available, is examined in order to investigate these hypotheses. This chapter incorporates data collected by Professor Roger Kitching in Panama, Brunei, Vietnam and Papua New Guinea, and data collected at Atherton, north Queensland by Louise Ashton. These data sets were collected using identical methods to those employed in the altitudinal gradient studies, and add extra power to our analyses of vertical stratification.

Chapter 6 – “Climate change monitoring in a beta diversity ‘hot spot’: a predictor set of altitudinally restricted moth species in tropical, sub-tropical and sub-alpine ecosystems, south-west China”, incorporates data collected across three altitudinal transects in tropical, subtropical and temperate forests, in Yunnan, China. Overall assemblage patterns from the three forest types are
compared, and from these baseline data sets, three sets of indicator species are identified, for monitoring of future distribution shifts.

Chapter 7 – Provides a synthesis of the research presented here and covers a wide range of different ecological questions concerning distributions of night-flying Lepidoptera. This chapter synthesises and evaluates the main findings of the research. Limitations of this research are explored and future directions for research are suggested.

References


Chapter 2
Theoretical background and literature review

Diversity

There are many definitions of ‘biodiversity’. Usually it refers to the variability within and between species and ecosystems (Magurran 2004). Hubbell uses a narrower definition of biodiversity “synonymous with species richness and relative species abundance in space and time. Species richness is the total number of species in a defined space at a given time, and relative species abundance refers to their commonness or rarity” (Hubbell 2001, p.3). Throughout this thesis, I will use Hubbell’s definitions of biodiversity based on richness and abundance. Alpha, beta and gamma diversity are terms that have been used in ecology to describe or characterise different scales of diversity (Whittaker 1960, Magurran 2004). However there has not been consistent usages of these terms in the ecological literature (Tuomisto 2010a). Throughout this thesis I will use the following definitions proposed by Tuomisto (2010a, b). Alpha diversity refers to the number of species in a particular sampling location or site; beta diversity, the number of species across a suite of sampling locations; and gamma diversity, the total number of species in a particular geographical area.

How many species of insects?

The diversity of life on earth is dominated by invertebrates, which make up an estimated 80% of the total number of described metazoan species (Fig. 2.1). E.O. Wilson (1987) referred to invertebrates as “the little things that run the world”; they are key drivers of ecosystem processes such as herbivory, decomposition and pollination. The large majority of terrestrial invertebrate diversity occurs in the tropics (Wilson 1992, Scheffers et al. 2012) and much of that occurs in the canopy (Stork et al. 1997). Insects are the most diverse invertebrate group with approximately 1.5 million species described (Fig.2.1).
Extrapolating from the number of beetle species found on twelve individual trees (*Luehea seemannii*) in Panama, Erwin (1982) estimated that there could be upwards of 30 million arthropod species worldwide, based on assumptions about species turnover, host specificity and the number of species in the canopy. Subsequent estimates have been considerably lower, between 2 and 10 million species, primarily due to evidence of much lower levels of host specificity, lower richness in the canopy, and lower turnover in beta diversity than first assumed (Gaston 1991, Stork 1993, Ødegaard 2000, Novotny et al. 2002, Hamilton et al. 2010, Basset et al. 2012).

In addition to insects contributing more than any other group to global diversity, they also make up much of the animal biomass on earth. Groups such as ants, termites and Collembola are hugely abundant, and have significant impact in shaping ecosystems. For example, insects are the most important herbivore group, consuming up to 25% of tropical rainforest foliage (Janzen 1981).

![Figure 2.1 Estimated number of described species of metazoans (image taken from Collen et al. 2012, Scheffers et al. 2012).](image)
Why are there so many species of insect?

Insect life has been highly successful and there have been several hypotheses as to why the insects have flourished. Fossil records suggest that speciation rates for insects have been higher than other terrestrial animals (Grimaldi and Engel 2005). Fossil evidence also suggests insects evolved during the Silurian period, 400 million years ago (mya), giving them plenty of time to speciate (Grimaldi and Engel 2005). Insects were amongst the first terrestrial animals and became highly successful as phytophages and pollinators, with many radiations linked to radiations in plants, especially their co-evolution with angiosperms (Grimaldi and Engel 2005). Insect physiology may be a driving factor in the success of insects. Insects are small, which has been suggested as a mechanism enabling partitioning into smaller niche space, allowing for higher levels of specialized host utilisation and resulting in greater levels of allopatric divergence (Strong et al. 1984). Many insects can fly, and so disperse successfully. Jointed arthropod exoskeletons provide strength and protect against desiccation (Grimaldi and Engel 2005). Serial appendages and metamerism allowed for highly specialized body parts. Additionally, the development of complete metamorphosis allowed for diapause, contributing to the utilization of a wide range of resources and domination of more extreme environments (Kukalova-Peck 1978). Insects have been able to dominate life on earth, through exhibiting a huge array of life history strategies including herbivory, predation, parasitism and decomposition. Short generation times, reproductive capacity and population numbers of insects may result in greater genetic variation, leading to high rates of speciation (Grimaldi and Engel 2005). Finally, based on fossil evidence, rates of extinction in insects appear to be lower than in other animals – many of the insect orders that arose in the Silurian are still extant today (Grimaldi and Engel 2005). These hypotheses are not mutually exclusive, and the hyper-diversity of insects is probably due to a combination of these factors.
Diversity across gradients – major ecological theories to explain observed patterns in diversity

Identifying the driving forces shaping diversity is a major theme in ecology (Hutchinson 1959) and is particularly significant in the context of climate change (Gaston 2000). Climatic gradients have commonly been used as an explanation for observed gradients in species diversity (Forster 1778, Wallace 1878). There is a complex set of literature demonstrating support for climate as a major factor shaping diversity, as well as a suite of other variables that change across climatic gradients, including biotic interactions, productivity and restricted geographic areas such as mountain tops (Pianka 1966). This thesis will explore ecological phenomena including the altitudinal and latitudinal patterns of community structure and vertical stratification. Here I give a brief overview of the relevant ecological theory related to studying distributions of insects across environmental gradients.

Altitudinal and latitudinal gradients

Latitudinal gradients in diversity are ubiquitous, and were first observed in 1799 when Alexander von Humboldt described patterns of diversity in plants across a South American latitudinal gradient (Hawkins 2001). There is a general trend, in a wide spectrum of organisms, for species richness to be highest at the equator and decrease towards the poles (Fischer 1960, Rosenzweig 1995). Theories to explain this gradient in diversity use a variety of explanatory factors including temperature, humidity and the pole-ward decrease in energy, water, environmental stability, and biome size and diversity. There is, however, little agreement (Hillebrand 2004). The only universal element that has been shown to shift predictably with latitude is solar radiation (Rohde 1992). Other explanations such as competition, predation, niche space, stability and productivity have produced mixed results, which appear to be influenced by the scale of each study (local, regional, landscape) and the body size and trophic level of the study organism (Hillebrand 2004).
Altitudinal gradients are excellent study systems for ecology, containing steep shifts in biotic and abiotic factors in a small geographic area (Hodkinson 2005). They have been used to study the driving forces and mechanisms that underlie patterns in diversity and community structure (Gagne 1979, Hebert 1980, Lieberman et al. 1996, Bravo et al. 2008). It has been theorised, and there is some empirical evidence, that the harsher environmental challenges presented at higher altitudes represent limiting factors in the distribution of species and, at lower altitudes, interactions among species become the most important factors shaping community assembly (Hoiss et al. 2012). The altitudinal stratification of species and assemblages is well documented but patterns vary between taxonomic groups, and the inter-correlation of factors across altitude reduces our ability to make statements of causality (Fischer et al. 2011).

**Patterns of richness across altitude**

Studies of species richness of insects along altitudinal gradients have largely demonstrated two patterns, a linear decline in richness with increasing altitude or a peak in richness at mid-elevations (Hagvar 1976, Janzen et al. 1976, Hebert 1980, Rahbek 1995). There are many factors that may drive patterns of insect richness across altitude, such as the season (Beck et al. 2010), plant assemblage structure, moisture and temperature. It has been suggested that mid-elevations are the most equable in terms of environmental conditions and plant resources, which would tend to produce mid-altitude peaks in diversity. Mid-altitude peaks in diversity are also predicted if they are areas of overlapping zonal habitats (or ecotones) (Lomolino 2008). Linear declines could occur as a result of the temperature lapse rate acting as a limiting factor or through increased primary productivity at lower elevations (Rahbek 1995). The species-area effect may also produce linear declines in richness, driven by decreasing available habitat with increasing altitude. A study by Nogués-Bravo et al. (2008) showed that larger-scale altitudinal gradients produced unimodal-shaped results, whilst small-scale gradients produced monotonic declines. A
controversial theory is the “mid domain effect” – a model that suggests that when random shuffling of species within a homogenous habitat occurs, species’ distributions overlap more in the centre, creating a mid-habitat peak in species richness. Mid-domain effect as a null model has been criticized for ignoring the gradients that are required to produce the range size distributions, and the absence of ecological or evolutionary processes (Hawkins et al. 2005).

*Environmental heterogeneity*

Habitat heterogeneity can be higher in the tropics than in temperate areas, which may produce a latitudinal gradient in diversity (Ricklefs 1977). Niche partitioning and structural complexity are fundamental ecological theories which have been hypothesised to explain diversity patterns across gradients. Many studies have shown positive relationships between habitat heterogeneity and diversity (Tews et al. 2004) including in birds (Poulsen 2002, Van Rensburg et al. 2002), mammals (Ecke et al. 2002, Williams et al. 2002) and, to a lesser extent, arthropods (Strong Jr and Levin 1979, Hill et al. 1995, Haslett 1997). In the case of high altitude tropical forests, they tend to be structurally simpler and less diverse, with shorter trees, which are often floristically distinct from lowland forests (Grubb et al. 1963, Gentry et al. 1995). The available niche space in high altitude forest can therefore be predicted to be lower than in the more complex lowland forests. Similarly, the structure and diversity of tropical forest is famously complex with steep vertical stratification of environmental microhabitats, from the understory to the canopy, whereas temperate forests tend to be dominated by a few species, and have less complexity in the vertical dimension (Basset 2001b).

*Niche partitioning and competition*

Competition has been suggested as an important driver of community structure (Hutchinson 1978), yet there remains substantial debate on its relative importance (Rosindell et al. 2012). Dobzhansky (1950) hypothesised
that competition was a highly important factor shaping communities, especially in tropical areas where other environmental constraints may not be limiting. It has been proposed that gradients of diversity may, in fact, be reflections of gradients in competition, with smaller niche space and greater niche partitioning in areas of high diversity (Macarthur 1965, 1969). Species in more stable environments in tropical and lowland areas may not be limited by environmental factors, and competition may play a much greater role. The importance of competition in shaping assemblages, however, has been hotly debated, especially in relation to arthropods. For example, Janzen (1973), suggested competition on a single host plant is a major factor shaping community structure. Lawton and Strong (1981), however, argued that many studies do not take account of the other driving forces that shape communities, such as biogeographical theory and the species-area relationship. Novotny et al. (2006), compared phylogenetically related trees in the tropics and temperate zones, and found no difference in the diversity or host specificity of folivorous insects per host plant. This result suggests that greater niche partitioning may not be a driving force for the higher diversity of insect herbivores in the tropics, and it may be more likely that the greater diversity of insects found in the tropics is directly related to the greater diversity of plants. Novotny’s results are concordant with those of Fiedler (1998), who found no difference between tropical and temperate diet specialisation of butterflies.

**Predation and herbivory**

A complementary idea to the competition hypothesis is the predation hypothesis, which proposes predation and parasitism are driving forces shaping community assembly, which in turn, produces lower levels of competition. Paine (1966) found that in marine intertidal organisms, predators maintain high diversity through suppressing the dominance of any one species. Herbivory is also an important force in shaping community assembly. Ants are a key insect predator in rainforests (Novotny et al. 1999, Floren et al. 2002). Several studies have found evidence that there are high rates of herbivory on
vegetation in the tropics (Sih et al. 1985, Novotny et al. 2006), particularly driven by large densities of ants (Jeanne 1979).

**Productivity**

Darwin (1872) suggested higher plant diversity would result in higher primary productivity, which has been supported with empirical evidence in some ecosystems (Tilman 1999). There has been a range of research investigating rates of primary productivity in the tropics versus temperate zone, as a driving force behind the latitudinal diversity gradient (MacArthur 1969). Connell and Orias (1964) used modelling to demonstrate that greater environmental stability leads to greater productivity, which in turn results in higher diversity. There is still major debate on whether productivity really does create greater diversity, and whether productivity really is higher in the tropics. Singh and Misra (1969) demonstrated that diversity was correlated with higher productivity in grasslands, however McNaughton (1968) found no such relationship between productivity and diversity. In a systematic review Waide et al. (1999) found that there were four main patterns relating to species richness and productivity in the literature; humped shaped (or unimodal), a linear decline, a linear increase or no trend. A meta analysis by Mittelbach et al. (2001) found that the relationship is usually unimodal, however there was no strong latitudinal pattern in the relationship, which may be scale dependent. Latitudinally, there may be differences in the productivity–diversity relationship, which has been shown to be positive in temperate zones, and unimodal in the tropics (Meelis et al. 2007). Meelis et al. (2007) suggested this pattern is driven by different evolutionary histories, as the temperate zone has had lower primary productivity for longer throughout its history, which has led to low speciation and low diversity. It may be challenging to produce evidence for a causal effect, if productivity produces higher richness, or if higher richness produces greater productivity, due to the circular nature of the productivity-diversity logic.
Species-area relationship

The species-area relationship describes the pattern of increasing area producing increasing richness, at a rate that eventually reaches asymptote in large areas (Lomolino 2008). It has been suggested that the species-area relationship (Connor et al. 1979) is one of the only ‘laws’ of ecology (Lomolino 2001), and is an important factor shaping distributions of diversity across altitudinal gradients. This pattern is well established and has been demonstrated in a range of ecosystems, and has led to the development of island biogeography theory (MacArthur and Wilson 1967). Large areas at the base of mountains support more diversity than small areas at the tops of mountains. Larger lower elevation areas capture greater resources, population sizes and habitat heterogeneity (Lomolino 2008). The species-area relationship can be seen as simply heuristic, but in small habitat patches, such as mountain tops and small islands, the association may be more complex, as the slope of the species-area relationship is greater for smaller areas, and therefore species richness may increase even with altitude (Lomolino 2008) . The species-area hypothesis has been demonstrated in hundreds of papers, and may be a simple way of explaining patterns of diversity, however, it does not incorporate other factors that shift along area gradients (Hodkinson 2005) including abiotic factors, pest pressure (Baltzer and Davies 2012) , competition and niche space (Connor et al. 1979).

Stability

Stability can refer to climatic stability or stability in a number of biotic factors such as primary production and biomass. Pimm (1984) suggested that relationships between diversity and stability can also include stability in abundances and resilience of populations. In terms of climate, stability theory suggests that because the tropiesent a more constant environment, with low seasonal variation, species are able to exploit finer niche space than in more extreme environments (MacArthur 1969). There have been a series of papers
that support this theory (Kushlan 1976, Zaret 1982, Givnish 2001) including a long term experimental study in grasslands by (Tilman 1996) who showed strong evidence for stability in more diverse communities. Longer growing seasons in the more climatically stable tropics may directly result in greater niche partitioning through time, for example, insect herbivores reaching their peak abundances at different times, with greater lengths of time in which conditions are appropriate. Doak et al. (1998) found that there is a probabilistic statistical relationship between stability and diversity associated with fluctuations in species’ abundances, without accounting for ecological interactions. Conversely, May (2001) used modelling to demonstrate that higher diversity produces lower stability. In addition, there have been several examples which have shown an inverse relationship between stability and diversity (McNaughton 1968).

**Biogeographical History**

In addition to contemporary factors (including environmental factors and inter-, intra-specific interactions), patterns of diversity will also be strongly influenced by historical and phylogenetic factors. Ecosystems which are older, and have been isolated from disturbance for a longer period may support higher diversity, if diversity is driven by long-term geographical and evolutionary patterns (Latham and Ricklefs 1993). The effective evolutionary time hypothesis (Rohde 1992), looks to historical factors and suggests that higher rates of speciation have occurred in the tropics, driven by higher energy availability, and more stable environments throughout evolutionary time (Gaston and Williams 1996, Jansson 2002, Jansson and Mats 2002). This theory in the context of gradients of diversity suggests that areas at higher altitudes and latitudes have been more disturbed by historical climate events (such as glaciations) than low altitudes and latitudes. Running counter to this, Simpson (1964) suggested that temperate zones have existed as long as tropical areas, and that there is little evidence that more recently glaciated areas have lower diversity. In addition, Sax (2008) showed that explanations which employ
differences in speciation rates or geological history between the tropics and temperate zones can be nullified by examining biogeographical patterns of introduced species, which show similar distribution patterns to the native species, and have not been influenced by these historical factors or speciation rates.

**Beta diversity**

Beta diversity (the variation of community composition between sites) of tropical rainforest has long been regarded as very high, however there has been wide debate on whether there actually is high turnover in beta diversity in low altitudes and latitudes. A pattern of high turnover of beta diversity has been shown for tropical species of plants and insects (Kitching et al. 2013, Condon et al. 2008, Beck and Chey 2007, Ødegaard 2006, Erwin 1991, Erwin 1982). Sampling along environmentally heterogeneous gradients or at large spatial scales, will produce higher estimations of beta-diversity. Additionally, undersampling assemblages will also result in overestimations of beta diversity (Tuomisto 2010a), which may be a significant issue for studies of hyper-diverse rainforest arthropods. The observed pattern of high beta diversity in tropical rainforest has long been considered a rule in ecology, however a landscape scale study by Novotny et al. (2007) found low levels of beta diversity in tropical insect herbivores, with little turnover in assemblages across distance in Papua New Guinea, a result that was also found in the lowland tropical rainforest of Panama by Basset et al. (2012). Environmental homogeneity is likely a major factor producing low turnover and the spatial scale and the target taxa of these studies may be an important factor in shaping the results (Kitching 2013). Condit et al. (2002) examined tropical tree species and found high turnover in the environmentally heterogenous landscape of Panama, but low turnover in the more homogenous lowland in Ecuador and Peru, concordant with Pitman et al. (1999) who also found low turnover in Peru. Other responses to this debate have shown energy availability (measured as
potential evapotransporation) may be the major factor driving patterns of beta diversity (Qian and Xiao 2012).

Kraft et al. (2011) suggest that the high turnover in beta diversity reported by some studies at lowland and low latitude sites may be an artefact of the locally available species pool (gamma diversity) and other ecological explanations of differences in beta diversity across gradients may not be necessary. In two separate responses Tuomisto and Ruokolainen (2012) and Qian et al. (2012) both questioned the appropriateness of the sampling and the analysis used by Kraft et al (2011) showing that the conclusions were not useful in understanding the drivers of beta diversity.

Beck et al. (2012) attempted to overcome any issues associated with sampling heterogeneous sites, or under-sampling of assemblages, by conducting extensive surveys of moths at different spatial scales. Their results showed strong evidence for turnover in assemblage composition in two different moth families, at the local, regional and landscape scales. One major difference that may be driving the different results found by these studies is the definition of what a ‘local’ sample is. Beck et al (2012) used ‘local’ to indicate an area (such as the radius of a mercury vapour light trap), whereas Novotny (2007) used trees belonging to a particular genera to examine local scales.

*Niche vs. neutral debate*

Relevant to the question of beta diversity turnover is deterministic versus stochastic explanations for distributions. This debate has centred around the neutral theory of community assembly, which employs random replacement as the major factor shaping diversity, and assumes equivalent levels of success and replacement among species (Hubbell 2001, Condit et al. 2002). Empirical evidence for and against the neutral theory has been developed, and in general, the neutral theory may be applied to stable and species-rich communities such as tropical rainforest trees (where the assumption of equivalence may be met).
A combination of niche and neutral theory can be employed, which incorporates both neutral process and niche differentiation as explanations for observed patterns of diversity at different scales. This was the case in Kitching et al. (2013) who found that turnover in beta diversity was apparent in primary rainforest moths, but not in logged-over forest, and both niche and neutral drivers may be acting at different scales.

**A combination of explanations**

A major issue with several of the hypotheses presented here is that there is high correlation between the major factors shaping diversity, which may be impossible to isolate. For example, primary productivity may be higher in the rainforest than the savannah, but there is also much greater habitat complexity, niche space, competition and climatic stability (Huston 1979). The suite of theories to explain gradients in diversity are not mutually exclusive; a synergistic approach, combining multiple explanations is probably necessary, as patterns of diversity may be driven by a combination of processes (Brown and Lomolino 1998).

Many of these theories are difficult to test and encompass a range of assumptions associated with each ecological theory, most significantly, the assumption of equilibrium, or ecosystem saturation, which has been shown to be inaccurate (Huston 1979). There is also significant difficulty in defining, measuring and comparing elements such as predation, competition, biogeographical history and niche space in real biological terms (Huston 1979). Despite extensive research into the subject of diversity across gradients, there is little agreement on the specific mechanisms driving latitudinal and altitudinal patterns of diversity (Ricklefs and Schluter 1993, Gaston 2000). Most studies that have sought to test one or more of these latitudinal hypotheses are based on higher-order animal or plant taxa, with a strong bias towards the northern hemisphere (Hillebrand 2004). There is still much to resolve in our
understanding of diversity. As a result, our understanding of the long-term impacts of human influence is also poorly defined.

_Climate change – current signals and predicted future impacts_

Over the course of the 20th century, climate change has encompassed a suite of environmental changes. Global average temperature has risen by 0.8ºC, atmospheric carbon dioxide has risen, the frequency of extreme heat waves has increased, sea ice has receded and global average sea level has increased by around 15 to 20 cm (IPCC 2007). Predictions of further climate warming of global average temperatures range between 1.4 and 5.8 ºC by the end of this century (IPCC 2007). Such rates of warming could well exceed the resilience and functioning of many ecosystems (The-World-Bank 2012).

Numerous studies on a wide range of taxa such as plants, insects, birds, mammals and fish have documented changes in species ranges, abundances and phenology, across terrestrial and marine ecosystems (Grabherr et al. 1994, Bale et al. 2002, Moller et al. 2004, Perry et al. 2005, Hickling et al. 2006, Parmesan 2006). Many groups have exhibited upwards shifts in distributions, including plants (Kullman 2001, Feeley et al. 2011), insects (Konvicka et al. 2003, Wilson et al. 2005) mammals, and birds (Hickling et al. 2006). Distributional shifts towards the poles have been documented in butterflies (Hill et al. 1999, Parmesan et al. 1999), birds (Thomas and Lennon 1999), fish (Perry et al. 2005) and insect herbivores (Bale et al. 2002). Such shifts may occur when species’ climatic envelopes (the limits of individual species’ tolerances of environmental variables such as precipitation and temperature), move as a result of changed environmental conditions (Kullman 2001, Walther et al. 2002, Battisti et al. 2006). Such poleward and upward shifts in distribution are only possible for those species with appropriate dispersal ability and only if suitable habitat is available for both colonisation and inter-site traversal.
The phenology, or timing of life history stages, which are driven by environmental cues, may be altered for individual species, which also affects the timing of interactions between species, such as between oak (*Quercus robur*) and winter moths (*Operophtera brumata*) (Visser and Holleman 2001) and between winter moths and the great tit (*Parus major*) (Visser et al. 1998). Plant life is predicted to elicit an array of climate driven signals, including phenological shifts as well as changes to growth rate, reproduction, photosynthesis and respiration.

Models based on the current distributions of species have demonstrated, under a range of scenarios, the expected future latitudinal and altitudinal shifts in a variety of taxa (Beaumont and Hughes 2002, Sekercioglu et al. 2008). Predictions about future shifts in distributions are often based on mapping ‘climatic envelopes’, and modelling shifts in these climatic zones. Other important factors that may have a profound impact on future distribution shifts are human disturbance and fragmentation of the landscape, isolating patches of habitat and thus inhibiting or even preventing dispersal, as well as interactions with other species, which will influence the actual distribution (Davis et al. 1998).

Climate change, over the course of the next century, will alter weather patterns (Pounds et al. 1999, IPCC 2007). Increased weather variability and extreme weather events (Easterling et al. 2000, IPCC 2001) are predicted to change ecosystem dynamics (Weltzin et al. 2003). These changes will result in a number of ‘winners’ - species that benefit from the changed conditions. However, species with low tolerances to climate change will be adversely affected, along with the suite of species interactions and ecosystem functions associated with them (McCarty 2001, Thomas et al. 2004). Climatic changes are predicted to be less severe in the tropics (Root et al. 2003, Deutsch et al. 2008), compared with the temperate zone, however, tropical species may be less tolerant of climatic change. For example, there is evidence that tropical species are less able to cope with warming possibly because they have evolved in
tropical environments with low temperature fluctuations (diurnally, seasonally and/or across years in recent historical time scales) (Janzen 1967, Addo-Bediako et al. 2000, Ghalambor et al. 2006, Dunn and Fitzpatrick 2012, Malhi 2012), which may lead to higher extinction rates in the tropics (Calosi et al. 2008, Tewksbury et al. 2008).

Mountains, distribution shifts and climate change

Mountain ecosystems, and their diversity, are under particular threat, as they are effectively climate islands, where shifting upwards or latitudinally with warming may not be possible (Foster 2001). The prediction for more frequent extreme weather events, such as heat waves, paints a grim picture for rainforest diversity; temperatures exceeding tropical species’ maximum thresholds may lead to shifts in distribution or, if this is not possible, local or complete extinction (Thomas et al. 2004). Such biological responses to climate change have already occurred in a variety of taxa and ecosystems (IPCC 2001, Walther et al. 2002, Parmesan and Yohe 2003). The precautionary principle demands that we minimise biodiversity loss for a myriad of reasons (Myers 1993), yet in the context of climate change and biodiversity loss, there are many unknowns. In a recent article in Nature by Barnosky et al. (2012), impending climate change impacts on biodiversity are described as “the perfect storm”: the combination of increased temperature, changes to precipitation and more extreme weather events, with the deepening problems associated with other human impacts, may lead to an irreversible state shift in the earth’s biosphere.

Climate change in an Australian context

Future effects of climate change will affect different parts of the globe in a wide range of ways. Average temperatures in Australia have increased by approximately 0.9°C since 1950, a higher figure than the average global temperature increase of 0.7°C (Braganza and Church 2011). Observed changes in climate in Australia have varied regionally, with eastern and south-western
Australia having experienced reduced rainfall, while north-west Australia has become wetter. Predicted changes to precipitation vary between a 60% increase to a 40% decrease in different parts of Australia (CSIRO 2001).

Many regions of Australia are predicted to become drier (Pittock and Wratt 2001). Predicted temperature increases are heavily influenced by estimations of emission levels over the next 60 years. Under a low-emissions scenario, Australian temperatures are expected to increase by 1 - 2.5°C, and by 2.2 - 5°C under a high emissions scenario (CSIRO 2007). Increased frequency and severity of extreme weather events are also predicted, such as the combination of increased temperature, drying and greater evaporation which will likely lead to increased fire risk, heat waves and flooding. Impacts of climate change in Australia are already apparent and include less extensive snow cover in the Snowy Mountains (Green and Pickering 2002), increased frequency, severity and extent of coral bleaching events along the Great Barrier Reef, Queensland (Brown 1996, Berkelmans et al. 2004), and substantial warming and increased salinity and acidification in the oceans around Australia (Braganza and Church 2011).

Climate change has been predicted to exacerbate environmental problems caused by human activity, such as soil loss, land salinization, habitat fragmentation and the impact of introduced plants and animals (Dukes and Mooney 1999, Pittock and Wratt 2001). Australian biota are predicted to suffer from significant range shifts, population declines and contraction, and extinctions, especially in areas with large numbers of regionally endemic species such as the Wet Tropics, the Great Barrier Reef and the eastern alpine areas (Hilbert et al. 2001, Pittock and Wratt 2001, Williams et al. 2003). Records and observations of changes to species’ distributions that have already occurred due to climate change in Australia are less numerous than those in the northern hemisphere because of a lack of historical data.
Climate change and insects

The historical and contemporary study of insects and their fossils has shown that insect lineages are highly successful, resilient and diverse. Although insects exhibit low extinction rates, probably due to the adaptive nature of the arthropod body plan (Grimaldi and Engel 2005), the observed and predicted rates of the current wave of climate change may be too rapid for adaptation. Worldwide climate change is expected to have a wide variety of impacts on insects through direct changes to temperatures, habitat availability and interspecific interactions (Thomas et al. 1999, Parmesan 2001, Axmacher et al. 2004, Menendez 2007). Documented shifts in distributions and abundances have been found in insects such as butterflies, beetles, moths and crickets (Parmesan 1996, Hill et al. 1999, Thomas et al. 2001, Hickling et al. 2006). There are also documented cases of extinctions in populations of butterflies (McLaughlin et al. 2002, Thomas et al. 2006) and predicted climate-driven shifts of inter-specific interactions, such as parasitoid-caterpillar interactions (Virtanen and Neuvonen 1999, Stiremann et al. 2005). Increased frequency of extreme weather events such as heat waves and drought will potentially have dramatic impacts on insect communities (Easterling et al. 2000, Rosenzweig et al. 2001). Researchers are becoming increasingly aware that these extreme weather episodes are playing a major role in the shifting distribution and local extinction of some insects, through exceeding physiological tolerances, driving early emergences (before food resources are available) and mortality of host plants (Parmesan et al. 2000).

Phenological changes have also been demonstrated for many insect species in Europe and the Americas (Walther et al. 2002), such as altered diapause periods in British aphids (Woiwod and Harrington 1994). Of major concern for conservation and forestry are increases in populations of pests, such as defoliators, driven by warm winters (Parmesan et al. 2000) and the reduction in reproductive success of native or endangered species because of unsynchronized life history events. Species at the edges of their thermal
tolerances may be able to adapt to new conditions by increasing their development times, depending on their phenotypic plasticity (Honěk 1996).

Canopy ecosystems are expected to be heavily impacted by future climatic change. The canopy is the major interface between the atmosphere and the forest (Parker et al. 1992). Some rainforests canopies have been shown to have a high diversity of insects, and contain a large proportion of canopy specialists (Basset 2001a). Rainforest canopies have been called ‘the last frontier’ of biological research (Wilson 1992) and are understudied because of significant logistical problems in accessing the canopy. Climate change impacts on the canopy may be severe, as these ecosystems are strongly associated with a range of atmospheric conditions not apparent elsewhere in the forest, including higher UV, temperature and evapotranspiration. Any shifts in these conditions may have dramatic impacts on canopy assemblages (Nadkarni and Solano 2002).

Other than widespread climate change, the major threat to terrestrial arthropod diversity is land clearing for agriculture and timber, which affects 31% of listed threatened species on the International Union for Conservation of Nature (IUCN) red list (Gerlach et al. 2012). Other threats include fragmentation driven by development, introduced species, changes to fire regimes, pollution and mining. Climate change has been identified as having a direct impact on 12% of species on the IUCN red list however, the ‘real’ figure is probably much larger (Gerlach et al. 2012). There is a need therefore, to identify which species (on a red list or not) are sensitive to climate, collect baseline data on their current extent and monitor distributions through time.
In order to gain a better understanding of how insects may respond to shifts in climate, a useful approach in predicting the impacts of altered climatic conditions on insects is to examine how insects have responded to climate changes over historical and geological time (Elias 1994). Insects, even those with low dispersal ability, did shift their ranges during glacial and interglacial periods (Parmesan 2001). Distribution shifts associated with climatic change have been shown in fossils from the Pleistocene, including the dung beetle *Aphodius holderei* (Scarabaeidae), which shifted from Britain to the Mediterranean during glaciation events (Grimaldi and Engel, 2005).

Those insect species endemic to mountain tops, with low dispersal abilities are of clear conservation concern because rapid climate change will mean adaptation *in situ* or moving to new habitats, both of which are often beyond the capabilities or physiological tolerances of many high altitude species (Hill et al. 1999, McLaughlin et al. 2002, Hodkinson 2005). In addition, future dispersal of insect assemblages in response to climatic change will be compounded by habitat fragmentation and loss. High altitude areas such as the *Nothofagus* patches (‘cool temperate rainforest’) in Lamington NP, Qld, have supported cool-adapted species through past periods of climatic shifts. Looking back at the expansion and contraction of rainforests in Australia, and the associated insect fauna, it can be predicted that further shifts in climate may well have a similar effect (Schneider and Williams 2005). However, the rapidity of anthropogenically-induced climatic shifts will obviate the normal responses of ecosystems, especially those systems based on immobile or long-lived organisms, such as mature forests and coral reefs. Overcoming the difficulties of studying the complex patterns associated with sensitive high altitude systems is vital if measures to minimise loss of diversity are to be taken (Coope 1970, Lemdahl 2000, Alley et al. 2003).
The use of altitudinal gradients as study systems for understanding ecology and ecosystem function, especially in tropical biomes where current knowledge is limited, has become increasingly popular due to the inherent research opportunities they provide (Malhi et al. 2010). Altitudinal gradients can be seen as a kind of space-for-time substitution approach (Pickett 1989), where adjacent climatic envelopes can be used as a model of climate warming. A 3°C change in temperature is equivalent to a shift of 300-400km in latitude or 500m in altitude (Beaumont and Hughes 2002). In the last decade the examination of altitudinal gradients has increased markedly, containing as they do, many ecotones within a small geographical area (Hodkinson 2005). In addition to the predictive power of climatic gradients, it is important to establish baseline information on the current distributions of biota across gradients, in order to monitor future shifts.

Describing the distributions of taxa across climatic gradients like altitudinal or latitudinal transects, is a way of examining how they may respond to future changes in climate (Inouye et al. 2000, Progar and Schowalter 2002, Andrew and Hughes 2005, Botes et al. 2006). One of the major criticisms of altitudinal studies, however, is that environmental and biological factors are often intercorrelated. Conversely, these correlations give altitudinal gradient studies the potential to explore these physical and biological factors and make predictions about how they will change (Körner 2007). Another caveat to using altitudinal gradients as a proxy for climate change is that some species may adapt in situ, therefore we will not observe distribution changes in these species.

Altitudinal gradients are a powerful tool, especially in the tropics, where there is less understanding of ecosystem ecology and function (Malhi et al. 2010), however they require careful consideration of co-founding factors that could be influencing observed altitudinal patterns, such as human disturbance, drought and regional climatic variation (Körner 2007). Using mountains in the tropics
is an especially effective research tool as mountainous areas have high diversity (driven in part by the altitudinal turnover in climate), high levels of endemism, and high conservation value (Malhi et al. 2010). Of particular importance is that a unique insight into long-term ecological processes like community turnover and adaptation can be gained through examining responses to altitude, which would not be possible in a laboratory situation (Malhi et al. 2010).

*Abiotic shifts across altitudinal gradients*

A number of abiotic factors, such as temperature and precipitation, change consistently with altitude and these factors influence the altitudinal distribution of insects. Temperature decreases as elevation increases; average temperatures drop by about 1.5°C for every 200m increase in elevation (Jacobson 2005, Strong et al. 2011). This figure, of course, is a generalisation of actual lapse rates, which vary depending on the region and local conditions such as seasonality, diurnality, topography, aspect, precipitation and cloud level (Lookingbill and Urban 2003). Insects, almost certainly, will be strongly influenced by temperature, which can affect the distribution of both the insects themselves and their host plants.

Precipitation generally increases with altitude (Fowler et al. 1988). In addition, moisture levels are highest where the cloud cap persists due to horizontal precipitation through direct contact between cloud and soil or vegetation. Increasing temperatures are predicted to increase the altitude at which vapour condenses thereby increasing the average cloud cap altitude on mountain tops and dramatically altering moisture levels and thus drying cloud forests (Pounds et al. 1999, Still et al. 1999, Williams et al. 2003). Insects can be affected physically by precipitation, for example, through desiccation due to drought, or indirectly through the effects of moisture levels on host plants (Schulze et al. 2001). Variability of precipitation patterns has a direct impact on insect species abundance and reproductive success, with some species exhibiting greater
success with increased rainfall whilst others are more successful during dry periods (Speight et al. 1999).

Another important abiotic factor that changes with altitude is soil nitrogen (N), which is influenced by climate, microclimate and temperature, and is a major factor shaping the vegetation assemblages at high altitudes (Huber et al. 2011). Structure, primary productivity and diversity of vegetation generally decrease with increasing altitude. Vegetation changes across altitudes have been attributed to soil properties including higher pH, lower soil fertility and increased occurrence of water-logging (Bruijnzeel and Veneklaas 1998, Coley 1998) at higher altitudes. With increasing altitude, leaves become smaller and less nutritious which can be directly related to changes in soil, and in turn, can affect the distribution and diversity of insect herbivores (Bruijnzeel and Veneklaas 1998, Brehm et al. 2003). Additionally, abiotic factors such as lower soil fertility at higher altitudes, influences forest structure. In rainforest ecosystems, forest structure generally changes from lowland forest with a tall canopy, to montane communities with stunted growth, which has implications for the availability of structural niches for insect herbivores (Brehm et al. 2003).

Mountain systems – sensitive climate change indicators

Mountain systems are also highly vulnerable to the impacts of climate change (Nadkarni and Solano 2002), if they are viewed as climatic ‘islands’ with the lowland areas in between mountains acting against possible dispersal of high altitude-adapted species. Mountain tops often have a high proportion of endemic species and range-restricted species (McDonald and Cowling 1995, Williams et al. 2003), a pattern noted by Holloway (1982) for Lepidoptera, primarily driven by the lower dispersal abilities of montane species. Altitudinal shifts in distributions may occur through a process of upwards species’ invasion, resulting in a shrinking of high altitude assemblages as they are out-competed by species from lower altitudes (Foster 2001). The combination of potential stresses from climate change impacts will heavily influence cloud
forest moth assemblages in mountain systems. The ecotonal areas of transition between cloud forest and lower altitude assemblages are predicted to show the first responses to climate change. It is predicted that the effects of climate change will result in a severe decline in suitable habitat for many montane species, ultimately resulting in the extinction of species with poor dispersal abilities (Hilbert et al. 2001, Williams et al. 2003, Krockenberger et al. 2004, Thomas et al. 2004, Parmesan 2006). Distance, fragmentation and climatic conditions may inhibit the ability of some species to shift to new locations (Ohlemuller et al. 2006). The high level of endemism associated with the high altitude forest and the sensitivity of this cloud forest to changing climate therefore make the monitoring, protection and management of these areas a priority.

Altitudinal gradients are potentially very useful for monitoring the likely impacts of climate change over time, especially when biological and environmental data are collected at fixed altitudes (Hodkinson 2005, Shoo et al. 2006). Detailed assessments of assemblages at fixed altitudes will provide a powerful tool for monitoring the impacts of climate change if a baseline set of indicators is established. Long–term ecological monitoring programs, where indicators can be assessed at fixed sites, may provide a meaningful assessment of ecosystem changes (Havstad and Herrick 2003). Altitudinal gradients are very useful for such long-term studies because they can be used both to make predictions based on various climate change scenarios, and also to monitor actual responses to change over time (Shoo et al. 2006). One of the major biases in current research using altitudinal gradients has been the tendency to examine only northern hemisphere or tropical forest ecosystems (Gagne 1979, Wolda 1987, Hodkinson 2005). A complex and variable problem like climate change requires studies in other areas of the globe. Although moths have been shown to be ideal indicators of climate change (Chen et al. 2009, Ashton et al. 2011), very little work has been done in Australia on the biology, distribution and climate responses of this group (Common 1990). Monitoring and understanding the complexities of climate change requires large, long-term
data sets in addition to descriptive work on the current distributions of species and populations. Both of these approaches have their limitations. However, it would seem that the best way forward is to implement a combination of the two and encourage collaboration among ecologists, managers and modellers, in order to improve the ability to predict, monitor and assess the impacts of climate change (Hughes 2003).

*Lepidoptera as indicator species*

Indicators are species which can be used to characterize a habitat, and can then be used in conservation, management or monitoring of change. Indicator species have become a popular and necessary method of assessing disturbance or change through time, in manageable and affordable ways. If we are to take action to mitigate loss or change of biodiversity, there is a need for useful indicator species studies which are rigorous, repeatable and easy to use (Balmford et al. 2005). When establishing an indicator species, (or a ‘predictor set’ of multiple indicator species (Kitching et al. 2000), there are several criteria that should be met. Indicator species should be proposed with a clear objective, easy to sample, occur in large enough abundances to be reliably encountered, easy to identify, and sampling should be cost-effective (McGeogh 1998). In order to establish which species are sensitive to the variable in question, baseline surveys need first to be conducted and from that point the indicators can be targeted for sampling in the future, which should be a quicker and cheaper process. The identification of indicators should involve rigorous statistical tests, establishing robust relationships which are consistent through time and space (McGeogh 1998).

Lepidoptera are a useful taxon for the rapid categorisation and monitoring of change in habitats via repeated sampling of indicators within the overall assemblage (Holloway 1985, Scoble 1995, Holloway 1998). Lepidoptera are the largest group of phytophagous insects (Romoser and Stoffolano 1998) and are taxonomically the best known insect order, with an estimated 50 000 total
species worldwide (Gaston 1991), belonging to 120 families, the biggest groups being Noctuoidea, Pyraloidea and Geometroidea. Lepidoptera have been used as indicators in a range of different ecosystems such as rainforests, temperate forests and agricultural systems (Beccaloni and Gaston 1994, New 1997, Brown and Freitas 2000, Ricketts et al. 2001). Lepidoptera meet the indicator criteria mentioned above: that is, abundant species are easy to sample in large numbers using automated light traps which are cost effective and easy to use. Many Lepidoptera are easy to identify based on external characteristics. Species that should be avoided for selection are rare species and cryptic or hard to identify species (Kitching et al. 2000) such as those moths belonging to the Tortricidae and Phycitinae.

Insects are ectotherms, and may be particularly useful as indicators of climate change, as their phenological events are triggered by particular temperature and precipitation cues (Frith and Frith 1985, Speight et al. 1999, Beaumont and Hughes 2002). Lepidoptera are useful in the development of such tools because of their almost universally herbivorous life histories (Common 1990) which means they are generally sensitive to floristic change. Ecological sampling methods such as light traps, may contain various tourist taxa, which are not local to the sampling site, including the highly vagile Sphingidae and some Noctuidae (Chey et al. 1997), which disperse over large distances (Common 1990). This problem can be avoided by using other groups within the Lepidoptera which have lower dispersal abilities (Doak 2000) and therefore respond in a discriminating way to other variables such as temperature and host plants. Many groups within the Lepidoptera have very low dispersal ability or are flightless, a characteristic that increases with altitude (Roff 1990). Families, subfamilies and tribes within the Lepidoptera may exhibit different suitability as indicators. Geometridae, for example, generally have fine-grained distribution patterns and have been used as indicators across a variety of ecological gradients (Holloway 1985, Holloway et al. 1992, Scoble 1995, Intachat et al. 1997, Kitching et al. 2000, Beck et al. 2002), whereas Noctuidae have been shown to be poor indicators along altitudinal gradients, but have been shown
to be useful indicators of disturbances such as fragmentation (Kitching et al. 2000).

Apart from the benefit of identifying indicator species, historical baseline data sets have been useful for identifying change through time, such as latitudinal (Hill et al. 2002, Lenoir et al. 2008) and altitudinal shifts (Chen et al. 2009), shifts in body size distribution (Gilchrist et al. 2004), and other shifts in assemblage structure (Wilson et al. 2005, Moritz et al. 2008, Raxworthy et al. 2008, Chown and McGeogh 2011). Butterflies and large moths, by virtue of their high visibility and attractiveness, have been well studied by both professional and amateur entomologists. This has resulted in a wealth of long-term distribution data for butterflies and moths in Europe (Harrington et al. 1999). This data is invaluable, and has allowed for descriptive studies of changes in distributions and phenology, that would have otherwise been undocumented. These include increased range in the northern limits of European butterflies, as they shift polewards, driven by climate warming (Pollard et al. 1993, Hill et al. 1999, Crozier 2003, Battisti et al. 2005, Menendez et al. 2008).

The almost total absence of historical data in the southern hemisphere and the tropics requires us to develop baseline data now, and use different methodological approaches, such as altitude as a proxy for climate, and modelling of distribution shifts (under various climate scenarios) based on knowledge of current distributions (Pearson and Dawson 2003). A good example of this in the Australian context is Beaumont and Hughes (2002) use of BIOCLIM (Bioclimatic analysis and prediction system) (Busby 1991), in modelling distributional changes of 24 Australian butterfly species. Models showed that even under a conservative climate change scenario of 0.8 – 1.4°C of warming, 88% of Australian butterfly species would suffer range contractions (Beaumont and Hughes 2002). Moths have been less readily adopted for studies predicting the impacts of climate change as much less is known about individual species’ life histories. We have very little information on the current distribution of species, and sparse information on host plants for Australian
species. A better understanding of Lepidoptera is crucial, as they occupy a large proportion of ecological niche space and interact with the environment and with other species in a highly significant way (Common 1990, Scoble 1995).
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Chapter 3

Altitudinal patterns of moth diversity in tropical and subtropical Australia

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To be submitted to Diversity and Distributions
Abstract

A major theme in modern ecology is describing and understanding how organisms are distributed. We established a series of altitudinal gradients, in order to describe how the patterns of a hyper-diverse herbivore group (night-flying Lepidoptera) change with altitude, in subtropical and tropical rainforest. We established two altitudinal transects in subtropical rainforest within the same region - Lamington National Park in south-east Queensland (latitude ca 28.7°S) and Border Ranges National Park, in north-east New South Wales (latitude ca 29.7°S). Four replicate 20m x 20m plots in each of five altitudinal bands were established. We established an analogous altitudinal transect in tropical rainforest at Mt Lewis National Park, in north Queensland. (latitude ca 17.5°S). Moths were sampled with two modified Pennsylvania light traps at each plot (one in the canopy and one in the understory) and run for three nights. Sampling was conducted at the beginning and end of the wet season. A total of 69677 individual moths were recorded across the three altitudinal transects, belonging to 2304 species. The two altitudinal gradients in the same region showed identical patterns of turnover across altitude, with the most distinctive assemblage occurring at the highest altitude. Some species were found to occupy a lower altitudinal range at Border Ranges than at Lamington, possibly due to slightly cooler conditions, produced by a south-westerly aspect. Moth assemblages at our tropical location showed a similar response to altitude with a distinct high altitude assemblage above 1000m a.s.l. These results suggest ubiquitous altitudinal stratification in tropical and sub-tropical Australian rainforests. Predictor sets of altitudinally restricted indicator species are presented. These indicators may be used to monitor future shifts in distributions predicted to occur with further climate change.
Introduction

Understanding patterns of diversity and the factors that underlie community structure are some of the most challenging and important ecological problems (Gaston 2000), and are requisite to understanding future changes driven by climate change. Mountain ecosystems and altitudinal gradients are notable for their high level of diversity (Körner 2000) and have become a key tool for understanding the forces that shape the distributions of organisms, making predictions about future responses to climate change and observing shifts in altitudinal ranges (Shoo et al. 2006, Fischer et al. 2011). This study compares the altitudinal distributions of night-flying Lepidoptera across three altitudinal gradients, two in sub-tropical rainforest within the same region and which have been influenced by the same biogeographical and historical forces, and one altitudinal transect in the Wet Tropics of north Qld, a location with different climatic and biogeographical features.

Across altitudinal gradients, steep environmental shifts occur in small geographical distances. Altitudinal gradients encompass suites of predictable microclimatic changes, including decreasing temperature (approx 0.75°C drop for every 100m), and increasing moisture and wind speed with increasing altitude (Hodkinson 2005). Of particular importance to mountain rainforest ecosystems is the average level of the cloud cap, which greatly increases precipitation levels above the cloud base. Under a range of climate change scenarios, the average cloud base is predicted to rise (Still et al. 1999), which may dramatically affect ecosystems currently located at the border between the cloud base and drier, lower altitudes (Pounds et al. 1999).

Many groups of organisms exhibit altitudinal stratification, with some species occupying very small ranges, leading to a high turnover in assemblage structure across altitudes. On the other hand, species that are able to cope with a wide range of environmental conditions may occur across an entire altitudinal
gradient. Biotic interactions add another layer of complexity. For example, herbivore distributions will be driven both by environmental factors and the distributions of their host plants, as well as a suite of other biotic interactions such as predation, parasitism and competition (Merrill et al. 2008).

Insects may respond to altitude (and latitude), in a variety of ways. Such responses include changes in morphology such as body size (both positivity and negatively correlated with altitude in different taxonomic groups), behaviour, reproduction, abundance and distribution (Krasnov et al. 1996, Sota 1996, Smith et al. 2000, Hodkinson 2005).

Generally, studies have found stratification in insect assemblage composition across altitude, including studies conducted in Lamington NP which showed stratification in moths (Ashton et al. 2011), beetles (Ødegaard and Diserud 2011), ants (Burwell and Nakamura 2011) and Collembola (Greenslade and Kitching 2011, Maunsell et al. 2012). In other parts of the world, studies have found similar patterns of altitudinal stratification in moths, beetles, frogs, mammals and plants (Auerbach and Shmida 1993, Brehm and Fiedler 2003, Escobar et al. 2005, Hemp 2006). Conversely, some studies have found little evidence of altitudinal zonation including in plants (Auerbach and Shmida 1993, Lieberman et al. 1996a) and invertebrates (Olson 1994). Different taxonomic groups may respond in different ways to altitude (Stork and Brendell 1990, Ødegaard and Diserud 2011) (see Chapter 4 for differences among moth families). Many species may be restricted to high altitudes, and many are endemic (Kessler 2002, Szumik et al. 2012).

The relationship between species richness and altitude has also been shown to be variable. The two major patterns are linear declines (Hebert 1980), or unimodal (humped) shaped patterns in species richness (Beck and Chey 2008). There are several factors which may influence observed patterns in species richness, including the altitudinal range of the gradient, which often reflects the degree of disturbance in lowland areas due to human impact (these disturbed areas usually being avoided by researchers). In such cases, it is not possible to incorporate the
full range of altitudinal heights within an ecosystem, and sampling points have to be placed in locations where intact forest is available. The scale or resolution at which altitudinal studies are conducted (i.e. the distance between altitudinal bands), may also have a large impact on observed patterns, and can, in fact, produce completely different patterns of species richness (hump shaped or linear) (Rahbek 2005, Nogués-Bravo et al. 2008).

**Climate change and indicator species**

Climate change is driving a range of biological responses (Steffen et al. 2009) and is predicted to lead to a range of severe impacts including species extinction, range contraction and mismatched phenologies of interacting species (Hughes 2000, Williams et al. 2003). Recent climate change has driven upward altitudinal shifts in distributions, which have been recorded for plants, insects, mammals, birds, frogs and amphibians (Hughes 2000, Walther et al. 2002, Konvicka et al. 2003, Wilson et al. 2005, Kelly and Goulden 2008, Lenoir et al. 2008, Chen et al. 2009). Further upward shifts in distributions are predicted for terrestrial biota (Sekercioglu et al. 2008, Kreyling et al. 2010, Laurance et al. 2011). These predicted shifts are complicated by a suite of other biotic interactions, important among which is the distribution of host plants for insect herbivores, which may result in a mismatch between available suitable climatic zones and available food resources if plants and herbivores respond to climate change differentially (Merrill et al. 2008).

In Australia there is a conspicuous lack of data on the impacts of climate change on the biota, especially invertebrates, driven by a paucity of historical data. In order to understand how species are responding to climate change, and the complex array of biotic and abiotic factors and feedback loops that may be involved, we first need to establish baseline data of current distributions. Large-scale biodiversity assessments to document species’ distributions can then be complimented by the selection of predictor sets (Kitching et al. 2000) of species, those which are closely associated with climatic zones, which can be monitored
through time. Here, we expand on a previous study of moth assemblages in Lamington NP (Ashton et al. 2011), in which the altitudinal distributions of moths were documented, and a suite of indicator species were suggested. Following that study, we have established two further altitudinal transects, one in nearby sub-tropical rainforest and one in tropical rainforest.

By sampling along an altitudinal transect in Border Ranges NP, within the same bioregion as the Lamington NP transect, we can make comparisons of assemblages in relatively close proximity to each other, but which present key environmental differences – in this case, aspect. Aspect is an important factor determining the structure of plant communities, and by extension, their insect herbivores. Aspect is particularly important for the subtropical rainforests of NSW and south-east Qld, especially in winter, where a south-facing slope may receive less than 10 hours of sunlight in a day (Laidlaw et al. 2011). The importance of aspect is reduced in tropical rainforests closer to the equator, where south and north facing slopes receive a similar amount of daily sunlight. We anticipated that the moth fauna of the Border Ranges transect would be similar to that found along the Lamington NP transect (established during the Investigating the Biodiversity of Soil and Canopy Arthropods (IBISCA-Qld transect)). Consequently, this new transect should provide insight into the influence of local environmental conditions on moth assemblages.

Tropical rainforest presents a different suite of environmental drivers. Accordingly, the logical next step was to incorporate into our research an analogous altitudinal transect in the Wet Tropics of north Qld, to assess patterns of altitudinal stratification in an area with very different climate, weather patterns and biogeographical history. Here, we seek to investigate whether tropical rainforest moths respond to the changes in environmental conditions across altitudes in a similar way to sub-tropical assemblages. We hypothesise that the altitudinal stratification of moth assemblages in this tropical area will show strong turnover across altitudinal zones, as environmental factors that shift with altitude may be a major constraining factor on tropical species, given that
tropical species may be less able to cope with a wide range of temperature fluctuations (Addo-Bediako et al. 2000, Tewksbury et al. 2008)

Through examining the macro moth assemblages across these three altitudinal gradients, we seek to address the following hypotheses;

H₁ (1) altitudinal distributions of moth assemblages will be different at different latitudes, with higher alpha and beta diversity at lower latitudes.
H₁ (2) the altitudinal distributions tropical, sub-tropical and sub-alpine moth assemblages will be correlated with the altitudinal structure of vegetation assemblages.
H₁ (3) family-level composition of moth assemblages will shift with increasing latitude, in association with vegetation assemblage composition.”

Additionally, baseline data on the current distributions of rainforest moths will enable future monitoring of changes in distributions, and a predictor set of indicator species will be proposed for each altitudinal transect.

**Methods**

*Lamington (LAM) and Border Ranges (BR) National Parks*

The Gondwana Rainforest of Australia (formerly known as the Central Eastern Rainforest Reserves Australia), was originally listed as a UNESCO World Heritage Area in 1986, and then extended in 1994 to include areas of rainforest in southeast Qld. The world heritage area consists of over 50 properties, from Newcastle, NSW, north to Brisbane, Qld, and contains the largest area of sub-tropical rainforest in the world. The area was assigned world heritage value and listed “as an outstanding example representing major stages of the earth’s evolutionary history, as an outstanding example representing significant ongoing geological processes and biological evolution, and containing important and significant
habitats for the *in situ* conservation of biological diversity” (ICUN 1994). These rainforest sites are recognised for their unique examples of evolutionary history, containing floral and faunal lineages that date back to the Carboniferous Period (Keto and Scott 1986, ICUN 1994), particularly high-altitude patches of *Nothofagus* and other evolutionary conserved species which were present on the Pangaean and Gondwanan continents.

The Investigating Biodiversity of Soil and Canopy Arthropods (IBISCA) Queensland Project, was located in Lamington NP (latitude ca 28°13'S), and ran between 2006 and 2010 (see Chapter 1 and Appendix 1 for an overview of results). This project established 20 permanent 20 m x 20 m study plots, across five elevational bands – 300m, 500m, 700m, 900m and 1100m a.s.l. (Figure 3.2). The changes in vegetation along this altitudinal transect have been described by (Laidlaw et al. 2011). The vegetation type is classified as complex notophyll vine forest at the 300m - 900m a.s.l. plots, and simple notophyll fern forest at the 1100m a.s.l. plots. Plant assemblages are altitudinally stratified, and highly correlated with soil properties, temperature and moisture (Laidlaw et al. 2011). Plots in the 300m a.s.l. altitudinal band were dominated by *Cleistanthus cunninghamii*, *Argyroderodon trifoliolatum* and *Capparis arborea*. The most dominant species at 500m a.s.l. included *Argyroderodon trifoliolatum*, *Cleistanthus cunninghamii* and *Baloghia inophylla*. The plots at 700m a.s.l. were dominated by *Argyroderodon trifoliolatum* and *Baloghia inophylla*, and at 900m a.s.l. by *Cyathea leichhardtiana* and *Caldcluvia paniculosa*. Plots at 1100m a.s.l., were dominated by *Polyosma cunninghamii*, *Cyathea leichhardtiana* and *Nothofagus moorei* (Antarctic Beech).

The physical environment of the IBISCA-Qld transect in Lamington NP has been described by (Strong et al. 2011), incorporating data from Bureau of Meteorology weather stations, temperature data loggers (in the understory and the canopy), and soil analysis (conducted by Phosyn Analytical Pty Ltd). All plots were located on soils derived from Cainozoic igneous rock, with a north-easterly aspect (with the exception of 300m and some 500m a.s.l. plots, which had southerly aspects).
Moisture increases at higher altitudes, a factor that is influenced by slope, orographic moisture and aspect. At the higher altitudes, wind speed, relative humidity and radiation are higher, while temperature is lower and less variable. Average annual temperatures range between 17.5°C at 300m a.s.l. to 12.5°C at 1100m a.s.l., an average drop of 1.17°C per 200m. Soil variables change with increasing altitude, with higher soil pH and calcium at lower elevations, and greater levels of soil moisture, organic matter and nitrate at higher elevations, a pattern driven by temperature and precipitation (Strong et al. 2011). This region is subject to strong seasonality, with pronounced wet and dry seasons. Evapotranspiration peaks in December and is the lowest in June and July (Morand 1996). The cloud cap sits between 800m and 900m a.s.l., which can provide between 40% of the total annual precipitation, and up to 70% in dry months (Hutley et al. 1997, Balston and Turton 2007).

Figure 3.1 Map of the IBISCA-Qld altitudinal transect in Lamington NP, Qld, showing the locations of the 20 study plots, 4 in each of 5 elevational bands.

Border Ranges NP (latitude ca 28.7 ºS), part of the Gondwana Rainforests of Australia, was established in 1979 and covers 318 km². Border Ranges NP was logged between 1965 and 1975, and targeted species were primarily
Argyroderdon trifoliolatum, Geissois benthamii and Araucaria cunninghammi (Shugart et al. 1980). Experimental plots in the area showed average basal area and diversity of logged plots had returned to similar levels found in primary forest after 35 years (Smith and Nichols 2005, Smith et al. 2005). The three wettest months are January, February and March, with a pronounced dry season in July, August and September (NSW-National-Parks-and-Wildlife-Services 2012). Average annual rainfall is between 2500 and 4000mm, and soils are kraznozems or ferrosols (Isbell 2002). As in the Lamington NP transect, the cloud cap sits between 800m and 900m a.s.l., and regulates moisture above this level.

Ibutton® temperature data loggers were placed at head height on all plots, programmed to record temperature once per hour and run between April 2010 and January 2011, with some gaps (a total of 236 days). Frequency distributions of average temperatures at each altitude (Figure 3.2) illustrate the drop in temperature with increasing altitude. The lapse rate observed between 10.04.2010 and 16.01.2011 was 0.944°C per 200m. The slightly lower lapse rate observed at Border Ranges may be driven by a number of factors. The average temperature at the 300m a.s.l. plots at Border Ranges was 15.6°C, compared to 17.5 °C at Lamington. This may be due to some Border Ranges plots being located in areas of cool air drainage, and the actual elevations of plots at Lamington, which were at an average of 265m a.s.l. as this was the available forest. The 500m a.s.l. (15°C at BR and 15.7°C at LAM and 1100 m a.s.l. (12.1°C at BR and 12.4°C at LAM) plots at Lamington and Border Ranges had similar observed average temperatures, however the 700m a.s.l. (13.5°C at BR, 15.4°C at LAM) and 900m a.s.l. (12.4°C a at BR and 14.2°C at LAM) were cooler at Border Ranges,
The altitudinal gradient at Border Ranges NP has the same design as the Lamington gradient, with 5 altitudinal bands (300m, 500m, 700m, 900m and 1100m a.s.l.) of 4 plots, with plots within each band separated by at least 400m (Figure 3.3). Where possible, all plots were located at least 100m away from watercourses, to avoid the compounding factors associated with the microhabitat conditions of cold drainage (and aquatic insects) and with south-westerly facing aspects. There is approximately 20km of continuous subtropical rainforest between the Border Ranges and Lamington transects.

Botanical surveys on the Border Ranges 20m x 20m plots were conducted by John Hunter, Stephanie Horton and Bill McDonald. All trees with a dbh greater than 5 cm were permanently tagged and identified. At the 300m a.s.l. plots, dominant tree species included *Archontophoenix cunninghamiana* and *Diospyros pentamera*, at 500m a.s.l. the flora was dominated by *Archontophoenix cunninghamiana*, *Argyroderondron trifoliatum* and *Eupomatia laurina*. At 700m a.s.l., the plots were dominated by *Sloanea australis*, *Atractocarpus benthamianus* and *Argyroderondron trifoliatum*, and at 900m a.s.l. by *Cyathea leichhardtiana*, *Caldcluvia paniculosa* and *Sloanea australis*. At the highest altitude plots, 1100m...
a.s.l., *Nothofagus moorei* is present at plot (a), and the other plots are dominated by *Atractocarpus benthamianus*, *Polyosma cunninghamii* and *Doryphora sassafras*. The low to mid altitudes of the transect are located within complex notophyll vine forest (Webb and Tracey 1978).

![Figure 3.3 Map of Border Ranges National Park transect showing the location of plots within five elevations bands; 300, 500, 700, 900 and 1100m a.s.l.](image)

*Mt Lewis National Park (ML)*

The Australian Wet Tropics World Heritage Area (WTWHA) is the largest area of rainforest in Australia, covering 2 million hectares, and was made a World Heritage Area in 1988. The Wet Tropics contains a high proportion of Australia’s flora and fauna, and a high proportion of endemic species (Stork et al. 2008). WTWHA is made up of a series of fragmented patches of rainforests ranging in latitude from 15° 30’ S to 19° 25’ S, and is home to a number of vulnerable and endemic species particularly susceptible to climate change (Williams et al. 2003). These patches are mainly in montane areas, approximately one third are above 600m a.s.l., as most of the lowland tropical rainforest has been cleared. Mt Lewis NP (latitude ca 17.5°S), is located 80kms north of Cairns, and protects areas of both primary and logged highland rainforest. The area was declared a National Park in December 2009, (combining it with Riflemead Forest Reserve) to become
Mt Lewis National Park, encompassing a total area of 229km². This area contains a number of endangered vertebrate species, many of which have undergone documented declines linked to climate change (Williams et al. 2003). The forest shifts from warm tropical rainforest to cloud forest at the higher altitudes, starting at around 900m a.s.l. This shift, driven by direct orographic precipitation from the cloud cap and cooler temperatures, is characterised by lower diversity, tree height, and leaf size (DERM 2010).

Figure 3.4 Map of Mt Lewis National Park transect, which is divided into five altitudinal bands (400m, 600m, 800m, 1000m and 1200m a.s.l.)

A pre-existing altitudinal transect, established by researchers from James Cook University has been used in a modified fashion for this study. The transect runs from 400m to 1200m a.s.l. The 600m, 800m, 1000m and 1200m a.s.l. plots are along the 28km long Mt Lewis Road, while the lowest plots, at 400m a.s.l., are located further down the range and are accessed from the Mossman - Mount Molloy Road (Figure 3.4). Within each altitudinal band the plots are at least 400m apart and within 50m of the altitudinal band (e.g. 1000m +/- 50m). Rainfall and temperature data were collected by researchers at James Cook University (JCU), Mt Lewis being one of seven altitudinal transects that are studied by JCU.
researchers in the Wet Tropics region. Temperature data was collected at one plot per elevation (plot a), between 01.01.2006 and 09.12.2008. Average annual temperatures range between 21°C at 400m a.s.l., to 16°C at 1200m a.s.l., an average decrease of 1°C per 200m (Figure 3.5). Daily rainfall data between 01.01.2006 and 01.01.2009, collated from data from the Bureau of Meteorology’s Australian Water Availability Project (http://www.bom.gov.au/awap/rain/index.jsp). Average annual rainfall ranged between 2140mm at 400m a.s.l., up to 2924mm at 1200m a.s.l. (Figure 3.6). These figures are estimations, based on data from surrounding areas, and extrapolated to the Mt Lewis plots using 5km grid data.

Plant identification of the Mt Lewis plots is ongoing. Two plots per altitude will be presented here. At the 400m a.s.l. plots, the vegetation assemblage was dominated by *Alstonia muelleriana* and *Cryptocarya lividula*. The 600m a.s.l. plots were dominated by *Brombya platynema*, *Argyroderdon peralatum* and *Mallotus polyadenos*, and the 800m a.s.l. plots were dominated by *Brombya platynema* and *Franciscodendron laurifolium*. At 1000m a.s.l. the dominant species include *Balanops australiana* and *Daphnandra repandula*, and at 1200m a.s.l. *Doryphora aromatic* and *Niemeyera sp. Mt Lewis. 

![Figure 3.5 Average annual temperature for Mt Lewis altitudinal transect (data courtesy of James Cook University).](image-url)
The major sampling tool used to capture moths in this research is the Pennsylvania light trap (Frost 1957), which uses a vertical UV actinic light bulb to attract night-flying insects, which hit clear plastic vanes and fall into a bucket below. The original Pennsylvania light trap design was modified, with a lightweight lid to exclude rain, larger space in the funnel above the bucket to let in large moths, and an automatic timer, allowing for sampling in remote locations (Figure 3.7) (Kitching et al. 2005). Traps were run from dusk to dawn, using 12 volt gel-cell batteries, and emptied and given a fully charged battery daily. The killing agent employed was Killmaster Pest Strip®, a Dichlorvos impregnated plastic strip, which was cut into one inch pieces, with two to three pieces placed in each trap. In each trap we placed pieces of egg carton to reduce the level of damage to moth specimens from beetles and other insects (which cling to the egg carton) and some paper towel, to absorb any moisture that might get into the trap. This method of sampling has yielded large samples of night-flying moths, often upwards of 1000 moths per night within a single trap.
All sampling methods have some level of bias, capturing as they do, a certain subset of the entire actual assemblage (Krebs 1999). There is an assumption that sampling methods are randomly sampling the community. This assumption is violated by light traps, as some moth species, and male and females within the same species may respond to UV lights in different ways (Southwood and Henderson 2000, Altermatt et al. 2009). However, this bias is consistent across all samples, those species that are attracted to light should be sampled randomly by these traps, which are an effective method of sampling arthropods, as long as they are used in a standardised way (Preston 1948). The size of the sample is often influenced by a variety of factors, including temperature, moon phase, precipitation and wind (Muirhead-Thomsom 1991, Yela and Holyoak 1997). In order to standardise the trap nights and to avoid problems of differing detectability of species within the assemblage, we have, in all cases, sampled over three nights, and have not sampled three days either side of the full moon.

Vertical stratification is an established concept in insect ecology (Schulze et al. 2001, Brehm 2007). Important questions about the relative diversity and endemism in the canopy and understory can be addressed through sampling of

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**Figure 3.7** Modified Pennsylvania light trap, hung at head height.
both canopy and ground assemblages. In addition, we aimed to sample as much of the night-flying moth fauna as possible. Through sampling both the canopy and ground fauna, we can get a better picture of the overall forest moth fauna (Beck et al. 2002). At all study plots two Pennsylvania light traps were run simultaneously at a plot on each trapping night, one trap at head height (ground trap) and one in the canopy. A modified compound bow (fish hunting bow), was used to shoot canopy lines with modified arrows, which had a weight attached to the front of the arrow, so that it fell to the ground after being shot into the canopy. The canopy traps were raised into the canopy, which differed in height between forest types and altitude, ranging between 15 and 35m. Ground traps were raised to approximately 2m above the ground, either by hanging them from a low branch or between two trees. (A detailed analysis of vertical stratification in moth assemblages is presented in Chapter 5.)

All moths with a forewing length greater than 1cm (loosely referred to as macrolepidoptera) were considered. In addition, all moths belonging to the superfamily Pyraloidea (that is, the families Crambidae and Pyralidae), regardless of their size, were also processed. Moth samples were sorted within two days of the collection of the sample, to prevent specimens becoming mouldy. Moths from each sample were sorted to morphospecies in field laboratories. A reference collection was established for each location. As these collections grew, additional moths that were readily recognisable were recorded and discarded. Any new specimens that could not be readily identified as belonging to an existing numbered morphospecies were pinned and preserved.

Sampling period

Each altitudinal transect was sampled at the beginning and end of the wet season. Lamington NP moth surveys were carried out between the 14th and the 30th of October 2006 and between the 10th of March and the 2nd of April 2007, as part of the IBISCA-Qld project. This research project was headed by Professor Roger Kitching, and Louise Ashton contributed to the field work, sorting,
identification and analysis (Ashton et al. 2011), which occurred prior to the commencement of this PhD research. This data has been included in this paper as it is the original baseline data with which we wish to make comparisons. Due to time constraints during the IBISCA Qld-project, two of the 300m a.s.l. plots were not sampled during the October 2006 session, and two of the 500m a.s.l. plots were not sampled during the March 2008 session. Field work at Border Ranges NP was conducted by Louise Ashton between the 4th and 22nd of April 2011, and between the 27th of October and 12th of November 2010 and field work at Mt Lewis NP was carried out between 21st Nov – 13th Dec 2009, and 1st – 18th of April 2011. Samples were collected over the course of four years; however this time period is not expected to have a major impact on the results, as any inter-annual variation will be outweighed by the variation across altitude and latitude.

Vegetation surveys

Vegetation surveys at Lamington NP were conducted by the Queensland Herbarium as part of the IBISCA-Qld project. At the Border Ranges transect, the same approach was employed as the Lamington transect, with permanent 20m x 20m plots established, all trees with a dbh greater than 5cm were permanently tagged, and identified by John Hunter, Stephanie Horton and Bill McDonald. The Mt Lewis transect was similarly permanently established, with all botanical identifications carried out by Bill McDonald from the Queensland Herbarium.

Analysis

Data from the three nights of collection in the canopy and understory at each plot were pooled, producing a single sample for each plot, and data collected at the beginning and end of the wet season were combined. The multivariate analysis package Plymouth Routines In Multivariate Ecological Research [PRIMER 6] (Anderson et al. 2008) was used to investigate differences in moth assemblages across altitudinal zones. Insect data sets are often characterised by a large number of rare species and a small number of abundant species which
overshadow patterns at the community level. Log transformations are commonly used in insect studies to overcome the influence of dominant species (Southwood and Henderson 2000), therefore we chose to log transform moth data prior to multivariate analysis.

We constructed dissimilarity matrices for each location (LAM, BR, ML) using the Bray–Curtis dissimilarity measure (Bray and Curtis 1957). From these matrices non-metric multi-dimensional scaling (NMDS) was conducted, set to 1000 random starts, to produce ordination plots illustrating the relationship among assemblages at different altitudes. Using the same dissimilarity matrices, we performed ‘Permutation-based Analysis of Variance’ [PERMANOVA] (Anderson et al. 2008) using 1000 permutations, to test for differences between a priori groups (i.e. five altitudinal zones). Another Bray–Curtis dissimilarity matrix for each location (LAM, BR, ML), was created, based on vegetation assemblage data (all trees with a dbh greater than 5cm) and the RELATE function in Primer 6 was used to perform a Mantel Test of correlation between the moth and vegetation assemblages, using Spearman’s rank correlation and 1000 permutations.

Moth assemblages at each altitudinal gradient were compared with plot-based environmental information (biotic and abiotic) using a distance-based linear model (DistLM) (Ardle and Anderson 2001) which was used to identify variables that were significantly correlated with the altitudinal moth assemblage structure. Lamington NP environmental data included altitude, tree species richness, number of fog events, air temperature variables (average, minimum and maximum) and a suite of soil properties – moisture, pH, organics, potassium, and carbon (collected by D. Putland during the IBISCA-Qld project). Border Ranges NP data included altitude, tree species richness and temperature variables (average, minimum and maximum). The Mt Lewis analysis incorporated air temperature variables (average, maximum and minimum), rainfall, altitude, and soil properties including sodium, nitrogen, calcium, clay and total organic content. The DistLM procedure models and analyses the relationship between multivariate data and predictor variables, using a distance matrix and
permutation. Many of these variables were highly correlated; sequential tests were employed to determine which combination of variables had the best explanatory power ($r^2$). Significant variables ($p < 0.05$) were superimposed onto moth assemblage ordination plots, to visually represent the relationships between environmental variables and moth assemblages. The direction of the each vector line represents the direction of change in each variable and the length of each line represents the strength of the relationship. The BEST procedure was also conducted in PRIMER 6, which identified what combination of environmental variables produces the greatest explanatory power when compared to the moth assemblages.

The total moth species pool, including those that were not sampled, was estimated using EstimateS (Cowell 2000). This analysis conducts random re-sampling of the existing data to provide an estimation of the total number of species, including those that were not encountered. This analysis was carried out to test the effectiveness of the sampling method, as it provides an estimate of what proportion of the total assemblage was caught, and to give an indication of the total moth diversity present at the study locations.

Indicator species were selected using a multi-step process. Firstly, IndVal (version 2.1 Dufrêne and Legendre 1997) analysis was conducted on all species with abundances greater than 40 individuals (any species with low abundance is likely to be too rare to be useful as an indicator). This analysis was conducted in the R statistical environment (R Development Core Team 2010), utilizing the IndVal procedure in the labdsv package (Roberts 2010). This method uses a randomization procedure to identify taxa that are indicative of a priori groups (i.e. each of five altitudes and their combinations). Based on the specificity (proportion of replicate plots, within groups, occupied by the species) and fidelity (proportion of the species within a group, across all replicates) of the species within a group or combination of groups, indicator values are calculated as a percentage. Taxa with a maximum indicator value of 100% are those that occur across all replicate plots (maximum fidelity) within a group or cluster of groups.
with none occurring in other groups (maximum specificity). We selected species with an indicator value greater than 0.7, producing a suite of species that are altitudinally restricted and common across the plots in each altitudinal band. Once this analysis had established statistically which species were altitudinally restricted and present within each altitudinal band, or groups of altitudinal bands, those species which are cryptic, hard to identify, or had not yet been assigned a scientific name were also removed from the final set of indicator species. Indicators were selected if they were highly restricted (e.g. only found at 1100m a.s.l.) or if they were restricted to two or three elevational bands (e.g. found at 500m, 700m, and 1100m a.s.l.). Both the highly restricted indicators and the indicators restricted to two or more bands of the altitudinal gradient are suitable as indicators, and may be useful in monitoring range of climate responses, including upwards shifts of entire extents, retraction from lower altitudes and local extinctions.

This analysis was conducted separately for each sampling session and an overall set of indicator species was produced for each altitudinal gradient (LAM, BR, and ML). Indicators have been selected from each sampling session, as indicators may depend on the season.

Historical moth distribution data was collected from several museums within Australia, including the Queensland Museum, Brisbane; the Australian National Insect Collection, Canberra; and the Australian Museum, Sydney. This involved targeting specimens of the indicator species to collate their locality which often included the altitude at which the specimen was caught. This collection data gives us some insight into the wider latitudinal and altitudinal distributions of the indicator species.

It should be noted that during the course of this research, there were two clear mass emergences, both during the November 2009 Border Ranges sampling session. There was a large number of specimens of the Sodgrass webworm *Herpetogramma licarsisalis* (Walker, 1859) (Pyraloidea – Crambidae), which was
especially abundant around the 900m a.s.l. plots. The other significant mass emergence was of hepialids, primarily at the 1100m a.s.l. plots. These mass emergences do not change the overall results of this study. When we ran analyses with and without these species there was no difference in the results; we therefore left singletons and doubletons in the datasets.

**Results**

During this study a total of 69677 individuals were caught and identified, belonging to 2304 species across the Border Ranges, Lamington and Mt Lewis plots (Chapter 3 Appendix Table 3.5). The number of species encountered was greatest in the tropics, with a total of 1134 species at Mt Lewis, 865 at Lamington, and 612 at Border Ranges.

**Lamington** – During the Lamington NP study, conducted in October 2006 and March 2007, a total of 11379 individuals were encountered, belonging to approximately 865 species. Species richness was greatest at 700m a.s.l., as was abundance (745 ± 124 individuals, belonging to 195 ± 24 species) (Table 3.1, Figure 3.8). Abundance Coverage Estimators (ACE) also showed that the total estimated species richness peaked at 700m a.s.l. (a total estimated number of 685 ± 17 species) (Figure 3.9). When interpreting the Lamington results, it is important to note that some of the 300m and 500m a.s.l. plots were under-sampled, therefore the lower richness and abundance, at 500m a.s.l. in particular (Figure 3.8), may be somewhat misleading. Using the ACE results to give an indication of the total species richness in each area, is one method of gaining a better understanding of the altitudinal patterns of richness, which show about the same levels of species richness at 300m and 500m a.s.l.. Generally, the ACE results indicate our sampling at Lamington recovered between 25% and 35% of the total species richness at each altitude, and across all altitudes, around 70% of the total richness (866 out of 1195 total species).
The NMDS ordination of Lamington moth assemblages (Figure 3.10 (a)) illustrates a strong turnover in moth assemblages with increasing altitude. PERMANOVA results show that pair-wise comparisons between the altitudinal bands were all significantly different, and there was no consistent shift in the Bray-Curtis dissimilarity across altitude, and the distance among the centroids of the assemblages from each elevational band (Table. 3.1). NMDS ordination plots with superimposed vectors illustrate the environmental variables that correlated significantly to the pattern of turnover in moth assemblages. At Lamington NP significant factors included altitude, fog events, temperature, and a suite of soil characteristics (Figure 3.11 (a), Table 3.2). Altitude, low temperature and medium temperature combined, produced the best explanatory correlation (83%).

There was a strong similarity of observed assemblage stratification across altitude between Lamington and Border Ranges (Figure 3.10 (a) and (b), Figure 3.12); indicating aspect was not a major influence on altitudinal patterns. The Lamington and Border Ranges transects shared 308 species, with a Bray-Curtis similarity value of 0.204. One pattern to note is that the 1100m a.s.l. plots at Lamington and Border Ranges are more similar to each other (Bray-Curtis similarity of 38.009), than they are to altitudes within the same catchment at lower altitude (e.g. 1100m and 700m a.s.l. have a similarity value of 32.3 at Lamington). This indicates that although the assemblages at each location have some different species (overall Bray-Curtis similarity value of 0.204), altitude plays a strong role in shaping the structure of these communities, and species are more similar to the equivalent altitudinal band 20km away. This also supports the assumption that spatial-auto correlation is not a major factor shaping the observed altitudinal patterns, as each altitudinal zone is generally more similar to the equivalent analogous assemblage 20km away, than to spatially closer assemblages at different altitudes.
Figure 3.8 Mean moth species richness (with standard error bars) across altitudinal gradients in two sampling occasions for LAM, BR and ML. Generally we found a mid-altitude peak in species richness.

Figure 3.9 Estimated (ACE) moth species richness (with standard error bars) across altitudinal gradients LAM, BR and ML. A mid-altitude hump in estimated richness is apparent for LAM and ML. BR however has significantly lower estimated species richness than LAM.
Table 3.1 Metrics of pairwise comparisons between adjacent altitudinal bands, for LAM, BR and ML; PERMANOVA results (t and P values), average Bray-Curtis similarity, and average distance among multivariate centroids. All altitudinal bands are significantly different (p > 0.05). There was no consistent pattern of increasing or decreasing similarity or distance among centroids across altitude.

<table>
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<tr>
<th>Location</th>
<th>Permanova</th>
<th>Average Bray-Curtis similarity</th>
<th>Distance among centroids</th>
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</tr>
<tr>
<td>300 and 500</td>
<td>1.801</td>
<td>0.036</td>
<td>25.976</td>
</tr>
<tr>
<td>500 and 700</td>
<td>1.439</td>
<td>0.026</td>
<td>35.029</td>
</tr>
<tr>
<td>700 and 900</td>
<td>1.577</td>
<td>0.028</td>
<td>38.236</td>
</tr>
<tr>
<td>900 and 1100</td>
<td>1.816</td>
<td>0.031</td>
<td>38.31</td>
</tr>
<tr>
<td>Border Ranges</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>300 and 500</td>
<td>1.301</td>
<td>0.037</td>
<td>50.175</td>
</tr>
<tr>
<td>500 and 700</td>
<td>2.106</td>
<td>0.031</td>
<td>46.803</td>
</tr>
<tr>
<td>700 and 900</td>
<td>1.940</td>
<td>0.035</td>
<td>50.589</td>
</tr>
<tr>
<td>900 and 1100</td>
<td>2.012</td>
<td>0.027</td>
<td>45.949</td>
</tr>
<tr>
<td>Mt Lewis</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>400 and 600</td>
<td>1.712</td>
<td>0.033</td>
<td>31.099</td>
</tr>
<tr>
<td>600 and 800</td>
<td>1.664</td>
<td>0.025</td>
<td>34.075</td>
</tr>
<tr>
<td>800 and 1000</td>
<td>1.717</td>
<td>0.036</td>
<td>29.353</td>
</tr>
<tr>
<td>1000 and 1200</td>
<td>1.561</td>
<td>0.03</td>
<td>35.64</td>
</tr>
</tbody>
</table>
Figure 3.10 NMDS ordinations of moth assemblages sampled at (a) LAM Oct 2006 and Mar 2007 (2D stress: 0.07), (b) B R in Apr and Nov 2010 (2D stress: 0.07) and (c) ML Nov 2009 and April 2010 (2D stress: 0.08).
Figure 3.11 NMDS ordinations for (a) LAM, (b) BR and (c) ML altitudinal transects with superimposed vectors. Only the significant variables were incorporated into this visual summary of variables that correlate with the observed moth assemblage pattern. The direction of each vector line indicates the positive or negative direction of the trend, and the length of each vector line indicates the strength of the relationship.
Border Ranges NP

Border Ranges NP sampling (Nov and Apr 2010), produced a total of 40859 individuals belonging to 612 species. EstimateS results indicated a total estimated assemblage of 694 ± 7 species, indicating we sampled about 88% of the total assemblage. Species richness was highest at 500m a.s.l. (180 species, 294 estimated species), which also had the highest encountered abundance. It should be noted that although the observed species richness was lower at 300m a.s.l. (147 species), the ACE estimate of total richness at 300m a.s.l. was the highest, with a total of 426 ± 8 estimated species (Chapter 3 Appendix, Table 3.5). Analysis of the correlation of environmental factors to the multivariate moth assemblage pattern indicated that low temperature, median temperature and altitude were significantly correlated. Superimposed vectors illustrate the strength of these relationships. (Figure 3.11 (b), Table 3.2). Low temperature and altitude were selected by the BEST procedure as the combination of variables that explained the most variation in moth assemblage composition (87%).

The NMDS ordination plot of moth assemblages at Border Ranges (Figure 3.10 (b)), showed a very similar pattern to the Lamington ordination (Figure 3.10 (a)), which is strong turnover in moth assemblages with increasing altitude. Pair-wise comparisons of moth assemblages between adjacent altitudinal bands were all significantly different, and there is no shift in Bray-Curtis similarity across altitude, and the distance among centroids (Table 3.2).
Table 3.2 Results of DISTLM analyses testing the correlation between environmental variables and moth assemblages, conducted with available environmental data at each altitudinal gradient. Non-significant variables (p>0.05 are shaded grey).

<table>
<thead>
<tr>
<th></th>
<th>Mt Lewis</th>
<th>Lamington</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tree rich</td>
<td>0.979</td>
<td>2.612</td>
</tr>
<tr>
<td>Low temp</td>
<td>4.761</td>
<td>5.718</td>
</tr>
<tr>
<td>High temp</td>
<td>5.079</td>
<td>3.249</td>
</tr>
<tr>
<td>Median temp</td>
<td>4.697</td>
<td>5.989</td>
</tr>
<tr>
<td>Altitude</td>
<td>4.971</td>
<td>5.765</td>
</tr>
<tr>
<td>Rainfall</td>
<td>4.944</td>
<td>4.441</td>
</tr>
<tr>
<td>Soil sodium</td>
<td>1.419</td>
<td>5.728</td>
</tr>
<tr>
<td>Soil nitrogen</td>
<td>2.485</td>
<td>4.750</td>
</tr>
<tr>
<td>Soil phosphorus</td>
<td>4.238</td>
<td>4.980</td>
</tr>
<tr>
<td>Soil carbon</td>
<td>1.126</td>
<td>4.040</td>
</tr>
<tr>
<td>Soil clay</td>
<td>3.084</td>
<td>4.272</td>
</tr>
<tr>
<td>Soil temp</td>
<td>4.864</td>
<td></td>
</tr>
</tbody>
</table>

Figure 3.12 NMDS ordination of both the LAM and BR moth assemblages, illustrating the similar pattern of altitudinal stratification along both altitudinal gradients.
During the two field seasons at Mt Lewis NP (Nov 2009 and Apr 2011), a total of 17258 individuals were collected, belonging to 1134 species, making it the most species rich location examined in this study. Rarefaction estimated a total assemblage of 1521.05 ± 11.18 species, indicating we sampled approximately 75% of the total assemblage (see Methods for a discussion on the limitations of estimators). The plots at 600m a.s.l. were most species rich, with a total of 250 species encountered, and an estimated total species richness of 988.54 ± 24.8. Abundance was also greatest at 600m a.s.l. (1357 individuals), however the second most abundant altitude was 1200m a.s.l. with 1171 individuals (Chapter 3 Appendix Table 3.5).

An ordination plot of moth assemblages at Mt Lewis NP (Figure 3.10 (c)) showed clear altitudinal stratification. One difference between the tropical and subtropical assemblage structure across altitude, was the clear distinction between the assemblages at 400m to 800m a.s.l. and those at 1000m and 1200m a.s.l.. Average Bray-Curtis similarity between 1200m and 1000m a.s.l. is 35.64, and between 1000m and 800m a.s.l. 29.35, meaning that there is a larger turnover in assemblages between the 800m to 1000m a.s.l. plots. This may be largely driven by the average level of the cloud cap, which sits at around 900m a.s.l. Superimposed vectors on the Mt Lewis NP moth assemblage ordination indicate several environmental and biotic variables that correlate significantly with observed moth assemblage patterns (Figure 3.11 (c)). BEST analysis indicated that the combination of high temperature, average temperature, soil temperature and altitude have the strongest explanatory power (92%).

**Indicator species**

A set of indicator species was identified for each location (LAM, BR and ML). Refer to Tables 3.6, 3.7 and 3.8 for tables and diagrams of each indicator species.
and their altitudinal extents, and Figures 3.16, 3.17 and 3.18 for photos of the indicator species. A suite of indicators for the Lamington location was presented in (Ashton et al. 2011), which was based on preliminary analysis identifying species which had at least 80% of the encountered individuals restricted to one or two altitudinal bands. At Lamington, a total of 15 species were selected. We note that the new indicator analysis has resulted in many of the same species as in our preliminary analysis (see page 383, Appendix 4), however there are several species which were not included after the more rigorous analysis. The taxonomic composition of the sets of indicator species at Lamington and Border Ranges were generally similar and dominated by Geometridae, however at the Mt Lewis transect, no Geometridae species were identified as good indicator species (Table 3.4).

At Border Ranges, 26 indicator species were found. There were seven overlapping indicators between Lamington and Border Ranges (Chapter 3 Appendix Table 3.7). All indicator species common to Lamington and Border Ranges belong to the family Geometridae, and are restricted to 700m a.s.l. and above. In all but one case, the altitude that these species indicate at Lamington is one altitudinal band higher than the altitude they are indicative of at Border Ranges. This pattern is consistent with temperature data collected between the two locations, which show that our plots at Border Ranges were, on average 1.3°C cooler, thereby allowing these cooler habitat-restricted species to extend to lower altitudes.

Collection data derived from museum specimens of the indicator species common between Lamington and Border Ranges, provide strong evidence that the altitude of the plots these species were collected from is influenced by their latitude (Table 3.3). For example, Xylostyla leptoxantha (found at 900m and 1100m a.s.l. at Lamington, and 700m, 900m and 1100m a.s.l. at Border Ranges), has been recorded at 1065m a.s.l. in the Bunya Mountains, Qld (ca 26° 29 S ), and as low as 245m in Coffs Harbour, NSW (ca 30°15 S). Two species found at lower altitudes further south, are also found at high altitudes in the same region –
Larophylla amimeta, (found at 620m a.s.l. at Cambewarra (ca 34° 46 S) and at 1585m a.s.l. at New England NP (ca 30° 29 S)), and Heterochasta conglobata (found at 1560m a.s.l. at Bellenden Ker, Qld (ca 17° 15 S), 900m a.s.l. at Paluma, Qld (ca 19° 1.7 S) and 700m a.s.l. at Border Ranges NP, NSW (ca 28° 7 S)). Indicator species identified at Lamington and Border Ranges, which have records from tropical forests, including Dyscheralcis crimnodes, Heterochasta conglobata and Eurychoria fictilis have records at or above 1500m a.s.l., with no observations at lower altitudes in these warmer tropical areas, suggesting that these species’ altitudinal distributions are restricted by temperature (and/or the other correlated factors that shift with altitude).
Table 3.3 Indicator species common between LAM and BR. In all but one case (*Dyscheralcis crimnodes*) the indicators at BR are present one altitudinal band below those at LAM. Museum records gathered for these species illustrate that indicators are found at higher altitudes in Nth Qld, and lower altitudes further south in NSW, supporting the hypothesis that these species’ distributions are primarily driven by temperature.

<table>
<thead>
<tr>
<th>Name</th>
<th>LAM (m a.s.l.)</th>
<th>BR (m a.s.l.)</th>
<th>Museum records location</th>
<th>Lat (S)</th>
<th>Altitude (m a.s.l.)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Xylodryas leptoxantha</em></td>
<td>900, 1100</td>
<td>700, 900, 1100</td>
<td>Bunya Mtns, QLD, Gibraltar Range, QLD, Acacia Plateau, NSW, Clyde Mtn, NSW, Cambewarra Mt NSW, Dorrigo NP, NSW, Mt Warning, NSW, Up Allyn R, NSW, Coffs Harbor</td>
<td>26°29, 29°28, 28°19, 35°24, 34°46, 30°22, 28°24, 32°10, 30°15</td>
<td>1065m, 950m, 915m, 730m, 620m, 520m, 500m, 455m</td>
</tr>
<tr>
<td><em>Dyscheralcis crimnodes</em></td>
<td>700, 900, 1100</td>
<td>900, 1100</td>
<td>Bellenden-Ker Nth QLD, Paluma QLD, Mt Bartie Frere QLD, Clyde Mt NSW</td>
<td>17°15, 19°1.7</td>
<td>1560m, 900m</td>
</tr>
<tr>
<td><em>Heterochasta conglobata</em></td>
<td>900, 1100</td>
<td>700, 900, 1100</td>
<td>Bellenden-Ker QLD, Mt Edith QLD, Mt Warning, NSW</td>
<td>19°0.6, 17°23, 35°24</td>
<td>1560m, 1500m, 731m</td>
</tr>
<tr>
<td><em>Eurychoria fictilis</em></td>
<td>900, 1100</td>
<td>700, 900, 1100</td>
<td>Bellenden-Ker QLD, Mt Edith QLD, Killarney NSW</td>
<td>19°0.6, 17°4.5</td>
<td>1560m, 1035m</td>
</tr>
<tr>
<td><em>Lyelliana dryophylla</em></td>
<td>900, 1100</td>
<td>700, 900, 1100</td>
<td>New England NSW, Conenac NSW, Killarney NSW, Cambewarra Mt NSW</td>
<td>30°29, 37°51, 28°18, 34°46</td>
<td>1585m, 900m, 920m, 620m</td>
</tr>
<tr>
<td><em>Larophylla amimeta</em></td>
<td>900, 1100</td>
<td>700, 900, 1100</td>
<td>Barrington Tops NSW, New England NSW, Springbrook NSW</td>
<td>31°56, 30°29, 28°11</td>
<td>1545m, 1615m, 700m</td>
</tr>
</tbody>
</table>

Table 3.4 Proportions of indicator species within moth families at each location. LAM and BR indicators are dominated by Geometridae; ML has no Geometridae indicators, but a large proportion of Arctiidae.

<table>
<thead>
<tr>
<th></th>
<th>Geometridae</th>
<th>Noctuidae</th>
<th>Pyraloidea</th>
<th>Arctiidae</th>
<th>Other</th>
</tr>
</thead>
<tbody>
<tr>
<td>LAM</td>
<td>60%</td>
<td>13%</td>
<td>7%</td>
<td>20%</td>
<td>0%</td>
</tr>
<tr>
<td>BR</td>
<td>54%</td>
<td>15%</td>
<td>15%</td>
<td>8%</td>
<td>8%</td>
</tr>
<tr>
<td>ML</td>
<td>0%</td>
<td>11%</td>
<td>11%</td>
<td>56%</td>
<td>22%</td>
</tr>
</tbody>
</table>
Figure 3.13 Species richness of trees (with standard error bars) (dbh > 5cm) across altitude at LAM and BR

Figure 3.14 Species richness of trees (with standard error bars) (dbh > 5cm) across altitude at ML
Tree assemblages across altitude

The total number of tree species encountered at each altitudinal transect was 114 species at Lamington, 109 species at Border Ranges (within the twenty 20m x 20 m study plots), and 146 species at Mt Lewis (from only two plots per altitude). There was no clear pattern of increasing or decreasing species richness across altitude at Lamington, Border Ranges (Figure 3.13) or Mt Lewis (Figure 3.14). NMDS ordinations of the vegetation assemblages at each altitudinal transect generally show a gradual turnover in assemblages with altitude, with some caveats.

Lamington NP vegetation assemblages formed discrete assemblages at 300m to 700m a.s.l., and the 900m and 1100m a.s.l. plots, which were distinct from each other Figure 3.15 (a). The pattern is confirmed by PERMANOVA pair-wise post hoc tests, which showed no significant difference between the 300m, 500m, and 700m a.s.l. altitudinal pairs, but a strong significant difference between the 900m and 1100m a.s.l. altitudinal pairs. (300 and 500 t = 1.49, P= 0.07, 500 and 700 t = 1.3, P= 0.08, 700 and 900 t = 2.47, P= 0.03, 900 and 1100 t = 2.03, P = 0.03). Plots at 1100m a.s.l. consisted of a different assemblage, characterized by simple microphyll fern forest, dominated by *Nothofagus moorei*. This unique high altitude assemblage is also reflected in the moth assemblages forming a separate grouping at 1100m a.s.l., as well as a suite of other taxa, including ants, beetles and Collembola.

The altitudinal structure of vegetation assemblages at Border Ranges NP (Figure 3.15 (b)), showed a similar pattern to the Lamington results, however three of the 700m a.s.l. plots group with the 900m and 1100m a.s.l. plots. As in the Lamington location, 1100m a.s.l forms a distinct assemblage, and is also categorized as simple microphyll fern forest, with the presence of *Nothofagus moorei*. When we combined the vegetation assemblage data of LAM and BR, ordinations show that the equivalent altitudinal assemblages at each location are similar, and respond in a similar way to altitude (Figure 3.15 (c)).
Here, we present vegetation results for two plots per altitude at Mt Lewis, as identification of these plots is ongoing. The NMDS ordination of the Mt Lewis vegetation (Figure 3.15 (d)), visually demonstrates strong altitudinal stratification with distinct groupings of the 400m to 800m a.s.l. plots and the 1000m to 1200m a.s.l. plots. Moisture data for this altitudinal transect indicates that the cloud cap sits between 800m and 1000m a.s.l., as there is a significant jump in moisture between these two elevational bands. Comparing the altitudinal structure of moth assemblages with these vegetation results, using Mantel tests, we found a significant correlation between the moth assemblages and the vegetation assemblages at Border Ranges (Rho = 0.55, p = 0.001), Lamington (Rho = 0.605, p = 0.001), and Mt Lewis (Rho = 0.776, p = 0.001). The Mt Lewis vegetation assemblages correlated the highest with the moth assemblages, which both show clear delimitation between 400m to 800m a.s.l. assemblages and the 1000m to 1200m a.s.l. assemblages.
Figure 3.15 NMDS ordinations of vegetation assemblages, based on presence/absence data and Bray-Curtis similarity matrices at (a) LAM (2D stress: 0.7), (b) BR (2D stress: 0.16), (c) BR and LAM combined and (d) ML (2D stress: 0.07).
Discussion

This study has addressed three main questions:
(1) does aspect influence patterns of diversity across altitude,
(2) what are the differences in altitudinal stratification between tropical and subtropical rainforest; and,
(3) how does vegetation assemblage structure relate to the altitudinal distributions of moth assemblages?
In this Discussion, the major findings will be explored, shortcomings examined, and future research that may stem from this work identified.

Differences between the two sub-tropical locations

During the IBISCA-Qld project, a range of target taxa were sampled along the Lamington NP altitudinal transect, and shown to exhibit clear altitudinal stratification (Kitching et al. 2013a). The next logical step after conducting this baseline study along one altitudinal gradient was to expand the design to incorporate more locations within the same region, allowing us to assess the generality of the previous results, and examine further ecological questions with greater scope. We established a second altitudinal transect with an analogous study design, in a nearby subtropical rainforest location, but with minor, albeit important, environmental differences (principally driven by aspect). This has allowed us to test the generality of the altitudinal zonation of subtropical rainforest moth assemblages, and to examine further how different sets of environmental variables can produce different patterns of altitudinal zonation. It is important to note however that we have sampled two transects in subtropical rainforest, and more replication is required before we can produce quantitative results.

We found slightly fewer species at the Border Ranges NP transect compared with that at Lamington NP, yet the main pattern of a stepwise turnover in moth
assemblages with increasing altitude, was the same. Aspect did not affect the pattern of altitudinal stratification. We found that there was a lower rate of change in temperature across altitude at Border Ranges NP (0.94°C/200m at BR, 1.17 °C/200m at LAM), which may be driven by the different aspect of this transect, the high rainfall levels that occurred during the year that temperature was recorded, and micro-habitat effects.

The small temperature differences between these locations may influence the altitudinal range of species. This is particularly apparent when we examine the indicator (i.e. altitudinally restricted) species that were common to the two locations, all of which belong to the family Geometridae and were restricted to 700m a.s.l. or above. Out of seven shared species, all but one had a distribution extending one altitudinal band lower at Border Ranges NP. This suggests that these species are particularly sensitive to temperature, and so occur at lower altitudes in the cooler Border Ranges. That these distributions are driven primarily by temperature is supported by the data collected from museum collections. These data indicate that the altitudinally restricted species common to both Lamington NP and Border Ranges NP are generally found at higher altitudes in the tropics, and at lower altitudes in forests further south.

Why is there a difference between tropical and sub-tropical assemblages?

We found strong altitudinal turnover in moth assemblages in both sub-tropical and tropical transects but there were, however, some key differences between them. The indicator, or altitudinally restricted, species identified at Lamington NP and Border Ranges NP, were dominated by Geometridae. The suite of indicators identified at Mt Lewis NP, located in the Wet Tropics, however, contained no geometrid species, and was instead dominated by Arctiidae (=Erebidae: Arctiinae) and Pyraloidea. Differences in the overall faunal composition of our tropical and sub-tropical study locations are examined in Chapter 4 where we show that this difference in the indicator species is not simply a reflection of changing proportions of major taxa. Both the sub-tropical
and tropical samples contained more or less similar proportions of geometrids (BR 38%; LAM 25%; ML 27%). Accordingly, we take the differences in the altitudinally restricted species as a strong difference between tropical and subtropical rainforests.

Another major difference between the tropical and sub-tropical locations is the clear faunal break-points at Mt Lewis NP between the 400m to 800m a.s.l. cluster of moth assemblage and the 1000m to 1200m a.s.l. cluster. This distinct zone of turnover may be driven by the elevation of the cloud cap. Data gathered from the Bureau of Meteorology, based on a 5km grid, indicates that there is a significant jump in average rainfall between 800m a.s.l. and 1000m a.s.l., a shift which is reflected in both moth and vegetation assemblages. Mountain cloud caps are lenticular and form through the process of orographic lift, where air is pushed from low to high elevations. Climate warming is predicted to raise the average level of the cloud cap (Pounds et al. 1999, Still et al. 1999). The turnover in moth assemblages above 1000m a.s.l. may be due, in part, to an average location of the cloud cap, which sits between 900m and 1000m a.s.l. at Mt Lewis NP.

At Lamington NP and Border Ranges NP, high altitude plots are characterized as simple microphyll fern forest dominated by *Nothofagus moorei*: a forest type that contrasts distinctly with the complex notophyll vine forests at lower elevations. Mt Lewis NP shows no such dramatic switch in forest type at the highest altitudes (although floral composition does change incrementally). We speculate, therefore, that the presence of the cloud cap above a.s.l. is the driver shaping both vegetation and insect herbivores. In the sub-tropical forest, the cloud cap may well be driving the dramatic shift in forest type, dominated by *Nothofagus moorei*, at the higher altitudes. In turn, this shift in forest type and available plant resources seem to be the stronger candidates in forming the insect assemblages, particularly of herbivores.
**Why is there a mid-elevation peak in species richness?**

In contrast with lower elevation rainforests, cloud forests are characterised as short in stature, less diverse, with high loads of epiphytes and ferns (Bruijnzeel and Hamilton 2000) and they typically support distinct biotic assemblages, associated with the high moisture levels (Lieberman et al. 1996b, Foster 2001). In our sub-tropical and tropical transects, this characterization of cloud forest, even though it is based on non-Australian systems, is accurate. We generally found unique assemblages and decreasing species richness above the cloud cap. Species richness peaked at mid-elevations in all of our transects, supporting previous results that have found mid-altitude peaks in moth assemblages (Brehm et al. 2007). There are several hypotheses that have been postulated to explain mid-altitude peaks in species richness. The literature promoting and discussing these has been reviewed in Chapter 2. In summary, the four contrasting explanations are:

1) the ‘mid-domain effect’ in which mid altitude peaks are produced by the random overlap of species' occurrences across altitude which are postulated to represent homogenous habitats;

2) mid-elevation peaks are the result of overlapping ecotones from adjacent ecosystems (e.g. the coincidence of the upper bounds of low elevation ecosystems with the lower bounds of the upper elevations ecosystems),

3) richness peaks at mid-elevations because they represent the most equable environmental factors for a majority of species (i.e. upper and lower extremes are avoided); and,

4) species-area effects could produce a mid-elevation peak when lower elevations have been substantially modified by human activities.

How do these alternative explanations help interpretation of our data from the sub-tropical and tropical transects? Hypothesis 1 is fundamentally a neutral explanation. As we have argued elsewhere (Kitching et al. 2013b) the most parsimonious explanation for moth distributions involves deterministic relationships with host plants. Accordingly, unless host plant distributions form a
mid-elevation peak, this explanation seems weak for moth distributions. There is no such peak in the plant data (see Fig 3.13 and 3.14). Hypothesis 2 is plausible for our transects. In all cases there is a meta-grouping in the plant analyses indicating the existence of an upper and a lower forest assemblage (Fig 3.15). This is somewhat less convincing in the tropical example but this could reflect the limited vegetation data we have available currently from those sites. Hypothesis 3 is again plausible but would require far more detailed information on tolerance regimes at the level of individual species than is currently available. Finally, hypothesis 4 is a likely contributor to the patterns we observe simply because, for all of our transects, it was not possible to sample below around 300m a.s.l. as most of the lower forest had been cleared (Nogués-Bravo et al. 2008). We suggest then, that a combination of hypotheses 2 and 4 are the best available explanations of the patterns we observed, but we note that hypothesis 3, on tolerance zones, cannot be completely discounted.

_Elevational gradients - indicators of climate change?_

High altitude communities are isolated from other mountain tops, and from lower elevation communities, and accordingly, have lower rates of immigration and higher rates of extinction (Lomolino 2001). Mountain tops can also act as climate refugia for cool-adapted species. During the Pleistocene, for example, tropical rainforests in north-eastern Australia repeatedly contracted into a series of small upland refugia, the distribution of which strongly influence current-day patterns of species diversity and elevational specialization (Winter 1988). Today most rainforest-endemic vertebrates in this region are upland or montane specialists, with the highest diversities found in what were evidently the largest and least irregularly-shaped refugia (Williams and Pearson 1997). The _Nothofagus moorei_ high altitude forests found in south-east Queensland and north-east New South Wales, are relicts of Gondwanan forest, which have contracted to a few high altitude patches (White 1986). Mountain ecosystems today represent areas of high conservation concern (Foster 2001), containing high numbers of endemic, endangered and climate sensitive species, often with small altitudinal ranges...
Mountain ecosystems are, by virtue of these features, also sensitive indicator systems, and may be used as early warning tools for the monitoring of climate change responses (Beniston et al. 1997). We have established three suites of altitudinally restricted moth indicator species in Australia. These insects are ideal to use as climate indicators, as our analysis of their general distributions show that they are highly sensitive to climate. They are also easy to identify and readily collected (Kitching and Ashton In Press).

Cloud forests are predicted to be particularly sensitive to climate change impacts (Pounds et al. 1999, Still et al. 1999, Foster 2001, Nadkarni and Solano 2002). An average temperature increase of 4°C by 2100 (a scenario that is perceived as being increasingly likely (The World Bank 2012)), would result in an 800m upward elevational shift in climatic conditions (Malhi and Phillips 2004). More optimistic climate change scenarios still predict upwards shifts of 450m (Loope and Giambelluca 1998). There is evidence from the Appalachian Mountains in the USA that the average cloud cap base is already shifting upwards (Richardson et al. 2002). In addition to climate warming, rising cloud levels, more variable weather, droughts and extreme weather events will also drive changes to sensitive cloud forests (Loope and Giambelluca 1998, McLaughlin et al. 2002).

Understanding the impacts of climate change on biodiversity has been termed the ‘grand challenge in ecology’, in which long-term monitoring is essential (Thuiller 2007). There is a growing recognition that in order to monitor and measure biodiversity change, standardized observation data needs to be incorporated into a global framework (Pereira et al. 2013). The Group on Earth Observations Biodiversity Observations Network (GEO BON) is an intergovernmental group which is developing a system of Essential Biodiversity Variables (EBV’s), which can be used in international monitoring programs using a collaborative approach based on voluntary contributions. The predictor sets of moths we have identified here are ideal candidates for incorporation into this program (which have been submitted to GEO BON). The suites of indicator species can be re-sampled by
organisations such as GEO BON, ecologists and land managers to assess how these species are responding to climate through time. Sampling at 10 to 15 year intervals are appropriate time-scale at which to monitor gradual climate-driven shifts. At 30 to 40 years we expect to see large-scale upwards shifts, such as those already documented in Borneo (Chen et al. 2009).

We have also expanded our baseline surveys to incorporate three altitudinal transects in China (see Chapter 5,) identifying predictor sets in tropical, subtropical and temperate forests in south-west China, which are similarly suitable for the EBV program, and can contribute unique insect biodiversity information in a location which is undergoing rapid biodiversity loss and where there is limited current knowledge of the biota.

We have also collaborated with other research groups to conduct meta-genomic analyses of our biodiversity surveys in China (Jia et al. In press). The combination of community composition and metagenomic surveys is an ideal coupling for meeting targets established by the Convention on Biological Diversity to understand biodiversity loss and changes in community composition.

The differences we observed across the suites of altitudinally restricted species, in Lamington NP (see Appendix 1) and the nearby Border Ranges NP (18 species at Lamington, 26 indicator species at Border Ranges, with 7 overlapping indicators, all of which belong to the family Geometridae) suggests that if we wish to conduct monitoring of altitudinal shifts in Lepidoptera, we first need to conduct baseline studies in individual locations. An appropriate indicator for one location may not be suitable at an adjacent location. The geographical range at which indicators can be presumed to be useful is an interesting question stemming from these results. Moth indicator species may only be useful within a local area of homogenous forest type, within the same catchment.
The predictor sets of altitudinally restricted moths form unique packets of information on a key group of insect herbivores. They present several strengths for monitoring climate-driven distribution shifts. The tropical gradient set of altitudinally restricted species are powerful, because these tropical species, with narrow altitudinal extents, are particularly vulnerable to climate change, since they may have a low range of thermal tolerance, due to the tropical climate producing lower fluctuations in temperatures (Laurance et al. 2011, Cadena et al. 2012). High altitude species are particularly at risk and may show early signs of climate driven responses (Dirnbock et al. 2011). Another sensitive area to monitor is the ecotone between cloud forest and lower altitude forest, as the drying in this area may also show early climate change responses (Foster 2001).

Vegetation and moth assemblages across altitude

Climatic factors highly influence the distributions of exothermic insects such as moths. However, in order to have a more complete understanding of what shapes their current and future distributions under climate change, vegetation profiles are a vital element. If we rely only on environmental variables to describe herbivore distributions, we may end up with overestimations, modelling them as occurring in areas where their host plants do not. Pellissier et al. (2012) found that when modelling the altitudinal distributions of butterflies, without incorporating information on host plants, overestimations occur at low altitudes, where biotic interactions may be more important in shaping community structure, and at high altitudes predictions are more accurate where environmental factors may be more limiting.

We found clear shifting of tree assemblages between low and high altitudes plots. Given that the average cloud base sits between 800m and 900m a.s.l. at Lamington NP, this pattern of separate high-altitude vegetation assemblages may be driven by the orographic precipitation that is available at these altitudes. The temperature data collected across Lamington NP and Border Ranges NP gradients indicated slightly cooler temperatures at most plots at Border Ranges.
than at the equivalent Lamington plots. We can hypothesise that the cloud cap base, which is highly influenced by local temperatures, may sit at a lower altitude (i.e. between 700m and 800m a.s.l. at BR, and between 800m and 900m a.s.l. at LAM), which would explain the grouping of vegetation assemblages into 300m and 500m a.s.l., and 700m –1100m a.s.l. categories, and the presences of shared moth indicators at one elevation lower at Border Ranges NP. Further work measuring cloud cap properties is underway at Lamington NP.

We found that both the moth assemblages and vegetation (trees with a dbh greater than 5cm) were altitudinally stratified, and that temperature and vegetation assemblages are both highly correlated with the distributions of moths. Other studies on beetles have found that vegetation is more significantly correlated with distributions than altitude (Werenkraut and Ruggiero 2012).

*Limitations and future research directions*

As these altitudinal gradients are located in tropical and sub-tropical rainforests of Australia, there is some level of disturbance at all locations. All areas are subject to a range of invasive plant, invertebrate and vertebrate species. Feral pigs have a particularly high impact, especially in the Wet Tropics, where their impacts are more severe in lowland areas (Mitchell and Mayer 1997). Some selective logging occurred in the Border Ranges and Mt Lewis transects, during the 1970’s, however the forest has mostly recovered from this disturbance (Smith et al. 2005). These results are based on sampling three altitudinal transects – one in tropical rainforest and two in sub-tropical rainforest, therefore quantitative comparisons are not possible. This limitation is important to recognise when interpreting the results so that over-generalisations are not made. The next step in this Australian research is to incorporate results from additional altitudinal survey, such as the work currently being conducted in Eungella National Park (c.a. 20.1°S) and future planned work at Dorrigo/New England National Park (c.a. 30.3°S).
Assemblage structure and productivity across altitudinal gradients will also be driven by a number of environmental factors other than just temperature and precipitation, including soil type (Kitayama and Aiba 2002). Any monitoring of biotic indicators of climate change should also incorporate careful measurement of a suite of environmental variables including temperature, moisture and soil properties.

This study has provided some insight into the distributions of moths in Australia, a continent where there has been very little work conducted on these key herbivores. To expand on these results, the rearing of larvae to quantify direct links to host plants is an ideal approach. This type of life-history information would greatly increase the robustness of our understanding of moth community structure. However, it is also labour intensive, and often records for species which are accessible only from ground sampling are made. Employing parataxonimists and volunteers may be one way forward in tackling these challenges (Basset et al. 2004). Another avenue of monitoring distributions of moth assemblages, which has been particularly successful in the U.K., is the contribution of amateur enthusiasts to national web-based data sets on the distributions of easily recognizable species, such as the national moth recording scheme (http://www.mothscount.org/text/57/county_moth_recorders.html). Although there is less of a strong culture of amateur entomology in Australia, establishing a programme similar to the ‘moths count’ database would encourage Australians to participate in natural history observation and conservation.

In terms of climate change responses, one clear avenue that stems from this research is to conduct laboratory-based experiments to quantify the thermal tolerances, particularly of the altitudinally restricted indicator species identified here. This would provide empirical evidence on how these species respond to increased temperatures, and give us a more robust picture of how they will respond to climate change.
In this chapter, we have established the robustness of the pattern of altitudinal stratification of moth assemblages in both tropical and sub-tropical rainforests, and established predictor sets of indicator species which may be sensitive to climate change. From here we will ask: what are the family and sub-family level differences across altitude (Chapter 4); is there vertical stratification in moth assemblages across altitude and latitude (Chapter 5); and, what are the differences between Australian rainforest moth assemblages, and those in forests with different biogeographical histories, climates and human impacts (Chapter 6)?
Acknowledgments

Lamington National Park data was collected during the IBISCA-Qld project, which was funded by the Department of State Development of the State of Queensland (a Smart State initiative), Griffith University, and the Queensland Museum, the Global Canopy Programme, NRM Qld and Qld National Parks Association. This project was driven by over 50 volunteers, many of whom helped in the collection of moth samples. D. Putland coordinated moth sampling, and collection was contributed to by J. Gray, D. Wright, K. Barton, C. Chavas-Bryant and J Bryant. During the course of field work for this research at Border Ranges NP and Mt Lewis NP John Grey helped and was able to contribute several months of his time. Other help was given by Sarah Maunsell, Casey Hall and Christy Harvey. Mt Lewis NP tree tagging was supervised by A. Nakamura. Conservation Volunteers Australia assisted with tree tagging at the Border Ranges transect. Funding for this project was provided by Griffith University and the Terrestrial Ecosystem Research Network (TERN) project.

References


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Chapter 3 Appendix

Table 3.5 Numbers of individuals, number of species and estimated and shared species encountered in LAM, BR and combined LAM and BR. Generally, we were able to sample between 70% and 90% of the total estimated species richness (ACE)

<table>
<thead>
<tr>
<th></th>
<th>Lamington</th>
<th>Total species</th>
<th>Estimated species</th>
<th>Total individuals</th>
</tr>
</thead>
<tbody>
<tr>
<td>All altitudes</td>
<td>865</td>
<td>1195.86 ± 23.1</td>
<td>11560</td>
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</tr>
<tr>
<td>300</td>
<td>173 ± 31.09</td>
<td>468.14 ± 20.26</td>
<td>582.5 ± 169.17</td>
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<tr>
<td>500</td>
<td>142.25 ± 52.67</td>
<td>461.63 ± 49.36</td>
<td>380.5 ± 173.56</td>
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</tr>
<tr>
<td>700</td>
<td>194.5 ± 24.41</td>
<td>684.89 ± 16.5</td>
<td>745 ± 124.03</td>
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</tr>
<tr>
<td>900</td>
<td>177 ± 30.22</td>
<td>656.81 ± 17.34</td>
<td>571.75 ± 166.08</td>
<td></td>
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<tr>
<td>1100</td>
<td>128.75 ± 13.35</td>
<td>393.1 ± 18.68</td>
<td>610.25 ± 194.46</td>
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<table>
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<th>Estimated species</th>
<th>Total individuals</th>
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<tr>
<td>300</td>
<td>147.75 ± 40.47</td>
<td>426.11 ± 8.52</td>
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<td>500</td>
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<td>700</td>
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<td>212.31 ± 10.77</td>
<td>1032.75 ± 209.01</td>
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<tr>
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<td>141 ± 12.35</td>
<td>203.68 ± 10.89</td>
<td>991.25 ± 484.23</td>
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<table>
<thead>
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<th></th>
<th>Mt Lewis</th>
<th>Total species</th>
<th>Estimated species</th>
<th>Total individuals</th>
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<td>17258</td>
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<td>400</td>
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<td>600</td>
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<tr>
<td>1000</td>
<td>143.5 ± 19.84</td>
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<td>701 ± 506.42</td>
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<tr>
<td>1200</td>
<td>169 ± 10.39</td>
<td>628.28 ± 19.04</td>
<td>1171 ± 231.91</td>
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Table 3.6 Moth species which met indicator species criteria as outlined in the Methods section (IndVal number greater than 0.7, occurred in numbers greater than 35 individuals, easy to identify), collected along the LAM transect in October 2006 and March 2008. See Figure 3.16 for photos of each indicator. The black bars indicate altitudinal restriction based on the indicator criteria.

<table>
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<tr>
<th>Species</th>
<th>Family</th>
<th>Subfamily</th>
<th>Genus</th>
<th>species</th>
<th>IndVal</th>
<th>P</th>
<th>Season</th>
<th>Fig.</th>
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<th>900</th>
<th>1100</th>
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<td>Asura</td>
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<td>0.729</td>
<td>0.014</td>
<td>Mar</td>
<td>1A</td>
<td></td>
<td></td>
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<td>Oct</td>
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<td></td>
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<td>Ectropis</td>
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<td>0.001</td>
<td>Mar</td>
<td>1D</td>
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<td>0.010</td>
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Table 3.7 Moth species which met indicator species criteria as outlined in the Methods section (IndVal number greater than 0.7, occurred in numbers greater than 35 individuals, easy to identify), collected along the BR transect in (a) April and (b) November 2010. See Figure 3.17 for photos of each indicator. The black bars indicate altitudinal restriction based on the indicator criteria.

<table>
<thead>
<tr>
<th>Species</th>
<th>Family</th>
<th>Subfamily</th>
<th>Genus</th>
<th>species</th>
<th>IndVal</th>
<th>P</th>
<th>Season</th>
<th>Fig.</th>
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Table 3.8 Moth species which met indicator species criteria as outlined in the Methods section, collected along the ML transect in November 2009 and April 2011. See Figure 3.18 for photos of each indicator. The black bars indicate altitudinal restriction based on the indicator criteria.

<table>
<thead>
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<th>Species</th>
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<th>Genus</th>
<th>species</th>
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<th>P</th>
<th>Season</th>
<th>Fig.</th>
<th>Altitude (m a.s.l.)</th>
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Figure 3.16 Altitudinally restricted moth species collected along the LAM transect, identified using our indicator selection criteria (see Table 3.6 for family and sub-family placements and altitudinal zonation). 1A, *Asura cervicalis* (Walker); 1B *Palpita unionalis* (Hubner); 1C, *Thallarcha homoschema* (Turner); 1D, *Ectropis bispinaria* (Guenée); 1E, *Dyscheralcis crimnodes* (Turner); 1F, *Thalatha bryochlora* (Meyrick); 1G, *Heterochasta conglobata* (Walker); 1H, *Xylodryas leptoxantha* (Turner); 1I, *Lyelliana dryophila* (Turner); 1J, *Larophylla amimeta* (Turner); 1K, *Eurychoria fictilis* (Turner); 1L, *Thallogama corticola* (Goldfinch); 1M, *Palaeosia bicosta* (Walker); 1N, *Thalatha trichroma* (Meyrick); 1O *Middletonia hemichroma* (Turner).
Figure 3.17 Altitudinally restricted moth species collected along the BR transect, identified using our indicator selection criteria (see Table 3.7 for family and sub-family placements and altitudinal zonation). 2A, Chorodna strixaria (Gueneé); 2B, Aethaloessa calidalis (Gueneé); 2C, Epidesmia tryxria (Gueneé); 2D, Ectropis fractaria (Gueneé); 2E, Lithosiinae spp. #1225; 2F, Pyrausta albisellaris (Hampson); 2G, Racotis maculata (Lucas); 2H, Noctuoidea spp. #74; 2I, Ethmia clytodoxa (Turner); 2J, Merodictya marmorata (Lucas); 2K, Termessa gratiosa (Walker), 2L, Comibaena mariae (Lucas); 2M, Yponomeuta myriosema (Turner); 2N, Syneora adelphodes (Meyrick); 2O, Anisozyga speciosa (Lucas). (cont. next page).
Figure 3.17 cont. Altitudinally restricted moth species collected along the BR transect (cont). 2P, Notodontidae spp # 216; 2Q, Xylodryas leptoxantha (Turner); 2R, Tyspanodes metachrysialis (Lower); 2S, Lophosigna catasticta (Turner); 2T, Heterochasta conglobata (Walker); 2U, Lyelliana dryophila (Turner); 2V, Larophylla amimeta (Turner); 2W, Dyscheralcis crimnodes (Turner); 2X, Maceda mansueta (Walker); 2Y, Middletonia hemichroma (Turner); 2Z, Noctuidae spp. #299.
Figure 3.18 Attitudinally restricted moth species collected along the ML altitudinal transect, identified with IndVal analysis, (see table 3.8 for family and sub-family placements and altitudinal zonations). 3A, *Teulisna bipunctata* (Walker); 3B, *Lyclene pyraula* (Vollenhoven); 3C, *Atteva charopis* (Turner); 3D, *Collinsa* sp; 3E, Lithosiinae spp #998; 2F, *Nyctimera luctuosa* (); 2G, *Nyctimera baulus* (Boisduval); 2H, *Maceda mansueta* (Walker); 2I, *Endotricha mesenterialis* (Walker).
Chapter 4

Rainforest moths and altitude: family to family differences in subtropical and tropical rainforests

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Abstract

Within the Lepidoptera, different moth families and subfamilies have contrasting life histories and, as such, respond differently to biotic and abiotic conditions. Here, we explore how the major moth family-groups respond to biotic and abiotic gradients associated with changing altitude, and to link moth family-level differences to their life history characteristics and vegetation changes across altitude. We sampled moths along elevational transects in sub-tropical rainforest at Border Ranges NP, NSW and Lamington NP, Qld, and tropical rainforest at Mt Lewis NP, Qld. Both sub-tropical transects spanned elevations from 300m to 1100m a.s.l.

Each transect consisted of 20 study plots, with four replicate plots within each of five elevational bands, separated by 200 vertical metres. Elevational bands at both subtropical transects were located at 300, 500, 700, 900, 1100m a.s.l., while at the tropical transect they were located at 400, 600, 800, 1000 and 1200m a.s.l. Each transect was sampled twice, at the beginning and the end of the wet season. A total of 69667 individuals were sampled belonging to 2304 species across our sub-tropical and tropical altitudinal transects.

The four largest family groups were investigated – Geometridae, Noctuidae, Pyraloidea (Crambidae + Pyralidae) and Arctiidae, which comprised between 82 to 85% of the total fauna sampled at each transect. Different family-groups responded differently to elevational change. Geometridae, Pyraloidea and Arctiidae all showed clear elevational signals, whereas Noctuidae did not. The proportion of species belonging to each of the target family-groups, and subfamilies within the Geometridae did not change consistently across elevation, in contrast to previous studies in Ecuador and Borneo, which showed strong elevational shifts in taxonomic composition. Differences in stratification amongst Lepidoptera families may be explained by parallel elevational patterns of vegetation, host plant information, and life histories across families. These results
may reflect the processes of community assembly across adjacent climates and inform the selection of indicator species for monitoring responses to future climate change.

Introduction

Habitat gradients provide an effective method of examining the ecological processes that drive community patterns and ecosystem dynamics (Pianka 1966, Whittaker 1972, Menge and Sutherland 1976). Recently there has been an increase in the use of altitudinal gradients to investigate climatic and other mechanisms driving species turnover and community assembly (Gagne 1979, Hebert 1980, Lieberman et al. 1996, Vázquez and Givnish 1998, Bravo et al. 2008). Altitudinal gradients are of particular interest because they contain many ecotonal shifts within a small geographical area, allowing for comparisons between adjacent, but environmentally contrasting sites (Butterfield et al. 1991, Körner 2007). With increasing altitude, a number of co-varying abiotic factors change in a predictable manner. Temperature decreases by approximately $0.6^\circ$C for every 100m increase in altitude (in dry air) (Jacobson 2005). There is a general pattern of increasing moisture levels with increasing altitude (Fowler et al. 1988) which, at the tops of forested mountains is commonly heavily influenced by the cloud cap. Moisture increases dramatically from the base of the cloud cap, due to horizontal precipitation in direct contact with soil and vegetation. These shifts in abiotic factors influence the distribution of organisms such as rainforest insects (Hodkinson 2005).

Assemblages of many groups of insects show clear patterns of turnover associated with altitude (Wolda 1987, Brehm et al. 2003, Botes et al. 2006, Dial et al. 2006, Burwell and Nakamura 2011). Studies of Lepidoptera along ecological gradients have been particularly useful in interpreting ecosystem changes because of their almost universally herbivorous life histories, which tightly link species to the availability of host plants (Holloway et al. 1992). Moth distributions may be influenced directly by factors such as precipitation and temperature through each
species’ physiological tolerance envelope or indirectly, through the distribution of host plants (Schulze et al. 2001). Moth assemblages have been demonstrated to respond to environmental changes in a variety of terrestrial ecosystems, including rainforests, temperate forests and agro-ecosystems (Beccaloni and Gaston 1994, New 1997, Brown and Freitas 2000, Ricketts et al. 2001) and selected moth species, subfamilies and families have frequently been identified as indicators of ecosystem change (Holloway 1985, Holloway et al. 1992, Scoble 1992, Intachat et al. 1997, Beck et al. 2002). Families within the Lepidoptera may respond in different ways to environmental gradients, driven by a range of factors including availability of host plants, thermal tolerances, competition and predation (Holloway 1987, Brehm and Fiedler 2003).

The families and subfamilies within Lepidoptera represent sets of species with often contrasting biologies in terms of life-history strategies, food-plant preferences and vagility (Common 1990) which, in studies elsewhere in the world, have underpinned differential responses to altitude (Brehm et al. 2003, Axmacher et al. 2004, Hilt and Fiedler 2005, Hodkinson 2005, Fiedler et al. 2008, Nöske et al. 2008). To gain further insight into the processes underlying community assembly along the forested climatic gradients that we have studied in tropical and subtropical Australia, we present results on distributions, diversity and similarity patterns of four major family-group moth taxa: the Geometridae, Arctiidae, Noctuidae and Pyraloidea'. Together, these four taxa make up approximately 82% of the total Australian moth fauna. In addition, we investigate elevational patterns in species richness in the geometrid subfamilies Ennominae, Geometrinae, Larentiinae, Oenochrominae and Sterrhinae. This family has been targeted for more in-depth analysis as it is relatively well known taxonomically; and has been a target group for many other elevational studies of moths, which have shown that the Larentiinae are particularly dominant at high altitudes

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1 In our analyses the family concepts of Arctiidae and Noctuidae follow those of Neilsen et al. (1996). In terms of the recently proposed classification of the Noctuoidea of Zahiri et al. (2011) our noctuid taxa translate as follows: Arctiidae becomes Noctuidae: Arctiinae and Noctuidae becomes ‘[Noctuidae-(Lymantriinae) + Arctiinae +Erebidae+Nolidae(partim)]’. 
We hypothesize that family-level differences in life histories, such as host plant requirements, physical tolerances and phenology, will produce dissimilar altitudinal responses across these sub-assemblages of moths.

We sampled moths along two altitudinal gradients in sub-tropical rainforest, and one altitudinal gradient in tropical rainforest, Queensland, Australia, to investigate a range of ecological questions. Here we focus on the differences among families and sub-families within the Lepidoptera across elevations. We established permanent transects in each of these locations, utilising the continuous mature rainforest available from about 300m a.s.l. to 1100m a.s.l. in the sub-tropics, and 400m to 1200m a.s.l. in the tropics. We sampled moth assemblages at the beginning and the end of the wet season at each location, in order to incorporate any temporal variation in moth family patterns. Through examining the family-level differences assemblages across these three altitudinal gradients, we seek to address the following hypotheses:

H₁ (1) families within the lepidoptera will respond to altitude in different ways, exhibiting contrasting patterns of species richness and assemblage structure across altitudinal gradients
H₁ (2) sub-families within the Geometridae with contrasting life-histories will respond to altitude in different ways
H₁ (3) the altitudinal distribution of families within the lepidoptera will be different between tropical and sub-tropical rainforests.

Methods

Experimental Design

This research was based on three altitudinal transects – two in sub-tropical rainforest (Border Ranges NP and Lamington NP) and one in tropical rainforest (Mt Lewis NP), Queensland, Australia. At each location we established 20 study
plots within a single catchment (Figure 4.1). Each plot comprised a central 20m x 20m square botanical plot. Four plots were located at each of five altitudes centred on 300m, 500m, 700m, 900m and 1100m a.s.l. at Border Ranges and Lamington, and 400m, 600m, 800m, 1000m and 1200m a.s.l. at Mt Lewis. Plots were located within 50m elevation of their target altitude. As well as altitude, study plots were chosen on the basis of accessibility and where possible they were non-riparian. We aimed that each should be at least 400 horizontal metres from any other plot, which was possible in most cases, except for two Border Ranges plots at 300m a.s.l. which were necessarily separately by approximately 250m. Each transect was sampled at the beginning and end of the austral wet season. At Border Ranges sampling was undertaken from the 4th to the 22nd of April 2011 (the end of the 2010-11 wet season) and from the 27th of October to the 12th of November 2011 (beginning of the 2011-12 wet season). At Lamington the plots were sampled from the 14th until the 30th of October 2006 and from the 10th of March until the 2nd of April 2007. Sampling at Mt Lewis occurred between 21st Nov – 13th Dec 2009, and 1st – 18th of April 2011.

Study sites

Subtropical rainforest

The Tweed Caldera located in south-eastern Queensland and north-eastern NSW, Australia, contains large tracts of more or less undisturbed sub-tropical rainforest (Hoback 2012). Biogeographically this region contains an unexpectedly biodiverse fauna, capturing the northerly range limits of many cooler adapted species and the southern limits of a suite of northerly taxa, the so-called McPherson-Macleay overlap zone (Burbridge 1960). Several National Parks are located within this bioregion, the largest of which are the Border Ranges NP in northern New South Wales and Lamington NP in south-east Queensland. This study was conducted along two subtropical altitudinal transects, through continuous rainforest, one in Border Ranges NP, NSW and the other in Lamington NP, Qld. These transects are separated by 20km of continuous rainforest, within the Gondwana Rainforests of Australia World Heritage Area.
Both locations share a climate in which a drier winters alternate with wetter summers. The Lamington plots were located on north-easterly slopes, and the Border Ranges plots on south-westerly slopes, to encompass different suites of environmental conditions. With increasing altitude, there is a shift from warmer conditions, drier soils and low organic soil carbon to lower temperatures with high soil moisture and soil organic carbon. The cloud cap, the lower limit of which sits between 800m - 900m a.s.l. depending on the season and weather conditions, has a strong influence on local climate, driven by higher orographic rainfall. A full account of the local and regional climate of the Lamington transect is presented in Strong et al. (2011) and Laidlaw et al. (2011). Broad vegetation types change from complex notophyll vine forest at the low and mid-altitudes to simple microphyll fern forest (sensu Webb and Tracey 1978) which only occurs above 1000m a.s.l. and is dominated by Antarctic Beech (Nothofagus moorei) (Hutley 2006).

Border Ranges National Park, ca 28º24S, 153º4.8E (hereafter 'Border Ranges') was established in 1979 and extended significantly in 1983. It encompasses 31 683 hectares of forested land of which 15 929 hectares lie within the Gondwana Rainforests of Australia WHA (Macdonald and Hunter 2010). Before establishment of the National Park the forest was selectively logged in places but in the ensuing 30 years has returned to a mature well-structured state (McDonald 2011). Our transect was established entirely within the Sheep Station Creek catchment (Figure 4.1 (a)) which is generally located on basaltic basement weathering to basic krasnozem soils (Beckman & Thomson 1976). All trees with a dbh greater than 5 cm were counted and identified to species in 2010 and 2011. A total of 111 tree species with dbh more than 5cm were recorded from these plots. Dominant trees within the 300m, 500m and 700m a.s.l. plots included Diospyros pentamera, Archontophoenix cunninghamiana and Argyrodendron trifoliatum. Above 900m a.s.l. there is a gradual reduction in tree diversity and at the highest elevations Antarctic beech, Nothofagus moorei is dominant. Other common species at and above 900m a.s.l. include Polyosma cunninghamii, Cyathea leichhardtiana, Doryphora sassafras and Atractocarpus benthamianus (R. J. Hunter & S. Horton, unpublished results).
Figure 4.1 Spatial arrangement of study plots along the three altitudinal transects (a) Border Ranges National Park, NSW; (b) Lamington National Park, West Canungra Creek catchment, Qld and (c) Mt Lewis National Park, Wet Tropics WHA, north Qld. Plot labels indicate the elevational band followed by the plot 'number', A-E.
**Lamington National Park**, ca 28°13’S, 153°8.6’E (hereafter ‘Lamington’) was established in 1915 and encompasses 20,590 hectares, all of which lies within the Gondwana WHA (McDonald 2010). The forests within the National Park have never been logged and, apart from the establishment of walking tracks, may be regarded as pristine. The study transect (the ‘IBISCA-Queensland transect’) (Figure 4.1(b)) was established entirely within the West Canungra Creek catchment. Soils and basement rock are very similar to those of Sheep Station Creek (Walter et al. 1998). The flora of the transect have been described in detail by Laidlaw et al. 2011a. A total of 282 species of tree with dbh greater than 5cm were recorded across the 20 plots. The lower elevation subtropical forest plots were dominated by species including *Argyrodendron actinophyllum*, *A. trifoliolatum* and *Pseudoweinmannia lachnocarpa* whereas the higher elevation forests had dominants including *Nothofagus moorei*, *Quintinia sieberi* and *Callicoma serratifolia* (Laidlaw et al. 2011). The principle difference between the two subtropical transects is that the Border Ranges plots generally have south-westerly aspects whereas the Lamington plots are largely north-westerly facing. The Lamington transect was established and extensively studied as part of the IBISCA-Queensland project: a major international, collaborative project (Kitching et al. 2011). A wide range of preliminary results from this project have been published (Kitching et al. 2011). Assemblages of ‘macrolepidoptera’ responded strongly to altitude and a number of attitudinally restricted species, including several confined to the high elevation ‘cloud’ forests above 900m a.s.l., were identified (see Chapter 2) (Ashton et al. 2011). These form part of a multi-taxon predictor set available for future monitoring of bioclimatic shifts.

**Tropical rainforest**

*Mt Lewis National Park* ca 16°33’S, 145°19.6’E. (hereafter ‘Mt Lewis’) is located in the Australian Wet Tropics World Heritage Area (WTWHA), and covers 229km² of primary and secondary rainforest. The area has undergone mining for alluvial tin and tungsten and some selective logging which targeted Kauri (*Agathis australis*)
and Red Cedar (*Toona ciliata*). The Mt Lewis transect consists of five altitudinal bands, 400m, 600m, 800m, 1000m and 1200m a.s.l., with five replicate plots in each. The 400m a.s.l. plots were accessed by the Mossman – Mt Molloy road, and all other plots were accessed from Mt Lewis Road (see figure 4.1 (c)) for a map of the Mt Lewis plots). As in the Border Ranges and Lamington transects, 20m x 20m plots were permanently tagged and trees with a dbh greater than 5cm were identified. Botanical identification was carried out by Bill McDonald of the Queensland Herbarium, and is still underway. The vegetation analyses presented here are based on two (of the four) plots per altitudinal band. Vegetation is characterized as complex notophyll vine forest, dominated by *Alstonia muelleriana* and *Cryptocarya lividula* at the 400m a.s.l. plots, which have been disturbed by logging and impacts of cyclones. Towards the lower end of the transect dominant species included *Brombya platynema*, *Argyroderon perlatum* and *Franciscodendron laurifolium*, and at the high altitude plots *Doryphora aromatic* and *Niemeyera* sp. “Mt Lewis” were dominant. Temperature, rainfall and other environmental data (presented in chapter 3) were collected by researchers at James Cook University, using weather stations and Bureau of Meteorology data.

**Moth Sampling**

Moths were sampled using modified Pennsylvania light traps (Frost 1957) fitted with 12 volt gel-cell batteries. Traps were set daily with a fully charged battery, and ran for about 12 hours from 6pm to 6am. The trap design employs a vertical actinic tube surrounded by three transparent vanes that knock down insects attracted to the light into a collecting bucket below. The bucket contained a Sureguard® resin strip impregnated with Dichlororvos™ insecticide which killed moths *in situ*. Traps were emptied daily and all arthropods caught were brushed into sample containers and taken back to a field laboratory and then the traps were re-set for the following night. Trapping occurred for three nights at each plot on each of the two sampling occasions at each location. Two traps were set simultaneously at each plot on each night, one located close to ground level and
one at 30-35m in the canopy above. Vertical stratification of moth species can result in distinct ground and canopy faunas (Schulze et al. 2001, Brehm 2007). Putting light traps at both ground and canopy level ensured the widest sampling of moth diversity. During each sampling period, there were scattered trap failures. At Border Ranges a total of 120 (20 plots x 3 nights x canopy and ground) were collected in April 2010 (end of the wet season), and 108 samples were collected in October/November 2010 (beginning of the wet season). At Lamington a total of 99 samples were collected in October 2006, and 108 in March 2007. At Lamington, two of the 500m a.s.l. plots in March 2007 and two of the 300m a.s.l. plots in October 2006 were not sampled, due to time constraints. At Mt Lewis a total of 115 samples were collected in November 2009, and 120 in April 2011.

All moths with a wing length greater than 1 cm were targeted for identification. Moths were sorted to morphospecies and each morphospecies was assigned a unique code number, pinned and dried. As sorting proceeded, a reference collection of at least 6 representatives of each morphospecies was assembled. Individuals in a given sample that could be readily identified as belonging to an existing numbered morphospecies were recorded in a data book, and those specimens that could not be identified were pinned and preserved. Consistent morphospecies numbers were assigned to all specimens collected across the four sampling periods at Lamington and Border Ranges. Morphospecies were identified to family level, and where possible as described species by reference to named specimens in the collections of the Queensland Museum, Australian National Insect Collection, Australian Museum or illustrated in Moths of Australia (Common 1990) and/or CSIRO’s Australian Moths Online (CSIRO 2004).

Analysis

Data from the maximum of 6 samples collected at each plot (three nights of trapping at canopy and ground level) were combined to produce one dataset per
plot. For multivariate analysis of community assemblage patterns across altitude, each sampling occasion (April and November 2010 at Border Ranges, October 2006, March 2007 at Lamington, and November 2009 and April 2011 at Mt Lewis) were analysed separately. Only moths belonging to the four major groups: Pyraloidea, Geometridae, Arctiidae and Noctuidae were targeted for analysis. Multivariate analyses were conducted using the package Plymouth Routines in Multivariate Ecological Research [PRIMER 6™] (Clarke and Gorley 2006), investigating the differences in moth assemblages across altitudinal zones. Permutational multivariate analysis of variance (PERMANOVA), carried out in PRIMER 6 with PERMANOVA+ add-on software (Anderson et al. 2008), was used to test for significant differences in assemblage composition between altitudinal groups, and was run using the Bray-Curtis dissimilarity measure (Bray and Curtis 1957), under 9999 permutations. Mantel tests comparing moth assemblages of each family with vegetation assemblages at each of the altitudinal plots, were conducted using the RELATE function in PRIMER6. PRIMER was also used to compare each moth assemblages with the available environmental variables for each location. BIOENV (Biological – Environmental relationships) procedure, based on Spearman’s rank and Euclidean distances, was used to produce correlations between environmental and moth assemblage data across altitude at each location. Environmental variables which were significantly correlated (p>0.05) with moth assemblages were superimposed onto NMDS ordination plots to indicate the direction and strength of each relationship.

We tested to see if the proportion of each target family group – Geometridae, Pyraloidea (Crambidae + Pyralidae), Arctiidae and Noctuidae, changed across elevations (at p < 0.05). We then repeated this analysis for subfamilies within the Geometridae – Ennominae, Geometrinae, Larentiinae, Sterrhinae and Oenochrominae. Binomial logistic regression was conducted in the R statistical environment (R Development Core Team 2011), to assess proportions of faunal composition of species richness across altitude for each family group. Logistic regression is recommended for analysis of this nature (rather than traditional arcsine transformations) as it allows for greater interpretability (Warton and Hui
We employed the generalized linear model: `model<-glm(y~Altitude,binomial)`, in which y (the ratio of each family or sub family to all other families or subfamilies) was modelled as a function of altitude, a continuous explanatory variable, assuming an error distribution from the binomial family. Model simplification was conducted by selecting the model in each analysis with the smallest Akaike information criterion (AIC).

Results

During the six field sessions conducted in this study, a total of 38715 individual moths belonging to 615 morphospecies were sampled at Border Ranges, 11379 individuals, belonging to 865 morphospecies were sampled at Lamington and at Mt Lewis, there were 17258 individuals, belonging to 1134 species. A mass emergence of the grass webworm, *Herpetogramma licarsisalis* (Walker, 1859) in April 2010 at Border Ranges resulted in 21425 individuals of this species being captured. This species is a pasture pest, and was observed in road-side grass areas along the altitudinal transect. We removed this species from the data, in order to examine community-level patterns without this highly dominant species, based on the assumption that it is probably not characteristic of rainforest assemblages, being a well known grass-feeding pest species (Common 1990). Accordingly, we have included 17290 individual moths in our Border Ranges analyses.

Altitudinal stratification

Results of PERMANOVA tests between adjacent pairs of altitudinal assemblages showed that Arctiidae and Geometridae showed the most consistent altitudinal stratification, and Pyraloidea and Noctuidae showed a lower degree of altitudinal stratification (Table 4.4 (a), (b), (c) and (d)). Geometridae showed strong altitudinal stratification, demonstrated by significant differences between
PERMANOVA pair-wise comparisons (Table 4.4 (a)). In the October 2006 sampling at Lamington however, all family groups displayed weak altitudinal stratification, which may be due to the smaller samples collected in this season (3490 individuals, compared with 7889 in March 2007). Pyraloidea exhibited strong altitudinal stratification at Mt Lewis, and at Border Ranges in April 2010, and weak altitudinal stratification at Border Ranges in November 2010 and at Lamington (Table 4.4 (b)). Arctiidae showed strong altitudinal stratification at all locations except between some altitudinal pairs at Mt Lewis in November 2009 (Table 4.4 (c)). Noctuidae showed the least altitudinal stratification (Table 4.4 (d)).

When we compared the moth family-level assemblage data with the available environmental data for each altitudinal transect, we found that Noctuidae showed the lowest correlation with environmental variables collected along the altitudinal gradients. See Table 4.1 (a), (b) and (c) for a summary of these results, and Tables 4.6, 4.7 and 4.8 for detailed results. At Lamington in October 2006, the Noctuidae did not correlate with any environmental factors (tree species richness, soil properties (moisture, pH, organic matter, potassium and carbon) fog events, temperature (maximum, minimum or median) or elevation. In the March 2007 results, however, assemblages of all families, including Noctuidae, were correlated with these environmental variables. At Border Ranges, Noctuidae correlated with low temperature and altitude, but no other factors. At Mt Lewis, all family assemblages correlated with altitude, rainfall, high, low and average temperatures, soil nitrogen and phosphorus in the November 2009, however in April 2011, Noctuidae was the only family that did not correlate with average, high and low temperature, soil nitrogen and soil phosphorus.

Other family groups had mixed responses to environmental variables. Geometridae were generally strongly correlated with most variables, especially at Mt Lewis. Arctiidae and Pyraloidea generally showed significant correlations with environmental variables. Plant species richness did not change predictably with altitude, and we generally found no significant correlations between moth family
assemblages and plant species richness. Some soil chemical properties, including soil sodium, calcium and carbon at Mt Lewis, were not significantly correlated with moth family assemblages across altitude,
Table 4.1 Summary of family level correlations (positive signs indicate a significant correlation, negative signs indicate no significant correlation) for available environmental data at Lamington, Border Ranges and Mt Lewis.

<table>
<thead>
<tr>
<th>Lamington</th>
<th>High temp</th>
<th>Low temp</th>
<th>Ave temp</th>
<th>Altitude</th>
<th>Plant rich</th>
<th>Soil K</th>
<th>Soil C</th>
<th>Fog events</th>
<th>Soil organics</th>
<th>Soil pH</th>
<th>Soil moist</th>
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</thead>
<tbody>
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<td></td>
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<td>Mar 07</td>
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<td>Mar 07</td>
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<tr>
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<td>+</td>
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<td>+</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>+</td>
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</tr>
<tr>
<td>Pyral</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
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<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
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<td>+</td>
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<table>
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<th>Border Ranges</th>
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<th>Ave temp</th>
<th>Altitude</th>
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<tr>
<td>Pyral</td>
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<tr>
<td>Arct</td>
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<td>Noct</td>
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<td>-</td>
<td>+</td>
<td>+</td>
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</table>

<table>
<thead>
<tr>
<th>Mt Lewis</th>
<th>High temp</th>
<th>Low temp</th>
<th>Ave temp</th>
<th>Rainfall</th>
<th>Altitude</th>
<th>Plant rich</th>
<th>Soil P</th>
<th>Soil N</th>
<th>Soil temp</th>
<th>Soil clay</th>
<th>Soil sodium</th>
<th>Soil carbon</th>
<th>Soil calcium</th>
</tr>
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<td>Apr 11</td>
<td>Nov 09</td>
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<td>Nov 09</td>
<td>Nov 09</td>
<td>Nov 09</td>
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</tr>
<tr>
<td>Geom</td>
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<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
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</tr>
<tr>
<td>Pyral</td>
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<td>+</td>
<td>+</td>
<td>-</td>
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<tr>
<td>Arct</td>
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<td>+</td>
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<td>-</td>
</tr>
<tr>
<td>Noct</td>
<td>+</td>
<td>-</td>
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<td>-</td>
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<td>-</td>
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<td>+</td>
<td>+</td>
<td>+</td>
</tr>
</tbody>
</table>

137
When we compared the patterns of assemblage composition of the four moth family groups to that of the vegetation we found that Geometridae and Pyraloidea were the most highly correlated (Table 4.2). Geometrid assemblages strongly correlated with vegetation at Border Ranges in April (Rho = 0.54, p = 0.001) and November (Rho = 0.51, P = 0.001), and at Mt Lewis in November 2009 (Rho = 0.56, P = 0.001). Pyraloidea were highly correlated with vegetation assemblages at Lamington in October 2006 (Rho = 0.62, P = 0.001) and Mt Lewis in November 2009 (Rho = 0.59, P = 0.001) and April 2011 (Rho = 0.53, P = 0.001). Arctiid assemblages were highly correlated with vegetation at Mt Lewis in April 2011 (Rho = 0.051, p = 0.001).

Table 4.2 Relationship between assemblage structure of moth families and vegetation. Assemblages of Geometridae and Pyraloidea were most highly correlated with vegetation composition. Spearman's rank correlations (Rho) less than 0.5 are shaded.

<table>
<thead>
<tr>
<th></th>
<th>BR APR</th>
<th>BR NOV</th>
<th>LAM OCT</th>
<th>LAM MAR</th>
<th>ML NOV</th>
<th>ML APR</th>
</tr>
</thead>
<tbody>
<tr>
<td>Geometridae</td>
<td>0.541</td>
<td>0.001</td>
<td>0.519</td>
<td>0.001</td>
<td>0.326</td>
<td>0.002</td>
</tr>
<tr>
<td>Pyraloidea</td>
<td>0.222</td>
<td>0.001</td>
<td>0.415</td>
<td>0.001</td>
<td>0.612</td>
<td>0.001</td>
</tr>
<tr>
<td>Arctiidae</td>
<td>0.344</td>
<td>0.001</td>
<td>0.259</td>
<td>0.001</td>
<td>0.412</td>
<td>0.096</td>
</tr>
<tr>
<td>Noctuidae</td>
<td>0.315</td>
<td>0.001</td>
<td>0.347</td>
<td>0.001</td>
<td>0.098</td>
<td>0.114</td>
</tr>
</tbody>
</table>
Summary of results

Pyraloidea generally did not show strong altitudinal stratification, except at our tropical location - Mt Lewis (Table 4.4 (b)). Pyraloidea were commonly significantly correlated with environmental variables at most locations and significantly correlated with the vegetation assemblage pattern at Mt Lewis, and at Lamington (in the October 2006 sample).

Geometridae showed strong altitudinal stratification - pair-wise comparisons between adjacent altitudinal bands were significantly different, except at Mt Lewis in November 2011, and Lamington in October (where samples were much smaller) (Table 4.4 (a)). On most occasions geometrid assemblages were significantly correlated with key environmental variables, including altitude, temperature and rainfall. Geometrid assemblages significantly correlated with the vegetation assemblage at Border Ranges, and Mt Lewis in November.

Arctiidae were strongly altitudinally stratified with significant differences in pair-wise tests between adjacent altitudinal bands at all locations except Mt Lewis in November 2011 (Table 4.4 (c)). Arctiidae were strongly correlated with most environmental vectors, including altitude, temperature and rainfall, at all plots. The arctiid assemblage was significantly correlated with the vegetation assemblages at Mt Lewis in April 2011 (with a Rho greater than 0.5) and significantly correlated at Border Ranges (in both seasons) and Lamington in March.

Noctuidae did not show strong altitudinal signals. Pair-wise comparisons between adjacent altitudinal bands generally showed no significant differences (Table 4.4 (d)). Noctuidae also exhibited the lowest correlation with environmental vectors, with no correlations at Lamington in October 2006, and Mt Lewis in April 2011. Noctuidae also showed the lowest degree of correlation to vegetation assemblages across altitude.

Species richness

At both Border Ranges and Lamington, Geometridae was the most diverse family, contributing 38% and 25% respectively to overall moth richness, while at Mt Lewis, Pyraloidea was most diverse contributing 34% of the total number of
species (Figure 4.2 (a-c)). Figure 4.3 (a-c) shows the proportional representation of each family, within each of the five altitudinal bands at the three locations. Conjointly the four target taxa (Geometridae, Pyraloidea, Arctiidae and Noctuidae) represented between 70% (900m a.s.l. plots at Lamington) and 84% (300m a.s.l. plots at Border Ranges) of our total moth species after the exclusions mentioned above. The proportion of families did not change across altitude at all locations (Table 4.3 (a)), with the exception of Geometridae at Lamington – where there was a slight increase with altitude.

The proportion of geometrid sub-families generally did not change with altitude (Table 4.3 (b)), with the exception of Lamington, where the number of species in each of the Geometrinae, Sterrhinae, Larentiinae and Oenochrominae were as low as 2 species at some elevations (Sterrhinae at 1100m a.s.l.) which produced a significant result. Figure 4.4 illustrates proportional representation of each of the geometrid subfamilies (Ennominae, Larentiinae, Oenochrominae, Geometriinae, Sterrhinae) to the overall geometrid species richness across altitude. Ennominae were the dominant subfamily at all locations and all altitudes, contributing 50% of the total Geometridae species at Border Ranges, 41% at Lamington and 59% at Mt Lewis.

Table 4.3 Results of z-test of proportion of species across altitude (a) families (Geometridae, Arctiidae, Pyraloidea, Noctuidae and others) and (b) Geometridae subfamilies (Ennominae, Geometrinae, Sterrhinae, Larentiinae and Oenochrominae) at Border Ranges, Lamington and Mt Lewis. Significant differences in the proportion of groups across altitude are shaded.

<table>
<thead>
<tr>
<th>(a)</th>
<th>Geometridae</th>
<th>Arctiidae</th>
<th>Pyraloidea</th>
<th>Noctuidae</th>
<th>Others</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>z</td>
<td>P</td>
<td>z</td>
<td>P</td>
<td>z</td>
</tr>
<tr>
<td>BR</td>
<td>0.630</td>
<td>0.471</td>
<td>-0.116</td>
<td>0.908</td>
<td>-0.063</td>
</tr>
<tr>
<td>LAM</td>
<td>4.058</td>
<td>0.001</td>
<td>-0.246</td>
<td>0.806</td>
<td>-1.136</td>
</tr>
<tr>
<td>ML</td>
<td>0.471</td>
<td>0.638</td>
<td>0.660</td>
<td>0.509</td>
<td>-0.772</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>(b)</th>
<th>Ennominae</th>
<th>Geometrinae</th>
<th>Sterrhinae</th>
<th>Larentiinae</th>
<th>Oenochrominae</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>z</td>
<td>P</td>
<td>z</td>
<td>P</td>
<td>z</td>
</tr>
<tr>
<td>BR</td>
<td>0.653</td>
<td>0.513</td>
<td>-0.547</td>
<td>0.585</td>
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</tr>
<tr>
<td>LAM</td>
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<td>0.241</td>
<td>-3.347</td>
<td>0.001</td>
<td>-3.447</td>
</tr>
<tr>
<td>ML</td>
<td>-0.132</td>
<td>0.895</td>
<td>-0.539</td>
<td>0.589</td>
<td>-0.034</td>
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</table>
Figure 4.2 The relative overall contributions of the major moth families (species richness) for two combined seasons at (a) Border Ranges, (b) Lamington and (c) Mt Lewis
Figure 4.3 Relative proportions of moth families' species richness at each altitudinal band for two combined seasons (the beginning and end of the wet season) at (a) Border Ranges, (b) Lamington and (c) Mt Lewis. The proportion of each of the families remains stable across altitudes.
Figure 4.4 Proportion of species richness (%) across altitude for each of the Geometridae subfamilies – Ennominae (ENNO), Geometrinae (GEOM), Sterrhinae (STER), Larentiinae (LARE) and Oenochrominae (OENO) at (a) Border Ranges, (b) Lamington and (c) Mt Lewis. Ennominae is the dominant subfamily at all altitudes and locations. There is no strong pattern of increasing or decreasing proportion of subfamilies at any of the altitudinal gradients. Figure (d) indicates the proportion of species richness within the Geometridae subfamilies.
Discussion

Our results show that families within the Lepidoptera may respond in different ways to environmental gradients. We found that the Noctuidae was the least altitudinally stratified family, and the other families that were targeted, Geometridae, Arctiidae and Pyraloidea (Crambidae + Pyralidae), exhibited much stronger altitudinal stratification. Additionally, we found that the taxonomic composition of moth assemblages did not change across altitude in subtropical or tropical Australian rainforests and there were no clear differences in altitudinal signals between our sub-tropical locations within the same region – Lamington and Border Ranges, or between sub-tropical and tropical rainforest altitudinal gradients at Mt Lewis. Our results contrast with other studies in the tropics which have shown that proportions of moth families shift dramatically across altitudes. Holloway (1987) found that patterns of species richness across altitude differed between families, with Geometridae increasing in species richness with increasing altitude (mainly through increased Larentiinae richness). We observed no altitudinal change in proportions of species at the family or subfamily level within the Geometridae. Here, we suggest some explanations for our results, based on the biology and life histories of the families and subfamilies.

We found no clear differences in the proportional representation of the major family groups to the species pool of moth assemblages between the sub-tropical and tropical locations, except an increase in the proportion of Pyraloidea encountered in the tropics. The proportional representation of major family groups as observed at each location generally reflected the Australia-wide proportions of moth families. For example, Geometridae represent 26% of described macrolepidopteran species (+ Pyraloidea) in Australia, and we found that 25% of species at Lamington were Geometridae, 38% geometrids at Border Ranges and 37% Geometridae at Mt Lewis. Pyraloidea, on the other hand, represent 24% of described Australian species (macrolepidoptera + Pyraloidea), and in our locations, represented 12% of species at Border Ranges, 20% of species
at Lamington, and 34% of species at Mt Lewis, indicating higher than average representation of Pyraloidea in the tropics, which are generally considered to be a tropical radiation (Common 1990).

The observed patterns of altitudinal distributions of different family groups are presumably the products of interacting niche dimensions for each species, within each family, reflecting their environmental tolerances and biological interactions. The survival of an individual moth will be determined by host plant availability, physical conditions for growth, availability of suitable pupation sites and its ability to avoid predators amongst many other factors (Common 1990). In Australia, there is very little information on the life histories of most moth species, however, it is possible to make generalisations based on the known food preferences of each family group. Studies of host specificity have indicated low rates of monophagy, and many tropical herbivores feed on multiple plant genera (Novotny et al. 2002). However, moths are thought to be somewhat family specific (Scoble 1992). A study of moth assemblages suggested that less than 10% of moth species feed on more than three families of plants (Bernays and Graham 1988). Therefore, acknowledging the limited information available on host plants of Australian rainforest moths, we are able to examine relationships between environmental factors, vegetation assemblages and moth herbivores across altitudinal gradients.

The four groups focused on for this study showed disparate patterns and have contrasting biological characteristics. Geometridae are a large family with an estimated 21000 species described worldwide (Scoble 1992), and 1300 described Australian species. Host plants vary widely and include woody vines, Eucalyptus, Acacia and gymnosperms. Geometridae showed strong altitudinal stratification, suggesting low vagility and close association with host plants across altitudes. Geometridae were the most species-rich family in our subtropical locations (and the second richest following Pyraloidea at our tropical location).
At Lamington, the proportional representation of Geometridae to species richness increased at the highest altitude plots, suggesting the environmental conditions at 1100 m a.s.l. are not a physiological constraint for this group. Harsher environmental conditions may be a disadvantage to non-geometrids, reflected in decreased proportions at high altitudes, when compared to Geometridae. Geometridae are able to fly at sub-zero temperatures, a physiological adaptation in some tympanate moths, which enable them to fly at low thoracic temperatures, due to their low wing loading (Heinrich and Mommsen 1984). Subfamily patterns within the Geometridae have been explored across altitudinal gradients in Borneo (Holloway 1987) and Ecuador (Brehm et al. 2003) and show that the proportional representation of species of Larentiinae is greater at higher altitudes. It has been suggested that the Larentiinae encountered at high altitudes are cool-adapted species (Holloway 1987). Brehm et al. (2003) suggested that an evolutionary advantage of adapting to cold, high altitude environments could be reduced predation due to a sharp decrease in bat numbers with increasing altitude. The Larentiinae (generally feeding on herbaceous plants (Holloway 1997)) did not exhibit any significant increase in proportional representation of species richness with increasing altitude. Ennominae (mainly feeding on woody plants) were the most species rich group across all altitudes, including the 1100 m a.s.l. plots. The dominance of Larentiinae at high altitudes found by others in the tropics does not hold true at our tropical or subtropical Australian locations. We note though, that our forest transects only reached 1200 m and 1100 m a.s.l. respectively, spanning a total of 800 m of elevation (for want of any higher forests), compared with more than 1800 m a.s.l. in Borneo and approximately 2000 m a.s.l. in Ecuador. Our relatively low Australian mountains may not allow for the more extreme environmental conditions which favour the Larentiinae elsewhere.

Arctiidae is a comparatively small family with an estimated 11000 species worldwide and 280 Australian described species (Common 1990). Arctiidae show high levels of montane endemism within the Syntominae, Arctiini and the genus Nyctemera in Borneo (Holloway 1986-2008). The subfamily Lithosiinae in
Australia are represented by about 70 genera, many of which are endemic (Common 1990). Many species of Arctiidae are polyphagous, feeding on herbaceous plants, however, host plants of Lithosiinae often include lichens, mosses and algae (Common 1990), which may account for the distribution of the high altitude endemics within this group. Lithosiinae were highly dominant in our samples, contributing 92% to the total number of Arctiidae encountered, in contrast with other studies (Fiedler et al. 2008). Among Ecuadorian Arctiidae, for example, Arctiinae was the most species rich subfamily (Fiedler et al. 2008).

The superfamily Pyraloidea (Crambidae + Pyralidae) is one of the largest groups of moths, with 16000 species described worldwide, and 1100 described Australian species. Pyraloids are usually small moths and generally more host specific (Loder et al. 1998), with large tropical radiations (Common 1990). Pyraloidea are often endophagous. Their host plants in Australia include Myrtaceae, Fabaceae, Moraceae, Euphorbiaceae and some mosses (Common 1990). There is a wide range of life history characteristics represented in this superfamily, including leaf-mining, wood-boring and leaf-rolling, and some non-herbivorous strategies such as predation and parasitism. The patterns of altitudinal stratification in Pyraloidea observed across the subtropical altitudinal gradients were not as clear as those shown in the Geometridae and Arctiidae. In tropical rainforest, however, there was a very clear pattern of altitudinal stratification.

Generally, there was little change in proportional representation of Pyraloidea between high and low altitude plots, at any location. This contrasts with the findings of Fielder et al. 2008, who encountered fewer Pyraloidea at high altitudes and suggested they may be less well adapted to harsh environments. Again, the clear altitudinal patterns in species richness found elsewhere may be related to the greater altitudinal heights of tropical mountains in Asia and South America.

Before a recent reclassification (Zahiri et al. 2011), the Noctuidae was the largest family within the Noctuoidea, with 35000 species described worldwide, and 1150 described Australian species. Many Australian Noctuidae are related to Oriental
and Papua New Guinean species, and many have wide distributions, including the Old World tropics (Common 1990). Host plants are mainly grasses and herbs and many species are polyphagous. Noctuidae generally did not show a clear altitudinal pattern which may result from their generalist feeding behaviour, and as they are robust flyers, they may have broad-scale distributions that are less restricted by altitude.

The most consistently attitudinally stratified family groups were the Arctiidae and Geometridae while Noctuidae exhibited little altitudinal stratification. Pyraloidea did show some altitudinal stratification, which was especially apparent in the tropics. Pyraloidea is a broad grouping of species with a wide range of life histories. Further taxonomic identification to family and subfamily level may identify groups within the Pyraloidea that respond to altitude.

Vegetation and moth distributions

Since moth distribution is often dependent on host plant distribution, it is useful to examine relationships between vegetation and moths. Consequently their altitudinal responses will be driven by a combination of biotic and abiotic factors. Previous moth studies have shown that the most important of these factors are likely to be associated changes in vegetation assemblages, temperature and precipitation, occurring along altitudinal gradients (Hodkinson 2005). Plant assemblage composition varies with altitude; generally the diversity of plants falls with increasing altitude and the structural composition of vegetation becomes simpler (Vázquez and Givnish 1998). Higher plant diversity and productivity at lower elevations may be due to drier, warmer conditions, as well as human disturbance pressures increasing environmental heterogeneity. Plant species richness can be directly correlated with a number of environmental conditions such as soil fertility and moisture. Vegetation assemblages at high altitudes can be attributed to shifts in soil properties, such as higher pH, lower soil fertility and

Studies of altitudinal distributions of invertebrates have concluded that climate is the factor shaping assemblages of spittlebugs (Whittaker and Tribe 1996), psyllids (Hodkinson et al. 1999), aphids, moths (Fiedler et al. 2008) and other herbivores (Hodkinson et al. 1998). Other studies of moth assemblages have shown that there is little evidence linking the diversity or richness of plant assemblages with moth assemblages (Axmacher et al. 2009), and that other factors, such as changes in abiotic factors along altitudinal gradients are more important in driving moth assemblage composition. Our results indicate that there are differences in the degree that moth assemblages correlate with vegetation amongst the different moth family groups. We found that assemblages of Geometridae, Arctiidae and Pyraloidea (especially in the tropical plots) were correlated with vegetation assemblages, but Noctuidae assemblages consistently showed no relationship with vegetation assemblages across altitude. Again, these differences may be driven by life history characteristics, and it is important to note that many factors, such as vegetation assemblage, temperature, precipitation and soil characteristics are intercorrelated across altitude. Further work involving linking individual species to their host plants is required to confirm this result.

Future shifts in altitudinal distributions

Many moth families respond sensitively to altitude, with current distributions predicted to shift upwards with further climate warming (Fiedler et al. 2008). Upwards shifts in distributions of moths have already been demonstrated in mountain systems with long-term data sets. An altitudinal study of moth assemblages on Mt Kinabalu, Borneo, over 40 years, showed significant uphill movement of Geometridae (Chen et al. 2010). Significantly, the high altitude species contracted their ranges at both their upper and lower margins, whereas species at lower elevations increased their upper boundaries more than they retreated from their lower boundaries, increasing their ranges. The probable
mechanisms for this pattern are the reduced land area at high altitudes, restricting the opportunities for upwards colonisation. This illustrates the vulnerability of high altitude moth species under climate warming. Complicating factors include availability of host plant vegetation, and invasion from lowland forests by competing species. The response of moth assemblages examined in this study will depend on the responses of individual species and will be complicated by interactions within each ecosystem, especially in the moisture sensitive cloud forest. It may be possible to measure distributional shifts as part of a future monitoring program; the use of a 'predictor set' of altitudinally restricted species is key to regular, economical ecological monitoring. We suggest that the strong altitudinal signals we observed in Geometridae, Arctiidae and Pyraloidea lends support for inclusion of these groups in studies monitoring altitudinal shifts.

Acknowledgments

We thank the IBISCA-Qld team and the volunteers who helped collect and sort moths in October 2006, March 2007 and January 2008 as part of the IBISCA Queensland Project, and John Grey who helped collect samples at all locations. Taxonomic assistance was provided by Ted Edwards at the Australian National Insect Collection. Thank you to Casey Hall, Heather Christensen, Steph Suess, Kyle Barton, Dean Wright, Cecelia Chavana-Bryant, Jake Bryant, Stefan Curtis, Kyran Staunton and Ellen Forster for helping in field and laboratory work. The Environmental Futures Centre at Griffith University provided financial support for this project, for which I am most grateful. Thank you to the Queensland Museum for allowing access to reference collections of moths. Many improvements have been made to this manuscript thanks to feedback from Jude Buckman and Bob Ashton.
References


Chapter 4 Appendix

Table 4.4 Summary of pair-wise post-hoc PERMANOVA tests between adjacent pairs of altitudinal bands at Lamington in October 2006 (LAM OCT) and March 2007 (LAM MAR), Border Ranges in April 2009 (BR NOV) and November 2009 (BR APR) and Mt Lewis in November 2009 (ML NOV) and April 2011 (ML APR) for (a) Geometridae and (b) Pyraloidea. Comparisons between 300 plots and other altitudes in October, and 500 plots and other altitudes in March at Lamington have been removed from this analysis due to uneven sampling of these plots.

(a) Geometridae

<table>
<thead>
<tr>
<th>Comparison</th>
<th>LAM OCT</th>
<th>LAM MAR</th>
<th>BR NOV</th>
<th>BR APR</th>
<th>ML NOV</th>
<th>ML APR</th>
</tr>
</thead>
<tbody>
<tr>
<td>300 &amp; 500</td>
<td>1.8</td>
<td>0.016</td>
<td>1.1</td>
<td>0.23</td>
<td>1.241</td>
<td>0.103</td>
</tr>
<tr>
<td>500 &amp; 700</td>
<td>0.9</td>
<td>0.488</td>
<td>1.8</td>
<td>0.022</td>
<td>1.9</td>
<td>0.014</td>
</tr>
<tr>
<td>700 &amp; 900</td>
<td>1.3</td>
<td>0.150</td>
<td>1.6</td>
<td>0.035</td>
<td>1.5</td>
<td>0.063</td>
</tr>
<tr>
<td>900 &amp; 1100</td>
<td>1.3</td>
<td>0.131</td>
<td>1.8</td>
<td>0.018</td>
<td>1.9</td>
<td>0.013</td>
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</table>

(b) Pyraloidea

<table>
<thead>
<tr>
<th>Comparison</th>
<th>LAM OCT</th>
<th>LAM MAR</th>
<th>BR NOV</th>
<th>BR APR</th>
<th>ML NOV</th>
<th>ML APR</th>
</tr>
</thead>
<tbody>
<tr>
<td>300 &amp; 500</td>
<td>1.2</td>
<td>0.188</td>
<td>1.3</td>
<td>0.173</td>
<td>1.290</td>
<td>0.022</td>
</tr>
<tr>
<td>500 &amp; 700</td>
<td>1.3</td>
<td>0.113</td>
<td>1.6</td>
<td>0.066</td>
<td>2.3</td>
<td>0.013</td>
</tr>
<tr>
<td>700 &amp; 900</td>
<td>1.3</td>
<td>0.162</td>
<td>1.4</td>
<td>0.091</td>
<td>1.7</td>
<td>0.054</td>
</tr>
<tr>
<td>900 &amp; 1100</td>
<td>1.2</td>
<td>0.183</td>
<td>1.5</td>
<td>0.069</td>
<td>1.5</td>
<td>0.086</td>
</tr>
</tbody>
</table>
Table 4.5 Summary of pair-wise post-hoc PERMANOVA tests between adjacent pairs of altitudinal bands at Lamington in October 2006 (LAM OCT) and March 2007 (LAM MAR), Border Ranges in April 2009 (BR NOV) and November 2009 (BR APR) and Mt Lewis in November 2009 (ML NOV) and April 2011 (ML APR) for (c) Arctiidae and (d) Noctuidae. Comparisons between 300 plots and other altitudes in October, and 500 plots and other altitudes in March at Lamington have been removed from this analysis due to uneven sampling of these plots.

<table>
<thead>
<tr>
<th>Comparison</th>
<th>Arctiidae</th>
<th></th>
<th></th>
<th>Noctuidae</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>LAM OCT</td>
<td>LAM MAR</td>
<td>BR NOV</td>
<td>BR APR</td>
<td>ML NOV</td>
<td>ML APR</td>
</tr>
<tr>
<td>300 &amp; 500</td>
<td>t P</td>
<td>t P</td>
<td>t P</td>
<td>t P</td>
<td>t P</td>
<td></td>
</tr>
<tr>
<td>500 &amp; 700</td>
<td>1.1 0.259</td>
<td>2.6 0.006</td>
<td>1.6 0.035</td>
<td>2.041 0.030</td>
<td>2.615 0.025</td>
<td></td>
</tr>
<tr>
<td>700 &amp; 900</td>
<td>1.1 0.286</td>
<td>2.1 0.013</td>
<td>2.5 0.010</td>
<td>1.211 0.167</td>
<td>2.750 0.024</td>
<td></td>
</tr>
<tr>
<td>900 &amp; 1100</td>
<td>1.3 0.172</td>
<td>2.8 0.003</td>
<td>2.6 0.012</td>
<td>1.104 0.302</td>
<td>1.789 0.032</td>
<td></td>
</tr>
</tbody>
</table>

| Comparison | | |
|------------|-----------|-------------|-----------|-----------|-------------|-------------|
|            | LAM OCT   | LAM MAR     | BR NOV    | BR APR    | ML NOV     | ML APR     |
| 300 & 500  | 1.2 0.170 | 1.1 0.30    | 1.548 0.033 | 1.937 0.028 |
| 500 & 700  | 1.3 0.122 | 1.5 0.07    | 1.101 0.297 | 1.115 0.295 |
| 700 & 900  | 1.1 0.299 | 1.5 0.068   | 2.1 0.01   | 2.213 0.030 | 1.289 0.079 |
| 900 & 1100 | 1.5 0.072 | 1.3 0.12    | 1.288 0.069 | 1.592 0.029 |
Table 4.6 Results of distance linear matrix analysis of correlation between family groups assemblages across altitude with available environmental data (average tree richness, soil properties (moisture, pH, organic content, potassium, and carbon), fog events, altitude, and temperature) at (a) Lamington in October 2006 and (b) March 2007. Non-significant correlations are shaded in grey (p>0.05)

<table>
<thead>
<tr>
<th></th>
<th>Lamington October 2006</th>
<th></th>
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<th></th>
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<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td><strong>Noctuidae</strong></td>
<td><strong>Pyraloidea</strong></td>
<td><strong>Arctiidae</strong></td>
<td><strong>Geometridae</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tree richness</td>
<td>0.721(0.825)</td>
<td>1.600(0.070)</td>
<td>1.565(0.126)</td>
<td>1.173(0.264)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Soil moist</td>
<td>1.499(0.074)</td>
<td>4.476(0.001)</td>
<td>3.165(0.001)</td>
<td>2.817(0.001)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Soil pH</td>
<td>1.179(0.254)</td>
<td>3.757(0.001)</td>
<td>2.860(0.002)</td>
<td>2.753(0.001)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Soil organ</td>
<td>1.519(0.067)</td>
<td>3.642(0.001)</td>
<td>2.889(0.002)</td>
<td>2.364(0.001)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fog events</td>
<td>1.485(0.078)</td>
<td>3.171(0.001)</td>
<td>2.836(0.002)</td>
<td>2.021(0.006)</td>
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<tr>
<td>Soil potas</td>
<td>1.168(0.283)</td>
<td>3.161(0.001)</td>
<td>2.099(0.017)</td>
<td>2.141(0.003)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Soil carbon</td>
<td>1.153(0.315)</td>
<td>3.801(0.001)</td>
<td>2.845(0.002)</td>
<td>2.727(0.001)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Altitude</td>
<td>1.137(0.337)</td>
<td>4.321(0.001)</td>
<td>3.460(0.001)</td>
<td>2.719(0.001)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>High temp</td>
<td>2.068(0.003)</td>
<td>2.292(0.011)</td>
<td>2.741(0.002)</td>
<td>1.714(0.025)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Low temp</td>
<td>1.192(0.252)</td>
<td>4.162(0.001)</td>
<td>3.334(0.001)</td>
<td>2.691(0.001)</td>
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<td></td>
</tr>
<tr>
<td>Ave temp</td>
<td>1.343(0.135)</td>
<td>4.291(0.001)</td>
<td>3.314(0.001)</td>
<td>2.784(0.001)</td>
<td></td>
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</table>

<table>
<thead>
<tr>
<th></th>
<th>Lamington March 2007</th>
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<th></th>
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</thead>
<tbody>
<tr>
<td></td>
<td><strong>Noctuidae</strong></td>
<td><strong>Pyraloidea</strong></td>
<td><strong>Arctiidae</strong></td>
<td><strong>Geometridae</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tree richness</td>
<td>2.511(0.003)</td>
<td>2.547(0.016)</td>
<td>2.782(0.014)</td>
<td>2.894(0.006)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Soil moisture</td>
<td>2.982(0.001)</td>
<td>6.792(0.001)</td>
<td>6.993(0.001)</td>
<td>5.723(0.001)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Soil pH</td>
<td>3.023(0.001)</td>
<td>4.922(0.001)</td>
<td>5.737(0.001)</td>
<td>5.029(0.001)</td>
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<td></td>
</tr>
<tr>
<td>Soil organs</td>
<td>2.872(0.001)</td>
<td>5.457(0.001)</td>
<td>6.010(0.001)</td>
<td>5.276(0.001)</td>
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<td></td>
</tr>
<tr>
<td>Fog events</td>
<td>2.897(0.001)</td>
<td>5.530(0.001)</td>
<td>5.420(0.001)</td>
<td>4.306(0.001)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Soil potassium</td>
<td>3.270(0.001)</td>
<td>4.433(0.003)</td>
<td>4.380(0.002)</td>
<td>4.312(0.002)</td>
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<tr>
<td>Soil carbon</td>
<td>2.708(0.002)</td>
<td>4.316(0.003)</td>
<td>5.277(0.002)</td>
<td>4.667(0.001)</td>
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<tr>
<td>Altitude</td>
<td>4.146(0.001)</td>
<td>6.006(0.001)</td>
<td>7.035(0.001)</td>
<td>6.033(0.001)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>High temp</td>
<td>2.141(0.008)</td>
<td>4.045(0.001)</td>
<td>4.342(0.002)</td>
<td>3.298(0.003)</td>
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<td></td>
</tr>
<tr>
<td>Low temp</td>
<td>4.215(0.001)</td>
<td>6.048(0.001)</td>
<td>6.333(0.001)</td>
<td>5.769(0.001)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Median temp</td>
<td>3.973(0.001)</td>
<td>6.492(0.001)</td>
<td>7.205(0.001)</td>
<td>5.964(0.001)</td>
<td></td>
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</table>
Table 4.7 Results of distance linear matrix analysis of correlation between family groups across altitude with environmental data (average tree richness, high temperature, low temperature, median temperature and altitude) at Border Ranges in April and November 2010.

<table>
<thead>
<tr>
<th></th>
<th>Border Ranges November 2010</th>
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</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Noctuidae</td>
<td>Pyraloidea</td>
<td>Arctiidae</td>
<td>Geometridae</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Pseudo-F</td>
<td>P</td>
<td>Pseudo-F</td>
<td>P</td>
<td>Pseudo-F</td>
</tr>
<tr>
<td>Tree richness</td>
<td>1.153</td>
<td>0.295</td>
<td>0.454</td>
<td>0.916</td>
<td>0.461</td>
</tr>
<tr>
<td>Low temp</td>
<td>3.303</td>
<td>0.003</td>
<td>7.114</td>
<td>0.001</td>
<td>5.505</td>
</tr>
<tr>
<td>High temp</td>
<td>1.209</td>
<td>0.246</td>
<td>0.922</td>
<td>0.480</td>
<td>2.601</td>
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<tr>
<td>Altitude</td>
<td>5.269</td>
<td>0.001</td>
<td>7.689</td>
<td>0.001</td>
<td>7.994</td>
</tr>
<tr>
<td>Average temp</td>
<td>2.247</td>
<td>0.029</td>
<td>2.792</td>
<td>0.010</td>
<td>2.453</td>
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</table>

<table>
<thead>
<tr>
<th></th>
<th>Border Ranges April 2010</th>
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<td>Noctuidae</td>
<td>Pyraloidea</td>
<td>Arctiidae</td>
<td>Geometridae</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Pseudo-F</td>
<td>P</td>
<td>Pseudo-F</td>
<td>P</td>
<td>Pseudo-F</td>
</tr>
<tr>
<td>Tree richness</td>
<td>0.552</td>
<td>0.909</td>
<td>0.637</td>
<td>0.756</td>
<td>0.785</td>
</tr>
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<td>Low temp</td>
<td>3.027</td>
<td>0.002</td>
<td>4.161</td>
<td>0.002</td>
<td>6.435</td>
</tr>
<tr>
<td>High temp</td>
<td>1.163</td>
<td>0.278</td>
<td>2.616</td>
<td>0.016</td>
<td>2.297</td>
</tr>
<tr>
<td>Altitude</td>
<td>4.265</td>
<td>0.001</td>
<td>3.701</td>
<td>0.001</td>
<td>12.60</td>
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<tr>
<td>Median temp</td>
<td>2.007</td>
<td>0.026</td>
<td>1.920</td>
<td>0.046</td>
<td>4.553</td>
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Table 4.8 Results of distance linear matrix analysis of correlation between family group assemblages across altitude with available environmental data (temperature, rainfall, altitude, soil properties (sodium, nitrogen, phosphorus, carbon, calcium, clay and temperature) and average plant species richness) at (a) Mt Lewis in November 2009 and (b) April 2011.

(a) Mt Lewis November 2009

<table>
<thead>
<tr>
<th></th>
<th>Noctuidae</th>
<th>Pyraloidea</th>
<th>Arctiidae</th>
<th>Geometridae</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Pseudo-F</td>
<td>P</td>
<td>Pseudo-F</td>
<td>P</td>
</tr>
<tr>
<td>High temp</td>
<td>4.465</td>
<td>0.001</td>
<td>4.373</td>
<td>0.001</td>
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<tr>
<td>Low temp</td>
<td>3.948</td>
<td>0.001</td>
<td>4.212</td>
<td>0.001</td>
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<tr>
<td>Rainfall</td>
<td>4.475</td>
<td>0.001</td>
<td>4.754</td>
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<tr>
<td>Altitude</td>
<td>4.010</td>
<td>0.001</td>
<td>3.879</td>
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<tr>
<td>Soil sodium</td>
<td>0.898</td>
<td>0.560</td>
<td>1.814</td>
<td>0.031</td>
</tr>
<tr>
<td>Soil nitrogen</td>
<td>2.452</td>
<td>0.009</td>
<td>1.808</td>
<td>0.028</td>
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<td>Soil phosphorus</td>
<td>4.805</td>
<td>0.001</td>
<td>3.428</td>
<td>0.001</td>
</tr>
<tr>
<td>Soil carbon</td>
<td>1.039</td>
<td>0.391</td>
<td>1.292</td>
<td>0.217</td>
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<td>Soil calcium</td>
<td>2.098</td>
<td>0.019</td>
<td>1.895</td>
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<tr>
<td>Soil clay</td>
<td>3.292</td>
<td>0.001</td>
<td>3.421</td>
<td>0.001</td>
</tr>
<tr>
<td>Soil temp</td>
<td>4.285</td>
<td>0.001</td>
<td>3.838</td>
<td>0.001</td>
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<tr>
<td>Plant sp. richness</td>
<td>0.728</td>
<td>0.743</td>
<td>1.188</td>
<td>0.248</td>
</tr>
<tr>
<td>Average temp</td>
<td>3.624</td>
<td>0.001</td>
<td>3.426</td>
<td>0.001</td>
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</table>

(b) Mt Lewis April 2011

<table>
<thead>
<tr>
<th></th>
<th>Noctuidae</th>
<th>Pyraloidea</th>
<th>Arctiidae</th>
<th>Geometridae</th>
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Chapter 5

Vertical stratification of moths in tropical, subtropical and temperate forest, across altitude and continents

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To be submitted to Biological Journal of the Linnaean Society
Abstract

Understanding the diversity and distribution of arthropods within rainforest canopies has been a major challenge in ecology, with little consensus. We report here on extensive cross-continental fieldwork over 17 years, collecting canopy and ground samples of nocturnal moths in a variety of different forest types, climates, altitudes, latitudes and areas with differing biogeographical history. Study locations included tropical and subtropical rainforest in Queensland (Qld) and New South Wales (NSW), Australia; tropical, subtropical and subalpine forest in Yunnan Province, China; tropical rainforest in Panama, Vietnam, Brunei and Papua New Guinea. We collected night-flying Lepidoptera at two vertical strata: in the upper canopy and at ground-level using modified Pennsylvania light traps. All moths with a forewing length greater than 1 cm were sorted and identified to morphospecies. A total of 102 033 moths were collected across all studies. There were consistent differences between canopy and ground assemblages at almost all rainforest locations, across altitudinal gradients, and in our sub-alpine location. There were no consistent patterns of differences in species richness or species composition between canopy and ground across altitude or latitude. Family-level analysis of selected datasets (Panama and Atherton), showed that Pyraloidea (Crambidae + Pyralidae), Arctiidae and Geometridae formed discrete assemblages in the canopy and ground layers, and the Noctuidae showed no vertical stratification. Analyses of life history information provide support for both behavioural and food-plant driven explanations of vertically compartmentalised assemblages.
Introduction

Tropical rainforests contain a significant proportion of the world’s animal diversity (Wilson 1992). At the level of species, most of this diversity is made up of arthropods, particularly insects (May 2010). It has long been hypothesised that the majority of tropical insect species are associated with the crowns of forest trees and their associated epiphytes (Novotny et al. 2003). Tropical canopy assemblages of a range of taxa can be highly diverse, including bats (Kalko and Handley 2001), arthropods (Sutton et al. 1983, Basset 2001) and canopy plants (Madison 1977). In 1982 Erwin estimated the canopy to have twice the number of beetle species than the understorey, and through extrapolation, estimated that the total number of tropical arthropods could be as high as 30 million species. Further work has suggested levels of host specificity and stratum specialization are much lower than assumed by Erwin (1982), and estimates of global diversity have been reduced to 5 ± 5 million (Ødegaard 2000, Hamilton et al. 2010, May 2010, Mora et al. 2011, Basset et al. 2012, Costello et al. 2013). Tropical databases, nevertheless, remain limited and localised. Questions of how many species are in the canopy, how vertically compartmentalised assemblages are, and to what degree canopy species are stratum-specialists, await resolution.

Forest canopies are the interface between the atmosphere and the biosphere (Basset et al. 2003b, Didham and Fagan 2003, Ozanne et al. 2003), presenting a unique suite of environmental conditions when compared with the understorey. These include a harsher ultraviolet regime, greater temperature fluctuations, evaporation rates and wind speeds (Lowman and Rinker 2004). Moving from the understorey to the upper canopy, a suite of environmental and biotic factors shift, creating a matrix of microclimates and potential ecological niche spaces. Nutrients and water availability change across strata, as does the floristic composition, leaf area, biomass and resource availability associated with these environmental factors. With the harsher conditions of the canopy, come unique plant responses and trophic interactions. Levels of leaf toughness tend to be
higher due to environmental stresses (Devries et al. 1997), which in turn influence insect herbivores. Levels of herbivory in the canopy, however, are not homogenous across forest types and regions (Basset 1992, Lowman and Heatwole 1992). Herbivory levels within forests can be influenced by a suite of environmental and biotic factors, including temperature, light levels, leaf age, seasonality as well as the richness and abundance of tree species (Lowman 1985).

Vertical stratification

Arthropod biodiversity in undisturbed rainforests has been shown to be strongly 'compartmentalised' with more or less isolated assemblages of species occupying, sometimes closely adjacent, habitat components within a forest (Basset et al. 1992, Walter et al. 1998, Amedegnato 2003, Wardhaugh et al. 2012a). The ‘vertical stratification’ of assemblages may refer to canopy versus upper canopy, many vertical layers of assemblages, or a contrast between ‘the canopy’ as a grouping and ‘the understorey’. It is important to recognise that the canopy may be highly variable, with a complex three dimensional structure (Richards 1984). Obviously the degree to which this compartmentalisation can be shown to occur has a substantial impact on the description of, and hypotheses to account for, the extraordinary arthropod diversity which is observed in such forests. Contrasts between the arthropod fauna of the canopy and ground layers in a forest are one of the key aspects of this proposed compartmentalisation (Basset et al. 2003a). Previous authors have discussed this stratification with particular reference to Collembola (Rodgers and Kitching 1998), Isoptera (Roisin et al. 2006), Araneae (Sorensen 2003), Acari (Aoki 1970) and Coleoptera (Stork and Grimbacher 2006). Work on the stratification of Lepidoptera is discussed below.

Vertical stratification of Lepidoptera

A few authors have looked explicitly at vertical stratification of Lepidoptera, comparing ground samples with equivalent canopy samples. A related, but separate concept to vertical stratification at the level of the community is the
concept of higher diversity in the canopy, which is also addressed in many studies of Lepidoptera comparing ground and canopy. Several papers have examined butterflies, a taxonomically well-known group, using trapping methods such as fruit-baited traps, netting and visual observations. DeVries et al. (2012) examined Costa Rican butterfly distributions, finding distinct communities in canopy and ground strata (consistent with earlier work) (DeVries 1988), and slightly higher diversity in the canopy. In Ecuador DeVries et al. (1999) found a similar result – vertically stratified butterfly assemblages. Rarefied estimations, however, suggested similar richness levels between canopy and ground. Fermon et al. (2003), examined butterflies in managed West African rainforest, finding stronger vertical stratification in less-disturbed forest than thinned-out sites, which may be due to the reduction of canopy resources including fruit in the latter. Beccaloni (1997) showed vertical stratification of Neotropical ithomiine butterflies, which correlated with the height of their host plants. Schulze et al. (2001) examined butterflies and night flying moths (Sphingidae and Erebidae: Arctiinae), employing fruit-baited traps, visual counts and a gauze tower light trap. Frugivorous butterflies declined in the canopy whereas nectar-feeding groups increased. The authors attributed these patterns principally to nectar availability and predator avoidance, with larval host-plant preferences playing only a minor role for some ground-zone species. In Australia there has been little work done on vertical stratification of Lepidoptera. A study of rainforest butterfly stratification at three locations in northern Queensland (Hill et al. 1992) found no evidence of stratification, and that the diversity of butterflies in the canopy was not higher than lower strata. A possible reason butterflies may not exhibit vertical stratification is that they are more vagile than many other arthropod species.

Several studies have targeted specific families within the Lepidoptera. Brehm (2007), for example, compared ground and canopy samples of arctiids (Erebidae: Arctiinae) and geometrids from rainforest in Costa Rica, demonstrating that the diversity of Arctiinae was greater in the canopy than at ground-level, with an inverse pattern for the Geometridae. He attributed these differences to the availability of larval resources in the different strata. Intachat and Holloway
(2000) worked in a lowland mixed dipterocarp forest (70 - 90m a.s.l.) in peninsular Malaysia. They examined Geometroidea alone, using Rothamsted light traps at 1m, 15m and 30m above the ground. Over 13 months of intensive trapping they found no significant differences; indeed they noted a decline in geometroid diversity at canopy level. Finally, Schulze and Fiedler (2003) compared assemblages of Pyraloidea from the ground and canopy within hill dipterocarp forest in Borneo (at 580m a.s.l.). Assemblages were significantly less diverse in the canopy than at ground level and few species could be designated as stratum specialists.

Any differences between assemblages of adult moths encountered at ground level compared with those encountered in the canopy may reflect either or both of the following two hypotheses. First, there may be two independent resident assemblages whose location as adults reflects the species' larval and oviposition preferences. Alternatively, or in addition, the adults may be stratifying behaviourally as they seek something other than food-plants on which to oviposit. Availability of nectar and/or mates (or mating locations) are the two obvious alternative resources which could produce vertical stratification (Basset et al. 2003a).

Latitudinal and altitudinal gradients allow us to investigate the forces driving patterns of diversity (Hillebrand 2004, Hodkinson 2005). It can be hypothesised that with increasing latitude, differences between canopy and ground communities may diminish. Canopy insect faunas have been shown to be less stratified and diverse in temperate forests (Fowler 1985, Schowalter and Ganio 1998) and it has been hypothesised that this is driven by accompanying low stratification of environmental conditions (Basset 2001). Conversely, at low latitudes, we may expect greater differences between canopy and ground assemblages (Stork et al. 1997), as tropical canopies present a suite of different environmental conditions, are structurally more complex and can be upwards of 45m from the understorey. With increasing altitude, a complimentary set of hypotheses can be made – vertical stratification may shrink with increasing
altitude, as the physical distance between canopy and understorey, forest complexity and variability in environmental conditions may be reduced.

In this paper we present the first global comparative analysis of canopy/ground comparisons of moth assemblages based on a series of rainforest canopy studies using comparable methodologies that include work in Panama, tropical and subtropical Eastern Australia, Papua New Guinea, Borneo, Vietnam, and tropical, subtropical and temperate China. Using all or selected parts of these extensive canopy and ground datasets from across continents, forest types and climates, we investigate the generality of vertical stratification of forest Lepidoptera. We specifically seek to address the following two hypotheses; (1) vertical stratification will decrease with increasing latitude, and (2) vertical stratification will decrease with increasing altitude. We examine (1) vertical stratification across bioregions, at different latitudes within regions, and at different altitudes within location, (2) levels of canopy richness compared with understorey richness, and (3) patterns of vertical stratification across different families within the Lepidoptera.

**Methods**

*Study areas and sampling designs*

During sampling carried out between 1995 and 2000 by Professor Roger Kitching (Paluma, north Queensland (2000); Oomsis, Papua New Guinea (2000); Cat Tien, Vietnam (1997), Kuala Belalong, Brunei (1995)), canopy-ground comparisons were carried out as part of extensive general arthropod and plant surveys of one hectare (ha) plots (see Kitching et al. 2001, 2005). Repeated surveys at Atherton, north Queensland were carried out on a 25 ha permanent plot established as part of the Terrestrial Ecosystem Research Network (TERN) Project. In Panama, surveys were part of the IBISCA Panama Project within a half hectare section of the San Lorenzo Protected Area (see Basset et al. 2007, Basset et al. 2012). In Australia, altitudinally stratified data sets from Border Ranges NP, north-eastern
NSW; Lamington NP, south-east Queensland; and Mt Lewis, northern Queensland were collected as part of larger projects examining the impact of altitude (as a surrogate for climate) on rainforest biodiversity. At each of these locations twenty replicate plots were established, four located at each of five altitudes. Each location was sampled twice, once at the onset of the wet season and once at its close. In a similar fashion, altitudinally stratified data from China derived from three permanent transects established in tropical rainforest (Mengla), broad-leaved evergreen forest (Ailao Shan) and subalpine conifer forest (Lijiang) all in Yunnan Province. Again twenty replicate plots were used, distributed in sets of five, over four altitudes. Each of the Chinese transects was sampled once. Site descriptions are collated from associated vegetation and environmental work, and from general sources. More detailed site descriptions can be found in Appendix 5.1 and Table 5.1 and 5.3.

<table>
<thead>
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<th>Location</th>
<th>Country</th>
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<th>Forest type</th>
<th>Design</th>
<th>Occasion</th>
<th>Total samples</th>
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<td>4 plots x 5 altitudinal bands</td>
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<td>235</td>
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<td>5 plots in 25 ha</td>
<td>Nov 2009 May 2010 Apr 2011</td>
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<td>3 plots in 1 ha</td>
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At all locations we sampled moth assemblages in both the canopy and at ground level. In almost all cases we circumvented the difficulties of canopy access (Basset et al. 2003b) by using a modified compound bow to shoot canopy lines - a safe and portable method allowing us easy access to all levels of the canopy. Canopy traps were hung from emergent branches, with the aim of locating traps at the top of the canopy. For the Panama studies a variety of access methods were used including a canopy crane (see Basset et al., 2007). In most locations, canopy traps were placed at a height of approximately 35 metres, but depending on the height of the canopy this sometimes varied. Ground traps were raised to approximately head height, around 1.5m.

All samples were taken using Pennsylvania-style light traps and each canopy and understorey trap was run for three nights (Frost 1957, Kitching et al. 2005). These traps comprise a vertical 8 watt actinic tube surrounded by three transparent vanes which knock insects down into a collecting funnel and bucket mounted below. The traps are powered by 12 volt gel-cell batteries. With a well maintained, fully charged battery the trap will remain illuminated for up to 12 hours. Both the trap and the battery are mounted within a frame with a rain-cover above them. This permits the trap to be suspended in the canopy when required. Insects are killed \textit{in situ} by including a strip of resin impregnated with Dichlorvos™ within the collecting bucket.

\textit{Sample sorting and taxonomy}

In all locations, except Panama, all moths with a forewing length greater than 1 cm (loosely referred to as macrolepidoptera) were considered. In addition, all moths belonging to the superfamily Pyraloidea (that is, the families Crambidae and Pyralidae), regardless of their size, were also processed. In Panama only Geometridae, Arctiidae and Pyraloidea were targeted. Moth samples were sorted within two days of the collection of the sample, to prevent specimens becoming
mouldy. Moths from each sample were sorted to morphospecies in field laboratories, and assigned to family where possible. A reference collection was established for each location. As these collections increased in size, additional moths that were readily recognisable were recorded and discarded. Any material that could not be readily identified as belonging to an existing numbered morphospecies was pinned, preserved and numbered. We are aware of the phylogeny of the Noctuoidea as presented by Zahiri et al. (2011). Here we use ‘Noctuidae’ sensu lato to represent the families Erebidae (less Arctiinae and Lymantriinae) and Noctuidae as proposed by Zahiri et al. Similarly, for pragmatic reasons, we retain the Arctiidae as a family and Arctiinae, Lithosiinae and Ctenuchinae as subfamilies, aware that these designations are downgraded to tribal status in the ‘new’ classification.

Data analysis

Data from all nights of collection at each plot were pooled, so that there was a single canopy and ground sample for each plot. Sorensen similarity values, based on datasets with singletons and doubletons removed and on presence/absence data, were extracted from similarity matrices produced in PRIMER (Plymouth Routines In Multivariate Ecological Research, version 6) (Clarke and Gorley 2006) for each plot. We illustrated the mean Sorensen similarity values for each plot (1ha plots) and altitudinal plots against altitude and latitude, to give a visual characterisation of patterns of change with increasing altitude and latitude. We plotted the difference in absolute species richness encountered in the canopy and ground at each plot, against latitude and altitude, to illustrate patterns of canopy or ground dominance across these gradients. Linear mixed-effects models (carried out in the R statistical environment) were used to test the effect of altitude, latitude and study design (single altitude, 1ha and 25ha plots, vs. 20m x 20m altitudinal gradient plots) on the Sorenson dissimilarity between canopy and ground, and the absolute difference in species numbers between canopy and ground. In this linear mixed-effects model, we specified latitude as a random effect and altitude and study design as fixed effects, under an assumed Poisson
distribution. All models were checked using diagnostic plots of both residuals and predictions of random effects (best linear unbiased predictions - BLUP) and found to be adequate.

The multivariate analysis package PRIMER 6 (Clarke and Gorley 2006) was used to investigate differences in moth assemblages between ground and canopy at single plots and across altitudinal zones. Moth data in this study was log transformed before analysis. Non-metric multi-dimensional scaling (NMDS) was used to produce ordination plots illustrating the relationship between plots, using the Bray-Curtis dissimilarity measure (Bray and Curtis 1957), set to 9999 random starts. We used permutational Analysis of Variance [PERMANOVA] in PRIMER 6 (Clarke and Gorley 2006) to test for significant differences among the a priori groups, canopy and ground, based on matrices of log-transformed data, created using the Bray-Curtis similarity index.

The total number of species, including an estimation of the species that were not encountered in each location, was calculated using the software package, EstimateS (Colwell 2009). We selected the Abundance Coverage Estimator (ACE), which was most suited to the moth abundance data sets. This analysis conducts random re-sampling of existing sample data at each plot, to provide an estimation of the total number of species that were not encountered. This tests the effectiveness of the sampling methods, indicating how much of the total assemblage is being caught, a question that is important to consider when using traps in the canopy, which may be subject to confounding factors such as varying influences of the moon, wind and rain (Yela and Holyoak 1997).

Some analyses were restricted to a particular superfamily - or family-level data sets from particular plots. These focussed on the four largest lepidopteran groups, Pyraloidea (Crambidae + Pyralidae), Geometridae, ‘Arctiidae’ and ‘Noctuidae’.

These groups were selected because of their contrasting biologies, their use as
target taxa in other ecological studies (including canopy-ground stratification) and the reasonable level of taxonomic information available for these groups (Holloway 1986-2008, Common 1990). Superfamily and family-level analyses were conducted on those data sets where moths were identified to an appropriate level: that is, Atherton and Panama. For these sub-sets we repeated those analyses conducted on the entire assemblage data. Panama data were enriched by the Janzen host plant data base (http://janzen.sas.upenn.edu/caterpillars/database.lasso), which we used to find host plant information on those species which were restricted to the canopy or the understorey.

Results

A total of 102,033 individual moths were sampled across the 15 sampling locations. Across all locations there was a clear pattern of vertical stratification, with distinctive assemblages in the canopy and understorey layers (see Appendix Table 5.4 and 5.5 for PERMANOVA results). There was no consistent pattern of increasing or decreasing vertical stratification (Sorensen dissimilarity) across latitude ($t = 0.805, P = 0.441$, Figure 5.1), altitude ($t = 1.584, P = 0.122$, Figure 5.2) or sampling design ($t = -1.423, P = 0.188$). Differences in the species richness between canopy and ground did not change across latitude ($t = 0.805, P = 0.441$, Figure 3) or altitude ($t = 1.584, P = 0.122$, Figure 4) or sampling design ($t = 0.449, P = 0.629$). These results indicate that there is no latitudinal or altitudinal gradient in the vertical stratification of moth assemblages. Appendix Figure 5.6 provides a visual representation of the proportion of species (with singletons and doubletons removed) that were restricted to the canopy, restricted to the understorey, and the proportion of species encountered in both the canopy and the understorey.

At all single altitude locations – Brunei, Vietnam, Paluma, Papua New Guinea, Panama and Atherton there was clear and statistically significant stratum differentiation (for a summary of PERMANOVA results see Appendix Table 5.4).
This pattern is illustrated by the NMDS (Non-Metric Multi Dimensional Scaling) ordination of the Panama data (Fig. 5b), which shows very clear separation between canopy and ground assemblages. The numbers of individuals and species which make up the samples analysed are presented in Appendix Table 5.5.
Figure 5.1 Mean Sorensen similarity values (with standard error bars) between canopy and ground moth assemblages for each location, plotted against latitude. Open circles are single altitude plots, closed circles are plots that were studied along altitudinal gradients. No pattern of increasing or decreasing similarity between canopy and ground across latitude is apparent.

Figure 5.2 Mean Sorensen similarity values (with standard error bars) between canopy and ground at each location plotted against elevation. Open circles are single altitude plots, closed circles are plots that were studied along altitudinal gradients. There is no consistent pattern of higher or lower differences in richness between canopy and ground across elevation.
Figure 5.3 Mean difference (with standard error bars) in species richness between canopy and ground plotted against latitude for all locations. Open circles are single altitude plots, closed circles are plots that were studied along altitudinal gradients. No trend in the difference in richness between canopy and ground is evident across latitude.

Figure 5.4 Mean difference (with standard error bars) between observed species richness in canopy and ground assemblages plotted against elevation. Open circles are 1ha plots, closed circles are plots that were studied along altitudinal gradients. There is no consistent pattern of difference between canopy and ground richness across elevation.
Figure 5.5 NMDS ordinations from selected data sets. Closed triangles are canopy assemblages, open triangles are ground assemblages at: (a) Panama, tropical rainforest (stress = 0.19), (b) Panama Arctiidae (stress = 0.17), (c) Panama Geometridae (stress = 0.2), (d) Atherton, Australia, tropical rainforest, Noctuidae (stress = 0.1), (e) Border Ranges, Australia, subtropical rainforest, November 2010 (stress=0.15), (f) Lijiang, China, subalpine conifer forest (stress = 0.11). All ordinations show strong separation of canopy and ground assemblages, except Noctuidae at Atherton.
Altitudinal Transects

At all three Chinese altitudinal gradients – Mengla, Ailao Shan and Lijiang - abundance and richness at ground level was higher than in the canopy. In contrast the Australian altitudinal gradients produced a mixture of ground and canopy dominance or, indeed, little difference between the two (Appendix Table 5.5). In our Australian tropical altitudinal transect at Mt Lewis, canopy samples were more speciose and had more individuals in the canopy in both sampling periods (except 1000m a.s.l. in April, which had 1286 individuals in the ground samples and 473 individuals in the canopy, but with similar species richness 162 and 128 respectively).

Across all altitudinal transects, an overall pattern of separation between canopy and ground assemblages was apparent (Appendix Table 5.5). Generally there was clear delimitation between canopy and ground strata, with only two exceptions in our extensive data sets (Australia: Border Ranges, April, 300m a.s.l. and Lamington, March 900m a.s.l.). Representative of the general pattern observed - clear separation of canopy and ground layers across altitude – results are presented for Border Ranges, Australia in November (Fig 5.5 (e)) and Lijiang, China (Fig 5.5. 1(b)).

Family-level analysis

Atherton, North Queensland

Across three sampling occasions (November 2009, May 2010 and April 2011), a total of 4090 individual moths were sorted and identified, belonging to 603 species. In the November 2009 samples, numbers of Pyraloidea, Noctuidae and Geometridae were fairly even, with the most species belonging to Pyraloidea (180 species). Arctiidae were least abundant with only 65 individuals belonging to 38 species. In May 2010, Geometridae were most speciose (280 individuals belonging
to 71 species), followed by Pyraloidea (190 individuals belonging to 53 species). Arctiidae were abundant (243 individuals), but represented by only 18 species. In April 2011, Pyraloidea were dominant (558 individuals, 73 species), followed by Geometridae (207 individuals, 62 species.). Estimated total species richness (ACE) for canopy and ground-level was not consistent across time. Generally, more Arctiid species occurred in the canopy. For other taxa, however, patterns of richness between canopy and ground were not consistent across years. Generally, the species richness of each taxon was quite similar in the canopy and on the ground - a result similar to that obtained for the entire multi-family analysis.

Geometridae, Arctiidae and Pyraloidea showed strong vertical stratification, with significantly different assemblages in canopy and ground samples, on all three sampling occasions. In contrast, there were no significant differences in the assemblages of Noctuidae between ground and canopy in any of the sampling periods. An ordination of the Noctuidae (Fig. 5.5 (d)) from the November 2009 Atherton sample provides a visual representation of this lack of this pattern (number of individuals = 442). A summary of these results is presented in Appendix Table 5.6.

Panama

Taking the three major taxa overall (Arctiidae, Geometridae and Pyraloidea) we sampled 1703 moths representing 420 species. Canopy versus understorey stratification was clear, with strong separation between the two assemblages (Figure 5c). Samples were dominated by Pyraloidea (957 individuals, 237 species) which were abundant and speciose in both the canopy (543 individuals, 172 species) and on the ground (414 individuals, 157 species). The Pyraloidea were dominated by the subfamily Spilomelinae (Crambidae). Eleven other subfamilies in both Crambidae and Pyralidae were represented by many fewer individuals and species. The Arctiidae (432 individuals, 74 species) were second most abundant but less speciose than the Geometridae (314 individuals, 109 species). Species richness of Arctiidae was similar in the canopy (272 individuals, 52 species) and at
ground level (160 individuals, 52 species). The arctiids were dominated by the subfamily Lithosiinae although both Ctenuchiinae and Arctiinae were well represented in all samples. Geometrids were somewhat more diverse in the canopy (130 individuals, 90 species) compared to ground-level (184 individuals, 72 species). The geometrids were dominated both in terms of abundance and richness by the Ennominae. Many fewer individuals of the Geometrinae, Larentiinae and Sterrhinae, made up virtually all of the remainder of the geometrids.

In the Panama data set, 68 species of moths were represented by ten or more individuals. For this subset, we classified species as ‘canopy specialists’ (more than 3.5 - 27 times as many individuals in the canopy than ground-level samples) or ‘layer generalists’ (less than 3 times as many individuals in the canopy compared with the ground traps). There were no ground specialists among these 68 species. For these 68 species, and assuming generic equivalences (that is, assuming that host plant records from any member of a genus would be informative about the feeding preferences of other members of the same genus), we extracted food plant information from the Janzen database for 31 species (Janzen and Hallwachs 2009). There were no host plant records for the genera containing the other 37 species. Table 5.2 summarises our findings from this preliminary analysis.

The first noteworthy feature is that 22 (32%) of these common species were ‘canopy specialists’ and were principally pyraloids and arctiids. The remaining 66 occurred more or less evenly across the two vertical layers. Of the 31 species for which we have some indication of host-plant relationships, 11 were canopy specialists. Canopy specialists in general showed lower degrees of host-plant specialization at both the plant generic and family levels. Both classes of moths (canopy specialists and layer generalists) contained species which fed on lianas, shrubs, understorey and canopy trees although individual species were sometimes much more specialized. Of the eight liana feeders, six were canopy specialists. It is also noteworthy that some lichen-feeding Lithosiinae (Arctiidae) occurred in both
canopy and ground samples as did some Acentropinae (Crambidae), the larvae of which are almost certainly aquatic (Scoble 1995).

Table 5.2 An analysis of the stratum and food-plant preferences of the most common species of moths within samples from the San Lorenzo Forest, Panama (see text).

<table>
<thead>
<tr>
<th>Statistic</th>
<th>Canopy Specialists</th>
<th>Stratum Generalists</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of species with &gt;10 individuals (%)</td>
<td>22 (32.4)</td>
<td>46 (67.6)</td>
</tr>
<tr>
<td>Number of ‘common’ species: Arctiidae</td>
<td>7</td>
<td>7</td>
</tr>
<tr>
<td>Number of ‘common’ species: Geometridae</td>
<td>1</td>
<td>13</td>
</tr>
<tr>
<td>Number of ‘common’ species: Pyraloidea</td>
<td>12</td>
<td>24</td>
</tr>
<tr>
<td>Number of all species with food plant records</td>
<td>10</td>
<td>20</td>
</tr>
<tr>
<td>Average number of food plant genera</td>
<td>4.80±1.916</td>
<td>8.26±2.738</td>
</tr>
<tr>
<td>Average number of food plant families</td>
<td>3.30±1.477</td>
<td>4.70±1.534</td>
</tr>
</tbody>
</table>

Having established that canopy and ground assemblages of moths are clearly and significantly separated within our data, here we seek to explain these differences. The high heterogeneity indicated in the datasets by these results is not, however, due to chance. The ordination plots (Fig. 1a – 1f) show a clear separation of moth assemblages from ground and canopy samples. This is all the more impressive given the relatively small number and overall size of some samples (e.g. Brunei, Panama, Paluma), and we can be more confident of the generality of these results shown also in our very large data sets (e.g. Papua NewGuinea, Vietnam, Mengla). Vertical stratification in different families within entire assemblages has also been established for the Atherton, Queensland location, for the Geometridae, Arctiidae and Pyraloidea. Noctuidae did not exhibit separation between ground and canopy strata. Ecological and life history characteristic differences in the Noctuidae may be driving this difference, and will be discussed below.
Discussion

The concept of vertical stratification is a fundamental tenet in ecology (Ozanne et al. 2003), and yet there remains little consensus on the degree to which vertical compartmentalisation occurs across different taxa. There have been many single location canopy studies on a range of taxa (Wardhaugh et al. 2012b). However, in order to understand the ecological and evolutionary processes involved, we first need descriptive data on vertical ecological patterns, across forest types, climates, and continents with contrasting biogeographic histories (Stork et al. 1997). Differences in sampling methods used in previous canopy studies have made wider interpretation difficult, confounding variation between studies. We employed a standardized approach to sampling canopy and understory arthropods across all our study sites. Through examining species’ responses to vertical structure, we can examine how important environmental heterogeneity and structural complexity are in shaping assemblages (Hubbell 2001, Chave and Leigh 2002, Kitching et al. 2013). Our results show that: (1) there is an overarching pattern of vertical stratification within forest moth assemblages across altitude, latitude and forest types; (2) species richness is not consistently higher in the canopy or ground layer and shows no relationship to latitude or altitude; and (3) in at least some locations, different lepidopteran families respond in different ways to the vertical structure of rainforest.

How ubiquitous is vertical stratification?

The clear distinction between ground and canopy assemblages across all our sites, at different altitudes, latitudes and forest types, supports the fundamental idea of vertical stratification in arthropods. Vertical stratification has been demonstrated in many groups of arthropods including moths, butterflies and beetles, mainly in tropical rainforests (Sutton et al. 1983, Beccaloni 1997, Basset et al. 2001, Brehm 2007). Studies that have found no evidence of stratification, have focused on butterflies (Hill et al. 1992), which may be driven by behavioural patterns.
other studies that have found no evidence of vertical stratification in forest arthropods have been carried out in temperate forests and these will be discussed below.

A potential hypothesis when examining vertical stratification across altitudinal and latitudinal gradients, would be to expect lower stratification at higher altitudes and latitudes, as the trees become shorter, lianas become sparser (Lieberman et al. 1996) and harsher environmental conditions may become limiting for some species. However, we did not find a pattern of decreasing stratification with increasing altitude or latitude. We found strong separation between canopy and ground assemblages at all of our high elevation sites, which were located at the highest possible elevation in each mountain system. In our temperate study location in sub-alpine conifer forest at Lijiang, China, canopy and ground assemblages were distinctly separated, even at 3800m a.s.l. It has been suggested that forest type is a major factor shaping differences in composition of canopy taxa, and that vertical stratification of arthropods in temperate forests is weak because the vertical dimension does not represent large changes in microclimate (Basset 2001). This is not supported by our results, in which we found no latitudinal pattern in vertical stratification. Our results are discordant with other temperate zone studies, which have shown dramatically lower abundance and richness of canopy arthropods (Preisser et al. 1998) and little to no evidence for vertical stratification (Fowler 1985, Schowalter and Ganio 1998, Corff and Marquis 1999).

Is the canopy richer than the ground?

When we examined patterns of abundance and richness, we found mixed results. Overall abundance and species richness were sometimes higher in the canopy and sometimes higher in the understorey, however there was no consistent pattern of dominance of the canopy over the ground fauna (or vice versa) across altitude or latitude. We demonstrate that for the hyper-diverse Lepidoptera, the canopy fauna is not necessarily more abundant or species rich compared to that on the
ground, which has important implications for current estimates of global biodiversity.

Sutton et al. (1983), found higher abundances of Lepidoptera in the canopy, something we also observed in Brunei, Papua New Guinea and Panama. When we examined total estimated species richness, however, there was little difference between canopy and ground. Basset et al. (2001), showed that insect herbivores were more speciose in the canopy than at ground-level in Gabon, in agreement with results for light trap insects in Zaire (Sutton and Hudson 1980). Our results are discordant with the idea that herbivore assemblages in the canopy are more diverse than in the understorey. Our Chinese altitudinal transects, located in tropical, sub-tropical and sub-alpine regions displayed higher levels of abundance and richness in the understorey at all altitudes. A possible explanation for this difference in China, is that human disturbance has produced a rich ground flora. Long-term management of the forest understorey, such as for the cultivation of medicinal plants, may have inflated habitat heterogeneity and diversity, thus leading to a higher diversity of associated moths.

Methodological Issues

Canopies are recognised as habitats of high diversity, however many studies of canopies have focused on sampling foliage with insecticidal fogging (Adis et al. 1998), a method which may fail to capture high levels of diversity attributable to more vagile groups of arthropods. Fogging surveys of rainforest canopies do not recover large numbers of Lepidoptera (e.g. Ellwood and Foster 2004), which sometimes contribute as little as 0.2% of the total species encountered (Erwin 1989). Flowers in the canopy are an important habitat for arthropods such as beetles, yet they are often not targeted in surveys of canopy species richness (Wardhaugh et al. 2012b). Epiphytes have been shown to host a large number of invertebrates. Epiphytes such as Asplenium, can contain a unique suite of species (Rodgers and Kitching 2011) and the inclusion of Asplenium can double previous estimates of total canopy biomass (Ellwood and Foster 2004). Using light traps,
we show that a hyper-diverse order, the night-flying Lepidoptera, (which may have diurnal resting sites away from the canopy foliage), are also under-represented in total estimates of total canopy diversity.

**Explanatory Hypotheses**

The clarity and ubiquity of the ground/canopy stratification we have identified precludes the idea that this is merely an accidental outcome reflecting our methodology. Two classes of explanation then exist to account for the stratification we have shown. These are not mutually exclusive.

The first explanation is that the species encountered within ground and canopy assemblages occur where they do because that particular stratum of the forest defines their life-time *habitat*. In other words, the adult insects we encounter in our traps reflect the larval assemblages which occur in that stratum. This in turn demands that the food resources of the species encountered at each level are themselves stratum-limited. Testing the veracity or otherwise of this hypothesis demands knowledge of the food plants of the species that dominate each level. The contrasting, but not mutually exclusive hypothesis is that encountering particular species in particular strata reflects a *behavioural* preference on the part of the adults of that species, the food-plants of which may actually occur elsewhere.

Support for food resource stratification has been found for butterflies in Borneo (Schulze et al. 2001) and Panama (Beccaloni 1997). In Costa Rica, Brehm (2007) showed strong stratification of geometrid and arctiid moths, associated with host plant height. Generally however, there is little information on food resource stratification for moths, which has made interpretation of observed differences in moth distributions difficult. In principle, testing this idea would involve knowing not only where particular species breed but also what their diel (diurnal vertical migration) shifts in flight level might be.
The above hypotheses require information on host plant associations if they are to be tested. Some information for Panamanian moths is available, cataloguing many years and many tens of thousands of rearings from adjacent Costa Rica (http://janzen.sas.upenn.edu/caterpillars/database.lasso). Accordingly we have made a preliminary analysis based on that data-base plus plant information available (Croat 1978).

The examination of food-plant records for the Panamanian samples suggests there is support for both hypotheses. The occurrence of moth species in the canopy which have larval habitats at ground level (such as the Acentropinae (Crambidae)), as also noted by Schulze and Fiedler (2003), is evidence that stratification may be behavioural. On the other hand, differences in food-plant specialization among canopy and ground sampled adults suggests that a substantial percentage of species are reflecting available larval resources within the stratum in which they are encountered. Only natural historical studies of individual species will allow species to be placed unequivocally in one or other category. This analysis also highlights the general value of food-plant compendia such as the Janzen website (Janzen and Hallwachs 2009), which represents a large amount of work, making it possible to link the species we are interested in to their host plants.

The work of (Brehm 2007) is most directly comparable to our Panama results, being conducted in lowland rainforest on the Caribbean slopes of Costa Rica. Brehm found a clear increase in the richness of Arctiidae for the canopy. We also found more arctiid individuals in the canopy, but observed species richness differed little between canopy (57 species) and ground (52 species). Geometrid species richness was greater in the understory in Brehm’s 2007 study, another pattern that was not apparent in our results (130 individuals of 62 species in the canopy; 184 individuals of 72 species on the ground), but we acknowledge that Brehm’s samples were larger than ours (total individuals 946 compared with 314 geometrid individuals in our case) so it is possible that larger samples may uncover similar patterns in the San Lorenzo forests. Differences between the two
studies could also be seasonal, as Brehm’s samples were collected from February to July (across 2 years) whereas our results are from late September and October. Certainly Brehm’s understorey samples contained a greater proportion of Larentiinae than did ours and this could be a seasonal effect (Brehm 2007).

Atherton, Queensland, sampling produced patterns similar to those from Panama - strong evidence of vertical stratification in Geometridae, Arctiidae and Pyraloidea. At both locations, Arctiidae and Pyraloidea were consistently more abundant and species rich in the canopy layer. Geometridae produced mixed results, often with higher abundances in the ground layer, but with similar species richness in the ground and canopy. The generally even distribution of Geometridae richness between canopy and ground, or a slight decline of Geometridae in the canopy, were also found in Borneo by Beck et al. (2002) and in Peninsular Malaysia by Intachat and Holloway (2000). The increase in abundance of Arctiidae in the canopy noted by Schulze et al. (2001) is consistent with our Atherton results. The lack of a clearly defined canopy fauna for the Pyraloidea as found by Schulze & Fielder (2003) is not reflected in our results.

During the Atherton study we were able to include the Noctuidae, which were unique among our analyses in exhibiting no clear stratification between canopy and ground assemblages. Noctuids were consistently more abundant in the canopy, while species richness was either equal between canopy and ground strata (Nov 2009), higher in the ground samples (May 2010) or higher in the canopy (Apr 2011). Many species of Noctuidae are robust, highly vagile, generalist monocot feeders, which could make them tourists across habitat types, with less habitat specificity than other restricted moth families such as Geometridae (Common 1990).

In both family-level analyses presented here (Panama and Atherton), moth assemblages within the Arctiidae, Geometridae and Pyraloidea showed strong vertical stratification. Any attempt, therefore, to assess the fauna of rainforests or
to develop monitoring protocols for on-going assessment of forest health must sample in the canopy as well as at ground level.

This study has been an extensive investigation of adult moths, focusing primarily on spatial distributions rather than indications of resource use. The community-level analyses we have presented now need to be complimented with detailed faunistic analyses, in which the specific taxa contributing to the vertically demarcated assemblages are examined both in terms of distribution, overlap and available natural history information. We have not set out to study vertical stratification at a more fine-grained scale, such as the effect of microhabitats in vertical space, or the degree to which assemblages form multiple vertical layers; however this is another area in which further research is necessary.

We have conducted extensive sampling over 20 years, collecting and identifying over 100,000 individual moths across altitudinal and latitudinal gradients. The major conclusion, based on sampling in many habitats, forest types and areas of differing biogeographical history, is that for night-flying moths, canopy assemblages are different from ground assemblages, but not necessarily more diverse. Obviously, this has important implications for research, which is often carried out either in the canopy or at ground level. These results suggest that, in forests, looking at one or the other may be misleading.

Acknowledgments

This paper is the product of many different projects, and would not have been possible without many funding bodies and volunteer help. Griffith University School of Environment and the Environmental Futures Centre supported all research presented here. Atherton research was funded Terrestrial Ecosystem Research Network (TERN); this data is available for use by other researchers (http://tern.org.au/). Lamington National Park data was collected during the IBISCA-Qld project, funded by the Qld Government Smart State Initiative,
Queensland Museum and The Qld National Parks Association. Border Ranges research would not have been possible without the botanical expertise of John Hunter, Stephanie Horton and Bill McDonald. Support was also provided by Conservation Volunteers Qld. Work in China was funded by the Qld-Chinese Academy of Science Biotechnology Fund, in collaboration with Xishuangbanna Tropical Botanic Garden and the Kunming Institute of Zoology. The IBISCA-Panama study was an initiative of Pro-Natura International, Ocean Vert, Blaise-Pascal University, the University of Panama and the Smithsonian Tropical Research Institute (STRI), with core funding from SolVin Solvay SA, STRI, and the United Nations Environment Programme, the Walcott fund of the Smithsonian Institution, the European Science Foundation and the Global Canopy Programme. Thank you to Nigel Stork for feedback and editing.

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Chapter 5 Appendix

Appendix 5.1 Study locations

Australia

Border Ranges (BR) National Park (NP), New South Wales (Latitude ca 28.2°S), encompasses 31683 ha of rainforest, 15 929 ha of which are within the Gondwana Rainforests of Australia World Heritage Area (WHA). A transect of 20 permanent, 20m by 20m square study plots were established, with four replicate plots (at least 400m apart) in each of five altitudinal bands placed across the available altitudinal range (300m, 500m, 700m, 900m, and 1100m a.s.l.). Generally, the transect runs from complex notophyll vine forest at the lower altitudes, to simple microphyll fern forest (Webb and Tracey 1978) at the higher altitudes. At the low and mid altitude plots – 300m, 500m and 700m a.s.l., dominant tree species include Diospyros pentamera, Archontophoenix cunninghamiana and Argyrodendron trifoliatum. At higher altitude plots – 900m and 1100m a.s.l., dominant species include Polyosma cunninghamii, Cyathea leichhardtiana, Doryphora sassafras and Atractocarpus benthamianus, with some Nothofagus moorei at the 1100m a.s.l. plots. All plots were located on basaltic krasnozem soils, with a south-westerly facing aspect. At each plot, one trap was placed in the canopy and one at head height and run for three nights. Due to time constraints and trap failures, a total of 228 samples were collected in the two seasons. Samples were collected between the 4th and 22nd of April 2011, and between the 27th of October and 12th of November 2011.

Lamington NP Queensland (LAM) (Latitude ca 28.13°S), was established in 1915, and covers 20590 ha of primary rainforest, lying within the Gondwana Rainforests of Australia WHA, and is separated by 12.5 km of continuous rainforest from the Border Ranges plots. Forest types are similar to those at Border Ranges with complex notophyll vine forest at low elevations being dominated by Argyrodendron actinophyllum, A. trifoliolatum and Pseudoweinmannia lachnocarpa while the simple microphyll fern forest at higher elevations is
dominated by *Nothofagus moorei*, *Quintinia sieberi* and *Callicoma serratifolia*. The flora of the transect is detailed by Laidlaw et al. (2011). This altitudinal transect has the same design as the Border Ranges NP transect, i.e. four, 20 x 20m plots located at least 400m apart, in each of five altitudinal bands (300m, 500m, 700m, 900m and 1100m a.s.l.). All plots were situated within the West Canungra Creek catchment, on Cainozoic ingenious rock, with north-westerly aspects (Strong et al. 2011). At each plot, one trap was placed in the canopy and one hung at head height, and run for three nights, producing a total of 207 samples in both sampling seasons. Sampling at Lamington NP occurred between the 14th and the 30th of October 2006 and between the 10th of March and the 2nd of April 2007.

**Mt Lewis NP, Queensland** (ML) (Latitude ca 17.5°S), is part of the Australian Wet Tropics World Heritage Area (WTWHA) and is located 80 kms north of Cairns, Qld. and protects an area of both primary and secondary highland rainforest. The area was declared a National Park in December 2009, (and combined with Riflemead Forest Reserve) to become Mt Lewis National Park, encompassing 229km². This area contains a number of endangered vertebrate species, many of which are predicted to decline under climate change (Williams and Hero 1998, Williams et al. 2003). The forest shifts from complex notophyll vine forest, to cloud forest at the higher altitudes, starting at around 900m a.s.l. This shift, driven by direct orographic precipitation from the cloud cap and cooler temperatures, is characterised by simpler community structure, tree height, and leaf size (DERM 2010). The transect runs from 400m – 1200m a.s.l., with 600m, 800m, 1000m and 1200m a.s.l. plots along the 28 km long Mt Lewis Road. At each plot, one trap was placed in the canopy and one at ground level, and run for three nights, producing a total of 235 samples across the two sampling occasions. Sampling at Mount Lewis was carried out from 21st Nov – 13th Dec 2009, and 1st – 18th of April 2011.

**Atherton, North Queensland** (Latitude ca 17.0°S) is a 25 ha permanent study plot, established as part of the CSIRO Rainforest Permanent Plots of North Queensland,
and funded by the Terrestrial Ecosystem Research Network (TERN), an interdisciplinary project which has established a series of permanent monitoring plots (Graham 2006). The plot is located 24 km northeast of Atherton, in Danbulla State Forest, which covers 12,672 ha. The plot is at 800 m a.s.l., and is based on metamorphic rock, with affinities to the xanthozem Great Soil Group (Graham 2006). The plot is characterized as complex notophyll vine forest (Tracey 1982), dominated by *Medicosma fareana*, *Flindersia laevicarpa* and *Ceratopetalum succirubrum* and the canopy ranges between 26 m and 40 m. This area was selectively harvested approximately 35 years ago but is relatively free from recent disturbance (Graham 2006). Light traps were placed at 5 points within the 25 ha plot, selected using a random number table. Moth sampling was carried out at the Atherton plot on three occasions: between the 10th and 20th of November 2009, between the 19th and 27th of May 2010 and between the 20th and 26th of April 2011. At each of the five points, one canopy trap was put into the upper canopy, and one trap was run at ground level, and run for three nights, producing a total of 90 samples across the sampling occasions.

*Paluma, North Queensland* (PL)(Latitude ca 18.5°S). Sampling was carried out on a one hectare plot, established at 1000 m a.s.l. on Mt Spec in Paluma Range National Park, which covers 10,700 ha near Townsville, Qld. The forest type is simple notophyll vine forest (Tracey 1982) and the area is based on granitic rock. Dominant tree species include *Apodytes brachysylis*, *Cryptocarya leucophylla*, *Brackenridgea nitida* and *Cryptocarya densiflora* (Laidlaw 1999). Three traps were run at ground level, and three in the canopy, for five nights, at least 40 m apart, producing a total of 30 samples. Sampling occurred between the 26th of Jan and 3rd of Feb 1999.

**Papua New Guinea**

*Oomsis, PNG* (PNG) (Latitude ca 6.5°S) is an area of lowland mixed species rainforest (Paijmans 1976) which was selectively logged around 45 years ago. The plot occurs at around 400 m a.s.l., with a mean annual rainfall of 4800 mm. Three
traps were put into the canopy, and three at ground level, located at random points within a 1 ha plot, at least 40m apart, and run for five nights, producing a total of 30 samples. Sampling occurred between the 22nd Jul and 3rd of Aug 2000.

**China**

We carried out sampling across altitudinal gradients at three different latitudes in Yunnan Province, China. The experimental design of the Chinese altitudinal transects was slightly different to that of the Australian altitudinal transects. In China there were five replicate plots at each of four altitudinal bands, rather than four replicates at each five altitudinal bands in Australia, due to less availability of forest across altitude.

**Ailao Shan** (Latitude ca 24.5°N). The Ailao Shan study location was in a 504 km² area of protected subtropical rainforest, in a reserve 200km south-west of Kunming. Plots were grouped into 4 altitudinal bands (2000m, 2200m, 2400m and 2600m a.s.l.) with five replicate plots in each. The mean annual temperature is around 11°C. Plots at the lower end of the transect (2000m a.s.l.) were dominated by *Claoxylon khasianu* (Euphorbiaceae), *Manglietia insignis* (Magnoliaceae) and *Lithocarpus truncates* (Fagaceae), with a dense understorey of bamboo at all plots. The density of the bamboo understorey decreased with increasing altitude. At 2200m a.s.l., plots were dominated by *Lithocarpus hancei* and *Camellia sinensis*, and at 2400m a.s.l., *Rhododendron leptothrium* (Ericaceae), *Eurya obliquifolia* (Ericales) and *Lithocarpus xylocarpus* (Fagaceae). The highest altitude plots (2600m a.s.l.) were dominated by *Castanopsis wattii* (Fagaceae) and *Rhododendron leptothrium* (Ericoideae) (Y. Tang et al. unpublished data). Each plot was sampled at canopy and ground level for three nights, producing 120 total samples. Moth sampling was carried out between the 1st and 20th of July 2011.

**Mengla** (Latitude ca 21.5°N). The Mengla tropical altitudinal gradient was located near the border of Laos, in the Xishuangbanna region of Yunnan. The average annual temperature is 21°C and the area is typified by a tropical monsoonal
climate, which is warm for the latitude, being as it is, edged by mountain ranges to the north. This area is the limit of tropical rainforest in the northern hemisphere (Hua 2003). The forest type at Mengla is closely allied with tropical South East Asian rainforest, with a very similar composition of plant families and genera but is less dominated by Dipterocarpaceae (Hua 2003). Plots were in four altitudinal bands (800m, 1000m, 1200m and 1400m a.s.l.) with five replicates in each. A total of 120 samples were collected. Moth sampling occurred between the 5th and 24th of July 2012.

Lijiang – (Latitude 27.0°N). Lijiang study plots were located around the Yulong Snow Mountain, Lijiang, a transitional zone between the Tibetan plateau and the north east Yunnan Plateau. This location has been modified by human impacts including Yak farming and an increasing tourist trade. The wet season is between May and October and the average temperature is 12.6°C annually (He et al. 2010). Altitudinal bands were at 3200m, 3400m, 3600m and 3800m a.s.l., with five replicate plots in each band. Due to time constraints, we sampled some plots until we caught at least 100 samples from both the canopy and the understorey, collecting a total of 92 samples (rather than the full 120 samples at the other altitudinal transects). Moths were sampled between the 9th and 22nd of August 2012.

Panama
The site is in the San Lorenzo Protected Area (Latitude ca 20.4°N). Field work in Panama took place in a lowland wet forest in the Parque Nacional San Lorenzo (Colón Province, Republic of Panama), growing on Chagres sandstone (late Miocene or early Pliocene; Pyke et al. 2001), in the vicinity of a tower crane yielding easy access to 0.92 ha of canopy (Wright et al. 2003). The study plots were approximately 100-120m a.s.l. This location averages 3139 mm of annual rainfall and an average annual air temperature of 26.0°C (1998-2002 data). The climate is wet year-round, with a comparatively drier season between January and mid-April (average length of dry season = 125 days - Chave et al. 2004). The crane stands in a six-hectare plot where all 22,400 trees of 238 species with a bole size of
1 cm dbh or greater have been identified, measured and mapped. This 6 ha of forest contains 3338 stems per ha (> 1 cm dbh) and a total basal area of almost 32 m² per hectare with trees up to 45 m tall. Liana abundance amounts to 2222 individuals and 0.776 m² of basal area per ha (greater than 0.5 cm diameter: Schnitzer 2005). At least 103 epiphyte species are present within the crane perimeter (Zotz 2004) and 119 liana/vine species have been recorded from the area (S.J. Wright, pers. comm.). The forest has been mostly free of severe disturbance for the past 150 years and is evergreen, with less than 3% loss in canopy cover by the end of the dry season (Condit et al. 2000, Condit et al. 2004). The most common plant species include Tovomita longifolia (Clusiaceae), Protium panamense (Burseraceae), Tachigali versicolor (Fabaceae) and Psychotria suerrensis (Rubiaceae), Brosimum utile (Moraceae), Aspidosperma spruceanum (Gentianales), Manilkara bidentata and Tapirira guianensis. Six traps were deployed at each plot, three at head height in the ground zone and three in the canopy, and run for 1 night, producing a total of 44 samples. The availability of a range of specialized canopy access devices enabled virtually all of the traps to be placed in the high canopy. Only moths belonging to the Arctiidae, Geometridae and Pyraloidea were targeted during this study. A single night’s trapping (with six traps) was run at each plot unless there was a trap malfunction, in which case further trap nights were added so that the trapping effort at each plot remained equal. Moths were sampled at 8 points within the 0.92 ha canopy crane plot, between September 27th and October 28th 2003.

**Vietnam**

*Cat Tien National Park* (Latitude ca 11.3°N). This plot was situated in Cat Tien National Park, Vietnam, which covers 720 km² of forest, in Dong Nai Provence, approximately 150 km north of Ho Chi Minh City. The climate is characterised as monsoonal tropical, with annual rainfall of around 2300 mm, and average monthly temperatures range from 15 - 35°C. The area has had some disturbance including logging and herbicides sprayed during the Vietnam War (Blanc et al. 2000). The forest is a semi-evergreen regeneration area with dominant species including Glochidion hypolencum (Phyllanthaceae), Lagerstroemia ovalifolia (Lithraceae),
Alphonsea gaudiana (Annonaceae) and Streblus asper (Moraceae). Three traps were placed in the canopy and three at ground-level at random locations within a 1 hectare plot, at least 40m apart. Sampling occurred in July 2002 and each light trap was run for 5 nights, producing a total of 30 samples.

Brunei

Batu Apoi National Park (Latitude ca 4.3°N). The Bruneian plot was located in the Batu Apoi National Park, Brunei Darussalam, Borneo, which covers 48,857 ha of primary rainforest. Our Brunei plot was at 50m a.s.l. approximately 500 km from the north-west coast of Borneo. The area has an average annual rainfall of 3900mm, and average temperatures range from 22.3 - 31.8°C. The area is characterized by quartz and kaolinite soils, and is a mixed dipterocarp lowland rainforest dominated by Fordia splendissima, Mallotus sp., Dillenia excelsa and Syzygium sp. (Laidlaw 1999). Three traps were run at ground level and three in the canopy, separated by at least 40m within a 1 ha plot, and run for five nights, producing a total of 30 samples. Moth sampling occurred between the 7th and 23rd of August 1995.

For a summary of all study locations, plots and sampling regimes see Table 5.1 and Appendix Table 5.3.
<table>
<thead>
<tr>
<th>Location</th>
<th>DATE</th>
<th>Lat Long</th>
<th>NUMBER OF TRAP NIGHTS</th>
<th>TOTAL MOTHS SAMPLED</th>
<th>CANOPY</th>
<th>GROUND</th>
<th>CANOPY</th>
<th>GROUND</th>
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<tbody>
<tr>
<td><strong>Australasia</strong></td>
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<tr>
<td>Border Ranges National Park, NSW</td>
<td>Apr 2011</td>
<td>28°24’S 153°05’E</td>
<td>60</td>
<td>60</td>
<td>4669</td>
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<tr>
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<td>13358</td>
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<td>60</td>
<td>1449</td>
<td>2040</td>
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<td>Nov 2009</td>
<td>17°06’S 145°37’E</td>
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<td>21</td>
<td>1034</td>
<td>571</td>
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<td>345</td>
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<td>1206</td>
<td>1176</td>
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<td>Mengla, Yunnan China</td>
<td>Jul 2012</td>
<td>24°03’N 101°19’E</td>
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<td>60</td>
<td>8511</td>
<td>11441</td>
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<td>Ailao Shan Ranges, Yunnan, China</td>
<td>Aug 2011</td>
<td>24°03’N 101°19’E</td>
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<td>60</td>
<td>851</td>
<td>11441</td>
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<td>Lijiang, Yunnan, China</td>
<td>Aug 2012</td>
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<td>8</td>
<td>8</td>
<td>758</td>
<td>945</td>
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<td>Oct 2008</td>
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<td>8</td>
<td>8</td>
<td>758</td>
<td>945</td>
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</table>

1. Target taxa were the Pyraloidea, Arctiidae and Geometridae only.
Table 5.4 Summary of results for ground and canopy level at each single altitude plot: Brunei (BRU), Panama (PAN), Vietnam (VIET), Paluma (PALU), Papua New Guinea (PNG), Atherton (AT) November 2009, May 2010 and April 2011. G=Ground, C=canopy; Rich = species richness, Abund = abundance.

<table>
<thead>
<tr>
<th>Location</th>
<th>Abund G</th>
<th>Abund C</th>
<th>G Rich</th>
<th>C Rich</th>
<th>G rich (ACE)</th>
<th>C rich (ACE)</th>
</tr>
</thead>
<tbody>
<tr>
<td>BRU</td>
<td>576</td>
<td>822</td>
<td>213 ± 9.9</td>
<td>241 ± 9.6</td>
<td>222.91 ± 15.01</td>
<td>250.78 ± 12.97</td>
</tr>
<tr>
<td>PAN</td>
<td>758</td>
<td>945</td>
<td>282 ± 12.6</td>
<td>290 ± 12.6</td>
<td>457.08 ± 31.39</td>
<td>493.2 ± 17.12</td>
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<tr>
<td>VIET</td>
<td>3618</td>
<td>3528</td>
<td>251 ± 9.0</td>
<td>217.6 ± 9.4</td>
<td>253.1 ± 9.26</td>
<td>239.6 ± 9.87</td>
</tr>
<tr>
<td>PALU</td>
<td>539</td>
<td>651</td>
<td>293 ± 14.4</td>
<td>313 ± 15.3</td>
<td>835.57 ± 80.06</td>
<td>1157.05 ± 85.56</td>
</tr>
<tr>
<td>PNG</td>
<td>1232</td>
<td>1795</td>
<td>365 ± 16.2</td>
<td>362 ± 15.5</td>
<td>921.34 ± 53.32</td>
<td>807.66 ± 65.12</td>
</tr>
<tr>
<td>AT NOV</td>
<td>581</td>
<td>1091</td>
<td>187 ± 12.2</td>
<td>212 ± 13.1</td>
<td>333.42 ± 12.89</td>
<td>402.63 ± 18.38</td>
</tr>
<tr>
<td>AT MAY</td>
<td>345</td>
<td>625</td>
<td>123 ± 10.5</td>
<td>148 ± 11.4</td>
<td>232.88 ± 9.48</td>
<td>298.81 ± 13.32</td>
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<td>AT APR</td>
<td>445</td>
<td>1003</td>
<td>134 ± 10.9</td>
<td>179 ± 12.5</td>
<td>236.65 ± 6.77</td>
<td>267.68 ± 6.88</td>
</tr>
</tbody>
</table>
Table 5.5 Canopy ground comparisons at each altitudinal band for the
altitudinal transects in Australia – Mt Lewis, Border Ranges, Lamington
(beginning and end of wet season) and China – Ailao Shan, Lijiang, Mengla
(single sampling occasions). These results consistently show strong
differences between the overall assemblages in the understorey and canopy.

Location

Alt

P
(perm)

Pseudo-F
/t

Abund
G

Abund C

Rich G

Rich C

Rich (ACE) G

Rich (ACE) C

ML Apr

400

0.023

1.4514

361

437

153±11.8

160±12.0

292.4 (± 18.85)

306.6 (± 20.07)

ML Apr

600

0.021

1.4304

939

3206

217±13.8

252±14.7

452.57 (± 23.61)

474.12 (± 17.24)

ML Apr

800

0.041

1.3246

837

986

192±13.1

163±12.2

370.21 (± 15.87)

346.39 (± 18.6)

ML Apr

1000

0.037

1.3867

1286

473

162±12.1

128±10.9

323.79 (± 15.94)

321.14 (± 32.55)

ML Apr

1200

0.029

1.4919

1339

1830

168±12.3

132±11.0

281.47 (± 8.52)

223.2 (± 13.23)

ML Nov

400

0.039

1.4631

474

528

141±10.9

137±10.8

286.57 (± 24.44)

272.01 (± 20.95)

ML Nov

600

0.024

1.7896

462

821

187±12.3

171±11.9

320.85 (± 13.38)

320.85 (± 13.38)

ML Nov

800

0.028

1.4342

272

447

109±9.8

133±10.6

231.14 (± 13.81)

260.19 (± 14.66)

ML Nov

1000

0.033

1.3734

466

579

118±10.2

82±8.6

230.48 (± 11.75)

159.26 (± 11.25)

ML Nov

1200

0.037

1.3039

955

560

128±10.5

107±9.7

229.18 (± 15.58)

166.51 (± 7.59)

BR Nov

300

0.025

1.2263

453

464

118±10.4

102±9.7

194.16 (± 9.01)

180.85 (± 10.79)

BR Nov

500

0.028

1.4715

1062

1408

137±11.2

158±11.9

199.28 (± 8.24)

266.66 (± 14.87)

BR Nov

700

0.031

1.391

978

1044

134±11.0

121±10.5

187.71 (± 7.47)

170.17 (± 10.89)

BR Nov

900

0.026

2.2888

585

1344

91±9.2

94±9.4

122.02 (± 4.28)

136.99 (± 9.77)

BR Nov

1100

0.03

1.6246

827

406

115±10.3

81±8.8

163.77 (± 7.38)

143.6 (± 4.24)

BR Apr

300

0.847

0.776

1679

2367

101±9.7

101±9.6

123.42 (± 5.03)

135.71 (± 7.11)

BR Apr

500

0.032

1.2818

1231

3027

118±10.4

132±10.9

164.71 (±7.06)

163.94 (± 5.05)

BR Apr

700

0.028

1.6238

899

1152

105±9.8

100±9.6

134.39 (± 4.58)

120.02 (± 4.9)

BR Apr

900

0.027

1.4901

12582

6029

122±10.6

86±8.9

150.64 (± 3.39)

107.71 (± 4.99)

BR Apr

1100

0.027

1.8339

2103

345

98±9.6

44±6.5

124.04 (± 3.52)

71.56 (± 6.67)

LAM Oct

500

0.023

1.2921

344

628

125±10.3

210±13.2

201.03 (± 11.44)

407.13 (± 17.97)

LAM Oct

700

0.305

1.0543

399

409

142±11.3

154±11.7

297.65 (± 13.03)

396.39 (± 29.82)

LAM Oct

900

0.028

1.4169

514

352

148±11.4

115±9.9

226.79 (± 11.28)

316.47 (± 43.6)

LAM Oct

1100

0.026

1.3291

336

83

107±9.8

39±6.1

175.51 (± 9.11)

88.78 (± 9.13)

LAM Mar

300

0.03

1.473

758

999

171±12.1

210±13.2

346.15 (± 22.34)

370.5 (± 12.54)

LAM Mar

700

0.032

1.4739

1153

1001

224±13.6

185±12.6

369.98 (± 16.28)

316.86 (± 10.6)

LAM Mar

900

0.226

1.0701

766

558

207±13.1

188±12.6

349.98 (± 17.38)

313.03 (± 21.18)

LAM Mar

1100

0.03

1.5962

1363

740

154±11.5

126±10.6

226.51 (± 9.32)

197.01 (± 10.36)

AS Jul

2000

0.01

1.3319

1916

1281

511±19.5

378±17.5

994.62 (± 28.47)

862.98 (± 32.22)

AS Jul

2200

0.014

1.4935

3945

3326

550±19.3

510±19.0

841.66 (± 24.33)

807.98 (± 19.42)

AS Jul

2400

0.007

1.5612

3575

1930

495±18.9

334±16.5

776.3 (± 22.42)

581.01 (± 12.01)

AS Jul

2600

0.008

1.9413

2586

1390

460±18.2

258±14.7

654.02 (± 15.47)

410.89 (± 14.02)

MG Jul

800

0.014

1.3737

1479

1339

569±21.7

522±21.1

1082.09 (± 23.97)

1152.82 (± 41.1)

MG Jul

1000

0.017

1.2002

2312

1783

805±24.8

625±22.6

1497.94 (±32.02)

1252.67 (± 47.2)

MG Jul

1200

0.008

1.3728

1775

1336

657±23.1

518±20.9

1221.97 (± 30.19

1095.31 (± 43.82)

MG Jul

1400

0.01

1.4006

1906

1277

718±23.9

553±21.5

1362.86 (± 32.98)

1195.45 (± 33.33)

LJ Aug

3200

0.011

1.706

3069

1574

284±13.5

227±12.5

378.92 (± 12.04)

330.12 (± 7.92

LJ Aug

3400

0.008

1.5732

1921

1324

210±12.5

205±12.5

290.68 (± 12.55)

305.73 (± 11.41)

LJ Aug

3600

0.004

1.5571

2195

1778

265±13.2

242±12.9

385.27 (± 11.47)

337.42 (± 10.06)

LJ Aug

3800

0.012

1.4546

1672

1655

224±12.98

183±11.9

309.59 (± 19.28)

251.67 (± 5.95)

206


Table 5.6 Summary of family level results – total abundance and species richness observed at each location, PERMANOVA test results comparing similarity of ground and canopy assemblages (p>0.05), abundance of each family in canopy and ground strata, observed and estimated total number of species (ACE) in canopy and ground strata, for family level datasets (geom = Geometridae, Pyral = Pyraloidea (Crambidae + Pyralidae), Arct = Arctiidae and Noct = Noctuidae) – at Panama and Atherton (Nov, 2009, May 2010, Apr 2011).

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<td>53</td>
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<td>2.93</td>
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<td>123</td>
<td>26 ± 4.8</td>
<td>37 ± 5.6</td>
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<td>3.83</td>
<td>34</td>
<td>209</td>
<td>9 ± 2.7</td>
<td>15 ± 3.4</td>
<td>10.8 ± 2.3</td>
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<tr>
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<td>1.27</td>
<td>24</td>
<td>46</td>
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<td>87.7±12.5</td>
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Figure 5.6 Bar graphs illustrating the number of species restricted only to the canopy, restricted only to the ground, and found in both the canopy and the ground at all location – Brunei, Paluma, Panama, Papua New Guinea, Vietnam, and Robson Creek, Atherton (RC), Mt Lewis, Mengla, Ailao Shan, Lijiang, Lamington, Border Ranges, Mt Lewis.
Chapter 6

Beta diversity in an Asian ‘hotspot’: moth turnover across altitudinal gradients in tropical, sub-tropical and sub-alpine forest, south-west China

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To be submitted to *Journal of biogeography*
Abstract

South-western China is widely acknowledged as a biodiversity ‘hotspot’: there are very high levels of endemism, and many environments are under significant anthropogenic threat. As part of a Queensland-Chinese Academy of Sciences Joint Biotechnology Project, we have established three permanent elevational transects in tropical (Mengla), sub-tropical (Ailao Shan) and sub-alpine (Lijiang) forest in central Yunnan Province (P. R. China). At each transect, twenty permanent study plots were established, five in each of four elevational bands separated by 200 vertical metres. Moths were sampled in August 2011, July 2012, and August 2012. Floristic surveys were conducted at all plots. Over all three altitudinal surveys, a total of 48358 individual moths, belonging to 4267 separate morphospecies, were sampled. When compared with moth assemblages collected using similar sampling protocols across elevational gradients in tropical and subtropical Australian rainforests, the assemblage of moths from the Chinese altitudinal gradients was more diverse. Clear differentiation of species assemblages was apparent across elevations in our Chinese results, which was also reflected in four of the most diverse subordinal groupings: the Pyraloidea, Geometridae, Arctiidae and Noctuidae. The presence of unique assemblages at the highest elevations is documented; these may well be under most threat from predicted climate change. Predictor sets of altitudinally restricted indicator species are proposed for each of the altitudinal gradients. These results add to our understanding of China’s biodiversity and can be used to monitor future changes to herbivore assemblages in a ‘hotspot’ of biodiversity.
Introduction

Conservation biologists have subscribed widely to the idea that there is a set of biodiversity ‘hotspots’ globally, in which levels of plant and animal diversity, endemism and vulnerability are exceptionally high. First proposed by Myers and Mittermeier as long ago as 1988, the idea has gained considerable traction and has, in part, underpinned national and international conservation policy settings ever since (Myers 1988, Mittermeier 1999, Myers et al. 2000). The original list of 25 locations has subsequently been added to substantially. However, the biological provinces of south-west China have featured as a ‘hotspot’ from the first inception of the idea. Myers et al. (2000) pointed out that this region has lost over 90% of its original primary vegetation, yet is still home to over 12000 species of plants, of which more than 25% are endemic. This richness is carried over, to a slightly lesser extent, to the vertebrate fauna. Immediately to the south of this region lies a second ‘hotspot’: Indo-Burma (Mittermeier et al. 1999).

The evolutionary and biogeographical reasons for this hyper-diversity are still a matter for debate. Certainly classical Palaearctic and Oriental faunas overlap here (Rongzu 1994, Wu and Yuan 1997). The highly dissected and geologically heterogeneous nature of this mountainous landscape plus the general parallel north-south trending mountain ranges play a part (Zhu 2002) in both engendering and maintaining this high diversity. The location of the region at the very core of mainland East Asia with large areas (before clearing) of habitat available at the latitude may also have acted to produce the very large species pool.

An essential part of the ‘hotspot’ concept has been the idea of vulnerability and endangerment which, in the original formulation, was interpreted as vegetation transformation and the lack of large, formally protected areas. Since then the threats represented by anthropogenic global warming and its likely impact on biodiversity have received increasing amounts of attention (Steffen et al. 2009).
Climate change is having a marked effect on biodiversity, through shifts in altitudinal and latitudinal range, local extinctions, changes in species composition and phenology, as well as a suite of difficult to measure ecosystem level impacts (Hughes 2000, IPCC 2007). The impact that climate change is having on biodiversity is difficult to measure, especially in areas such as south-west China where there is very little historical information about distributions of taxa.

Yunnan Province of south-west China contains over 50% of China's plant species and over 55% of China's fauna (Young and Zhi-Jun 2003). It is comprised of large areas at low latitude and also high altitude, contains many different climatic zones and ecosystem types and has an exceptionally high diversity of flora and fauna (Ellwood and Foster 2004). Western Sichuan and the Yunnan-Guizhou plateaux have experienced a clear warming trend and a decline in rainfall days over the last 40 years of the 20th century. Biodiversity reduction, ecosystem degradation and desertification have followed these changes (2nd National Assessment, 2011).

Yunnan Province contains a large range of ecosystems, from sub-alpine forests near the border of Tibet in the north, to tropical rainforests in the south which are continuous with those of Laos. The region is of particular interest. First, although it lies within a biodiversity ‘hotspot’ it has been little studied. Second, the forests of south-west China are under threat from a suite of interacting factors, including climate change and land clearing. Yunnan Province contains several mountain reserves, which have been designated protected National Parks, yet clearing of mountain cloud rainforest is still occurring in this highly modified and fragmented landscape (Shi and Zhu 2009). Third, climate change in China over the last 50 years has raised annual mean surface air temperature at a slightly higher rate than the global average (Ding et al. 2007). It is predicted that climate change will have a marked effect in East Asia, mostly in line with global predictions including significant increases in temperature, increased
precipitation and more frequent extreme weather events (Ding et al. 2007, IPCC 2007).

Little attention, in general, has been paid to invertebrates in conservation assessments yet terrestrial arthropods are, on the one hand, key drivers of ecological processes (Wilson 1987) and, on the other, excellent predictors of environmental change (Basset et al. 1998). Understanding how selected arthropod assemblages will change with climate is therefore important in understanding likely future changes in diversity and the processes driven by diversity.

Forested altitudinal gradients representing sets of adjacent climates are excellent tools for such studies (Rahbek 1995, 2005, Fiedler and Beck 2008, Grytnes et al. 2008, Fischer et al. 2011, Kitching et al. 2011), encompassing, as they do, a range of environmental factors that shift in a predictable way. Altitudinal gradients allow us to examine a range of shifting environmental factors in a small geographical area. For every 100 m of increased altitude, the temperature decreases by around 0.6ºC (Jacobson 2005). In addition, a suite of other environmental factors shift, including soil chemical properties (Strong et al. 2011) and precipitation, a factor often confounded by the presence of a cloud cap (Laidlaw et al. 2011). The cloud cap modifies community structure, through orographic precipitation, where moisture transfers directly from cloud to the surface of soil and vegetation, influencing a suite of environmental factors including soil moisture, organics and pH (Weathers 1999). There are important implications for cloud forests in the context of climate warming, as increased temperatures are predicted to raise the average level of the cloud base (Still et al. 1999, Laidlaw et al. 2011). Given the high level of endemism in tropical cloud forest systems, this is an area of conservation concern (Aldrich et al. 1997).

Altitudinal gradients are unique study systems yet it is important to understand the range of inter-correlated environmental and biological factors that can shift
with altitude before any conclusions about causation relating to the distributions of plants and animals are made. The impacts of these factors may be mutually confounding such that it is not clear which factor or combination of them is driving the patterns observed. Having acknowledged this limitation, it is also important to emphasise that altitudinal gradients are sometimes the only way in which to study the effects of climate change on ecological communities given a lack of historical data, as is the case in China. Examination of the assemblages of invertebrates’ sites along an altitudinal gradient in a series of other taxonomic groups (to be presented elsewhere) with shifting environmental conditions, allows us to observe the current responses of different species, make predictions about how they will respond to climate change based on their current climatic envelopes, and monitor range shifts through time with ongoing surveys of target taxa.

Lepidoptera is an ideal group for use in climate monitoring, alone or as part of a multi-taxon monitoring tool kit, because they are sensitive to environmental variables such as temperature and moisture and their herbivorous life history ties them closely with larger community-level shifts (Holloway et al. 1992, Schulze et al. 2001). Moths are also a practical study group as they are easy to sample in large numbers using automated light traps, allowing for strong statistical power, and they are a relatively well known group taxonomically (Holloway 1986-2008). Lepidoptera have been used extensively as indicators elsewhere, in studies of vegetation health, restoration and fragmentation (New 1997, Brown and Freitas 2000, Kitching et al. 2000, Chey 2006, Lomov et al. 2006), and as a study of taxa along latitudinal and altitudinal gradients (Axmacher et al. 2004, Brehm et al. 2007).

As part of a collaborative project between the state government of Queensland, Australia, and the Chinese Academy of Sciences we examined changes in moth diversity along three forested gradients within Yunnan Province, south-west China. Altitudinal gradients were established at Lijiang – sub-alpine temperate
forest (27°N), Ailao-Shan – subtropical rainforest (24°N) and Mengla – tropical rainforest (22°N). The Lijiang transect lies within, and the Ailao Shan transect is immediately adjacent to the South Central China biodiversity ‘hotspot’, while the Mengla transect is situated in the small area of Chinese territory which Mittermeier et al. (1998) placed in the Indo-Burma ‘hotspot’.

Through examining the altitudinal distributions of macro moth assemblages across three altitudinal transects – tropical, sub-tropical and sub-alpine, we seek to address the following hypotheses:

H₁ (1) altitudinal distributions of moth assemblages will be different at different latitudes, with higher alpha and beta diversity at lower latitudes
H₁ (2) the altitudinal distributions tropical, sub-tropical and sub-alpine moth assemblages will be correlated with the distributions of vegetation
H₁ (3) family-level composition of moth assemblages will shift with increasing latitude, in association with vegetation assemblage composition.

Methods

Study sites

Three permanently marked altitudinal transects were established in Yunnan Province, south-west China in tropical (Mengla), subtropical (Ailao Shan) and temperate (Lijiang) forests, each separated by approximately 300 km (Figure 6.1). At each of the altitudinal transects, environmental data is currently being recorded, with ibutton temperature loggers at 3 of the 5 plots at each altitude. Ibuttons have been placed in leaf litter, at understorey height (2m above ground) and in the canopy. In addition, soil moisture measurements are being recorded.
The tropical rainforest altitudinal transect was located near Bubeng, Mengla, in the Xishuangbanna Region, close to the international border with Laos. The climate is characterized as tropical and monsoonal, with a pronounced wet season between May and October and a dry season between November and April. The average annual temperature at Mengla is 21°C, with an average annual rainfall of 1,530mm, of which 281mm falls during the dry season.

Figure 6.1 Map of locations of Chinese altitudinal gradients, located in tropical (Mengla), subtropical (Ailao Shan) and temperate (Lijiang) forests each separated by approximately 300 km.

Five replicate 20m x 20m plots in four elevational bands (800m, 1000m, 1200m and 1400m a.s.l.) were established (Figure 6.2) and all trees with a dbh greater than 5cm were identified and permanently tagged and identified by collaborating botanists. Plots at 800m a.s.l. were dominated by Parashorea chinensis and Pittosporopsis kerrii, those at 1000m a.s.l. by Aporusa yunnanensis and
Pittosporopsis kerrii, those at 1200m a.s.l. by Castanopsis echinocarpa and Lithocarpus truncates, and those at 1400m a.s.l. by Castanopsis mekongensis and Lithocarpus truncatus. Moths were sampled between the 5\textsuperscript{th} and 24\textsuperscript{th} of July 2012, using the sampling protocol identical to those techniques employed in the Australian altitudinal transects (presented in Chapter 3).

Figure 6.2 Study sites at Mengla (21°3N); five replicate plots, A to E, in each of four elevational bands (800m, 1000m, 1200m and 1400m a.s.l.).

Ailao Shan (Latitude ca 24.5°N).
Located within the larger Ailao Mountains Reserve, the sub-tropical altitudinal transect was located within the Qian Jia Zai area, about 200 km south-west of Kunming (Figure 6.3). The Ailao Mountains Reserve is a protected forest covering 504km\textsuperscript{2}. The sub-tropical climate of the Qian Jia Zai area has an average temperature of 11°C, with average annual rainfall around 1900mm. The Ailao Mountains occur at a major climatic border between the south-west and south-east monsoon systems of China (Young and Zhi-Jun 2003).
At Ailao Shan, 20 permanent study plots were established, consisting of five replicate plots at each of four altitudinal bands, 2000m, 2200m, 2400m and 2600m a.s.l. (Figure 6.3). Each 20m x 20m plot was permanently marked, and all trees with a dbh greater than 5 centimetres were tagged and identified by collaborating botanist T Yong. The lowest altitude plots (2000m a.s.l.) were dominated by *Claoxylon khasianu* (Euphorbiaceae), *Manglietia insignis* (Magnoliaceae) and *Lithocarpus truncates* (Fagaceae), plots at 2200m a.s.l. by *Lithocarpus hancei* (Fagaceae), *Camellia sinensis* (Theaceae) and *Cyclobalanopsis stewardiana* (Fagaceae), those at 2400m a.s.l. by *Rhododendron leptothrium*, *Lithocarpus xylocarpus* (Fagaceae), *Eurya obliquifolia* (Theaceae) and *Eura paratetragonocladia* (Theaceae), and the highest altitude plots at 2600m a.s.l. by *Castanopsis wattii* (Fagaceae) and *Rhododendron leptothrium* (Ericoideae) (Y. Tang et al. unpublished data). Bamboo was a large component of the understory at 2000m a.s.l., but declined with increasing altitude.

Figure 6.3 Ailao Shan sub-tropical altitudinal transect (24°N); five replicate plots, A-E, in each of four elevational bands (2000m, 2200m, 2400m and 2600m a.s.l.).
Moths were sampled between the 1st and 20th of July 2011, using the previously described protocols. Our methods of sorting to morphospecies were validated by a metabarcoding technique, in which half of each moth sample was preserved in 100% alcohol and then processed by Doug Yu at the Kunming Institute of Zoology. The results of the metabarcoding showed equivalent patterns of altitudinal zonation in the moth assemblages as the traditional techniques we used (Jia et al. In press). Analogous analysis is currently underway for our other altitudinal gradient moth samples.

**Lijiang (Latitude 27.0°N)**

Our Lijiang site was located on Yulong Snow Mountain, a massif consisting of thirteen peaks, the highest of which, Shanzidou, reaches 5596m a.s.l. (Ren et al. 1957). This area is a transitional zone between the south-east Tibetan plateau and the north-east Yunnan Plateau. The Lijiang region has been affected by climate warming, with records showing that mean temperatures were 1.17°C higher between 1999 and 2008, when compared with 1979-1988 (Wang et al. 2010), and precipitation has generally increased since the 1980’s (He et al. 2010). Historically, the Yulong Mountain area contained 19 glaciers, with an average surface area of 11.6 km², the most southerly glaciers in China. These glaciers have retreated and reduced in number to 15, with an average surface area of 8.5 km², a reduction in glacier surface area of 26.8% since 1957. (Rai 2005, Wang et al. 2010). This area is also under substantial environmental pressures from steadily increasing tourist visitation (Wang et al. 2010). Precipitation in Lijiang is highest from May to October and the average temperature is 12.6°C annually (He et al. 2010).

Four altitudinal bands were identified at 3200m, 3400m, 3600m and 3800m a.s.l., with five replicate plots in each band (Figure 6.4). At Lijiang, all 20m x 20m plots were permanently marked, trees with a dbh greater than 5cm were permanently tagged and identified by collaborating botanist Z. Sun. At 3200m a.s.l. the dominant plant species were *Abies forrestii* (Pinaceae) and *Quercus pannosa*
(Fagaceae), at 3400m a.s.l. dominant species included *Abies georgei* (Pinaceae) and *Quercus pannosa* (Fagaceae), and at both the 3600m and 3800m a.s.l. elevational bands, the dominant tree species was *Abies georgei* (Pinaceae). Moths were sampled at Lijiang between the 9\textsuperscript{th} and 22\textsuperscript{nd} of August 2012.

Moths were sampled using the same protocols established during sampling of Australian altitudinal transects. At Mengla and Ailao Shan, a trap was situated at ground level and another in the canopy at each plot and both were run for three nights, producing a total of 120 samples from each transect. Due to time constraints, at Lijiang, some plots were sampled for only two nights, or until we encountered at least 100 individuals (either 2 or 3 nights) in each layer (canopy and ground), producing a total of 98 samples. (See Chapter 3 for a detailed description of moth traps, processing and identification procedures.) Collections of pinned voucher specimens from these surveys have been deposited in the Kunming Institute of Zoology, Kunming.

![Figure 6.4 Study plots at Lijiang (27°9N), five replicate plots, A-E, in each of four elevational bands (3200m, 3400m, 3600m and 3800m a.s.l.)](image)
Analysis

Non-metric multi-dimensional scaling (NMDS) was used to produce ordinations to visualise altitudinal patterns, displayed by assemblages of all macrolepidoptera, and by four diverse family-groups (Geometridae, Arctiidae, Pyraloidea and Noctuidae\(^1\)). Ordinations were generated from matrices of comparisons between plots, based on log transformed abundance data, using the Bray-Curtis similarity measure (Bray and Curtis 1957), with 999 permutations. Permutational multivariate analysis of variance (PERMANOVA) was used to test for differences among the *a priori* altitudinal groups. PRIMER 6 with PERMANOVA+ add-on software (Anderson et al. 2008) was used to run PERMANOVA tests, using a Bray-Curtis similarity measure. We used rarefaction to estimate total species richness within each elevational band using the Abundance-Based Estimator (ACE) (Chao and Lee 1992) in Estimate S (version 8.0.0) (Colwell 2004). We used a Mantel test (RELATE function in PRIMER 6 PERMANOVA+) to test whether altitudinal patterns of plant and moth assemblages were significantly correlated with moth assemblages across altitudes at all locations. The BEST function was used to calculate Spearman’s rank correlations (BIOENV) between the elevation of plots, their tree species richness and the composition of their moth assemblages. Binomial logistic regression was conducted in the R statistical environment (R Development Core Team 2011), to assess changes in the family level faunal composition of species richness across altitude. We tested to see if the proportion of each target family, Geometridae, Pyraloidea (Crambidae + Pyralidae), Arctiidae and Noctuidae, changed across elevations (at p < 0.05), at each of our locations (Mengla, Ailao Shan and Lijiang). We used the generalized linear model: model<-glm(y~Altitude,binomial), in which y (the ratio of a particular family to all other families) is modelled as a function of a single continuous explanatory variable (called Altitude), using an

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\(^1\) In our analyses the family concepts of Arctiidae and Noctuidae follow those of Neilsen et al. (1996). In terms of the recently proposed classification of the Noctuoidea of Zahiri *et al.* (2011) our noctuoid taxa translate as follows: Arctiidae becomes Noctuidae: Arctiinae and Noctuidae becomes ‘[Noctuidae-(Lymantriinae) + Arctiinae +Erebidae+Nolidae(*partim*)]’.
error distribution from the binomial family. The step function was then used to simplify the model by identifying the model with the smallest Akaike information criterion (AIC), a method commonly used in model selection.

IndVal analysis (Dufrene 1999) was used to identify moth species indicative of particular altitudes or ranges of altitudes. The IndVal analysis was carried out using the R statistical environment, utilizing the labdsv package (Roberts 2007, R Development Core Team 2011), which uses a permutation based procedure to quantify species fidelity and specificity to groups of sites (in our case altitudinal bands) using the formula:

\[
\text{IndVal}_{ij} = A_{ij} \times B_{ij} \times 100
\]

\[
A_{ij} = \frac{N_{\text{indiv}}_{ij}}{N_{\text{indiv}}_i}
\]

\[
B_{ij} = \frac{N_{\text{site}}_{ij}}{N_{\text{site}}_j}
\]

Where \( \text{IndVal}_{ij} \) is the indicator value of species \( i \) in cluster \( j \)

\( A_{ij} \) is specificity, \( N_{\text{indiv}}_{ij} \) is the mean number of individuals of species \( i \) that are across plots of group \( j \)

\( B_{ij} \) is fidelity, \( N_{\text{site}}_{ij} \) is the number of sites in cluster \( j \) that contain species \( i \) (Dufrene and Legendre 1997).

We selected species as suitable indicators if they were represented by more than 40 individuals and had an IndVal value greater than 0.7. When selecting indicator species, we sought species that were common, easy to recognize and altitudinally restricted. In the analyses presented here, we have determined statistically which species have high indicator values, and occurred in large enough numbers to be easily encountered. In order for the suites of indicator species to be utilized successfully, future taxonomic identification and removal of species that are hard to identify will be necessary.
Results

Across all three altitudinal transects, a total of 48358 individual moths were sampled, belonging to 4267 morphospecies. At the Mengla tropical rainforest altitudinal gradient, we sampled a total of 13213 individuals, belonging to 2160 morphospecies, 866 of which were singletons. Abundance Coverage Estimation (ACE) produced an estimation of 3206 ± 11 species, suggesting we sampled approximately 67% of the total fauna. At Ailao Shan we collected 19952 moths belonging to 1438 morphospecies. Estimation of total species richness (ACE) was 2105 ± 76; we therefore sampled approximately 68% of the estimated fauna at Ailao Shan. At Lijiang, we collected 15193 individuals, belonging to 669 species. Estimation of total species richness (ACE) was 812 ± 3 suggesting we sampled approximately 82% of the moth fauna.

There was no clear relationship between moth species richness and altitude at Mengla (Figure 6.5 (a)) and Lijiang (Figure 6.5(c)), while there is a slight trend of declining species richness with altitude at Ailao Shan (Figure 6.5 (b)). At Mengla both observed and estimated species richness was fairly even across altitudes, with the greatest richness at 1000m a.s.l. (1091 observed, 1866 estimated species). At Ailao Shan the species richness was highest at 2200m a.s.l. (738 observed, 1099 estimated) with a slight decrease at the highest altitude plots (528 observed, 746 estimated species at 2600m a.s.l.). At Lijiang, there was no clear pattern of change in observed species richness across altitude, however estimated species richness declined linearly with altitude. Mengla had the highest proportion of species represented by singletons and doubletons, 55%, followed by Ailao Shan with 51%, and Lijiang with 37%. The number of species with less than 10 individuals was greatest at Mengla (87%), followed by Ailao Shan (78%) and Lijiang (70%).
Figure 6.5 Total numbers of total observed species encountered (light grey bars), and total estimated species (dark grey bars) in each elevational band at (a) Mengla, (b) Ailao Shan and (c) Lijiang.
Species assemblages exhibited high levels of altitudinal stratification at all three study locations. At Mengla, there was clear stratification between altitudinal bands, which was confirmed by significant differences in assemblage composition between all altitudinal bands pair-wise PERMANOVA tests, between all adjacent altitudinal bands (Table 6.1., Figure 6.6 (a)). At Ailao Shan there was clear step-wise turnover in the moth assemblages, with the 2000m a.s.l. plots forming the most distinct and most dispersed grouping (Figure 6.6 (b)). All pair-wise comparisons of altitudinal bands were significantly different (Table 6.1). Lijiang moth assemblages were also strongly altitudinally stratified, with the highest altitude moth assemblages (3800m a.s.l.) the most loosely associated altitudinal grouping Figure 6.6 (c)). This may be driven by the presence of high-altitude, vagile tourist species. All adjacent pairs of altitudinal bands of moth assemblages were significantly different (Table 6.1).

### Table 6.1 Results of PERMANOVA tests of the entire moth assemblages, between adjacent altitudinal bands at Mengla, Ailao Shan and Lijiang

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<th>800 &amp; 1000 m a.s.l.</th>
<th>1000 &amp; 1200 m a.s.l.</th>
<th>1200 &amp; 1400 m a.s.l.</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Mengla</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>t</td>
<td>1.47</td>
<td>1.62</td>
<td>1.41</td>
</tr>
<tr>
<td>P</td>
<td>0.01</td>
<td>0.008</td>
<td>0.006</td>
</tr>
<tr>
<td><strong>Ailao Shan</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>t</td>
<td>2.38</td>
<td>2.06</td>
<td>1.89</td>
</tr>
<tr>
<td>P</td>
<td>0.009</td>
<td>0.006</td>
<td>0.009</td>
</tr>
<tr>
<td><strong>Lijiang</strong></td>
<td>3200 &amp; 3400</td>
<td>3400 &amp; 3600</td>
<td>3600 &amp; 3800</td>
</tr>
<tr>
<td>t</td>
<td>1.88</td>
<td>1.82</td>
<td>2.41</td>
</tr>
<tr>
<td>P</td>
<td>0.01</td>
<td>0.007</td>
<td>0.005</td>
</tr>
</tbody>
</table>

A Mantel test indicated that vegetation assemblages and moth assemblages were significantly correlated at Mengla (Rho = 0.852, P = 0.001), Ailao Shan (Rho = 0.77, P = 0.001) and Lijiang (Rho = 0.61, P = 0.001). Altitude was highly correlated with moth assemblages at Mengla (91.5%), Ailao Shan (72%) and Lijiang (91.2%).

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Figure 6.6 NMDS Ordination plots of (a) Mengla (tropical) moth assemblages across four elevational bands (800m, 1000m, 1200m and 1400m a.s.l.) (stress + 0.07), (b) Ailao Shan (sub-tropical) moth assemblages across four elevational bands (2000m, 2200m, 2400m and 2600m a.s.l.) (stress = 0.06) and (c) Lijiang (sub-alpine) moth assemblages across four elevational bands (3200m, 3400m, 3600m and 3800m a.s.l.) (stress = 0.05).
Moth family-level composition changed with latitude. In particular, contribution of the Geometridae to the overall moth fauna was greatest at sub-alpine Lijiang (57% of total species (320 species)) declined at Ailao Shan (39% of total species (502 species)), and was lowest at tropical Mengla (22% of total species (432 species)), where the faunal composition of families was more even (Figure 6.7). There were very few species of Pyraloidea encountered at Lijiang (10 species, 2% of total species), in comparison with the diverse Pyraloidea fauna at Ailao Shan (16% of total species (206 species)) and Mengla (17% of total species (330 species)). This may be due to the rainforest versus sub-alpine contrast, as the Pyraloidea is considered a tropical radiation (Common 1990).

Generally, when examined separately, all moth families were altitudinally stratified in a similar way to the entire assemblages (Appendix Tables 6.4, 6.5 and 6.6). The only exception to this was when we encountered very few species, such as in the Pyraloidea and Arctiidae at Lijiang. A summary of pair-wise PERMANOVA tests of altitudinal stratification of individual moth families at each altitudinal gradient is provided in Appendix Table 6.5. Across altitudes, there were no clear shifts in the taxonomic composition of moth assemblages (Figure 6.8, Table 6.2). Generally the overall proportions of moth families were consistent across altitudinal bands, with the exception of Noctuidae at Lijiang, the proportion of which increased with altitude (Figure 6.8, Table 6.2).
Figure 6.7 Subordinal composition of the overall moth fauna at (a) Mengla, (b) Ailao Shan, and (c) Lijiang, when considering the hyperdiverse family-groups Geometridae, Noctuidae, Pyraloidea (Crambidae + Pyraustiinae) and Arctiidae. “Others”, includes all other families of macrolepidoptera such as those within the Bombycoidea and Tortricoidea and the Sphingidae, Notodontidae, Lymantriidae and Lasiocampidae.
Figure 6.8 Proportions of family-groups at each altitudinal band at (a) Mengla, (b) Ailao Shan, and (c) Lijiang. See Table 6.2 for results of tests of proportions.
Table 6.2 Test of proportions of target families across altitudes at each location – Mengla (MG), Ailao Shan (AS) and Lijiang (LJ). Significant differences \((p < 0.05)\) in the proportion of groups across altitude are shaded.

<table>
<thead>
<tr>
<th></th>
<th>Geometridae</th>
<th>Arctiidae</th>
<th>Pyraloidea</th>
<th>Noctuidae</th>
<th>Others</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(z) (P)</td>
<td>(z) (P)</td>
<td>(z) (P)</td>
<td>(z) (P)</td>
<td>(z) (P)</td>
</tr>
<tr>
<td>MG</td>
<td>-0.456 0.648</td>
<td>-0.566 0.572</td>
<td>-0.810 0.418</td>
<td>-0.548 0.584</td>
<td>-0.524 0.6</td>
</tr>
<tr>
<td>AS</td>
<td>1.876 0.060</td>
<td>1.266 0.205</td>
<td>1.310 0.19</td>
<td>1.856 0.063</td>
<td>1.848 0.064</td>
</tr>
<tr>
<td>LJ</td>
<td>-0.407 0.684</td>
<td>-0.672 0.502</td>
<td>1.203 0.229</td>
<td>2.550 0.010</td>
<td>1.060 0.289</td>
</tr>
</tbody>
</table>

*Indicator species*

We identified 26 indicator species at tropical Mengla, 86 at sub-tropical Ailao Shan and 28 at sub-alpine Lijiang (see Appendix Tables 6.7, 6.8 and 6.9 for detailed lists of indicator species). The faunal composition of indicator species varied across latitude, Geometridae contributed the most to indicators in Lijiang (69%), followed by Ailao Shan (51%) and Mengla (28%) (Table 6.3). This can be directly related to the overall faunal composition at each of these locations, which was heavily dominated by Geometridae at sub-alpine Lijiang, whereas overall species composition at Mengla was more evenly distributed across the moth families (see Figure 6.7 (a), (b) and (c)).

Table 6.3 Faunal composition of altitudinally restricted indicator species at (a) Mengla, (b) Ailao Shan and (c) Lijiang. Geometridae accounted for the highest numbers of indicators in all three locations, 28% at tropical Mengla, 51% at sub-tropical Ailao Shan, and 69% at sub-alpine Lijiang.

<table>
<thead>
<tr>
<th></th>
<th>Geometridae</th>
<th>Noctuidae</th>
<th>Pyraloidea</th>
<th>Arctiidae</th>
<th>Other</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lijiang</td>
<td>69%</td>
<td>22%</td>
<td>0%</td>
<td>4%</td>
<td>5%</td>
</tr>
<tr>
<td>Ailao Shan</td>
<td>51%</td>
<td>12%</td>
<td>18%</td>
<td>15%</td>
<td>4%</td>
</tr>
<tr>
<td>Mengla</td>
<td>28%</td>
<td>12%</td>
<td>24%</td>
<td>16%</td>
<td>20%</td>
</tr>
</tbody>
</table>
Discussion

This study, located in China’s south-west, a biodiversity ‘hotspot’ vulnerable to climate change and other human impacts, investigated patterns of diversity in a major insect herbivore group which has been neglected in ecological research in this region. We found that moths in tropical, subtropical and temperate forest form altitudinally stratified assemblages, and are suitable as climate change bioindicators, such as those that have been developed for Australian locations (Ashton et al. 2011, Greenslade and Kitching 2011) and those described in Chapter 3.

Biodiversity ‘hotspot’

Our results support the idea of a biodiversity ‘hotspot’ in this region; the moth fauna was very species rich at all three altitudinal gradients, 2160 species in tropical rainforest at Mengla, 1448 in subtropical rainforest at Ailao Shan and 669 in sub-alpine forest Lijiang especially when compared to similar transects and sampling intensity in tropical (Mt Lewis, 1134 species) and subtropical (Lamington, 865 species) Australian rainforests. The species-area effect may be a major factor producing high species richness in Yunnan, located in a central area of the Eurasian continent, and at overlapping bioregions (Palaearctic and Indomalaya) with contrasting biogeographical histories, in combination with the effect of a highly heterogeneous mountainous landscape. Australian rainforests, on the other hand, are restricted to small remnant patches. Furthermore, the altitude of the Yunnan Province varies from 6740m a.s.l. (Meili Snow Mountain) down to 76m a.s.l. (Red River) (Ellwood and Foster 2004), and latitudinally from tropical monsoonal Asia in the south, to the temperate montane plateau in the north-west. This wide variation in the altitude, latitude and corresponding environmental conditions results in Yunnan Province being home to many different ecosystem types, and much of the biodiversity of China (Ellwood and Foster 2004).
Altitudinal and latitudinal patterns of moth assemblages

The highly altitudinally stratified moth assemblages at all three locations suggest that altitude (or some associated correlate) is important in structuring moth communities. All four major moth family groups (Geometridae, Arctiidae, Pyraloidea and Noctuidae) also exhibited strong altitudinal zonation in tropical, sub-tropical and temperate locations. We found the faunal composition at sub-alpine Lijiang was dominated by Geometridae (57% of species); at subtropical Ailao Shan, Geometridae accounted for 40% of species, and at tropical Mengla, Geometridae accounted for 22% of species. This latitudinal gradient in the proportion of geometrid richness may be driven by cool-adaptation of the Geometridae. Members of the subfamily Larentiinae (Rydell and Lancaster 2003), in particular, have the ability to fly at low thoracic temperatures, and have been shown to exploit high altitude, cooler habitats where there is reduced predator pressure (Holloway 1987, Brehm and Fiedler 2003). At tropical Mengla, Noctuidae were the most diverse family, contributing 40% of species richness, and this location was where Pyraloidea, generally considered a tropical radiation (Common 1990), were best represented. We did not find any shifts in the faunal composition of moth assemblages across altitude at any of our locations, contrasting with the findings of Holloway (1987). Further exploration at the sub-family level may reveal compositional changes across altitude, as was shown for geometrid sub-families (Brehm and Fiedler 2003).

Indicator species

The highly diverse rainforest ecosystems in Yunnan are under threat from a range of intercorrelated environmental pressures, including habitat loss and fragmentation, driven by a large population (Ozanne et al. 2003, Ellwood and Foster 2004). In tandem with many environmental impacts, climate change has already had significant effects on the region (Ding et al. 2007), and is predicted to have future impacts in line with global predictions (Ding et al. 2007, IPCC 2007).
In order to monitor the impacts of climate change in Yunnan Province through time, we suggest the use of a ‘predictor set’ (Kitching et al. 2011) of altitudinally restricted species. Indicator analysis produced three suites of species (one for each altitudinal transect) that were restricted altitudinally, and found to have a high fidelity across these altitudinal bands. At sub-tropical Ailao Shan, China, there was a large number of indicator taxa in comparison to a comparable study at Lamington National Park, in subtropical Australia (84 versus 18 species respectively (Ashton et al. 2011)) which may be directly related to the size of the regional species pool (1438 species at Ailao Shan, 865 at Lamington and 612 at Border Ranges National Park).

Climate change is already having a marked impact on the altitudinal and latitudinal distributions of Lepidoptera, however most observed distribution shifts are from temperate areas in Europe and the USA, where long-term data sets are available (Parmesan et al. 1999, Hill et al. 2002, Wilson et al. 2005, Gonzalez-Megias et al. 2008, Forister et al. 2010). A lone exception is a historical data set of moths from Mt Kinabalu, Borneo, that allowed Chen et al. (2009) to document an average uphill shift of 67m in geometrid moth assemblages between 1965 and 2007. These upslope shifts in moths’ assemblages may be a direct response to changes in temperature, a response to shifts in host plants, or a combination of different species and community level interactions and physiological responses. Our study provides invaluable baseline data for an area of mountain forests that has been little examined in terms of arthropod assemblages. This analysis will contribute to a multi-taxon monitoring tool which can be monitored through time. Further work, including DNA bar-coding, is currently being conducted on the moth collections by collaborating Chinese scientists, with special attention given to the indicator species, which may help in the utilization of these indicators in future research and monitoring.

We have set up a group of permanent, replicated altitudinal plots which can be monitored through time. Vegetation has been identified on these plots, and a suite of environmental variables (temperature, precipitation, soil properties) are
being monitored through time. Measurement of a range of environmental variables is an important element to include in any altitudinal study, in order to help examine the inter-correlation of environmental factors and species distributions across altitude. It is also important to note that study areas we examined are all within-biome transects, they do not transverse multiple biomes, as our intent is to reduce the confounding factors that can occur across altitudinal gradients. This study did not examine seasonal variation in altitudinal patterns of moth assemblages, however seasonality can influence the distribution of moth assemblages across altitudes (Beck et al. 2010), and this should be considered in any future comparative work on these altitudinal gradients. The next step in this project is to combine these results into multi–taxon, intra – China analysis, and inter-continental analysis, examining the generality of our results across China and Australia in tropical and sub-tropical rainforest.

Acknowledgments

This project would not have been possible without the help of many volunteers and collaborators who assisted with all aspects of field work in China. We thank J. Shillcock, S. Curtis, M. Laidlaw, S. Maunsell, C. Hall, H. Huang, L. Qie, S. Huang, Z. He, G. Li, J. Luo, D. Yu, K. Xu and W. Wang. This work is supported by the Queensland Government, the Chinese Academy of Science, Griffith University, Xishuangbanna Tropical Botanical Garden, Queensland Museum, Queensland Herbarium and the Kunming Institute of Zoology.
References


Chapter 6 Appendix

Table 6.4 Pair-wise comparisons of moth assemblages between altitudinal groups at Mengla, for each of the major moth families, Geometridae, Noctuidae, Pyraloidea and Arctiidae. All pair-wise comparisons of adjacent bands are significant (P>0.05).

<table>
<thead>
<tr>
<th>Comparison</th>
<th>Geometridae</th>
<th>Noctuidae</th>
<th>Pyraloidea</th>
<th>Arctiidae</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>t</td>
<td>P</td>
<td>t</td>
<td>P</td>
</tr>
<tr>
<td>800 and 1000</td>
<td>1.533</td>
<td>0.007</td>
<td>1.285</td>
<td>0.007</td>
</tr>
<tr>
<td>1000 and 1200</td>
<td>1.765</td>
<td>0.005</td>
<td>1.395</td>
<td>0.005</td>
</tr>
<tr>
<td>1200 and 1400</td>
<td>1.375</td>
<td>0.005</td>
<td>1.384</td>
<td>0.008</td>
</tr>
</tbody>
</table>

Table 6.5 Ailao Shan pair-wise comparisons of moth assemblages between adjacent altitudinal groups, for all moths encountered, showing t and P values. P values for all pair-wise comparisons are significant at Ailao Shan, with the exception of Pyraloidea between 2400m a.s.l. and 2600m a.s.l., where there was some overlap in assemblages.

<table>
<thead>
<tr>
<th>Comparison</th>
<th>Geometridae</th>
<th>Noctuidae</th>
<th>Pyraloidea</th>
<th>Arctiidae</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>t</td>
<td>P</td>
<td>t</td>
<td>P</td>
</tr>
<tr>
<td>2000 and 2200 m</td>
<td>2.22</td>
<td>0.004</td>
<td>2.02</td>
<td>0.003</td>
</tr>
<tr>
<td>2200 and 2400 m</td>
<td>2.52</td>
<td>0.002</td>
<td>1.55</td>
<td>0.033</td>
</tr>
<tr>
<td>2400 and 2600 m</td>
<td>2.05</td>
<td>0.003</td>
<td>1.76</td>
<td>0.022</td>
</tr>
</tbody>
</table>

Table 6.6 Lijiang pair-wise comparisons of moth assemblages between adjacent altitudinal pairs (3200m and 3400m, 3400m and 3600m, 3600m and 3800m a.s.l.). All pair-wise comparisons were significant, with the exception of Pyraloidea between 3400m and 3600m a.s.l., and Arctiidae between 3400m and 3600m a.s.l., and 3600m and 3800m a.s.l., which may be driven by the very low number of individuals belonging to these families encountered at these plots.

<table>
<thead>
<tr>
<th>Comparison</th>
<th>Geometridae</th>
<th>Noctuidae</th>
<th>Pyraloidea</th>
<th>Arctiidae</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>t</td>
<td>P</td>
<td>t</td>
<td>P</td>
</tr>
<tr>
<td>3200 and 3400</td>
<td>1.873</td>
<td>0.006</td>
<td>1.827</td>
<td>0.009</td>
</tr>
<tr>
<td>3400 and 3600</td>
<td>1.971</td>
<td>0.009</td>
<td>1.760</td>
<td>0.008</td>
</tr>
<tr>
<td>3600 and 3800</td>
<td>2.704</td>
<td>0.009</td>
<td>2.128</td>
<td>0.01</td>
</tr>
</tbody>
</table>
Table 6.7 Morphospecies number, family, altitudinal distributions, and Indicator values for each of the altitudinally restricted indicator morphospecies at Mengla.

<table>
<thead>
<tr>
<th>Species number</th>
<th>Family</th>
<th>Altitude</th>
<th>Indicator value</th>
</tr>
</thead>
<tbody>
<tr>
<td>2239</td>
<td>Geometridae</td>
<td>0800m</td>
<td>0.75</td>
</tr>
<tr>
<td>2045</td>
<td>Noctuidae</td>
<td>0800m</td>
<td>0.8663</td>
</tr>
<tr>
<td>2025</td>
<td>Crambidae</td>
<td>08,10,1200m</td>
<td>0.9486</td>
</tr>
<tr>
<td>2038</td>
<td>Arctiidae</td>
<td>08,10,1200m</td>
<td>0.9333</td>
</tr>
<tr>
<td>2196</td>
<td>Crambidae</td>
<td>08,1000m</td>
<td>0.8069</td>
</tr>
<tr>
<td>2063</td>
<td>Limacodidae</td>
<td>08,1000m</td>
<td>0.869</td>
</tr>
<tr>
<td>2049</td>
<td>Lasiocampidae</td>
<td>08,1000m</td>
<td>0.7303</td>
</tr>
<tr>
<td>2021</td>
<td>Crambidae</td>
<td>08,1000m</td>
<td>0.8407</td>
</tr>
<tr>
<td>2754</td>
<td>Geometridae</td>
<td>10,12,1400m</td>
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</tr>
<tr>
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<td>Arctiidae</td>
<td>10,12,1400m</td>
<td>0.7885</td>
</tr>
<tr>
<td>2594</td>
<td>Geometridae</td>
<td>10,12,1400m</td>
<td>0.8955</td>
</tr>
<tr>
<td>2039</td>
<td>Arctiidae</td>
<td>10,12,1400m</td>
<td>0.7611</td>
</tr>
<tr>
<td>2295</td>
<td>Erebidae</td>
<td>10,12,1400m</td>
<td>0.7746</td>
</tr>
<tr>
<td>2344</td>
<td>Crambidae</td>
<td>10,12,1400m</td>
<td>0.8829</td>
</tr>
<tr>
<td>2775</td>
<td>Pyralidae</td>
<td>10,12,1400m</td>
<td>0.8627</td>
</tr>
<tr>
<td>2527</td>
<td>Notodontidae</td>
<td>10,12,1400m</td>
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</tr>
<tr>
<td>2419</td>
<td>Erebidae</td>
<td>1000m</td>
<td>0.7188</td>
</tr>
<tr>
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<td>Geometridae</td>
<td>1000m</td>
<td>0.7167</td>
</tr>
<tr>
<td>2939</td>
<td>Erebidae</td>
<td>12,1400m</td>
<td>0.7</td>
</tr>
<tr>
<td>2325</td>
<td>Crambidae</td>
<td>12,1400m</td>
<td>0.8298</td>
</tr>
<tr>
<td>2458</td>
<td>Lymantriidae</td>
<td>12,1400m</td>
<td>0.7468</td>
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<tr>
<td>2809</td>
<td>Geometridae</td>
<td>12,1400m</td>
<td>0.9545</td>
</tr>
<tr>
<td>2730</td>
<td>Lymantriidae</td>
<td>12,1400m</td>
<td>1</td>
</tr>
<tr>
<td>2803</td>
<td>Geometridae</td>
<td>12,1400m</td>
<td>0.9701</td>
</tr>
<tr>
<td>2719</td>
<td>Arctiidae</td>
<td>1200m</td>
<td>0.9</td>
</tr>
</tbody>
</table>
Table 6.8 Altitudinally restricted species (indicator value of 0.7+) at Lijiang, showing morphospecies numbers, family, altitudinal distributions and Indicator values.

<table>
<thead>
<tr>
<th>Species number</th>
<th>Family</th>
<th>Altitude</th>
<th>Indicator value</th>
<th>Species number</th>
<th>Family</th>
<th>Altitude</th>
<th>Indicator value</th>
</tr>
</thead>
<tbody>
<tr>
<td>5325</td>
<td>Geometridae</td>
<td>32</td>
<td>0.7814</td>
<td>5037</td>
<td>Geometridae</td>
<td>32,34,36</td>
<td>1</td>
</tr>
<tr>
<td>5231</td>
<td>Geometridae</td>
<td>32</td>
<td>0.7529</td>
<td>5027</td>
<td>Geometridae</td>
<td>32,34,36</td>
<td>0.8</td>
</tr>
<tr>
<td>5127</td>
<td>Geometridae</td>
<td>32</td>
<td>0.9608</td>
<td>5024</td>
<td>Erebidae</td>
<td>32,34,36</td>
<td>0.9689</td>
</tr>
<tr>
<td>5085</td>
<td>Geometridae</td>
<td>32</td>
<td>0.8077</td>
<td>5020</td>
<td>Erebidae</td>
<td>32,34,36</td>
<td>0.9242</td>
</tr>
<tr>
<td>5071</td>
<td>Geometridae</td>
<td>32</td>
<td>0.9333</td>
<td>5018</td>
<td>Geometridae</td>
<td>32,34,36</td>
<td>0.9703</td>
</tr>
<tr>
<td>5047</td>
<td>Geometridae</td>
<td>32</td>
<td>0.8889</td>
<td>5017</td>
<td>Erebidae</td>
<td>32,34,36</td>
<td>0.7963</td>
</tr>
<tr>
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<td>Geometridae</td>
<td>32</td>
<td>0.8</td>
<td>5016</td>
<td>Erebidae</td>
<td>32,34,36</td>
<td>1</td>
</tr>
<tr>
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<td>Geometridae</td>
<td>32</td>
<td>1</td>
<td>5014</td>
<td>Geometridae</td>
<td>32,34,36</td>
<td>0.9845</td>
</tr>
<tr>
<td>5019</td>
<td>Geometridae</td>
<td>32</td>
<td>0.9024</td>
<td>5007</td>
<td>Geometridae</td>
<td>32,34,36</td>
<td>0.9797</td>
</tr>
<tr>
<td>5011</td>
<td>Uraniidae</td>
<td>32</td>
<td>0.925</td>
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Table 6.9 Altitudinally restricted species (IndVal values of 0.7+, more than 40 individuals) for Ailao Shan altitudinally restricted indicator species, showing morphospecies number, family, altitudinal distributions and indicator values.

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Chapter 7

Synthesis

“The most pressing problem is the protection of living diversity, not just mega fauna, and if we are to provide solutions, then entire habitats and ecosystems must be protected. Only as insightful and determined stewards can we continue to appreciate the greatest evolutionary success story in the history of life on earth.”

Evolution of the Insects (Grimaldi and Engel 2005).

Summary of research

This chapter will re-visit the questions raised in the Introduction, summarise the findings of this research, address limitations, and propose future research directions. This PhD research was initiated after the conclusion of the IBISCA-Qld project in 2008. The IBISCA-Qld project examined patterns of diversity in many taxa, across an altitudinal gradient (Kitching et al. 2011) and found a large suite of taxa, including moths (Ashton et al. 2011), beetles (Ødegaard and Diserud 2011), ants (Burwell and Nakamura 2011), Collembola (Greenslade and Kitching 2011) and plants (Laidlaw et al. 2011) that were altitudinally stratified. A suite of altitudinally restricted species was suggested for inclusion in a ‘predictor set’, which could be re-sampled through time to monitor altitudinal shifts in distributions. Several issues arose from the IBISCA-Qld project. It was difficult, for example, to make assertions about the ubiquity of the patterns of diversity we observed during the IBISCA-Qld project, as that study was based on a single altitudinal gradient. Using the IBISCA-Qld results as a baseline for comparison with altitudinal gradients in
other locations, as described, *inter alia*, in this thesis, allows us to make more general statements about patterns of diversity, vertical stratification and family-level patterns across altitude and latitude. We have successfully carried out moth sampling that is directly comparable to the IBISCA-Qld project, in the nearby Border Ranges and distant Mt Lewis in the Wet Tropics, at the beginning and end of the wet season in each case. We have also been able to expand the investigation to elevational gradients in south-western China, which has added a new dimension to this research, examining how the patterns of diversity across altitude and latitude may differ in China, an area with a very different biogeographical history. Overall, this project has allowed us to investigate several different, yet complimentary, aspects of environmental gradients. This final chapter recaps the main findings and puts them into the context of the relevant ecological theories which have been discussed at length in Chapter 2.

The major research aims of this study have been as follows.

*(1) To assess the richness and assemblage structure of moths along a series of altitudinal gradients within continuous forests, along the east coast of Australia, and south-west China.*

During the course of this research, we carried out an ambitious and extensive study into the altitudinal distributions of forest moths in Australia and China, sampling, sorting and identifying a total of 118,035 individuals belonging to 6571 species. Our results showed that the altitudinal stratification of moths is ubiquitous across different latitudes, forest types, biogeographic areas and climatic zones that we examined. In addition to the moth surveys, collaborating botanists identified all trees with a dbh greater than 5 cm on each of the 20m x 20m plots which comprised the foci of our moth sampling. Moth assemblages and temperature and vegetation composition were intercorrelated across altitude.

When we compared results from Lamington NP and Border Ranges NP, which were altitudinal transects within the same biogeographical sub-region, comprising
the same elevational ranges and vegetation types, yet presenting different aspects, we found that aspect did not have a strong influence on either moths or plant assemblages, with both groups exhibiting similar patterns of altitudinal stratification along both transects. We did note however, that the moth assemblages at the two transects, separated by only 20 km of rainforest, were different (with a Bray-Curtis similarity of only 0.2), pointing to high turnover in diversity even at this small geographical scale.

(2) Examine the differences in assemblage turnover at different taxonomic resolutions across altitude and latitude.

Our Australian family-level analyses showed that the Geometridae, Arctiidae and Pyraloidea consistently showed strong altitudinal zonation across all our study sites, regardless of forest type, latitude and biogeographic region. Noctuidae did not show significant altitudinal zonation in any of the Australian transects. This may be attributable to their life history characteristics, as many noctuoids are generalist grass feeders and are often highly vagile. Subfamilies within the Geometridae did not respond differentially to altitude, conflicting with patterns described from Ecuador (Brehm and Fiedler 2003, Fiedler et al. 2008), Tanzania (Axmacher et al. 2004) and Borneo (Holloway 1987). In all these three regions shifting taxonomic composition of the proportions of geometrid sub-families across altitude was apparent.

Three major family-level patterns emerged from the Chinese altitudinal gradients located at three different latitudes. First, all of the moth family groups examined (Geometridae, Pyraloidea, Arctiidae and Noctuidae), exhibited significant altitudinal stratification. This is important to note as the Noctuidae generally showed no pattern of altitudinal stratification in our Australian sites. This result and the applied biogeographic contrast warrants further investigation, including life history analysis. Second, we found a latitudinal gradient in the relative contribution of species of Geometridae to the overall richness of moth species. Geometridae were dominant at our sub-alpine transect (57% Geometridae species),
relatively less dominant but still the most speciose family at our sub-tropical transect (39%), and displayed similar species richness to other diverse families (such as Noctuidae) at our tropical site (22% of species were Geometridae). This pattern may be, in part, driven by the ability of geometrids to fly at very low thoracic temperatures (Rydell and Lancaster 2003), allowing them to dominate the sub-alpine sites. Finally, we found very few species of Pyraloidea and Arctiidae at the sub-alpine transect (2% and 1% respectively). This supports the idea that Pyraloidea are, in general, a tropical radiation (Common 1990), and that Arctiidae diversity increases towards the tropics (Brehm 2009). We recognise, when discussing the faunal composition of assemblages at different latitudes, that these results are confounded by altitude and it is important to keep the altitudinal nature of these data sets in mind when discussing the ecological meaning of these patterns.

(3) Investigate the vertical stratification of moth species richness and assemblage structure, across altitude, latitude and forest type.

During all field work conducted as part of this research, canopy and ground layers were sampled simultaneously at all sites in order to investigate patterns of vertical stratification, and to ensure the widest possible sampling of the moth assemblages. We were able to combine data collected during the candidature of this PhD research (Border Ranges, Mt Lewis, Mengla, Ailao Shan and Lijiang), with data collected by Professor R. L. Kitching in previous field surveys (Panama, Paluma, Vietnam, Papua New Guinea and Brunei), and data collected by L. A. Ashton as part of the Terrestrial Ecosystems Research Network (TERN) project on the Atherton Tablelands, far north Queensland. This produced a powerful data set, based on sampling of over 100,000 individual moths. This analysis showed a universal pattern of vertical stratification at all study locations, and the degree of vertical stratification showed no significant relationship with either latitude or altitude. It was found that, in general, species richness was similar in the canopy and ground layers, a pattern which did not shift across latitude and altitude. These results are important in the context of current ecological literature, as there is
vigorous, on-going debate on the degree of vertical stratification, and the species richness of the canopy. Our use of night-flying Lepidoptera, sampled in the same way across many locations, provides strong evidence for vertical stratification, in a hyper-diverse order that is sometimes neglected in canopy studies.

As indicated, canopy-ground stratification was apparent across all altitudes and latitudes in China, including the temperate sub-alpine transect, in contrast to other temperate zone studies of vertical stratification in moths, which have found no stratification in temperate zone forests (Fowler 1985, Schowalter and Ganio 1998). In contrast to Australia, understory moth assemblages were generally more species-rich than their corresponding canopy assemblages, perhaps as a result of long-term, low intensity, human management of Chinese forests through activities such as the cultivation of herbs in the understory.

During the course of this research, and in combination with previous research conducted by Kitching (between 1995 and 2008) we found strong evidence for the vertical stratification of moth assemblages, and, in the case of Panama, we have been able to link the vertical stratification of some species to the vertical distribution of their host-plants. Linking individual species to the vertical distribution of their larval host-plants seems to be the key to understanding the mechanisms driving the vertical stratification of adult moths. Patterns of vertical stratification may be driven by larval host-plant preferences, the behaviour of adult moths or, more likely, a combination of both. Differing patterns of host use and adult behavioural patterns may explain different levels of vertical stratification, which may shift across species, genus, sub-families and families. The dominance of particular families and subfamilies in particular vertical layers, across altitude and latitude, is a clear next-step in this research. This need has also been identified as an important ecological question by other researchers (Brehm 2009). Our preliminary family-level analysis of tropical Australian moth data showed that (as for the altitudinal stratification of Australian moth assemblages), the degree of vertical stratification differed amongst family-groups. Specifically, Geometridae, Arctiidae and Pyraloidea formed distinctive understorey and canopy assemblages,
whereas Noctuidae did not, perhaps as a result of their larval host-plant preferences, or their high vagility as adults. The next step in this research is to examine the vertical stratification of the assemblages of family-groups across our altitudinal and latitudinal transects.

(4) Examine and compare the patterns of altitudinal and latitudinal shift in moth assemblages in Australia with those found in mainland China.

Our study of moth assemblages across three altitudinal gradients, in tropical, subtropical and temperate forests of Yunnan Province, China, was an excellent opportunity to examine the diversity and distributions of moths in a location which has been little studied. Collaborating with scientists from the, Xishuangbanna Tropical Botanical Garden and the Kunming Institute of Zoology (Chinese Academy of Sciences), has enabled us to conduct a successful project in China, with few if any of the impediments reported by some workers (Hvistendahl 2013). We established three permanent altitudinal transects that can be re-sampled in the future, and have made extensive moth collections. Three field sessions, each one month long, produced a total of 48358 individual moths, belonging to 4267 species. The results of this work indicate that altitudinal stratification of moth assemblages is a ubiquitous phenomenon, with moths responding strongly to altitude at all three latitudes - tropical, subtropical and temperate.

(5) Identify which species are most important in driving altitudinal and latitudinal changes in assemblage structure and which may be useful as indicator species for monitoring faunal distribution shifts of insects in Australia and China.

Building on the previous results of the IBISCA-Qld project, which suggested a predictor set of moths which were altitudinally stratified (Appendix 1), this study applied a rigorous statistical method to identify indicator taxa (IndVal analysis) and produced predictor sets of altitudinally sensitive species for each location. These predictor sets of altitudinally restricted species can be monitored through
time, to detect altitudinal shifts in distribution. We found that within the same sub-biogeographic region (Lamington and Border Ranges) the identities of species in each predictor set can be different, emphasising the importance of conducting baseline surveys in a range of locations.

In addition to our Australian work, we also established three predictor sets of moth species for the three Chinese altitudinal gradients in tropical, sub-tropical and temperate forests. These altitudinal transects have been permanently tagged and will be managed primarily by the Xishuangbanna Tropical Botanical Garden. The voucher collection of moth specimens is deposited in the Zoology Museum of the Institute of Zoology, Kunming. As a result of the work described in this thesis, a collaborative bar-coding project is currently underway with researchers at the Kunming Institute of Zoology, who are bar-coding all moths collected during the research, with special attention to the altitudinally restricted ‘indicator’ species. This bar-coding analysis, and further taxonomic identification, is required before the predictor sets of indicator species produced for our Chinese transects can be presented as a usable tool for future monitoring and management.

Similarities between the faunal composition of indicator species between our Australian and Chinese sites are apparent. In general, we found fewer altitudinally restricted indicator species at our tropical sites - 26 at Mengla and 9 at Mt Lewis, compared with 84 at Ailao Shan and 26 at Border Ranges, which is surprising given how much larger the regional species pool is in the tropics. The lower number of indicators in the tropics may, in part, be due to greater numbers of rare species, which are unlikely to be identified as statistically significant indicators given the methodology we employed (even if they are altitudinally restricted). The IndVal protocol is based both on specificity (restriction to a particular altitude) and fidelity (frequency of occurrence within sites across an altitudinal band). We also found that in the tropical locations (Mt Lewis and Mengla) there were significantly fewer geometrid indicator species, when compared with the other locations, which may be related to the generally observed decrease in Geometridae with increasing latitude.
As one of the main foci of this research has been to establish baseline data that can be used to monitor the impacts of a changing climate, all effort has been made to make the data available to future researchers. Firstly, the Australian collections of pinned and identified moths made during this study have been deposited in the Terrestrial Ecology Laboratory at Griffith University. Additionally, the Chinese collections are held at the Kunming Institute of Zoology. Both collections are available to visiting researchers. Secondly, once publication is completed, the original datasets will be made publicly available online through the researchgate site (www.researchgate.net). Thirdly, the predictor sets of indicator species will be submitted to the Group on Earth Observations, Biodiversity Observations Network (GEO BON) (http://www.earthobservations.org/geobon.shtml), which will make the data collected during this research available to other researchers, with the main aim of inclusion in biodiversity monitoring schemes.

*Estimating species richness and similarity*

This research project involved intensive study sessions, with over 100,000 individual moths caught and identified to morpho-species across all sampling efforts. This work involved many one and two-month intensive field sessions, extensive help from field volunteers and collaborators, and comprehensive post-field work: laboratory work and identification, which involved visiting multiple collections (Australian National Insect Collection, Kuranda Sphingidae collection, Griffith University terrestrial arthropod collection) and museums (Queensland Museum, Australian Museum). The projects involved in this PhD research received funding from Griffith University, Conservation Volunteers Australia, the Terrestrial Ecosystems Research Network, the Queensland Government and the Chinese Academy of Science. With this substantial input of effort, driven by many volunteer field workers, an appropriate question we might ask is: did we sample a large proportion of the moth fauna in each of our study locations? I addressed this issue using EstimateS (Colwell 2009), which employs random re-sampling of datasets to estimate total species richness in a given location. In general, we
sampled a surprisingly large proportion of the estimated total moth fauna. At our Australian locations, we sampled 75% in tropical rainforest at Mt Lewis and in subtropical rainforest, 87% at Border Ranges and 70% at Lamington, and at our Chinese sites 67% at tropical Mengla, 68% at subtropical Ailao Shan and 82% at temperate Lijiang. Of course, these are estimates, based on our sampling at each of these locations. They do, however, provide a rough guide as to the total richness of the species pool at each of these locations. These overall richness estimates are also confounded by altitude and, again, are only intended as a method of comparison between analogous study designs. The percentage of moth species that we encountered compared with the total estimated assemblage at each altitude separately is lower than when we examine the entire assemblage across all altitudes. This difference between the estimations of total richness at each altitudinal layer and entire assemblages may be because many species are shared across altitudes and, accordingly, were sampled multiple times, reducing the estimation of total species richness.

**Limitations**

**Altitudinal gradients**

A major advantage of using altitudinal gradients as study systems, is the ability to examine real-world responses to suites of environmental conditions, rather than simplified, simulated laboratory environments (Hodkinson 1999). This quality, allowing for studies of assemblage-wide responses, is clearly important when examining complex and diverse rainforest systems. Across altitudinal gradients, many abiotic factors change predictably, including moisture, temperature and soil chemistry. Biotic factors also change with altitude, including species richness, niche dimensionality, body size, rates of competition, predation and parasitism (Terborgh 1973, Sivinski et al. 2000, Taniguchi and Nakano 2000, Kubota et al. 2007, Boyle 2008, Fischer et al. 2011). Criticisms of the altitudinal gradient approach to ecological questions, include the complexity involved in making
statements of causality, when so many inter-correlated factors change with altitude (Körner 2007, Fischer et al. 2011). We have attempted not to make generalizations that go beyond the scope of the altitudinal gradients we have examined; any general conclusions will come from the replication of many altitudinal gradients across latitudes, biogeographical histories and climatic zones. When using altitudinal gradients to study the impacts of climate change on insects it is important to recognize that many species may be able to adapt in situ, and will not show any climate-driven response, however, many of the altitudinally restricted species we have identified will be unable to adapt during rapid climate warming and we predict species which are climatically sensitive to exhibit a climate response. Another unavoidable limitation is that this research has only covered three altitudinal transects, and further replication of altitudinal transects in different locations will allow for quantities comparisons to be made. Further work is currently being conducted on sampling additional altitudinal transects and is described in the ‘future directions’ section below.

One limitation of the Chinese altitudinal gradients is that we were only able to survey each transect once, due to time and financial constraints. When we examined the Australian altitudinal transects, we did so at the beginning and end of the wet season, and found very little difference in the overall patterns of moth assemblages across altitude. It is not unreasonable to assume, therefore, that if we had sampled the Chinese altitudinal gradients at a different time of year, we would have produced the same qualitative result as we did in Australia. We hypothesize that there would be little seasonal effect on overall assemblage structure through time. However, the identities of the individual species that we encountered will shift between months, annually and inter-annually. Further work, however, on the seasonality of the ecological patterns of moth assemblages across altitude and latitude we have described here is necessary, especially in the Chinese locations, before we make such assumptions. Through placing the original IBISCA-Qld Lamington results in the context of the broader geographical region, incorporating a tropical zone altitudinal gradient, and examining analogous transects in China,
we have demonstrated some heterogeneity in distribution patterns between continents (such as the dominance of the ground layer and its fauna in China). However, the overall results of altitudinal stratification across gradients, the major moth families that respond strongly to altitude, and the ubiquity of discrete canopy and understory assemblages, have been demonstrated across all our gradients.

Spatial autocorrelation is a common concern for any ecological study that examines patterns across gradients (Legendre 1993). It is important to establish that the observed turnover in moth assemblages is driven by the suite of environmental differences across altitude and not simply because of the spatial arrangement of sites. An effective method for overcoming this is to establish additional plots that are at the same elevation, but on a different side of the same mountain, or an adjacent mountain. A test of auto-spatial correlation was conducted for ants at Lamington National Park (C. Burwell and A. Nakamura pers. comm.), which showed that the ant assemblages at the same altitudes at different locations were more similar than geographically closer assemblages at different altitudes. This pointed to altitude being the primary factor shaping the altitudinal distributions of ant assemblages, rather than any artefact of geographic distance. We conducted a similar test, by sampling the moth assemblages at Lamington NP and 20km away at Border Ranges NP. This showed that although the assemblages between these two regions contain many different species, which points to high species turnover at this scale, the overlapping species common between the two altitudinal gradients were found at the same altitudes, and we can therefore posit that spatial autocorrelation is not responsible for our observed altitudinal stratification of assemblages.

*The taxonomic impediment*

Another relatively recent and important methodological addition for ecological studies of Lepidoptera is the use of bar-coding and meta-bar-coding molecular
techniques. Our Chinese altitudinal research has been enhanced through collaboration with the metabarcoding research group at the Kunming Institute of Zoology (under the direction of Professor Doug Yu), and has enabled the validation of metabarcoding for community-level analysis of light trap Lepidoptera. Half of each sample collected from our Chinese altitudinal gradients was processed and categorised using next generation metabarcoding technology. The results of our traditional morphospecies identification and the metabarcoding identification were highly statistically correlated in terms of both alpha and beta diversity, and produced the same altitudinal signals (Jia et al. In press). We do, however, stress the importance of a combination of both metabarcoding and traditional identification, as the use of metabarcoding to characterize mass assemblage samples does not provide any meaningful life-history information for the species involved. A shortage of taxonomic expertise may necessitate a shift towards more metabarcoding-based research and, as the financial costs of this emerging technology decline and the accuracy of analysis improves, the use of metabarcoding may become ubiquitous, and provide rigorous, repeatable and efficient community-level results for ecologists. The combination of this style of research with extensive life history information may help bridge the short-fall between available taxonomic experts and the need for rapid biodiversity assessments.

The notion that a decline in practising taxonomists will result in the loss of many rainforest species before they have been described, has been questioned recently (Costello et al. 2013). These authors provide an optimistic analysis of the rates of new species description versus estimated extinction rates. Estimates of the diversity of rainforest arthropods, once as high as 30 million species (Erwin 1982), have been reduced to more conservative estimates of about 6.1 million species (Basset et al. 2012, Hamilton et al. 2012). Publication rates describing new species have steadily increased over the last 30 years, especially in developing countries. In Australia, around half of the estimated 20 000 species of Lepidoptera have been described (Common 1990). Our Australian collections have approximately 16% of species which have been identified as described species, and our identification
efforts have primarily been focused on the Geometridae, Pyraloidea and Arctiidae. Identifications have been made based on resources including books, online resources and by visiting several museums in Australia, together with assistance from Mr Ted Edwards at the Australian National Insect Collection. In Australia, many families remain neglected, and the taxonomic impediment has become exacerbated as Australian taxonomic capacity decreases (Cassis et al. 2007). The low availability of taxonomic advice and expertise has been a somewhat limiting factor during this research, and has prevented the inclusion of some families. This is also true for our Chinese collections, which although they are being bar-coded, are not taxonomically identified. Major projects working on digitising insect collections, such as those currently under way at the Australian National Insect Museum, are a positive step towards ameliorating this problem.

Future directions

The IBISCA approach and the benefits of collaboration

The IBISCA (‘Investigating Biodiversity of Soil and Canopy Arthropods’) research approach was developed initially by Yves Basset, Bruno Corbara and Hector Barrios (Basset et al. 2007) for a vertical stratification study conducted in Panama. The core concept of the IBISCA approach is to engage numerous scientists from across the world, with a range of specialties, to participate in relatively short-term field sessions simultaneously, in order to address a specific ecological question. This approach was successful in producing collaborations and strong data sets with convincing results, such as the recent Science publication based on the IBISCA-Panama project, which addressed an on-going ecological problem of how many species of arthropods occur in tropical rainforests (Basset et al. 2012)

Since the IBISCA Panama project, the IBISCA model has been applied to several other major studies in different countries and addressing different ecological
questions, including IBISCA-Vanuatu (Tardieu and Barneoud 2007), IBISCA-Queensland, IBISCA-Auvergne and, most recently, IBISCA-Papua New Guinea. The IBISCA-Queensland project was highly successful and, as has been described in this thesis, we have built on its results, expanding into new altitudinal gradients, and collaborating with the Chinese Academy of Sciences (QCAS) incorporating three altitudinal transects in south-west China. The results presented in this thesis are based primarily on Lepidoptera data collecting during these projects. In addition, the collaborative IBISCA approach has allowed us to work with other ecologists studying plants, ants, beetles, Homoptera, Collembola, parasitoids and galling insects, at the same sites using the same general experimental design (Bito et al. 2011, Burwell and Nakamura 2011, Greenslade and Kitching 2011, Ødegaard and Diserud 2011). Powerful further results from this work will be produced in multi-authored, multi-taxon collaborative papers. We are currently preparing for publication the results from the QCAS project from China and Australia. Our first publication will address the turnover in beta diversity across altitude and latitude. There has been considerable debate in the ecological literature regarding how high universal beta diversity is in tropical rainforests (Novotny et al. 2007, Beck et al. 2012, Tang et al. 2012). We now have data on beta diversity turnover across altitude and latitude, for moths, vegetation, ants and beetles, in Australia and China, and the combination of these data sets should provide a strong contribution to this ongoing debate.

This research has established baseline data which can be used to assess future impacts of climate change. This data, however, has value beyond simply setting baselines for future research: it has added to our knowledge of how a hyper-diverse insect group is distributed across environmental gradients - altitudinally, latitudinally and vertically. An intrinsic quality of this type of extensive baseline research is the novel and comprehensive faunistic and biogeographical data sets that are generated concerning groups of organisms for which very little existing information has been available. In both Australia and China, there is a paucity of information on the diversity and distributions of forest moths. Significantly, we
have had the unique opportunity to work in the forests of mainland China, a study that was highly successful because of our collaboration with our Chinese associates at the Xishuangbanna Tropical Botanical Garden and Kunming Institute of Zoology. Future collaborative work will also involve the inclusion of an intermediate altitudinal gradient (between Mt Lewis and Lamington/Border Ranges) located at Eungella National Park (ca 20°51’S), with field work beginning in March 2013. This altitudinal gradient will add to our previous results and produce an even more comprehensive analysis of altitudinal and latitudinal patterns of diversity in Australia. Less certain plans may extend the studies further south into the rainforest of New South Wales.

**Climate change**

Climate change, once considered to be a less important and immediate threat in the tropics in comparison with deforestation and other human impacts, is now recognized as one of the most serious environmental problems there (Kirschbaum et al. 1996). There has, however, been little information collected on climate change and biotic responses in tropical rainforests, and models and predictions of climate change impacts have wide uncertainty (Corlett 2012). The fourth IPCC reports addressed the immediate and long-term problems associated with climate change in tropical forests, especially changes to precipitation regimes (IPCC 2007, Zelazowski et al. 2011). The paucity of direct, data-based, tropical climate change research is now a clear gap in our understanding, and limits our ability to predict, mitigate or adapt to future responses. It is now largely recognised that climate change is occurring at a rate in line with the higher rate of the climatic warming scenarios (Betts et al. 2011). It is therefore important that when we discuss future responses to climate change that it is in the context of as much as 4°C or even higher increases in average global temperatures (New et al. 2011).

Tropical rainforest mountains are hotspots of biodiversity and endemism, acting as climate islands with unique and isolated assemblages (Myers et al. 2000, Rodríguez-Castañeda et al. 2010). Mountain areas are predicted to be heavily
impacted by climate change, as they contain steep temperature and precipitation gradients (Lawler et al. 2009). The levels of the bases of cloud caps, a significant factor shaping cloud forest assemblages, is predicted to increase in altitude (Foster 2001), although predictions on how cloud formation will be impacted by climate change are complex and may impact upon different locations in different ways (Foster 2010, Lawton et al. 2010). Monitoring the cloud cap heights and how much time forests are immersed in cloud cap is a complex problem which is being approached using a range of methods including quantitative measurements of cloud immersion and the use of remote sensing and modelling (Lawton et al. 2010). Warming of 4°C is equivalent to around a 500m upslope shift in climatic conditions, which may push assemblages upwards, drive biodiversity loss and generate novel ecosystems (Foster 2001). Given the serious and rapid nature of predicted impacts of climate change on mountain systems, it is vital to monitor both biotic and abiotic responses if conservation planning for preserving diversity is to have any hope of success. We have established, to date, six permanent altitudinal transects - a significant research output which can be utilized by other researchers to monitor altitudinal changes throughout time. We have collected extensive environmental data at many of these sites, including temperature data at Border Ranges, Lamington (Strong et al. 2011) Mengla, Ailao Shan and Lijiang. Cloud cap measurements at several sites around Lamington NP, which are being conducted by Dr M. J. Laidlaw of the Queensland Herbarium, will allow for a more detailed understanding of fluctuations in the cloud cap, and how this shapes assemblage structure, and importantly, track any upwards shifts in the average cloud base through time.

During the course of this research we have identified a series of ‘predictor sets’ for each altitudinal gradient. These ‘predictor sets’ contain species that were restricted altitudinally, found in large numbers and easy to identify, and can be monitored through time, to track any distributional shifts that may occur. Overall, geometrids were best represented amongst the indicator species from our sub-tropical and sub-alpine transects. Species of Geometridae have been used extensively elsewhere
as indicators of environmental change, as they are often tightly linked to their habitat types (Holloway 1998, Intachat et al. 1999, Kitching et al. 2001, Beck et al. 2002). In tropical rainforest in Australia (Mt Lewis), however, most indicator species were from the Arctiidae, whereas in tropical rainforest in China (Mengla) indicator species were more evenly distributed among the family groups examined. The Arctiidae, in general, appear a useful indicator group, as they also tend to display high habitat fidelity (Fiedler et al. 2007, Hawes et al. 2009, Ferro and Melo 2011), and some host plant information is available for this group, which allows for studies which tie their distributions to that of their host plants (Holloway 1985). Species within the Noctuoidea tended to be less altitudinally restricted, and also be harder to identify, making them generally less useful as indicator species.

Altitudinal gradients can be used as early warning systems for monitoring climate change responses (Loope and Giambelluca 1998, Shoo et al. 2006) and the baseline data we have established for moths (and other researchers have collected for ants, beetles, plants) is vital in detecting these responses. The predictor sets of moths identified here, should be employed with indicator species from other taxa (such as ants), in combination with continued recording of environmental variables (including temperature and precipitation). This data can be employed for monitoring shifts in distributions in several ways. Insects, and particularly moths, have already been used to demonstrate shifts in distributions, in cases where long term historical data sets are available (Chen et al. 2009, Bässler et al. 2013). We suggest similar use of the suites of indicators we have outlined (i.e. repeated monitoring through time). The use of meta-bar-coding is another direction for monitoring future distribution shifts, and may be especially useful for large- scale monitoring and when taxonomic expertise is not available (Jia et al. In press). Specific resources to make our data available for future research have been outlined above.

One caveat to the use of indicator species is that it may be necessary to conduct baseline surveys at each location in order for indicator species can be selected. We
found a different suite of indicators between Lamington and Border Ranges National Parks (separated by 20km), and although there was some overlap in indicators (primarily Geometridae restricted to high altitudes) the predictor sets at each location consisted of different species. Using indicator species at each location to monitor distribution shifts can provide a valuable research tool, and will allow for greater understanding of assemblage change and how joint distributions of herbivores and their host plants shift, which in turn has significant implications for ecosystem function. Incorporating these results with similar work using different taxa at different geographical locations, we can create a globally coherent understanding of range shifts (Parmesan and Yohe 2003, Laurance et al. 2011) as well as more detailed local and regional scale analyses (Shoo et al. 2012).

The distributional shifts of species are unlikely to occur at the same rate. Less vagile taxa, for example, may be slower to respond and this may result in the assembly of novel communities and local extinctions of species with low dispersal abilities, resulting from their inability to track shifting climatic envelopes (Parmesan 2006, Williams and Jackson 2007). The multi-taxon approach proposed here should provide a robust methodology that captures a broad range of species-level responses.

**Future directions – methodology**

*Bioclimatic modelling*

During this research, distributional data on those species identified as indicators from Australian altitudinal transects has been collated from museum specimens (Queensland Museum, Australian National Insect Collection, and Australian Museum). Although beyond the scope and time frame of this PhD research, the next logical step for utilisation of this data is to incorporate it into bioclimatic models. Work of this kind has been done in Australia for butterflies (Beaumont and Hughes 2002) and vertebrates (Williams et al. 2003, Meynecke 2004), however
there has been little modelling of moth distributions, probably due to the lack of widely available historical and contemporary data sets. The moth data we have gathered from insect collections, although patchy, provides a first approximation of the distributions of those altitudinally restricted moths. Through modelling the latitudinal and altitudinal climate envelopes of these species, it may be possible to make predictions about how they will respond, both altitudinally and latitudinally, to further climate warming. A more sophisticated approach but one which demands far greater and more complete data sets and natural historical knowledge, would be to incorporate host plant distributions, and dispersal abilities, into such modelling efforts (Araujo and Luoto 2007, Merrill et al. 2008).

An important direction for monitoring shifts in distributions is the use of technologies such as remote sensing and GIS mapping of the distributions of vegetation types. This GIS mapping of individual species’ distributions is currently being conducted by a range of government and academic researchers, and is a cost effective method of monitoring large scale shifts in ecosystems (Havstad and Herrick 2003). These distribution maps and predictions of further range shifts of plant species can be combined with larval host-plant lists of individual moth species, such as those included in our predictor sets, and used to predict and monitor distribution changes. Accurate recording of environmental variables is vital in order to link climatic changes to further distribution shifts in moth taxa. Micro-logging technology, such as the ibutton® temperature and humidity loggers, are a useful tool, and more advanced weather stations can monitor fog events accurately. Observations of microhabitat conditions, information on slope and solar radiation also need to be incorporated into models in order to produce detailed distribution shift scenarios, incorporating possible climate refugia and allowing more sophisticated and accurate climate change predictions to be made (Lookingbill and Urban 2003). The gap in our knowledge of this kind of data in some areas of Australia and China is evident, as climate models are often based on broad regional weather stations.
Establishing a causal relationship

A limiting factor of altitudinal studies is in the difficulty of establishing causality: that is, identifying the particular factors, abiotic or biotic, that drive species distributions across altitudes and latitudes. In terms of climate change, it may also be difficult to distinguish biological responses that are due to climate change from those arising from other environmental changes, such as southern oscillation climatic cycles, which can also cause increased temperatures and changes to cloud caps (Aiba and Kitayama 2002, Walther et al. 2002). A major challenge of future research is to determine direct causal relationships between distribution shifts and climate change (Shoo et al. 2006). The most parsimonious explanation for shifts in distribution shifts in our insect herbivore study group will likely be a combination of climatic changes and changes in host plant distributions. One method of establishing direct links to temperature changes is to use experimental manipulations to examine how individual species respond to temperature through measuring the thermal and moisture tolerances of plants and insects. This can be done in a laboratory environment or through selecting altitudinally restricted species and re-locating them to lower altitudes.

In order to establish the strength of biotic and abiotic variables shaping the distributors of insects, we suggest resurveying the vegetation assemblages of our permanent study plots through time, in combination with re-sampling environmental variables including temperature, moisture and soil chemical properties. This may show the vegetation assemblage shifting at a slower rate than the insects, a result already apparent in Europe (Bässler et al. 2013). Linking individual indicator species to their host plants is a challenging, but potentially insightful exercise which may help understand joint-species responses to climate change. This information, in combination with the potential modelling methods discussed above, may provide a more detailed picture of climate change responses and real-world shifts in fundamental and realised niche space (Fordham et al. 2013).
Light traps

Total catch at light traps may reflect a number of biases and influences, including the light-trap light capture radius which may vary between 1m and 25m (Baker and Sadovy 1978, Muirhead-Thomsom 1991), and differences in how moth species respond to light; some may not be attracted to light at all. Additionally, a number of environmental factors will influence the set of moths trapped each night. For example, a light trap positioned in the canopy on a steep slope, may effectively be closer to the ground level of adjacent trees, than the rest of the canopy, leading to the question: is this really sampling the ‘canopy’ or some combination of canopy and understory? Physical vegetation structure may also influence light trap efficiency. More open vegetation, for example, may result in the capture of larger numbers of ‘tourist’ taxa which may not be associated with the area in which the trap is situated. We acknowledge that we sampled using a single type of trap, and thus inherently collected a biased selection of the entire lepidopteran assemblage. Such biases, however, exist for all trap types, and we make the assumption that at least our biases are the same for all trapping occasions and locations. To address these concerns, we endeavoured, where possible, to position the light traps in the same vegetation type, avoid interference from moon light (by ceasing trapping three nights either side of the full moon), water bodies and light gaps.

Throughout the four years of my PhD candidature, using Pennsylvania light traps, several modifications and improvements have been made by Professor Roger Kitching and Mr Bruce Mudway (Griffith University mechanical workshop). These include a light-weight metal lid to keep out rain, an enlarged bucket funnel hole to allow larger moths to enter the trap and stabilizing plastic attachments to help keep the plastic veins vertical. A vital element which has been added to these light traps is 12 volt, 10 amp automatic timers (sourced from Rainbow Power Company http://www.rpc.com.au/catalog/digital-timer-12volt-p-2108.html). Using these timers allowed us to go into the field in the morning, empty traps, and reset the traps with a fresh battery to turn on automatically at dusk. This innovation made it possible to visit sampling sites only once a day, freeing the rest of the day for
sorting catches in a field laboratory. Future light trap design innovations may include employing a more lightweight battery. Light trap weight could also be reduced by using banks of LED lights in place of the actinic UV bulbs currently employed (Cohnstaedt et al. 2008). Caution is advised however, because of difficulties in quantifying the radius of attraction of LED light traps as they emit different wavelengths of light from the traditional actinic UV bulbs (which is why they require less energy), and attract fewer moths, making direct comparisons to studies that use UV actinic light more complex. This type of research could be augmented by employing other established methods to sample Lepidoptera, including baited traps and hand collecting and rearing of larvae.

**Moths and mountains – what do we know now?**

This research has sought to address many ecological questions related to the distributions of forest moths in mountain ecosystems, through examining altitudinal and latitudinal gradients within Australia and Asia. Moths have been shown to be ideal research taxa; they are diverse and able to be caught in large numbers and they respond sensitively to their environment. Moths are key insect herbivores, and yet very few community studies of moths have been carried out in Australia and Asia.

In addition to the topical applications of this research to understanding the impacts of climate change, this research has relevance to more general themes of community ecology, such as the major factors shaping the diversity and distributions of assemblages. We found strong evidence for stratification across altitudinal gradients, identified variations between families of moths along altitudinal gradients at different latitudes, and found strong evidence for vertical compartmentalisation of forest moth assemblages. Climate change has already impacted upon the distributions and phenologies of plants and insects, and will continue to drive changes to species and assemblages, creating novel communities (Williams and Jackson 2007, Jackson and Sax 2010). Mountain systems are
particularly threatened by climate change, with the potential for many high altitude endemics to become extinct (Williams et al. 2003). In order to avoid the most serious consequences of climate change, we need to combine efforts to reduce the rate of climate warming with increased efforts to monitor and ameliorate the impacts of climate change on ecosystems. This research has produced tools for monitoring shifts driven by climate change and, through our collaboration with other researchers in Australia and overseas, has aimed to create a better understanding of the impacts of climate change on the terrestrial biota.
References


Appendix 1 – Published Paper

Macrolepidopteran assemblages along an altitudinal gradient in subtropical rainforest - exploring indicators of climate change

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ABSTRACT

Moth assemblages have been widely used to estimate patterns of beta-diversity in forest ecosystems. As part of the IBISCA-Queensland project we examined patterns of diversity in a large subset of night-flying moths along an altitudinal gradient in subtropical rainforest. The permanent IBISCA-Queensland transect located in Lamington National Park, south-east Queensland, Australia, spans altitudes from 300 metres (m) to 1100 m above sea level (a.s.l.) within continuous, undisturbed rainforest. We sampled four replicate plots at each of five altitudes (300, 500, 700, 900, 1100 m a.s.l.). A total of 11 379 individual moths were sampled, belonging to approximately 865 morphospecies. Moth assemblages displayed a strong altitudinal signal at each of two sampling periods (October 2006 and March 2007). The results show that cloud forest above 900 m a.s.l. where Nothofagus moorei becomes dominant, contains a number of moth species that are restricted to the high elevation forest and these species may be most threatened by climatic change. The analyses presented here suggest a set of 18 moth species which may be useful as part of a multi-taxon predictor set for future monitoring of the impact of global warming on forest biodiversity.

Climate change is having a marked effect on terrestrial ecosystems, as evidenced by poleward and elevational shifts in the distributions of many species of plants and animals (Bale et al. 2002; Grabherr et al. 1994; Hickling et al. 2006; IPCC 2007; Parmesan 1996). The IBISCA-Queensland project aimed to quantify the relationship between climate and biodiversity along an altitudinal gradient in subtropical rainforest and, by so doing, develop robust measures for future monitoring of climate change impacts (Kitching et al., this volume). This paper investigates moth assemblages along this altitudinal gradient, and suggests a group of moth species that may be used to monitor altitudinal shifts in distributions.

It has been predicted that climatic warming, over the course of the next century will cause an increase in global average temperature of...
between 1.4ºC and 5.8ºC (IPCC 2007). Changes to climatic conditions are likely to result in increased weather variability and extreme weather events (Easterling et al. 2000), leading to dramatic changes in ecosystem dynamics (Weltzin et al. 2003). The responses of ecosystems to climate change are wide and varied, and are confounded by species interactions and feedback relationships. Species interactions may enable some groups to adapt to new conditions, for example, through shifts in community composition and simplification of food webs (Suttle et al. 2007). However, changed conditions may exceed the environmental thresholds for many species leading to changes in distribution or, if this is not possible, local or even global extinction (Pounds et al. 1999; Thomas et al. 2004). Biological responses due to climate change, such as distribution shifts and phenological changes, have already been measured in a variety of taxa and ecosystems (Parmesan & Yohe 2003; Walther et al. 2002).

Studies of altitudinal gradients are an effective method of investigating and monitoring the impacts of climate change because they allow for a wide range of changing environmental variables to be observed over small geographical areas. They provide ideal situations to explore how species distributions may be associated with, and limited by, climatic factors, while minimising confounding historical factors that influence species distributions over latitudinal gradients (Fiedler & Beck 2008; Shoo et al. 2006). Altitudinal gradients potentially provide insight into climate change impacts, because they encompass steep temperature and moisture gradients, leading to stratified environmental parameters and faunal assemblages (Hodkinson 2005; Shoo et al. 2006). Many studies have shown that montane cloud forests are highly sensitive to, and threatened by, climate change (Foster 2001; Nadkarni & Solano 2002; Pounds et al. 1999; Still et al. 1999; Williams et al. 2003).

A medium-range climate change scenario predicts an average global temperature increase of 4ºC over the next 100 years, which would push current climate envelopes around 800 m upwards in altitude (Malhi & Phillips 2004). Even an optimistic climate change scenario predicts upward shifts in climatic envelopes of up to 450 m (Loope & Giambelluca 1998). However, these estimates are likely to vary regionally and will also depend on local conditions. Despite this, the estimates are of particular concern because cloud forest ecosystems often encompass rare and endemic species with limited altitudinal ranges (Foster 2001). Some plant species in tropical montane forests, for example, display ranges of less than 300 m (Loope & Giambelluca 1998).

IBISCA-Queensland was a collaborative, international investigation of patterns of diversity and ecosystem processes along an altitudinal gradient. This study investigated which species are sensitive to climatic variability associated with increasing altitude and therefore most likely to be sensitive to climate change and, by doing so, sought to establish current baseline information, laying the foundation for longer-term monitoring programs. Study sites for this project are located in the UNESCO World Heritage listed Lamington National Park, noted for its isolated patches of montane, Antarctic Beech (Nothofagus moorei) dominated, ‘cool temperate’ rainforest.

The collaborative approach of the IBISCA-Queensland project involved a broad range of taxonomic and ecological specialists each working to a fixed experimental design. This helped ensure that a wide range of taxa were studied, producing a multi-faceted baseline dataset describing a range of invertebrate and plant assemblages. The culmination of the study will be a powerful ‘predictor set’ (Kitching 1993) that can be re-sampled in the future in order to monitor impacts of climate change. In this paper we examine the potential of moths for inclusion in this predictor set. Monitoring protocols such as those which will be created by this study will provide important tools for understanding biotic responses to climate change, subsequently facilitating adaptive management strategies.
that encompass such responses. Moths are potentially particularly useful in this regard because they are diverse, relatively well-known taxonomically and, as herbivores, reflect closely the vegetational health of the forest (Kitching et al. 2000; Scoble 1995). They are also sensitive to environmental variables, being strongly affected by temperature and precipitation and resource limiting factors such as food availability (Holloway et al. 1992). Moths have been used as indicators of environmental change and the success of restoration in a variety of different terrestrial ecosystems, such as rainforests, temperate forests and agro-ecosystems (Beccaloni & Gaston 1994; Brown & Freitas 2000, New 1997; Ricketts et al. 2001).

The current study posed the following two questions by sampling moth assemblages along an altitudinal transect within the subtropical forest of Lamington National Park.

1. Do moth assemblages change with altitude?
2. If so, which moth species show the strongest altitudinal signal thus making them potentially appropriate indicators of future climate change within Lamington National Park?

METHODS

Study site

Lamington National Park is a protected area of forests covering 206 km² and includes the Lamington Plateau, which is located across the Queensland-New South Wales border, a part of the larger Tweed Caldera region (Willmont 2004). Lamington National Park is part of the Gondwana Rainforests of Australia, a group of eight national parks in south-east Queensland and north-east New South Wales, and has been World Heritage listed since 1994. The area mainly lies upon Cainozoic igneous rock, derived from volcanic eruptions. Lamington plateau was formed by a now extinct shield volcano, centred at Mount Warning, in north-eastern New South Wales (Stevens 1997).

The altitudinal transect that is the basis of the IBISCA-Queensland project was established in continuous rainforest within the Green Mountains section of Lamington National Park and encompasses a steep temperature and moisture gradient (Strong et al., this volume). The transect encompasses altitudes between 300 and 1100 m a.s.l. with four replicate plots located within coarse elevational bands centred upon altitudes of 300, 500, 700, 900 and 1100 m a.s.l. Lower elevation plots (300 and 500 m a.s.l.) are located within the valley of West Canungra Creek. Middle and high elevation plots (700 m a.s.l. and above) are located along the western slopes of the same valley, along the access road to Green Mountains, O’Reilly’s Guesthouse and the Border Track leading to Mount Bithongabel. Lower altitude plots are characterised by dryer, hotter conditions and the high altitude sites experience lower temperatures and higher moisture levels (Strong et al., this volume). The cloud cap, the lower limit of which sits between 800 and 900 m a.s.l depending on season and weather conditions, is likely to have a strong influence on local climate.

The rationale for the overall project and the locations of study plots are presented by Kitching et al. (this volume). Strong et al. (this volume) describe the climate and soil conditions prevailing across the selected altitudes. Laidlaw et al. (this volume) describe vegetation changes along the transect. The low elevation plots at 300 m a.s.l. are classified as complex notophyll vine forest (sensu Webb and Tracey 1978) dominated by Hoop Pine (Araucaria cunninghamii). The mid-elevation plots, 500, 700, 900 and 1100 m a.s.l., are also complex notophyll vine forest (McDonald & Hunter 2008). The highest altitude plots at 1100 m a.s.l. are simple microphyll fern forest dominated by Antarctic Beech (Nothofagus moorei).

Moth collection and identification

Trap design. Moths were sampled using modified Pennsylvania light traps (Frost 1957; Kitching et al. 2005) fitted with 12 volt gel-cell batteries. Traps employed a vertical actinic tube, producing short
wavelength blue light. This tube was surrounded by three transparent vanes that intercepted and knocked down insects attracted to the light into a bucket below. The bucket contained a Sureguard® resin strip impregnated with Dichlorvos™ insecticide which killed moths in situ. Traps were set daily and ran for 12 hours from 6 pm to 6 am.

Two Pennsylvania light traps were run simultaneously on a plot on each trapping night, with one trap at ground level and one in the forest canopy. Canopy traps were raised to a height of approximately 35 metres, depending on the height of the canopy, and ground traps were raised a few metres above the ground and hung from a low branch. The light traps were placed at both ground and canopy level to ensure a broader sampling of moth diversity (Brehm 2007; Beck et al. 2002; Schulze et al. 2001).

**Sampling regime.** Sampling took place in October 2006 and March 2007. Two traps (ground and canopy) were set simultaneously for three nights at each plot. Traps were emptied daily and all arthropods caught were transferred to sample containers and taken to a field laboratory. In total, 120 samples were collected in the first sampling period, from 14th to 31st October 2006, and 108 samples were collected in the second sampling period, from 10th March to 2nd April 2007. Two of the four 500 m a.s.l. plots were not sampled in March 2007 due to time constraints. In order to minimise the negative effect of moonlight on catches (Muirhead-Thomson 1991; Yela & Holyoak 1997; Nowinszky 2004) no trapping was carried out five days either side of the full moon.

**Processing catches.** Moths with a wing length of 1 cm or more were processed, thus representing the macrolepidoptera. In addition, all moths belonging to the superfamily Pyraloidea (i.e. the families Crambidae and Pyralidae), regardless of their size, were also processed. This group was targeted in addition to the macrolepidoptera because of the relatively good resources available for the identification of many subgroups within the Pyraloidea (Common 1990).

Based on external characteristics, moths were sorted to species, hereafter referred to as ‘morphospecies’ and each morphospecies was assigned a unique code number. As sorting proceeded, a reference collection including at least one representative of each morphospecies was assembled. Individuals in a given sample that could be readily identified as belonging to an existing, numbered morphospecies were recorded and discarded. Identification to generic and species level was carried out principally by comparison with the reference collections available in the Queensland Museum, Brisbane, Australia. Identified material from previous surveys in the Lamington region held by the Arthropod Biodiversity Laboratory at Griffith University was also used in addition to printed and electronic resources (Common 1990; www. ento.csiro.au/anic/moths.html).

**ANALYSIS.**

Data from the paired canopy and ground-level traps across three trap nights were pooled into one dataset for each plot. Quantitative samples of insects are often characterised by zero-inflated data with a small number of very abundant species and this was found to be the case in our samples. Multivariate analyses were based on the proportion of species within samples and these were log transformed in order to reduce the impact of highly dominant species. The multivariate analysis package Plymouth Routines in Multivariate Ecological Research [PRIMER 6™] (Clarke & Gorley 2006) was used to investigate patterns of moth assemblages across altitudinal zones.

Permutational multivariate analysis of variance (PERMANOVA) was conducted in PRIMER 6 with PERMANOVA+ add-on software (Anderson et al. 2008), testing for significant differences in the moth assemblage composition among a number of a priori groups, in this case the five altitudinal bands. This analysis was run with 9999 permutations, using the Bray-Curtis dissimilarity measure (Bray & Curtis 1957). The pair-wise post-hoc comparisons of each altitudinal group were used here to explore differences between altitudinal bands. Owing to time constraints, in
the October 2006 sampling session, only three of the 300 m a.s.l. sites were sampled, and in March 2007 only two of the 500 m a.s.l. sites were sampled. Because of this discrepancy pair-wise comparisons between altitudes for the 500 m sites in the March 2007 have been excluded to avoid unbalanced replication.

The Bray-Curtis dissimilarity measure (Bray & Curtis 1957) was also used to create a distance matrix. From this matrix, non-metric multi-dimensional scaling (NMDS), set to 100 random starts, was used to produce ordination plots illustrating the relationship of moth assemblages among sampling sites. The NMDS approach to analysis has been adopted successfully in similar studies of moths, and is useful in detecting patterns in assemblages that tend toward high diversity and low evenness (Beck & Chey 2008; Brehm & Fiedler 2004; Fielder et al. 2008).

Relationships between environmental variables and overall moth assemblage composition were investigated using the Distance-based Linear Model (DistLM) function in PERMANOVA+. Marginal tests available within the DistLM procedure investigate which environmental variables are significantly correlated to the variation in moth assemblage composition. The vectors of significant environmental variables were then superimposed on NMDS ordinations of moth assemblages. The length of vectors indicates the strength of the correlation and their direction indicates whether the environmental variables were positively or negatively correlated with the observed patterns of assemblage composition. Environmental vectors which were measured as part of the IBISCA-Qld project included soil moisture, soil organics, tree species richness and median temperature. The methods of collection of this environmental data are summarised by Strong et al. and Laidlaw et al. (this volume). A metric called ‘fog events’ was also used, indicating days when weather data recorders showed periods of 100% atmospheric humidity, thought to reflect fog events, although some inaccurate readings may result from the data loggers being wet from rainfall.

We also investigated the extent of variation in moth assemblage explained by spatial-auto correlation, in comparison to altitudinal differences. To this end, latitudes and longitudes of the site locations were first centred and rotated using PCA ordination with PRIMER 6, and the resultant x and y coordinates were used to generate a between-site distance matrix based on Euclidean distance measures. Similarly, another distance matrix (based on Euclidean distance measures) was generated using altitudinal differences between sites. Two separate Mantel tests (available from the RELATE routine within PRIMER 6) were conducted to calculate correlation coefficients and associated P values between distance matrices of moth assemblages and site locations, and moth assemblages and altitudinal differences.

RESULTS

A total of 11,379 moths belonging to 865 morphospecies was sampled in this study; 3,376 individuals in October 2006 and 7,658 in March 2007. Samples collected in October 2006 showed a mid-elevation peak in species richness which was highest at 500 m a.s.l. No such peak was apparent in the March 2007 data, although it should be noted that sampling effort at 500 m a.s.l. in March 2007 was restricted to two sites.

Ordination plots of moth assemblages sampled in October 2006 (Fig. 2a) and March 2007 (Fig. 2b) show a clear altitudinal signal in assemblage structure between 300 and 1100 m a.s.l. The PERMANOVA analysis indicated a highly significant relationship between altitude and moth assemblages for both the October 2006 (pseudo-F = 2.95, P = 0.001) and March 2007 datasets (pseudo-F = 5.13, P = 0.0001). Pair-wise post-hoc comparisons, testing between each of the altitudinal groups (Table 1), showed that most altitudinal groups were significantly different from each other, with the exception of 500 and
FIG. 1. Mean moth species richness (± 1 x standard deviation) at each sampled elevation in October 2006 (black bars) and March 2007 (open bars). In March 2007, only two of the four 500 m a.s.l plots were sampled, therefore the complete range is shown for this sampling occasion.

FIG. 2. NMDS ordination plots of moth assemblages, based on log transformed proportion of morpho-species, collected in (a) October 2006 and (b) March 2007. Only three of the 300 m a.s.l plots were sampled in October 2006, and only two of the 500 m a.s.l plots during March due to time constraints. Superimposed vectors are environmental parameters significantly correlated to the assemblage composition.
Macrolepidopteran assemblages along an altitudinal gradient

TABLE 1. Results of pair-wise post-hoc comparisons of moth assemblages between altitudinal (m a.s.l.) groups for October 2006 and March 2007 (500 m sites have been excluded from March 2007 analysis due to low replication), showing degrees of freedom (df), t and P values. Analyses were based on log transformed proportions of morphospecies.

<table>
<thead>
<tr>
<th>Comparison</th>
<th>df</th>
<th>t</th>
<th>P</th>
<th>df</th>
<th>t</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>300 and 500 m</td>
<td>5</td>
<td>1.85</td>
<td>0.030</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>300 and 700 m</td>
<td>5</td>
<td>1.83</td>
<td>0.029</td>
<td>6</td>
<td>2.32</td>
<td>0.028</td>
</tr>
<tr>
<td>300 and 900 m</td>
<td>5</td>
<td>2.02</td>
<td>0.028</td>
<td>6</td>
<td>2.35</td>
<td>0.029</td>
</tr>
<tr>
<td>300 and 1100 m</td>
<td>5</td>
<td>2.02</td>
<td>0.026</td>
<td>6</td>
<td>3.55</td>
<td>0.031</td>
</tr>
<tr>
<td>500 and 700 m</td>
<td>6</td>
<td>1.28</td>
<td>0.057</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>500 and 900 m</td>
<td>6</td>
<td>1.69</td>
<td>0.030</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>500 and 1100 m</td>
<td>6</td>
<td>2.02</td>
<td>0.029</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>700 and 900 m</td>
<td>6</td>
<td>1.26</td>
<td>0.062</td>
<td>6</td>
<td>1.60</td>
<td>0.028</td>
</tr>
<tr>
<td>700 and 1100 m</td>
<td>6</td>
<td>1.69</td>
<td>0.030</td>
<td>6</td>
<td>2.86</td>
<td>0.028</td>
</tr>
<tr>
<td>900 and 1100 m</td>
<td>6</td>
<td>1.39</td>
<td>0.025</td>
<td>6</td>
<td>2.05</td>
<td>0.026</td>
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</tbody>
</table>

TABLE 2. Average similarities between and within altitudinal (m a.s.l.) groups, based on log transformed proportions of morphospecies, from four plots at each altitudinal band collected in (a) October 2006 and (b) March 2007.

<table>
<thead>
<tr>
<th></th>
<th>300m</th>
<th>500m</th>
<th>700m</th>
<th>900m</th>
<th>1100m</th>
</tr>
</thead>
<tbody>
<tr>
<td>a) October 2006</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>300m</td>
<td>44.89</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>500m</td>
<td>24.23</td>
<td>40.16</td>
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<td></td>
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<tr>
<td>700m</td>
<td>21.89</td>
<td>33.36</td>
<td>36.34</td>
<td></td>
<td></td>
</tr>
<tr>
<td>900m</td>
<td>16.18</td>
<td>25.60</td>
<td>32.24</td>
<td>37.27</td>
<td></td>
</tr>
<tr>
<td>1100m</td>
<td>12.96</td>
<td>14.45</td>
<td>19.95</td>
<td>27.23</td>
<td>32.03</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th>300m</th>
<th>500m</th>
<th>700m</th>
<th>900m</th>
<th>1100m</th>
</tr>
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<tr>
<td>b) March 2007</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>300m</td>
<td>50.83</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>500m</td>
<td>20.14</td>
<td>38.30</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>700m</td>
<td>22.12</td>
<td>37.79</td>
<td>42.23</td>
<td></td>
<td></td>
</tr>
<tr>
<td>900m</td>
<td>16.43</td>
<td>23.01</td>
<td>28.12</td>
<td>36.03</td>
<td></td>
</tr>
<tr>
<td>1100m</td>
<td>07.73</td>
<td>11.77</td>
<td>14.06</td>
<td>26.44</td>
<td>56.23</td>
</tr>
</tbody>
</table>

Marginal tests within the DistLM routine showed the same six environmental variables significantly correlated with moth assemblages collected in both October 2006 and March 2007. Changes in moth assemblages with increasing altitude were positively correlated to soil moisture (October, $F = 3.6$, $P = 0.0001$; March, $F = 6.4$, $P = 0.0001$), soil organic content (October, $F = 3.2$, $P = 0.0001$; March, $F = 5.5$, $P = 0.0001$) (presumably reflecting slower breakdown processes induced by lower temperatures) as well as fog events (October, $F = 2.6$, $P = 0.0004$; March, $F = 5.2$, $P = 0.0001$) (100% atmospheric humidity, from which we may infer a higher frequency of fog events and rainfall), whereas reverse trends were found for median temperature (October, $F = 3.7$, $P = 0.0001$; March, $F = 6.5$, $P = 0.0001$), soil pH (October, $F = 3.4$, $P = 0.0001$; March, $F = 5.0$, $P = 0.0001$) and tree species richness (October, $F = 1.7$, $P = 0.027$; March, $F = 2.8$, $P = 0.007$) (Figures 2a and 2b).

Mantel tests showed a high correlation between moth assemblages and altitude (correlation 700 m, and 700 and 900 m, but only in the October 2006 results, when fewer moths were collected.

TABLE 2. Average similarities between and within altitudinal (m a.s.l.) groups, based on log transformed proportions of morphospecies, from four plots at each altitudinal band collected in (a) October 2006 and (b) March 2007.
coefficient (Rho) of 0.84, \( P < 0.002 \) in March, and Rho = 0.73, \( P < 0.001 \) in October). However, moth assemblages were also equally highly correlated with the geographic arrangement of the sites (Rho = 0.85, \( P < 0.001 \) in March, and Rho = 0.728, \( P < 0.001 \) in October).

The moth assemblages of plots at 1100 m a.s.l. were clearly differentiated from those at other elevations, particularly in the March sample (Fig. 2b), and featured a number of moth species not found at lower elevations. The average similarity between altitudinal groups, summarised in Table 2, demonstrates decreasing assemblage similarity with increasing distance between altitudinal groups, indicating strong altitudinal turnover of moth assemblages with altitude.

**Species with altitude-restricted distributions**

As a first step towards nominating which species might be useful as indicators of climate change at particular elevations, or ranges of elevations, and hence promising candidates for future monitoring, we identified species with restricted altitudinal distributions (Table 3). For this we selected species represented by at least 30 specimens with at least 80% of the catch restricted to one or a small range of altitudes. In total there were 28 such taxa, 18 of which we have thus far been able to identify with confidence to species level. Of these 18 species (and using the 80% criterion mentioned above) nine were characteristic of a single altitude; three to 300 m, one to 700 m and five to 1100 m a.s.l. A further six species were commonly spread over two altitudes; one from 700 – 900 m and five from 900 – 1100 m a.s.l. Finally, three species occupied less restricted altitude ranges; one from 300 – 700 m.

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### Table 3. Altitudinally restricted moth species collected along the IBISCA-Queensland transect in Lamington National Park based on combined data from samples taken in October 2006 and March 2007. Only species that were represented by 30 or more individuals included. The black bars indicate the altitude or range of altitudes at which at least 80% of the total number of individuals were restricted.

<table>
<thead>
<tr>
<th>Species</th>
<th>Family</th>
<th>Subfamily</th>
<th>Fig.</th>
<th>Altitude (m a.s.l.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Termessa gratiosa</td>
<td>Arctiidae</td>
<td>Lithosiinae</td>
<td>3A</td>
<td></td>
</tr>
<tr>
<td>Rhimphelea sceletalis</td>
<td>Crambidae</td>
<td>Pyraustinae</td>
<td>3B</td>
<td></td>
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<tr>
<td>Lyclene structa</td>
<td>Arctiidae</td>
<td>Lithosiinae</td>
<td>3C</td>
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<tr>
<td>Asura cervicalis</td>
<td>Arctiidae</td>
<td>Lithosiinae</td>
<td>3D</td>
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<tr>
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<td>Lacturidae</td>
<td></td>
<td>3E</td>
<td></td>
</tr>
<tr>
<td>Palaesia bicosta</td>
<td>Arctiidae</td>
<td>Lithosiinae</td>
<td>3F</td>
<td></td>
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<tr>
<td>Ectropis bispinaria</td>
<td>Geometridae</td>
<td>Ennominae</td>
<td>3G</td>
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</tr>
<tr>
<td>Hesychopa chionora</td>
<td>Arctiidae</td>
<td>Lithosiinae</td>
<td>3H</td>
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<tr>
<td>Xylodryas leptoxantha</td>
<td>Geometridae</td>
<td>Ennominae</td>
<td>3I</td>
<td></td>
</tr>
<tr>
<td>Aboetheta pteridomona</td>
<td>Crambidae</td>
<td>Pyraustinae</td>
<td>3J</td>
<td></td>
</tr>
<tr>
<td>Eurychoria fictilis</td>
<td>Geometridae</td>
<td>Ennominae</td>
<td>3K</td>
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<td>Lyelliana dryophila</td>
<td>Geometridae</td>
<td>Ennominae</td>
<td>3L</td>
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<tr>
<td>Larophylla amimeta</td>
<td>Geometridae</td>
<td>Ennominae</td>
<td>3M</td>
<td></td>
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<tr>
<td>Unplaced genus crimnodes</td>
<td>Geometridae</td>
<td>Ennominae</td>
<td>3N</td>
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<tr>
<td>Heterochasta conglobata</td>
<td>Geometridae</td>
<td>Larentiinae</td>
<td>3O</td>
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<tr>
<td>Lychnographa heroica</td>
<td>Geometridae</td>
<td>Ennominae</td>
<td>3P</td>
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<td>Thalatha trichroma</td>
<td>Noctuidae</td>
<td>Amphipyrinae</td>
<td>3Q</td>
<td></td>
</tr>
<tr>
<td>Middletonia hemichroma</td>
<td>Geometridae</td>
<td>Ennominae</td>
<td>3R</td>
<td></td>
</tr>
</tbody>
</table>
FIG. 3. Altitudinally restricted moth species collected along the IBISCA-Queensland transect in Lamington National Park (see Table 3 for family and subfamily placements). A, Termessa gratiosa (Walker); B, Rhimphalea sceletalis Lederer; C, Lycline structa (Walker); D, Asura cervicalis Walker; E, Eustixis laetifem (Walker); F, Palaeosia bicosta (Walker); G, Ectropis bispinaria (Guenée); H, Hesychopa chionora (Meyrick); I, Xylocryas leptoxantha (Turner); J, Aboetheta pteridonoma Turner; K, Eurychoria fictilis (Turner); L, Lyelliana dryophila Turner; M, Larophylla amimeta Turner; N, Unplaced genus crinodes (Turner); O, Heterochaeta conglobata (Walker); P, Lychnographa heroica Turner; Q, Thalatha trichroma (Meyrick); R, Middletonia hemichroma. (Turner).
and two from 700 –1100 m a.s.l. These altitudinally restricted species represented five families. The ‘lower elevation species’, those characteristic of plots from 300 to 700 m a.s.l., comprised three lithosiine arctiids and a single pyraustine crambid. In contrast, species characteristic of higher elevations (900 –1100 m a.s.l.) were principally geometrids (nine ennomines and one larentiine) with one amphipyrine noctuid and a pyraustine crambid. Species restricted to mid-elevations (500–700 m a.s.l.) were, in general, scarce. The two species we identified in this category comprised a lithosiine arctiid and the lacturid, *Eustixis laetifera*.

**DISCUSSION**

The main objective of this study was to document changes in moth assemblages along an altitudinal gradient within continuous rainforest. We have demonstrated that there are characteristic assemblages of species at each elevation in two seasons and have identified particular species with indicator potential. In this discussion we examine potential explanations for these patterns and the potential impacts of climate change upon them. We discuss the likely generality of our results and avenues for further research.

The occurrence of a species in a particular sample results from a multiplicity of factors. These may be methodological or biological. Methodologically we acknowledge that we are sampling only night-flying, light-attracted moths. This is a subset of all moths but, nevertheless, is sufficiently large to provide a degree of confidence to identify community patterns from which usable management tools can be derived. Light traps are relatively easy to use and produce large samples. Poor catches can result from their use on cold and/or windy nights and bright moonlight undoubtedly adversely affects catches on clear nights (Nowinszky 2004). Any moth trapping programme must be flexible enough to substitute additional sampling nights in response to the occasionally unsuccessful trap night. A more serious issue concerning the repeatability and representativeness of light-trap samples is that of seasonality. There are undoubtedly different assemblages of moth species flying at different times of the year. Further, even for a particular species, there will be a peak time of flight activity and the first emergents or last survivors of a species, appearing in trap catches, may give a false impression of rarity. We have partly addressed this problem by sampling on two different occasions (and a third not reported on here). Nevertheless, any comparisons using results of the kind we have reported must aim to target a comparable season. Of course, year-long sequences of catches would be useful in resolving the issue of seasonality across species. There are, however, no such datasets available for any subtropical Australian location. Even where such datasets available, the highly variable Australian climate would, quite possibly, prevent the drawing of general conclusions concerning species diversity from a single year’s data. We suggest the large sample sizes and the fact that rather similar patterns emerged from two quite different sampling periods lends a good deal of credibility to the conclusions. We note also that singletons or doubles (i.e. species that appear only once or twice within our samples) had little impact on the results of multivariate ordinations (results not presented here).

Ecologically, the presence or absence of a particular species at a particular elevation will be determined by the limiting dimensions of the niche of each species. These may be physico-chemical dimensions such as temperature, moisture and soil chemistry, or biological variables based on interactions with food-plants, competitors and natural predators. The physico-chemical variables are dimensions of the fundamental niche of the species and reflect the evolved physiological tolerances of the species concerned. Biological interactions add dimensions to the niche space which define the realised niche of the species and usually define a hypervolume nested within that circumscribed by the fundamental niche dimensions (Hutchinson 1957). We say ‘usually’ because, in rare instances, mutualistic interactions
may expand the niche of a species beyond the volume defined by its physiological tolerances to physio-chemical factors. It would be in line with general niche theory (see for example Dobzhansky 1950; McCoy 1990) to suppose that species restricted to altitudes presenting more extreme and challenging microclimates, would be more likely to be restricted by their physiological tolerances of climatic extremes, whereas those species spread across altitudes, presumably comfortably within their physiological envelopes, are more likely to be restricted by biological interactions. Biological interactions that may restrict the spatial distribution of moths are likely to include the presence or absence of acceptable food-plants and the suite of predators and parasitoids co-occurring with them.

Our nomination of moth species which may be useful as indicators is preliminary. As other species are firmly identified, so additional, usable, range-restricted species can be added to the list. Further statistical characterisation of the ‘attachment’ of these species to particular altitudinal ranges is in progress. Of course, one set of information that would assist in explaining these patterns are lists of the larval food plants of these species. Very little published information is available on this subject (www-staff.it.uts.edu.au/~don/larvae). There is general agreement that larvae of many lithosines feed on lichens and this has been confirmed for Termessa gratiosa and Palaeosia bicosta. Given that montane and boreal lichen distributions are predicted to shift under climate change (Ellis et al. 2007), these species feeding on lichens may be of conservation concern.

There is published food-plant data available for only one of the remaining species, Ectropis bispinaria (Geometridae: Ennominae), which is highly polyphagous, being recorded from species of Rutaceae, Lauraceae, Rosaceae and Proteaceae with all families being well represented in the flora of the Lamington rainforest. Larval rearing by one of us (D. Bito) adds Monimiaceae (Daphnandra micrantha) and Sapindaceae (Arytera divaricata and A. dystilis) to this list. Other species within the lacturid genus Eustixis have been reared from Ficus spp. and this association might reasonably be expected for E. laetifera. Unpublished rearing records provide a few additions. Among the ennomines, Middletonia hemichroma has been reared from Nothofagus moorei (Nothofagaceae), Quintinia verdonii (Quintiniaceae) and Syzygium crebrinerve (Myrtaceae); and Dyscheralcis crimnodes has been reared from Neolitsea australiensis (Lauraceae) and Pentaceras australis (Rutaceae) (D. Bito, unpub. data).

Testing these explanatory hypotheses related to the altitudinal distributions of species is restricted by insufficient data on both host plants and natural enemies. We have some, albeit sparse, data on food-plants but we have virtually no information on parasitoid loads. Both deficiencies point to likely rewarding future areas of investigation. The IBISCA-Qld Project has generated substantial samples of micro-Hymenoptera through Malaise trapping (see Boulter et al., this issue) and further analysis of these samples may provide more insight into their likely significance in structuring moth assemblages.

The existence of clear cut patterns of altitudinally delimited moth assemblages, with particular species having clearly restricted altitudinal distributions, suggests that selected moth taxa will be useful in tracking any upward shifts in distribution and invasions of higher altitudes – a likely consequence of global warming. It also suggests that the highly distinctive upper elevation assemblage must be regarded as vulnerable and of conservation concern. The patterns we have identified are concordant with studies of other taxa that formed part of the IBISCA-Qld Project and with other studies of moths on altitudinal gradients elsewhere (Fiedler et al. 2008; Brehm & Fiedler 2003). Our results suggest that the most sensitive altitudes to target for monitoring in the relatively short-term (say over 20-30 years) will be those at 700 m
a.s.l. and above, where cloud base fluctuations are predicted to alter ecosystem structure and dynamics (Laidlaw et al. this issue). This conforms with the opinions of earlier authors who have suggested that such ecotones are the areas that will show the strongest signals of climate change (Parmesan & Yohe 2003).

The selection of suitable indicator species depends on several criteria. An effective indicator needs to be present in large numbers, be easily recognisable, as well as being sensitive to environmental variables (Holloway 1998; Scoble 1995). Moth groups that are sensitive to floristic change and which have low vagility, such as the Geometridae and some Pyralidae, fulfil these criteria and have been demonstrated to be good indicators across a variety of ecological investigations (Beck et al. 2002; Holloway 1985; Kitching et al. 2000; Scoble 1995).

The set of moth species identified will be usefully incorporated as part of a ‘predictor set’ of arthropod and plant species, reflecting different trophic levels and guilds within the rainforest community. This will be significant for the ecological monitoring of future changes in ecosystem composition and function (Kitching 1993; McGeogh 1998).

The generality of our results is inevitably a potential point of contention. Firstly, we have examined only a single gradient within a single biome and a single catchment at one latitude. Although it is likely, as a general principal, that the higher taxa we have identified are likely to be useful generators of indicator species at other rainforest locations, no claims for generality of our results beyond the target locations can be (or is) made. Wider distribution records (as well as altitudinal information) for the indicator species are being collected from the Australian National Insect Collection, Canberra, and other museums. Future research will target additional rainforest transects within Australia at a range of scales. In particular, the local role of aspect and the continental role of latitude require investigation. This work is in progress.

Clearly, because of the way sites are necessarily distributed across the altitudinal gradient, geographic distances between sites will be correlated with moth assemblages. It is impossible to separate how much of this correlation is driven by inter-site distances and how much by the effects of altitude per se. However, the most parsimonious and most ecologically sensible explanation is that moth assemblages are more highly influenced by altitude (and the suite of environmental variables that are associated with altitude). Further work at additional altitudinal gradients, such as at Border Ranges National Park, will help test this hypothesis.

The analyses we have presented here are the first, necessarily, preliminary results of the Lepidoptera studies within the IBISCA-Queensland project. Further analyses examining responses on a family by family basis, formal quantification of ‘indicator values’ (Dufrene & Legendre; 1997), and comparisons of the ground-zone catches with those from the canopy, will probably also be informative.

ACKNOWLEDGEMENTS

This work was conducted as part of the IBISCA-Queensland Project and as such we are deeply grateful to the Department of State Development of the State of Queensland for the Smart State funding which made this project possible. Their generous funding was matched by funding from Griffith University, the Queensland Museum, the Queensland Herbarium, the Global Canopy Programme (Oxford), NRM Queensland (SEQ Catchments) and the Queensland National Parks Association. The project also received cash support from the federal Department of Environment, Heritage and the Arts and O’Reillys’ Rainforest Resort. We thank IBISCA-Qld team and the volunteers who helped collect and sort moths in October 2006, March 2007 and January 2008.
as part of the IBISCA Queensland project, particularly John Gray, Heather Christensen, Kyle Barton, Dean Wright, Cecilia Chavana-Bryant, Jake Bryant, Stefan Curtis, Kyran Staunton and Eileen Forster for their help in field and laboratory work. Thanks also to Aki Nakamura for his valuable guidance with statistical analyses and to Geoff Thompson for photographing and preparing the plate of moths. The Environmental Futures Centre at Griffith University, Queensland, provided financial support for this paper, for which we are most grateful. We thank the Queensland Museum for allowing access to their reference collections of moths. Many improvements have been made to this manuscript thanks to feedback from Jude Buckman, Bob Ashton and Kyran Staunton.

LITERATURE CITED


Ashton et al.


Macrolepidopteran assemblages along an altitudinal gradient


