Community parameters of Auchenorrhyncha (Hemiptera: Insect) along altitudinal gradients in subtropical and tropical rainforests in Australia

Francesca Florence Dem BSc (Hons, MSc)

Griffith School of Environment
Science, Environment, Engineering and Technology
Griffith University

Submitted in fulfilment of the requirements of the degree of Doctor of Philosophy
April 2015
Synopsis

Gradients in altitude are used frequently to understand how species respond to changes in local climatic conditions and are therefore a robust tool for predicting how species and communities in montane environments may respond to changes in climate. It is important that we understand how species richness patterns and interactions are affected by current changes in climate if we are to make sensible predictions about how biodiversity and ecosystem function will be affected by climate change. Further, while studies have shown a strong gradients in species richness and species turnover that accompany altitude, little is known about how species at different heights in forests and how plant-insect herbivore interactions respond to altitude.

This challenge has been addressed here by examining the changing distribution patterns of the taxonomic group, Auchenorrhyncha, which are an important group of plant sucking herbivores, with altitude, in vertical forest columns and of their associated host plants. Herbivorous insects, including leafhoppers and planthoppers interact with their host plants in complex networks, but relatively little is known about how these relationships will be and are being affected by changes in climate. In order to determine how altitudinal changes in climatic conditions affect distribution patterns of Auchenorrhyncha, I quantified these communities along two altitudinal gradients, one in eastern Australian subtropical rainforest and the other in northern Australian tropical rainforest. In doing so, I aimed to: 1) examine the distribution patterns of Auchenorrhyncha along altitudinal gradients, 2) examine the vertical structure of
Auchenorrhyncha within forests, their feeding-guild structure and how these may change with altitude, and 3) examine nymphal herbivore load to determine their distribution patterns on different plant species and how this might change with altitude.

Data on the distribution patterns of leafhoppers and planthoppers were obtained by collecting using light and Malaise traps at altitudes situated along gradients, encompassing altitudes ranging from 400-1200m for the tropical transect and 300-1100m for the subtropical transect, over two sampling seasons. Adult Auchenorrhyncha were sorted and identified to morphospecies. Information on the herbivore-host plant relationship was obtained by hand collecting Auchenorrhyncha nymphs on plants within the subtropical transect. Collections of samples were only restricted to nymphs as rearing of nymphs is difficult and time-consuming.

Auchenorrhyncha are generally poorly documented in Australia, particularly in their native rainforest habitats, as in many parts of the world, and this research has provided new data on this important insect herbivore group this is. The total species richness of Auchenorrhyncha recorded from the light and Malaise traps across both altitudinal gradients was 365, representing 22 713 individuals in 17 families. The tropical transect had more species (274) than the subtropical transect (188), however, it had less individuals (6 809) than the subtropical transect (15 904). At both altitudinal gradients, species distribution patterns showed that lower altitudes tended to have a greater diversity of Auchenorrhyncha than higher altitudes. Beta-diversity, that is, the turnover of species, of Auchenorrhyncha across altitudes was not affected by altitude.
The total number of morphospecies recorded from light trap samples across all altitudes from both transects was 318, representing 20,813 individuals. For each forest strata across both transects, canopy samples produced 246 species with a total abundance of 13,349, and the understorey samples produced 265 species, representing 7,464 individuals. Altogether, there were 17 families in both the tropical and subtropical transects, which shared a proportion of 0.70 families. Differences in vertical structure of distribution patterns also showed a strong gradient in altitude, in understorey communities. Canopy and understorey assemblages contributed equally to Auchenorrhyncha communities and their species turnover with altitude also were similar, with communities closer to each other having similar composition than those further away.

Overall there was no strong gradient in nymph incidence on plants with increasing altitude. There was seasonal variation in nymph incidence both in the pooled community and at each altitude. Herbivore load showed no correlation with host plant species abundance. However, there was a significant correlation between the total number of nymphs and total number of plant individuals per plant species across altitudes. Patterns of distribution of nymphs on host taxa showed an effect of host species abundance.

My results provide strong evidence that altitude affects distribution patterns of Auchenorrhyncha. However, altitude did not affect herbivore load and nymph incidence on host taxa. Climate change may potentially lead to changes in species and feeding-guild distribution patterns, as well as plant-insect herbivore relationships. Distribution
patterns of nymphs on host plants between altitudes differed among plant taxa. My research has demonstrated that species diversity and the vertical structure of Auchenorrhyncha within forests changes along altitudinal gradients in tropical and subtropical rainforests in Australia. It also demonstrated that the interaction of herbivore species and their host plants changes with altitude, but the interaction was impacted more by plant species abundance and leaf-flush than altitude.
Statement of originality

I hereby declare that the material contained in this thesis has not previously been submitted for a degree or diploma at any university. Further, all the work herein was written solely for this thesis and submitted as partial completion of a postdoctoral degree, and to the best of my knowledge, this thesis contains no material previously published or written by another person except where due reference is made in the thesis itself.

_______________________________
Francesca Florence Dem
Table of contents

Synopsis..................................................................................................................ii

Statement of originality.........................................................................................vi

Table of contents..................................................................................................vii

List of figures.........................................................................................................x

List of tables.........................................................................................................xiv

Acknowledgements..............................................................................................xvi

Chapter 1: Introduction, aims and thesis outline..............................................1

1.1. Introduction.....................................................................................................1
1.2. Aims...............................................................................................................3
1.3. Thesis structure.............................................................................................4

Chapter 2: General introduction to Auchenorrhyncha.........................................6

2.1. Biology and life history................................................................................6
2.1.1. General introduction................................................................................6
2.1.2. Mating systems and reproduction.........................................................7
2.1.3. Feeding-guilds and their feeding strategies..........................................10
2.2. Determinants of Auchenorrhyncha dynamics........................................12

Chapter 3: Theoretical background and literature review................................14

3.1. Introduction..................................................................................................14

3.2. Diversity patterns across gradients- major ecological theories to explain
    observed diversity patterns............................................................................14
3.2.1. Latitudinal gradient..............................................................................15
3.2.2. Altitudinal gradient ................................................................. 16
3.2.3. Vertical gradient ................................................................. 16
3.3. Richness patterns across altitudes ........................................... 17
  3.3.1. Habitat heterogeneity ....................................................... 19
  3.3.2. Niche partitioning and competition .................................... 20
  3.3.3. Primary productivity and biotic interactions ....................... 21
  3.3.4. Evolution and biogeographic history ............................... 24
  3.3.5. Energy hypothesis .......................................................... 26
  3.3.6. Species-area relationship ................................................. 27
3.4. Herbivory and host specialization ......................................... 29
3.5. Climate change and biodiversity ........................................... 31
  3.5.1. Impacts of climate change ............................................... 31
  3.5.2. Climate change in an Australian context .......................... 34
  3.5.3. Climate change and insects ............................................. 35

Chapter 4: General methods ......................................................... 38
  4.1. Study locations ................................................................. 38
  4.2. Community sampling ....................................................... 45
    4.2.1. Sampling of adult insects ............................................ 46
  4.3. Insect specimen dissection and identification ....................... 51

Chapter 5: Altitudinal distribution patterns of Auchenorrhyncha along gradients in subtropical and tropical rainforests in Australia ......................... 53
  5.1. Abstract ............................................................................. 53
8.4. Potential impacts of climate change on insect species and host plants........135

8.5. Future directions.................................................................136

References..................................................................................138

List of figures

Figure 4.1. Map of Border Ranges NP showing the five altitudinal sites (300m, 500m, 700m, 900m, 1100m a.s.l) and the four replicated plots within each band...........40

Figure 4.2. Frequency distribution of average temperature for each altitude, recorded using Ibutton temperature loggers at all plots at each of the five altitudinal sites (300m, 500m, 700m, 900m, 1100m a.s.l) between the period 10th July 2010 and 6th January 2011 (Ashton 2013, PhD dissertation, Griffith University)......................41

Figure 4.3. Map of Mt Lewis National Park transect. Altitudinal bands are at 400m, 600m, 800m, 1000m and 1200m a.s.l. Four 20m x 20m replicated plots are located at each altitude.................................................................44

Figure 4.4. Modified Pennsylvania light trap, hung at head height. (Photo courtesy of L. Ashton).................................................................49

Figure 4.5. Latest modified Malaise trap set up in the forest to trap flying insects.....51

Figure 5.1. Proportions of each family collected at the tropical (i, ii) and subtropical (iii, iv) transects. (i, ii) abundance collected at each transect (families with 20 or less individuals are grouped as ‘other families’). (ii, iv) species sampled at each transect (families with 10 or less species are grouped as ‘other families’).................64

Figure 5.2. The relationship between the observed number of species (i, ii), rarefied species richness (iii, iv) and extrapolated number of species (v, vi), and altitude respectively for each transect (a, b). Error bars on rarefied data (iii, iv) are 95% confidence intervals.........................................................65
Figure 5.3. Individual based rarefaction and extrapolation curves from five reference samples (filled black circles) for each transect (i, tropical transect; ii, subtropical transect). Individuals were rarefied down to the smallest number of individuals (unbroken black lines) and extrapolated to the highest number of individuals (broken black lines) in the samples for the respective study location. 66

Figure 5.4a. Principle Coordination Axes for all the sites at each altitude at the tropical transect, taking into account environmental variables. 68

Figure 5.4b. Principle Coordination Axes for all the sites at each altitude at the subtropical transect, taking into account environmental variables. 68

Figure 5.5. Relationship between altitudinal difference and Sørensen insect similarity between sites at different altitudes. There is no significant correlation between altitudinal difference and similarity for both transects (a, b). All pairwise comparisons between five study sites from each transect were used. Each marker is one paired comparison. 69

Figure 5.6a. Distribution of altitudinal range of species across altitudes at the different transects. Most species at both transects have narrow altitudinal ranges. 70

Figure 5.6b. Correlation between altitudinal range and altitudinal midpoint of species at the tropical and subtropical transect. There is no significant correlation at either transect, so that species at low elevations have similar range size as those at high altitudes (Pearson correlations, Mt Lewis, r= 0.21, N=274, P>0.05; Border Ranger, r = 0.51, N=188, P>0.05). The sizes of the markers indicate the number of sites (1-5) where the species is recorded. 70

Figure 6.1. The relationship between altitude and species richness at the canopy and understory levels recorded at the tropical (a) and subtropical (b) transects. Both relationships showed significant correlations between the two variables for both canopy and understory assemblages. 87

Figure 6.2. Distribution of canopy and understory assemblages at each altitude observed for each transect (a, b). The number of species did not differ between canopy and understory at each altitude (Two-sample T-test: tropical transect, T-test = 2.78, d.f =4, P<0.05; subtropical transect, T-test = 2.78, d.f =4, P<0.05). 87

Figure 6.3. Distribution of feeding-guild assemblages at each altitude within each of the transects. Phloem-feeding species are more dominant than xylem- and mesophyll-
feeding species (one-sample T-test = 2.78, d.f =4, P<0.05, tropics; one-sample T-test = 2.78, d.f=4, P<0.05, subtropics)……………………………………………………………………..88

**Figure 6.4.** The number of shared and unique species recorded at the canopy understorey levels. Distribution for pairs of adjacent altitudes at the tropical and subtropical transects……………………………………………………………………..90

**Figure 6.5.** Proportion of shared and unique species for each feeding-guild between canopy and understorey, across altitudes at each study location (a, b)……………….91

**Figure 6.6.** Sørensen and Chao-Sørensen insect similarities between altitudes for the canopy and understorey communities within the tropical (i, ii) and subtropical transect (iii, iv)…………………………………………………………………………………………………………………………92

**Figure 6.7.** NMDS ordinations matrices of species composition among samples across altitudes and forest strata at each plot within the tropical transect……………………………93

**Figure 6.7.** NMDS ordinations matrices of species composition among samples across altitudes and forest strata at each plot within the subtropical transect………………….94

**Figure S6.1.** Distribution of feeding-guild assemblages among altitudes and between canopy and understorey at the tropical transect. The number of species per feeding-guild did not differ, both among altitudes and between forest strata………………….101

**Figure S6.2.** Distribution of feeding-guilds assemblages among altitudes and between forest strata at the subtropical transect. The number of species per feeding-guild differed among altitudes, but did not differ between canopy and understorey………..101

**Figure S6.3.** NMDS ordinations matrices of species composition among latitudes, altitudes, plot sites and forest strata for the subtropical and tropical transects combined. BR – stands for Border Ranges NP (subtropical transect); ML – stands for Mt Lewis NP (tropical transect)…………………………………………………………………………………………………………………………………………..103
Figure 7.1. Percentages of nymph abundance collected from each plant family in both seasons combined across altitudes. Plant families with 10 or fewer individuals are grouped together as ‘other families’. .................................................................114

Figure 7.2a. Percentages of nymph abundance recorded on plant families sampled at the start of the wet season. Plant families with 10 or fewer individuals are grouped together as ‘other families’ .................................................................114

Figure 7.2b. Percentages of nymph abundance on plant families at the end of the wet season. Plant families with 10 or fewer individuals are grouped together as ‘other families’ .................................................................115

Figure 7.3a. Nymph incidence and distribution on plant species between seasons across altitudes. Only plant species from which nymphs were collected in both seasons are represented .................................................................117

Figure 7.3b. Nymphal abundance sampled at each altitude at the start and end of wet season. There were more nymphs collected at the start of wet season than at end of it (two-sample T-test = 0.254, d.f. = 4, P>0.05) .................................................................118

Figure 7.4a. Distribution of nymph incidence on selected plant species. Herbivore incidence was examined among plant species that were each represented by five or more nymphs in three consecutive altitudinal bands. Black bars represent plant species abundance and grey bars represent nymph abundance ........................................118

Figure 7.4b. Distribution of nymph incidence on selected plant families. Herbivore incidence was examined among plant families that were each represented by five or more individuals in three consecutive altitudes. Black bars represent plant family abundance and grey bars represent nymph abundance ........................................119

Figure 7.5a. Relationship between average number of nymphs and plant species abundance across altitudes. There was no correlation between herbivore load and plant abundance (Pearson’s correlation, r = -0.03, R² = 0.001, N = 31, P>0.05) ........................................119

Figure 7.5b. Relationship between total nymph incidence and total number of plant individuals across altitudes. There was a significant correlation between the number of nymphs and plant abundance (Pearson’s correlation, r = 0.91, R² = 0.82, N = 31, P<0.05) .................................................................120
Figure 7.6. Relationship between nymph abundance and plant species richness among altitudes (Pearson correlation, r = -0.57, R²=0.33, N=5, P>0.05). Trees with dbh >5cm are identified and used in the analyses. Dotted triangles represent each altitudinal site……………………………………………………………………121

Figure S7.1. Nymph abundance collected on each plant species. Plant species with five or more nymphs are represented…………………………………………………………………………126

List of tables

Table 4.1. List of Auchenorrhyncha families in their respective feeding-guilds……..46

Table 5.1. Number of species and their abundance in each family recorded at the tropical and subtropical transect respectively……………………………………………………65

Table S5.1. Abundance and ranges of morphospecies of common families recorded at each altitudinal transect. Morphospecies with 100 or more individuals across altitudes are represented…………………………………………………………………………75

Table 6.1. Summary of the pair-wise PERMANOVA test for altitudes, strata and the interaction effect of altitude and stratum for the subtropical transect.............93

Table 6.2. Summary of the pair-wise PERMANOVA test for altitudes, strata and the interaction effect of altitude and stratum for the subtropical transect.............94

Table S6.1. ACE species richness estimator. Mean number of species at each altitude for canopy and understorey communities for the respective transect.................102

Table S6.2. ACE species richness estimator. Mean number of species of feeding-guilds at each altitude for both forest strata for the respective transect...............102

Table S6.3. Summary of the pair-wise PERMANOVA test for latitudes, altitudes and strata, and their interaction effects for both transects combined...............103
Table S6.4. Summary of the pairwise post-hoc PERMANOVA test between canopy and understorey communities at each altitude at the subtropical transect. Respective canopy and understorey samples at each plot site per altitude were combined. 104

Table S6.5. Summary of the pairwise post-hoc PERMANOVA test between canopy and understorey communities at each altitude at the tropical transect. Respective canopy and understorey samples at each plot site per altitude were combined. 104

Table 7.1. Dominant plant species (greater than 5 cm dbh) within each altitudinal band sampled at Border Ranges National Park, New South Wales. 111

Table S7.1. List of plant taxa from which nymphs were sampled from different altitudes. 124

Table S7.2. Nymph abundance sampled from different plant species at each altitude at the subtropical transect. 125
Acknowledgements

First and foremost, I thank my supervisors Professor Roger Kitching, Professor Nigel Stork, Professor Jane Hughes and Dr Murray Fletcher for their valuable advice, support and mentoring me throughout my PhD. I am endlessly grateful to Professor Vojtech Novotny for his advice and encouragement before and throughout my PhD. I am also grateful to the Australian Government and Griffith University for offering a Griffith University Postgraduate Research Scholarship (GUPRS) and Griffith University International Postgraduate Research Scholarship (GUIPRS) which funded this PhD program. I also thank the Griffith School of Environment, the Environmental Futures Research Institute and the Griffith University Higher Degree Research Office for providing academic and development support, and additional financial support.

I am grateful to the NSW Government for providing a research permit to do field work at Border Ranges National Park and the Queensland Government for providing a research permit to work at Mt Lewis National Park.

This research could not have been achieved without the hard work and assistance of Eric Brus, who assisted me both in the field and the laboratory and John Gray for volunteering to help me in the field. A special thank you to Dr Sarah Maunsell for giving valuable advice and assistance with regard to field work. I am also grateful to Dr Louise Ashton for the endless hard work in the field collecting light trap samples which was the major part of my data.

I thank members of my laboratory group for their friendship and for providing valuable suggestions in regard to many aspects of my research, particularly Dr Louise Ashton, Dr Sarah Maunsell, Casey Hall, Dr Akihiro Nakamura and Legi Sam. I am very grateful to Dr Sarah Maunsell, Dr Louise Ashton and Elliot Leech who, in additional to my supervisors provided comments on drafts of this thesis. Over the course of my PhD, I
have enjoyed sharing an office with Dr Sarah Maunsell, Casey Hall, Legi Sam, Maryam Esfandbod and Amy Baker, whom I thank for their company.

I am forever indebted to my parents, Michael Dem Miro and Agnes Mare for their unconditional support, encouragement and influencing my view of education since when I started school. I thank my siblings and my relatives, especially my cousin Fr. Alois Kaumu for their encouragement and time which was very important to me when at times I feel like missing home and family. Finally, I thank my husband Eric Brus for his never-ending patience, support and assistance throughout my PhD program.
Chapter 1. Introduction, aims and thesis outline

1.1. Introduction

Herbivorous insects and their host-plants make up a large percentage of global terrestrial biodiversity and also play vital roles as consumers and producers (Price 2002). Much of this diversity is observed within forests, especially tropical rainforests where many species remain undescribed (Godfray et al. 1999; Novotny et al. 2006; Schuldt et al. 2010). The interaction of herbivores and their host plants present disparate and intricate relationships within complex food webs, yet little is known about specificity levels and diet breath within these interactions (Forister et al. 2015; Novotny et al. 2010). Plant-herbivore interaction is one of the most common and consequential ecological associations on this planet (Ohgushi 2005; Singer et al. 2004). Variation in diet specialization is clearly an important driving factor in numerous ecological and evolutionary processes (Büchi & Vuilleumier 2014; Devictor et al. 2008) and is crucial in maintaining the provision of ecosystem services (Albrecht et al. 2007; Thebault & Loreau 2006).

It is widely accepted that climate change has, and will continue to have effects on biodiversity and on the distribution of species (Rasmann et al. 2014; Telwala et al. 2013). The effect of climate change on species, however, depends on the interaction of abiotic and biotic factors which ultimately determine their current geographical ranges and populations (Franco et al. 2006; Hickling et al. 2006). Currently, there is gap in our understanding of the effect of climate change on species interactions, particularly in Australia (Williams et al. 2008). In order to make sensible predictions on the likely effects of climate change on species and their interactions (Pearson & Dawson 2003;
Thuiller et al. 2008; Van der Putten et al. 2010), it is important that we first understand how species response to current climatic gradients (Suttle et al. 2007; Walther 2010).

Altitudinal gradients encompass climatic and environmental factors, such as area, net primary productivity, vertical stratification and geometric constraints (reviewed by Nogués-Bravo et al. 2008). Species respond to such gradients over relatively small spatial scales, and hence studies investigating the distribution of species and their patterns of interaction along altitudinal gradients, are very important, since they contribute to our understanding of diversity of patterns and ecological communities affected by clines in climate within localized areas (Chen et al. 1999; Oommen & Shanker 2005). Within altitudinal gradients, the spatial scale at which species are present allows better comparisons of ecological and diversity patterns, as opposed to latitudinal gradients (Körner 2007). Steep increases in altitude over small distances in montane environments, result in rapid and relative changes in environmental conditions, especially with respect to local climate (reviewed by Dobrowski 2011; Fridley 2009). Over the last 50 years, the effect of altitude on species richness and composition have been the focus of numerous biodiversity surveys, especially in mountainous regions across the globe (Kessler et al. 2011; Kitching et al. 2011; Sanders et al. 2003; Werner et al. 2007).

One important question is the pattern of species turnover in community assemblages along altitudinal gradients (Kitching et al. 2011; reviewed by Lomolino 2001). Many species are narrowly distributed attitudinally or are only found at mountain tops, especially in the tropics, which harbour a higher percentage of endemic species, as a result of poor dispersal conditions (Janzen 1967). Consequently, mountain ecosystems
are particularly more vulnerable to climate change (Lawrance et al. 2011). An important, but generally unanswered question is, do community-level changes resulting from climate change translate into changes in herbivore-host plant breath or in vertical stratification of species assemblages? There have been only a few studies that investigate herbivore host specificity levels or vertical community assemblages affected by plant species composition and climate change that accompany altitudinal changes (Ashton et al. 2016; Benadi et al. 2013; but see Ramos-Jilberto et al. 2010).

1.2. Aims

The work described in this thesis addresses the challenges of understanding how patterns of species distribution are affected by climate change in Auchenorrhyncha (leafhopper and plant hopper insect herbivores) and their presumed host plants. I have quantified the relationships and distribution of this group and its host plant along two altitudinal transects (except for Goal 3, which was investigated only in the subtropical transect) in tropical and subtropical rainforests in eastern Queensland. I used observational methods to determine how altitude and host plant species affect distribution patterns and herbivore load.

On commencing this research, I had the following goals:

1. To examine the distribution patterns of Auchenorrhyncha along altitudinal gradients.

2. To examine the vertical structure of distribution patterns of Auchenorrhyncha herbivore species’ and feeding-guilds and the altitudinal association of these patterns.
(3) To examine herbivore-host plant association with a view to determine the specificity levels of these associations, and whether these might change with altitude. Unfortunately, the DNA barcoding of nymphs and adults that I had proposed did not work out and I have instead used actual plant-herbivore species records, and observations of nymph herbivore load to determine their distribution patterns on plant taxa and how this changes with altitude.

1.3. Thesis structure

In addressing my goals I have organised my thesis as a series of chapters which will be revised as manuscripts for submission to journals (except this Chapter, Chapter 2, General Introduction to Auchenorrhyncha, Chapter 3, Theoretical Background and Literature review, Chapter 4, General Methods and Chapter 8, General Discussion).

Chapter 2 entitled ‘General introduction to Auchenorrhyncha’, gives an introduction to my study organisms. This provides an overview of their biology and life history, including mating systems and reproduction, feeding-guilds and their feeding strategies.

This is followed by a ‘Theoretical background and literature review’ chapter (Chapter 3) which reviews diversity patterns across gradients, including altitudinal gradients. It also explores major theories and hypotheses, such as environmental heterogeneity, niche partitioning and competition, primary productivity and biotic interactions, energy hypothesis, and species-area relationship. This review also covers other areas that are relevant to this thesis, including herbivory and host specialization, global climate change impacts, climate change in Australia and the impacts of climate change on insects.
Following this, is a ‘General Methods’ chapter (Chapter 4), which provides details about the study areas, sampling methods and species sorting, including the dissection and identification techniques used.

Chapter 5 is the draft of a manuscript entitled ‘Altitudinal distribution patterns of Auchenorrhyncha along transects in subtropical and tropical rainforests in Australia’. This manuscript presents new information on distribution patterns of leafhoppers and planthoppers at different altitudes in different rainforest systems in Australia.

Chapter 6 is the draft of the second manuscript entitled ‘Vertical stratification of herbivore and feeding-guild assemblages of Auchenorrhyncha along altitudinal gradients in subtropical and tropical forests in Australia’. This manuscript investigates vertical species and feeding-guild assemblages and composition and the effect of altitude on these patterns.

Chapter 7 is the draft chapter of the third manuscript entitled ‘Auchenorrhyncha nymphs, host plants and altitude in the understorey of an Australian subtropical rainforest’. This manuscript investigates the relationship of nymph abundance and host plants, and how this changes with altitude and/or season. It takes into account relative abundance of potential host plants in the forest and counts of nymphs on these plants.

Chapter 8 concludes the thesis, with a General Discussion and conclusions of the main issues explored in the previous chapters.

Relevant ‘Supplementary Material’ is provided following each chapter. References are provided at the end of the thesis rather than with each chapter.
Chapter 2

General introduction to Auchenorrhyncha

2.1. Biology and life history

2.1.1. General introduction

Auchenorrhyncha is one of the suborders of Hemiptera, the insect group that is the largest and by far the most successful of the hemimetabolous insects. The Auchenorrhyncha fauna of Australia comprises the cicadas, spittlebugs, plant hoppers and leafhoppers. This group is characterized by its complex tymbal acoustic system and aristoid antennal flagellum and range in length from 1 to 110mm. Auchenorrhyncha have very uniform wings which are either membranous or hardened at which both wings, including venation are well developed (Carver et al. 1991). The two infraorders of Auchenorrhyncha, namely Fulgoromorpha and Cicadomorpha, occur in all major zoogeographical regions, except the Antarctic (Holzinger et al. 2002), and are found in every major biome, from tropical rainforests to the arctic tundra (O’Brien & Wilson 1985). The majority of the species occur in the tropics and subsequently in the subtropics, practically in every ecosystem (Deitz et al. 2008; Ceotto & Bourgoin 2008; Virla et al. 2008). Except Cicadoidea, all species of Auchenorrhyncha either jump or hop, as flight capability is very costly and has negative consequences on their reproductive capacities. As a consequence, Auchenorrhyncha use the energy available mostly to enhance quality reproduction rather than on flight investment (Denno et al. 1989).

Cicadomorpha species are grouped into three super families that are well established on morphological criteria: Cicadoidea (cicadas); Cercopoidea (spittlebugs and
froghoppers); and Cicadelloidea (leafhoppers, sharpshooters, treehoppers) (Dietrich 2005). All cicadas have similar features and behavior, except Tettigarctidae in which the venation is complete on the forewing and the nodal line is clearly developed, and also their adults have the tendency to make themselves unseen during the day, often feeding under bark. A majority of the cercopids have very similar characteristics to cicadelloids or leafhoppers. They can be differentiated from their wing venation, and in their biology and the structures of their nymphs. Cicadelloidea is a very diverse superfamily comprising three families. The identification of the species of Cicadomorpha is difficult because of their tremendous diversity (Hamilton 1995; Whitcomb et al. 1994) and recent studies suggested that there are more than 90% of tropical species that are yet to be described (Hodkinson & Casson 1991). Fulgoromorpha on the other hand, comprise the single super family Fulgoroidea (planthoppers) (Carver et al. 1991; Denno & Roderick 1990), which consists of 21 different families (Ceotto & Bourgoin 2008). Planthopper families are among the largest and diverse of all insects, and yet are not well documented (Wilson & Wheeler 1992) except for members of the family Delphacidae (Asche 1990).

2.1.2. Mating Systems and Reproduction

Reproduction is the most significant platform of life history theory, however, traits such as dispersal and diapause are also important components of an insect life history as they synchronize reproduction with favorable resources (Denno & Dingle 1981; Denno et al. 1989; Knight et al. 1991). Like most Hemiptera, Auchenorrhyncha can reproduce sexually or asexually (den Bieman 1988a; Denno & Roderick 1990). Prior to sexual activities, initial courtships are achieved through establishing communication among
individuals of both sexes, either through airborne signals by cicadas, delphacids, cicadellids and membracids (Ossiannilsson 1949) or substrate vibrations by planthoppers (Booij 1982; Ichikawa 1976). There are several different behavioural functions that acoustic signals serve which includes male aggression, male recognition, location and attraction, and courtship and mate choice (Claridge 1985a, b; Ichikawa 1982). The exchanges of signals are general at first, but eventually narrowed down to a duet and are also species-specific (Booij 1982; Claridge 1985b). Sexual reproduction can be achieved by, side by side as in many Cicadelloidea and Fulgoroidea. In some fulgoroids, asexual reproduction specifically known as parthenogenetic reproduction, in the form of pseudogamy is practised, in which case during mating the male only takes part in the insemination process and does not contribute any genetic material to the offsprings (den Bieman 1988b). Sperm may remain for long periods within the female awaiting egg maturation (Carver et al. 1991).

Eggs and in-stars of Auchenorrhyncha are laid and protected in a number of ways and it differs among the different groups. Planthoppers are the most outstanding wax producers among insects, using the wax produced by the wax glands on the anal tubes of females to enhance reproduction and fecundity (Calvert & Wilson 1986; Holder & Wilson 1992; Yang & Yeh 1994). Secretion of wax is only found in adults of a few species of fulgoroids, however, it is very common in juvenile fulgoroids (Liang 2001; Lucchi & Mazzoni 2004). Some families oviposit their eggs and nymphs in dark habitats usually in soil adjacent to the base of a host plant, feeding on stem bases or roots underground (Ceotto & Bourgoin 2008; Sfroza et al. 1999). Emerged adults fly to the upper sections of their host plants, which may not be necessarily their natal host plant (Wilson & Tsai 1982). In some circumstances, both the nymphs and the adults feed on roots underground (Hoch & Horvath 1989). Leafhoppers oviposit their eggs in
the branches or near the leaf midrib (Demichelis & Bosco 1995; Virla & Paradell 2002) or in the mesophyll of leaves (Claridge & Wilson 1976; Gillham 1991), and protect their egg masses, nymphs and newly emerged adults by means of brochosomes, secretions produced in the Malpighian tubules (Hix 2001; Rakitov 2002, 2004; Velema et al. 2005). A recent study has shown that a species of leafhopper utilizes the formation of gall and uses it as a reproduction site (Rakitov & Appel 2012). Spittlebugs and froghoppers lay their eggs on foliage and on stems and twigs, and protect their eggs and nymphs under white frothy foam like spittle while undergoing development (Biedermann 2003; Dem et al. 2013). The production and functions of these different structures (i.e. wax, brochosomes, spittle foam) are still unclear at large, however, it is widely accepted by the majority of these studies as a protection to the eggs and nymphs from predators, parasites, pathogens, harmful radiation (Emeljanov 2009; Hix 2001; Rakitov 2002, 2004; Velema et al. 2005) and also as a protective mechanism to minimize desiccation of eggs and juveniles (Arzone 1986; Hix 2001). Nymphs of Auchenorrhyncha look like wingless adults and have a metamorphosis process that does not involve a pupa (Calvert & Wilson 1986; Carver et al. 1991; Holder & Wilson 1992). The nymphs undergo 5 instar moulting processes, before reaching maturity, in which the stages of the instars can be distinguished by different body characteristics, such as body dimensions, morphological traits and colouration patterns (Cargnus et al. 2012; Manurung et al. 2005; Virla & Paradell 2002). Most species, on average take about 4 to 6 weeks to complete their development cycle, from egg to adult (McPherson & Wilson 1995; Virla & Paradell 2002; Wheeler & Wilson 1987).
2.1.3. Feeding-guilds and their feeding strategies

Studies of feeding behavior in plant tissues of phytophagous Hemiptera have shown that there are three distinct feeding sites of piercing-sucking insects. They are xylem, phloem vascular tissue and non-vascular tissues including the mesophyll of leaves (Tonkyn & Whitcomb 1987), hence the feeding-guild names, xylem-, phloem-, and mesophyll-feeders. Auchenorrhyncha is one of the insect groups which have both the larvae and the adults that feed on plants (Demichelis & Bosco 1995; Virla et al. 2008) and feeding may take place after oviposition. All are free-living and phytophagous, mostly feeding on phloem and xylem tissue of angiosperms (Bentz & Townsend 2005; Hoddle et al. 2003; Novotny 1994; Rakitov & Appel 2012). All members of Fulgoroidea feed predominantly on phloem tissues (Carver et al. 1991; Denno & Roderick 1990) of woody or herbaceous plants. However, some planthopper families feed on mosses, fungi, horsetail or ferns (Carver et al. 1991; Wilson et al. 1994). On the contrary, all members of Cicadoidea and Cercopoidea feed primarily on the xylem (Biedermann 2003). In Cicadelloidea, majority of the families feed on phloem, except two subfamilies of Cicadellidae, in which members of the tribes Cicadellini and Proconnini (Cicadellinae), commonly referred to as sharpshooters have shown to be xylem-feeders (Novotny & Wilson 1997; Rakitov & Dietrich 2001; Virla et al. 2008) and the subfamily Typhlocybinae to be mesophyll-feeders (Demichelis & Bosco 1995; Gillham 1991; Hunter & Backus 1989).

Nutrient quantity and quality among these feeding sites vary significantly and are largely determined by the chemical make-up of the plant fluids. The xylem tissues transport soluble mineral nutrients in large quantities in a continuous flow from the roots to the aerial parts of plant. However, although these fluids contain a wider range
of organic and inorganic nutrients, they are an unbalanced source of amino acids for insects and, the quality is very poor and in very low concentrations, unlike those in phloem or mesophyll cells (Andersen et al. 1989). On the other hand, phloem tissue provides a very different food resource for insects, composing of a great variety of amino acids and their amides, in which the nutrient quality is slightly higher and in high concentrations than in xylem (Pate 1976; Tonkyn & Whitcomb 1987). In comparison to xylem and phloem fluid, mesophyll tissue has a higher advantage because of its location, providing yet a better food resource for piercing-sucking insects. Since the mesophyll layer is where photosynthesis takes place and is where the products of photosynthesis are stored, it contains very high quality nutrients in very high concentrations of sugar and amino acids (Tonkyn & Whitcomb 1987). However, regardless of the differences in tissue sap quality, each feeding guild of Hemipterans does face some practical difficulties during penetration of host and ingestion, although the degree of difficulty varies, from trying to cope with xylem pressure tension (Cheung & Marshall 1973; Novotny & Wilson 1997) to locating and attempting to minimize the risk of destroying the tiny phloem sieve tubes (Campbell et al. 1982) and maximizing an adequate intake of rich food (Pollard 1968; Tonkyn & Whitcomb 1987).

Auchenorrhyncha have very highly modified mouthparts, including several specialized features (Anderson et al. 2006; Dai et al. 2014; Zhao et al. 2010) to enhance effective feeding. All three feeding-guilds feed by either penetrating through plant stems and sucking out vascular fluids (Fritschi et al. 2007; Hamilton & Whitcomb 2010) or piercing between leaf cells and extracting the liquid contents (Dong & Huang 2013; Hamilton 1997). Auchenorrhyncha uses one of the two different feeding mechanisms. Firstly, lacerate- and-flush, in which stylets move continuously or at irregularly, producing watery saliva (digestive enzymes) in the absence of a sheath. Secondly,
salivary sheath, in which insects seal their stylet tips into a vascular cell through a sheath made of solidifying saliva (Backus *et al*. 2005; Joost *et al*. 2006; Leopold *et al*. 2003; Miles 1972; Nickel 2003; Wang *et al*. 2008). The former strategy is being used mostly by mesophyll-feeders and the latter being used by most taxa, mostly xylem- and phloem-feeders (Backus *et al*. 2005, 2012; Hunter & Backus 1989; Tonkyn & Whitcomb 1987). Although, all three feeding guilds of Auchenorrhyncha use piercing sucking stylets to ingest plant liquids, there are distinct behavioural strategies involved in the movement of stylets and type of plant tissues exploited (Backus 1988). Variation in these strategies is strongly correlated at least at the infraorders level and guild type.

2.2. Determinants of Auchenorrhyncha

Host plant diversity and quality, and natural enemies are known to play key-roles in determining insect herbivore communities (Janzen 1973; Perner *et al*. 2005; Price *et al*. 1980; Sedlacek *et al*. 1988), and as a consequence, understanding interactions between these have become key areas of study in ecology. Communities of herbivorous insects associated with plant communities have a higher number of species in the understorey (Novotny 1992; Novotny & Leps 1997), yet they are in low abundance (Janzen 1973; Wolda & Wong 1988). However, most insects do not occupy the complete range of their host plants, but rather establish their distribution relating to the quality of their host plants (Hodkinson *et al*. 2001). Host plant nutrition, especially nitrogen is a prominent factor in understanding insect-plant relationships, life history patterns and population dynamics of herbivorous insects. Other factors such as habitat structure and plant architecture (Lawton 1983; Nickel & Hildebrandt 2003; Strong *et al*. 1984) are often ignored, but appear to be also important factors determining population size and distribution of herbivorous insects.
Auchenorrhyncha is a comparatively well-known group of insect-herbivores, especially in Europe and the USA (Biedermann et al. 2005; Waloff 1980), where the ecology of some species or taxa are better-studied than many others. The effects of host plant quality (Awmack & Leather 2002; Denno & Roderick 1990; Prestidge & McNeil 1983), plant abundance (Novotny & Basset 1998; Novotny & Leps 1997), plant species composition (Bennett & O’Grady 2012; Novotny 1991), plant architecture (Brown et al. 1992; Lewinsohn et al. 2005; Reid & Hochuli 2007), successional age of the plant community (Hollier et al. 1994; Huusela- Veistola & Vasanainen 2000) and habitat structure (Györffy & Karsai 1991; Kruess & Tscharntke 2002; Novotny 1995) have all been demonstrated to show a major influence on Auchenorrhyncha dynamics. Natural enemies of Auchenorrhyncha such as parasites/parasitoids, fungal pathogens and predators have also been known to play an important role in influencing their dynamics (Tipping & Mizell 2004; Virla et al. 2008; Wang et al. 2008). The most investigated natural enemies of Auchenorrhyncha are insect parasitoids which can be grouped into two subgroups: egg parasitoids and nymph/adult parasitoids (Hesami et al. 2009; Virla & Paradell 2002; Waloff 1975). Auchenorrhyncha eggs are mainly parasitized by Hymenoptera, while the nymphs and adults by several different insect taxa, including Dryinidae (Hymenoptera), Elenchidae (Strepsiptera) and Pipinculidae (Diptera) (Guglielmino 2000; Stapley 1976; Waloff 1980). Parasitism rate is often highest where host density is high (Cronin & Strong 1993; Waloff 1975), and the greatest mortality of Auchenorrhyncha is due to the deaths of eggs (Solomon 1973). The eggs of Auchenorrhyncha are also predated upon by some families of Hemiptera and the nymphs and adults mostly by spiders. Other groups such as carabid beetles and ants are also important predators, but to a lesser extent (Denno & Roderick 1990; Perkins 1905).
Chapter 3

Theoretical background and literature review

3.1. Introduction

In this chapter, I give an overview of the theoretical background and literature relating to species richness patterns across different taxa, including insects, taking into account aspects including, diversity patterns across gradients, species richness across altitude, environment heterogeneity, niche partitioning and competition, productivity gradients and biotic interactions, the ‘energy’ hypothesis and species-area relationships. Given my focus on insect herbivores, I also provide an overview of host specialization, host breadth and the factors involved in determining host specificity in herbivorous insects. Finally, I discuss the possible effects of climate change on species diversity patterns across altitudes and latitudes, species range shifts and shifts in host plants.

3.2. Diversity patterns across gradients- major ecological theories to explain observed diversity patterns.

Identifying the factors that determine and shape diversity patterns is an important theme in ecology (Jentsch & Beierkuhnlein 2003) and is crucial in the context of climate change (Gaston 2000). In particular, natural gradients in climate have been used frequently to explain large-scale diversity patterns (Frouz et al. 2003; McLaughlin et al. 2002; Pounds et al. 1999). Other explanations include other biotic factors (notably species-species interactions), productivity gradients and geographical locations (Ghalabor et al. 2006).
This study investigates ecological phenomena, including altitudinal and latitudinal patterns of community structure and vertical stratification. Here I explore some of the key ecological concepts related to insect distributional patterns across environmental gradients.

3.2.1. Latitudinal gradients

The most striking observed ecological pattern in diversity along latitudinal gradients—that species richness is greatest in the tropics and rapidly decreases towards the poles—was made by Alexander von Humboldt, more than two centuries ago (von Humboldt 1807). It is now widely recognised that species richness of most taxa, mostly in terrestrial ecosystems, shows a negative linear patterns from the equator towards the poles (Bannister et al. 2012; Rahbek & Gaves 2001; Weiser et al. 2007). In contrast, the existence of such pattern in the marine environment has been surprisingly controversial, (Ellingsen 2002; Rex et al. 2005; Roy et al. 2000; Witman et al. 2004). Many theories have been proposed to explain this diversity pattern, using a wide range of explanatory factors, including temperature, humidity, poleward decrease in energy availability, and biome size and diversity (Brown & Lomolino 1998; Currie et al. 2004; Lambers et al. 2002). Other explanations such as evolutionary mechanisms, biotic interactions, niche space and productivity have also been considered (Gaston 1996; Mittelbach et al. 2007; Turner 2004) and appear to be influenced by scale of study and the trophic level of the subject organism (Hillebrand 2004). Studies of diversity along latitudinal gradients have focused also on energy availability and habitat heterogeneity (Jetz & Rahbek 2002; Riklefs 2004). However, despite the many theories put forward, the pattern still lacks a convincing mechanistic explanation (Hillebrand 2004; Rhode 1992; Willig et al. 2003). These theories are further explored later in this chapter.
3.2.2. Altitudinal gradients

Using altitudinal gradients rather than altitudinal gradients to study diversity patterns and community structure is often favoured because it exploits steep gradients in abiotic and biotic factors (Hodkinson 2005) that affect diversity patterns over short spatial scales. Accordingly, altitudinal gradients have been used to study the driving forces that support the patterns of diversity and community structure encompassing, as they do, gradients in environmental, ecological and geographical factors such as climate, area, primary productivity and geometric constraints (Gagne 1979; Nogués-Bravo et al. 2008; reviewed by Sanders & Rahbek 2012). Theories have demonstrated that at higher altitudes species diversity patterns are more affected by the demanding environmental conditions presented whereas, at lower altitudes, community assemblages are mostly shaped by biotic factors (Hoiss et al. 2012). Altitude restricted assemblages of species are well documented, but patterns differ among taxonomic groups (Fischer et al. 2011; Nogués-Bravo et al. 2008).

3.2.3. Vertical gradients

Patterns of vertical stratification of organisms from the ground surface upward or downward are dependent on study systems (reviewed by Basset et al. 2003a), such as vegetation (Basset et al. 2001; Tangah et al. 2004), lakes (Serra et al. 2007; Zadereev et al. 2012), soil and litter (Rodgers & Kitching 1998; Wilkie et al. 2010), as well as available habitat components (Walter et al. 1998; Wardhaugh et al. 2006), food resources, and abiotic parameters, such as temperature and light (Parker 1995; Smith et al. 1992). The vertical stratification of rainforests from the ground level to the upper
canopy, reflects differences in microclimate, habitats and available food resources at various forest strata (Schowalter & Ganio 1998; Schulze et al. 2001; Tanabe 2002). Species assemblage patterns have been documented for a wide range of taxa, both in temperate and tropical forest ecosystems (Heymann et al. 2002; Jayson & Mathew 2003; Pereira et al. 2010; Walther 2002). The majority of studies show that species richness along forest vertical stratification is at its highest at the canopy level (Basset et al. 2001; Davis et al. 2011; Stork & Grimbacher 2006), arguably others show a similarity in species richness pattern among levels (Coots et al. 2012; Pereira et al. 2010; Sutton et al. 1983).

This thesis

In this thesis, I have examined patterns of species richness in selected insect herbivores (the Auchenorrhyncha) across altitudinal gradients in subtropical and tropical rainforests. In the remainder of this review, I focus on those factors which may be important in analysing and interpreting the patterns I observed.

3.3. Richness patterns across altitude

Altitudinal studies of biotic diversity have received much attention over the last 50 years, principally because altitudinal gradients may show rapid species turnover over very short distances with associated high levels of endemicity (Fu et al. 2006; Kessler 2000). Such gradients and the observed species turnover are strongly implicated in generating high regional species diversity. Studies of species distributional patterns along altitudinal gradients show, in general, one of two principal patterns. Species richness may simply decrease with increasing altitude (Begon et al. 1990; Lawton et
The four main reasons suggested for the high elevation decline are:

“(1) reduced habitat area at high elevations,
(2) reduced resource diversity at high elevations,
(3) increasing harsh environments at high elevations, and
(4) reduced primary productivity at high elevations” (reviewed by McCoy 1990).

When a mid-altitudinal peak is evident, two distinct processes have been proposed by way of explanation, viz.

1) Species occurrence at their higher and lower limits reflects environmental contraints, with populations at the high altitudes affected mostly by climatic severity (coolness or wetness) and resource restrictions, and those at the low altitudes by climatic severity (hotness) and predation. This leads to a net accumulation of species in the mid-altitudes (Gagne 1979; Randall 1982a; Smiley & Rank 1986).

2) Recent studies have suggested, as an alternative that mid-altitude peaks are not the result of any overarching biological properties, but merely reflect geometric constraints imposed by the environment (Colwell et al. 2009; VanDerWal et al. 2008). Geometric constraints refers to particular geographical range of a species, within a bounded geographical domain (e.g. altitude, latitude). The increasing overlap of species ranges towards the centre of a shared geographical domain is due to geometric boundary constraints in relation to the distribution and of species; range size and midpoints (Colwell & Lees 2000; reviewed by Colwell et al. 2004). Indeed, these constraints may affect species distributions in general and not just those on altitudinal gradients (Colwell & Lees 2000). Imposing geometric constraints on the random placement of
species generates a humped-shaped pattern of species richness (termed the ‘mid-domain effect’, MDE), simply because most altitudinal ranges fall in the middle section of the geographical domain (Colwell & Lees 2000), with the potential of species to exist outside the observed limits curtailed by the non-existence of habitats at those additional locations. Range, domain size and the frequency distribution of range size strongly influence the predictions of the MDE (Colwell et al. 2004; VanDerWal et al. 2008).

Even though the MDE may be generated solely on the basis of available space and not based on biotic and abiotic factors (Colwell et al. 2004), the phenomenon, nevertheless, has been confirmed in studies that measured abiotic and/or biotic factors (Lees et al. 1999; Rahbek 2005; Willig & Lyons 1998). Other factors such as type of dataset (Kluge et al. 2006), sampling effort (Rahbek 1995) and scale effect may also underlie observed patterns of species richness (Hillebrand 2004; Rahbek 2005; Willig et al. 2003).

3.3.1. Environmental heterogeneity

Environmental heterogeneity is a fundamental structuring agent determining the species diversity of organisms (Chase & Leibold 2003; McClain & Barry 2010). Heterogeneous environments are predicted to contain more complex and higher diversity of species assemblages (Dufour et al. 2006; Ricklefs & Schluter 1993; Tews et al. 2004) because they contain a greater number of partitionable niches and structural complexity (MacArthur & MacArthur 1961; Nickel & Hildebrand 2003). Habitat heterogeneity can be higher in the tropics than the temperate regions (Ricklefs 1977) which, in turn may produce higher species richness and greater tolerance for coexistence of species in the tropics than in the temperate areas (Connell & Orias
Patterns in species richness have shown positive relationships between habitat heterogeneity and diversity, in taxa such as mammals (Williams et al. 2002), birds (Goetz et al. 2007), and plants (Ricklefs 1977) and, to a lesser extent, arthropods (Bowden & Buddle 2010; Haslett 1997).

Within tropical forest biomes, high altitude forests tend to be structurally simpler and less diverse (Aiba & Kitayama 1999), with shorter trees and less diverse vegetation composition (Aiba & Kitayama 1999; reviewed by Ashton 2003). The availability of potential niche space in low altitude forests is predicted to be greater than in the less complex higher altitude forests. The same principle may apply within the vertical structure of forests, from the understory to the canopy with the structure and diversity of habitat components in the canopy of tropical forests being more complex compared with less structured and diverse temperate forests (Basset 2001). These patterns in the vertical plane will, by analogy, intensify the contrast seen along altitudinal gradients.

### 3.3.2. Niche partitioning and competition

The concept of the niche is central to ecological theory yet classically has had different definitions where each definition takes into account different factors such as abiotic, food preferences, microclimates, habitat and the position of a species in the ecosystems and food webs (Elton 1927; Grinnell 1917; Hutchinson 1959). Essentially, classical ecological theory suggests that the coexistence of consumer species is fostered by use of different resources, leading to a greater resource use and more intense ‘species packing’ leading to higher species richness (Finke & Snyder 2008). Resource use by a species, however, is often confounded with other species-specific attributes (Fründ et al. 2013; Kusch et al. 2004; Reid et al. 2013). Variation in resource use can generally be
classified with reference to space, time and food resources which are attributes that
serve as key dimensions which define ecological niches in coexisting organisms

The `traditional' explanation for long-term species’ coexistence is that each specializes
on different resources or parts of a resource, leading to a minimization in competition
among interspecific organisms (Armstrong & McGehee 1980). The idea of interspecific
competition as an ecological mechanism has existed since at least Darwin (1859), but
more recent studies show that competition may be a relatively weak ecological force
because it has only been shown to be elevated in some taxa, such as birds (Jankowski et
al. 2012; MacArthur & Levins 1964) and plants (File et al. 2012; Milbau et al. 2007).
Community level mechanisms sometimes referred to as `diffuse’ competition in which
the well-being of an organism is affected by all the species sharing its niche space may
be a more important mechanism in seeking explanations for patterns at the community
level (Comins et al. 1992; Minot 1981). Indirect competition, in which coexisting
organisms use resources, happens when intra- or interspecific species exploit a
particular resource at different times or on different parts of the resource (Denno et al.
1995; Petersen & Sandström 2001).

3.3.3. Primary productivity and biotic interactions

The relationship between primary productivity and diversity has been of particular
interest to ecologists and is still strongly debatable (Mittelbach et al. 2001;
Rosenzweig 1992). Species richness patterns of plants and animals along primary
productivity gradients show one of several patterns:

(1) a hump-shaped relationship between productivity and diversity,
(2) a monotonic increase in diversity with productivity,
(3) a monotonic decrease in diversity with productivity, and

Variation in observed primary productivity-diversity patterns reflect both differences in study design and the different responses of organisms as well as geographical and ecological scale (Horner-Devine et al. 2003; reviewed by Scheiner & Willig 2005). Primary productivity-diversity relationships are well-studied in taxa, such as terrestrial plants and not in others such as microorganisms and any generalizations, therefore, may be biased towards the better studied taxa (Horner-Devine et al. 2003; Mittelbach et al. 2001).

Two of the patterns of altitudinal distribution of the primary productivity-diversity relationship, the negative monotonic (pattern 3) (Bhattarai & Vetaas 2003; Pausas 1994; Stevens 1992) and the humped-shaped (pattern 1) (Dunn et al. 2006; Watkins et al. 2006) are observed for plants. Floristic species richness and diversity may be determined by one or more environmental gradients. These include temperature, nutrients, water and light (Erelli et al. 1998; see references in Pausas & Austin 2001). For instance, at high altitudes, low temperatures rather than photosynthesis tend to restrict growth (Pollack 1990; Pollack et al. 1984), suggesting that plants accumulate carbohydrates for their growth and maintenance requirements, leading to the production of carbon-based secondary metabolites (Ayres 1993; Hems and Mattson 1992). If this is the case, then plants growing at low temperature may be less palatable to herbivores than the foliage from plants growing at higher temperatures (Erelli et al. 1998). Where insects’ food plants occur over a wide altitudinal range, then environmental differences over that range will produce variation in their suitability to
support insect growth and development (Hodkinson 2005). In particular, exposure to less favourable abiotic factors, shorter growing season and poorer soils will affect the phenology, size, morphology, physiology and chemistry of the plants with consequences for the dependent insect population (Kronfuss and Havranek 1999). Consequently, plant species growing in less favourable environmental conditions may be less attractive to insect herbivores in general (reviewed by Price 1991). Some, of course, will be specifically adapted to these ‘unfavourable’ conditions, but these will likely be few in numbers. The distribution and variety of herbivorous insects are primarily determined by the availability of their host plants in suitable conditions to support growth and development (Strong et al. 1984). Dillon and his colleagues (2006) suggested that many features of insect altitudinal distributions may come from correlated variation in floristic composition and associated nutritional resources. The higher the diversity of plant species, the higher the number of insect species (Lewinsohn et al. 2005; Novotny et al. 2006). On the other hand, it is widely argued that stressed plants under a wide range of unrelated environmental factors are able to provide quality food to their insect herbivore communities, because stress in plants can cause an increase in soluble nitrogen in the tissues of plants (Brodbeck et al. 1987; Larsson 1989; White 1984).

Species interactions also play an important role in determining diversity and population size, particularly of herbivores (Novotny & Leps 1997). Variation in biotic factors may affect the outcomes of trophic interactions by altering effects on insect herbivores (Hunter & Price 1992). Information on the interactions among host plants and herbivorous insect, their parasites and/or predators are often required for a complete understanding of the population dynamics of species along elevational gradients. Such studies are scarce, but often provide simple explanations for changes in insect
abundance of the studied species over its altitudinal range (Hodkinson 2005; Maunsell et al. 2015). Like diversity patterns displayed by the majority of taxa, parasitism declines with an increase in altitude (Randall 1982a; b), and other studies reported similar patterns of parasitism along elevational gradients (refer to Table 3, Hodkinson 2005). Similarly, the availability of a prey type for a free-living predator may have a significant effect on the presence or absence of organisms in a particular locality (see references in Guevara & Aviles 2007). Studies on predation rates show monotonic patterns with increasing elevation (Gilbert & Gregoire 2003; Wiggins et al. 2001). However, reliable data on changes in predation rate with altitude, however, are even fewer than for rates of parasitism (Hodkinson 2005).

3.3.4. Evolution and biogeographic history

The factors that regulate species diversity patterns involve a complex mixture of ecological, evolutionary and biogeographical processes (Ackerly et al. 2006; Ricklefs 2007). It is widely accepted that several factors, such as the differences in geography (Darwin 1858; Wallace 1878), climate regimes (Dobzhansky 1950; Francis & Currie 2003) and historical (Currie et al. 1999; Fischer 1960) processes have all affected the patterns of species diversity observed at different latitudes. These explanations have been summarized into two main hypotheses; (1) time and area hypothesis, and (2) diversification rate hypothesis.

The time and area hypothesis explains that the tropics accumulate species over a longer period than temperate regions, allowing more opportunity for diversification. In addition, tropical environments are older than temperate climates and hence, allow for longer effective time for speciation (Stephen & Wiens 2003). Further, the greater
expansion of tropical biomes, especially during the early Cenozoic, could enhance higher speciation rates due to area effects on diversification rates and extinction (Chown & Gaston 2000; Fine & Ree 2006; Rosenzweig 1995). Recent discussions of the time and area hypothesis have focused on the distribution of tropical environments during early portions of the Cenozoic, throughout the different time periods, especially the mid Palaeocene to early Eocene, with the poles becoming warmer and a reduction in temperature from the equator to the poles (Sluijs et al. 2006). These changes in climate due to glacial activities have disproportionally affected species and lineages at high latitudes (Lavergne & Molofsky 2006; Xu et al. 2009; Zachos et al. 2001). Recently, phylogenetic information have been used to provide additional supporting evidence for the time hypothesis, by showing relationships between the tropics and temperate taxa (Cadotte et al. 2008; Leibold et al. 2004). Many diverse lineages have their ancestors from the tropics, and temperate taxa clades often branches off the tropical ancestors, implying their origin from tropical groups with older evolutionary roots (Farrell & Mitter 1993; Jablonksi et al. 2006; Judd et al. 1994; Ricklefs 2005; Wiens et al. 2006). The idea that many clades have originated in the tropics, but relatively few have speciated and transited to temperate climates (Farrell et al. 1992; Hawkins et al. 2006; Wiens & Donoghue 2004), is because of the range limit in many taxa corresponding to climatic isoclines, suggesting that certain traits such as freezing tolerance present significant barriers to extending their ranges into the temperate regions (Fine 2001; Wiens et al. 2006).

‘The diversification rate hypothesis holds that tropical regions diversify faster due to higher rates of speciation (caused by increased opportunities for the evolution of reproductive isolation, or faster molecular evolution, or the increased importance of
biotic interactions), or due to lower extinction rates’ (Mittelbach et al. 2007). The diversification rate is based on time over evolutionary period, hence the evolutionary speed theory considers historical factors and suggest that higher speciation rates and consequently species richness occurring in the tropics is being driven by high energy availability and undisturbed environments throughout evolutionary time (Fischer 1960; Wright et al. 2003). This theory suggests that species diversity in the temperate regions is affected by climate while in the tropics by biotic interactions (Darwin 1859; Dobzhansky 1950; Wallace 1878). Many hypotheses have been proposed to explain why rates of diversification might differ between temperate and tropical regions (Allen et al. 2002; Brown & Lomolino 1998; Dynesius & Jansson 2000; Fedorov 1966; Gentry 1969; Janzen 1967; Ricklefs & Schluter 1993; Schemske 2002; Terborg 1973), whereas fewer hypotheses focus on rates of extinction (Fischer 1960; Rosenzweig 1995). There is accumulating evidence for higher diversification rates in the tropics compared to the temperate regions in many taxa, partly due to greater tropical speciation. This evidence is based on both palaeontological (Flessa & Jablonski 1996; Stelhi & Wells 1971) and phylogenetic studies (Baraclough et al. 1998; Genung et al. 2014), and observe for marine and terrestrial groups (Buzas et al. 2002; Jablonski et al. 2006; Jacksons & Williams 2004; Roy & Pandolfi 2005), plants and animals (Cardillo 1999; Davis et al. 2004), vertebrates and invertebrates (Cardillo 1999; Coyne & Orr 1997)

3.3.5. Energy hypothesis

The energy hypothesis is a climatically based idea that claims that energy availability generates and maintains high species richness. It has been a current point of debate since from the beginnings of biogeography (von Humboldt 1807) and has gained support from a large number of studies which have quantified the relationship between
species richness and climate variables (reviewed by Wright et al. 1993). Two driving mechanisms have been proposed.

One version of the hypothesis proposes that energy constraints richness through successive upward trophic interactions (Brown & Maurer 1987; Hutchinson 1959). This recognises that plants directly or indirectly, form the base of all terrestrial food webs and plant richness is limited primarily by solar energy and water availability (Currie 1991). In turn this limits herbivore richness and subsequently, predators and so forth up the food chain. This means that species richness is limited by energy flowing through food webs rather than the total energy entering a geographical area (Huston 1994; Mittelbach et al. 2001).

The second version of the hypothesis is that ‘ambient energy’ inputs are important rather than food availability (von Humboldt 1807). Explanations including climatic stability, environmental stability, seasonality and harshness are incorporated under ‘ambient energy’. The concept is that organisms inhabiting environments at high latitudes (and by extension higher altitudes) are faced with far more harsh conditions than their low-latitude counterparts (reviewed by Willig et al. 2003). This is because ambient energy decreases from the equator towards the poles and varies with seasons, thus as a result species richness decreases with increasing latitude reflecting seasonal decline in ambient energy with increasing distance from the equator (Currie 1991; Hawkins et al. 2003; Turner et al. 1987).

### 3.3.6. Species-area relationship

One of the earliest explanations proposed to explain patterns of species richness was the species-area relationship (Arrhenius 1921; Gleason 1922; Öckinger et al. 2010) and it
remains, empirically at least, one of the most robust. Recently, ecologists have shown an increasing interest in the issue of spatial scale and biodiversity (Fridley et al. 2006; Krishnamani et al. 2004; Triantis et al. 2008). Many hypotheses have been proposed to explain the shape of the species-area curve (Connor & McCoy 2001; Rosenzweig 1995; Tjørvel & Tjørvel 2008). Fundamentally increasing species richness is correlated with increasing area at an ever-diminishing rate that eventually reaches an asymptote for large areas (Barnosky et al. 2005). Based on the species-area relationship, species richness is higher in the tropics than in temperate and polar regions because tropical regions comprise larger areas (Rosenzweig 1995; Terborgh 1973). This pattern is well established and shown in different types of ecosystems for a variety of taxa (Lomolino 2001b). The subsequent development of the theory of island biogeography rests heavily on this observed empirical pattern (MacArthur & Wilson 1967).

Empirical studies along altitudinal gradients often use this relationship to explain species richness patterns, based on the assumption that rapidly decreasing area with altitude will have large effect on the number of species at particular altitudes (Davies & Smith 1997; Novotny & Leps 1997; Rahbek 1997). Lower altitudes on a mountain tend to have a larger area than higher locations (Körner 2000), consequently capturing greater resources, population size and habitat heterogeneity (Kadmon & Allouche 2007; Shen et al. 2009). In some regions, however, the mid-altitudes may have larger area particularly if there are broad valleys forming a compromise between steep valleys at low altitudes and steeper terrain at higher altitudes (Grytnes & McCain 2007). Further, the lowland below 500m includes much larger area than any other altitude globally across most geographic regions. Because of the differences in species patterns along altitudinal gradients, it is important to evaluate this pattern on a regional scale (Grytnes
& McCain 2007; Rahbek 2005), since areas of altitudinal belts may differ with latitude. The species-area relationship may seem a simple tool for explaining diversity patterns, but it does not take into account other factors that shift along the same areal gradient (Hodkinson 2005) including abiotic factors, competition and habitat heterogeneity (McCain & Grytnes 2010).

3.4. Herbivory and host specialization

The ranges of host plant of herbivorous insects is a key determinant of the occurrence of particular herbivore species forming the fundamental resource base for the insect species concerned. The type availability of host plants, in turn will influence their population dynamics and interactions with other herbivorous species, predators and parasites. The range of current host plants also provide a record of past evolutionary interactions between the herbivore and plant lineages (Novotny et al. 2002b). The species involved in plant/insect interactions, comprise more than 40% of all global terrestrial biodiversity (Price 2002), most of it concentrated in tropical forests. Herbivores are often classified as mono-, olio- or polyphagous in their feeding habits, or, simply as generalists and specialists (Novotny & Basset 2005). Since there is no universal definition of these oft-used terms, it is useful to use the better defined concepts of species-, genus- and family-specialist (Barone 1998). A herbivore species is considered to be specialist at one or other of these levels if it is feeding on a single plant species, more than one plant species within a genus or within a single plant family.

Many members of Auchenorrhyncha, the subject of this study, (leafhoppers, planthoppers and their relatives) either feed on a single plant species or several plant species within a genus (Claridge & Wilson 1976; Stewart 1988).
The fact remains, however, that measuring host specificity is complex and limitations include sampling limited numbers of host plant species and lineages. Other problems include too short sampling periods yielding samples too small for quantitative analyses, or insects are sampled destructively which makes it impossible to carry out successful feeding/rearing experiments and the associated study of immature stages (Dem et al. 2013; Novotny et al. 2002a). Even in large sample sizes, many insect species and taxa are recorded as specialists (Novotny et al. 2002b; Novotny et al. 2005a). Host specialization differs between particular insect herbivores, different taxonomic groups and the host plant studied (Basset 1992). Consequently, host specificity is often underestimated, largely due to the effect of sample size, i.e. rare specialized species are missed and/or some of the host plants are not sampled for generalists which then falsely appear more specialized than they actually are. It is very important, therefore, to consider the phylogenetic relationships of host plants (Novotny & Basset 2005) to get a clear understanding of how an insect herbivore selects its host plant. Phylogenetic constraints on host plant selection may be investigated as a relationship of species turnover among plant-species specific herbivore assemblages and the phylogenetic distances among host plants involved (Novotny et al. 2002a).

Host specialization in herbivores is determined by how each herbivore species or feeding-guild chooses its host plant. Although plants provide insects with ready-made food, they have developed controlling factors such as nutrient quality and defensive mechanisms that defend them from overexploitation by insect (and other) herbivores (Speight et al. 1999). Host plant selection includes synchronization of host plant quality and availability (Novotny & Basset 1998; Reich 1995) as well as coping with and adaptation to unfavourable environmental conditions (Biedermann 2003; Hix 2001). In
addition, some plant species have evolved use of the `time and space’ concept in which they rely on their rarity (in terms of plant species abundance) and not synchronization (time factor) with the herbivore species’ reproduction and development periods (Fowler & Lawton 1982; Hamilton 1964; Lowman 1985). The connection between plant phenology and the life-histories of herbivorous insects is also important (Aide 1992; Borchert 1994; Hunter et al. 1997). Host plant selection by herbivores is affected by plant defense mechanisms, such as physical (Eigenbrode 2004; Howe & Schaller 2008; Znidarcic et al. 2008), chemical (Bidart-Bouzat & Imeh-Nathaniel 2008; Després et al. 2007; Schuler 2011) and biological (Degenhardt et al. 2009; Rudgers 2004; Wynne-Edwards 2001) defenses.

3.5. Climate change and biodiversity

3.5.1. Impacts of climate change

Climate change, specifically global warming, has resulted in a wide range of environmental changes over the last 100 years. Global average temperature has risen by approximately 0.85°C during the past century and is continuing to increase (IPPC 2014a). Atmospheric CO₂ concentrations have increased by 2.0 ± 0.1 ppm yr⁻¹ over the last decade. Precipitation has generally increased in temperate regions, but downward trends dominate the tropics over the last five decades. Global average precipitation change is -1.54 ± 4.50 over that last 50 years (Becker et al. 2013). Mean sea level rose by 0.19 m over the last century at a rate that has been larger than the mean rate during the previous two millennia. Over the 21st century, global temperature rise is predicted to exceed 1.5°C, with uncertainty in the emissions of CO₂ as it depends on each region and industrial activities. Extreme precipitation is expected to increase with warming, with a median increase of 7% °C⁻¹. Australia’s continental average temperature has elevated by
0.16°C per decade since the last 6 decades, and by 2070, mean temperatures will have increased by 1.0 - 5.0 °C (IPCC 2014b). Total annual rainfall has increased by approximately 15 % in two-thirds of Australian states (Hughes 2003). For the remaining of this century, projected amount of rainfall will vary between states and localities, with precipitation increasing in some areas and decreasing in others (IPCC 2014b).

A wide range of taxa, including birds, mammals, insects, plants and fish in both marine and terrestrial ecosystems have been shown to have changed in their ranges, abundances and phenology as a result of global warming (Hughes 2000; Møller 1994; Perry et al. 2005; Rasmann et al. 2014; Telwala et al. 2013). Range shifts have been reported across many taxa including plants (Michalet et al. 2014), birds (La Sorte et al. 2009), mammals (Hickling et al. 2006) and insects (Bale et al. 2002). Evidently, butterflies, birds and insect herbivores are good examples of groups that have shown to have shifted their ranges upwards towards the poles (Bale et al. 2002; Franco et al. 2006; Thomas & Lennon 1999). Species shift their ranges when their climatic boundaries are no longer suitable for their survival as a result of changes in their environment (Moore & Huntington 2008; Walther et al. 2002).

The phenology of species may respond to changes in climate as much as the timing of their development stages are driven by environmental factors. Such as in phenology may in turn affect mutualistic relationships, interspecific synchronization events such as prey-predator interactions and plant-herbivore systems, with adverse consequences to ecosystems and ecosystem functioning (Bartomeus et al. 2013; Ovaskainen et al. 2103; Visser & Booth 2005). Impacts upon plant life are predicted to include changes in quality (Bidart-Bouzat et al. 2005; Caldwell et al. 2007), phenology and
synchronization (Bale et al. 2002; Root et al. 2003) as well as growth rate, reproduction, respiration and photosynthesis (Garbutt & Bazzaz 1984; Leakey et al. 2009a; Soon et al. 1999).

Alterations in weather patterns caused by climate change are predicted to occur over the next 100 years (IPCC 2014a; Williams et al. 2007). Weather variability and extreme weather events, such as heatwaves, extreme precipitation and coastal flooding (Coumou & Rahmstorf 2012; IPCC 2014a) are predicted to change species distribution, species richness, species composition as well as ecosystem structure and function (Grimm et al. 2013; Pounds et al. 1999; Thuiller et al. 2008). These changes will have an adverse effect on the majority of the species, especially those with narrow climatic and geographical range, and low tolerances to climatic changes (Janzen 1967; Thomas et al. 2004). Species may either continue to exist in their current range or respond to changing environmental conditions with range expansion, contractions or shifts (reviewed by Thomas 2010). Comparatively speaking, climatic changes are predicted to be less drastic in tropical than temperate regions (Deutsch et al. 2008). Tropical species, however, may be more challenged than their temperate counterparts, as they may have a low ability for adaptation to warming both in terms of maximum heat tolerance and/or annual temperature variability (Bonebrake & Mastrandrea 2010; Ghalabor et al. 2006; Janzen 1967), which may lead to a higher vulnerability to extinction rate especially in the lowland tropics (Calosi et al. 2008; Hughes 2003).

Mountain regions and their diversity are potentially especially vulnerable to climate change where shifting upwards (or polewards) may be physically impossible (Thuiller et al. 2005). On the other hand, mountain regions may be a good sink as they may provide climatic refuge for displaced lowland species (reviewed by Pauli et al. 1996;
Peñuelas & Boada 2003; Xu et al. 2009). An increase in the frequency of extreme temperatures exceeding species’ thresholds, may cause species to extend their ranges upward or towards higher latitudes, or where this is not possible, may result in extinction either locally, continentally or at a regional scale (Thomas et al. 2004). Predictions of changes in extreme weather patterns and events, such as heatwaves and flooding resulting from anthropogenic activities, pose potential threats to ecosystems and diversity (Palmer & Räisänen 2002).

3.5.2. Climate change in an Australian context

Australia’s continental average temperature has elevated by ±0.94°C since the beginning of the 19th century (Fawcett et al. 2012; IPCC 2014b), with the greatest warming over subtropical inland regions. Since 1950, temperature over oceans have also increased by 0.11-0.12°C per decade for northwest and northeast Australia and up to 0.2°C per decade in the region of the East Australian Current (IPCC 2014b; Lough & Hobday 2011). Further warming this century over Australia is predicted to be greatest over inland and least in coastal areas, and in the south and northeast areas (CSIRO & BoM 2007; Prowse & Brook 2011). Projected mean temperature rise increases across Australia by 2030 ranges from 0.5-1.5°C (IPCC 2014b). The long-term trend in average temperature in the whole of Australia is very clear where warming occurred in all seasons, with the strongest warming in spring and the weakest in summer; night temperatures increased more rapidly than day time temperature (CSIRO & BoM 2007).

Rainfall in Australia, in general, has decreased over most regions since mid-1990 (Hope et al. 2010), with variations among regions and seasons (Bates et al. 2008;
Potter et al. 2010). However, rainfall in northwest Australia has increased over the last 50 years (Jones et al. 2009). Annual rainfall is predicted to further decline in southern Australia, with the greatest drop during winter (Moise & Hudson 2008). On the other hand, the direction of future change in rainfall in other regions remains unclear (Watterson 2012). By 2030, projected rainfall changes are -15% to +10% in the northern areas and -10% in southern areas (CSIRO & BoM 2007).

Australia is the world’s second most arid continent, and because of this more than 80 percent of its annual rainfall is lost through evaporation or transpiration, resulting in less ‘effective’ precipitation (Hughes 2011), which makes it impossible for the soils to hold any water for long periods. Model projections have indicated that droughts will present an even greater challenge in the future than they do now (Nicholls 2005; Pittock & Wratt 2001). As air temperature increases, the frequency of extreme hot weather events is expected to increase unevenly (Stott et al. 2004). There would be more frequent extremes of heat and high rainfall in the far north and extremes of heat and low rainfall in the south (IPCC 2014b). Impacts of climate change in Australia are already apparent, such as shortening of the snow period and its depth (Nicholls 2005), sea level rise (CSIRO & BoM 2007), coral bleaching (Berkelmans et al. 2004; Hughes 2011) and increased salinity and acidification in the oceans around Australia (Braganza & Church 2011). The Australian fauna and flora are predicted to face climatic change challenges such as range shifts, population reduction and contraction, and extinction (Pittock & Wratt 2001; Williams et al. 2003).

3.5.3. Climate change and insects

Insects are the most diverse group of non-marine animals, with different species inhabiting a range of terrestrial and aquatic habitats in every major biome. They are
among the group of organisms likely to be substantially affected by climate change because climate and temperature in particular, has a strong direct influence on their development, reproduction and survival (Bale et al. 2002). In addition, insects have short life cycles and high reproductive rates and, enhanced by their dispersal ability, they are more likely to respond quicker to climate change through range shifts in contrast to long-lived organisms such as plants and vertebrates (Menéndez 2007). Such shifts in species range may lead to changes in the relationships of the insects, their host plants and parasitoids (Harrington et al. 1999; Singer & Parmesan 1993). Insects therefore are likely to present taxa which may be suitable indicators in the study of climate change.

The direct effects of temperature on insects will vary among species, depending on their existing environments and life-histories, habitats, behavior and ability to adapt. Polyphagous species are less likely to be affected by climate change than those species with narrow trophic niches (Bale et al. 2002). Other factors likely to change in response to climate change include physiology (Dahlhoff et al. 2008; Karban & Strauss 2004), and synchronization (Bale et al. 2002; Root & Hughes 2005) which are also important in accounting for species dynamics.

Herbivorous insects have a profound relationship with their host plants. For many years, biologists have been fascinated by the effects of host plant quality, predation/parasitism and abiotic factors on insect herbivore populations (Dethier & MacArthur 1964; White 1984). More recently, ecologists have become interested in how such interactions may be affected by the transitions that have already taken place, either directly or indirectly, in natural ecosystems as a result of an anthropogenically changing climate. Changes in quality (Bidart-Bouzat et al. 2005; Caldwell et al. 2007), phenology and
synchronization (Bale et al. 2002; Root et al. 2003) of host plants will have an adverse effect on its insect herbivores by modification of the population dynamics of both host and herbivore. The on-going emissions of greenhouse gases such as CO$_2$ into the atmosphere will have an adverse effect on host plant quality. Increased CO$_2$ may have positive consequences such as increasing photosynthetic rates (Leakey et al. 2009b), plant growth rates (Soon et al. 1999), plant population growth (Garbutt & Bazzaz 1984) and the nitrogen: carbon ratio (Hughes & Bazzaz 2001). An elevation in CO$_2$, however, may also have negative impacts such as a reduction in nitrogen concentration in plant tissues, which will then reduce plant-nutrient quality (Ayres 1993; Cotrufo et al. 1998; Taub et al. 2008). An increase in CO$_2$ may also enhance plant chemical defenses by increasing concentration of anti-feedant chemicals (Bidart-Bouzat et al. 2005; Heyworth et al. 1998). Ayres (1993), for instance, reported that insects feeding on plants grown under enhanced CO$_2$ conditions experienced low survival, a reduction on growth rate and extended development time. Such responses, may in turn, lead to changes in host-plant use either spatially or temporally.
Chapter 4

General Methods

4.1. Study location: Border Ranges (BR) and Mt Lewis (ML) National Parks

Altitudinal distributional patterns of Auchenorrhyncha as well as their association with their host plants are investigated and quantified within montane subtropical and tropical rainforests of eastern Queensland. Field work sites have been established at two locations; one at Border Ranges National Park (longitude 28°21'35"S, latitude 152°59'10"E) in northern New South Wales and Mt Lewis National Park (longitude 16°30'35"S, latitude 145°13'22"E) in north Queensland, but primary field work was executed at Border Ranges National Park. The decision to base primary fieldwork at Border Ranges was made on the basis of the stretch of the rainforest as well as the accessibility to large altitudinal belts provided by the Tweed Range Road. Given that the sites would need to be visited regularly over the course of the field work, this was also considered important.

Border Ranges National Park

Border Ranges National Park lies to the south of the New South Wales-Queensland border and has a land area of 15929 hectares (McDonald 2010). This national park is part of the Gondwana rainforests of Australia which contains a series of groupings of 8 national parks and reserves distributed between Newcastle and Brisbane and contains the largest area of subtropical rainforest in the world. These rainforests are further classified into four principal types, including subtropical dry, warm temperate, cool temperate (McDonald & Hunter 2010) and the Antarctic rainforests (Floyd 1990). The Gondwana rainforests provide habitat for a range of rare and threatened plant and
animal species, making them internationally significant with respect to conservation (Adam 1987). They are of evolutionary significance as they contain the most ancient types of vegetation, including ferns and conifers, and provide an interesting living link with the evolution of Australia (Hunter 2003). The Antarctic rainforest flora is only present in northern New South Wales, making this region of international significance and should be of conservation priority (Floyd 1990).

Border Ranges National Park is part of the Shield Volcano Group of the World Heritage Site Gondwana Rainforests of Australia. Its area encompasses humid subtropical to warm temperate transitional zone and the environment (climatic conditions, aspects, plant composition and distribution) is largely controlled by topography and soil type (Graham et al. 1976). The Border Ranges region which includes the McPherson Range, Tweed Range, Lamington Plateau and Levers Plateau, were formed from the erosion of the Tweed volcano over many years (Adam 1987). Border Ranges National Park along with several other adjacent parks (the Border Group) are recognized as a biodiversity hotspot (DECCW NSW 2010). Rainforests stand on different soil types broken down from basaltic and rhyolite (McDonald 2010; Monroe & Stevens 1976). Areas of rainforest types at Border Ranges NP are 13,295 ha (subtropical), 725 ha (warm temperate), 5 ha (cool temperate) and 6,835 ha (dry temperate) (Floyd 1989).

Descriptions of the major forest systems include complex notophyll vine and low microphyll vine forest at the lowland forests, and at the slopes and uplands, there is a huge variation in the sclerophyll vegetation from tall wet sclerophyll forest to mountain heath (Graham et al. 1976). Within the region of the Tweed Caldera Group, the average monthly summer temperatures ranges between 24.1°C maximum and 19.7°C minimum on the coast and 21.5°C and 17.7°C in the ranges. In winter, averages are 21.0°C and
14.4°C on the coast and 17.8°C and 12.3°C in the ranges (McDonald 2010). The annual rainfall from the March to October is 65-70% and high intensity rainfall is predominant (McDonald 2010).

Five altitudinal locations (300m 500m, 700m, 900m, 1100m a.s.l) were established, each with four 20m x 20m replicated sites (Figure 4.1), with plots within each band 400m apart in distance. Where possible, location of all plots were targeted to be no more than 100m from water channels, to avoid compounding factors associated with microhabitat of aquatic ecosystems and with aspects related to south-westerly direction.

![Figure 4.1. Map of Border Ranges NP showing the five altitudinal bands (300m, 500m, 700m, 900m, 1100m a.s.l) and the four replicated plots within each band.](image)

Vegetation surveys were conducted at each of the 20m x 20m plots. 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*, *Argyroderon trifoliatum* and *Eupomatia laurina*. The plots at 700m a.s.l were dominated by *Sloanea australis*, *Atractocarpus benthamianus* and *Argyroderon 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*.

*Ibutton* temperature data loggers were placed at arm’s reach on all plots, set to record hourly mean temperature from July 2010 to January 2011, with 236 days of missing recordings as a result of technical faults with the temperature data loggers. Frequency distribution of average temperatures at each altitude displays a negative correlation between temperature and altitude (Figure 4.2). The overall drop-off in temperature with increasing altitude is 0.9°C for every 200m. Average temperature at each altitude ranges from 12-15°C, but comparatively 700m and 900m were cooler than other bands.

![Figure 4.2. Frequency distribution of average temperature for each altitude, recorded using Ibutton temperature data loggers.](image-url)
Ibutton temperature loggers at all plots at each of the five altitudes (300m, 500m, 700m, 900m, 1100m a.s.l.) between the period 10th July 2010 and 6th January 2011 (Ashton 2013, PhD dissertation, Griffith University).

Mt Lewis National Park

Mt Lewis National Park has a total area of 229km² and lies 60km north-west of Cairns, North Queensland and is within the Wet Tropics World Heritage Area (WTWHA). WTWHA was officially declared in 1988 and stretches for about 450km between Cooktown and Townsville. Mt Lewis NP is formed from geological activities (sedimentation) in the Wet Tropics about 42 million years ago. These sediments piled up, compressed, folded and lifted, creating a series of mountain ranges. Much of the landscape today in the Wet Tropics was from metamorphic rocks formed by immense pressure and heat. For over 10 million years, long stable period caused mountains to continue to rise, but were also influenced by the prolonged processes of erosion. Eventually the granite was exposed and the covering of rocks was weathered. Basalt creates the most fertile soil while granites and metamorphic rocks are more acidic and their soils are less fertile. The soils from most of the area are formed from granite (http://www.derm.qld.gov.au/parks/mount-lewis/culture.html; Wiltshire 1986).

Comprising nearly 900 000 ha, the world heritage is predominant wet tropical rainforests. Although, rainforest represents the major vegetation type, other types such as open eucalypt forests, wetlands (Melaleuca spp.) and mangrove forests are also considered biologically significant. Structural diversity of the rainforests of the Wet Tropics is extremely high and is related to factors such as rainfall, soil type, soil drainage, altitude, aspects and evolutionary history (Wiltshire 1986). Rainforests differ accordingly, where complex multistorey vine forests reflect rich soils and warmer
wetter climate, and poorer soils in the drier areas presents a simple vine forests while the higher wetter altitudes are dominated by ferns (Tracey & Webb 1975; Wiltshire 1986). Rainforest structure is significantly affected by altitude, showing variation in floristic composition between low and high altitudes. In contrast, this region has the only extant stands of complex mesophyll vine forest. The Wet Tropics is also dominated by the endemic Fan Palm, *Licuala ramsayi* which are found in small islands on poorly lowland soils (Wiltshire 1986). Floristic diversity in the area is extremely high with the likelihood that it has about 75 percent of rainforest plant families in Australia. It also has a high species richness of endemic species (Johnson & Briggs 1975; Stork et al. 2008). Important individual species include *Austrobaileya scandens*, *Idiospermum australiense*, *Galbalimima baccata* and *E. Bennetti* (Wiltshire 1986).

Climate and weather at Mt Lewis are very pleasant and satisfactory, that is the climate and weather presents suitable environments for organisms. At lower altitudes, maximum summer temperatures are around 30 °C while winter temperatures can fall below 10 °C. The highest amount of rainfall is experienced in the wet season, between December and April (http://www.derm.qld.gov.au/parks/mount-lewis/about.html).

Mt Lewis NP study design is very similar to the Border Ranges NP. A pre-existing altitudinal transect, established by colleagues from James Cook University (JCU) has been modified and used in the current study. The transect ranges from 400m to 1200m a.s.l. at an interval of 200m. All altitudinal sites are located along Mt Lewis Road, while the 400m band is further down the range. At each of the altitude, four 20m x 20m plots, separated by at least 400m were established (Figure 4.3).
Rainfall and temperature data were collected by researchers at JCU. Temperature data was collected at one plot per altitude (plot a), during the period from January 1, 2006 to January 1, 2008. Average annual temperatures range between 21°C at 400m a.s.l. to 16°C at 1200m a.s.l., an average decline of 1°C per 200m. Daily rainfall data was taken from the Bureau of Meteorology’s Australian Water Availability Project (http://www.bom.gov.au/jsp/awap/rain/index.jsp) which was collected between January 1, 2006 and January 1, 2009. Average annual rainfall ranged between 2140mm at 400m a.s.l. up to 2924mm at 1200m a.s.l. Extrapolation of data from surrounding areas within a 5km grid data was necessary to make estimations relevant to Mt Lewis plots.
Mt Lewis plots vegetation data are incomplete as it is still ongoing, as a result only 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*. At the 600m, they were dominated by *Brombya platynema*, *Argyrodendron peralatum* and *Mallotus polyadenos*, and the 800m a.s.l. plots were dominated by *Brombya platynema* and *Franciscodendron laurifolium*. At 1000m a.s.l. plots, the dominant species include *Balanops australiana* and *Daphnandra repandula*, and at 1200m a.s.l. *Doryphora aromatic* and *Niemeyera sp. Mt Lewis.*

4.2. Community sampling

All species of Auchenorrhyncha are the subject of this study. This group is one of the lineages of Hemiptera, although recent analyses indicated that it may be a paraphyletic taxon (Sorensen *et al*.1995). All species of Auchenorrhyncha are sap sucking herbivores, members of one of the three guilds (see Novotny and Wilson 1997 for details); (i) xylem-feeding Cercopoidea, Cicadoidea, Cicadellidae: Cicadellini (sensu Hamilton 1983); Cicadellinae sensu (Young 1968) and Mileewini (their position is unclear; they were treated as xylem-feeders, based on the observations from the study by Novotny and Basset (1998); (2) mesophyll-cell-feeding: Cicadellidae: Typhlocybinae; and (3) phloem-feeding: remaining Auchenorrhyncha and Sternorrhyncha. All three guilds were of prime concern in the present study: (i) xylem-feeders; Cercopoidea and Cicadellidae: Cicadellini (ii) mesophyll-feeders; Typhlocybinae and (iii) phloem-feeders; remaining Cicadormorpha and Fulgoroidea (note the present study does not include Sternorrhyncha which forms another important component of the phloem-feeding guild). As in almost any other studies, the above guilds are in fact ‘taxon guilds’ (*sensu* Simberloff and Dayan 1991), i.e. groups
defined both by their food resource and phylogenetic lineage. Subsequently, families of Auchenorrhyncha are assigned accordingly, particularly with reference to their food resources and feeding-behaviour (Table 4.1).

<table>
<thead>
<tr>
<th>phloem-feeders</th>
<th>xylem-feeders</th>
<th>mesophyll-feeders</th>
</tr>
</thead>
<tbody>
<tr>
<td>Achilidae</td>
<td>Cercopidae</td>
<td>Cicadellidae</td>
</tr>
<tr>
<td>Cicadellidae</td>
<td>Aphrophoridae</td>
<td>- subfamily</td>
</tr>
<tr>
<td>Flatidae</td>
<td>Cicadidae</td>
<td>Typhocytinae</td>
</tr>
<tr>
<td>Fulgoridae</td>
<td>Cicadellidae</td>
<td></td>
</tr>
<tr>
<td>Issidae</td>
<td></td>
<td>- tribe Cicadellini</td>
</tr>
<tr>
<td>Meenoplidae</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Membracidae</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nogodinidae</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ricaniidae</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tropiduchidae</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

4.2.1. Sampling of adult insects

There are no widely applicable, standardized sampling protocols for sampling Hemiptera, in particular Auchenorrhyncha within their native rainforest habitats (Moir et al. 2005). This is surprising, given that Auchenorrhyncha are present in nearly all terrestrial ecosystems and occur in greater abundances representing one of the species-rich groups of herbivorous invertebrates (Gaston 1991) and play important roles in ecosystems functioning (Kruess & Tscharntke 2002; Nickel & Hildebrandt 2003; Virolainen et al. 2000).

The two primary collection techniques used here were light trapping and malaise trapping. The altitudinal transects and study designs are exactly the same as the one used by a colleague, former PhD student (Louise Ashton, PhD, Environmental Futures Research Institute, Griffith University). In fact, the insect group (Auchenorrhyncha,
Hemiptera) that I am doing research on were collected together with her specimens (moths) during the same light trapping nights (major part of my data); hence the methods (excluding Malaise traps) and trapping night dates were as exact as hers. Both light and Malaise trapping methods were used in both the subtropical and tropical transects. All Auchenorrhyncha specimens from both trapping techniques were later pulled out in the laboratory and stored in alcohol. All families and feeding-guilds (xylem-, phloem-, and mesophyll-feeders) were included in the study (refer to Table 4.1).

*Light trapping*

The major sampling tool used to collect Auchenorrhyncha in this research is the Pennsylvania light trap. This 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 light-weight 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 (Kitching *et al.* 2005)(Figure 4.4). 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 Dichlororvos impregnated plastic strip, which was cut into one inch pieces, with two to three pieces placed in each trap” (L.Ashton, PhD dissertation, Environmental Futures Research Institute, Griffith University 2013). In each trap, paper towels were placed in to lower humidity in the trap as much as possible. Although, this method is mostly used to catch moths (Ashton *et al.* 2016; Wolda 1996), it has also been well documented to be an efficient way to capture Auchenorrhyncha (Casson & Hodkinson 1990; Wolda 1980), In addition, from personal observations, it has yielded large samples of
Auchenorrhyncha in the current study and also from my MSc. Project (Dem 2013, unpublished data) which was conducted in Papua New Guinea. All collection techniques have some level of bias, even when studying a subset(s) of the entire natural assemblage (Krebs 1999). Light traps are mostly used to capture flying insects, especially moths, however, capture efficiency may be affected by responses to the UV light (Altermatt et al. 2009). This same principle may also apply to other insect groups, including Auchenorrhyncha which are also attracted to the light. However, this bias is similar across all samples, as those species that are attracted to light should be sampled to an equivalent regime by this trap. Thus, this is an effective method of sampling arthropods, as long as they are used in a standardised manner (Preston 1948). On the contrary, Auchenorrhyncha are difficult to sample as they are and the samples tend to be low when using single sampling technique.

Sampling efficiency is often influenced by different factors, including temperature, moon phase, precipitation and wind (Muirhead-Thomsom 1991; Yela and Holyoak 1997). In order to standardise the trap nights and to be able to have as much as possible similar catches relating to species assemblages, we sampled over three nights, avoiding three days before or after the full moon.

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. The canopy traps were raised into the canopy using ropes, with the height above ground varying 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.
Each altitudinal transect was sampled at the beginning and end of the wet season. Field work at Border Ranges NP was conducted by Louise Ashton between the 4 and 22 April 2011, and between the 27 October and 12 November 2010. Mt Lewis NP field work was executed from 21 November to 13 December 2009, and 1 to 18 April 2011.

Malaise trapping

The Malaise trap, originally invented by Dr. Rene Malaise, is a reliable trap for many groups of insects (Malaise 1937; Oldroyd 1959). Since 1958, three modified versions of the trap have been made over the last century, differing in dimensions, nylon type and with each succeeding version better than the last. The trap version used here is the latest version that was constructed by the Entomology Department at the University of Queensland. It is of much stronger build and durability, with dimensions of 7.7cm in length and 9cm and width. A light canvas is attached along the ridge pole, main seams and edges, with a strip horizontally across the middle of the centre panel (Gressitt &
Gressitt 1962) which reaches down to the ground. Transparent catching cylinders with built-in inverted funnel are attached at the entrance end for insect storage. Like light traps, Malaise traps are also designed to capture flying insects that fly onto the vertical panel of the mesh. Once insects land on the panel, they will make their way to the top of the net and become trapped in the roof, where the top of the trap comes in conjunction with the vertical panel, and into the collecting cylinders (Paulson 2005).

A very important thing to consider when placing the trap is finding the ideal location and position to enhance efficient sampling (http://mississippientomologicalmuseum.org.msstate.edu/collection.preparation.methods/Malaise.traps.htm), which relates to several factors, such as local circumstances of topography, density or lack of vegetation, relation to wind and water. Suitable locations vary depending on the vegetation type and study design. The majority of insects that are trapped are usually very mobile in terms of flight. Insect groups mostly trapped, include Hymenoptera (highest representation), Diptera, and Lepidoptera; others are represented more or less equally (Gressitt & Gressitt 1962).

Each altitudinal transect was sampled at the beginning and end of the wet season. Field work at Border Ranges NP was conducted from 19 November to 9 December 2012, and 19 March to 18 April 2013, and field work at Mt Lewis was carried out from 6 to 29 March 2013, and 18 to 29 October 2013. At each of the altitudinal site, one Malaise trap (Figure 4.5) was set up anywhere on the ground (considering the spot is at least level and also easy access to tie the top ends of the trap to nearby standing stems) within each of the replicated plots and left untended for 10 days. Ethanol (alcohol) was used as a preservative in the collection chamber of the trap. After 10 days, insects were
transferred from the cylinder containing alcohol into proper storage containers and brought back to the laboratory for sorting.

![Figure 4.5. Latest modified Malaise trap set up in the forest to trap flying insects.](image)

4.3. Insect specimen dissection and identification

After sampling, insects were sorted and identified to species in the laboratory based on both the external morphology and genitalia dissection (Bartlett et al. 2011; Dietrich 2005; Fletcher & Lariviere 2001). The morphologies of both male and female genitalia are very distinct in different species, and although this is a very time-consuming method, and required a thorough check on both the physical morphology and genital segment, it is extremely accurate. Accordingly, it can be stated here, with confidence, that sorting was to species rather than the more common morphospecies of insect community surveys. As in many insect groups, including Auchenorrhyncha, identification of species relies to a large extent of dissection of the male genitalia, particularly the shape of the aedeagus. Unfortunately, this technique cannot be used for
nymphs which have to be matched up with adults and hence sorting of nymphs is far less accurate. In addition, because most of the families have very soft wings and, once the wings are damaged, this makes identification difficult.

The male genital segment was dissected from the abdomen under the microscope and left in 10 % potassium hydroxide (KOH) for 24 hours, and then rinsed with ethanol. This helps to wash away muscles and other tissues that might be blocking the aedeagus from a clear view when looking at it under the microscope. The aedeagus was sketched and the representative specimen preserved in glycerol in a small plastic tube was pinned underneath the mounted specimen. Subsequently, one or two representatives of the species were kept in a reference collection that I created.

Upon completion of identification, insects were also allocated into their specific feeding-guilds: xylem-, phloem- or mesophyll-feeders, using the scheme of Novotny et al. (2010).
Chapter 5

Altitudinal distribution patterns of Auchenorrhyncha along transects in subtropical and tropical rainforests in Australia.

5.1. Abstract

1. Species distribution patterns along environmental gradients are important in characterizing community structure, especially as they are driven by the local climatic conditions. This study may be the first in Australia to investigate Auchenorrhyncha along altitude and latitudes, and little is known about species assemblages of Auchenorrhyncha that is relatively understudied in the tropics, including Australia. Despite this, Auchenorrhyncha may be highly vulnerable to climate change, as they have a very close relationship with their host plants.

2. Here, I present new information on the distribution patterns of Auchenorrhyncha among different altitudes and between latitudes in tropical and subtropical rainforests in Australia.

3. Leafhoppers and planthoppers were recorded along two altitudinal transects, ranging from 400-1200m a.s.l. for the tropical transect and 300-1100m a.s.l. for the subtropical transect.

4. A total of 22,713 individuals of 365 species and 17 families were sampled across latitudes, with 274 species from the tropical transect and 188 from subtropical transect. 177 and 91 species were unique to the tropical and subtropical transect respectively. Altitude had a significant effect on species
diversity of Auchenorrhyncha assemblages at each transect. Insect communities between pairwise altitudinal sites were similar in composition for each transect, with species from both transects having very narrow altitudinal ranges.

5. The gap in the current study is the ecological aspect of it, which is the missing information on the host plant records of Auchenorrhyncha, which may have provided a clear explanation on the distribution patterns of Auchenorrhyncha along such gradients.

**Keywords:** Auchenorrhyncha, altitudinal gradient, latitude gradient, climate change, distribution patterns, species range.

### 5.2. Introduction

Species distributional patterns along environmental gradients are vitally necessary to characterize community structure, especially as much as they are driven by the local climatic conditions (Sanders *et al.* 2003; Werner *et al.* 2007). A fundamental issue that has fascinated biologists is how climate shapes variation in the physiology, ecology and evolution of organisms (Ghalabor *et al.* 2006). In addition to abiotic factors, biologists have also been aware that biotic factors are also important in influencing the conditions and the capability of an organism to continue its generation (Pelliissier *et al.* 2013; Van der Putten *et al.* 2010). Consequently, investigations of the patterns of species diversity and the roles of abiotic and biotic factors that may explain patterns of species diversity have been a fertile field of study for biologists.
There has been an increasing interest in environmental gradients such as altitudinal
gradients in recent decades, principally because they may exhibit steep shifts in species
turnover over very short distances and are strongly implicated in generating high
regional species diversity (reviewed by Lomolino 2001a; Rohde 1992). Patterns in
species richness show either a monotonic decline with altitude (Maveety et al. 2011;
Péré et al. 2013) or a unimodal distribution (Fu et al. 2007; Janzen et al. 1976).
Explanations for the decline in species richness at high altitudes include smaller habitat
area, lower resource diversity and primary productivity, and the increasing harsh
environmental conditions compared to lower altitudes (Lawton et al. 1987). Unimodal
patterns may reflect climatic severity (low temperature, high precipitation) and resource
restrictions imposed predominantly at higher altitudes, and at lower altitudes by
climatic severity (high temperature, dessication challenges) and high predation
pressures, resulting in optimal environmental conditions at mid-altitudes (reviewed by
McCoy 1990). Recently, modelling of the natural geometric constraints of altitudinal
ranges have been shown to produce a humped-shaped pattern in species richness
(Colwell & Hurtt 1994), the model being called the ‘mid-domain effect’ (MDE). This
concept takes into account species range, domain size and frequency distribution of
range, and does not take into consideration abiotic and biotic factors (Colwell et al.
2004; VanDerWal et al. 2008). However, as a result of habitat heterogeneity, the
monotonic and unimodal patterns may not be observed on mountain tops, possibly
because increasing slopes and habitat isolation on mountain tops may contain more
species, which may produce an opposite trend to the monotonic decline pattern
(Laurance et al. 2011). Patterns in species richness may be caused by a combination of
several factors, including both abiotic and biotic factors; however, recent debate on the
likely driving forces behind these patterns is largely due to changes in climate.
The average temperature of the earth has risen by approximately 0.85°C during the past century and is continuing to increase (IPCC 2014a; Menéndez 2007). Atmospheric CO₂ concentrations has increased by 2.0 ±0.1 ppm yr⁻¹ over the last decade. Precipitation has generally increased in temperate regions, but downward trends dominate the tropics over the last five decades. Global averaged precipitation change is -1.54 ± 4.50 mm over the last 50 years (Becker et al. 2013). Mean sea level rose by 0.19 m over the last century at a rate that has been larger than the mean rate during the previous two millennia. Over the 21st century, global temperature increase is predicted to exceed 1.5°C, with uncertainty in the emissions of CO₂ as it depends on each region and industrial activities. Extreme precipitation is expected to increase with warming, with a median increase of 7% °C⁻¹. Australia’s continental average temperature has elevated by 0.16°C per decade over the last six decades, and by 2070, mean temperatures will have increased by 1.0 -5.0 °C (IPPC 2014b). Total annual rainfall has increased by approximately 15% in two-thirds of Australian states (Hughes 2003). For the remaining of this century, projected amount of rainfall will vary between states and localities, with precipitation increasing in some areas and decreasing in others (IPCC 2014b).

Assemblage patterns of insects along altitudinal gradients have become of special importance as interests have focused on likely impacts of climate change (Erelli et al 1998; Merrill et al. 2008). The study of the ecology of species along an altitudinal gradient may provide baseline information on the likely response of both species and communities to climate change at any one point over time. Climate change has forced many insect species to shift their distribution ranges towards higher altitudes and latitudes (Chen et al. 2009; reviewed by Hill et al. 2011; Sekercioglu et al. 2008). There
is clear evidence for range shifts poleward and towards higher altitudes in temperate regions, but less for the tropics due to lack of long-term datasets (Colwell et al. 2008; Parmesan & Yohe 2003). If a similar trend were to be observed in the tropics, species living at lower altitudes will move upwards to cooler environments, with those species living on mountain tops having nowhere cooler to move to. Insects are very sensitive to temperature change, especially those species with narrow-thermal tolerances (Deutsch et al. 2008). Investigation of insects along altitudes and latitudes have shown that species are moving up to high altitudes and latitudes (Anderson et al. 2008; Pöyry et al. 2009; Warren et al. 2001) and withdrawing their presence at low altitude and latitude (Chen et al. 2011; Franco et al. 2006; Wilson et al. 2005). A long-term study of moth assemblages along an altitudinal gradient over 42 years at Mt Kinabalu, Sabah revealed that climate change is indeed causing species to shift their ranges upslope, with 102 montane species moving an average of 67m upwards over that period (Chen et al. 2009). Consequently, species experience a contraction in their ranges (Dahlhoff et al. 2008), which may still provide some space above the maximum recorded altitude for species at low altitudes and latitudes. Unfortunately, this presents a situation that may have cause some species at mountain tops to go extinct (Thomas et al. 2004; Williams et al 2007), as they would encounter a small area availability. These circumstances have led to changes in species distribution and population (Adler et al. 2007; Tylianakis et al. 2008).

The direct effects of temperature on insects are likely to vary among species, depending on the environments they live in, their life-histories, habitats and their ability to adapt. Polyphagous species are less likely to be affected by climate change than monophagous species with narrow niches (Bale et al. 2002). Other factors such as physiology
species interactions (Menéndez 2007), insect phenology and synchronization (Bale et al. 2002; Root & Hughes 2005) are also affected by temperature change. The predicted impacts of temperature on terrestrial invertebrates is that most species may still be vulnerable, even those with wide climatic range, as a result they are forced to shift ranges under climate change, leading to reduction in their ranges (Beaumont & Hughes 2002). Many herbivorous invertebrates are also likely to be affected by reductions in plant quality as atmospheric CO₂ increases, which may result in higher mortality rates, longer development times and reduced adult body mass (Johns & Hughes 2002; Lawler et al. 1997).

Insects are most likely to be affected by climate change because climate has a strong direct influence on their development, reproduction and survival (Bale et al. 2002). Moreover, insects have a short life cycle and high reproductive rates, so they are more likely to respond quicker to climate change than long-lived organisms such as plants and vertebrates (Menéndez 2007), which makes them suitable for the study of climate change.

Through investigating Auchenorrhyncha assemblages between the two altitudinal gradients, I aim to address the following research questions: (1) what is the species richness (alpha diversity) of Auchenorrhyncha at different altitudes and how does the species composition change between altitudes (beta diversity)? (2) are there differences in patterns of alpha and beta diversity of Auchenorrhyncha assemblages between subtropical and tropical rainforests? and (3) what are the distribution and range sizes of Auchenorrhyncha along altitudinal gradients?
5.3. Methods

5.3.1. Study locations and study design – refer to Chapter 4 (sub-chapter 4.1)

5.3.2. Adult insects sampling – refer to Chapter 4 (sub-chapter 4.2)

5.3.3. Insect specimens sorting and identification- refer to Chapter 4 (sub-chapter 4.3).

5.3.4. Data analysis

At both study locations, samples collected on separate occasions from each altitude were pooled for analyses. Analyses were carried out for counts of individual adult leafhoppers and planthoppers, and counts of species from each family from both the Malaise and light trappings combined.

Community richness is expressed as the proportion of individuals and species in each family at each altitude. Another parameter also describing community richness is the number of species observed at each altitude (species richness). In addition, rarefied species richness were obtained for the lowest possible number of individual for each altitude for the respective study location. Their relationships were expressed by regression and their significance was tested using Pearson correlation test. Individual-based rarefaction and extrapolation curves for each altitude for the respective study location were interpolated and extrapolated from reference samples. Rarefied species richness was calculated down to the smallest possible number of individuals among the samples from each study location (i.e. Mt Lewis, 892 individuals and Border Ranges, 156 individuals). Extrapolated species richness was rarefied to the highest number of individuals among the samples from each study location (i.e. Mt Lewis, 2067
individuals and Border Ranges, 12 471 individuals). EstimateS 9.1.0 is used in the calibration of rarefaction and extrapolation of incidence data (Colwell 2013).

Principle Coordinates Analyses (PCoA) were conducted for each dataset (incidence, presence/absence) in order to see if there was a turnover in composition of leafhoppers and planthoppers among altitudes. These analyses were calibrated using PRIMER v6 software (Anderson, Gorley and Clarke 2008; Clarke & Gorley 2006). Both datasets were square-root transformed in order to minimize the effect of highly abundant species. Similarity matrices were created for all datasets using the Bray-Curtis Index from which all PCoA plots were constructed. The effect of environmental variables was assessed using the distance-based linear models (DistLM) (McArdle & Anderson 2001). The most parsimonious model that best explained insect assemblages and composition was obtained by using step-wise procedure and a modified Akaike’s Information Criterion (AICc) (Anderson, Gorley & Clarke 2008). To see if there is a relationship between the environmental variables and the biological data, and which of the environmental variables best explained most of the variation, RELATE and BEST functions in Primer were respectively used, using Spearman rank correlation from 4999 permutations.

Sorensen index of similarity in EstimateS 9.1.0 (Colwell 2013) was used to estimate community similarity between different altitudes. The relationships between similarity and altitude were tested using Pearson correlation. The significance of correlation between altitude and pair-wise similarity values for all pairs for the five sites from each study location was tested using Mantel test.
The altitudinal distribution of species was evaluated in two ways, as (i) altitudinal range, which quantifies the extent of altitudinal distribution of each species and is calculated as: maximum altitude – minimum altitude, and (ii) altitudinal midpoint, which quantifies the position of each species and is calculated as: the (minimum altitude + maximum altitude)/2. The Kolmogorov-Smirnov test was used to determine if species from the tropical and subtropical transects have similar altitudinal range size. To test if there is a difference in the number of species having similar altitudinal range between the tropical and subtropical transects, a Chi-squared two-sample test was used. The significance of correlation between altitudinal range and altitudinal midpoint is tested using Pearson’s correlation coefficient.

5.4. Results

Community descriptions and assemblages

A total of 22,713 individuals of 365 species were collected, with 274 species from the tropical transect, 188 on the subtropical transect, 97 species shared between transects, 177 species unique to the tropical transect and 91 species unique to the subtropical transect. However, the tropical transect had a lower abundance (6,809) than the subtropical transect (15,904). Across both transects, 17 families were encountered, with 14 families shared between transects. Cercopidae and Cicadidae were recorded only within the tropical transect and Aphrophoridae was only recorded within the subtropical transect (Table 5.1). The mean number of species at each altitude on the tropical transect was 55 (SD = ±2.67) with 16 families represented. Cicadellidae is the most species rich family which comprised approximately 50% of the total species, followed by Achilidae with 13%. Cicadellidae was also the most numerically abundant family.
with an approximate abundance proportion of 0.5, followed by Achilidae with a proportion of 0.22 of the entire population. The species richness of families differed across altitudes, with some families become less diverse with increasing altitudes, while other become more diverse toward higher altitudes (Figure 5.1i, ii). The mean number of species at each altitude on the subtropical transect was 17.6 species (S.D = ±48.76) with 15 families collected. Cicadellidae was the most species-rich family, followed by Derbidae, Cixiidae and Achilidae (Figure 5.1iii, iv). The four most numerically abundant families, recorded across all altitudes were Cicadellidae (>50%), followed by Derbidae, Cixiidae and Achilidae (Table S5.1).

Table 5.1. Number of species and their abundance in each family recorded at the tropical and subtropical transect respectively.

<table>
<thead>
<tr>
<th>Families</th>
<th>tropical transect</th>
<th></th>
<th>subtropical transect</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Species richness</td>
<td>Family abundance</td>
<td>Species richness</td>
<td>Family abundance</td>
</tr>
<tr>
<td>Aphrophoridae</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>17</td>
</tr>
<tr>
<td>Nogodinidae</td>
<td>0</td>
<td>0</td>
<td>5</td>
<td>24</td>
</tr>
<tr>
<td>Dictyopharidae</td>
<td>1</td>
<td>5</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Fulgoridae</td>
<td>1</td>
<td>3</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Meenoplidae</td>
<td>2</td>
<td>5</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Ricaniidae</td>
<td>2</td>
<td>5</td>
<td>1</td>
<td>4</td>
</tr>
<tr>
<td>Membracidae</td>
<td>3</td>
<td>6</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Cicadidae</td>
<td>4</td>
<td>18</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Cercopidae</td>
<td>5</td>
<td>682</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Tropiduchidae</td>
<td>5</td>
<td>58</td>
<td>3</td>
<td>13</td>
</tr>
<tr>
<td>Issidae</td>
<td>7</td>
<td>27</td>
<td>7</td>
<td>39</td>
</tr>
<tr>
<td>Delphacidae</td>
<td>17</td>
<td>233</td>
<td>7</td>
<td>574</td>
</tr>
<tr>
<td>Derbidae</td>
<td>18</td>
<td>216</td>
<td>15</td>
<td>3144</td>
</tr>
<tr>
<td>Cixiidae</td>
<td>20</td>
<td>648</td>
<td>11</td>
<td>975</td>
</tr>
<tr>
<td>Flatidae</td>
<td>21</td>
<td>180</td>
<td>6</td>
<td>50</td>
</tr>
<tr>
<td>Achilidae</td>
<td>35</td>
<td>1467</td>
<td>22</td>
<td>887</td>
</tr>
<tr>
<td>Cicadellidae:</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>non-Typhlocybina</td>
<td>79</td>
<td>2632</td>
<td>54</td>
<td>9597</td>
</tr>
<tr>
<td>Typhlocybinae</td>
<td>54</td>
<td>618</td>
<td>51</td>
<td>574</td>
</tr>
</tbody>
</table>

The observed number of species recorded from light and Malaise traps at each altitude at both transects showed a very strong significant correlation with altitude (Pearson’s correlation, Mt Lewis, r = -0.96; N=5; P<0.05; Border Rangers, r = -0.97, N=5, P<0.05,
Figure 5.2i, ii). Both relationships were described by a linear regression, so that the number of species decreases with increasing altitude. This was supported by the strong correlations between square root number of individuals and square root number of species at both transects (Pearson’s correlation, Mt Lewis, r = -0.93; N=5; P<0.05; Border Ranges, r = -0.87; N=5; P<0.05), so that in all correlations the number of species at each altitude is influenced by the number of individuals. This was also being supported when the number of species were rarefied for each altitude, although for the subtropical transect, the significance is weak (Pearson’s correlation, Mt Lewis, r = 0.87, N=5, P<0.05; Border Ranges, r = -0.44, N=5, P<0.05, Figure 5.2iii, iv). Further, extrapolated species richness and altitude showed significant relationships for both transects (Pearson’s correlation, Mt Lewis, r = -0.86, N = 5, P<0.05; Border ranges, r = 0.87, N=5, P<0.05, Figure 5.2v, vi). Interpolated curves for both transects and extrapolated curves for the tropical transect have not yet reached asymptotic levels, however, the extrapolated curves for the subtropical transect (500, 700, 900 and 1100 m) have already levelled-off to the most abundant reference sample (Figure 5.3).
Figure 5.1. Proportions of each family collected at the tropical (i, iii) and subtropical (iii, iv) transects. Graphs (i, iii) show proportion of family abundance collected at each transect (families with 20 or less individuals are grouped as ‘other families’), and graphs (ii, iv) show species from each family collected at each transect (families with 10 or less species are grouped as ‘other families’).
Figure 5.2. The relationship between the observed number of species (i, ii), rarefied species richness (iii, iv) and extrapolated number of species (v, vi), and altitude respectively for each transect (a, b). Error bars on rarefied data (iii, iv) are 95% confidence intervals.
Community similarity and altitudinal distribution

Dissimilarity matrices of community assemblages of Auchenorrhyncha as revealed by PCoA showed slightly different patterns among altitudes between tropical and subtropical assemblages. Based on incidence data, insect communities in the tropics were grouped into low, mid and high-altitudes. However, presence/absence data showed a different pattern for the mid-altitudes where the two communities have different species composition and yet are all strongly correlated to all environmental variables (Figure 5.4a). All environmental variables were strongly correlated with the biological data, however, the environmental variable that best explained the patterns in the communities was altitude (Spearman rank, $r = 0.89$, Rho = 0.89, P<0.1). Community similarities were significantly related to all environmental variables included in the
distance-linear model, except for soil sodium, soil carbon, soil clay, soil nitrogen, soil calcium and plant species richness. In all stepwise comparisons, the most parsimonious model to explain the multivariate data included altitude only, which explains about 30% of the variation in the patterns ($R^2 = 0.3$, $P < 0.001$). The subtropical insect communities have similar species composition patterns to those of the tropical communities, but based on presence/absence data, 300m and 1100m each have very different community composition whereas 500m, 700m and 900m have very similar assemblages. Correlations between the biota and environmental variables showed a very weak, but significant correlation ($Rho = 0.33$, $P < 0.05$, Figure 5.4b), however, the patterns in assemblages are best explained by a combination of variables, with altitude alone explaining most of the variation, followed by the combination of altitude and temperature (both correlations $> 0.5$, $Rho = 0.52$, $P > 0.005$). Community similarities were not significantly related to the environmental variables included in the distance-linear model, except for altitude and temperature. In all stepwise comparisons, the most parsimonious model selected from all environmental variables to explain the multivariate data included altitude only, which altogether explain about 50% of the variation. Insect community similarities between altitudes did not decrease with increasing differences in altitude, for either of the tropical and subtropical communities. Sorensen insect similarity showed that regardless of whether or not the communities are closer or further away from each other, they have similar community composition (Mt Lewis, $r = -0.82$, $N=10$, $P > 0.05$; Border Ranges, $r = -0.77$, $N=10$, $P > 0.05$, Mantel Test, Figure 5.5).
Figure 5.4a. Principle Coordination Axes for all the plot sites combined the tropical transect, taking into account environmental variables.

Figure 5.4b. Principle Coordination Axes for all the plot sites combined the subtropical transect, taking into account environmental variables.
Figure 5.5. Relationship between altitudinal difference and Sorensen insect similarity between sites at different altitudes. There is no significant correlation between altitudinal difference and similarity for both transects (a, b). All pairwise comparisons between five study sites from each transect were used. Each marker is one paired comparison.

The distribution of altitudinal ranges showed that majority of the species recorded at each transect had narrow altitudinal ranges as they were found either at a single or two adjacent sites, with a range of 0-200m (K-S test = 0.128, N=2, P>0.05, Figure 5.6a). However, there were more species at the tropical transect than the subtropical transect, having similar range sizes ($\chi^2 = 168.68$, d.f = 4, P<0.05, Figure 5.6a). This finding was supported by the determination of species range size expressed by the correlation of each species altitudinal range and midpoint. The correlation between the variables is not significant, indicating that range size does not change with elevation (Pearson’s correlation, tropical transect, r = 0.21, N=274, P>0.05; subtropical transect, r = 0.51, N=188, P>0.05, Figure 5.6b).
Figure 5.6a. Distribution of altitudinal range of species across altitudes at the different transects. Most species at both transects have narrow altitudinal ranges.

![Distribution of altitudinal range of species across altitudes at the different transects. Most species at both transects have narrow altitudinal ranges.](image)

Figure 5.6b. Correlation between altitudinal range and altitudinal midpoint of species at the tropical and subtropical transect. There was no significant correlation at either transect, so that species at low elevations have similar range size as those at high altitudes (Pearson correlations, Mt Lewis, r = 0.21, N=274, P>0.05; Border Ranger, r = 0.51, N=188, P>0.05). The sizes of the markers indicate the number of sites (1-5) for which the species was recorded.

![Correlation between altitudinal range and altitudinal midpoint of species at the tropical and subtropical transect.](image)
5.5. Discussion

**Species richness and assemblages**

This study showed that both the altitude and latitude affected species diversity for the respective forest ecosystem i.e. the tropical and subtropical forests, except for the two lower altitudes at each transect. The two lower altitudes at the subtropics each had higher overall species abundance than their counterpart altitudes in the tropics, resulting in the overall species abundance to be higher in the subtropics. However, the opposite was observed for species richness, in which the tropics had higher species richness than the subtropics. This is also true for the rarefied species richness among altitudes at both forest types, which showed that altitude has a strong significant effect on species richness. However, the weak significance shown by the regression of rarefied number of species and altitude at the subtropical transect suggests that the very large differences in species abundance between samples can be a contributing factor to explaining differences in species richness between the two forest systems. This conclusion is supported by the rarefaction of species individuals for each altitude where the number of species increases with increasing number of individuals, suggesting that species abundance is also an important underlying determinant of community distributional patterns along environmental gradients, such as altitude (Colwell *et al.* 2012; Janzen *et al.* 1976). I am not aware of any study on the altitudinal and latitudinal stratification of leafhoppers and planthoppers in Australia. Since it is generally accepted that the species richness of most animal groups, particularly insect groups, decreases with altitude (Fischer *et al.* 2011; Williams *et al.* 2007) and latitude (Bale *et al.* 2002). I hypothesized that the species richness and total abundance of leafhoppers and plant hoppers in the tropics would be greater than the subtropics. This hypothesis was true for
species richness, but not species abundance. The overall population for leaf hoppers and plant hoppers, as well as the overall population recorded at each altitude, showed that the subtropical transect supported more individuals than the tropical transect. This may be due to the incidence of very few abundant species, especially few species from the Cicadellidae family, and one species from the Derbidae family that had caused this huge difference in the overall population. This could in turn reflect the effect of plant species richness (Laidlaw et al. 2011) since leafhoppers and plant hoppers depend entirely on plants (Dem et al. 2013; Novotny et al. 2010). However, populations fluctuate enormously depending on a range of conditions, and plant species richness is unlikely to be the driver for differences in abundance. It seems more likely that other factors such as differences in levels of parasitism and predation are responsible for such differences (Virla et al. 2008). The rarefaction curves for each altitude at both study locations was still increasing at a very steep rate, indicating that there are more species yet to be sampled. At the subtropical transect, the extrapolated curves have already reached asymptotic levels, even to the highest sample abundance. This could be due to an effect of plant community differences among altitudes and the differences in the seasons between the tropics and the subtropics, which may potentially affect species richness abundance (Novotny & Basset 1998; Schuldt et al. 2010). Comparatively, there are differences in altitudinal zone communities between the tropics and subtropics; (i) the lower-altitudes at the subtropical transect had extremely high species abundance, but lower species richness than the lower-altitudes at the tropical transect, and (ii) higher-altitudes at the subtropical transect had lower species richness and abundance than the higher altitudes at the tropical transect. These differences in communities between altitudinal-zones could be due to high pressure from natural enemies, temperature and/or effect of plant species composition (Novotny et al. 2005b;
Wang et al. 2008). For instance, at the lower altitudes (400m and 600m) at the tropical transect, the plots and the whole surrounding area are dominated by lawyer cane (*Calamus australis*), which stretches from the ground-level into the canopy.

*Community similarity*

Species are clearly grouped into the low-, mid-, and high-altitude assemblages for both tropical and subtropical transects. As one begins to move high up the mountains or nearer the equator, variation in environmental conditions become larger, and as a result community similarity decreases with each community having its own unique species. However, altitude had no significant effect on community similarity between adjacent altitudinal sites. Environmental factors such as abiotic (temperature, precipitation) and plant species composition change at a constant rate, which resulted in similar insect composition. This is not surprising as communities of phytophagous Hemiptera, including Auchenorrhyncha have been reported to exhibit a high level of similarity between adjacent latitudes (Andrew & Hughes 2005). As I have predicted, based on the idea that great differences in environmental variations would affect community similarity. My results did not suggest this otherwise, but that increasing altitudinal differences did not have a significant effect between each pairwise comparison of altitudinal sites. Increasing altitudinal differences did not have a significant effect on community similarity between each pairwise comparison of sites, as we predicted, based on the great differences in environmental variations (Axmacher et al. 2004). This could be because I used an altitudinal scale that is small (VanDerWal et al. 2008) with only 200m between adjacent altitudes. This might result from the trends in the microclimate which resembles plant communities being very similar or the altitudinal sites are all on one side of the mountain.
The size of the altitudinal range of a species is a very important ecological characteristic as it demonstrates the distribution boundaries of an organism which may be limited by the species’ ability to adapt and cope with the changing microclimate and/or the availability of its food resources. Organisms that have larger range size are better able to adapt and survive with changes in the environment than species with smaller range size. Here I have shown that Auchneorrhyncha have very narrow range sizes. Isolation on mountains and topological barriers make insects vulnerable if they need to move upslope to avoid rising temperatures. Whether a species can adapt or cope with the conditions of the new environment depends on its adaptability. This is a serious problem for many tropical species with narrow altitudinal ranges (Colwell et al. 2008). Numerous species have shifted their ranges in response to the changes in the climate, especially temperature, during the past decades (e.g. Parmesan & Yohe 2003; Thomas et al. 2001). Herbivorous insects depend on the availability of their host plants for survival and reproduction. If the species of host plants they normally feed on are not available or have not move upwards, then they may need to find alternative hosts. This may be problematic for host-specific species of Auchneorrhyncha. Plants at higher altitudes maybe less palatable because of low temperatures which reduce their quality (Erelii et al. 1998). Lower nutrient quality may affect the ability of Auchenorrhyncha species to survive or reproduce.
## S5 SUPPLEMENTARY MATERIALS

### Table S5.1. Abundance and ranges of morphospecies of common families recorded at each altitudinal transect. Morphospecies with 100 or more individuals across altitudes are represented

<table>
<thead>
<tr>
<th>Morphospecies</th>
<th>300 m</th>
<th>400 m</th>
<th>500 m</th>
<th>600 m</th>
<th>700 m</th>
<th>800 m</th>
<th>900 m</th>
<th>1000 m</th>
<th>1100 m</th>
<th>1200 m</th>
</tr>
</thead>
<tbody>
<tr>
<td>ACHI001</td>
<td>216</td>
<td>27</td>
<td>18</td>
<td>6</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ACHI002</td>
<td>60</td>
<td>18</td>
<td>17</td>
<td>30</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ACHI004</td>
<td>148</td>
<td>1</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ACHI025</td>
<td>126</td>
<td>7</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ACHI016</td>
<td>8</td>
<td>49</td>
<td>441</td>
<td>214</td>
<td>80</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ACHI044</td>
<td>47</td>
<td>35</td>
<td>17</td>
<td>17</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CICA004</td>
<td>61</td>
<td>254</td>
<td>156</td>
<td>336</td>
<td>71</td>
<td>68</td>
<td>40</td>
<td>54</td>
<td>1</td>
<td>218</td>
</tr>
<tr>
<td>CICA010</td>
<td>436</td>
<td>4</td>
<td>1</td>
<td>13</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CICA012</td>
<td>25</td>
<td>105</td>
<td>96</td>
<td>20</td>
<td>67</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CICA023</td>
<td>150</td>
<td>20</td>
<td>19</td>
<td>6</td>
<td>11</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CICA042</td>
<td>7336</td>
<td>35</td>
<td>9</td>
<td>130</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CICA043</td>
<td>70</td>
<td>35</td>
<td>8</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CICA045</td>
<td>131</td>
<td>95</td>
<td>170</td>
<td>75</td>
<td>19</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CICA067</td>
<td>108</td>
<td>67</td>
<td>129</td>
<td>29</td>
<td>11</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CICA116</td>
<td>34</td>
<td>89</td>
<td>11</td>
<td>1</td>
<td>5</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CERC004</td>
<td></td>
<td>15</td>
<td>24</td>
<td>143</td>
<td>171</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CERC001</td>
<td>16</td>
<td>22</td>
<td>54</td>
<td>62</td>
<td>160</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CIXI004</td>
<td>105</td>
<td>17</td>
<td>22</td>
<td>27</td>
<td>13</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CIXI014</td>
<td>6</td>
<td>11</td>
<td>37</td>
<td>57</td>
<td>18</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CIXI006</td>
<td>5</td>
<td>29</td>
<td>56</td>
<td>32</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CIXI007</td>
<td>547</td>
<td>234</td>
<td>24</td>
<td>11</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>DELP010</td>
<td>288</td>
<td>11</td>
<td>27</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>DELP004</td>
<td>153</td>
<td>4</td>
<td>33</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>DERB002</td>
<td>1965</td>
<td>552</td>
<td>33</td>
<td>148</td>
<td>45</td>
<td>175</td>
<td>24</td>
<td>33</td>
<td>13</td>
<td></td>
</tr>
<tr>
<td>TYPH004</td>
<td>47</td>
<td>53</td>
<td>55</td>
<td>16</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>TYPH068</td>
<td>190</td>
<td>6</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Chapter 6

Vertical stratification of herbivore and feeding-guild assemblages of Auchenorrhyncha along altitudinal gradients in tropical and subtropical forests in Australia.

6.1. Abstract

1. There is some debate as to how arthropod species are distributed between the ground layers and canopy in tropical forests. Such studies suggest that arthropods are as diverse as or more diverse in the canopy than the understorey. How exactly species are distributed vertically in forest stands and how this distribution changes along altitudinal and latitudinal gradients has been little explored. Herbivores comprise a large proportion of insects in tropical forests and yet their distribution among forest strata and even along altitudinal gradients has been poorly documented.

2. These gaps are addressed here by investigating species distribution of Auchenorrhyncha herbivores and their feeding-guilds between canopy and understorey along altitudinal gradients, in order to determine if the number of herbivore species and feeding-guilds vary between forests strata and between altitudes.

3. Auchenorrhyncha adults were collected over two sampling seasons using light traps which were placed in the understorey and canopy at each site along a subtropical and tropical altitudinal gradient. The tropical transect ranged from 400-
1200m a.s.l. and the subtropical transect from 300-1100m a.s.l., with sample sites at altitudinal intervals of approximately 200m on both transects.

4. Across altitudes and forest strata, I collected a total of 243 species of Auchenorrhyncha from a total of 5689 individuals within the tropical transect and 15125 individuals representing 159 species within the subtropical transect. The relationship between species richness and altitude was significant for each forest strata within each transect. Also, I found that, canopy and understorey communities contribute equally to Auchenorrhyncha assemblages. Feeding-guild assemblages were dominated by phloem-feeders, both at each altitude and across altitudes. Insect community similarity decreases with altitude and the closer the communities are to each other, the more similar they are in species composition.

**Keywords**: arthropods, diversity, assemblage composition, altitude, vertical stratification, herbivores, feeding-guilds, Auchenorrhyncha.

### 6.2. Introduction

The upper canopy of tropical forest is where the atmosphere meets the biosphere and hence is where most photosynthesis and flowering occurs (Ozanne *et al.* 2003). It also harbours a major portion of the arthropods and other organisms that are dependent on these resources (Wardhaugh 2014; Wardhaugh *et al.* 2013). Lack of suitable access has meant that canopy has been poorly studied until recently (Shaw 2004). There has been a greater focus on canopy arthropods since that time (see Basset *et al.* 2003a; Dial *et al.* 2006; Stork *et al.* 1997). These studies suggest that while arthropods are generally
equally or less diverse in the understorey than canopy in tropical forests (Brehm 2007; Stork & Grimbacher 2006; Ulyshen et al. 2010), the opposite pattern is frequently observed in temperate forests (Coots et al. 2012; Hirao et al. 2009; Ulyshen & Hanula 2007). These results notwithstanding, there remain many considerable unanswered questions about canopy-ground patterns, in no small part because of the wide variety of forest types and insect groups remaining to be investigated (Charles & Basset 2005; Maguire et al. 2014; Vance et al. 2007). To date, few studies have described differences in vertical stratification of arthropod diversity in forest stands along altitudinal and latitudinal gradients (Ashton et al. 2016). Arthropods, because of their small size and ectothermic physiology are particularly sensitive to climate change (Thomas et al. 1994) and should respond to local and regional gradients in temperature and rainfall (Monte-Alegre et al. 2005; Progar & Schowalter 2002). Variation among species in response to environmental gradients (Schowalter et al. 1999) and vertical stratification within and among altitudes and latitudes, contributes also to species diversity at the wider landscape level.

Terrestrial food webs in association with living plants may well represent 75% of global terrestrial biodiversity, and about 40% of these food networks are plant-herbivore food webs (Godfray et al. 1999; Price 2002; Wilson 1988). Forest canopies contain a large fraction of the green biomass of any forest and are largely responsible for the forests’ primary productivity. In spite of this, few studies have documented the distribution of herbivores and their feeding-guilds among forests strata, especially within heterogeneous canopy crowns (Basset et al. 2001; Corff & Marquis 1999; Grimbacher & Stork 2007). The distribution of herbivorous insects may be affected by several factors, including vertical gradients in physio-chemical environmental factors, many of
which are strongly inter-correlated (i.e. from the understorey to the upper canopy) (Basset et al. 2001; Schowalter et al. 1986). The implications for the distribution of insect herbivores along vertical gradients in tropical forests may be profound. Insect herbivores foraging and feeding in the upper canopy encounter serious dessication challenges during the day and water condensation at night (Basset et al. 2001). Further, the high intensity of light in the canopy can alter leaf quality and, in consequence, influence the feeding behaviour and oviposition patterns of herbivores (Basset 1991; Lowman 1992a). Conversely, the availability of young leaves is greater due to increased leaf production, in the upper canopy than understorey. Young leaves have been shown to be more palatable and nutritious than mature leaves (Basset et al. 1992; Lowman 1992b; Novotny & Basset 1998).

Since the distribution of herbivores along forest vertical gradients has been rarely determined, it is difficult to make generalizations. In addition, due to the difficulty of sampling and identifying herbivore species, no consistent pattern of vertical stratification has been observed, but three different patterns have emerged; (i) some species are more abundant lower in the canopy (Kato et al. 1995), (ii) others are abundant higher within the canopy (Meagher & Hull 1987), and (iii) others are distributed equally (reviewed by Brown et al. 1997).

Herbivorous insects, in particular the Auchenorrhyncha, and their feeding-guilds are poorly studied and documented in the tropics. However, potentially this group is an excellent subject of study since they rely on continuous flows of nutrients within the xylem and phloem and have close relationships with their host plants (Dem et al. 2013). Accordingly, along ecological gradients, their distribution will likely be mostly affected

In this study I test the following inter-connected hypotheses using standard community level descriptors.

1. Herbivore and feeding-guild species richness in each forest stratum decreases with altitude.
2. Species richness of herbivores in the canopy is greater than in the understorey.
3. There were no differences in species richness among feeding-guilds at each altitude.
4. Species richness within feeding-guilds differs both between forest strata and among altitudes.
5. There were no differences in insect community similarity among altitudes for canopy and understorey assemblages.

6.3. Methods

6.3.1. Study sites and sampling design - refer to Chapter 4 (sub-chapter 4.1.)

6.3.2. Adult insect sampling – refer to Chapter 4 (sub-chapter 4.2, Light trapping).

6.3.3. Specimens sorting and identification - refer to Chapter 4 (sub-chapter 4.3)
6.3.4. Data analyses

At each of the altitudinal gradient, specimens from both sampling occasions from each altitude were pooled for analyses. In addition, respective forest stratum from each altitude had data from all four plots pooled for analyses.

Relationships between altitude and species richness recorded for forest strata (canopy or ground) were examined using regression techniques and species-specific correlations were tested by Pearson’s correlation analysis. To test for differences in species richness between understorey and canopy communities, a Two-sample T-test was used. A One sample T-test was used to test for differences in species richness among feeding-guilds at each altitude. Further, differences in species richness of particular feeding-guilds among altitudes and between forest strata, as well as the effect of interaction between altitude and forest strata were tested using repeated measure analyses of variance. This form of analysis seeks significant effects for each of the variables separately. All the above tests were calibrated using the XLSTAT version 5.0.1 software.

Community similarity between adjacent altitudes were compared and described in terms of the number of shared and unique species at low and high altitudes for each forest stratum. In addition, the proportion of species in each feeding-guild across altitudes was compared again in terms of the number of shared and unique species across the canopy and understorey. Further, exploration of similarity was carried out by calculating Sorensen and Chao-Sorensen (Colwell 2013) similarities between canopy and understorey communities at different altitudes for each transect. Chao-Sorensen
similarity index attempts to take into account non-observed species based on the proportion of singletons and doubletons sampled from each of the forest stratum (Chao et al. 2005). The relationships between altitude, in terms of altitudinal differences and canopy, and understorey respectively were correlated using Pearson’s correlation and the significances of correlations in all cases were tested using Mantel Test (Mantel 1967). Non-metric multidimensional scaling (NMDS) ordinations were used to characterize similarities among samples across altitudes and forest strata for the tropics and subtropics respectively. NMDS ordinations of both regions (tropics and subtropics) combined were also constructed, considering latitude, altitude and forest stratum as factors affecting community similarities. First, raw values were log-transformed in order to decrease the effect of highly abundant species. All these ordinations were based on prior calculations of Bray-Curtis indices from which PCoA (Principle Coordination Analyses) plots were constructed. To test for significance differences in community assemblages among altitudes and between forest strata within each region, PERMANOVA with a post hoc test was used to test for the interactive effect of altitude and forest stratum on community similarities. The significances of groupings and differences within the ordinations were tested using PERMANOVA (permutation-based analysis of variance) procedure of Anderson et al. (2008), using Monte Carlo tests from 4 999 permutations. PRIMER v6 statistical software (Clarke & Gorley 2006; Anderson, Gorley & Clarke 2008) was used to perform the ordinations.
6. 4. Results

Community composition and assemblages

The total number of morphospecies recorded from light trap samples across all altitudes from both transects was 318, representing 20 813 individuals. Canopy samples at both transects produced 246 species from a total abundance of 13 349. Total species richness of Auchenorrhyncha from the understorey light traps for both transects was 7 464 individuals representing 265 species. There were 17 families represented in the tropical and subtropical transects: more than 70% of them occurred in both transects. Fifteen families were recorded from the tropical transect and 14 families from the subtropical transect. The families Cicadidae, Cercopidae and Membracidae were recorded only from the tropical transect and, Aphrophoridae and Nogodinidae only from the subtropical transect.

The Mt Lewis transect

For the tropical transect, species richness across altitudes and forest strata was 243. Species richness from the canopy was 185 from a total of 3 091 individuals. The understorey assemblages was represented by 2 597 individuals of 199 species. All families, except Dictyopharidae were shared between canopy and understorey across all altitudes. Individuals of Dictyopharidae were only present in the canopy, particularly at the low- and mid-altitudes. There are significant correlations between altitude and the number of species recorded at the canopy and understorey levels. Species richness at both canopy and understorey decreases with altitude (Pearson’s correlation: canopy, \( r = 0.98, R^2 = 0.97, N=5, P<0.05 \); understorey, \( r = -0.80, R^2 = 0.64, N =5, P<0.05 \), Figure
6.1). The same trend is observed for species abundance against altitude for the canopy samples (Pearson’s correlation, \( r = -0.94, N =5, P<0.05 \)). Species abundance for understorey samples, however, was not significantly correlated with altitude. Here there appears to be a mid-altitudinal peak (Pearson’s correlation, \( r = 0.003, N =5, P>0.05 \)). The number of species did not differ between canopy and understorey at each altitude (Two-sample T-test = 2.78, d.f =4, P>0.05, Figure 6.2).

Generally, the observed trend was that species richness of canopy and understorey communities among different altitudes showed that canopy communities were species rich at lower altitudes, and the understorey communities were species rich at higher altitudes. All three feeding-guilds of Auchenorrhyncha were present across all altitudes and in both the canopy and understorey. The order of dominance of feeding-guilds across all altitudes was phloem-feeders > mesophyll-feeders > xylem-feeders, with species proportions of 0.79, 0.18 and 0.03 respectively. There were significant differences in species richness among feeding-guilds at each altitude, where the phloem feeding-guild had a higher proportion of species than xylem and mesophyll feeding-guilds at each altitude (One-sample T-test = 2.78, d.f =4, P<0.05, Figure 6.3a). Further, assemblages of each feeding-guild were similar, both among altitudes and between forest strata (Repeated measures ANOVA: altitude, \( F = 4.94, P>0.05 \); forest strata, \( F = 0.01, P>0.05 \), Figure S6.1). In support of these significances, the effect of the interaction between altitude and forest strata produced a similar pattern (Repeated measures ANOVA, \( F = 0.09, P>0.05 \)).
The number of species estimated by ACE species richness estimator, in the canopy and understorey at each altitude, respectively showed an overall species richness of two and three species less than the observed number of species (Table S6.1). Estimation of species richness within feeding-guilds at each altitude, showed an overall species richness of 27 and 13 more species for phloem- and mesophyll-feeders respectively, and none for the xylem-feeders, to the observed species richness for each guild (Table S6.2).

**Border Ranges transect**

Within the subtropical transect, overall species richness across altitudes and forest strata was 159, representing 15 125 individuals. Species richness within the canopy was 120 with an abundance of 10 258 individuals and at the ground, a total of 124 species representing 4 867 individuals was recorded. Both canopy and ground shared more than 50% of the total species across altitudes, with 22% and 25%, respectively, unique to canopy and ground. All families, except the Dictyopharidae, Fulgoridae and Meenoplidae were shared between canopy and understorey across all altitudes. These unique families were only present within canopy communities and are only sampled from lower altitudes. The correlation between altitude and the number of species for each forest strata showed a monotonic pattern (Pearson’s correlation: canopy, \( r = -0.94, R^2 = 0.89, N=5, P<0.05 \); understorey, \( r = -0.91, R^2 = 0.83, N=5, P<0.05 \), Figure 6.1). In a similar fashion, the relationship between altitude and species abundance for both canopy and understorey showed weaker, but significant correlations (Pearson’s correlation: canopy, \( r = -0.77, R^2 =0.60, N =5, P<0.05 \); understorey, \( r = -0.75, R^2 =0.56, N=5, P<0.05 \)). Although, there were more species in the canopy than understorey, the results were not statistically different (Two-sample T-test = 2.78, d.f = 4, P>0.05,}

85
Figure 6.2). All three feeding-guilds were present at each altitude and in both canopy and understorey communities. The order of dominance of feeding-guilds in the pooled community is phloem-feeders > mesophyll-feeders > xylem-feeders, with species proportions of 0.74, 0.25 and 0.01 respectively. At each altitude, there were more phloem-feeding species than other feeding-guilds (One-sample T-test = 2.78, d.f = 4, P<0.05, Figure 6.3b). Altitude did not have a significant effect on the number of species within feeding-guilds, but species richness within each feeding-guild was affected by forest strata (Repeated measures of ANOVA: altitude, F =250.78, d.f =4, P<0.05; forest strata, F = 0.008, d.f = 4, P>0.05, Figure S6.2). Further, the combined effect of altitude and forest strata showed similar effect to that impacted by forest strata.

The number of species estimated by ACE species richness estimator, in the canopy and understorey at each altitude, respectively showed an overall species richness of 70 and 67 species more than the observed species richness for each forest strata (Table S6.1). Further, estimation of species richness of feeding-guilds at each altitude, showed an overall species richness of 21 and 6 species more, respectively for phloem- and mesophyll-feeders and none for the xylem-feeders, to the species richness observed for each feeding-guild (Table S6.2).
Figure 6.1. The relationship between altitude and species richness at the canopy and understory levels recorded at the tropical (a) and subtropical (b) transects. Both relationships showed significant correlations between the two variables for both canopy and understory assemblages. Filled-dots represent canopy samples and non-filled dots represent understory samples.

Figure 6.2. Distribution of canopy and understory assemblages at each altitude observed for each transect (a, b). The number of species did not differ between canopy and understory at each altitude (Two-sample T-test: tropical transect, T-test = 2.78, d.f = 4, P < 0.05; subtropical transect, T-test = 2.78, d.f = 4, P < 0.05).
Figure 6.3. Distribution of feeding-guild assemblages at each altitude within the tropical transect and subtropical transects. Phloem-feeding species were dominant than xylem- and mesophyll-feeding species (one-sample T-test = 2.78, d.f =4, P<0.05, tropics; one-sample T-test = 2.78, d.f.=4, P<0.05, subtropics).

Community similarity

Turnover of insect species between adjacent altitudes was examined, particularly with respect to shared and unique species at low and high altitudes, for each forests stratum. The number of shared and unique species starts to decrease between the 400m x 600m levels for the canopy samples and the 600m x 800m for the understorey samples on the tropical transect (Figure 6.4). At the subtropical transect, the number of shared and unique species starts to decrease at the 300m x 500m comparison for both canopy and understorey assemblages (Figure 6.4). Also, beta diversity of feeding-guild species across altitudes are compared and described related to the shared and unique species between canopy and understorey. Phloem- and xylem-feeding guilds each shared more than 50% of their species between canopy and understorey, and mesophyll-feeding
guild had most of its species present only in the canopy on the tropical transect. Interestingly, all xylem-feeding species present in the canopy are also present at the understorey level (Figure 6.5). At the subtropical transect, phloem- and mesophyll-feeding guilds each had 50 percent of shared species, and almost equal proportion of the remaining species unique to each forest strata in their respective guild. The xylem-feeding guild, on the other hand, had a 100% species shared between canopy and understorey (Figure 6.5). Insect community similarity between altitudes decreases with increasing altitudinal differences for both canopy and understorey communities within each transect. Sorensen similarity indicated that communities closer to each other had similar composition than those further away from each other (Pearson’s correlation: tropical transect, \( r = 0.80, N = 5, P < 0.05 \), Figure 6.6i; subtropical transect, \( r = 0.74, N = 5, P < 0.05 \), Figure 6.6iii, Mantel test). Chao-Sorensen similarity for the tropical transect showed a similar pattern to the Sorensen similarities (Pearson’s correlation, \( r = 0.80, N = 5, P < 0.05 \), Mantel Test, Figure 6.6ii). There was no significant difference in similarities between altitudes for both canopy and understorey communities within the subtropical transect (Pearson’s correlation, \( r = -0.09, N = 5, P > 0.05 \), Mantel Test, Figure 6.6iv).
Figure 6.4. The number of shared and unique species recorded at the canopy and understorey levels. Distribution for pairs of adjacent altitudes at the tropical and subtropical transects.
Figure 6.5 Proportion of shared and unique species for each feeding-guild between canopy and understorey, across altitudes at each study location (a, b).
Figure 6.6. Sorensen and Chao-Sorensen insect similarities between altitudes for the canopy and understorey communities within the tropical (i, ii) and subtropical transect (iii, iv).

Dissimilarity matrices of community assemblages of Auchenorrhyncha between latitudes (regions) were different, however, patterns of altitudinal stratification were similar between the two regions Canopy and understorey differences in similarity showed a distinct separation at the highest altitude at the subtropical transect. The opposite pattern was observed for the tropical transect, where the lowest altitude had a distinct community composition from the rest of the altitudinal sites ((Figure S6.3, Table S6.3). For the subtropical transect, interaction effects between altitude and forest
stratum on community similarities was significant (Table 6.1, Figure 6.7). Post-hoc analysis showed that canopy and understorey were significantly different at 1100m plot sites only (Table S6.4). Unlike the subtropical transect, the tropical transect showed marginally significant interaction effects (Table 6.2, Figure 6.8). Poct-hoc analysis showed that canopy and understorey strata were significantly different at 400m plot sites only (Table S6.5).

Table 6.1. Summary of the pair-wise PERMANOVA test for altitudes, strata and the interaction effect of altitude and stratum for the subtropical transect.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>SS</th>
<th>MS</th>
<th>Pseudo-F</th>
<th>P(perm)</th>
<th>Unique perms</th>
</tr>
</thead>
<tbody>
<tr>
<td>Altitude</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(nAl)</td>
<td>4</td>
<td>33260</td>
<td>8315.1</td>
<td>6.0457</td>
<td>0.0002</td>
<td>4969</td>
</tr>
<tr>
<td>Stratum (St)</td>
<td>1</td>
<td>5963.6</td>
<td>5963.6</td>
<td>4.336</td>
<td>0.0002</td>
<td>4971</td>
</tr>
<tr>
<td>nAlxSt</td>
<td>4</td>
<td>10300</td>
<td>2575.0</td>
<td>1.8722</td>
<td>0.0002</td>
<td>4963</td>
</tr>
<tr>
<td>Res</td>
<td>30</td>
<td>41261</td>
<td>1375.4</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>39</td>
<td>90785</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Figure 6.7. NMDS ordinations matrices of species composition among samples among altitudes and forest stratum at each plot site within the subtropical transect.
Table 6.2. Summary of the pair-wise PERMANOVA test for altitudes, strata and the interaction effect of altitude and stratum for the subtropical transect.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>SS</th>
<th>MS</th>
<th>Pseudo-F</th>
<th>P(perm)</th>
<th>Unique perms</th>
</tr>
</thead>
<tbody>
<tr>
<td>nAltitude (nAl)</td>
<td>4</td>
<td>35352</td>
<td>8838.1</td>
<td>4.9266</td>
<td>0.0002</td>
<td>4954</td>
</tr>
<tr>
<td>Stratum (St)</td>
<td>1</td>
<td>6286.3</td>
<td>6286.3</td>
<td>3.5042</td>
<td>0.0002</td>
<td>4977</td>
</tr>
<tr>
<td>nAl x St</td>
<td>4</td>
<td>8576.7</td>
<td>2144.2</td>
<td>1.1952</td>
<td>0.0848</td>
<td>4952</td>
</tr>
<tr>
<td>Res</td>
<td>30</td>
<td>53818</td>
<td>1793.9</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>39</td>
<td>1.04E+05</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Figure 6.8. NMDS ordinations matrices of species composition among samples among altitudes and forest stratum at each plot site within the subtropical transect.

6.5. Discussion

This is the first study on altitudinal and vertical stratification effects on species and feeding-guilds assemblages of Auchenorrhyncha in Australian rainforest. The results provide strong support for three of my hypotheses, with quantitative measures of species and feeding-guilds assemblages all affected by altitude and forest strata as separate factors and also the interactive effect of both factors. I did not, however, prove my hypothesis of greater species richness in the canopy than understorey, and that the
number of species within feeding-guilds would be similar between canopy and understorey and among altitudes. The significant effect of altitude on the number of species for each forest stratum in both study locations reflect differences in environmental conditions (Lawton et al. 1987; reviewed by McCoy 1990), although patterns in vertical stratification were similar between both regions As one moves towards higher altitudes, climatic conditions become more challenging and less suitable for lowland species. On the other hand, species’ abundance of ground assemblages were not affected by altitude and my best explanation for this is that the trends were a result of idiosyncratic, presence of a few extraordinary abundant species at each altitude, such as a species from Achilidae family at 800m and 1000m, a Cicadellidae species at 400m and a Cercopidae species at 1200m. McCoy (1990) showed a similar result for Auchenorrhyncha except Cicadellidae, displaying no altitudinal effect on species abundance. A possible cause is that perhaps there were many more rare species occurring at only some altitudes. Likewise, a similar explanation could be applied to forest stratification along altitudinal gradients, where most species may tend to be present at the canopy than the understorey level. The canopy assemblages at the tropical transect, were more species-rich at the lower altitudes than the higher altitudes. My results were not supported by other studies that investigated vertical stratification of insects in different forest types (Coots et al. 2012; DeVries et al. 1997). Possible explanation for this pattern would be a result of extreme exposure to wind and cloud cover at higher elevations (Chazdon & Fetcher 1984) and cloud cover, and less towards light factor (Davis & Sutton 1998).

Two main patterns of species richness between canopy and understorey have been observed by others. First, that species richness is higher in the understorey than canopy
(DeVries et al. 1997; Larrivée & Buddle 2009; Schulze et al. 2001), and second, that species richness is higher in the canopy than understory (Basset et al. 2001; Charles & Basset 2005; Roisin et al. 2006). My results of vertical stratification of Auchenorrhyncha between forest strata at each altitude conformed to neither of these patterns, but showed a non-significant difference in species richness between the two strata. Similarities in microclimate and uniformity in vegetation columns are potential contributing factors (Wardhaugh et al. 2012; Yoda 1974), in that, a large proportion of species at each plot site, particularly canopy species, were able to forage between canopy and understory when necessary (Southwood et al. 2005). The effect of tourist species could also affect community composition and similarity (Ødegaard 2004) between canopy and understory. Further, sampling techniques employed may have affected the outcome of the community composition between forest strata. Using only a single sampling method may not sampled the majority of the Hemiptera species Moir et al., (2005). It is important to employ a combination of sampling techniques and also determine which combination of techniques are best, to maximize the richness of Hemiptera collected (Buffington & Redak 1998; Standen 2000). Several factors, such as purpose of study and location (Cranston & Trueman 1997; New 1998), vegetation structure (Moir et al. 2005; Novotny 1992) and time (Moir et al. 2005) are equally important to consider when choosing sampling methods in order to maximize sampling efficiency.

Feeding-guilds showed very distinct variation in species-richness, both at each altitude and across altitudes. Other studies have supported my results indicating that there are more phloem-feeders than xylem- and mesophyll-feeders feeding on forest plants (Dem et al. 2013; Basset 1999b; Novotny & Basset 1998). Factors such as, effects of host
plant diversity and quality (Perner et al. 2005; Sedlacek et al. 1988), play key-roles in
determining diversity of herbivorous insects and their feeding-guilds. The majority of
Auchenorrhyncha species prefer to feed on phloem rather than xylem and leaf
mesophyll cells, basically because of the higher nutrient content in phloem. In addition,
unlike the specialist mesophyll-feeders, phloem-feeders are often generalists (Baje et al.
2014), feeding on many plant species. I found that there were few xylem-feeders across
all altitudes. This may be due to the fact that humidity level is very high on mountains
and increases with altitude. Because xylem-feeders have to cope with xylem pressure
tension, and also protect their eggs and nymphs in spittle-foams, their energy is all used
up trying to withstand the cold environment as well as cope with xylem pressure
(Andersen et al. 1992; Brodbeck et al. 1993; Novotny & Wilson 1997; Redak et al.
2004)., therefore less energy is spent on reproduction, resulting in a low fecundity
success It may also be that, through evolutionary processes, xylem-feeders speciate,
coupled with shifts in their host plants (Price 2007). Since xylem-feeders are specialists,
the low species richness may be a result of narrow diet-breath (Dem et al. 2013;
Forister et al. 2015; Novotny & Wilson 1997). Altitude and forest strata respectively
had no significant effect on species assemblages per feeding-guild, except at the
subtropical transect, the number of species per feeding-guild was affected by forest
strata. This may suggest that community assemblages were affected by the interactive
effect of altitude and forest strata. Studies have suggested that there is a distinct canopy
fauna and that surveys conducted only on understorey biota missed a substantial
component of forest biodiversity, probably due to the differences in the light
environment among forest vertical strata (Beck & Schulze 2000; Hill et al. 2001) and
the larger quantities of diverse resources, i.e. young foliage, fruits and flowers at the
canopies (Lowman & Moffett 1993).
Community similarity, the number of species shared between altitudinal zones, decreases with increasing altitude, due to differences in environment becoming larger towards higher altitudes, therefore each community having its own unique species (Andrew & Hughes 2005). However, with increasing forest heights, all three feeding guilds shared more than 50% of their species between canopy and understorey. In general, there was no difference in community similarity between canopy and ground at each of the plots, which leads to the overall similarity in the pooled community.

Environmental factors, such as plant composition and microclimate change at a constant rate between adjacent or nearby micro-communities, which resulted in a higher proportion of species being shared. Xylem-feeding guild showed an interesting, yet different pattern in the composition of unique species. At the tropical transect, all xylem-feeders present in the canopy were also present in the understorey, which comprised only of species from the Cicadidae and Cercopidae families. Biologically, Cicadidae species lay their eggs in the ground and emerge to the surface when matured (Dardar et al. 2012; Maier 1982). Hence one would find them mostly in the understorey. While at the subtropical transect, the only two xylem-feeding species, which were both Aphrophoridae species, were both shared between forest strata. Because xylem-feeders lay their eggs and protect their nymphs in spittle-foams while undergoing development (Biedermann 2003), these species tend to move between canopy and understorey levels, in order to locate suitable egg deposition locations or possibly trying to locate quality food resources, since their feeding preferences are largely determined by differences in xylem nutrient content among plant species (Andersen et al. 1992; Brodbeck et al. 1990) and plant parts (Horsfield 1977), and also respond to diurnal changes in xylem chemistry (Brodbeck et al. 1993). The proportion of variability in community composition among samples across altitudes, sites and forest strata, generally showed
very strong gradients for both tropical and subtropical transects. Communities from both regions, and among altitudes showed clear separation in species composition. This could be a result of differences in plant composition and abiotic factors among altitudes (Sobek et al. 2009) or latitudes or resource quantity (Lowman & Moffett 1993) and quality among altitudes and between forest strata. The distinct insect community at the 1100m plots may be due to mountain ecosystem isolation, resulting especially from differences in abiotic factors. Also, the distinct community composition at the 400m plots was likely due to differences in plant composition and vegetation layers.

Differences in community similarities between samples may also be affected by species abundances. Several shared species between any two of the altitudes or subsets of altitudes or between forest strata, tend to be inclined towards the altitude (s) or stratum to which they were most abundant. Other reasonable explanations, particularly related to similarities among plot sites were due to forest disturbances in the understorey or canopy either within the plot or the immediate surroundings.

Conclusions

I have demonstrated that like any other insect groups, species richness of insect herbivores decreases in the canopy and understorey along altitudinal gradients, showing a strong gradient effect, consistent across the two altitudinal gradients. Comparatively, species richness of herbivores between forest strata did not show a strong vertical gradient. Besides other non-herbivore insect groups, insect herbivores present a very interesting phenomena, because not only do they respond to variability in environmental conditions between forest strata, but also to biological conditions, most importantly plant composition and host plant quality. Auchenorrhyncha makes an excellent study group because they, with the exception of mesophyll-feeders, depend
entirely on live plants, and the respective feeding-sites of their feeding-guilds display variation in nutrient quality and quantity. By measuring species diversity of herbivores along a vertical gradient, this study contributes an extra information on Auchenorrhyncha to the few studies that documented diversity distribution of insect herbivores and feeding-guilds between canopy and understorey.
Figure S6.1. Distribution of feeding-guilds assemblages among altitudes and between canopy and understory at the tropical transect. The number of species per feeding-guild did not differ, both among altitudes and between forest strata.

Figure S6.2. Distribution of feeding-guilds assemblages among altitudes and between forest strata at the subtropical transect. The number of species per feeding-guild differed among altitudes, but did not differ between canopy and understory.
**Table S6.1.** ACE species richness estimator. Mean number of species at each altitude for the canopy and understorey communities for the respective transect.

<table>
<thead>
<tr>
<th>Transect</th>
<th>Altitude (m)</th>
<th>Observed</th>
<th>ACE Mean</th>
<th>ACE SD</th>
<th>Observed</th>
<th>ACE Mean</th>
<th>ACE SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>tropics</td>
<td>400</td>
<td>121</td>
<td>121.59</td>
<td>±49.28</td>
<td>83</td>
<td>179.32</td>
<td>±32.24</td>
</tr>
<tr>
<td></td>
<td>600</td>
<td>106</td>
<td>211.48</td>
<td>±25.18</td>
<td>95</td>
<td>231.2</td>
<td>±18</td>
</tr>
<tr>
<td></td>
<td>800</td>
<td>81</td>
<td>245.51</td>
<td>±15.97</td>
<td>87</td>
<td>257.88</td>
<td>±13.2</td>
</tr>
<tr>
<td></td>
<td>1000</td>
<td>37</td>
<td>267.88</td>
<td>±10.15</td>
<td>73</td>
<td>276.19</td>
<td>±7.09</td>
</tr>
<tr>
<td></td>
<td>1200</td>
<td>24</td>
<td>282.95</td>
<td>±4.8</td>
<td>49</td>
<td>288.33</td>
<td>0</td>
</tr>
<tr>
<td>sub-tropics</td>
<td>300</td>
<td>99</td>
<td>67.88</td>
<td>±39.93</td>
<td>97</td>
<td>106.08</td>
<td>±42.01</td>
</tr>
<tr>
<td></td>
<td>500</td>
<td>59</td>
<td>134.96</td>
<td>±37.15</td>
<td>50</td>
<td>152.63</td>
<td>±28.51</td>
</tr>
<tr>
<td></td>
<td>700</td>
<td>29</td>
<td>163.15</td>
<td>±26.34</td>
<td>26</td>
<td>169.56</td>
<td>±25.51</td>
</tr>
<tr>
<td></td>
<td>900</td>
<td>33</td>
<td>179.61</td>
<td>±17.98</td>
<td>34</td>
<td>186.08</td>
<td>±10.42</td>
</tr>
<tr>
<td></td>
<td>1100</td>
<td>6</td>
<td>190.33</td>
<td>±6.64</td>
<td>7</td>
<td>191.26</td>
<td>0</td>
</tr>
</tbody>
</table>

**Table S6.2.** ACE species richness estimator. Mean number of species of feeding-guilds at each altitude for both forest strata for the respective transect.

<table>
<thead>
<tr>
<th>Transect</th>
<th>Altitude (m)</th>
<th>Observed</th>
<th>ACE Mean</th>
<th>ACE SD</th>
<th>Observed</th>
<th>ACE Mean</th>
<th>ACE SD</th>
<th>Observed</th>
<th>ACE Mean</th>
<th>ACE SD</th>
<th>Observed</th>
<th>ACE Mean</th>
<th>ACE SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>tropics</td>
<td>400</td>
<td>120</td>
<td>127.9</td>
<td>±23.8</td>
<td>3</td>
<td>7.11</td>
<td>±1.48</td>
<td>24</td>
<td>33.95</td>
<td>±15.48</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>600</td>
<td>113</td>
<td>168.2</td>
<td>±13.52</td>
<td>5</td>
<td>8.55</td>
<td>±1.59</td>
<td>24</td>
<td>46.33</td>
<td>±9.26</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>800</td>
<td>93</td>
<td>191.1</td>
<td>6.43</td>
<td>5</td>
<td>8.2</td>
<td>±1.68</td>
<td>24</td>
<td>50.11</td>
<td>±7.55</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>1000</td>
<td>73</td>
<td>206.8</td>
<td>±7.29</td>
<td>5</td>
<td>8.2</td>
<td>±0.41</td>
<td>6</td>
<td>54.47</td>
<td>±7.22</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>1200</td>
<td>46</td>
<td>217.9</td>
<td>0</td>
<td>5</td>
<td>8</td>
<td>0</td>
<td>6</td>
<td>56.81</td>
<td>0</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>sub-tropics</td>
<td>300</td>
<td>92</td>
<td>60.72</td>
<td>±34.83</td>
<td>1</td>
<td>1.37</td>
<td>±0.49</td>
<td>37</td>
<td>20.76</td>
<td>±15.07</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>500</td>
<td>60</td>
<td>94.37</td>
<td>±26.98</td>
<td>2</td>
<td>1.74</td>
<td>±0.44</td>
<td>10</td>
<td>31.36</td>
<td>±14.19</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>700</td>
<td>33</td>
<td>114.1</td>
<td>±15.34</td>
<td>0</td>
<td>1.98</td>
<td>±0.14</td>
<td>6</td>
<td>37.44</td>
<td>±13.07</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>900</td>
<td>35</td>
<td>126.7</td>
<td>±11.38</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td>8</td>
<td>41.89</td>
<td>±9.83</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>1100</td>
<td>9</td>
<td>138.8</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>46.18</td>
<td>0</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table S6.3. Summary of the pair-wise PERMANOVA test for latitudes, altitudes and strata, and their interaction effects for both transects combined.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>SS</th>
<th>MS</th>
<th>Pseudo-F</th>
<th>P(perm)</th>
<th>Unique perms</th>
</tr>
</thead>
<tbody>
<tr>
<td>Region (Re)</td>
<td>1</td>
<td>60155</td>
<td>60155</td>
<td>37.961</td>
<td>0.0002</td>
<td>4986</td>
</tr>
<tr>
<td>Altitude (nAl)</td>
<td>4</td>
<td>37381</td>
<td>9345.3</td>
<td>5.8974</td>
<td>0.0002</td>
<td>4945</td>
</tr>
<tr>
<td>Stratum (St)</td>
<td>1</td>
<td>7598.3</td>
<td>7598.3</td>
<td>4.7949</td>
<td>0.0002</td>
<td>4962</td>
</tr>
<tr>
<td>RexnAl</td>
<td>4</td>
<td>31232</td>
<td>7807.9</td>
<td>4.9272</td>
<td>0.0002</td>
<td>4951</td>
</tr>
<tr>
<td>RexSt</td>
<td>1</td>
<td>4651.5</td>
<td>4651.5</td>
<td>2.9353</td>
<td>0.0002</td>
<td>4960</td>
</tr>
<tr>
<td>nAlxSt</td>
<td>4</td>
<td>9473.1</td>
<td>2368.3</td>
<td>1.4945</td>
<td>0.0006</td>
<td>4950</td>
</tr>
<tr>
<td>RexnAlxSt</td>
<td>4</td>
<td>9403.6</td>
<td>2350.9</td>
<td>1.4835</td>
<td>0.0004</td>
<td>4950</td>
</tr>
<tr>
<td>Res</td>
<td>60</td>
<td>95080</td>
<td>1584.7</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>79</td>
<td>2.55E+05</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Figure S6.3. NMDS ordinations matrices of species composition among latitudes, altitudes, plot sites and forest strata for the subtropical and tropical transects combined. BR – stands for Border Ranges NP (subtropical transect); ML – stands for Mt Lewis NP (tropical transect).
**Table S6.4.** Summary of the pairwise *post-hoc* PERMANOVA test between canopy and understorey communities at each altitude at the subtropical transect. Respective canopy and understorey samples at each plot site per altitude were combined.

<table>
<thead>
<tr>
<th>Altitude (metres)</th>
<th>300</th>
<th>500</th>
<th>700</th>
<th>900</th>
<th>1100</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Comparison</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>canopy x understorey</td>
<td>1.11</td>
<td>0.32</td>
<td>1.21</td>
<td>0.22</td>
<td>1.09</td>
</tr>
</tbody>
</table>

**Table S6.5.** Summary of the pairwise *post-hoc* PERMANOVA test between canopy and understorey communities at each altitude at the tropical transect. Respective canopy and understorey samples at each plot site per altitude were combined.

<table>
<thead>
<tr>
<th>Altitude (metres)</th>
<th>400</th>
<th>600</th>
<th>800</th>
<th>1000</th>
<th>1200</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Comparison</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>canopy x understorey</td>
<td>1.70</td>
<td>0.04</td>
<td>1.47</td>
<td>0.09</td>
<td>1.23</td>
</tr>
</tbody>
</table>
Chapter 7

Auchenorrhyncha nymphs, host plants and altitude in the understorey of an Australian subtropical rainforest.

7.1. Abstract

1. The distribution and abundance of herbivorous insects on plants are affected by numerous factors, such as plant traits and the distribution and species composition of the host plants. However, the impact of environmental factors on the distribution of herbivores has been little studied. Most studies on the ecology and community structure of insects focus on adults and yet for most species the majority of the life cycle is spent in the larval/nymphal stages when most feeding occurs.

2. The abundance of Auchenorrhyncha nymphs on subtropical understorey plants was, therefore, studied along an altitudinal gradient in Australia. The altitudinal transect ranged from 300 - 1100m, with altitudinal sites at intervals of 200m. Nymphs were hand collected at each altitude and the plant species from which they were collected were identified and recorded.

3. A total of 1337 nymphs were collected from 63 plant species, representing 35 plant families, across seasons and altitudes. Overall, across altitudes, seasonal variation in nymph abundance was significant, with nymphs more abundant at the start of wet season than at the end. Further, similar results were shown for each altitude, where there were more nymphs collected at the start than at the
end of wet season. My results suggest otherwise that, altitude and plant taxa richness were not strong predictors of nymph load (i.e. average number of nymphs per plant individual sampled for each plant species). It seems more likely that factors such as, plant species abundance and leaf flush seem more reasonable predictors.

4. The limitation of this study is that it could not provide precise information on host plant specificity of individual Auchenorrhyncha species, but it provides baseline information on nymph abundance on presumed host plants at different altitudes.

**Keywords:** nymph load, host plants, plant-insect herbivore interaction, altitude, seasonal variation, understorey.

### 7.2. Introduction

The global terrestrial biodiversity constitute at least 40% plant-herbivore food webs (Price 2002). The close relationship between herbivorous insects and their host plants (Bennett & O’Grady 2012; Novotny *et al.* 2010) is a very important evolutionary aspect, as both represent the most abundant life on the planet (Schoonhoven *et al.* 2005). Depending on the manner in which herbivorous insects consume plants, they can be broadly categorized into ectophagy (including leaf chewing and sap sucking) and endophagy (including leaf mining, galling and stem boring). Ectophagous herbivory is better studied than endophagous herbivory (reviewed by Sinclair & Hughes 2010). In order to understand the impact of insect herbivores on their host plants, it is important to quantify the variation in the amount of leaf damage and the composition of insect
herbivores that feed on these plants (Marquis 1991). Despite the importance of understanding patterns of plant-herbivore interactions, comprehensive studies of tropical plant-herbivore food webs are lacking (Novotny et al. 2010). For instance, some herbivore taxa or guilds are better studied than others, which may falsely represent distribution patterns in the entire food web. In fact, more than 50% of such studies only focused on leaf-chewing herbivores, particularly caterpillars (Lewinsohn & Roslin 2008; Novotny & Basset 2005) while most other feeding-guilds, such as leaf-miners and sap-sucking insect herbivores are often neglected.

The distribution of herbivorous insects on tropical foliage is influenced by many factors, most influentially by local factors, which may be important for insect herbivores of tropical rain forests (Basset 1996). Such important factors include rainfall (Bullock & Solis-Magallanes 1990; Wilf et al. 2001), patterns of leaf production (Aide 1993; Basset 1999a), vegetation texture (Denno & Roderick 1991; reviewed by Lawton 1983) and abundance of natural enemies (Majer 1993). However, studies investigating the relative significance of these different factors on whole communities of insect herbivores on tropical vegetation are scarce (Basset 1996). On the other hand, plants from both temperate and tropical forests are badly affected, particularly on their growth, reproduction and photosynthetic capacity by insect herbivores (Kaitaniemi et al. 1999; Morrison & Reekie 1995; Mothershead & Marquis 2000).

Plant-herbivore interactions have been mostly studied in the lowlands, usually either on a single or several plant taxa at a single altitude (Dem et al. 2013), or several sampling locations with different altitudes (Novotny et al. 2005b). These studies mostly examined the effects of host plants and composition on insect herbivore dynamics, even
so beta diversity of insect herbivores on diverse vegetation also varied with altitude (Novotny et al. 2005a). This issue could be achieved by separating beta-diversity of plants from that of their insect herbivores by the analyses of herbivore assemblages on a particular plant species at different altitudes. However, such studies are surprisingly very scarce (Allison et al. 1993). On a local scale, such studies have often been neglected along altitudinal gradients until recently, where it is beginning to gain much attention, especially in the tropics (Maunsell et al. 2015). This same concept could be applied to investigate beta-diversity of herbivore assemblages on a particular plant species at different altitudes. Further, because altitudinal gradients provide steep environmental gradients, such as temperature, rainfall and predation (Givnish 1999), herbivore species turnover patterns could also be examined using these environmental factors apart from plant species turnover (Novotny et al. 2010).

The Auchenorrhyncha, including leaf, plant and froghoppers, is a relatively well-known group of insect herbivores (Waloff 1980), representing more than 10% of all herbivore species in the local community (Baje et al. 2014; Basset et al. 2012). The effects of host plant quality (Novotny & Basset 1998), plant architecture (Brown et al. 1992), plant species composition (Novotny 1991) and successional age of plant community (Hollier et al. 1994) have all been shown to hugely influence Auchenorrhyncha dynamics. While the mesophyll-feeders are easy to rear in order to determine their host plants, the sap-feeders are difficult to rear from nymphs to adults as the phloem and xylem species require live plants (Dem et al. 2013). Host plants of Auchenorrhyncha nymphs have been studied in the tropics for agricultural pests (Witt & Edwards 2000), but there are no quantitative studies from tropical rainforests.
Because of the difficulties in rearing Auchenorrhyncha nymphs, particularly the phloem- and xylem-feeders, nymph abundance was used as an indicator to examine their distribution on plant species at different altitudes. In this chapter I examine the following inter-connected questions (re-stated here as testable hypotheses):

1) Does the incidence of Auchenorrhyncha nymphs on plants within subtropical rainforest simply reflect the abundance of potential host plants?

**Testable Hypothesis:** the patterns of nympHAL abundance counts are closely correlated with the availability of that plant species across all altitudinal sites.

2) Does the incidence of nymphs on woody plants in the forest understorey differ from altitude to altitude?

**Testable Hypothesis:** the strength of the correlation between the patterns of nymphal abundance and the availability of plant species will differ with altitude.

3) Do Auchenorrhyncha nymphs prefer/avoid plants in particular plant families? (and, if so, do these patterns differ with altitude?)

**Testable Hypothesis:** Does the counts of nymphs, when aggregated by plant family, produce a rank order different from that observed in the plant community itself? (either for the entire set of altitudes or for plot sites aggregated by altitude)

### 7.3. Methods

Spatial variation in the levels of abundance of Auchenorrhyncha nymphs was investigated on plants within the subtropical rainforests of northeast New South Wales. Fieldwork was conducted along an altitudinal gradient at Border Ranges National Park.
7.3.1. Study locations and sampling design— refer to Chapter 4 (sub-chapter 4.1: Border Ranges National Park).

As part of a wider study, four 20m x 20 m plots were marked out within each of five altitudes (300m 500m, 700m, 900m, 1100m a.s.l). Within each of these bands, the replicate plots were at least 400m from the next plot at that altitude. Vegetation surveys of the 20m x 20m plots were conducted by co-workers (Mr John Hunter, Dr Bill McDonald and Dr Stephanie Horton). All trees, palms and tree-ferns with a dbh greater than 5cm were permanently tagged and identified. The most abundant tree species’ at each altitudinal level are shown in Table 7.1.
Table 7.1. Dominant plant species (greater than 5 cm dbh) within each altitudinal site sampled at Border Ranges National Park, New South Wales.

<table>
<thead>
<tr>
<th>ALTITUDINAL SITE (METRES ASL)</th>
<th>DOMINANT TREE SPECIES</th>
<th>FAMILY</th>
</tr>
</thead>
<tbody>
<tr>
<td>300</td>
<td><em>Archontophoenix cunninghamiana</em></td>
<td>Areecaceae</td>
</tr>
<tr>
<td></td>
<td><em>Diospyros pentamera</em></td>
<td>Ebenaceae</td>
</tr>
<tr>
<td>500</td>
<td><em>Archontophoenix cunninghamiana</em></td>
<td>Areecaceae</td>
</tr>
<tr>
<td></td>
<td><em>Argyrodertron trifoliatum</em></td>
<td>Malvaceae</td>
</tr>
<tr>
<td></td>
<td><em>Eupomatia laurina</em></td>
<td>Eupomatiaceae</td>
</tr>
<tr>
<td>700</td>
<td><em>Sloanea australis</em></td>
<td>Elaeocarpaceae</td>
</tr>
<tr>
<td></td>
<td><em>Atractocarpus benthamianus</em></td>
<td>Rubiaceae</td>
</tr>
<tr>
<td></td>
<td><em>Argyrodertron trifoliatum</em></td>
<td>Malvaceae</td>
</tr>
<tr>
<td>900</td>
<td><em>Cyathea leichhardtiana</em> (a tree-fern)</td>
<td>Cyatheaceae</td>
</tr>
<tr>
<td></td>
<td><em>Caldcluvia paniculosa</em></td>
<td>Cunoniaceae</td>
</tr>
<tr>
<td></td>
<td><em>Sloanea australis</em></td>
<td>Elaeocarpaceae</td>
</tr>
<tr>
<td>1100</td>
<td><em>Nothofagus moorei</em></td>
<td>Nothofagaceae</td>
</tr>
<tr>
<td></td>
<td><em>Atractocarpus benthamianus</em></td>
<td>Rubiaceae</td>
</tr>
<tr>
<td></td>
<td><em>Polyosma cunninghamii</em></td>
<td>Escallonioaceae</td>
</tr>
<tr>
<td></td>
<td><em>Doryphora sassafras</em></td>
<td>Atherospermataceae</td>
</tr>
</tbody>
</table>

1. dominant on one plot only although a characteristic dominant of this altitude.

7.3.2. Nymph sampling and sorting

Sampling of nymphs took place in September/October 2012 and March 2013. That is, at the start and at the end of the wet season respectively. At each 20m x 20m plot, nymphs were sought on the foliage of every understorey plant (excluding ferns and palms, for identification reasons), spending two hours at each of the plots. Nymphs were hand collected and stored in small vials, in which all nymphs seen and collected from the
same plant individual were all put in the same vial. Sampling was only restricted to dry days to avoid the possibility of biased sampling, particularly of smaller individuals and also to sample as many nymphs as possible. From personal observations over 2 years (Dem et al. 2013) animals, especially terrestrial insects generally become inactive when the vegetation is wet. Plant species from which nymphs were collected were later identified. In the laboratory, nymphs collected from each plant individual were counted using a stereo-microscope.

7.3.3. Data analyses

Counts of nymphs are presented graphically in relation to proportion and percentages of plant species and family. At the family level, plant families from which 10 or fewer individual nymphs were collected were grouped together as ‘other families’. Combined data across all altitudes was used as well as data for each altitude. Seasonal data could not be used to examine diversity patterns among plant taxa as it was insufficient. To test for differences in nymph distribution patterns on each plant species across altitudes, only plant species from which nymphs were collected in both seasons were used. Chi-squared test was then used to test for differences in the number of nymphs collected between the two seasons across altitudes. A Two-sample T-test was used to see if the number of nymphs collected at each altitude across all plants sampled varied significantly between sampling seasons. To examine patterns of herbivore incidence among plant species among altitudes, the selection of the four plant species and the four plant families used in the analyses was based on the selection criteria that, if each plant taxa had five or more nymphs collected from it at each altitude at three consecutive altitudinal sites. Further, correlations of herbivore load (i.e. average number of nymphs per plant individual sampled for each plant species) and total number of nymphs,
respectively on plant species abundance were represented for individual altitude as well as across altitudes. Host plant species with less than five individuals were excluded from the analyses.

7.4. Results

The diversity of plant taxa from which nymphs were collected was greater at the start of wet season than at the end of it. Twenty-four plant species and 8 plant families had nymphs at the start of the wet season and three plant species and plant families had nymphs at the end of wet season. The remaining plant taxa had nymphs collected from them during both sampling seasons (Table S7.1). Total nymph abundance across plant species within each altitude decreases with increasing altitude (Table S7.2).

The total number of nymphs collected on plants across all altitudes was 1,337, with the numbers at each altitude in the order of highest to lowest being 300m (470) > 500m (445) > 1100m (191) > 700 m (133) > 900m (98). In total, 871 nymphs were collected at the start of wet season and 466 nymphs at the end of wet season. Overall, nymph incidence varied among plant species, and the highest percentages of nymphs encountered were on Sloanea australis (21%), Doryphora sassafras (13%), the vine Cissus antarctica (11 %) and Eupomatia laurina (10%) (Figure S7.1). Further, the percentage of nymphs associated with particular plant families across altitudes, ranged from 1 to 21% (Fig 7.1). Overall, at the start of wet season, most nymphs were collected from Sloanea australis (22%), Eupomatia laurina (12%) and Cissus antarctica (11%), and at the end of wet season, most nymphs were collected from Doryphora sassafras (26%), Sloanea australis (19%) and Cissus antarctica (11%). Percentages of nymphs
sampled at the start of wet season were highest in the plant families Vitaceae (34 %), Sapindaceae (11 %) and Malvaceae (10 %) (Figure 7.2a), and at the end of wet season, Atherospermataceae, Elaeocarpacaeae and Vitaceae had most of the nymphs sampled from them, with 26%, 22% and 12% respectively (Figure 7.2b).

Figure 7.1. Percentages of nymph abundance collected from each plant family in both seasons combined across all altitudes. Plant families with 10 or fewer individuals were grouped together as ‘other families’.

Figure 7.2a. Percentages of nymph abundance recorded on plant families sampled at the start of wet season. Plant families with 10 or fewer individuals are grouped together as ‘other families’.
Across altitudes, nymph incidence on plants was higher at the start of wet season than at the end of it ($\chi^2 = 122.68$, d.f. = 1, P<0.05, Figure 7.3a). Although, relative nymph abundance at each altitude showed that there were more nymphs collected at the start of wet season than at the end of it, statistically there was no significant difference in nymph incidence between seasons (Two-sample T-test = 0.254, d.f. = 4, P>0.05, Figure 7.3b.). Patterns of nymph incidence on particular host species between altitudes differed among plant species, as revealed by the four selected plant species that had the highest number of nymphs, which together made up 42.7% of the total plant individuals sampled. Some plant species had more nymphs at lower altitudes, others had more at the higher-altitudes, yet some had similar nymph abundance across the entire altitudinal band and some had a decreasing pattern of nymph incidence with increasing altitude (Figure 7.4a). In addition, the distribution of nymphs on the four selected plant families
showed similar patterns between altitudes as that shown by the selected plant species (Figure 7.4b). Nymph load on woody plants both across altitudes (Pearson’s correlation, \( r = -0.03, \ R^2 = 0.001, \ N = 31, \ P > 0.05, \) Figure 7.5a) and at each altitude showed no correlations. On the other hand, there were correlations between nymph incidence and plant species abundance, both across altitudes ((Pearson’s correlation, \( r = 0.91, \ R^2 = 0.82, \ N = 31, \ P < 0.05, \) Figure 7.5b) and for each altitudinal band.
Figure 7.3a. Nymph incidence and distribution on plant species between seasons across altitudes. Only plant species from which nymphs were collected in both seasons are represented.
Figure 7.3b. Nymphal abundance sampled at each altitude at the start and end of wet season. There were more nymphs collected at the start of wet season than at the end of it (Two-sample T-test = 0.254, d.f. = 4, P < 0.05).

Figure 7.4a. Distribution of nymph incidence on selected plant species. Herbivore incidence was examined among plant species that were each represented by five or more nymphs in three consecutive altitudinal bands. Black bars represent plant species abundance and grey bars represent nymph abundance.
Figure 7.4b. Distribution of nymph incidence on selected plant families. Herbivore incidence was examined among plant families that were represented by five or more individuals in three consecutive altitudes. Black bars represent plant family abundance and grey bars represent nymph abundance.

Figure 7.5a. Relationship between average number of nymphs and plant species abundance across altitudes. There was no correlation between herbivore load and plant abundance (Pearson’s correlation, $r = -0.03$, $R^2 = 0.001$, $N = 31$, $P > 0.05$)
Figure 7.5b. Relationship between total nymph incidence and total number of plant individuals across altitudes. There was a significant correlation between the number of nymphs and plant abundance (Pearson’s correlation, r=0.91, $R^2=0.82$, N=31, P<0.05).

7.5. Discussion

The distribution of insect herbivore and/or their larvae present on any vegetation type or on particular plant is influenced by many factors. In particular, local factors such as biological (Virla et al. 2008; Wang et al. 2008), ecological (Basset 1996; Reid & Hochuli 2007) and environmental (reviewed by Sinclair & Hughes 2010) factors may be important for insect herbivores and their larvae. Unlike the concealed groups of insect herbivore larvae (Cueveas-Reyes et al. 2006; reviewed by Sinclair & Hughes 2010), Auchenorrhyncha nymphs are non-concealed and are usually far more vulnerable to natural enemies (Hesami et al. 2009) and harsh environmental conditions, especially high or low temperature, presenting dessication and mycosis problems which is very high at the egg stage, because of their stationary position (Hix 2001). The effect of temperature could be the most possible explanation that could be used in the current study to describe the distributional pattern of nymph abundance among altitudes,
however, the 1100m site had higher nymph abundance than the 700m and 900m sites. This pattern has been influenced by the large number of nymphs collected from *Nothofagus moorei* at 1100m, which could be the result of a mass production of eggs at one time in order to enhance maximum survival. Plant species richness seems a less important factor affecting nymph incidence among altitudes, as there was no clear pattern of decreasing or increasing species richness among altitudes (Figure 7.6). As reflected by the four selected plant taxa used in the analyses as representations of the plant community, plant abundance may be a strong predictor of nymph abundance than plant species richness.

![Graph](image)

**Figure 7.6.** Relationship between nymph abundance and plant species richness among altitudes (Pearson correlation, $r = -0.57$, $R^2=0.33$, N=5, $P>0.05$). Trees with dbh $>$5cm are identified and used in the analyses. Dotted triangles represent each altitudinal site.

Plant quality is an important factor in determining herbivore population dynamics (Novotny & Basset 1998), which in turn is affected by seasonal variations in leaf, flower and seed production (Reich 1995). Members of Auchenorrhyncha have a very close relationship with their host plants, and not only that they are present where their host plants are, but also on the quality of their host plants (Novotny & Basset 1998). My
results of nymph abundance variation between seasons and also among altitudes, possibly reflect an effect of leaf flushing and quality. Rainfall enhances new leaf flushes (Bullock & Solis-Magallanes 1990) in which young leaves are more palatable to herbivores because young leaves are easier to chew and digest than matured leaves (Schädler et al. 2003). From observations in the field, there were more leaves flushing during the start of wet season and very little at the end of it. However, factors such as plant defense mechanism, i.e. ‘escape in space and time’ may come into play in certain cases here. For instance, plant families Meliaceae, Monimiaceae, Pennantiaceae and Polyosmaceae all had nymphs sampled from them during both sampling seasons, however, they had more nymphs collected on them during the end of wet season than at the start of it (Figure 7.2a, b), which may suggest that they have escape in time to avoid the mass production and breakout of insects during the start of wet season that synchronized with the leaf flushing period (Yukawa 2000).

Limitations

At this stage, it is difficult to identify Auchenorrhyncha nymphs to species level due to time limit and practical reasons, such as lack of taxonomic expertise and knowledge on the different families. Some Auchenorrhyncha families are better-studied than others, either taxonomically (Hoch & Dem 2011; Sforza et al. 1999) or ecologically (Gillham 1991). It may be possible to identify nymphs in their late instars development to family level (Biedermann 2003; Cargnus et al. 2012), however, nymphs collected in the current study were mostly in their 2nd and 3rd instars which makes identification difficult due personal lack of expertise in this area. Recently, molecular keys have been proposed as an alternative method to identify nymphs (Bertin et al. 2010a, b) using
molecular markers with certainty at species level without knowing the identity of parents (Cargnus et al. 2012).

Auchenorrhyncha is one of the insect groups which has both the adult and larvae feed on plants (Hernández et al. 2011; Virla et al. 2008). It could be suggested that the host plants of Auchenorrhyncha are those that are fed on by their larvae, since the larvae are mostly stationary and less mobile. Unlike other herbivorous insect groups, the only way to rear Auchenorrhyncha nymphs (except mesophyll-feeders, see Baje et al. 2014) to adults is to rear them on live plants (Dem et al. 2013) as they rely on a continuous flow of soluble nutrients in the plant xylem and phloem. However, as I am not able to do that here, due to reasons such as site accessibility and time limitation, I initially proposed to use molecular techniques as an alternative to match sequences of nymphs and adults in order to identify the nymphs. After several attempts doing molecular laboratory work, this did not turned out well due to circumstances beyond my control. As a result, it is not possible at this stage to determine what herbivore species feeds on what plant species, instead I have decided to use nymph abundance on plant species at each altitude to describe nymph abundance distribution on plant taxa along altitudinal gradient.
### Table S7.1. List of plant taxa from which nymphs were sampled from different plant species at different altitudes.

<table>
<thead>
<tr>
<th>PLANT FAMILY</th>
<th>PLANT SPECIES</th>
<th>PLANT FAMILY</th>
<th>PLANT SPECIES</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alangiaceae</td>
<td>Alangium villosum</td>
<td>Monimiaceae</td>
<td>Palmeria foremani*</td>
</tr>
<tr>
<td>Apocynaceae</td>
<td>Melodinus australis</td>
<td></td>
<td>Palmeria racemosa</td>
</tr>
<tr>
<td>Araliaceae</td>
<td>Cephalalaria cephalobotrys Polycias elegans</td>
<td></td>
<td>Wilkiea austroachestenlandica</td>
</tr>
<tr>
<td>Arecaeae</td>
<td>Linospadix monostachya</td>
<td>Myrtaceae</td>
<td>Acmena smithii</td>
</tr>
<tr>
<td>Atherospermataceae</td>
<td>Doryphora sassafras</td>
<td></td>
<td>Syzygium crebrinerve</td>
</tr>
<tr>
<td>Bignoniaceae</td>
<td>Pandorea jasminoides</td>
<td>Nothofagaceae</td>
<td>Nothofagus moorei</td>
</tr>
<tr>
<td>Capparaceae</td>
<td>Capparis arborea</td>
<td>Pennantiaceae</td>
<td>Pennantia cunninghamii</td>
</tr>
<tr>
<td>Cardiopteridaceae</td>
<td>Citronella moorei</td>
<td>Polyosmaceae</td>
<td>Polyosma cunninghamii</td>
</tr>
<tr>
<td>Cunoniaceae</td>
<td>Calcluvia paniculosa Geissos benthamii Guioa semiglaucna</td>
<td>Primulaceae</td>
<td>Embelia australiana</td>
</tr>
<tr>
<td>Elaeocarpaceae</td>
<td>Sloanea australis</td>
<td>Proteacea</td>
<td>Orites excelsus</td>
</tr>
<tr>
<td></td>
<td>Sloanea woolii*</td>
<td>Quintiniaceae*</td>
<td></td>
</tr>
<tr>
<td>Euphorbiaceae</td>
<td>Ballogia inophyla</td>
<td>Ripogonaceae</td>
<td>Ripogonum elseyanum</td>
</tr>
<tr>
<td>Eupomatiaceae</td>
<td>Eupomatia laurina</td>
<td>Rosaceae</td>
<td>Rubus nebulosus</td>
</tr>
<tr>
<td>Fabaceae</td>
<td>Austroteenisia glabristyla Derris involuta</td>
<td>Rubiaceae</td>
<td>Atractocarpus benthamianus</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lamiaceae</td>
<td>Clerodendrum floribundum</td>
<td>Rutaceae</td>
<td>Halfordia kendack</td>
</tr>
<tr>
<td>Lauraceae</td>
<td>Beilschmiedia obtusifolia Cinnamomum olivera Cryptocarya obovata Cryptocarya erythroxylon Eudandra grassiflora Litsea reticulata Neolitsea dealbata</td>
<td>Salicaceae</td>
<td>Scolopia braunii</td>
</tr>
<tr>
<td></td>
<td>Sapindaceae</td>
<td>Alectryon subcinereus</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Arytera divaricata</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Elattostachys nervosa</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Mischocarpus australis</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Sarcorpteryx stipata</td>
<td></td>
</tr>
<tr>
<td>Malvaceae</td>
<td>Argyrodendron actinophyllum</td>
<td>Smilacaceae</td>
<td>Smilax australis</td>
</tr>
<tr>
<td></td>
<td>Argyrodendron trifoliatum Brachychiton acerifolius</td>
<td>Symplocaceae</td>
<td>Symplolcus thwaitesii</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Melliaceae</td>
<td>Anthocarpa nitidula</td>
<td>Winteraceae</td>
<td>Tasmannia insipida</td>
</tr>
<tr>
<td></td>
<td>Dysoxylum fraserianum Dysoxylum rufum</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Malvaceae</td>
<td>Argyrodendron actinophyllum</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Argyrodendron trifoliatum Brachychiton acerifolius</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
plant taxa from which nymphs were sampled only at the start of wet season; bold with asterick- plant taxa from which nymphs were sampled only at the end of wet season. The remaining plant species supported nymphs at both seasons.

Table S7.2. Nymph abundance sampled from different plant species at each altitude at the subtropical transect.

<table>
<thead>
<tr>
<th>Plant species</th>
<th>300m</th>
<th>500m</th>
<th>700m</th>
<th>900m</th>
<th>1100m</th>
<th>Plant species</th>
<th>300m</th>
<th>500m</th>
<th>700m</th>
<th>900m</th>
<th>1100m</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acmena smithii</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td></td>
<td></td>
<td>Guioa semiglauca</td>
<td>4</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Alectryon subcinereus</td>
<td>1</td>
<td>5</td>
<td></td>
<td></td>
<td></td>
<td>Halfordia kendack</td>
<td>4</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Alangium villosum</td>
<td>2</td>
<td>3</td>
<td></td>
<td></td>
<td></td>
<td>Linospadix monostachyi</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Anthocarpa nitidula</td>
<td>1</td>
<td>9</td>
<td></td>
<td></td>
<td></td>
<td>Litsea reticulata</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Argyrodendron actinophyllum</td>
<td>3</td>
<td>10</td>
<td>7</td>
<td>1</td>
<td></td>
<td>Melodinus australis</td>
<td>16</td>
<td>4</td>
<td>9</td>
<td>7</td>
<td>32</td>
</tr>
<tr>
<td>Arystera divaricata</td>
<td>1</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td>Mischocarpus australis</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Argyrodendron trifoliolatum</td>
<td>22</td>
<td>22</td>
<td>3</td>
<td></td>
<td></td>
<td>Morinda jasminoides</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Atractocarpus benthamianus</td>
<td>6</td>
<td>7</td>
<td>5</td>
<td></td>
<td></td>
<td>Myrsine subsessilis</td>
<td>2</td>
<td>7</td>
<td>5</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>Austrotenisia glabristyloa</td>
<td>1</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
<td>Neolitsea dealbata</td>
<td>11</td>
<td>5</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Balogia inophylla</td>
<td>1</td>
<td>11</td>
<td>4</td>
<td></td>
<td></td>
<td>Nothofagus moorei</td>
<td>57</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Beilschmiedia obtusifolia</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Orites excelsus</td>
<td>4</td>
<td>1</td>
<td>3</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Brachychiton acerifolius</td>
<td>1</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td>Pandorea jasminoides</td>
<td>1</td>
<td>4</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Callicheia paniculosa</td>
<td>3</td>
<td></td>
<td>2</td>
<td></td>
<td></td>
<td>Palmeria racemosa</td>
<td>2</td>
<td>8</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Capparis arborea</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Pennantia cunninghamii</td>
<td>3</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cephalanthea cephalobotrys</td>
<td>2</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
<td>Pennantia cunninghamii</td>
<td>4</td>
<td>10</td>
<td>1</td>
<td>8</td>
<td></td>
</tr>
<tr>
<td>Cissus antarctica</td>
<td>150</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Polyosma cunninghamii</td>
<td>5</td>
<td>1</td>
<td>6</td>
<td>9</td>
<td>2</td>
</tr>
<tr>
<td>Citronella moorei</td>
<td>5</td>
<td>2</td>
<td>2</td>
<td>1</td>
<td></td>
<td>Polyscias elegans</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cinnamomum olivera</td>
<td>4</td>
<td>1</td>
<td>1</td>
<td>3</td>
<td></td>
<td>Quintinia verdonii</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cissus sclerophylla</td>
<td>14</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td>Ripogonum elseyanum</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Clerodendrum floribundum</td>
<td>1</td>
<td></td>
<td>1</td>
<td></td>
<td></td>
<td>Rubus nebulosa</td>
<td>2</td>
<td>3</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cryptocarya erythroxylon</td>
<td>6</td>
<td>10</td>
<td>1</td>
<td>1</td>
<td></td>
<td>Sarcopteryx stipata</td>
<td>7</td>
<td>7</td>
<td>5</td>
<td>2</td>
<td>5</td>
</tr>
<tr>
<td>Cryptocarya ochotrya</td>
<td>3</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Scopalia braunii</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Derris involuta</td>
<td>1</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
<td>Sloanea australis</td>
<td>129</td>
<td>71</td>
<td>41</td>
<td>18</td>
<td>22</td>
</tr>
<tr>
<td>Diploglossis australis</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Sloanea woollsii</td>
<td>10</td>
<td></td>
<td></td>
<td></td>
<td>1</td>
</tr>
<tr>
<td>Doryphora sasasifra</td>
<td>147</td>
<td>7</td>
<td>5</td>
<td>15</td>
<td></td>
<td>Smilax australis</td>
<td>1</td>
<td>8</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dysoxylum fraserianum</td>
<td>8</td>
<td></td>
<td>2</td>
<td>2</td>
<td></td>
<td>Syzygium creberneire</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dysoxylum pumilum</td>
<td>2</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td>Symphlocus thwaitesii</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Elattostachys nervosa</td>
<td>6</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
<td>Tasmaniania insipida</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Embelia australiana</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Tetrastigma nitens</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Endiandra classiflora</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Triunia youngiana</td>
<td>3</td>
<td>24</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Eupomatia laurina</td>
<td>66</td>
<td>68</td>
<td></td>
<td></td>
<td></td>
<td>Wilkiea austroqueenslandica</td>
<td>3</td>
<td>4</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Geisosis benthamii</td>
<td>1</td>
<td>3</td>
<td></td>
<td></td>
<td></td>
<td>Wilkiea hueguliana</td>
<td>5</td>
<td>7</td>
<td>5</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure S7.1. Nymph abundance collected on each plant species. Plant species with five or more nymphs are represented.
Chapter 8

General discussion and conclusions

8.1. Introduction

In this thesis, I set out to describe the species assemblage patterns and herbivore loads of Auchenorrhyncha on plants distributed along two altitudinal gradients in subtropical and tropical rainforests in Australia and to determine how these are affected by changes in climate associated with increasing altitude. In doing this, I had recognised that there is a general lack of understanding of plant-herbivore relationships and how these might be affected by changing plant species composition and local climate, which may be a reflection of global climate change (Bale et al. 2002; Williams et al. 2008). My research has demonstrated that for Auchenorrhyncha, there is variation in species richness along altitudinal gradients within forests as well as within forest vertical stratification in tropical and subtropical Australia. However, herbivore load on host plants did not appear to change with increasing altitude in subtropical Australia. Generalizing these results to other regions, forest types and insect herbivore groups or guilds is difficult and requires additional documentation, similar to that presented in this study. Nonetheless, these results are of relevance to a relatively wide audience, including those interested in plant-insect herbivore interactions, vertical stratification, altitudinal gradients and climate change.

Here, I revisit the research goals outlined in Chapter 1 followed by a discussion of the use of altitudinal gradients in climate change research. The discussions will include, briefly, other factors of climate change that have not been measured in the current
study, as well as potential responsive shifts in herbivore host plant to climate. I conclude by providing recommendations for future studies in this area of research.

8.2. Revisiting aims

This research has examined the distribution patterns of Auchneorrhyncha along altitudinal gradients (Goal 1, Chapter 5).

Prior to this study, there have been no investigations of the effect of altitude on the distribution of Auchenorrhyncha assemblages in Australia (but see Andrew & Hughes 2005). Therefore, the research presented in this thesis adds data to and builds on the literature of studies that examined the effect of altitude on other insect groups (Chen et al. 2009; Zou et al. 2014). A relatively high percentage of Auchenorrhyncha morphospecies in their native rainforest habitats, which previously have not been examined in Australia, have now been recorded and their distribution ranges have been identified. Two families of Auchenorrhyncha have only been recorded in the tropical transect and were found across the entire range, and one family was recorded as only found in the subtropical transect and was recorded only at lower altitudes. Just as in other insect groups, Auchenorrhyncha assemblages change with altitude and latitude, and as a result of their current geographical or altitudinal distributions, the majority of species would still have some area above their maximum limits to shift to under the current climate change. However, some rare species will be vulnerable to both direct climatic changes and indirect effects via changes to their hosts’ distribution (Andrew & Hughes 2005; Hodkinson & Bird 1998).
Taxonomic information on native Australian Auchenorrhyncha of economic importance is well advanced (Fletcher & Dangerfield 2002; Pilkington et al. 2004) compared to that for the native community in rainforest systems (Fletcher 2008; Van Achterberg et al. 1991). Consequently, specimens in the current study could not be precisely identified to species level. All specimens were identified as morphospecies in their respective families and the methods used to sort to species were more sophisticated than those used in many ecological studies. Improvement in taxonomy and phylogenetic information may provide a more effective method of species identification.

Several families, mostly the xylem-feeders, were less in both species number and abundance across altitudes within each of the transect, which implies compensating less energy on feeding due to the high tension pressure of xylem (Redak et al. 2004) or perhaps more likely nutrient contents of xylem, in terms of amino acids were insufficient, affecting their development, survival and host plant selection (Brodbeck et al. 1990). Further experiments may provide a more robust explanation as to whether the diversity of species is affected by altitude, host plants, amino acids or a combination of these and other factors (Brodbeck et al. 2004; Fielding et al. 1999).

This research has examined the vertical structure of distribution patterns of Auchenorrhyncha herbivore species and feeding-guilds and the altitudinal association of these patterns (Goal 2, Chapter 6).

In Australia, this is one of the only two studies that so far have investigated the effect of vertical stratification on insect-plant species assemblages associated with altitude. More generally, it has contributed to the growing body of research that seeks to explore and understand diversity patterns along forest vertical planes (Longino & Nadkarni 1990;
Schulze et al. 2001), encompassing other gradients such as light, temperature and primary productivity (Basset et al. 2001; Walther 2002). Vertical stratification patterns of species assemblages of Auchenorrhyncha have also been documented, without the host plant component in different regions (Casson & Hodkinson 1990; Wolda 1980). My work also contributes to the growing number of datasets that are available to determine community assemblage variations in forest vertical strata. Importantly, it has focused on arguably the most fundamental interaction of insects with plants. Furthermore, I have sought to explore how herbivore feeding-guilds change with altitude.

Vertical stratification of assemblages within forest strata showed a monotonic relationship with altitude, with both strata contributing equally to community assemblages. Similar stratification patterns were observed in other insect groups, such as beetles, which showed that the understorey and canopy contributed equally to biodiversity (Stork & Grimbacher 2006). Species richness of Auchenorrhyncha within feeding-guilds was not affected by altitude and forest strata within the tropical transect. However, within the subtropical transect, forest strata showed a strong gradient on species assemblages within feeding-guilds. Differences in similarities may suggest that the microclimate between altitudes or plot sites, and the different vertical layers of the vegetation had a larger effect than altitude (Wardhaugh et al. 2012). Factors such as food resources, alternative resources (such as mates, mating locations) and stratum lifetime habitat are acknowledged to be the most influential factors affecting diversity patterns along forest vertical strata (Ashton et al. 2016; Basset et al. 2003), while temperature, and plant species richness and composition are the most important factors along altitudinal or latitudinal gradients (Basset et al. 2001; Hodkinson 2005). In the
current study, the low number of species at higher altitudes may have been due to the demanding environment. Also, the observation that species richness was similar in the canopy and understory may be because of the similarity in the vegetation layers at each plot site and/or the similarity in the microclimate between either forest strata at each plot or between adjacent altitudes.

As discussed in chapter 6, phloem-feeders were species rich across all altitudes and between forest strata. On the other hand, the xylem feeding-guild was less diverse, in which both species richness and species abundance were very low at each forests stratum, altitude and across altitudes. These feeding-guilds may be important in maintaining herbivore species diversity and it would certainly be crucial to examine the contents of amino acids on host plants since feeding-sites on plants vary largely in nutrient quality and concentration (Andersen et al. 1989). Humidity levels may potentially affect species distribution, particularly xylem-feeders as their feeding-strategy is more energy-demanding than phloem- and mesophyll-feeders (Novotny & Wilson 1997). An important question is whether certain plant taxa acts as ‘keystone’ hosts in supporting herbivore and diverse range of feeding-guilds. Would the removal or loss of these taxa lead to extinction of some insect herbivores and certain feeding-guilds? This question has not been explored in this study but could investigated using perhaps a single plant taxon which potentially is a host to particular herbivore species or all feeding-guilds at specific altitudes or across the entire gradient.
This research has **examined herbivore-host plant association with a view to determining the specificity levels of these associations, and whether these might change with altitude** (Goal 3, Chapter 7).

The relationship between plant and an insect herbivore is an important evolutionary phenomena (Schoonhoven *et al.* 2005), which also describes diversity patterns. Ecologically, herbivorous insects are grouped into feeding-guilds, depending on the manner in which they feed (Novotny *et al.* 2010; reviewed by Sinclair & Hughes 2010). Their distribution is influenced by many factors, such as pattern of leaf production, rainfall and natural enemies (Aide 1993; Bullock & Sulis-Magallances 1990; Majer 1993). Auchenorrhyncha has a very close relationship with their host plants, such as not only do they follow their host plants but also on the quality of their hosts (Novotny & Basset 1998; Reich 1995). My work contributes to the investigation of the distribution of herbivore load on host plants and how this changes with altitude. Importantly, it provides baseline information on herbivore incidence on plants and how this might change with altitude and host plant shifts due to climate change in future.

Seasonal variation in nymph incidence is significant in that there were more nymphs collected at the start of wet season than at the end of it across all altitudes. The distribution of nymphs among altitudes differed among plant taxa, which was supported by the non-significant correlations between herbivore load and plant species abundance, both across altitudes and for each altitudinal band. On the other hand, relationship between the total number of nymphs and plants showed very strong significant correlations. Factors such as leaf flush, temperature and altitude may affect the distribution of nymphs. In the current study, leaf flush and plant abundance are likely to be the strongest factors rather than altitude and/or temperature.
As discussed in chapter 7, some plant families had nymphs collected from them at the start of wet season and others had nymphs collected from them at the end of it. Also, plant families that had nymphs collected from them in both seasons, surprisingly had more nymphs collected from them the end of wet season than at the start of it. Here, these plants avoided the synchronization period of insect herbivores to the leaf flushing period and delayed their leaf flushing period until the end of wet season. The important question is, do plants employ a synchronization mechanism to avoid mass breakout of insect herbivores or do insect herbivores change their host plants with increasing altitude? Either of the question is explored in the current study, but one possible way to explore this, would be to investigate particular plant taxa that has a wide range or particular herbivore taxa along the entire gradient.

8.3. Drivers of biological variation along altitudinal gradients

Altitudinal gradients are an efficient system to investigate diversity patterns and community structure, and their responses to a range of environmental variables (Körner 2000; reviewed by Nogués-Bravo et al. 2008). Determining which environmental factors is the strongest predictor of diversity and aspects of the structure of communities, however, is difficult because many factors co-vary with altitude (Sundqvist et al. 2013). In cases where I tested the effect of both altitude and temperature or altitude and vertical stratification (Chapters 5 & 6) on community assemblages, community similarities were affected by either a single factor or a combination of both factors. Further, variables that change as a direct effect of altitude, such as temperature and humidity, may be confounded by other factors that reflect regional phenomena, such as topography or seasons (Bruun et al. 2006; Janzen 1973).
In this study, several other variables (such as temperature, plant species richness, precipitation) that were measured along the environmental gradient co-varied with altitude, therefore their individual effect cannot be singled out as the strongest predictor (Chapter 5). It is important to use experimental manipulations to adequately determine which environmental variables have the most effect on insect responses. Temperature and available host plants, for example, may be more important than factors such as precipitation in determining species distribution patterns and their relationships with host plants (Lawton et al. 1987). There are also other variables, such as humidity and area availability within altitudinal sites, but these also co-vary with altitude.

Experimental manipulation of a particular variable or a group of interactive variables may clearly show whether/not patterns of species assemblages are affected by these variables. Further, it is highly likely that the observed patterns were a result of a combination of variables rather than a single variable (Bruun et al. 2006; Merrill et al. 2008).

In spite of these issues, altitudinal gradients remain a phenomenal mechanism for investigating effects of abiotic factors on patterns of community assemblages. The advantage of using altitudinal gradient is that it encompasses a range of factors which change with increase in altitude. Regardless of not knowing precisely which variables are responsible for the variation in community assemblages, it is highly possible that these distributions would be affected by changes in climate (Walther 2010; Wilson et al. 2005). In addition, mountain ecosystems provide a less effective dispersal environment, resulting in a greater number of rare and endemic species, which may be

8.4. Potential impacts of climate change on insect species and host plants

Based the data and analyses in this thesis, I make some predictions about how Auchenorrhyncha communities and their host plants will be affected by climate change.

1. Species that are currently present at lower altitudes may shift their ranges to higher altitudes and those that occupy higher altitudes may become extinct as they have very narrow ranges.

2. Leafhopper and planthopper species residing in forest canopies may move down towards the understory.

3. Herbivore load on host plants may either increase with altitude or produce a mid-altitudinal peak in abundance as a result of changes in climate and host plants.

Communities of leafhoppers and planthoppers may not be affected directly by climate, but indirectly through other factors. These are briefly discussed below;

It is highly likely that Auchenorrhyncha communities will be affected through changes in their host plants. Changes in quality, phenology and synchronization of host plant will have an adverse effect on its herbivore population dynamics (Bidart-Bouzat et al. 2005; Cramer et al. 2001). Furthermore, synchronization, phenology and physiology of insects which are also important in influencing species dynamics, will also be affected
by changes in climate (Hughes 2000). Factors such as increasing CO₂ levels may also positively affect photosynthetic rates, growth rates and nitrogen-carbon ratio to the advantage of sap sucking insects (Hughes & Bazzaz 2001).

8.5. Future directions

Generalization of patterns found in this study to other insect groups and feeding-guilds and other locations will require additional datasets on the distribution and host plants of Auchenorrhyncha, since this group is scarcely investigated in Australia, particularly in their native rainforest habitat.

Auchenorrhyncha has a very close relationship with their host plants and because they rely on a continuous flow of soluble nutrients in the vascular tissues, the only way to have profound records of their host plants is to rear them on live plants. However, rearing of nymphs is time-consuming and rearing success is very low (Dem et al. 2013). Fortunately, modern techniques of molecular procedures may solve this issue by matching of the sequences of nymphs to adults and subsequently determining their host plants. It is important to include host plants of Auchenorrhyncha with abiotic factors associated with altitude because, unlike other herbivore groups, they could not function without continuously feeding on their hosts.

Inclusion of identification of host plants in future studies along altitudinal gradients will not only provide datasets of herbivore-host plant records, but most importantly it will provides new data of possible changes in host plant with altitude due to climate change. Further, it will also provide baseline information of the host specificity levels of
particular herbivore species and feeding-guilds that also may change in future as a result of changes in climate.
References


http://mississippientomologicalmuseum.org.msstate.edu/collection.preparation.method


IPCC (2014b) IPCC 2014. Working Group II AR5 Chapter 5: an assessment on the intergovernmental panel on climate change.


Goecke & Und Evers, Keltern.


significant units in the *Platyleurastridula* L. species complex (Hemiptera: Cicadellidae) in the Cape Floristic Region, South Africa. *Molecular Ecology*, 16, 2574-2588.


