



Lianas, trees and insect herbivory

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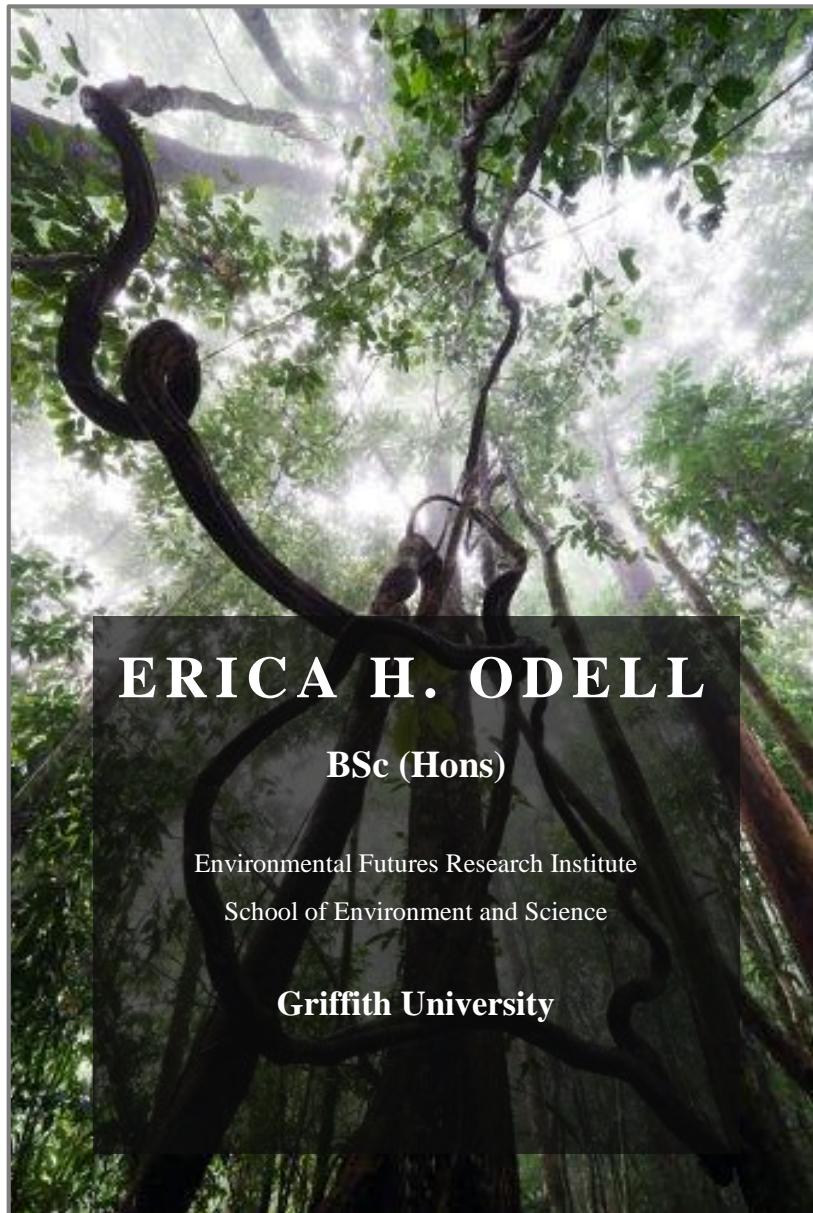
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LIANAS, TREES & INSECT HERBIVORY



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

May 2018

S Y N O P S I S

Erica H. Odell

Lianas, trees and herbivory

Insect herbivory is a key ecological process which mediates the structure, functioning and maintenance of forests. Studies of insect herbivory in tropical forests typically focus on trees whereas the contributions of other plant types, particularly climbing plants, remains undervalued and under studied. Lianas, or woody climbing plants, are important ecosystem contributors. Per unit basal area, lianas support substantially more leaves than trees and typically comprise 20-40% of the above ground leaf biomass in rainforests. This indicates a likely function in insect herbivory. Little data, however, exists which quantifies the importance of their contribution to overall ecosystem dynamics, particularly in contrast with trees. Information on the contributions of other plant types to herbivory are necessary if we are to fully appreciate the role of lianas in herbivory and understand the ways in which forests and associated processes may shift given anticipated environmental and vegetation changes.

This thesis aims to address this knowledge gap and demonstrate the value of lianas in supporting herbivory and associated insect assemblages. I aim to establish the need for a better understanding of liana-supported insect herbivory, quantify the trophic link among different plant types and insects in two contrasting rainforests, and determined the influence of structural and chemical leaf traits.

First, I determine the need for liana focussed herbivory research by providing a comprehensive review of the literature.

Second, I examine the temporal changes in liana and tree communities over two decades in a 1 ha plot of Australian subtropical rainforest. It is firmly established that lianas are increasing in Neotropical rainforest. In other bioregions, however, the pattern is less clear and derived from few sources. In Australia, where the factors influencing vegetation dynamics may differ, no such studies exist. I found liana abundance and biomass increased substantially from 2005 to 2015 while tree abundance remained stable from 1995 to 2015. Tree biomass also rose considerably, but at approximately half the rate of lianas. Based on the structure of liana and tree communities, I suggest increasing atmospheric CO₂ to be the most probable explanatory hypothesis over changes in rainfall or tree mortality. Given the results presented here and other documented increases in liana abundances globally, it is concerning we do not know more about the ecosystem services they provide.

Third, theoretical and empirical evidence suggests lianas may be an important food source for phytophagous insects. I address this hypothesis by two methods. First, in a literature-based study I assess the relative use of lianas as host plants for Australian butterflies. Second I make quantitative assessments

of herbivore damage in the canopy of a tropical Chinese rainforest and the understory of a subtropical Australian rainforest based on new, primary data.

Lianas, and vines alike, are hypothesised to be important food plants for butterflies. This speculation, however, has never been formally tested. Based on available food plant information of Australian butterflies, I found lianas to be an important food source for butterfly caterpillars in rainforests and their use as host plants to be greater than what simple plant diversity would predict. Interestingly, butterflies feeding on climbing plants had significantly greater incidences of monophagy than those feeding on trees. The patterns of host plant use and specialisation on trees and lianas are similar to those found in phytophagous rainforest beetles elsewhere.

If lianas support greater diversity and abundances of foliar feeding insects than trees, we would expect this to be reflected by asymmetrical incidences of herbivore damage across the two plant types. I found no overall significant difference across plant types in neither the canopy of a tropical Chinese rainforest or the understory of a subtropical Australian rainforest, providing further support for this hypothesis. I did however observe that; 1) lianas influence their host's leaf traits, most likely through inputs of nitrogen rich leaf litter around the base of their hosts, 2) under drought conditions lianas may reduce the amount of herbivory occurring on their host trees, and 3) leaf traits important for predicting herbivory are not consistent across plant types.

Through the combination of studies, I have shown that lianas are an important food source for herbivorous insects at least as much so as trees. The results of this thesis have helped close the knowledge gap in our understanding of herbivory and demonstrate the importance of lianas in supporting insect assemblages. Without understanding the contributions of other plant types to herbivory (and the associated insect faunas they support) we are unable to make accurate models and predictions about their future. Given lianas are increasing in many tropical rainforests, including those studied here, it is concerning that not more is known about their contributions to herbivory and their relationships with the insect herbivores they support – this thesis goes part way to allay this concern.

STATEMENT OF ORIGINALITY

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

Erica H. Odell

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JOURNAL ARTICLES ARISING FROM THIS THESIS

Chapters 2, 3, 5 and 6 in this thesis are written as manuscripts prepared for publication in scientific journals. Chapter 4 forms part of a wider study which is in preparation for publication. One manuscript is in review at *Biological Reviews* and others are prepared for publication and will be submitted to journals shortly after the submission of my thesis. These manuscripts are co-authored with other researchers and my contribution to each co-authored paper is outlined at the front of the relevant chapter. Appropriate acknowledgement of those who contributed to the research but did not qualify as authors is made in each manuscript or in the *Acknowledgements* section of this thesis. The bibliographic details for these manuscripts are;

Chapter 2

Odell E, Stork N, Kitching R (in review) Lianas and host trees compared: critical similarities, differences and contributions to herbivory. *Biological Reviews*

Chapter 3

Odell E, Laidlaw M, Yong T, MacDonald W, Kitching R (prepared manuscript) Trees and lianas in an Australian subtropical rainforest: change and stasis over two decades.

Chapter 4

Odell E, Kitching R (in preparation) The consumption of vines and trees by butterfly larvae: a comparative study of well-known rainforest faunas.

Chapter 5

Odell E, Min C, Kitching R, Nakamura A (prepared manuscript) Insect folivory on trees and lianas in a tropical rainforest canopy.

Chapter 6

Odell E, Stork N, Kitching R (prepared manuscript) Lianas and trees: insect folivory and leaf traits in an Australian subtropical rainforest.

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CHAPTER 1

Introduction and Thesis Outline

1.1 INTRODUCTION

This thesis examines the relative impacts of insect herbivory on trees and associated climbing plants (vines and lianas) within Old-World rainforests. In particular it focusses on the community level expression of this ecological process and its consequences. The approach taken combines primary data collection, analyses of leaf chemistry, a literature review and formal comparative analyses.

The green food-web

Herbivory, the feeding of animals on living plant parts, is a key ecological process which mediates the structure, functioning and maintenance of forests (Schowalter, 2016). Global diversity and ecosystem processes, including primary production, plant population dynamics and nutrient cycling, are all intimately linked with herbivory (Metcalfe et al., 2014, Lamarre et al., 2012). Food-webs founded on primary production, whereby solar energy fixed by plants through photosynthesis is released into terrestrial food-webs through herbivory, are aptly named ‘green food-webs’, while those centred on detritus are termed ‘brown food-webs’(Ingham et al., 1985, Cebrian, 1999, Cebrian and Lartigue, 2004). In ‘brown’ food-webs energy is released to higher trophic levels by the process of decomposition. Together, these two processes form the only terrestrial mechanisms whereby energy is liberated into ecosystems.

Ground-based measures of herbivory typically estimate losses of approximately 5-10 percent of total net primary production in forests (Mattson and Addy, 1975, Kozlov et al., 2015a). These estimates, however, may significantly underestimate the extent of herbivory in different strata or forests of various types and quality. For example, herbivory is generally greater in the canopy, compared with the understory, where leaf biomass as well as herbivore density and diversity is substantially higher (Basset et al., 2008, Charles and Basset, 2005). There is also evidence to support both positive and negative correlations of herbivory with diversity (Jactel and Brockerhoff, 2007, Kambach et al., 2016, Brezzi et al., 2017, Vehviläinen et al., 2007) but it is difficult to generalise or draw conclusions across studies about the impact of diversity. The comparability of results among studies is highly contentious due to differences in environmental conditions, locations, seasons and methodologies.

Herbivory by insects and other invertebrates can be further classified based on feeding behaviour (eg. mining, galling, chewing) or by the plant part consumed (e.g. wood feeding, bud feeding, leaf feeding, root feeding). Leaf feeding, or folivory, is the most dominant form of herbivory and one of the best studied. Investigations have focussed on chewing damage, generally for methodological reasons as it is

relatively easy to measure (Heinrich and Collins, 1983, Aide and Zimmerman, 1990, de la Cruz and Dirzo, 1987, Stastny and Agrawal, 2014). The frequency of studies on leaf chewing (in contrast to other forms of herbivory) has led to the assertion that both leaf feeding and chewing are the dominant forms of herbivory and the most impactful (Wint, 1983, de la Cruz and Dirzo, 1987, Eichhorn et al., 2007, Heinrich and Collins, 1983, Turcotte et al., 2014). The large scale impacts of the full suite of different types of herbivory on an individual plant are complex, however, challenging to measure and broad generalisation are weakly based. Many classes of herbivory, such as, root feeding have received little attention. Furthermore, although studies assessing individual-based impacts of herbivory are of value, their applicability and usefulness in understanding broad-scale patterns and impacts of herbivory at the community and ecosystem level are limited. Studies of individual species do not necessarily reflect processes occurring within the community at large and provide limited information on how herbivory may affect community stability or resilience.

Insect herbivores

Plant-based terrestrial food-webs support approximately 75% of global biodiversity (Price, 2002) and the ecological and evolutionary importance of plant-herbivore interactions is widely appreciated (Schmitz 2008; Futuyma & Agrawal 2009). Insects are, by far, the dominant herbivore group in terms of diversity, abundance, biomass and estimated impacts (Janzen, 1983, Price, 2002, Maron and Crone, 2006, Wilson, 1987). Insect herbivores contribute several tonnes of biomass per hectare to tropical forests compared with just a few kilograms for vertebrates, and are estimated to consume anywhere from two to six times more leafy biomass per hectare annually compared with vertebrates (Dajoz, 2000). Inevitably, insect herbivores therefore, exert a substantial influence over the maintenance and regulation of ecosystem processes (Wilson, 1987, Reynolds et al., 2000).

Globally, insect herbivores affect more forest area than disease outbreaks (although they may play a role in exacerbating such outbreaks) and severe weather (van Lierop et al., 2015). The impacts of insect folivory can range from negligible grazing to wholesale mortality of leaves, branches, whole crowns and entire forest stands. Some populations of insect herbivores, particularly Coleoptera, Lepidoptera and Hymenoptera, have the capacity to cause rapid and dramatic change in forest dynamics (Schowalter, 2016, Maron and Crone, 2006, Lowman and Morrow, 1998, Reichle et al., 1973). Douglas fir tussock moths (*Orgyia pseudotsugata*) and Hemlock loopers (*Lambdina fiscellaria*), for example, can completely defoliate a mature host tree within one to two seasons (Cooke et al., 2007). Many insect groups are also important seedling feeders which kill seedlings outright or significantly reduce their growth and competitive ability (Mills, 1983, Crawley, 1989). These insects are of particular importance in the early stages of plant community assembly for suppressing recruitment of dominant species and increasing plant heterogeneity in forests (Bagchi et al., 2014, Carson and Root, 1999, Wright, 2002).

Plant types and herbivory

Interest in plant-herbivore interactions has generally focused on the interactions occurring among a few species or groups of species rather than within entire forest stands or ecosystems (Rinker and Lowman, 2004). Studies of herbivory in tropical forests centre primarily around trees (Kozlov et al., 2015a).

Quantitative herbivory data on plant types (ie. lianas, grasses, ferns etc.) other than trees (and, to a lesser extent, shrubs) is lacking as are comparisons across plant types. Research into plant functional types focuses predominantly on their differing responses to environmental and climatic conditions, and consequent changes within the plant community and structure (Box, 1996, Schnitzer and Carson, 2010, Oosterhoorn and Kappelle, 2000). Comparisons of the ways in which different plant functional types interact with, and support fauna (and the associated food-webs), however, are rare.

Leaf loss on ferns from insect herbivores is comparable to that on trees at *ca* 10% (Winkler et al., 2005, Hendrix and Marquis, 1983, Rinker and Lowman, 2004, Coley and Barone, 1996), while insect mediated leaf loss on palms is reported between *ca* 2-6% (Stiegel et al., 2017). These figures are, however, based on a limited suite of available studies and are not specific to herbivory in rainforests. Herbivory on bromeliads and orchids was historically assumed to be low and, although leaf loss on these plant types is typically lower than other dominant plant functional groups, both commonly have high levels of non-leaf herbivory (such as damage to meristematic tissues and flowers), and may be important for insects feeding on plant parts other than leaves (Winkler et al., 2005).

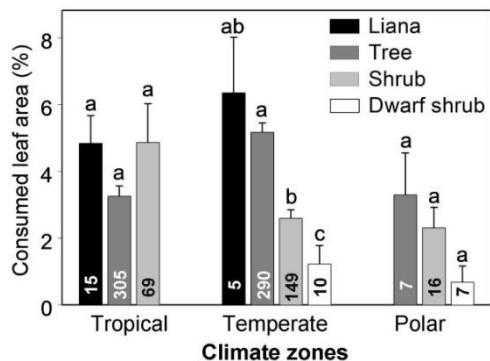


Figure 1.1 Percent leaf area loss from insect herbivores, after Kozlov et al. (2015a). The number of species information is gathered from is shown within bars. Significant differences are indicated by different letters.

Growth strategies and anti-herbivore defence strategies often differ across plant types and functional groups. For example, silicon is a common anti-herbivore defence in the blades of grasses but is in low concentrations in tree and shrub foliage where lignin and phenols are more abundant herbivore defences (Cornelissen et al., 2004, Massey et al., 2006, Hartley et al., 2016, Barbehenn and Peter Constabel, 2011, Cooke and Leishman, 2011, Coley et al., 1985, Moore and Jung, 2001). These different anti-herbivore defences operate via different mechanisms, target different species and have different effects on the outcomes. Similarly, there is evidence to suggest that trees with contrasting functional roles and growth strategies accumulate herbivory differently. Fast growing pioneer tree species frequently incur greater herbivore damage than slower growing species (Coley, 1988, Salgado-Luarte and Gianoli, 2017). Background foliar losses from insects are significantly different between trees and shrubs despite many shared phenotypic characteristics (Figure 1.1) (Kozlov et al., 2015b, Kozlov et al., 2015a). Herbivory data on climbing species, specifically woody climbing species, is, however, scarce for both tropical and temperate zones despite their abundance and diversity in these regions.

A meta-analysis of available data (collected from 20 species of liana and 595 species of trees) showed greater herbivory on lianas compared with trees in tropical and temperate regions (Kozlov et al., 2015a). However, the statistical significance of these differences in herbivory between plant types could not be confirmed due to the limited information available from climbing species (Figure 1.1). Furthermore comparisons among these studies may be confounded as the data were gathered under variable environmental conditions, from different forest types, sites, years, seasons, strata and using differing methodologies. The scarcity of information on climbing species, notably lianas, is concerning given trends in their distributions and communities over recent decades and their importance within tropical forests (Wright et al., 2004, Chave et al., 2008, Schnitzer and Bongers, 2011, Phillips et al., 2002, Laurance et al., 2014).

Lianas

Lianas are a type of woody climbing vines that lack the necessary attributes to support independent vertical growth (Figure 1.2). As a result, they are structurally parasitic on other elements, principally trees, to access the forest canopy and associated light resources. In contrast to true parasites, however, they draw no nutritional resources from their hosts by remaining rooted to the ground throughout their life (Putz and Mooney, 1991). By forgoing this major investment in structural tissues, lianas are able to increase resource capture by enhancing their foliage and vascular systems. These attributes also extend to non-woody (generally shorter stemmed) herbaceous vines, also referred to as creepers and twiners.

Lianas are probably the single most important physiognomic feature in tropical rainforests (Croat, 1978, Gentry, 1991), although here ‘tropical’ should be taken to include both tropical and subtropical forests. They may also be absent from otherwise more or less characteristic rainforests on tropical oceanic islands. At ground level, lianas usually constitute less than 5% of the basal area of rainforests (Schnitzer et al., 2012), while in the canopy they may compose up to 40% of the leafy biomass (Schnitzer and Bongers, 2002, Gentry, 1991). Per unit basal area, liana support substantially more leaves than trees and many small stemmed lianas, as little as 2-3cm diameter at breast height (DBH), have the ability to reach the canopy (Kurzel et al., 2006) where they contribute further to diversity and architectural complexity. In contrast, trees of the same DBH would require several decades of growth before they could contribute to canopies. The contribution of lianas to the architectural complexity of forests is unparalleled. They provide an abundance of habitat for invertebrates and vertebrates alike and are an essential source of connectivity between tree crowns, and between vertically stratified habitats.

Both leafy biomass and architectural complexity are important factors for predicting the complexity and nature of insect within forest communities, and by proxy, herbivory. The availability and biomass of leaves is a better predictor of insect abundance than plant quality or palatability (Whitfeld et al., 2012) and insect diversity is typically greater on architecturally more complex plants (Lawton, 1983, Basset, 2001, Leite et al., 2017). Given the substantial contribution of lianas, and climbing plants alike, to both

leafy biomass and architectural complexity, it is likely they play an important role in supporting and maintaining insect assemblages and herbivory. This role may become increasingly ecologically important as global change in ecosystems favours the growth and development of lianas (Wright et al., 2004).



Figure 1.2 Lianas, or woody climbing plants, using host trees to access forest canopies. They are important physiognomic features of rainforests and substantial contributors to primary production.

1.2 THESIS OUTLINE

As indicated in my opening statement, this thesis aims to address the importance of lianas as a food source for herbivorous insects (Figure 1.3). With the exception of Chapter 1 and Chapter 7 the thesis is structured as a series of published and unpublished manuscripts which have been prepared for submission to peer reviewed journals in accordance with Griffith University policy on PhD theses as published and unpublished papers (Griffith University, 2017). In Chapters 2, 3, 5, and 6 I specifically address lianas (woody climbing vines), while in Chapter 4 I extend the discussion to both lianas and creepers (non-woody herbaceous vines).

Chapter 2 of this thesis is a broad literature review which emphasises the need to consider liana herbivory differently from that of trees due to key differences in aspects of their leaf traits and life histories. This review provides the context for the thesis and discusses much of the foundational information regarding herbivory, lianas and their possible roles in insect herbivory. The subsequent data chapters are based on independent studies. Chapter 3 examines temporal trends in liana abundances and highlights the paucity of Australian and subtropical based studies. By understanding temporal trends in liana demographics we will be able to better predict their future importance within forest dynamics (Figure 1.3). Information on the insect herbivore assemblages relying on lianas as food plants, in contrast with those on trees, is essential for understanding the importance of lianas for ecosystem processes (Figure 1.3). This is examined in Chapter 4 where the use of climbing and non-climbing plants as butterfly host plants relative

to their diversity within ecosystems, specifically rainforest, is determined. It is intended that the analysis of Australian data presented in this Chapter will be augmented by comparable analyses from other biogeographic regions (in progress but beyond the scope of this thesis) before final submission for publication. Chapter 5 quantifies canopy insect herbivory in a tropical dipterocarp-dominated rainforest in Mengla, China using a canopy crane to measure broad scale patterns in herbivory among lianas, their hosts and trees with and without lianas. Chapter 6 similarly quantifies liana and tree herbivory but in a subtropical rainforest of south-east Queensland, Australia, and correlates patterns in herbivory with different leaf traits on lianas and trees. Baseline information such as that presented in Chapters 5 and 6 is largely absent from the literature and is essential in understanding liana-insect interactions (Figure 1.3). Chapter 7 concludes the thesis by providing a general discussion of the findings in light of its overarching aims and identifies possible directions for future research.

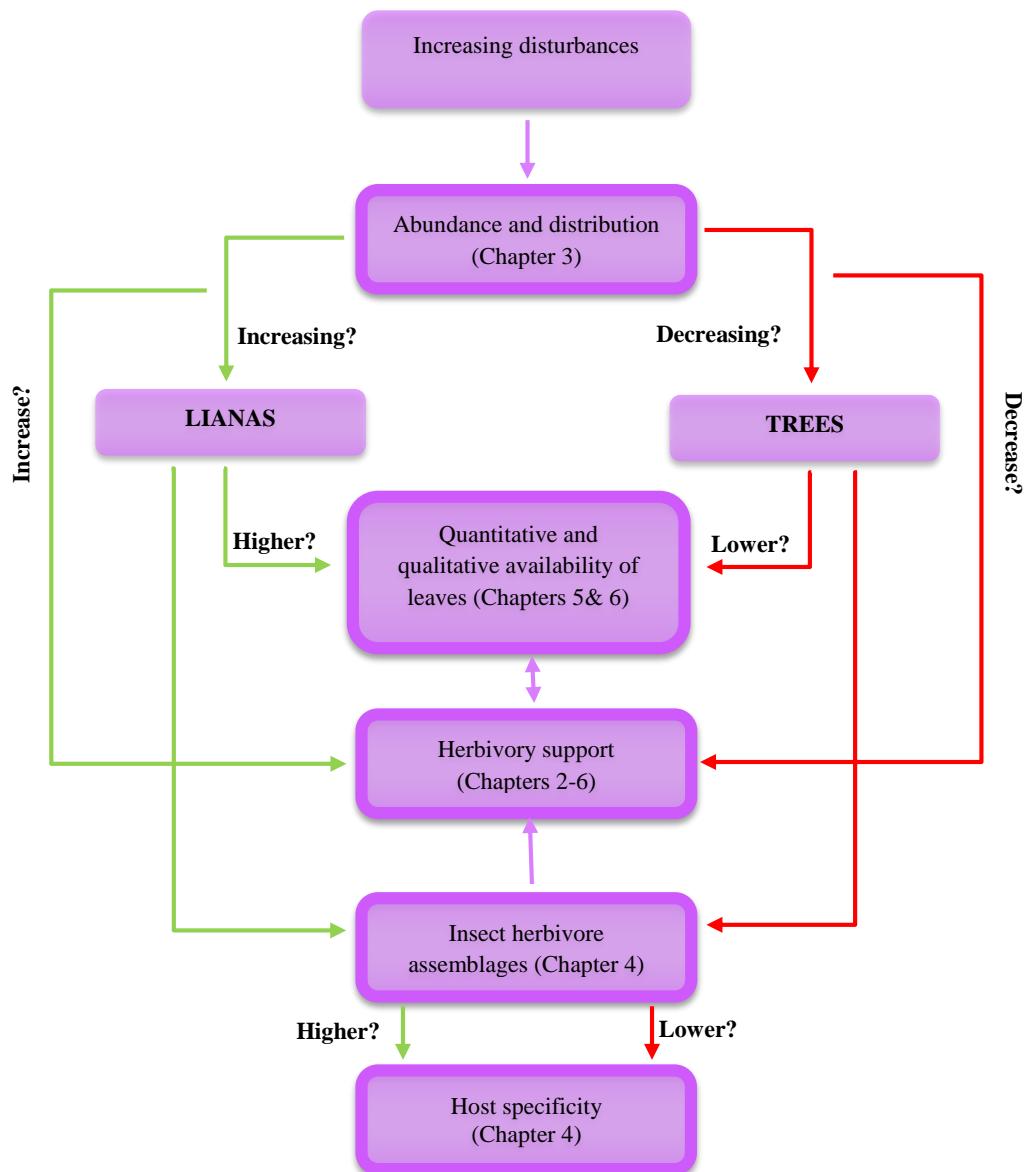


Figure 1.3 Conceptual framework for investigating and comparing herbivory on lianas and trees. Lianas follow the pathway indicated in green, and red indicates the likely pathway followed by trees. Topics investigated in this thesis are shown in bold outlines.

CHAPTER 2

STATEMENT OF CONTRIBUTION TO CO-AUTHORED PAPER

Chapter 2 is a co-authored paper which has been submitted for publication in *Biological Reviews*. The bibliographic details of the co-authored paper, including all authors, are:

Odell E, Stork N, Kitching R (in review) Lianas and host trees compared: critical similarities, differences and contributions to herbivory. *Biological Reviews*.

My contribution to this chapter involved reviewing all cited literature, data collection, creation of all figures and tables, and writing of the manuscript. My co-authors are my supervisors, they provided guidance and assisted with the direction, structure and editing of the manuscript.

(Signed) _____
Erica H. Odell

(Date) 10 May 2018

(Countersigned) _____
Supervisor: Roger L. Kitching

(Date) 10 May 2018

(Countersigned) _____
Supervisor: Nigel E. Stork

(Date) 10 May 2018

CHAPTER 2

Lianas and host trees compared: critical similarities, differences and contributions to herbivory

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2.1 ABSTRACT

The presence and abundance of woody climbers ('lianas') is one of the main features that characterises rainforests. They are thought to be the single most important physiognomic structure differentiating tropical from temperate forests. Historically, lianas have been viewed as structural parasites since they require the assistance of trees to achieve vertical growth and access canopies potentially leading to stunted tree growth, increased tree mortality, reduced host resource acquisition and inhibited tree regeneration. In contrast, lianas influence community assembly resulting in increased species richness, more complex diversity mosaics, and greater architectural heterogeneity. However, their role in community wide plant-insect interactions and how this affects ecosystem processes, such as herbivory, is little known.

Lianas are the second largest contributor to leaf matter in rainforests (after canopy trees) and, in some forest systems produce up to 40% of the above ground green leafy biomass. In light of this, I hypothesize that lianas may be as important as trees in supporting insect herbivores and, consequently, driving species diversity in rainforests. Much of our current understanding of insect herbivory in rainforests comes from observations of large canopy trees and saplings. However, since liana leaves have distinct structural, chemical and phenological properties independent of phylogenetic relatedness, inferences and conclusions about herbivory gathered from data on trees may not apply.

I present evidence of their widespread phylogenetic distribution in three parts of the world (subtropical and tropical Australia and Panama), and discuss how some of the key differences in the phenology and quality of leaves between lianas and trees potentially make lianas an equally or more attractive and palatable food source. These factors may have important and even beneficial consequences for their host trees, and for aspects of ecosystem dynamics such as nutrient cycling. Since many studies now indicate that lianas are increasing in abundance in tropical forests as a possible consequence of climate change, understanding their role in supporting and maintaining biodiversity is increasingly necessary. Much remains to be determined about the ways in which lianas contribute to, support and maintain the ecosystems in which they exist and conclude by identifying major knowledge gaps.

Keywords: liana, host tree, herbivory, insect, rainforest

2.2 INTRODUCTION

Plant based food-webs support approximately 75% of global biodiversity, and are dominated by herbivorous insects and other arthropods (Price, 2002). Rainforests are the most complex and diverse of terrestrial biomes and maintain a large proportion of herbivorous species. Much of our current understanding of insect herbivory in rainforests comes from the study of large canopy trees and saplings, which are the primary contributors to leaf biomass in those forests (Hladik, 1978, Pichon et al., 2015, Hegarty, 1991 , Wright et al., 2004, Pragasan and Parthasarathy, 2005). Woody climbers - ‘lianas’ - are, however, important physiognomic structures within rainforests and although they rarely exceed 5% of the total biomass (Schnitzer et al., 2012), they commonly comprise 20-40% of the abundance and species richness of woody stems (Schnitzer and Bongers, 2002, Gentry, 1991), and may contribute up to 40% of above ground leaf biomass, leaf litter, leaf area and productivity (Table 2.1) (Hladik, 1978, Pragasan and Parthasarathy, 2005, Tang et al., 2012). The biomass and ecological significance of lianas appear to be increasing gradually as global change in ecosystems favours their growth and development (see Table 2.2), possibly as a direct photosynthetic response to carbon dioxide enrichment (Wright et al., 2004, Cernusak et al., 2013, Schnitzer and Bongers, 2011).

Table 2.1. Relative contributions of lianas and trees to leaf litter production in tropical and subtropical forests. Ranges are provided for BCI, Panama and Coromandel Coast, India as data is extracted from multiple years or sites. Wright et al. (2004) provides reliable evidence that the relative contribution of lianas to leaf litter production has increased over a 17 year period.

Location	Forest type	Years	Tree	Liana	Source
Gabon	Tropical seasonal rainforest	1971-1972 (Jun-Aug)	62%	38%	Hladik (1978)
Badrala Forest, Madagascar	Semi-deciduous tropical forest	May 2008 – Apr 2009	83%	17%	Pichon et al. (2015)
BCI, Panama	Tropical seasonal rainforest	Nov 1985 – Dec 2002	83-87%	11-17%	Wright et al. (2004)
Coromandel Coast, India	Tropical dry evergreen forest	2003 (Jan-Dec)	61-71%	29-39%	Pragasan and Parthasarathy (2005)
Brisbane, Australia	Subtropical rainforest	24 months (years not stated)	76%	24%	Hegarty (1991)

An understanding of the importance of lianas in ecosystems as supporters of animal biodiversity (and the subsequent food-webs created) is essential if ecosystem processes creating and maintaining biodiversity are to be appropriately appreciated and managed. At present, research about lianas has focused heavily on their impacts to host trees and saplings, their responses to disturbance and succession pathways. In contrast, the way in which lianas support ecosystems, maintain species diversity and contribute to

herbivore dynamics is poorly understood. Virtually all hypotheses regarding the contribution of lianas to food-webs and animal biodiversity require study (see below).

Here I show that lianas are an important food source for many herbivorous insects and that there are key differences in critical aspects of these resources compared with trees, independent of phylogenetic relatedness. I discuss how some of the key differences in the quality and availability of leaves between lianas and the trees with which they co-exist may well make lianas an attractive and palatable food source. At the level of the ecosystem, these properties may also have beneficial consequences for the host trees and nutrient cycling in general. In this review, I discuss mainly woody climbing species (lianas), however many of these insights can be extended to non-woody vine species.

2.3 LIANAS

Lianas are woody climbing plants which lack the necessary structures to support independent vertical growth and thus rely on structural support from other elements (principally trees) to access canopies and the light resources they provide (Schnitzer and Bongers, 2002). Unlike hemi-epiphytes and other parasitic plants they draw no resources from their hosts, but may compete with their hosts for above and below ground resources and cause direct or indirect physical modifications to their hosts' canopies (Schnitzer et al., 2005, Tobin et al., 2012). Like epiphytes they rely on their host trees for structural support but differ in remaining rooted to the ground and drawing nutrients from the soil (Putz and Mooney, 1991), often at considerable distances from their host trees (Parren et al., 2005). Earlier research into rainforest ecology often overlooked or omitted lianas (Nadkarni, 1988, Denslow, 1987, Lloyd et al., 1995), but there has been a recent expansion of interest in their roles within forest (particularly rainforest) ecosystems (Table 2.1 and 2.2). It is now widely accepted that lianas are significant components of tropical rainforests and are thought to be the single most important physiognomic structure differentiating tropical from temperate forests (Croat, 1978).

Individual level impacts of liana-host associations have been of central focus to liana research and management, the impacts of which have tended to be measured in terms of host tree growth, reproductive output and mortality (Putz, 1984, Stevens, 1987, Schnitzer et al., 2000, van der Heijden and Phillips, 2009). Lianas stunt tree growth (Schnitzer et al., 2011), increase tree mortality (Ingwell et al., 2010), reduce resource acquisition by host trees (Schnitzer and Carson, 2010), inhibit tree regeneration (Alvira et al., 2004), and alter gap-phase processes (Schnitzer et al., 2000, Schnitzer and Carson, 2001). They are also heavily associated with disturbances, anthropogenic impacts and edge effects (Ledo and Schnitzer, 2014, Tang, 2007, Magrach et al., 2014). In some instances, when abundant lianas can smother other plants and completely inhibit forest regeneration leading to a semi-stable 'subclimax' (Schnitzer and Carson, 2010, Alvira et al., 2004). From a community level perspective, however, the impacts of lianas on ecosystems and processes are quite different. In many rainforests, lianas enhance species richness, strengthen diversity mosaics, create architectural complexity, generate higher levels of inter-species competition, encourage gene flow between ground and arboreal populations by providing transport

routes, and support different herbivore-predator communities (Ødegaard, 2000b, Stork, 1987, Álvarez-Cansino et al., 2015, Parthasarathy, 2015). Accordingly, the presence of large lianas and liana diversity are generally accepted as robust indicators of more mature, undisturbed forest stands (Campbell, 2016, Castello et al., 2017).

Table 2.2 Long-term temporal trends of liana abundances in tropical, sub-tropical and temperate forests. Patterns of increasing liana abundances in tropical forests is well established, but the extent of this phenomenon in sub-tropical and temperate forests requires further data.

¹ long-term permanent plot/s

Location	Forest	Abundance	Study length	Reference
	Type			
Amazon, Brazil ¹	tropical	increase	14 years	Laurance et al. (2014)
Costa Rica ¹	tropical	increase	8 years	Yorke et al. (2013)
Barro Colorado Island, Panama ¹	tropical	increase	30 years	Schnitzer et al. (2012)
French Guiana ¹	tropical	increase	8 years	Chave et al. (2008)
Amazon, Bolivia	tropical	increase	14 years	Foster et al. (2008)
Amazon, Central and South America ¹	tropical	increase	20 years	Phillips et al. (2002)
Congo ¹	tropical	stable	13 years	Ewango (2010)
Gabon	tropical	decrease	13 years	Caballé and Martin (2001)
South Carolina, USA ¹	subtropical	increase	22 years	Allen et al. (2007)
South-east Queensland, Australia ¹	subtropical	increase	10 years	This thesis (Chapter 3)
Wisconsin, USA	temperate	stable	45 years	Londré and Schnitzer (2006)

The direct negative impacts that lianas have upon host trees has been hypothesised to be inconsequential as lianas generally root sufficient distances away from the base of host trees minimising the likelihood of below ground competition for substrate nutrients. Furthermore, the frequent turnover of liana leaves may provide a source of nutrients around the base of its host trees, resulting in a more commensalistic (rather than parasitic) relationship (Tang et al., 2012).

2.4 LIANA DIVERSITY AND PHYLOGENETICS

(1) Diversity

The climbing habit of vines and lianas was an early innovation of land plants and has arisen successfully on numerous independent occasions throughout the evolutionary history of plants (Gentry, 1991, Gianoli, 2015). Climbing functional groups of plants are best represented within the angiosperms but are also present in gymnosperms and ferns. Updated estimates of the ubiquity of climbing plants suggests that 75% of all dicotyledonous orders and a third of all seed bearing families have at least one representative climber (Gianoli, 2015).

The habit of climbing is associated with enhanced clade diversification, that is to say, lineages with climbing species tend to have greater species richness than those without (Rios et al., 2014). Gianoli (2004) postulated this may occur as a result of the expanded niche dimensions opened up by the climbing process, which maximises interactions with a wide array of antagonistic and mutualistic species, which in turn, promotes diversification. Gentry (1991) also suggested a correlation between specialised mechanisms of climbing and high speciosity in plant families. This hypothesis awaits quantitative analysis, however, there is some evidence to suggest that there is no such macroevolutionary pattern of an association between climbing mode and diversification (Gianoli, 2015).

Lianas are common across many biomes and, contrary to popular pre-conceptions, are abundant in some temperate forests. They do, however, reach peak abundance, maximal taxonomic diversity, and structural diversity in tropical forests (Schnitzer and Bongers, 2002, Mascaro et al., 2004, Putz, 1984, Givnish and Vermeij, 1976, Schnitzer, 2005). In tropical forests, lianas typically constitute 19-30% of species diversity (Appanah et al., 1993, Putz and Chai, 1987, Jongkind and Hawthorne, 2005) compared with 9-19% in subtropical forests (Cai and Song, 2000) and 5-7% in temperate forests (Gentry, 1991). The diversity, abundance and distribution of lianas are largely explained by abiotic factors such as water availability, temperature, seasonality and disturbance regime (Schnitzer, 2005, Schnitzer and Bongers, 2002, Laurance et al., 2001, Dewalt et al., 2000, Babweteera et al., 2000, Schnitzer and Carson, 2001). Liana diversity and abundance is often at its greatest at forest edges and within light-gaps (Tang, 2007, Laurance et al., 2001). This has led to the over generalised classification of lianas as early successional and gap dependent ‘pioneer’ species (Dewalt et al., 2000), despite a wide range being shade tolerant and present within closed canopy mature forests (Putz, 1984, Putz and Chai, 1987).

(2) *Phylogenetics*

Although climbing as a habit has multiple origins, lianas (as well as non-woody vines) share many convergent ecophysiological traits that they do not share with nearer tree relatives (Rios et al., 2014, Angyalossy et al., 2012). For example, lianas in general have enhanced photosynthetic and dark-adapted respiration rates, greater foliar concentrations of nitrogen, lower anti-herbivore chemical defences, and lower leaf mass area and specific leaf area (Rios et al., 2014, Asner and Martin, 2012, Han et al., 2010, Tang et al., 2012). There is also evidence of differential foliar phosphorus concentrations between lianas and trees; although, this variation is minor and its significance unclear (Zhu and Cao, 2010, Cai and Bongers, 2007, Salzer et al., 2006). Collectively, these factors demonstrate patterns of ecophysiological trait variation among tree and liana species that is independent of phylogenetic relatedness.

The phylogenetic distribution of climbing species (woody and non-woody species alike) among dicotyledonous rainforest plant families in Australia and BCI with 10 or more species (see Table 2.3 and Figures 2.1-2.3) is comparable to global estimates by Gianoli (2015) and Gentry (1991). Climbing species accounted for 17%, 24% and 34% of regional diversity (Table 2.3), and were spread across more than 60% of families in both subtropical/temperate and tropical Australia, and BCI, respectively.

The relative diversity of climbing species within rainforests was greatest at low latitudes. This pattern reflects the general species distribution of climbing plants.

Table 2.3 Comparison of the occurrence of lianas and other creepers in three rainforests. Only dicotyledonous families which occurred with more than ten species are included. ‘Lianas’ in this case include some non-woody creepers and non-liana species refers specifically to woody plants i.e. trees (herbaceous species were excluded from the analysis). Sources of information for the Australian analysis are Harden et al. (2006 & 2007) and Hyland et al. (2010), and for the Panamanian example, Croat (1978). Note that in the case of the Australian locations data were abstracted from regional floras whereas the BCI data were abstracted from the flora of that island alone (54m²). Percent contributions of lianas/non-lianas to regional species richness (excluding herbaceous plants) are included in brackets. Associated phylogenies are shown in Figures 2.1-2.3.

Location	Total families with >10 species	Number of non-liana species	Number of liana species	Families with no lianas	Families with 50<99% lianas	Families with 100% lianas
Subtropical and temperate rainforests of Australia (ca 28.2°S)	26	639 (83.0%)	131 (17.0%)	9 (34.6%)	2 (7.7%)	1 (3.8%)
Wet Tropics, tropical Australia (ca 17.3°S)	35	978 (75.8%)	312 (24.2%)	11 (31.4%)	1 (2.9%)	5 (14.3%)
Barro Colorado Island, Republic of Panama (9.2°N)	22	343 (63.3%)	199 (36.7%)	7 (31.8%)	4 (18.2%)	3 (13.6%)

A single family in subtropical/temperate Australia comprised entirely of climbing species (Vitaceae) (Figure 2.1), whereas several specialist climbing families are present in tropical floras (Australia: Aristolochiaceae, Menispermaceae, Convolvulaceae, Vitaceae, Cucurbitaceae, BCI: Convolvulaceae, Cucurbitaceae, Passifloraceae) (Figures 2.2 and 2.3). Apocynaceae and Fabaceae were among the top three most speciose families of climbers for each of the floras assessed. It is interesting to note however, that climbing species are largely absent from the Myrtaceae, Australia’s dominant plant family (and also the dominant family within the Australian elements of this analysis) (Figures 2.1 and 2.2). As a whole, climbers are poorly represented within the malvids. Similarly, Australian Sapindaceae included very few climbing species while Sapindaceae on BCI was dominated by vines (Figures 2.1- 2.3).

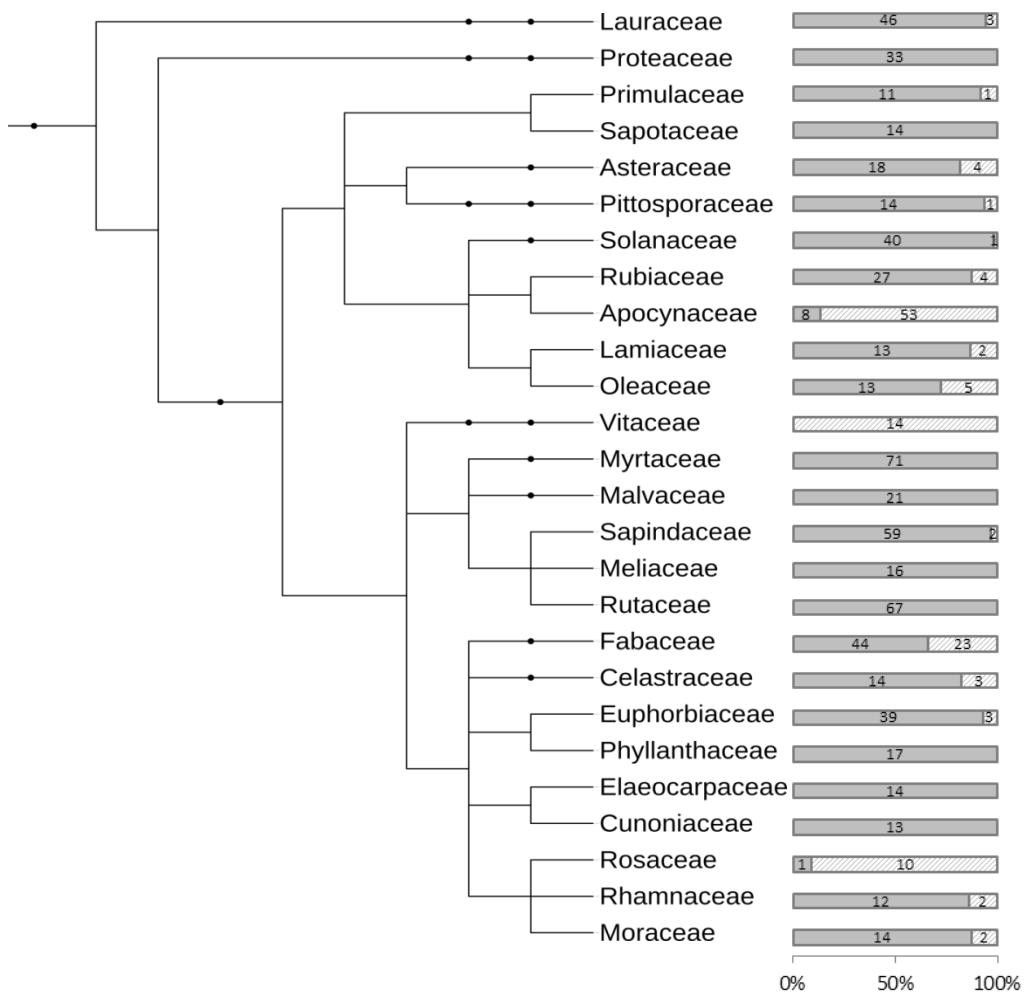


Figure 2.1 Evolutionary relationships of Australian temperate and subtropical dicotyledonous rainforest plant families with ≥ 10 species. Bar graphs depict the species richness of woody species i.e. trees and shrubs (dark grey) and climbing plants (hatching). Climbing plants are represented in 17 of the 26 families displayed. Within bar labels indicate the number of species. Data was extracted from Harden et al. (2006 & 2007) and phylogenies were generated using an online phylogenetic tree generator (Letunic, 2017) based on NCBI taxonomy. Note herbaceous species were excluded from the analysis.

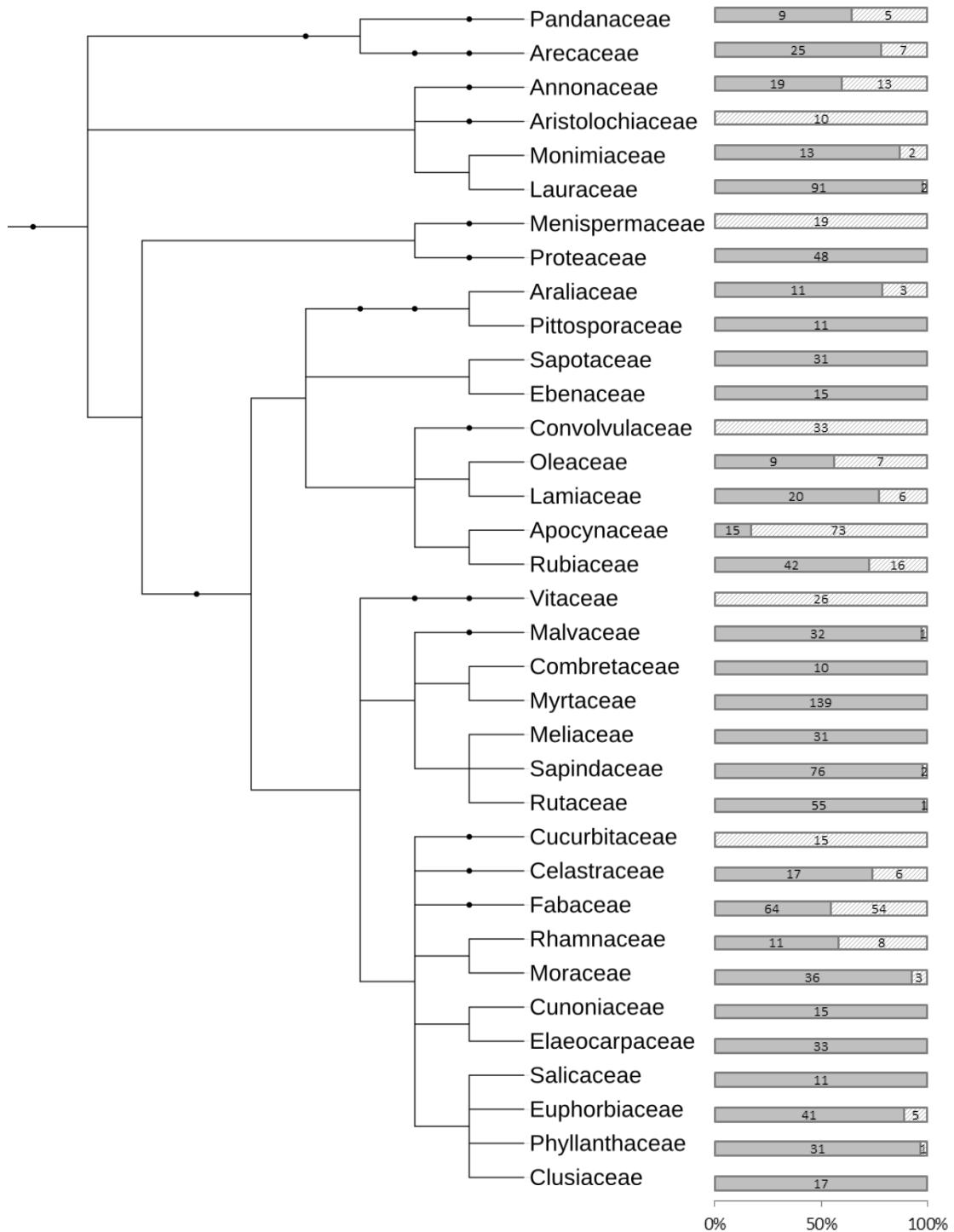


Figure 2.2 Evolutionary relationships of dicotyledonous rainforest plant families in tropical Australia with ≥ 10 species. Climbing plants are represented in 25 of the 36 families displayed. Data is extracted from Hyland et al. (2010). Description follows as in Figure 2.1.

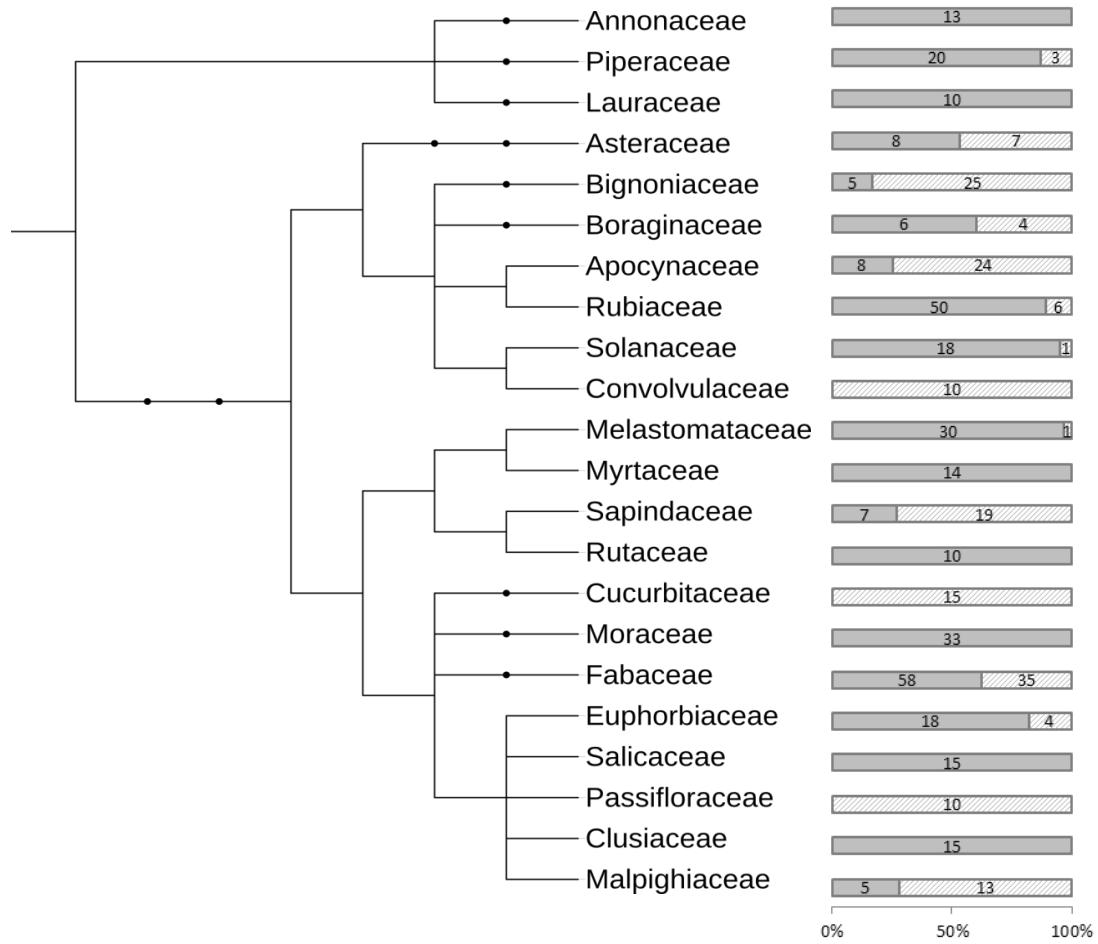


Figure 2.3 Evolutionary relationships of dicotyledonous rainforest plant families on Barro Colorado Island, Panama with ≥ 10 species. Climbing plants are represented in 15 of the 22 families displayed. Data were abstracted from Croat (1978). Description follows as in Figure 2.1.

2.5 LIANAS AS A RESOURCE FOR HERBIVORES

Few clear general patterns of herbivory have been identified linking plant communities with their insect herbivores (Metcalfe et al., 2014, Endara and Coley, 2011, Moles et al., 2011), largely due to the complex nature of plant-insect interactions. One well supported pattern, however, is the general preference by herbivores for young expanding leaves over mature leaves (Coley, 1980, Aide, 1993, Aide, 1992, Basset, 1992). Although species-specific exceptions to this rule exist (for example the larvae of the regent skipper, *Euschemon rafflesiae*, which feed on leathery leaves of *Wilkeia* species (Braby, 2000, Harden et al., 2006)), the presence of soft, young expanding leaves can largely predict the occurrence of herbivory (Basset, 1992, Raupp and Denno, 1983). Several factors appear to drive this preference, including: higher nitrogen content, lower foliar biochemical defences and poorly developed structural defences (Furlan et al., 1999, White, 1984, Aide, 1993, Feeny, 1976, Cunningham et al., 1999, Wright and Cannon, 2001). These aspects of leaf quality can be usefully applied to predict local and larger-scale patterns of herbivory. In tree leaves, these leaf qualities diminish rapidly as the leaf reaches full expansion,

presenting only a small window of opportunity for optimal herbivore exploitation. For herbivores feeding on lianas, however, this may not be the case. It has been suggested (but seldom tested) that lianas; invest little energy in chemical and structural defences, store high levels of nutrients in their leaves, and exhibit a phenology in which newer leaves may be available more often and/or more consistently than trees.

A quantitative comparison of herbivory on lianas and trees in Papua New Guinea (PNG) found the difference in relative leaf loss was greater on trees than lianas (trees = 12.5-13.7%, lianas = 6.2-10.7%), although this difference was only significant at one of the two sites (Wint, 1983) (Table 2.4). In contrast, de la Cruz and Dirzo (1987) observed greater relative leaf loss on lianas compared to trees (trees = 8.17%, lianas = 10.87%), albeit insignificant (Table 2.4). These estimates of relative leaf loss on lianas are, however, likely underestimates as liana leaves have shorter life spans compared to tree leaves, which reduces the duration each liana leaf is exposed to potential herbivory. Although the available data, of which I am aware, on the relative leaf loss of lianas and trees is limited, it indicates lianas may contribute substantially, if not equally, to rainforest insect folivory. Further research, however, is needed to confirm this assumption.

Table 2.4 Relative contributions of trees and lianas to herbivory from within a single location and period of time. The number of species sampled shown in brackets. Relative leaf loss on trees compared to lianas was only significantly different in PNG south ($p<0.01$). It is important to note estimates of relative leaf loss on lianas are likely underestimated due to shorter leaf-life spans compared to trees which reduce the duration each liana leaf is exposed to potential herbivory.

Location	Forest type	Tree	Liana	Reference
Mexico	Tropical rainforest	8.17% (13)	10.87% (6)	de la Cruz and Dirzo (1987)
PNG (north)	Tropical rainforest	12.5% (7)	10.7% (11)	Wint (1983)
PNG (south)	Tropical rainforest	13.7% (23)	6.2% (20)	Wint (1983)
Borneo	Tropical rainforest	5.39% (72)	4.96% (9)	Peñuelas et al. (2013)

If the aforementioned leaf characteristics (structural and chemical defences, nutritional quality and phenology) are indeed accurate and important general predictors of insect herbivory, we can hypothesise that lianas are likely to be considerable and potentially keystone supporters of insect herbivory in rainforests and that this interaction may become even more important if, as predicted (discussed above), lianas continue to increase in abundance in response to climate change and other anthropogenic influences.

(1) Chemical and structural defences

Plants have developed a wide array of chemical and structural mechanisms to defend against herbivory. Such defences reduce a plant's palatability and digestibility, and may reduce the fitness of herbivores feeding upon them. Little is known about the differences in structural defences between liana and tree leaves. However, chemically they have been observed to be notably different, with defence chemicals largely lacking in liana life forms (see below).

Chemical defences. Asner and Martin (2012) assessed the chemical composition of 7274 species of tropical liana and tree leaves. Mass based concentration of metabolic chemicals associated with light-capture, growth and maintenance were approximately 15% greater in lianas than in trees, whereas structural and defence chemicals were 9% lower in lianas than in trees ($p>0.05$). Such allocation priorities are typical of pioneer species and other species with enhanced growth, such as lianas (Kursar and Coley, 2003).

Plant species with lower levels of chemical defences have been shown to have higher vulnerability to herbivory (Paré and Tumlinson, 1999, Levy et al., 2005) and those with greater concentrations of chemical defences are, in general, grazed upon by insect herbivores less than their counterparts with fewer chemical defences if all other factors are controlled (Coley, 1983, Coley and Barone, 1996, Bidart-Bouzat and Imeh-Nathaniel, 2008). Accordingly, the lower foliar biochemical defences possessed by lianas pose a reduced threat to herbivores, and therefore may make lianas a preferred food source. There are notable exceptions to this generalisation, especially for lianas in families such as the Asclepiadaceae, Passifloraceae and Aristolochiaceae which are characterised plesiomorphically by their possession of strong (principally vertebrate targeted) anti-feedant chemicals. These plants in turn have been exploited by specialist insect herbivores which sequester the vertebrate toxins as a defence mechanism leading to specific insect radiations associated with those vertebrate-protected clades of plants (Ackery and Vane-Wright, 1984, Nishida, 1994, Kitching and Scheermeyer, 1993) .

The configuration of arthropod assemblages (in terms of diversity, specialisation and network complexity) should alter to reflect the availability of suitable food plants (i.e. those poorly defended against insect attack). In principle, a lack of chemical defences should encourage grazing on lianas by more generalist herbivores as insect specialist interactions are more likely to develop in association with plants that possess chemical protection (Coley and Barone, 1996, Pellissier et al., 2012). Against this idea is the notion that polyphagous herbivores may be better adapted to cope with chemical defences as they are exposed to a greater variety of such defences which may have led to the selection of individuals who could survive ingesting an assortment of toxins. Some larger monophagous species, in contrast, benefit from hosts with low chemical defences, such as the assemblages of Costa Rican saturnid moths which feed on plants with low to no foliar chemicals (Janzen, 1984). Observations of Coleoptera by Ødegaard (2000b), also showed beetle specialisation on lianas to be equal to, if not greater than specialisation on trees.

Structural defences. For many insects, the epidermis is the first point of contact for a herbivore and the primary barrier that must be overcome. Plants have developed a wide range of structural defences to deter herbivores such as tough lignified and waxy cuticles, trichomes and raphides to deter herbivores (War et al., 2012). These defences may block herbivory or slow rates of consumption. They may also deter oviposition and subsequent establishment of populations of larval herbivores (Handley et al., 2005, Haddad and Hicks, 2000). Trichomes, raphides, lignin and other structural defences also cause internal physical damage to the herbivores when ingested, interfering with digestion, behaviour and mobility (Dalin and Bjorkman, 2003, Mithofer and Boland, 2012, Hanley et al., 2007).

No assessment has been made of the relative occurrence of foliar structural defences across lianas and trees. However, lower leaf mass per unit area (LMA) and reduced levels of foliar structure chemicals (Asner and Martin, 2011) suggest a reduced investment by lianas in structural defences. This should be reflected in the levels of herbivory between trees and lianas. Taxonomic information on structural traits (such as; raphides, domatia, waxy cuticle etc.) is available for various regional liana and tree floras and could provide the basis for a comparative analysis.

(2) Nutrition

The importance of foliar nutritional quality for an insect herbivore differs between species depending on specific biological requirements for growth and development (Boppré, 1990). Nitrogen and phosphorus are commonly considered to be universally important for insect nutrition. They are vital to many metabolic processes and can limit development and influence herbivore fitness (Mattson and Scriber, 1987, Awmack and Leather, 2002). Apple et al. (2009) observed maximal larval growth rates (of lepidopterans) on lupin leaves with intermediate to high leaf phosphorus concentrations and concluded that phosphorus may mediate the plant herbivore interaction. In contrast, Metcalfe et al. (2014) found leaf area loss greatest on leaves with lower foliar phosphorus. The results may not be at odds, but simply reflect the use of two different response variables of the same phenomenon. Low phosphorus levels per unit leaf area may drive greater consumption in order to maintain appropriate intake of nutrients. Further experimentation looking at both responses jointly is required.

For a consumer, it is arguably important to consume the greatest amount of nutrients for the lowest effort. One strategy to achieve this is to consume leaves with the highest nutritional value (i.e. high nitrogen and phosphorus). This may in part explain a preference of insect herbivores for young leaves which commonly sequester greater levels of nitrogen than older leaves (Reich et al., 1992, Basset, 1992, Furlan et al., 1999).

Foliar concentrations of nitrogen and phosphorus have been found at greater concentrations in the leaves of lianas compared with the leaves of their tree counterparts (Zhu and Cao, 2010, Cai and Bongers, 2007, Kazda and Salzer, 2000, Asner and Martin, 2011). If the nutritional quality of available food plants is

indeed an important factor regulating insect herbivory (Coley 1983), we can hypothesise that liana leaves will be a more attractive and nutritionally advantageous food source for insects than trees. In turn, this may mitigate the amount of herbivory on host trees (as discussed further below).

(3) Phenology & availability

The quantitative and qualitative availability of plant resources play a key role in herbivory and these features are, in turn, a reflection of the phenology of the plants concerned. If palatable or suitable leaves are not available when insect herbivores require them, the herbivores survival/fitness is potentially reduced. If a food plant is reliably available with palatable young leaves and this coincides with the seasonal feeding of an insect then the risks associated with an insect relying on that plant is minimized and survival more likely. Many fluctuations in insect abundances can be linked to the availability of their food plants (Dempster and Pollard, 1981, Zhu et al., 2015). Phenological coincidence, or its lack, is also an important factor in the evolution of host-plant specialisation or generalisation on the part of the insect herbivores concerned (Singer and Parmesan, 2010, Navarro-Cano et al., 2015, Bernays and Chapman, 1994).

Development of defensive chemicals and structural barriers are plant adaptations that may minimise herbivory. These defences, however, are not always a possibility for physiologically young, developing leaves. For example, a tough epidermal layer is an effective defence but is incompatible with leaf expansion (Aide and Londono, 1989, Coley and Barone, 1996, Moles and Westoby, 2000). Similarly the allocation of secondary metabolites to young rapidly expanding leaves risks the possibility of auto-toxicity (Coley and Barone, 1996, Asao and Asaduzzaman, 2012). Without these defences, plants must rely on alternative mechanisms to protect young leaves. One such mechanism for the minimisation of herbivory is through modifying leaf phenology. Three different phenological strategies have been suggested. Firstly, plants may advance or delay leaf flush to coincide with the season when insect herbivores are least abundant; thus minimising predation of young leaves (Coley, 1982, Aide, 1992, Coley and Barone, 1996, Murali and Sukumar, 1993). Second, plants within or across species may synchronously produce vast quantities of leaves to swamp the demands of coincident herbivores, with the assumption that at least some will survive intact to maturity (Lieberman and Lieberman, 1984). Third, plants may shed and produce new leaves more frequently, so that the effects of herbivory are minimised.

Insect herbivores will be at minimum levels of abundance and activity when environmental conditions are least optimal for survival; this corresponds to the dry season in the seasonal tropics and subtropics, or the winter in cooler climates. In cool climates with severe winters the deciduous habit or other forms of plant dormancy obviate the herbivory issue. In the tropics and subtropics, however, trees that exploit a dry season to flush their leaves experience less herbivory on both young and mature leaves (Murali and Sukumar, 1993). Although this may be useful for avoiding insects, dry season water stress may limit leaf production. Presumably for those species which flush at this time the benefits of leaf production during the dry season are outweighed by the potentially greater costs of herbivory during the wet season. This

strategy may not be viable for plants in forests with weak, unpredictable and/or short dry seasons or extreme water limitation.

For species where dry season leaf production is not viable, synchronised leaf flushing may be an alternative. Tree species that show high levels of synchronicity in leaf production are less likely to experience insect damage to young leaves (Lieberman and Lieberman, 1984). This is most likely because insect herbivores actively seek young leaves, and therefore the chance that any particular young leaf will be damaged decreases as the number of concurrently available young leaves increases (Coley and Barone 1996). The well-known mass flowering and fruiting of the dipterocarps in south-east Asia (Appanah, 1993), and other mast flowering and fruiting events may represent such a herbivore avoidance strategy across species.

These two temporal strategies decrease the proportion of damage caused to young leaves by insect herbivores and are presumably beneficial to the survival of the individual plant, but limit the way in which they can cope with herbivory throughout the year. A third strategy, however, may be useful for mitigating the impacts of herbivore damage, while sustaining a degree of herbivory.

Fast growing species, such as lianas may be able to tolerate greater levels of herbivory than slower growing trees due to differences in leaf life spans, leaf production periods and greater turnover of leaves. The life span of liana leaves is shorter than those of self-supporting species. In one study, the life span of liana leaves was 8.50 ± 0.43 months compared with 10.16 ± 0.50 months for trees (Zhu and Cao, 2010) while another found that lianas produced new leaves for 200 ± 74 days compared to trees which only produced new leaves for 157 ± 97 days (Ødegaard, 2000b). Greater levels of leaf turnover most likely do not physically reduce the proportion of damage caused to young leaves by insect herbivores but alternatively may help to alleviate and minimise the time to recovery. If we assume the impacts of herbivore damage only persist until the leaf is replaced, then the impacts of herbivory at the level of the entire plant will be far more short-lived for those species with faster rates of leaf turnover. Such a strategy may appear to be wasteful, but is offset by low (or no) investment in chemical defences. This is evidenced in lianas, compared with trees, by their lower investments into leaf construction costs per unit area (Zhu and Cao, 2010) and significantly lower leaf mass per unit area (Reich et al., 1992). Further, as leaves age, their photosynthetic capacity, nitrogen contents and relative growth rates decline (Reich et al., 1992, Zhu and Cao, 2010). These effects can be obviated by frequent leaf turnover.

Rates of leaf turnover and phenology are two important characteristics that underlie a food plant's availability and reliability. As the life-span of liana leaves is significantly shorter than those of other growth forms (Zhu and Cao, 2010) and their leaf production periods are longer than those of trees (Ødegaard, 2000b), they are able to provide a reliable source of young and more palatable leaves to insect herbivores for greater durations. As old leaves are shed, new, more palatable and nutritious ones become available, thereby providing effective and stable support to herbivores that rely upon them. Lianas may also be important for providing a suboptimal, temporary, alternative food source when the availability of

a preferred non-liana food plant is low. The lack, in many cases, of structural and chemical defences increases their availability to generalist herbivores and can provide temporary support to weakened tropic interactions. The use of lianas as an alternative food source during times of scarcity of more seasonal food plants has been observed in mammals (Moscovice et al., 2007). Accordingly, frequent replacement of leaves will maintain accelerated growth rates (Reich et al., 1992, Loomis, 1997) while providing valuable resources to insect herbivores.

2.6 LIANA-HOST INTERACTIONS AND HERBIVORY

The spatial proximity of plants plays an important role in mediating many ecosystem processes such as; resource availability, growth, reproduction, facilitation and herbivory (Karban, 1997, Barbosa et al., 2009, Reader et al., 1994, Armas and Pugnaire, 2011). Neighbouring plants may be beneficial or detrimental to a focal plant depending on the characteristics of both the focal and neighbouring plant species (Callaway, 1995). These factors may either aid or reduce a focal plant's fitness depending on its response to herbivory (Bergvall et al., 2006, Agrawal, 2000). Plant neighbours may impact positively upon another individual's capacity to tolerate herbivory by reducing the impacts of environmental stresses that might have otherwise limited that individuals ability to compensate for these stresses (Callaway, 1995). Similarly, a closely associated unpalatable plant neighbour may deter and protect a focal plant from insect herbivores (Tahvanainen and Root, 1972). Neighbouring plants, however, may also be disadvantageous. In some cases, plant neighbours attract and facilitate colonisation of a focal plant by insect herbivores (Karban, 1997, Barbosa et al., 2009, Hambäck et al., 2000) resulting in increased herbivory. Many neighbouring plants compete for the same limited resources during post-herbivory stages and may hinder an individual's ability to recover from herbivore induced damage.

One of the closest spatial relationships between pairs of plant species is between a liana and its host. The impacts of tree-tree spatial proximity may differ to that of liana-host due to differences in leaf traits, below-ground resource competition (or lack thereof) and degree of environmental buffering. Impacts of liana-host associations, such as those on reproduction and mortality, have been documented (Wright et al., 2005, Ingwell et al., 2010, Putz, 1984, Stevens, 1987), but little information is known about how liana-host associations affect herbivory and faunal communities. Despite the great number of faunal inventories of tropical forests, few have specifically compared arthropod communities between lianas, their hosts, and liana-free trees (Schnitzer et al., 2015). Stork (1991), who used knockdown insecticides to collect insects from trees in Borneo found that highest numbers of insect species were collected from trees with a high liana and epiphytic load, but this has not been tested more widely (Table 2.5).

Foaham (2002) investigated the impacts of liana-cutting on herbivory upon trees and found that insect herbivory on trees was greatest in forests where lianas had been removed. This implies lianas may alleviate levels of host-tree herbivory, perhaps by increasing the density of leaves surrounding and 'camouflaging' their host. However, more research and replicated studies are required to confirm the generality of these results.

As discussed earlier, direct competition for below ground resources between lianas and hosts may not be as great as commonly presumed as lianas are generally rooted away from their host tree. The rapid turnover of lianas leaves may even be beneficial to the resource acquisition of host trees as they are able to acquire nutrients from elsewhere, transport it to their leaves which later mulch the soil surrounding the base of their host (Tang et al., 2012). Empirical evidence for or against this phenomenon is needed.

2.7 FAUNAL COMMUNITIES AND LIANAS

Reduced investment in defence chemicals in favour of faster foliage growth as shown in lianas should give rise to associations with more generalist herbivores. However, the best known liana-arthropod associations are those of highly specialized plant feeders. Some of the best documented examples include those of Heliconiinae butterflies and Passifloraceae (Smiley, 1978, Benson, 1978), Ithomiinae butterflies and Solanaceae (Trigo and Motta, 1990), and Baridini (Curculionidae) and *Hylaeogena* (Buprestidae) beetles and Bignoniaceae (Ødegaard, 2000b). Specialisation of insect herbivores on lianas may be related to the elevated levels of nitrogen in liana leaves as nitrogen content is an important factor for specialist herbivores, particularly those feeding on chemically well-defended families as it may help overcome the impacts of defences lowering feeding efficiency (Volf et al., 2015).

These highly specific and well-known examples of herbivore-host relationships are almost certainly not at random, nor a representative sample of herbivore-liana interactions in general. They have generally been selected for study because of *a priori* knowledge of high levels of specialisation. The more general role of lianas in structuring arthropod faunal communities is less well understood. Local liana abundance has been hypothesised to be more important than tree identity in determining faunal similarity (Stork, 1987). This in part may be attributable to the unique physiognomic contribution of lianas to the structural complexity of ecosystems. However, the significance of habitat structural complexity in the maintenance of diversity within arthropod communities is poorly understood and merits further attention.

From the few available studies that have focused on faunal assemblages on trees and lianas, several have observed elevated arthropod abundance and diversity on lianas compared with trees and on trees associated with lianas compared to trees without lianas (Ødegaard, 2000b, Wolda, 1979, Dial et al., 2006, Adams et al., 2017, Walter, 1994). However, most of these assessments focus on a single order of arthropods and don't make multi-taxon comparisons (see Table 2.5). This limits the potential to understand how the presence of lianas influences interactions and patterns of co-existence between arthropod orders. Whether or not differences in faunal compositions on lianas compared with trees is explained by characteristics of the liana (such as phenolics or greater availability of new foliage) or simply an increase in overall plant diversity remains unclear.

Lianas play an important role in shaping local arboreal ant assemblages. Trees hosting lianas on average have greater ant species richness and different community compositions than trees without lianas (Adams

et al., 2017). Several mechanisms may explain these differences. Firstly, lianas overcome the insular nature of tree crowns by increasing connectivity with other trees in the canopy allowing for greater mobility of ant species. Secondly, lianas increase habitat complexity and niche availability. Thirdly, extra-floral nectaries (EFN) are rare on trees but are common on lianas and are a popular food source for ants and other insects (Blüthgen et al., 2000, Blüthgen and Fiedler, 2002). Fourthly, as mentioned above, lianas may simply increase proximal plant species richness and available foliage.

Table 2.5. Examples of plant-insect interactions and influence of plant type (i.e. liana, tree) on arthropod assemblages. ¹ tropical rainforest, ² subtropical rainforest

Location	Arthropod group	Focal plant/s	Impact of lianas	Reference
Panama ¹	Coleoptera	Trees, lianas	<ul style="list-style-type: none"> Maintain local species diversity Trees and lianas support equal numbers of beetle species Specialisation greater on lianas Support different guilds 	Ødegaard (2000b)
Borneo ¹	Arthropoda	Trees, lianas	<ul style="list-style-type: none"> Assemblage correlated to liana and tree foliar elements Abundance increases with liana foliage density 	Dial et al. (2006)
Borneo ¹	Arthropoda	Trees (notes on vines and epiphytes)	<ul style="list-style-type: none"> Epiphyte/vine load significant effect on faunal similarity 	Stork (1987)
BCI, Panama ¹	Formicidae	Trees, lianas	<ul style="list-style-type: none"> Lianas influence arboreal ant assemblages Different ant assemblages on trees with and without lianas Ant species richness greater on trees with lianas than without 	Adams et al. (2017)
Amazon, Venezuela ¹	Formicidae	Trees, lianas, epiphytes	<ul style="list-style-type: none"> Liana and epiphyte EFN common food source for ants (rare on trees). Aggregations of ant species feeding on lianas were commonly found on trees, but rare on epiphytes 	Blüthgen et al. (2000)

Table 2.5 Continued

Location	Arthropod group	Focal plant/s	Impact of lianas	Reference
QLD, Australia ¹	Formicidae, Hemiptera, Homoptera	Trees, lianas	<ul style="list-style-type: none"> · Visitation rates (VR) to hemipterans by ants was significantly greater on lianas compared to trees · VR to homopterans by ants was greatest on lianas · Majority of tritrophic aggregation sites were found on lianas 	(Blüthgen and Fiedler, 2002)
Panama ¹	Homoptera	Trees, lianas	<ul style="list-style-type: none"> · Correlation between number of vines and homopteran density · Vines influence the suitability of tree canopies for homopterans 	Wolda (1979)
QLD, Australia ^{1,2}	Arachnida: Acari	Trees, lianas	<ul style="list-style-type: none"> · Mite density greater on lianas than trees 	Walter (1994)

2.8 OPEN QUESTIONS

I have noted throughout this review, instances where key questions concerning the role of lianas in forest ecosystems remain in need of clarification or, in some cases lack relevant studies. In this final section I place a selection of these comments in their wider context and attempt to set a future research agenda for liana-herbivore studies.

One of the main hindrances to an improved understanding and appreciation of the contribution of lianas within ecosystems is the lack of data on liana-insect interactions. Research on lianas is beginning to attract attention, but mostly still focusses on the roles of lianas in disturbance and successional dynamics, or biogeographical patterns and temporal changes in abundances (Laurance et al., 2014, Londré and Schnitzer, 2006, Laurance et al., 2001, Schnitzer and Bongers, 2011, Roels and Verbeeck, 2016, Caballé and Martin, 2001, Ledo and Schnitzer, 2014). Little quantitative data exists, comparing the amount of herbivory on lianas with herbivory on trees, the interactions occurring between different plant functional groups and insect herbivores, or the function of lianas in ecosystems and the significance of that role in biodiversity maintenance, and/or ecosystem functioning, structure and stability. Available evidence suggests their role is of significance for many critical functional ecosystem properties. The many open questions will benefit from further focussed field studies in appropriate locations from cross-regional meta-analyses, and from carefully designed manipulative experiments.

(1) *Herbivory*

Much of our understanding of insect herbivory in rainforests comes from the study of large canopy trees and saplings. However, difference in leaf traits between lianas and trees, including, structural chemical, and phenological properties, suggest inferences and conclusions about herbivory gathered from data on trees cannot simply be extended to lianas. Community wide pairwise comparisons and comparisons within taxa would be useful in quantifying the relative contribution of lianas compared with trees to ecosystem processes such as herbivory, and the mechanisms influencing these processes. The amount of leaf loss on lianas compared with trees (and between trees with lianas compared with those without) can be quantified using the image processing software package ImageJ and correlated with patterns to leaf traits such as leaf toughness, total phenols, nitrogen, carbon, and phosphorus. Further investigation is required to understand the influence of other leaf traits, particularly structural (such as; raphids, domatia, hair etc.), and patterns of phenology, seasonal variability and climatic influences.

(2) *Host-plants*

The relative use of lianas as host-plants for arthropods is poorly known. Butterflies (represented by Papilioidea and Hesperioidae) are arguably the most taxonomically well-known and best resolved insect taxa globally. Most are highly folivorous and inventories of their larval identities, life histories and larval host plants are extensive for many regions. Lianas, and vines alike, are hypothesised to be important food plants for butterflies. However, this speculation has never been formally tested. This provides an ideal framework to critically assess the relative contribution of lianas compared with trees as larval food-plants (particularly in rainforests) and determine differences in the degree of host specialisation between the two plant functional groups. Wider questions related to other herbivore taxa, guilds and locations require further investigation.

(3) *Liana abundances*

It is well established that liana abundances are increasing within the Neotropics (Laurance et al., 2014, Schnitzer and Bongers, 2011, Yorke et al., 2013, Chave et al., 2001). In Paleotropical, subtropical and temperate regions, however, temporal patterns in the distribution and abundance of lianas have received much less attention and no such studies are available for Australia. Historical records of liana and tree abundances are available for south-east Queensland (e.g. Laidlaw et al. 2000 and Tang 2007). This site was re-surveyed in 2015 and similarly shows increasing in liana abundances (unpublished). However, the relevance of this study within the wider context of Australian rainforests requires the establishment of additional long-term monitoring sites which incorporate lianas into their inventories.

(4) Arthropod assemblages

The differences (or similarities) in arthropod assemblages on lianas compared with trees has been little studied and few include multi-taxon approaches (see Table 2.5). Arthropod assemblages could be determined using traditional sampling techniques such as hand collection, beating and feeding trials, and more modern techniques such as meta-barcoding or gut contents. The resulting data would allow for community level comparisons of arthropod assemblages and the reconstruction of fine-scale food webs existing on each plant type, and between trees associated with lianas compared to those without.

Collection of additional data would assist with the determination of subsidiary hypothesis such; as how lianas structure and influence species distribution and diversity throughout forests and the mechanisms underlying this. Understanding the potential role of lianas as determinants of local species richness is essential to predicting future patterns of biodiversity because, as noted earlier, they are the second biggest contributor to leaf biomass and accordingly should exert a large influence over herbivore assemblages.

2.9 CONCLUSIONS

- 1) Lianas are important physiognomic components of forests and the second largest contributor of primary production (Hladik, 1978, Hegarty, 1991 , Pragasan and Parthasarathy, 2005). Accordingly, they should exert a large influence over herbivore communities. Their contributions to ecosystems, in terms of leaf biomass and production, may surpass that of trees if their abundances and dominance continue to increase.
- 2) Much of our current understanding of insect herbivory in rainforests comes from the study of large canopy trees and saplings. However, inferences and conclusions about herbivory developed from data on trees cannot simply be extended to lianas due to distinct ecophysiological variation in leaf traits independent of phylogeny (Angyalossy et al., 2012, Rios et al., 2014).
- 3) Although lianas are not monophyletic, their leaf traits differ significantly to those of trees in terms of chemical and structural defences, nutritional quality and phenology (Cai and Bongers, 2007, Zhu and Cao, 2010, Asner and Martin, 2012, Rios et al., 2014). These differences will produce different rates of herbivory.
- 4) Lianas support different herbivore assemblages compared with trees, and increase arthropod species richness on the trees with which they associate. Whether or not this is explained by the distinct qualities of lianas leaves, or through improvement of habitat complexity and niche availability, or simply an increase in overall plant diversity remains unclear.
- 5) Many rudimentary questions require attention and have been outlined here. Studies specifically investigating the dynamics of herbivory on lianas (and the impacts this has on their hosts and overall ecosystem functioning), are needed to develop a holistic understanding of herbivory in forests.

CHAPTER 3

STATEMENT OF CONTRIBUTION TO CO-AUTHORED PAPER

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My contribution to the chapter involved field work and data collection, data analysis and writing of the manuscript. Melinda Laidlaw and Tang Yong contributed historical vegetation data. Bill MacDonald assisted with field work and identification of plants. Roger L. Kitching is my supervisor and assisted with conceptualisation, the scope and structure of the manuscript and editing.

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CHAPTER 3

Trees and lianas in an Australian subtropical rainforest: change and stasis over two decades

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3.1 ABSTRACT

Changes in the floristics of a subtropical rainforest were monitored over a 20 year period (surveys in 1995, 2005 and 2015) on a permanent 1 ha reference plot at Lamington National Park ($28^{\circ}13'S$, $153^{\circ}07'N$, 900m asl) in south-east Queensland, Australia. All trees with a diameter at breast height (DBH) $>5\text{cm}$, and lianas $>2\text{cm}$ were included in the study. On each sampling occasion DBH, position within the plot, and species was recorded. Lianas were added to the database in 2005.

Liana abundances increased by 13% over the 10 years from 2005 to 2015 whereas the number of tree stems was stable from 1995-2015. Liana biomass rose 23% over the decade, while tree biomass increased slower at 13.5% for the same period. Using liana and tree structure, I determined the influence of rainfall, tree mortality and carbon dioxide (CO_2) enrichment on the observed floristic changes. There was little evidence to suggest that rainfall and tree mortality were driving patterns in liana abundances. Based on changes in the structure and assembly of liana and tree communities, I suggest that the most probable explanatory hypothesis driving increases in liana abundances on this plot is increasing atmospheric CO_2 and the consequent accelerated forest dynamics.

This increase in liana abundance and biomass is similar to those observed in tropical rainforests around the world, particularly the Neotropics.

3.2 INTRODUCTION

Rainforests cover less than 2% of the global land surface, yet are home to 50% of all extant terrestrial species and provide invaluable environmental, economic and social benefits (Corlett and Primark, 2011). Rainforest coverage has declined dramatically in recent decades owing primarily to logging, deforestation, agriculture and road construction (Hansen et al., 2013, FAO & JRC, 2012), and is under further threat from climate change. Declines in species diversity and associated ecosystem functions such as productivity and carbon cycling are well documented (Loreau et al., 2001, Hooper et al., 2012). One of the most notable recent structural changes occurring within rainforests is the increase in the abundance and biomass of lianas (woody vines) in tropical forests (Laurance et al., 2014, Schnitzer and Bongers, 2011, Yorke et al., 2013).

Australian rainforests are estimated to have covered up to 80 000 km² in the late eighteenth century ranging from cool temperate forests in Tasmania through to the lowland tropical forests of far northern Queensland. Approximately one quarter of this remained in 1981 (Webb and Tracey, 1981) distributed in patches along the eastern seaboard, with smaller patches of monsoonal and other wet forests in the north and north-west. The most extensive remnants are in the Wet Tropics (*ca* 760 km²), in the higher elevation subtropics of south-eastern Queensland and north-eastern New South Wales (*ca* 600 km²) and in the western half of Tasmania (*ca* 456 km²) (Webb and Tracey, 1981).

In this paper I describe changes in forest structure that have occurred over a twenty year period in a subtropical Australian rainforest. I place particular emphasis on changes in the richness and abundance of lianas and trees that have occurred in these quantities over a ten-year period. I do this in the context of a wider study on the relative importance of lianas in subtropical forests particularly their role as resources for insect herbivores (Odell, 2018). Placing the dynamics of the liana assemblage in context necessitates wider measures of the entire tree flora, which I also present here.

Lianas (woody vines) are important physiognomic components of rainforests and their high abundance is one of the key properties that distinguishes rainforests from other forest types. Of course, they may be present in non-rainforests, but generally in low abundances and diversity. Lianas typically reach peak abundance and diversity in highly seasonal tropical forests (Gentry, 1991, DeWalt et al., 2015, Schnitzer, 2005) where they contribute substantially to many ecosystem properties and functions including; diversity mosaics, habitat heterogeneity, structural complexity, leaf litter and productivity (Wright et al., 2004, Gentry, 1991, Croat, 1978). In tropical ecosystems, lianas contribute up to 20-40% of the leaf litter, above ground leaf biomass and diversity of woody species (Putz and Chai, 1987, Jongkind and Hawthorne, 2005, Appanah et al., 1993, Pragasan and Parthasarathy, 2005, Wright et al., 2004, Hladik, 1978), compared with 9-20% in subtropical forests (Cai and Song, 2000, Hegarty, 1991) and 5-7% in temperate forests (Gentry, 1991). They also significantly alter tree dynamics, gap-phase processes, nutrient cycling and carbon sequestration (Phillips et al., 2002, Schnitzer and Bongers, 2002). In subtropical and temperate rainforests however, inferences about their importance and roles in forest

dynamics rest only on a handful of studies (Londré and Schnitzer, 2006, Allen et al., 2007). Aspects of the ecology of lianas, with respect to their importance in hosting biodiversity and as a food source for phytophagous insects has been reviewed in Chapter 2 of this thesis.

In tropical ecosystems, liana abundances and biomass are increasing in response to a combination of climate change and disturbance (Chave et al., 2008, Schnitzer et al., 2012, Yorke et al., 2013, Laurance et al., 2014). Long-term increases in liana abundances have been documented primarily in the Neotropics and include an 8 year (1997-2007) study in Costa Rica (Yorke et al., 2013), a 10 year (1992-2002) study in French Guiana (Chave et al., 2008), a 14 year study (1997-2014) in the Amazon (Laurance et al., 2014), and a 30 year (1979-2007) study in Panama (Schnitzer et al., 2012). In the Palaeotropics, however, trends identified in liana abundances are derived from only two studies with contrasting results. Forests in the Congo exhibit stable liana abundances (Ewango, 2010) whereas in Gabon liana abundances decreased (Caballé and Martin, 2001). Changes in lianas in subtropical and temperate forests are documented in only two studies, both from North America. Allen et al. (2007) examined subtropical/warm temperate forests in South Carolina and Londré and Schnitzer (2006) reviewed the situation in a temperate forest in Wisconsin. Hitherto there have been no published studies from Australia addressing temporal changes in lianas or their associated vegetation communities.

Three hypotheses have been proposed to explain increasing liana distributions, abundance, and biomass; 1) increasing disturbance, 2) change in rainfall regimes, and/or 3) enrichment of atmospheric carbon dioxide (CO₂). In general, these hypotheses have arisen from fully tropical datasets outside of Australia (Laurance et al., 2014, Phillips et al., 2002, Wright et al., 2004, Ingwell et al., 2010, Chave et al., 2008). Their applicability to subtropical and temperate liana assemblages and Australian forests remains to be explored. Differences in environmental factors, such as the seasonality of rainfall and the duration of the dry season, may alter the responsiveness of liana assemblages to said factors between continents. Determining landscape level changes in the distribution and spatial patterns of lianas is necessary to predict the overall responses of forests, and the ecological processes and interactions upon which lianas have the largest impact. This will further generate insight into the mechanisms controlling liana species distributions and abundances within an Australian landscape (Laurance et al., 2014).

Hypothesis 1: Change, disturbance, accelerated forest dynamics and tree mortality

Within any patch of forest, community changes between any two time periods reflect the coincident operation of three processes. Firstly, recruitment into the youngest (or smallest) size class being considered may add to overall abundance, basal area and species diversity. Secondly, age (or size) specific mortality will counteract these positive impacts. Finally, age (or size) structures of trees or lianas within the forest will grow from one size category to the next. The contrasts among the positive and negative impacts of these concurrent processes will produce observable, community level changes.

Liana abundances are greatest in areas of disturbance. Within mature forests, natural disturbance is primarily generated by treefalls. More than 90% of adult lianas survive treefalls (Putz, 1984) which allows them rapidly colonize the resulting light gap (Schnitzer et al., 2000), principally through clonal propagation (Ledo and Schnitzer, 2014). They then influence the subsequent successional pathways (Schnitzer and Carson, 2010). In contrast, the probability of survival for trees affected by tree falls is low (van der Meer and Bongers, 1996). Rates of tree mortality and turnover are increasing in forests (Laurance et al., 2014, Phillips and Gentry, 1994, Lewis et al., 2004, Laurance et al., 2009) and extreme environmental events are projected to become increasingly unpredictable and severe in response to climate change (IPCC, 2014). We may expect lianas to continue increasing as these events change gap dynamics within forests.

Where treefalls and disturbance are the primary drivers of liana assemblages, liana distributions are expected to be highly aggregated (Ledo and Schnitzer, 2014, Schnitzer and Carson, 2001) and their stems, within aggregations, to be of similar sizes. In areas of severe and/or prolonged disturbance, liana assemblages may also be dominated by fewer species that can withstand such disturbance. In forests where lianas are recruited into the understory and liana recruitment is temporally continuous we would expect more variation of stem sizes (Schnitzer et al., 2012).

Hypothesis 2: Rainfall regimes

Lianas are most abundant in both drier and highly seasonal rainforests (Schnitzer, 2005, Parthasarathy et al., 2004, Gentry, 1991). The density of most rainforest plant groups increases with precipitation (Dattaraja and Sukumar, 2004, Clinebell et al., 1995, Gentry, 1982, Gentry, 1995). Lianas deviate from this general pattern and increase with decreasing rainfall (Schnitzer, 2005). Lianas have extremely efficient vascular systems and have deeply penetrating roots which allows them to exploit otherwise inaccessible stores of water and nutrients in soils. Because lianas can access these reservoirs, they are able to capitalize on the increased availability of dry season solar radiation and respond with elevated growth rates (Angyalossy et al., 2012, Schnitzer et al., 2005). If trends of increased dry periods and seasonality continue and even intensify, as climate change models predict (IPCC, 2014), lianas should be at a competitive advantage compared with other woody species.

If rainfall or lack thereof, is the driving factor influencing liana distributions (as opposed to gap dynamics *per se*), lianas should be randomly distributed across the landscape and increases in the number of liana stems should be coupled with an increase in liana basal area, presumably across all size classes. We would also expect uniformity of tree DBH within smaller stem-size classes reflecting decreased growth rates but high and synchronous rates of recruitment when rainfall does occur.

Hypothesis 3: Atmospheric CO₂ enrichment

Concentrations of atmospheric CO₂ have increased rapidly over the past century from <320ppm in 1960 to >400ppm today (Dlugokencky and Tans, 2017). This change may be a significant factor influencing the distribution of lianas in forests (Schnitzer and Bongers, 2011, Cernusak et al., 2013, Wright et al., 2004), that is, directly rather than through CO₂ induced climate change. Both trees and lianas grown under elevated CO₂ conditions exhibit increased growth rates, particularly in the low light conditions of the understory (Korner, 2003, Cernusak et al., 2013)(Körner 2009). The response of lianas to CO₂ enrichment, however, may be greater than that of trees because of their ability to access deep soil stores of resources more efficiently (Tobin et al., 2012)(see above). The positive effect of CO₂ enrichment on plant growth rates may diminish if atmospheric CO₂ concentrations exceed plant physiological thresholds (Korner, 2003). In addition, the benefits of elevated CO₂ on plant growth rates may be obviated if thermal thresholds are exceeded (Cernusak et al., 2013, Doughty, 2011). The ways in which these physiological thresholds differ (if at all) among various plant functional groups is unclear. If thresholds for lianas significantly exceed those of trees facilitating an increasing dominance of lianas, forests could experience a dramatic change not only in diversity and community composition, but also in the overall physiognomy and, in turn, the ecosystem services they provide, such as CO₂ sequestration (Phillips et al., 2002, Schnitzer and Bongers, 2002).

If elevated atmospheric CO₂ is driving changes in liana abundances and biomass, we would expect liana abundances in forests globally to increase, that is, provided there are no synergistic or countervailing effects with other factors. In addition, within forests we would expect to see not only an increase in the number of stems, but also an increase of basal area for all stem size classes, and potentially a lower rate of turnover in liana stems.

3.3 METHODS

Study Site - Lamington National Park

Lamington National Park conserves one of the most extensive patches (*c.* 20,600km²) of sub-tropical rainforest in Australia (see Figure 3.1). The Park preserves the northern sector of the Tweed shield caldera and is complemented by several rainforest-dominated National Parks in far northern New South Wales (McDonald, 2010). The vegetation formally designated as ‘subtropical rainforest’, also referred to as complex notophyll vine forest (Webb, 1978), is loosely divided into a lowland sub-form below 800–900 m asl, and a cooler sub-form above that elevation (McDonald and Hunter, 2010).

The Park contains large areas of highly diverse subtropical rainforest in its lower elevations with smaller contiguous areas of *Nothofagus*-dominated ‘cool temperate’ rainforest at higher elevations. Small enclaves of *Ceratopetalum*-dominated ‘warm temperate’ rainforests are contained within the subtropical areas generally reflecting more acid substrates (McDonald and Hunter, 2010). Floristically, Lamington

National Park (and adjacent parks) falls within an area of overlap between humid sub-tropical and warm temperate regions known as the Macpherson-Maclay overlap zone (Burbidge, 1960) leading to an exceptional regional diversity and heterogeneity. The Park is a part of the multi-property ‘Gondwana Rainforests of Australia’, World Heritage Area (Kitching et al., 2010).



Figure 3.1 Location map of Lamington National Park and study site. Inset of Queensland shows the extent of this map within the state.

The one-hectare plot

In 1995 a one-hectare reference plot was established and used for floristic and arthropod surveys (Laidlaw et al. 2000). Since then, this plot has been used frequently for a variety of ecological studies (Watkins et al., 2017, Rodgers and Kitching, 1998, Rodgers and Kitching, 2011) . The plot lies in subtropical rainforest at 900m asl on a north-north-west facing ridge ($28^{\circ}13'S$, $153^{\circ}07'E$). Complex notophyll vine forests dominate mid elevations (McDonald and Hunter, 2010) characterised by Sterculiaceae, Euphorbiaceae, Cunoniaceae, Rutaceae and Lauraceae (Laidlaw et al., 2000). Before the present study, the vegetation of the plot has been comprehensively surveyed twice; first in 1995 by Laidlaw et al. (2000) and again in 2005 by Tang (2005). This study describes a third survey (completed in 2015) and analyses the floristic compositional and structural changes of the one-hectare plot over 20 years.

1995 floristic survey. In 1995, all trees on the 1 ha plot with a diameter at breast height (DBH, 1.3m) equal to or greater than 5cm were identified. Their diameters were measured and their positions plotted within the plot. Lianas were not included in this initial survey. Further information regarding site selection and survey procedure is described in Laidlaw et al. (2000).

2005 floristic survey. The second floristic survey of the 1 ha plot was conducted in 2005(Tang, 2007). This survey followed identical protocols to the previous survey for recording trees but also included

lianas for the first time. Tree DBHs were re-measured and any new individuals with DBH equal or greater than 5cm were identified and their positions plotted. A few earlier mis-identification were corrected and the nomenclature updated. In addition, all lianas with a DBH greater than 2cm were surveyed and their species, DBH and location recorded. Additional information regarding survey methodology may be found in Tang (2007).

2015 Floristic survey

In 2015, the 1 ha plot was surveyed for the third time. As before, the site was subdivided into one hundred 10m x 10m grid squares. All tree stems equal to or greater than 5cm DBH, and all lianas with a DBH greater than 2cm were included in the survey. The circumference and position of each individual in the plot were recorded. A permanent tag was attached to each individual that met the criteria, this step was not included in previous surveys and was done so to improve continuity between surveys and for the ease of future surveys. All individuals were identified by Dr. W. McDonald of the Queensland Herbarium.

The floristic information was digitised using ArcMap GIS software (ESRI, 2011). Data from the three surveys (1995, 2005 and 2015) were aligned and comparative analyses of the structural and compositional change of the one-hectare plot over the 20 years were carried out (see below).

I note that *Ficus watkinsiana* was present on the plot and data for this species recorded; however, it was excluded from all analyses as DBH measurements were often confounded by the DBH of the host tree and could not be accurately determined. If these measurements were included in the analysis it would have compromised the integrity of basal area measurements and biomass estimates.

Rainfall and temperature

Rainfall and temperature data for the period 1995-2014 were sourced from the Bureau of Meteorology's online database (Bureau of Meteorology, 2013). Rainfall data were collected from the nearest weather station (Green Mountains, Station number 40182) located 2.4km from the study site. No rainfall data were available from the Green Mountain's weather station for November-December 2008; January, February, August and September 2009; April-July 2010. For these months information were obtained from the next nearest weather station (O'Reilly's, Station number 40931). No single weather station collected temperature data for the entire period between 1995 and 2015. Temperature data were collated from the Canungra (Station number 40582), Hinze Dam (Station number 40584) and Beaudesert (station number 40983) weather stations to create a complete dataset.

Data analysis

Data analysis was approached at two levels: that of the entire assemblage of trees or lianas, and then on a species by species basis for the most dominant members of the assemblage.

Assemblage level (α) diversity

To compare the chronological change in over forest stand dynamics, standard diversity metrics, Shannon's H and Fisher's α , were calculated. Both Shannon's H and Fisher's α are commonly used metrics for characterising species diversity. Both summarise richness and abundance (and hence evenness) in a single number potentially useful for comparative purposes. Shannon's H is widely, if often inappropriately, used (Magurran, 2004, Southwood, 1978). Its principal shortcoming, a sensitivity to small sample sizes especially in highly diverse situations, does not apply to our data given all individuals in the statistical population were included. Fisher's α is based empirically on the assumption that species' abundances conform to a log_e series, the slope of which is the index (Southwood, 1978). Because of this it tends to emphasize common species over rarer ones.

Importance values were determined for each species recorded on the plot based on a formula by Cottam and Curtis (1956) which uses relative density, dominance and frequency to calculate an index of a species importance. This metric was used in the analysis of the first survey and is a useful mechanism to compare historical changes on the plot. Species Importance Values (SIV) were determined using the formula;

$$\text{SIV} = (\text{relative density} + \text{relative dominance} + \text{relative frequency}) \times 100$$

where;

Relative density = number of trees of a species / total number of trees

Relative dominance = total basal area of species/total basal of all species

Relative frequency = abundance of a species / total number of sub-plots

Family importance values (FIV) were calculated using the formula of Mori et al 1983;

$$\text{FIV} = \text{Relative diversity} + \text{Relative density} + \text{Relative dominance}$$

where;

Relative diversity = number of species in family/total number of species

Relative density = number of stems/total number of stems

Relative dominance = basal area/total basal area

Biomass estimates

Tree biomass estimate

In a similar fashion, tree circumference (and thus DBH) has also been usefully applied to estimate total tree biomass. Many allometric equations have been proposed to determine total tree above ground

biomass (TAGB), of which most yielded relatively similar results (Baker et al., 2004a). Here I have used the equation developed by Chave et al. (2001) to estimate TAGB of individual trees;

$$\ln(\text{TAGB}) = \alpha + b \ln(\text{dbh})$$

Where α is -2.0, and b is 2.42. These values were derived by Chave et al. (2001) from observations and measurements obtained from a forest in French Guiana. At the very largest sizes, tree diameter is likely to overestimate tree biomass, however, at the stand level the linear correlation between basal area and above ground biomass will hold (Chave et al., 2004, Baker et al., 2004b). In this model DBH is expressed in centimetres and TAGB is the estimated above ground dry weight biomass of the tree in kilograms.

Liana biomass estimate

The stem size of a liana is directly related to its biomass (Gehring et al., 2004, Gerwing and Farias, 2000, van der Heijden and Phillips, 2009, Schnitzer et al., 2006). Therefore the biomass of a liana can be estimated reasonably confidently by determining its DBH. Total liana above ground biomass (LAGB) can be approximated through the equation developed by Schnitzer et al. (2006);

$$\text{LAGB} = e^{(-1.484 + 2.657 * \ln(\text{DBH}))}$$

In this model DBH is expressed in centimetres, while LAGB is the predicted above ground oven dry weight of the liana in kilograms.

Population level changes

For population level comparisons, the six most dominant species of trees and lianas were selected for further analysis to determine population changes in abundances and size structure through time. Significant changes to the distribution of size structure across years were determined using X^2 tests for each of the selected species. The null hypothesis assumed the distribution of individuals in different size classes did not change through time.

Liana-tree interactions

The effect of tree dynamics on liana abundances and biomass was tested within the 100 sub-plots for both 2005 and 2015. A generalised linear model (GLM) with Gaussian error distributions was fitted to the data in R studio (RStudio, 2016). Predictors (tree mortality, biomass and recruitment) were standardized prior to analysis so effect sizes could be compared directly.

3.4 RESULTS

Assemblage level (α) diversity

Variation in the calculated Fishers α of trees was minimal from 1995 to 2015, and showed a hump shape distribution which peaked in 2005. Shannon's H for trees showed a slight decline from 1995 to 2015 as did both Shannon's H and Fishers α for lianas from 2005 to 2015. Changes, however, in neither Fishers α nor Shannon's H for trees or lianas was of concern and remained within a narrow range.

Trees

Patterns in the structure and composition of the tree stand remained consistent between 1995 and 2015, however some apparent anomalies were present in the 2005 dataset. The density of stems on the 1 ha plot was 1239 stems in 1995, and 1213 stems per hectare in 2015. In 2005, however, the number of stems on the plot increased considerably to 1369 stems (Table 3.1) and caused a significant shift in the size distribution of stems when compared with both 1995 and 2015 (X^2 , $p<0.001$). Changes in the density of stems was greatest for individuals 5-10cm DBH. The number of stems in this size class varied by approximately 18-20% over the 20 year period (Figure 3.2). A 6.5% decline in the number of stems 10-40cm DBH was observed from 1995 to 2015, while stems >40cm DBH rose by 13%. Basal area across the entire plot increased by approximately 3m² between 1995-2005 and by 4m² between 2005-2015 despite the number of trees >40cm DBH remaining stable from 2005 to 2015, and a decrease in number of stems in all other size classes. The distribution of trees within size classes and the spatial distribution of trees over time was stable as expected.

In 2005, 254 recruits and 124 deaths (individuals that could not be aligned with prior/subsequent data records) were observed in comparison with the 1995 data. The 2015 survey detected 87 further recruits but recorded 243 deaths; which were largely the result of 'new' recruits from the previous survey dying off (Figure 3.3). Tree mortality for 2005-2015 was greater across all size classes compared with 1995-2005, but was greatest in recruits and individuals >50cm DBH. Mortality for trees >50cm DBH increased from 1 death in 1995-2005, to 13 deaths for 2005-2015. Large tree mortality was initially overestimated for 1995-2005 as some trees were recorded as standing dead (or were missing from the records) during the 2005 survey, but were in fact alive and included in the 2015 survey. Large tree mortality is likely overestimated for 2005-2015 as there was no change in the number of large trees in this period and the appearance of the plot did not suggest the loss of 13 large trees.

Tree species richness declined from 1995 to 2015 but showed similar data peaks in 2005. Seventy-eight species were recorded in 1995 and 75 in 2015, but peaked at 80 species in 2005. Fluctuations of species richness were largely due to the appearances and disappearances of singletons and doubletons. For example a singleton of *Elaeodendron australis* recorded in 2005 could not be reconciled with individuals

recorded on the plot in either 1995 or 2015. This may be a misidentified individual; although the species is common in the region and may represent a short-lived vagrant on the plot.

Tree community composition separated into three distinct groupings based on their DBH; small (5-20cm DBH), medium (20-40cm DBH) and large trees (>40cm DBH). Overall, community composition fluctuated minimally throughout the observed 20 years. Minor changes in community composition were identified in small and medium trees. The composition of large/canopy individuals also showed few changes (Appendix 3.5).

Thirty three families were represented on the plot and were present during 1995, 2005 and 2015 with the exception of the Fabaceae which was represented by a single individual that died sometime between the 2005 and 2015 surveys. The 10 most abundant families accounted for approximately 80% of all stems found on the one-hectare plot. Of these families, four experienced declines of more than 10%; Lauraceae (-17%), Proteaceae (-22%), Rutaceae (-19%) and Euphorbiaceae (-11%). Lauraceae, Rutaceae and Euphorbiaceae were all classified within the top 5 most important families on the plot by Laidlaw et al. (2000). Conversely, dramatic population increases were observed in Monimiaceae and Phyllanthaceae (both identified in the top 10 abundant families). The number of Monimiaceae stems more than doubled from 1995 to 2005, and was the result principally of an increase in *Wilkiea hugeliana*. Phyllanthaceae, similarly increased >30% over the 20 years due to a rapid population growth in the sole species, *Actephila lindleyii*. Approximately 60% of families identified on the plot were represented by a single species.

The three families with the highest FIV from 1995-2005 were Rutaceae, Rubiaceae and Sapindaceae. However, the FIV of Sapindaceae had the greatest reduction out of all families over the 20 year period and was replaced by Phyllanthaceae in 2015, who had the greatest increase in FIV from 1995-2015.

The most diverse families identified based on their relative diversity were Rutaceae, Sapindaceae, Myrtaceae, Lauraceae and Proteaceae. These families accounted for 48% of the observed diversity. Relative diversity increased in both Rutaceae and Myrtaceae over the 20 years, while Sapindaceae (and to a lesser extent, Lauraceae) experienced a large decline. Sapindaceae also experienced declines in relative density and dominance. Three quarters of all families experienced no change in relative diversity. For a complete list of FIV and SIV for all families and species found on the plot please see Appendix 3.1.

Lianas

From 2005 to 2015 liana abundance increased 13%. A total of 283 liana stems >2cm DBH were recorded on the plot in 2005, and 320 stems in 2015. Of these stems only 10 in 2005 and 13 in 2015 were >10cm DBH. Lianas in the smallest size class (2-4cm DBH) saw the biggest increase in number of stems from 161 in 2005, to 187 in 2015 (Figure 3.2). This pattern was replicated, but to a lesser degree, throughout all size classes. From 2005 to 2015, medium sized lianas (6-8cm DBH) and large lianas (>10cm DBH) increased 36% and 30% respectively. Out of the 100 subplots, at least one liana was recorded in 83

subplots and only 34 subplots had new liana recruits from 2005 to 2015. Overall, a total of 101 new liana recruits were observed. Accordingly, basal area of lianas in the 1 ha increased from 0.56m² to 0.67m². Additionally, growth habits of the species roots would result in an inflated stem count. Twenty-two percent of liana stems recorded in the 2005 survey could not be aligned with individuals encountered in 2015 (Table 3.1, Figure 3.3). It is assumed these individuals perished in this time.

Over the two survey periods 22 different species of liana were recorded on the plot; 18 in 2005 and 19 in 2015. This consisted of 10 families across both survey years (with the addition of Araliaceae in 2005). Fabaceae and Apocynaceae were the two most dominant families on the one-hectare plot; reflecting principally the abundances of *A. glabristyla* and *M. australis* (see below). Moraceae, Rubiaceae and Vitaceae were also identified as important families by their FIV (Appendix 3.3). Relative dominance of both Fabaceae and Apocynaceae decreased while Moraceae, Rubiaceae and Vitaceae increased, suggesting a shift to a more evenly distributed liana family composition. Apocynaceae was the only family to experience a decline in abundance. This was a direct reflection on the reduction in the *P. fulva* population (see below). Community composition of lianas was more dynamic over time compared with trees (Appendix 3.5) and mid-sized liana communities (6-10cm DBH) varied most.

Biomass estimates

The biomass of both trees and lianas increased consistently across surveys. The biomass of trees increased 4 times more between 2005 and 2015 than it did between 1995 and 2005 (Table 3.1). Unfortunately, there are no other comparable studies from the region with which comparisons can be made and the magnitude of the biomass changes confirmed. If this increase in biomass is an accurate reflection of change in the 1 ha plot and as there was no significant change in the number of stems from 1995 to 2015, we can infer that the biomass increase is due to trees increasing in DBH not an increase in the number of trees.

Liana biomass also increased from 2005 to 2015. Their rate of biomass increase (19%) between 2005 and 2015 was, however, greater than the rate of biomass accumulation for the same period in trees (12%). The increase in liana biomass was due to both an increase in the number of stems and an increase in the DBHs of individuals. Overall, lianas contributed >1% to the biomass of the plot.

Population level changes

Trees

The composition of dominant tree species showed little change though time. *Atractocarpus benthamiana*, *Actephila lindleyi*, and *Baloghia inophylla* were prominent in the sub-canopy and dominated the stand numerically. *A. lindleyii* was the only dominant species whose distribution of individuals across size classes changed significantly through time (X^2 , p<0.05) (Figure 3.4). *Argyrogendron trifoliatum*, *Ackama*

paniculosa and *A. actinophyllum* were the dominant canopy species and represented over 40% of canopy (>40cm DBH) individuals. None showed significant changes in the size distribution of individuals through time (X^2 , $p>0.05$). Only 15 species were represented by 20 or more individuals. These species remained constant over the 20 years with the exception of *Lenwebbia prominens* which declined by 40%.

Table 3.1 Summary of the one-hectare plot's forest dynamics

	1995	2005	2015
Trees			
Species Richness	78	80	75
No. of Stems	1239	1369	1213
Basal area (m ²)	70.49	73.16	77.86
Family richness	33	33	32
Shannon's H	3.37	3.39	3.32
Fisher's alpha	17.87	19.29	17.99
Recruits	-	254	87
Deaths since previous survey	-	124	243
Biomass estimate (kg)	686 968	705 756	801 143
Lianas			
Species Richness	-	18	19
No. of Stems	-	283	320
Basal area (m ²)	-	0.56	0.67
Family richness	-	10	11
Shannon's H	-	2.06	1.99
Fisher's alpha	-	4.59	4.42
Recruits	-	-	101
Deaths since previous survey	-	-	63
Biomass estimate (kg)		5946	7319

The SIV of dominant sub-canopy species shifted significantly from 1995 to 2015. *A. lindleyii* increased substantially over the 20 years while the SIV of *B. inophylla* declined. These two species recorded the greatest change in SIV, however the changes in stand structure were only significant for *A. lindleyii* (X^2 , $p<0.05$). All dominant canopy species (*A. trifoliatum*, *A. paniculosa* and *A. actinophyllum*) experienced minor declines in SIV (Appendix 3.2) although changes to their stand structure were not significant (X^2 , $p>0.05$).

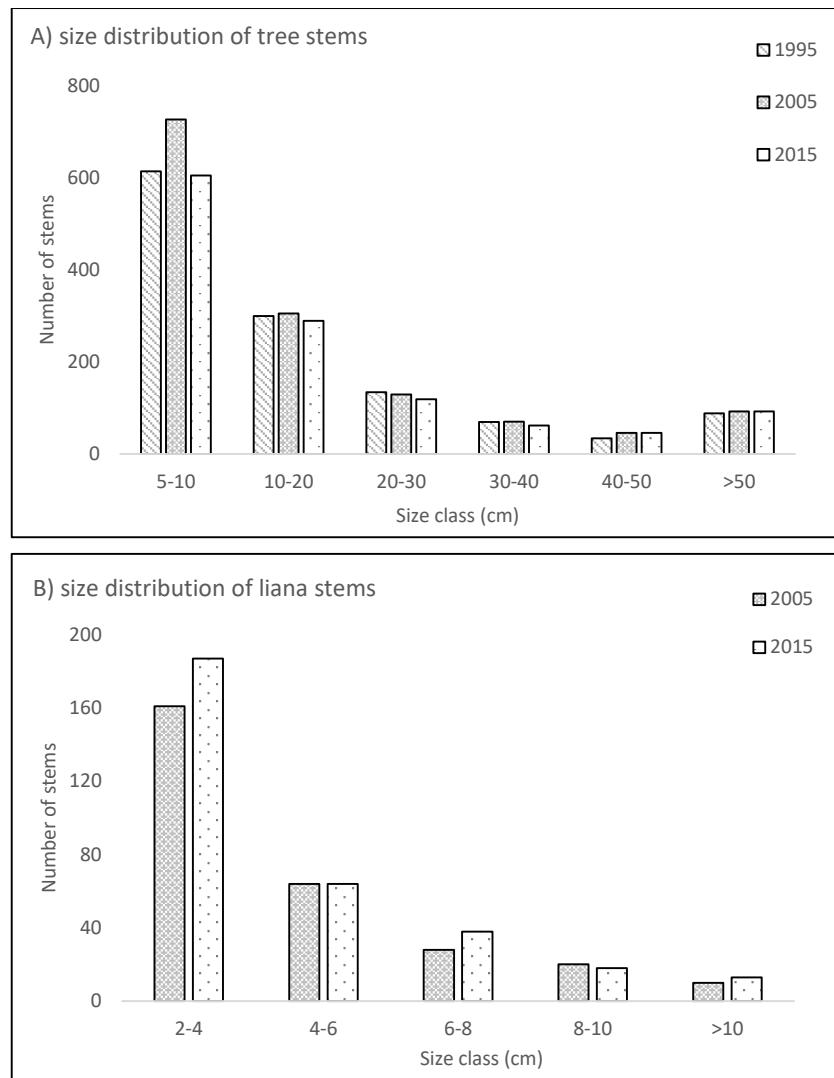


Figure 3.2 Size distribution of A) tree and B) liana stems on the 1 ha plot in 1995 (striped), 2005 (grey hatch), and 2015 (spots). The number of tree stems >10cm DBH was stable across years, as were the number of liana stems >4cm DBH.

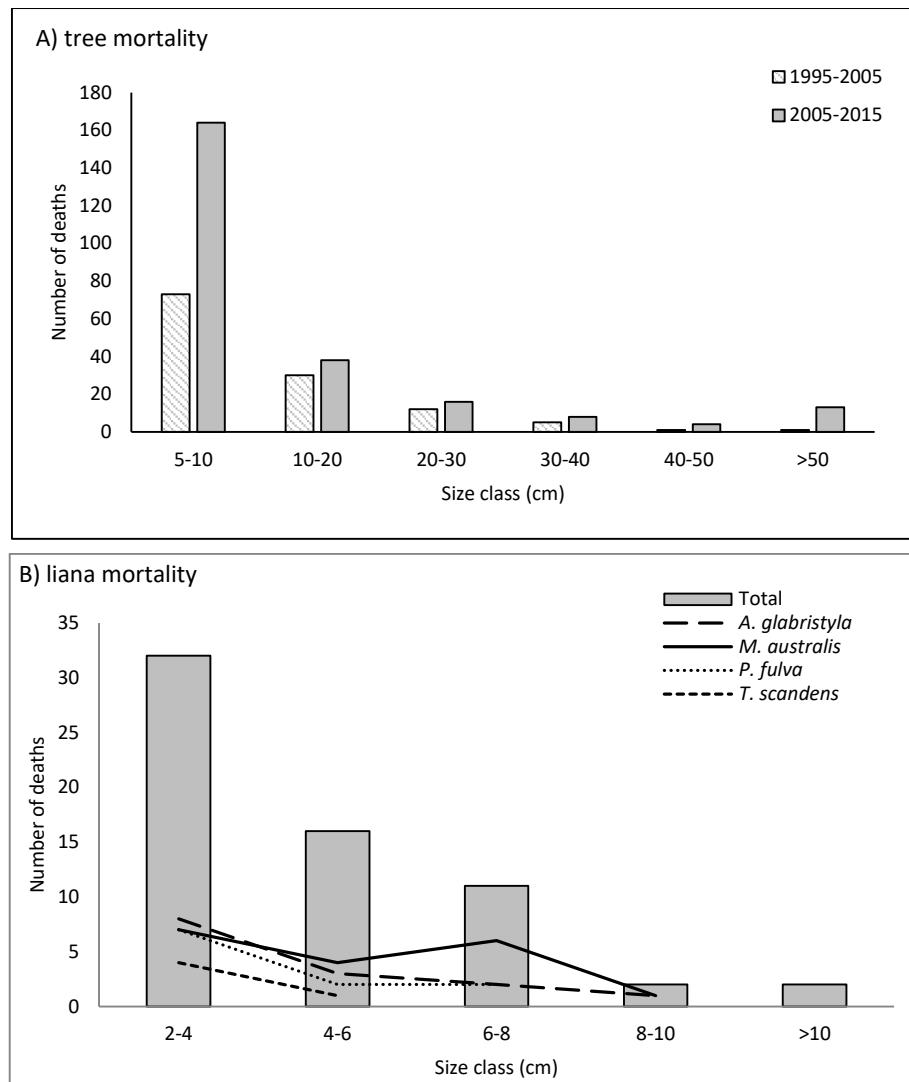


Figure 3.3 Mortality of A) trees between 1995-2005 (striped) and 2005-2015 (grey) and B) lianas between 2005-2015 (grey). Tree mortality was greatest between 2005-2015 across all size classes. The high rate of small tree mortality between 2005-2015 is likely attributed to drought and environmental stress following an inflated recruitment period between 1995-2005. Mortality was similarly greatest in smaller stemmed lianas. Overlayed lined graphs show mortality for dominant liana species. Dominant liana species contributed less than a third to mortality within stems 2-4cm DBH.

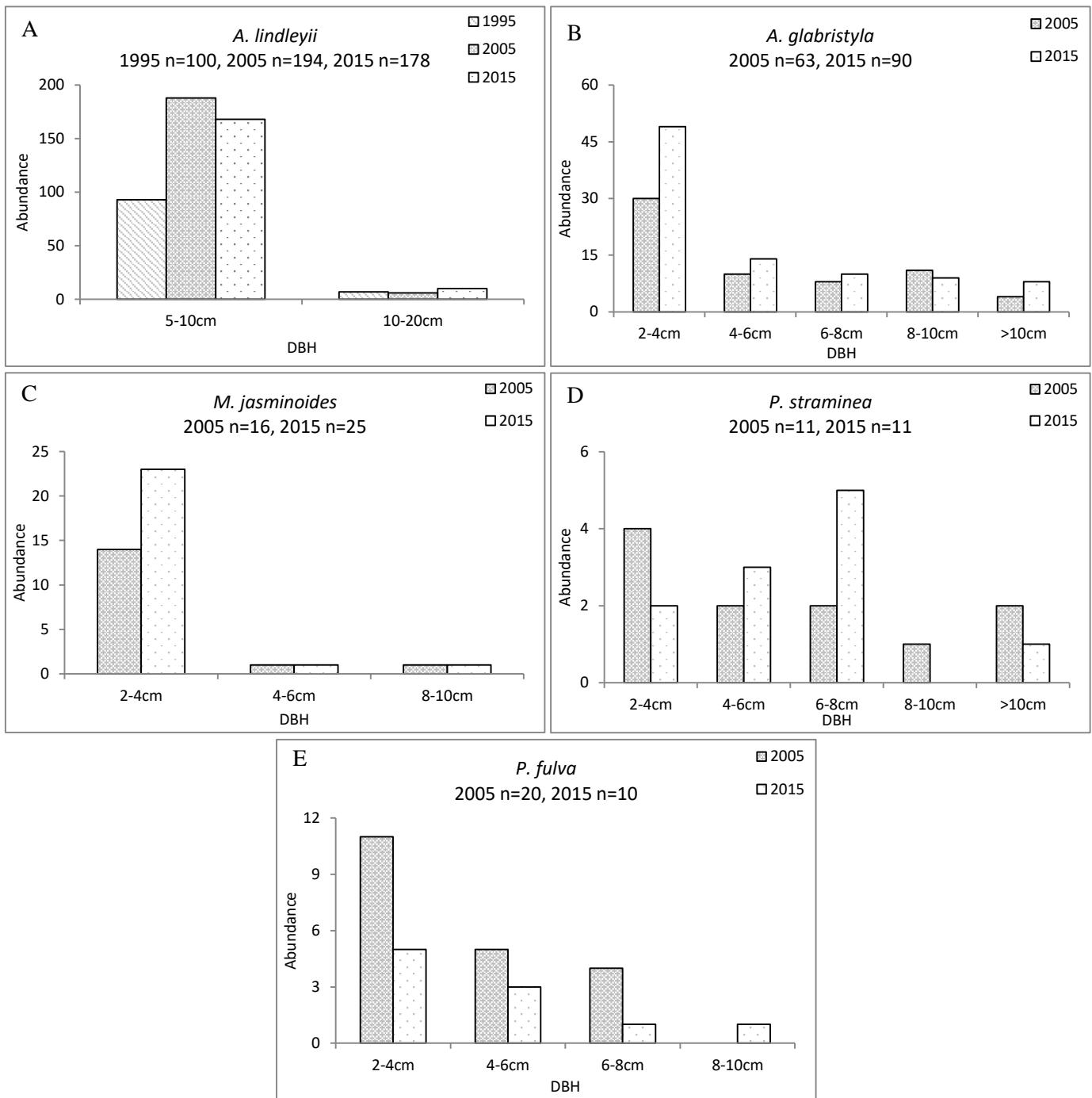


Figure 3.4 Changes in the size distribution of stems in 1995 (stripes), 2005 (hatch) and 2015 (spots). There was a significant change in the size distribution of A) *A. lindleyii* between 1995-2005, 2005-2015 and 1995-2015 (χ^2 , $p<0.001$, $p<0.05$, $p<0.001$), B) *A. glabristyla* (χ^2 , $p<0.001$) and C) *G. jasminoides* (χ^2 , $p=0.05$). Marginally significant differences were found in the size distribution of D) *P. straminea* (χ^2 , $p<0.1$) and E) *P. fulva* (χ^2 , $p<0.1$).

Lianas

Austroqueenslandica glabristyla and *Melodinus australis* were the two most dominant lianas on the plot. *M. australis* abundances were consistent from 2005 to 2015. The number of *A. glabristyla* stems

increased significantly by 43% between 2005 and 2015 (X^2 , $p<0.001$) (Figure 3.4). Increases occurred across all size classes but was greatest in 2-4cm DBH stems. All other species abundances remained stable over the 10year period, with the exception of *Gynochthodes jasminoides* (+56%), *Trophis scandens* (+34%) and *Parsonia fulva* (-50%). These changes in abundances were marginally significant only for *G. jasminoides* and *P. fulva* (X^2 , $p=0.05$ and $p<0.1$ respectively) (Figure 3.4). *P. straminea* abundances were stable from 2005 to 2015. There was, however, a significant shift in the size distribution of individuals (X^2 , $p<0.05$) (Figure 3.4). In 2005, *P. straminea* showed a typical size distribution with 2-4cm DBH stems being the most common size class and >10cm DBH the least. By 2015, the size distribution had shifted to a hump shaped distribution with 6-8cm DBH individuals the most common.

These fluctuations were reflected in the changes to SIV values across years (Appendix 3.4). All five of the aforementioned species were identified as important by their SIV, along with *Cissus sterculiifolia*.

Liana-tree interactions

Tree mortality, biomass and recruitment showed no significant relationship (GLM, $p>0.05$) with liana abundances, nor did liana biomass with tree mortality or recruitment in both 2005 and 2015. Tree biomass was, however, positively correlated to liana biomass in both 2005 and 2015 (GLM, $p<0.02$). As tree biomass increased, so did the biomass of lianas.

Rainfall and temperature

Average annual temperatures for the region have risen approximately 1.5°C from 1995 to 2015 with average summer temperatures experiencing a slightly greater increase than average winter temperature. This has been coupled with changes in seasonal rainfall. Dry season rainfall declined over the 20year period while wet season rainfall increased. These changes to the temperature and rainfall regime are more typical of a tropical climate. The duration between peaks in wet season rainfall have extended and reflect changes in ENSO events.

3.5 DISCUSSION

The data collected in this study provides a basis for further work on the dynamics of the studied forest. Additional surveys may be conducted in future years, perhaps with shorter intervals and/or considering other components such as saplings, and height.

Assemblage level (α) diversity

Trees

The number of tree recruits was inflated in 2005 most likely due to favourable weather conditions the previous year which promoted tree growth. Light penetration may have also improved due to small canopy gaps created from increased storm activity and rainfall in 2004, further aiding small tree growth. Following 2005, south east Queensland entered an El Niño period, producing drought and below average rainfall for 3 consecutive years. A large proportion of these recruits recorded in the 2005 survey did not survive which inflated the estimate of tree mortality substantially in 2015. The loss of the recruits on the 1 ha plot is likely due to the aforementioned harsh environmental conditions which followed 2005(McDowell et al., 2008). Diebacks of small stemmed individuals and seedlings were reported from other sites in the region following El Niño (Laidlaw et al., 2011). Higher mortality in small stemmed individuals is typical, although there is no consensus on the shape of the relationship between tree size and survival (Ma et al., 2016, Green et al., 2014). The likelihood of mortality decreases with size because the ability to withstand environmental stress improves with increasing basal area (Lang and Knight, 1983, van Mantgem et al., 2009, Mueller et al., 2005, Niinemets, 2010, Anderegg and Anderegg, 2013, He et al., 2005). Furthermore, small individuals may be more sensitive to habitat variables than larger trees as they are subject to greater competition pressures (Van Gunst et al., 2016, Ruiz-Benito et al., 2013) since larger trees are typically found in preferred habitats due to environmental filtering (Yang et al., 2016).

The peak in tree diversity during 2005 is likely the result of chronological overlap in species with few individuals from 1995 and 2015. For example singletons of *Pittosporum lancifolium*, *Acmena ingens* and *Rhodomyrtis psidioides* were absent from the 1995 survey, but were present in subsequent surveys. Similarly, a singleton of *Acacia melanoxylon* was present in 1995 and 2005, but disappeared from the plot in 2015.

The composition and structure of the dominant canopy tree species on the plot was stable over time. This temporal stability in the canopy community is expected for longer lived species, such as those forming the canopy. However, the presence of these dominant tree species has declined in the seedling layer of this region (Laidlaw et al., 2011). Long-term reductions in these species may be expected if there are fewer saplings present to replace the loss of mature trees. Other less dominant species in important families have also declined in abundances. Of the 10 most abundant families (more than 50 individuals), seven showed declines in their abundances, four of which experienced declines greater than 10% in the number of individuals over the study period (Lauraceae, Proteaceae, Rutaceae, Euphorbiaceae). The decline in the number of stems in these families is attributable to the decline of only a few species; *Cinnamomum virens*, *Orites excelsa*, *Acronychia* species and *B. inophylla*. Lauraceae, Rutaceae, Euphorbiaceae were identified within the top five most important families in 1995 (Laidlaw et al., 2000) but as of 2015, only Rutaceae has retained its position in the top five most important families on the plot. The loss of

individuals in these families was replaced by Phyllanthaceae and Mimosaceae individuals. These declines indicate a loss of compositional and structural heterogeneity.

There was no decline in the productivity of the plot as tree basal area and biomass between both 1995-2005 and 2005-2015 increased. This increase may be explained in part by the CO₂ fertilisation hypothesis and is supported by the parallel increase in liana basal area. Confirmation of this trend of increasing biomass is required and will be possible with continued periodic inventories of the plot.

Lianas

Our study suggests that subtropical rainforests of Australia are undergoing change and that this change parallels changes observed elsewhere in tropical forests with lianas increasing in abundance and biomass (Laurance et al., 2009, Phillips et al., 2002, Londré and Schnitzer, 2006, Wright et al., 2004, Yorke et al., 2013). The increase in liana abundance in our subtropical plot averaged across the time period was 1.3% per year and falls in line with forests in tropical regions which have reported annual liana increases of 1-4% per year (Laurance et al., 2014, Schnitzer et al., 2012, Phillips et al., 2002).

The variability of rainfall in Queensland is strongly influenced by El Niño Southern Oscillation events (Hughes et al., 2003) which confound the interpretation of temporal trends. While total annual rainfall in south-east Queensland showed no overall change, data from weather stations near our study site showed that summers were becoming wetter and winters potentially drier. In addition, the period between heavy rainfall years increased. This is consistent with current climate projections for the region which predict more extended drought durations (IPCC, 2014, C.S.I.R.O. and Bureau of Meteorology, 2015).

Predictions of rainfall magnitude and periodicity, on the other hand, are less certain.

Greater seasonality and variability of inter-annual rainfall has been correlated with increases in liana abundances in tropical rainforests (DeWalt et al., 2010, Schnitzer, 2005). Similarly tropical liana abundances and basal area increase with decreasing rainfall (Schnitzer, 2005). Although I observed increases in liana abundances, basal area and biomass, corresponding trends in the rainfall regime were weak. If decreased rainfall is driving liana patterns we would expect to see accompanying declines in tree abundances, basal area and biomass. Lianas are known to increase at the expense of trees under conditions of increasing rainfall seasonality and declining total rainfall (Schnitzer and Bongers 2002, 2011). I found no evidence of such trends in the tree community during the course of our study (1995-2015) suggesting factors other than rainfall are influencing liana distributions in our study area. The response times of tree species, nevertheless, may well be much longer than those of lianas and our twenty year dataset may not be long enough to detect changes in the structure of the tree assemblage. I note, however, that this data was collected from multiple weather stations, the closest of which resided over 1km away. The lack of a corresponding rainfall dataset of the site itself produces uncertainty over the true influence of rainfall on the forest plot dynamics.

Although I did not implicitly examine the influence of CO₂ on forest dynamics, inferences about its impact can be drawn from the responses of the liana and tree communities. Increased atmospheric CO₂ promotes both liana and tree growth. Atmospheric CO₂ concentrations increased markedly between 1995 and 2015, from ~360ppm to ~400ppm (Dlugokencky and Tans, 2017). If CO₂ fertilization has promoted accelerated growth rates, increased plant competition, as well as increased tree mortality, recruitment and senescence would also be predicted (Laurance et al., 2014). I found some evidence to support this hypothesis. Increased CO₂ fertilization should also translate into increased liana fecundity and recruitment. This would explain the substantial increase in small stemmed lianas observed in this study, and the increase in basal area and biomass of lianas in larger size classes.

If elevated CO₂ concentrations have influenced the vegetation dynamics within our plot, it may have mitigated any negative effect of liana abundance on tree biomass. In the tropics factors such as thermal thresholds may limit the benefits of elevated CO₂ on tree growth and productivity. Trees in subtropical regions however, may not be limited by their thermal thresholds as they are further from their thermal maximum and, accordingly, can capitalise on elevated atmospheric CO₂. An increase in liana abundances triggered by increasing atmospheric CO₂ aligns with hypotheses of accelerating forest dynamics (Laurance et al., 2014), as both productivity and plant growth would be increased. The observed increases in both tree and liana biomass and basal areas support this.

The acceleration of forest dynamics, specifically tree mortality and disturbances, is also hypothesised to promote increases in liana abundances and distributions and is discussed later.

Population level changes

Trees

There were notable shifts in the SIV and FIV of some species and families from 1995-2005. In 1995 the SIV of two dominant sub-canopy species, *A. lindleyii* and *B. inophylla* was comparable with very little differences in their population dynamics. By 2015, however, *B. inophylla* individuals had reduced significantly while *A. lindleyii* had increased considerably and is now the dominant species. Little life history information is available for these rainforest plants. Both flourish in the shade of drier rainforests, with well drained soils. Of the available information, no particular feature or adaptation suggests *A. lindleyii* should be out-competing *B. inophylla*. Theoretically, species of the same shade tolerance class and strata within the rainforest should exhibit similar responses to the same environmental factors (Ma et al., 2016). Several other sub-canopy species (*Denhamia celastroides*, *Lenwebbia prominens*, *Tasmannia insipida*) also showed sharp declines in their abundances.

L. prominens population was dramatically reduced following the discovery of myrtle rust in Australia in 2010. The causal factors behind the other declines were not determined in this investigation, although they likely follow other declines in species diversity in Australia (Waldron et al., 2017). As this study

was conducted in a national park with minimal human disturbance, we can assume that the likely drivers of these species declines are due to environmental related changes and not anthropomorphic influences such as logging. In contrast with these declines, *Wilkiea hugeliana* abundances increased substantially over the past 20 years. The sub-canopy of the 1 ha plot has become more homogenous over time. This loss of complexity may have consequences for ecosystem functioning, faunal communities and for spatial heterogeneity complexity.

Lianas

The most dominant liana species on the plot did not change across years indicating some level of stability within their populations. Most species abundances increased or remained stable with the exception of *Parsonsia fulva*. The reason behind the decline in *P. fulva* is unknown at the moment due to limited available life history information. Populations of congeners, however, were stable and did not suffer the same reduction.

A. glabristyla account for over 70% of the net increase in liana abundances and was the most important species driving the change. Little species specific information is available on the life history of *A. glabristyla* to explain why this species may have benefitted more than others. However, nitrogen fixing Fabaceae, may benefit from elevated atmospheric CO₂ (Cernusak et al., 2013).

Liana-tree interactions

Tree mortality was greater between 2005-2015 than between 1995-2005. This was largely attributable to loss of small trees <10cm DBH. The number of tree recruits observed between 1995-2005 was inflated most likely due to favourable weather conditions the previous year which promoted an exceptional level of recruitment. Following 2005, south east Queensland entered an El Nino period, causing drought and below average rainfall for 3 consecutive years. A large proportion of these recruits did not survive, inflating tree mortality substantially in 2015. The loss of these recruits is likely due to the aforementioned harsh environmental conditions which followed 2005 and not related to the increase in lianas. Mortality of large stemmed trees (>50cm DBH) increased substantially from 1995-2015, from 1 death per decade to 13 deaths per decade. This increase is in part due to a misalignment in the data as not all individuals could be confidently matched to records obtained in the previous surveys. Tree mortality from 1995-2005 was initially estimated to be greater as some alignments of the data were missed, and some trees appeared dead (or missed) during the 2005 survey but were in fact alive and had recovered to some degree by 2015. Although, this does not account entirely for the substantial difference, tree mortality between 2005-2015 may be slightly lower than stated here.

Declines in tree abundance and biomass are associated with increasing liana distributions in the tropics (Magrach et al., 2014, Schnitzer et al., 2012, Schnitzer et al., 2000). This study, however, found that although there was an increase in liana abundances between 2005-2015, there was no substantial change

in the total number of trees between 1995-2015 with the exception of the discussed anomalies in new recruits. We also found that tree biomass increased substantially over the last decade despite minimal fluctuation in the number of stems (specifically medium and large stems, DBH>20cm) from 1995-2015. This may, however, be due to human error in measuring DBHs, a problem with the biomass equation (which tends to over-estimate biomass for large sized trees) or a true reflection of change occurring within the plot. Furthermore, GLMs correlating tree mortality to liana abundance and biomass within subplots shows no significant relationship (although I acknowledge the potential influence of pseudo-replication on the outcome of this analysis). Despite liana abundances having increased by 13% in the last decade, neither tree mortality nor tree growth has been affected. The increase in tree growth across time may support the hypothesis that forest turnover is accelerating leading, *inter alia*, to increases in lianas.

Few studies of long term changes in liana and tree communities from which comparisons can be made exist for subtropical forests. None are available for Australia. However, our study suggests that subtropical and tropical forests may respond differentially to increases in liana abundances, although the driving mechanisms may be the same. Our focus on a single hectare, of course, limits the extent to which any region generality can be claimed.

Implications of increased lianas

Increases in liana abundances are predicted to have a number of impacts on tropical and subtropical forest tree communities (Schnitzer and Bongers, 2002, Paul and Yavitt, 2011). Many descriptions of lianas promote the idea that they have an antagonistic relationship with trees, notably shade-tolerate species. For example, it is suggested increases in liana abundances will favour the growth and survival of pioneer species as they are ‘less vulnerable’ to climbing plants than shade-tolerant species (Putz, 1984, Ingwell et al., 2010). This may lead us to suspect that if shade-tolerant species are more susceptible to climbing by lianas then their biomasses would positively reflect one another. However, the biomass of pioneer species has been positively correlated to the biomass of lianas and is hypothesised to enhance survival of pioneer species by inhibiting shade-tolerant species (Schnitzer et al., 2000). This conclusion, however, may be in incorrect as seedling survival of shade-tolerant species is limited within gaps as they may not be able to withstand the harsher conditions (Canham, 1989, Lu et al., 2018). They may not necessarily be present in low abundances due to higher liana abundances but rather in reflection of unfavourable environmental conditions.

Lianas in gaps may favour shade tolerant species in the long term. Lianas help close the canopy after a disturbance which buffers the harsh environmental conditions of forest gaps for shade tolerant species. Although liana abundances in our study substantially increased from 2005-2015, I did not observe any significant changes in the distribution or abundance of well-known short or long lived pioneer species. As noted earlier, the duration of this study may have been too short to detect the influence of increasing lianas abundances on floristic communities.

Lianas are also predicted to have a sizeable impact on the carbon storage capacity of forests by reducing growth rates, survival and biomass of trees (van der Heijden and Phillips, 2009, Durán and Sánchez-Azofeifa, 2015). Carbon storage is closely related to biomass, particularly for species with high wood densities (Gao et al., 2015, Malhi et al., 2006, Houghton et al., 2009). In tropical forests, tree biomass has a strong negative relationship with liana abundance (Laurance et al., 2014) suggesting that the carbon storage potential of forests will decline with increasing liana abundances. Where this correlation exists, it may reflect liana abundances supressing tree biomass or liana abundances increasing due to extrinsic differential mortality events (thereby decreasing tree biomass). The causal relationship, however, is difficult to ascertain. As I observed consistent increases in tree biomass over 20 years, the carbon storage capacity of this patch of forest has likely not been negatively affected by the increase in liana abundance and biomass. The effects of increasing liana abundances on forest carbon storage may be different in subtropical forests compared with tropical forests, where CO₂ enrichment may effectively negate the effect of lianas on tree growth.

In contrast, tree biomass is largely dictated by the biomass of woody parts (i.e. trunk and branches) and can be a poor surrogate for crown and foliage cover of individuals. It is possible that while the biomass of trees remained stable, their contribution to canopy foliage may have declined and been displaced by foliage from lianas. Future studies addressing changes in liana and tree abundances should incorporate estimates of crown cover and changes in cover. Drones and LiDE images will be an important source of canopy cover data, however the ability to identify specific individuals and/or species from these images is challenging. Canopy cranes on the other hand may provide a more pragmatic approach to monitoring changes in canopy cover of lianas and trees.

3.6 SUPPLEMENTARY INFORMATION

Appendix 3.1 Tree Family Importance Values

Family	Abundance	Abundance	Abundance	FIV 1995	FIV 2005	FIV 2015
	1995	2005	2015			
Akaniaceae	5	5	4	1.72	1.61	1.65
Alangiaceae	1	1	1	1.40	1.32	1.40
Araliaceae	1	6	4	1.40	1.68	1.65
Araucariaceae	7	8	8	1.92	1.86	2.02
Atherospermataceae	53	59	53	5.61	5.46	5.70
Celastraceae	12	15	8	2.29	3.57	1.98
Cunoniaceae	112	117	107	13.17	12.27	12.95
Ebenaceae	45	51	50	4.99	4.92	5.48
Elaeocarpaceae	1	1	1	1.40	1.32	1.40
Escalloniaceae	1	1	1	1.40	1.32	1.40
Euphorbiaceae	131	132	116	11.94	10.70	10.93
Eupomatiaceae	3	4	4	1.56	1.53	1.65
Fabaceae	1	1	0	1.40	1.32	0.00
Lamiaceae	14	13	12	2.47	2.21	3.64
Lauraceae	63	61	52	14.37	13.14	12.26
Malvaceae	4	5	5	1.64	1.61	1.73
Meliaceae	20	21	17	5.58	6.51	6.68
Mimosaceae	116	126	106	13.57	12.99	12.99
Monimiaceae	33	71	63	6.61	8.81	7.83
Moraceae	6	6	7	3.24	3.03	3.33
Myrtaceae	42	46	33	11.30	13.29	13.26
Oleaceae	11	22	15	2.21	2.82	2.55
Phyllanthaceae	135	196	178	12.23	15.21	16.01
Pittosporaceae	3	4	3	2.88	2.79	2.88
Proteaceae	67	66	52	10.72	9.74	9.59
Quintiniaceae	16	13	13	2.61	2.18	2.39
Rhamnaceae	14	4	3	2.45	1.54	1.57
Rubiaceae	148	168	146	14.60	14.47	14.69
Rutaceae	123	118	100	23.17	22.22	24.11
Salicaceae	4	7	5	1.64	1.75	1.73
Sapindaceae	34	35	29	15.92	13.75	11.62
Thymelaeaceae	2	12	11	1.48	2.11	2.23
Winteraceae	10	10	5	2.12	1.96	1.73

Appendix 3.2 Tree Species Importance values

Species	Abundance	Abundance	Abundance	SIV	SIV	SIV
	1995	2005	2015	1995	2005	2015
<i>Acacia melanoxylon</i>	1	1		1.12	1.12	
<i>Ackama paniculosa</i>	67	65	63	80.03	78.81	76.32
<i>Acronychia baueuerlenii</i>	4	5	5	4.35	5.40	5.45
<i>Acronychia laevis</i>	1			1.08		
<i>Acronychia octandra</i>	30	28	26	36.02	33.49	31.14
<i>Acronychia pubescens</i>	22	17	12	24.08	18.43	13.17
<i>Acronychia suberosa</i>	30	30	25	33.33	33.14	27.74
<i>Actephila lindleyi</i>	137	194	178	149.35	209.12	193.59
<i>Akania bidwillii</i>	5	5	4	5.47	5.43	4.39
<i>Alangium villosum</i>	1	1	1	1.09	1.09	1.10
<i>Anthocarapa nitidula</i>	1	2	2	1.10	2.17	2.19
<i>Araucaria cunninghamii</i>	7	8	8	11.29	12.76	12.62
<i>Archidendron grandiflorum</i>	8	8	7	8.80	8.75	7.74
<i>Argyrodendron actinophyllum</i>	33	33	29	46.44	44.75	41.95
<i>Argyrodendron trifoliolatum</i>	79	82	70	100.09	105.50	94.68
<i>Atractocarpus benthamianus</i>	142	160	143	154.94	173.20	156.09
<i>Auranticarpa rhombifolia</i>	2	3	2	2.31	3.39	2.32
<i>Baloghia inophylla</i>	132	131	116	147.37	145.78	129.85
<i>Brachychiton acerifolius</i>	4	5	5	4.43	5.47	5.51
<i>Cinnamomum virens</i>	30	32	30	33.77	35.54	33.68
<i>Citronella moorei</i>	6	8	7	6.52	8.62	7.61
<i>Citrus australasica</i>	1	1	1	1.08	1.08	1.09
<i>Clerodendrum floribundum</i>			1			1.09
<i>Cryptocarya erythroxylon</i>	1	1	1	1.32	1.34	1.38
<i>Cryptocarya foveolata</i>	1	1		1.17	1.18	
<i>Cryptocarya obovata</i>	3	4	3	3.74	5.25	3.26
<i>Cupaniopsis flagelliformis</i>	2	2	2	2.17	2.16	2.18
<i>Decaspermum humile</i>	4	4	3	4.37	4.34	3.28
<i>Denhamia celastroides</i>	13	14	8	14.16	15.12	8.73
<i>Diospyros pentamera</i>	50	51	50	57.88	58.80	58.14
<i>Diploglottis australis</i>	2	2	1	2.34	2.39	1.31
<i>Doryphora sassafras</i>	52	57	53	57.36	62.45	58.57
<i>Dysoxylon fraserianum</i>	10	8	5	12.10	9.73	5.78
<i>Dysoxylum rufum</i>	1	1	1	1.17	1.16	1.19
<i>Elaeodendron australe</i>		1			1.08	
<i>Elattostachys nervosa</i>	2	3	2	2.17	3.23	2.17
<i>Emmenosperma alphoniooides</i>	5	4	3	6.02	5.04	3.78
<i>Endiandra muelleri</i>	7	7	5	7.88	7.82	5.70
<i>Eupomatia laurina</i>	3	4	4	3.26	4.31	4.35
<i>Flindersia australis</i>	3	3	3	3.95	4.17	4.08

Species	Abundance	Abundance	Abundance	SIV	SIV	SIV
	1995	2005	2015	1995	2005	2015
<i>Gossia bidwillii</i>	2	2	2	2.26	2.27	2.27
<i>Guioa semiglauca</i>	1	1		1.08	1.08	
<i>Halfordia kendack</i>	15	15	13	17.50	17.05	15.36
<i>Harpullia alata</i>	1			1.09		
<i>Helicia glabriflora</i>	2	2	2	2.22	2.20	2.22
<i>Jagera pseudorhus</i>	1	2	2	1.09	2.16	2.18
<i>Karrabina benthamiana</i>	12	14	13	14.11	16.36	14.76
<i>Lenwebbia prominens</i>	25	19	15	27.30	20.59	16.36
<i>Litsea reticulata</i>	10	11	11	15.91	14.68	18.07
<i>Melicope micrococca</i>			1			1.09
<i>Mischocarpus anodontus</i>	2			2.23		
<i>Mischocarpus australis</i>	3	3	4	3.64	3.54	4.74
<i>Neolitsea australiensis</i>	1	2	2	1.09	2.16	2.19
<i>Notelaea johnsonii</i>	14	22	15	15.30	23.77	16.36
<i>Orites excelsus</i>	51	47	41	58.66	53.92	47.23
<i>Pentaceras australe</i>	8	11	7	9.09	12.19	7.92
<i>Phaleria chermsideana</i>	11	12	11	12.07	13.08	12.10
<i>Pittosporum lancifolium</i>	1	1	1	1.09	1.08	1.09
<i>Polyosma cunninghamii</i>	1	1	1	1.09	1.08	1.09
<i>Polyscias elegans</i>	1	6	4	1.09	6.50	4.36
<i>Pseudoweinmannia lachnocarpa</i>	32	34	31	43.34	45.34	42.54
<i>Psychotria simmondsiana</i>	2	6	3	2.17	6.46	3.26
<i>Quintinia verdonii</i>	16	11	13	17.56	11.98	14.28
<i>Rhodamnia argentea</i>	1	1	1	1.10	1.25	1.25
<i>Rhodomyrtus psidioides</i>	2	2	1	2.17	2.15	1.09
<i>Rhysotoechia bifoliolata</i>	1	1	1	1.08	1.08	1.09
<i>Sarcomelicope simplicifolia</i>	2	2	1	2.39	2.35	1.27
<i>Sarcopteryx stipata</i>	18	18	17	20.19	19.96	19.12
<i>Scolopia braunii</i>	4	7	5	4.39	7.59	5.49
<i>Sloanea woollsii</i>	1	1	1	1.08	1.08	1.09
<i>Stenocarpus salignus</i>	6	6	4	6.53	6.49	4.40
<i>Stenocarpus sinuatus</i>	7	5	5	7.99	5.69	5.72
<i>Streblus brunonianus</i>	1	1	1	1.09	1.08	1.09
<i>Synoum glandulosum</i>	8	9	9	9.24	10.29	10.38
<i>Syzygium crebrinerve</i>	7	7	7	8.43	8.43	8.53
<i>Syzygium ingens</i>		1	1		1.08	1.09
<i>Syzygium smithii</i>	4	3	3	4.35	3.25	3.27
<i>Tasmannia insipida</i>	10	9	5	10.86	9.71	5.43
<i>Vitex lignum-vitae</i>	13	12	11	15.99	14.80	13.46
<i>Wilkiea austroqueenslandica</i>	5	7	6	5.45	7.57	6.54
<i>Wilkiea huegeliana</i>	30	64	57	32.55	68.90	61.91

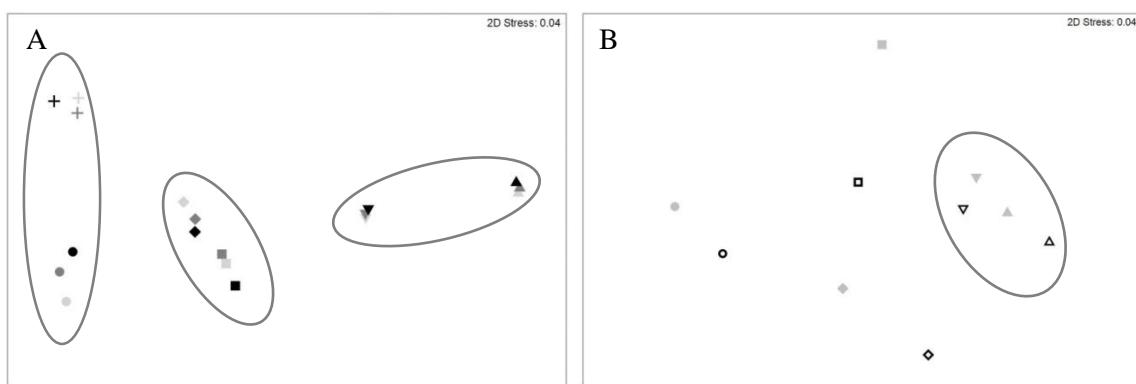
Appendix 3.3 Liana family importance values

Family	Abundance	Abundance	FIV 2005	FIV 2015
	2005	2015		
Apocynaceae	131	122	2.15	1.94
Araliaceae	1		0.01	
Dilleniaceae	1	1	0.02	0.01
Fabaceae	74	100	1.43	1.72
Monimiaceae	6	5	0.11	0.08
Moraceae	35	49	0.54	0.73
Myrsinaceae	6	5	0.09	0.07
Piperaceae	1	1	0.01	0.01
Rubiaceae	16	25	0.24	0.36
unknown		1		0.01
Vitaceae	12	12	0.22	0.27

Appendix 3.4 Liana species importance values

Species	Abundance	Abundance	SIV 2005	SIV 2015
	2005	2015		
<i>Austrosteenisia glabristyla</i>	63	90	125.57	156.97
<i>Caesalpinia subtropica</i>	2	1	2.97	1.38
<i>Celastrus subspicatus</i>	8	8	12.63	11.77
<i>Cephalaria cephalobotrys</i>	1		1.47	
<i>Cissus hypoglauca</i>	2	2	3.08	3.90
<i>Cissus sterculiifolia</i>	9	10	17.81	23.01
<i>Derris involuta</i>	1	1	1.48	1.56
<i>Embelia australiana</i>	6	5	8.99	7.19
<i>Ficus henneana</i>		2		2.74
<i>Gynochthodes jasminoides</i>	16	25	24.11	36.49
<i>Hibbertia scandens</i>	1	1	1.52	1.50
<i>Melodinus australis</i>	95	95	152.84	147.35
<i>Palmeria foremanii</i>	3	5	4.72	7.61
<i>Palmeria scandens</i>	3		6.56	
<i>Parsonsia fulva</i>	20	10	32.23	16.65
<i>Parsonsia longipetiolata</i>	5	4	7.64	6.19
<i>Parsonsia straminea</i>	11	11	22.04	20.72
<i>Parsonsia velutina</i>		2		2.73
<i>Piper hederaceum</i>	1	1	1.45	1.45
<i>Tetrastigma nitens</i>	1		1.42	
<i>Trophis scandens</i>	35	47	54.48	70.35
unknown		1		1.43

Appendix 3.5 nMDS ordination of A) tree and B) liana assemblages in different size classes based on a Euclidean Distance Resemblance Matrix generated from standardized proportional log(x+1) transformed data. A clear separation in the tree community exists between small (5-20cm DBH), medium (20-40cm DBH) and large trees (>40cm DBH). Separation of the liana assemblage between different size classes is less apparent, although smaller lianas (2-6cm DBH) tended to cluster together. Different size classes of trees showed little variation in the community structure over the 20year survey period while liana assemblages were much more variable. Symbology A) Light grey = 1995, dark grey = 2005, black = 2015. \blacktriangle = 5-10cm DBH, \blacktriangledown = 10-20cm DBH, \blacksquare = 20-30cm DBH, \blacklozenge = 30-40cm DBH, \bullet = 40-50cm DBH, \blackplus = >50cm DBH. Stress = 0.04. Symbology B) 2005 (grey, closed markers) and 2015 (black, open markers). \blacktriangle = 2-4cm DBH, \blacktriangledown = 4-6cm DBH, \blacksquare = 6-8cm DBH, \blacklozenge = 8-10cm DBH, \bullet = >10cm DBH. Stress = 0.04.



CHAPTER 4

STATEMENT OF CONTRIBUTION TO CO-AUTHORED PAPER

Chapter 4 is a co-authored paper which is intended for publication alongside additional comparable analysis from other biogeographic regions. The bibliographic details of the co-authored paper, including all authors, are:

Odell E, Kitching R (in preparation) The consumption of vines and trees by butterfly larvae: a comparative study of well-known rainforest faunas.

My contribution to this chapter involved data collection, analysis and writing of the manuscript. My co-author is my supervisor and provided guidance with regards to the direction, structure and editing of the manuscript.

(Signed) _____
Erica H. Odell

(Date) 10 May 2018

(Countersigned) _____
Supervisor: Roger L. Kitching

(Date) 10 May 2018

CHAPTER 4

The consumption of vines and trees by butterfly larvae: a comparative study of the Australian fauna¹

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4.1 ABSTRACT

Vines are hypothesised to play an important role in the maintenance of high local species diversity and may support high levels of co-evolutionary radiations with insects. Yet, little is known about the interactions between vines and insects, or the ways in which they support herbivory at the community level and maintain arthropod diversity.

I performed a literature based analysis of the feeding habits of Australian butterfly caterpillars to test the hypothesis that vines and other climbing plants are preferred host plants over trees, especially in rainforests. Significantly more species of butterflies were found to feed on climbing plants than their relative diversity within rainforests predicted, and significantly greater levels of overall monophagy was found in butterflies that fed on vines than was expected. Feeding on climbing plants was positively correlated to diversity within butterfly families in rainforests, although, only when lycaenids were removed. In contrast however, monophagy was negatively correlated to diversity of butterfly families.

Difference in the characteristics of butterfly assemblages across plant functional groups are likely influenced by plant architecture, length of growing season and availability of new leaves. It is likely the patterns found here, of host plants and host specificity between plant functional groups are replicated in other insect taxa and that vines are at least as important as trees for herbivory and for the maintenance of local species richness of butterflies, particularly in rainforests. I performed this study in the context of a wider research project and intend to analyse other geographic locations with well-known butterfly fauna (such that of Barro Colorado Island and Sri Lanka) and flora. Herbivory on vines, in contrast with trees, merits further investigation.

¹ It is proposed that, before publication, this analysis be extended to include two additional rainforest butterfly faunae: a Neotropical (Panama) and an Afrotropical (Benin, West Africa) case study. These additional analyses fall beyond the present scope of this thesis.

4.2 INTRODUCTION

Vines, both woody and non-woody, are the second most dominant plant grown form in rainforests after trees and contribute substantially in terms of species richness, leafy biomass and production (Hladik, 1978, Pichon et al., 2015, Hegarty, 1991 , Pragasan and Parthasarathy, 2005, Wright et al., 2004). Vines are regarded as the single most important physiognomic feature differentiating tropical and temperate forests and their role within gap dynamics is well recognised (Schnitzer et al., 2000, Letcher, 2015, Schnitzer and Carson, 2001, Schnitzer and Carson, 2010).

Vines are widespread throughout the plant kingdom. In Australia, climbing species are found in more than 60% of dicotyledonous rainforest plant families (see Chapter 2) and are important contributors to species diversity in canopies. In one hectare of Australian subtropical rainforest, canopy trees (>30cm DBH) make up approximately 23% of overall plant diversity compared to 20% contributed by vines (see Chapter 3). In a tropical Australian rainforest a survey of 19 tree species encountered 11 species of vines infesting the sampled trees (Tng et al., 2016, Cox et al., in review). In some forest canopies, vines are more species rich than trees. For example, in Barro Colorado Island, Panama, canopy tree species contribute 15.4% to the total angiosperm diversity whereas vines constitute 19.4% (Croat, 1978). Many small stemmed vines, only 2-3cm in diameter at breast height, have the ability to reach the forest canopy (Kurzel et al., 2006) where they generally contribute 18-40% of the leafy biomass (Hladik, 1978, Pichon et al., 2015, Pragasan and Parthasarathy, 2005, Wright et al., 2004, Hegarty, 1991). Compared with trees of the same DBH, vines support substantially more leaves per unit basal area (Putz 1983, Gerwing and Farias 2000). Given their contribution to diversity and primary production within forests, it is likely vines are important food plants for many herbivorous arthropods.

Despite their significant representation and recognised importance within forests, studies specifically addressing their contribution to ecosystem functioning outside of disturbance processes are few. Such studies that exist of insect herbivory in forests have focused largely on trees, as has research into the community wide ecosystem function of herbivory (Coley, 1982, Basset, 1991, Metcalfe et al., 2014, Poorter et al., 2004, de la Cruz and Dirzo, 1987, Nooten and Hughes, 2013). Little is known about the interactions between vines and insects, or the ways in which they support herbivory at the community level and maintain arthropod diversity.

Vines are hypothesised to play an important role in the maintenance of high local species diversity (Stork, 1987, Wolda, 1979), possibly by supporting high levels of co-evolutionary radiations with insects. Enhanced clade diversification is common among climbing plants (Rios et al., 2014). This may be a product of the expanded niche dimensions opened up by the climbing process, which maximises interactions with a wide array of antagonistic and mutualistic species, which in turn, promotes diversification (Gianoli, 2004). Plant feeding among insects has been attributed to accelerated diversification among insect lineages. In general, the diversity of plants is significantly and positively correlated to the diversity of insects (Kemp and Ellis, 2017). Whether or not these radiations occurred as

a result of sequential evolution whereby insects colonized and radiated on diversifying plants (Winkler and Mitter, 2008, Wheat et al., 2007), or as a result of a co-evolutionary ‘arms-race’ is unresolved (Ehrlich and Raven, 1964, Becerra et al., 2009, Futuyma and Agrawal, 2009). Therefore, enhanced clade diversification in vines should beget diversification in associated insect herbivore clades (Janz et al., 2006) particularly in lineages such as Lepidoptera which have among the fastest diversification rates of any insect order (Wiens et al., 2015).

If co-radiations are a common phenomenon among vines and insects as hypothesised, vines will be important hosts for a substantial proportion of insects relative to their diversity within specific ecosystems and will be important for structuring ecosystems and maintenance of local species diversity. As potential hosts for insect herbivores, vines may offer several advantages to the insects concerned (see Chapter 2). Leaves of vines may contain fewer insect-directed antifeedants (although some clades contain well known vertebrate-directed anti-feedants which some insects may sequester as defensive compounds themselves) (Ehrlich and Raven, 1964, Opitz and Müller, 2009, Nishida, 2014). Further, and correlated with this, vines show greater temporal turnover in leaves with more frequent flushing and, in consequence, more frequently available food stuffs for insect herbivores (Zhu and Cao, 2010, Ødegaard, 2000b).

With the exception of Ødegaard (2000b) who studied phytophagous beetles on vines and trees, most vine-insect interactions are known from highly specific interactions within taxonomically rich insect groups such as those of *Heliconius* butterflies and Passifloraceae, ithomiine butterflies and Solanaceae, and *Hylaeogena* beetles and Bignoniaceae. These examples have generally been selected for study because of *a priori* knowledge of high levels of specialisation. However, Ødegaard (2000b) also observed greater levels of host specificity of beetles feeding on vines compared with those feeding on trees at the level of the assemblage.

Traditional calculations of host specificity typically assess the specialisation of a group of organisms within a narrow location (Ødegaard, 2000b, Morrow, 1977, Novotny et al., 2002, Mawdsley and Stork, 1997, May, 1990). Species may be effectively specialized in a particular location if other suitable host plants are not present, but may not be specialised at a larger or continent-wide scale. Ødegaard (2000b) points out that, “*testing of host specificity can never be accurate unless all possible plant species in the total range of the insect species are included (i.e. one can never prove monophagy)*”. In addition, host specificity data are often limited by small sample sizes, insufficient duration of study (leading to an oversight of all host plant taxa used), or the insects are sampled destructively which prevents feeding experiments and the study of immature stages (Novotny et al., 2002). However, for studies of well-known faunas, such as Lepidoptera, they may only be marginally constrained by the aforementioned limitations due to the wealth of available knowledge (although Ødegaard’s (2000) logic remains).

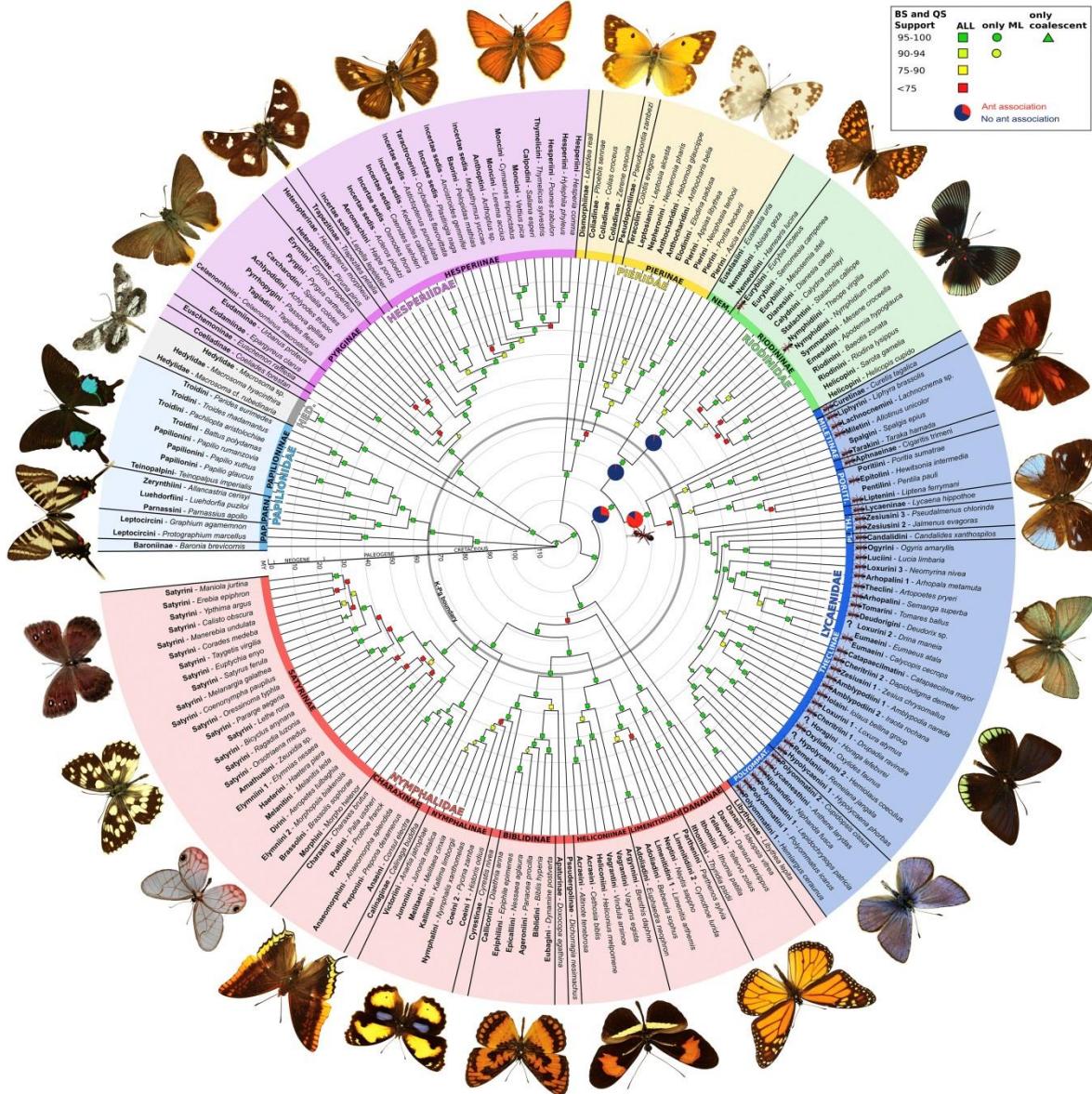


Figure 4.1 Dated, molecular phylogeny of butterflies based on molecular data from 207 taxa (352 loci, >151,000 bps) representing 98% of all tribes. Image from Espeland et al. (2018). This phylogeny places Papilionidae (pale blue) as the sister group to all other butterflies, followed by Hesperiidae (purple). Pieridae(yellow) is strongly supported as a sister group to Nymphalidae (red) and Lycaenidae (darker blue). Further description of this phylogeny is in Espeland et al. (2018).

The Lepidoptera (moths and butterflies) is the largest lineage of virtually exclusively phytophagous insects and, together, are the most speciose herbivore per 10m³ of tropical forest (Rinker and Lowman, 2004, Schoonhoven et al., 2005). Butterflies (traditionally represented by the superfamilies Papilioidea and Hesperioidae – but see Espeland et al. (2018)) are arguably among the most taxonomically well-known and best resolved insect taxa globally (see Figure 4.1). Most butterflies are exclusively folivorous and the larval identities, life histories and host plant records are extensive for many regions including; Australia (Orr and Kitching, 2010), North America (Scott, 1986), Europe (Haahtela et al., 2011), Kenya (Larsen, 1996b) and the West Indies (Hernandez, 2004b). This level of knowledge is unparalleled in other insect orders and presents a unique opportunity to test hypotheses about the interactions occurring

between insects and different life forms. Vines and lianas are frequent food plants of butterflies, especially in rainforest (Orr and Kitching, 2010, Braby, 2000, Larsen, 1996a, Hernandez, 2004a, van der Poorten and van der Poorten, 2016) and may be important and preferred food plants for butterflies. However, this speculation has never been formally tested. The key evolutionary and ecological question then becomes ‘are vines and lianas over-represented as butterfly food-plants, within local floras.

Comparative studies of the ways in which vines and trees interact with and support insect herbivores contribute to a holistic understanding of herbivory in forests. This study aims to test how vines (including lianas and other climbers) compare with trees as host taxa for butterfly larvae in rainforests using available data sources relating to the Australian butterfly fauna. I determine the relative use of vines and the trees on which they climb as larval host plants and discuss implications for biodiversity maintenance and within-species specialisation.

I hypothesise the following;

1. Vines will be host plants of more butterfly species than their relative diversity predicts,
2. There will be minimal overlap of species feeding on both trees and vines,
3. Butterflies feeding on vines will exhibit greater specialisation,
4. Enhanced diversification in clades with climbing species should beget greater diversity in butterfly lineages with more species feeding on vines,
5. Concentrations of elements important to metabolic processes and growth (namely nitrogen and phosphorus) found in vine leaves compared to tree leaves would result in larger butterflies (as determined by male forewing lengths) feeding on vines.

Here, I define non-climbing woody species (including shrubs) as ‘trees’, and non-woody and woody climbing species, alike, as ‘vines’.

4.3 METHODS

Butterflies

Using available information compiled in Orr and Kitching (2010) and Braby (2000), data were collected on the biology and habits of Australian butterflies and their larval host plants. Larval host plants were assigned to one of several types describing the plant functional group (e.g. tree, herb, vine, epiphyte, grass, sedge, succulent etc). Where possible I differentiated between the primary/most common host plant taxa and secondary plant taxa that are less commonly used. Host plant records that were obtained in artificial, laboratory-base encounters were omitted from this study to reflect most closely natural host plant preferences. Species with information missing about their food plants or life histories were excluded. I selected as ‘rainforest’ butterflies those that select such forests as their primary (sometimes original) habitat while acknowledging that less frequent use of other ecosystem types by these species do occur. Data on male forewing lengths was also obtained and used as a proxy for size.

Butterflies were categorized by their host plant type as tree feeders (woody non climbing plants), herb feeders, vine feeders (woody and non woody climbing species), grass feeders, mixed feeders (utilized multiple host plant types) or other (includes species feeding on cactus, mistletoe, ferns, as well as carnivorous species). Species were defined as ‘monophagous’ if their larvae fed on a single genus of host plant (see below).

Flora

It was infeasible to collate data on all Australian vegetation. As an alternative I opted to gather vegetation data solely on rainforests as their floristics are well known and vines are important features and the second largest contributor to primary production within these systems after trees (Hegarty, 1991 , Tang et al., 2012, Hladik, 1978).

Information on the diversity of rainforest floras (specifically trees, shrubs and vine) was obtained for temperate and subtropical Australia and tropical Australia. Sources of information for temperate and subtropical rainforests were Harden et al. (2006 & 2007), and for tropical forests, Hyland et al. (2010). Complete floristic data on grass and herbaceous species could not be sourced.

Data analysis

Species frequencies were produced using IBM SPSS Statistics Data Editor (IBM Corp, 2016). Chi squared (χ^2) values were calculated to test for significant variation between observed and expected results. I calculated the expected value of butterflies feeding on a specific plant type in rainforests by dividing the total number of rainforest butterflies, by the relative diversity of the plant type within rainforests. χ^2 values were only calculated for butterflies feeding on woody and climbing species (i.e. trees vs. vines) as I was unable to source complete floristic data for plant types such as grasses and herbs in rainforests.

Specialisation

For the purposes of this study specialisation was characterised based on the number of genera of (primary) host plant taxa a species feeds on. If a species fed on a single genus of plant taxa the species was considered to be ‘monophagous’. Species feeding on 4+ genera of host taxa were considered ‘polyphagous’, and those in between ‘oligophagous’. I also note many of the butterfly species included in our study occur outside Australia and may have a wider range of host plant species extra-liminally. Nevertheless, our geographical scope is continental. Certainly the depth and breadth of available knowledge on Australian butterflies allows us to draw more accurate conclusions concerning host specialisation/monophagy than would be possible for any other comparably large taxonomic group.

Following this categorization, X^2 expected values of monophagy were calculated. The proportions of monophagous butterflies was expected to be equal for both trees and vines and were calculated by dividing the total number of monophagous rainforest butterflies by the total number of butterflies found in rainforests.

Diversification and climbing host plants

Correlations between clade richness, the proportion of butterfly species using climbing host plant, and the degree of specialisation were tested by fitting linear regression models to log-transformed data in R (RStudio, 2016). Response variables (i.e. the number of species utilising climbing host plants and the number of monophagous, oligophagous and polyphagous species) were standardised into proportions to account for variation in richness among clades.

Adult Size

Differences in the forewing length of butterflies feeding on trees compared with those feeding on climbing species were compared statistically using t-tests.

4.4 RESULTS

Flora

In subtropical and temperate Australia, 217 of the 1004 species listed were identified as either a vine or liana and contributed 21.6% to the floristic diversity of rainforests overall. In the tropics, vines contributed 27.3% to the regional floristic diversity of rainforests and were represented by 434 species out of 1156 species for the region (see Table 4.1). Vines occurred in ~65% of families with more than 10 species, and showed no phylogenetic partitioning (see Chapter 2).

Table 4.1 Floristic diversity of climbing and woody plant species in Australian rainforests. Sources of information for temperate and subtropical rainforests were Harden et al. (2006 & 2007), and for tropical forests, Hyland et al. (2010). On average, climbing species contribute 24.5% to the relative diversity of rainforests.

	Climbing species	Woody species	Total
Subtropical and temperate Australian rainforest	217 (21.6%)	787 (78.4%)	1004
Tropical Australian rainforest	434 (27.3%)	1156 (72.7%)	1590

Butterflies

Out of the 409 species listed in the available resources, complete information was available for a total of 370 species representing all known Australian families. Less than half (42%) of all species were commonly found in rainforests, 84 of which listed no other habitat type. Papilionidae had the highest affinity for rainforest habitats with 76% of species commonly observed in this habitat type. Less than half of the species in all other families inhabited rainforest. Hesperiidae had the lowest proportion of species (36%) found in rainforest (see Table 4.2).

Table 4.2 Summary of butterfly data collection separated by family. Complete information was available for 90% of Australian butterflies.

Family	No. of species included	Proportion of taxa with complete information	No. inhabiting rainforest	Proportion of taxa inhabiting rainforest
Hesperiidae	116	0.96	42	0.36
Lycaenidae	131	0.89	51	0.39
Nymphalidae	75	0.89	37	0.49
Papilionidae	17	0.85	13	0.76
Pieridae	31	0.86	14	0.45
TOTAL	370	0.90	157	0.42

Table 4.3 Summary of *all* Australian butterflies feeding within each host plant category. Percent of total fauna feeding in each plant type is included in brackets.

Family	No. of species	Host plant type					
		Vines	Trees	Grass	Herbs	Mixed	Other
Hesperiidae	116	9 (7.8%)	11 (9.5%)	66 (56.9%)	24 (20.7%)	0 (0%)	6 (5.2%)
Lycaenidae	131	14 (12.4%)	64 (48.9%)	0 (0%)	5 (3.8%)	17 (13.0%)	31 (23.7%)
Nymphalidae	75	15 (20.0%)	12 (16.0%)	33 (44.0%)	9 (12.0%)	4 (5.3%)	2 (2.7%)
Papilionidae	17	6 (35.3%)	10 (58.8%)	0 (0%)	0 (0%)	1 (5.9%)	0 (0%)
Pieridae	31	5 (16.1%)	12 (38.7%)	0 (0%)	1 (3.2%)	5 (16.1%)	8 (25.8%)
TOTAL	370	49 (13.2%)	109 (29.5%)	99 (26.8%)	39 (10.5%)	27 (7.3%)	47 (12.7%)

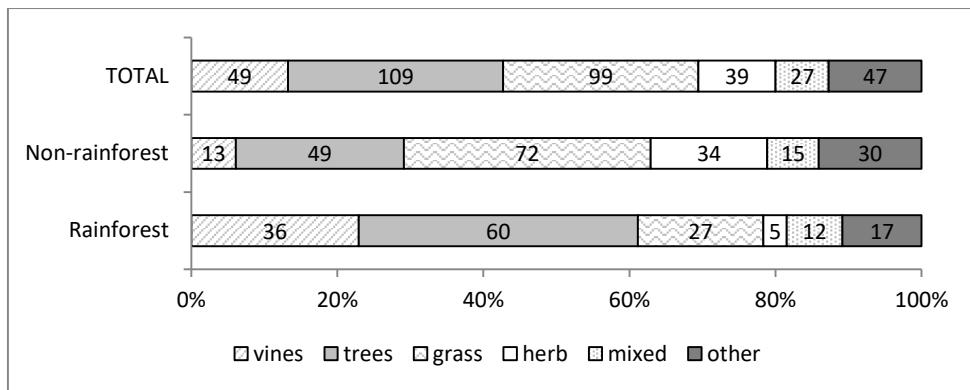


Figure 4.2 The number of Australian butterflies feeding in different plant categories in rainforest and non-rainforest habitats.

Host-plants

Vines, trees and grasses were the three dominant food plant types and contributed to over half of all families food plants. Ninety-three percent of all butterflies fed within a single food plant category, demonstrating a high fidelity of species to plant growth type (Table 4.3).

In non-rainforest areas, grasses were the most commonly used host plant type, whereas, not surprisingly, vines were the least common (see Figure 4.2). In rainforests, however, vines were the second most commonly used food plant type after trees. Butterflies feeding on vines were nearly three times more likely to be found in rainforest than non-rainforest habitats. The utilization of vines (largely lianas) as host plants increased in rainforests across all families but this increase was most dramatic in families that relied heavily on grasses in non-rainforest habitats. The dominant food plant type of Hesperiidae (principally Hesperiinae) and Nymphalidae (principally Satyrinae) in non-rainforest environments is grass, while vines are utilized minimally or not at all. In rainforest, these families increased their dependence on vine, although I note this switch often involved contrasting subfamilies (Pyrginae and Coeliadinae in the case of hesperiids and a wide range of non-satyrines in the case of the nymphalids).

When the contribution of ‘leafy’ host plants (vines, trees or a combination of both) to diet breadth were analysed in isolation, butterflies used vines as host plants nearly twice as often in rainforests (33.3%) compared with non-rainforest habitats (16.9%).

In rainforests, 96 species of butterflies fed exclusively on either vines or trees. I calculated expected X^2 values by dividing the total number of vines and trees feeding butterflies by the average relative diversity of each plant type in rainforests. These figures were used to calculate X^2 values. In rainforests, I recorded 36 species feeding on vines, and 60 feeding on trees (Table 4.4). These figures were significantly different from the expected values ($X^2=8.75$, df=1, $p<0.003$, n=93). I expected to observe 23.5 butterflies using vines as host plants and 69.5 butterflies using trees, based on the relative diversity of each of these plant types in rainforests. Vines were used as host plants significantly more than their relative diversity

predicted ($X^2=13.83$, df= 4, p<0.01, n=36). Vine host plants were used by all Australian butterfly families and 65% of all subfamilies. Use of climbing host plants showed no apparent phylogenetic signal with rainforest genera (although this was not formally tested) (Figure 4.3). X^2 values were also calculated for rainforest vine feeding butterflies in different families. Their utilization by Nymphalidae and Hespiridae were double the expected values, whereas the observed use by Lycaenidae and Pieridae were as expected. The contribution of vines to butterfly host plant taxa exceeds their contribution to floral diversity in rainforests.

Table 4.4 Summary of Australian *rainforest* butterflies feeding within each host plant category. Percent of total rainforest fauna feeding on each plant type shown in brackets.

Family	No. of species	Host plant type					
		Vines	Trees	Grass	Herbs	Mixed	Other
Hesperiidae	42	9 (21.4%)	9 (21.4%)	16 (38.1%)	2 (4.8%)	0 (0%)	6 (14.3%)
Lycaenidae	51	9 (17.6%)	29 (56.9%)	0 (0%)	0 (0%)	8 (15.7%)	5 (9.8%)
Nymphalidae	37	11 (29.7%)	9 (24.3%)	11 (29.7%)	3 (8.1%)	2 (5.4%)	1 (2.7%)
Papilionidae	13	5 (38.5%)	7 (53.8%)	0 (0%)	0 (0%)	1 (7.7%)	0 (0%)
Pieridae	14	2 (14.3%)	6 (42.9%)	0 (0%)	0 (0%)	1 (7.1%)	5 (35.7%)
TOTAL	157	36 (22.9%)	60 (38.2%)	27 (17.2%)	5 (3.2%)	12 (7.6%)	17 (10.8%)

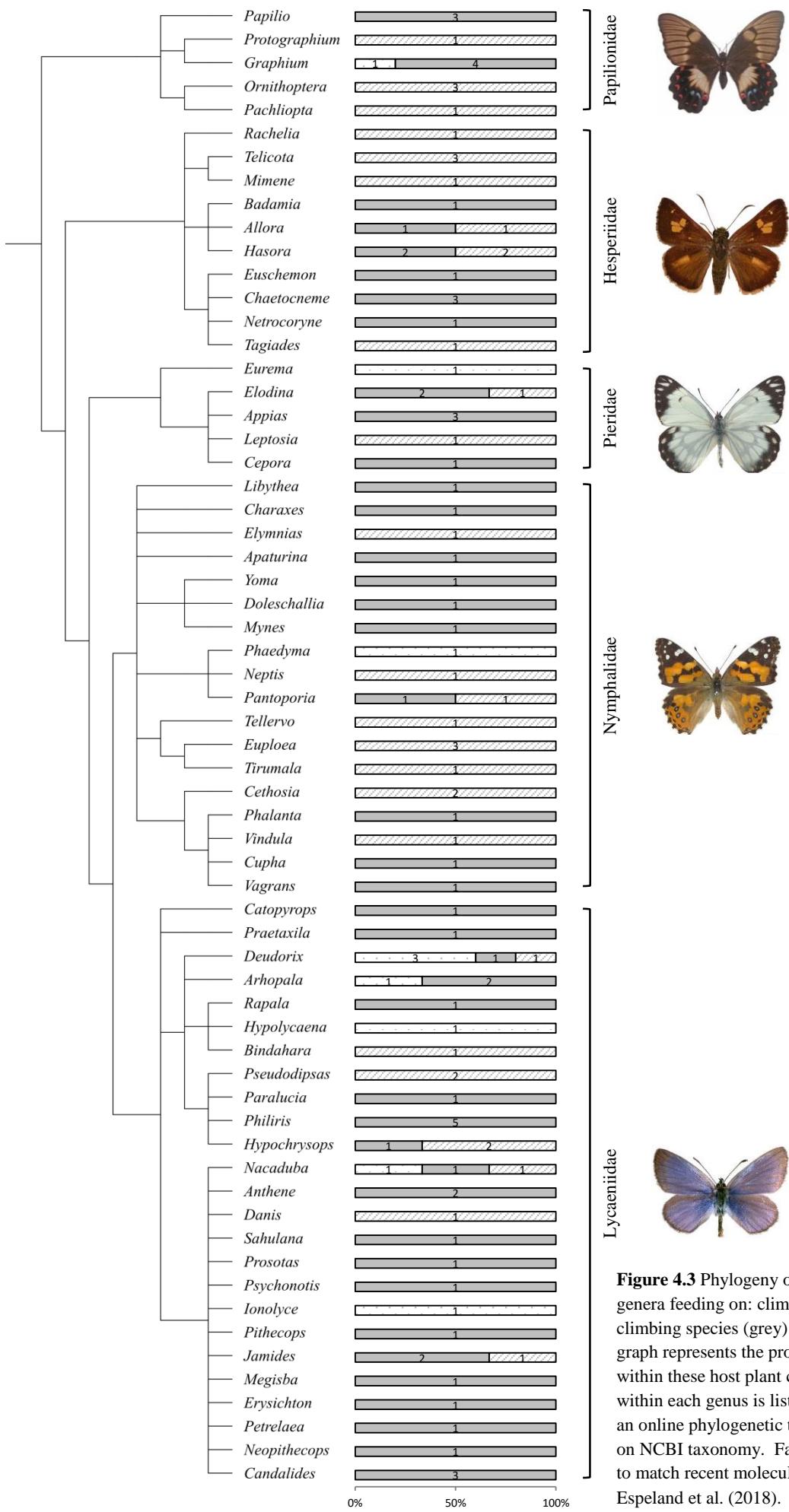


Figure 4.3 Phylogeny of Australian rainforest butterfly genera feeding on: climbing species (striped); woody non-climbing species (grey); or both (spotted). The adjacent bar graph represents the proportion of each genera feeding within these host plant categories. Number of species within each genus is listed. Phylogenies were created using an online phylogenetic tree generator (Letunic, 2017) based on NCBI taxonomy. Families were, however, constrained to match recent molecular taxonomic placement by Espeland et al. (2018).

Specialisation

Monophagy, characterised here as feeding on a single genus of plant, was exhibited by 61.6% of butterfly species and was greatest in vine feeders. Nearly 90% of all vine feeders were monophagous, compared with tree feeders who exhibited monophagy in only 60.6% of species (Table 4.5). As expected, species feeding on more than one plant type (mixed) exhibited the greatest levels of polyphagy. Sixteen percent of all tree feeders were classified as polyphagous, whereas no species feeding on vines fed on more than 3 genera of host plant.

If we assume the proportion of monophagy is equal among butterflies feeding on different plant types (specifically vines and trees), we would expect to observe 34.1 monophagous vine feeders and 75.9 monophagous tree feeders. However, I observed a significantly different ratio of monophagous butterflies ($X^2=4.15$, $df=1$, $p<0.05$, $n=110$) favouring vine feeding species. Monophagy was found in 44 vine feeding and 66 tree feeding butterflies species.

Table 4.5 The number of host plant genera used by butterflies feeding on different plant types. The proportion of butterflies feeding on x genera within a specific plant type are in brackets.

Plant Type	Number of host plant genera					
	1	2	3	4+	carnivorous	Total
Vines	44 (89.8%)	3 (6.1%)	2 (4.1%)	0 (0%)	0 (0%)	49
Trees	66 (60.6%)	22 (20.2%)	4 (3.7%)	17 (15.6%)	0 (0%)	109
Grass	66 (66.7%)	16 (16.2%)	8 (8.1%)	9 (9.1%)	0 (0%)	99
Herbs	31 (79.5%)	4 (10.3%)	2 (5.1%)	2 (5.1%)	0 (0%)	39
Mixed	6 (22.2%)	5 (18.5%)	0 (0%)	16 (59.3%)	0 (0%)	27
Other	15 (31.9%)	14 (29.8%)	3 (6.4%)	5 (10.6%)	10 (21.3%)	47
TOTAL	228 (61.6%)	64 (17.3%)	19 (5.1%)	49 (13.2%)	10 (2.7%)	370

Diversification and climbing host-plants

I found a weak negative association at the family level between species richness and the proportion of butterflies feeding on vines ($n=5$, $p=0.06$) when habitat choice was not considered. Families with greater

species richness had proportionally fewer climbing host plants. When rainforest species were analysed in isolation no correlation was found ($n=5$, $p<0.05$). However, when lycaenids were removed (for reasons discussed below) from the model, a significant positive correlation was returned ($n=4$, $p<0.02$). As the richness of a family increased the proportion of climbing host plants increased accordingly. However, this correlation was only observable at the family level and not at the level of subfamily.

Similarly, there was a negative correlation between the proportion of monophagous species and richness within sub-families ($n=21$, $p=0.02$), and remained even with lycaenids removed. As the proportion of monophagous species increased within a sub-family, species richness declined. However, 38% of subfamilies were represented by a single individual (all of which were monophagous). When this analysis was re-tested at the family level this effect disappeared ($n=5$, $p=0.19$) most likely due to a small sample size.

Adult size

Overall, species feeding on vines had a significantly larger forewing length than species feeding on non-climbing woody plants (t test, $n=158$, $p<0.05$). However the response within families was variable. Both Papilionidae and Nymphalidae feeding on vines had larger (but not statistically significant) forewing lengths than those that fed on trees ($p>0.05$). In contrast, Hesperiidae and Pieridae feeding on trees had significantly larger forewings than species feeding on vines ($p<0.05$). The forewing length of Lycaenidae species showed no response to food plant type.

4.5 DISCUSSION

I expected to observe that the use of vines as butterfly host plants reflected their relative diversity within ecosystems, especially rainforest. I observed, however, significantly more species of butterflies feeding on vines than the relative diversity of such plants predicted, and significantly greater levels of overall monophagy in butterflies that fed on climbing species than expected. Of course, the results derived here are only as reliable as the degree of comprehensiveness of host plant information. I performed this study in the context of a larger project and intend to replicate this analysis on other well-known butterfly faunas.

Host plant use

Host plant selection in many phytophagous insects is hypothesised to be governed primarily by ovipositional behaviour and chemoreception, with adaptations to the biochemical profile of the host plant a secondary process (Becerra and Venable, 1999, Jermy, 1984, Thompson and Pellmyr, 1991). Vines, however, typically produce fewer anti-herbivore defence chemicals and olfactory cues than trees (Asner and Martin, 2012). Presumably, vines form insect associations via non-chemosensory mechanisms such

as leaf quality, availability and apparentness. I use these factors to discuss the elevated use of vines as host plants compared with trees.

Firstly, vines produce new leaves for longer periods throughout the year than trees and the availability of young leaves is an important predictor of insect herbivores (Aide, 1992, Aide, 1993, Basset, 1992, Coley, 1980). The longer the availability of new and palatable leaves, the greater the likelihood for interactions with a greater number of herbivores that are able to use them as a food source (Lawton and Schroder 1977, Niemelä 1982, Niemelä et al. 1982). This in turn should promote vine-insect food plant associations and may in part explain the discrepancy I found in observed and expected values of host plants.

Secondly, the availability of desirable leaf traits may also give rise to host plant associations. The nutritional quality of leaves of vines is hypothesised to be superior to leaves of trees as they contain higher concentrations of chemicals important for metabolic processes and growth (N and P) (Mattson and Scriber, 1987, Awmack and Leather, 2002), and contain fewer defensive chemicals which may be toxic and/or reduce the nutritional value of the leaf by interfering with absorption (Sharma et al., 2009, Barbehenn and Peter Constabel, 2011, Mithofer and Boland, 2012). The lack of defensive compounds found in many vines may be advantageous for butterfly species which lack the ability to convert or sequester these chemicals and may further explain the greater use of vines as host plants. Furthermore, vine host plants may be of particular use for early instars which tend to be more sensitive to toxins than later instars.

Thirdly, vines increase habitat structural complexity and provide a greater diversity and abundance of micro-habitats that may be suitable for many butterflies/caterpillars which, in turn, may promote vine-butterfly associations. Vines (specifically woody lianes) provide important microhabitats for many phytophagous beetles feeding within Bignoniaceae, Rhamnaceae, Sapindaceae and Vitiaceae (Ødegaard, 2000b) which has promoted radiations in many of these beetle clades. Similar diversifications promoted by the structural complexity of vines may have occurred in other insect lineages, such as butterflies, but requires further investigation. It is probable vines offer concealment and protection for caterpillars from predators and may provide thermal refuges, optimal for growth and survival, by buffering local environmental and microclimatic conditions. Future investigations would benefit from determining the abundances and survival rates of larvae on climbing plants in comparison with trees.

Host specificity

Monophagy in butterflies was significantly more prevalent in species feeding on vines than those feeding on trees. Ødegaard (2000b) similarly found a higher degree of effective specialisation of beetles associated with vines (specifically lianas) than trees. Analyses of this nature are lacking for other insect faunas and geographic locations which limits more broad-scale generalisations of patterns. However, the alignment of these results, from within the two most prominent herbivorous lineages, suggests this pattern

may be widespread among phytophagous insects and merits further investigation among other faunas. Similar analyses could be performed on the butterfly faunas of Sri Lanka and Barro Colorado Island, Panama and could be further usefully compared with other geographic zones depauperate of rainforest such as Europe and North America.

The same factors which may have promoted greater use of vines as host plants may have equally contributed to greater levels of monophagy in vine feeding species. Greater availability of new leaves, as provided by vines (Zhu and Cao, 2010, Ødegaard, 2000b), may be more advantageous to monophagous species as these species rely more heavily on the availability of new leaves than polyphagous species (Cates, 1980, Cates, 1981). Availability of leaves is likely important for monophagous insects as they are unable to switch to alternative food sources during times of scarcity and rely more heavily on the likelihood of phenological overlap between host plant leaf availability and larval feeding periods.

In contrast, elevated biofoliar chemical defences in young tree leaves is hypothesised to promote specialisation (Janzen and Waterman, 1984). I am unaware of any literature regarding the chronology of chemical defences in vine leaves and are therefore unable to comment on the relevance of this hypothesis to insects feeding on vines. Chemical defences are however, significantly lower in mature vine leaves compared with tree leaves (Asner and Martin, 2012) and low to no chemical defences in plants has been linked to monophagy in saturniid moths (Janzen, 1984). Explaining monophagy becomes an interesting problem where no special biochemical or morphological apparatus are required to access the food (Levins and MacArthur, 1969). In the absence of biofoliar traits to promote specialisation, alternative characteristics must promote monophagy.

Diversification and climbing host-plants

I found a weak negative association at the family level between species richness and proportion of butterflies feeding on vines (when habitat was not considered). This association contradicts our hypothesis that enhanced diversification in clades with climbing species should generate greater richness in butterfly lineages with greater vine feeding species. Although this hypothesis may still be valid at a global scale, it is not observable within the Australian butterflies due to distinct characteristics of the Australian fauna compared to the fauna of other well-known regions. The diversity of butterflies in Australia is relatively low in contrast to other comparable regions and highly endemic (Austin et al., 2004, Ackery, 1991). The Family Riodinidae is absent, and over 30% of subfamilies and 50% of genera recorded here were represented by only a single species, including several globally diverse lineages such as, *Ornithoptera*, *Pachliopta*, *Acraea*, *Neptis* and *Polyura*. Australia is also peripheral to ranges of other notable diverse groups such as, *Graphium*, *Eurema*, *Delias*, *Euploea*, *Hypolimnas*, *Hypochrysops*, *Tagiades*, *Mimene* and *Notocrypta* (Ackery, 1991), although their richness within Australia is notably lower. It may also be noteworthy that although insect (but not butterfly) radiations with Myrtaceae are extensive in Australia (Austin et al., 2004), no vines originate from this family within Australia, and are largely depauperate from the malvids as a whole (see Chapter 2). Furthermore, very few butterflies feed

on *Eucalyptus* (Myrtaceae) or Proteaceae (Braby, 2000), two dominant and characteristic floras of the Australian landscape.

It is also of importance that lycaenid butterflies, the most speciose butterfly family (overall and in rainforests) reported here, have the highest proportion of obligately ant-associated species of any zoogeographical region (Austin et al., 2004). Ants are known to defend trees against vines (Janzen, 1969, Rickson, 1977, Heil et al., 2001, Janzen, 1966), which may have structured the food-plant association of ant-attended butterflies. Similarly the prevalence of carnivorous species within the group confounds the data. When lycaenids removed from the rainforest specific analysis, I found a strong positive correlation at the level of the family between the proportion of climbing host plants and richness within rainforests.

Co-radiations among speciose butterfly lineages and vines are known. For example, Heliconinae includes 45-50 genera of butterflies which feed almost exclusively on Passifloraceae vines (Gilbert, 1982). Given known food plant records, radiations between Troidini feeding on Aristolochiaceae vines, Biblidinae feeding on Euphorbiaceae vines and Danainae feeding on Asclepidaceae vines are highly probable. The Australian representatives of these groups follow these patterns and consume climbing food-plants. Interestingly, although perhaps coincidentally, Heliconinae, Troidini and Danainae all possess intricate mimicry complexes (Joron, 2005, Benson, 1978, West, 1994, Brown and Benson, 1974).

The negative correlation between butterfly richness and proportion of butterflies feeding on vines may have been impacted by the high degree of specialisation of butterflies feeding on vines. The oscillation hypothesis predicts more species in clades with greater diversity of host-plant use i.e. polyphagy, (Janz et al., 2006, Janz and Nylin, 2008). In contrast, the musical chairs hypothesis suggests speciation is driven by host plant switching, without changes in niche breadth (Hardy and Otto, 2014), this hypothesis further predicts that speciation events should be associated with a trait shift from polyphagy to monophagy. I found a significant negative correlation between the proportion of monophagous species and the speciosity within clades. This result supports the oscillation hypothesis and corresponds to the negative correlation I observed between butterfly richness and proportion of butterflies feeding on vines.

There was no apparent phylogenetic signal between using climbing host plants and rainforest butterfly genera. Many butterfly clades, however, have recently been shown to be poly and paraphyletic (Espeland et al., 2018) and require higher level taxonomic revision. A pattern may be evident under a revised taxonomy, however given the multiple origins of climbing within dicotyledonous plants; it is probable the use of vines within butterflies will reflect this pattern.

Adult size

I hypothesised that the greater concentrations of elements important to metabolic processes and growth (namely nitrogen and phosphorus) found in vine leaves compared to tree leaves would result in larger butterflies (as determined by male forewing lengths) feeding on vines. Although I found a significant

difference in the forewing length of butterflies between vine-feeding and tree-feeding species, the response within families was variable. This may be due in part to the different growth strategies species employ. Janzen (1984) hypothesised two mechanisms by which moths may attain large sizes. Moths with food-plants of high nutritional quality should achieve a large size relatively quickly, while moths with nutritionally poor food-plants can achieve the same size with longer developmental times.

Through additional analyses may be able to determine if host plant choice can predict characteristics of their associated butterfly faunas. For example, insects feeding on hosts-plants with greater nutrient contents tend to have faster developmental times compared to those feeding on less nutritious or chemically well-defended host plants (Janzen, 1984) therefore by knowing a butterflies host plant is a vine we may be able to predict elements of its life history strategy.

Vines are important food sources for many phytophagous insects and are at least as important as trees for the maintenance of local species richness of butterflies, particularly in rainforests. The mechanisms that drive these patterns likely involve plant architecture, length of growing season and availability of new leaves. Herbivory on vines, in contrast with trees, merits further investigation. I performed this study in the context of a wider research project and intend to analyse other geographic locations with well-known butterfly fauna (such that of Barro Colorado Island, Benin and Sri Lanka) and flora.

CHAPTER 5

STATEMENT OF CONTRIBUTION TO CO-AUTHORED PAPER

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My contribution to this chapter involved all field work and data collection, analysis and writing of the manuscript. Akihiro Nakamura and Min Cao are my Chinese collaborators and assisted with the organisation of my trip, access to the canopy crane and provided methodological advice. My supervisor, Roger L. Kitching, assisted with the direction and editing of the manuscript.

(Signed) _____

(Date) 10 May 2018

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CHAPTER 5

Insect folivory on trees and lianas in the upper canopy of a tropical rainforest

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5.1 ABSTRACT

In rainforests, lianas commonly comprise 20-40% of the above ground leafy biomass, yet, in contrast to co-occurring trees and shrubs, few studies have quantified the herbivore damage inflicted upon them. I addressed this knowledge gap by measuring leaf herbivory from the canopy of lianas, their host trees and from trees without lianas in a *Parashorea chinensis* (Dipterocarpaceae) dominated rainforest in southwest China. Access to the canopy was made possible using one of a network of canopy cranes recently established in Chinese forests. This study sets the scene for more detailed studies of the process of insect herbivory in these fragmented and remnant forests and between plant types.

I quantified herbivory using digital methods from 18,758 leaves from 89 lianas and 66 trees, on which lianas were present on 45. Herbivory on lianas accounted for approximately 48% of all leaf area loss within the forest. I found no difference in the level of leaf herbivory on lianas (6.0%) compared with trees (6.4%), or between trees hosting lianas (6.2%) and liana-free trees (6.8%). I hypothesised that levels of herbivory on host trees may increase the more liana species it hosted but observed no significant correlation between the number of lianas and amount of host tree herbivory. This suggests lianas support the herbivory processes at a level equivalent to trees and the presence of a liana (or lianas), does not increase the susceptibility of its host to herbivory.

5.2 INTRODUCTION

Rainforest canopies

Estimates of herbivory calculated from ground-based measurements typically suggest losses of leaf area in rainforests of roughly 5-10% (de la Cruz and Dirzo, 1987, Mattson and Addy, 1975). These estimates have been scaled-up and used as surrogates for stand-wide herbivory (Rinker and Lowman, 2004, Lowman, 1985). This approach however, may underestimate herbivory substantially or misrepresent patterns of herbivory in the canopy where high levels of light and temperatures encourage foraging and ovipositing among insects (Basset et al., 2003). In addition to leaf biomass, density of new leaves and arthropod abundances and diversity are generally greater in the canopy compared with the understory (Basset et al., 2008, Charles and Basset, 2005).

Rainforest canopies are one of the most species-rich terrestrial habitats, but among the least explored (Erwin, 1982, Basset et al., 2003, Basset et al., 2008, Bohlman, 2015). Access to forest canopies poses obvious challenges for canopy science. The formation of a global network of canopy cranes holds the promise of alleviating this problem by improving ease of access and allowing for the establishment and long-term maintenance of a high number of sampling points within a study area (Stork et al., 1997b). Hitherto, these cranes have been used predominantly to study tree physiology and vegetation structure with only *ca* 10% of published studies exploring epiphytes, epiphylls, and endophytes (Nakamura et al., 2017, Zotz, 2007, Zotz and Schultz, 2008, Nieder et al., 2000). A further *ca* 18% of studies using cranes investigated arthropods, and to a lesser extent, herbivory (Nakamura et al., 2017, Ødegaard, 2000b, Basset et al., 2015, Blüthgen et al., 2000). China has the potential to become a leader in this new approach to canopy science having recently established eight cranes within its borders (Nakamura et al., 2017, Wu et al., 2016).

Quantitative information on canopy herbivory is scarce, and estimates of herbivory are often calculated from less than 30 leaves per individual (Coley, 1983, Poorter et al., 2004, Aide and Zimmerman, 1990), and/or from a small number of species (Nooten and Hughes, 2013, Basset, 1991, Lowman, 1985). This degree of sampling effort reflects the time-consuming nature of accurately and electronically measuring herbivory. These earlier methods based on small sample sizes, have the potential to both over- and under-estimate ‘true’ herbivory when used to generalise community and stand-wide herbivore damage.

Insect herbivory

The consumption of plants by insects is a key ecological process which mediates the structure, functioning and maintenance of forests (Schowalter, 2016) and is of substantial fundamental and economic importance. Herbivory in rainforests has been well documented on trees and saplings (Coley,

1983, Bassett, 1991, Kambach et al., 2016, Eichhorn et al., 2007, Poorter et al., 2004) but is less-known for other common plant functional groups.

For epiphytes, authors have suggested that levels of insect herbivory in rainforests are low (Hendrix and Marquis, 1983, Schneider, 1982, Lowe, 1898). These estimates however have been at best semi-quantitative and may be critiqued both for their limited sampling and the estimation techniques employed. More comprehensive studies of herbivory on tropical epiphytic ferns estimate leaf loss of *ca* 10%, comparable with estimates of herbivory on trees (Winkler et al., 2005, Hendrix and Marquis, 1983, Rinker and Lowman, 2004, Coley and Barone, 1996). Herbivory on bromeliads and orchids has similarly been assumed to be low and, although leaf loss on these plant types is typically lower than expected, both commonly have high levels of non-leaf herbivory (such as damage to meristematic tissues and flowers) (Winkler et al., 2005), and may be important for insects feeding on plant parts other than leaves.

A recent review of the literature by Kozlov et al. (2015a), examined herbivory on different woody plant functional groups and, highlighted the global lack of quantitative data on herbivory on plants other than trees. They particularly emphasised the dearth of information on woody climbing species (lianas). For these climbing plants, even less data is available from which to estimate broad-scale herbivory and the contrasts, if any, between trees and lianas (de la Cruz and Dirzo, 1987, Peñuelas et al., 2013). There is but a single study that has investigated herbivory on lianas (and other climbing plants) in contrast with trees in a rainforest canopy (Wint, 1983). This study examined herbivory on lianas and trees in Papua New Guinea (PNG) and found the difference in relative leaf loss was greater on trees than lianas at one site, but was comparable at the second site (trees = 12.5-13.7%, lianas = 6.2-10.7%) (Wint, 1983). In contrast de la Cruz and Dirzo (1987) observed greater relative leaf loss on seedlings of lianas compared to seedlings of trees (trees = 8.17%, lianas = 10.87%), albeit insignificant.

This paucity of information is all the more surprising given the substantial overall contributions of lianas to leaf biomass and diversity in rainforests. Lianas support substantially more leaves per unit basal areas than trees and typically constitute 20-40% of leaf biomass in forests (Hegarty, 1991 , Wright et al., 2004, Pragasan and Parthasarathy, 2005). In terms of dicotyledonous species richness they are equally diverse as trees in the canopies of both subtropical and tropical rainforests (Croat, 1978)(see Chapters 2 and 3). In canopies, lianas support equivalent numbers of phytophagous beetle species as do trees (Ødegaard, 2000b) and, in Australian rainforests, host more species of butterflies than their relative diversity predicts (see Chapter 4). If lianas support a comparable, if not greater, diversity and abundance of foliar feeding insects as trees, then then we would expect to this to be reflected by equivalent levels of herbivore damage.

The gaps in our knowledge of herbivory on lianas is all the more concerning given the well-documented increase in liana numbers within rainforests (see Chapters 2 and 3), possibly driven by anthropogenic global change (Laurance et al., 2014, Schnitzer, 2005).

In this paper we quantify herbivory from the canopies of lianas and trees, and from trees with and without lianas at a single point in time. I hypothesise (1) there will be no difference in herbivory between lianas and trees, and (2) trees hosting lianas will incur different amounts of herbivory to liana-free trees due to either associational susceptibility (leading to an increase in tree herbivory) or resistance (leading to a decrease in herbivory)(Barbosa et al., 2009, Agrawal et al., 2006, Plath et al., 2012).

5.3 METHODS

Study site

The Xishuangbanna Tropical Rainforest Ecosystem Station (XTRES) is located in Bubeng, Mengla, in the Xishuangbanna prefecture of Yunnan, China, near the Laotian border (101°34'E, 21°36'N) (Figure 5.1). The region hosts over 5,000 species of vascular plants, comprising 16% of China's total plant diversity and is included in the Indo-Burma biodiversity hotspot (Cao et al., 2006). The climate is monsoonal and characterised by a pronounced wet season between May and October, and a dry season between November and April. More than 80% of the average annual rainfall (1530mm) falls in the wet season (Lan et al., 2012) and mean annual temperature (21.4°C) is warm for the latitude (Fei et al., 2018). This area is the limit of tropical rainforests in the northern hemisphere (Hua, 2003).

The profile of the forest plot parallels that of other tropical south east Asian rainforests and has a similar physiognomic characteristics, floristic composition and species richness but is less dominated by Dipterocarpaceae (Hua, 2003, Zhu, 2017). In the hectare surrounding the crane, there are approximately 119 species of trees (unpublished) of which *Pittosporopsis kerrii* (Icacinaceae) and *Parashorea chinensis* (Dipterocarpaceae) dominate the stand in both the emergent and sapling layers (Lan et al., 2012). In a nearby hectare of tropical rainforest in Mengla 38 species of lianas were recorded and *Byttneria grandifolia* was shown to be the most important liana species (Lu et al., 2009). Overall lianas comprise ~24% of total species richness but only account for 0.8-1.4% of the above ground biomass (Lu et al., 2009, Zheng et al., 2006).

The XTRES canopy crane was constructed in 2013 as part of an initiative to establish canopy research in China. The crane itself is 80m tall with a jib length of 60m facilitating access to *ca* 1 ha of canopy through a gondola which is lifted from the ground, raised above the canopy and lowered anywhere in the arc of the 55m long arm (Figure 5.1). All canopy trees and lianas in the hectare surrounding the crane are tagged at ground level and identified. There is, however, no mapping or geospatial data of the floristics from the canopy. Other cranes have mapped and identified the crowns of individuals using GIS which allows for sampling of targeted species and individuals and accurate spatial information (Stork, 2007).

In the 1 ha surrounding the crane there are more than 190 species of tree >1cm diameter at breast height (DBH) and approximately 52 identified species of canopy trees (defined here as > 20cm DBH) from 197

individuals. *Parashorea chinensis* accounts for 23% of all canopy trees while 22% of species consist of 5 or fewer individuals.

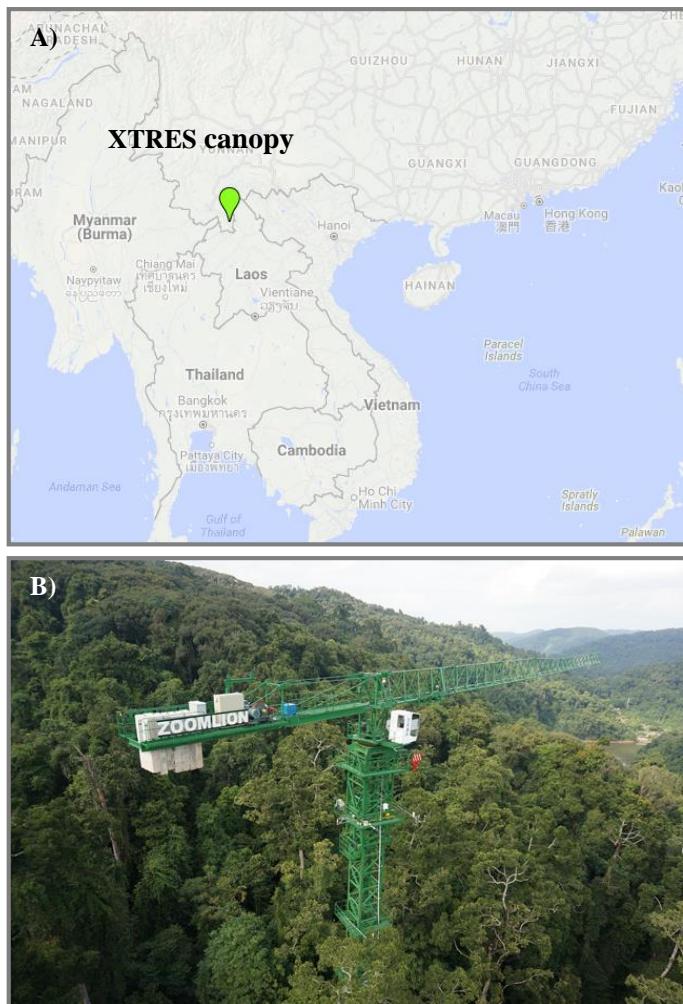


Figure 5.1 A) Location of the XTRES canopy crane. It is located near the China-Laos international border in Southern Yunnan, China. B) XTRES canopy crane. The crane's arm allows researchers direct access to the canopy of 1ha of tropical rainforest. Image by XTBG

Sampling

Mature leaves were collected in August 2015 from the canopy of the XTRES crane site. Leaves were sampled from trees without lianas and from trees with lianas and their associated lianas using the canopy crane. At least 100 leaves were collected from most individuals. For a few large leaved individuals, such as *Byttneria aspera* (whose leaves can be over 25cm long and 17cm wide) and *Ficus langkokensis* (with leaves up to 25cm long and 9cm wide), collections were a little smaller.

Family-level taxonomic matching across lianas and trees, although desirable, was impossible so it was elected to sample as many species and individuals as possible. Replicate samples within individual plant species were obtained wherever possible. This broad-brush approach should encompass a wide diversity of leaf traits such as nutritional values, structural and chemical defences, to account for variation across higher taxa, and between functional groups.

To minimise issues associated with pseudo-replication, the canopies of sampled trees were at least 10m apart. Folivorous insects, particularly juvenile morphs, generally have limited foraging ranges (Heinrich, 1979, Hassell and Southwood, 1978, Jones, 1977, Cain et al., 1985, Harcourt, 1961) and intervals of 10m between sampled trees are typically sufficient to ensure independence.

Herbivory analysis

Sampled leaves were pressed and dried before being photographed on a white background using a camera attached to a tripod parallel to the leaf surface. Images were then transferred to a computer where the background, shadows and any unwanted pixels were removed using Adobe Photoshop CS3 Extended. Leaf margins affected by herbivory were approximated and drawn in to calculate leaf area loss (herbivory). Herbivory was calculated using the software program *ImageJ* (Rasband, 2016). Using a macro subroutine, images were loaded onto the software platform, converted to black and white formats and leaf area calculated with ‘damage’ both included and excluded. Herbivory was calculated by subtracting leaf area ‘holes’ excluded from leaf area ‘holes’ included. Final figures were expressed as percent leaf area lost per individual. All obvious forms of insect herbivory damage (e.g. chewing, mining, and skeletonisation) were included but were not quantified separately. All leaf loss was assumed to be the result of insect folivory as arboreal vertebrate herbivores are no longer present on the plot.

Data analysis

Significant differences in herbivory between 1) trees with and without lianas and 2) trees and lianas were verified by t-tests. Correlations between the number of lianas and herbivore damage to host trees was tested by fitting a linear regression model to standardized data in R (RStudio, 2016).

5.4 RESULTS

I sampled 18,758 leaves from 66 trees (*ca* 34% of accessible canopy trees) and 89 lianas consisting of 39 species of tree (in addition to 5 unidentified individuals likely belonging to 4 additional species) and 20 species of lianas (plus an additional 34 unidentified individuals likely constituting a further 10-20 species). This represented approximately 75-83% of canopy tree species and 36% of all tree individuals accessible by the crane. At the time of this study, lianas surrounding the crane site had not yet been identified. Alternatively, I relied on regional field identification guides as well as expert and local knowledge. Species that could not be identified were assigned a morpho-species code.

Lianas were present on 45 individuals of the 66 trees sampled, of which 24 had a single liana, 10 had two lianas and 11 had three or more lianas.

I found no significant difference in the total or mean leaf area loss between lianas (total=6.0%, mean=5.66% \pm 0.5) and trees (total=6.4%, mean=5.76% \pm 0.6) (t test, p>0.05), nor did I observe a

difference in leaf area loss between trees with (total=6.2%, mean=5.8% \pm 0.7) and without lianas (total=6.8%, mean 5.9% \pm 1.2) (t test, $p>0.05$), although leaf loss on trees without lianas was marginally higher (see Figure 5.2). Furthermore, I observed no significant correlation between leaf area loss on trees with lianas and the number of lianas (LM, $p>0.05$).

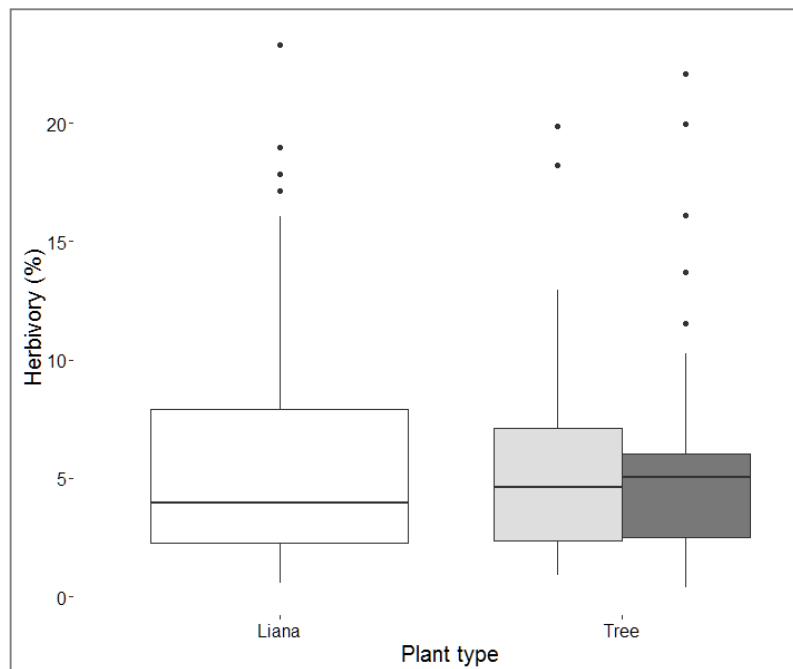


Figure 5.2 Box plot of herbivory on lianas (white), trees with lianas (light grey) and trees without lianas (dark grey) expressed as a proportion of damage to total leaf area. There was no significant difference in herbivory between lianas and trees ($p>0.05$), or between trees with and without lianas ($p>0.05$).

The influence of family could not be reliably determined due to asymmetrical and low sample sizes in many families, the large number of unknown species (particularly lianas) and the small proportion of families where lianas and trees were sympatric. The sampled lianas, however, were phylogenetically widely distributed (Appendix 5.1). For families with three or more individuals, herbivory was shown, under a linear model, to be significantly influenced by family in only Annonaceae ($p<0.05$) and Malvaceae ($p<0.05$) (Table 5.1). These families contained both trees and lianas, albeit in low numbers, and interacted significantly with plant type (Annonaceae, $p<0.05$, Malvaceae, $p<0.01$). Mean and total leaf area loss was greatest on trees within Annonaceae compared to lianas, while in Malvaceae this pattern was reversed and leaf area loss was greatest on lianas. This may be attributable to differences in quantitative and qualitative availability of leaves between the two families, or difference in herbivore assemblages. Nevertheless, contrasting patterns between families and species such as the one found here require further attention. A summary of all families is detailed in Appendix 5.2.

Table 5.1 Summary of lianas and trees sampled in each family with 3 or more individuals. Significant differences in herbivory determined by a linear model is indicated by *** p<0.001, **p<0.05, *p<0.1, however, the small sample sizes within families limit the reliability of these results. ¹ denotes significant interaction of plant type with family. A complete summary of all families can be found in Appendix 5.2.

Family	LIANAS			TREES			TOTAL		
	No. individuals sampled	Total leaf area loss (%)	Mean leaf area loss (%)	No. individuals sampled	Total leaf area loss (%)	Mean leaf area loss (%)	No. individuals sampled	Total leaf area loss (%)	Mean leaf area loss (%)
Annonaceae	3	4.06	3.85	2*	15.76	11.32	5*** ¹	9.66	6.84
Clusiaceae				3	4.08	4.47	3	4.08	4.47
Dipterocarpaceae				8	4.74	4.39	8	4.74	4.39
Ebenaceae				4	6.24	5.47	4	6.24	5.47
Elaeocarpaceae				3	11.74	9.51	3	11.74	9.51
Euphorbiaceae				6	5.96	4.68	6	5.96	4.68
Fabaceae	6	6.02	5.97	1	5.04	5.04	7	5.86	5.84
Fagaceae				4	11.19	11.40	4	11.19	11.40
Lardizabalaceae	8	5.45	5.88				8	5.45	5.88
Malvaceae	5***	17.11	17.15	2***	6.33	6.29	7*** ¹	14.63	14.05
Menispermaceae	4	4.24	3.92				4	4.24	3.92
Moraceae				7	2.21	2.16	7*	2.21	2.16
Pennantiaceae				3	4.54	4.98	3	4.54	4.98
Rubiaceae	15	6.15	5.87	1*	2.28	2.28	16	5.81	5.65
Sapindaceae				3	5.23	5.11	3	5.23	5.11
Verbenaceae	7	3.56	3.52				7	3.56	3.52

5.5 DISCUSSION

Much of our current understanding of insect folivory in rainforests comes from observations of large canopy trees and saplings. Yet 20-40% of the leaf biomass is made up of leaves from other plant types, principally lianas (Pragasan and Parthasarathy, 2005, Wright et al., 2004). Inferences and conclusions about herbivory gathered from data on trees may not apply to other plant types. For example, lianas and trees exhibit distinct ecophysiological trait variation in terms of structural, chemical and phenological properties that are independent of phylogenetic relatedness (Rios et al., 2014, Asner and Martin, 2012, Gianoli, 2015). Therefore factors influencing herbivory may contrast among plant functional groups. This suggests the importance of lianas in insect herbivory has been overlooked. Accordingly, quantifications of herbivore damage among plant types (i.e. lianas and trees) is the first step to understanding how different plant types support herbivory, insect diversity and ecosystems at large. In this study, I have quantified herbivory from lianas, their host trees, and trees without lianas. Overall, no differences in herbivory among groups was observed. This suggests lianas provide support to forest-wide herbivory processes equivalent to trees, and that the presence of a liana (or lianas) does not increase herbivory on its host.

Under ideal conditions, leaves would have been sampled from lianas and trees belonging to the same families to account for possible phylogenetic influences and liana-tree combinations would have been replicated. Such a sampling design is rarely possible. Few replicate liana-tree combinations were available, and few families on the plot were represented by both liana and tree species (a phenomenon I have encountered elsewhere, see Chapter 3). When such co-occurrences did occur they were in low abundances and often inaccessible. At the time of this study, no mapping of the canopy floristics had been completed and I relied on local expertise to identify plants for sampling. Botanical information on liana species, however, is not well known in the region and many species could not be identified by experts. In addition, fine-scale geospatial data was not possible using the available GPS equipment. Changes in the positioning of the crane often yielded no change in the GPS coordinates. Other cranes have addressed this issue by fixing a compass to the gondola and adding ‘tick’ marks with measurements to the arm of the crane (Stork, 2007).

The ‘snapshot method’ of quantifying leaf herbivory used here is the most common approach to measuring herbivory (Lowman, 1995). It does not, however, account for temporal variability in herbivory, nor does it account for whole leaf herbivory. As a result, herbivory is generally underestimated using this methodology. Given these limitations and the uniformity of herbivory assessment across plant types in this study, estimates of leaf loss on trees likely provide a reasonable representation of tree herbivory at the study site at the given point in time since a large proportion of canopy individuals and species were sampled. However, estimates of herbivory on lianas presented here may be an underestimate as liana leaves turnover more rapidly than do those on trees and each individual liana leaf captures herbivory for a shorter time-span than tree leaves (Zhu and Cao, 2010, Ødegaard, 2000b).

The similarity in herbivore damage between trees and lianas suggest lianas are as important for herbivory as trees and likely support similar densities and/or diversity insects per species as trees. Coleoptera (beetles) and Lepidoptera (moths and butterflies) are the two most speciose and abundant groups of insects in rainforests (Rinker and Lowman, 2004). In Panama, the diversity and abundance of phytophagous beetle species on lianas is statistically indistinguishable from that on trees (Ødegaard, 2000b). In addition, lianas are used as butterfly host plants in Australian rainforests more frequently than what their diversity within floras would predict (Chapter 4). Interestingly, both of these studies found greater specialisation of insects on lianas than on trees. Assemblages of other arthropod groups, such as Hymenoptera, Heteroptera, Homoptera and Acari, are similarly influenced by lianas (Walter, 1994, Wolda, 1979, Blüthgen and Fiedler, 2002, Blüthgen et al., 2000, Adams et al., 2017, Stork, 1987, Dial et al., 2006). The density of mites, for example, is greater on lianas than on trees (Walter, 1994); and lianas provide important sources of extra floral nectaries and at small scales lianas support different food webs from trees (Blüthgen and Fiedler, 2002).

I suggest Orthoptera and Phasmatodea deserve more attention. Although less speciose, they are often very abundant and individuals are frequently large and voracious. Large, highly mobile and abundant

polyphagous taxa, such as these, indiscriminately remove considerable quantities of leaf matter. This may obscure patterns in herbivory of other highly diverse, or small, taxa such as Coleoptera and Lepidoptera. For example, many species of Coleoptera are small, and/or rare and thus would not have contributed greatly to measurements of herbivory. Differences in patterns of herbivory from these taxa, therefore, would have gone undetected with the method used here. The exclusion of large polyphagous species, such as those discussed, may be necessary for future studies examining differences in herbivory between trees and lianas.

Furthermore, both lianas and trees supply resources for phytophagous insects other than leaves, such as; buds, fruits, extra floral nectaries, wood, roots, flowers and tendrils. Support to these different feeding guilds likely varies between plant types. For example, lianas are an important source of extra floral nectaries for Hymenoptera and Hemiptera, and tendrils, which support a large fauna of specialist beetles, are largely unique to climbing plants (Ødegaard 2000). Comparisons of herbivory on these plant parts across plant types requires investigation.

The arthropod assemblages on host trees are also likely influenced by the presence or absence of lianas. Ant species richness has been found to be greater on trees with lianas (Adams et al., 2017) and the density of homopterans in canopy tree crowns is higher on trees hosting lianas as they improve habitat suitability (Wolda, 1979). Changes in the herbivore assemblages, particularly in abundance, on host trees may influence the amount of herbivore damage they incur.

I hypothesised that associational susceptibility or resistance would result in differences in the amount of herbivore damage on trees with and without lianas. For example, palatable plant neighbours, such as lianas which invest little in herbivore defences (Asner and Martin, 2012) may increase herbivory on a focal host plant by attracting herbivores. In contrast, plant neighbours that are unpalatable may decrease herbivore damage on a focal plant species. Neighbouring climbing plants may also facilitate colonisation of insect herbivores on to a focal plant and increase the density of foliage surrounding host trees which may either serve to reduce herbivory by ‘camouflaging’ their host by lowering the probability that any one leaf is attacked, or increase the apprenency of a host tree therefore increasing insect visitation and herbivory. Our results show no difference in herbivory between trees with and without lianas. This may be because lianas attract predominantly specialist herbivores thereby exerting no influence of herbivory on their host trees, or because any ‘camouflaging effect’ provided by the added liana leaf biomass is obviated by the probable greater densities of arthropods on trees with lianas compared to those without.

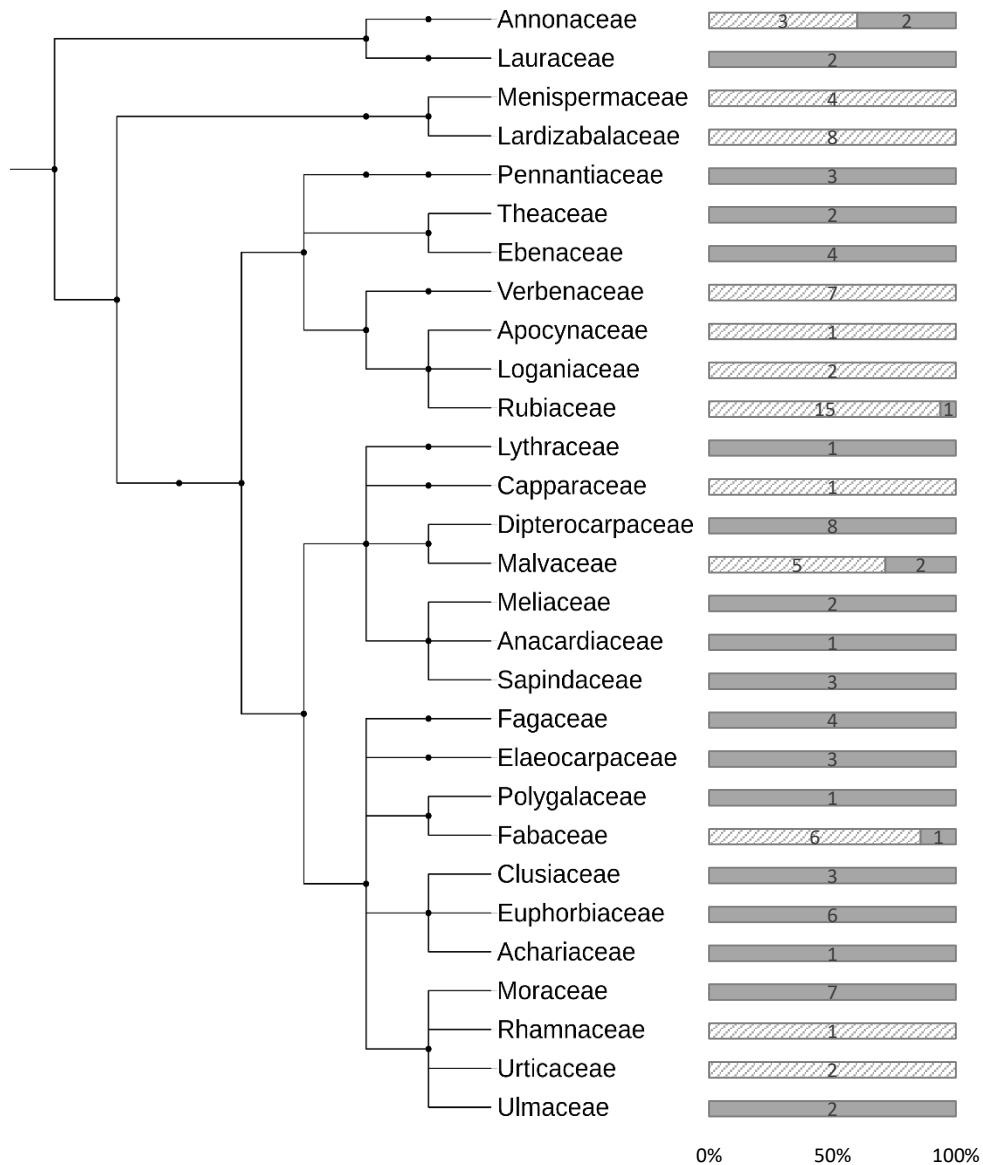
Given the evidence that suggests lianas are an important food source for herbivorous insects it is imperative they are not overlooked when considering ecosystem processes such as herbivory. Further studies specifically addressing differences in herbivory and the diversity and abundance of arthropod assemblages between lianas, their hosts and liana-free trees are needed in order to adequately understand key ecosystem processes and the mechanisms controlling the diversity and distribution of insects in rainforests. In addition detailed studies of herbivory on lianas from the insects ‘perspective’ would

provide some much needed insight. Many of the open questions depend on the identity of the taxa involved, and their associated range, abundance and host specificity.

I conclude by emphasizing the utility of the XTRES canopy crane at Mengla, China, and by implication the wider network of such facilities, opening opportunities for detailed ecological studies of forest canopies.

5.6 APPENDICES

Appendix 5.1 Phylogeny of families sampled created using an online phylogenetic tree generator (Letunic, 2017) based on NCBI taxonomy. The corresponding bar graph represents the number of lianas (white striped) and trees (grey) sampled within each family (figures listed within). Sampled lianas have a wide phylogenetic distribution.



Appendix 5.2 Summary of the number of lianas and trees sampled in each family. Significant differences in herbivory determined by a linear model is indicated by *** p<0.001, **p<0.05, *p<0.1, however, the small sample sizes within families limit the reliability of these results.

Family	LIANAS			TREES			TOTAL		
	No. individuals sampled	Total leaf area loss (%)	Mean leaf area loss (%)	No. individuals sampled	Total leaf area loss (%)	Mean leaf area loss (%)	No. individuals sampled	Total leaf area loss (%)	Mean leaf area loss (%)
Achariaceae				1*	6.16	6.16	1	6.16	6.16
Anacardiaceae				1	2.09	2.09	1	2.09	2.09
Annonaceae	3***	4.06	3.85	2	15.76	11.32	5	9.66	6.84
Apocynaceae	1	4.74	4.74				1	4.74	4.74
Capparaceae	1	1.09	1.09				1	1.09	1.09
Clusiaceae				3	4.08	4.47	3	4.08	4.47
Dipterocarpaceae				8	4.74	4.39	8	4.74	4.39
Ebenaceae				4	6.24	5.47	4	6.24	5.47
Elaeocarpaceae				3	11.74	9.51	3	11.74	9.51
Euphorbiaceae				6	5.96	4.68	6	5.96	4.68
Fabaceae	6	6.02	5.97	1	5.04	5.04	7	5.86	5.84
Fagaceae				4	11.19	11.40	4	11.19	11.40
Lardizabalaceae	8	5.45	5.88				8	5.45	5.88
Lauraceae				2	6.23	6.46	2	6.23	6.46
Loganiaceae	2	3.72	3.87				2	3.72	3.87
Lythraceae				1	2.14	2.14	1	2.14	2.14
Malvaceae	5	17.11	17.15	2	6.33	6.29	7*	14.63	14.05
Meliaceae				2	4.05	3.95	2	4.05	3.95
Menispermaceae	4	4.24	3.92				4	4.24	3.92
Moraceae				7	2.21	2.16	7	2.21	2.16
Pennantiaceae				3	4.54	4.98	3	4.54	4.98
Polygalaceae				1	5.28	5.28	1	5.28	5.28
Rhamnaceae	1	4.56	4.56				1	4.56	4.56
Rubiaceae	15	6.15	5.87	1	2.28	2.28	16	5.81	5.65
Sapindaceae				3	5.23	5.11	3	5.23	5.11
Theaceae				2	4.90	5.47	2	4.90	5.47
Ulmaceae				2	12.27	13.54	2	12.27	13.54
Unknown	34	5.04	5.08	7	6.80	6.48	41	5.42	5.32
Urticaceae	2	2.08	2.09				2	2.08	2.09
Verbenaceae	7	3.56	3.52				7	3.56	3.52
TOTAL	74	6	5.66±0.5	46	6.4	5.76±0.6	129	6.2	5.7±0.4

CHAPTER 6

STATEMENT OF CONTRIBUTION TO CO-AUTHORED PAPER

Chapter 6 is a co-authored paper which has been prepared for publication. The bibliographic details of the co-authored paper, including all authors, are:

Odell E, Stork N, Kitching R (prepared manuscript) Lianas and trees: insect folivory and leaf traits in the mid- and sub-canopy of an Australian subtropical rainforest.

My contribution to this chapter involved all field work and data collection, chemical analyses, statistical analysis and writing of the manuscript. My co-authors are my supervisors and provided guidance with the direction of the project and assisted with the structure and editing of the manuscript.

(Signed) _____

(Date) 10 May 2018

Erica H. Odell

(Countersigned) _____

(Date) 10 May 2018

Supervisor: Roger L. Kitching

(Countersigned) _____

(Date) 10 May 2018

Supervisor: Nigel E. Stork

CHAPTER 6

Lianas and trees: insect folivory and leaf traits in the mid- and sub-canopy of an Australian subtropical rainforest

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6.1 ABSTRACT

The presence of woody climbers, commonly known as lianas, is one of the main features that characterises rainforests. In some forests lianas contribute up to 40% of the above ground green leafy biomass. Such ubiquity and abundance in rainforests indicates a likely functional importance of lianas, particularly for herbivores. Much of our understanding of insect herbivory in rainforests comes from the study of large canopy trees and saplings. However, difference in leaf traits between lianas and trees, including, structural, chemical, and phenological properties, suggest inferences and conclusions about herbivory gathered from data on trees cannot simply be extended to lianas. Information which quantifies the contribution of each functional group, and the roles they play in supporting herbivory is needed. Understanding the role and relative importance of lianas in rainforests may be of wider significance as liana biomass and abundances increase in response to global warming.

In May of 2016 and 2017, leaves were collected from 36 liana individuals and 57 individual trees (29 of which hosted the sampled lianas) in a subtropical rainforest in Queensland, Australia. Leaf damage was quantified from over 100+ leaves for each individual using the software package *ImageJ*, and leaf traits such as leaf toughness, total phenols, and elemental concentrations, were determined.

A total of 14,746 leaves were assessed for herbivory damage and leaf traits. Trait analyses suggest distinct ecophysiological variation in leaf chemistry, leaf structure and herbivory between trees and lianas; and between trees with lianas compared to trees without lianas. Liana leaves had a significantly lower tensile strength than tree leaves, greater concentrations of nitrogen and lower quantities of phenols. Interestingly, leaves from trees associated with lianas had significantly greater foliar nitrogen concentrations and marginally more phosphorus than leaves on trees without lianas. I also found differential responses of herbivory to leaf traits for each of the plant types and a lack of consistency among the variables influencing herbivory on trees and lianas. Herbivory on trees was best predicted by models that included total phenols, nitrogen and leaf toughness whereas herbivory on lianas was most usefully determined by total phenolic, carbon, and phosphorus and nitrogen concentrations. Herbivory on trees hosting lianas were also influenced by the nitrogen concentration of their lianas leaves. I also found

evidence to suggest lianas mitigate herbivory on their host trees, particularly during times of environmental stress.

I conclude that inferences and conclusions about herbivory developed from data on trees cannot simply be extended to lianas. As lianas are important components of forests and the second largest contributor of primary production in these systems, studies specifically investigating the dynamics of herbivory on lianas (and the impacts this has on their hosts and overall ecosystem functioning), are needed to develop a holistic understanding of herbivory in forests.

6.2 INTRODUCTION

One of the key characteristics that define and identify rainforests is the presence of lianas (Richards, 1996, Gentry, 1991, Schnitzer and Bongers, 2002, Schnitzer et al., 2015). These long-stemmed, flexible, woody climbers are often considered to be parasitic in as much as they use other plants as physical scaffolds. However, unlike physiologically parasitic plants, lianas root in the soil, drawing no nutritional resources from their host but simply rely on hosts for architectural support (Schnitzer, 2015). The detrimental impacts of lianas to host trees are well documented. Lianas stunt tree growth (Ingwell et al., 2010) , increase tree mortality (Ingwell et al., 2010, Schnitzer and Bongers, 2002), reduce host tree reproductive output (Putz, 1984), alter gap-phase processes (Schnitzer et al., 2000), inhibit tree regeneration (Alvira et al., 2004), and compete with hosts for both above and below ground resources (García León et al., 2017). However, when liana infestation rates are low (<50% crown infestation) the effects of these harmful impacts upon individual host trees are negligible (Ingwell et al., 2010). From an ecosystem perspective, where the outcomes are measured differently, lianas provide several beneficial functions. For example, the suppression of tree regeneration promotes intermediate levels of disturbance which increases habitat complexity and overall species diversity by allowing other species the opportunity to grow, thereby maintaining optimal levels of interspecies competition (Connell, 1978).

Research into the roles of lianas in ecosystems has increased substantially in recent decades and it is now widely accepted that lianas are important components of tropical rainforests, both numerically and physically (Schnitzer et al., 2015, Tang et al., 2012). They are thought to be the single most important physiognomic feature differentiating tropical from temperate forests (Croat, 1978) and the presence of large lianas often serves as a robust indicator of more mature, undisturbed forest stands (Castello et al., 2017, Campbell, 2016). Lianas, and their non-woody creeper relatives, are abundant in tropical rainforests and make up a substantial proportion of the canopy. Although lianas generally only comprise 20-25% of the diversity of woody species (Gentry, 1991, Putz, 1984, DeWalt et al., 2015), and 5% of the total biomass (Schnitzer et al., 2012, DeWalt and Chave, 2004) of undisturbed tropical forests, they contribute disproportionately to the above ground leaf biomass (AGLB) and leaf litter. In tropical forests, AGLB and leaf litter commonly comprise 30-40% liana leaves (Hladik, 1978, Pragasan and Parthasarathy, 2005). When compared with trees of the same diameter at breast height (DBH), lianas support significantly more leaves per unit basal area (Putz, 1983, Gerwing and Farias, 2000). On Barro

Colorado Island, Panama, the basal area of large (>10cm) lianas increased 4.5% over a 17 year period. This in turn, saw a 50% increase in the relative contribution of liana leaves to overall forest litter production (Wright and Calderón, 2006). Similar increases in the abundance and contribution of lianas to tropical forest ecosystems are widely documented (Schnitzer and Bongers, 2011, Ingwell et al., 2010, Laurance et al., 2014, Yorke et al., 2013, Chave et al., 2008, Phillips et al., 2002, Foster et al., 2008, Allen et al., 2007) and has been linked to a warming global environment.

Insect herbivory

Insect herbivory is important for the structure, functioning and maintenance of healthy forests and affects key ecosystem processes, including; primary production; plant growth, reproduction, survival, nutrient cycling and soil quality. Herbivory dynamics between plants and insects has focused on large canopy trees and saplings (Nooten and Hughes, 2013, Eichhorn et al., 2007, Coley, 1982, Lamarre et al., 2012) whereas interactions occurring between insect assemblages and lianas, and the possible associated impacts on their hosts, have been largely overlooked (but see Ødegaard 2000). Given the substantial contribution of lianas to primary production in forests, their interactions with insect herbivores are likely to be important.

Estimates of foliar herbivory in various ecosystems are available for trees but are rarer for lianas (Kozlov et al., 2015a). Herbivory has been quantified on juvenile liana individuals (Aide and Zimmerman, 1990, de la Cruz and Dirzo, 1987), and on mature lianas following herbivore outbreaks (Van Bael et al., 2004), but comparisons of herbivory on trees and lianas are generally lacking (see Chapter 2).

Leaf traits

Lianas and trees are likely to exhibit distinctly different leaf traits (most notably, nutritional, structural, chemical, and phenological properties). As a consequence, inferences and conclusions about herbivory gathered from data on trees may not be useful for understanding patterns of herbivory on lianas or making generalisations across plant types.

Nutritional quality

Compared with the leaves of trees, lianas should possess greater foliar concentrations of both nitrogen and phosphorus due to differences in life history strategies and prioritisation of resources (Asner and Martin, 2011, Cai and Bongers, 2007, Kazda and Salzer, 2000, Zhu and Cao, 2010). If the nutritional quality of available food plants is an important factor regulating insect herbivory, as suggested by Coley (1983), then we can hypothesise that liana leaves will be a more attractive and a nutritionally more advantageous food source for insects than trees. In turn, this may mitigate the amount of herbivory on host trees (see below).

Structural defences

Contrasts in structural defences between lianas and trees, such as trichomes, raphids and domatia, have not been broadly investigated. However, lower leaf mass per unit area (LMA) and lower levels of foliar chemicals linked to structure (Asner and Martin, 2011) suggest a reduced investment of lianas in structural defences, particularly leaf toughness, compared to trees. Leaf toughness is a useful predictor of herbivory in trees (Kitajima and Poorter, 2010, Stiegel et al., 2017, Carmona et al., 2011) but may not be useful for modelling herbivory on species with soft leaves such as lianas.

Chemical defences

Anti-herbivore defence chemicals may make plants less palatable and anti-nutritive (Mithofer and Boland, 2012, Coley, 1983). Liana leaves have significantly fewer defence chemicals compared with trees (Asner and Martin, 2011). Lower levels of biofoliar chemical defences pose a reduced threat to herbivores and may influence food preferences and patterns in herbivory. I suggest lianas may be a more palatable and nutritive food source for herbivores and patterns of herbivory may differ between lianas and trees.

Phenological availability

The quantitative and qualitative availability of plant resources play a key role in herbivory. Rates of leaf turnover are reported to be greater in lianas compared with those of trees (Zhu and Cao, 2010). Leaf production in lianas is not limited to the wet season and occurs throughout the year and times of environmental stress (Pichon et al., 2015). These phenological characteristics result in the availability of new, palatable leaves throughout the year and suggest lianas are a reliable food source, particularly for insect species that need to feed for extended periods throughout the year (Janzen, 1984).

Liana-host interactions and insect herbivory

It is becoming increasingly apparent that plant-herbivore interactions strongly depend, in a predictable way, on the community context in which they occur (Björkman and Hambäck, 2003, Stiling et al., 2003, Baraza et al., 2006, Strauss and Irwin, 2004). The impacts of tree-tree spatial proximity may differ to those of between lianas and their host trees due to differences in leaf traits, below-ground resource competition and degree of environmental buffering. Impacts of liana-host associations, such as those on reproduction and mortality, are well documented (Wright et al., 2005, Ingwell et al., 2010, Putz, 1984, Stevens, 1987). In contrast, little information is available on how liana-host associations affect herbivory processes. Foaham (2002) found that insect herbivory on tree leaves was greatest in forests where lianas had been removed. Similarly, Piirainen et al. (2014) found that tree leaf herbivory was lowest in forest gaps where liana infestation was high. These studies suggest lianas may help to reduce levels of host leaf

herbivory. However, studies specifically addressing this question at the level of the community are lacking.

In this paper I address the variations in leaf traits between trees and lianas; identify correlations between herbivory, leaf traits, and plant type; and discuss the associational impacts between host trees and their lianas.

6.3 METHODS

Study site

Lamington National Park lies roughly 100km south of Brisbane in south-east Queensland and covers an area of 20,600 hectares. The Park is one of the largest remaining areas of continuous sub-tropical rainforests in Australia and is part of the World Heritage Gondwanan Rainforest. This region forms part of the Macpherson range which straddles the remnants of the Mt Warning shield volcano's erosion caldera (Stevens, 1977) and are surrounded by drier forests. The historical complexity of geological activity in the region has produced high levels of environmental heterogeneity, creating a diverse mosaic of topography and microclimates ideal for supporting both temperate and sub-tropical species. Elements of northern and southern biota are found here in a region known as the McPherson-Macleay overlap zone (Burbidge, 1960). These two factors combined to produce the high levels of structural and biotic complexity seen in the region. The floristics of the park have been detailed by McDonald and Thomas (1990).

The climate of South-east Queensland has distinct summer-autumn wet seasons and cool, dry winters (June-August). Temperatures of Lamington National Park commonly reach 35°C in the summer and occasionally will dip as low as 0°C in the winter. Above average temperatures for 2015 and 2016 (Bureau of Meteorology, 2016a, Bureau of Meteorology, 2017a) with an average summer temperature of 30°C and 21.5°C in the winter (data for the whole of 2017 are not yet publically available). Regional annual rainfall averaged 1563mm between 1995 and 2016; 2016-2017 saw below average rainfall with 2016 being considered a ‘drought year’. The last dry period for the park was from 2000-2007 and it had entered another dry, El Nino period as of 2014.

Lamington National Park is an ideal location for this study for three primary reasons. 1) The regional floristics are well known, 2) arboreal mammals and non-insectivorous herbivores are largely absent, and 3) most of the plant species have been DNA barcoded (Shapcott et al., 2015).

Most of the park comprises complex notophyll vine forest in the lower elevations to simple microphyll fern forest above 950masl. This continuous forest is part of the patchwork of post-glacial rainforest remnants surviving along the eastern seaboard of Australia from Cape York to Tasmania (Webb, 1978). This study was conducted within a one-hectare permanent reference plot of complex notophyll vine forest

($28^{\circ}13'S$, $153^{\circ}07'N$, 900m asl) at Lamington National Park (see Figure 6.1). The floristics of the plot is well known and the woody-plant diversity was first documented in 1995 by Laidlaw et al (2000). The plot has since been re-surveyed twice; once by Tang (2005) in 2005 and again in 2015 (detailed in Chapter 3 of this thesis). Seventy-six tree species are found within the one hectare plot along with 19 species of lianas. The plot's stand structure is dominated by sub-canopy elements with half of all stems recorded having a diameter at breast height (DBH) less than 10cm. The two most abundant species on the plot, *Actephila lindleyii* (Phyllanthaceae) and *Atractocarpus benthamianus* (Rubiaceae), fall into this category. The canopy layer ranges from 20-40m above the ground and is occupied primarily by *Argyrodendron actinophyllum*, *A. trifoliatum* (both Flacourtiaceae), *Ackama paniculosa* (Cunoniaceae) and *Pseudoweinmannia lachnocarpus* (Cunoniaceae). These four species form the major elements of the canopy along with two species of liana: *Melodinus australis* (Apocynaceae) and *Austrosteenisia glabristyla* (Fabaceae). The understory is comprised of a dense covering of seedlings and ferns. The liana, *Cephalaria cephalobotrys* (Araliaceae) proliferates in this layer.



Figure 6.1 Map of the 1 ha plot located in subtropical rainforest at Lamington National Park ($28^{\circ}13'S$, $153^{\circ}07'N$, 900m asl)

Leaf Collection

Mature leaves were collected during May 2016 after the summer season when insects are most active, but before the seasonal peak in leaf fall. This was done so to ensure that the entire season's insectivorous feeding history was captured in the samples.

Leaf samples from trees with and without lianas and the lianas they supported were obtained from the mid-canopy using tree climbing techniques and from the sub-canopy (approximately 4-8m above the ground) with the assistance of a long reach pruning pole. Sampled trees were at least 10m apart to limit issues associated with pseudo-replication. For the most part, folivorous insects, particularly juvenile morphs, have fairly limited foraging ranges (Heinrich, 1979, Hassell and Southwood, 1978, Jones, 1977, Cain et al., 1985, Harcourt, 1961). An interval of at least 10m between sampled individuals should be sufficient to mitigate this effect. A balanced sampling design was not possible due to the random nature and availability of accessible species. To overcome the unbalanced sampling approach but still achieve a statistically valid result, it was decided to have a larger sample size for trees and lianas. Replicate samples within individual plant species were obtained when possible.

Measurements of leaf toughness were taken within an hour of removal (see below) and a portion of leaves from each sample was immediately placed inside a zip lock bag and chilled *in situ* before being transferred to a freezer for later chemical analyses.

In May 2017 sampling focussed on the two most dominant sub-canopy species of tree (*Actephila lindleyi* and *Atractocarpus benthamianus*) and the lianas they supported, when present. Herbivory was measured on leaves from ten individuals of each species were sampled; five supporting a single liana and five that did not. These individuals were not analysed for their structural or chemical properties, although a sub-sample of leaves have been preserved for possible future analysis.

Leaf toughness

Leaf toughness measures were taken in field within an hour of removal from the plant. A Geotester pocket penetrometer with a 2.5mm probe was used to approximate the unconfined compressive strength of leaves. The accuracy of these instruments can be variable depending on; the user, the angle at which the device is held, the angle at which the probe penetrates the leaf and the speed at which the device is pressed down at a constant speed. To reduce such variation, measurement methodology was standardized by fitting the penetrometer into a bench press and placing it on a flat surface to take measurements. Leaves were positioned on the stage of the bench press and firmly held in place. The penetrometer was gently pushed down on the upper surface of the leaf until it was pierced. Measurements were taken by the same person at four different points on the leaf; the tip, the base, near the central vein, and near the edge, while making sure to avoid main veins. Leaf toughness measurements were performed on three undamaged mature leaves from each individual.

Herbivory

Leaf samples were pressed and dried before being scanned using a Cannon LiDE 120 scanner. Images were then processed in Adobe Photoshop CS3 Extended to remove the background, shadows and any unwanted pixels. In areas where leaf margins had incurred herbivore damage, the missing margin was approximated and drawn in. Herbivore damage was calculated using the software program *Image J* (Rasband, 2016). A macro subroutine was used to load the images onto the software platform, convert them to black and white formats, and to measure the amount of leaf area when leaf damage was included and excluded. Herbivory was measured as percent leaf area lost per individual and was calculated by subtracting leaf area _{damage excluded} from leaf area _{damage included}. All obvious forms of insect herbivory damage were included in the study (see Figure 6.2). Different damage types (such as chewing, mining and skeletisation) were not quantified separately and were considered together in the analysis. All forms of damage and leaf loss were assumed to be inflicted by insect herbivores as are no arboreal vertebrate herbivores in this region of Australia.

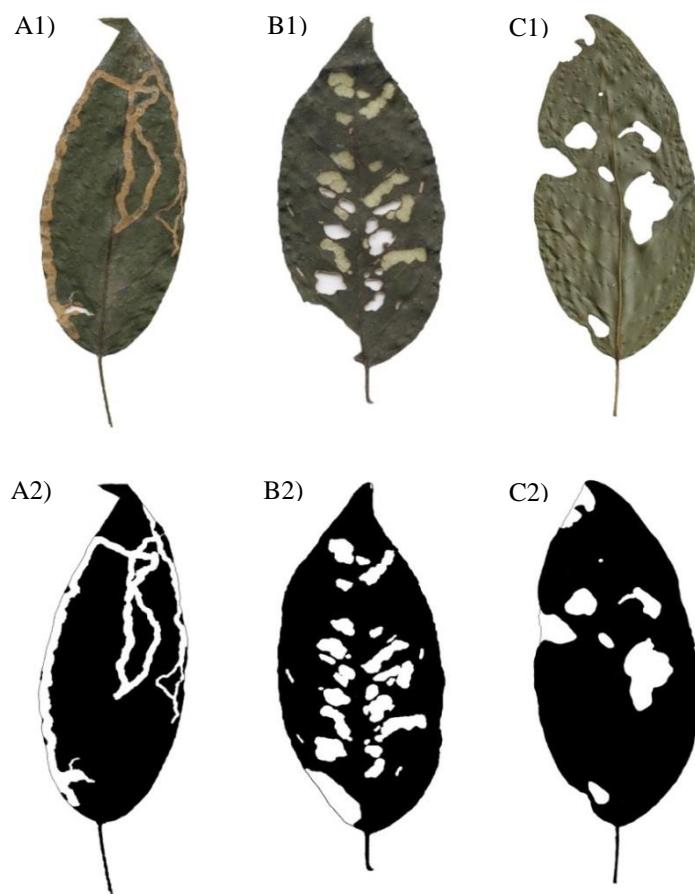


Figure 6.2 Example of three main damage types, A1) mining, B1) skeletonising, C1) chewing, and the processed image (A2, B2, C2) from which leaf area loss was calculated.

Chemical analyses

Plant materials collected for chemical analysis were immediately bagged and placed on ice in the field and transferred to a freezer upon return to the laboratory.

Nitrogen and Carbon

Total carbon and nitrogen in samples were determined using an automated dry combustion, Dumas method (Saint-Denis and Goupy, 2004) by Leco TruMac CN- analyzer, Leco Corporation, USA. Plant material dried in an oven at 60°C for 72 hours were ground and weighed portions loaded into the machine for analysis. Samples were combusted at 1250°C.

Phosphorus

Inductively coupled plasma mass spectrometry was used to determine total phosphorus in the collected leaf samples. Plant material was dried in an oven at 60°C for 72 hours until completely dry and milled into a fine powder. Weighed portions (0.5g) of the ground samples were placed into digestion tubes with 8ml of concentrated nitric acid and mixed thoroughly with a vortex mixer. Samples were placed into a digestion rack and left to predigest for 24 hours. Predigested samples were combined with 2ml of concentrated perchloric acid and exposed to a digestion block temperature sequence. The temperature sequence for the acid digestion block of leaf samples is 120 minutes at 80°C, 60 minutes at 125°C, 18 minutes at 180°C and 18 minutes at 205°C, after which samples were then left to cool overnight. Acid digested samples were flushed into 50ml volumetric flasks and made to volume with deionised water. Diluted samples were then filtered into flasks using Whatman (No 42) filter papers. Samples were then sent to a laboratory for total phosphorus determination on a Shimadzu UV-spectrophotometer measured at a wavelength of 880nm.

Phenolics

Total phenolic content of leaves was determined spectrophotometrically using the Folin Ciocalteu method for total phenol determination (Folin and Ciocalteu, 1927). This method is routinely used for the determination of phenolic content in leaves (Ainsworth and Gillespie, 2007, Sengul et al., 2009, Sulaiman and Balachandran, 2012, Singleton et al., 1999). Plant materials were freeze dried and ground to a fine powder. Phenols were extracted from 0.5g of ground leaf matter and mixed with 50ml of an 80:20 ethanol:water solution. Samples were then placed on to an orbital shaker for 1hour. The extracts were filtered through Whatman (No. 1) filter paper and diluted 10-fold with deionised water. Aliquots (1ml) of the diluted sample were transferred to test tubes and mixed with 5ml of 10% v/v dilution of Folin Ciocalteu reagent and 4ml of 7.5% w/v Na₂CO₃. The test tubes were left to develop for 1 hour at room temperature, after which the absorbance was measured at 765nm. The concentration of phenols in the test

samples were derived from a calibration curve generated using known concentrations of gallic acid and are expressed as gallic acid equivalent values (GAE).

Data analysis

Exploratory analysis of the data was performed using box plots where trees were assigned one of two treatments to assess the effect of lianas to hosts; 1) trees without lianas, and 2) trees with lianas.

Correlations between percent leaf loss, leaf traits and plant type was tested by fitting generalised linear models (GLM) to the data in R (RStudio, 2016). Response variables were standardised into proportions (with the exception of leaf toughness), with non-normally distributed errors. For non-normally distributed data, such as this, GLMs can be usefully applied to build regression models while retaining the integrity of the response variables (McCullagh and Nelder, 1983). Most appropriate models were determined based on whichever generated the lowest AIC values.

6.4 RESULTS

A total of 10,839 leaves in 2016 and 3,907 in 2017 were assessed for herbivory loss in this study. In 2016 61 plants (n=36 trees and 25 lianas) were samples and 30 plants in 2017 (n=20 trees and 10 lianas). Of the 37 trees sampled in 2016; 18 were canopy individuals and 19 were associated with one or more lianas. This first round of samples aimed to include a wider diversity of tree species to develop a more general ecosystem wide approximation of herbivory. In total, samples were collected from 11 species of trees and 14 species of liana in 2016. In 2017, sampling was limited to the two most common species of trees to better understand the impact of liana/host associations and herbivory. Leaves were collected from 10 *Actephila lindleyii* (5 with lianas and 5 without), 10 *Atractocarpus benthamianus* (5 with lianas and 5 without), and 10 associated lianas.

Herbivory

Mean leaf area lost was $4.7 \pm 0.5\%$ and $4.3 \pm 1.0\%$ for lianas in 2016 and 2017 respectively. Trees had a higher mean leaf area lost at $6.1 \pm 0.7\text{--}1.2\%$ for both years. This is approximately a 32% difference in herbivory between the two plant groups. However, this difference was only formally significant ($p < 0.01$, $n = 61$) for the 2016 samples which were much larger than those of 2017 as indicated above (see Figure 6.3 and Table 6.1). In general, the presence of a liana had a negligible and insignificant impact on the level of herbivory upon the host ($p > 0.05$, $n = 56$).

The relationship between lianas and host trees and the impact to herbivory was investigated further in two species; *Atractocarpus benthamianus* and *Actephila lindleyii*.

Atractocarpus benthamianus

Throughout both 2016 and 2017 *A. benthamianus* individuals without lianas lost significantly more leaf area to insect herbivores than individuals with lianas ($p<0.05$, $n=18$). GLM analyses found the relationship between liana herbivory and tree herbivory significant ($p<0.05$, $n=20$). As liana herbivory increased, tree herbivory decreased. (see Figure 6. and Table 6.1)

Actephila lindleyii

During the first sampling season, *A. lindleyii* individuals associated with a liana were consumed by insect herbivores marginally less than their counterparts without lianas ($p<0.1$, $n=9$). During the following season however, this pattern was reversed; individuals with lianas incurred more herbivore damage than individuals without ($p<0.05$, $n=10$). Out of the 5 *A. lindleyii* associated with lianas assessed in 2016, only one incurred greater levels of herbivory than its associated liana. The following season (2017), this pattern was also reversed (see Figure 6.4 and Table 6.2).

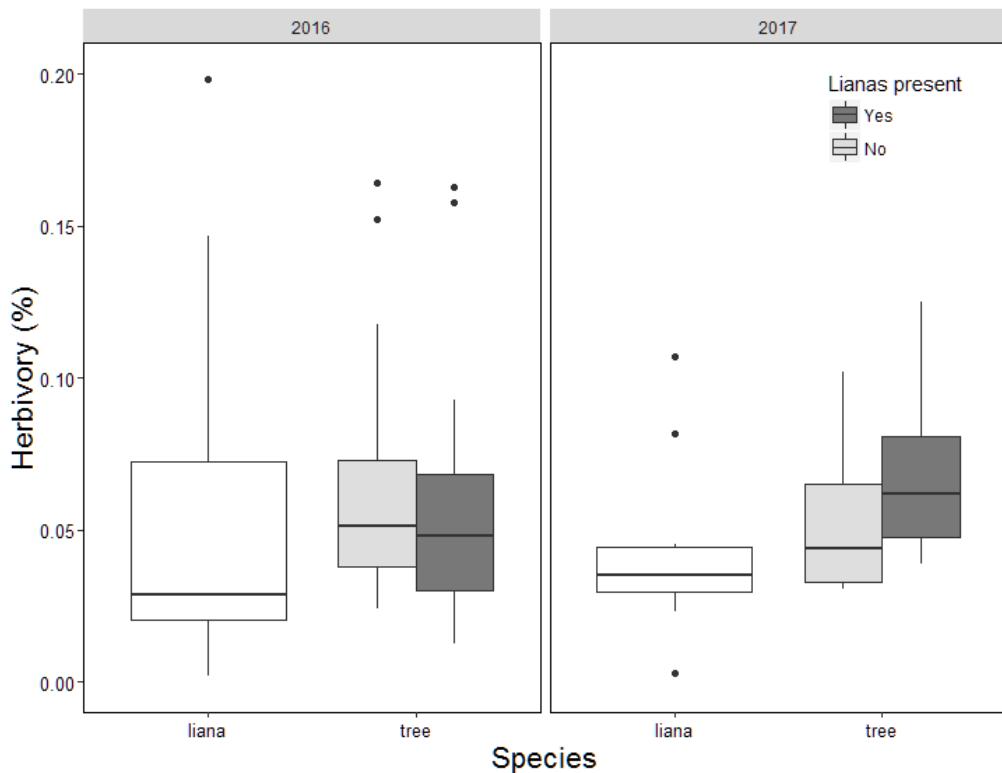


Figure 6.3 Total herbivory for 2016, 2017 and the two years combined. Herbivory is expressed as a percentage of leaf area lost or damaged. Lianas (white), trees with a liana (dark grey), trees without a liana (light grey). See Table 6.1 for additional information.

Table 6.1 Summary of herbivory for A) trees and lianas and B) trees with and without lianas based on GLM.
Significant results are in bold ($p < 0.05$).

A	Mean lianas (%)	Mean trees (%)	p
2016	4.7 ± 0.5 (n=25)	6.1 ± 0.7 (n=36)	0.004
2017	4.3 ± 1.0 (n=10)	6.1 ± 1.2 (n=20)	0.2

B	Mean with lianas (%)	Mean without lianas (%)	p
2016	5.7 ± 0.9 (n= 18)	6.5 ± 0.6 (n= 18)	0.278
2017	7.0 ± 1.2 (n=10)	5.2 ± 0.9 (n=10)	0.274

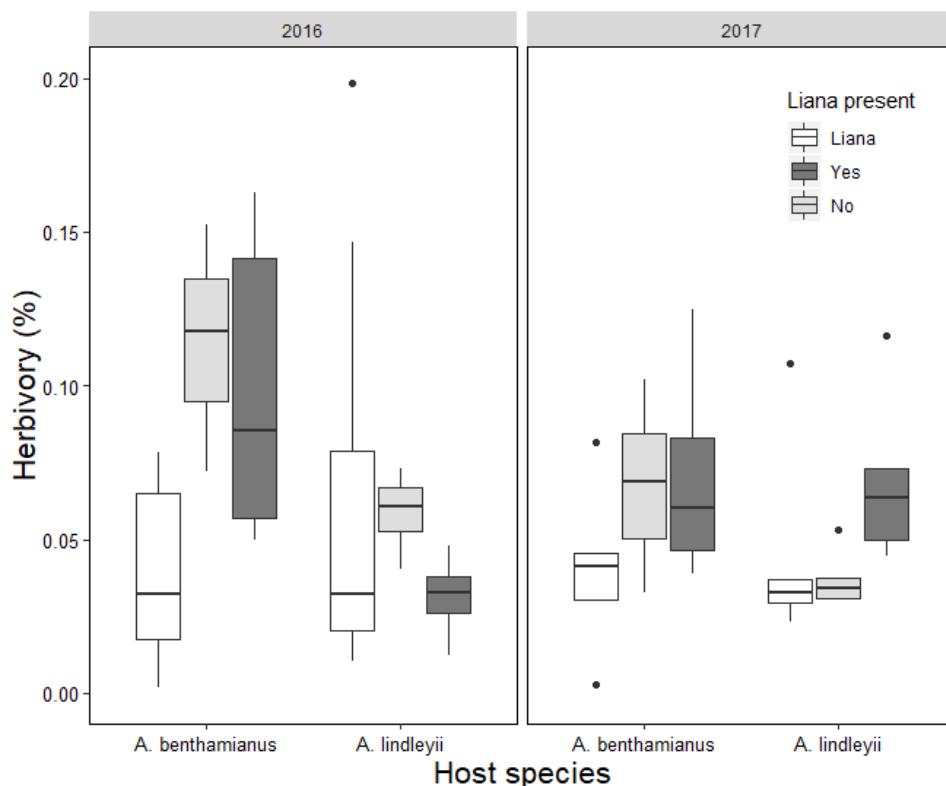


Figure 6.4 Box plots of leaf herbivory on *A. lindleyii* and *A. benthamianus* in 2016, 2017. Herbivory is expressed as a percentage of leaf area lost or damaged. Lianas (white), trees with a liana (light grey), trees without a liana (dark grey). See Table 6.2 for additional information.

Table 6.2 Summary of differences in leaf herbivory for *A. lindleyii* and *A. benthamianus* between trees with and without lianas based on GLM. Significant results are shown in bold ($p<0.05$).

Species	Year	Mean with lianas (%)	Mean without lianas (%)	p
<i>A. lindleyii</i>	2016	3.29 ± 1.8 (n=5)	5.86 ± 1.3 (n=4)	0.07
	2017	6.95 ± 2.0 (n=5)	3.71 ± 1.5 (n=5)	0.03
<i>A. benthamianus</i>	2016	8.67 ± 1.6 (n=5)	11.39 ± 1.2 (n=3)	0.23
	2017	7.08 ± 1.5 (n=5)	6.77 ± 1.1 (n=5)	0.85

Leaf traits

Nitrogen

Concentrations of nitrogen in tree and liana leaves did not differ significantly (GLM, $p>0.05$, $n=61$). Interestingly however, nitrogen concentrations in the leaves of trees with lianas were significantly greater than leaves from trees without lianas ($p<0.05$) (see Figure 6.5 and Table 6.3). When trees with lianas were excluded from analysis the difference between nitrogen concentrations of liana and tree leaves became significant.

Foliar concentrations of nitrogen were an important predictor of leaf area removed by herbivory and interacted significantly with plant type ($p<0.05$) (see Figure 6.6 and Table 6.4).

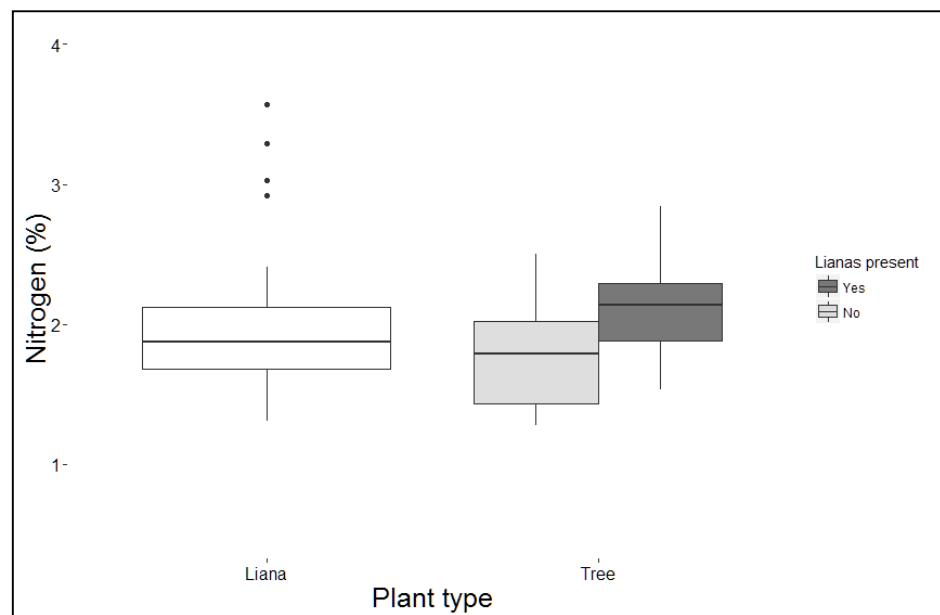


Figure 6.5 Box plots of total foliar nitrogen concentration separated into lianas (white), and trees with (dark grey) and without (light grey) lianas determined from the May 2016 samples. Concentrations of nitrogen did not differ significantly between tree and liana leaves ($p>0.05$), but differed significantly between trees with and trees without lianas ($p<0.05$).

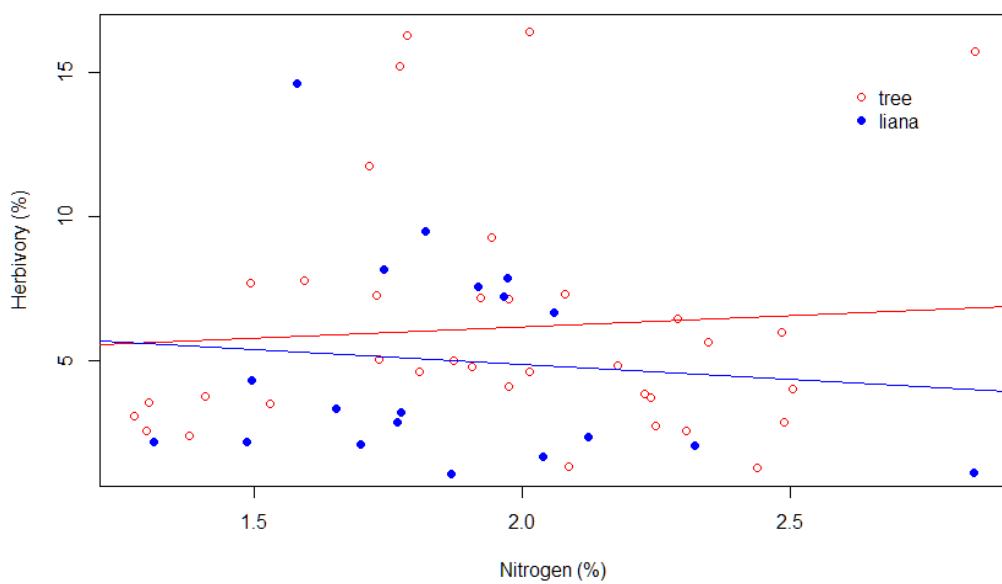


Figure 6.6 Linear relationships of foliar nitrogen concentrations to percent leaf area removed by herbivory in lianas (blue) and trees (red). Herbivory correlated significantly to leaf nitrogen content and showed a significant interaction effect with plant type ($p<0.05$).

Carbon

Mean concentrations of foliar carbon was greater in lianas than in tree leaves, but not statistically significant (GLM, $p>0.05$, $n=61$) (see Figure 6.7 and Table 6.3). Foliar concentrations of carbon corresponded to the level of herbivory in both plant types (GLM, $p<0.05$, $n=61$); although no interaction affect was observed (see Figure 6.8 and Table 6.4).

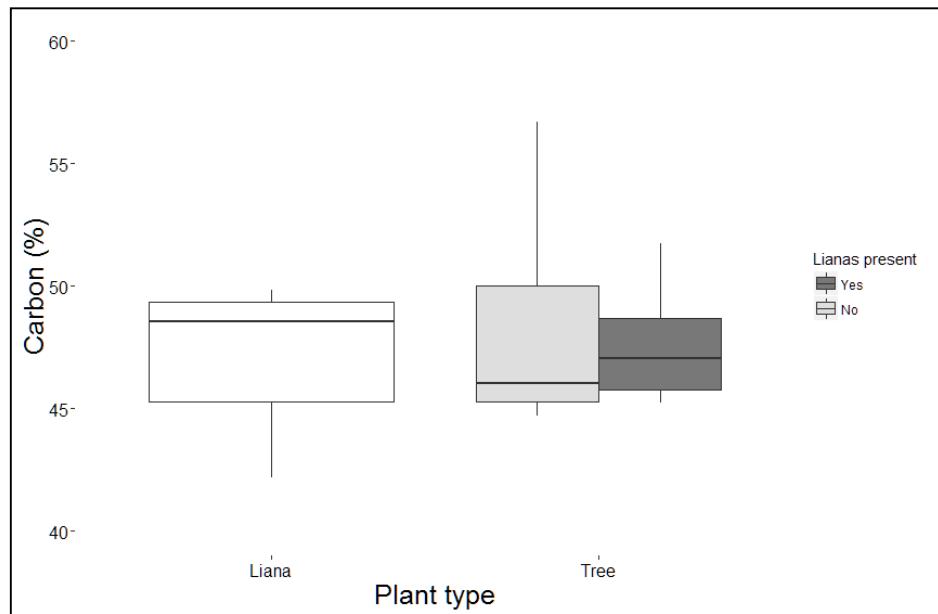


Figure 6.7 Box plots of total foliar carbon concentration separated into lianas (white), and trees with (dark grey) and without (light grey) lianas determined from the May 2016 samples. Carbon did not differ significantly between liana and tree leaves ($p>0.05$), nor between trees with and without lianas ($p>0.05$).

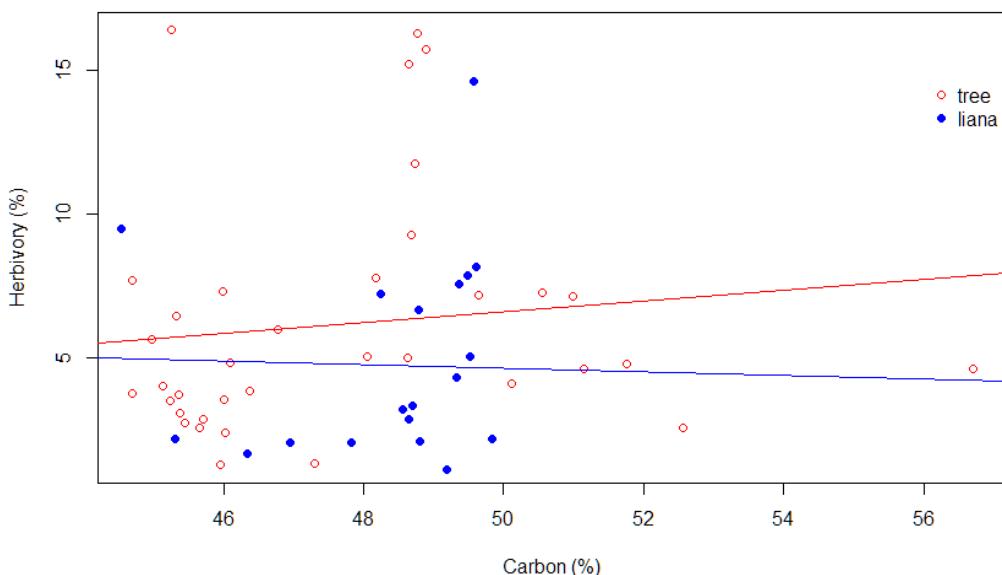


Figure 6.8 Linear relationships of foliar carbon concentrations to leaf area lost to herbivory in lianas (blue) and trees (red). Herbivory was shown to significantly correlate to foliar carbon concentration ($p<0.05$).

Leaf Toughness

Lianas and trees had highly significant differences in the toughness of their leaves (GLM, $p<0.01$, $n=61$), with liana leaves having a considerably lower tensile strength than tree leaves (see Figure 6.9 and Table 6.3). GLM analyses showed a strong relationship between the leaf toughness and levels of herbivory in trees ($p<0.001$, $n=36$) but not in lianas (see Figure 6.10 and Table 6.4). A significant interaction between leaf toughness and plant type was observed when predicting herbivory ($p<0.05$, $n=61$).

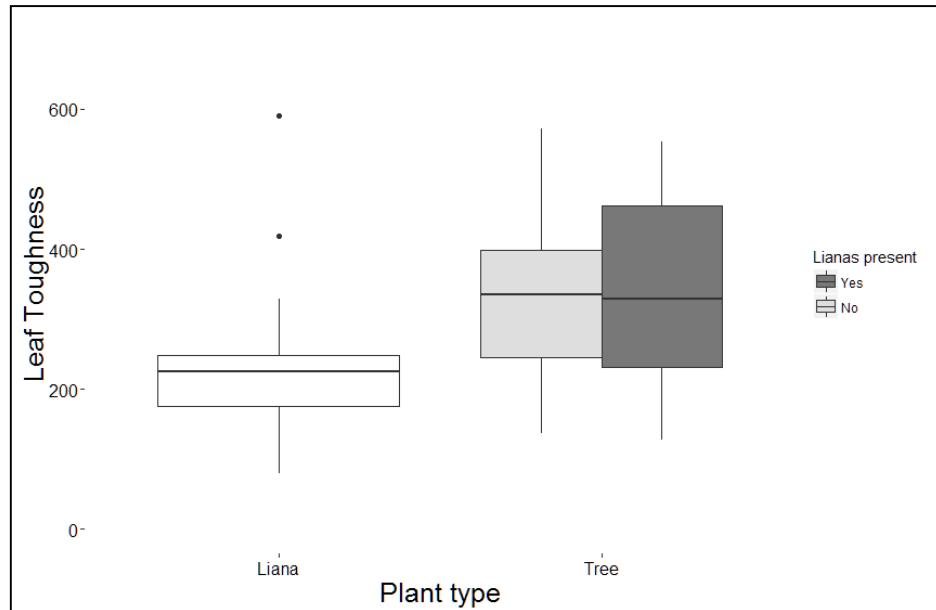


Figure 6.9 Box plots of total foliar leaf toughness concentration separated into lianas (white), and trees with (dark grey) and without (light grey) lianas determined from the May 2016 samples. Leaves from lianas were significantly softer than leaves from trees ($p<0.05$).

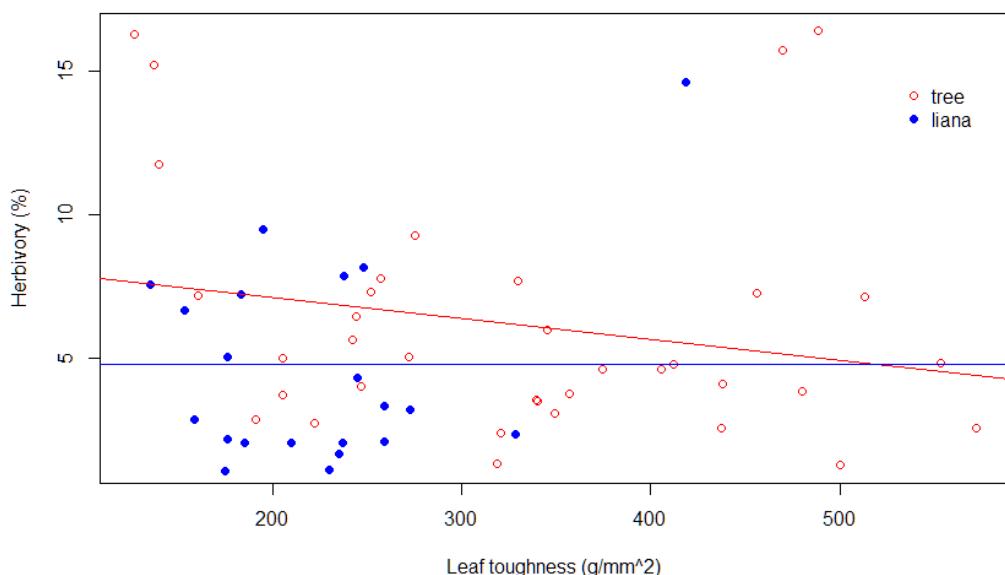


Figure 6.10 Linear relationships of foliar leaf toughness concentrations to leaf area lost to herbivory in lianas (blue) and trees (red). Leaf toughness correlated strongly to herbivory in trees ($p<0.05$) but not in lianas ($p>0.05$).

Phenols (chemical defences)

Foliar phenolic concentrations did not differ significantly between lianas and trees (GLM, $p>0.05$, $n=61$), however there were distinct differences in trends between the two groups that may be significant with a larger sample size. Liana leaves typically possessed lower concentrations of phenols and tended to have lower variability in their ranges. There was also a trend for trees with lianas to have lower levels of phenols than trees without lianas. When trees with lianas were removed from the analysis, differences in foliar phenolic concentrations became significant, albeit weakly ($p<0.1$) (see Figure 6.11 and Table 6.3).

Phenolic concentrations of leaves were significantly correlated to levels of herbivory and interacted significantly with plant type ($p<0.05$) (see Figure 6.12 and Table 6.4). Overall, phenolic concentration was more useful in predicting herbivory on trees than on lianas.

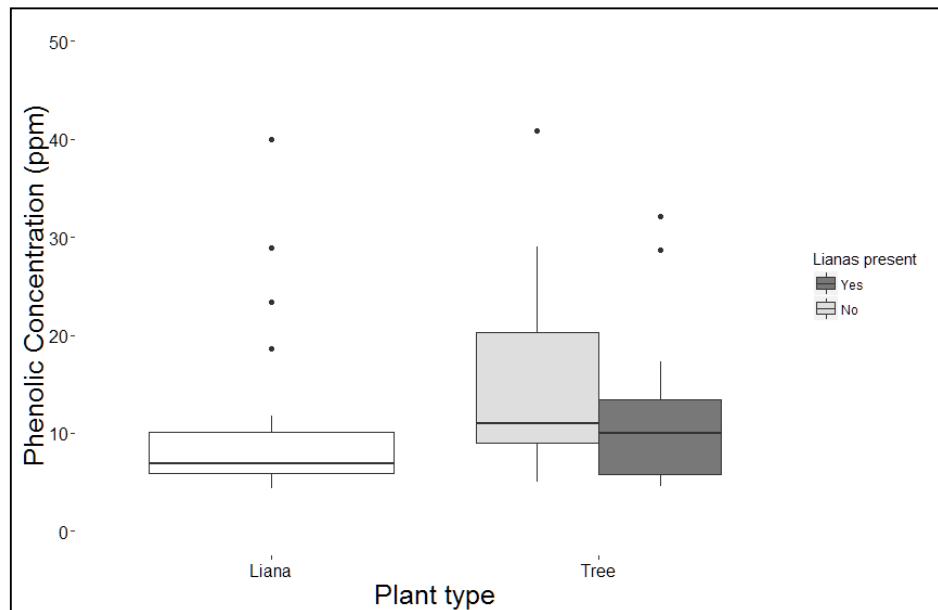


Figure 6.11 Box plots of total foliar phenol concentration separated into lianas (white), and trees with (dark grey) and without (light grey) lianas determined from the May 2016 samples. Phenolics did not differ significantly between liana and tree leaves ($p>0.05$), although when trees with lianas were removed from the analysis a significant difference was shown ($p<0.05$).

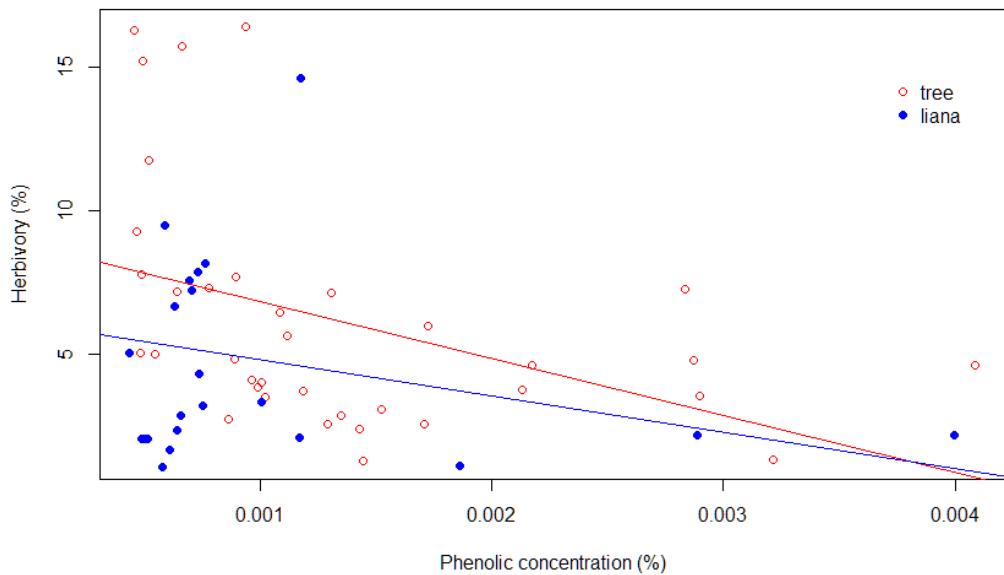


Figure 6.12 Linear relationships of foliar phenol concentrations to leaf area removed by herbivory in lianas (blue) and trees (red). Phenolic concentrations of leaves were significantly correlated to levels of herbivory and interacted significantly with plant type ($p<0.05$).

Phosphorus

Mean leaf phosphorus concentration between lianas and trees did not differ significantly (GLM, $p>0.05$, $n=61$). Trees with and without lianas exhibited a marginally significant difference in the concentration of phosphorus in their leaves ($p<0.1$) (see Figure 6.13 and Table 6.3). Foliar phosphorus concentration was significantly correlated to the level of herbivory observed in trees ($p<0.01$) but not in lianas ($p>0.05$) (see Figure 6.14 and Table 6.4).

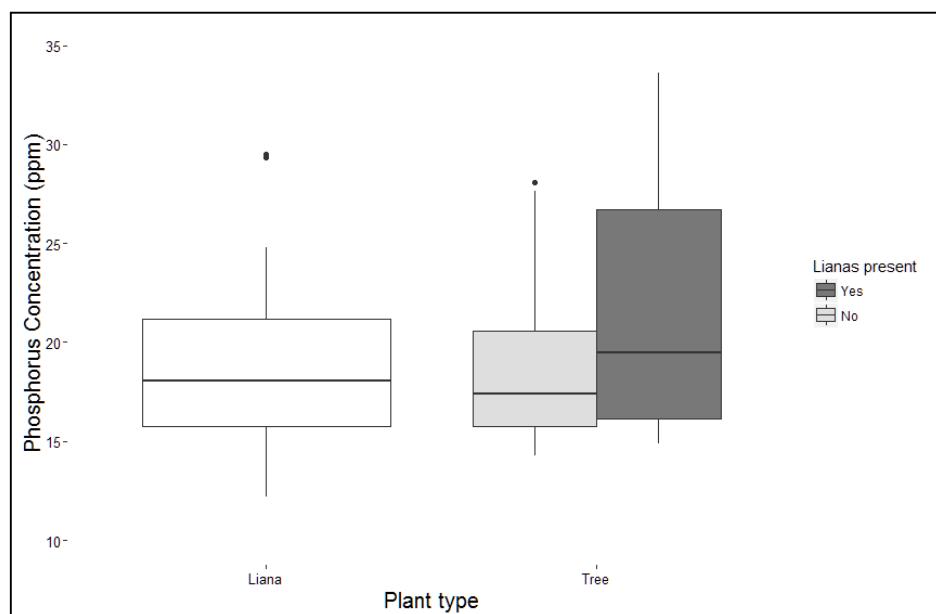


Figure 6.13 Box plots of total foliar phosphorus concentration separated into lianas (white), and trees with (dark grey) and without (light grey) lianas determined from the May 2016 samples. Phosphorus concentrations in the leaves of lianas and trees did not differ significantly.

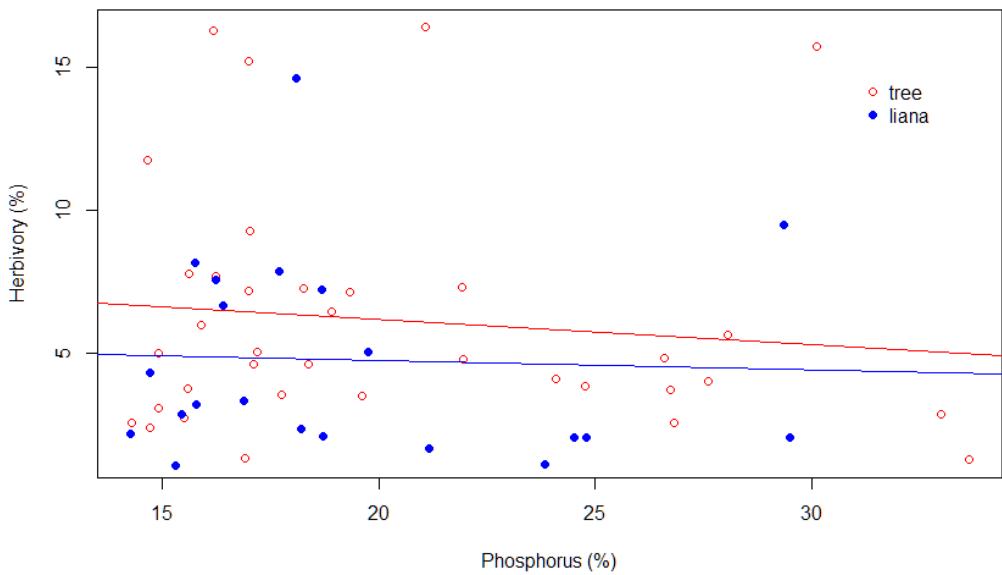


Figure 6.14 Linear relationships of foliar phosphorus concentrations to leaf area removed by herbivory in lianas (blue) and trees (red). Phosphorus concentrations of leaves were significantly correlated to herbivory in trees ($p<0.05$), but not in lianas ($p>0.05$).

Table 6.3 GLM output of differences between leaf traits of A) lianas ($n=25$) and trees ($n=36$), and B) trees with ($n=18$) and without lianas ($n=18$). Significant outcomes are in bold ($p<0.05$).

* $p<0.05$ when trees with lianas excluded from comparisons

** $p<0.1$ when trees with lianas excluded from comparisons

A	p (liana vs. tree)	Mean (liana)	Mean (tree)	Effect size
Carbon	0.91	47.58 ± 0.5	47.65 ± 0.7	-0.03 (small)
Nitrogen	0.26*	2.09 ± 0.1	1.95 ± 0.1	0.30 (small)
Leaf Toughness	<0.001* (tree > liana)	230.53 ± 23.0	332.79 ± 30.0	-0.89 (large)
Phenols	0.16**	10.24 ± 1.8	13.47 ± 2.3	-0.36 (small)
Phosphorus	0.35	18.98 ± 1.0	19.81 ± 1.3	-0.14 (small)

B	p (with vs. without)	Mean (without)	Mean (with)	Effect size
Carbon	0.64	47.87 ± 0.6	47.44 ± 0.9	0.15 (small)
Nitrogen	0.02 (with > without)	1.80 ± 0.09	2.11 ± 0.1	-0.85 (large)
Leaf Toughness	0.72	325.23 ± 29.6	340.35 ± 41.9	-0.12 (small)
Phenols	0.27	15.12 ± 2.1	11.81 ± 2.9	0.38 (small)
Phosphorus	0.1	18.75 ± 1.3	20.87 ± 1.8	-0.32 (small)

Table 6.4 Output from GLM analyses correlating leaf traits to herbivory and plant type (liana n=25, tree n=36).

Nitrogen, leaf toughness and phenols interacted significantly with plant type. The model that best predicted herbivory included these 3 variables along with plant type. Significant outcomes are in bold ($p < 0.05$).

A	p (type:liana, n=25)	p (type:tree, n=36)	Interaction
Carbon	0.014	0.003	no
Nitrogen	0.025	0.079	0.015
Leaf Toughness	0.128	0.003	0.039
Phenols	0.236	0.0002	0.051
Phosphorus	0.303	0.003	no

Leaf traits and herbivory

Leaf traits that best predicted herbivory were different for lianas and trees under generalised linear models. Herbivory on lianas was most usefully determined by total phenols, phosphorus, carbon and nitrogen concentrations. Herbivory on trees, in contrast, was best predicted using models that incorporated total phenols and nitrogen concentration, and leaf toughness. However when predicting herbivory on trees hosting lianas the most useful variables were tree leaf toughness and phenolic concentration, and liana nitrogen concentration.

6.5 DISCUSSION

Herbivory

Leaf herbivory was inconsistent across years with several differences in herbivory between different plant types and between host and non-host trees being significant in 2016 but not in 2017. Leaf area loss on lianas accounted for 33% and 20% of total herbivory in 2016 and 2017, respectively. Liana species richness, however, only accounted for 20% of the woody species diversity in the one hectare plot. Leaf area loss may reflect the availability of total above ground leaf biomass of each plant type, however this metric was not determined in this study.

From 2016 to 2017, Australia experienced a change in ENSO events from El Nino to La Nina, which resulted in changes to the temperature and rainfall regime. Between January and May, South-east Queensland received below average rainfall in 2016, but received above average rainfall in 2017 (Bureau of Meteorology, 2016b, Bureau of Meteorology, 2017b). Monthly temperatures were above average during January to May in both 2016 and 2017 (Bureau of Meteorology, 2016b, Bureau of Meteorology, 2017b). These shifts in weather patterns would have affected both insect and plant population dynamics resulting in variation of herbivory across years.

Insect herbivore populations fluctuate accordingly with weather patterns. Drought reduces growth, fecundity and increases mortality (Koricheva et al., 1998). During times of environmental stress, chewing insects are reported to perform better on stressed fast growing plants (i.e. lianas) than on stressed slow growing plants (i.e. trees) (Koricheva et al., 1998). The differential performance of chewing insects on fast and slow growing plants may reflect stress induced changes in leaf chemistry (such as nitrogen and secondary metabolites), or stress-related changes in the nutritional requirements of the insects themselves. Consequently, in the present study insects feeding on lianas may have responded better to below average rainfall than insect populations feeding on trees which may explain the greater contribution of lianas to herbivory in 2016 compared to 2017.

Similarly, water availability drives leaf production in many species. During times of water stress, leaf production is suppressed (Farooq et al., 2012) and triggered when drought, or the dry season is broken (Larcher, 2003, Borchert et al., 2002, Wolda, 1978). However this phenomenon is commonly documented in tree species and may not be a primary mechanism underlying leaf phenology in lianas (Pichon et al., 2015). Lianas continue to grow during dry periods (Schnitzer, 2005) and under experimental drought and water stressed conditions show no change in leaf production (Cavelier et al., 1999, Schnitzer and Bongers, 2011). These phenological traits underlie the quantitative and qualitative availability of liana leaves throughout the year and may be of use to herbivores as an alternative food source during times of scarcity or environmental stress, such as those observed in 2016. This may in part explain the disproportionate herbivory observed on lianas in 2016 compared to their overall contribution diversity. As 2017 was not limited by precipitation, the utilization of lianas in herbivory more closely resembled their contribution to diversity.

It is important to note, however, that lianas likely contribute more to total leaf area loss than reported here. Leaf turnover is greater on lianas than trees, consequently the liana leaves I analysed capture herbivory from a shorter time period than the tree leaves observed.

Leaf Traits

These results confirm that the leaves of lianas and trees exhibit distinct ecophysiological variation in traits. Lianas possessed softer leaves with higher nitrogen and lower phenolic concentrations than their tree counterparts. These findings align with those of Asner and Martin (2012) who found similar leaf trait variation in a pan-tropical analysis of lianas and trees. They reported elevated levels of foliar nitrogen in conjunction with lower concentrations of phenols, tannins and lignin in the leaves of lianas. Leaves with higher nutrient concentrations and low phenolic levels are reported to decompose faster (Aerts and Chapin, 1999) which suggests that liana leaves decompose more rapidly than tree leaves, and thus are efficient cyclers of nutrients through ecosystems.

The observed differences in leaf traits between the two plant groups are likely not simply a reflection of phylogenetic relatedness (Rios et al., 2014, Gentry, 1991) but rather an example of convergent evolution

among climbing species. The relationship between leaf traits of different plant types and patterns of species divergence could be further investigated with phylogenetic analytical tools such as phylogenetic generalised least squares (PGLS), Blomberg's K (Blomberg et al., 2003) and Pagel's λ (Pagel, 1999). However, as the climbing habit has evolved independently on several occasions, and the phylogenetic distribution of liana species sampled in this study are not phylogenetically conserved (see Chapter 2), it is unlikely these analyses will uncover any correlation between the observed leaf traits from this study and phylogenetic relatedness.

Some of the differences between liana and tree leaf traits were disguised by the apparent confounding influence of the lianas upon their host's leaf traits. Trees with lianas exhibited significantly greater foliar nitrogen concentrations, marginally significant higher phosphorus concentrations, and generally tended to have lower levels of phenols suggesting a decreased investment in chemical defences in response to the liana association.

Elevated foliar concentrations of nitrogen and phosphorus in trees associated with lianas may be influenced by the greater levels of leaf turnover in lianas. Tang et al. (2012) hypothesised that as lianas turn over their leaves, the resulting leaf litter mulches the soil which may promote the development of a source of nutrients around the base of their host tree. As soil chemistry is positively correlated with leaf chemistry, particularly for nitrogen and phosphorus (He et al., 2014, Pereira-Silva et al., 2012, Vitousek et al., 1995, Hobbie and Gough, 2002, Reich and Oleksyn, 2004), it is reasonable to assume that this mechanism may be the underlying cause for the significant difference in leaf nitrogen between trees with and without lianas.

Trees associated with a liana exhibited lower levels of leaf phenolic concentration. Phenol production is induced in many plant species as a response to microbe and insect herbivory (War et al., 2012). The corresponding herbivory analysis from 2016 identified decreased herbivory on trees with lianas. It is possible that increased foliar phenol levels observed in trees without lianas are a reflection of this phenomenon. Alternatively, host trees may benefit from not expending additional resources on phenolic production as the presence of a liana increases proximal leaf biomass which acts as a sort of 'camouflage' for host species impacting on the 'apparency' of the host-tree's leaves to potential herbivores. In turn, the host tree may not need to produce as much chemical defence in order to achieve the same reduction in herbivore pressure.

Herbivory and leaf traits

Leaf herbivory on trees was significantly correlated with all leaf traits assessed, but on lianas herbivory was significantly correlated only with levels of nitrogen and carbon. Interestingly trees and lianas showed inverse correlations for both nitrogen and carbon. As liana foliar nitrogen and carbon increased, herbivory decreased. The opposite was true of trees. Given these different responses of herbivory to the same leaf traits and the variability of leaf traits important to herbivory between different plant types it is

clear that conclusions about herbivory obtained from data on trees cannot simply be extended to lianas. Studies specifically focussing on general community wide trends between herbivory and lianas are necessary and will provide a meaningful contribution to our overall understanding of herbivory in forests.

Models that best predicted herbivory also differed between plant types. Herbivory on lianas was best determined by total phenolic, carbon and nitrogen concentrations. Herbivory on trees, in contrast, was best predicted using models that incorporated total phenolic and nitrogen concentration, and leaf toughness. Both models incorporate elements important to leaf nutrition (nitrogen) and palatability (phenols, carbon and leaf toughness) but their impact on herbivory was different between trees and lianas. Total phenolic concentration was the only variable common across models and the only variable in which herbivory on both trees and lianas exhibited similar responses. From our models, leaf traits contributing to palatability appeared to be more important in determining levels of herbivory than leaf traits associated with nutritional quality. This trend confirms the results of Poorter et al. (2004) which found leaf traits relating to palatability, rather than nutritive value, are more important determinants of leaf herbivory.

Leaf feeding in different groups of insects will reflect their responses to differences in leaf traits on lianas and trees. Insects feeding on trees may favour different leaf qualities to those feeding on lianas. However, we know very little about the arthropod assemblages, and the subsequent food webs, supported by lianas in comparison to trees and other life forms. Even if differences in arthropod assemblages were known, the life histories of many insects and their dietary requirements are elusive.

Associational susceptibility and resistance to herbivory

There was no significant difference in the amount of leaf loss to herbivory on trees hosting lianas compared with trees alone. However, the two focal plant species, *A. lindleyii* and *A. benthamianus*, exhibited trends which suggested that trees with lianas may incur less damage than trees alone. These trends may be significant with a greater sample size as the amount of herbivory on individuals was highly variable. The underlying mechanisms of this observation are unclear. I suggest that the additional proximal leaf biomass contributed by lianas may have provided some degree of environmental buffering or camouflage during this period of water scarcity (Callaway, 1995). In forest gaps, where the micro climatic conditions parallel some of the conditions experienced during drought, climber infestation has been linked to increased host survival due to a reduction in herbivore pressure (Piironen et al., 2014).

Most studies investigating the response of arthropod assemblages to drought have focused on herbivorous arthropods but rarely look at the overall shift in arthropod networks, particularly those involving predator communities. Frampton et al. (2000) reported a negative effect of drought on predator communities, while many have documented positive impacts of drought on populations of herbivorous pests (Dale and Frank, 2017, Wallner, 1987, Mattson and Haack, 1987, Raffa et al., 2008). The biomass of arthropods is strongly correlated to primary production (Bell, 1985), as leaf production persists in lianas even during

periods of water stress, arthropod communities on trees associated with lianas may remain more complex and ‘balanced’ during these periods, than those on trees without lianas.

CHAPTER 7

General Discussion

7.1 DISCUSSION

This thesis has addressed a crucial knowledge gap concerning the value of lianas in supporting herbivory and associated insect assemblages and quantifying the relative contribution of both lianas and their host trees to herbivory.

In this thesis I have shown the following;

1. There is a lack of information regarding herbivory on plant types other than trees, especially lianas given their ubiquity and singular leaf traits (Chapter 2).
2. Lianas are phylogenetically widespread at small and large scales (Chapter 2).
3. Lianas are increasing in abundance in subtropical rainforests possibly in response to elevated atmospheric CO₂. In contrast to tropical rainforests, however, tree abundances in subtropical rainforests have not declined in response to increasing liana abundances (Chapter 3).
4. Lianas (and vines alike) are key host plants for butterflies in Australian rainforests. They are used at least equally, if not more than trees, and have given rise to a greater proportion of monophagous/specialised interactions with phytophagous insects (Chapter 4).
5. Leaf area loss resulting from insect herbivory is equivalent between lianas and trees in the canopy of tropical rainforests (Chapter 5) and in the understorey/sub-canopy of subtropical rainforests (Chapter 6).
6. Lianas and trees have distinct and contrasting ecophysiological variation in leaf traits independent of phylogenetic relatedness (Chapter 6).
7. Patterns of herbivory and leaf traits useful for predicting herbivory differ between lianas and trees. This suggests hypotheses and conclusions inferred from data on trees may not apply to lianas (Chapter 6).

This chapter concludes the thesis by providing a general discussion of the main themes covered (i.e. lianas, insect herbivory, global change and its impacts), and places the findings within the wider context of important ecological questions including estimates of global species richness and changes in ecosystems given present and future global environmental changes. In addition, the limitations of this research and suggestions for potential directions of future research are discussed.

7.2 LIANAS, INSECTS & HERBIVORY

The relationships between plants and their insect herbivores is essential for approximating global species richness. As knowledge of these relationships improves so to do estimates of global species richness. Just how great global species richness is, is an important ecological question (Ødegaard, 2000a, Erwin, 1982, Hamilton et al., 2010, Stork et al., 2015). Estimates of tropical insect diversity in the late twentieth century relied on a series of extrapolations following measures of the diversity of Coleoptera in a very limited set of Neotropical trees resulting in a (gu)estimate of 30 million species (Erwin, 1982). The basis of this extrapolation was that the set of insects encountered on a tree were largely host-specific either as herbivores or herbivore-specific natural enemies. The accuracy and reliability of the serial multipliers involved in this estimate have been widely criticised (May, 1990, Stork, 1988, Hamilton et al., 2011, Hamilton et al., 2010). Other methodologies now converge on a global estimate of between 5 and 7 million species of insect worldwide (Stork et al., 2015, Ødegaard, 2000a, Castello et al., 2017, Hamilton et al., 2013, Stork, 2018), still far beyond the 1.3 million or so species currently named.

In the present context the key multiplier within the Erwin (1982) estimate is that of host specificity. The question of host specificity has subsequently been much refined. The specificity of insects feeding on different plant parts (e.g. leaves, flowers, buds, meristems) and different forms of leaf herbivory (e.g. chewing, mining, galling) is now relatively well documented (Mawdsley and Stork, 1997, Novotny et al., 2002, Barone, 1998, Smiley, 1978). In contrast, few studies have looked at how host specificity differs among plant functional groups (e.g. trees, shrubs, grasses, lianas, or even between pioneer vs shade tolerant species). Ødegaard (2000b) who examined host specificity of phytophagous beetles feeding on trees and lianas is a notable exception to this trend. Ødegaard's (2000b) study, has not been replicated, nor tested on other insect taxa. In Chapter 4, I addressed this knowledge gap in part by examining the types of host plants preferred by butterflies in Australian rainforests, and found that lianas and other climbing plants supported a diverse assemblage of host specific species. In contrast, trees supported fewer monophagous species. I have expanded upon this chapter here, to discuss its wider implications in species richness estimation. Estimates of host specificity are typically generated from data on insects feeding on trees and often produce low estimates of host specificity (Stork et al., 1997a, Mawdsley and Stork, 1997, Basset, 1996). Host specificity, however, may be considerably greater on lianas compared with trees. In general, life form (that is the plant functional groups) may well be a critical aspect to consider when determining the effective specialisation of insects and in turn species richness.

Ødegaard (2000a) proposed a method to incorporate information on plant functional group into Erwin's (1982) calculation. With a greater availability of data on host specificity, Erwin's (1982) initial estimate of species richness can be revised and verified against real data. There are, however, still too few studies available on the host specificity of insects across plant functional groups for a valid meta-analysis. Future work, needs to expand upon the foundational work of Ødegaard (2000b) and the further analyses presented in Chapter 4. Future research on the influence of plant functional groups on herbivore host

specificity within and between communities should further reduce the uncertainty of global estimates of species richness.

If lianas are important for maintaining species diversity – particularly host specific species diversity – then understanding their roles and the mechanism by which they maintain diversity is essential for understanding forest dynamics at large. An important consideration if such forests are to be conserved.

Studies of host specificity are often constrained by limited or unreliable records. Traditionally, species host plant data are determined from in situ field observations and/or more or less artificial experimental feeding in laboratories. DNA barcoding of gut contents, on the other hand, presents a unique opportunity to greatly improve host plant information. DNA barcoding of gut contents has been effectively used to determine host plants for insects (Jurado-Rivera et al., 2009, Avanesyan, 2014, Hardwick, in prep). This approach is of course limited by the available genetic information on plant species to determine matches. However, host plant information need not be constrained by time consuming observational studies and host plant data of canopy species can much more readily be determined. The value and effectiveness of this method will improve as taxonomic coverage in regional genetic botanical inventories grows.

Once the relative importance of lianas as a resource for herbivores is established, as has been shown here, then food-webs that depend on these plants for their energetic base can be constructed using network analyses (Lau et al., 2017, Proulx et al., 2005, Allesina et al., 2005, Ulanowicz, 2004). This network approach usually considers a species to be of greater ecological importance if it is a highly connected node within an ecological network, or has unique interaction patterns (Proulx et al., 2005, Jordán et al., 2009, Dunne et al., 2002). Multiple, comparative datasets are required to perform such analyses effectively. Food plant data is lacking for most phytophagous insects, especially in the tropics and few datasets exist detailing the feeding habits and biomass removal of phytopagous insects from both lianas and trees for specific ecosystems (although this information could be improved with future DNA analysis of gut contents, discussed above). In addition, inadequate knowledge of adult/juvenile association limits such datasets further (although molecular based identification methods are also improving capacity in this regard (Raso et al., 2014, Valdez-Moreno et al., 2010). Three potentially useful datasets do exist for Parque Natural Metropolitano, Republic of Panama, upon which preliminary analyses demonstrating the importance of lianas as a food source could be conducted. Observational feeding data of phytophagous Coleoptera on lianas and trees collected by Ødegaard (2000b) analysed in tandem with existing site vegetation data, and liana and tree herbivory assessments of Wright & Samaniego (unpublished data) could provide a useful indication of the contribution of lianas to such ecosystem dynamics.

Simulations will also play a role in future understanding of the role of lianas in ecosystems. One study of interest would be to develop a model of a complex food web and remove the lianas from the network to observe and predict how systems respond in their absence (*cf* Morris et al., 2004). Further, parameters pertaining to trees could be altered under simulated conditions and the ability of lianas to provide support and stability to communities during times of change observed. Our lack of information on liana biology

could, however, limit the potential of such simulations as realistic parameter values may be hard to obtain.

7.3 GLOBAL CHANGE & LIANAS

Throughout this thesis, I have discussed lianas largely in terms of relatively undisturbed rainforests and made reference to their likely growing importance given present and future anthropogenic disturbances. Here, I discuss in more detail the wider implications of global change on liana communities and the likely increased importance of lianas as host-plants for herbivores and for the maintenance of diversity and ecosystem functioning (Figure 7.1).

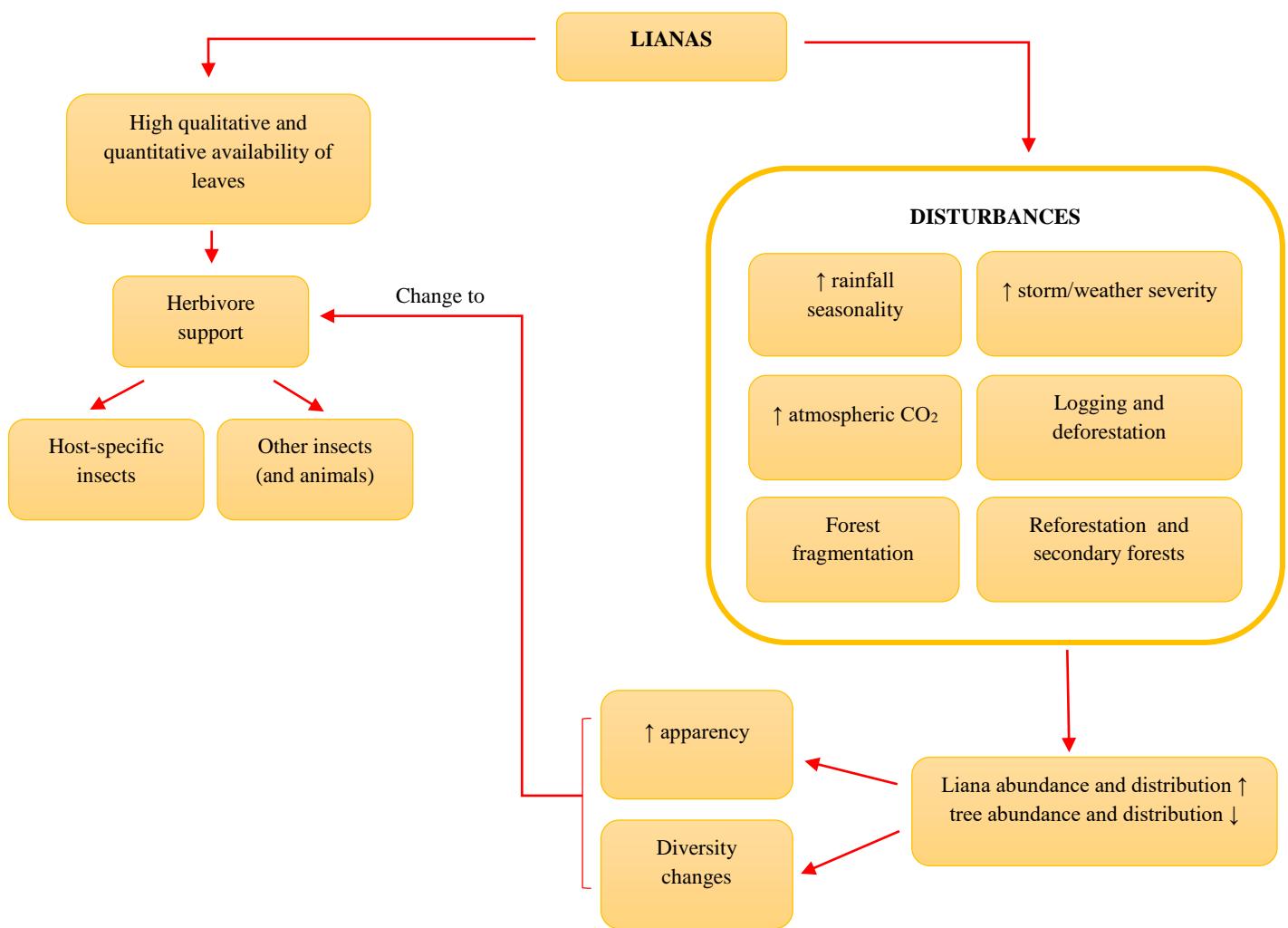


Figure 7.1 Conceptual model illustrating how lianas may become more important for supporting herbivory and maintaining biodiversity. Liana abundances and distributions will likely increase in response to present and future disturbances. Tree abundances may decrease in response to these disturbances, resulting in an increased reliance of herbivores on lianas.

Changing liana abundances

Detecting long-term patterns in liana abundances, and vegetation in general, is a necessary task for monitoring change in rainforests, particularly in response to climate and other anthropogenic disturbances. Determining shifts in their abundances and distributions is essential for understanding the functional importance of lianas, particularly under predicted future global climate scenarios. In Chapter 3, I showed that lianas are increasing in abundance and biomass in Australian subtropical rainforests. This increase is most likely in response to elevated atmospheric CO₂, although changes to the rainfall regime and accelerated forest dynamics cannot be ruled out as contributing factors altogether and likely act with elevated atmospheric CO₂.

Increases in liana abundances and the underlying mechanisms driving vegetation changes are most reliably determined from the Neotropics where meticulous and comprehensive long term datasets have been maintained from large plots, across multiple sites and regions (Laurance et al., 2014, Schnitzer et al., 2012, Yorke et al., 2013, Chave et al., 2008, Foster et al., 2008, Phillips et al., 2002). Several comprehensive liana datasets originate from Barro Colorado Island (BCI), Panama, where liana abundances have been documented for over 30 years (Schnitzer et al., 2012), liana leaf litter production, seed production and seedling densities have been recorded for more than 17 years (Wright et al., 2004) and precipitation has been documented (Schnitzer, 2005). Schnitzer (2005) hypothesised increases in liana abundances and leaf litter production on BCI are driven by precipitation and greater aseasonality, although does not discount the likely influences of changes to the disturbance regime and atmospheric CO₂. In contrast, changes in liana abundances in the Brazilian Amazon show no relationship to the local rainfall regime, but alternatively correlate with metrics of accelerated forest dynamics, such as tree mortality, disturbance and atmospheric CO₂ enrichment (Laurance et al., 2014). The relationship between disturbances and increased liana abundance is well-known (Campbell et al., 2018, Roels and Verbeeck, 2016, Ledo and Schnitzer, 2014, Addo-Fordjour et al., 2012), however, the impact of CO₂ is more difficult to establish and is founded largely in theory rather than by direct evidence of a causal relationship. Studies explicitly testing this relationship are needed. The explanatory hypotheses proposed by Schnitzer (2005) and Laurance et al. (2014) are in no way mutually exclusive and likely act in tandem to drive changes in liana abundances and distributions.

Long-term datasets on lianas, such as those for Neotropical rainforests, are rare in comparison with the available historical datasets of trees. Vegetation surveys in Australia have historically and routinely centred on trees, such as the permanent rainforest plots of CSIRO and the Long Term Ecological Research Network (LTERN) which were established in 1971 (Bradford et al., 2014b). Even the 1 ha plot discussed in Chapter 3 of this thesis initially focused on tree floristics, with an inventory of lianas being added 10 years later (Laidlaw et al., 2000, Tang, 2007). Including lianas in vegetation surveys is becoming increasingly common practice, particularly for large permanent research plots. Tng et al. (2016) published a recent vegetation survey of the 42ha Daintree Rainforest Observatory (DRO) permanent plot (established 20 years ago) which included a comprehensive dataset of lianas >1cm DBH.

Bradford et al. (2014a) also included lianas in the vegetation surveys of the Robson Creek 25ha plot on the Atherton Tablelands. The criteria for this study, however, uses a cut-off of stems >10cm DBH. This cut-off has resulted in only larger stemmed lianas being recorded and the majority of the liana assemblage being over-looked. Standard protocols for surveying lianas have been developed by Gerwing et al. (2006) and Schnitzer et al. (2008) and should be more widely adopted. The establishment of liana inventories are invaluable additions to the vegetation datasets of both the DRO and Robson Creek plots and could be usefully resurveyed in five to ten years to corroborate the findings presented here. However, monitoring of additional environmental variables (such as rainfall, temperature, storm activity, tree mortality and primary productivity) is pivotal if underlying mechanisms driving change are to be accurately identified.

Long-term permanent monitoring plots, such as the one described in this thesis, are needed and are becoming increasingly valuable resources for ecological research. Few other historical datasets of lianas and trees exist within Australia. The only sites that I am aware of suitable for the re-surveying of lianas and trees in the present are those of Gallagher and Leishman (2012) established in 2009. This data was, however, completed from ten small 0.3 ha plots and may be spatially insufficient to capture changes in abundances or the underlying ecosystem processes driving the change in these parts. Nevertheless, available literature on changes in liana abundances from temperate forests is virtually non-existent (with the exception of Londré and Schnitzer (2006)). The existing plots could be expanded upon to determine if they are representative of the larger spatial scale and converted into larger plots for future long-term monitoring.

An important distinction I have shown, which contrasts with Neotropical datasets, is the increase in liana abundances in subtropical Australian rainforests has not (as of yet) occurred detectably at the expense of the tree community. Other long-term records of rainforest trees throughout the eastern tropics and subtropics of Australia show similar temporal stability in the tree communities (Bradford et al., 2014b), although complementary records of liana abundances are not available. Atmospheric CO₂ enrichment enhances both liana and tree growth, but in the tropics may be obviated if thermal thresholds are exceeded. In subtropical rainforest tree communities, where they are further from their thermal maxima, trees may still be able to exploit this resource and effectively compensate for the effects of increasing liana distributions on tree mortality and growth. This effect, however, may be temporary and tree declines may be observed with continued monitoring if thermal thresholds of lower latitudinal species are exceeded.

Anthropogenic change and lianas

Anthropogenic change affects forests globally, and today, is mostly driven through; fragmentation, land-use change, hunting/ defaunation, logging and climate change (Wright, 2010). These changes have significant impacts on the liana communities and internal ecology of forests. Understanding how these changes affect liana communities and the associated ecosystem functions is essential for maximizing the

conservation value of lianas in supporting forest diversity, maintenance and functioning given anthropogenic perturbations.

Biodiversity hotspots retain less than 15% of their natural intact vegetation, half of which sits below the critical threshold of less than 10% (Sloan et al., 2014) beyond which declines in biodiversity is precipitous (Lande, 1987, Bascompte and Sole, 1996, Tilman et al., 1994), and most of which is impacted by fragmentation. Forest fragmentation is globally ubiquitous and fragmented forests represent a substantial proportion of remaining forest areas (Riitters et al., 2016, Bhagwat, 2015). An estimated 70% of all remaining forests lie within 1km of a forest edge (Haddad et al., 2015). Forest edges support significantly greater liana abundances and favour climbing guilds adapted for using small trees as trellises (Campbell et al., 2018, Tang, 2007). At forest edges, lianas may help to ‘seal’ the forest edge faster than trees alone (Campbell et al., 2015). This ‘sealing’ effect may help to reduce the distance edge effects penetrate into fragments (Tang, 2007, Campbell et al., 2015) for example by reducing light penetration, desiccation, and canopy openness.

At forest edges, abundances of liana seedlings are usually negatively correlated with those of tree seedlings, resulting in assumptions that liana seedlings limit, or out compete, tree seedlings. It is more likely, however, that this occurs due to other extrinsic underlying mechanisms, since in forest interiors liana and tree seedlings form a positive correlation (Tang, 2007). Low tree seedling abundances are more likely found at forest edges as tree seeds in forest edge environments struggle to germinate (even under ideal laboratory conditions), whereas liana seeds do not (Tang, 2007). High densities of lianas at forest edges may also help to close canopies faster, thereby improving understory conditions for the germination of tree seeds and return conditions to those of intact forests quicker. High densities of canopy lianas may, however, limit light resources for seedlings and stall regeneration. There is altogether a poor understanding of how liana canopy processes positively and negatively connect with ground/understory processes. Observational studies of liana densities and diversity at forest edges and the penetration of forest edge disturbances are needed to determine the effects of lianas (and their densities) on edge processes and their potential role for forest management and restoration. Experimental manipulations by liana removal at recently formed forest edges (in comparison to edges left to natural successional processes) should provide corroborating evidence.

Understanding the role of lianas in forest edge processes may also be of benefit for interpreting their role in reforestation and how they could be used to manipulate forest regeneration. Losses of tropical forest cover to deforestation are estimated at $\sim 64,000 \text{ km}^2 \text{ yr}^{-1}$, but are offset in part by the reforestation of abandoned lands through natural regeneration processes (Wright, 2010, Aide et al., 2013). This underlines the likely present and future importance of secondary forests for species conservation given declines in primary forests (Chazdon et al., 2009). The biodiversity driving role of lianas may also increase in parallel given increasing disturbances and CO₂ fertilisation. Although often viewed as an obstacle to forest restoration, the role of lianas in reforestation (and forest maintenance for that matter) is almost certainly more complex than currently presumed.

A healthy liana assemblage may assist in returning ecosystem functionality in secondary forests by increasing the diversity of both plants and animals, especially if they are, in general, desirable food-plants of a range of herbivores (Campbell, 2016, Ødegaard, 2000b)(and see Chapter 4). However, Chazdon et al. (2009) reported only *ca* 40% of tree and liana genera found in primary forests are also found in secondary forests. This study, however, represents but a single data point for lianas from secondary forests which had multiple historical land uses. Roeder et al. (2010) found that secondary forests regenerating on land exposed to minimal disturbances (such as selective felling only) produce liana communities similar to those found in primary forests. In comparison, in regions exposed to multiple perturbations (such as clear felling, pasture use and burning) liana communities in post-disturbance forests present similar densities but much lower diversity (Roeder et al., 2010). How land-use history affects the dynamics and direction of regeneration, the return of ecosystem functions, and how this compares with primary forests needs to be properly assessed.

Very high abundances of aggressive lianas may, suppress forest regeneration and ‘swamp’ young trees. In these instances liana removal may well be necessary (Marshall et al., 2017). That having been said, overuse of this management tool may lead to greater herbivore stress on the remaining trees (Foaham, 2002) and, in due course, a slower accrual of biological diversity in general. In forest management in general, how lianas are treated will depend very much on what the goal of management is. Forests used for timber extraction of high-value trees will likely require a different approach from that aimed at maximising overall biological diversity. Mixed models of establishment and a patchwork approach would provide a useful basis for future research. Of course invasion by *exotic* lianas and creepers will likely produce a different response.

Nonetheless, understanding the importance of lianas in edge and reforestation processes particularly with respect to herbivory and maintenance of diversity, cannot be wholly appreciated until their functions within intact forests are known. At present, little is known about the comparative functional importance of lianas, trees and other plant functional groups, with regards to herbivory. Information as rudimentary as redundancy, patterns of consumption and differences in the associated herbivore assemblages are lacking. In the absence of such fundamental baseline data, the roles of lianas and other plant types in the functioning of primary forest ecosystems cannot be appropriately valued. Only once this information is available can we evaluate effectively how these roles may shift under anthropogenic change.

The impact of lianas on ecosystem functions can be determined by observing and comparing biodiversity and functions along liana gradients. A useful liana gradient has been developed by the Sabah Biodiversity Experiment, where lianas have been experimentally removed (or left intact) from restoration sites of varying ages (Hector et al., 2011). The Forest Restoration Climate Experiment (FoRCE) have also established permanent field plots in restoration sites with varying degrees of liana-cutting in Tanzania, and are establishing sites in Australia (Marshall et al., 2017, Marshall and Pfeifer, 2017). Possible directions for research are as simple as determining changes in arthropod assemblages or the

amount of herbivory occurring across sites of different liana abundances and diversity. Understanding the implications of phylogenetic and spatial auto-correlation will, however, be essential in the interpretation of results.

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