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The ecological response of lianas to habitat fragmentation of a tropical rainforest

MASON JAMES CAMPBELL

B.Sc James Cook University

B.Sc (Hons) Australian National University

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DECLARATION

I declare that this thesis is my own work and has not been submitted in any form for another degree or diploma at any University or other institution of tertiary education.

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Statement of contribution of others

Nature of Assistance	**Contribution**	**Names, Titles and Affiliations of Co-Contributors**
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Abstract

More than half of the pre-industrial cover of tropical forest has been lost. Tropical forests are the pinnacle of terrestrial diversity, and thus their destruction threatens global biodiversity more than any other contemporary human practice. As forests are cleared, isolated fragments of the original vegetation are left, surrounded by new habitat types. This forest fragmentation is occurring on an immense scale throughout the tropical regions of the world, with estimates suggesting that fragments now comprise as much as 46% of the remaining tropical forested area. Furthermore, as tropical deforestation and land-use conversion continue unabated the proportion of tropical forests in fragments will increase.

After deforestation, fragmentation likely poses the biggest threat to global diversity. Fragmentation threatens diversity as it alters the environmental and ecological characteristics of tropical forests, degrading their ability to support biodiversity. Moreover, fragmentation degrades the complex system of ecological interactions that occur within tropical forests. Yet, despite this, forest fragments preserve many rare and endangered species and threatened ecosystems and are thus valuable for biodiversity conservation. However, if the conservation values of tropical forest fragments are to be maximized they must not only be retained but their internal ecological interactions must be effectively managed.

Determining how lianas (woody vines) interact with trees and other flora within fragmented tropical forests is important for effective biodiversity conservation. Lianas threaten tree diversity within fragments as they can proliferate and infest trees causing their host structural stress whilst competing with them for resources. Liana infestation can also lead to decreased tree seedling recruitment, damage to saplings, decreased tree growth and fecundity, and increased tree mortality. Consequently, lianas can have fragment-wide impacts that can result in the decline or extirpation of vulnerable tree species or guilds leading to a depauperate tree community. Within this thesis I examined the ecological mechanisms underlying the detrimental interaction between lianas and their tree hosts, the drivers of the positive liana (*sensu lato*) response to forest fragmentation and the ecological impacts of lianas on other members of the vegetative community of forest fragments. This study occurred within the intact and fragmented forests of the Atherton Tableland, northeastern Queensland, Australia.

First, to assess liana abundance and tree infestation rates I examined the relationship between these parameters and their environmental and ecological drivers at a landscape level (comparing fragmented to intact forest) and within forest fragments (23-58 ha). Within these sites, I also examined the response of the liana climbing guild composition to fragmentation. Fragmentation increased liana abundance and altered liana-host tree interactions and the composition of liana climbing guilds. I found that the increased disturbance of fragment edges and in particular the increase in light and climbing trellis availability within fragments, was significantly related to the increase in liana abundance. However, the rate of liana infestation of trees was not only positively related to liana abundance but also liana size (diameter at breast height), with large lianas predominantly occurring within less disturbed areas of fragments. As such, an alleviation of liana impacts upon forest fragments could occur through effective management of the disturbance of fragment edges and large liana management (i.e. cutting).

Second, very little research exists on the impact of lianas on non-tree life forms of the vegetative community of tropical forests. Epiphytes comprise a significant component of tropical forest diversity and provide resources for a diverse community of resident species. To assess the impact of lianas on epiphytic ferns within fragments I compared their respective abundances and spatial arrangements to that of the resident trees. I found that lianas compete intensely with epiphytes on the edges of forest fragments for the structural hosts (trees) needed by both life forms. This competition imperils epiphytic ferns and the reliant diversity of fauna they support. As the first study of its kind, my finding of lianas negatively impacting Old World epiphytic ferns should focus research on liana-epiphyte interactions both within the region and throughout the tropics.

Third, rattans (climbing palms) are arguably the world’s most important non-timber forest product and emblematic of the Old World climbing plant community. Yet, rattan species of many regions are threatened with extinction through forest conversion, landscape modification and unsustainable harvesting. Though monocotyledonous rattans are included as lianas (*sensu lato*) within landscape ecological studies, it is unknown whether they respond similarly to fragmentation and ecological and environmental drivers. I examined how fragmentation has impacted rattan abundance and demography. I found a strong proliferation of rattans and in particular adult rattans in response to fragmentation. Again this proliferation is due to the increased disturbance of forest fragments and the subsequent decreased canopy cover. My findings also provide new insight into the world of climbing plant competition, with rattan proliferation possibly occurring at the expense of lianas due to rattans superior inter-host colonization ability which allows them to infest more widely-spaced tree hosts in heavily-disturbed forest fragments. This hypothesis provides a basis for future research whose outcomes could influence stocking densities of rattans allowing for maximization of rattan output whilst minimizing liana management costs.

Fourth, the vast majority of the liana literature provides almost constant reminders of the negative impact lianas have on trees, forest dynamics and forest functioning. As our understanding of lianas increases it is becoming clear, however, that lianas are a diverse and integral component of a functioning tropical forest. Consequently, for the first time, I synthesized information from across diverse topics dealing with lianas to provide a focused assessment of the potential for lianas to expedite rain forest recovery. The restoration practices I and my colleagues suggested are the first time an explicit list of potential liana uses within restoration has been constructed. Moreover, the listing of these suggested practices allows for field trials by restoration practitioners.

The findings reported in this thesis further our understanding of the ecological responses of lianas (*sensu lato*) to tropical forest fragmentation. In particular, they provide information on liana ecology within the fragments of the World Heritage listed tropical forests of northeastern Australia. This information will be informative to rain forest managers of the region, who are tasked with conserving these exquisite and irreplaceable forests. The results corroborate the literature on many fundamental points of liana ecology and forest dynamics, while providing new insights into the relationship among the lianas, rattans, trees and epiphytes of forest fragments.

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General Introduction

Tropical forest fragmentation

It is currently estimated that tropical forests are being lost at a rate of 8.5 million hectares per year with the average area deforested increasing by 200,000 hectares annually (Hansen et al. 2013, Mercer 2015). Deforestation rarely removes all pre-existing vegetation in a given area (Laurance and Bierregaard Jr 1997). Rather, the process results in fragmentation; whereby isolated fragments of the original vegetation remain surrounded by new habitat types (Wilcove et al. 1986). Fragmentation of tropical closed-canopy forests is globally ubiquitous though its extent is regionally variable (Wade et al. 2003, Bhagwat 2014, Haddad et al. 2015). Across the world's extant tropical closed-canopy forests, estimates suggest that 46% are fragmented (Mercer 2015) and that approximately 70% of the total forested area is within 1 km of a forest edge (Haddad et al. 2015, Riitters et al. 2016). Moreover, the global extent of remnant fragments will continue to increase with continuing deforestation (Achard et al. 2002, Wright 2005, Broadbent et al. 2008, Haddad et al. 2015, Riitters et al. 2016).

The process of forest fragmentation occurs in conjunction with deforestation. When combined, these two anthropogenic impacts are believed to represent the single greatest threat to terrestrial biodiversity (Dirzo and Raven 2003, ter Steege et al. 2015); imperiling much of the >50% of global biodiversity thought to reside within tropical forests (Scheffers et al. 2012, Pimm et al. 2014). Tropical forest fragmentation can be deleterious to many plant species as it leads to the modification of a variety of physical and biological conditions that can alter habitat quality and disrupt ecological interactions (e.g. see reviews by Fahrig 2003, Fischer and Lindenmayer 2007, Laurance et al. 2011, Magrach et al. 2014a). For instance, forest fragmentation greatly increases the area of forest-edge habitat, which exposes the surviving biota to numerous environmental changes, known as edge effects (Laurance and Yensen 1991, Laurance 1997a, Laurance et al. 2002). Some edge effects include increased light penetration, increased desiccation and increased wind disturbance (Wilcove et al. 1986, Williams-Linera 1990, Laurance and Yensen 1991, Laurance and Curran 2008, Briant et al. 2010, Laurance et al. 2011, Magnago et al. 2015). Furthermore, edge effects can lead to the loss of large trees and increase the rate of tree turnover, further exacerbating forest disturbance (Laurance et al. 2000, Laurance et al. 2002, Laurance et al. 2006a, Laurance and Curran 2008, Oliveira et al. 2008, Pütz et al. 2014). Not only does fragmentation lead to the alteration of environmental conditions and biological processes individually, but these individual influences may also act synergistically, substantially increasing their individual impacts and further threatening forest biota (Laurance et al. 2014a). The effects of fragmentation may not occur immediately; deleterious impacts upon resident biodiversity, ecological interactions and forest functions may take years to become fully apparent (Terborgh et al. 2001, Laurance et al. 2002, Laurance et al. 2011, Laurance et al. 2014a, Haddad et al. 2015).

Forest fragments, though degraded, act as important biodiversity repositories in many landscapes, often preserving rare and endangered plant species and threatened ecosystems (e.g. Guindon 1996, Tabanez and Viana 2000, Arroyo-Rodriguez and Mandujano 2006, Muthuramkumar et al. 2006, Arroyo-Rodriguez et al. 2009). They may also be important ‘stepping stones’ facilitating faunal movements in fragmented landscapes (Tischendorf and Fahrig 2000, Baum et al. 2004, Saura et al. 2014). Moreover, the importance of remnant tropical forest fragments for biodiversity conservation will continue to increase with continued tropical forest loss (Achard et al. 2002, Hansen et al. 2008, Hansen et al. 2013, Bhagwat 2014). For example, areas where secondary forests have regenerated are far more diverse when remnants of primary forest were present, than in landscapes that were completely denuded of native vegetation (Sloan et al. 2015).

However, maximizing the conservation values of forest fragments requires not only that they are retained, but that they are managed effectively, which necessitates an understanding of their ecology and the species they still sustain. For instance, not all tropical-forest plant species are deleteriously affected by fragmentation. Early successional tree species are well known to proliferate in fragmented forests (Laurance 1997a, Laurance et al. 1997, Laurance et al. 1998a, Laurance et al. 2000, Laurance et al. 2002, Laurance et al. 2006a, Laurance et al. 2006b). Lianas are also known to respond positively to forest fragmentation (Oliveira et al. 1997, Viana et al. 1997, Laurance et al. 2001a, Magrach et al. 2014b) but much remains to be learned about the specific mechanisms involved and the nature and magnitude of their impacts on their tree hosts (Laurance et al. 2001a, Schnitzer and Bongers 2002, Magrach et al. 2014b, Schnitzer 2015b).

What are lianas?

Lianas are woody climbing plants that remain rooted to the ground throughout their lifetime (Schnitzer 2015a). They are an significant component of tropical rainforests and have been described as the single most important physiognomic feature differentiating tropical from temperate rainforests (Croat 1978). Once a conspicuous omission within ecological studies of tropical rainforests (e.g. "the ecology of lianas is virtually a blank"; Jacobs 1976)), research into lianas within tropical forests has expanded rapidly within the last few decades (Schnitzer et al. 2015c).

Figure 0.1 The weight of large lianas can place considerable structural stress on infested trees, as can be seen in the figure above with the author (MJC) included for scale.

The principal difference between lianas and trees is that lianas forgo major investment in structural supportive tissue in exchange for increased resource interception (and consequently growth) by means of enhanced leaf and root production (Ogawa et al. 1965, Putz 1983, Hegarty 1991a, Schnitzer and Bongers 2002, Wyka et al. 2013). A consequence of this growth strategy is that lianas must utilize tree hosts as trellises to reach the forest canopy and acquire light (Schnitzer and Bongers 2002). Liana infestation of trees can be quite common. For instance, in both Neotropical and Southeast Asian forests, 40-75% of all large (≥ 10cm diameter) trees typically bear at least one liana (Putz 1983, Putz and Chai 1987, Campbell and Newbery 1993, Ingwell et al. 2010).

For trees, liana infestation is detrimental, as the additional weight that lianas impose upon host trees results in structural stress leading to reduced tree growth, reduced fecundity, an increase in limb breakage and infested trees increasing in stem diameter at the expense of height to support the additional weight of lianas (Stevens 1987, Schnitzer et al. 2000, Grauel and Putz 2004, Schnitzer et al. 2005, Kainer et al. 2006, Nabe-Nielsen et al. 2009, Ingwell et al. 2010). Infesting lianas also compete with their host tree for light, soil nutrients and soil moisture (Perez-Salicrup and Barker 2000, Chen et al. 2008, Tobin et al. 2012, Toledo-Aceves 2015). The structural stresses and increased resource competition lianas impose upon infested trees results in increased tree mortality (Putz 1984b, Ingwell et al. 2010) and a subsequent decline in forest carbon storage (Durán and Gianoli 2013, Heijden et al. 2013, Heijden et al. 2015a, Heijden et al. 2015b). Furthermore, lianas can alter tree community composition by adversely affecting some tree species (and successional guilds) more intensely than others (Campbell and Newbery 1993, Schnitzer and Bongers 2002, Ingwell et al. 2010, Schnitzer and Carson 2010). Lianas may also influence the spatial arrangement of trees within a forest as they proliferate in zones of high disturbance, such as treefall gaps and forest edges, limiting tree seedling recruitment, damaging tree saplings and stalling tree succession (Stevens 1987, Schnitzer and Carson 2001, Schnitzer et al. 2005, Ingwell et al. 2010, Schnitzer and Carson 2010). Consequently, determining the how lianas interact with trees and other flora within fragmented forests and understanding the nuances of how lianas respond to fragmentation (Laurance et al. 2001a, Schnitzer and Bongers 2002, Magrach et al. 2014b, Schnitzer 2015b) is very important if we are to better manage the complexity and richness of tropical closed-canopy forest fragments.

Overview of the Thesis

In Chapter 1, I review the literature examining lianas and their response to fragmentation in tropical closed-canopy forests of the world, seeking to evaluate current knowledge, identify unifying themes and uncover critical knowledge gaps.

Global liana diversity varies both spatially and temporally, peaking in the humid tropics in conjunction with the distribution of closed-canopy forests (Gentry 1991, Schnitzer and Bongers 2002, DeWalt et al. 2015). However, variation in regional liana diversity occurs due to local environmental and ecological conditions, the evolutionary history of a region’s flora and, more recently, human impacts (e.g. Gentry 1991, Laurance et al. 2001a, Schnitzer and Carson 2001, Schnitzer and Bongers 2002, Durigon et al. 2013, Ledo and Schnitzer 2014, DeWalt et al. 2015). Human impacts (such as forest fragmentation) on tropical forests are increasing in intensity concurrently with human population expansion (Edelman et al. 2014, Gerland et al. 2014) and are widespread in their spatial extent (Wade et al. 2003, Kettle and Koh 2014). As such, human impacts on tropical forests will likely be the main driving force that shapes future patterns of regional liana diversity. Consequently, it is important that we understand the impact that large-scale human processes such as forest fragmentation will have on liana diversity, particularly as lianas typically constitute one third of woody plant species richness in tropical forests (Schnitzer et al. 2012, Parthasarathy 2015, Schnitzer et al. 2015a).

In Chapter 2, I review the literature on the response of liana diversity to threatening anthropogenic processes, including forest fragmentation, with the specific aim of predicting how these processes will likely affect future liana community diversity.

Fragmentation of tropical closed-canopy forests alters ecological interactions between resident species (Fagan et al. 1999, Laurance et al. 2011, Magrach et al. 2014a, Chávez-Pesqueira et al. 2015) as a product of changes in abiotic and biotic conditions (Williams-Linera 1990, Laurance 1997a, Williams-Linera et al. 1998, Harper et al. 2005, Magnago et al. 2015). Understanding the impact of fragmentation upon the ecological interactions between trees and lianas is of particular importance given the detrimental impact lianas can have on tree communities (Campbell and Newbery 1993, Schnitzer and Bongers 2002, Paul and Yavitt 2011, Heijden et al. 2015a) and forest carbon storage (Durán and Gianoli 2013, Heijden et al. 2015a, Heijden et al. 2015b). Previous work has identified a consistent trend of liana proliferation within forest fragments concurrent with increased liana infestation of trees (Laurance et al. 2001a) which is associated with increased disturbance of forest fragments (Laurance et al. 2000, Laurance 2002, Laurance et al. 2002, Laurance and Curran 2008, Laurance et al. 2011). These affects are known to provide conditions that favor lianas, such as an increase in the availability of light (Schnitzer and Bongers 2002, Schnitzer and Bongers 2005, Schnitzer and Carson 2010, Schnitzer and Bongers 2011, Ledo and Schnitzer 2014) and an increase of suitably sized climbing trellises (Putz 1984b, Putz and Chai 1987, Balfour and Bond 1993). However, it is likely that fragmentation also influences tree community composition through differential effects on tree species associated with morphological traits that influence liana infestation success. These traits include bark morphology and chemical composition (Putz 1980, Boom and Mori 1982, Talley et al. 1996, Carsten et al. 2002, Heijden et al. 2008), presence of buttresses (Black and Harper 1979, Putz 1980, Boom and Mori 1982), leaf shedding and leaf and stem flexibility (Maier 1982, Putz 1984a, Rich et al. 1987), tree/trellis diameter (Putz 1984b, Clark and Clark 1990, Pérez-Salicrup et al. 2001, Perez-Salicrup and de Meijere 2005), presence of spines (Maier 1982, Putz 1984a, Rich et al. 1987), and the availability of tree hosts and their distance form lianas (Muthuramkumar et al. 2006, Arroyo-Rodriguez and Toledo-Aceves 2009, Roeder et al. 2015). Further, synergisms among these traits also likely exist (Sfair et al. 2016).

As such, a comparative examination of selected morphological traits of trees and their association with liana infestation rates, between intact and fragmented forests, may be of use as a proxy to determine whether forest fragmentation alters liana-tree interactions. Furthermore, liana climbing guilds utilize trellises of different diameters (Putz 1984b, Putz and Chai 1987, Balfour and Bond 1993) whose availability is likely altered by forest fragmentation and in particular the increased rate of forest disturbance (Laurance et al. 2000, Laurance 2002, Laurance et al. 2002, Laurance and Curran 2008, Laurance et al. 2011). As such, it is likely that fragmentation not only alters the abundance of trees that possess different morphological traits, but that this, in turn, also influences the liana community itself.

In Chapter 3, I present the first of my empirical results comparing liana infestation of trees bearing specific “liana-defensive” traits and contrast the community composition of liana climbing guilds between fragments and nearby intact forests.

Many of the detrimental impacts that lianas have on infested host trees and tree communities are becoming better known (e.g. see reviews within Schnitzer and Bongers 2002, Schnitzer 2015a, Schnitzer 2015b). For instance, lianas limit tree seedling recruitment, damage saplings, compete with trees for limited resources, stall tree succession and increase tree mortality (Stevens 1987, Schnitzer and Carson 2001, Schnitzer et al. 2005, Ingwell et al. 2010, Schnitzer and Carson 2010). Lianas are also known to alter tree community composition by competing more intensely with some tree species (and successional guilds) than others (Campbell and Newbery 1993, Schnitzer and Bongers 2002, Paul and Yavitt 2011, Heijden et al. 2015a), as mentioned above. However, little is known about the impact lianas have on other vegetative components of the forest community. For instance, the impact lianas have upon epiphytic plants has not been explored despite the fact that epiphytes are major contributors to the vascular plant diversity of tropical forests (Gentry and Dodson 1987) and support a diverse community of reliant animal and plant species (Ellwood et al. 2002, Freeman and Freeman 2009). However, given that epiphytic plants root on the surface of host tree trunks and branches (Benzing 2004) and that lianas require host trees for structural support, it seems plausible that as large trees are lost from forest fragments (Laurance et al. 1997, Laurance et al. 1998a, Laurance et al. 2000) epiphytes may suffer from competition with lianas. To test this hypothesis, in Chapter 4 I examine how edge effects shape the spatial distribution of lianas and epiphytic ferns in forest fragments.

In Chapter 5, I examine the impact that forest fragmentation has on rattan abundance and their ecological interactions with trees. Rattans (climbing species within the palm family, Arecaceae) are a distinct and abundant component of Old World liana communities (Gentry 1991, Dransfield et al. 2008) and one of the world’s most valuable non-timber forest products (Ros-Tonen 2000, Sastry 2002). Ecological assessments of closed-canopy forests often combine information on rattans with that of woody, dicotyledonous lianas (Gentry 1991). However, the relatively narrow evolutionary lineage of monocotyledonous rattans (Dransfield 2001, Dransfield et al. 2008, Baker 2015) has resulted in comparatively constrained physiological and morphological traits compared to dicotyledonous lianas. For instance, although rattans compete with and structurally parasitize tree hosts similarly to lianas (Putz and Chai 1987, Putz 1990, Gentry 1991), they differ from them in that they exhibit no secondary growth, instead relying on their primary-formed vascular system for the entire life of a stem (Tomlinson and Huggett 2012). This means that unlike lianas rattans generally lack the capacity to branch and rarely re-root their stems to the soil surface (Dransfield 1978).

Consequently, rattans differ from lianas in the ways they interact with their tree hosts (Putz 1990a). Understanding how rattans respond to forest fragmentation and their ecological interactions with resident trees would allow for increased effectiveness of rattan management for both conservation and rattan-production values (Siebert 2012).

The current literature on lianas is predominantly focused on the many negative impacts that lianas have on trees and tropical forests (however see Schnitzer 2015a, Schnitzer 2015b). This focus on the negative impacts of lianas is potentially justified given that they alter large-scale processes such as forest carbon storage (Heijden et al. 2015a, Heijden et al. 2015b). Nevertheless, very little attention has been given to the positive roles that lianas might play within tropical forests. Though some works do exist, most of them are limited to faunal resource provisioning (e.g. Yanoviak and Schnitzer 2013, Arroyo-Rodríguez et al. 2015) and the economic potential of groups such as rattans (Siebert 2012). However, the early-successional guild type that many lianas occupy (DeWalt et al. 2000, Paul and Yavitt 2011) along with the associated traits they exhibit (such as rapid leaf production (Wyka et al. 2013)) support an examination of their potential role in facilitating tropical forest restoration. The current practice of excluding lianas from most restoration plantings (at least initially) because of the potential threat that they pose to planted trees requires re-examination. For instance, exclusion of lianas from restoration plantings ignores the fact that under certain conditions lianas contribute to forest-wide biodiversity (Ødegaard 2000, Arroyo-Rodríguez et al. 2015, DeWalt et al. 2015), assist in regulating forest microclimate (Campanello et al. 2007, Wyka et al. 2013) and can increase forest-wide processes such as nutrient turnover through enhanced and rapid leaf litter production (Putz 1983, Hegarty 1991a, Wyka et al. 2013). Consequently, in Chapter 6, I examine published studies on liana ecology and identify themes to propose possible strategies by which restoration plantings of tropical forests could be aided by the inclusion of specific liana species or guilds. I performed this in the hope that a practical examination of these strategies might aid effective restoration practices. Implementation of effective restoration continues to increase in importance given the vast area of tropical forests have already been cleared (Lewis et al. 2015) and future projections under current clearing rates (Hansen et al. 2008, Hansen et al. 2013, Mercer 2015) are alarming.

Supplementary Section

I highlight some additional materials that I have produced during my PhD within a Supplementary Section of this thesis. These are articles undertaken during my candidature that depart from the geographic locale of my PhD, deviate from my specific PhD theme (liana ecology and ecological interactions within fragmented tropical forests), or are of a more general nature (such as popular articles). Nevertheless, they are included to provide broader perspectives on tropical forests, forest fragments and lianas, and to illustrate that my activities have included efforts to address some issues beyond the immediate scope of my doctoral thesis.

Figure 0.2 Tropical forest fragments form a considerable component of the world heritage listed “Wet Tropics” forests of northeastern Australia.

Finally, this doctoral thesis is wide-ranging, examining topics as diverse as potential patterns in future liana diversity through to lianas and forest fragment restoration. It is however, unified in being an examination of liana ecology and ecological interactions within fragmented forests. Overall, this thesis aims to provide a better understanding of the ecological interactions occurring between lianas and other vegetation types in fragmented tropical closed-canopy forests. It is hoped that this knowledge will assist managers in planning and implementing biodiversity conservation practices in fragments, especially those with high conservation value such as the fragments that represent a component of the world heritage listed “Wet Tropics” forests of northeastern Australia (UNESCO 1988) that I have studied herein. Moreover, given the general lack of knowledge on ecology of tropical Australian liana species (Schnitzer and Bongers 2011), the information contained within this thesis will contribute to the understanding of global patterns in liana abundance and ecology. Most importantly, it is hoped that the knowledge on liana ecology and interactions identified within the thesis will not just aid liana management within forest fragments, but contribute to the conservation of the magnificent and majestic rain forest ecosystem and the captivating species which call it home.

Chapter 1 The ecological effects of lianas in fragmented forests

This chapter is based upon a paper published by Campbell et al. (2015), with minimal format and content edits:

Campbell, M., W. F. Laurance, and A. Magrach. 2015. Ecological effects of lianas in fragmented forests. Pages 447-454 *in* S. A. Schnitzer, F. Bongers, R. Burnham, and F. E. Putz, editors. *Ecology of lianas*. Wiley-Blackwell Publishing, Oxford.

Statement of contribution of others:

Campbell wrote the first draft of the chapter. The subsequent drafts were revised by Campbell with editorial input from Laurance and Magrach. Laurance created the figures.

Overview

Understanding how biodiversity persists in the small fragments of forest that remain in many tropical regions is a vital priority. If lianas flourish in fragmented forests, as is expected, then they might have a wide array of ecological effects, including those on biodiversity. In this chapter, I review available studies on liana communities and liana–tree interactions in fragmented tropical forests. Although much remains unknown, it is apparent that lianas often increase dramatically in abundance in fragmented forests, especially those with large amounts of forest edge or recurring canopy disturbance. Where lianas are particularly abundant, they reduce tree survival, growth, fecundity, and regeneration. Abundant lianas also alter tree-community composition and reduce forest carbon storage, though the magnitude of these effects is variable and not fully understood. Finally, liana proliferation at the expense of trees affects rain forest fauna that are dependent on resources provided by trees such as fruits, nectar, foliage, and tree cavities, as well as fauna that capitalize on liana resources. If lianas benefit markedly in the future from rising atmospheric CO_2 levels or other global change phenomena, then they will become even more dominant in fragmented forests.

Introduction: tropical forest fragmentation

Whether by happenstance or design, deforestation rarely removes all pre-existing vegetation in a given area (Laurance and Bierregaard Jr 1997), but leaves isolated fragments of the original vegetation surrounded by new habitat types (Wilcove et al. 1986). This process of habitat fragmentation leads to the modification of a variety of biological and physical processes within the fragmented forests that can be deleterious to the constituent species and their ecological interactions (e.g. see reviews by Fahrig 2003, Fischer and Lindenmayer 2007, Laurance et al. 2011). However, remnant forest fragments now represent a large proportion of the remaining tropical forested area (Achard et al. 2002, Broadbent et al. 2008, Haddad et al. 2015) and despite their degradation, they provide an important biodiversity repository for many landscapes including the preservation of many rare and endangered species and threatened ecosystems (e.g. Guindon 1996, Tabanez and Viana 2000, Arroyo-Rodriguez and Mandujano 2006, Muthuramkumar et al. 2006, Arroyo-Rodriguez et al. 2009). The importance of remnant tropical forest fragments for biodiversity conservation increases with continued worldwide tropical forest loss (Achard et al. 2002, Broadbent et al. 2008).

Maximization of the conservation values of forest fragments requires that they are not only retained, but are managed effectively, which necessitates an understanding of their ecology. One potentially important, yet minimally examined component of fragmented tropical forests is the liana community: how lianas respond to forest fragmentation and the antagonistic interaction that they have with their tree hosts (Fig. 1.1, Jacobs 1976, Schnitzer and Bongers 2002, Toledo - Aceves 2015).

Figure 1.1 Lianas proliferating along an abrupt forest edge in Gabon, central Africa (photo by William Laurance).

Fragmentation effects on liana diversity

Lianas generally comprise 20–25% of the woody species diversity in undisturbed tropical forest (Putz 1984b, Gentry 1991, Appanah et al. 1992, DeWalt et al. 2015) but can be as high as 35% of the species in some forests, such as the one on Barro Colorado Island, Panama (Schnitzer et al. 2015b). During the loss of forest concurrent with the initial fragmentation process, local extirpation of many sparsely distributed species of trees and lianas can occur, resulting in decreased landscape-scale species diversity (Laurance et al. 1999, Zhu et al. 2004). After the initial forest loss, however, liana diversity is usually proportionally greater in forest fragments (relative to trees) than in comparable undisturbed forest, with this enhanced diversity linked to increased forest edge area and elevated disturbance levels (Laurance 1997a, Oliveira et al. 1997, Laurance et al. 2001a, Schnitzer and Bongers 2002, Zhu et al. 2004).

Although an increase in local liana diversity compared to trees within forest fragments is the more common trend, two major factors can potentially depress liana diversity in fragments. First, fragmentation results in a number of potential impacts on populations and communities, such as genetic drift, isolation of breeding populations, propagule-dispersal limitation, and pollination limitation through local extirpation of obligatory dispersers or pollinators, which may decrease the diversity of both trees and lianas within forest fragments (e.g. Aizen and Feinsinger 1994, Young et al. 1996, Benitez-Malvido and Martinez-Ramos 2003). Second, a collapse in the availability of structural hosts (available trees) within heavily disturbed forest fragments can also reduce liana diversity (Muthuramkumar et al. 2006, Arroyo-Rodriguez and Toledo-Aceves 2009, Addo-Fordjour et al. 2012a). This host loss can occur through both continued anthropogenic disturbances within fragments (e.g. repeated logging; Muthuramkumar et al. 2006, Arroyo-Rodriguez and Toledo-Aceves 2009) or through cascades of impacts initiated by forest loss and fragmentation (e.g. enhanced tree mortality (Laurance et al. 1998a, Laurance et al. 2000, Laurance et al. 2006a), such as edge effects, that alter forest microclimate and increase wind damage (Kapos 1989, Williams-Linera 1990, Laurance and Curran 2008).

Forest fragmentation effects on liana abundance

Fragmentation of once-continuous primary forests results in a considerable increase in landscape-wide liana abundance and rates of tree infestation (Laurance 1997a, Oliveira et al. 1997, Viana et al. 1997, Laurance et al. 2001a, Benitez-Malvido and

Martinez-Ramos 2003). There are three main reasons for the increase in liana abundance. First, the area of forest edge greatly increases within fragmented forest landscapes (Laurance and Yensen 1991) and forest edges are preferential liana habitat (Figs. 1.2 and 1.3, Laurance 1997a, Oliveira et al. 1997, Laurance et al. 2001a, Londre and Schnitzer 2006). Second, elevated rates of large tree mortality, turnover and treefall-gap creation (Laurance et al. 1997, Laurance et al. 1998a, Laurance et al. 2000, Hill and Curran 2003, Laurance et al. 2006a) occur in many forest fragments, which again enhance the amount of available disturbed and well-lit habitat preferred by lianas (Schnitzer and Bongers 2002, Schnitzer and Bongers 2011). Finally, initial forest loss and fragmentation may lead to a greater area of forest regeneration ("younger" forest), which again harbors an increased liana abundance and diversity when compared to equivalent unfragmented ("older") forest (DeWalt et al. 2000, Letcher and Chazdon 2009a, Letcher 2015).

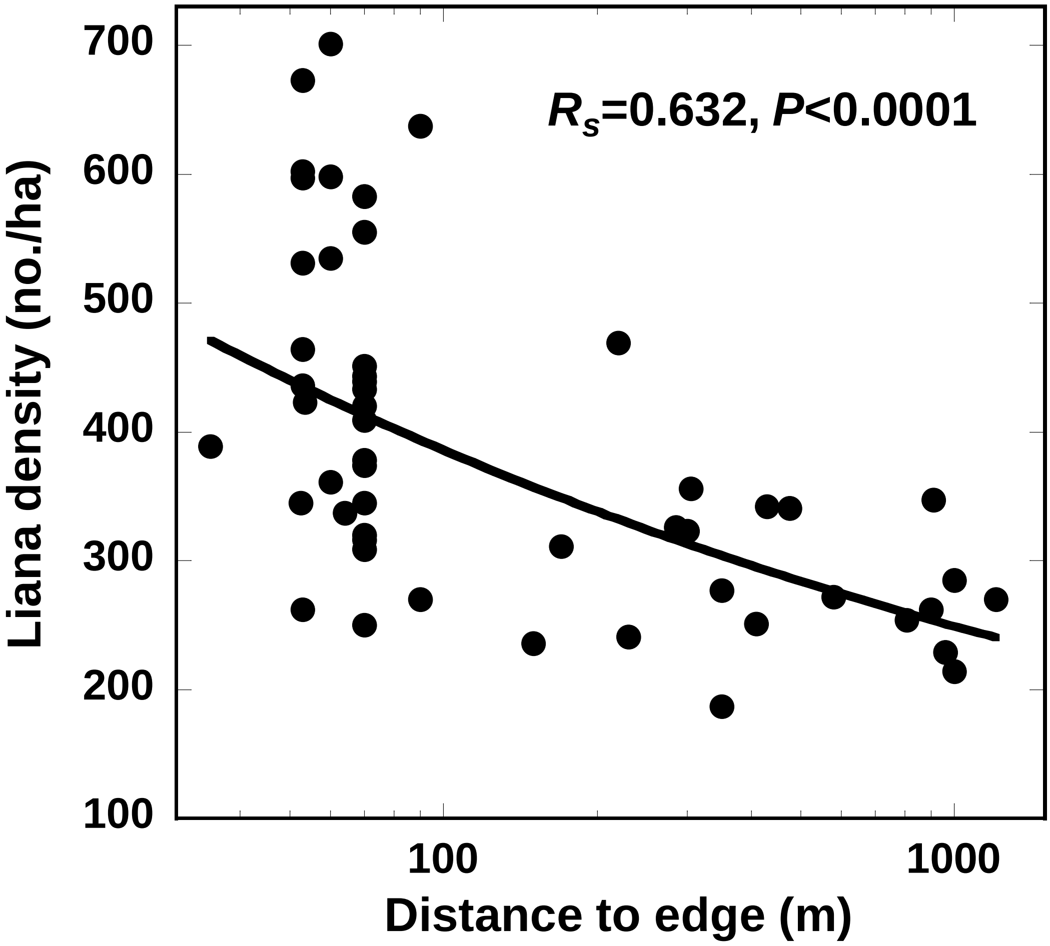

Figure 1.2 Lianas tend to increase near the abrupt, artificial boundaries of forest fragments. Shown is the number of liana stems (≥ 2 cm diameter) within 1-hectare plots as a function of

distance of plots from the nearest forest edge, in the rain forests of the central Amazon (results from a Spearman rank correlation).

Liana impact upon fragmented vegetation communities

Any increase in liana abundance may be highly detrimental to the tree community of a fragmented forest due to the enhanced structural stress and increased resource competition experienced by trees infested with lianas (Fig. 1.1, Putz 1984b, Stevens 1987, Schnitzer and Bongers 2002, Schnitzer et al. 2005, Toledo ‐ Aceves 2015). Liana infestation may even contribute to the death of individual trees (Putz 1984b, Clark and Clark 1990, Schnitzer and Bongers 2002, Ingwell et al. 2010, Heijden et al. 2015a). Consequently, a fragment-wide decline or extirpation of vulnerable tree species may occur, changing the composition and diversity of the tree community (Laurance et al. 1997, Laurance et al. 2001a, Laurance et al. 2006b, Heijden et al. 2015a). This problem is particularly pertinent for “vulnerable” tree species whose morphology leads to a high probability of liana infestation (Putz 1980, 1984a, Hegarty 1991b, Talley et al. 1996, Schnitzer and Bongers 2002) and for tree species that are isolated from other sub-populations or otherwise restricted in their potential for recruitment (Young et al. 1996).

Lianas may also hasten the decline of tree species diversity within forest fragments via their differential impact on different successional guilds of trees. Traits that serve as liana “defense,” such as fast growth, large leaves, and few branches, occur more often in pioneer or secondary succession species than in large mature-phase (shade-tolerant) tree species (Putz 1980, 1984a, Clark and Clark 1990, Schnitzer and Bongers 2002). Consequently, mature-phase tree species host lianas more frequently (Clark and Clark 1990, Laurance et al. 2001a, Schnitzer and Bongers 2002, Schnitzer and Carson 2010), and increased liana abundance within forest fragments may contribute to their decline or loss (Phillips and Gentry 1994, Laurance et al. 2000, Laurance et al. 2001a, Laurance et al. 2006a). The loss of mature-phase tree species may be exacerbated through a synergism with the enhanced wind shear and altered microclimates that forest fragments experience (Kapos 1989, Williams-Linera 1990, Laurance and Curran 2008), accelerating the alteration of the tree community composition (Laurance et al. 1998a, Laurance et al. 2006a). A third mechanism by which lianas may alter the tree composition of a forest fragment is via their impact upon the succession process itself. Lianas can alter the succession pathway and eventual vegetation type, or arrest succession within treefall gaps (Schnitzer et al. 2000, Schnitzer and Carson 2001, Schnitzer and Bongers 2002, Schnitzer and Bongers 2005, Toledo-Aceves and Swaine 2008, Schnitzer and Carson 2010, Letcher 2015, Toledo‐Aceves 2015). Additionally, lianas may promote treefall-gap formation by elevating tree mortality (Putz 1984b, Clark and Clark 1990, Schnitzer and Bongers 2002, Schnitzer 2015c) and collateral damage during a treefall event (Appanah and Putz 1984, Putz 1984b). Accordingly, an increased liana abundance may alter the succession of the tree community and the formation of a canopy gap, promoting the loss of mature-phase tree species in fragments (Oliveira et al. 1997, Viana et al. 1997).

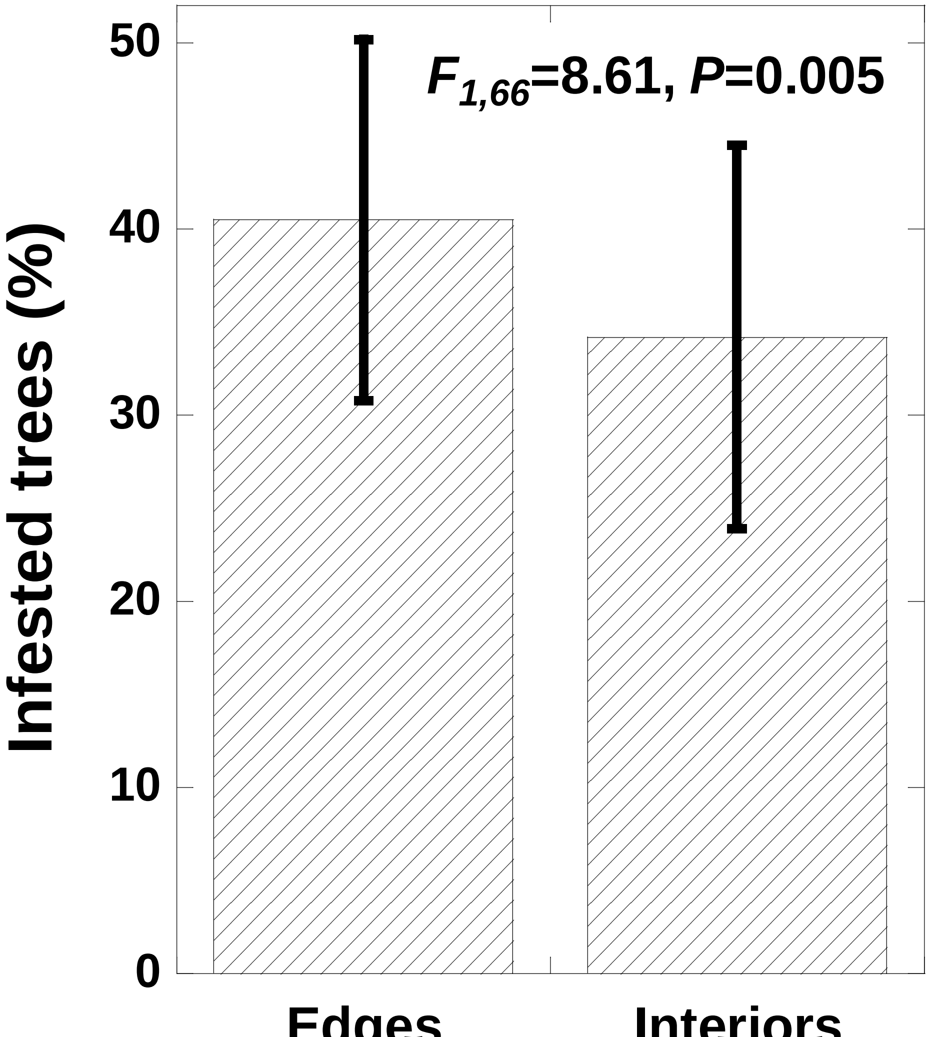

Figure 1.3 In Amazonian forests, liana infestation rates (the proportion of trees with at least one liana) are higher near forest edges than in forest interiors (results from a one-way ANOVA; adapted from Laurance et al. 2001a).

Forest biomass

In addition to altering the composition of the tree community, lianas can also suppress tree biomass in fragments (Laurance et al. 1997, Nascimento and Laurance 2004, Heijden et al. 2015a). When lianas are abundant, they can kill or reduce growth in trees and thereby reduce the ability of fragmented forests to sequester and store carbon (Fig. 1.4, Laurance et al. 1997, Laurance et al. 1998b, Laurance et al. 2001a, Phillips et al. 2002, Nascimento and Laurance 2004). Any increase in liana biomass is relatively negligible and does not offset the loss of tree biomass, because lianas generally comprise less than one-tenth of the aboveground biomass even in disturbed forests (Hegarty and Caballe 1991, DeWalt et al. 2000, Gerwing and Farias 2000, Schnitzer et al. 2014). Given that tropical forests store ~44% (or 228 billion tons of carbon, Baccini et al. 2012) of the globe's terrestrial vegetation-derived carbon (Dixon et al. 1994, Phillips et al. 1998, Malhi and Grace 2000), liana effects on fragmented forest biomass could have nontrivial impacts on the global carbon cycle (Heijden et al. 2015a).

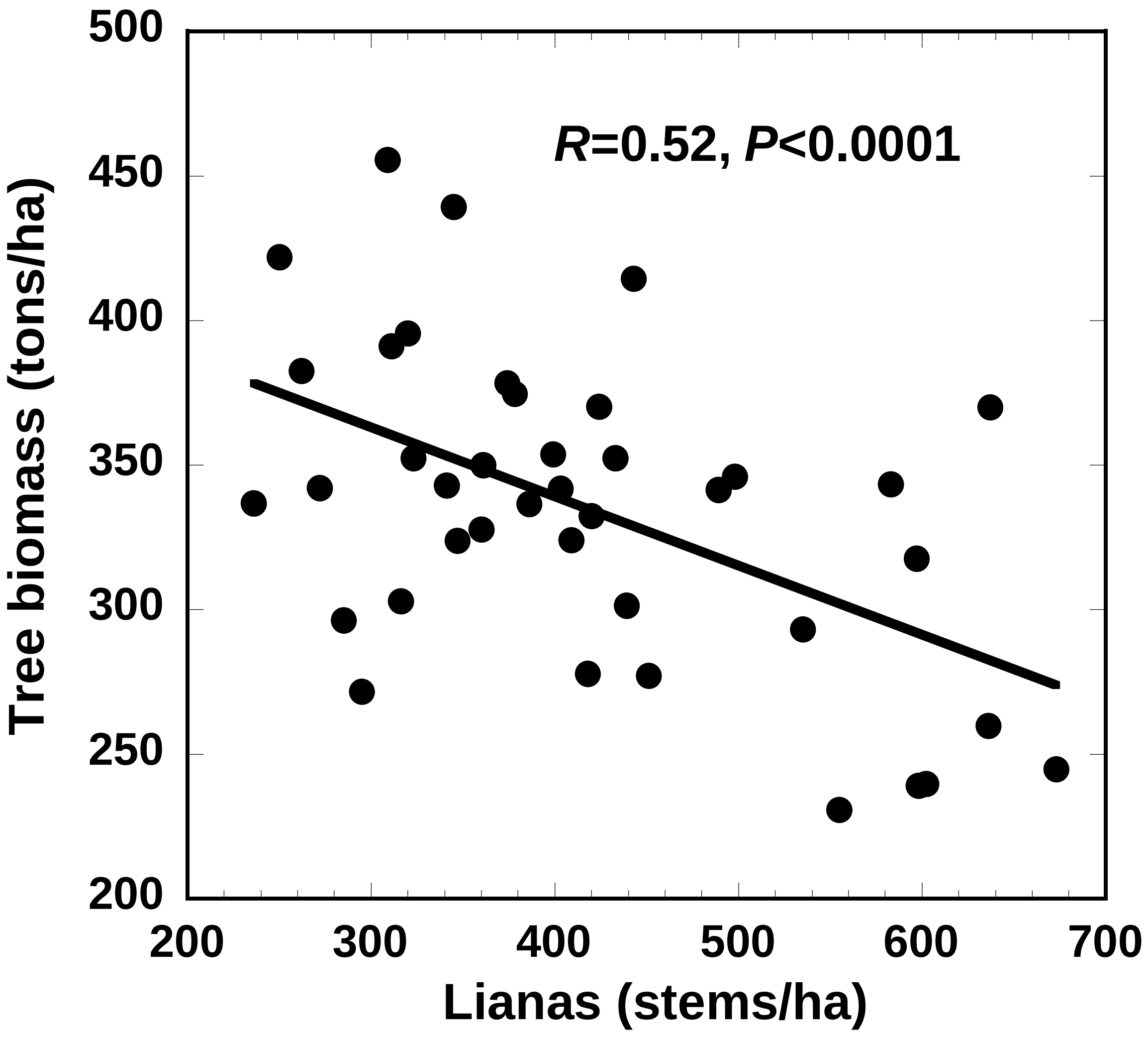

Figure 1.4 Lianas are negatively correlated with the aboveground biomass of live trees in Amazonian forests (results from a Pearson correlation; adapted from Laurance et al. 2001a). This negative relationship can arise both because lianas reduce tree survivorship and growth and because external disturbances, such as windstorms, can fell or damage trees and thereby create disturbed conditions favored by lianas.

Future liana increase within fragmented forests

Lianas seem likely to increase in abundance in fragmented forests for three reasons. First, future climatic predictions suggest tropical storms will become more frequent and increase in intensity (Emanuel 2005, Elsner et al. 2008) and trees in fragmented forests are known to display an increased vulnerability to wind damage (Laurance and Curran 2008). Therefore, in the future, forest fragments are likely to experience elevated tree turnover rates, greater vegetation disturbance, and substantial changes in forest microclimates (Webb 1958, Turton and Siegenthaler 2004, Laurance and Curran 2008), all of which could favor lianas (Putz 1984b, Schnitzer and Bongers 2002).

Second, lianas achieve their peak abundance in tropical forests with a pronounced dry season (Gentry 1991, Schnitzer 2005, DeWalt et al. 2010, DeWalt et al. 2015) and rainfall in many tropical regions is projected to increase in seasonality (Malhi and Wright 2004). A transition from wetter to more seasonal forest types would favor an increase in liana abundance (Schnitzer and Bongers 2011, Schnitzer 2015c). This process might be magnified in fragmented forests because forest edges are often prone to desiccation (Kapos 1989, Williams-Linera 1990, Briant et al. 2010, Magnago et al. 2015).

Finally, liana growth rates may increase proportionately more than tree growth rates in response to rising atmospheric CO_2 levels (Granados and Korner 2002, Phillips et al. 2002, Schnitzer and Bongers 2011, however see Marvin et al. 2015). If so, there could be a shift in the competitive interactions between trees and lianas in fragmented forests even more in favor of lianas (Tabanez and Viana 2000, Dalling et al. 2012). However, the extent of any potential increase in liana growth might be somewhat ameliorated if increased air temperatures limit the duration of transpiration periods (Betts et al. 1997).

Conclusion

Fragmented forests are ubiquitous in tropical landscapes and are occasionally the last surviving remnants of rare habitats and species for which conservation is an urgent priority. Given the potent role that lianas can play in some fragmented forests, and are likely to play in the future, understanding how lianas affect forest ecology and ecological interactions is a key priority. In some circumstances, control and management of lianas might be necessary if lianas are having major deleterious impacts on rare ecosystems or species.

Acknowledgments

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Chapter 2 Liana diversity and the future of tropical forests

This chapter is based upon a paper published by Campbell et al. (2015), with minimal format and content edits:

Campbell, M., A. Magrach, and W. F. Laurance. 2015. Liana diversity and the future of tropical forests. Pages 255-274 *in* N. Parthasarathy, editor. *Biodiversity of Lianas*. Springer International Publishing.

Statement of contribution of others:

Campbell wrote the first draft of the chapter other than the sections on logging, climate change and hunting which were written by Magrach. The subsequent drafts were revised by Campbell with editorial input from Magrach and Laurance. Campbell created all the figures other than figure 2.1 which was created by Laurance.

Abstract

Lianas contribute substantially to the total species richness of tropical forests, accounting for up to a quarter of the woody plant diversity. However, liana diversity is intrinsically linked with forest condition and consequently is altered by human-induced forest modifications. Multiple environmental drivers including forest fragmentation, logging and climate change are impacting tropical forests; the extent and intensity of their effects will likely define future global liana diversity.

Introduction

Globally, liana diversity is both spatially and temporally heterogeneous (Gentry 1991, Schnitzer and Bongers 2002, DeWalt et al. 2015). Liana diversity peaks in tropical climes where it is intrinsically linked with the distribution of closed-canopy forests (Gentry 1991). However, within the closed-canopy forests of the tropics, there is considerable regional variation in liana diversity in response to local environmental or ecological conditions and the evolutionary history of a region's flora (Gentry 1991, Hegarty and Clifford 1991, Schnitzer and Bongers 2002, Gianoli 2004, Schnitzer 2005, Durigon et al. 2013, DeWalt et al. 2015).

Regional liana diversity also varies over time, as both the lianas and the forests they inhabit respond to changes in the prevailing environmental conditions and, more recently, human impacts (Laurance et al. 2001a, Phillips et al. 2002, Schnitzer et al. 2011, Addo-Fordjour et al. 2012a, Addo-Fordjour et al. 2012b, Addo-Fordjour et al. 2013, Laurance et al. 2014b). Human impacts on forests will likely shape future patterns of regional liana diversity due to their broad spatial extent and increasing intensity as the human population continues to expand (Gerland et al. 2014).

Here I focus on some of the more influential impacts that humans are currently having on tropical forests and how these affect local liana diversity. The impacts I assess include deforestation, forest fragmentation, logging and other silvicultural practices, forest disturbance, climate change and hunting. Finally, I conclude by examining the implications that these human impacts will likely have on the liana diversity of future tropical forests.

Liana Diversity and Anthropogenic Forest Modifications

Deforestation

Any discussion on tropical closed-canopy forests and the retention of species diversity therein must begin with deforestation, the single biggest threat to tropical biodiversity (Dirzo and Raven 2003, Gibson et al. 2011). In fact, approximately half of the original tropical closed-canopy forest and its constituent biodiversity has already been lost due to deforestation (Wright 2005). Moreover, tropical forests continue to be lost at an alarming rate (Hansen et al. 2008, Asner et al. 2009, Hansen et al. 2013).

Lianas are highly vulnerable to deforestation as they rely on the trees of the tropical closed-canopy forests for structural support (Gentry 1991). Additionally, lianas are vulnerable to deforestation as many liana species are sparsely distributed (Gentry 1991, Laurance et al. 2001a, Parthasarathy et al. 2004, Santos et al. 2009). For such rare species, localized extirpation may occur in the heavily degraded landscapes and small forest remnants created in the aftermath of deforestation (Laurance et al. 1999). Deforestation has surely resulted in the local extirpation of many liana species and any tropical region facing the loss of closed-canopy forests on a broad-scale are likely to exhibit a concurrent decline in their resident liana diversity.

Forest Fragmentation

Tropical deforestation rarely results in the removal of all pre-existing vegetation in a given area (Laurance and Bierregaard Jr 1997).The resulting landscape is often a matrix of isolated forest fragments surrounded by new habitat types (Wilcove et al. 1986). Forest fragmentation is occurring on an immense scale throughout the tropical regions of the globe (Haddad et al. 2015) with nearly 9000 fragments of <100km^2 in area generated from 1999 to 2002 in the Brazilian Amazon alone (Broadbent et al. 2008). With continuing deforestation, the extent of remnant fragments will continue to increase (Achard et al. 2002, Wright 2005, Broadbent et al. 2008).

One by-product of forest fragmentation is that it greatly increases the area of forest edge, which exposes the surviving biota to numerous environmental changes associated with these edges, such as increased light penetration and desiccation (Wilcove et al. 1986, Williams-Linera 1990, Laurance and Yensen 1991, Laurance 2008, Briant et al. 2010, Magnago et al. 2015). Additionally, the forest edge offers lianas an increased availability of climbing trellises (Putz 1984b, Williams-Linera 1990, Balfour and Bond 1993, Chittibabu and Parthasarathy 2001, Londre and Schnitzer

2006). The increased desiccation, light and climbing trellises within forest fragments and in particular at forest edges is often a result of the higher level of disturbance and tree-turnover found there (Laurance et al. 1997, Laurance et al. 2000, Laurance and Curran 2008, Briant et al. 2010, Laurance et al. 2011). The juxtaposition of ecological and environmental traits in forest fragments and in particular forest edge habitat favors liana growth requirements and as a result these areas often have high liana diversity (Fig. 2.1, Laurance et al. 2001a, Zhu et al. 2004, Mohandass et al. 2014).

Although fragmentation increases liana abundance and diversity on forest edges it can also lead to a decline in overall species diversity at regional scales. This decline in regional diversity may occur as a direct consequence of the fragmentation process itself through mechanisms such as genetic drift, isolation of breeding populations, propagule-dispersal limitation, and pollination limitation (Aizen and Feinsinger 1994, Young et al. 1996, Lienert 2004, Hernandez-Stefanoni 2005). These fragmentation processes are especially likely to impact lianas that are rare (Laurance et al. 1999), although the extent of the impact of each particular process on lianas specifically is still poorly understood. However, given that the percentage of rare liana species within any tropical forest region is not insignificant (Gentry 1991, Laurance et al. 2001a, Parthasarathy et al. 2004, Santos et al. 2009), it is important to better understand how such rare species are affected by fragmentation.

Liana diversity within forest fragments may also decline as the result of additional anthropogenic impacts after fragmentation. For instance, heavy disturbance (see section below) within fragments often leads to a considerable decline in intra-fragment and thus regional liana diversity (Muthuramkumar et al. 2006, Arroyo-Rodriguez and Toledo-Aceves 2009, Addo-Fordjour et al. 2012b, Mohandass et al. 2014). It is believed that the decline in liana diversity in heavily disturbed fragments may be due to a decrease in the availability of structural hosts (trees) for lianas to climb (Heijden and Phillips 2008, Arroyo-Rodriguez and Toledo-Aceves 2009, Addo-Fordjour et al. 2012b). This loss of potential tree hosts can result from logging, from tree damage via other anthropogenic resource extraction, or from a progressive decay in fragment condition over time (Oliveira et al. 1997, Laurance et al. 2000, Laurance and Curran 2008). Fragment decay can be driven by elevated tree mortality and turnover from increased wind damage and unfavorable microclimatic changes near forest edges (Kapos 1989, Williams-Linera 1990, Laurance et al. 1998a, Laurance et al. 2000, Laurance et al. 2006a, Laurance and Curran 2008, Magnago et al. 2015) and by edge-related fires (Cochrane and Laurance 2002, 2008). Consequently, regional liana diversity in areas with a low to moderate level of fragment disturbance are more likely to retain their liana diversity than are those suffering heavy disturbance (Muthuramkumar et al. 2006, Arroyo-Rodriguez and Toledo-Aceves 2009, Addo-Fordjour et al. 2012b, Mohandass et al. 2014).

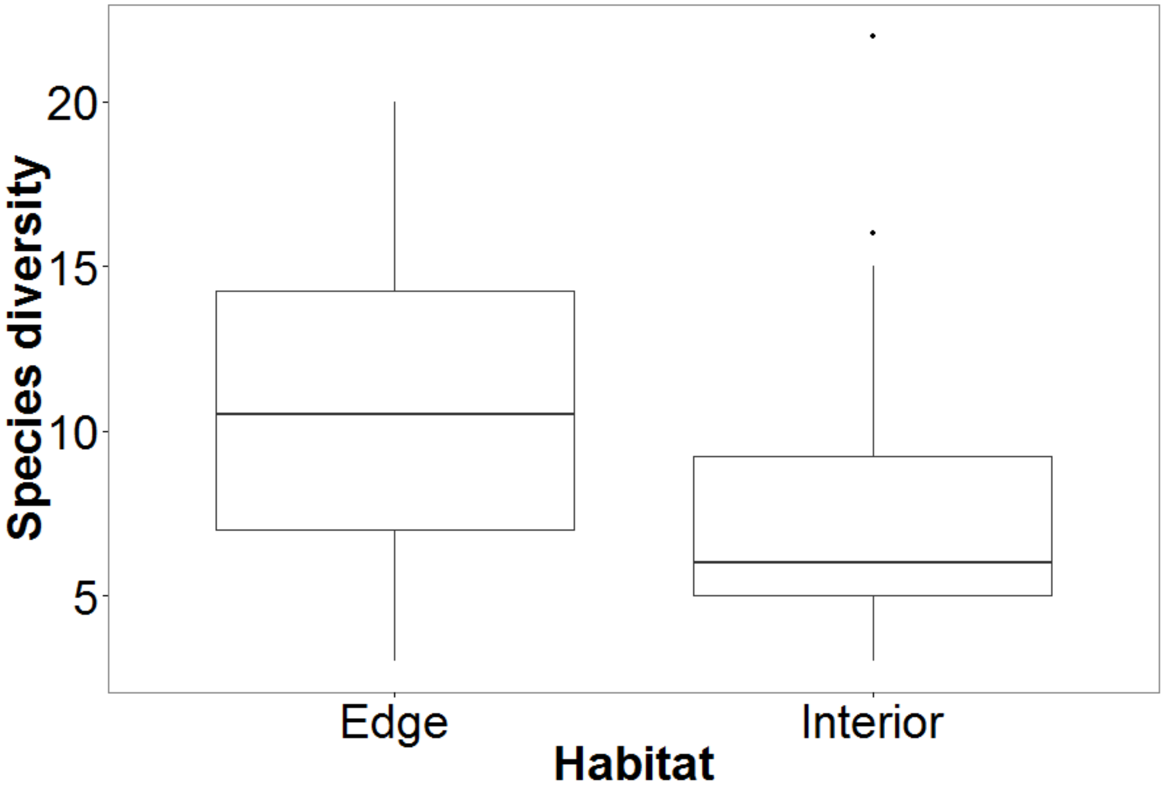

Figure 2.1 Lianas are significantly more diverse on the edge of forest fragments than in their interior (Laurance et al. 2001a).

Logging and other Silvicultural Practices

Selective logging has varied impacts on regional liana diversity. Selective logging is a major driver of forest degradation across the tropics, with ~20% of all tropical forests logged between 2000 and 2005 (Asner et al. 2009). Globally, more than 400 million hectares of tropical forest are in logging estates (Blaser et al. 2011). Selective logging, via the felling of canopy trees, collateral killing of many other trees, and the creation of logging roads and skid trails (Laporte et al. 2007), modifies the local microclimate by reducing canopy cover. A loss in canopy cover causes a decline of many forest-interior specialists and an increase in abundance of disturbance-tolerant and edge-adapted taxa, including most species of lianas (Laurance et al. 2001a, Schnitzer et al. 2004, Parren and Doumbia 2005, Arroyo-Rodriguez and Toledo-Aceves 2009, Ding and Zang 2009, Schnitzer and Bongers 2011). However, the overall response of regional liana species richness to logging varies considerably depending upon the intensity and type of logging applied (Fox 1968, Gerwing and Vidal 2002, Gerwing 2006). Additionally, selective logging of forests has been suggested to unequally impact individual liana species by altering the availability of climbing trellises in certain size classes and thus favoring lianas of certain climbing guilds (Ding and Zang 2009).

The increase in liana abundance in logged forests has received considerable attention given their effects on important timber trees. Timber trees may suffer increased tree mortality and stem deformation in forests with high liana abundance (Putz and Mooney 1991, Ingwell et al. 2010). Lianas also compete with timber trees for light and nutrients, lowering tree growth rates (Schnitzer et al. 2005, Wright et al. 2005, Tobin et al. 2012). It has been suggested that cutting lianas might be a mechanism (but expensive, Perez-Salicrup et al. 2001) by which to improve the value of production forests (Gerwing and Uhl 2002, Alvira et al. 2004, Schnitzer et al. 2004). Liana cutting has also been suggested to improve seed production of certain timber tree species by 50-100% and hence enhance their recruitment (Nabe-Nielsen et al. 2009). However, liana cutting might considerably reduce the conservation value of logged forests by diminishing liana diversity and their valuable role in ecosystem functioning (Schnitzer and Bongers 2002). In particular, the loss of localized liana diversity through deliberate cutting may impact faunal inhabitants by reducing food resources, arboreal walkways and nesting sites (Fig. 2.2, Gentry 1991, Asensio et al. 2007, Thorpe et al. 2009, Ansell et al. 2011, Yanoviak and Schnitzer 2013, Arroyo-Rodríguez et al. 2015). Such practices can have long-term effects on liana communities. For example, after pre-logging liana cutting, the local liana community of one logged forest was found to display a reduction in animal-dispersed liana species (Gerwing and Vidal 2002) and an increase in vegetatively reproducing liana species (Gerwing 2006).

Another intervention prescribed by silviculturalists to decrease liana abundance in logged forests is controlled burning. Burning leads to a disproportionate increase in liana mortality compared with that of trees and consequently is likely to cause a decrease in local liana diversity (Gerwing 2001, Balch et al. 2011). Burning also causes changes in liana community composition, because burn-induced mortality rates vary among different species and size classes of lianas (Balch et al. 2011). Additionally, burning favors liana species that are able to coppice after fires (Gerwing 2001). Finally, previously burnt stands are more susceptible to further burns (Cochrane et al. 1999, Gerwing 2001) and subsequent burn events may further impact liana diversity resulting in a magnified degradation of the liana community.

A better understanding of both the direct and indirect implications of selective logging on liana communities is needed in order to determine the direction and extent of changes to local and regional liana diversity. However, it appears likely that liana diversity will be maintained within selectively logged forests (Ding and Zang 2009) but decline in logged forests where lianas are cut or burnt (Gerwing and Vidal 2002, Balch et al. 2011). Consequently, a balanced perspective between the negative impacts of lianas on timber production and the positive impacts of liana diversity on associated ecosystem functioning and faunal support must be reached when determining regional forest-usage strategies (Gerwing and Vidal 2002).

Figure 2.2 Liana cutting during logging operations may threaten liana diversity and with them their reliant faunal counterparts.

Forest Disturbance

Disturbance of the forest canopy, soil and micro-climatic conditions can occur through both human-induced and natural environmental processes. Spatially, these disturbances can range in size from a single treefall to forest-wide disturbances such as canopy defoliation following cyclones or hurricanes (Turton and Siegenthaler 2004). Small-scale forest disturbance often occurs through treefalls, which usually disturb an area of forest only tens of metres in extent. However, even though a single treefall may be spatially small, the amount of treefall disturbance throughout a forest is closely linked with the maintenance of forest-wide liana diversity (Schnitzer and Carson 2001, Schnitzer and Bongers 2005, Ledo and Schnitzer 2014).

It is believed that abundant treefall gaps maintain liana diversity in forests, as lianas are proportionately more diverse in treefall gaps than other interior forest locations (Schnitzer and Carson 2001, Ledo and Schnitzer 2014). Lianas are successful within treefall gaps as they can both colonize gaps in high numbers and survive in gaps for a long period of time (Schnitzer and Bongers 2005). Lianas take possession of treefall gaps so successfully because as well as colonizing treefall gaps through seed and seedling banks as do trees, they can also colonize through surviving the treefall event itself and subsequently regrowing (Putz 1984b) and through long-distance clonal growth (Penalosa 1984, Yorke et al. 2013). Once lianas have colonized a treefall gap they can survive there for long periods of time, which again enhances their localized diversity (Oliveira et al. 1997, Schnitzer et al. 2000, Schnitzer and Bongers 2005). Lianas are also successful at retaining possession of forest gaps because they often form dense “tangles” in the gap that may prevent tree-seedling establishment and damage tree saplings (Fig. 2.3, Schnitzer and Carson 2010). Liana proliferation in treefall gaps may stall tree succession by increasing tree mortality, which may even change the successional trajectory of the gap vegetation (Schnitzer et al. 2000, Schnitzer and Carson 2001, Schnitzer and Bongers 2005, Schnitzer and Carson 2010). Consequently, small-scale disturbance of tropical forests through treefalls often leads to the maintenance of high regional liana diversity (Schnitzer and Carson 2001, Dalling et al. 2012, Anbarashan and Parthasarathy 2013, Ledo and Schnitzer 2014).

Large-scale disturbance of tropical closed-canopy forests can occur through anthropogenic processes such as forest fragmentation, climate change (such as an increase in intensity and frequency of cyclones or droughts) and selective logging. Following the large-scale disturbance of a forest, liana diversity peaks as the forest reaches an intermediate successional age and then may slowly decline in mature forest (DeWalt et al. 2000, Letcher and Chazdon 2009a). It has been suggested that the peak in liana diversity in intermediate-aged forest corresponds with the availability of liana-limiting resources such as light and climbing trellises within the forest (Putz 1984b, DeWalt et al. 2000). In addition, liana recruitment into forests may increase by up to 500% after disturbance (Benitez-Malvido and Martinez-Ramos 2003). However, such recruitment is not even across all liana species and thus the disturbance may alter local liana-community composition and possibly reduce overall local liana diversity (Benitez-Malvido and Martinez-Ramos 2003). Finally, recent studies suggest that excessive disturbance of a forest may result in a collapse of local liana diversity (Addo-Fordjour et al. 2009, Addo-Fordjour et al. 2012a, Addo-Fordjour et al. 2013).

Globally, there is a prodigious amount of tropical forest currently suffering from myriad anthropogenic disturbances (Achard et al. 2002, Hansen et al. 2008, Haddad et al. 2015). This is likely to increase in future as humanity places more demands on the resources of tropical forests (e.g. Seto et al. 2012, Gerland et al. 2014, Laurance et al. 2014c). However, disturbed future tropical forests are likely to maintain high regional liana diversity if these disturbances can be managed so that they are both spatially and temporally variable and of low to medium intensity.

Figure 2.3 Liana tangles in treefall gaps limit tree regeneration during forest succession and enable the maintenance of localized liana diversity**.**

Climate Change

Long-term changes in liana communities within undisturbed forests are currently occurring (Phillips et al. 2002, Wright et al. 2004, Laurance et al. 2014b). In particular, researchers have observed that liana abundance, recruitment, productivity and biomass have been increasing, at least in the New World tropics (Wright et al. 2004, Laurance et al. 2014b). Three main hypotheses have been proposed to explain the increase in liana abundance in undisturbed forests:

1. Elevated atmospheric CO_2 concentration is enabling increased liana growth and fecundity (Granados and Korner 2002, Körner 2009, however see Marvin et al. 2015);

2. Seasonal droughts (Fu et al. 2013, Cai et al. 2014) disproportionately benefit lianas as they are often more resilient to dry conditions than trees (Schnitzer 2005, Cai et al. 2009, Chen et al. 2015), and;
3. Increasing tree mortality and turnover in forests is creating additional treefall gaps, which favors lianas (Putz 1984b, Schnitzer et al. 2000, Dalling et al. 2012).

These mechanisms are not mutually exclusive and it is possible that a combination of all three is leading to the observed changes (Laurance et al. 2014a). However, recent research comparing leaf-chemical traits in trees and lianas across the tropics (Asner and Martin 2012) suggests that the systematic differences found between trees and lianas in leaf nutrient concentrations (in particular N, P and Ca) may act to favor the growth of lianas under elevated CO_2. This finding gives more importance to CO_2 fertilization as a potential major driver of rising liana productivity (Granados and Korner 2002, Korner 2004, Laurance et al. 2014b, however see Marvin et al. 2015). Although the findings mentioned above specifically relate to liana abundance and productivity increases, this long-term trend could influence regional liana diversity as well. If the increase in liana abundance and productivity in response to increasing atmospheric CO_2 concentration is species specific (Condon et al. 1992), the liana community composition within forests may be altered. As such, studies to determine, whether and how, long-term changes in liana diversity in undisturbed forests are occurring in apparent response to climate change and rising atmospheric CO_2 concentration should be a priority.

In addition to increasing atmospheric CO_2 concentration, a current gradual increase in El Niño Southern Oscillation (ENSO) intensity and the amplitude of its oscillations might intensify droughts across many tropical forests, especially those of the western Pacific (Tudhope et al. 2001, Malhi and Wright 2004, Power et al. 2013, Cai et al. 2014). As mentioned above, intensified droughts or extended dry seasons may give lianas a competitive advantage over trees in tropical forests (Schnitzer 2005, DeWalt et al. 2010, however see van der Sande et al. 2013, Chen et al. 2015). Continued drought might also contribute to increased tree mortality and turnover, facilitating forest disturbance and favoring lianas (Ledo and Schnitzer 2014). However, if these droughts result in excessively depleted deep-soil moisture, liana mortality may also increase (Nepstad et al. 2007), potentially leading to a localized diversity decline. As well as increased drought-induced liana mortality, future climatic conditions may lead to the demise of suitable host trees (Laurance et al. 2001b, Nepstad et al. 2007), potentially resulting in negative, indirect consequences for liana diversity, as host-tree availability has been identified as a major determinant of liana success (Heijden and Phillips 2008, Arroyo-Rodriguez and Toledo-Aceves 2009, Addo-Fordjour et al. 2012b).

A final future impact of climate change that may result in increased tree turnover in tropical closed-canopy forests is a predicted increase in the frequency and intensity of cyclones (also known as hurricanes or typhoons)(Emanuel 2005, Elsner et al. 2008, Mendelsohn et al. 2012). These intense events often destroy much of the canopy cover of affected forests, leading to high-disturbance and high-light conditions (Turton and Siegenthaler 2004). In addition, forests in cyclonic and hurricane zones may not reach successional maturity due to high levels of disturbance and tree turnover (Whigham et al. 1991). As a consequence of these cyclonic impacts and their associated environmental conditions, liana abundance and diversity may increase at the expense of local tree abundance and diversity (Webb 1958, Putz 1984b, Allen et al. 2005).

Hunting

The unsustainable hunting of vertebrates is one of the more insidious anthropogenic impacts influencing modern tropical forests, with important indirect impacts on their resident liana diversity. Unsustainable hunting occurs on a vast scale throughout the tropics with very few regions not touched by its influence (Bennett et al. 2002, Corlett 2007, Peres and Palacios 2007, Abernethy et al. 2013). Moreover, hunting often occurs simultaneously with, and is promoted by, other forest-degrading processes such as logging and road construction (Laurance et al. 2009, Laurance et al. 2014c). Hunting is a major threat to targeted faunal communities, whose localized extirpation may lead to the demise of seed predators and dispersers and thus substantially impact many plant species (Muller-Landau 2007, Wright et al. 2007). For instance, the competitive ability of large-seeded liana species may be improved (Wright et al. 2007) due to decreased predation by hunted fauna (however see Peres and Palacios 2007). Additionally, the localized extirpation of animal seed dispersers may favor wind-dispersed liana species (Fig. 2.4, Wright et al. 2007).

Neotropical liana communities have a disproportionate representation of wind-dispersed species (Gentry 1991) and appear to be regenerating increasingly well in forests that have been hunted (Wright et al. 2007). Thus, wind-dispersed lianas are likely to maintain their diversity and potentially increase their abundance in heavily hunted Neotropical forest regions. However, the competitive ability of animal-dispersed lianas in these regions may decline, altering liana community composition. Outside the Neotropics, in some tropical regions such as north Queensland (Australia), the majority of liana species bear fleshy fruits (Australian tropical rainforest plants edition 6.1 2010). The lianas in these regions require animal dispersers and thus may suffer much of the negative consequences of hunting that their fleshy-fruited tree counterparts do (Muller-Landau 2007, Wright et al. 2007). Of course, the degree to which hunting influences liana seed dispersal or predation depends on the prevalence of hunting within the particular region (which is minimal in tropical Australia). As a result, the impact of hunting on regional liana diversity and community composition will likely be region-specific and determined by the combination of hunting intensity and the proportion of animal- and wind-dispersed lianas within the local flora.

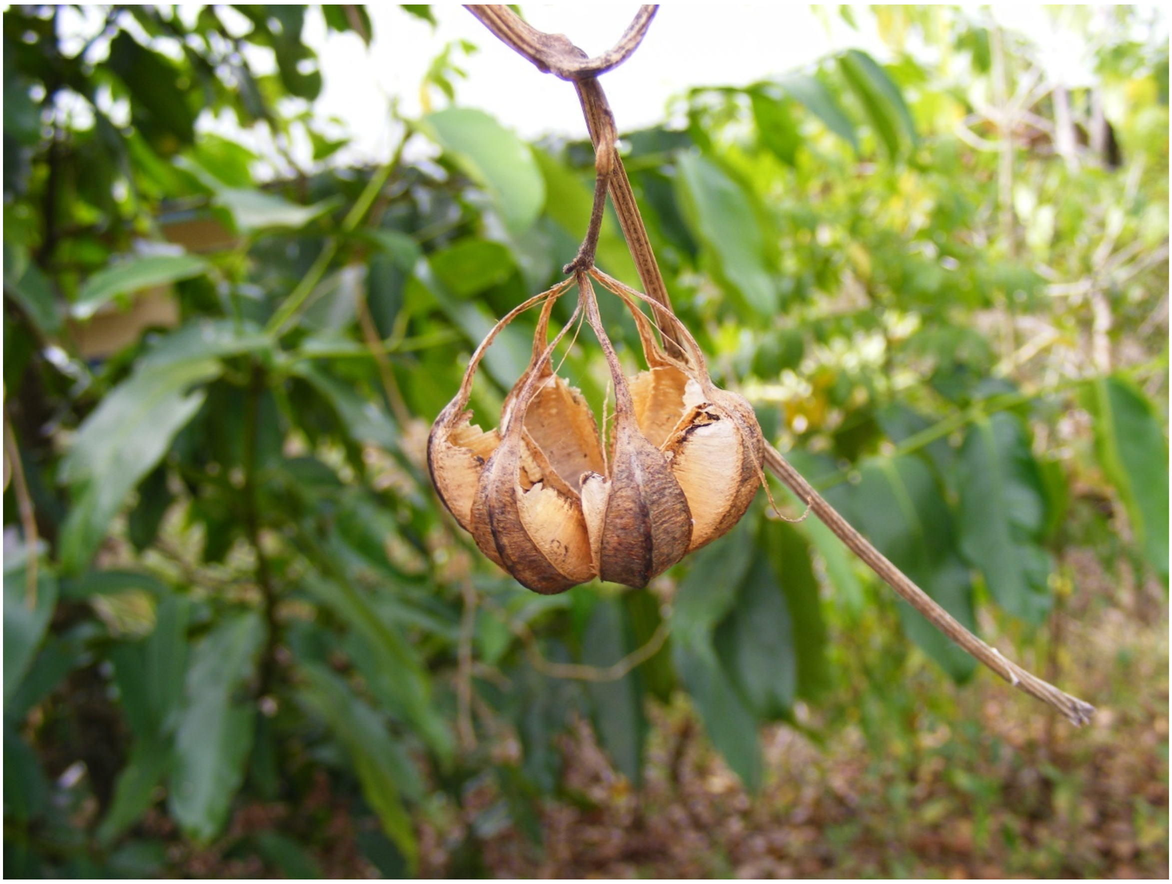

Figure 2.4 An empty seed pod of the wind-dispersed liana *Aristolochia acuminata* Lam. after a successful dispersal event. Hunting is suggested to competitively advantage wind-dispersed liana species over those dispersed by animals, as wide-scale, unsustainable hunting results in the localized extirpation of many bird and mammal species throughout the tropics.

Conclusion

Human impacts on tropical closed-canopy forests are unequivocally modifying regional liana diversity patterns. Besides substantial liana-diversity declines in tropical regions experiencing deforestation, human impacts are also modifying liana diversity in the remaining forests in an often complex manner. To continue to unravel these patterns I suggest that researchers focus specifically on assessing liana-diversity responses to each human impact. It appears that the often-overarching changes in liana abundance and biomass found in many studies to date may ‘drown out’ any fine-scale changes in liana community composition. In fact, when examined closely, it seems that many of the human impacts on tropical forests studied to date may be unequally favoring certain guilds or species of lianas at the expense of others (Tab. 2.1). Consequently, although liana abundance may remain high in the human-impacted forests of the future, it appears likely that their community compositions will be altered (Tab. 2.2). Given the complexity of ecological interactions within tropical forests, any alteration to liana community composition is likely to have a variety of flow-on effects for ecosystem functioning and for fauna that rely on liana resources (Gentry 1991, Yanoviak and Schnitzer 2013).

Table 2.1 Liana traits influenced by human impacts on tropical closed-canopy forests.

Human impact on tropical forest	Liana traits favored	Liana traits disadvantaged	Source(s)
Deforestation and Forest Fragmentation	Spatially common	Spatially rare	Laurance et al. (1999)
Forest Fragmentation	Forest edge specialists/full sun-tolerant	Forest interior specialists/full sun-intolerant	Arroyo-Rodriguez and Toledo-Aceves (2009) Laurance et al. (2001a) Mohandass et al. (2014) Zhu et al. (2004)
Forest Fragmentation and climate change	Desiccation tolerant species	Desiccation intolerant species	Cai et al. (2009) Schnitzer (2005)
Burning (logging management practice)	Fire tolerant	Fire intolerant	Balch et al. (2011) Gerwing (2001)
Logging	Persistent seed bank, Re-sprouting/ coppicing from fallen and prostrate stems	Non-persistent seed bank (unless reduced impact logging), No re-sprouting/ coppicing from fallen and prostrate stems	Gerwing (2006) Gerwing and Vidal (2002)
Logging (Mid successional stage)	Stem-twining climbers	Tendril climbers	Ding and Zang (2009)
Logging (Early successional stage)	Tendril climbers	Stem-twining climbers	DeWalt et al. (2000) Muthuramkumar and Parthasarathy(2000)
Forest disturbance	Species using stolon/clonal treefall gap colonization	Species not using stolon/clonal treefall gap colonization	Penalosa (1984) Yorke et al. (2013)
Forest disturbance	Disturbance induced germination	Non- disturbance induced germination	Benitez-Malvido and Martinez-Ramos (2003)
Climate change	Species more receptive to elevated CO_2	Species less receptive to elevated CO_2	Condon et al. (1992) Granados and Korner (2002) Korner (2009)
Hunting (seed predation)	Large seeded species	Small seeded species	Wright et al. (2007)
Hunting (seed dispersal)	Wind dispersal	Animal dispersal	Wright et al. (2007)

Table 2.2 Human impacts and their effect on regional liana diversity.

Human impact on tropical forest	Impact	Reason	Source(s)
Deforestation	Regional liana diversity decline	Direct loss of lianas and loss of liana host trees	Laurance et al. (1999)
Forest fragmentation	Maintenance or proportional increase in regional liana diversity	Increased availability of forest edge habitat	Arroyo-Rodriguez and Toledo-Aceves (2009) Laurance et al. (2001a) Mohandass et al.(2014) Zhu et al. (2004)
Forest fragmentation	Regional liana diversity decline and community composition change	Differential species recruitment following disturbance	Benitez-Malvido and Martinez-Ramos (2003)
Forest fragmentation	Regional liana diversity decline	Direct loss of lianas or loss of suitable host trees	Addo-Fordjour et al. (2012b) Arroyo-Rodriguez and Toledo-Aceves (2009) Laurance et al. (1999) Heijden and Philips (2008)
Logging and associated forest management practices	Liana community composition change	Alteration in availability of climbing trellises	Ding and Zang (2009)
Logging and associated forest management practices	Regional liana diversity decline and community composition change	Forest burning and liana cutting	Balch et al. (2011) Chittibabu and Parthasarathy (2001) Gerwing (2001, 2006) Gerwing and Vidal (2002)
Forest disturbance	Maintenance or proportional increase in regional liana diversity	Enhanced resource availability and suitable growing conditions	Anbarashan and Parthasarathy (2013) Laurance et al. (2001a) Ledo and Schnitzer (2014) Malizia and Grau (2008) Schnitzer and Bongers (2002, 2013) Schnitzer and Carson (2001)
Forest disturbance	Regional liana diversity decline	Heavy disturbance may result in the direct damage of lianas and loss of host trees	Addo-Fordjour et al. (2012b, 2013)
Climate change	Liana community composition change	Species specific response to increased atmospheric CO_2	Condon et al. (1992) Granados and Korner (2002) Korner (2009)
Hunting	Liana community composition change	Loss of pollinators and seed predators and dispersers	Wright et al. (2007)

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Chapter 3 Tropical forest fragmentation increases liana abundance and alters liana-host tree interactions

This chapter is based upon a paper in preparation:

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Statement of contribution of others:

Campbell collected the data with some initial assistance from Magrach. Campbell analyzed the data with advice from Edwards. Campbell wrote the first draft of the chapter. The subsequent drafts were revised by Campbell with editorial input from Edwards and Laurance. Campbell created the figures and tables.

Abstract

Closed-canopy forests are being rapidly fragmented across much of the tropical world. Determining the impacts of fragmentation on ecological processes enables better management and improves species-conservation outcomes. Lianas are ubiquitous in the tropics and have detrimental and potentially complex interactions with their host trees. These effects can include reduced tree growth and fecundity, elevated tree mortality, alterations in tree-species composition, degradation of forest succession, and a substantial decline in forest-carbon storage. I examined the impact of fragmentation on the liana community and liana-host tree interactions in rainforests of the Atherton Tableland in north Queensland, Australia. I compared the liana and tree community, the traits of liana-infested trees, and determinants of the rates of tree infestation within five forest fragments (23-58 ha in area) and five nearby intact-forest sites. Fragmented forests experienced considerable disturbance-induced degradation at their edges, resulting in a significant increase in liana abundance. This effect penetrated to significantly greater depths in forest fragments than intact forests. Additionally, the composition of the liana community in terms of climbing guilds was significantly different between fragmented and intact forests, likely because forest edges had more small-sized trees favoring particular liana guilds which preferentially use these for climbing trellises. Sites that had higher liana abundances also exhibited higher infestation rates of trees, as did sites with the largest lianas. However, large lianas were associated with low disturbance forest sites. In conclusion, forest fragmentation significantly altered the abundance and community composition of lianas and their ecological relationships with trees, with liana impacts on trees being elevated in fragments relative to intact forests.

Introduction

Habitat fragmentation is globally ubiquitous (Wade et al. 2003, Bhagwat 2014, Riitters et al. 2016). In fact, it is currently estimated that 70% of the world's remaining forest is within 1 km from a forest edge (Haddad et al. 2015). This is important as the fragmentation of forests and associated edge effects can reduce biodiversity and degrade forest functioning (e.g. Saunders et al. 1991, Laurance et al. 2000, Laurance et al. 2002, Fahrig 2003, Laurance et al. 2011, Magrach et al. 2014a). For instance, forest fragments are estimated to possess 13-75% less diversity than comparable non-fragmented forests (Haddad et al. 2015) with the majority of the lost diversity often the most iconic components, such as big trees and large mammals (Laurance 1997b, Chiarello 1999, Laurance et al. 2000, Oliveira et al. 2008, Gibson et al. 2013). In addition, forest fragmentation is also known to alter or degrade many beneficial ecological processes, such as pollination and seed dispersal, which occur between the remnant biota (Terborgh et al. 2001, Laurance et al. 2002, Magrach et al. 2014a, Peh et al. 2014, Campbell et al. 2015a).

In the tropics, large-scale deforestation has resulted in forest fragments now representing a substantial proportion of the remaining forested area in many regions such as the Atlantic forest of Brazil, West Africa, and the Atherton Tableland of northeastern Australia (Winter et al. 1987, Ribeiro et al. 2009, Ouedraogo et al. 2011). In such regions, forest fragments provide the primary or sole repository for the preservation of many rare and endangered species and threatened ecosystems (Guindon 1996, Arroyo-Rodriguez and Mandujano 2006, Arroyo-Rodriguez et al. 2009). Maximizing the conservation values of forest fragments requires that fragments are not only retained, but are managed effectively. Effective management necessitates an understanding of their internal ecology.

One of the major ecological interactions altered by fragmentation is the relationship between trees and lianas (woody vines), as fragmentation has been previously associated with an increase in liana abundance (Laurance 1997a, Laurance et al. 2001a, Magrach et al. 2014b). Lianas detrimentally impact trees by limiting seedling recruitment, damaging saplings, decreasing tree growth and fecundity, competing with trees for limited resources, and increasing tree mortality (Stevens 1987, Schnitzer et al. 2000, Schnitzer et al. 2005, Ingwell et al. 2010, Schnitzer and Carson 2010, Pasquini et al. 2015, Reid et al. 2015). In addition, lianas can modify the functioning of a forest by reducing carbon storage capacity (Durán and Gianoli 2013, Heijden et al. 2013, Schnitzer et al. 2014), re-distributing nutrients (Powers et al. 2004, Schnitzer and Bongers 2011, Kazda 2015), altering tree-species composition (Clark and Clark 1990, Laurance et al. 2001a, Schnitzer and Bongers 2002), threatening epiphytic ferns (Magrach et al. 2014b), and limiting or changing the trajectory of tree-species succession within treefall gaps (Schnitzer et al. 2000, Schnitzer and Carson 2001, Schnitzer and Bongers 2005, Schnitzer and Carson 2010). Thus, lianas have significant impacts on both the biota and functioning of remnant forest fragments. Understanding the ecological interactions between lianas and their host trees is critical for successfully managing remnant forest fragments, especially those with high conservation value.

There is strong support for the observation that lianas preferentially impact certain ecological “guilds” of tree species such as late-successional/climax species (Clark and Clark 1990, Schnitzer et al. 2000, Laurance et al. 2001a, Campbell et al. 2015a), although there is little evidence that this occurs at a species-specific level (Hegarty 1991b, Pérez-Salicrup et al. 2001, Garrido-Perez and Burnham 2010). The enhanced liana infestation rates in particular tree guilds is likely due to their advanced age (and thus time available for possible infestation) and the character traits they possess (Hegarty 1991b, Schnitzer and Bongers 2002). Such traits include bark morphology and chemical composition (Putz 1980, Boom and Mori 1982, Talley et al. 1996, Carsten et al. 2002, Heijden et al. 2008), buttresses (Black and Harper 1979, Putz 1980, Boom and Mori 1982), leaf shedding and leaf and stem flexibility (Maier 1982, Putz 1984a, Rich et al. 1987), tree/trellis diameter (Putz 1984b, Clark and Clark 1990, Pérez-Salicrup et al. 2001, Perez-Salicrup and de Meijere 2005), spines (Maier 1982, Putz 1984a, Rich et al. 1987), liana-host distance and availability (Muthuramkumar et al. 2006, Arroyo-Rodriguez and Toledo-Aceves 2009, Roeder et al. 2015), liana phylogeny (Zulqarnain et al. 2016) and synergisms among these traits (Sfair et al. 2016). As such, a comparative assessment of the tree traits between intact and fragmented forests, and their association with liana infestation, may be of use as a proxy to determine how forest fragmentation impacts liana-tree interactions and contributes to increased liana abundance within fragmented forests (Laurance et al. 2001a).

The total abundance of lianas is known to be positively associated with forest edges and areas of disturbance (Putz 1984b, Laurance et al. 2001a, Laurance et al. 2014b, Ledo and Schnitzer 2014, Magrach et al. 2014b, Mohandass et al. 2014). High liana abundances at forest edges is likely due to edge effects (e.g. Williams-Linera 1990, Murcia 1995, Laurance et al. 2002, Harper et al. 2005), in particular to the increased availability of climbing trellises (i.e. smaller-stemmed trees) (Putz 1984b, Williams-Linera 1990, Balfour and Bond 1993, Chittibabu and Parthasarathy 2001, Londre and Schnitzer 2006). Moreover, forest edges are often more disturbed than forest interiors (Laurance et al. 1997, Laurance et al. 2000, Laurance and Curran 2008, Briant et al. 2010, Laurance et al. 2011, Magnago et al. 2015) resulting in increased desiccation and light levels. These conditions preferentially favor lianas over trees, through mechanisms such as differential recruitment success and resource-interception capacity (Oliveira et al. 1997, Perez-Salicrup and Barker 2000, Andrade et al. 2005, Schnitzer and Carson 2010, Ledo and Schnitzer 2014, Chen et al. 2015). Consequently, it is important that any study of liana-tree interactions examine the spatial distribution of lianas in relation to forest edges.

Analyzing the abundance of lianas within guilds between intact and fragmented forests can also be used to assess liana-host tree interactions. For example, assessing the proportion of lianas within climbing guilds can reveal the current trellis availability and thus the successional state of the forest (Putz 1984b, Hegarty and Caballe 1991, Laurance et al. 2001a, Mohandass et al. 2014). This is possible because lianas within different climbing guilds utilize trellises of differing maximal diameter (Putz 1984b, Putz and Chai 1987, Putz 1990a, Balfour and Bond 1993). For instance, climbers that attach with adhesive roots are not limited by trellis (i.e. tree branch or trunk) size, whereas main-stem twining and branch climbers use larger trellises (branches) than do tendril and hook climbers (Putz 1984b, Putz and Chai 1987, Putz 1990a, Balfour and Bond 1993).

Here I compare the response of lianas to forest fragmentation and liana-host tree interactions in fragmented and intact forests, within the heavily fragmented landscape of the Atherton Tableland in northeastern Australia. In this study I aimed to a) determine the influence of fragmentation on liana abundance, tree infestation rates, and liana size (diameter at breast height [DBH]) by identifying the environmental and ecological predictors associated with these measures at the landscape level (fragmented vs intact forests). I also assessed b) whether tree morphological traits (tree bark type, or buttressing) and their location, with respect to the forest edge, influenced liana infestation rates within fragmented and intact forests. Finally, I examined c) whether the liana community climbing-guild composition varied by forest type (fragmented or intact) and how this relationship was affected by the distance to the forest edge.

Methods

Study Area

My study was located on the Atherton Tableland, north-eastern Queensland, Australia (Fig. 3.1 a). The Atherton Tableland is an upland, hilly plateau ranging in elevation from ~600-1100 m. Mean annual precipitation of sites within the study area range from 1400-3000 mm due to a localized north-west (low) to south-east (high) rainfall gradient. Irrespective of mean rainfall, all sites receive most of their annual rainfall during a pronounced wet season from January to April. The area is also prone to cyclonic episodes during the wet season with 45 cyclonic impacts recorded for the Wet tropics bioregion (within which the Atherton Tableland is found) over the period 1858–2011 (Turton 2012). Cyclonic impacts cause increased precipitation and wind damage in affected forests (Turton and Siegenthaler 2004, Turton and Stork 2009).

The local vegetation of the study area are remnants and regrowth of a larger rain forest expanse that previously covered the Atherton Tableland, now isolated by a predominantly agricultural land-use matrix (Fig. 3.1 a). Deforestation of this area has been extensive with over 76,000 ha cleared for cattle pasture and crop lands (Winter et al. 1987). Much of the remaining forested areas are isolated forest fragments in an agricultural land-use matrix of cattle pastures, croplands, and rural residences (Winter et al. 1987, WTMA Management 2009). Additionally, most of the remnant rain forest vegetation has been selectively logged for valuable hardwood timber species such as Red Cedar (*Toona ciliata*) (Society 1979, 1995, Pearson 2008). Nevertheless, many of these forest fragments form a large part of the greater Wet Tropics World Heritage area (UNESCO 1988). In a global analysis of mammal, bird, and amphibian faunal conservation values, this area ranked as the second most irreplaceable natural World Heritage site, the sixth overall in terms of global irreplaceability on the basis of all species, and eighth on the basis of threatened species (Bertzky et al. 2013, Le Saout et al. 2013).

The remnant vegetation of the area is described as complex mesophyll vine forest and notophyll vine forest (regional ecosystem 7.8.2 and 7.8.4), with drier areas transitioning into complex semi-evergreen notophyll vine forest (regional ecosystem 7.8.3) (Tracey 1982, Herbarium 2015). Within the complex mesophyll vine forest, multiple intact canopies may be present with the upper canopy averaging a height of 20-40m and emergent trees reaching to 55m (Tracey 1982, Herbarium 2015). Deciduous tree species are rare; however woody lianas, epiphytes and ferns are common resulting in a complex forest structure (Tracey 1982).

Fragments are generally found overlying volcanic soils, namely krasnozems, and topographically occur on level to gently undulating plains and gently undulating to undulating rises (Malcom et al. 1999). Intact forests are mostly located on steeper mountainous areas that were less conducive to logging and on relatively nutrient-poor granite and rhyolite-derived soils that restricted their suitability to agriculture (Malcom et al. 1999).

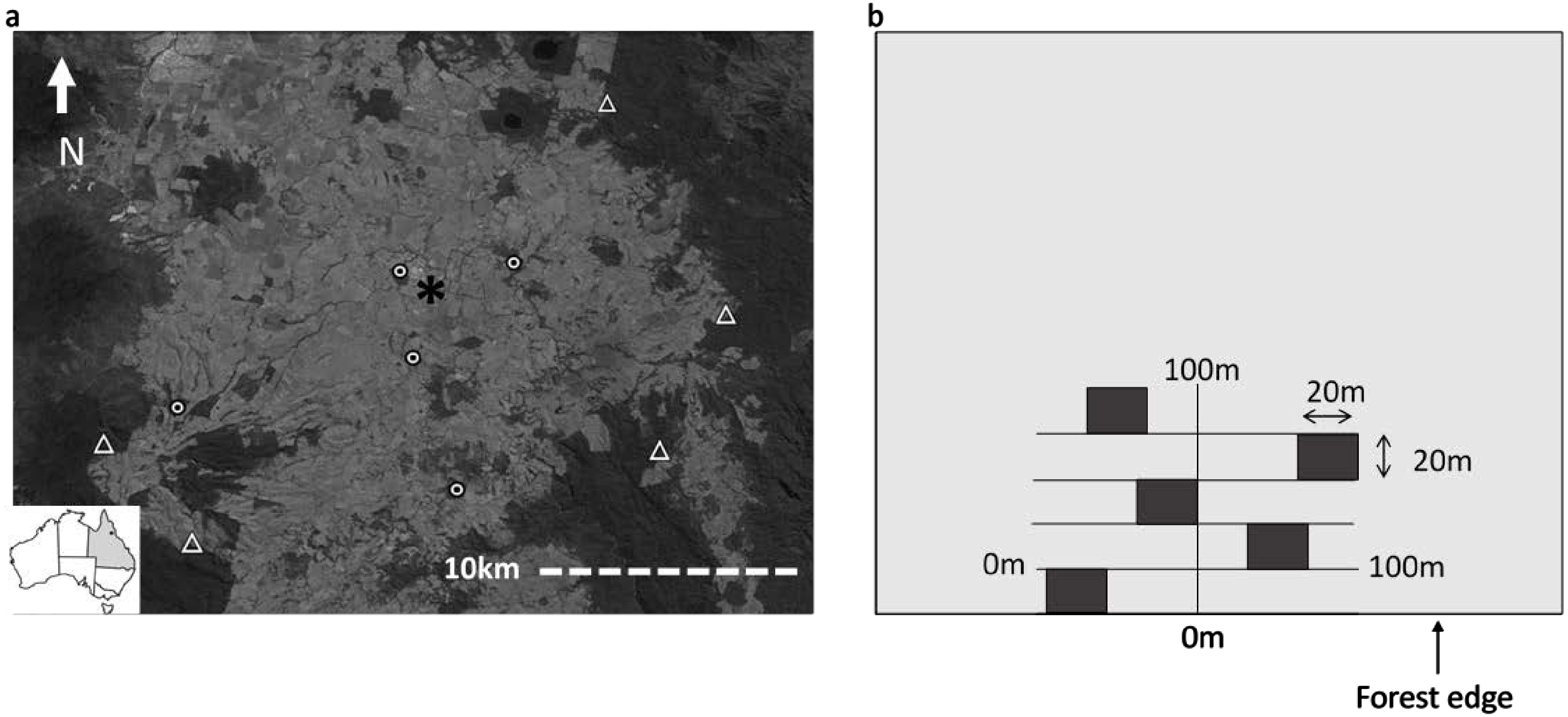

Figure 3.1 a) Location of the ten study sites on the Atherton Tablelands, Australia. Study sites are indicated as triangles for intact forests and circles for fragmented forest. Malanda as the nearest town is indicated with an asterix; **b)** Illustrates the design of vegetation sampling at each study site wherein five 20 x 20 m plots were stratified and randomly placed with respect to the forest edge.

Study sites and sampling design

Ten sites were selected for study, comprising five forest fragments and five sites in nearby intact rain forest (Fig. 3.1 a). Forest fragments were selected to minimize variation in total area, ranging from 23-58 ha, and thus limit patch-area effects on liana abundance (Laurance et al. 2001a, Mohandass et al. 2014). Intact-forest sites were selected to be as close as possible to the fragments, with the largest between-site distance for all sites being <23 km. Inter-site distance was minimized to lessen variation in environmental variables known to influence liana abundance; in particular rainfall, elevation, and soil type (Laurance et al. 2001a, Schnitzer and Bongers 2002, Schnitzer 2005, DeWalt et al. 2010, DeWalt et al. 2015). Finally, fragments were selected to ensure that they were all created prior to 1950 (i.e. ⩾ 60 years since isolation) and are currently surrounded by cattle pastures to lessen possible confounding effects of fragment age or surrounding matrix type.

At each site I used a linear transect to establish five 20 x 20 m plots stratified at 5 distance classes perpendicular to the forest edge (0–20 m, 20–40 m, 40–60 m, 60–80 m, 80–100 m; Fig. 3.1 b). This design was used because edge effects are known to significantly influence liana abundance (Laurance et al. 2001a, Laurance et al. 2014a, Magrach et al. 2014b) and result in ecological and environmental changes in fragmented landscapes (e.g. Williams-Linera 1990, Murcia 1995, Laurance et al. 2002, Harper et al. 2005). At each distance, plots were randomly located along a 100 m-long transverse transect (Fig. 3.1 b) to increase their statistical independence.

Liana measures

From March 2012 to February 2014, liana abundance, DBH, and climbing guild were determined for each liana within all individual plots at each of the 10 sites. Liana abundance was determined by counting all liana stems ⩾1 cm DBH within each plot. Unless clearly joined, stems were assumed to be individual lianas (genets) but were not excavated to determine whether each stem was linked to nearby stems (vegetatively propagated ramets). The location for DBH measurement of each liana stem was determined as per current methodology (Gerwing et al. 2006, Schnitzer et al. 2006, Schnitzer et al. 2008). Additionally, each liana was assigned to one of five climbing guilds: mainstem twiner, branch twiner, tendril climber, root climber, and scrambler (Putz 1984b) and trees (⩾10 cm DBH) used as climbing supports were identified and given a unique tag number.

Environmental and structural parameters of fragmented and intact forests

To characterize the environmental and ecological conditions of fragmented and intact forest sites I examined physical and structural parameters of forests which are known to influence liana abundance, identified using the liana literature. Parameters examined included: canopy cover (%), number of fallen logs (⩾ 10cm diameter), plot elevation (m), plot slope (degrees), mean annual rainfall (mm), mean dry quarter (July-September) rainfall, plot distance to forest edge (m), tree abundance, tree DBH (cm), tree bark type, tree buttressing and plot carbon storage (tonnes/ha).

To assess forest disturbance two measures were examined for each plot: canopy cover and the number of fallen trees (⩾ 10cm diameter). Canopy cover was estimated at the four corners and the center of each plot, and was measured by averaging four spherical densitometer readings taken facing the cardinal directions (N, E, S, W) at each point. The number of fallen trees (⩾10 cm diameter) was counted within each plot.

To determine physical traits of plots I examined their slope and elevation. The degree of slope of each plot was calculated using a clinometer, whilst elevation of all sites was assessed using climatic model interpolations data provided by the Wet Tropics Management Authority, Cairns, Australia (WTMA 2009). These data were also assessed to determine the annual rainfall (mm) and dry quarter rainfall (July-September, mm) of sites.

The structural parameters of fragmented and intact forest sites were examined through assessment of the resident rattan (*Calamus* spp.) population, tree population and plot live carbon storage assessment. Relative rattan abundance was recorded for each plot. At the four corners of each plot, line intercept transects of 3 m were established in the four cardinal directions. Along these transects, individual rattan stems that intercepted the line, and up to 1.8 m in height above it, were counted. For each plot, the 16 transect values were then summed to produce a relative abundance estimate of rattan abundance per plot. However, any rattan stems that intercepted the line transect but could be distinguished as coming from a previously encountered rattan clump were disregarded.

The tree population was assessed by counting all trees (⩾10 cm DBH) within each plot and measuring their DBH at 1.3 m height or above any buttresses. Trees were also scored into bark type categories of “smooth”, “rough”, or “shedding” and buttress categories of “present” or “absent”. These classifications were visually determined by the same researcher throughout the study (MJC).

Live plot carbon storage was estimated by combining carbon above ground estimates of all live trees ⩾ 10cm and lianas ⩾ 1cm within a plot. Initially, liana biomass was calculated using the liana specific allometric equation developed by Schnitzer et al. (2006):

$$AGB = \exp[-1.484 + 2.657 \ln(D)]$$

In this model, D is the diameter at 130 cm from the roots (with the location determined as per Gerwing et al. (2006)) expressed in centimetres, while AGB is the predicted above ground oven-dry weight of the liana in kilograms.

Tree above ground biomass (ABG) was calculated using the allometric equation developed by Chave et al. (2005) (see below) as Preece et al. (2012) compared the accuracy of multiple biomass estimation methods for forests within the Wet Tropics bioregion and concluded that the Chave et al. (2005) allometric provided the best and most reliable estimate for the region. To convert AGB into biomass carbon storage I used a conversion factor of 0.47 which is the recommended value from the Intergovernmental Panel for Climate Change for tropical forests (IPCC 2006). In addition, AGB was calculated using wood density estimates at the reported default value for Australian tropical forests of 0.5 g cm^{-3} (500 kgm^{-3}) (Department of Climate Change and Energy Department of Climate Change and Energy Efficiency 2010). Consequently, tree AGB estimates were calculated using the following equation:

$$AGB = \rho * \exp(-1.499 + 2.148\ln(dbh) + 0.207(\ln(dbh))^{2} - 0.0281(\ln(dbh))^{3})$$

Where AGB is measured in kg, dbh is measured in cm, and ρ is wood density measured in g cm^{-3}.

Above ground biomass estimates for both lianas and trees were then converted to carbon estimates using the formula:

Carbon = AGB*0.47

Data analysis

Environmental and structural parameters of fragmented and intact forests

Disturbance and forest gap dynamics along with the availability and size of trees (liana supports) are known to be the major drivers of the distribution of lianas within forests (Schnitzer et al. 2000, Schnitzer and Bongers 2005, Schnitzer and Carson 2010, Ledo and Schnitzer 2014). To assess these traits within fragmented and intact forests, canopy cover, tree abundance and tree DBH were compared along with their relationships with the previously identified (see above) environmental and structural parameters (other than tree bark type and buttressing which, due to sample size limitations, were assessed in log-linear models below). The relationship between these response variables and the environmental and structural parameters were compared using individual Generalized Linear Mixed Models (GLMMs) in the glmmADMB (Fournier et al. 2012) and lme4 (Bates et al. 2015) packages.

Prior to model generation I checked for correlated predictor variables following the protocol of Zurr et al. (2010).One variable was subsequently removed the mean dry quarter rainfall. To prevent undue influence of any explanatory variable due to unit of measurement, all explanatory variables used in the model were standardized ((x - mean(x)) / SD(x)). Standardizing in this manner has the additional benefit that the effects sizes of all variables included in the model can be directly compared via model coefficients. Additionally, as there were five plots within each site (stratified by forest edge distance), plots were not fully independent. As such, I included site ID as a random effect. Consequently, in each model-fitting exercise I selected *a priori* a global model in which the response variable (tree abundance, tree DBH and canopy cover) was examined as a function of the following variables (with the response variable removed from this list in their respective GLMM): number of fallen logs (⩾ 10cm diameter), plot elevation (m), plot slope (degrees), mean annual rainfall (mm), plot distance to forest edge (m), tree abundance, tree DBH (cm), and plot carbon storage (tonnes/ha), relative rattan abundance, liana abundance, liana DBH and proportionate liana infestation of trees, canopy cover (%), tree abundance, tree DBH (cm), and interactions between the terms where appropriate. The most parsimonious models were then determined using backwards, stepwise regression with selection based on lowest AIC model values using the drop1 function of Program R (R Core Team 2015). The most parsimonious model was defined as that which included the minimum number of terms to produce the best possible explanation of the response variable (lowest AIC value), and may or may not have contained traditionally significant ($p < 0.05$) variables. Tree abundance was examined using a poisson GLMM, and tree DBH and canopy cover were examined using individual gamma GLMMs with log link. Canopy cover was also logit transformed prior to model initiation.

The influence of fragmentation on liana infestation of trees, liana abundance and liana DBH

Once I had quantified the variation in canopy cover, tree abundance and tree DBH between fragmented and impact forests and their interactions with the environmental and structural parameters, I then construct individual GLMMs to identify the influence of fragmentation on a) the proportion of trees infested by lianas per plot, b) liana abundance per plot, and c) liana size (DBH). All model construction and fitting was performed as per the previous methods (see above). The proportion of trees infested by lianas was examined using a binomial GLMM with a logit link, liana abundance using a negative binomial GLMM, and the liana DBH examined using a gamma GLMM with log link. Furthermore, where examination of the residuals from the final model revealed incorrect model fit, model fit was further improved by including a quadratic term. This occurred after checking residual diagnostics for models describing the proportion of trees infested by lianas and liana abundance, with curvature in both cases related to distance to the forest edge (see results).

Host tree morphology and forest effects

A log linear model (Poisson with log link) was used to determine the relationship between host-tree morphological traits and the impact of forest effects. These were assessed by examining the relationship between the categorical variables of tree buttress presence (yes or no), tree bark type (smooth, rough, or shedding), forest type (fragmented or intact), distance to the forest edge (0-20m, 20-40m, 40-60m, 60-80m and 80-100m), and whether a tree was infested by one or more lianas (yes or no).

Infesting liana climbing guilds, forest type and environmental traits

To determine the relationship between infesting liana traits and the impact of forest effects I used a log linear model as per the tree-host traits model above. I compared the categorical variables: liana climbing guild type (branch climber, hook climber, mainstem twiner, root climber, scrambler, tendril climber, unknown), forest type (fragmented or intact), distance to the forest edge (0-20m, 20-40m, 40-60m, 60-80m and 80-100m), and whether a tree was infested by lianas (yes or no).

All analyses were performed in Program R (R Core Team 2015).

Results

Environmental and structural parameters of fragmented and intact forests

Tree abundance was significantly lower in fragmented forests than in intact forests but was higher on forest edges than forest interiors (Tab. A1). As expected, tree abundance was significantly and positively related to forest live carbon, however, it was significantly and negatively related to altitude (Tab. A1).

Tree size (DBH) was significantly higher in fragmented forests than in intact forests and was also higher in sites with greater canopy cover, at higher altitude, where large lianas were present and sites with greater live forest carbon (Tab. A2).

Canopy cover was significantly lower in fragmented that intact forests and was lower on forest edges than forest interiors (Tab. A3). The reduction in canopy cover also penetrated significantly further into the edges of fragmented than intact forests (Tab.A3). Canopy cover was also found to be significantly and negatively related to altitude (Tab. A3).

Environmental and structural predictors of tree infestation by lianas

Tree infestation by lianas was not significantly related to forest type (fragmented or intact) (Tab. 3.1) with an average of ~29% (S.E. ± 0.024) of trees infested in fragments and ~32 % (S.E.± 0.029) in intact forest. Tree infestation by lianas was significantly and positively related to increasing liana abundance, liana DBH, canopy cover, and mean annual rainfall

(Tab. 1, Fig. 2). Of these parameters, liana abundance had the greatest influence on the proportional liana infestation of trees with the highest relative effect size of 0.517 (S.E. ± 0.079) (Tab 3.1).Tree infestation by lianas significantly decreased with increasing tree abundance but was parabolically related to the forest edge distance with more trees infested by lianas on forest edges and in forest-interior plots and fewer in those plots in between (Tab. 3.1, Fig. 3.2).

Environmental and structural predictors of liana abundance

At the landscape level, I recorded a total liana abundance of 2124 (n) stems. Liana abundance was significantly and positively related to forest fragmentation and an increase in the number of fallen logs in a forest (Tab. 3.2, Fig. 3.3). However, liana abundance significantly decreased with an increase in forest carbon storage (Tab. 3.2, Fig. 3.3). Liana abundance was also significantly and parabolically related to forest edge distance with more lianas on forest edges and in forest-interior plots and fewer in those plots in between (Tab. 3.2, Fig. 3.3). Moreover, there was a significant interaction between forest type (fragmented or intact) and the distance to the nearest forest edge (Tab. 3.2, Fig. 3.3). Of all parameters tested, forest-edge distance had the largest influence on liana abundance with a relative effect size of -0.750 (S.E. ± 0.162) (Tab. 3.2).

Environmental and structural predictors of liana DBH

Liana DBH was significantly and positively related to tree-infestation rates and tree DBH and there was a positive but non-significant relationship between liana DBH and tree abundance (Tab. 3.3, Fig. 3.4). Conversely, liana DBH was negatively related to an increase in liana abundance and site slope (Tab. 3.3, Fig. 3.4). Of the examined parameters, the number of liana infested trees had the largest positive influence on liana DBH with a relative effect size of 0.137 (S.E. ± 0.034; Tab 3. 3). Conversely, liana abundance was the most negatively related parameter to liana DBH with a relative effect size of -0.115 (S.E. ± 0.037) (Tab 3.3).

Host-tree morphology and forest effects on liana-infestation rates

The probability of a tree hosting a liana was primarily determined by its distance to the forest edge, with fragmentation status, tree bark type, or possession of buttresses having a limited affect (Tab. 3.4). However, there was a mildly significant four-way interaction among tree infestation by lianas and forest type, bark type, and buttress presence (Tab. 3.4).

Infesting liana climbing guilds, forest type and environmental traits

Lianas that infested trees varied by both their distance to the forest edge and fragmentation status of the forest patch (Tab. 3.5). Moreover, the abundance of lianas within individual climbing guilds varied, and differences between responses of different climbing guilds was associated with both the distance to the forest edge and forest fragmentation (Tab. 3.5).

Table 3.1 The most parsimonious generalized linear mixed model (binomial) for the influence of forest fragmentation effects and environmental and forest structural parameters on proportional tree infestation by lianas. Forest edge distance = mid- distance of plot to the forest edge (m) and this was analyzed using a quadratic term based on initial residual diagnostics. All explanatory variables were standardized prior to the analysis ((x - mean(x)) / SD(x)).

	Estimate	SE	Z value	P
Intercept	-1.086	0.122	-8.881	< **0.001**
Forest edge distance	-0.040	0.107	-0.379	0.704
Quadratic term forest edge distance ($x_1 + x_1^2$)	0.234	0.102	2.286	**0.022**
Liana abundance	0.517	0.079	6.481	< **0.001**
Tree abundance	-0.232	0.083	-2.798	**0.005**
Liana DBH	0.202	0.064	3.114	**0.001**
Canopy Cover	0.216	0.091	2.364	**0.018**
Mean annual rainfall	0.161	0.063	2.528	**0.011**

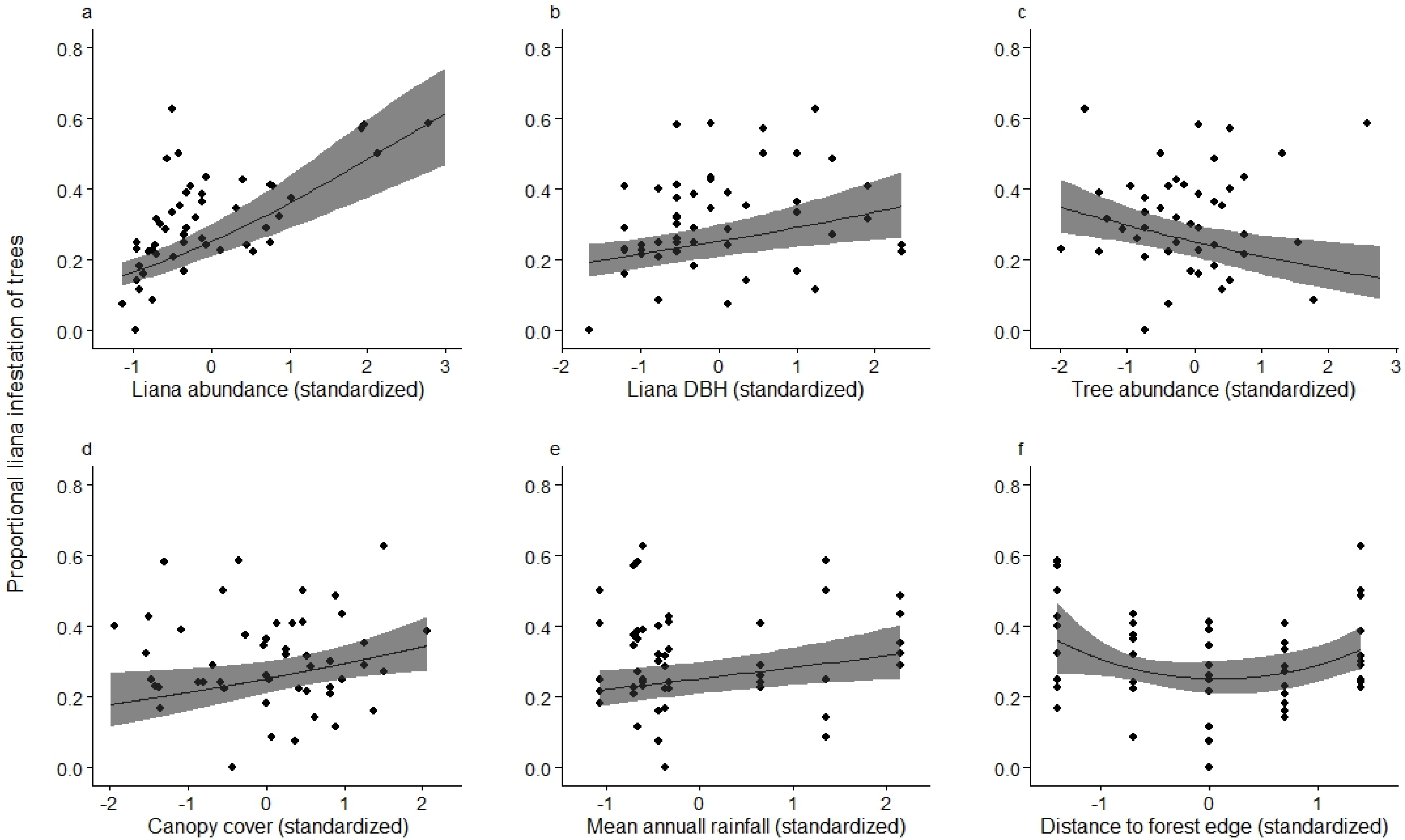

Figure 3.2 The relationship between proportional tree infestation by lianas and **a)** liana abundance, **b)** liana DBH, **c)** tree abundance, **d)** canopy cover**, e)** mean annual rainfall and **f)** mid plot distance to the forest edge. The trend lines are predicted values and shaded areas represent the 95% confidence intervals.

Table 3.2 The most parsimonious generalized linear mixed model (negative binomial) for the influence of forest fragmentation effects and environmental characteristics on liana abundance. Forest edge distance = mid-distance of plot to the forest edge (m) and this was analyzed using a quadratic term based on initial residual diagnostics. All explanatory variables were standardized prior to the analysis ((x - mean(x)) / SD(x)).

	Estimate	SE	Z value	P
Intercept	2.839	0.186	15.25	< **0.001**
Forest edge distance (m)	-0.750	0.162	-4.61	< **0.001**
Quadratic term forest edge distance ($x_1 + x_1^2$)	0.499	0.116	4.27	< **0.001**
Forest type (Fragmented)	0.427	0.202	2.11	**0.035**
Tree abundance	0.180	0.122	1.47	0.140
Carbon	-0.307	0.083	-3.68	< **0.001**
Altitude	0.156	0.092	1.70	0.089
Fallen logs	0.156	0.078	2.01	**0.044**
Canopy cover	0.246	0.142	1.73	0.083
Forest edge distance : Forest type interaction	0.520	0.164	3.16	**0.001**

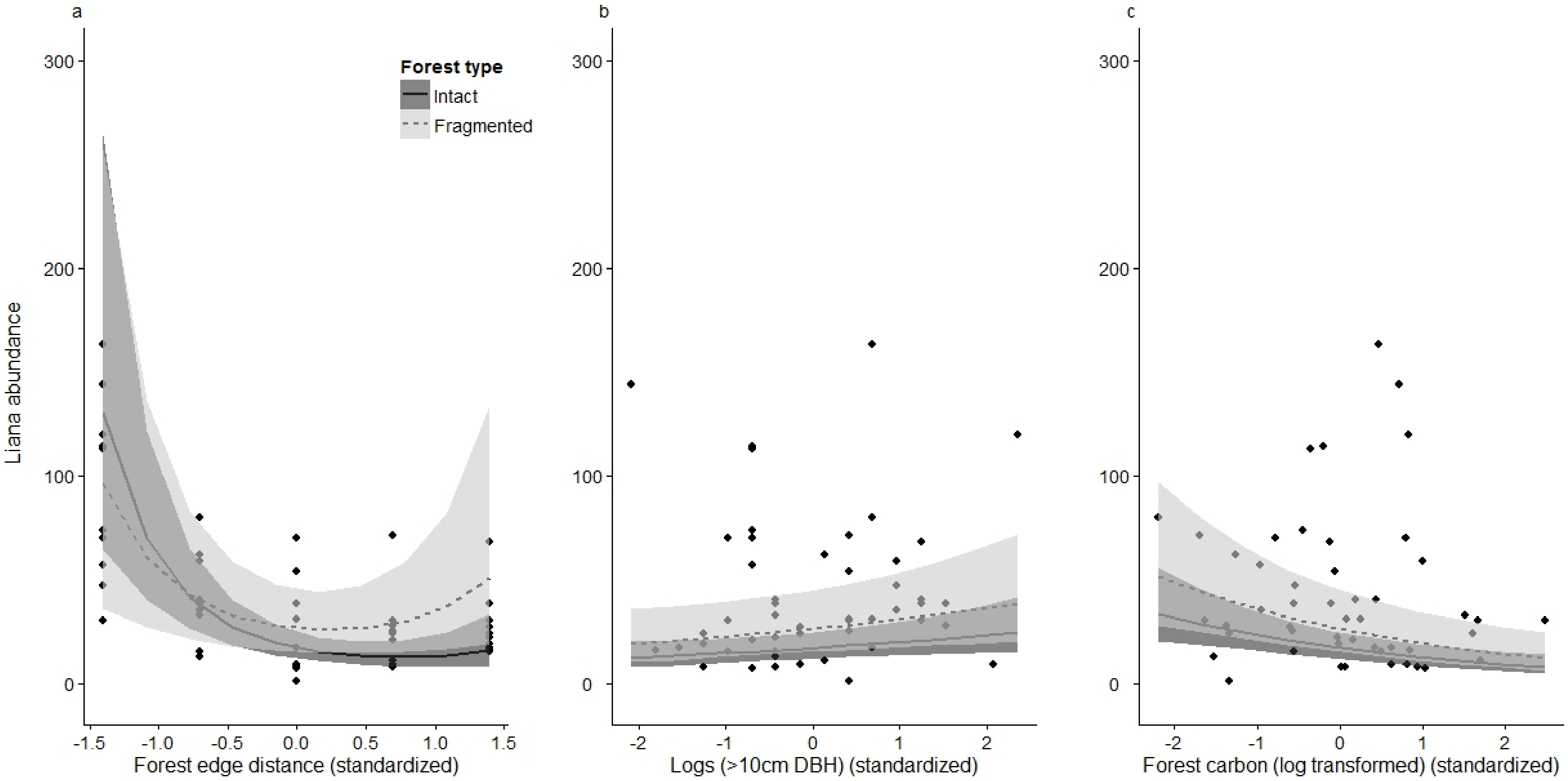

Figure 3.3 The relationship between liana abundance and the interaction of forest type and **a)** distance to the nearest forest edge, **b**) fallen logs, and **c)** stored forest carbon (log10 transformed). The individual trend lines are predicted values and show the significant interaction forest type and forest edge distance. Shaded areas represent the 95% confidence intervals.

Table 3.3 The most parsimonious generalized linear mixed model (gamma log link) for the influence of forest fragmentation effects and environmental characteristics on liana diameter breast height. Liana diameter breast height (cm) was measured as per current standard protocols (Gerwing et al. 2006, Schnitzer et al. 2006, Schnitzer et al. 2008). All explanatory variables were standardized prior to the analysis ((x - mean(x)) / SD(x)).

	Estimate	SE	t value	P
Intercept	0.542	0.026	20.56	< **0.001**
Proportionate liana infestation of trees	0.137	0.034	3.97	< **0.001**
Liana abundance	-0.115	0.037	-3.11	**0.001**
Tree diameter breast height (DBH)	0.073	0.028	2.55	**0.010**
Tree abundance	0.061	0.032	1.92	0.054
Slope	-0.081	0.027	-2.94	**0.003**

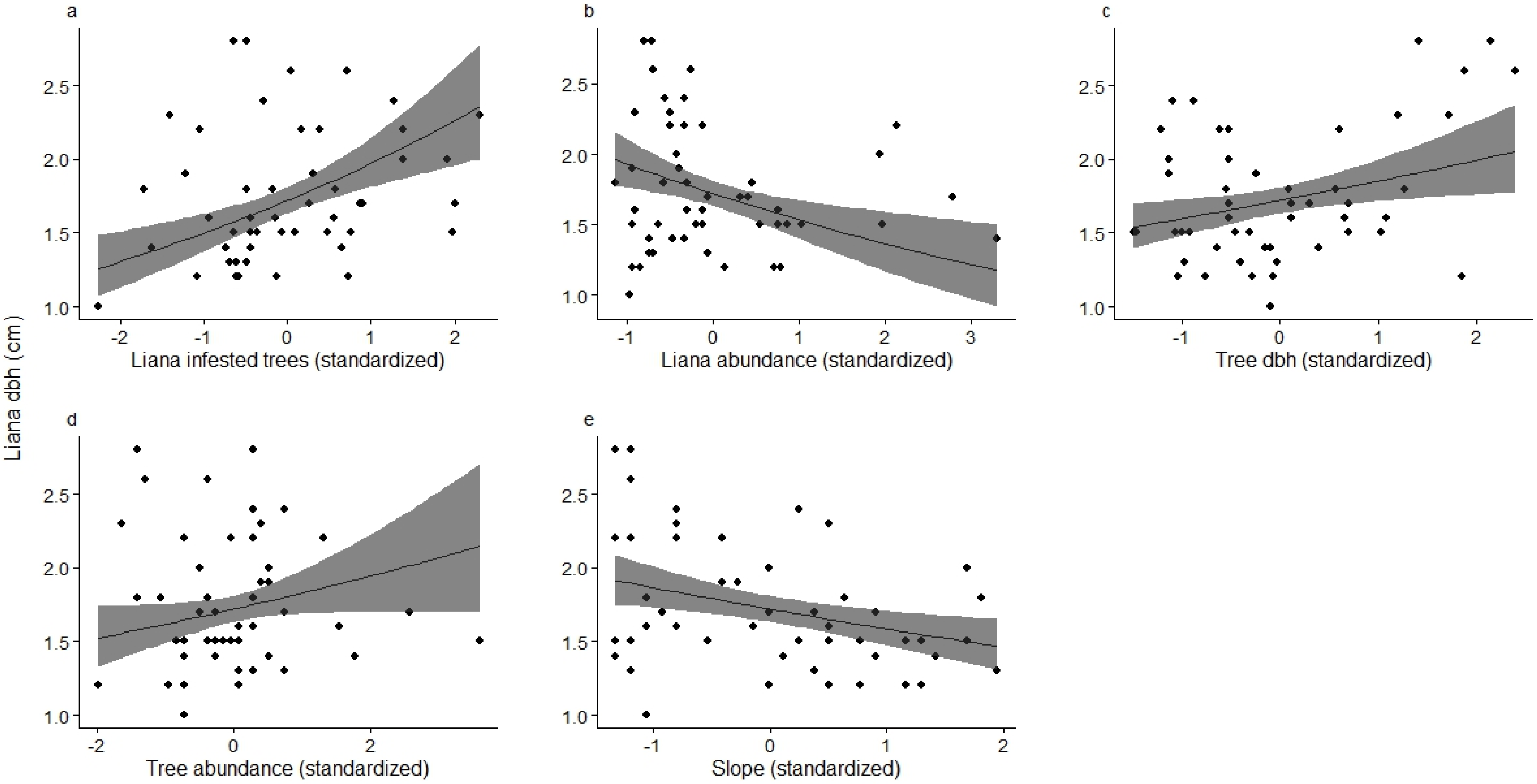

Figure 3.4 The relationship between liana diameter breast height (DBH) and **a)** proportion of trees infested by lianas, **b)** liana abundance, **c)** tree DBH, **d)** tree abundance, and **e)** slope. The trend lines are predicted values and shaded areas represent the 95% confidence intervals.

Table 3.4 The analysis of deviance for a log-linear model investigating association between: trees infested with lianas (yes or no), forest type (fragmented or intact), distance to the forest edge (0-20m, 20-40m, 40-60m, 60-80m and 80-100m), buttress presence (yes or no), and bark type (smooth, rough, or shedding). Df =degrees of freedom. Non-significant higher-interaction terms were removed whereas lower-order non-significant terms were retained if they were nested within a significant higher-interaction term.

	Df	Deviance	Residual Df	Residual Deviance	P
Null	NA	NA	119	3005.451	NA
Tree infested	1	220.284	118	2785.166	< **0.001**
Forest type	1	17.823	117	2767.343	< **0.001**
Edge	4	32.012	113	2735.331	< **0.001**
Buttress	1	0.519	112	2734.813	0.471
Bark type	2	2549.900	110	184.913	< **0.001**
Tree infested:Forest	1	2.801	109	182.113	0.094
Tree infested:Edge	4	32.352	105	149.761	< **0.001**
Forest:Edge	4	2.127	101	147.634	0.712
Tree infested:Buttress	1	0.969	100	146.665	0.325
Forest:Buttress	1	6.529	99	140.136	**0.011**
Edge:Buttress	4	5.919	95	134.217	0.205
Tree infested:Bark	2	0.752	93	133.464	0.687
Forest:Bark	2	1.376	91	132.089	0.503
Edge:Bark	8	8.596	83	123.492	0.377
Buttress:Bark	2	11.811	81	111.681	**0.003**
Tree infested:Forest:Edge	4	9.285	77	102.396	0.054
Tree infested:Forest:Buttress	1	0.596	76	101.800	0.440
Tree infested:Edge:Buttress	4	7.735	72	94.065	0.102
Forest:Edge:Buttress	4	9.627	68	84.437	**0.047**
Tree infested:Forest:Bark	2	2.847	66	81.590	0.241
Tree infested:Edge:Bark	8	7.572	58	74.018	0.476
Forest:Edge:Bark	8	13.426	50	60.593	0.098
Tree infested:Buttress:Bark	2	5.318	48	55.275	0.070
Forest:Buttress:Bark	2	1.025	46	54.250	0.599
Edge:Buttress:Bark	8	11.283	38	42.967	0.186
Tree infested:Forest:Edge:Bark	8	15.273	30	27.694	0.054
Tree infested:Forest:Buttress:Bark	2	6.704	28	20.991	**0.035**

Table 3.5 The analysis of deviance for a log-linear model investigating association between: forest type (fragmented or intact), liana climbing guild (branch climber, hook climber, mainstem twiner, root climber, scrambler, tendril climber, unknown), distance to the forest edge (0-20m, 20-40m, 40-60m, 60-80m and 80-100m), whether the liana infested a tree (yes or no). Df =degrees of freedom. Non-significant higher-interaction terms were removed whereas lower-order non-significant terms were retained if they were nested within a significant higher-interaction term.

	Df	Deviance	Residual Df	Residual Deviance	P
Null	NA	NA	139	3043.548	NA
Forest	1	12.064	138	3031.484	< **0.001**
Guild	6	1032.740	132	1998.744	< **0.001**
Edge	4	679.871	128	1318.874	< **0.001**
Infesting liana	1	75.781	127	1243.092	< **0.001**
Forest:Guild	6	95.485	121	1147.607	< **0.001**
Forest:Edge	4	97.822	117	1049.785	< **0.001**
Guild:Edge	24	341.774	93	708.012	< **0.001**
Forest:Infesting liana	1	7.825	92	700.187	**0.005**
Guild:Infesting liana	6	211.509	86	488.678	< **0.001**
Edge:Infesting liana	4	14.513	82	474.165	**0.006**
Forest:Guild:Edge	24	372.679	58	101.486	< **0.001**
Forest:Guild:Infesting liana	6	22.505	52	78.981	< **0.001**
Guild:Edge:Infesting liana	24	42.878	28	36.103	**0.010**

Discussion

Liana abundance and habitat fragmentation

From my results, it is clear that habitat fragmentation has significantly altered the liana community and the ecological relationship between lianas and trees within rainforests of the Atherton Tableland. For example, I found forest fragmentation to result in a significant increase in liana abundance. Furthermore, whereas liana abundance was significantly higher on the edges of both forest types, this effect penetrated further into the edges of fragmented than intact forests (Tab. 3.2, Fig. 3.3). It is likely that the increase in liana abundance at greater distances within fragmented forests is primarily due to increased disturbance on fragment edges (Tab. 3.2, Fig. 3.3). For example, canopy cover (a proxy for forest disturbance) was significantly less within fragmented forests than that in intact forests (Tab. A3). Furthermore, canopy cover decreased significantly in response to proximity to the forest edge in both forest types but this occurred at a significantly greater rate in fragmented forests (Tab. A3). A decrease in canopy cover, such as is found on forest edges or in tree fall gaps, is well known to favor liana proliferation, often at the expense of tree recruitment, tree succession, tree growth, and forest carbon storage (Schnitzer et al. 2000, Schnitzer and Carson 2001, 2010, Schnitzer et al. 2014).

As well as increasing in response to lowered canopy cover, liana abundance was also found to increase significantly in association with an increasing frequency of fallen logs (⩾ 10cm diameter) within a plot (Tab. 3.2, Fig. 3.3); an indicator of past forest disturbance (e.g. Attiwill 1994). Moreover, liana abundance significantly decreased with increasing forest carbon storage (Tab. 3.2, Fig. 3.3), which is strongly positively associated with the presence of large trees (Slik et al. 2013) indicative of low rates of forest disturbance (Laurance et al. 1998a, Laurance et al. 2000, Laurance et al. 2002, Laurance et al. 2006a). Numerous studies have shown that fragment edges experience higher levels of disturbance that those of intact forests (Williams-Linera 1990, Laurance and Yensen 1991, Saunders et al. 1991, Murcia 1995, Laurance 1997a, Laurance et al. 1997, Laurance et al. 2001b, Cochrane and Laurance 2002, Laurance et al. 2002, Harper et al. 2005, Laurance et al. 2006b, Laurance and Curran 2008, Oliveira et al. 2008, Tabarelli et al. 2008, Laurance et al. 2011, Magrach et al. 2014b) with others identifying localized forest disturbance as the primary driver of local liana abundance within a forest (Laurance et al. 2001a, Schnitzer and Bongers 2011, Ledo and Schnitzer 2014, Schnitzer 2015c). Thus my results of liana abundance increasing in response to disturbance are supported by previous findings of forest disturbance resulting in liana proliferation (Ledo and Schnitzer 2014).

Liana infestation of trees

The proportion of trees infested by lianas did not differ significantly between fragmented and intact forests (Tab. 3.1). Nevertheless, the proportion of trees infested by lianas was found to be driven by both ecological and environmental factors (Tab. 3.1, Fig. 3.2). For instance, liana abundance was a significant predictor of the infestation rates of trees (Tab. 3.1). As distance to the forest edge itself strongly influences liana abundance, increased disturbance near the edges of forest fragments is not only driving differences in the spatial pattern of liana concentration but also the probability that individual trees will be infested (Fig. 3.2a, Laurance 1997a, Laurance et al. 2001a). In fact, recent studies suggest that the mere proximity of lianas to potential host trees may be a primary determinant of host tree selection by lianas (Roeder et al. 2015) and thus an increase in local liana abundance (due to forest disturbance) would lead to an increase in local tree infestation probabilities.

The probability of trees infestation by lianas was not solely attributable to liana abundance. One other important factor was the size of lianas (DBH), with a higher fraction of trees infested at sites with a larger median liana size than at sites with a smaller median liana size (Tab. 3.1, Fig. 3.2b). Thus, I found that the median size of lianas at a site could be a good predictor of liana impact upon trees. This was previously noted by Putz (1990b) who stated that “estimates of liana diameter growth rates are useful in predicting total liana leaf area and thus the effects of lianas on their supporting trees”. However, unlike liana abundance, median liana size within a fragment was positively related to decreased disturbance and the prevalence of mature forest traits (Hegarty and Caballe 1991, Letcher 2015). For instance, I found median liana size (DBH) to be positively and significantly related to factors associated with mature successional forest traits such as larger tree diameter, increasing canopy cover and decreasing tree abundance and negatively associated with factors associated with disturbed forest sites such as increasing slope and liana abundance (Tabs. 3.1 and 3.2, Figs. 3.2, 3.4 b, c and e). Therefore, while sites with larger lianas (DBH) significantly contributed to tree infestation rates their prevalence was significantly related to areas of forest with mature forest traits (Tab. 3.3, Fig. 3.4; Hegarty and Caballe 1991, Letcher 2015).

While both increased liana abundance and size (DBH) significantly contributed to liana infestation rates of trees within a forest, increased liana abundance was associated with sites of forest disturbance (Tab. 3.1, Fig. 3.2; Putz 1984b, Laurance et al. 2001a, Ledo and Schnitzer 2014) whilst large lianas (DBH) occurred at mature forest sites (Tab. 3.3, Fig. 3.4; Hegarty and Caballe 1991, Letcher 2015). As such, it is likely that patterns of disturbance and subsequent succession combine to determine liana infestation rates of trees within forest fragments. For example, initial forest disturbance can facilitate liana recruitment and abundance (Ledo and Schnitzer 2014), with subsequent forest canopy closure in these areas retaining lianas in the forest canopy (i.e. in general those ⩾ 2cm; Kurzel et al. 2006). These individual lianas increase in size, but canopy closure precludes additional liana stems successfully reaching the canopy (Putz 1984b, Letcher and Chazdon 2009a, Letcher 2015). Consequently, tree infestation and liana size distributions within forest fragments likely reflects forest dynamics and liana community age with distinct differences in community composition between larger lianas in older (less disturbed) areas and smaller lianas in younger forest sections (i.e. recently disturbed) (Letcher 2015) (Tabs. 3.1, 3.2, 3.3 and Figs. 3.2, 3.3, 3.4).

Infesting liana climbing guilds and host tree traits and their response to forest effects

Liana infestation of trees has previously been linked to the morphological and ecological traits of lianas themselves (e.g. the trellis size-use of liana-climbing guilds; Putz 1984b, Putz and Chai 1987). I found fragmentation of the rain forest significantly influenced liana infestation of trees (Tab. 3.5), and these effects, in turn, resulted in substantial shifts in the relative abundance of liana climbing guilds (Tab. 3.5). Proportions of total stems in different liana climbing guilds varied significantly in response to forest edge distance within and between both fragmented and intact forests (Tab. 3.5). It is likely that the variation in liana guild composition between fragmented and intact forests can again be attributed to increased disturbance of fragmented forest edges (Laurance 1997a, Oliveira et al. 1997, Laurance and Curran 2008, Tabarelli et al. 2008). Disturbance is known to result in the proliferation of usually smaller successional trees and earlier successional forests (Laurance 1997a, Laurance 2002, Laurance et al. 2002, Laurance et al. 2006b, Tabarelli et al. 2008, Chazdon 2014). These recruits increase the availability of smaller-sized climbing trellises (i.e. small trees and branches), which are favored by tendril climbers and stem twiners which also proliferate there. Lianas that utilize larger climbing trellises (e.g. branch twiners) are more frequently found in mature forest (Putz 1984b, Putz and Chai 1987, Schnitzer and Bongers 2002). Consequently, much of the changes in liana community-composition and infestation rates in fragmented forests can be attributed to the effects of disturbance in determining the availability of different-sized climbing trellises.

Morphological attributes of trees have also been suggested to influence the probability of liana infestation. For Both, tree bark type (Putz 1980, Boom and Mori 1982) and buttress presence (Putz 1980, Boom and Mori 1982) have been noted as potential liana inhibitors. For instance, it has been suggested that flaky barked trees may shed lianas whilst smooth bark trees may decrease the success of liana attachment (Putz 1984b). Meanwhile, tree buttressing has been hypothesized to act as a mechanical barrier, preventing liana proximity and therefore attachment (Black and Harper 1979). However, as has been found in previous studies (Putz 1980, Boom and Mori 1982), I found that neither tree bark type nor buttress presence significantly influenced the probability of hosting a liana (Tab. 3.4), despite the fact that buttress presence varied significantly across forest types and in conjunction with distance to the forest edge (Tab. 3.4).

Prediction of future liana impacts upon fragmented forests

It is clear that multiple environmental and ecological determinants influence liana infestation of trees (Tab. 3.3, Fig. 3.2; Putz 1980, 1984b, a, Hegarty 1991b, Schnitzer and Bongers 2002, Heijden et al. 2008) and that these determinants likely interact synergistically (Heijden et al. 2008, Laurance et al. 2014a, Sfair et al. 2016). Further, attributes of the liana community (abundance, size distribution class, and climbing guild) all respond to these influences. Nevertheless, liana abundance alone is often used as a proxy to infer likely liana impact (and future impact) on fragmented forests (e.g. Wright 2010, Schnitzer et al. 2011, Campbell et al. 2015b). However, my findings identified liana size distribution as a possible indicator of the inherent and potential rate of liana infestation of trees within a forest and future liana impact (Fig. 3.1). Thus, they confirm those of previous studies on liana community size (DBH) distributions (Phillips et al. 2002, Phillips et al. 2005). Individual trees experiencing liana infestation are well known to experience reduced growth, reduced fecundity, limb damage, increased resource competition and increased mortality rates (Putz 1984b, Stevens 1987, Schnitzer et al. 2005, Ingwell et al. 2010, Reid et al. 2015). Lianas are already known to significantly impact forest community processes such as decreasing forest carbon storage capacity (Heijden et al. 2013, Schnitzer et al. 2014, Heijden et al. 2015a, Heijden et al. 2015b), arresting forest succession (Schnitzer and Bongers 2005, Schnitzer and Carson 2010, Paul and Yavitt 2011, Tymen et al. 2015) and causing differential mortality between host species (Clark and Clark 1990, Schnitzer and Bongers 2002). The contribution to these impacts made by large lianas is often not determined. And, as above, most focus is on liana abundance. Consequently, when assessing tropical closed-canopy forests for liana impacts and determining future management strategies, as well as the clearly justifiable assessment of overall liana abundance (Tab. 3.1, Fig.3.2a), considerable useful information may be attained through the regular assessment of the liana size (DBH) frequency distributions for all lianas at each site (Fig. 3.1).

Conclusion

Forest fragmentation significantly alters the abundance and community composition of lianas and their ecological relationships with trees. Liana abundance increased significantly within fragmented forests in response to the increased disturbance of fragmented forest edges. However, liana infestation rates of trees were not significantly different between fragmented and intact forests. Infestation rate was not only influenced by liana abundance but also by a liana populations size (DBH) distribution. Abundance and size distribution responded in opposite ways to environmental drivers, potentially explaining the finding of no significant difference in infestation rates of trees between existing in fragmented and intact forests. Finally, the increased disturbance of forest edges resulted in a shift in the composition of liana climbing guilds, likely due to a change in the size of available climbing trellises.

Acknowledgements

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Chapter 4 Edge effects shape the spatial distribution of lianas and epiphytic ferns in Australian tropical rain forest fragments

This chapter is based upon a paper published by Magrach et al. (2014), with minimal format and content edits:

Magrach, A., J. Rodríguez-Pérez, **M. Campbell**, and W. F. Laurance. 2014. Edge effects shape the spatial distribution of lianas and epiphytic ferns in Australian tropical rain forest fragments. *Applied Vegetation Science* **17:** 754-764.

Statement of contribution of others:

Magrach and Campbell developed the main research question and collected the field data together. Magrach wrote the first draft of the paper other than the description of the study area in the methods section which was written by Campbell. The subsequent drafts were revised by Magrach with editorial input from Campbell, Laurance and Rodriguez-Pérez. Rodríguez-Pérez also provided statistical input. Magrach constructed the figures and tables.

Abstract

Question: In fragmented forests, edge effects lead to changes in the distribution of plant species. In particular, tropical forest edges are increasingly dominated by lianas. Will this increase in lianas lead to changes in their interactions with other plant morphological groups? If so, will this alter the local distributions and abundance of other species?

Location: Plots located at increasing distances from the nearest forest edge and in remnant fragments of rain forest in the Atherton Tablelands, far northeast Queensland, Australia.

Methods: I mapped the distribution of trees, lianas and epiphytic ferns to better understand the role of forest disturbance in shaping their competitive and facilitative interactions. I then used specific spatial point-process analyses to examine the effects of the spatial distribution of trees on the presence and abundance of lianas and epiphytic ferns.

Results: Tree aggregation near forest edges was lower than that in the interior. The higher abundance of lianas near edges was associated with increased spatial segregation between lianas and epiphytic ferns. This segregation suggests there is competition between these two functional groups, and that lianas, being much more abundant, probably outcompete epiphytic ferns.

Conclusions: The ability of lianas to thrive in disturbed tropical rain forests appears to reduce the abundance of epiphytic ferns, probably via direct competition for space. Epiphytic ferns provide unique microclimates and harbor much biodiversity, and their decline could negatively affect many animals and plants that rely upon them.

Key words: Atherton Tablelands; Competition; Edge effects; Forest fragmentation; Plant–plant interactions; Point-pattern analysis

Introduction

Tropical forests worldwide are being cleared and disturbed (Wright 2005, 2010, Laurance et al. 2012), leading to rapid changes in the distribution of many species (Fahrig 2003). Among the most studied effects of forest disturbance are those related to forest edges, which are artificial, often abrupt boundaries between remnant forest fragments and the modified habitats around them (Murcia 1995, Laurance et al. 2002, Ries et al. 2004, Harper et al. 2005, Lindenmayer and Fischer 2006, Laurance et al. 2011). The creation of these new edges leads to a proliferation of pioneer plant species in detriment of long-lived ones that might have been common before disturbance (Laurance et al. 2000, Laurance et al. 2006b). These changes in the identity of the species in the edge community invariably lead to modifications in the persistence and distribution of many organisms as well as to alterations in plant demography (Murcia 1995, Jules 1998). This in turn can lead to important changes in ecological interactions between species (Fagan et al. 1999), to the extinction of some species (Laurance et al. 2000) and eventually to the formation of new ecological communities near forest edges (Ries et al. 2004). In some cases, edge effects can lead to a marked homogenization of edge communities (Tabarelli et al. 2008), with important consequences for functional diversity and ecosystem functioning across the landscape.

In tropical plant communities, one of the most conspicuous edge effects is an increase in the abundance of lianas (woody vines; Laurance et al. 2001a, Schnitzer and Bongers 2011). Lianas are a widespread feature of tropical forests globally (Hegarty and Caballe 1991, DeWalt et al. 2015) and become particularly abundant in tree-fall gaps and sites affected by disturbance (Putz 1984b, Schnitzer and Bongers 2002, Schnitzer and Bongers 2005, Schnitzer and Carson 2010). The proliferation of lianas in fragmented and disturbed forests (Schnitzer and Bongers 2011) has been demonstrated in tropical Australia (Laurance 1997a), south-eastern Brazil (Oliveira et al. 1997), the Amazon Basin (Laurance et al. 2001a, Phillips et al. 2002, Benitez-Malvido and Martinez-Ramos 2003, Foster et al. 2008) Panama (Wright et al. 2004, Wright and Calderón 2006), French Guiana (Chave et al. 2008) and Costa Rica (Rutishauser 2011). Many of these studies evaluate the impact that lianas have on their host trees (Schnitzer and Bongers 2002, Paul and Yavitt 2011, Schnitzer and Bongers 2011). However, abundant lianas could also cause other ecological changes in tropical forests. Vegetative reproduction and facilitation processes between different species of liana (Pinard and Putz 1994) lead to clumped spatial patterns and clustering, especially near forest edges (Schnitzer and Bongers 2011). Given the relative paucity of places to establish within tropical forests, such clumping could lead to patchy interspecific competition with other plant functional groups, such as epiphytes, that also rely on trees for support.

Epiphytes (those that root on the surface of tree trunks and branches but do not harm the host, *sensu* Benzing 2004) (those that root on the surface of tree trunks and branches but do not harm the host, *sensu* Benzing 2004) are major contributors to vascular plant diversity and biomass (Gentry and Dodson 1987), and play key roles in nutrient cycling (Benzing 1998, Muñoz et al. 2003). Of special relevance in tropical Australia are epiphytic ferns (Cummings et al. 2006), which support diverse communities of animals and plants, including a variety of bird (Cruz-Angon and Greenberg 2005), reptile (Freeman and Freeman 2009) and invertebrate (Ellwood et al. 2002) species, some of which have obligate relationships with their host epiphytes. These 'islands' of unique habitat might be sensitive to forest disturbance (Wenzhang et al. 2008), but the mechanisms responsible for this sensitivity are uncertain. One possible explanation is that epiphytes suffer from competition with other co-occurring plants, such as lianas. If this were the case, I might be able to detect this interspecific competition between both functional groups via increased spatial segregation at small scales. In addition, given the increased presence of lianas near forest edges, I would expect this spatial segregation to be more frequent there.

Here I assess whether and how forest fragmentation alters the ecological interactions between lianas and epiphytic ferns in tropical Queensland, where lianas thrive under disturbed conditions (Laurance 1997a). My aim is to determine whether fern-liana-tree interactions have a strong spatial component (see Raventós et al. 2011) and to address three specific questions: (1) do lianas and epiphytic ferns respond to edge effects; (2) do they interact in space; and (3) do they compete for the use of trees? My findings may help to reveal how competition for supporting trees helps to structure rain forest plant communities.

Methods

Study Site

The study was carried out on the Atherton Tableland in NE Queensland, Australia (Fig. 4.1). Mean annual precipitation ranges from 2000 to 3000 mm at different locations, and rainfall is highly seasonal, peaking from January to April. The rain forests in the study area are complex notophyll vine-forests (Tracey 1982, Herbarium 2015), ranging in height from 20 to 40 m, and are dominated by the following tree species: *Agathis microstachya* (Araucariaceae), *Ficus* spp. (Moraceae), *Flindersia brayleyana* (Rutaceae), *Geissois* *biagiana* (Cunoniaceae), *Cryptocarya onoprienkoana* (Lauraceae), *Argyrodendron peralatum* (Malvaceae), *Castanospermum australe* (Fabaceae) and *Cardwellia sublimis* (Proteaceae). Lianas and epiphytes are common throughout these forests (Tracey 1982, Cummings et al. 2006), with lianas known to increase in disturbed areas (Laurance 1997a).

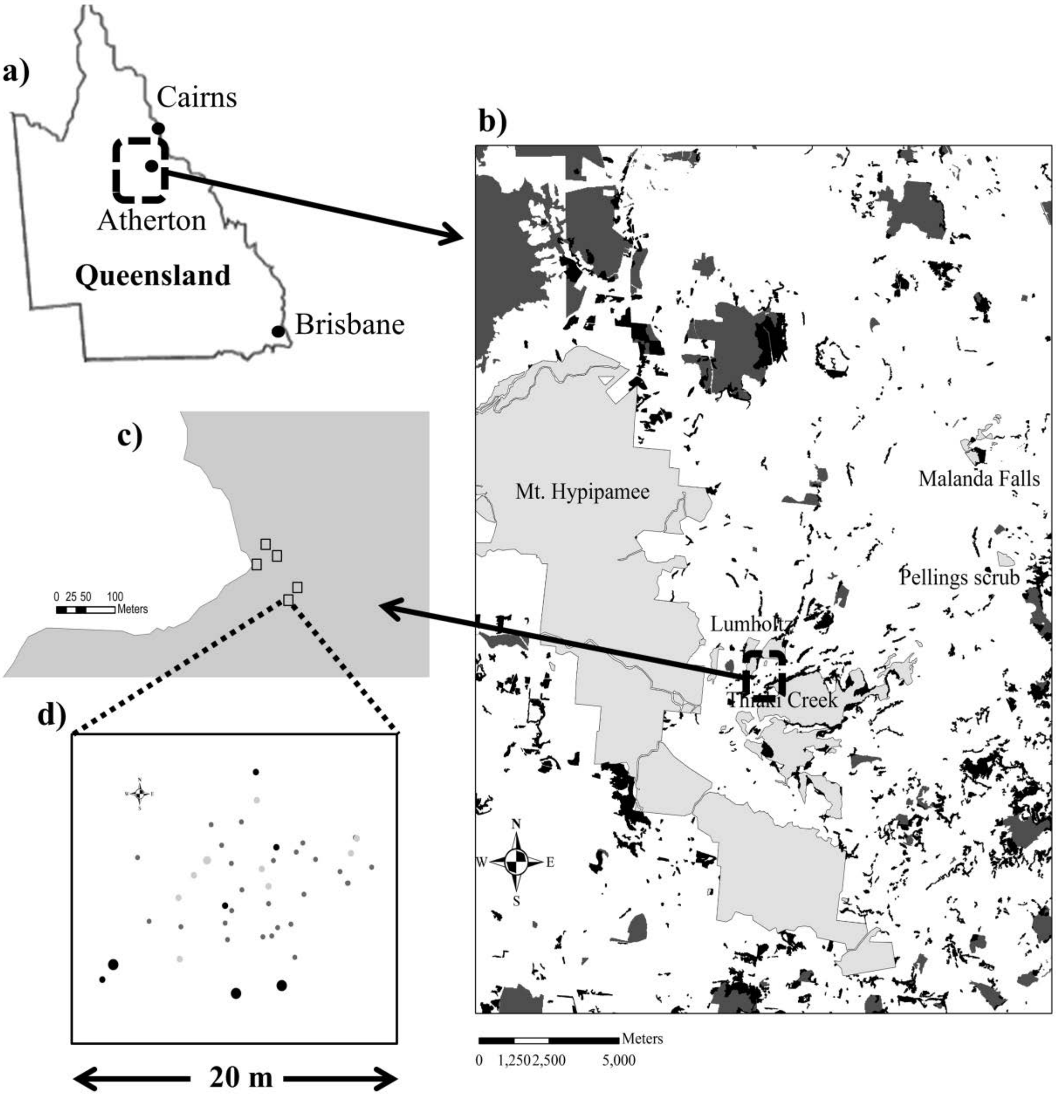

Figure 4.1 a) Map showing study area location in northeast Queensland, Australia. **b)** Location of forests in Atherton Tablelands. Dark grey areas indicate primary forest, black areas represent secondary forest and light grey areas show the fragments sampled in the study. **c, d)** Example of one of the plots measured inside one of the forests. **c)** Location of five plots in relation to forest edge. **d)** Trees measured inside a particular plot (located 80–100 m from the nearest forest edge). In light grey are trees with lianas, dark grey is trees with no epiphytes or climbers and black is trees with epiphytic ferns. Different sized circles indicate different loads of lianas and epiphytic ferns.

Queensland tropical forests are listed among 200 ecoregions that should be prioritized for global conservation due to their vulnerable status (Olson and Dinerstein 2002) and biologically unique nature. These forests have historically suffered heavy logging and land clearing for agriculture (Goosem et al. 1999). Clearing in the study area began with European colonization around 1909 and proceeded rapidly until the 1940s, then slowed in the following decades (Winter et al. 1987, Society 1995). Currently, most primary forest in the study area comprises forest fragments ranging from 1 to 600 ha in area, surrounded by cattle pastures and secondary forests, most of which are under some form of protection. The main threats currently faced by forests are due to isolation, edge effects and invasive species, although present plant distributions could reflect past disturbances (Dupouey et al. 2002, Lindborg and Eriksson 2004). Steeper, more nutrient-poor areas to the south, west and east of the Atherton Tablelands sustain larger, continuous forests.

The forests of the Atherton Tablelands harbor several species of epiphytic fern, among the most common of which are those in the genera *Asplenium* (Aspleniaceae) and *Platycerium* (Polypodiaceae). *Asplenium* creates a unique microclimate in the forest (Cummings et al. 2006) and harbors important invertebrate communities (Ellwood et al. 2002), whereas *Platycerium* has important functions in capturing and retaining moisture in the forest canopy (Cummings et al. 2006). There are >390 species of liana known in the study area, belonging to four main families, Apocynaceae, Convolvulaceae, Fabaceae and Vitaceae (Research 2010). These lianas have an array of climbing strategies that include mainstem twiners, branch twiners, tendril climbers, root climbers and scramblers (see Putz 1984b). Like other lianas worldwide, they frequently reproduce vegetatively. However, whereas lianas in the New World contain many wind-dispersed species (Gentry 1991), those in Australian tropical forests, similar to others found in Central African and some Asian regions, often have fleshy fruits (Research 2010) presumably adapted for animal dispersal.

Plot measures

From April to June 2012 I examined five primary rain forest fragments ranging from ca. 18 to 9500 ha in area. Within each fragment I located five 20 9 20-m plots at increasing distances from the nearest forest edge (0–20 m, 20–40 m, 40–60 m, 60–80 m, 80–100 m; see Fig. 4.1), following a linear transect perpendicular to the edge. To avoid possible interactions due to the presence of other neighboring edges within a forest fragment (Porensky and Young 2013), all plots were located >150 m from any second edge. In addition, I tried to avoid the eastern faces of the fragments, which are more exposed to cyclonic activity. I measured canopy cover in the four corners and centre of each plot, by averaging at each point four spherical densitometer readings taken at cardinal directions.

For each tree, liana and epiphytic fern in my plots, I recorded their spatial location with a handheld GPS (Garmin GPSMAP 62). To increase precision, I averaged 50–100 GPS measurements for each plant, and corrected GPS measurements using known waypoints. I also measured the DBH of each tree ≥10 cm and recorded the number of lianas and epiphytic ferns using that tree for support. Fern abundance was evaluated by counting individual ferns from the forest floor using binoculars; individual species can be distinguished once their reproductive fronds have developed. However, I counted only ferns with a basal diameter of ≥10 cm (where basal diameter is the area of contact between fern and host tree; Cummings et al. 2006). I also measured the DBH of all lianas ≥1 cm in DBH at 1.3 m from the rooting point, following recent protocols (Gerwing et al. 2006, Schnitzer et al. 2006, Schnitzer et al. 2008), and recorded all trees (≥10 cm DBH) that they used as support (although lianas can also climb over trees with DBH < 10 cm). Each liana was assigned to one of five climbing guilds: mainstem twiner, branch twiner, tendril climber, root climber and scrambler (Putz 1984b). For each plot, I calculated the 'morphological diversity' of lianas and epiphytic ferns using Shannon's diversity index (H), based on the proportions of plants in the two fern genera and five liana climbing guilds.

Data analysis (between plots)

I analyzed the collected data (including tree abundance, and liana and fern presence and abundance per plot) using generalized linear mixed-effect models (GLMMs) with package glmmADMB in R 2.15.0 (R Foundation for Statistical Computing, Vienna, AT). 'Fragment' was always included as a random variable, given the dependence of plots within the same fragment. I created all possible model combinations using the dredge function in the MuMIn package and then selected all models with ∆AIC < 2 and calculated averaged confidence intervals for all variables included in the subset of best-performing models (Burnham and Anderson 2002).

Data analysis (within plots)

I used techniques of spatial point-pattern analysis (Wiegand and Moloney 2004, Law et al. 2009) to describe the locations of host trees, and the presence/absence and abundance of lianas and epiphytic ferns. The spatial explicit distribution of plants carries information about the processes that are currently operating or that occurred in the past, and hence I can infer ecological processes with the analysis of the spatially explicit distribution of points (Law et al. 2009). Analyses were performed using the software PROGRAMITA (Wiegand and Moloney 2004). For each plot, I performed spatial point-pattern analyses of host trees at three levels: (1) the spatial structure of trees within the forest, which gives us the spatial scale over which lianas and ferns interact; (2) the spatial distribution of host trees with lianas or ferns; and (3) the spatial pattern of the presence and abundance of ferns on host trees occupied by lianas (see Raventós et al. 2011). The former analyses were based on the theory of 'unmarked' (i.e. the points only depend on the spatial location of host trees) and 'marked' point patterns (i.e. apart from location, each tree carries marks, such as species identity, epiphyte type colonizing it or size; Illian et al. 2008).

For each analysis and plot, I calculated the summary statistics for the observed and simulated (null) point-process models. I used simulations (199 replicates) to estimate the envelopes encircling the 95% range of values of summary statistics under a given point-process model (i.e. the 5th lowest and highest values). Departures from the point-process models occurred if the observed summary statistics were outside the simulation envelopes (Wiegand and Moloney 2004, Illian et al. 2008). I also used Diggle's (2003) goodness of fit (GoF) test to assess the overall fit of null models for a given test statistic (Loosmore and Ford 2006). If the rank of the test was >200, the data showed a significant departure from the null model, with an error rate $\alpha = 0.05$.

Given that I was interested in obtaining global results while using the full statistical power of my data, I combined the summary statistics of different plots using techniques for replicated patterns (Law et al. 2009). These techniques allow for the combination of all summary statistics into a single 'master' statistical test that basically represents the average of the summary statistics of each plot, weighted by the number of focal points in the focal pattern (Illian et al. 2008, Raventós et al. 2011). In other words, I focused on the average process, rather than on the potential variability for each individual plot (for a similar study following the same methodology, see Raventós et al. 2011). I thus pooled my plots into interior (60–100 m from edge) and edge (0–60 m from edge) categories, as these were relatively distinct. For ferns, however, I grouped my results by fragment as there was little difference between forest edges and interiors (see Results).

Spatial distribution of trees

To describe the pattern of tree aggregation with distance from the forest edge I carried out 'unmarked' point-pattern analyses (Diggle 2003, Wiegand and Moloney 2004, Illian et al. 2008) using the univariate pair-correlation function $g(r)$ (Diggle 2003, Illian et al. 2008). For each distance, the significance of the observed *g(r)* describing tree aggregation was evaluated against a random pattern (null model) generated by randomly drawing an identical tree number for each plot. Analyses were carried out separating edge and interior plots.

Spatial distribution of ferns and lianas

In this case I analyzed whether the spatial pattern of host trees with and without lianas or ferns was randomly distributed. The latter analyses are based on the use of null models of random labelling: I randomly assigned the pattern of trees with the labels (a) with and without lianas, and (b) with and without ferns, conditional on the observed tree distribution. Specifically, I used the univariate mark-connection function $p11(r)$, where trees with lianas or ferns (type 1) were compared to the distribution of trees without lianas or ferns (type 2; Diggle 2003, Illian et al. 2008). If $p11(r)$ of the observed pattern showed a positive departure from that of the null model [i.e. $p11\ (r) > p1p1(r)$], the presence of either lianas or ferns was significantly clustered at scale r, conditional on tree distribution. I used the bivariate function $p12(r)$ to further explore the spatial relationship between trees with (type 1) or without (type 2) lianas or ferns. Attraction (or segregation) between type 1 and type 2 groups occurs if observed $p12(r)$ shows positive (or negative) departures from that of the null model. I did not detect differences between edge and interior plots (results not shown), and I thus carried out these analyses combining all plots.

Spatial distribution of ferns dependent on lianas

I used a trivariate random labelling (e.g. Raventós et al. 2011) to test whether trees with and without lianas differed in their probability of bearing ferns. I contrasted the observed point pattern to an expected null model of random fern distribution conditional on host trees (Raventós et al. 2011). With this null model, ‘fern presence’ was randomly shuffled among host trees, leaving the observed liana presence on trees fixed. Analyses were carried out for both edge and interior plots. I did not analyze the effect of ferns on lianas because ferns were much less abundant than lianas (see Results).

Spatial abundance of lianas and ferns

To examine the spatial pattern of the abundance of lianas or ferns on host trees, I used the univariate r-mark correlation function $k_{m1}(r)$ (Stoyan and Stoyan 1994, Getzin et al. 2008). In each plot null models were generated randomly, shuffling the mark m (i.e. liana or fern abundance on host trees) over the observed tree distribution. If the analysis of liana abundance on trees departed negatively from the null model [i.e. $k_{m1}(r) < 1$], then this means that host trees with high loads of lianas are free of trees with low loads of lianas (i.e. inhibition of lianas). By contrast, a positive departure from the null model of the liana abundance [i.e. $k_{m1}(r) > 1$] would indicate that host trees with high loads of lianas are also surrounded by trees with low loads of lianas (i.e. mutual facilitation of lianas). The same procedure could be extrapolated to fern abundance. Analyses for liana abundance were carried out for edge and interior plots, while all plots were combined for fern abundance.

Furthermore, the bivariate mark-correlation function $k_{m1,\,m2}(r)$ gives the mean mark product of the number of lianas ($m1$) and ferns ($m2$) on trees at distance r. If the host trees have smaller than average marks $m1$ and $m2$ when they are closer together, there is inhibition; if they have larger than average marks when they are closer together, there is mutual facilitation. To test for a significant correlation of the $m2$ marks dependent on the position of $m1$ marks (i.e. spatial abundance of ferns dependent on that of lianas; see above for a similar analysis for lianas or fern presence), I used a null model where $m1$ marks were fixed and $m2$ marks were randomly shuffled among all trees (with and without lianas or ferns). The former analyses were carried out combining all plots.

Results

Analysis of lianas and ferns between plots

Across the 25 plots in my five forest fragments, I recorded 889 trees, 882 lianas and 98 epiphytic ferns. Tendril climbers were the most abundant liana climbing guild (40% of all lianas), followed by mainstem twiners (29%), branch twiners (18%) and root climbers and scramblers (13%). *Asplenium* spp. were the most abundant of the ferns sampled (73%). Comparing edge and interior plots, I found that lianas were twice as abundant in general in edge plots as in interior ones (mean ± SE = 24.5 ± 5.72 and 12.38 ±3.14, respectively), and that all of the liana climbing guilds were more abundant near forest edges (Tab. 4.1). They were also morphologically more diverse on edges than interiors based on the Shannon diversity index (Tab. 4.1).

The abundance of trees per plot was not explained by any of the variables included in my GLMM models (Tab. 4.2). However, lianas were more frequently present and abundant near forest edges and on larger trees (Tab. 4.2). Fern presence and abundance were both higher in plots with less canopy cover and larger trees. Also, ferns declined near forest edges (Tab. 4.2).

Table 4.1 Values of abundance for the different liana guilds and Shannon's diversity index for the edge and interior plots.

	Edge	Interior	X^2
Branch Twiners	21 ± 9.7	4.5 ± 3.5	**18.69*****
Mainstem Twiners	26 ± 4.5	17.5 ± 0.5	**3.79***
Root Climbers	12.33 ± 7.33	6.5 ± 1.5	**3.95***
Tendril Climbers	38.66 ± 19.22	21 ± 8	**11.49*****
Shannon Diversity	0.95 ± 0.09	0.58 ± 0.12	**5.94***

***$P < 0.0001$, *$P < 0.05$.

Distribution of lianas and ferns within plots

Point-pattern analyses revealed that trees were unevenly distributed within plots, occurring at nearest-neighbor distances (*r*) of roughly 2-3 m (Fig. 4.2a, b). At local distances of $r <$ 0.5 m, trees in interior plots showed stronger clustering than did trees in edge plots.

In all plots, host trees with ferns were aggregated within 5–6 m of each other (Fig. 4.2c). Trees with lianas were spatially segregated beyond 8 m (Fig. 4.2d), which may be attributed to an uneven distribution of trees within plots. Furthermore, trees with ferns and lianas were clustered and separated from those without ferns and lianas at distances of 2.1 m (Fig. 4.2e) and 0.6–1.5 m (Fig. 4.2f), respectively. In other words, host trees with ferns were clustered and separated from those without ferns. However, I found a finer aggregation for host trees with and without lianas than for those with or without ferns (i.e. segregation between trees with and without lianas is higher as it appears at distances under 2 m, coinciding with the distance at which tree aggregation stabilizes; see above).

Additionally, I found a significant lower probability of ferns in the vicinity of trees with lianas, but only at distances beyond 1.2 m in edge plots (Fig. 4.3a). For interior plots, the observed data did not depart from the null model, except for distances >9 m (Fig. 4.3b), probably due to an uneven distribution of trees within plots (see Fig. 4.2d for a similar result).I observed a random pattern of fern abundance on host trees (Fig. 4.3c, joining all plots). I observed mutual exclusion of trees with high and low loads of lianas at small distances (between 0.6 and 1.5 m), but only for edge plots (Fig. 4.3d,e); in other words, edge plots have clusters of host trees with high liana loads, and that probably favors high competition with ferns. Finally, I detected a random pattern in the association between the abundance of lianas and ferns (Fig. 4.3f). That is, competitive interactions are only apparent when analyzing the presence of lianas and ferns.

Table 4.2 Results for the average of the subset of best performing models selected. Numbers indicate 95% confidence intervals.

	Tree abundance	Liana presence	Liana load	Fern presence	Fern abundance
Fragment size	-0.003 ± 0.0014$^{\text{n.s.}}$	-0.003, 0.02$^{\text{n.s.}}$	-0.003, 0.02$^{\text{n.s.}}$	-0.01, 0.004$^{\text{n.s.}}$	-0.01, 0.002$^{\text{n.s.}}$
Distance to edge	-0.004 ± 0.0014$^{\text{n.s.}}$	**-0.34, -0.04****	**-0.32, -0.06****	**0.016. 0.36****	-0.06, 0.32
Canopy cover		-0.06, 0.02$^{\text{n.s.}}$	-0.06, 0.01$^{\text{n.s.}}$	**-0.15, -0.05****	**-0.14, -0.03****
Log tree size		**0.18, 0.75****	**0.27, 0.82****	**1.24, 1.93****	**1.57, 2.39****
Liana presence				-0.51, 0.33$^{\text{n.s.}}$	
Fragment size x Distance to edge		-0.006, 0.0008$^{\text{n.s.}}$		-0.004, 0.005$^{\text{n.s.}}$	-0.24, 0.69$^{\text{n.s.}}$

Bold letters indicate significant effects. n.s., non-significant effects. ***P* < 0.001.

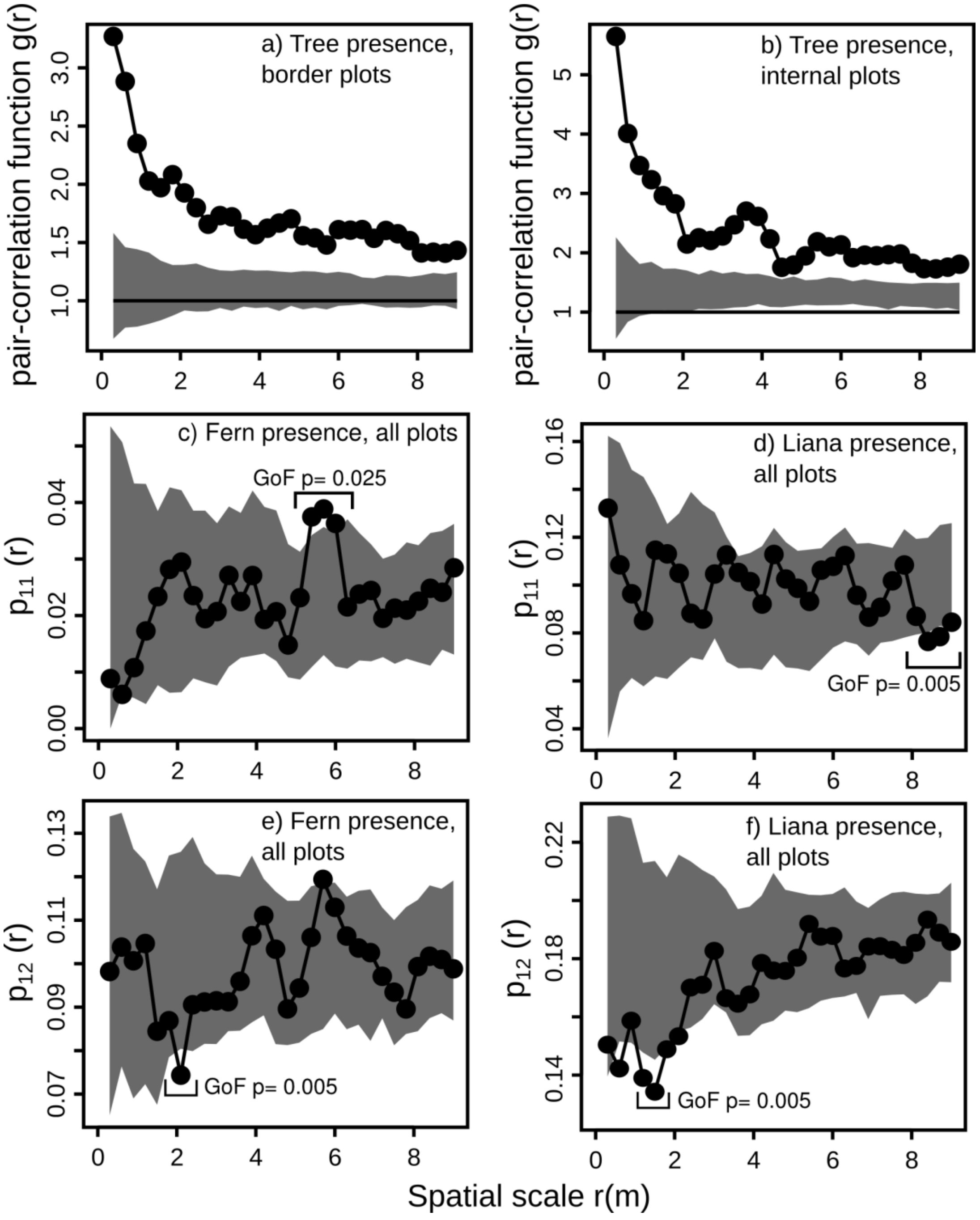

Figure 4.2 Analyses of the spatial distribution of trees, ferns and lianas. The pair correlation functions *g(r)* were used to estimate the tree distribution in edge **a)** and internal plots **b)**. The univariate mark-connection functions *p11(r)* were used to explore the spatial structure of trees occupied by ferns **c)** and lianas **d)** over all trees. The bivariate mark-connection functions *p12(r)* was used to test if there was spatial differentiation between host trees with and without ferns **e)** or lianas **f)**. The functions estimated from the observed point pattern (lines with dots) were contrasted to the simulation envelopes (grey polygons) derived from 199 runs of the null model chosen in each analysis (see further details in Methods). In **a)** and **b)**, the expected results of the functions under a random pattern are shown as black lines. For a given analysis, I further computed the goodness of fit (GoF) test for the intervals of distances of observed data departing from simulation envelopes (distances between brackets).

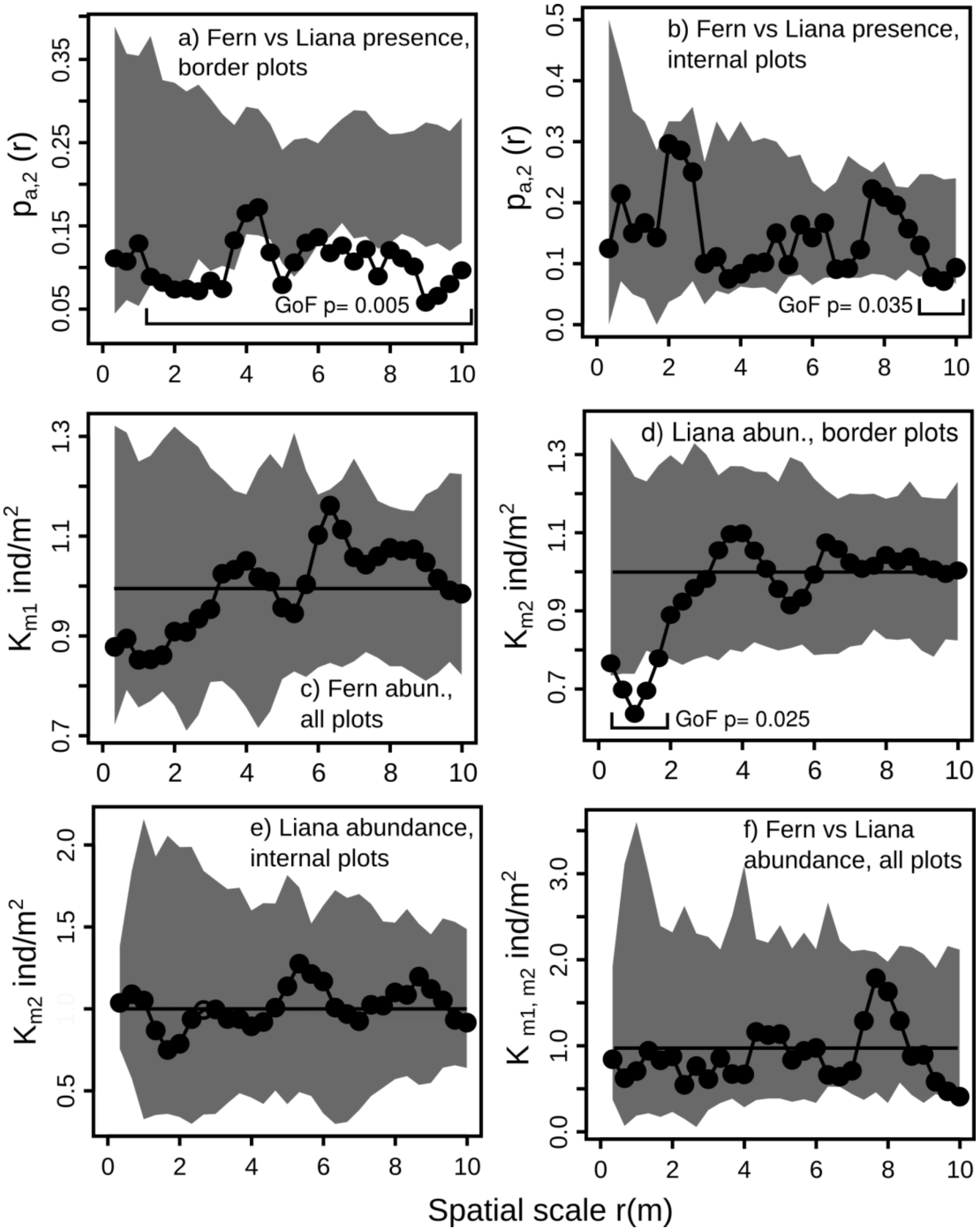

Figure 4.3 Analyses of spatial distributions of presence and abundance of ferns and lianas. Probability *p_a,2(r)* that a fern (subscript 2) was present at distance *r* from a tree occupied by a liana (subscript a) in border **a)** and internal plots **b)**. The univariate *r*-mark correlation functions *km1* and *km2* give the mean fern abundance in all plots **c)** and the mean liana abundances in border **d)** and internal **e)** plots, at distance *r* from a host tree. **e)** The bivariate mark-correlation function *km1,m2* tests the mean product of fern abundances dependent on the liana abundance (ind m^{-2}). For further conventions, see Fig. 4.2.

Discussion

My study is the first to suggest that lianas may have an impact on plant species other than trees, namely epiphytic ferns. Previous studies have shown that lianas can negatively affect their tree hosts, especially in disturbed forests where they become hyper-abundant (e.g. Putz 1984b, Laurance et al. 2001a, Schnitzer and Bongers 2002, Paul and Yavitt 2011, Schnitzer and Bongers 2011). In disturbed environments, lianas may affect trees negatively by loading heavily on their crowns (Putz and Mooney 1991), competing for light, water (Perez-Salicrup and Barker 2000, Pérez-Salicrup et al. 2001) and soil nutrients (Schnitzer et al. 2005), reducing tree growth and reproduction (Lowe and Walker 1977, Putz 1984b, Schnitzer and Bongers 2002), suppressing tree regeneration in canopy gaps (Schnitzer et al. 2000) and accelerating tree turnover rates (Laurance et al. 2001a). My analysis suggests that following disturbance, trees become an increasingly aggregated resource for climbing and epiphytic plants, grouped in clusters of roughly 2–3 m in diameter, particularly dense in forest interiors. The lower numbers of trees and the large increases in liana abundances in edge environments (twice as abundant as in the interior), together with the probable increase in liana re-sprouting near edges in response to increased light levels, is apparently translated into clumped distributions of lianas and epiphytic ferns. The lower abundances of epiphytic ferns in edge environments may very well reflect a response to abiotic drivers such as humidity, which is lower in these areas. However, the presence of ferns within plots with less canopy cover suggests this is not the only feature determining their distribution, and that a lack of suitable hosts for colonization is also limiting their distribution. Indeed, my finding that in edge plots, epiphytic ferns were less abundant near lianas (within ca. 1 m), suggests the existence of a high interspecific competition between them. Certainly, the prodigious re-sprouting ability of lianas enhances the creation of massive clumps of them around small groups of trees (Benitez-Malvido and Martinez-Ramos 2003). This, coupled with their high specific leaf area, allows them to allocate large amounts of canopy leaves above their hosts, competing aggressively with trees (Schnitzer and Bongers 2011) and leaving relatively little space available for other lianas and epiphytic plants. And such a pattern is supported by the data for distances < 2 m. Specifically, I found a clustering of host trees with high liana loads at edge plots, which is probably leading to a high intra- and interspecific competition at local scales. However, although epiphytic ferns were largely excluded from using trees colonized by lianas in my study area, the reverse could actually be true as in certain other systems, where ants inhabiting epiphytic ferns have been found to actively exclude lianas from attaching to their host trees (Tanaka and Itioka 2011, see also Fayle et al. 2012).

My results suggest that lianas with tendril climbing mechanisms are more abundant than the other guilds. Although tendril climbers are generally thought to require smaller (<10 cm diameter) supports (Putz 1984b), many species found in my study area initially use their tendrils to attach to small trees but, when fully grown, drop their tendrils and sometimes twine completely around the branches or trunks of trees. Lianas bearing these kinds of climbing mechanisms are probably the first to colonize small trees, acting then as facilitators for other lianas to further colonize host trees and contributing to the creation of clumps of lianas (Pinard and Putz 1994). Therefore, re-sprouting and potential facilitation processes between types of liana seems to create groups of trees with large amounts of lianas in close vicinity, hindering the colonization of epiphytic ferns, especially so near forest edges.

A key caveat of my study is that I measured morphological plant guilds rather than individual species (see Fayle et al. 2009 for differences in the distribution of species of Asplenium ferns). However, I observed a clear pattern of fern displacement in relation to trees with lianas, despite the large spatial heterogeneity of lianas in edge plots. This strong response (especially apparent when analyzing the presence of epiphytic ferns in host trees with lianas) would probably be even stronger if species were analyzed separately. Larger sample sizes for both ferns and lianas would be needed to assess species-specific analyses, and such studies with a taxonomic component will help in understanding the mechanisms behind the patterns observed in this paper.

In summary, my results suggest important differences in the composition of epiphytic and climbing plants between the edges and interiors of forest fragments in my study area. Edge ecotones seem to be the domain of lianas with detrimental effects upon epiphytic ferns. The vital importance of ferns in tropical forests in Australia (Cummings et al. 2006) and their apparent decline in fragmented forests might have cascading impacts on animals and plants that depend on them.

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Chapter 5 Forest disturbance drives rattan proliferation in tropical rain forest fragments

This chapter is based upon a paper in preparation:

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Statement of contribution of others:

Campbell collected the data with some initial assistance from Magrach. Campbell analyzed the data with advice from Magrach and Edwards. Campbell wrote the first draft of the chapter. The subsequent drafts were revised by Campbell with editorial input from Edwards, Magrach, and Laurance. Campbell created the figures and tables.

Please note: for ease of reading, some information which reiterated that previously provided within Chapter 3 has been removed, please see referral notes where applicable.

Abstract

Human-induced forest fragmentation poses one of the largest single threats to tropical rain forest diversity yet its impact on rattans (climbing palms) has remained virtually unexplored. Rattan is arguably the world's most valuable non-timber forest product although current levels of harvesting and land-use change, such as forest fragmentation, place wild populations at risk. I examined the impact of forest fragmentation on rattan abundance, demography and ecology within the forests of the Atherton Tablelands of northeastern, Australia. I assessed the community abundance of rattans, and separately the component adult (> 3 m) and juvenile (⩽ 3 m) rattan abundance in five intact forests and five forest fragments (23-58 ha) to determine their response to a range of environmental and ecological parameters. My study found that fragmented forests had less canopy cover and supported higher abundances of rattans than intact forests. Fragment size and edge penetration distance significantly affected adult rattans, with greater numbers observed in smaller fragments and near edges. The presence of other climbing plants was also significantly correlated with juvenile rattan abundances. My findings suggest that the proliferation of rattans within fragmented rain forests is predominantly due to canopy disturbance of forest edges and the subsequent increase in suitable, high-light habitat for rattans. However, the response of adult and juvenile rattans to fragmentation and edge effects are not consistent. I propose that managed forest fragments may provide potential economic benefits where rattans are harvested as a forest product though in fragments whose primary function is conservation rattan management and control may be required.

Introduction

Deforestation of tropical rainforests rarely removes all pre-existing vegetation in a given area (Laurance and Bierregaard Jr 1997), but leaves isolated fragments of the original vegetation surrounded by new habitat types (Wilcove et al. 1986). Fragmentation of tropical forests is globally pervasive and increasing in extent (Wade et al. 2003, Bhagwat 2014, Riitters et al. 2016), with forest fragments now representing 46% of the remaining forested area (Mercer 2015). Forest fragments support less species than comparable intact forest (Fahrig 2003, Haddad et al. 2015). The estimated 13-75% lost diversity (Haddad et al. 2015) that occurs in fragments has been associated with habitat alteration due to the degradation of a variety of biological and physical processes (e.g. see reviews by: Laurance et al. 2002, Fahrig 2003, Fischer and Lindenmayer 2007, Laurance et al. 2011). For instance, one by-product of forest fragmentation is that it greatly increases the area of forest edge habitat (Laurance 1991b). In fact, current estimates suggest 70% of the world's remaining forest is within 1 km from a forest edge (Haddad et al. 2015). Proximity to a newly-created forest edge exposes the surviving biota to numerous environmental changes associated with edges, such as: increased light levels, increased desiccation, and greater temperature variability (Williams-Linera 1990, Laurance et al. 2002, Briant et al. 2010). These environmental changes are a consequence of increased disturbance found on forest edges due to mechanisms such as an increase in the rate of large tree loss and tree-turnover (Laurance 1997a, Laurance et al. 2000, Laurance and Curran 2008, Laurance et al. 2011). In addition, forest fragmentation threatens species' long-term persistence through the degradation of beneficial ecological interactions such as pollination and seed dispersal, between the remnant biota (Terborgh et al. 2001, Laurance et al. 2002, Magrach et al. 2014a, Peh et al. 2014, Campbell et al. 2015a).

Despite their degraded state, forest fragments are often the sole means of preservation for many rare and endangered species and threatened ecosystems within heavily deforested regions (Guindon 1996, Arroyo-Rodriguez and Mandujano 2006, Arroyo-Rodriguez et al. 2009). Consequently, retention of forest fragments is of high importance for species and community conservation at regional spatial scales (Guindon 1996, Arroyo-Rodriguez and Mandujano 2006, Arroyo-Rodriguez et al. 2009). If the conservation values of forest fragments are to be preserved, fragments must not only be retained but effectively managed. This necessitates an understanding of their internal biota and ecology.

The majority of work on fragmentation has involved the study of trees. Indeed, the response of forest trees to fragmentation has received considerable focus (e.g. Laurance et al. 1998a, Laurance et al. 2000, Laurance et al. 2002, Laurance et al. 2006a, Laurance et al. 2011). However, despite the high diversity of non-tree life forms in tropical forests (Gentry and Dodson 1987) the potential impact of forest fragmentation on this forest component is less well known. For instance, even though rattans are one of the World's most valuable non-timber forest products (Ros-Tonen 2000, Sastry 2002) and the existence of many wild populations is under threat (Dransfield 1987, Hirschberger 2011), how rattans respond to forest fragmentation has yet to be explored.

"Rattan" is the generic term used to describe climbing species within the palm family Arecaceae (subfamily Calamoideae) (Dransfield 2001). Within Arecaceae, rattans represent roughly one fifth of the currently described taxa; comprising 13 genera and ~600 species (Uhl and Dransfield 1987, Dransfield et al. 2008). The majority of these species (~400 spp.) belong to the genus *Calamus* L. (Dransfield et al. 2008, Baker 2015). *Calamus* is the most diverse genus within Arecaceae (Dransfield et al. 2008) and one of the most diverse genera of all climbing plants (Gentry 1991). *Calamus* is widely distributed throughout the Old World humid tropics ranging from Africa, through much of Asia to Australasia and parts of the Pacific region (e.g. Fiji). The *Calamus* genus attains maximum diversity in the closed-canopy forests of south-east Asia, where their predominance is a striking characteristic of Asian liana communities (Gentry 1991, Dransfield et al. 2008).

Economically, rattans are used extensively for furniture, basket making and construction making them a valuable non-timber forest product (Ros-Tonen 2000, Sastry 2002). The use of rattan by rural communities has persisted for centuries (De Beer and McDermott 1989, Dransfield and Manokaran 1994). Historically, most rattan has been harvested from wild populations in primary forests (Dransfield and Manokaran 1994), yet overharvesting along with continued land clearing has left many rattan species threatened with extinction (Dransfield 1987, Hirschberger 2011). Understanding how rattan abundance responds to forest fragmentation would allow for increased effectiveness of rattan management for production (Siebert 2012).

Few studies have explored the response of wild populations of rattans to the concurrent alteration of multiple environmental traits imposed by fragmentation. However, individual environmental traits are known to strongly influence rattan abundance. For example, in general, rattan abundance increases in moderate to high light conditions (Siebert 2012), in well drained soils (Dransfield 1992, Siebert 1993, Watanabe and Suzuki 2008, Siebert 2012) and peaks in abundance at mid-elevations (~1000m) (Putz and Chai 1987, Siebert 2005, Stiegel et al. 2011). However, species-specific rattan responses have been identified for light-availability, soil type, elevation and soil moisture (Siebert 1993, 2012, Thonhofer et al. 2015) some of which are contradictory (Siebert 1993, Stiegel et al. 2011). For instance, in a study of two species of *Calamus* in Indonesia Siebert (1993) identified *C. zollingeri* Becc. as displaying a positive relationship with light intensity whilst *C. exilis* Griff. abundance was negatively related to light intensity. Determining which environmental variables positively relate to rattan abundance and whether synergisms exist would allow for the improved conservation of wild rattan populations (Siebert 2012).

Rattans are generally included in forest assessments as lianas *sensu lato* (Gerwing et al. 2006). While both rattans and lianas are climbing-plants, are structurally dependent on trees (Putz and Chai 1987, Putz 1990a, Gentry 1991), and proliferate in disturbed environments (Putz 1990a, Siebert 1993, Bøgh 1996, Laurance 1997a, Laurance et al. 2001a) they differ in important ways. Within forests, rattans function differently from true lianas. As monocotyledons, they exhibit no secondary growth (Tomlinson and Huggett 2012) and rarely re-root their stems to the soil surface (Dransfield 1978). This lessens their ability for long-distance clonal colonization of tree-fall gaps (Yorke et al. 2013). Rattans also lack the capacity to branch (Dransfield 1978) resulting in difficulty maintaining canopy position during the stem elongation necessary for their leaf production (Putz 1990a). Furthermore, rattans interact differently with their tree hosts. Unlike tendril-climbing or stem-twining lianas (Putz 1984b, Putz and Chai 1987), rattans can utilize large diameter supports by embedding into tree branches or trunks (Isnard and Rowe 2008a, Rowe and Isnard 2009) using recurved hooks on flagella (a modified inflorescence) or cirri (extensions of the leaf rachis) (Putz 1990a, Isnard and Rowe 2008a, Rowe and Isnard 2009). Thus rattans depend more on the spatial arrangement of supports rather than on the alignment of a series of successively taller, small diameter supports that are required by true lianas (Putz and Chai 1987). Rattans can also span larger inter-support gaps than most lianas (Putz 1984b, 1990a). This is because a lack of secondary growth means young rattan stems are of a similar size to mature stems and are considerably more rigid than vine leader shoots (with additional rigidity provided by leaf sheaths (Isnard and Rowe 2008b)) (Putz 1990a). Increased rigidity also means young rattan stems do not require structural support as early in plant development as vine leader shoots (Putz 1990a). As a consequence, rattans generally access the canopy through smaller, more vertical openings in the overstorey (Siebert 2012) and use larger supports over larger intra-support distances than many lianas could (Putz and Chai 1987). Therefore, despite the inclusion of rattans with lianas within forest assessments (Gerwing et al. 2006), rattans are likely to respond differently to the enhanced disturbance within forest fragments (Laurance et al. 2002, Laurance et al. 2006a, Laurance et al. 2011). Nevertheless, it is yet to be determined how rattans respond to forest fragmentation, and whether these responses differ from those of lianas (Laurance 1997a, Laurance et al. 2001a, Magrach et al. 2014b). Furthermore, a single rattan “response” to fragmentation may not be expected as adult rattans are reliant on structural hosts (trees) whilst juveniles are free-standing (Putz 1990a). Consequently, juvenile rattans may respond differently to environmental and ecological variables than adult rattans (Thonhofer et al. 2015, Browne and Karubian In Press). For instance, juvenile rattans in Indonesian forests were found to show a stronger relationship to ecological and spatial factors than adult rattans, possibly due to differential microhabitat preferences (Thonhofer et al. 2015). Juvenile arboreal palms have also been observed to display a greater sensitivity to edge effects than adults in a study of Ecuadorian forests (Browne and Karubian In Press). These findings suggest that the demographic structure of rattan communities may be altered both temporally and spatially by forest fragmentation. As juvenile rattans constitute up to half the abundance of understory plants in some tropical forests (Siebert 2012) it is important for both conservation and production values to ascertain whether their response to fragmentation is consistent with that of adult rattans.

Here, I report on the effect of forest fragmentation on total rattan community abundance and demographic structure at both a landscape level (comparing fragmented versus intact forests) and local level (within fragments), in a long-term (~100 years) fragmented-forest landscape of northeastern, Australia. I aimed to; a) determine the influence of fragmentation on total rattan abundance and rattan demographic structure (by looking at the component juvenile and adult rattan abundance separately), and b) identify the environmental and ecological predictors associated with these measures. I predicted that the highly-disturbed environmental conditions found within forest fragments would favor an increase in total community, juvenile and adult rattan abundance. However, I predicted that adult and juvenile abundances would respond differently to environmental factors due to adult rattans reliance on structural hosts (trees) as opposed to their free-standing juveniles (Putz 1990a).

Methods

Study area

My study was located on the Atherton Tableland, north-eastern Queensland, Australia (Fig. 3.1 a). The Atherton Tableland is a hilly upland plateau ranging in elevation from ~600-1100 m.a.s.l. Mean annual precipitation ranges from 1400 to 3000 mm due to a localized north-west (low) to south-east (high) rainfall gradient, with a pronounced wet season from January to April (Bureau of Meterology 2016). The region is also prone to cyclones with 45 cyclonic impacts recorded for the region from the years 1858 to 2011 (Turton 2012). Cyclone impacts can range from elevated precipitation to severe canopy damage of forest trees (Turton and Siegenthaler 2004, Turton and Stork 2009).

Forests in the study area are described as complex mesophyll and notophyll rainforests (Tracey 1982, Herbarium 2015). These are structurally similar to those of the Indo-Malay region (Metcalfe and Ford 2009) and contain abundant rattans. Four of the eight species of *Calamus* present in Australia are found in the area: *C. australis* Mart., *C. caryotoides* A.Cunn. ex Mart., *C. moti* F.M.Bailey, and *C. radicalis* H.Wendl. & Drude (Dowe 2010, Centre for Australian National Biodiversity Research 2010). These forests have not experienced rattan harvesting since harvesting is uncommon in the region and most forests are protected. Vegetation of the study area comprises primary remnants, secondary forests and large rain forest areas on surrounding mountain ranges. Deforestation here began in the early 1900's and proceeded rapidly with most forest clearance occurring within three decades (Society 1979, Winter et al. 1987, Smith 1991, Society 1995). The study area is now heavily fragmented with remaining vegetation fragments spatially isolated by a predominantly agricultural land use matrix (Fig. 3.1a). Additionally, most of the remnant rain forest vegetation has, at some time in the past, been exposed to selective logging for valuable hardwood timber species such as Red Cedar (*Toona ciliata*) (Eacham Historical Society 1979, 1995, Pearson 2008).

Fragments are generally found overlying volcanic soils, namely krasnozems, and topographically occur on level to gently undulating plains and gently undulating to undulating rises (Malcom et al. 1999). Larger remnant intact forests are mostly located on steeper mountainous areas that were less conducive to logging and on poor nutrient granite and rhyolite-derived soils that restricted their suitability to agriculture (Malcom et al. 1999).

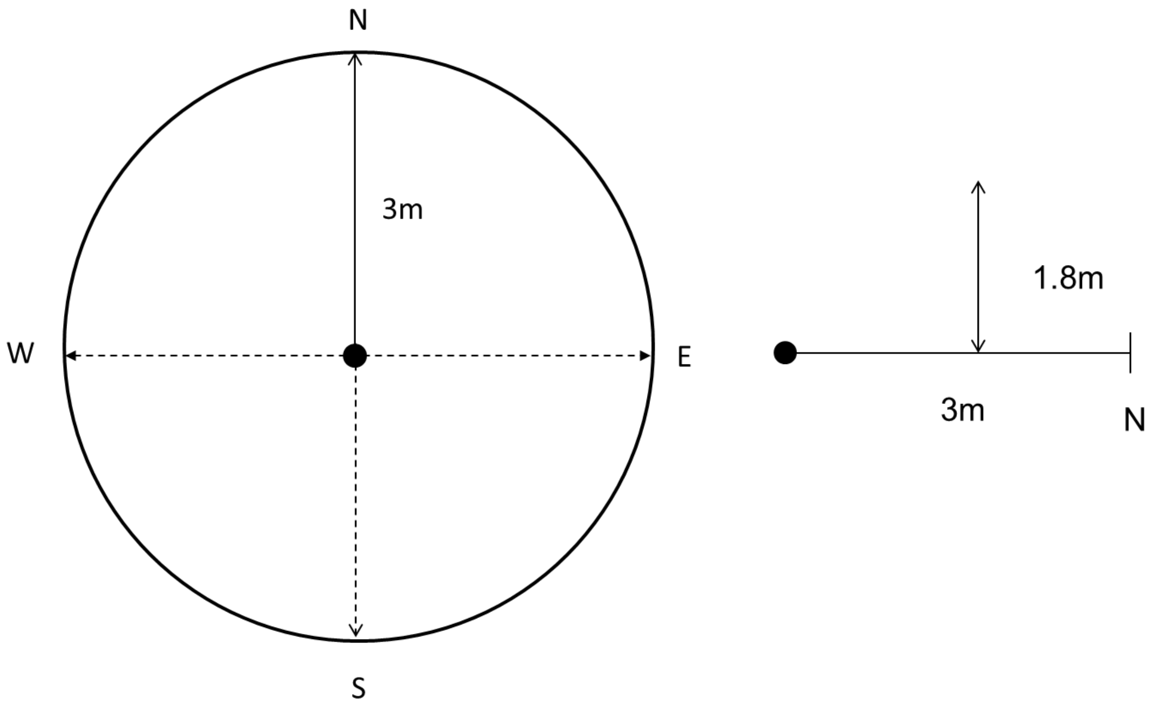

Figure 5.1 Relative rattan abundance measurement protocol. All rattan stems encountered along a 3m long by 1.8m high transect facing north were counted unless they were noted to arise from a previously encountered rattan clump. In addition, each counted rattan stem was classified as ≤ 3m or > 3m in height/length. This procedure was then repeated for identical transects facing the other three cardinal directions with all transects originating from a central point. Finally, this entire process was repeated in the remaining three corners of each plot and the 16 transect values summed to gain an overall representative value of rattan abundance per 20m^2 plot.

Rattan measures

Over the period March 2012 to February 2014, rattan abundance was recorded at five 20 x 20m plots in 10 forest sites (Fig. 3.1b) five in forest fragment sites and five in intact forest sites (50 plots in total). At the four corners of each plot, line intercept transects of 3 m were established in the four cardinal directions. Along the transects, individual rattan stems that intercepted the line, including those up to 1.8 m in height above it, were counted (Fig. 5.1). For each plot, the 16 samples were summed to produce a relative abundance estimate of rattans. Any rattan stems that intercepted the line transect and could be distinguished as coming from a previously encountered rattan clump were disregarded. Finally, to ascertain rattan population demography, all sampled rattans were categorized as either juvenile (≤ 3m) or adult (> 3m). I used a similar method of aging rattans as Thonhofer et al. (2015) in their study from central Sulawesi, however, I chose a 3 m cut off for the category of juvenile rattans rather than 1 m as this was the height at which rattans transitioned from free standing to utilizing tree hosts.

The second aim of my study was to identify the environmental and ecological predictors associated with rattan abundance and demography at both the landscape and local level. To identify these I collected information on known correlates of rattan and liana abundance (e.g. those identified within Siebert 1993, Laurance et al. 2001a, Schnitzer and Bongers 2002, Siebert 2012, Ledo and Schnitzer 2014) for incorporation in the individual generalized linear mixed models (GLMMs) listed below (see Data Analysis subheading for full description). Parameters examined included: liana abundance, tree abundance, tree DBH (cm), tree bark type, tree buttressing, canopy cover (%), number of fallen logs (⩾ 10cm diameter), plot elevation (m), plot slope (degrees), mean annual rainfall (mm), mean dry quarter (July-September) rainfall, plot distance to forest edge (m), and plot carbon storage (tonnes/ha).

Liana and tree measures

The abundance of lianas (≥ 1 cm diameter breast height: DBH) was determined for five 20 x 20 m plots at each of the 10 sites as per standard methodology (Gerwing et al. 2006, Schnitzer et al. 2006, Schnitzer et al. 2008). Liana stems were counted as individuals unless clearly joined and were not excavated to determine vegetative propagation. Tree abundance and size (≥10 cm DBH) was also measured with tree size measured at 1.3m above the ground or 10 cm above buttresses.

Forest disturbance and localized environmental parameters

Two measures of forest disturbance were determined for each plot: canopy cover and the number of fallen trees (≥ 10cm diameter). Canopy cover was estimated at the four corners and the center of each plot, measured by averaging four spherical densitometer readings taken facing the cardinal directions (N, E, S, W) at each point. The number of fallen trees (⩾10 cm diameter) was counted within each plot.

To determine physical traits of plots I examined their slope and elevation. The degree of slope of each plot was calculated using a clinometer, whilst elevation of all sites was assessed using climatic model interpolation data provided by the Wet Tropics Management Authority, Cairns, Australia (WTMA 2009). These data were also accessed to determine the annual rainfall (mm) and dry quarter rainfall (July-September, mm) of sites.

Plot live carbon was used to compare the structural parameters of fragmented and intact forest sites. This was estimated by combining carbon from above ground estimates of all live trees (≥ 10cm DBH) and lianas (≥ 1cm DBH) within a 20 x 20 m plot. Liana above-ground biomass (AGB) was calculated using the liana specific allometric equation developed by Schnitzer et al. (2006):

$$AGB = \exp[-1.484 + 2.657 \ln(D)]$$

where D is the diameter at 130 cm from the roots (Gerwing et al. 2006) expressed in centimetres, while AGB is the predicted above ground oven-dry weight of the liana in kilograms.

Tree above ground biomass (ABG) was calculated using the allometric equation developed by Chave et al. (2005) (see below) as Preece et al. (2012) compared the accuracy of multiple biomass estimation methods for forests within the Wet Tropics bioregion and concluded that the Chave et al. (2005) allometric provided the best and most reliable estimate for the region. To convert AGB into biomass carbon storage I used a conversion factor of 0.47 which is the recommended value from the Intergovernmental Panel for Climate Change for tropical forests (IPCC 2006). In addition, AGB was calculated using wood density estimates at the reported default value for Australian tropical forests of 0.5 g cm^{-3} (500 kgm^{-3}) (Department of Climate Change and Energy Department of Climate Change and Energy Efficiency 2010). Consequently, tree AGB estimates were calculated using the following equation:

$$AGB = \rho^* \exp(-1.499 + 2.148 \ln(dbh) + 0.207 (\ln(dbh))^2 - 0.0281(\ln(dbh))^3)$$

Where AGB is measured in kg, dbh is measured in cm, and ρ is wood density measured in g cm^{-3}.

Landscape variables

Data on forest fragment characteristics were collected from the aforementioned climatic model interpolations data and assessed using the program Fragstats (McGarigal et al. 2002). Parameters assessed included: fragment area (m^2), fragment perimeter (m), fragment isolation (m), fragment shape (perimeter/minimum possible perimeter for a fragment that size) and fragment proximity which is a measure of isolation which also includes the proportion of similar vegetation within distinct buffer zones (1000 m and 5000m) surrounding individual fragments.

Data analyses

Rattan abundance and demography: intact vs fragmented forests

I evaluated the influence of landscape and environmental parameters on rattan abundance and demography using individual, negative binomial, generalized linear mixed models (GLMMs). Prior to model generation I checked for correlated predictor variables through examination of the variance inflation factor (VIF) and eliminated those that showed a VIF > 3 following the protocol of Zurr et al. (2010). This resulted in the removal of the mean dry quarter rainfall variable. Additionally, as there were five plots within each site (stratified by forest edge distance), plots were not fully independent. As such, I included site ID as a random effect. In each model-fitting exercise I selected *a priori* a global model in which the response variable (total rattan abundance, juvenile abundance, and adult abundance per plot) was examined as a function of the following nine environmental and ecological drivers: forest state (intact vs. fragmented), edge distance, liana abundance, tree abundance, number of fallen logs, canopy cover, mean annual rainfall, altitude and slope. I additionally included the interaction between forest state and edge distance. Model analysis was performed using the R package *glmmADMB* (Skaug et al. 2012).

The most parsimonious model was determined using a multimodel inference approach (Burnham and Anderson 2002) where I ran all combinations of models using function *dredge* in package *MuMIn* (Bartoń 2013) and selected the best model based on Akaike information criteria values (AIC). Whenever I had more than one plausible model (i.e., when Δ AIC < 2 for more than one model, (Burnham and Anderson 2002)) I computed average estimates for each variable across all models. This procedure was followed for model fitting for each response variable.

Rattan abundance and demography: within forest fragments

I used the subset of forest fragment sites (i.e. excluded intact forest sites) to evaluate the effect of the fragment specific traits such as fragment area, fragment isolation, fragment shape and fragment proximity, on the response variables of total rattan abundances and the abundance of juvenile and adult rattans per plot. Again, these impacts were assessed in conjunction with the previously mentioned environmental and ecological drivers (listed below) known to influence rattan abundance. Analyses were preformed using individual GLMMs and followed the procedure mentioned above. Full models here included the following explanatory variables: fragment size, fragment shape, fragment isolation, fragment proximity, distance to the forest edge, liana abundance, tree abundance, number of fallen logs, canopy cover, mean annual rainfall, altitude and slope. I followed the same procedure outlined above for model fitting, selection and averaging.

Environmental traits of fragmented and intact forests

Disturbance and forest gap dynamics along with the availability and size of trees (as rattan supports) are known to be the major drivers of the distribution of rattans and lianas within forests (Putz 1990a, Schnitzer et al. 2000, Schnitzer and Bongers 2005, Schnitzer and Carson 2010, Ledo and Schnitzer 2014). To assess these traits within fragmented and intact forests, canopy cover and tree abundance were compared along with their relationships with the previously mentioned (see above) environmental and ecological drivers. Assessment was again determined using individual GLMMs. For full description see Chapter 3 (subheading “Environmental and structural parameters of fragmented and intact forests”).

Program R (R Core Team 2015) was used for all statistical analyses.

Results

Rattan abundance and demography: intact vs fragmented forests

At a landscape level, I recorded a total relative rattan abundance of 3023 (n) stems ~70% of which were found in fragmented forests (n=2128) and the remaining ~30% in intact forests (n=895) (Fig. 5.2). Within the total rattan community, adult rattans (n=2763) comprised >90% of the recorded stems, whilst juvenile rattans (n=260) contributed < 10 % (Fig. 5.2). Despite considerable variation in environmental and ecological traits (Tab. 5.1, Tabs. A1, A2 and A3), forest state (fragmented or intact) was the only significant predictor of total and adult rattan abundance within the landscape, with more rattans occurring in fragmented than intact forests (Fig. 5.2, Tab.

5.2). Additionally, adult and total rattan abundances displayed a positive relationship with distance from the forest edge whilst the relationship between juvenile rattan abundance and distance from the forest edge was negative, though these relationships were not significant.

Rattan abundance and demography: within forest fragments

Within fragmented forests, juvenile, adult and total rattan abundance was significantly and negatively related to: fragment area and canopy cover. The abundance of juvenile rattans was also significantly and negatively related to plot elevation and positively to liana abundance, whereas adult rattans were significantly and negatively influenced by tree abundance. Furthermore, total rattan abundance was positively associated with liana abundance and negatively with plot slope and tree abundance (Tab. 5.3). Interestingly, in contrast with the findings at the landscape level, within fragments, adult rattan abundance displayed a negative relationship to distance from the forest edge whilst the relationship with juvenile rattan abundance and distance from the forest edge was positive, though these relationships again were not significant (Tab. 5.3).

Environmental traits of fragmented and intact forests

Canopy cover was significantly lower in fragmented than intact forests and was lower on forest edges than forest interiors (Tab. A3). This decreased canopy cover also penetrated significantly further into the edges of fragmented than intact forests (Tab. A3). Canopy cover was also found to be significantly and negatively related to altitude (Tab. A3).

Tree abundance was significantly lower in fragmented forests than in intact forests but was higher on forest edges than forest interiors (Tab. A1). Furthermore, tree abundance was significantly and positively related to forest live carbon however it was significantly and negatively related to altitude (Tab. A1).

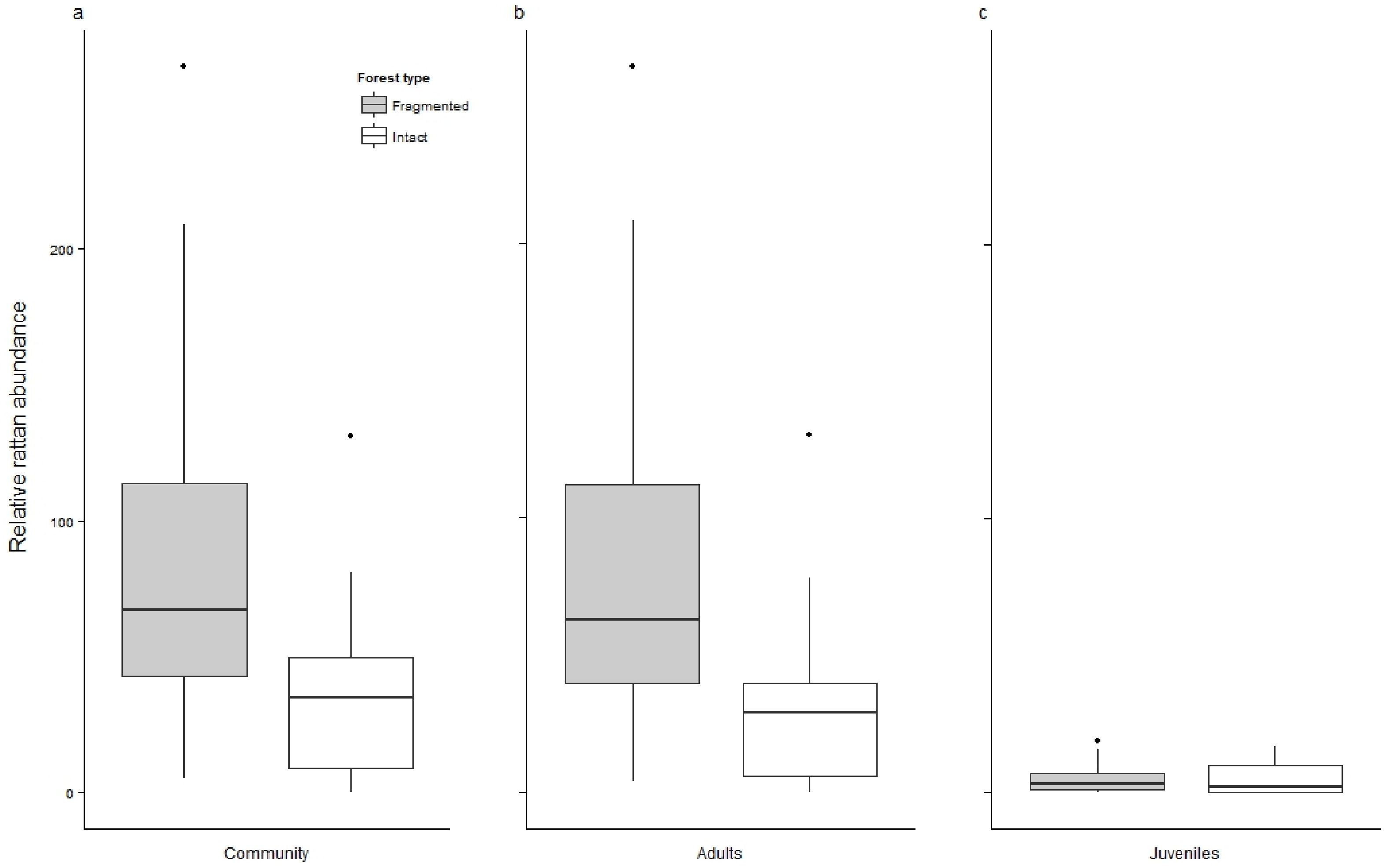

Figure 5.2 Relative abundance of the **a)** Total rattan community, and component **b)** Adult rattans (>3m in length) and **c)** Juvenile rattans (≤ 3m in length) in fragmented and intact forests of the Atherton Tablelands, northeastern Australia.

Table 5.1 Mean and range of the environmental and ecological traits assessed to determine their influence on rattan abundance in the fragmented and intact forests of the Atherton Tablelands, northeastern Australia.

	Fragmented	Intact
	Mean (Range)	Mean (Range)
Liana abundance	39.28 (7-120)	45.68 (1-163)
Tree abundance	27.08 (13-44)	33.68 (24-62)
Fallen logs	8.04 (1-16)	7 (0-13)
Canopy Cover (%)	97.01 (92.77-99.63)	97.63 (85.64-99.72)
Slope (°)	10.48 (3-28)	15.72 (7-27)
Altitude (m.a.s.l)	784.4 (710-940)	810 (670-1010)
Mean annual rainfall (mm)	2008 (1660-2489)	2337.8 (1831-3218)

Table 5.2 Results of model averaged, generalized linear mixed models (negative binomial) examining the Landscape Level (fragmented and intact forests) response of **a)** total rattan abundance, **b)** juvenile rattan (≤ 3m in length) abundance and **c)** adult rattan (> 3m in length) abundance to forest fragmentation and environmental parameters.

	Estimate	Std. Error	Adjusted SE	z value	P
a) Total rattan abundance					
(Intercept)	4.522	0.374	0.382	11.853	< **0.001**
Forest type (Intact)	-0.855	0.287	0.295	2.901	**0.004**
Fallen logs	-0.045	0.039	0.041	1.111	0.267
Distance from forest edge	0.005	0.005	0.005	0.947	0.344
Liana abundance	-0.002	0.003	0.003	0.681	0.496
Tree abundance	-0.012	0.017	0.018	0.662	0.508
b) Juvenile rattan abundance					
Intercept	1.096	0.665	0.677	1.617	0.106
Slope	0.031	0.02	0.021	1.483	0.138
Tree abundance	0.022	0.021	0.021	1.047	0.295
Rainfall	< 0.001	< 0.001	< 0.001	0.871	0.384
Liana abundance	-0.004	0.005	0.005	0.738	0.46
Distance from forest edge	-0.003	0.006	0.006	0.576	0.565
c) Adult rattan abundance					
Intercept	4.453	0.406	0.413	10.788	<**0.001**
Forest type (Intact)	-0.946	0.3	0.308	3.071	**0.002**
Fallen logs	-0.047	0.041	0.042	1.111	0.267
Distance from forest edge	0.006	0.005	0.005	1.102	0.271
Liana abundance	-0.015	0.018	0.019	0.785	0.432
Tree abundance	-0.002	0.003	0.004	0.609	0.542

Table 5.3 Results of model averaged, generalized linear mixed models (negative binomial) examining the Fragment (within fragmented forests only) response of **a)** total rattan abundance, **b)** juvenile rattan abundance (≤ 3m long) and **c)** adult rattan abundance (> 3m in length) to forest fragmentation and environmental parameters.

	Estimate	Std. Error	Adjusted SE	z value	P
a) Total rattan abundance					
Intercept	18.215	6.727	6.846	2.661	**0.008**
Fragment area	-0.003	0.001	0.001	4.607	**<0.001**
Canopy cover	-0.131	0.056	0.057	2.279	**0.023**
Slope	-0.037	0.018	0.018	2.043	**0.041**
Liana abundance	0.01	0.004	0.004	2.178	**0.029**
Fragment shape	0.441	0.225	0.231	1.911	0.056
Tree abundance	-0.057	0.015	0.016	3.638	**<0.001**
Altitude	-0.003	0.001	0.001	1.908	0.056
Fallen logs	-0.043	0.031	0.032	1.366	0.172
b) Juvenile rattan abundance					
Intercept	28.029	10.194	10.448	2.683	**0.007**
Fragment area	-0.002	0.001	0.001	2.171	**0.03**
Canopy cover	-0.25	0.095	0.098	2.549	**0.011**
Distance from fragment edge	0.014	0.007	0.007	1.845	0.065
Altitude	-0.006	0.003	0.003	2.099	**0.036**
Liana abundance	0.018	0.008	0.009	2.056	**0.04**
Slope	0.036	0.022	0.022	1.616	0.106
Fragment shape	0.41	0.271	0.278	1.476	0.14
c) Adult rattan abundance					
Intercept	16.761	7.169	7.276	2.304	**0.021**
Fragment area	-0.003	0.001	0.001	4.398	**<0.001**
Canopy cover	-0.126	0.058	0.059	2.135	**0.033**
Slope	-0.039	0.02	0.02	1.934	0.053
Liana abundance	0.008	0.004	0.005	1.83	0.067
Tree abundance	-0.059	0.017	0.017	3.469	**0.001**
Fragment shape	0.483	0.242	0.249	1.942	0.052
Altitude	-0.003	0.001	0.002	1.672	0.095
Fallen logs	-0.05	0.034	0.035	1.416	0.157
Distance from fragment edge	-0.009	0.005	0.005	1.743	0.081
Fragment isolation	<0.001	<0.001	<0.001	1.334	0.182

Discussion

The fragmentation of the rainforests of the Atherton tablelands of north Queensland, Australia, has resulted in significantly higher total rattan abundance, and in particular, adult rattan abundance than similar, intact, forest locations. In fact, at a landscape level whether a forest was fragmented or not was the single best predictor of total and adult rattan abundance, in this study. The proliferation of rattans in response to forest fragmentation is similar to that found for woody-dicotyledonous lianas (Chapter 3, Laurance et al. 2001a, Laurance et al. 2014a) and suggests that fragmentation promotes environmental or ecological changes which favor both types of climbing plants (rattans and lianas). However, juvenile rattan abundance was not significantly different between the two forest states, and forest type was not retained in any of the selected models used to describe juvenile rattan abundance. That no single model including forest type was retained (i.e. all had a Δ AIC > 2) strongly suggests forest type (i.e. intact vs. fragmented) exerts very limited influence on the abundance of juvenile rattans.

Within forest fragments, light availability had a significant positive influence on rattan abundance. Sites with lower canopy cover had greater total, adult and juvenile rattan abundances than sites with high canopy cover. This finding supports previous reports of rattans proliferating in disturbed, high-light sites (Tomlinson 1979, Bøgh 1996, Laurance 1997a) and the observations of Siebert (2012) who stated that “light is the most important determinant of rattan species composition, densities and growth rates” for South-East Asian rattan communities. Furthermore, I found that fragments had significantly lower canopy cover than intact forests and reduced canopy cover penetrated significantly further into the edges of fragmented than intact forests. The decreased canopy cover in fragments can result in changes to microclimatic conditions (Camargo and Kapos 1995, Laurance et al. 2002, Laurance et al. 2011, Magnago et al. 2015) including increased light availability (Turton and Freiburger 1997). This result also supports numerous studies which have shown that fragment edges experience higher levels of disturbance that those of intact forests (Saunders et al. 1991, Murcia 1995, Laurance et al. 2002, Harper et al. 2005, Laurance et al. 2011). Interestingly, however, when the response of rattans to forest edges was examined within individual demographic classes (adult and juveniles) the findings were not consistent between them. For instance, at a landscape level, adult rattans displayed a positive relationship to forest edge distance and juveniles a negative relationship, whilst the reverse relationships were true for the abundances of both groups when examined in fragmented forests alone. Whilst these finding were non-significant, they suggests that juvenile rattans may respond differently to adult rattans in how they react to the environmental and ecological alterations found on fragmented forest edges (Thonhofer et al. 2015, Browne and Karubian In Press). Whether the contrary responses are due to light availability alone or some other mechanisms (e.g. seed dispersal limitation or structural host limitation in fragmented forests) remains to be tested. It can, however, be concluded that the increased disturbance of fragment edges leads to a general increase in rattan abundance, even though adult and juvenile rattan responses to fragmentation and edge effects were not consistent.

Further support that forest disturbance drives an increase in rattan abundance in fragments was my finding that fragment area was significantly and negatively related to juvenile, adult and total rattan abundance. Fragment area is negatively correlated with tropical forest disturbance with smaller fragments likely to experience significantly higher levels of disturbance which is chronic (Laurance 1991b, Laurance 2002, Laurance et al. 2002, Laurance et al. 2006a, Laurance et al. 2011). This disturbance is the consequence of elevated rates of large tree mortality, turnover and treefall-gap creation (Laurance et al. 1997, Laurance et al. 1998a, Laurance et al. 2000, Hill and Curran 2003, Laurance et al. 2006a) mostly on fragment edges due to wind-disturbance, desiccation, and micro-climate alteration (Williams-Linera et al. 1998, Briant et al. 2010, Laurance et al. 2011, Magnago et al. 2015). In corroboration, there was a positive relationship between rattan abundance and fragment shape, where more dissected fragments with greater edge exposure (Laurance 1991b, Hill and Curran 2005), were found to display greater rattan abundances (Tab. 3).

In my study, lianas and rattans appear to have similar habitat preferences, with both increasing in abundance in response to fragmentation (Chapter 3). For instance, analogous with rattans, lianas are renowned for proliferation in response to forest disturbance (Laurance et al. 2001a, Ledo and Schnitzer 2014), peaking in areas of high-light availability such as forest edges and treefall gaps (Schnitzer et al. 2000, Schnitzer and Carson 2001, Schnitzer and Bongers 2005, Schnitzer and Carson 2010). These findings lend further credence to the assertion that rattans proliferate in fragments due to disturbance and possible increased light availability (Tomlinson 1979, Dransfield and Manokaran 1994, Bøgh 1996, Laurance 1997a, Siebert 2012). However, though adult rattan abundance was positively related to liana abundance this relationship was not significant. It is plausible that whilst adult rattans proliferate in the disturbed and high-light environments within which lianas are found, there is considerable competition between these ecologues (functional ecological analogues) for essential structural supports (tree hosts). For instance, the capacity of lianas to branch and their highly specialized climbing apparatus dedicated for attachment to smaller climbing trellises (Putz 1984b, Putz and Chai 1987, Hegarty 1991b), may provide a competitive advantage in areas with smaller climbing trellises (Penalosa 1984, Putz 1984b), such as the edges of forests and regenerating treefall gaps (Schnitzer et al. 2000, Schnitzer and Carson 2001, Schnitzer and Bongers 2005, Schnitzer and Carson 2010), areas in fragmented forests which have previously been found to exhibit increased liana abundances (Oliveira et al. 1997, Viana et al. 1997, Laurance et al. 2001a, Magrach et al. 2014b).

Rattan abundance would increase within fragments if altered environmental conditions provide them a competitive advantage for host trees colonization. Though speculative, this mechanism could explain why adult rattan abundance increased in forest fragments with respect to forest edges. Beyond a certain threshold the number of supports available (trees), not the access to sufficient light, becomes the limiting factor for both rattan and liana abundance (Hegarty and Caballe 1991). I found fragments had significantly less trees than intact forests (however I did not examine trees <10 cm DBH) and thus potential structural hosts. A collapse in tree abundance often occurs within heavily disturbed forest fragments (Laurance et al. 1997, Laurance et al. 2002, Laurance et al. 2006a) and this has previously been found to result in reduced liana abundance and diversity linked to increased competition for hosts (Muthuramkumar et al. 2006, Arroyo-Rodriguez and Toledo-Aceves 2009, Addo-Fordjour et al. 2012b, Addo-Fordjour et al. 2013). Given lower tree abundances within fragments and their significantly lower canopy cover (Tabs. S1, S2), it is plausible that climbing plants must span larger distances between successive supports. Young rattans are comparatively rigid meaning they do not require structural support as early as vine leader shoots (Putz 1990a). Rattans also possess flagella or cirri often several metres long (Putz 1990a). As a consequence of both these traits, rattans possess a superior ability to span larger inter-support distances than lianas (Putz 1990a). Furthermore, the ability of rattans to embed into tree branches and trunks (Isnard and Rowe 2008a, Rowe and Isnard 2009), allows them to attach to and climb larger supports (which are themselves further apart) than could most lianas (Putz 1984b, 1990a, Isnard and Rowe 2008a, Rowe and Isnard 2009). If correct, this hypothesis would also explain the lack of any detectable response of juvenile rattan abundance to fragmentation as free-standing, juvenile rattans, would not be affected by inter-host distances unlike adults. Whilst, this hypothesis of rattan and dicotyledonous liana competition and host distance is as yet un-tested, their specialized morphology and restricted monocotyledonous phylogeny (Isnard and Rowe 2008a, Isnard and Rowe 2008b, Rowe and Isnard 2009, Couvreur et al. 2014), suggest that rattans function as a specialized sub-component within the broader climbing plant community.

In addition, the above hypothesized competition for climbing supports may be one of many as yet unknown ancillary processes contributing to the lack of response to fragmentation by juvenile rattans. For instance, there is considerable variation in light-level preferences of rattan species in some South-East Asian forests (Siebert 1991). Unfortunately, there is very little known of the responses to light availability for the species occurring in this study. Furthermore, it is unclear whether differences in light-level preferences occur between different age classes of rattan species or communities studied here or elsewhere in the world. Additionally, further insight could be had by examining even earlier life history stages. For example, I did not examine rattan seedling recruitment in this study. Rattans possess fleshy fruits whose principle means of dispersal are birds and mammals (Dransfield 1992, Dransfield 2001, Dowe 2010, Siebert 2012). Fragmentation and associated impacts (e.g. increased hunting; Wright et al. 2007) are known to differentially alter the populations of many birds and mammals (e.g. Laurance 1991a, 1997b, Terborgh et al. 2001, Gibson et al. 2013) and thus potential rattan dispersers. As such, patterns of dispersal of rattan propagules within-and-between forest fragments could also be influential in setting overall abundances.

Conclusion

Rattans proliferate in the fragmented rain forests of tropical north-eastern Australia. This proliferation is likely due to an increase in the canopy disturbance in fragments leading to an increase in light availability. However, the response of adult and juvenile rattans to fragmentation and edge effects are not consistent suggesting different underlying mechanisms may determine their distribution and abundances. Adult rattans may proliferate in fragments as their ability to span larger inter-support distances could allow them to better colonize the widely-spaced tree hosts that occur in forest fragments, potentially outcompeting dicotyledonous lianas.

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Chapter 6 Can lianas assist in the restoration of rain forest fragments?

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Statement of contribution of others:

Campbell developed the main research question. Campbell wrote the first draft of the chapter other than the sections on lianas and insects which were written by Odell. The subsequent drafts were revised by Campbell with editorial input from Laurance, Edwards, Odell and Mohandass. Campbell constructed all figures and tables.

Abstract

Can the strategic incorporation of lianas (woody vines) into rain forest restoration plantings enhance biodiversity-conservation outcomes? Lianas are an integral component of primary tropical rainforests yet are often omitted from rain forest restoration plantings as they may damage trees and compete with them for resources. However, there is increasing evidence that many ecological and physiognomic characteristics of lianas may be of some value to restoration plantings, at least in certain contexts. Here I propose strategies for experimentally incorporating lianas into rainforest-restoration plantings to explore whether they can expedite rain forest establishment and enhance biodiversity-conservation outcomes.

Key words: Afforestation, Reforestation, Regeneration, Revegetation, Vines

Resumen

¿Puede la incorporación estratégica de lianas a plantaciones que buscan restaurar la vegetación de las selvas húmedas, mejorar los resultados para la conservación y la biodiversidad? Las lianas son un componente integral de las selvas húmedas tropicales, sin embargo, son omitidas frecuentente en plantaciones que buscan restaurar bosques, ya que estas pueden dañar los árboles y competir con ellos por recursos. No obstante, evidencia creciente indica que muchas características ecológicas y físicas de las lianas pueden tener cierto valor para las plantaciones de restauración, por lo menos en algunos contextos. Nosotros proponemos estrategias para la incorporación experimental de lianas a las plantaciones de restauración, con el fin de explorar si las lianas pueden acelerar el establecimiento de la vegetación, mejorando así los resultados para la conservación y la biodiversidad.

Palabras clave: Aforestación, lianas, reforestación, regeneración, revegetación

Introduction

Lianas limit seedling recruitment, damage saplings, compete with trees for limited resources and increase tree mortality (Stevens 1987, Schnitzer et al. 2005, Ingwell et al. 2010, Schnitzer and Carson 2010, Schnitzer et al. 2014), resulting in their deliberate exclusion from rainforest-restoration efforts. However, as knowledge of liana ecology increases (Putz and Mooney 1991, Schnitzer and Bongers 2002, Schnitzer and Bongers 2011), it is becoming apparent that they often play an integral role in supporting local biodiversity and overall forest functioning. Consequently, it is possible that many of their ecological and physiognomic characteristics could be strategically exploited to enhance and accelerate rain forest restoration processes. Here I propose questions to be answered by the experimental incorporation of strategic liana plantings into rain forest restoration efforts (Tab. 6.1) in the hope that these will be trialed and their value to restoration practitioners determined. Additionally, I suggest why I think these liana-planting strategies could potentially expedite rain forest establishment and improve biodiversity-conservation outcomes.

Table 6.1 Potential topics for experimental examination using strategic liana plantings in rain forest restoration plots.

1. Does planting lianas on the edge of rain forest restoration plots result in the rapid obtainment of a preferential forest interior micro-climate leading to a decrease in shade-intolerant weed species incursions?
2. Does the planting of a liana and tree species mix expedite closed-canopy attainment and limit shade-intolerant weed abundance?
3. Does incorporating lianas into deciduous-rain forest restoration plantings assist in minimizing weed incursions?
4. Does the addition of lianas to restoration plantings increase nutrient turnover and soil biota diversity?
5. Does planting lianas in locations with exposed soil surfaces aid in soil erosion mitigation and limit localized shade-intolerant weed germination?
6. Does planting lianas on deciduous rain forest restoration plot edges result in a decrease in low-intensity fire incursions?
7. Does planting lianas on restoration plot edges lessen wind damage in early successional stages?
8. Does planting lianas at restoration sites containing a heavy undesirable tree species load decrease tree vigor, abundance and recruitment?
9. Could linear plantings of lianas within restoration corridors aid faunal dispersal?
10. Could faunal movement within restoration plantings be guided by densely-planting thorny lianas or rattans?
11. Does incorporating lianas into restoration plantings support enhanced mammalian and insect diversity through the provision of additional food resources?
12. Could including lianas within restoration plantings lessen herbivorous insect damage to planted trees?
13. Does the addition of liana species with conspicuous fruits and flowers to restoration site plantings aid in the passive introduction of tree species and novel genetic material?
14. Can the practical impediments to liana incorporation in restoration plantings be overcome?

Weed management, soil management and soil fauna support

1. **Does planting lianas on the edge of rain forest restoration plots result in the rapid obtainment of a preferential forest interior micro-climate leading to a decrease in shade-intolerant weed species incursions?**

Comprising on average only 4-5% of the total biomass of a lowland moist rain forest (Putz 1983, DeWalt and Chave 2004), lianas produce up to 40% of all leaves in the forest (Hladik 1974, Putz 1983, Gentry 1991, Hegarty 1991a). Hence, leaf-litter production from lianas in tropical forests is much greater than would be expected from their biomass contribution alone (Tang et al. 2012). Additionally, lianas produce leaves rapidly in comparison to most canopy-forming trees because their leaves typically have a low leaf-mass-to-area ratio (LMA) and a short lifespan (Cai et al. 2009, Zhu and Cao 2010, Asner and Martin 2012, Wyka et al. 2013). The prodigious and rapid leaf output of lianas might be beneficial to the restoration process, and could be used to limit the incursion of shade-intolerant weeds into semi-established restoration plots. To test this idea, lianas would need to be planted on the forest edge to vegetatively ‘seal’ it (Williams-Linera 1990, Hegarty and Caballe 1991, Strayer et al. 2003, Harper et al. 2005), thereby creating a dark forest-interior, unsuitable for shade-intolerant weed colonization (Williams-Linera 1990, Goosem and Tucker 2013). Planting lianas along restoration-plot margins in conjunction with bushy tree or shrub species (to act as climbing trellises), might allow for faster and more complete ‘sealing’ of forest edges than would occur by using tree species alone (Schnitzer 2005, Paul and Yavitt 2011, Wyka et al. 2013). If so, this edge sealing would be an important contribution to restoration efforts as weeds are “probably the most important obstacle to ecological restoration… and may completely stop … or deflect succession” in restoration plots (Goosem and Tucker 2013).

In support of this edge-planting strategy, lianas are known to be more abundant on primary and remnant forest edges than in their interiors (Putz 1984b, Laurance et al. 2001a, Zhu et al. 2004, Magrach et al. 2014b, Mohandass et al. 2014). Therefore, dense planting of lianas on restoration-plot edges may simply hasten edge sealing due to this underlying successional process (Williams-Linera 1990, Oliveira et al. 1997, Chazdon 2014). As an added benefit, restoration plots that have been sealed by lianas may also suffer less from detrimental forest edge effects, such as increased light penetration and desiccation (Laurance et al. 2000, Laurance et al. 2002). However, if this planting strategy were undertaken, it is likely that the trees on the edge of the restoration plots would also suffer proportionally more deleterious impacts due to increased liana infestations, than that which occurs “naturally” for trees on the edge of primary and remnant forests (Laurance et al. 2001a). This may be a trade-off regeneration practitioners would need to accept if they were to include lianas in restoration edge-plantings. Regardless, an experimental examination of the value of planting lianas on restoration plot edges would enable comparison of the costs and benefits of this planting strategy.

2. **Does the planting of a liana and tree species mix expedite closed-canopy attainment and limit shade-intolerant weed abundance?**

Planting lianas among juvenile trees in an existing restoration plot would allow one to assess their value for use as a means of reducing the time required until forest canopy-closure. A key goal for rain forest restoration is minimizing the time to establish a closed-canopy because this helps to eliminate shade-intolerant weed species, thereby decreasing weed-management costs (Wagner et al. 2011). Additionally, restoration sites with a closed canopy may provide suitable conditions for the passive recruitment of shade-tolerant, forest-interior tree species (Chazdon 2014), thereby increasing the biodiversity value of the site. Canopy establishment within rainforest-restoration sites using pioneer tree species alone often takes many years (Goosem and Tucker 2013). Lianas, due to their rapid growth rates (Schnitzer 2005, Paul and Yavitt 2011, Wyka et al. 2013), may significantly accelerate canopy closure as they can potentially cover large areas of forest canopy within short periods, as they have previously been found to do following a disturbance (Webb 1958, Catterall et al. 2008). An experiment to determine whether planting lianas within semi-established restoration plots accelerates canopy-closure, and at what cost to the resident trees this occurs, would provide restoration practitioners with the emperical data with which to assess the ecological value of lianas in this role. Additionally, experimentally evaluating lianas as a means of rapid canopy closure, would allow for the determination of the economic costs versus benefits associated with the differing planting strategies of either a dense tree seedling planting without lianas or a less dense tree spacing with them.

Admittedly, integrating liana and tree planting for faster canopy establishment would likely result in a lowered forest canopy height (Oliveira et al. 1997, Chazdon 2014). Additionally, the greater abundance of lianas within plantings could potentially increase tree damage and reduce tree growth rates and fecundity (Stevens 1987, Schnitzer et al. 2005, Ingwell et al. 2010, Schnitzer and Carson 2010). As the restored forest approached maturity, however, liana abundance would likely decline due to natural successional processes (DeWalt et al. 2000, Letcher and Chazdon 2009a, Letcher and Chazdon 2009b). Moreover, if the desired outcome of the restoration process was to obtain a closed-canopy in the shortest possible time, a decrease in tree health may be a lesser concern. For example, rapid canopy closure at the expense of tree health may be the priority when creating a faunal movement corridor to link isolated remnant forest blocks (Lamb et al. 1997). Such a corridor might require rapid closed-canopy establishment at the expense of tree health to facilitate the earliest possible useage by animals, since the local extinction of animal species in isolated forest fragments can occur relatively quickly (Gibson et al. 2013).

3. Does incorporating lianas into deciduous-rain forest restoration plantings assist in minimizing weed incursions?

Incorporating lianas into deciduous rain forest restoration plantings could potentially assist in minimizing weed incursions. Within seasonal rainforests, many canopy tree species are deciduous or dormant during periods of water stress (Givnish 2002). When canopy trees shed leaves an increased penetration of light into the forest provides the ground-layer vegetation with an enhanced level of photosynthetically active radiation (PAR) (Lee 1989, Lerdau et al. 1992). In addition, canopy trees are often “dormant” during periods of deciduousness and as such provide decreased competition for soil resources such as water and nutrients (Álvarez-Cansino et al. 2014, Souza et al. 2014). As a consequence, deciduous forests often experience considerable weed incursions particularly during periods of water stress (Latch 2006). Lianas often retain their canopy (however see Hegarty 1991a) and remain photosynthetically active during periods of water stress at locations where forest trees are deciduous (Schnitzer 2005). They can remain evergreen and photosynthetically active due to their proportionately large root investment when compared to trees (Restom and Nepstad 2004, Schnitzer 2005, Wyka et al. 2013) and efficient vascular system, both of which enhances their ability to access and use ground water (Schnitzer 2005, Chen et al. 2015). Thus, lianas could potentially be used to minimize weed incursions at deciduous forest restoration sites, especially during periods of water stress, through limiting the availability of PAR and competing for limited soil resources (Álvarez-Cansino et al. 2014, Wright et al. 2015).

4. Does the addition of lianas to restoration plantings increase nutrient turnover and soil biota diversity?

The limited availability of soil nutrients, particularly plant-available nitrogen, commonly impedes restoration efforts (Uhl et al. 1988, Holl 1999). Nutrient limitation is often a result of slow mineralisation because of a lack of soil biota (Persson 1989). Soil organisms are imperative to ecosystem functioning and contribute significantly to nutrient cycling, decomposition, mineralisation, and maintenance of soil structure (Lee and Foster 1991, Lavelle et al. 2006, Wagg et al. 2014). Soil organisms are often lacking in restoration sites as a consequence of previous site-management practices (Oddsdottir et al. 2008, Wagg et al. 2014). The inclusion of lianas into restoration plantings could rapidly augment soil organic matter through fast leaf production and turnover (Hladik 1974, Putz 1983, Gentry 1991, Hegarty 1991a, Oddsdottir et al. 2008, Cai et al. 2009, Zhu and Cao 2010, Asner and Martin 2012, Wyka et al. 2013, Wagg et al. 2014) which may in turn increase the abundance of soil fauna. As a consequence, improved soil health and nutrient mineralisation rates would result. If lianas were found to provide any improvement to soil health and nutrient mineralisation rates this function may be particularly beneficial for restoration sites located on nutrient limited soils.

Can lianas support beneficial soil arthropods in restoration plantings? Liana leaves differ from leaves of other plants in a variety of ways (Wyka et al. 2013). In general, liana leaves have lower leaf mass per unit area (LMA) and higher nutrient concentrations compared to leaves from trees and shrubs (Reich et al. 1992, Kazda and Salzer 2000, Tang et al. 2012, Wagg et al. 2014). As a result, leaves from lianas may decompose faster (however see Santiago 2010) and produce more nutritious organic matter for soil organisms (Tang et al. 2012). This feature has been suggested to create a source of nutrients around the base of host trees (Tang et al. 2012), and may also provide some insight as to why lianas are often linked with nutrient-rich soils (Vitousek and Denslow 1986, Putz and Chai 1987, Gentry 1991). Encouraging the return of beneficial soil arthropods through decomposing liana leaf litter in restoration plantings could additionally, potentially promote the decomposition of associated tree litter.

5. Does planting lianas in locations with exposed soil surfaces aid in soil erosion mitigation and limit localized shade-intolerant weed germination?

Lianas could potentially assist in decreasing soil erosion at restoration sites through the increased addition of leaves to the soil surface. In the tropics, bare soils are often prone to erosion (El-Swaify et al. 1982) and nutrient leaching due to heavy rainfall (e.g. Cahn et al. 1993). The rapid addition of leaves to the soil surface of restoration sites by lianas could potentially act as a mechanism of “natural mulching”, limiting the impact of raindrops and decreasing soil erosion (Geddes and Dunkerley 1999, Hartanto et al. 2003, Sayer 2006). Additionally, any augmentation of vegetative material to the soil surface by lianas could potentially slow the overland flow of surface water during rainfall events and promote water infiltration into the soil (Hartanto et al. 2003, Sayer 2006). As a potential additional benefit, liana leaves on the soil surface may decrease the amount of bare soil available for weed species to colonize (Chalker-Scott 2007).

Site protection and management

6. **Does planting lianas on deciduous rain forest restoration plot edges result in a decrease in low-intensity fire incursions?**

Experimentally planting lianas within restoration plots would permit the determination of their value for improving several site protection and management issues, such as the minimization of low-intensity fire incursions. The ability of lianas to maintain an evergreen canopy during periods of water-stress (Schnitzer 2005, Chen et al. 2015) as well as their production of new leaves along fire-vulnerable forest edges (Cochrane and Laurance 2002) may make combustion of these forests less likely (Uhl et al. 1988, Cochrane 2003). There are two reasons for this. First, an evergreen canopy may retain higher sub-canopy humidity levels through the trapping of transpired moisture (Uhl et al. 1988, Cochrane 2003). Second, the new leaves that lianas produce along fire-vulnerable forest edges (Cochrane and Laurance 2002) are less flammable than older leaves due to their higher moisture contents (Kauffman et al. 1988). One possible negative aspect of planting lianas on forest edges to limit fire incursions is that, as mentioned previously, lianas produce proportionately more leaf-litter than trees (Hladik 1974, Putz 1983, Gentry 1991, Hegarty 1991a), which could potentially increase the fuel load of a restoration site. Consequently, experimentally determining whether lianas do indeed limit low-intensity fire incursions into restoration plots may be of significant value, particularly as fire is a major and increasing cause of forest damage in many tropical forest regions (Cochrane and Laurance 2002, Cochrane 2003, Cochrane and Laurance 2008, Balch et al. 2011).

7. **Does planting lianas on restoration plot edges lessen wind damage in early successional stages?**

Determining the value of lianas as a means of reducing wind damage to restoration plantings is another site protection issue worthy of experimental exploration. Restoration sites are often forest fragments and as such suffer significantly more wind damage than do non-fragmented forests (Laurance and Curran 2008). Lianas may help minimize some wind impacts as they are known to bind trees together, protecting them against wind damage (Putz 1984b), and this in turn reduces wind-induced gap formation in young forest stands (Garrido-Pérez et al. 2008). However, lianas have also been found to enhance wind induced-tree falls in older forest stands and increase tree mortality by pulling down adjacent trees when a treefall does occur (Appanah and Putz 1984, Putz 1984b, Garrido-Pérez et al. 2008). Consequently, experimental studies of lianas in restoration plots should determine both the overall value of lianas as a means of reducing wind damage to forests and the temporal management requirements to reduce negative effects i.e. when, and if, management is required to remove them as the forest ages.

8. Does planting lianas at restoration sites containing a heavy undesirable tree species load decrease tree vigor, abundance and recruitment?

Lianas could potentially be a useful restoration site management tool for decreasing woody-weed abundance and vigor prior to tree planting. Lianas compete strongly with trees for limited soil and light resources, increase tree mortality and decrease both tree establishment success and fecundity (Stevens 1987, Schnitzer et al. 2005, Kainer et al. 2006, Ingwell et al. 2010, Schnitzer and Carson 2010, Schnitzer et al. 2014). Consequently, dense plantings of lianas at restoration sites containing an undesirable tree species composition may be a relatively inexpensive and efficient ancillary method of decreasing undesirable tree species abundances. This practice could reduce management costs prior to site clearing and planting. Granted, the cost and labor requirements of planting lianas may be quite high and the lianas in turn may require removal themselves prior to site preparation. However, if a non-clonal liana species was used and the locations of the plantings were recorded (Tab. 6.2), liana removal could potentially be cheaper and less arduous than the management of the uncontrolled undesirable tree species.

Table 6.2 Cautionary notes on the experimental planting of lianas during rain forest restoration.

1. Lianas should be planted away from desirable trees to prevent underground competition
2. Lianas should be planted near desired trees only after the trees are established and structurally capable of supporting the weight of lianas
3. Preferentially use liana species that predominantly reproduce sexually to prevent excessive site colonization through the clonal pathway
4. Preferentially avoid using liana species that climb by main stem twinning as they may girdle and damage desirable trees. Other liana climbing types that may be substituted for main stem twiners include those that climb by tendrils, hooks/spines or adventitious roots
5. Preferentially use liana species that are indigenous to the local region as many exotic species of lianas are serious rain forest weeds. Additionally, indigenous liana species are likely to better handle localized climate, topographical and altitudinal conditions
6. If lianas are to be removed once a fully functioning tree species canopy is established, then their location must be carefully recorded for future re-location. Additionally, single stemmed (non-clonal) species should be selected for efficient future removal (cutting)
7. Lianas can damage small trees and suppress natural succession if they are planted too early in the restoration process or left on site without management

Faunal conservation and lianas in restoration plots

9. Could linear plantings of lianas within restoration corridors aid faunal dispersal?

Facilitating the safe movement of endangered faunal species across fragmented landscapes is often a major reason for initiating rain forest restoration efforts (Lamb et al. 1997, Tucker 2000). Consequently, restoration sites often exist as corridors between larger blocks of rainforest; created to aid animal movement (e.g. Lamb et al. 1997, Rosenberg et al. 1997, Tucker 2000). Experimental, strategic planting of lianas within restoration corridors could be done to determine whether they enhance faunal dispersal capabilities, as lianas are well known to function as both aerial pathways (i.e. natural rope bridges) and nesting sites for a diverse array of animal species (Fig. 6.1) (Gentry 1991, Rendigs et al. 2003, Asensio et al. 2007, Yanoviak and Schnitzer 2013, Arroyo-Rodríguez et al. 2015). Furthermore, experimentation could determine whether lianas allow animals to traverse corridors while remaining in the canopy (Goosem 2012), thereby lessening the risk of ground predation by both wild and domestic predators (Andrén 1995, Newell 1999).

10. Could faunal movement within restoration plantings be guided by densely-planting thorny lianas or rattans?

Restoration practitioners often wish to focus animal movements; for example, by directing them towards strategically placed road culverts, or away from dangers such as nearby roads. This is frequently achieved via the erection of expensive artificial barriers such as fences (Taylor and Goldingay 2003). Dense stands of liana or rattan species that possess prodigious thorns or spines often form an almost impenetrable “wall” of vegetation that limits both large-animal and human movement (M. Campbell, pers. obs.). Thorny lianas are often especially prevalent in areas of past disturbance such as treefall gaps (Fig. 6.1) (Schnitzer et al. 2000, Schnitzer and Bongers 2002). Consequently, strategic linear “wall” plantings of thorny liana or rattan species in areas of high disturbance such as the forest edges of restoration sites (Williams-Linera 1990, Laurance and Yensen 1991, Murcia 1995, Laurance et al. 2002, Harper et al. 2005), could be trialed as a short-term, cost-effective and natural alternative to artificial barrier erection.

Figure 6.1 Upper photo left: The flowers of the Burny Bean (*Mucuna gigantea*) liana host aphids which in turn are farmed for their “honey dew” by Green Ants (*Oecophylla smaragdina*). **Upper right photo:** A Green Ring Tail Possum (*Pseudochirops archeri*) uses a liana to traverse the rain forest canopy. **Bottom-left photo**: A recent treefall clearing is fully colonized by the rattan known as Yellow Layer Cane (*Calamus moti*) preventing large animal and human movement. **Bottom-right photo:** The fearsome spines on the canes of the Yellow Layer Cane (*Calamus moti*).

Lianas as a food source and a distraction for herbivores

11. **Does incorporating lianas into restoration plantings support enhanced mammalian and insect diversity through the provision of additional food resources?**

Lianas produce leaves that are less chemically and/or structurally protected than those of many tree species (Zhu and Cao 2010, Asner and Martin 2012, Wyka et al. 2013). As a result, lianas often provide an important component of the overall food intake of mammalian folivores (leaf eaters), particularly under localized conditions where tree diversity is reduced (i.e. degraded forest fragments) (Lambert et al. 2006, Wong et al. 2006, Asensio et al. 2007, Dunn et al. 2012, Arroyo-Rodríguez et al. 2015). Restoration plots are often tree-species poor due to time and resource constraints (Goosem and Tucker 2013). Consequently, the experimental addition of liana species to restoration plantings could determine whether their presence results in an increase in the abundance and rate of site usage of mammalian folivores.

Lianas also play an important role in the structuring and maintenance of local arthropod diversity. Many phytophagous beetles and Lepidopterans are intimately linked to lianas and depend solely on their availability for survival (Benson 1978, Ødegaard 2000, Orr and Kitching 2010). Lianas aid insect diversity by creating a variety of complex and suitable habitats (Fig. 6.1) (Erwin 1983, Stork et al. 1997) and are at least as important a food source for herbivorous insects as canopy trees (Ødegaard 2000). This importance may be due to the fact that, as mentioned above, liana leaves in general contain less foliar biochemical defenses than tree leaves (Asner and Martin 2012). Additionally, in general, lianas direct greater concentrations of nitrogen and phosphorus to their leaves than trees (Reich et al. 1992, Cai and Bongers 2007, Zhu and Cao 2010, Asner and Martin 2012) both of which are important for supporting many energetic and cellular processes in insects (Throop and Lerdau 2004, Bobbink and Hicks 2014). Liana leaves are thus more nutritious and pose a considerably lower threat to insects than tree leaves. Furthermore, lianas turnover leaves faster than trees (Cai et al. 2009, Zhu and Cao 2010, Asner and Martin 2012, Wyka et al. 2013) and young leaves are generally attacked by insects more often than are older leaves, presumably because of their higher palatability and digestibility (Reichle et al. 1973, Coley 1998). It is likely these features are of great importance to maintaining insect herbivore assemblages, particularly during the dry season when new leaves and other food sources may be scarce. Consequently, experimentally including lianas within restoration plantings may be used to determine whether they are of assistance in enhancing localized arthropod diversity and conservation.

12. **Could including lianas within restoration plantings lessen herbivorous insect damage to planted trees?**

Herbivory can often be problematic during the early stages of regeneration, especially for young trees. Intensively grazed individuals may suffer reduced developmental rates (Bergvall et al. 2006) and a lowered capacity to compensate for other environmental stressors (Stone and Bacon 1994, Willis et al. 1995, Louthan et al. 2013). Lianas could potentially decrease insect herbivory of trees within restoration sites by acting as a "distraction" to herbivorous insects. Again, this might be expected as a function of liana leaves representing a high quality and quantity food source (as described above). For instance, Foaham (2002) found that insect herbivory on trees was greatest in forests where lianas had been removed, suggesting liana presence within restoration plots could potentially aid in mitigating insect herbivory of trees. Furthermore, there are potential flow-on benefits. For example, if lianas were found to lessen insectivorous herbivore pressure on trees, restoration practitioners could potentially decrease insecticide usage, possibly resulting in less accidental negative impacts on important non-targeted insect species such as predatory insects and beneficial soil arthropods.

Lianas as an attraction for seed dispersers

13. **Does the addition of liana species with conspicuous fruits and flowers to restoration site plantings aid in the passive introduction of tree species and novel genetic material?**

Many restoration sites are established using a framework-species approach because of the cost-efficient nature of this method (Goosem and Tucker 1995). This restoration technique aims to incorporate a few highly fecund and often conspicuous, flower- or fruit-producing tree species within plantings to attract seed dispersers [usually frugivorous birds or bats]; with the aim of increasing the likelihood of further passive introductions of tree species [through droppings] and genetic material to the site (Goosem and Tucker 1995, Goosem and Tucker 2013, Sritongchuay et al. 2014). Many liana species are both prolific flower and fruit producers (Menninger 1970, Wright and Calderón 2006, Boulter et al. 2009), providing copious food resources that attract both pollinators and frugivores (Benson 1978, Snow 1981, Hodgkison et al. 2003, Asensio et al. 2007, Kilgore et al. 2010, Ansell et al. 2011). For instance, Boulter et al. (2009) found liana flowers to be, on average, more colorful than those of the resident tree species in the rain forest of Australia's Wet Tropics bioregion. Similarly, Ansell et al. (2011) found logged Bornean rainforests with a high abundance of lianas contained higher bird species richness, in particular obligate frugivores, than forests with a low liana abundance**.** Furthermore, lianas may have the potential to enhance the sustained attraction of seed dispersers to forests as Wright and Calderon (2006) found in their long-term study (17 years) of the Barro Colorado Island forest where lianas have exhibited a significantly greater increase in both flower and fruit production over time than the resident tree species. Consequently, the experimental inclusion of lianas into restoration plantings could enable the determination of their value for attracting pollinators and frugivorous seed dispersers to restoration sites as a means of facilitating passive tree species and genetic diversity introductions in both the immediate and long-term.

14. Can the practical impediments to liana incorporation in restoration plantings be overcome?

As well as determining the ecological value of lianas to rain forest restoration, resolving the practical and economic constraints of liana usage would need to occur prior to their regular incorporation into restoration plantings. For instance, it is likely that lianas would not be easy to maintain in a plant nursery setting because their growth habit would require regular cutting back and structural support prior to planting out. However, this restriction may not be overly onerous as climbing plants are widely used in the horticultural trade (Menninger 1970) and as such initial practical advice may be sought there and subsequently built upon.

In addition to the maintenance of lianas within nurseries, ascertaining the appropriate time to plant them during restoration trials would be vital if the strategy is to be successful. In particular, lianas require a tree trunk or foliage (trellis) of a suitable diameter to climb (Putz 1984b) and in certain cases these may not be available until planted trees are several years old. Conversely, if lianas were introduced at the initial tree planting stage their vigorous growth may overwhelm and smother tree seedlings as they do in forest treefall gaps (Schnitzer and Bongers 2002, Schnitzer and Carson 2010, Schnitzer et al. 2014). Consequently, trials of liana plantings during different restoration successional phases and in conjunction with different trellis partners (e.g. shrubs, trees and fallen logs) would likely allow the strategy conferring maximum efficiency and effectiveness to be determined.

As well as determining the correct temporal usage of lianas in restoration plantings, understanding their effective spatial usage could be an initial practical and economic consideration. For example, determining how many lianas should be incorporated into a planting and how this changes depending upon the required outcome or goal (as per sub-headings above) would enable increased efficiency in their ecological and economic usage. Additionally, determining how planting density interacts with the scale of the restoration effort, is vital foundation knowledge especially when determining the economic viability of the practice.

Table 6.3 Desirable liana traits for restoration experimentation.

Desirable trait	Potential benefits for experimental exploration*
1. High leaf production and turnover	-Enhance forest edge sealing and shade-intolerant weed species exclusion (1) -Increase nutrient turnover and soil biota diversity (4) -Lessen soil erosion (5)
2. Rapid growth rate	-Enhance forest edge sealing, forest canopy closure and shade-intolerant weed species exclusion (1, 2)
3. High nutrient content in leaves	-Increase nutrient turnover and soil biota diversity (4) -Support faunal site usage and abundance (11) -Lessen herbivorous insect damage to planted trees (12)
4. Evergreen canopy with regular new leaf production	-Decrease weed abundance in deciduous rainforests (3) -Decrease low-intensity fire incursions (6) -Lessen soil erosion (5)
5. Good inter-tree linkage capabilities	-Limit wind damage to young forests (7) -Enhance faunal dispersion capabilities and lessen their predation by ground dwelling predators (9)
6. High competitive resource capture rate and negative impacts on trees#	-Decrease undesirable tree: vigor, abundance and recruitment (8)
7. Heavily armed stems and leaves with a capability to grow in dense stands	-Guide animal movement (10)
8. Palatable foliage with low levels of structural and chemical defence	-Enhanced mammalian and insect diversity through food provision (11) -Lessen herbivorous insect damage to planted trees through distraction (12)
9. Species possessing animal dispersed, conspicuous fruits and flowers with high nectar and other "attractant" properties	-Attract seed dispersers and pollinators to aid in the passive introduction of tree species and novel genetic material (13)

Note this trait is desirable solely for restoration sites containing a heavy undesirable tree species load and is not compatible with the other proposed usages of lianas in restoration plantings
*Numbers in brackets represent the experimental topic for investigation as per Table 6.1

Discussion

Since the reinvigoration of liana ecological research in the 1970s, evidence of the negative impacts of lianas on rain forest trees has been accumulating (Stevens 1987, Schnitzer et al. 2005, Ingwell et al. 2010, Schnitzer and Carson 2010, Schnitzer et al. 2014). It is now abundantly clear that lianas damage saplings, compete with trees for limited resources, prevent tree recruitment in canopy gaps and increase tree mortality (e.g. Stevens 1987, Schnitzer et al. 2005, Ingwell et al. 2010, Schnitzer and Carson 2010, Schnitzer et al. 2014). However, this strong flow of empirical evidence may be masking the fact that liana species (and the ecological strategies they employ) are often nearly as diverse as the tree species with which they compete (e.g. Gentry 1991, Pérez-Salicrup et al. 2001, Schnitzer and Bongers 2002). Thus, complete exclusion of all liana species from restoration plantings in response to the potential threat that individiual species or climbing guilds display ignores the now equally abundant fact that some lianas, under certain conditions, can support considerable biodiversity (Benson 1978, Snow 1981, Ødegaard 2000, Hodgkison et al. 2003, Lambert et al. 2006, Wong et al. 2006, Asensio et al. 2007, Kilgore et al. 2010, Orr and Kitching 2010, Ansell et al. 2011, Dunn et al. 2012, Arroyo-Rodríguez et al. 2015), assist in regulating forest microclimate (Kochummen and Ng 1977, Campanello et al. 2007, Wyka et al. 2013) and are invaluable in forest wide processes such as nutrient turnover through enhanced and rapid leaf litter production (Hladik 1974, Putz 1983, Gentry 1991, Hegarty 1991a, Schnitzer 2005, Paul and Yavitt 2011, Tang et al. 2012, Wyka et al. 2013).

In addition to supporting biodiversity and aiding ecological and geochemical processes, the fact that many liana species are themselves rare (Gentry 1991, Laurance et al. 2001a, Parthasarathy et al. 2004, Santos et al. 2009) and threatended with localized extinction due to anthropological threats, may alone, justify their inclusion in biodiversity restoration plantings. For instance, numerous studies of geographically distinct rainforests have found that lianas make up a considerable proportion of the local woody plant diversity (e.g. Gentry 1991, Pérez-Salicrup et al. 2001, Schnitzer and Bongers 2002) of which rare liana species often comprise a substantial fraction (Gentry 1991, Laurance et al. 2001a, Parthasarathy et al. 2004, Santos et al. 2009). As such, it is highly likely that they are threatened by the same deleterious effects of deforestation and forest degradation (e.g. fragmentation) as rare tree species (Laurance et al. 1999, Fahrig 2003, Lienert 2004). Consequently, excluding all liana species from restoration efforts, and in particular rare liana species, may result in the loss of considerable localized liana diversity with likely flow-on effects to reliant faunal species.

Selectively utilizing the morphological features and ecological functions of liana species by strategically incorporating (Tabs. 6.1, 6.2 and 6.3) them within rain forest restoration efforts may have the potential to considerably enhance restoration efficiency and biodiversity conservation outcomes. However, the magnitude of any benefit can only be determined through the outcomes of experimental plantings. It is clear that including lianas in restoration efforts will be costly in terms of funds, time and labor. Moreover, if done incorrectly (Tab. 6.2), excessive on-site liana abundance could occur (Yorke et al. 2013, Ledo and Schnitzer 2014). Yet, the current practice of complete liana exclusion from restoration sites followed by eventual self-recruitment is equally fraught with costs. For instance, allowing for liana species self-recruitment is likely to result in a resident liana community composition that is non-representative of the landscape-wide species composition (Oliveira et al. 1997, Laurance et al. 1999, Laurance et al. 2001a, Fahrig 2003) as it is determined by dispersal capabilities and site locality (Fahrig 2003, Lienert 2004). Intrinsically, a local liana community that represents a small subset of the landscape-wide community is likely to support lower levels of biodiversity, especially in forests where a high degree of mutualism exists (Magrach et al. 2014a). Additionally, allowing self-recruitment may result in a high abundance of lianas occurring in non-preferred areas of restoration plots increasing overall management costs. Conversely, deliberate planting of lianas allows for the spatial location and liana community composition to be determined, at least to a reasonable extent, *A priori* and thus species and their relative distributions can be tailored to match management goals.

Until the benefits and costs of strategic liana usage in restoration efforts are experimentally quantified I can only guess at their potential value for restoration practitioners and ultimately restored forests. As such, I propose that lianas with selected traits (Tab. 6.3) be experimentally and strategically incorporated into rain forest restoration plantings (Tabs. 6.1 and 6.2) to assess whether they can enhance biodiversity conservation and expedite rain forest restoration efforts. As primary rainforests throughout the world continue to be deforested and degraded (Dirzo and Raven 2003, Asner et al. 2009, Hansen et al. 2013), maximizing the efficiency and effectiveness of rain forest restoration techniques is becoming increasingly essential for the long-term sustainability of this ecosystem and its constituent biota.

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Synthesis

Background

Tropical forests are the most diverse terrestrial ecosystem on earth (Dirzo and Raven 2003, Scheffers et al. 2012). However, in many tropical regions continued deforestation and conversion to human-dominated landscapes imperil these forests (Dirzo and Raven 2003, Lewis 2006, Lewis et al. 2015, Mercer 2015). In fact, it is estimated that more than half of the pre-industrial tropical forest cover is already lost (Wright 2005). As forests are cleared it is rare for all the pre-existing vegetation to be removed (Laurance and Bierregaard Jr 1997). Rather, isolated fragments of the original vegetation remain surrounded by new habitat types (Wilcove et al. 1986). Fragmentation of tropical forests is globally ubiquitous with estimates suggesting that as much as 46% of the remaining tropical forested area exists as fragments (Mercer 2015) and that 70% lies within 1 km of a forest edge (Haddad et al. 2015). As tropical deforestation and land-use conversion continues (Hansen et al. 2008, Asner et al. 2009, Hansen et al. 2013), the proportion of tropical forests in fragments will increase along with their importance for biodiversity conservation (Hansen et al. 2013, Bhagwat 2014, Haddad et al. 2015).

Fragmentation alters the environmental and ecological characteristics of tropical forests which results in a loss of biodiversity (Laurance et al. 2011, Haddad et al. 2015). For instance, fragments are estimated to lose 13-75% of the diversity they previously had as intact forests (Haddad et al. 2015). This loss occurs due to the degradation of a variety of biological and physical processes within fragments (e.g. see reviews by: Laurance et al. 2002, Fahrig 2003, Fischer and Lindenmayer 2007, Laurance et al. 2011). Although fragments are less diverse than intact forests, they often represent the last preserve of many rare and endangered species and ecosystems (e.g. Guindon 1996, Tabanez and Viana 2000, Arroyo-Rodriguez and Mandujano 2006, Muthuramkumar et al. 2006, Arroyo-Rodriguez et al. 2009). They can also be important ‘stepping stones’ facilitating faunal movements in fragmented landscapes (Tischendorf and Fahrig 2000, Baum et al. 2004, Saura et al. 2014). Fragments may even act as biological repositories, supporting species that can be used in future restoration of deforested landscapes. For instance, in areas where remnants of primary forest are present, secondary forests are larger, more diverse and regenerating more rapidly than in landscapes stripped of native vegetation (Sloan et al. 2015).

Tropical forests possess the most complex system of ecological interactions known to occur on land (Myers 1984). However, within fragments, the altered environmental and ecological conditions (Laurance 1997a, Williams-Linera et al. 1998, Laurance et al. 2002, Laurance et al. 2011, Magnago et al. 2015) can disrupt these interactions (Fagan et al. 1999, Terborgh et al. 2001, Magrach et al. 2014a, Peh et al. 2014, Chávez-Pesqueira et al. 2015) potentially leading to species loss (Laurance et al. 2002, Laurance et al. 2011). The degradation of ecological interactions does not equally impact remaining species as the new conditions can result in ecological cascades which favor the proliferation of “winner” species at the expense of declining “loser” species (McKinney and Lockwood 1999, Laurance et al. 2002, Laurance et al. 2011, Tabarelli et al. 2012, Magrach et al. 2014a, Arroyo-Rodríguez and Melo 2016). Consequently, effective assessment and subsequent management of the ecological interactions occurring within fragments will maximize their conservation values.

Lianas are known “winners” of the ecological contests occurring within forest fragments, proliferating extensively (Chapter 3; Oliveira et al. 1997, Viana et al. 1997, Tabanez and Viana 2000, Laurance et al. 2001a, Magrach et al. 2014b) and responding positively to the increased levels of forest disturbance (Ledo and Schnitzer 2014). Liana proliferation in fragments is highly detrimental to the tree community as trees infested with lianas suffer enhanced structural stress and increased resource competition (Putz 1984b, Stevens 1987, Schnitzer and Bongers 2002, Schnitzer et al. 2005, Schnitzer and Carson 2010). Consequently, lianas can limit tree seedling recruitment, damage saplings, decrease tree growth and fecundity, and increase tree mortality (Putz 1984b, Stevens 1987, Campbell and Newbery 1993, Schnitzer et al. 2000, Schnitzer et al. 2005, Ingwell et al. 2010, Schnitzer and Carson 2010, Reid et al. 2015). These impacts can lead to the fragment-wide decline or loss of particular tree species or guilds (Putz 1980, 1984b, Clark and Clark 1990, Schnitzer and Bongers 2002), resulting in changes to the composition and diversity of the tree community (Laurance et al. 1997, Laurance et al. 2001, Laurance et al. 2006b, Heijden et al. 2015) and a significant reduction in carbon storage capacity (Heijden et al. 2013, Schnitzer et al. 2014, Heijden et al. 2015a, Heijden et al. 2015b). Therefore, understanding the ecological mechanisms underlying the interactions between lianas and their tree hosts, and the drivers of the positive response of lianas to forest fragmentation, is of utmost importance for diversity conservation in fragmented landscapes.

This doctoral thesis explored a variety of themes relevant to the ecological interactions of lianas (*sensu lato*) and trees within forest fragments in tropical Australia. It also examined the underlying mechanisms behind the positive response of lianas to fragmentation. In this final chapter the key findings from previous chapters (3-6) are integrated in the context of liana ecology within tropical forest fragments. The aim of this chapter is to synthesize the central findings of the thesis and to suggest future research avenues.

Tropical forest fragmentation increases liana abundance and alters liana-host tree interactions

My results from Chapter 3 clearly demonstrate that forest disturbance is the primary driver of liana abundance and their subsequent tree infestation rates within forest fragments (Laurance et al. 2001a, Ledo and Schnitzer 2014, Magrach et al. 2014b). Furthermore, my findings suggest that the proliferation of lianas in forest fragments (Oliveira et al. 1997, Viana et al. 1997, Tabanez and Viana 2000, Laurance et al. 2001a, Magrach et al. 2014b) occurs in response to the increased disturbance at fragment edges (Laurance 1997a, Oliveira et al. 1997, Laurance et al. 2000, Harper et al. 2005, Tabarelli et al. 2008, Laurance et al. 2011, Chaplin-Kramer et al. 2015) and the extent to which these effects penetrate from fragment edges toward interiors. Thus any attempt to manage liana proliferation within forest fragments must primarily focus on the protection of vulnerable fragment edges. For instance, mechanisms such as buffer plantings of trees on forest edges (Goosem and Tucker 2013) and liana cutting (Appanah and Putz 1984, Gerwing and Uhl 2002) could mitigate liana proliferation on fragment edges. Whilst my findings corroborate those of previous studies, I also found that liana infestation rates of trees were not only related to liana proliferation in disturbed forest conditions but also the presence of large established lianas in less-disturbed forest conditions. This suggests that mitigation of liana infestation in forest fragments through managing forest disturbance at edges alone would likely prove ineffective, but may work in conjunction with management (i.e. liana cutting) to reduce large lianas within less disturbed areas.

On average, lianas provide a third of the woody plant diversity of a forest (DeWalt et al. 2015, Parthasarathy 2015, Schnitzer 2015a, Schnitzer 2015b). However, previous research has found that whilst low to intermediate levels of disturbance may favor liana diversity (Laurance et al. 2001a, Schnitzer and Bongers 2002, Ledo and Schnitzer 2014, Mohandass et al. 2014), chronic or intense disturbance can result in a reduction of liana diversity due to a decrease in the number of available tree hosts (Hegarty and Caballe 1991, Toledo-Aceves and Swaine 2008, Arroyo-Rodriguez and Toledo-Aceves 2009, Addo-Fordjour et al. 2012a). In Chapter 3, I identified a significant modification to the composition of the liana climbing guilds within fragmented forests. This shift in community composition is due to a broader change in the forest structure of fragments where the death of canopy trees has created forest gaps that are subsequently filled by many smaller stems (DeWalt et al. 2000, Laurance et al. 2000, Laurance et al. 2002, Laurance et al. 2006a, Laurance et al. 2006b, Laurance et al. 2011). Plants regenerating in forest gaps provide smaller climbing trellises that appear to benefit liana guilds such as tendril climbers, at the expense of liana guilds with structural or mechanical adaptations for larger-sized trellises (e.g. branch climbers) (Putz 1984b, Putz and Chai 1987, DeWalt et al. 2000, Letcher 2015). Thus future research could investigate if the loss of liana diversity in highly-disturbed forest fragments is due to treefall gaps dynamics and forest succession and the differential impacts of these upon liana climbing guilds, including whether this has a phylogenetic component.

Edge effects shape the spatial distribution of lianas and epiphytic ferns in Australian tropical rain forest fragments

A diverse array of negative impacts are now known to affect trees infested with lianas (e.g. see reviews by: Schnitzer and Bongers 2002, Schnitzer 2015a, Schnitzer 2015b). In fact, most stages of a tree’s life history including seedling recruitment, sapling and tree growth, fecundity and even mortality risk are vulnerable to the detrimental impacts of lianas (Putz 1984b, Stevens 1987, Campbell and Newbery 1993, Schnitzer et al. 2000, Schnitzer et al. 2005, Ingwell et al. 2010, Schnitzer and Carson 2010, Reid et al. 2015). While there is extensive literature on liana-host tree interactions (see Chapter 3 and references therein) very little, if any, literature exists on the impact of lianas on non-tree plant life forms. Epiphytes comprise a significant component of tropical forest plant diversity (Gentry and Dodson 1987) and contribute to total diversity as habitat and resources for a diverse community of resident species (Ellwood et al. 2002, Cruz-Angon and Greenberg 2005, Freeman and Freeman 2009). In Chapter 4, I found that lianas compete intensely with epiphytes for the structural hosts (trees) on the edges of forest fragments. As the first study of its kind, my finding that lianas negatively impact epiphytic ferns should prompt rapid research on liana-epiphyte interactions both within the region and throughout the tropics. This is especially timely, given the current increase in liana abundance occurring throughout most tropical forests (Schnitzer and Bongers 2011), and particularly in the Neotropics (Schnitzer 2015c).

Forest disturbance drives rattan proliferation in tropical rain forest fragments

The forests of the Old World tropics are currently experiencing some of the fastest rates of conversion to human-modified landscapes occurring on the planet (Achard et al. 2002, Hansen et al. 2013, Mercer 2015). This conversion places at risk some of the most biodiverse terrestrial habitats known (Myers et al. 2000, Dirzo and Raven 2003) and with that also risks the economic potential that their sustainable usage could provide (FAO 2010). For instance, rattans are arguably the world's most important non-timber forest product (Sastry 2002), yet many species are threatened by forest conversion and unsustainable harvesting (Dransfield 1987, Hirschberger 2011). In Chapter 5, I examined how human-induced fragmentation has impacted rattan abundance and demography. This research is one of very few studies that provides ecological information on rattan response to fragmentation without the confounding effects of harvesting. I found a strong proliferation of rattans and in particular adult rattans in response to fragmentation, which (as with lianas) appears to be associated with an increase in disturbance and the higher light availabilities this generates. Interestingly, my findings provide a speculative insight into the world of climbing plant competition. I hypothesized that rattan proliferation may occur at the expense of lianas due to rattans possessing greater inter-host colonization ability. This biomechanical trait better allows rattans to infest more widely-spaced tree hosts in heavily-disturbed forest fragments than lianas. This hypothesis provides a basis for future research, the outcomes of which could influence stocking densities of rattans allowing for maximization of rattan output whilst minimizing liana management costs. Furthermore, the observed increase in rattan abundance could be linked to future research on the economic benefits of sustainable management of this resource within the Australian wet-tropics region.

Can lianas assist in rain forest restoration?

The vast majority of the liana literature provides almost constant reminders of the negative impact lianas have on trees, forest dynamics and forest functioning. Conversely, only a small component of the literature addresses the potential benefits lianas may provide (Schnitzer 2015a, Schnitzer 2015b), although many of these studies only mention the benefits of lianas when referring to their value for faunal resource provisioning (e.g. Lambert et al. 2006, Wong et al. 2006, Asensio et al. 2007, Dunn et al. 2012). As our knowledge of lianas increases (Schnitzer et al. 2015c) it is becoming clear that these life forms are a diverse and integral component of a functioning tropical forest (Croat 1978, DeWalt et al. 2015) with both negative and positive influences on forest processes. Consequently, in Chapter 6, for the first time, I synthesized information from across diverse topics dealing with lianas to provide a focused assessment of the potential for lianas to expedite rain forest recovery in restoration plantings. Given the current rate of tropical forest clearing and degradation (Hansen et al. 2008, Asner et al. 2009, Haddad et al. 2015, Mercer 2015) the restoration practices suggested within this Chapter are provided with the explicit aim that their potential to enhance restoration be fully explored in future research, especially through field trials by restoration practitioners.

Concluding remarks

The findings reported in this thesis further our understanding of the ecological response of lianas (*sensu lato*) to tropical forest fragmentation. In particular they provide information on liana ecology within the fragments of the World Heritage listed (UNESCO 1988) tropical forests of northeastern Australia. This information will be directly informative to rain forest managers of the region, who are tasked with conserving these exquisite and irreplaceable forests (Bertzky et al. 2013, Le Saout et al. 2013). The results corroborate the literature on many fundamental points of liana ecology and forest dynamics, while providing new insights into the relationship between lianas, rattans and other vegetative members of forest fragments. Continued investigation into these relationships will likely produce even more exciting and practical ecological data that can be used to better understand and manage the rain forest ecosystem.

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Appendices

Appendix 1

Table A1 Generalized linear mixed model (Poisson with log link) for the impact of forest fragmentation effects and environmental characteristics on tree abundance. Only the significant explanatory variables are shown. Forest edge distance = mid-distance of plot to the forest edge. All explanatory variables were standardized prior to the analysis ((x - mean(x)) / SD(x)).

	Estimate	SE	Z value	P
Intercept	3.499	0.037	93.60	< **0.001**
Forest edge distance	-0.092	0.032	-2.81	**0.004**
Liana abundance	0.044	0.030	1.45	0.147
Tree DBH	-0.053	0.032	-1.66	0.096
Plot forest carbon	0.090	0.028	3.15	**0.001**
Altitude	-0.088	0.027	-3.24	**0.001**
Forest Type (Fragmented)	-0.215	0.058	-3.71	< **0.001**

Table A2 Generalized linear mixed model (gamma with log link) for the impact of forest fragmentation effects and environmental characteristics on tree diameter breast height (DBH). Only the significant explanatory variables are shown. All explanatory variables were standardized prior to the analysis ((x - mean(x)) / SD(x)).

	Estimate	SE	t value	P
Intercept	2.863	0.025	110.22	< **0.001**
Liana DBH	0.068	0.017	3.95	< **0.001**
Plot forest carbon	0.043	0.017	2.52	**0.011**
Altitude	0.068	0.019	3.59	< **0.001**
Calamus spp. relative abundance	0.038	0.020	1.92	0.054
Canopy cover	0.038	0.018	2.08	**0.037**
Forest Type (Fragmented)	0.127	0.040	3.17	**0.001**

Table A3 Generalized linear mixed model (gamma log link) for the impact of forest fragmentation effects and environmental characteristics on logit transformed proportional canopy cover. Only the significant explanatory variables are shown. Forest edge distance = mid-distance of plot to the forest edge (m) and this was analyzed using a quadratic term (x1 +x12) to enable better model fit. All explanatory variables were standardized prior to the analysis ((x - mean(x)) / SD(x)).

	Estimate	SE	t value	P
Intercept	1.606	0.039	41.09	< **0.001**
Forest edge distance	0.237	0.030	7.79	< **0.001**
Quadratic term forest edge distance ($x_1 + x_1^2$)	-0.142	0.028	-5.10	< **0.001**
Forest type (Fragmented)	-0.172	0.045	-3.75	< **0.001**
Proportionate liana infestation of trees	0.046	0.023	1.94	0.051
Altitude	-0.064	0.020	-3.11	**0.001**
Forest edge distance : Forest type interaction	-0.127	0.042	-3.03	**0.002**

Appendix 2

Publications produced during PhD candidacy including those in press and under review

Publications

- Alamgir, M., **M.J., Campbell**, S.M. Turton, P.L. Pert, W. Edwards and W.F. Laurance. In Press. Degraded tropical rain forests possess valuable carbon storage opportunities in a complex, forested landscape. *Nature Scientific Reports* **6:**30012.
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- Mohandass, D., **M.J. Campbell**, X-S., Chen, A.C., Hughes, X., Deng and Q-J., Li. Under review. Flowering and fruiting phenology of woody trees in the tropical-seasonal rainforest, south-western China. *Plant Ecology and Evolution*.

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