Liana effects on tree functional groups and carbon balance in a lowland tropical forest, Panama and an analysis of progress in remote sensing of lianas

Ashley D.C. Proctor BSc (Hons)

20322381

Thesis submitted to the University of Nottingham
for the degree of Master of Research

September 2021

Acknowledgements

I would like to thank Dr Geertje M.F. van der Heijden and Dr Doreen S. Boyd for their invaluable and continued support and guidance throughout the duration of my postgraduate study. I am also grateful for the support of my friends, family, and partner in what has been a difficult and uncertain year.

Contents

List of Figures

List of Tables

Abstract

1. Lianas (or vines) are woody climbers that root in the ground and utilise the structure of neighbouring trees to ascend into the forest canopy. These plant forms are found in forests globally, although they are particularly prevalent seasonal and lowland forests of the neotropics where they make up a significant proportion of woody species and stems. Lianas infest host trees and can dominate forest canopies, often described as structural parasites, lianas compete intensely with trees for sunlight and belowground resources without investing in their own supporting structure.
2. Research interest in lianas has increased substantially in recent decades, though they remain understudied compared to other plant forms. **Chapter 1** reviews the increasingly comprehensive and geographically broad evidence base documenting the competitive effect of lianas upon host trees. Liana infestation has a significant and detrimental impact on tree growth, mortality, reproduction, and regeneration. Ultimately this reduces the capacity of trees to sequester and store carbon, a globally important ecosystem service provided by tropical forests. Furthermore, some evidence suggests that lianas are disproportionately affecting shade-tolerant carbon dense tree genera, contributing to a decline in these species. Reports of increasing liana abundance in the neotropics adds to the urgency for further research into the extent, magnitude, and mechanisms by which lianas effect the carbon balance in tropical forests.
3. Studying tropical forest canopies is challenging, as such relatively little is known about the distribution of lianas in forest canopies. Remote sensing is an emerging research method that has overcome some of the shortfalls associated with standard field surveys and can provide new and critical insights into liana ecology. **Chapter 2** provides the first systematic assessment of the progress in the use of remote sensing to further understand the (i) spatial and temporal distributions, (ii) structure and biomass, (iii) responses to environmental conditions, and (iv) diversity, of lianas. The possibilities offered by new and future advances in remote sensing technology to study lianas, and the further data requirements needed, are then considered. For unanswered research questions to be resolved, liana ecology needs remote sensing.
4. **Chapter 3** is the first study to report findings from a large-scale liana removal experiment for which there is more than 3-4 years of data. I consider eight census years of data from an ongoing liana-removal experiment in Gigante, Panama to address the paucity of research into how lianas impact carbon accumulation in trees with differing life histories and functional traits. Tree biomass growth was 49.21% lower in liana-infested plots over the eight-year period. This is attributed to a growth release in low wood density pioneer species in the four years after removal, which shifts towards high wood density shade tolerant species dominating growth contributions to overall forest carbon in the latter four census years. My findings also support the notion that severity of crown infestation dictates the magnitude of liana effect on tree biomass growth. This study highlights the need to quantify the contribution of species functional groups to forest carbon balance in order to better understand potential future liana effects. With reports of increasing liana abundance, my findings present a worrying picture of the resilience of tropical forests to persist as a functioning global carbon sink.
5. *Synthesis*. Our understanding of liana ecology and the relationship between these plant forms and carbon balance in tropical forests has increased rapidly. Observational studies, removal experiments, repeated plot censuses and the rapidly evolving applications of remote sensing have provided new insights into the nature of lianas and their interactions with the tropical forests they infest. This study adds to these foundations for future liana research by presenting a thorough review of existing literature, a critical analysis of the integration of remote sensing and

an assessment of disproportionate lianas effects on tree functional groups. With the current state of tropical forest decline, urgent knowledge gaps must be addressed now more than ever.

Introduction

Lianas are woody vines that root in the ground and utilise the structure of neighbouring plants to climb into the forest canopy. Unlike trees, lianas are not self-supporting past their juvenile stage. Lianas are an integral and widespread feature of tropical forests, making up a significant proportion of woody stems and woody species (Gentry, 1991; Appanah et al., 1993). Over 10,000 species of lianas have been recorded from approximately 977 genera and 119 families of climbers (Acevedo-Rodríguez et al., 2015; Gentry, 1991). These plant forms are particularly prevalent in neotropical seasonal and lowland forests (Dalling et al., 2012), though can also be found in temperate, paleotropical and subtropical forests. Mean liana species richness is greatest in Africa (39.1 ±7.1), followed by Asia (36.2 ±17.0), then South America (33.7 ±10.9) and Central America and Mexico (28.2 ±5.5; based on 0.1 ha lowland forest sites; Schnitzer and Bongers, 2002). As well as contributing to forest species richness, these plant forms provide additional structure and food resources which support avian and faunal communities (Odell et al., 2019; Schnitzer et al., 2020a).

Lianas also have a significant effect on the carbon balance of tropical forests, which account for approximately half of the terrestrial carbon sink (Feldpausch et al., 2012). Lianas are structural parasites (Ewers et al., 2015), using the physical support of nearby trees to ascend upwards and deploy their leaves atop the forest canopy, intercepting valuable available light. Lianas also compete intensely with trees for below-ground resources, such as water and soil nutrients (Collins et al., 2016; Smith-Martin et al., 2019). As such, liana infestation can significantly impact growth and survival of host trees, whilst suppressing the regeneration of new recruits (van der Heijden et al., 2015). Furthermore, the greater the severity of crown infestation, the greater the magnitude of liana effect on host trees (Kainer et al., 2006; Visser et al., 2017). In addition, due to their principal investment into foliage over woody stem tissue, lianas account for a marginal proportion of forest biomass, failing to account for the biomass they displace in trees (van der Heijden and Phillips, 2009a). Thus, liana infestation reduces the ability of tropical forests to store and sequester carbon (Durán and Gianoli, 2013; Durán and Sánchez-Azofeifa, 2015).

Climate change and drought events are said to be adding to a decline in carbon-dense high wood density tree species, contributing to a shift toward low wood density tree species with higher turnover and lower carbon residence time (Brienen et al., 2020). Lianas may also be catalysing this trend by disproportionately affecting tree groups with certain functional traits. Some evidence suggests high wood density trees, typically slow-growing shade-tolerant species, suffer more frequent and severe liana infestation than low wood density trees, typically pioneer species (Visser et al., 2018; Muller-Landau and Visser, 2019). How tolerant host trees are to varying levels of liana infestation also differs between functional groups (Visser et al., 2017). What is lesser known, is to what extent this impacts carbon accumulation between different tree functional groups.

Research interest into lianas has increased substantially in recent decades, although compared to other plant forms, lianas remain understudied (Marvin et al., 2016). With reports of increasing liana abundance in recent years, their effect on the carbon balance of tropical forests is likely to intensify (Phillips et al., 2002; Schnitzer and Bongers, 2011). Therefore, it is important now more than ever for research to focus on understanding and quantifying liana effect on forest-level carbon accumulation. A key tool in the advancement of liana research is remote sensing, acquiring liana information from a distance, whether it be from spaceborne, airborne or terrestrially mounted sensors (Lechner et al., 2020). Remote sensing technologies present the opportunity to study lianas over greater spatial and temporal scales, with potentially greater accuracy and lower operational costs compared against traditional ground-based methods (Watts et al., 2012). Remote sensing of liana ecology is an emerging research area (Waite et al., 2019; Chandler et al., 2021a; 2021b). Key unknowns pertaining to liana distribution, structure and diversity remain relatively unexplored. As the two disciplines converge, it is hoped that answers to the most pressing questions in liana ecology become less elusive. This thesis seeks to illuminate the role of liana infestation on carbon storage in tropical forests using experimental data as well as considering how advances in remote sensing of liana ecology may help progress this field of research.

Aims and Objectives

Main Aim

Assess the effect of lianas on the contribution of tree functional groups to the carbon balance of tropical forests and analyse the use of remote sensing to address key unknowns in liana research.

Objectives

Firstly, I intend to review the existing literature covering the nature of lianas, their role in tropical forests, their effect on the viability of tropical forests to function as a global carbon sink and how remote sensing contributes to this knowledge base. Secondly, I will focus specifically on remote sensing of liana ecology and identify areas to improve the fusion of these two disciplines in the future (Objective 1). Finally, using data from a long-term and large-scale liana removal experiment in Gigante, Panama (full site description in section 3.4.1) I will analyse and quantify the effect of varying levels of liana infestation on differing tree functional groups (Objective 2). This thesis will thus address the following objectives:

Objective 1. Review the progress in remote sensing of lianas and identify the underpinning data, methodologies and technological advances needed to further develop this field.

Objective 2. Investigate how liana infestation differentially impacts the contribution of tree functional groups to forest-level carbon accumulation in Gigante, Panama.

Chapter 1: Literature Review

1.1 Overview

Lianas are an integral and characteristic feature of tropical forests, accounting for up to 25% of woody stems and 35% of woody species (Gentry, 1988; Gentry, 1991; Gerwing and Farias, 2000; DeWalt and Chave, 2004; Schnitzer and Bongers, 2011; Schnitzer et al., 2012; Durán and Gianoli, 2013; Durán and Sánchez-Azofeifa, 2015; A. Wright et al., 2015). Rooting in the ground, lianas shoot upwards, often utilising the structure of nearby trees to climb and ascend to the forest canopy (Gentry, 1985). In contrast to trees, lianas are characterized by long and pliable stems (Putz, 1984), rapid growth and stem turnover (Phillips et al., 2005), extensive root systems (Chen et al., 2015; Smith-Martin et al., 2020) and large leaf area relative to their stem diameter (Medina-Vega et al., 2021). Once a largely ignored element of tropical forest research, studies of lianas have become increasingly numerous over the past three to four decades (Schnitzer et al., 2015a), with the number of publications increasing faster than any other topic within tropical ecology (Schnitzer et al., 2015b).

Liana stem density is fairly equal across the Central Americas and Africa (351 and 374 individuals ha^{-1}, respectively), with South America hosting slightly higher densities of liana stems (462 individuals ha^{-1}; Poulsen et al., 2017). Mean liana density in Asia is roughly half that of the other continents at 223 individuals ha^{-1} (DeWalt et al., 2015). Liana infestation can vary greatly between forests, often dominating in seasonal and lowland areas (Balfour and Bond, 1993; Dalling et al., 2012). The most severe infestations have been documented in a lowland dry to moist 'liana forest' in Bolivia (86% of trees; Perez-Salicrup et al., 2001) and a lowland moist forest in Cameroon (80% of trees; Parren and Doumbia, 2005).

Lianas play an important role in influencing forest physiognomy and species richness, as well as providing food and structure to support animal communities (Morellato and Leitao-Filho, 1996; Odegaard, 2000; Gianoli, 2015; César et al., 2017; Odell et al., 2019; Schnitzer et al., 2020a). However, it has been long understood that lianas have detrimental effects on their host trees (Featherly, 1941; Putz, 1982; Putz, 1984a; Putz, 1984b), essentially acting as structural parasites (Stevens, 1987; Muller-Landau and Pacala, 2020). They do this by competing strongly both above- and below-ground with trees for valuable light, soil nutrients and water (Toledo-Aceves, 2015). By these means lianas have a detrimental impact on tree growth (van der Heijden and Phillips, 2009a), survival (Phillips et al., 2005; Ingwell et al., 2010), reproduction (Kainer et al., 2006; Nabe-Nielsen et al., 2009; García León et al., 2018) and regeneration (Schnitzer et al., 2000; Schnitzer and Carson, 2010). For these reasons, liana infestation can suppress tree biomass and reduce above-ground carbon storage in tropical forests (Chave et al., 2001; Malhi et al., 2006; Durán and Gianoli, 2013; Ledo et al., 2016), as evidenced by reduced carbon uptake in liana-infested plots compared to liana-removed plots in liana removal experiments (van der Heijden et al., 2015; 2019; Estrada-Villegas et al., 2020). This effect on tree biomass is not compensated by the presence of lianas themselves as due to their lower investment in woody biomass, lianas displace more carbon than they account for (van der Heijden and Phillips, 2009a). Furthermore, some studies point towards a disproportionate impact of lianas on shade-tolerant species (Muller-Landau and Visser, 2019), perhaps contributing to the decline in dominance of these carbon dense genera (Laurance et al., 2004; Brienen et al., 2020).

The effect of lianas on forest biomass and carbon uptake could worsen given recent reports of increasing liana abundance (Phillips et al., 2002; Schnitzer and Bongers, 2011), which may have potential global ramifications for the rate of climate change. Further research quantifying liana effect on the carbon balance of tropical forests is therefore paramount to increase our understanding of the potential future effects on this crucially important ecosystem. Despite growing research interest in this field in recent years, unknowns such as the relationship between tree functional traits and liana effect are still to be resolved.

1.2 Tropical Forests

Despite only covering ~7.7% of the Earth's land surface (Myers, 1988; World Bank, 2016), tropical forests are thought to account for ~55% (471 Pg) of the terrestrial carbon sink (Pan et al., 2011; Feldpausch et al., 2012) and ~50% of sequestered terrestrial carbon (Beer et al., 2010; Hubau et al., 2020). This is understood to increase by a further 1.2 Pg C annually (Lewis et al., 2009), although this figure is changing with ongoing shifts in climate. Carbon sequestration is one of many globally important ecosystem services tropical forests provide, with any changes to the balance of tropical forest carbon potentially having worldwide implications for climate change. Tropical forests contain a wide array of plant growth forms, including trees, (hemi-)epiphytes, shrubs, herbs and lianas (Richards et al., 1996) and are thought to host over half the planets biodiversity (Lewis et al., 2015).

Recent studies have concluded that the global tropical carbon sink is declining (Brienen et al., 2015; Baccini et al., 2017; Hubau et al., 2020), with radial growth rates in some tropical forests showing a decrease (Clark et al., 2003; Feeley et al., 2007). Simultaneously, data from Amazonia suggests carbon-dense shade-tolerant plant genera with high wood density have reduced in dominance (such as *Duroia*, *Endopleura* and *Lacunaria*; Laurance et al., 2004). Tropical forests are thus experiencing a shift toward trees with an accelerated life span, increasing forest-level mortality and stem turnover, which in turn reduces their ability to function as a carbon sink (Brienen et al., 2020). These changes are exacerbated by increasingly frequent and severe drought events in the tropics, causing further mortality and stunting growth, subsequently reducing forest carbon sequestration and stores (Malhi and Wright, 2005; Phillips et al., 2009; Lewis et al., 2011; Fu et al., 2013; Feldpausch et al., 2016). These worsening climate events are projected to continue and intensify over the coming decades (Marengo et al., 2012; Boisier et al., 2015; Duffy et al., 2015). Furthermore, reported increases in the rate and severity of liana infestation are likely to contribute to the decline in the carbon sink function of tropical forests (Lewis et al., 2004; Ingwell et al., 2010; Schnitzer and Bongers, 2011).

1.3 Liana effects

This section pertains solely to liana effects on host and neighbouring trees in terms of growth, mortality, reproduction, and regeneration. Liana effects on the wider ecosystem and on landscape scale carbon accumulation are considered in later sections.

1.3.1 Growth

Lianas compete intensely with trees for light and below-ground resources, which can have a significant impact on the growth of host and neighbouring trees. A multitude of studies have now documented and quantified the effect of liana infestation on tree growth rates in the neotropics (e.g. Whigham, 1984; Gerwing, 2001; Peña-Claros et al., 2008; see below references) . For example, an early study on Barro Colorado Island, Panama (BCI) found that liana-free *Luehea seemannii* trees grew twice as fast as severely infested individuals over a 10-year period (Putz, 1984a). Similarly, growth rates doubled in liana removed trees in lowland Bolivia just one year after lianas were cut (Pérez-Salicrup and Barker, 2000), with growth rates in two shade-tolerant species in sub-tropical Argentina increasing by over 100% after two years (Campanello et al., 2007). In a more comprehensive Panamanian study on BCI, all ~2,000 liana-infested trees that survived a ten-year resampling period experienced reduced growth when compared against liana-free trees (Ingwell et al., 2010). In Peru, van der Heijden and Phillips (2009a) documented growth reductions of up to 84% for liana-infested individuals. Liana cutting in timber tree species has also been shown to increase growth and, in turn, yield (Alvira et al., 2004; Lussetti et al., 2016). However, it may take up to five years on average for growth-rates to recover to that of liana-free individuals (Grogan and Matthew Landis, 2009), suggesting that liana effects on host tree growth are lasting. When lianas were removed from the common timber tree *Prioria copaifera* in plots in Panama, radial growth had doubled five years after treatment (Grauel and Putz, 2004). The competitive effect lianas exert on trees can be much greater than neighbouring trees of similar biomass (Tobin et al., 2012; A. Wright et al., 2015). Sap velocity, a proxy for radial growth (Álvarez-Cansino et al., 2015), in canopy trees increased by ~8% only days after competing lianas were cut, whereas cutting of neighbouring tree saplings had no such effect (Tobin et al., 2012). Further evidence suggests the severity of liana load carried by trees has a significant positive correlation with the magnitude of effect on growth (van der Heijden and Phillips, 2009a; Grogan and Matthew Landis, 2009; Smith et al., 2017; Visser et al., 2017).

The difference in effect of above- and below-ground liana competition on tree growth is still debated in the literature. A key limiting factor for individual tree growth in tropical forests is light availability (Graham et al., 2003; Schnitzer et al., 2005). The unique growth strategy of lianas ensures their leaves are optimized for reaching and overlaying the forest canopy by deploying their leaves atop those of their host tree (Avalos et al., 1999; Kurzel et al., 2006; Asner and Martin, 2012; Schnitzer, 2018). Liana leaves are thought to account for approximately one-fifth of canopy foliage, based on removal experiments in central Panama (van der Heijden et al., 2013; Rodríguez-Ronderos et al., 2016; Estrada-Villegas et al., 2020). Lianas are therefore effective above-ground competitors, reducing the photosynthetic capacity of even the tallest canopy trees (Avalos et al., 1999; Avalos and Mulkey, 1999; Ingwell et al., 2010; Fauset et al., 2017). In an extensive study across Amazonia, infested trees in high light conditions (crown completely exposed to vertical and lateral light) had significantly lower growth compared to individuals in poorly lit canopies (Reis et al., 2020). This suggests that liana competition in high light environments is dominated by above-ground competition for canopy light (Malizia and Grau, 2006).

Other growth-limiting resources in tropical forests are water and soil nutrients. Tropical plants compete intensely for these valuable below-ground resources (Coomes and Grubb, 2000; Lewis and Tanner, 2000; Tanner and Barberis, 2007), especially in the case of lianas and trees (Toledo-Aceves and Swaine, 2008a; Toledo-Aceves, 2015; Álvarez-Cansino et al., 2015; De Deurwaerder et al., 2018). However, the number of lianas rooted near the trunk of a tree is strongly correlated with the degree of liana infestation in the tree crown (Clark and Clark, 1990; van der Heijden and Phillips, 2009a; Ingwell et al., 2010), which makes disentangling above- and below-ground effects complicated. Nevertheless, some studies have concluded that below-ground liana competition has the strongest effect on tree growth (Dillenburg et al., 1993a; Toledo-Aceves and Swaine, 2008a). Whigham (1984) and Schnitzer et al. (2005) found no significant difference in growth rates between trees under below-ground competition only, and trees under both above- and below-ground competition in North America and Panama respectively. As such, below-ground competition elicits the strongest effect on tree growth in these instances. Further studies of *Liquidambar styraciflua* support this notion, as despite significantly reduced light availability in infested trees, growth responses were more closely related to below-ground nitrogen availability (Dillenburg et al., 1993b), a commonly growth-limiting soil nutrient (Field and Mooney, 1986). It should be noted that the bulk of studies supporting below-ground competition as the dominant effect on tree growth are based on tree seedlings or saplings (Dillenburg et al., 1993a; 1993b; Schnitzer et al., 2005; Toledo-Aceves and Swaine, 2008a). Therefore, it is possible that during ontogeny there is a shift in dominance from below-ground liana competition in juveniles to above-ground competition in adult trees. Overall, regardless of the relative contributions of above- and below-ground competition on tree growth, a growing body of evidence supports the significant effect of lianas on tree growth and carbon sequestration.

1.3.2 Mortality

Both intense competition for light and below-ground resources and the mechanical stress of carrying severe liana loads can increase mortality risk of trees that host lianas (Phillips et al., 2005; Ingwell et al., 2010; McDowell et al., 2018). Phillips et al. (2005) found that a third of tree basal area lost through mortality over 24 years was attributed to infestation by large lianas (≥10 cm diameter) across a series of upper Amazonian forest sites in Peru. This study also indicated that trees infested by large lianas had a 56% greater risk of mortality compared to liana-free trees, which increased to 200% when only those trees ≥50 cm diameter were considered (Phillips et al., 2005). Furthermore, the severity of liana infestation inflates mortality risk, with heavily infested trees (≥75% crown occupancy) twice as likely to die than trees with lower levels of liana infestation (≤25% crown occupancy; Grogan and Matthew Landis, 2009; Ingwell et al., 2010; Smith et al., 2017). In addition, liana-induced tree mortality can also cause the collateral death of neighbouring trees when a large tree dies and collapses. Lianas often tie tree crowns together, meaning that if one tree dies and falls, this can break and uproot neighbouring trees (Putz, 1984a; Appanah and Putz, 1984; Garrido-Pérez et al., 2008). When this is accounted for, mortality risk increases further by at least 3% (Phillips et al., 2005).

1.3.3 Reproduction

Liana infestation can also limit tree reproduction, with a growing body of evidence showing a negative relationship between the presence of lianas and the flowering and fruiting success of trees, which has a knock on effect on their reproductive output (Stevens, 1987; Wright et al., 2005; Kainer et al., 2006; Dalling and John, 2008; Fonseca et al., 2009; Klimas et al., 2012; Kainer et al., 2014; Tymen et al., 2016). For example, fruiting was significantly reduced in *Chrysophyllum lucentifolium* trees with ≥50% liana crown occupancy compared against liana-free trees in Brazil (Fonseca et al., 2009). Furthermore, in a Bolivian study, liana infested trees had reduced seed viability compared against liana-free trees, with trees hosting lianas in more than 20% of their crown not producing any seeds at all (Nabe-Nielsen et al., 2009). In addition, the severity of infestation also alters the magnitude of liana effect on reproduction, with liana load correlating negatively with fecundity (Stevens, 1987; Wright et al., 2005; Kainer et al., 2006; Nabe-Nielsen et al., 2009; Klimas et al., 2012). Deformation of the tree crown, constraining and breaking fruitful tree branches (Putz, 1995; Kainer et al., 2006; Kainer et al., 2007), as well as reducing canopy light availability (Phillips, 1993; Kainer et al., 2014), are key mechanisms by which lianas reduce tree reproduction. On a community-level, García León et al. (2018) found that fruiting of canopy trees was 173% more likely two years after liana removal. Liana-limited reproduction of canopy trees and associated reductions in seed dispersal may have knock-on effects on recruitment rates and species diversity (Clark et al., 2007). This could constrain niche diversification and may have a destabilizing effect on tree and animal populations and composition over time (García León et al., 2018).

1.3.4 Regeneration

Lianas may also impact tree regeneration, particularly in treefall gaps (Schnitzer et al., 2000; Toledo-Aceves and Swaine, 2008b; Schnitzer and Carson, 2010; Paul and Yavitt, 2011; Tymen et al., 2016). Strong plant-plant interactions, specifically interspecific liana-tree competition, can disturb the natural succession in tropical forests (A. Wright et al., 2015; Estrada-Villegas et al., 2020). In heavily disturbed sites, regenerating areas are often dominated by lianas (Hegarty and Caballé, 1991; Gerwing, 2001), suppressing the growth and survival of regenerating trees at the seedling phase and thus maintaining a low-canopy state (Schnitzer et al., 2000; Schnitzer and Carson, 2000; Pasquini et al., 2015; Martínez-Izquierdo et al., 2016; Tymen et al., 2016). Lianas can further disadvantage regenerating trees by adding to their mechanical load, creating shorter and more stout tree trunks (Toledo-Aceves and Swaine, 2007; Dias et al., 2017). In turn, this further increases their susceptibility to infestation and ultimately increases mortality risk (Gilbert et al., 2006; Ribeiro et al., 2016; Reis et al., 2020). Schnitzer and Carson (2010) found that liana-infested treefall gaps had 46% lower tree recruitment and 55% lower growth compared to liana-removed treefall gaps over a period of 8 years. These findings are consistent with other studies of treefall gaps in Panama (Grauel and Putz, 2004; Schnitzer, 2005; Schnitzer et al., 2014b; Martínez-Izquierdo et al., 2016), Brazil (César et al., 2016) and Bolivia (Naturales, 2001). Similarly, in secondary forest plots in Agua Salud, central Panama, the effect of lianas increased during succession. Regenerating trees suffered 19% lower growth in five year old forests, increasing to 47% lower growth in 60 year old forests compared to plots with a lower ratio of lianas to trees (Lai et al., 2017). Evidence for liana suppressed tree regeneration is also found in the palaeotropics (Toledo-Aceves and Swaine, 2008a; 2008b; Marshall et al., 2017). However, liana effect on early successional tree growth is not universally supported. Estrada-Villegas et al. (2021) found no evidence for suppressed tree regeneration in their liana removal experiment in a tropical dry forest, although this was largely attributed to local factors such as a lack of water. All in all, lianas have a doubly negative effect on tree regeneration, firstly by constraining fruit and flower production, and secondly by competing heavily with regenerating seedlings (García León et al., 2018).

1.4 Disproportionate effects on tree functional groups

1.4.1 Evidence

The effect of lianas on different tree functional groups is not equal, with liana infestation in different tree species varying between 10% and 90%, and liana load from 34% to 63% in forest plots on BCI (Muller-Landau and Visser, 2019). Pioneer species often experience lesser degrees of liana infestation, whereas shade-tolerant species generally account for a disproportionate amount of infested trees, often with greater liana loads (Putz, 1984a; Putz, 1984b; Putz, 1984c; Clark and Clark, 1990; Campbell and Newbery, 1993; Schnitzer et al., 2000; Carsten et al., 2002; Schnitzer and Bongers, 2002; Alvira et al., 2004; van der Heijden et al., 2008; van der Heijden and Phillips, 2009a; Schnitzer and Carson, 2010; S. Wright et al., 2015; Reis et al., 2020). For instance, in a large-scale Amazonian study, 78.3% of the dominant shade-tolerant *Micropholis venulosa* species were infested by lianas, whereas the common fast-growing *Schefflera morototoni* species suffered significantly less (32.1%; Reis et al., 2020). Equally, multiple studies have found fast-growing *Cecropia* trees to exhibit extremely low levels of infestation (Croat, 1978; Putz, 1984b; Brokaw, 1985; Clark and Clark, 1990; Ingwell et al., 2010). This is partially explained by their common association with *Azteca* ants, which are known to remove climbing vines (Janzen, 1969; Janzen, 1973; Schupp, 1986). However, Putz and Holbrook (1988) observed scarce liana infestation of *Cecropia* species in Malaysia despite *Azteca* ants not being present in Malaysia.

Shade tolerance can be represented by a species position on the slow-fast life-history axis, the trade-off between growth and survival (Wright et al., 2010; Visser et al., 2017). Typically, a species higher up the slow-fast axis has greater light requirements. Some evidence points towards a positive correlation between shade tolerance and liana infestation in Central America (Muller-Landau and Visser, 2019) and the palaeotropics (Lowe and Walker, 1977). Disproportionate liana infestation on species with differing life-history traits has also been observed in regenerating tree saplings (Naturales, 2001; Toledo-Aceves and Swaine, 2008b). In regenerating treefall gaps, slow-growing shade-tolerant tree species such as *Dipteryx oleifera* were predominantly constrained by lianas (A. Wright et al., 2015), whereas pioneer species grew virtually unabated (Schnitzer et al., 2000;

Schnitzer and Carson, 2010; César et al., 2017). Therefore, lianas are posited to have pervasive effects on tree-tree competition, by disproportionately advantaging certain species, by competing more intensely with others (Schnitzer and Bongers, 2002; Schnitzer et al., 2011).

However, not all studies support this relationship between shade-tolerance and susceptibility to infestation and exceptions to this general trend do exist. Studies in Argentina and Panama found slim to no evidence supporting a significant relationship between tree functional traits and the frequency or severity of liana infestation (Malizia and Grau, 2006; and Martínez-Izquierdo et al., 2016 respectively). Additionally, some pioneer tree species have been observed to suffer from heavy liana infestation (e.g. *Alchornea costaricensis, Miconia argentea* and *Sloanea terniflora*), alongside shade-tolerant species and those with unknown life-history traits (Ingwell et al., 2010).

1.4.2 Driving mechanisms

Pioneer and shade-tolerant tree species differ predominantly in their inherent growth rates. Tree growth rate is posited to be a determining factor in susceptibility to liana infestation (Laurance et al., 2001), correlating negatively with risk of infestation (Clark and Clark, 1990; van der Heijden et al., 2008; Reis et al., 2020). The increased susceptibility of shade-tolerant, typically slow-growing trees to liana infestation may simply be a function of the increased time they are exposed to potential infestation compared against fast-growing species of the same size (Lowe and Walker, 1977; Laurance et al., 2001; Perez-Salicrup et al., 2001; van der Heijden et al., 2008; Fadrique and Homeier, 2016). Additionally, fast growing species are able to outgrow and detach their lianas as long leaves and branches are shed (Carse et al., 2000; van der Heijden et al., 2008; Ingwell et al., 2010).

Tree size is also associated with susceptibility to liana infestation (Clark and Clark, 1990; Carsten et al., 2002; Pérez-Salicrup and De Meijere, 2005; Poulsen et al., 2017). Larger and older trees more frequently host lianas, as well as harbouring the heaviest liana loads (Clark and Clark, 1990; Nabe-Nielsen, 2001; Chittibabu and Parthasarathy, 2001; Malizia, 2003; Phillips et al., 2005; Fadrique and Homeier, 2016). In addition to an extended period of exposure, large trees receive the most canopy light, and therefore are a more preferable host to lianas (Phillips et al., 2005). Smaller, non-canopy trees experience fewer instances of liana infestation (Muller-Landau and Visser, 2019), although they are often used as a stepping-stone to reach the canopies of taller trees (Putz, 1995; van der Heijden et al., 2008).

In addition to life-history variation, morphological traits such as stem flexibility, leaf length, bark roughness and trellis availability may also impact susceptibility of different tree species to liana infestation (Balfour and Bond, 1993; Carse et al., 2000; Carsten et al., 2002; van der Heijden et al., 2008). Trunk infestation is reduced in tree species with tall branch-free boles (Campbell and Newbery, 1993; Balfour and Bond, 1993; Muthuramkumar and Parthasarathy, 2001; Chittibabu and Parthasarathy, 2001; Malizia, 2003; Campanello et al., 2007) and smooth bark (Putz, 1984b; Talley et al., 1996a; 1996b; Carsten et al., 2002; Malizia, 2003; Campanello et al., 2007; van der Heijden et al., 2008). The absence of available trellises makes the architecture of such trees (e.g. *Dipterocarpaceae*) not conducive to climbers (Campbell and Newbery, 1993; Balfour and Bond, 1993; S. Wright et al., 2015), which are rarely able to climb the trunks of such trees directly (Putz, 1984b). Tree species with narrow and shallow crowns may also be less susceptible to liana infestation (Putz, 1984b; Campanello et al., 2007), as trees with large crown diameter are at greater risk of lateral invasion from infested neighbouring trees (Putz, 1984b; Carse et al., 2000; Malizia, 2003; Malizia and Grau, 2006; Campanello et al., 2007; van der Heijden et al., 2008). Furthermore, infested trees are more susceptible to further invasion as existing lianas facilitate aggregation of other climbers (Putz, 1982; 1984b; Nabe-Nielsen, 2001; Perez-Salicrup et al., 2001; Campanello et al., 2007). Putz's (1984b) study found that stiff-trunked tree species were more susceptible to infestation, with flexible trunks snapping or dislodging lianas as they sway. In addition, large leaved species (>50 cm length) were observed to suffer less infestation as climbers were dislodged as leaves shed (Putz, 1984b). This is understood to be why palm species commonly exhibit minimal infestation rates (Putz, 1984a; 1984b; Carse et al., 2000; Perez-Salicrup et al., 2001; van der Heijden et al., 2008).

1.4.3 Tolerance

A hitherto ignored factor is not only the susceptibility of differing tree species to liana infestation, but also the tolerance of tree species as liana hosts. A commonly accepted ecological theory regarding interspecific competition is that hosts better adapted to enduring parasitism have a competitive advantage (Holt et al., 1994). Many of the aforementioned studies document variation in liana prevalence amongst different tree species, though fail to consider variation in tolerance to liana infestation between species functional groups. Presumably this is because tolerance is hard to quantify, requiring long term datasets on tree species vital rates and growth across different life stages (Muller-Landau and Visser, 2019). A novel 28-year study in Panama by Visser et al. (2017) was the first to evaluate the interspecific relationships between liana infestation and tolerance in tree species with different life-history traits. They found that fast-growing species had significantly lower rates of survival when infested, with low shade-tolerance eliciting a strong relationship with low liana tolerance (Visser et al., 2017). This contrasts with the commonly held assumption that because shade-tolerant species have disproportionately high levels of infestation, they are seemingly more vulnerable to infestation and are subsequently disproportionately disadvantaged. These previous conclusions may have been affected by a survivorship bias in fast-growing trees. As recent long-term studies show that liana-induced mortality is high in fast-growers, static studies will only consider those that survive, thus underestimating the scale and effect of infestation in fast-growing tree species.

Liana tolerance is partially contingent on the species-specific demand for particular above- and below-ground resources (Campanello et al., 2007; Toledo-Aceves and Swaine, 2008a). Fast-growing species may have a lesser tolerance to liana infestation as they tend to be more reliant upon abundant light (Kitajima, 1994; Stewart and Schnitzer, 2017), as well as soil water and nutrient reserves (Asner and Martin, 2012). Light-wooded fast-growers are also more prone to stem breakage and resulting mortality due to liana mechanical stress (Paciorek et al., 2000; Larjavaara and Muller-Landau, 2010). On the other hand, shade-tolerant species benefit from crown, stem and leaf traits more suited to tolerating this added competition (Kitajima, 1994; Kohyama et al., 2003; Kitajima et al., 2005). For these reasons, shade-tolerance has a significant positive correlation with liana tolerance (Visser et al., 2018; Muller-Landau and Visser, 2019). As host tolerance and liana prevalence within a tree species are antagonistic, no significant relationship between shade-tolerance and liana burden exists (Visser et al., 2017). All things considered, the burden of lianas in terms of the number of infested individuals, the liana load and the effect of lianas on growth between species is predominantly governed by host tolerance (Muller-Landau and Visser, 2019). As such, this metric is pivotal in studying the disproportionate effect of lianas on different tree functional groups.

1.4.4 Shift in tree composition

Disproportionate liana effects on certain tree functional groups may induce a shift in tree composition from slow-growing dense-wooded species to fast growing light-wooded tree species (van der Heijden and Phillips, 2009a; Durán and Sánchez-Azofeifa, 2015; García León et al., 2018; Visser et al., 2017), which have 15% less dense wood on average based on over one thousand trees censused in Peru (van der Heijden et al., 2008). This could reduce the capacity of tropical forests to sequester and store carbon by 34% (Bunker et al., 2005). This shift may already be occurring, with mean wood density decreasing in Peru (van der Heijden et al., 2013) and Amazonia over the last three decades, a pattern driven by stagnation and decline in slow-growing shade-tolerant species (Laurance et al., 2004). With liana induced effects potentially working in unison with increased atmospheric CO_2, the observed increase in dominance of fast-growing species over recent decades may be further exacerbated (Laurance et al., 2004; Phillips et al., 2004; Brienen et al., 2020). However, it is currently not yet known if and how lianas disproportionately affect certain tree species, nor how this may contribute to the carbon balance of tropical forests.

1.5 Forest carbon effects

1.5.1 Evidence

A reduction in the capacity of tropical forests to sequester and store carbon is the most dangerous and globally important ramification associated with liana prevalence (Schnitzer et al., 2011). Early studies have estimated that liana infestation can reduce stand-level above-ground carbon accumulation by 10%, equivalent to 0.25 Mg C ha^{-1} year^{-1} (van der Heijden and Phillips, 2009a). An observational study of 145 tropical forests across 5 continents concluded that liana presence in trees ≥10 cm diameter, those which store and sequester the most carbon (DeWalt and Chave, 2004; Stephenson et al., 2014; Lutz et al., 2018), reduced above-ground carbon stocks by up to 50% (Durán and Gianoli, 2013). Additionally, a liana removal experiment in central Panama found 21.9% lower above-ground carbon in liana-infested plots (Estrada-Villegas et al., 2020). Similar experimental methods on BCI by van der Heijden et al. (2015) reported a ~76% lower overall carbon uptake in liana-infested plots compared against liana-removed plots after three years, equivalent to 2.43 Mg C ha^{-1} year^{-1}.

Owing to their nature of using trees for structural support, lianas can afford to invest predominantly into foliage and not costly stems (Putz, 1983; Avalos and Mulkey, 1999; Gerwing, 2004; Selaya et al., 2007; Cai et al., 2007; Tang et al., 2012; Ewers et al., 2015). As such, lianas make up only a minimal proportion of woody biomass, commonly less than 5% (Ogowa, 1965; Kato, 1978; Gentry et al., 1987; Hegarty and Caballé, 1991; Nascimento and Laurance, 2002; DeWalt and Chave, 2004; Kirby and Potvin, 2007; Clark et al., 2008; Schnitzer et al., 2012; Schnitzer et al., 2014). This means that lianas only partly compensate for the carbon stored in the stems they displace, replacing just 33% in Peru (van der Heijden and Phillips, 2009a), 24% in Panamanian treefall gaps (Schnitzer et al., 2014) and as little as 8% in Brazil (Laurance et al., 1997).

Furthermore, lianas may also contribute to a shift in carbon residence time. Due to their heavy investment in foliage, leaves make up the majority of net primary productivity in liana-infested plots, to the detriment of woody stems (van der Heijden et al., 2015). Moreover, liana stems have considerably higher turnover rates (Mascaro et al., 2004), with even the largest lianas (≥10 cm diameter) exhibiting recruitment and mortality rates three times greater than neighbouring trees of comparable size (Phillips et al., 2005). Consequently, in liana-infested plots, fixed carbon is released back to the atmosphere at a faster turnover rate than in liana-free plots (Powers et al., 2009; Galbraith et al., 2013; Tymen et al., 2016).

1.5.2 Models

There are increasing calls for the unignorable impact of lianas on tropical forests to be included in future carbon dynamics models (Phillips et al., 2002; van der Heijden et al., 2013; McDowell et al., 2018; Kumar and Scheiter, 2019). di Porcia e Brugnera et al. (2019) pioneered this by introducing a liana plant functional type into an Ecosystem Demography Model (Moorcroft et al., 2001; Medvigy et al., 2009). This novel study found that lianas reduced forest primary productivity by 2.6% after 70 years, translating to a 20 tC ha^{-1} reduction in above-ground biomass. This liana plant functional type was subsequently improved by Meunier et al. (2020) to better represent plant hydraulics and root water uptake as well incorporating inventory data. Emerging work from Meunier et al. (2021) has incorporated three years of inventory data from a liana removal experiment in Gigante, Panama (van der Heijden et al., 2015) with this improved model to more accurately simulate liana effects on carbon storage. After 10 years the simulated difference in carbon storage between liana-removed and liana-infested plots remained significant, with net above-ground biomass 1.7 kg C m^{-2} greater in the absence of lianas (Meunier et al., 2021). Further modelling efforts must include lianas in future projections to accurately represent the likely changes in tree dynamics and forest carbon stocks over the coming century (Phillips et al., 2002; Phillips et al., 2005; van der Heijden and Phillips, 2009a; Durán and Gianoli, 2013; van der Heijden et al., 2013; Verbeeck and Kearsley, 2016; di Porcia e Brugnera et al., 2019; Estrada-Villegas et al., 2020). However, this comes with its own issues as complex interactions between lianas and trees as well as insufficient global data presents a unique task for modelers (Schnitzer et al., 2016).

1.6 Increasing Liana Abundance

1.6.1 Evidence

With the effect of lianas on forest carbon dynamics becoming ever more apparent, studies evaluating what controls their abundance and how this is changing are becoming ever more important. The evidence for increasing liana abundance (stem density), liana infestation (number of trees hosting lianas), severity of liana infestation (% crown occupancy) and liana biomass (combined basal area) in the neotropics is growing (Phillips et al., 2002; Schnitzer and Bongers, 2011; Schnitzer, 2015). In addition, the speed of these changes are understood to be significantly greater relative to all other tropical forest plant species (Schnitzer and Bongers, 2002; Chave et al., 2008).

Increases in liana abundance were first observed by Phillips et al. (2002) in Amazon forest plots, with stem numbers doubling over a 20 year period. Satellite-imagery supports this increase, with liana-dominated patches expanding by 59% over a similar time period in the Bolivian Amazon (Foster et al., 2008). Old-growth Amazon forests have also experienced growing liana abundance (Benitez-Malvido and Martinez-Ramos, 2003; Laurance et al., 2014). Liana biomass is recorded to be increasing at a 60% faster rate than trees in Amazonia, which are reportedly declining in stem density (Chave et al., 2008). In a forest on BCI, Panama, 47% of trees suffered liana infestation in 1979 (Knight, 1975; Putz, 1984a). By 2007, the proportion of infested trees in this forest had increased to 73.6% (Ingwell et al., 2010). Additionally, liana stem density had increased by 140% in this location (Schnitzer et al., 2012) and liana foliage and flower production increased markedly over a similar time period (Wright et al., 2004; Wright and Calderon, 2006). Severity of infestation on BCI has also changed, with the number of trees suffering a high liana load (≥75% crown occupancy) increasing by 65% between 1996 and 2007 (Ingwell et al., 2010). Evidence for increasing liana prevalence is also documented in Costa Rica (Enquist and Enquist, 2011), Ecuador (Smith et al., 2017), Puerto Rico (Hogan et al., 2017) and South Carolina (Allen et al., 2007).

Despite the wealth of evidence supporting increasing liana abundance, the generality of this trend may not be consistent across the neotropics, or indeed the globe. In Argentina, liana stem density declined over a 12-year period and basal area increase was muted in comparison to neotropical studies (Ceballos and Malizia, 2017). However, this may be due to a marked reduction in anthropogenic disturbance and tree mortality in this study, with local conditions potentially overriding global trends. Contrastingly, studies in tropical Africa oppose the pattern of increasing liana prevalence observed across the Americas (Caballé and Martin, 2001; Ewango, 2010; Bongers et al., 2020). Between 1979 and 1992 liana density decreased by 20% at a site in Gabon (Caballé and Martin, 2001). Similarly, across two plots in the Democratic Republic of Congo liana abundance decreased by 33% between 1994 and 2007, although this was largely attributable to the collapse of the dominant liana species *Manniophyton fulvum* (Ewango, 2010). A subsequent study in this location supported the decrease in liana abundance, although instead suggested a lack of forest disturbance for this decline (Bongers et al., 2020), perhaps again indicating that local conditions may take precedent over general global changes. Despite a convincing bulk of evidence supporting an increase in liana abundance in the Americas, further study in Africa, Asia and Australia are needed to confirm or deny the generality of this trend (Schnitzer and Bongers, 2011; Poulsen et al., 2017). This study location bias in liana abundance research towards the neotropics mirrors a broader trend in tropical ecology (Martin et al., 2012).

1.6.2 Drivers of increasing liana abundance

As manipulative studies of the required temporal and spatial scale are too difficult, existing data supporting the mechanisms thought to control liana prevalence are purely correlative. Existing research points towards the interrelated and synergistic effect of rising evapotranspirative demand, increased natural and anthropogenic disturbance, changing land use and enhanced atmospheric CO_2 (Phillips et al., 2002; Schnitzer and Bongers, 2011).

1.6.2.1 Evapotranspirative demand

High seasonality is common in neotropical forests (Feng et al., 2013; Allen et al., 2017) In turn, canopy photosynthesis in trees and lianas differs between seasons (Guan et al., 2015). Contrary to most other tropical plants, liana abundance correlates well with reduced mean annual precipitation and increased seasonality at a pantropical scale (Schnitzer, 2005; DeWalt et al., 2010; Schnitzer and Bongers, 2011; Manzané-Pinzón et al., 2018), although this is not significant in the neotropics (van der Heijden and Phillips, 2008). As such, lianas are hypothesized to have a seasonal growth advantage over trees in dry periods (Schnitzer, 2018; Schnitzer and van der Heijden, 2019), by which they gather and utilise water more efficiently (Schnitzer, 2005; Andrade et al., 2005; Cai et al., 2009; Sánchez-Azofeifa et al., 2009; De Deurwaerder et al., 2018), thus allowing them to maintain steady growth in contrast to dormant trees (van der Heijden et al., 2019).

A recent five-year study of >1,000 canopy trees and >500 lianas in Panama found that absolute and relative growth of lianas was highest in the dry-season (Schnitzer and van der Heijden, 2019), with lianas attaining 50% of their annual growth over the 4-month dry period compared to 25% in canopy trees. Furthermore, during the 2015/16 El Niño drought tree growth virtually stopped, whereas lianas were able to grow unabated (Schnitzer and van der Heijden, 2019). Further studies in Panama (van der Heijden et al., 2019), as well as southwestern China (Zhu and Cao, 2009; Cai et al., 2009), also support enhanced liana growth in the dry season. This seasonal growth advantage may also be amplified in juvenile lianas, with liana saplings experiencing up to seven-times greater growth in the dry season compared to tree saplings (Schnitzer et al., 2005). If increasing evapotranspirative demand was responsible for higher liana abundance and biomass, one would expect to see greater liana prevalence in seasonally dry forests compared to aseasonal forests (Schnitzer, 2005). Such patterns were observed by Parthasarathy et al. (2014) in peninsular India, where the highest liana densities are found in seasonal forests. Similarly, Swaine and Grace's (2007) study in Ghana demonstrated that lianas were more dominant in seasonally dry forests (1,000 mm rainfall year^{-1}; 43% of woody species) than in wet forests (2,000 mm rainfall year^{-1}; 30% of woody species). This trend is also exemplified in Panama, where seasonally dry forests had significantly higher liana stem density (1044 individuals ha^{-1}) than wet forests (729 individuals ha^{-1}; Dalling et al., 2012).

The consensus as to why lianas benefit from increased evapotranspirative demand is their competitive advantage over trees under scarce water events. Liana species are known to benefit from greater stomatal control in their leaves compared to trees during droughts and dry periods (Cai et al., 2009; Chen et al., 2015; Campanello et al., 2016; Maréchaux et al., 2017; Werden et al., 2018). As such, lianas are able to maintain high hydraulic conductivity in periods of drought, whereas trees are instead likely to succumb to embolism (van der Sande et al., 2019). This is evidenced in lowland Bolivia where liana-removed trees had a less-negative leaf water potential throughout the dry season compared to infested trees (Pérez-Salicrup and Barker, 2000). Additionally, as liana stems are not relied on for structural support, liana stems are more porous than trees with a higher xylem vessel density, allowing for more efficient water transport (Ewers et al., 1991; Fu et al., 2016; Werden et al., 2018). Furthermore, deep liana roots are also posited to facilitate uptake of scarce water reserves in dry periods (Gartner et al., 1990; Ewers et al., 1990; Fisher and Ewers, 1995; Holbrook and Putz, 1996; Restom and Nepstad, 2001; Restom and Nepstad, 2004; Andrade et al., 2005; Isnard and Feild, 2015; Chen et al., 2015; Collins et al., 2016). However, more recent evidence refutes this (de Azevedo Amorim et al., 2018), with others suggesting that liana roots are instead spread wider and shallower than tree roots (Johnson et al., 2013; Smith-Martin et al., 2020), in turn taking advantage of the limited precipitation by intercepting it in the topsoil at the detriment of deeper tree roots (Andrade et al., 2005; Collins et al., 2016; De Deurwaerder et al., 2018).

The seasonal growth advantage of lianas can also be explained by their ability to better capitalise on increased light availability in the dry season (Wright and van Schaik, 1994; Graham et al., 2003). Firstly, because they are not limited by reduced water resources in the same way as trees (Schnitzer, 2005; Schnitzer, 2018; Schnitzer and van der Heijden, 2019) and secondly, because lianas are more likely to retain (Putz and Windsor, 1987; Kalácska et al., 2005) or produce new leaves in the dry season (Opler et al., 1991), whereas as many as one-third of tree leaves can be lost (Condit et al., 2000).

As the strength and frequency of dry periods in the tropics has intensified in recent decades (Malhi and Wright, 2005; Fu et al., 2013), a trend expected to continue into the future (Marengo et al., 2012; Boisier et al., 2015; Duffy et al., 2015), the seasonal growth advantage of lianas over trees is likely to increase, as will their abundance. It is important to note that although liana abundance increases in dry periods, this does not also mean that the effect of lianas on tree carbon differs between seasons (van der Heijden et al., 2019). It does however indicate that the year-round effect of lianas on tree carbon may increase with increased drying and increasing liana abundance.

1.6.2.2 Natural Disturbance

The most frequent form of natural disturbance in tropical forests is tree mortality, and subsequent treefall, causing gaps in the forest canopy (Brokaw, 1985; Denslow, 1987; Hubbell et al., 1999; Schnitzer et al., 2014). An estimated 1-2% of canopy trees collapse each year (Swaine et al., 1987; Phillips and Gentry, 1994; van der Meer and Bongers, 2001), with mortality rate in old-growth forests increasing further in recent decades (Phillips et al., 2004). A regeneration period of 8-10 years minimum is needed for trees to refill a treefall gap (Brokaw, 1985). Consequently, it can be assumed that up to 20% of tropical forests are undergoing gap-phase regeneration at any one time (Schnitzer et al., 2014).

Lianas are often the first to take advantage of disturbed areas (Ledo and Schnitzer, 2014). Plentiful light availability and subdued tree competition provide ideal growing conditions for generating lianas (Putz, 1984b), which recruit and proliferate rapidly in these high resource gaps (Hegarty and Caballé, 1991; Horvitz et al., 1998; Schnitzer et al., 2000; Schnitzer and Carson, 2001; van der Heijden and Phillips, 2008; Schnitzer and Carson, 2010; Dalling et al., 2012; Schnitzer et al., 2014a). Lianas can invade laterally from neighbouring understories (Putz, 1984a; Putz, 1984b; Penalosa, 1984; Schnitzer et al., 2000; Pérez-Salicrup and De Meijere, 2005; Yorke et al., 2013). Alternatively, following treefall events, lianas that are dislodged and fall back to the forest floor are able to re-root and survive in 90% of instances (Alvira et al., 2004), though it may be months or years before they again reach the forest canopy (Putz, 1984a; Schnitzer et al., 2000; Phillips et al., 2005; Ingwell et al., 2010; Yorke et al., 2013). Recent and widespread reports of increasing tree mortality and forest turnover due to increasing temperatures (Clark, 2004; Malhi and Wright, 2005), atmospheric CO_2 (Laurance et al., 2004; Brienen et al., 2020), nutrient deposition (Phillips and Gentry, 1994; Körner, 2006; Wright, 2010) as well as increasingly frequent drought and El Nino events (Slik, 2004; Li et al., 2008; Zhang et al., 2008; Phillips et al., 2009) may be increasing the amount of treefall gaps (Schnitzer and Bongers, 2011). In the same way, lianas themselves may contribute to increasing mortality, thus creating a positive feedback loop where treefall and canopy gaps increase, further increasing liana prevalence and tree mortality and so on (Schnitzer and Bongers, 2002; Schnitzer and Bongers, 2011; Visser et al., 2017). With a high proportion of tropical forests undergoing gap-phase regeneration at any one time, added to the fact that factors driving tree mortality and treefall are intensifying, natural disturbances may give rise to liana prevalence in the future (Schnitzer et al., 2000; Schnitzer and Carson, 2001; Laurance et al., 2014).

1.6.2.3 Anthropogenic disturbance

In addition to natural disturbances, anthropogenic impacts (e.g. logging) and land use changes may also contribute to increasing liana abundance by creating more treefall gaps and forest edges (Gerwing, 2001; Parren and Doumbia, 2005; Addo-Fordjour et al., 2009; Hogan et al., 2017; Magnago et al., 2017; Campbell et al., 2018). Deforestation and selective logging is a global and growing issue that has a doubly negative impact on tree biomass (Asner et al., 2005; Wright, 2005; Laurance et al., 2009; Wright, 2010). Firstly, by removing fertile and mature trees, thus limiting reproduction, (Nabe-Nielsen et al., 2009) and secondly, by producing more canopy gaps by which lianas can rapidly proliferate and stall tree regeneration (Grauel and Putz, 2004; Schnitzer and Carson, 2010).

A marked increase in secondary forests in the tropics (Wright, 2005), chiefly due to areas being abandoned after human use (e.g. farmland, timber production; Chazdon, 2003), may also increase liana abundance. The combination of high light and trellis availability in young secondary forests provides ideal conditions for liana infestation (Balee and Campbell, 1990; Madeira et al., 2009). Thus, liana numbers peak in secondary forests a few decades after abandonment (DeWalt et al., 2000; Letcher and Chazdon, 2009; Barry et al., 2015; César et al., 2017).

The issue of forest fragmentation from new roads and linear infrastructure is also intensifying in the tropics (Laurance et al., 2009; Campbell et al., 2018). This creates new forest edges in which lianas tend to occupy extensively (Laurance et al., 2001; Londré et al., 2006; Magnago et al., 2017; Jones et al., 2017), largely owing to favourable light conditions and available trellises (Putz, 1984a). An increase in forest fragmentation is likely to cause an associated increase in liana abundance by indirectly altering forest structure to be more conducive to liana proliferation (Schnitzer and Bongers, 2011; Campbell et al., 2015; César et al., 2017; Campbell et al., 2018; Reis et al., 2020). This may also give rise to tree mortality at forest edges (Laurance et al., 2001).

Another, more direct human impact on liana prevalence is hunting for bushmeat, which reduces the density of certain mammal populations. This benefits lianas by reducing seed dispersal by animals in competing tree species (Wright et al., 2007), thus allowing wind dispersing liana species to reproduce more effectively (Gentry, 1991). With human populations and demand for resources ever growing, anthropogenic disturbance in tropical forests is likely to continue to benefit liana prevalence, ever-increasing their role in forest dynamics (Schnitzer and Bongers, 2002; Durán and Sánchez-Azofeifa, 2015).

1.6.2.4 Atmospheric CO_2

In addition to enriched atmospheric CO_2 accelerating forest turnover and indirectly benefitting liana proliferation through increased natural disturbances (Schnitzer and Bongers, 2011; Brienen et al., 2020), enriched atmospheric CO_2 may also directly benefit liana prevalence (Laurance et al., 2014). Due to having a larger photosynthetic capacity and reduced biomass investment compared to trees (Zhu and Cao, 2009; Cai et al., 2009; Asner and Martin, 2012; Wyka et al., 2013), lianas have a greater leaf area to whole plant biomass ratio (Putz, 1983; Mohan et al., 2006), meaning they are able to better take advantage of greater atmospheric CO_2. Lianas also benefit from leaves with greater photosynthetic rate per area and lower construction costs (Zhu and Cao, 2010), further benefitting their capacity to respond to elevated CO_2. Lianas may gain a further competitive advantage over trees in the dry season as they can take advantage of increased atmospheric CO_2 without being limited by scarce water resources in the same way as trees (Cernusak et al., 2013; Battipaglia et al., 2013). The relationship between elevated CO_2 and stimulated liana growth has been demonstrated experimentally in temperate liana species (Hättenschwiler and Korner, 2003; Belote et al., 2004; Mohan et al., 2006; Zotz et al., 2006). Tropical lianas have also been shown experimentally to respond positively to elevated CO_2, although existing studies are limited to juvenile lianas in laboratory conditions (Condon et al., 1992; Körner and Arnone, 1992; Granados and Körner, 2002). Furthermore, these studies do not compare the response of lianas with co-occurring tropical trees. A recent experiment by Marvin et al. (2015) found that both liana and tree seedlings experienced enhanced growth with CO_2 enrichment, with no significant difference in response between species over 7-months. As such, no empirical data supports increasing atmospheric CO_2 as a direct cause of increasing liana abundance as of yet (de Azevedo Amorim et al., 2018).

1.7 Remote Sensing

Remote sensing can be defined as acquiring information about a target from a distance and without direct contact. This is most commonly in reference to, but not limited to, the collection of Earth imagery from sensors mounted on airborne or spaceborne platforms. The sensors used for Earth observation (EO) can be passive, such as optical sensors which receive solar radiation across a spectrum of visible light and infrared; or they can be active, whereby a signal is emitted and received such as in Light Detecting and Ranging (LiDAR) and Synthetic Aperture Radar (SAR) technologies. Platforms can range in scale from multi-satellite constellations in space, airborne planes and helicopters, down through to small drones, Unmanned Aerial Vehicles (UAVs) and terrestrial mounted sensors (Lechner et al., 2020). This section describes the importance of resolution in the field of remote sensing, as well as highlighting existing applications of remote sensing in tropical ecology. The application of remote sensing in liana ecology specifically is reviewed and analysed in detail in Chapter 2.

Each platform and sensor combination has benefits and drawbacks regarding their various resolutions. There are four measures of resolution relevant to commonly used remotely sensed data (Wulder et al., 2009). First is spatial resolution, which pertains to the pixel size of a remotely sensed image, this being the size of the smallest discernible element picked up by a sensor (Yu et al., 2006). For example, 30 m spatial resolution may allow one to distinguish between an urban area and a forest, but not between a car and a tree. For ranging sensors, such as LiDAR, spatial resolution is commonly described by its point density, measured in hits per square metre (Jakubowski et al., 2013). Secondly, temporal resolution describes how often a sensor revisits an area. This can be annually or hourly depending on the platform. In the case of satellite-mounted sensors, greater temporal resolution often correlates with lower spatial resolution (e.g. Landsat; Wu et al., 2016; Yang et al., 2021). It should also be noted that images collected from optical sensors with low temporal resolution are more susceptible to being confounded by cloud cover (Asner, 2001). Thirdly, spectral resolution refers to the number and size of particular wavelength intervals along the electromagnetic spectrum, or ‘bands’, picked up by a sensor. A sensor may be panchromatic (one band), multispectral (several bands) or hyperspectral (many fine bands); with the latter being considered to have the greatest spectral resolution (Goetz et al., 1985; Vane et al., 1993). As different materials or surfaces reflect different electromagnetic wavelengths, sensors with greater spectral resolution are better able to distinguish between materials (van Leeuwen, 2009). Finally, radiometric resolution, commonly expressed in ‘bits’, pertains to the range and detail of information contained within each pixel (Lillesand and Kiefer, 2000). The nature of the object being remote sensed governs the necessary resolutions required to provide accurate detection.

In recent decades remote sensing methods have revolutionised tropical forest research, first providing data on changing forest extent (Iverson et al., 1989), later assessing metrics such as forest structure (Lim et al., 2003), canopy height (Hu et al., 2016) and diversity (Durán et al., 2019). In addition, active sensors have produced otherwise unobtainable 3D data, such as digital terrain and canopy models (Clark et al., 2004), as well as being able to detect minute differences in reflectance intensity between different tree species (Cao et al., 2016). The advancing capabilities and use of UAV technology in particular have transformed how researchers are able to assess and monitor canopy vegetation (Getzin et al., 2012; Paneque-Gálvez et al., 2014; Baena et al., 2017; Carr and Slyder, 2018; Baena et al., 2018; Buters et al., 2019). High spatial resolution UAV imagery (millimetres; Nakamura et al., 2017) of forest canopies has been used to estimate biomass (Kachamba et al., 2016), biodiversity (Zhang et al., 2016) and monitor forest recovery (Zahawi et al., 2015). Such capabilities present exciting new research methods for studying liana ecology (see Chapter 2).

Chapter 2: Making (remote) sense of lianas[1]

2.1 Abstract

Lianas (woody vines) are an abundant and diverse plant group, particularly in tropical ecosystems. Lianas use trees for structural support to reach the forest canopy, often deploying leaves atop of their host tree, thus they are likely a common feature of forest canopies. Yet, relatively little is known about the actual distribution of lianas in tropical forests. This knowledge gap is urgent to address because lianas compete strongly with trees, reduce forest carbon uptake and are thought to be increasing across the tropics. Lianas can be difficult to study using traditional field methods. Their pliable stems often twist and loop through the understorey making it difficult to assess their structure, location and biomass as well as the extent of their canopy. Furthermore, lianas remain relatively understudied compared to trees, because liana stems are commonly omitted from standard field surveys. Remote sensing can help overcome some of these obstacles and provide critical insights into liana ecology, but to date there has been no systematic assessment of that contribution. We review progress to date in studying liana ecology using ground-based, air-borne and space-borne remote sensing in four key areas: (i) spatial and temporal distributions, (ii) structure and biomass, (iii) responses to environmental conditions, and (iv) diversity, demonstrating their great potential for rapid advances in our knowledge and understanding of liana ecology. We then consider the data requirements to underpin improved use of remote sensing in liana ecology, the role of technological advances and the types of methods and experimental designs that should be prioritised to advance remote sensing of lianas in the future. The particular characteristics of lianas make them difficult to study by ground-based field methods. However, our review shows that remote sensing is an emerging tool that is ideally suited to study lianas, and will continue to improve with recent developments in sensor and platform technology. It is surprising, therefore, how little liana ecology research has utilised remote sensing to date – this should rapidly change if urgent knowledge gaps are to be addressed. In short, liana ecology needs remote sensing.

---

[1] Geertje M.F. van der Heijden*, Ashley D. C. Proctor*, Kim Calders, Christopher Chandler, Richard Field, Giles M. Foody, Sruthi M. Krishna Moorthy, Stefan Schnitzer, Catherine Waite & Doreen S. Boyd. (in review). Making (remote) sense of lianas. Journal of Ecology**.

**These authors contributed equally to the manuscript.*

***Manuscript is currently undergoing minor revisions following external review and editorial inputs. Acceptance into journal is pending reassessment of revised manuscript. Information is correct as of date of original submission.*

2.2 Introduction

Advances in remote sensing now allow the study of tropical forests at local, regional and global scales. Importantly, remote sensing enables the study of the difficult-to-access forest canopy layer, helping quantify above-ground biomass and diversity (e.g. Asner et al., 2017; Saatchi et al., 2011), as well as responses of tropical forests to environmental change and human disturbances (e.g. Reiche et al., 2015; Wigneron et al., 2020). However, the vast majority of remote sensing research in tropical forests has focussed exclusively on trees, or at least has attempted to (e.g. Gillespie et al., 2008; Saatchi et al., 2011; Wigneron et al., 2020). Tropical forests contain a wide array of plant growth forms, including (hemi-)epiphytes, shrubs, herbs and lianas (woody climbing plants; Richards et al., 1996). Despite still being understudied compared to trees, lianas commonly contribute 25% of the rooted woody stems and 35% of the woody plant species (Gentry, 1991; Schnitzer & Bongers, 2002; Schnitzer et al., 2012; van der Heijden et al., 2013). Lianas can also contribute up to 40% of the forest leaf area (van der Heijden et al., 2013), which means they are a particularly common feature of tropical canopies (Ingwell et al., 2010; Waite et al., 2019; Chandler et al., 2021b).

Liana field studies have become increasingly numerous in recent decades (Schnitzer et al., 2015), and have greatly furthered our knowledge of lianas and their impacts on tropical forests in general (briefly reviewed below). However, the use of remote sensing to study lianas and their impacts on ecosystem function and processes is still in its infancy. In this review, we argue that new advances in remote sensing are making it an essential tool and solution to amplify our knowledge of liana ecology and, therefore, tropical forest ecology as a whole.

2.2.1 Differences between lianas and trees

The most obvious and definitional difference between lianas and trees is whether they are self-supporting as adults. In contrast to trees, lianas are not self-supporting past their juvenile stage and instead use the architecture of adjacent trees to reach the forest canopy (Putz, 1984; Stevens, 1987). The lack of self-supporting architecture is complemented by differences in key life history traits of lianas compared to trees (Asner & Martin, 2015; Isnard & Feild, 2015; Maréchaux et al., 2017; Rowe & Speck, 2015; Santiago et al., 2015; Zhu & Cao, 2009). For example, lianas are characterised by fast-growing, elongated and pliable stems (Putz, 1984) with rapid community turnover rates (Phillips et al., 2005), wide vessels (Ewers et al., 1991) and extensive root systems (Chen et al., 2015; Smith-Martin et al., 2020). Few lianas reach diameters greater than 10 cm (Schnitzer et al., 2012), but stem lengths can be far longer and most lianas ≥2 cm diameter have already reached the forest canopy (Kurzel et al., 2006). Moreover, lianas often support a large leaf area relative to their diameter (Hegarty & Caballé, 1991; Medina-Vega et al., 2021; Putz, 1983). Despite typically constituting less than 5% of forest woody biomass (DeWalt & Chave, 2004; Schnitzer et al., 2012), lianas therefore contribute disproportionately (relative to stem diameter) to forest canopy productivity and leaf area, compared with trees (van der Heijden et al., 2015; van der Heijden et al., 2013).

Lianas possess a range of functional traits, some associated with a rapid resource acquisition strategy (Collins et al., 2016). For example, compared with trees, lianas possess higher specific root length and lower root tissue density and root diameter, suggesting they may more efficiently explore the soil for resources by constructing fine roots (Collins et al., 2016; Smith-Martin et al., 2019). Key leaf traits and leaf chemistry associated with lianas (Asner & Martin, 2012; Cai et al., 2009; Sánchez-Azofeifa et al., 2009; Zhu & Cao, 2010) suggests that they may have an increased photosynthetic capacity (Collins et al., 2016), but invest less in foliar structure and defence than trees (Asner & Martin, 2012; Visser et al., unpublished data). This may give lianas an advantage over trees in certain conditions. For example, lianas are thought to respond vigorously to disturbance (Ledo and Schnitzer, 2014) and to gather and utilize water more efficiently (Schnitzer, 2005; De Deurwaerder et al., 2018). Lianas may, therefore, thrive better in seasonally dry and disturbed environments than trees do (DeWalt et al., 2015; Schnitzer, 2005; 2018).

2.2.2 Importance of lianas in forests

The reliance of lianas on trees for structural support allows them to directly affect many forest ecological processes. For example, once they reach the top of the forest canopy, lianas deploy most of their leaves above those of their host trees (Avalos & Mulkey, 1999; Rodríguez-Ronderos et al., 2016) and aggressively compete with their host tree for light (Avalos et al., 1999; Avalos and Mulkey, 1999; Fauset et al., 2017). Lianas also compete below-ground with trees for nutrients and water as their root and vascular systems are posited to facilitate more efficient uptake of below-ground resources (Andrade et al., 2005), especially during dry periods (Álvarez-Cansino et al., 2015; De Deurwaerder et al., 2018; Meunier et al., 2020). As liana–tree competition is often stronger than tree–tree competition (Tobin et al., 2012), trees hosting lianas experience reduced growth (van der Heijden & Phillips, 2009a), increased mortality risk (Phillips et al., 2005; Ingwell et al., 2010) and reduced reproductive success (García León et al., 2018), thereby negatively affecting the forest carbon balance and cycle (van der Heijden et al., 2013; 2015). Furthermore, due to their high abundance in tree fall gaps, lianas can arrest and redirect gap-phase regeneration and forest succession (Estrada-Villegas et al., 2020; Schnitzer, Dalling, & Carson, 2000), maintaining disturbed areas in a low-canopy state for years (Pasquini et al., 2015; Schnitzer & Carson, 2000; Tymen et al., 2016).

However, tropical forests may also benefit from lianas. For example, lianas may protect trees from lightning strikes (Yanoviak, 2013) and wind damage (Putz, 1984). Lianas also provide alternative pathways into the tree crown, nesting spots and perches for tropical fauna, and food resources, especially during the dry season when many trees are leafless (Adams et al., 2017; Schnitzer et al., 2020; Yanoviak & Schnitzer, 2013). The presence of lianas, therefore, maintains faunal diversity and may contribute to complex trophic interactions in tropical forests (Schnitzer, 2018). However, although different tree species do not appear to be equally affected by lianas, the effect of lianas on tree species diversity and composition is less clear (van der Heijden and Phillips, 2008; Visser et al., 2017; 2018).

Lianas may, therefore, influence many ecosystem processes in tropical forests, such as biogeochemical and water cycling and litter decomposition (Collins et al., 2016; Hättenschwiler et al., 2005; Reichstein et al., 2014). Studying lianas is therefore important not only because it provides further insight into lianas themselves, but also because it fundamentally increases our understanding of the functioning and diversity of the entire tropical forest ecosystem (Schnitzer, 2018).

2.2.3 Remote sensing of lianas and trees

The recent realisation that lianas are important contributors to tropical forest dynamics, and should therefore not be ignored, brings forth the need to develop methods and experiments for measuring and monitoring them in tropical forests. However, tropical forests are dense, hard-to-access ecosystems, which can cause obstacles for field-based research (Balzotti et al., 2010). Traditionally, liana-focussed, and often plot-based, studies have utilised time- and labour-intensive, field-based data collection methods reliant on human surveying from the ground (van der Heijden et al., 2010). Although liana stems can be measured accurately from the ground, limited visibility means that assessing liana occupancy in the canopy is exceedingly difficult and error-prone (Waite et al., 2019). In short, although the demand for data on lianas is clear, the status quo on liana data capture does not meet this demand.

Remote sensing offers new solutions that can both complement and expand upon existing ground-based field methods, providing data on lianas that have been previously obscured or unobserved. Remote sensing provides an all-encompassing view of tropical forests at larger spatial and temporal scales than ground-based measurements (Foody, 2003; Lechner et al., 2020) and allows measurements of the life forms within them (Calders et al., 2020), whilst also enabling improved repeatability at lower operational cost per unit area (Carr & Slyder, 2018; Watts et al., 2012). Recent advances in both the spectral and spatial domain of air and space-borne, as well as ground-based remote sensing, may therefore offer critical insights into liana geography, their levels of forest canopy infestation, and their change in canopy infestation over time, which are not feasible with traditional ground-based measurements.

While our knowledge on liana ecology would benefit from remote sensing to meet pressing information needs, to date there has been no systematic assessment of exactly how remote sensing can contribute to these needs. This review seeks to outline how remote sensing can advance tropical forest ecology by elucidating the role of lianas in tropical forests. For simplicity, herein we make (remote) sense of lianas with respect to four main areas of liana ecology: (i) spatial and temporal liana distributions; (ii) liana structure and biomass; (iii) responses of lianas to environmental conditions; and (iv) liana species diversity. Measuring and monitoring these four areas can be largely achieved by air- and space-borne sensors. Remote sensing from below the canopy can also be performed from the forest floor, and may be linked to the top-of-the canopy view better understand the distribution of lianas throughout the entire forest strata (Figure 2.1).

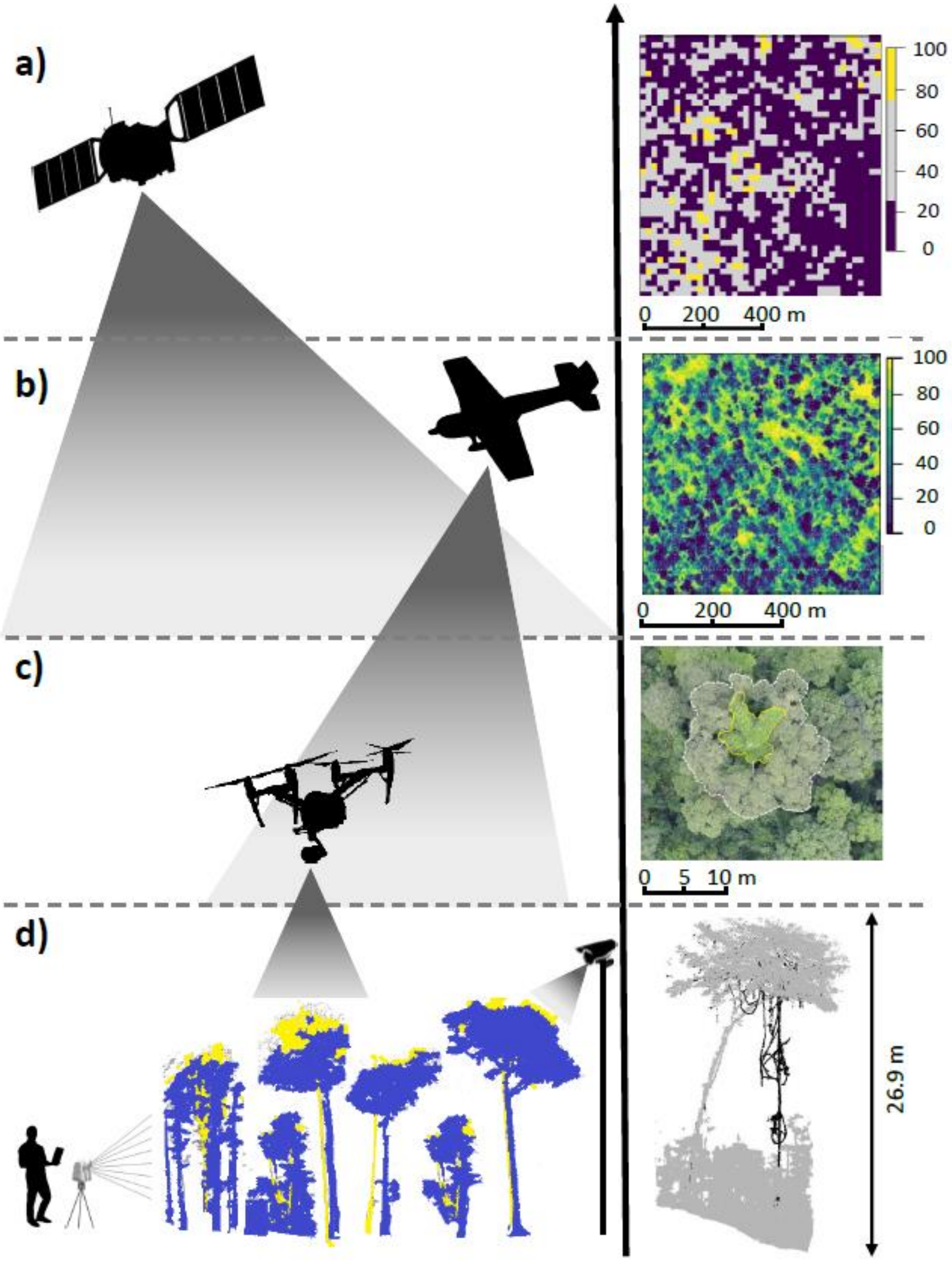

Figure 2.1 – To make remote sense of lianas, different combinations of sensors and platforms are (to be) used. For example: spatial and temporal liana distributions (section 2.3.1) can benefit from Sentinel-2 satellite data (Chandler et al., 2021a; see panel (a)) and airborne hyper-spectral and LiDAR data (e.g., Chandler et al., 2021b; see (b)). Insight into liana species diversity (section 2.4) may come from UAV data (e.g., Waite et al., 2019; see (c)). For liana structure and biomass measures (section 2.3.2), Terrestrial Laser Scanning (e.g., Krishna Moorthy et al., 2020; see (d)) is useful. For understanding responses of lianas to environmental conditions (section 2.4) a proximal sensor mounted on a pole or work using a field spectroradiometer may provide suitable data – see (d). The examples given here are not exhaustive; selection of suitable remote sensing approaches will be determined by underpinning data available (section 2.5.1), access to relevant technologies (section 2.5.2) and method and experimental design (section 2.5.3).

2.3 Key areas to expand liana research with remote sensing

2.3.1 Spatial and temporal distributions of lianas

To-date, locally field-based data collection through fieldwork across plots has been the predominant approach to assess spatial and temporal distributions in liana infestation, and their effects in tropical, subtropical and temperate forests. These field data have inferred levels of liana stem density and infestation across continents, regions or landscapes, indicating that liana distributions can vary considerably between forests, both within and among continents (DeWalt et al., 2015; DeWalt et al., 2010; Gentry, 1991; Schnitzer, 2005; van der Heijden & Phillips, 2008, 2009a). However, the drivers of within-forest and broad-scale variation in liana distribution is an active area of study (e.g., Parolari et al. 2020). Further studies of liana biogeography across a large geographical extent and covering a wide range of environmental variables are therefore urgently needed to elucidate the drivers of liana success across tropical forests on global, regional and landscape scales.

Field-based research has also shown that lianas have proliferated across the Neotropics (Phillips et al., 2002; Schnitzer and Bongers, 2011), with the longest-running study estimating that the abundance of lianas ≥10 cm diameter relative to trees increased by 1.7-4.6% a year from 1980 to 2000 (Phillips et al., 2002). However, studies outside the Neotropics indicate this may not be a universal trend across the tropics (Bongers et al., 2020; Schnitzer & Bongers, 2011). The drivers responsible for changes in liana abundance are still unknown, though several putative mechanisms have been proposed, such as elevated atmospheric CO_2 concentrations, increased disturbance and enhanced intensity and length of (seasonal) droughts (Schnitzer and Bongers, 2011; Parolari et al., 2020). Furthermore, we currently also do not know whether the rate of change in liana density across large geographical areas has changed in relation to pre-2000s levels (Phillips et al., 2002). Research is therefore urgently needed to test i) whether the increase in liana abundance in the Neotropics has accelerated, decelerated or remained similar to that pre-2000, ii) whether patterns of change are similar across the tropics and in which geographical areas changes are most pronounced, and iii) which local and/or global drivers are responsible for these temporal changes in liana abundance and infestation. This is important as changes in liana proliferation may have a knock-on effect on the carbon sink function of tropical forests, with potentially important ramifications for global change (van der Heijden et al., 2015).

Lianas reduce the ability of mature and secondary tropical forests to absorb and store carbon (Estrada-Villegas et al., 2020; Tymen et al., 2016; van der Heijden & Phillips, 2009a; van der Heijden et al., 2015; van der Heijden et al., 2019). However, liana-induced reductions on the carbon balance of tropical forests may differ across forests. For example, recent evidence suggests that liana–tree competition decreases with forest age (Estrada-Villegas et al., 2020) and may be dependent on the degree of liana infestation, as forests with a high presence of lianas generally store less carbon (Durán and Gianoli, 2013). However, the small number of studies focussing on liana ecology across space and time, as well as our lack of understanding on the spatial and temporal distributions of lianas, makes extrapolating the effects of lianas across broader geographical scales difficult. Increasing our knowledge about what drives spatial and temporal distributions in liana infestation across tropical forests will therefore not only assist in increasing our knowledge about liana biogeography itself, but also in making generalisations about liana-induced effects on the carbon dynamics of tropical forests.

Thus, the status quo is that our knowledge of liana distribution is via field-based liana studies that are limited spatially, have relatively long census intervals (e.g. Ingwell et al., 2010; Wright et al., 2015), focus predominantly on large lianas (≥ 10 cm diameter; Phillips et al., 2002) and/or are primarily from the Neotropics (Phillips et al., 2002; van der Heijden & Phillips, 2008). These limitations restrict our ability to understand spatial and temporal distributions in lianas as well as their effects on tropical forest functioning. Disturbance history (via LANDSAT; Pflugmacher et al., 2012) and drought (via metrics like Standardized Precipitation-Evaporation Index (SPEI); Marín et al., 2018) can be remotely sensed and, together with other environmental variables, correlated with spatial or temporal changes in liana abundance. However, to be able to do this, we need to be able to monitor lianas over much broader geographical scales, including across environmental gradients and forest types, and with a higher temporal frequency than is currently possible with field-based studies. Using remote sensing to routinely map liana infestation across space and time is, therefore, a key goal in liana ecology.

2.3.1.1 Current contribution of remote sensing

The feasibility of utilizing the contiguous and frequent coverage afforded by remote sensors, particularly those that are space-borne, is dependent on the ability of the deployed sensors to detect the liana infestation in the forest canopy. That is, the view from above must allow us to discriminate the lianas from the trees in the scene. Several studies have now indicated that lianas can indeed be differentiated from trees in the spectral domain, with most studies indicating that liana leaves have higher reflectance around 550 nm (green) and 2500nm (short-wave infrared; SWIR) and present more distinctive peaks and troughs than trees in the medium and longwave infrared region (MLWIR), whilst trees may have higher reflectance in the NIR (800-1200 nm) (Castro-Esau et al., 2004; Guzmán & Sanchez-Azofeifa, 2021; Guzmán et al., 2018; Hesketh & Sánchez-Azofeifa, 2012; Kalacska et al., 2007; Sánchez-Azofeifa et al., 2011; Sánchez-Azofeifa & Castro-Esau, 2006; Figure 2.2a and 2.2b). Most of these leaf-level differences remain discernible at the canopy scale, which allows differentiation between liana infested and liana-free trees (Marvin et al., 2016; Chandler et al., 2021b; Figure 2.2c).

Combining hyperspectral data and LiDAR data from an airborne sensor within a machine learning framework demonstrated accurate landscape-scale mapping of areas of high (≥50%) liana presence in the forest canopy both in seasonally dry (Marvin et al., 2016) and aseasonal (Chandler et al., 2021b) forests. However, more subtle differences in liana infestation may be more difficult to discern (Marvin et al. 2016; Chandler et al., 2021b). Spectral differences between lianas and trees appear to be more prominent in dry and seasonal forests and during the dry season (Castro-Esau et al., 2004; Hesketh & Sánchez-Azofeifa, 2012; Sánchez-Azofeifa et al., 2009), whereas the spectral properties of liana and tree leaves converge in wet and in aseasonal forests (Avalos et al., 1999; Chandler et al., 2021b). The ability to discern liana leaves in aseasonal forest canopies would permit the potential to estimate liana abundance in tropical forests worldwide (Chandler et al., 2021b) and should enable landscape-scale comparisons of liana infestation across different forest landscapes. Combining hyperspectral data may also assist in assessing the drivers of spatial distribution of liana infestation on the landscape scale by using variables such as disturbance, forest structural and topographical measures as predictor variables (cf. Marvin et al., 2016). With repeated sampling, the change in liana abundance across large swaths of tropical forests can be assessed to get a better idea of the rate of tropical liana change, along with insights into the potential drivers.

Exploiting the spatial domain for measuring liana presence and degree of liana infestation has been possible through the recent proliferation of unoccupied aerial vehicle (UAV) technology, one of the more affordable and accessible remote sensing platforms. Lianas have been successfully detected in forest canopies and gaps using ultra-fine resolution imagery, down to centimetre resolution, from UAVs fitted with both RGB (Waite et al., 2019), visible to NIR (Li et al., 2018) and thermal sensors (Yuan et al., 2019). Waite et al. (2019) expanded beyond detecting only the presence of lianas in tree canopies to also assess the degree of liana infestation in tree canopies. Although the spatial extent over which UAV technology can be used for monitoring liana presence is limited, its main advantage lies in its capacity for high-frequency deployment to monitor temporal changes in liana infestation.

Whereas both occupied and unoccupied airborne sensors have the potential to provide high resolution imagery to detect liana presence and abundance, they are realistically limited to landscape-scale studies (<10,000 km^2). For larger scales, such are regional, continental, or global, satellites remain the only remote sensing platform with the potential of facilitating both broad-scale and temporally frequent assessment of liana infestation. Only a few studies have used satellite data to identify liana infestation and assess temporal patterns in liana infestation (e.g. Foster et al., 2008 – EO-1 Hyperion and Landsat TM and ETM+, Tymen et al., 2016 – Landsat TM). However, these studies were either based on dry season images and/or limited to the detection of liana-dominated patches. It is therefore unclear whether these models can feasibly be transferred to predict liana infestation across broad geographical scales. Further development of suitable methods is needed to allow the identification of lianas in forest canopies and across different environments.

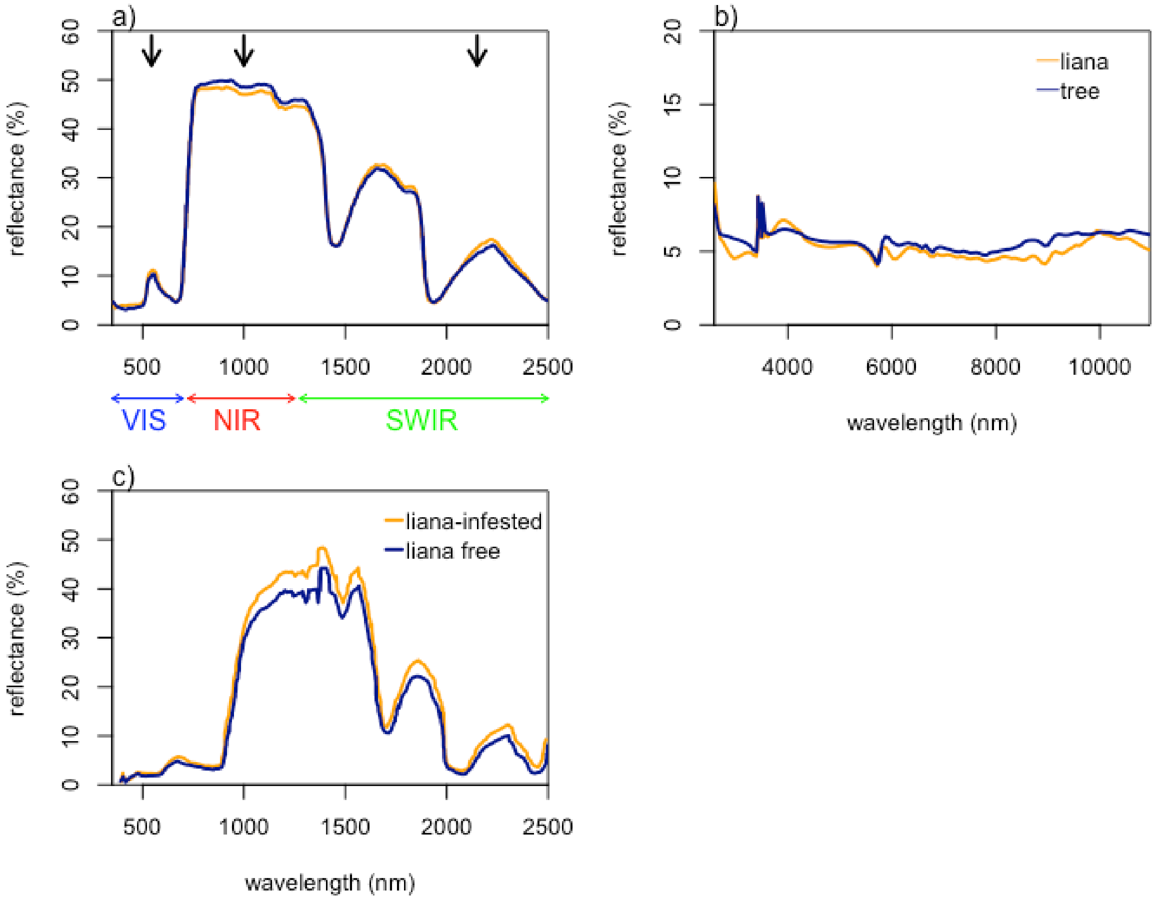

Figure 2.2 – Characteristic reflectance spectra: a) Visible (VIS) to near-infrared (NIR) to short-wave infrared (SWIR; from Kalacska et al., 2007) reflectance of liana and tree leaves; b) mid- to long-wave infrared (MLWIR; from Guzmán and Sánchez-Azofeifa, 2021) of liana and tree leaves; c) VIS-NIT-SWIR reflectance for liana-infested (≥75% crown covered by lianas) and liana-free tree crowns (from Chandler et al., 2021b). Black arrows in a) indicate the areas where literature indicates there is greatest spectral separability between liana and tree leaves.

2.3.2 Liana structure and biomass

The ability to accurately quantify liana biomass is imperative to better understand the role that lianas play in the carbon balance and cycle of tropical forests. The negative effects of lianas on tree above-ground biomass and biomass growth in tropical forests are well established. However, evidence that lianas themselves are unable to offset the displacement of tree carbon that they cause (van der Heijden et al., 2013) is generally based on both assumptions of liana biomass allocation patterns and liana allometric models to calculate liana biomass and biomass change.

Our ability to accurately quantify the contribution of lianas to above-ground biomass and biomass change in forests is constrained by the limited number of studies investigating liana allometry (Addo-Fordjour & Rahmad, 2013a, 2013b; Gehring et al., 2004; Schnitzer et al., 2006). These studies have produced different liana allometric models, with liana biomass calculation diverging considerably, depending on the allometric model used (Miao et al., 2016). As these studies are based on destructive harvesting of liana individuals, sample sizes are usually small; with the largest pantropical study including only 424 lianas, they only sparsely replicate across species and include very limited numbers of large lianas (Schnitzer et al., 2006). The large variation in liana allometric models between studies may also indicate that liana allometry and biomass allocation patterns may be caused by differences in species identity, climate, edaphic conditions or forest type (Schnitzer et al., 2006; Smith-Martin et al., 2020).

Furthermore, due to the complex growth form of lianas (Figure 2.3), some measurements (e.g. liana diameter) are much easier to obtain in the field than others (e.g. liana length) and allometric models are usually based on liana stem diameter only. However, liana stems are generally thinner but much longer than those of trees (Selaya and Anten, 2008), with lianas often assumed to allocate more biomass to leaves than to stems compared to trees (Castellanos et al., 1989; Putz, 1983; van der Heijden et al., 2015; 2019; Wyka et al., 2013). Yet recent research has indicated that lianas may invest proportionally as much biomass in stems as trees do, potentially by making up what they miss in stem diameter by extended stem length (Smith-Martin et al., 2020; Figure 2.3). The relationship between liana diameter and liana length and biomass may therefore not be as strong as that for trees (Krishna Moorthy et al., 2020; Schnitzer et al., 2006) and multiple studies have shown that, unlike trees, lianas are structurally and mechanically only weakly constrained to diameter (Condon et al., 1992; Putz & Mooney, 1991; Putz, 1990). Consequently, liana above-ground biomass estimates based on diameter measurements alone may be subject to considerable error, limiting our understanding of the contribution of lianas to functioning, productivity and structure in forests across the world. To accurately quantify the contributions of lianas to forest biomass and to fully understand the role of lianas in forest processes, we urgently need more information on liana structure and biomass allocation patterns from a range of forests worldwide.

Figure 2.3 – TLS imagery of four lianas from Nourages, French Guiana, having similar diameters (6 or 10 cm), but exhibiting different structures, length and biomass, which illustrates the complex and variable growth form of lianas compared to trees (adapted from Krishna Moorthy et al., 2020).

2.3.2.1 Current contribution of remote sensing

Terrestrial Laser Scanning (TLS) is an active remote sensing technique, which can be used to measure structural parameters such as height, diameter, above-ground biomass and Leaf Area Index (LAI) from LiDAR-derived 3D point clouds (Atkins et al., 2018; Béland et al., 2014; Calders et al., 2015; Strahler et al., 2008). It has advanced swiftly in the last decade (Calders et al., 2020; Dassot et al., 2011; Owen et al., 2021; Richardson et al., 2014). Although the use of this technology to study lianas has lagged behind that of trees (Krishna Moorthy et al., 2019), TLS now enables distinguishing liana stems from trees in point cloud data with great precision and accuracy (Bao et al., 2018; Krishna Moorthy et al., 2019). Thus, TLS is progressing the study of liana allometry and quantification of liana biomass (Krishna Moorthy et al., 2020). Liana extraction from co-registered point clouds is still challenging (Krishna Moorthy et al., 2019), but work in French Guiana has indicated that by obtaining detailed information on liana structure below the canopy, TLS methods may provide more accurate liana biomass estimations than traditional field-based methods (Krishna Moorthy et al., 2020). This methodology, in combination with a machine learning-based algorithm to semi-automatically extract liana woody points from plot-level TLS data, could facilitate long-term and reliable monitoring of liana biomass to enhance understanding of the dynamics of plot-based liana infestation, structure and biomass (Krishna Moorthy et al., 2019; 2020). Additionally, as this methodology has the potential to assess the complete above-ground liana structure, it could be an invaluable tool to comprehensively investigate allometric scaling relationships in lianas (cf. Krishna Moorthy et al. 2020), e.g. including both diameter and length (or length only) in allometric relationships to calculate biomass, and liana biomass allocation patterns, of which much is currently still unknown.

2.4 Liana responses to environmental conditions

Although our understanding of how lianas respond to their environment has increased over the last few decades, there are two main areas where our understanding is still lacking, despite being vitally important to predict and understand how changing environmental conditions may affect lianas in the future. The first concerns the response of lianas to elevated atmospheric CO_2 conditions, which has been one of the explanations for the observed liana proliferation (e.g. Schnitzer & Bongers, 2011). Although CO_2 enrichment experiments have shown a strong response of lianas to elevated CO_2 (Granados and Körner, 2002; Zotz et al., 2006; Marvin et al., 2015), these studies were mainly performed on seedlings or understorey plants and, therefore, are unlikely to represent the response of adult lianas to elevated CO_2 concentrations. Additionally, not all studies have shown a stronger effect for lianas than trees (e.g. Marvin et al., 2015). How lianas respond to elevated CO_2 concentrations, and whether their response is different from trees, requires further testing.

Second, climate change is expected to increase the amount of water stress in many parts of the tropics and there are numerous studies which have shown that lianas grow well during periods of prolonged water stress (Schnitzer & van der Heijden, 2019; van der Heijden et al., 2019). During drought conditions, lianas can photosynthesize more and maintain a healthier water status than co-occurring trees (Cai et al., 2009; Zhu and Cao, 2010; Chen et al., 2015; Maréchaux et al., 2017). However, a key unknown is how and where lianas find sufficient water to maintain their water status during the dry season (Schnitzer, 2018). Some studies have suggested that lianas tap into deeper water sources (e.g. Chen et al., 2015; Holbrook & Putz, 1996) whilst others imply that, by exploring larger areas of the top soil, lianas efficiently capture any precipitation in the dry season (De Deurwaerder et al., 2018; Smith-Martin et al., 2020). Additionally, lianas may deal with drought by reaching maximum photosynthesis early in the day after which they can close their stomata to prevent water loss during the hottest parts of the day (Schnitzer, 2018). However, the exact strategies employed by lianas to thrive during periods of drought stress remain unknown.

2.4.1.1 Current contribution of remote sensing

Responses to water stress and CO_2 are visible in the leaf spectral reflectance (Chemura et al., 2017; Chou et al., 2017; Gray et al., 2010; Ihuoma & Madramootoo, 2019; Nunes et al., 2019; Figure 2.2a) and hyperspectral remote sensing is showing promise to estimate photosynthesis in periods of stress (Barnes et al., 2017). The use of proximal sensors above the forest canopy, which record frequent spectral information, could provide information on the timing of water uptake and photosynthesis. Furthermore, using high resolution hyperspectral (visible through thermal wavelengths) data to monitor, for example, evapotranspiration of lianas and trees using drought and Free Air CO_2 Enrichment experiments in which lianas are present, or even natural phenomena such as El Niño events (e.g. van der Heijden et al. 2019), could also allow investigation of whether lianas and trees differ in their response to environmental change. Combining data on liana growth, survival, reproduction and recruitment with remote sensing could therefore prove essential in elucidating how lianas and trees respond to drought and elevated CO_2, and whether a potential difference in response may give lianas an advantage over trees in dealing with changing environmental conditions.

2.4.2 Liana species diversity

A key challenge in ecology is to increase our understanding of the mechanisms behind the broad-scale species distributions and composition (Schnitzer, 2018). Although lianas are known to contribute up to 35% to overall tropical forest diversity (Gentry, 1991; Schnitzer & Bongers, 2002; van der Heijden & Phillips, 2009b), rather little is known about what controls liana species diversity and composition across space and time. Most knowledge about liana diversity and species composition comes from small plot-based studies (many 0.1 ha), several larger plots of up to 50 ha (DeWalt et al., 2010; Gentry, 1991; Schnitzer et al., 2012) and field occurrence collections (Meyer et al., 2020). However, the limited spatial coverage of these studies has restricted our ability to predict liana diversity across larger geographical scales. Furthermore, studies focussing on temporal patterns of liana diversity and composition are still scarce (Caballé and Martin, 2001; Swaine and Grace, 2007). With global warming driving pronounced changes in both climatic conditions and disturbance across the tropics (Garcia et al., 2014), investigating the responses of liana species to these changes is crucial to predict future liana species distributions. Furthermore, it is currently unknown whether the liana proliferation observed in Neotropical forests is consistent across taxa or is driven by the proliferation of certain taxa only. If liana species diverge in their response to changing environmental conditions, phylogenetic differences in liana communities may provide an explanation for the different rates of liana proliferation across the world (Schnitzer and Bongers, 2011).

Plot-based studies are limited in the extent to which they can answer these questions. Field identification of lianas is often difficult and time-consuming, as fruits and flowers of lianas, which are often needed for identification, are often located high up in the forest canopy. Furthermore, due to the high diversity of lianas in tropical forests and the relatively small plot sizes, most species are locally rare (e.g. Mascaro et al., 2004). Top-of-canopy remote sensing technologies that would enable liana diversity mapping across the landscape and over time would substantially increase our understanding of the contribution of lianas to plant diversity in the tropics. Including lianas in biodiversity mapping will aid conservation efforts as, despite their importance to forest composition and diversity, lianas are still often overlooked in management, conservation and restoration actions.

2.4.2.1 Current contribution of remote sensing

Remote sensing technologies in combination with machine learning technologies have enabled the mapping of tree species richness and composition as well as distributions of individual tree species in tropical forest canopies, mainly based on differences in spectral patterns (e.g. Féret & Asner, 2012; Ferreira et al., 2019; Foody & Cutler, 2006). There is some evidence that liana species can be differentiated from each other as well as from tree species, based on their spectral reflectance (Hesketh and Sánchez-Azofeifa, 2012). However there have, so far, been no attempts to use remote sensing to either map liana diversity or identify liana species, probably due to the difficulty in reliably distinguishing tree from liana leaves in the forest canopy and that of differentiating between liana species, as multiple liana species can be present in the crown of a single tree.

2.5 Current limitations for remote sensing lianas

Lianas have been cited as an impediment in remote sensing of tropical forests, with a realisation that their presence alters the remotely sensed signal of trees (Laybros et al., 2019; Sánchez-Azofeifa et al., 2011). Thus, the ability to distinguish lianas and their traits from trees via remote sensing would be a major step forward, not only for our knowledge of liana ecology but also for the general field of tropical ecology. Despite the promise revealed by studies thus far, there is little strategy apparent in the fields of remote sensing and/or liana ecology to take this step forward optimally. We suggest that going forward activity in the following endeavours are required: (a) underpinning data, (b) technological innovation and (c) methods and experimental design. We use these to illustrate how the blend of each activity could support making (remote) sense of lianas and discuss each below.

2.5.1 Underpinning data

The need for appropriate, high-quality and standardised data for future use and interpretation of remote sensing analyses is no different in liana ecology than in the wider field of tropical ecology.

There are three principal sets of underpinning data required for advancing remote sensing of lianas. These data include: (i) liana trait measurements; (ii) spectral reflectance data for a wide range of liana species; and (iii) field-based measurements of liana biomass, abundance and infestation spatially distributed across sites. These data are required to produce models of the interactions between the liana property of interest and the remote sensing data being used. Once models are established, extrapolation across the rest of the remotely sensed datasets are possible.

A rapid expansion of such measurements would afford an improved comparability and confidence in future remote sensing of lianas, as well as development of methods to extract required liana metrics from remotely sensed data. Both should inform any technological development specific to the field of liana ecology. The challenge is how to achieve this data collection efficiently and, for optimal impact, within a framework that enables data sharing for mutual collaboration between all involved. There are existing plot networks and initiatives that could be used for this purpose. Examples include ForestGEO (Davies et al., 2021); the Global Ecosystems Monitoring (GEM) network (Malhi et al., 2021) and the Forest Observation System (Schepaschenko et al., 2019). The latter currently hosts aggregate data from plots contributed by several existing networks (e.g., the RAINFOR, CTFS-ForestGEO, AfriTRON, T-FORCES, IIASA network, TmFO and AusCover).

Building on existing plot networks would be advantageous because the infrastructure for field-based measurements are already established (e.g., stems ≥10 cm – e.g. Phillips et al., 2002; crown occupancy index – e.g. van der Heijden et al., 2010). Standardized protocols (Gerwing et al., 2006) that will directly aid in understanding remotely sensed liana measurements will be advantageous. Although these plots are often used to support remote sensing studies (e.g. Marselis et al., 2020), even relatively large plots (e.g., 50 ha) may be too small for airborne and satellite-based remote sensing. Additional investigation to determine a minimum usable plot size and/or shape for liana and tree censuses would, therefore, be beneficial.

Alongside developing optimal plot data, efforts to build an accessible database of spectra of all liana species would be advantageous, particularly for species diversity measurements (section 2.4.2). Our current knowledge on spectral properties of liana comes mainly from deploying field-based instrumentation within forests (e.g. as per Nunes et al., 2019 on trees), destructively sampling to enable laboratory-based measurement (Asner and Martin, 2012) and extracting spectra from airborne hyperspectral instrumentation (Marvin et al., 2016; Chandler et al., 2021b). The latter may not produce end-member spectra of optimal use. Thus, currently spectral knowledge across liana species is lacking. Existing spectral libraries, such as the ECOSTRESS spectral library (https://speclib.jpl.nasa.gov/; Meerdink et al., 2019), the EcoSIS database (https://ecosis.org/; Wagner et al., 2019) and the USGS spectral library (Kokaly et al., 2017), do not contain any liana species. Even for tropical tree species there are very few spectra. Further, many leaf and canopy traits vary systematically in relation to life history and leaf phenology among plant groups, but this variation may be small in comparison to the large variability across interspecific, intraspecific, phenotypic, and ontogenetic levels of natural vegetation (Detto & Xu, 2020; Werden et al., 2018; Wu et al., 2018). Thus, enhancing the knowledge base of spectral responses of both lianas and trees would be extremely beneficial for the ultimate goal of remotely sensing lianas. Baseline data of other remotely sensed measurements would also be useful; for example there are very few TLS data on trees infested with lianas. This prevents innovation in technology, but also in methods, to easily sense and extract liana measures from the laser scans.

2.5.2 Technological Innovation

Applying existing terrestrial, airborne and spaceborne sensing (using both spectral and ranging instrumentation) to lianas would bring considerable benefits for liana ecology. However, current studies are limited in number (see Table 2.1). This could be due to lack of opportunity (relating to section 2.5.1), but also likely because the current remote sensing technologies available are not ideal for the study of liana ecology. To measure liana infestation over time and space, cutting-edge space-borne systems with improved spatial resolution coupled with enhanced spectral resolution are essential. The coarse-scale resolution of current satellite datasets can be problematic as one single pixel may be occupied by multiple tree crowns. The liana spectral signal on these pixels will therefore not be easily observed as liana infestation can be patchy both within and amongst tree crowns and a single tree crown can be infested by multiple liana species. Furthermore, the heterogeneity in reflectance from forests growing in different environmental regimes may inhibit the detection of liana infestation over larger geographical scales, especially if any differences in reflectance between liana-infested and non-infested pixels are smaller than differences between forest types. Lastly, cloud-free satellite data from tropical forests can be difficult to obtain (Foster et al., 2008; Tymen et al., 2016), which may limit the ability to assess changes in liana infestation, depending on the temporal resolution of the system.

Despite this seemingly endless list of challenges, an exploratory study by Chandler et al. (2021a) demonstrated that liana infestation was positively related to Sentinel-2 MSI greenness (at 10 m spatial resolution) across primary and selectively logged aseasonal forest of Sabah, Borneo. Given the temporal frequency afforded by the constellation of Sentinel-2 satellites (and similarly other constellation systems with higher spatial resolutions, e.g., PlanetScope, Pléiades Neo) this bodes well for monitoring of infestation across regions and continents (improving, in particular, the chances of cloud-free data at desired repeat rates [e.g. prior to, within and after an ENSO event]). Other beneficial satellite sensor developments include hyperspectral missions (e.g., DESIS and PRISMA), along with others on the horizon for the routine capture of hyperspectral data (e.g. https://news.satnews.com/2021/03/18/pixxel-to-build-worlds-highest-resolution-hyperspectral-satellite-array/) and of thermal emission from canopies at a much higher spatial resolution (e.g. from Landsat OLI, Terra ASTER). These tend to be commercial satellites (e.g. Satellite Vu - https://www.satellitevu.com/), so they would need substantial investment to be used at the continental scales for which they would bring most benefit to liana ecology (https://news.mongabay.com/2020/09/new-partnership-brings-high-resolution-satellite-imagery-of-the-tropics-to-all/). Nonetheless, these could be used locally to showcase the utility of spectral data across the spectrum, at high spatial resolution, for: i) measurement of liana infestation, (ii) monitoring of areas of known infestation to better understand their dynamics and function, and iii) to serve as a data input to scaling from plots to other satellites. Occupied and unoccupied platforms carrying a suite of sensors would also be useful here. NASA Goddard's G-LiHT – an airborne system with LiDAR, Hyperspectral, and Thermal Imaging (Cook et al., 2013) – is one such example. It was designed to simultaneously retrieve biochemical and structural data from forests.

As our knowledge of liana diversity and liana structural and functional properties increases through increased observational, experimental, and modelling efforts, we can improve and tailor the design of liana-specific remote sensing platforms and sensors. Within certain geographies it may be the case that specific liana/tree assemblages may be discerned at specific wavelength combinations and so inform custom-built systems (either for proximal or airborne/spaceborne sensing). As Balzarolo et al. (2011) note, this approach is common at European flux sites, where the goal is to fuse eddy covariance and tower-based optical measurements. The latter are made by systems (multi- or hyperspectral) which incorporate discrete distinct wavebands, each sensitive to a specific vegetation parameter. Existing systems such as the Cropscan or Cimel radiometers could be adapted, or novel sensors produced (e.g. use of light emitting diodes for monitoring vegetation reflectance in narrow spectral bands – Ryu et al., 2010). As the manufacture of remote sensing systems become ever more democratised through expansion in capability and access to UAVs, cubesats, etc. (Baena et al., 2018; Santilli et al., 2018), the adaption of existing technologies for liana ecology specifically should be possible in the future.

As stated in section 2.5.1, the principal underlying necessity for remote sensing of lianas is having sufficient plot-based knowledge across the tropics underpinning this approach. Such expansion in plot-based measurements should also afford an understanding that the contributions of the upcoming and more novel spaceborne systems such as FLEX (Moreno et al., 2006; Drusch et al., 2017), EnMAP (Guanter et al., 2015), Zhuhai-1 (Jiang et al., 2019) and GEDI (Dubayah et al., 2020) can make to liana ecology. Maybe there is a calling for a liana ecology specific satellite sensor?

2.5.3 Methods and Experimental Design

In the long term, progress in remote sensing technology and underpinning ground data capture for remote sensing liana ecology would require innovation in methods to extract the required information from the data, understand its quality and ascertain experimental designs for determining the optimal remote sensing approaches for liana ecology. Developments in pattern recognition, data fusion and super-resolution analyses (e.g., Kaya et al., 2019; Ling et al., 2020) are required; the recent advances in spatial data science using machine learning and deep learning algorithms (Ma et al., 2019) offer new opportunities to improve existing methods and develop new ones specifically for liana ecology. However, we should not underestimate the challenges involved. For example, data-hungry methods require data that we still do not have (see section 2.5.1). Nonetheless, as the number of studies using remote sensing for liana ecology increases, they may provide answers to questions on transferability of models developed at particular climatic/floristic compositions to others (e.g. Foody, 2003). Answers to how recently proposed approaches in remote sensing for tropical forests, such as the spectral species concept (Féret and Asner, 2014) should also become apparent. Increasing spectral data will also allow theoretical radiative transfer modelling to increase understanding of what might be possible using remote sensing (Visser et al., unpublished data).

In the short term, several opportunities could be pursued. One relates to sharing of existing remote sensing measurements. Similar to plot-based initiatives, there are many examples of combining remote sensing datasets for a common aim – for example, for calibration and validation of new satellite sensors using occupied airborne data, or developing UAV data collection protocols (e.g., Cunliffe et al., in press). This community-based approach could be extended beyond the scientific community to the citizen scientist. As a case in point, Waite et al. (2019) and Norashikin et al. (2021) relied on visual interpretation of liana infestation in the UAV imagery collected. This sort of work could be done using now readily available citizen science platforms (e.g. CitizenGrid, Zooniverse), which vary in ask with respect to task type, level of user required, and user freedom (Liu et al., 2021). Understanding exactly what our understanding of liana ecology requires from the remotely sensed data would be important here, to frame the task. For instance, as the presence of lianas in the tree crown directly affects tree growth, it may be important to distinguish tree crown occupancy levels below 50% (e.g. Ingwell et al., 2010). Another short-term opportunity would be to build up remote sensing capability in the already running experimental plots that feature lianas (serendipitously or otherwise), for example, Free Air CO_2 Enrichment, drought and rainfall exclusion and liana removal experiments. Establishing a sensor(s) network on a range of platforms, along with the detailed ground measurements already being undertaken, would be extremely beneficial in understanding optimal scaling methods, any links between remotely sensed responses observed below the canopy and above the canopy, and to determine protocols for remotely sensed measurements of lianas (in the same way as for other metrics and traits of forests, e.g., Duncanson et al., 2021).

2.6 So, can we make remote sense of lianas?

The short answer is not yet, though the long answer is more nuanced. We argue that current and future remote sensing will play a key role in liana ecology and will contribute to filling many of the gaps in liana ecological knowledge by enabling the study of lianas on unprecedented spatial and temporal scales and in unprecedented detail. However, we have also indicated where further technological innovations, methods and experimental design or underpinning field-based data are currently still limiting the use of remote sensing in liana ecology. Future efforts to circumvent current constraints need liana ecologists and remote sensing experts to collaborate to make both (remote) sense of both lianas and tropical forests as a whole.

Though this review focussed on four key areas of liana ecology, as our understanding of the ecological systems within which lianas thrive increases, this will also open up novel possibilities for use of remote sensing to measure them and further potential to increase our knowledge of liana ecology. For example, presently the role for RADAR systems is not immediately obvious. However, it could be the case that understanding the effects of lianas on below-ground processes, of which little is currently known, could demand the use of ground-penetrating radar (e.g. Zou et al., 2020). Furthermore, being able to accurately map liana abundance over time, in combination with future missions to estimate biomass in tropical forests (e.g. BIOMASS - Quegan et al., 2019), would be particularly useful to understand the effects of lianas on forest structure and biomass. In turn, such studies could inform liana ecology directly. Further, advances to identify tree and liana species using remote sensing will enable monitoring of liana-driven changes in forest species composition. Understanding of all these liana impacts is essential for better predicting the fate of tropical forests and their carbon balance in a changing climate.

It is fair to say that, to date, remote sensing of tropical forests has mainly ignored lianas, which is problematic because lianas affect forest dynamics and respond differently to changes in some environmental conditions than trees do (e.g. Schnitzer et al., 2000; van der Heijden et al., 2019), and the presence of lianas may alter the signal of the forest being remotely sensed (e.g. Chandler et al., 2021b; Figure 2.2). In turn, lianas may distort efforts to remotely sense tropical forests, leading to measurement error in the biophysical parameters of trees. Satellite-observed changes in spectral reflectance in response to climatic changes (e.g. Saleska et al., 2007) may therefore be complicated (cf. Anderson et al., 2010) by the differential responses of lianas and trees. Given that lianas are here to stay, we hope this review prompts much needed activity within a new sub-field of remote sensing, or is it ecology...

Table 2.1 – Overview of sensors and platforms used in studies using remote sensing for liana ecology to-date. Each study is referred to in the main text.

Sensor	Platform	Citation
UniSpec Spectral Analysis System (306–1138 nm @ <10nm sampling)	Laboratory Analysis	Castro-Esau et al. (2004)
UniSpec Spectral Analysis System (306–1138 nm @ <10nm sampling)	Laboratory Analysis	Guzmán and Sánchez-Azofeifa (2021)
1. UniSpec Spectral Analysis System (306–1138 nm @ <10nm sampling); 2. Agilent 4100 ExoScan Fourier Transform Infra-Red (FTIR) spectrometer (8000–11000 nm across 301 wavebands)	Laboratory Analysis	Guzmán et al. (2018)
ASD FieldspecFR Spectrometer (350 – 2500 nm @ 1.4 nm sampling between 350-1050 nm & 2 nm between 1000-2500 nm)	Field Sampling by hand	Hesketh and Sánchez-Azofeifa (2012)
ASD FieldspecFR Spectrometer (350 – 2500 nm @ 1.4 nm sampling between 350-1050 nm & 2 nm between 1000-2500 nm)	Field Sampling by hand	Kalacska et al. (2007)
Portable Spectrometer (400 –1100 nm @ 10nm sampling).	Field Sampling by hand	Sánchez-Azofeifa et al. (2009)
RIEGLVZ400 terrestrial laser scanner (multiple return time-of-flight; narrow infrared laser beam @ 1550 nm)	Field sampling using tripod	Bao et al. (2018)
RIEGLVZ400 terrestrial laser scanner (multiple return time-of-flight; narrow infrared laser beam @ 1550 nm)	Field sampling using tripod	Krishna Moorthy et al. (2019)
RIEGLVZ400 terrestrial laser scanner (multiple return time-of-flight; narrow infrared laser beam @ 1550 nm)	Field sampling using tripod	Krishna Moorthy et al. (2020)
UniSpec Spectral Analysis System (306–1138 nm @ <10nm sampling)	Construction Crane	Sánchez-Azofeifa and Castro-Esau (2006)
Integrated three-waveband (RGB) high-quality Sony EXMOR 1/2.3″ 12- megapixel camera, with a narrow 94° field of view lens (35 mm format equivalent: 20 mm)	DJI Phantom 3 Advanced Quadcopter UAV	Waite et al. (2019)
Micasense RedEdge 3 camera with 5 wavebands (@ 475 nm; 560 nm; red 668 nm; 717 nm and 840 nm).	RotorKonzept® RK-8x multicopter UAV	Li et al. (2018)
1. Micasense RedEdge 3 camera with 5 wavebands (@ 475 nm; 560 nm; red 668 nm; 717 nm and 840 nm). 2. FLIR TAU® 2 FLIR 640 broadband camera (@ 7500 to 13500 nm).	RotorKonzept® RK-8x multicopter UAV	Yuan et al. (2019)

1. Leica ALS50-II - 8W class 4 laser with radiation at 1064 nm recording up to four discrete returns for each emitted pulse. 22cm pulse footprint and point density ranging between 2.80 and 3.16 per m^2. 2. Specim FENIX hyperspectral sensor (380–2500 nm), with 448 contiguous channels, sampled at (2.9 nm) in the visible-to-near infrared (VNIR) ranged from 380 to 970 nm with a spectral resolution of 3.5 nm; in the shortwave infrared (SWIR) spectra were sampled (5.7 nm) from 970 to 2500 nm with a spectral resolution of 12 nm.	UK's Natural Environmental Research Council's Airborne Research Facility (NERC-ARF) Dornier 228–201 airplane, flying at 65.6–71.6 ms^{-1} at an altitude of 2335–2429m.	Chandler et al. (2021b)
1. Full-spectral range (visible-to-shortwave infrared) imaging spectrometer spectral radiance in 481 contiguous channels spanning the 252–2648 nm wavelength range. 2. Visible-to-near infrared (VNIR) imaging spectrometer, The VNIR imaging spectrometer collects 288 contiguous spectral bands over a smaller range (365–1052 nm) 3. Fullwaveform light detection and ranging (LiDAR) - a dual laser, scanning waveform system capable of operating at 500,000 laser shots per second. the LiDAR point density was 2 shots m^{-2}.	Carnegie Airborne Observatory (CAO) Airborne Taxonomic Mapping System (AToMS)	Marvin et al. (2016)
1. Hyperion hyperspectral sensor (400-2500 nm) across 220 wavebands at a spatial resolution of 30m. 2. ETM+ multispectral sensor with 8 wavebands across 400-2400 nm and 1070-1270 nm and spatial resolutions of 15m (panchromatic); 30m (visible/NIR/SWIR) and 60m (thermal).	1. EO-1 satellite 2. Landsat-7 satellite	Foster et al. (2008)
TM multispectral sensor with seven spectral bands across 450-2350nm and 1040-1250nm and spatial resolutions of 30m in the reflective bands and 120m in the thermal band.	Landsat-5 satellite	Tymen et al. (2016)
Multispectral Instrument (MSI) hyperspectral sensor with 13 wavebands	Sentinel-2 satellite	Chandler et al. (2021a)

across 443-2190 nm) and spatial resolutions of 10m, 20m and 60m.	

Chapter 3: Liana-driven differences in the contribution of tree functional groups to the carbon balance of a tropical forest in Gigante, Panama

3.1 Abstract

Tropical forests are globally important terrestrial carbon stores. It has been well documented that lianas (climbing woody vines) suppress forest carbon accumulation by reducing growth, suppressing recruitment, and increasing mortality in tropical trees. What is lesser known is to what degree the liana effect on carbon accumulation differs between tree functional groups. I consider an eight-year dataset from an ongoing liana experiment in Gigante, Panama. Tree biomass growth and recruitment were significantly higher in liana-removed plots over the census period. Net biomass change was also greater in removal plots, predominantly due to elevated mortality in liana-infested plots. However, high variation in mortality data meant these differences were not statistically significant. Growth in infested plots also differed with the severity of crown infestation. Pioneer species experienced a marked growth release immediately after liana removal, although eventually shade-tolerant species dominated growth contributions to overall carbon accumulation in removal plots. A growing divide in carbon accumulation between liana-removed and -infested plots in shade-tolerant trees validates reports of a liana-induced decline in these carbon-dense species. Future research efforts should focus on how different tree functional groups respond to varying levels of liana infestation, to better quantify how this will affect the viability of tropical forests to sequester and store carbon.

3.2 Introduction

Lianas are distinguishing and key elements of tropical forests, contributing substantially to the proportion of woody stems (25%) and woody species (35%; Schnitzer et al., 2012; A. Wright et al., 2015). Lianas also have a significant impact on the carbon balance of tropical forests, despite often constituting less than 10% of above-ground woody biomass themselves (DeWalt and Chave, 2004). Intense competition with trees for light (Tobin et al., 2012), as well as below-ground resources such as water and soil nutrients (Toledo-Aceves, 2015), means that the influence of lianas on forest-level carbon accumulation extends beyond simply their own woody biomass contributions. In recent decades it has been well documented that lianas have a detrimental effect on the growth (van der Heijden and Phillips, 2009a), recruitment (Schnitzer and Carson, 2010; García León et al., 2018), and mortality (Ingwell et al., 2010) of tropical forest trees. This ultimately suppresses their ability to sequester and store carbon (Durán and Gianoli, 2013; van der Heijden et al., 2015), a globally important ecosystem service provided by tropical forests which is vital for moderating climate worldwide. Furthermore, the greater the severity of liana infestation, the larger the magnitude of liana effect on host tree carbon accumulation. Moreover, the effects of liana infestation on the capacity of tropical forests to function as a carbon sink are likely to accelerate in the coming years given reports of increasing liana abundance in the neotropics (Phillips et al., 2002; Schnitzer and Bongers, 2011).

The increasingly unignorable impact of lianas on tree carbon stores comes at a time where the tropical carbon sink is already considered to be in decline (Brienen et al., 2015; Hubau et al., 2020). This is predominantly attributed to a changing climate and more severe drought events causing decreased growth and increased mortality (Phillips et al., 2009). However, another concerning change is a shift in dominance from shade-tolerant tree genera, an inherently slow-growing and carbon dense functional group, to species with a more accelerated life span, typically fast-growing individuals with low wood density and high stem turnover (Brienen et al., 2020). Evidence for these changes has already been observed in the neotropics (Laurance et al., 2004; Phillips et al., 2004; van der Heijden et al., 2013). It has been posited that lianas may be contributing to this shift, by disproportionately impacting shade-tolerant species and tree functional groups (Muller-Landau and Visser, 2019). A decreasing trend in the dominance of these carbon dense genera is estimated to potentially reduce tropical forest carbon storage by as much as 34% (Bunker et al., 2005). Evidence for more severe infestation in shade-tolerant species does exist (Lowe and Walker, 1977; van der Heijden et al., 2008; Muller-Landau and Visser, 2019), although this relationship is not universal (Malizia and Grau, 2006; Martínez-Izquierdo et al., 2016). Furthermore, the capacity of tree species to tolerate liana infestation, that is to withstand significant impacts on growth and survival, may vary between tree functional groups (Visser et al., 2017).

The paucity of research into how lianas impact carbon accumulation in trees with differing life histories forms the basis of the rationale for the present study. Given shade-tolerant carbon dense genera are inherently slow growing, whereas pioneer species typically occupy a different position on the slow-fast life-history axis, these functional groups can be divided using wood density as an intrinsic proxy measure for differences in species-specific functional traits (Suzuki, 1999; Muller-Landau, 2004; Van Gelder et al., 2006; Poorter et al., 2008; van der Heijden et al., 2008). I consider a dataset from the ongoing liana removal experiment in Gigante, Panama, which documents over 3,800 lianas and trees (≥1 cm diameter) in order to assess forest-level impacts of liana infestation on ecosystem dynamics (van der Heijden et al., 2015; Álvarez-Cansino et al., 2015; Martínez-Izquierdo et al., 2016; Rodríguez-Ronderos et al., 2016; Adams et al., 2017; García León et al., 2018). This chapter analyses the data from the first eight years (2011-2019) of the experiment, focusing on 2,799 trees over ≥10 cm diameter.

3.3 Aims and objectives

3.3.1 Main Aim

To assess the effect of liana infestation on the contribution of tree functional groups to forest-level carbon accumulation.

3.3.2 Objectives

1. Assess the effect of lianas on net biomass accumulation, biomass growth and mortality across the eight-year census period.
2. Investigate whether lianas differentially affect tree species with different life history traits, as indicated by their wood density.
3. Assess whether the severity of liana infestation prior to liana removal affects the rate of tree carbon accumulation in the removal and control plots

3.4 Methods

3.4.1 Site description and experimental design

The liana removal experiment was carried out on the Gigante Peninsula, Republic of Panama. The site is located on the mainland adjacent to Barro Colorado Island (BCI) and is situated within the Barro Colorado Nature Monument (BCNM; 9.15°N, 79.85°W; Figure 3.1). A mix of early and late secondary seasonally moist lowland forest covers the Gigante Peninsula (Schnitzer and Carson, 2010; Álvarez-Cansino et al., 2015; García León et al., 2018). Average daily temperature in the BCNM is 27.5°C, with a mean annual precipitation of approximately 2,600 mm per year and a distinct four-month dry season from mid-December through April where rainfall rarely exceeds 100 mm per month.

In 2008, sixteen 80 x 80 m (0.64 ha) plots situated 116–1,690 m apart were located within floristically and structurally similar areas of the ~60-year-old secondary forest area of Gigante Peninsula (Figure 3.1). Plots with similar liana biomass and tree structure were paired and randomly assigned treatments i.e., either liana removal or to be left as unmanipulated control plots (hereafter referred to as removal and control plots respectively). In 2008, all lianas and trees ≥1 cm diameter at breast height (DBH; diameter at ~1.3 m above the forest floor or above buttresses) in the central 60 x 60 m area of each plot were measured. This was repeated in 2011 immediately prior to liana removal. Average above-ground tree biomass within the 16 plots was 75.1 Mg C ha^{-1}, in keeping with similar aged neotropical secondary forests (Saldarriaga et al., 1988; Marín-Spiotta et al., 2007). The forest in Gigante was heavily infested with lianas, with over 86% of trees ≥10 cm diameter in the plots carrying lianas in their crown. Prior to removal, there were no significant differences between liana biomass, density and infestation rate between the removal and control plots (van der Heijden et al., 2015).

In March 2011, lianas were removed from the eight removal plots. Using machetes, lianas were severed near the forest floor, but were not removed from the tree to avoid damaging the tree crown. Any liana debris was left in the plots to decompose. To ensure removal plots remained liana-free, all resprouting lianas were cut monthly for the first 2 months and bimonthly for the next 6 months. Plots were subsequently monitored and resprouting liana stems cut every 3–4 months. Both control and removal plots were visited at the same time and with the same frequency to avoid visitation effect (Cahill et al., 2001; Schnitzer et al., 2002). The liana load carried by trees was assessed before liana removal using the Crown Occupancy Index (COI), a five-point ordinal scale index from zero to four (Clark and Clark, 1990; van der Heijden et al., 2010). A tree with a COI of 0 is defined as having no lianas in its crown, a COI of 1 has 1-25% liana leaf crown coverage, 2 between 26-50%, 3 between 51-75%, and 4 greater than 75%.

Four months prior to treatment, in November 2010, dendrometer bands were installed 10 cm above DBH to monitor growth of all dicotyledonous trees ≥10 cm DBH in the central 60 × 60 m (0.36 ha) area of all removal and control plots, leaving a 10 m buffer zone at the plot edge to prevent lianas rooting outside of the plot infesting the core plot area. Tree stem diameter and diameter growth has since been measured biannually at the beginning of the wet season (end of April) and dry season (beginning of January) using dendrometer bands and electronic callipers and correcting for stem curvature. Mortality events and new recruits ≥10 cm DBH were also recorded at these regular intervals. This study thus considers a dataset consisting of 2,799 trees (170 species) across an eight-year census period.

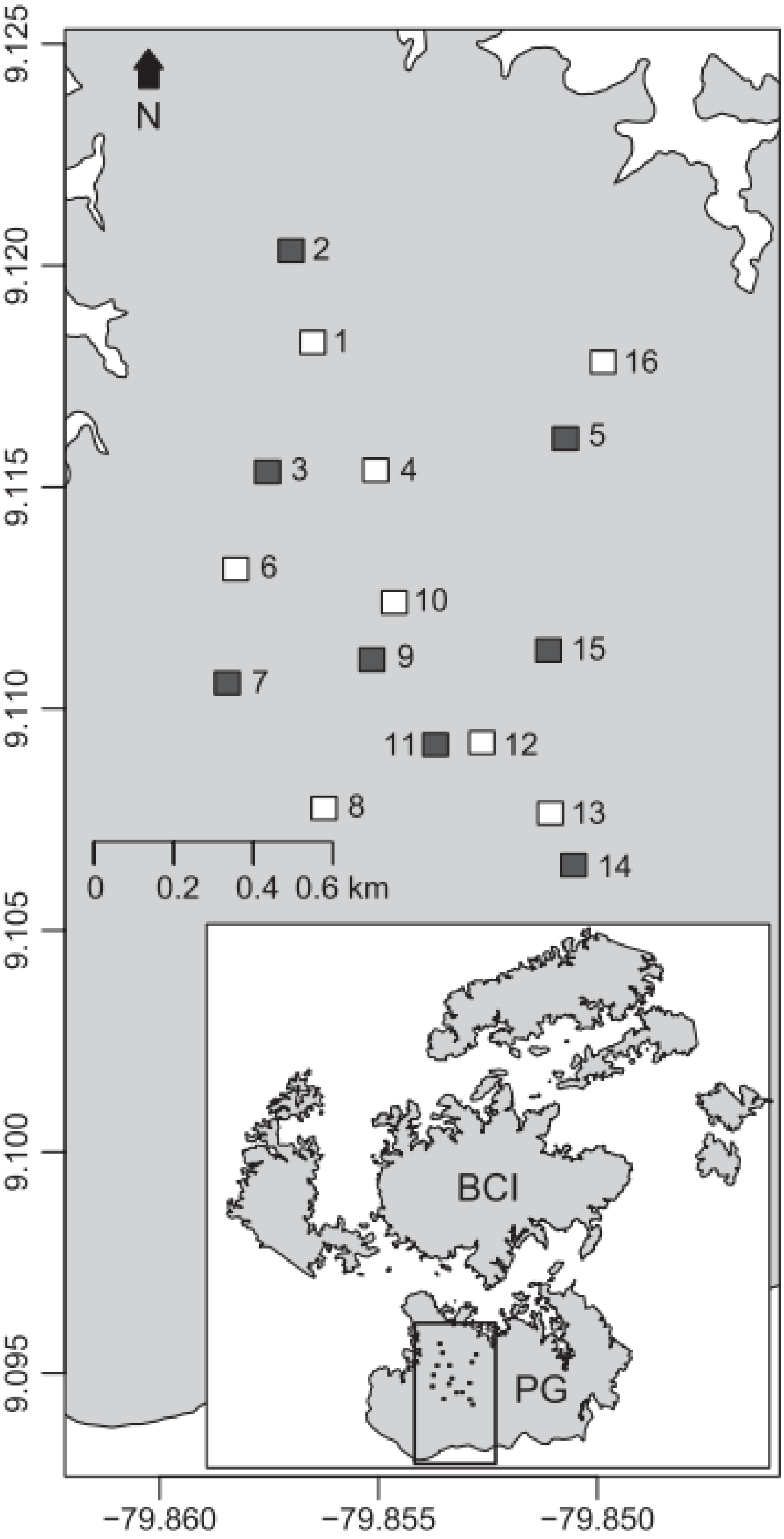

Figure 3.1 – Map of the liana removal experiment in Gigante, Panama. The 16 plots are divided into eight control plots (white squares) and eight removal plots (dark grey squares). The map insert illustrates the position of the liana removal experiment in relation to the adjacent Barro Colorado Island (BCI) and wider Barro Colorado Nature Monument (BCNM). Figure taken from van der Heijden et al. (2019).

3.4.2 Biomass calculations

Above-ground biomass of each tree stem was calculated from tree diameter measurements, wood density and estimated height using an allometric equation appropriate for tropical moist forests (Chave et al., 2014). Tree height was inferred from diameter using a height-diameter Weibull equation based on 6,256 trees in the Gigante Peninsula (van der Heijden et al., 2015). Locally gathered wood density values were available for the majority of tree species in the plots (Wright et al., 2010), when these were not available, data from the Global Wood Density Database were used (Zanne et al., 2009; Chave et al., 2009). In the rare occurrence where species-specific wood density was not available, genus or family-level wood density averages were used as per the methods of Lewis et al. (2009). For exceptional circumstances where stems were not represented in either database (0.3% of stems), a site-based average of 0.62 g m^{-3} was used. Species specific wood carbon-fraction values were used to convert tree biomass estimates from Mg dry mass to Mg C, when these were not available an average wood carbon-fraction of 47.35% was used (Martin and Thomas, 2011). Palms were excluded from all analyses as mature stems grow apically as opposed to radially (Rich et al., 1986). Furthermore, palms rarely exhibit liana infestation and were thus deemed unlikely to exhibit a significant response to removal (van der Heijden et al., 2008). As palm biomass was similar across removal and control plots (van der Heijden et al., 2015), their exclusion is unlikely to affect the overall results.

Net biomass change for each year of the experiment was defined as the difference between standing tree biomass at the end of the year and the beginning of the year, calculated by the sum of growth and recruitment minus mortality. Tree biomass growth was defined as the difference in tree biomass between the years for stems that were alive between censuses, and plot-level tree biomass growth was calculated by summing the individual biomass growth of all living tree stems within a plot. Tree biomass recruitment for each year was calculated by summing the biomass of the new stems that reached the 10 cm diameter threshold. Tree biomass mortality for each year was calculated by summing the biomass of all dead stems of the census before mortality occurred. Absolute liana effect on tree biomass growth and net biomass change was calculated as the difference between medians in removal and control plots. All plot-level biomass metrics were annualised and converted to Mg C ha^{-1} $year^{-1}$. Due to the short census periods (~4-8 months), it is assumed that all recruitment and mortality events were measured. Therefore, no corrections were made to include stems which may have recruited and subsequently died unobserved within a census period (Talbot et al., 2014). To control for the impact of tree size when comparing between COI classes, I used relative individual biomass growth (% $year^{-1}$), which was calculated as the annualised difference in tree biomass between two censuses and divided by its biomass in the first census multiplied by 100 (see equation 1).

Equation 1

(a)

$$\frac{biomass_2 - biomass_1}{biomass_1} * 100 = \text{relative biomass growth (\%)}$$

(b)

$$\frac{\text{relative biomass growth (\%)}}{date_2 - date_1} = \text{relative biomass growth (\% year}^{-1}\text{)}$$

Whereby $biomass_1$ refers to individual tree biomass in the first census, $biomass_2$ refers to individual tree biomass in the last census, $date_1$ refers to the numerical date of the first census, and $date_2$ refers to the numerical date in the final census.

3.4.3 Statistical analyses

Tests for difference between control and removal treatments for median biomass growth, recruitment, mortality, and net biomass change utilised a bootstrapping approach (van der Heijden et al., 2015; 2019). This approach permits direct comparisons between treatments and wood density classes in a single analysis without complicated post hoc testing. The bootstrapping approach calculated 100,000 realisations of the absolute liana effect between treatments as well as between the size of this effect between wood density classes. These iterations were used to calculate the median, upper and lower boundaries of the 95% confidence interval (CI) as the 50th, 97.5th and 2.5th percentiles respectively, of the differences in liana effect between treatments and the size of liana effect between wood density classes. These differences were considered significant when the CI of the difference did not include zero (van der Heijden et al., 2015). To test whether the effect of lianas on tree functional groups was related to life history traits, similar bootstrap analyses were used to compare within wood density classes, with individual trees divided into low (≤ 0.49), medium (>0.49 - ≤ 0.69), and high (≥ 0.69) wood density classes (van der Heijden and Phillips, 2009). Wood density in this instance is used as a proxy for functional traits related to light-tolerance and inherent growth rates (See Appendix 2; Suzuki, 1999; Muller-Landau, 2004; van der Heijden et al., 2008). All statistical analyses were conducted using R 4.0.2 (R Core Team, 2021).

3.5 Results

3.5.1 Liana effects on forest-level metrics

Median forest-level tree biomass growth was 1.30 (95%-bootstrap CI 1.08-1.57) Mg C ha^{-1} year^{-1} in control plots and 2.59 (95%-bootstrap CI 2.22-2.75) Mg C ha^{-1} year^{-1} in liana-removed plots between 2011 and 2019. As such, lianas reduced forest-level tree biomass growth by 49.21% (38.46-56.80% 95%-bootstrap CI) over the eight-year census period. Yearly biomass growth was significantly higher in removal plots in all eight census years (Figure 3.2B), consistent with the notion of a strong competitive effect of lianas upon tree growth. Similarly, biomass recruitment was significantly greater in liana-removed plots over the eight-year census period. However, yearly biomass recruitment between treatments was only significantly different in years one and three (Figure 3.2C). Conversely, biomass mortality was greater in control plots (1.35 [0.80-2.29 Mg C ha^{-1} year^{-1} 95%-bootstrap CI]) than removal plots (0.73 [0.49-2.61 Mg C ha^{-1} year^{-1} 95%-bootstrap CI]). Whereas, due to high variability between plots, this difference was not statistically significant across the eight-year census period (see Appendix 1a; Figure 3.2D).

Taken together, this amounts to a net change in biomass of -0.13 [-0.56 – 0.75] and 2.19 [0.05 – 2.44] Mg C ha^{-1} year^{-1} in the control and removal plots respectively, a difference of 2.11 Mg C ha^{-1} year^{-1} over the eight-year period (-0.19 – 2.73, 95%-bootstrap CI; see Appendix 1a). Yearly net biomass change however was significantly greater in removal plots than control plots in five out of the eight census years and only marginally so in other years (Figure 3.2A). The contribution of each forest metric to yearly net biomass change differed between treatments on average. In control plots, biomass mortality accounted for 48.4 ±8.6% of net biomass change, closely followed by biomass growth at 47.6 ±8.0% and recruitment making up the remaining 4.0 ±1.9%. Whereas, in removal plots, biomass growth accounted for a much larger proportion of net biomass change at 65.2 ±7.5%. Biomass mortality accounted for a much lower proportion of net biomass change at 28.9 ±8.5% in removal plots and recruitment was higher than in control plots at 5.9 ±2.4%.

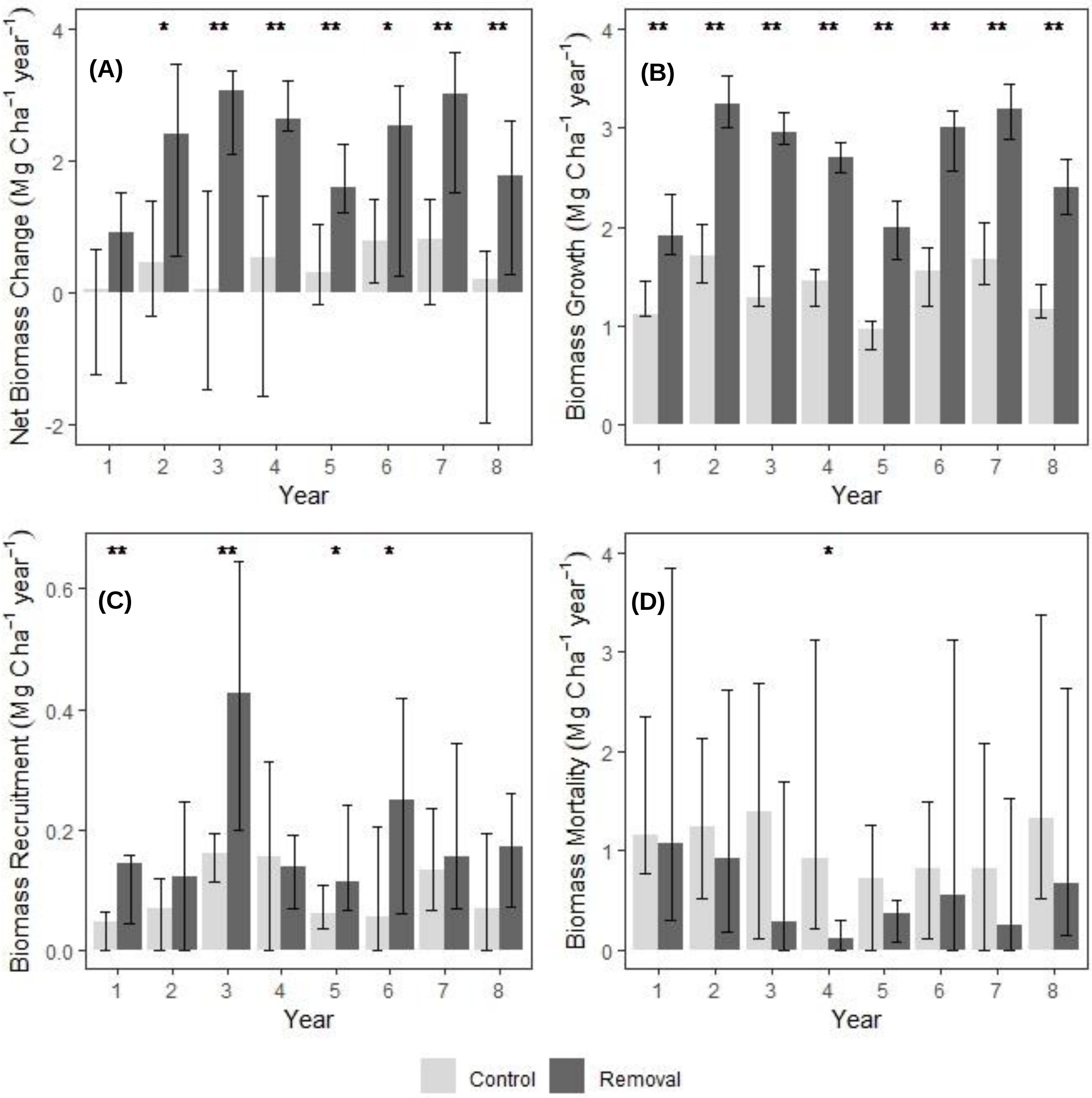

Figure 3.2 – Bar plots denoting median and 95% bootstrap Confidence Interval (CI) for yearly plot-level A) net tree biomass change, B) tree biomass growth, C) tree biomass recruitment, and D) tree biomass mortality (Mg C ha^{-1} year^{-1}) over an eight year census period. Significant differences between control plots (liana infested) (n=8, light grey boxes) and removal plots (liana removed) (n=8, dark grey boxes) are indicated by ** for 95% bootstrap CI, and * for 90% bootstrap CI.

3.5.2 Liana effect per wood density class

Wood density was used as a proxy for tree functional traits. Of the 2,799 recorded trees, 499 individuals (43 species) fell into the low wood density class, 1,313 individuals (89 species) were in the medium wood density class and 987 individuals (38 species) were in the high wood density class. Differences in net biomass change between treatments remained insignificant over the eight-year census period when split by wood density class. However, some yearly treatment differences were significant in each wood density class (see Figure 3.3a, Appendix 1b). Contrastingly, tree biomass growth remained significantly greater in removal plots than control plots for all wood density classes when averaged over the eight-year census period. When these data were further split by census year, absolute liana effect remained significant for most years (see Figure 3.3b, Appendix 1c).

The size of the difference in biomass growth and net biomass change between treatments differed between wood density classes in each census year (Figure 3.3). The trend in these biomass differences over the eight census years also differed between wood density classes (Figure 3.4). On a plot-level, all three wood density groups contributed to the total difference in biomass growth and net biomass change between the treatments in all eight years. However, the size of these contributions varied between wood density class over time.

In the first four years, low wood density species contributed most to biomass growth and the additional carbon uptake in removal plots, taking up on average 0.51 Mg C ha^{-1} $year^{-1}$ more in the removal plots than in the control plots. In contrast, trees in the high wood density class only sequestered an average of 0.40 Mg C ha^{-1} $year^{-1}$ during this period. After year four, the contribution of the different wood density classes to the increase in biomass growth in removal plots shifted (Figure 3.4B). High wood density species contributed on average 0.52 Mg C ha^{-1} $year^{-1}$ to the liana-induced difference in biomass growth over the latter four census years, whereas low wood density species only contributed 0.35 Mg C ha^{-1} $year^{-1}$. As such, the relative contributions of each wood density class, a proxy for tree functional groups, shifted from low wood density to high wood density individuals over the course of the eight-year census period.

Contrastingly, the relative contribution of each wood density class to net biomass change over the eight-year census period did not follow such a clear shift from low to high dominance. Instead, the wood density class with the greatest contribution to biomass change varied interchangeably from high-wood density dominance to a slight low wood density dominance twice over the eight-year period (Figure 3.4A). Furthermore, the size of the difference in contribution to net biomass change between wood density class varied on a much greater scale than biomass growth. In census year four, low wood density species contributed 0.56 Mg C ha^{-1} $year^{-1}$ to net biomass change whereas species in the high wood density class only accounted for 0.35 Mg C ha^{-1} $year^{-1}$. However, in the sixth census year this had flipped, with high wood density species now contributing the most to net biomass change at 0.72 Mg C ha^{-1} $year^{-1}$, with low wood density species contributing only 0.15 Mg C ha^{-1} $year^{-1}$.

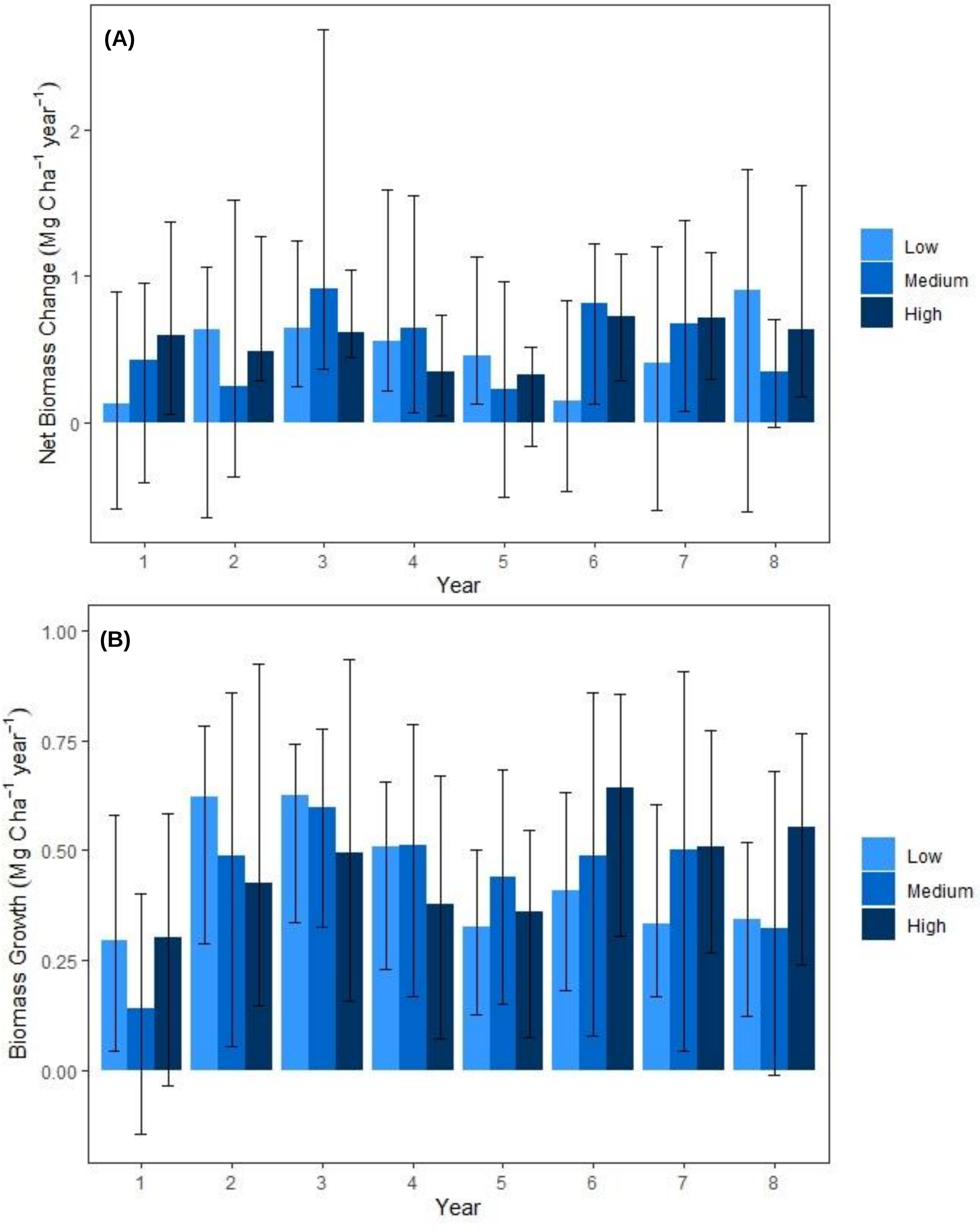

Figure 3.3 – Bar plot denoting median and 95% bootstrap confidence interval of yearly plot-level A) net tree biomass change, and B) tree biomass growth (Mg C ha^{-1} year^{-1}) for each wood density class (low [≤0.49], medium [>0.49 - ≤0.69], high [≥0.69]). Error bars not overlapping 0 indicates biomass growth or net biomass change for the wood density class were significantly higher in the liana removed plots. There were no significant differences in tree biomass growth, nor net tree biomass change, between the wood density classes in any census year (95%-bootstrap).

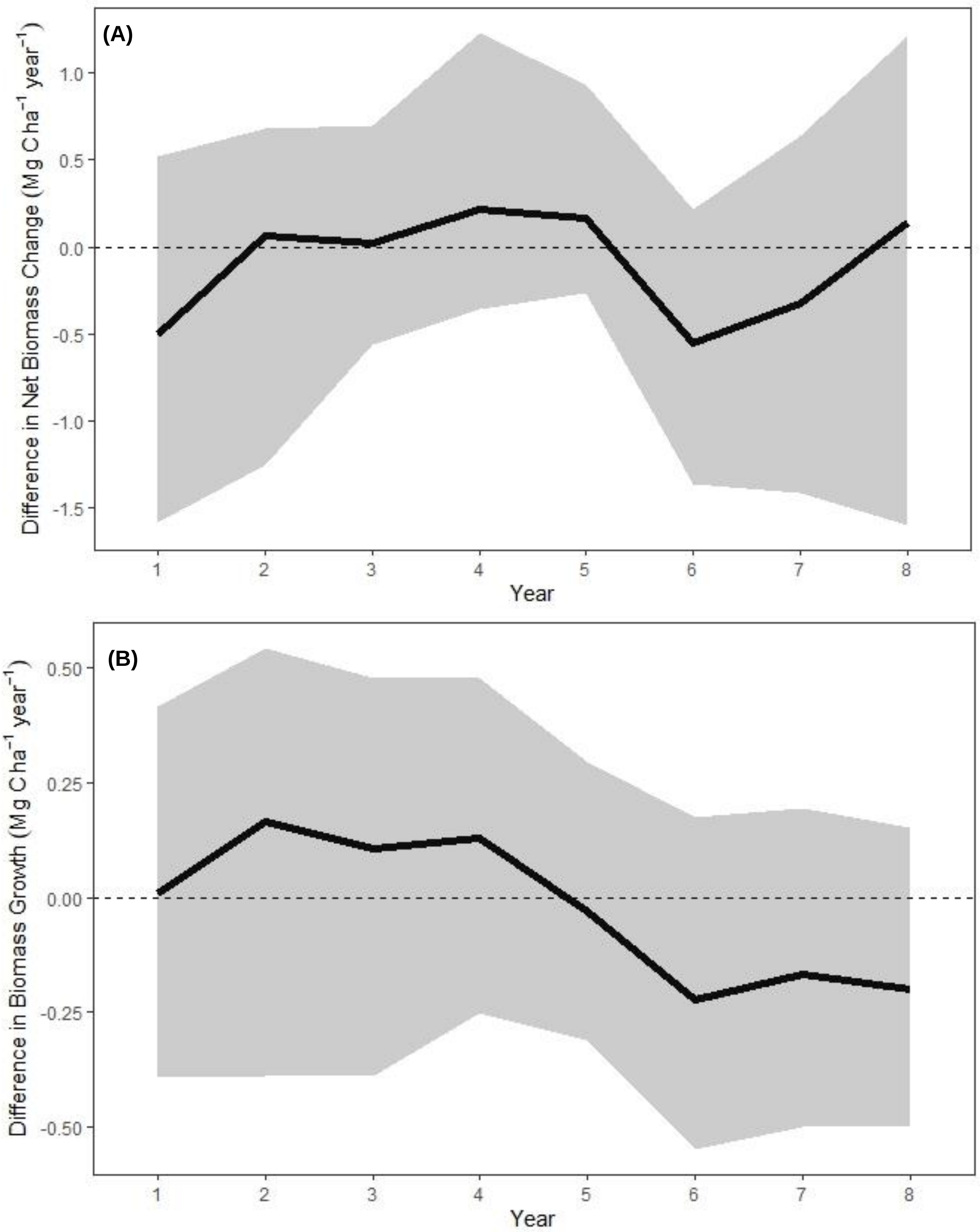

Figure 3.4 – Plot-level differences (black line) in yearly A) net tree biomass change, and B) tree biomass growth (Mg C ha^{-1} year^{-1}) between low wood density and high wood density classes over the eight-year census period. Error represented by light grey confidence envelope (95%-bootstrap). Confidence envelope overlapping 0 indicates no significant difference between low and high wood density classes in any census year.

3.5.3 Infestation severity and relative tree biomass growth

Prior to removal, 86.23% of trees across all 16 plots suffered some degree of liana crown infestation (Table 3.1A), with the other 13.77% experiencing no direct above-ground competition from lianas (COI = 0). This infestation rate exceeds neighbouring old-growth forest on BCI (73.6%; Ingwell et al., 2010) and is more similar to that of 'liana forests' in lowland Bolivia (86%; Perez-Salicrup et al., 2001) and lowland moist forests in Cameroon (80%; Parren and Doumbia, 2005). The majority of trees had a COI class of 1 (29.59%), and 36.41% of individuals were considered to be severely infested (>50% crown covered by liana leaves (COI classes 4 and 5). Relative tree biomass growth averaged over the entire eight-year census period was significantly greater in liana-removed plots than in control plots for each COI class (Figure 3.5). Average COI in low wood density species was greater than that of high wood density species (2.12 vs. 1.88 for high and low wood density species respectively; Table 3.1B), and this difference was statistically significant (Wilcoxon rank sum test, p < 0.01). Between COI classes, there was significantly greater relative growth in trees with no crown infestation (COI = 0) compared to trees with >75% of their crown covered by lianas (COI = 4) in control plots. No other statistically significant differences in relative biomass growth were found between COI classes in control plots. Contrastingly, in the removal plots, relative biomass growth did not differ significantly amongst any COI classes.

Table 3.1 – Infestation severity across 2,403 trees with recorded Crown Occupancy Index (COI) prior to treatment. A) Percentage of trees per COI class, and B) average COI per wood density class and Wilcoxon Rank sum test for difference.

A) Crown Occupancy Index distribution	
COI	Percentage
0	13.77%
1	29.59%
2	20.22%
3	18.77%
4	17.64%
B) Differences in Crown Occupancy Index per wood density class	
Wood Density class	Average COI
Low	2.12
High	1.88
Difference	p = 0.002406

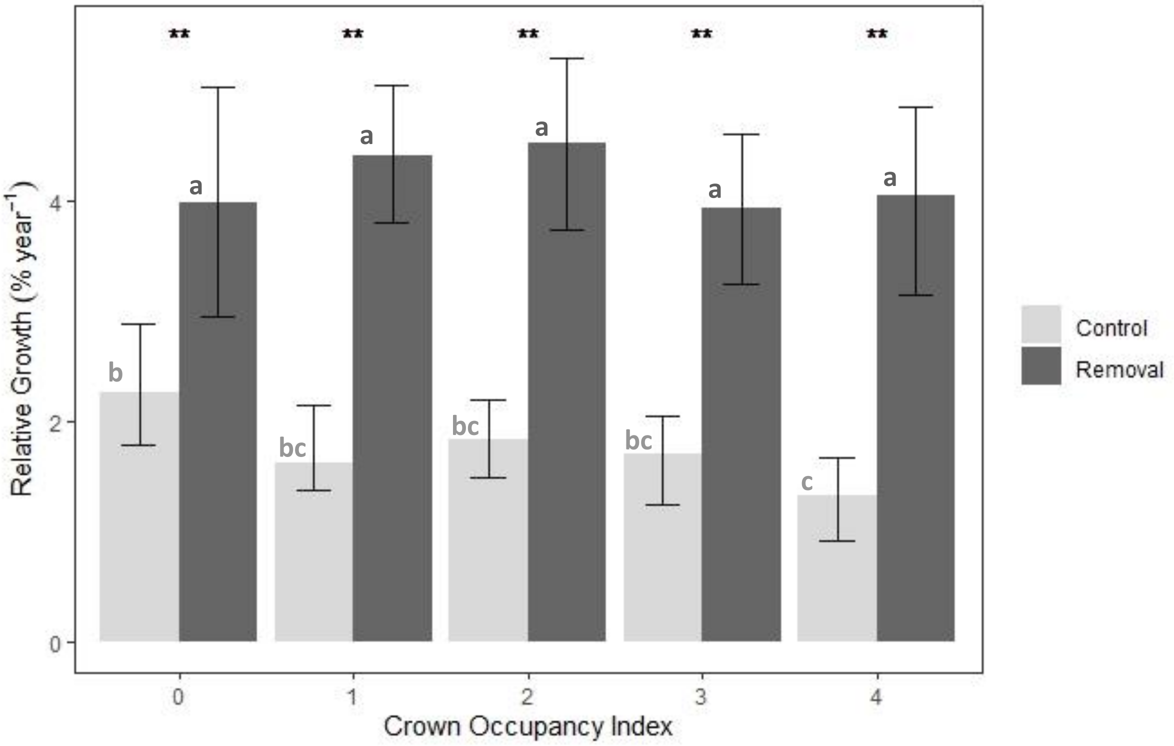

Figure 3.5 – Bar plot denoting median and 95% bootstrap Confidence Interval (CI) in relative tree growth (% year^{-1}) over the entire eight-year census period between treatments split by Crown Occupancy Index, whereby 0 is 0%, 1 is 1-25%, 2 (26-50%), 3 (51-75%), and 4 (>75%) of the crown covered by liana leaves, respectively. Significant differences in relative growth between trees in control plots (liana infested) (light grey boxes) and removal plots (liana removed) (dark grey boxes) treatments are indicated by ** for 95% bootstrap CI, and * for 90% bootstrap CI. Differences in relative growth between COI classes within treatments are indicated by letters a, b and c, only the difference between COI 0 and 4 in control plots is significant.

3.6 Discussion

3.6.1 Lianas and forest metrics

This study is the first to report findings from a large-scale liana removal experiment for which there is more than 3-4 years of data. This is also the first time the effect of lianas on different tree functional types has been analysed and quantified. My findings add to the increasingly comprehensive body of evidence supporting the significant effect of liana infestation in reducing forest-level carbon accumulation in the neotropics.

The difference in net biomass changes between liana-infested and liana-removed plots across this now eight-year dataset (2.11 Mg C ha^{-1} year^{-1}) is comparable to the earlier study by van der Heijden et al. (2015) which considered the first three years of the liana removal experiment (2.43 Mg C ha^{-1} year^{-1}). This difference however is much larger than another three year study in Peru (0.25 Mg C ha^{-1} year^{-1}; van der Heijden and Phillips, 2009), although this study utilised an observational approach as opposed to experimental liana removal. Net biomass change differences between treatments in the present study also far exceed figures reported in a previous experiment in Gigante over a similar time frame (0.121 Mg C ha^{-1} year^{-1}; Schnitzer et al., 2014), though this earlier research was limited to treefall gaps, not plot-level carbon accumulation.

Enhanced tree biomass growth was the prominent driver in greater net biomass change in removal plots. In this analyses, liana-infested plots had 49.21% lower tree biomass growth than liana-removed plots over the eight-year period. This is almost identical to the study by Schnitzer et al. (2014), whereby liana-infested treefall gaps had 49.78% lower growth than liana-free treefall gaps. Another liana removal experiment in Agua Salud, Panama, found tree biomass growth was only reduced by 18% in liana-infested plots (Estrada-Villegas et al., 2020), although this only considered a four-year long dataset. A noticeable dip in biomass growth and net biomass change in census year 5 was associated with the 2015–2016 El Niño, the third strongest drought recorded in Panama (Schnitzer and van der Heijden, 2019; van der Heijden et al., 2019).

Biomass mortality was 39.5% higher in liana-infested plots compared to removal plots, although high variability between plots meant this difference was not statistically significant, which is likely to be a result of the stochastic nature of mortality events (van der Heijden et al., 2015). Greater mortality was responsible for nearly half of net biomass changes in liana-infested plots, in combination with arrested growth and recruitment contributing to a negative overall net biomass change across the eight-year census period. Reduced tree biomass recruitment in control plots was consistent with fierce interspecific competition with lianas in juvenile stages (Schnitzer et al., 2005; Schnitzer and Carson, 2010). This difference in net tree biomass change is unlikely to be compensated by lianas as their unique growth strategy, characterised by low investment in stem biomass and greater investment in leaf foliage, means lianas account for a small fraction of biomass contributions to forest carbon (van der Heijden and Phillips, 2009a). Lianas typically account for as little as 24% of tree biomass they displace (Schnitzer et al., 2014). Furthermore, liana effect on net biomass change is accelerated given the faster turnover of liana stems (Mascaro et al., 2004; Phillips et al., 2005), and reduced carbon residence time of foliage compared to stem biomass (van der Heijden et al., 2015), meaning fixed carbon is released at a faster rate in infested plots (Powers et al., 2009; Galbraith et al., 2013).

3.6.2 Disproportionate impacts on functional groups

Tree biomass growth within each wood density class, used here as a proxy for species position on the slow-fast life-history axis, was significantly greater in liana-removed plots than infested plots over the eight-year period, as well as in the majority of census years. This suggests trees suffer from liana infestation regardless of functional traits. Conversely, differences in net biomass change between treatments in each wood density class are not significant over the eight-year period, which is attributable to large variation in mortality data. Despite this, yearly liana effect on net biomass change is significant across some census years within each wood density class. However, for both biomass growth and net change, the magnitude of the liana effect in each year is not equal, and the relative contributions of each wood density class to plot-level carbon accumulation differ over the eight-year census period.

In the initial three to four years following liana removal, low wood density species have a marked growth release (Figure 3.4B). This is likely due to newly formed canopy gaps, previously occupied by lianas, increasing the amount of available light in these areas. Trees with low wood density, commonly referred to as pioneer species, are extremely light-demanding and can grow rapidly in abundant water, nutrient, and high-light conditions (Kohyama et al., 2003; Kitajima et al., 2005). In the absence of lianas, these pioneer species are able to rapidly take advantage of these available niches and therefore experience a surge in growth (Kitajima, 1994; Stewart and Schnitzer, 2017). Additionally, similar to previous studies in the BCNM (Ingwell et al., 2010), low wood density species were more likely to carry a high liana load in their canopy (Table 3.1b). This is contrary to the commonly cited relationship between shade tolerance and infestation severity (Lowe and Walker, 1977; van der Heijden et al., 2008; Muller-Landau and Visser, 2019), although much evidence for this relationship is based on regenerating tree saplings (Naturales, 2001; Toledo-Aceves and Swaine, 2008b; A. Wright et al., 2015) and other notable exceptions in adult trees exist (Malizia and Grau, 2006; Martínez-Izquierdo et al., 2016). Furthermore, susceptibility to infestation is also governed by traits such as trellis availability and stem flexibility (Balfour and Bond, 1993; van der Heijden et al., 2008), not solely life-history. As such, greater initial COI in low wood density species in Gigante likely contributed to a larger liana burden, which following removal may have subsequently led to a higher growth release. Enhancing the contribution of low wood density species to overall forest-level carbon accumulation during this period.

Between census years four and five, the proportion of carbon accumulation made up by pioneer species growth dwindles. This is likely because any initial growth release caused by high-light conditions in newly available canopy gaps is expected to saturate as these gaps are filled. Thus, there is a shift in growth contribution to more shade-tolerant species, typically individuals with high wood density. This shift also coincides with severe drought events associated with the 2015/16 El Niño, despite the fact shade tolerance typically exhibits a negative relationship with drought tolerance (Niinemets and Valladares, 2006). Nevertheless, between 2015 and the most recent census in 2019, individuals with high wood density dominate biomass growth contributions to forest-level carbon accumulation in removal plots (Figure 3.4B). It is suggested that these trends in growth contributions also apply to net biomass changes, although the inclusion of sporadic mortality and recruitment events contribute to a more complicated picture of carbon accumulation in different wood density classes (Figure 3.4A).

The eventual dominance of shade-tolerant species contributions to forest-level biomass growth mirrors a commonly accepted relationship between wood density and carbon accumulation, whereby high wood density species are responsible for the largest proportion of above-ground biomass carbon stores (Baker et al., 2004). If, as expected, high wood density shade-tolerant species are to persist in making up the majority of growth contributions thereafter, the importance of this tree functional group to the carbon storage capacity of these tropical forests is invaluable.

As the difference in biomass growth in high wood density trees between liana-infested and liana-removed plots grew increasingly wider over the census period, this suggests lianas may be disproportionately impacting shade-tolerant, carbon-dense and typically larger species (Muller-Landau and Visser, 2019), contributing to a forest-wide shift toward species with lower wood density and more accelerated life spans (Laurance et al., 2004; Phillips et al., 2004; van der Heijden et al., 2013; Brienen et al., 2020). Such a decline in shade-tolerant genera presents a significant threat to the viability of tropical forests as a carbon sink, which account for over 50% of global terrestrial carbon stores (Pan et al., 2011; Feldpausch et al., 2012). Further investigation is needed into the disproportionate effect of lianas on tree functional groups. These relationships need to be more well defined, their likely impact on global tropical forest carbon accumulation quantified, and their impact on future forest carbon estimates incorporated into models.

3.6.3 Infestation Severity and Growth

Significantly higher relative biomass growth in individuals growing in liana removed plots in each COI class suggests that lianas have a detrimental impact on trees regardless of crown infestation severity. Relative biomass growth differed between treatments even for trees with no liana crown infestation. This is likely due to a combination of lianas shading trees they did not directly infest, and below-ground competition. With competition for water and soil nutrients between trees and neighbouring lianas being fierce (Toledo-Aceves, 2015; Álvarez-Cansino et al., 2015; De Deurwaerder et al., 2018), some studies conclude that below-ground liana impacts affect tree biomass growth more so than above-ground competition even in the most severely infested trees (Dillenburg et al., 1993a; Toledo-Aceves and Swaine, 2008a).

The observed difference in relative biomass growth between COI classes zero and four in control plots supports the notion that the severity of liana infestation translates to the magnitude of liana effect. Evidence for this relationship is common in existing literature (van der Heijden and Phillips, 2009a; Grogan and Matthew Landis, 2009; Visser et al., 2017). For example, a study in Ecuador found severely liana infested trees only grew a third as fast compared to trees with no crown infestation (Smith et al., 2017). These findings are concerning given reports of increasing infestation severity in recent years (Ingwell et al., 2010). It is suggested by Grogan and Matthew Landis (2009) that lianas have a lasting impact on tree growth following removal. As there were no significant differences in relative biomass growth between COI classes in removal plots, this study does not support this notion. Further to this, differences in biomass growth and recruitment between treatments in the first census year (Figure 3.2) suggest any legacy impact of lianas is not significant.

3.6.4 Limitations and future study

This analysis falls short in that, ideally, the impact of varying infestation severity on growth and mortality should also be tested amongst wood density classes. Some evidence suggests a relationship between shade-tolerance and liana tolerance (Visser et al., 2017; Muller-Landau and Visser, 2019), with trees with differing functional traits being able to tolerate different severities of liana infestation. Crown occupancy, as a measure of the severity of liana load, is a key metric in further understanding liana effects on forest-level carbon. Where possible, future censuses in forest plots and removal experiments should consider how COI variability impacts metrics of tree growth and mortality. Future studies should follow the methodology of repeated censuses, allowing for patterns in the liana effect on forest metrics to be analysed over time. Further research efforts should focus on the disproportionate impact of lianas on differing tree functional groups, as well as attempting to better quantify these differences and their likely effects on the future carbon sink capacity of global tropical forests. This would help inform targeted forest management and conservation aimed at liana control.

3.7 Conclusion

Here I provided evidence from the ongoing liana removal experiment in Panama for the continuing detrimental effect of lianas on forest-level carbon accumulation even eight years after lianas were removed. Lianas significantly reduced tree growth and recruitment, whilst simultaneously increasing mortality risk (Figure 3.2), in line with the findings of comparable experimental and observational studies. Furthermore, these effects correlated positively with the severity of crown infestation (Figure 3.5). The liana effect on trees with varying functional traits and life histories changed over the census period, with light-demanding pioneer species initially contributing most to carbon accumulation as they begin to occupy canopy gap niches, but with the contribution of shade-tolerant, carbon-dense tree species starting to dominate towards the end of the eight-year period. The growing divide in carbon accumulation between treatments in shade-tolerant trees validates reports of a universal decline in these species across the neotropics, whereby disproportionate liana impacts in combination with climate change are causing a shift towards species with lower wood density. These effects combine to produce a concerning picture of the future of tropical forests to persist as a functioning global carbon sink.

Conclusion

This study has reviewed our current understanding of liana ecology whilst also contributing to the ever-expanding field of liana research. As we learn more about the significant contributions of lianas to species diversity, forest structure and forest carbon, more questions arise surrounding the drivers of their abundance, their specific impacts on different tree species and improved methods to detect and quantify them. The current state of tropical forest decline and changes in climate add to the urgency of addressing these knowledge gaps in liana research.

The extensive review of previous investigations into liana effects on host trees in Chapter 1 came to the unignorable consensus that liana infestation in tree crowns has a three-fold detrimental impact on the capacity of tropical forests to store and sequester carbon. Firstly, by constraining host tree growth, secondly by increasing host tree mortality risk, and thirdly by suppressing reproduction and regeneration of tree recruits. For the first time, these liana effects were quantified in a large-scale removal experiment censused biannually over an eight-year period (Chapter 3). In line with existing literature, tree biomass growth and recruitment in liana-removed sites in Gigante was significantly higher than in infested plots. Furthermore, despite high variability meaning the differences weren't statistically significant, mortality in liana infested plots was also 39.5% higher than liana removed plots, in line with similar studies (Phillips et al., 2005).

Evidence for increasing liana abundance in the neotropical realm were presented and reasons for these changes were analysed. Current data however did not support a similar increase in liana abundance in the palaeotropics. Much of the studies cited in Chapter 1 relied on traditional field sampling methods, the need to develop methods for identifying and quantifying lianas using remote sensing is now paramount to enable repeatable and accurate future study. Understanding whether changing liana abundance has accelerated, decelerated, or remained the same since these pre-2000 field studies will have extraneous impacts on present and future carbon balance in tropical forests. Similar remote sensing efforts called for in Chapter 2 may also be able to verify claims regarding declining stem density in Amazonian trees (Chave et al., 2008). Remote sensing could also provide an insight into whether these patterns of change are consistent across the tropics or if they are more pronounced in certain geographical areas than others.

The use of remote sensing in liana research is still in its infancy, although progress is being made. The short answer to 'can we make remote sense of lianas?', is not yet. However, our systematic assessment of progress in this area has indicated that with further technological innovations and underpinning field-based data, our understanding of liana spatial and temporal distribution, structure and biomass, responses to environmental conditions and diversity can vastly improve. The integration of these disciplines relies on further collaboration between liana ecologists and remote sensing experts. Our understanding of liana impacts, facilitated by remote sensing, is essential to better predict the fate of tropical forests and their carbon balance in a changing climate.

My review in Chapter 1 identified a reduction in the dominance of carbon-dense shade-tolerant genera, although the role of lianas in this decline were poorly understood. Using data from the liana-removal experiment in Gigante, Panama, this study was the first to quantify differing liana effects on carbon accumulation in different tree species functional groups (Chapter 3). I found that low wood density trees experienced a rapid growth release in response to liana removal and reduced competition for light, although high wood density species eventually dominated contributions to forest-level carbon accumulation after this stimulation had worn off. Additionally, my findings validate concerns that lianas are contributing to a widespread decline in carbon-dense high wood density species, causing a shift towards species with lower wood density and reduced carbon residence time.

Taken together, this thesis presents a concerning outlook on the future of tropical forests to persist as a functioning global carbon sink. The findings presented in Chapter 3 showed a net decrease in forest biomass in liana-infested plots over the eight-year census period. This is in line with multiple studies reporting a marked decline in tropical forests (Brienen et al., 2015; Baccini et al., 2017; Hubau et al., 2020), made worse by a shift towards tree species with higher turnover and lower carbon residence time (Brienen et al., 2020). Future research efforts must continue to quantify and assess the role lianas play in contributing to the globally important carbon balance of tropical forests.

References

Acevedo-Rodríguez, P., Acherman, J.D. and Anderson, C. 2015. Lianas and climbing plants of the Neotropics. *Smithsonian*. [Accessed 24 April 2022]. Available from: https://naturalhistory.si.edu/research/botany/research/lianas-and-climbing-plants-neotropics.

Adams, B.J., Schnitzer, S.A. and Yanoviak, S.P. 2017. Trees as islands: canopy ant species richness increases with the size of liana-free trees in a Neotropical forest. *Ecography*. **40**(9), pp.1067–1075.

Addo-Fordjour, P., Obeng, S., Addo, M.G. and Akyeampong, S. 2009. Effects of human disturbances and plant invasion on liana community structure and relationship with trees in the Tinte Bepo forest reserve, Ghana. *Forest Ecology and Management*. **258**(5), pp.728–734.

Addo-Fordjour, P. and Rahmad, Zakaria B. 2013a. Development of allometric equations for estimating above-ground liana biomass in tropical primary and secondary forests, Malaysia. *International Journal of Ecology*.

Addo-Fordjour, P. and Rahmad, Zakaria B. 2013b. Mixed Species Allometric Models for Estimating above-Ground Liana Biomass in Tropical Primary and Secondary Forests, Ghana. *ISRN Forestry*., pp.1–9.

Allen, B.P., Sharitz, R.R. and Goebel, P.C. 2007. Are lianas increasing in importance in temperate floodplain forests in the southeastern United States? *Forest Ecology and Management*. **242**(1), pp.17–23.

Allen, K., Dupuy, J.M., Gei, M.G., Hulshof, C., Medvigy, D., Pizano, C., Salgado-Negret, B., Smith, C.M., Trierweiler, A., Van Bloem, S.J., Waring, B.G., Xu, X. and Powers, J.S. 2017. Will seasonally dry tropical forests be sensitive or resistant to future changes in rainfall regimes? *Environmental Research Letters*. **12**(2), p.023001.

Álvarez-Cansino, L., Schnitzer, S.A., Reid, J.P. and Powers, J.S. 2015. Liana competition with tropical trees varies seasonally but not with tree species identity. *Ecology*. **96**(1), pp.39–45.

Alvira, D., Putz, F.E. and Fredericksen, T.S. 2004. Liana loads and post-logging liana densities after liana cutting in a lowland forest in Bolivia. *Forest Ecology and Management*. **190**(1), pp.73–86.

Anderson, L.O., Malhi, Y., Aragão, L.E.O.C., Ladle, R., Arai, E., Barbier, N. and Phillips, O. 2010. Remote sensing detection of droughts in Amazonian forest canopies. *New Phytologist*. **187**(3), pp.733–750.

Andrade, J.L., Meinzer, F.C., Goldstein, G. and Schnitzer, S.A. 2005. Water uptake and transport in lianas and co-occurring trees of a seasonally dry tropical forest. *Trees - Structure and Function*. **19**(3), pp.282–289.

Appanah, S., Gentry, A. and LaFrankie, J. 1993. Liana diversity and species richness of Malaysian rain forests. *Journal of Tropical Forest Science*. **6**, pp.116–123.

Appanah, S. and Putz, F.E. 1984. Climber abundance in virgin dipterocarp forest and the effect of pre-felling climber cutting on logging damage. *Malaysian Forester*. **47**, pp.335–342.

Asner, G.P. 2001. Cloud cover in Landsat observations of the Brazilian Amazon. *International Journal of Remote Sensing*. **22**(18), pp.3855–3862.

Asner, G.P., Knapp, D.E., Broadbent, E.N., Oliveira, P.J.C., Keller, M. and Silva, J.N. 2005. Selective logging in the Brazilian Amazon. *Science*. **310**(5747), pp.480–482.

Asner, G.P. and Martin, R.E. 2015. Canopy chemistry expresses the life-history strategies of lianas and trees *In*: S. A. Schnitzer, F. Bongers, R. J. Burnham and F. E. Putz, eds. *Ecology of Lianas*. Oxford, UK: Wiley-Blackwell, pp.299–308.

Asner, G.P. and Martin, R.E. 2012. Contrasting leaf chemical traits in tropical lianas and trees: implications for future forest composition. *Ecology Letters*. **15**(9), pp.1001–1007.

Asner, G.P., Martin, R.E., Knapp, D.E., Tupayachi, R., Anderson, C.B., Sinca, F., Vaughn, N.R. and Llactayo, W. 2017. Airborne laser-guided imaging spectroscopy to map forest trait diversity and guide conservation. *Science*. **355**(6323), pp.385–389.

Atkins, J.W., Bohrer, G., Fahey, R.T., Hardiman, B.S., Morin, T.H., Stovall, A.E.L., Zimmerman, N. and Gough, C.M. 2018. Quantifying vegetation and canopy structural complexity from terrestrial LiDAR data using the forestr r package. *Methods in Ecology and Evolution*. **9**(10), pp.2057–2066.

Avalos, G. and Mulkey, S.S. 1999. Seasonal Changes in Liana Cover in the Upper Canopy of a Neotropical Dry Forest. *Biotropica*. **31**(1), pp.186–192.

Avalos, G., Mulkey, S.S. and Kitajima, K. 1999. Leaf optical properties of trees and lianas in the outer canopy of a tropical dry forest. *Biotropica*. **31**(3), pp.517–520.

de Azevedo Amorim, T., Nunes-Freitas, A.F. and Rosado, B.H.P. 2018. Revisiting the hypothesis for increasing liana abundance in seasonal forests: a theoretical review. *Plant and Soil*. **430**(1–2), pp.1–6.

Baccini, A., Walker, W., Carvalho, L., Farina, M., Sulla-Menashe, D. and Houghton, R.A. 2017. Tropical forests are a net carbon source based on aboveground measurements of gain and loss. *Science*. **358**(6360), pp.230–234.

Baena, S., Boyd, D.S. and Moat, J. 2018. UAVs in pursuit of plant conservation - Real world experiences. *Ecological Informatics*. **47**, pp.2–9.

Baena, S., Moat, J., Whaley, O. and Boyd, D.S. 2017. Identifying species from the air: UAVs and the very high resolution challenge for plant conservation. *PLOS ONE*. **12**(11), p.e0188714.

Baker, T.R., Phillips, O.L., Malhi, Y., Almeida, S., Arroyo, L., Di Fiore, A., Erwin, T., Killeen, T.J., Laurance, S.G., Laurance, W.F., Lewis, S.L., Lloyd, J., Monteagudo, A., Neill, D.A., Patino, S., Pitman, N.C.A., M. Silva, J.N. and Vasquez Martinez, R. 2004. Variation in wood density determines spatial patterns in Amazonian forest biomass. *Global Change Biology*. **10**(5), pp.545–562.

Balee, W. and Campbell, D. 1990. Evidence for the successional status of liana forest (Xingu River Basin, Amazonian Brazil). *Biotropica*. **22**, pp.36–47.

Balfour, D.A. and Bond, W.J. 1993. Factors Limiting Climber Distribution and Abundance in a Southern African Forest. *The Journal of Ecology*. **81**(1), p.93.

Balzarolo, M., Anderson, K., Nichol, C., Rossini, M., Vescovo, L., Arriga, N., Wohlfahrt, G., Calvet, J.-C., Carrara, A., Cerasoli, S., Cogliati, S., Daumard, F., Eklundh, L., Elbers, J.A., Evrendilek, F., Handcock, R.N., Kaduk, J., Klumpp, K., Longdoz, B., Matteucci, G., Meroni, M., Montagnani, L., Ourcival, J.-M., Sánchez-Cañete, E.P., Pontailler, J.-Y., Juszczak, R., Scholes, B. and Martín, M.P. 2011. Ground-Based Optical Measurements at European Flux Sites: A Review of Methods, Instruments and Current Controversies. *Sensors*. **11**(8), pp.7954–7981.

Balzotti, C.S., Petersen, S.L., Terry, R.E., Scherer, A.K. and Golden, C. 2010. Remote sensing as a tool for tropical ecology. *Geography Compass*. **4**(8), pp.993–1012.

Bao, Y., Moorthy, S. and Verbeeck, H. 2018. Towards extraction of lianas from terrestrial lidar scans of tropical forests *In*: *International Geoscience and Remote Sensing Symposium (IGARSS)*. Valencia, Spain: Institute of Electrical and Electronics Engineers Inc., pp.7544–7547.

Barnes, M.L., Breshears, D.D., Law, D.J., van Leeuwen, W.J.D., Monson, R.K., Fojtik, A.C., Barron-Gafford, G.A. and Moore, D.J.P. 2017. Beyond greenness: Detecting temporal changes in photosynthetic capacity with hyperspectral reflectance data. *PLoS ONE*. **12**(12), p.e0189539.

Barry, K.E., Schnitzer, S.A., van Breugel, M. and Hall, J.S. 2015. Rapid Liana Colonization along a Secondary Forest Chronosequence. *Biotropica*. **47**(6), pp.672–680.

Battipaglia, G., Saurer, M., Cherubini, P., Calfapietra, C., Mccarthy, H.R., Norby, R.J. and Francesca Cotrufo, M. 2013. Elevated CO2 increases tree-level intrinsic water use efficiency: Insights from carbon and oxygen isotope analyses in tree rings across three forest FACE sites. *New Phytologist*. **197**(2), pp.544–554.

Beer, C., Reichstein, M., Tomelleri, E., Ciais, P., Jung, M., Carvalhais, N., Rödenbeck, C., Arain, M.A., Baldocchi, D., Bonan, G.B., Bondeau, A., Cescatti, A., Lasslop, G., Lindroth, A., Lomas, M., Luyssaert, S., Margolis, H., Oleson, K.W., Roupsard, O., Veenendaal, E., Viovy, N., Williams, C., Woodward, F.I. and Papale, D. 2010. Terrestrial gross carbon dioxide uptake: Global distribution and covariation with climate. *Science*. **329**(5993), pp.834–838.

Béland, M., Baldocchi, D.D., Widlowski, J.L., Fournier, R.A. and Verstraete, M.M. 2014. On seeing the wood from the leaves and the role of voxel size in determining leaf area distribution of forests with terrestrial LiDAR. *Agricultural and Forest Meteorology*. **184**, pp.82–97.

Belote, R.T., Weltzin, J.F. and Norby, R.J. 2004. Response of an understory plant community to elevated [CO2] depends on differential responses of dominant invasive species and is mediated by soil water availability. *New Phytologist*. **161**(3), pp.827–835.

Benitez-Malvido, J. and Martinez-Ramos, M. 2003. Impact of Forest Fragmentation on Understory Plant Species Richness in Amazonia. *Conservation Biology*. **17**(2), pp.389–400.

Boisier, J.P., Ciais, P., Ducharne, A. and Guimberteau, M. 2015. Projected strengthening of Amazonian dry season by constrained climate model simulations. *Nature Climate Change*. **5**(7), pp.656–660.

Bongers, F., Ewango, C.E.N., Sande, M.T. and Poorter, L. 2020. Liana species decline in Congo basin contrasts with global patterns. *Ecology*. **101**(5).

Brienen, R.J.W., Caldwell, L., Duchesne, L., Voelker, S., Barichivich, J., Baliva, M., Ceccantini, G., Di Filippo, A., Helama, S., Locosselli, G.M., Lopez, L., Piovesan, G., Schöngart, J., Villalba, R. and Gloor, E. 2020. Forest carbon sink neutralized by pervasive growth-lifespan trade-offs. *Nature Communications*. **11**(1), pp.1–10.

Brienen, R.J.W., Phillips, O.L., Feldpausch, T.R., Gloor, E., Baker, T.R., Lloyd, J., Lopez-Gonzalez, G., Monteagudo-Mendoza, A., Malhi, Y., Lewis, S.L., Vásquez Martinez, R. and et al. 2015. Long-term decline of the Amazon carbon sink. *Nature*. **519**(7543), pp.344–348.

Brokaw, N.V.L. 1985. Gap-phase regeneration in a tropical forest. *Ecology*. **66**(3), pp.682–687.

Bunker, D.E., DeClerck, F., Bradford, J.C., Colwell, R.K., Perfecto, I., Phillips, O.L., Sankaran, M. and Naeem, S. 2005. Species loss and aboveground carbon storage in a tropical. *Science*. **310**(5750), pp.1029–1031.

Buters, T.M., Bateman, P.W., Robinson, T., Belton, D., Dixon, K.W. and Cross, A.T. 2019. Methodological Ambiguity and Inconsistency Constrain Unmanned Aerial Vehicles as A Silver Bullet for Monitoring Ecological Restoration. *Remote Sensing*. **11**(10), p.1180.

Caballé, G. and Martin, A. 2001. Thirteen years of change in trees and lianas in a Gabonese rainforest. *Plant Ecology*. **152**(2), pp.167–173.

Cahill, J.F., Castelli, J.P. and Casper, B.B. 2001. The Herbivory Uncertainty Principle: Visiting Plants Can Alter Herbivory. *Ecology*. **82**(2), p.307.

Cai, Z.Q., Poorter, L., Cao, K.F. and Bongers, F. 2007. Seedling growth strategies in bauhinia species: Comparing lianas and trees. *Annals of Botany*. **100**(4), pp.831–838.

Cai, Z.Q., Schnitzer, S.A. and Bongers, F. 2009. Seasonal differences in leaf-level physiology give lianas a competitive advantage over trees in a tropical seasonal forest. *Oecologia*. **161**(1), pp.25–33.

Calders, K., Adams, J., Armston, J., Bartholomeus, H., Bauwens, S., Bentley, L.P., Chave, J., Danson, F.M., Demol, M., Disney, M., Gaulton, R., Krishna Moorthy, S.M., Levick, S.R., Saarinen, N., Schaaf, C., Stovall, A., Terryn, L., Wilkes, P. and Verbeeck, H. 2020. Terrestrial laser scanning in forest ecology: Expanding the horizon. *Remote Sensing of Environment*. **251**, p.112102.

Calders, K., Newnham, G., Burt, A., Murphy, S., Raumonen, P., Herold, M., Culvenor, D., Avitabile, V., Disney, M., Armston, J. and Kaasalainen, M. 2015. Nondestructive estimates of above-ground biomass using terrestrial laser scanning. *Methods in Ecology and Evolution*. **6**(2), pp.198–208.

Campanello, P.I., Garibaldi, J.F., Gatti, M.G. and Goldstein, G. 2007. Lianas in a subtropical Atlantic Forest: Host preference and tree growth. *Forest Ecology and Management*. **242**(2–3), pp.250–259.

Campanello, P.I., Manzané, E., Villagra, M., Zhang, Y.J., Panizza, A.M., di Francescantonio, D., Rodriguez, S.A., Chen, Y.J., Santiago, L.S. and Goldstein, G. 2016. Carbon allocation and water relations of lianas versus trees *In*: G. Goldstein and L. Santiago, eds. *Tropical tree physiology*. Cham, Germany: Springer, pp.103–124.

Campbell, E.J.F. and Newbery, D.M.C. 1993. Ecological relationships between lianas and trees in lowland rain forest in Sabah, East Malaysia. *Journal of Tropical Ecology*. **9**(4), pp.469–490.

Campbell, M., Laurance, W.F. and Magrach, A. 2015. Ecological effects of lianas in fragmented forests *In*: S. A. Schnitzer, F. Bongers, R. J. Burnham and F. E. Putz, eds. *Ecology of Lianas*. Chichester, UK: John Wiley & Sons, Ltd, pp.443–450.

Campbell, M.J., Edwards, W., Magrach, A., Alamgir, M., Porolak, G., Mohandass, D. and Laurance, W.F. 2018. Edge disturbance drives liana abundance increase and alteration of liana–host tree interactions in tropical forest fragments. *Ecology and Evolution*. **8**(8), pp.4237–4251.

Cao, L., Coops, N.C., Innes, J.L., Dai, J., Ruan, H. and She, G. 2016. Tree species classification in subtropical forests using small-footprint full-waveform LiDAR data. *International Journal of Applied Earth Observation and Geoinformation*. **49**, pp.39–51.

Carr, J.C. and Slyder, J.B. 2018. Individual tree segmentation from a leaf-off photogrammetric point cloud. *International Journal of Remote Sensing*. **39**(15–16), pp.5195–5210.

Carse, L.E., Fredericksen, T.S. and Licona, J.C. 2000. Liana - Tree species associations in a bolivian dry forest. *Tropical Ecology*. **41**(1), pp.1–10.

Carsten, L.D., Juola, F.A., Male, T.D. and Cherry, S. 2002. Host associations of lianas in a south-east Queensland rain forest. *Journal of Tropical Ecology*. **18**(1), pp.107–120.

Castellanos, A.E., Mooney, H.A., Bullock, S.H., Jones, C. and Robichaux, R. 1989. Leaf, Stem, and Metamer Characteristics of Vines in a Tropical Deciduous Forest in Jalisco, Mexico. *Biotropica*. **21**(1), pp.41–49.

Castro-Esau, K.L., Sánchez-Azofeifa, G.A. and Caelli, T. 2004. Discrimination of lianas and trees with leaf-level hyperspectral data. *Remote Sensing of Environment*. **90**(3), pp.353–372.

Ceballos, S.J. and Malizia, A. 2017. Liana density declined and basal area increased over 12 y in a subtropical montane forest in Argentina. *Journal of Tropical Ecology*. **33**(4), pp.241–248.

Cernusak, L.A., Winter, K., Dalling, J.W., Holtum B, J.A.M., Jaramillo, C., Körner, C., Leakey, A.D.B., Norby, R.J., Poulter, B., Turner, B.L. and Wright, S.J. 2013. Tropical forest responses to increasing atmospheric CO 2 : current knowledge and opportunities for future research. *Functional Plant Biology*. **40**, pp.531–551.

César, R.G., Holl, K.D., Girão, V.J., Mello, F.N.A., Vidal, E., Alves, M.C. and Brancalion, P.H.S. 2016. Evaluating climber cutting as a strategy to restore degraded tropical forests. *Biological Conservation*. **201**, pp.309–313.

César, R.G., Rother, D.C. and Brancalion, P.H.S. 2017. Early Response of Tree Seed Arrival After Liana Cutting in a Disturbed Tropical Forest. *Tropical Conservation Science*. **10**, p.194008291772358.

Chandler, C.J., van der Heijden, G.M.F., Boyd, D.S. and Foody, G.M. 2021a. Detection of Spatial and Temporal Patterns of Liana Infestation Using Satellite-Derived Imagery. *Remote Sensing 2021, Vol. 13, Page 2774*. **13**(14), p.2774.

Chandler, C.J., van der Heijden, G.M.F., Boyd, D.S., Cutler, M.E.J., Costa, H., Nilus, R. and Foody, G.M. 2021b. Remote sensing liana infestation in an aseasonal tropical forest: addressing mismatch in spatial units of analyses M. Disney & K. Anderson, eds. *Remote Sensing in Ecology and Conservation*. **7**(3), pp.397–410.

Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G. and Zanne, A.E. 2009. Towards a worldwide wood economics spectrum. *Ecology Letters*. **12**(4), pp.351–366.

Chave, J., Olivier, J., Bongers, F., Châtelet, P., Forget, P.M., Van Der Meer, P., Norden, N., Riéra, B. and Charles-Dominique, P. 2008. Above-ground biomass and productivity in a rain forest of eastern South America. *Journal of Tropical Ecology*. **24**(4), pp.355–366.

Chave, J., Réjou-Méchain, M., Búrquez, A., Chidumayo, E., Colgan, M.S., Delitti, W.B.C., Duque, A., Eid, T., Fearnside, P.M., Goodman, R.C., Henry, M., Martínez-Yrízar, A., Mugasha, W.A., Muller-Landau, H.C., Mencuccini, M., Nelson, B.W., Ngomanda, A., Nogueira, E.M., Ortiz-Malavassi, E., Pélissier, R., Ploton, P., Ryan, C.M., Saldarriaga, J.G. and Vieilledent, G. 2014. Improved allometric models to estimate the aboveground biomass of tropical trees. *Global Change Biology*. **20**(10), pp.3177–3190.

Chave, J., Riéra, B. and Dubois, M.A. 2001. Estimation of biomass in a neotropical forest of French Guiana: Spatial and temporal variability. *Journal of Tropical Ecology*. **17**(1), pp.79–96.

Chazdon, R.L. 2003. Tropical forest recovery: Legacies of human impact and natural disturbances. *Perspectives in Plant Ecology, Evolution and Systematics*. **6**(1–2), pp.51–71.

Chemura, A., Mutanga, O. and Dube, T. 2017. Remote sensing leaf water stress in coffee (Coffea arabica) using secondary effects of water absorption and random forests. *Physics and Chemistry of the Earth*. **100**, pp.317–324.

Chen, Y.-J., Cao, K.-F., Schnitzer, S.A., Fan, Z.-X., Zhang, J.-L. and Bongers, F. 2015. Water-use advantage for lianas over trees in tropical seasonal forests. *New Phytologist*. **205**(1), pp.128–136.

Chittibabu, C. V. and Parthasarathy, N. 2001. Liana diversity and host relationships in a tropical evergreen forest in the Indian Eastern Ghats. *Ecological Research*. **16**(3), pp.519–529.

Chou, S., Chen, J.M., Yu, H., Chen, B., Zhang, X., Croft, H., Khalid, S., Li, M. and Shi, Q. 2017. Canopy-level photochemical reflectance index from hyperspectral remote sensing and leaf-level non-photochemical quenching as early indicators of water stress in maize. *Remote Sensing*. **9**(8), pp.1–17.

Clark, C.J., Poulsen, J.R., Levey, D.J. and Osenberg, C.W. 2007. Are plant populations seed limited? A critique and meta-analysis of seed addition experiments. *American Naturalist*. **170**(1), pp.128–142.

Clark, D.A. 2004. Tropical forests and global warming: Slowing it down or speeding it up? *Frontiers in Ecology and the Environment*. **2**(2), pp.73–80.

Clark, D.A., Piper, S.C., Keeling, C.D. and Clark, D.B. 2003. Tropical rain forest tree growth and atmospheric carbon dynamics linked to interannual temperature variation during 1984-2000. *PNAS*. **13**(10), pp.5852–5857.

Clark, D.B. and Clark, D.A. 1990. Distribution and effects on tree growth of lianas and woody hemiepiphytes in a costa rican tropical wet forest. *Journal of Tropical Ecology*. **6**(3), pp.321–331.

Clark, D.B., Olivas, P.C., Oberbauer, S.F., Clark, D.A. and Ryan, M.G. 2008. First direct landscape-scale measurement of tropical rain forest Leaf Area Index, a key driver of global primary productivity. *Ecology Letters*. **11**(2), pp.163–172.

Clark, M.L., Clark, D.B. and Roberts, D.A. 2004. Small-footprint lidar estimation of sub-canopy elevation and tree height in a tropical rain forest landscape. *Remote Sensing of Environment*. **91**(1), pp.68–89.

Collins, C.G., Wright, S.J. and Wurzburger, N. 2016. Root and leaf traits reflect distinct resource acquisition strategies in tropical lianas and trees. *Oecologia*. **180**(4), pp.1037–1047.

Condit, R., Watts, K., Bohlman, S.A., Pérez, R., Foster, R.B. and Hubbell, S.P. 2000. Quantifying the deciduousness of tropical forest canopies under varying climates. *Journal of Vegetation Science*. **11**(5), pp.649–658.

Condon, M.A., Sasek, T.W. and Strain, B.R. 1992. Allocation Patterns in Two Tropical Vines in Response to Increased Atmospheric CO 2. *Functional Ecology*. **6**(6), p.680.

Cook, B.D., Corp, L.A., Nelson, R.F., Middleton, E.M., Morton, D.C., McCorkel, J.T., Masek, J.G., Ranson, K.J., Ly, V. and Montesano, P.M. 2013. NASA goddard's LiDAR, hyperspectral and thermal (G-LiHT) airborne imager. *Remote Sensing*. **5**(8), pp.4045–4066.

Coomes, D.A. and Grubb, P.J. 2000. Impacts of root competition in forests and woodlands: A theoretical framework and review of experiments. *Ecological Monographs*. **70**(2), pp.171–207.

Croat, T.B. 1978. *Flora of Barro Colorado Island*. Stanford: Stanford University Press.

Cunliffe, A.M., Brazier, R.E., Graham, H.A., Myers-Smith, I.H., Boer, M.M., Clark, P.E., Cramer, M.D., Encinas-Lara, M.S., Escarzaga, S.M., Fernández-Guisuraga, J.M., Fisher, A.G., Gillespie, B.M., Hanan, N.P., Hanggito, M.S., Havrilla, C.A., Karl, J.W., Lyons, M.B., Mauritz, M.E., McIntire, C.D., Méndez-Barroso, L.A., Power, S.C., Sauer, K.J., Smit, J.L., Steele, C.M., Vargas, S.A. and Villarreal, M.L. 2020. Drone-derived canopy height predicts biomass across non-forest ecosystems globally. *bioRxiv*.

Dalling, J.W. and John, R. 2008. Seed limitation and the coexistence of pioneer trees species *In*: W. P. Carson and S. A. Schnitzer, eds. *Tropical forest community ecology*. Oxford, UK: Wiley - Blackwell Publishing, pp.242–253.

Dalling, J.W., Schnitzer, S.A., Baldeck, C., Harms, K.E., John, R., Mangan, S.A., Lobo, E., Yavitt, J.B. and Hubbell, S.P. 2012. Resource-based habitat associations in a neotropical liana community. *Journal of Ecology*. **100**(5), pp.1174–1182.

Dassot, M., Constant, T. and Fournier, M. 2011. The use of terrestrial LiDAR technology in forest science: Application fields, benefits and challenges. *Annals of Forest Science*. **68**(5), pp.959–974.

Davies, S.J., Abiem, I., Abu Salim, K., Aguilar, S., Allen, D., Alonso, A., Anderson-Teixeira, K., Andrade, A., Arellano, G., Ashton, P.S., Baker, P.J., Baker, M.E., Baltzer, J.L., Basset, Y., Bissiengou, P., Bohlman, S., Bourg, N.A., Brockelman, W.Y., Bunyavejchewin, S., FRP Burslem, D., Cao, M., Cárdenas, D., Chang, L.-W., Chang-Yang, C.-H., Chao, K.-J., Chao, W.-C., Chapman, H., Chen, Y.-Y., Chisholm aa, R.A., Chu ab, C., Chuyong ac, G., Clay ad, K., Comita ae, L.S., Condit af, R., Cordell ag, S., Dattaraja ah, H.S., Adalardo de Oliveira ai, A., den Ouden aj, J., Detto ak, M., Dick, C., Du al, X., Duque am, A., Ediriweera an, S., Ellis, E.C., Laurier Engone Obiang, N., Esufali, S., Ewango ao, C.E., Fernando ap, E.S., Filip ar, J., Fischer as, G.A., Foster at, R., Giambelluca au, T., Giardina ag, C., Gilbert av, G.S., Gonzalez-Akre, E., Gunatilleke aw, I.N., Gunatilleke aw, C., Hao ax, Z., Hau ay, B.C., He az, F., Ni ba, H., Howe bb, R.W., Hubbell bc, S.P., Huth bd, A., Inman-Narahari be, F., Itoh bf, A., Janík bg, D., Jansen aj, P.A., Jiang bi, M., Johnson, D.J., Andrew Jones bj, F., Kanzaki bk, M., Kenfack, D., Kiratiprayoon bl, S., Král bg, K., Krizel, L., Lao, S., Larson bm, A.J., Li bn, Y., Li bo, X., Litton bp, C.M., Liu bq, Y., Liu br, S., Lum bs, S.K., Luskin bt, M.S., Lutz bu, J.A., Truong Luu bv, H., Ma al, K., Makana ao, J.-R., Malhi bw, Y., Martin bx, A., McCarthy, C., McMahon by, S.M., McShea, W.J., Memiaghe bz, H., Mi al, X., Mitre, D., Mohamad ca, M., Monks cb, L., Muller-Landau, H.C., Musili cc, P.M., Myers cd, J.A., Nathalang, A., Min Ngo bs, K., Norden ce, N., Novotny cf, V., O, M.J., cg, B., Orwig ch, D., Ostertag ci, R., Papathanassiou cj, K., Parker ck, G.G., Pérez, R., Perfecto cl, I., Phillips cm, R.P., Pongpattananurak cn, N., Pretzsch co, H., Ren al, H., Reynolds cp, G., Rodriguez cq, L.J., Russo cr, S.E., Sack bc, L., Sang cs, W., Shue by, J., Singh, A., Song ct, G.-Z.M., Sukumar cu, R., Sun, I.-F., Suresh cu, H.S., Swenson cb, N.G., Tan ca, S., Thomas cv, S.C., Thomas cw, D., Thompson cx, J., Turner, B.L., Uowolo ag, A., Uriarte cy, M., Valencia cz, R., Vandermeer, J., Vicentini, A., Visser ak, M., Vrska da, T., Wang ax, X., Wang db, X., Weiblen dc, G.D., Whitfeld dd, T.J., Wolf bb, A., Joseph Wright, S., Xu bn, H., Leong Yao de, T., Yap df, S.L., Ye dg, W., Yu dh, M., Zhang bq, M., Zhu ba, D., Zhu al, L., Zimmerman di, J.K. and Zuleta, D. 2021. ForestGEO: Understanding forest diversity and dynamics through a global observatory network. *Biological Conservation*. **253**, p.108907.

Denslow, J.S. 1987. Tropical Rainforest Gaps and Tree Species Diversity. *Annual Review of Ecology and Systematics*. **18**(1), pp.431–451.

Detto, M. and Xu, X. 2020. Optimal leaf life strategies determine Vc,max dynamic during ontogeny. *New Phytologist*. **228**(1), pp.361–375.

De Deurwaerder, H., Hervé-Fernández, P., Stahl, C., Burban, B., Petronelli, P., Hoffman, B., Bonal, D., Boeckx, P. and Verbeeck, H. 2018. Liana and tree below-ground water competition-evidence for water resource partitioning during the dry season. *Tree Physiology*. **38**(7), pp.1071–1083.

DeWalt, S.J. and Chave, J. 2004. Structure and Biomass of Four Lowland Neotropical Forests. *Biotropica*. **36**(1), pp.7–19.

DeWalt, S.J., Schnitzer, S.A., Alves, L.F., Bongers, F., Burnham, R.J., Cai, Z., Carson, W.P., Chave, J., Chuyong, G.B., Costa, F.R.C., Ewango, C.E.N., Gallagher, R. V., Gerwing, J.J., Amezcua, E.G., Hart, T., Ibarra-Manríquez, G., Ickes, K., Kenfack, D., Letcher, S.G., Macía, M.J., Makana, J.-R., Malizia, A., Martínez-Ramos, M., Mascaro, J., Muthumperumal, C., Muthuramkumar, S., Nogueira, A., Parren, M.P.E., Parthasarathy, N., Pérez-Salicrup, D.R., Putz, F.E., Romero-Saltos, H.G., Sridhar Reddy, M., Sainge, M.N., Thomas, D. and Melis, J. van 2015. Biogeographical patterns of liana abundance and diversity *In*: Stefan A. Schnitzer, Frans Bongers, Robyn J. Burnham and Francis E. Putz, eds. *Ecology of Lianas*. Chichester, UK: John Wiley & Sons, Ltd, pp.131–146.

DeWalt, S.J., Schnitzer, S.A., Chave, J., Bongers, F., Burnham, R.J., Cai, Z., Chuyong, G., Clark, D.B., Ewango, C.E.N., Gerwing, J.J., Gortaire, E., Hart, T., Ibarra-Manríquez, G., Ickes, K., Kenfack, D., Macía, M.J., Makana, J.-R., Martínez-Ramos, M., Mascaro, J., Moses, S., Muller-Landau, H.C., Parren, M.P.E., Parthasarathy, N., Pérez-Salicrup, D.R., Putz, F.E., Romero-Saltos, H. and Thomas, D. 2010. Annual Rainfall and Seasonality Predict Pan-tropical Patterns of Liana Density and Basal Area. *Biotropica*. **42**(3), pp.309–317.

DeWalt, S.J., Schnitzer, S.A. and Denslow, J.S. 2000. Density and diversity of lianas along a chronosequence in a central Panamanian lowland forest. *Journal of Tropical Ecology*. **16**(1), pp.1–19.

Dias, A.S., dos Santos, K., dos Santos, F.A.M. and Martins, F.R. 2017. How liana loads alter tree allometry in tropical forests. *Plant Ecology*. **218**(2), pp.119–125.

Dillenburg, L.R., Whigham, D.F., Teramura, A.H. and Forseth, I.N. 1993a. Effects of below-and aboveground competition from the vines Lonicera japonica and Parthenocissus quinquefolia on the growth of the tree host Liquidambar styraciflua. *Oecologia*. **93**, pp.48–54.

Dillenburg, L.R., Whigham, D.F., Teramura, A.H. and Forseth, I.N. 1993b. Effects of vine competition on availability of light, water, and nitrogen to a tree host (Liquidambar styraciflua). *American Journal of Botany*. **80**(3), pp.244–252.

Drusch, M., Moreno, J., Del Bello, U., Franco, R., Goulas, Y., Huth, A., Kraft, S., Middleton, E.M., Miglietta, F., Mohammed, G., Nedbal, L., Rascher, U., Schuttemeyer, D. and Verhoef, W. 2017. The FLuorescence EXplorer Mission Concept-ESA's Earth Explorer 8. *IEEE Transactions on Geoscience and Remote Sensing*. **55**(3), pp.1273–1284.

Dubayah, R., Blair, J.B., Goetz, S., Fatoyinbo, L., Hansen, M., Healey, S., Hofton, M., Hurtt, G., Kellner, J., Luthcke, S., Armston, J., Tang, H., Duncanson, L., Hancock, S., Jantz, P., Marselis, S., Patterson, P.L., Qi, W. and Silva, C. 2020. The Global Ecosystem Dynamics Investigation: High-resolution laser ranging of the Earth's forests and topography. *Science of Remote Sensing*. **1**, p.100002.

Duffy, P.B., Brando, P., Asner, G.P. and Field, C.B. 2015. Projections of future meteorological drought and wet periods in the Amazon. *Proceedings of the National Academy of Sciences of the United States of America*. **112**(43), pp.13172–13177.

Duncanson, L., Armston, J., Disney, M., Avitabile, V., Barbier, N., Calders, K., Carter, S., Chave, J., Herold, M., MacBean, N., McRoberts, R., Minor, D., Paul, K., Réjou-Méchain, M., Roxburgh, S., Williams, M., Albinet, C., Baker, T., Bartholomeus, H., Bastin, J.F., Coomes, D., Crowther, T., Davies, S., de Bruin, S., De Kauwe, M., Domke, G., Dubayah, R., Falkowski, M., Fatoyinbo, L., Goetz, S., Jantz, P., Jonckheere, I., Jucker, T., Kay, H., Kellner, J., Labriere, N., Lucas, R., Mitchard, E., Morsdorf, F., Naesset, E., Park, T., Phillips, O.L., Ploton, P., Puliti, S., Quegan, S., Saatchi, S., Schaaf, C., Schepaschenko, D., Scipal, K., Stovall, A., Thiel, C., Wulder, M.A., Camacho, F., Nickeson, J., Román, M. and Margolis, H. 2021. Aboveground Woody Biomass Product Validation Good Practices Protocol. Version 1.0 *In*: *Good Practices for Satellite Derived Land Product Validation*. Land Product Validation Subgroup (WGCV/CEOS), p.236.

Durán, S.M. and Gianoli, E. 2013. Carbon stocks in tropical forests decrease with liana density. *Biology Letters*. **9**(4), pp.3–6.

Durán, S.M., Martin, R.E., Díaz, S., Maitner, B.S., Malhi, Y., Salinas, N., Shenkin, A., Silman, M.R., Wieczynski, D.J., Asner, G.P., Bentley, L.P., Savage, V.M. and Enquist, B.J. 2019. Informing trait-based ecology by assessing remotely sensed functional diversity across a broad tropical temperature gradient. *Science Advances*. **5**(12), p.eaaw8114.

Durán, S.M. and Sánchez-Azofeifa, G.A. 2015. Liana Effects on Carbon Storage and Uptake in Mature and Secondary Tropical Forests *In*: N. Parthasarathy, ed. *Biodiversity of Lianas*. Springer International Publishing, pp.43–55.

Enquist, B.J. and Enquist, C.A.F. 2011. Long-term change within a Neotropical forest: Assessing differential functional and floristic responses to disturbance and drought. *Global Change Biology*. **17**(3), pp.1408–1424.

Estrada-Villegas, S., Hall, J.S., van Breugel, M. and Schnitzer, S.A. 2021. Lianas do not reduce tree biomass accumulation in young successional tropical dry forests. *Oecologia*. **195**(4), pp.1019–1029.

Estrada-Villegas, S., Hall, J.S., Breugel, M. and Schnitzer, S.A. 2020. Lianas Reduce Biomass Accumulation in Early-Successional Tropical Forests. *Ecology*. **101**(5), p.e02989.

Ewango, C.E.N. 2010. *The liana assemblage ofa Congolian rainforest. Diversity structure and function*. PhD Thesis. Wageningen University, Netherlands.

Ewers, F.W., Fisher, J.B. and Chiu, S.T. 1990. A survey of vessel dimensions in stems of tropical lianas and other growth forms. *Oecologia*. **84**(4), pp.544–552.

Ewers, F.W., Fisher, J.B. and Fichtner, K. 1991. Water flux and xylem structure in vines *In*: F. E. Putz and H. A. Mooney, eds. *Biology of Vines*. Cambridge, UK: Cambridge University Press, pp.127–160.

Ewers, F.W., Rosell, J.A. and Olson, M.E. 2015. Lianas as structural parasites *In*: U. Hacke, ed. *Functional and Ecological Xylem Anatomy*. Cham: Springer International Publishing, pp.163–188.

Fadrique, B. and Homeier, J. 2016. Elevation and topography influence community structure, biomass and host tree interactions of lianas in tropical montane forests of southern Ecuador K. Woods, ed. *Journal of Vegetation Science*. **27**(5), pp.958–968.

Fauset, S., Gloor, M.U., Aidar, M.P.M., Freitas, H.C., Fyllas, N.M., Marabesi, M.A., Rochelle, A.L.C., Shenkin, A., Vieira, S.A. and Joly, C.A. 2017. Tropical forest light regimes in a human-modified landscape. *Ecosphere*. **8**(11), pp.e02002, 1–15.

Featherly, H.T. 1941. The effect of grapevines on trees. *Oklahoma Academy of Science*. **21**, pp.61–62.

Feeley, K.J., Joseph Wright, S., Nur Supardi, M.N., Kassim, A.R. and Davies, S.J. 2007. Decelerating growth in tropical forest trees. *Ecology Letters*. **10**(6), pp.461–469.

Feldpausch, T.R., Lloyd, J., Lewis, S.L., Brienen, R.J.W., Gloor, M., Monteagudo Mendoza, A., Lopez-Gonzalez, G., Banin, L., Abu Salim, K., Affum-Baffoe, K., Alexiades, M., Almeida, S., Amaral, I., Andrade, A., Aragão, L.E.O.C., Araujo Murakami, A., Arets, E.J.M.M., Arroyo, L., Aymard C., G.A., Baker, T.R., Bánki, O.S., Berry, N.J., Cardozo, N., Chave, J., Comiskey, J.A., Alvarez, E., de Oliveira, A., Di Fiore, A., Djagbletey, G., Domingues, T.F., Erwin, T.L., Fearnside, P.M., França, M.B., Freitas, M.A., Higuchi, N., Iida, Y., Jiménez, E., Kassim, A.R., Killeen, T.J., Laurance, W.F., Lovett, J.C., Malhi, Y., Marimon, B.S., Marimon-Junior, B.H., Lenza, E., Marshall, A.R., Mendoza, C., Metcalfe, D.J., Mitchard, E.T.A., Neill, D.A., Nelson, B.W., Nilus, R., Nogueira, E.M., Parada, A., Peh, K.S.-H., Pena Cruz, A., Peñuela, M.C., Pitman, N.C.A., Prieto, A., Quesada, C.A., Ramírez, F., Ramírez-Angulo, H., Reitsma, J.M., Rudas, A., Saiz, G., Salomão, R.P., Schwarz, M., Silva, N., Silva-Espejo, J.E., Silveira, M., Sonké, B., Stropp, J., Taedoumg, H.E., Tan, S., ter Steege, H., Terborgh, J., Torello-Raventos, M., van der Heijden, G.M.F., Vásquez, R., Vilanova, E., Vos, V.A., White, L., Willcock, S., Woell, H. and Phillips, O.L. 2012. Tree height integrated into pantropical forest biomass estimates. *Biogeosciences*. **9**(8), pp.3381–3403.

Feldpausch, T.R., Phillips, O.L., Brienen, R.J.W., Gloor, E., Lloyd, J., Lopez-Gonzalez, G., Monteagudo-Mendoza, A., Malhi, Y., Alarcón, A., Álvarez Dávila, E., Alvarez-Loayza, P., Andrade, A., Aragao, L.E.O.C., Arroyo, L., Aymard C., G.A., Baker, T.R., Baraloto, C., Barroso, J., Bonal, D., Castro, W., Chama, V., Chave, J., Domingues, T.F., Fauset, S., Groot, N., Honorio Coronado, E., Laurance, S., Laurance, W.F., Lewis, S.L., Licona, J.C., Marimon, B.S., Marimon-Junior, B.H., Mendoza Bautista, C., Neill, D.A., Oliveira, E.A., Oliveira dos Santos, C., Pallqui Camacho, N.C., Pardo-Molina, G., Prieto, A., Quesada, C.A., Ramírez, F., Ramírez-Angulo, H., Réjou-Méchain, M., Rudas, A., Saiz, G., Salomão, R.P., Silva-Espejo, J.E., Silveira, M., ter Steege, H., Stropp, J., Terborgh, J., Thomas-Caesar, R., van der Heijden, G.M.F., Vásquez Martinez, R., Vilanova, E. and Vos, V.A. 2016. Amazon forest response to repeated droughts. *Global Biogeochemical Cycles*. **30**(7), pp.964–982.

Feng, X., Porporato, A. and Rodriguez-Iturbe, I. 2013. Changes in rainfall seasonality in the tropics. *Nature Climate Change*. **3**(9), pp.811–815.

Féret, J.B. and Asner, G.P. 2014. Mapping tropical forest canopy diversity using high-fidelity imaging spectroscopy. *Ecological Applications*. **24**(6), pp.1289–1296.

Féret, J.B. and Asner, G.P. 2012. Semi-supervised methods to identify individual crowns of lowland tropical canopy species using imaging spectroscopy and lidar. *Remote Sensing*. **4**(8), pp.2457–2476.

Ferreira, M.P., Wagner, F.H., Aragão, L.E.O.C., Shimabukuro, Y.E. and de Souza Filho, C.R. 2019. Tree species classification in tropical forests using visible to shortwave infrared WorldView-3 images and texture analysis. *ISPRS Journal of Photogrammetry and Remote Sensing*. **149**, pp.119–131.

Field, C. and Mooney, H.A. 1986. The photosynthesis-nitrogen relationship in wild plants *In*: T. J. Givnish, ed. *Perspectives on plant competition*. San Diego, California: Academic Press, pp.25–55.

Fisher, J. and Ewers, F. 1995. Vessel dimensions in liana and tree species of Gnetum (Gnetales). *American Journal of Botany*. **82**(11), pp.1350–1357.

Fonseca, M.G., Vidal, E. and Maës dos Santos, F.A. 2009. Intraspecific Variation in the Fruiting of an Amazonian Timber Tree: Implications for Management. *Biotropica*. **41**(2), pp.179–185.

Foody, G.M. 2003. Remote sensing of tropical forest environments: Towards the monitoring of environmental resources for sustainable development. *International Journal of Remote Sensing*. **24**(20), pp.4035–4046.

Foody, G.M. and Cutler, M.E.J. 2006. Mapping the species richness and composition of tropical forests from remotely sensed data with neural networks. *Ecological Modelling*. **195**(1–2), pp.37–42.

Foster, J.R., Townsend, P.A. and Zganjar, C.E. 2008. Spatial and temporal patterns of gap dominance by low-canopy lianas detected using EO-1 Hyperion and Landsat Thematic Mapper. *Remote Sensing of Environment*. **112**(5), pp.2104–2117.

Fu, P.-L., Liu, W.-J., Fan, Z.-X. and Cao, K.-F. 2016. Is fog an important water source for woody plants in an Asian tropical karst forest during the dry season? *Ecohydrology*. **9**(6), pp.964–972.

Fu, R., Yin, L., Li, W., Arias, P.A., Dickinson, R.E., Huang, L., Chakraborty, S., Fernandes, K., Liebmann, B., Fisher, R. and Myneni, R.B. 2013. Increased dry-season length over southern Amazonia in recent decades and its implication for future climate projection. *Proceedings of the National*

Academy of Sciences of the United States of America. **110**(45), pp.18110–18115.

Galbraith, D., Malhi, Y., Affum-Baffoe, K., Castanho, A.D.A., Doughty, C.E., Fisher, R.A., Lewis, S.L., Peh, K.S.H., Phillips, O.L., Quesada, C.A., Sonké, B. and Lloyd, J. 2013. Residence times of woody biomass in tropical forests. *Plant Ecology and Diversity*. **6**(1), pp.139–157.

García León, M.M., Martínez Izquierdo, L., Mello, F.N.A., Powers, J.S. and Schnitzer, S.A. 2018. Lianas reduce community-level canopy tree reproduction in a Panamanian forest. *Journal of Ecology*. **106**(2), pp.737–745.

Garcia, R.A., Cabeza, M., Rahbek, C. and Araujo, M.B. 2014. Multiple Dimensions of Climate Change and Their Implications for Biodiversity. *Science*. **344**(6183), pp.1247579–1247579.

Garrido-Pérez, E.I., Dupuy, J.M., Durán-García, R., Ucan-May, M., Schnitzer, S.A. and Gerold, G. 2008. Effects of lianas and Hurricane Wilma on tree damage in the Yucatan Peninsula, Mexico. *Journal of Tropical Ecology*. **24**(5), pp.559–562.

Gartner, B.L., Bullock, S.H., Mooney, H.A., Brown, V.B. and Whitbeck, J.L. 1990. Water transport properties of vine and tree stems in a tropical deciduous forest. *American Journal of Botany*. **77**(6), pp.742–749.

Gehring, C., Park, S. and Denich, M. 2004. Liana allometric biomass equations for Amazonian primary and secondary forest. *Forest Ecology and Management*. **195**(1–2), pp.69–83.

Van Gelder, H.A., Poorter, L. and Sterck, F.J. 2006. Wood mechanics, allometry, and life-history variation in a tropical rain forest tree community. *New Phytologist*. **171**(2), pp.367–378.

Gentry, A. and Dodson, C. 1987. Contribution of Nontrees to Species Richness of a Tropical Rain Forest. *Biotropica*. **19**(2), pp.149–156.

Gentry, A.H. 1985. An ecotaxonomic survey of Panamanian lianas *In*: W. G. D'Arcy and M. D. Correa, eds. *The Botany and Natural History of Panama*. St Louis, Missouri, USA: Missouri Botanical Garden, pp.29–42.

Gentry, A.H. 1988. Changes in plant community diversity and floristic composition on environmental and geographical gradients. *Annals of the Missouri Botanical Garden*. **75**, pp.1–34.

Gentry, A.H. 1991. The distribution and evolution of climbing plants. *In*: F. E. Putz and H. A. Mooney, eds. *The Biology of Vines*. Cambridge: Cambridge University Press, pp.3–49.

Gerwing, J.J. 2004. Life history diversity among six species of canopy lianas in an old-growth forest of the eastern Brazilian Amazon *In*: *Forest Ecology and Management* [Online]., pp.57–72. [Accessed 15 October 2020]. Available from: https://epublications.marquette.edu/liana_articles/324.

Gerwing, J.J. 2001. Testing liana cutting and controlled burning as silvicultural treatments for a logged forest in the eastern Amazon. *Journal of Applied Ecology*. **38**(6), pp.1264–1276.

Gerwing, J.J. and Farias, D.L. 2000. Integrating liana abundance and forest stature into an estimate of total aboveground biomass for an eastern Amazonian forest. *Journal of Tropical Ecology*. **16**(3), pp.327–335.

Gerwing, J.J., Schnitzer, S.A., Burnham, R.J., Bongers, F., Chave, J., DeWalt, S.J., Ewango, C.E.N., Foster, R., Kenfack, D., Martínez-Ramos, M., Parren, M., Parthasarathy, N., Pérez-Salicrup, D.R., Putz, F.E. and Thomas, D.W. 2006. A standard protocol for liana censuses. *Biotropica*. **38**(2), pp.256–261.

Getzin, S., Wiegand, K. and Schöning, I. 2012. Assessing biodiversity in forests using very high-resolution images and unmanned aerial vehicles. *Methods in Ecology and Evolution*. **3**(2), pp.397–404.

Gianoli, E. 2015. Evolutionary implications of the climbing habit in plants *In*: S. A. Schnitzer, F. Bongers, R. J. Burnham and F. E. Putz, eds. *Ecology of Lianas*. Chichester: John Wiley & Sons, Ltd, pp.239–250.

Gilbert, B., Wright, S.J., Muller-Landau, H.C., Kitajima, K. and Hernandéz, A. 2006. Life history trade-offs in tropical trees and lianas. *Ecology*. **87**(5), pp.1281–1288.

Gillespie, T.W., Foody, G.M., Rocchini, D., Giorgi, A.P. and Saatchi, S. 2008. Measuring and modelling biodiversity from space. *Progress in Physical Geography*. **32**(2), pp.203–221.

Goetz, A.F.H., Vane, G., Solomon, J.E. and Rock, B.N. 1985. Imaging spectrometry for earth remote sensing. *Science*. **228**(4704), pp.1147–1153.

Graham, E.A., Mulkey, S.S., Kitajima, K., Phillips, N.G. and Wright, S.J. 2003. Cloud cover limits net CO2 uptake and growth of a rainforest tree during tropical rainy seasons. *Proceedings of the National Academy of Sciences of the United States of America*. **100**(2), pp.572–576.

Granados, J. and Körner, C. 2002. In deep shade, elevated CO2 increases the vigor of tropical climbing plants. *Global Change Biology*. **8**(11), pp.1109–1117.

Grauel, W.T. and Putz, F.E. 2004. Effects of lianas on growth and regeneration of Prioria copaifera in Darien, Panama. *Forest Ecology and Management*. **190**(1), pp.99–108.

Gray, S.B., Dermody, O. and Delucia, E.H. 2010. Spectral reflectance from a soybean canopy exposed to elevated CO 2 and O3. *Journal of Experimental Botany*. **61**(15), pp.4413–4422.

Grogan, J. and Matthew Landis, R. 2009. Growth history and crown vine coverage are principal factors influencing growth and mortality rates of big-leaf mahogany *Swietenia macrophylla* in Brazil. *Journal of Applied Ecology*. **46**(6), pp.1283–1291.

Guan, K., Pan, M., Li, H., Wolf, A., Wu, J., Medvigy, D., Caylor, K.K., Sheffield, J., Wood, E.F., Malhi, Y., Liang, M., Kimball, J.S., Saleska, S.R., Berry, J., Joiner, J. and Lyapustin, A.I. 2015. Photosynthetic seasonality of global tropical forests constrained by hydroclimate. *Nature Geoscience*. **8**(4), pp.284–289.

Guanter, L., Kaufmann, H., Segl, K., Foerster, S., Rogass, C., Chabrillat, S., Kuester, T., Hollstein, A., Rossner, G., Chlebek, C., Straif, C., Fischer, S., Schrader, S., Storch, T., Heiden, U., Mueller, A., Bachmann, M., Mühle, H., Müller, R., Habermeyer, M., Ohndorf, A., Hill, J., Buddenbaum, H., Hostert, P., van der Linden, S., Leitão, P., Rabe, A., Doerffer, R., Krasemann, H., Xi, H., Mauser, W., Hank, T., Locherer, M., Rast, M., Staenz, K. and Sang, B. 2015. The EnMAP Spaceborne Imaging Spectroscopy Mission for Earth Observation. *Remote Sensing*. **7**(7), pp.8830–8857.

Guzmán, J.A., Rivard, B. and Sánchez-Azofeifa, A. 2018. Discrimination of liana and tree leaves from a Neotropical Dry Forest using visible-near infrared and longwave infrared reflectance spectra. *Remote Sensing of Environment*. **219**, pp.135–144.

Guzmán, J.A. and Sánchez-Azofeifa, A. 2021. Prediction of leaf traits of lianas and trees via the integration of wavelet spectra in the visible-near infrared and thermal infrared domains. *Remote Sensing of Environment*. **259**, p.112406.

Hättenschwiler, S. and Korner, C. 2003. Does elevated CO2 facilitate naturalization of the non-indigenous Prunus laurocerasus in Swiss temperate forests? *Functional Ecology*. **17**(6), pp.778–785.

Hättenschwiler, S., Tiunov, A. V. and Scheu, S. 2005. Biodiversity and litter decomposition in terrestrial ecosystems. *Annual Review of Ecology, Evolution, and Systematics*. **36**, pp.191–218.

Hegarty, E.E. and Caballé, G. 1991. Distribution and abundance of vines in forest communities *In*: F. E. Putz, ed. *The Biology of Vines*. Cambridge, UK: Cambridge University Press, pp.313–334.

van der Heijden, G.M.F., Feldpausch, T.R., Herrero, A. de la F., van der Velden, N.K. and Phillips, O.L. 2010. Calibrating the liana crown occupancy index in Amazonian forests. *Forest Ecology and Management*. **260**(4), pp.549–555.

van der Heijden, G.M.F., Healey, J.R. and Phillips, O.L. 2008. Infestation of trees by lianas in a tropical forest in Amazonian Peru. *Journal of Vegetation Science*. **19**(6), pp.747–756.

van der Heijden, G.M.F. and Phillips, O.L. 2008. What controls liana success in Neotropical forests? *Global Ecology and Biogeography*. **17**(3), pp.372–383.

van der Heijden, G.M.F. and Phillips, O.L. 2009a. Liana infestation impacts tree growth in a lowland tropical moist Forest. *Biogeosciences*. **6**(10), pp.2217–2226.

van der Heijden, G.M.F. and Phillips, O.L. 2009b. Environmental effects on Neotropical liana species richness. *Journal of Biogeography*. **36**(8), pp.1561–1572.

van der Heijden, G.M.F., Phillips, O.L. and Schnitzer, S.A. 2015. Impacts of lianas on forest-level carbon storage and sequestration *In*: S. A. Schnitzer, F. Bongers, R. J. Burnham and F. E. Putz, eds. *Ecology of Lianas*. Chichester, UK: John Wiley & Sons, Ltd, pp.164–174.

van der Heijden, G.M.F., Powers, J.S. and Schnitzer, S.A. 2019. Effect of lianas on forest-level tree carbon accumulation does not differ between seasons: Results from a liana removal experiment in Panama N. Norden, ed. *Journal of Ecology*. **107**(4), pp.1890–1900.

van der Heijden, G.M.F., Powers, J.S. and Schnitzer, S.A. 2015. Lianas reduce carbon accumulation and storage in tropical forests. *Proceedings of the National Academy of Sciences of the United States of America*. **112**(43), pp.13267–13271.

van der Heijden, G.M.F., Schnitzer, S.A., Powers, J.S. and Phillips, O.L. 2013. Liana Impacts on Carbon Cycling, Storage and Sequestration in Tropical Forests. *Biotropica*. **45**(6), pp.682–692.

Hesketh, M. and Sánchez-Azofeifa, G.A. 2012. The effect of seasonal spectral variation on species classification in the Panamanian tropical forest. *Remote Sensing of Environment*. **118**, pp.73–82.

Hogan, J.A., Mayorquín, S., Rice, K., Thompson, J., Zimmerman, J.K. and Brokaw, N. 2017. Liana dynamics reflect land-use history and hurricane response in a Puerto Rican forest. *Journal of Tropical Ecology*. **33**(2), pp.155–164.

Holbrook, N.M. and Putz, F.E. 1996. Physiology of tropical vines and hemiepiphytes: plants that climb up and plants that climb down *In*: S. S. Mulkey, R. L. Chazdon and A. P. Smith, eds. *Tropical Forest Plant Ecophysiology*. Boston, MA: Springer, pp.363–394.

Holt, R.D., Grover, J. and Tilman, D. 1994. Simple rules for interspecific dominance in systems with exploitative and apparent competition. *American Naturalist*. **144**(5), pp.741–771.

Horvitz, C.C., Pascarella, J.B., McMann, S., Freedman, A. and Hofstetter, R.H. 1998. Functional roles of invasive non-indigenous plants in Hurricane-affected subtropical hardwood forests. *Ecological Applications*. **8**(4), pp.947–974.

Hu, T., Su, Y., Xue, B., Liu, J., Zhao, X., Fang, J. and Guo, Q. 2016. Mapping Global Forest Aboveground Biomass with Spaceborne LiDAR, Optical Imagery, and Forest Inventory Data. *Remote Sensing*. **8**(7), p.565.

Hubau, W., Lewis, S.L., Phillips, O.L., Affum-Baffoe, K., Beeckman, H., Cuní-Sanchez, A., Daniels, A.K., Ewango, C.E.N., Fauset, S., Mukinzi, J.M., Sheil, D., Sonké, B., Sullivan, M.J.P., Sunderland, T.C.H., Taedoumg, H., Thomas, S.C., White, L.J.T., Abernethy, K.A., Adu-Bredu, S., Amani, C.A., Baker, T.R., Banin, L.F., Baya, F., Begne, S.K., Bennett, A.C., Benedet, F., Bitariho, R., Bocko, Y.E., Boeckx, P., Boundja, P., Brienen, R.J.W., Brncic, T., Chezeaux, E., Chuyong, G.B., Clark, C.J., Collins, M., Comiskey, J.A., Coomes, D.A., Dargie, G.C., de Haulleville, T., Kamdem, M.N.D., Doucet, J.L., Esquivel-Muelbert, A., Feldpausch, T.R., Fofanah, A., Foli, E.G., Gilpin, M., Gloor, E., Gonmadje, C., Gourlet-Fleury, S., Hall, J.S., Hamilton, A.C., Harris, D.J., Hart, T.B., Hockemba, M.B.N., Hladik, A., Ifo, S.A., Jeffery, K.J., Jucker, T., Yakusu, E.K., Kearsley, E., Kenfack, D., Koch, A., Leal, M.E., Levesley, A., Lindsell, J.A., Lisingo, J., Lopez-Gonzalez, G., Lovett, J.C., Makana, J.R., Malhi, Y., Marshall, A.R., Martin, J., Martin, E.H., Mbayu, F.M., Medjibe, V.P., Mihindou, V., Mitchard, E.T.A., Moore, S., Munishi, P.K.T., Bengone, N.N., Ojo, L., Ondo, F.E., Peh, K.S.H., Pickavance, G.C., Poulsen, A.D., Poulsen, J.R., Qie, L., Reitsma, J., Rovero, F., Swaine, M.D., Talbot, J., Taplin, J., Taylor, D.M., Thomas, D.W., Toirambe, B., Mukendi, J.T., Tuagben, D., Umunay, P.M., van der Heijden, G.M.F., Verbeeck, H., Vleminckx, J., Willcock, S., Wöll, H., Woods, J.T. and Zemagho, L. 2020. Asynchronous carbon sink saturation in African and Amazonian tropical forests. *Nature*. **579**(7797), pp.80–87.

Hubbell, S.P., Foster, R.B., O'Brien, S.T., Harms, K.E., Condit, R., Wechsler, B., Wright, S.J. and Loo De Lao, S. 1999. Light-gap disturbances, recruitment limitation, and tree diversity in a neotropical forest. *Science*. **283**(5401), pp.554–557.

Ihuoma, S.O. and Madramootoo, C.A. 2019. Sensitivity of spectral vegetation indices for monitoring water stress in tomato plants. *Computers and Electronics in Agriculture*. **163**, p.104860.

Ingwell, L.L., Joseph Wright, S., Becklund, K.K., Hubbell, S.P. and Schnitzer, S.A. 2010. The impact of lianas on 10 years of tree growth and mortality on Barro Colorado Island, Panama. *Journal of Ecology*. **98**(4), pp.879–887.

Isnard, S. and Feild, T.S. 2015. The evolution of angiosperm lianescence: a perspective from xlem structure-function *In*: S. A. Schnitzer, F. Bongers, R. J. Burnham and F. E. Putz, eds. *Ecology of Lianas*. Chichester, UK: John Wiley & Sons, Ltd, pp.221–239.

Iverson, L.R., Graham, R.L. and Cook, E.A. 1989. Applications of satellite remote sensing to forested ecosystems. *Landscape Ecology*. **3**(2), pp.131–143.

Jakubowski, M.K., Guo, Q. and Kelly, M. 2013. Tradeoffs between lidar pulse density and forest measurement accuracy. *Remote Sensing of Environment*. **130**, pp.245–253.

Janzen, D.H. 1969. Allelopathy by Myrmecophytes: The Ant Azteca as an Allelopathic Agent of Cecropia. *Ecology*. **50**(1), pp.147–153.

Janzen, D.H. 1973. Dissolution of Mutualism between Cecropia and Its Azteca Ants. *Biotropica*. **5**(1), p.15.

Jiang, Y., Wang, J., Zhang, L., Zhang, G., Li, X. and Wu, J. 2019. Geometric processing and accuracy verification of Zhuhai-1 hyperspectral satellites. *Remote Sensing*. **11**(9).

Johnson, D.M., Domec, J.C., Woodruff, D.R., McCulloh, K.A. and Meinzer, F.C. 2013. Contrasting hydraulic strategies in two tropical lianas and their host trees. *American Journal of Botany*. **100**(2), pp.374–383.

Jones, I.L., Peres, C.A., Benchimol, M., Bunnefeld, L. and Dent, D.H. 2017. Woody lianas increase in dominance and maintain compositional integrity across an Amazonian dam-induced fragmented landscape. *PLoS ONE*. **12**(10).

Kachamba, D., Ørka, H., Gobakken, T., Eid, T. and Mwase, W. 2016. Biomass Estimation Using 3D Data from Unmanned Aerial Vehicle Imagery in a Tropical Woodland. *Remote Sensing*. **8**(11), p.968.

Kainer, K.A., Wadt, L.H.O., Gomes-Silva, D.A.P. and Capanu, M. 2006. Liana loads and their association with Bertholletia excelsa fruit and nut production, diameter growth and crown attributes. *Journal of Tropical Ecology*. **22**(2), pp.147–154.

Kainer, K.A., Wadt, L.H.O. and Staudhammer, C.L. 2007. Explaining variation in Brazil nut fruit production. *Forest Ecology and Management*. **250**(3), pp.244–255.

Kainer, K.A., Wadt, L.H.O. and Staudhammer, C.L. 2014. Testing a silvicultural recommendation: Brazil nut responses 10 years after liana cutting. *Journal of Applied Ecology*. **51**(3), pp.655–663.

Kalacska, M., Bohlman, S., Sanchez-Azofeifa, G.A., Castro-Esau, K. and Caelli, T. 2007. Hyperspectral discrimination of tropical dry forest lianas and trees: Comparative data reduction approaches at the leaf and canopy levels. *Remote Sensing of Environment*. **109**(4), pp.406–415.

Kalácska, M., Calvo-Alvarado, J.C. and Sánchez-Azofeifa, G.A. 2005. Calibration and assessment of seasonal changes in leaf area index of a tropical dry forest in different stages of succession. *Tree Physiology*. **25**(6), pp.733–744.

Kato, R. 1978. Plant biomass and growth of increment studies in Pasoh Forest Rewerve. *Malayan Nature Journal*. **30**, pp.211–224.

Kaya, A., Keceli, A.S., Catal, C., Yalic, H.Y., Temucin, H. and Tekinerdogan, B. 2019. Analysis of transfer learning for deep neural network based plant classification models. *Computers and Electronics in Agriculture*. **158**, pp.20–29.

Kirby, K.R. and Potvin, C. 2007. Variation in carbon storage among tree species: Implications for the management of a small-scale carbon sink project. *Forest Ecology and Management*. **246**(2–3), pp.208–221.

Kitajima, K. 1994. Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance of 13 tropical trees. *Oecologia*. **98**(3–4), pp.419–428.

Kitajima, K., Mulkey, S.S. and Wright, S.J. 2005. Variation in crown light utilization characteristics among tropical canopy trees. *Annals of Botany*. **95**(3), pp.535–547.

Klimas, C.A., Kainer, K.A., Wadt, L.H., Staudhammer, C.L., Rigamonte-Azevedo, V., Correia, M.F. and Da Silva Lima, L.M. 2012. Control of Carapa guianensis phenology and seed production at multiple scales: A five-year study exploring the influences of tree attributes, habitat heterogeneity and climate cues. *Journal of Tropical Ecology*. **28**(1), pp.105–118.

Knight, D.H. 1975. A Phytosociological Analysis of Species-Rich Tropical Forest on Barro Colorado Island, Panama. *Ecological Monographs*. **45**(3), pp.259–284.

Kohyama, T., Suzuki, E., Partomihardjo, T., Yamada, T. and Kubo, T. 2003. Tree species differentiation in growth, recruitment and allometry in relation to maximum height in a Bornean mixed dipterocarp forest. *Journal of Ecology*. **91**(5), pp.797–806.

Kokaly, R.F., Clark, R.N., Swayze, G.A., Livo, K.E., Hoefen, T.M., Pearson, N.C., Wise, R.A., Benzel, W.M., Lowers, H.A., Driscoll, R.L. and Klein, A.J. 2017. *USGS Spectral Library Version 7* [Online]. [Accessed 13 May 2021]. Available from: https://doi.org/10.3133/ds1035.

Körner, C. 2006. Forests, biodivsity and CO2: surprises are certain. *Biologist*. **53**(2), pp.82–90.

Körner, C. and Arnone, J.A. 1992. Responses to elevated carbon dioxide in artificial tropical ecosystems. *Science*. **257**(5077), pp.1672–1675.

Krishna Moorthy, S.M., Bao, Y., Calders, K., Schnitzer, S.A. and Verbeeck, H. 2019. Semi-automatic extraction of liana stems from terrestrial LiDAR point clouds of tropical rainforests. *ISPRS Journal of Photogrammetry and Remote Sensing*. **154**, pp.114–126.

Krishna Moorthy, S.M., Raumonen, P., Van den Bulcke, J., Calders, K. and Verbeeck, H. 2020. Terrestrial laser scanning for non-destructive estimates of liana stem biomass. *Forest Ecology and Management*. **456**, p.117751.

Kumar, D. and Scheiter, S. 2019. Biome diversity in South Asia - How can we improve vegetation models to understand global change impact at regional level? *Science of the Total Environment*. **671**, pp.1001–1016.

Kurzel, B.P., Schnitzer, S.A. and Carson, W.P. 2006. Predicting liana crown location from stem diameter in three Panamanian lowland forests. *Biotropica*. **38**(2), pp.262–266.

Lai, H.R., Hall, J.S., Turner, B.L. and van Breugel, M. 2017. Liana effects on biomass dynamics strengthen during secondary forest succession. *Ecology*. **98**(4), pp.1062–1070.

Larjavaara, M. and Muller-Landau, H.C. 2010. Rethinking the value of high wood density. *Functional Ecology*. **24**(4), pp.701–705.

Laurance, W.F., Andrade, A.S., Magrach, A., Camargo, J.L.C., Valsko, J.J., Campbell, M., Fearnside, P.M., Edwards, W., Lovejoy, T.E. and Laurance, S.G. 2014. Long-term changes in liana abundance and forest dynamics in undisturbed Amazonian forests. *Ecology*. **95**(6), pp.1604–1611.

Laurance, W.F., Goosem, M. and Laurance, S.G.W. 2009. Impacts of roads and linear clearings on tropical forests. *Trends in Ecology and Evolution*. **24**(12), pp.659–669.

Laurance, W.F., Laurance, S.G., Ferreira, L. V., Rankin-de Merona, J.M., Gascon, C. and Lovejoy, T.E. 1997. Biomass collapse in Amazonian forest fragments. *Science*. **278**(5340), pp.1117–1118.

Laurance, W.F., Oliveira, A.A., Laurance, S.G., Condit, R., Nascimento, H.E.M., Sanchez-Thorin, A.C., Lovejoy, T.E., Andrade, A., D'Angelo, S., Ribeiro, J.E. and Dick, C.W. 2004. Pervasive alteration of tree communities in undisturbed Amazonian forests. *Nature*. **428**(6979), pp.171–175.

Laurance, W.F., Pérez-Salicrup, D., Delamônica, P., Fearnside, P.M., D'Angelo, S., Jerozolinski, A., Pohl, L. and Lovejoy, T.E. 2001. Rain forest fragmentation and the structure of Amazonian liana communities. *Ecology*. **82**(1), pp.105–116.

Laybros, A., Schläpfer, D., Féret, J.-B., Descroix, L., Bedeau, C., Lefevre, M.-J. and Vincent, G. 2019. Across Date Species Detection Using Airborne Imaging Spectroscopy. *Remote Sensing*. **11**(7), p.789.

Lechner, A.M., Foody, G.M. and Boyd, D.S. 2020. Applications in Remote Sensing to Forest Ecology and Management. *One Earth*. **2**(5), pp.405–412.

Ledo, A., Illian, J.B., Schnitzer, S.A., Wright, S.J., Dalling, J.W. and Burslem, D.F.R.P. 2016. Lianas and soil nutrients predict fine-scale distribution of above-ground biomass in a tropical moist forest G. Zotz, ed. *Journal of Ecology*. **104**(6), pp.1819–1828.

Ledo, A. and Schnitzer, S.A. 2014. Disturbance and clonal reproduction determine liana distribution and maintain liana diversity in a tropical forest. *Ecology*. **95**(8), pp.2169–2178.

van Leeuwen, W.J.D. 2009. Visible, near-IR, and shortwave IR spectral characteristics of terrestrial surfaces *In*: T. A. Warner, G. M. Foody and M. Nellis, eds. *The SAGE Handbook of Remote*

Sensing. London: SAGE Publications Ltd, pp.33–50.

Letcher, S.G. and Chazdon, R.L. 2009. Lianas and self-supporting plants during tropical forest succession. *Forest Ecology and Management*. **257**(10), pp.2150–2156.

Lewis, S.L., Brando, P.M., Phillips, O.L., Van Der Heijden, G.M.F. and Nepstad, D. 2011. The 2010 Amazon drought. *Science*. **331**(6017), p.554.

Lewis, S.L., Edwards, D.P. and Galbraith, D. 2015. Increasing human dominance of tropical forests. *Science*. **349**(6250), pp.827–832.

Lewis, S.L., Lopez-Gonzalez, G., Sonké, B., Affum-Baffoe, K., Baker, T.R., Ojo, L.O., Phillips, O.L., Reitsma, J.M., White, L., Comiskey, J.A., Djuikouo K, M.N., Ewango, C.E.N., Feldpausch, T.R., Hamilton, A.C., Gloor, M., Hart, T., Hladik, A., Lloyd, J., Lovett, J.C., Makana, J.R., Malhi, Y., Mbago, F.M., Ndangalasi, H.J., Peacock, J., Peh, K.S.H., Sheil, D., Sunderland, T., Swaine, M.D., Taplin, J., Taylor, D., Thomas, S.C., Votere, R. and Wöll, H. 2009. Increasing carbon storage in intact African tropical forests. *Nature*. **457**(7232), pp.1003–1006.

Lewis, S.L., Malhi, Yadvinder and Phillips, Oliver L. 2004. Fingerprinting the impacts of global change on tropical forests Y. Malhi & O. L. Phillips, eds. *Philosophical Transactions of the Royal Society B: Biological Sciences*. **359**(1443), pp.437–462.

Lewis, S.L. and Tanner, E.V.J. 2000. Effects of above- and belowground competition on growth and survival of rain forest tree seedlings. *Ecology*. **81**(9), pp.2525–2538.

Li, W., Campos-Vargas, C., Marzahn, P. and Sanchez-Azofeifa, A. 2018. On the estimation of tree mortality and liana infestation using a deep self-encoding network. *International Journal of Applied Earth Observation and Geoinformation*. **73**, pp.1–13.

Li, W., Fu, R., Juárez, R.I.N. and Fernandes, K. 2008. Observed change of the standardized precipitation index, its potential cause and implications to future climate change in the Amazon region. *Philosophical Transactions of the Royal Society B: Biological Sciences*. **363**(1498), pp.1767–1772.

Lillesand, T.M. and Kiefer, R.W. 2000. *Remote Sensing and Image Interpretation* 4th ed. New York: John Wiley & Sons.

Lim, K., Treitz, P., Wulder, M., St-Onge, B. and Flood, M. 2003. LiDAR remote sensing of forest structure. *Progress in Physical Geography: Earth and Environment*. **27**(1), pp.88–106.

Ling, F., Li, Xinyan, Foody, G.M., Boyd, D., Ge, Y., Li, Xiaodong and Du, Y. 2020. Monitoring surface water area variations of reservoirs using daily MODIS images by exploring sub-pixel information. *ISPRS Journal of Photogrammetry and Remote Sensing*. **168**, pp.141–152.

Liu, H., Dörler, D., Heigl, F. and Grossberndt, S. 2021. Citizen Science Platforms *In*: K. Vohland, A. Land-Zandstra, L. Ceccaroni, R. Lemmens, J. Perelló, M. Ponti, R. Samson and K. Wagenknecht, eds. *The Science of Citizen Science*. Cham: Springer, pp.439–459.

Londré, R.A., Schnitzer, S.A., Londr, R.A. and Schnitzer1, S.A. 2006. The Distribution of Lianas and Their Change in Abundance in Temperate Forests over the past 45 Years. *Ecology*. **87**(12), pp.2973–2978.

Lowe, R.G. and Walker, P. 1977. Classification of Canopy, Stem, Crown Status and Climber Infestation in Natural Tropical Forest in Nigeria. *The Journal of Applied Ecology*. **14**(3), p.897.

Lussetti, D., Axelsson, E.P., Ilstedt, U., Falck, J. and Karlsson, A. 2016. Supervised logging and climber cutting improves stand development: 18 years of post-logging data in a tropical rain forest in Borneo. *Forest Ecology and Management*. **381**, pp.335–346.

Lutz, J.A., Furniss, T.J., Johnson, D.J., Davies, S.J., Allen, D., Alonso, A., Anderson-Teixeira, K.J., Andrade, A., Baltzer, J., Becker, K.M.L., Blomdahl, E.M., Bourg, N.A., Bunyavejchewin, S., Burslem, D.F.R.P., Cansler, C.A., Cao, K., Cao, M., Cárdenas, D., Chang, L.W., Chao, K.J., Chao, W.C., Chiang, J.M., Chu, C., Chuyong, G.B., Clay, K., Condit, R., Cordell, S., Dattaraja, H.S., Duque, A., Ewango, C.E.N., Fischer, G.A., Fletcher, C., Freund, J.A., Giardina, C., Germain, S.J., Gilbert, G.S., Hao, Z., Hart, T., Hau, B.C.H., He, F., Hector, A., Howe, R.W., Hsieh, C.F., Hu, Y.H., Hubbell, S.P., Inman-Narahari, F.M., Itoh, A., Janík, D., Kassim, A.R., Kenfack, D., Korte, L., Král, K., Larson, A.J., Li, Y. De, Lin, Y., Liu, S., Lum, S., Ma, K., Makana, J.R., Malhi, Y., McMahon, S.M., McShea, W.J., Memiaghe, H.R., Mi, X., Morecroft, M., Musili, P.M., Myers, J.A., Novotny, V., de Oliveira, A., Ong, P., Orwig, D.A., Ostertag, R., Parker, G.G., Patankar, R., Phillips, R.P., Reynolds, G., Sack, L., Song, G.Z.M., Su, S.H., Sukumar, R., Sun, I.F., Suresh, H.S., Swanson, M.E., Tan, S., Thomas, D.W., Thompson, J., Uriarte, M., Valencia, R., Vicentini, A., Vrška, T., Wang, X., Weiblen, G.D., Wolf, A., Wu, S.H., Xu, H., Yamakura, T., Yap, S. and Zimmerman, J.K. 2018. Global importance of large-diameter trees. *Global Ecology and Biogeography*. **27**(7), pp.849–864.

Ma, L., Liu, Y., Zhang, X., Ye, Y., Yin, G. and Johnson, B.A. 2019. Deep learning in remote sensing applications: A meta-analysis and review. *ISPRS Journal of Photogrammetry and Remote Sensing*. **152**, pp.166–177.

Madeira, B.G., Espírito-Santo, M.M., Neto, S.D.Â., Nunes, Y.R.F., Arturo Sánchez Azofeifa, G., Wilson Fernandes, G. and Quesada, M. 2009. Changes in tree and liana communities along a successional gradient in a tropical dry forest in south-eastern Brazil. *Plant Ecology*. **201**(1), pp.291–304.

Magnago, L.F.S., Magrach, A., Barlow, J., Schaefer, C.E.G.R., Laurance, W.F., Martins, S.V. and Edwards, D.P. 2017. Do fragment size and edge effects predict carbon stocks in trees and lianas in tropical forests? N. Norden, ed. *Functional Ecology*. **31**(2), pp.542–552.

Malhi, Y., Girardin, C., Metcalfe, D.B., Doughty, C.E., Aragão, L.E.O.C., Rifai, S.W., Oliveras, I., Shenkin, A., Aguirre-Gutiérrez, J., Dahlsjö, C.A.L., Riutta, T., Berenguer, E., Moore, S., Huasco, W.H., Salinas, N., da Costa, A.C.L., Bentley, L.P., Adu-Bredu, S., Marthews, T.R., Meir, P. and Phillips, O.L. 2021. The Global Ecosystems Monitoring network: Monitoring ecosystem productivity and carbon cycling across the tropics. *Biological Conservation*. **253**, p.108889.

Malhi, Y., Wood, D., Baker, T.R., Wright, J., Phillips, O.L., Cochrane, T., Meir, P., Chave, J., Almeida, S., Arroyo, L., Higuchi, N., Killeen, T.J., Laurance, S.G., Laurance, W.F., Lewis, S.L., Monteagudo, A., Neill, D.A., Vargas, P.N., Pitman, N.C.A., Quesada, C.A., Salomão, R., Silva, J.N.M., Lezama, A.T., Terborgh, J., Martínez, R.V. and Vinceti, B. 2006. The regional variation of aboveground live biomass in old-growth Amazonian forests. *Global Change Biology*. **12**(7), pp.1107–1138.

Malhi, Y. and Wright, J. 2005. Late twentieth-century patterns and trends in the climate of tropical forest regions *In*: Y. Malhi and O. L. Phillips, eds. *Tropical Forests and Global Atmospheric Change*. Oxford: Oxford University Press, pp.3–16.

Malizia, A. 2003. Host tree preference of vascular epiphytes and climbers in a subtropical montane cloud forest of northwest Argentina. *Selbyana*. **24**(2), pp.196–205.

Malizia, A. and Grau, H.R. 2006. Liana-host tree associations in a subtropical montane forest of north-western Argentina. *Journal of Tropical Ecology*. **22**(3), pp.331–339.

Manzané-Pinzón, E., Goldstein, G. and Schnitzer, S.A. 2018. Does soil moisture availability explain liana seedling distribution across a tropical rainfall gradient? *Biotropica*. **50**(2), pp.215–224.

Maréchaux, I., Bartlett, M.K., Iribar, A., Sack, L. and Chave, J. 2017. Stronger seasonal adjustment in leaf turgor loss point in lianas than trees in an Amazonian forest. *Biology Letters*. **13**(1).

Marengo, J.A., Chou, S.C., Kay, G., Alves, L.M., Pesquero, J.F., Soares, W.R., Santos, D.C., Lyra, A.A., Sueiro, G., Betts, R., Chagas, D.J., Gomes, J.L., Bustamante, J.F. and Tavares, P. 2012. Development of regional future climate change scenarios in South America using the Eta CPTEC/HadCM3 climate change projections: Climatology and regional analyses for the Amazon, São Francisco and the Paraná River basins. *Climate Dynamics*. **38**(9–10), pp.1829–1848.

Marín-Spiotta, E., Silver, W.L. and Ostertag, R. 2007. Long-term patterns in tropical re- forestation: Plant community composition and aboveground biomass accumulation. *Ecological Applications*. **17**(3), pp.828–839.

Marín, P.G., Julio, C.J., Dante Arturo, R.T. and Daniel Jose, V.N. 2018. Drought and Spatiotemporal Variability of Forest Fires Across Mexico. *Chinese Geographical Science*. **28**(1), pp.25–37.

Marselis, S.M., Abernethy, K., Alonso, A., Armston, J., Baker, T.R., Bastin, J.F., Bogaert, J., Boyd, D.S., Boeckx, P., Burslem, D.F.R.P., Chazdon, R., Clark, D.B., Coomes, D., Duncanson, L., Hancock, S., Hill, R., Hopkinson, C., Kearsley, E., Kellner, J.R., Kenfack, D., Labrière, N., Lewis, S.L., Minor, D., Memiaghe, H., Monteagudo, A., Nilus, R., O'Brien, M., Phillips, O.L., Poulsen, J., Tang, H., Verbeeck, H. and Dubayah, R. 2020. Evaluating the potential of full-waveform lidar for mapping pan-tropical tree species richness. *Global Ecology and Biogeography*. **29**(10), pp.1799–1816.

Marshall, A.R., Coates, M.A., Archer, J., Kivambe, E., Mnendendo, H., Mtoka, S., Mwakisoma, R., de Figueiredo, R.J.R.L. and Njilima, F.M. 2017. Liana cutting for restoring tropical forests: a rare palaeotropical trial. *African Journal of Ecology*. **55**(3), pp.282–297.

Martin, A.R. and Thomas, S.C. 2011. A reassessment of carbon content in tropical trees. *PLoS ONE*. **6**(8), p.23533.

Martin, L.J., Blossey, B. and Ellis, E. 2012. Mapping where ecologists work: Biases in the global distribution of terrestrial ecological observations. *Frontiers in Ecology and the Environment*. **10**(4), pp.195–201.

Martínez-Izquierdo, L., García, M.M., Powers, J.S. and Schnitzer, S.A. 2016. Lianas suppress seedling growth and survival of 14 tree species in a Panamanian tropical forest. *Ecology*. **97**(1), pp.215–224.

Marvin, D.C., Asner, G.P. and Schnitzer, S.A. 2016. Liana canopy cover mapped throughout a tropical forest with high-fidelity imaging spectroscopy. *Remote Sensing of Environment*. **176**, pp.98–106.

Marvin, D.C., Winter, K., Burnham, R.J. and Schnitzer, S.A. 2015. No evidence that elevated CO2 gives tropical lianas an advantage over tropical trees. *Global Change Biology*. **21**(5), pp.2055–2069.

Mascaro, J., Schnitzer, S.A. and Carson, W.P. 2004. Liana diversity, abundance, and mortality in a tropical wet forest in Costa Rica. *Forest Ecology and Management*. **190**(1), pp.3–14.

McDowell, N., Allen, C.D., Anderson-Teixeira, K., Brando, P., Brienen, R., Chambers, J., Christoffersen, B., Davies, S., Doughty, C., Duque, A., Espirito-Santo, F., Fisher, R., Fontes, C.G., Galbraith, D., Goodsman, D., Grossiord, C., Hartmann, H., Holm, J., Johnson, D.J., Kassim, A.R., Keller, M., Koven, C., Kueppers, L., Kumagai, T., Malhi, Y., McMahon, S.M., Mencuccini, M., Meir, P., Moorcroft, P., Muller-Landau, H.C., Phillips, O.L., Powell, T., Sierra, C.A., Sperry, J., Warren, J., Xu, C. and Xu, X. 2018. Drivers and mechanisms of tree mortality in moist tropical forests. *New Phytologist*. **219**(3), pp.851–869.

Medina-Vega, J.A., Bongers, F., Schnitzer, S.A. and Sterck, F.J. 2021. Lianas explore the forest canopy more effectively than trees under drier conditions. *Functional Ecology*. **35**(2), pp.318–329.

Medvigy, D., Wofsy, S.C., Munger, J.W., Hollinger, D.Y. and Moorcroft, P.R. 2009. Mechanistic scaling of ecosystem function and dynamics in space and time: Ecosystem Demography model version 2. *Journal of Geophysical Research*. **114**(G1), p.G01002.

van der Meer, P. and Bongers, F. 2001. Tree-Falls and Canopy Gaps: Patterns of Natural Disturbance *In*: F. Bongers, P. Charles-Dominique, P. M. Forget and M. Théry, eds. *Nouragues: Monographiae Biologicae, vol 80*. Dordrecht: Springer, pp.243–250.

Meerdink, S.K., Hook, S.J., Roberts, D.A. and Abbott, E.A. 2019. The ECOSTRESS spectral library version 1.0. *Remote Sensing of Environment*. **230**, p.111196.

Meunier, F., van der Heijden, G.M.F., Schnitzer, S.A., De Deurwaerder, H.P.T. and Verbeeck, H. 2021. Lianas significantly reduce aboveground and belowground carbon storage. *Frontiers in Forests and Global Change*.

Meunier, F., Verbeeck, H., Cowdery, B., Schnitzer, S.A., Smith-Martin, C.M., Powers, J.S., Xu, X., Slot, M., De Deurwaerder, H.P.T., Detto, M., Bonal, D., Longo, M., Santiago, L.S. and Dietze, M. 2020. Unraveling the relative role of light and water competition between lianas and trees in tropical forests: A vegetation model analysis. *Journal of Ecology*. **109**(1), pp.519–540.

Meyer, L., Kissling, W.D., Lohmann, L.G., Hortal, J. and Diniz-Filho, J.A.F. 2020. Deconstructing species richness–environment relationships in Neotropical lianas. *Journal of Biogeography*. **47**(10), pp.2168–2180.

Miao, Z., Koerner, S.E., Medjibe, V.P. and Poulsen, J.R. 2016. Wanted: new allometric equations for large lianas *and* African lianas. *Biotropica*. **48**(5), pp.561–564.

Mohan, J.E., Ziska, L.H., Schlesinger, W.H., Thomas, R.B., Sicher, R.C., George, K. and Clark, J.S. 2006. Biomass and toxicity responses of poison ivy (Toxicodendron radicans) to elevated atmospheric CO2. *Proceedings of the National Academy of Sciences of the United States of America*. **103**(24), pp.9086–9089.

Moorcroft, P.R., Hurtt, G.C. and Pacala, S.W. 2001. A method for scaling vegetation dynamics: The ecosystem demography model (ED). *Ecological Monographs*. **71**(4), pp.557–586.

Morellato, P.C. and Leitao-Filho, H.F. 1996. Reproductive Phenology of Climbers in a Southeastern Brazilian Forest. *Biotropica*. **28**(2), p.180.

Moreno, J.F., Asner, G.P., Bach, H., Belenguer, T., Bell, A., Buschmann, C., Calera, A., Calpe, J., Campbell, P., Cecchi, G., Colombo, R., Corp, L.A., Court, A., Cutter, M.A., Disney, M., Dudelzak, A., D’Urso, G., Fernandes, R., Flexas, J., Gege, P., Gielen, B., Gitelson, A., Gloor, E.U., Gower, J., Green, R.O., Hill, J., Jacquemoud, S., Jia, L., Kneubühler, M., Laurila, T., Lewis, P., Lobb, D., Magnani, F., Maier, S.W., Marek, M. V., Martinez, A., Martinez-Cobo, P., Mazzinghi, P., Menenti, M., Merton, R., Middleton, E., De Miguel, E., Miller, J., Mohammed, G., Milton, E.J., Morales, F., Moya, I., Nedbal, L., Knorr, W., Ottlé, C., Olioso, A., Pace, S., Palucci, A., Pedros, R., Peltoniemi, J., Peñuelas, J., Plaza, A., Polcher, J., Rascher, U., Reuter, R., Rosema, A., Roujean, J.L., Saito, Y., Saugier, B., Schaepman, M., Serrano, J.B., Settle, J.J., Sierra, M., Sobrino, J., Stoll, M.P., Bob Su, Z., Tobehn, C., Tremblay, N., Valcke, R., Verhoef, W., Veroustraete, F., Verstraete, M. and Zarco-Tejada, P. 2006. Fluorescence explorer (FLEX): An optimised payload to map vegetation photosynthesis from space *In*: *AIAA 57th International Astronautical Congress, IAC 2006*. American Institute of Aeronautics and Astronautics Inc., pp.2065–2074.

Muller-Landau, H.C. 2004. Interspecific and Inter-site Variation in Wood Specific Gravity of Tropical Trees. *Biotropica*. **36**(1), pp.20–32.

Muller-Landau, H.C. and Visser, M.D. 2019. How do lianas and vines influence competitive differences and niche differences among tree species? Concepts and a case study in a tropical forest. *Journal of Ecology*. **107**(3), pp.1469–1481.

Muller-Landau, H.C. and Pacala, S.W. 2020. What determines the abundance of lianas and vines? *In*: A. Dobson, R. D. Holt, D. Tilman and E. T. Borer, eds. *Unsolved Problems in Ecology*. Oxford: Princeton University Press, pp.239–264.

Muthuramkumar, S. and Parthasarathy, N. 2001. Tree-liana relationships in a tropical evergreen forest at Varagalaiar, Anamalais, Western Ghats, India. *Journal of Tropical Ecology*. **17**(3), pp.395–409.

Myers, N. 1988. Tropical Forests and Their Species Going, Going … ? *In*: E. O. Wilson, ed. *Biodiversity*. Washington, D.C.: National Academy Press, pp.28–35.

Nabe-Nielsen, J. 2001. Diversity and distribution of lianas in a neotropical rain forest, Yasuní National Park, Ecuador. *Journal of Tropical Ecology*. **17**(1), pp.1–19.

Nabe-Nielsen, J., Kollmann, J. and Peña-Claros, M. 2009. Effects of liana load, tree diameter and distances between conspecifics on seed production in tropical timber trees. *Forest Ecology and Management*. **257**(3), pp.987–993.

Nakamura, A., Kitching, R.L., Cao, M., Creedy, T.J., Fayle, T.M., Freiberg, M., Hewitt, C.N., Itioka, T., Koh, L.P., Ma, K., Malhi, Y., Mitchell, A., Novotny, V., Ozanne, C.M.P., Song, L., Wang, H. and Ashton, L.A. 2017. Forests and Their Canopies: Achievements and Horizons in Canopy Science. *Trends in Ecology and Evolution*. **32**(6), pp.438–451.

Nascimento, H.E.M. and Laurance, W.F. 2002. Total aboveground biomass in central Amazonian rainforests: A landscape-scale study. *Forest Ecology and Management*. **168**(1–3), pp.311–321.

Naturales, R. 2001. Effect of liana cutting on tree regeneration in a liana forest in Amazonian Bolivia. *America*. **82**(2), pp.389–396.

Niinemets, U. and Valladares, F. 2006. Tolerance to shade, drought, and waterlogging of temperate northern hemisphere trees and shrubs. *Ecological Monographs*. **76**(4), pp.521–547.

Norashikin, F., Ibrahim, B., Aziz, S.N.A., Musfiroh, J. and Kamarul Ariffin, H. 2021. Estimation of liana infestation above canopy in Bukit Bakar recreational park, Kelantan using an unmanned aerial vehicle. *IOP Conference Series: Earth and Environmental Science*. **736**(1), p.012049.

Nunes, M.H., Both, S., Bongalov, B., Brelsford, C., Khoury, S., Burslem, D.F.R.P., Philipson, C., Majalap, N., Riutta, T., Coomes, D.A. and Cutler, M.E.J. 2019. Changes in leaf functional traits of rainforest canopy trees associated with an El Nino event in Borneo. *Environmental Research Letters*. **14**(8), p.085005.

Odegaard, F. 2000. The relative importance of trees versus lianas as hosts for phytophagous beetles (Coleoptera) in tropical forests. *Journal of Biogeography*. **27**(2), pp.283–296.

Odell, E.H., Stork, N.E. and Kitching, R.L. 2019. Lianas as a food resource for herbivorous insects: a comparison with trees. *Biological Reviews*. **94**(4), pp.1416–1429.

Ogowa, H. 1965. Comparative ecological studies on three main types of forest vegetation in Thailand. *Nature and Life in Southeast Asia*. **4**, pp.49–80.

Opler, P.A., Baker, H.G. and Frankie, G.. 1991. Seasonality of climbers: a review and example from Costa Rican dry forest *In*: F. E. Putz and H. A. Mooney, eds. *The Biology of Vines*. Cambridge: Cambridge University Press, pp.377–391.

Owen, H.J.F., Flynn, W.R.M. and Lines, E.R. 2021. Competitive drivers of interspecific deviations of crown morphology from theoretical predictions measured with Terrestrial Laser Scanning.

Journal of Ecology. **109**(7), pp.2612–2628.

Paciorek, C.J., Condit, R., Hubbell, S.P. and Foster, R.B. 2000. The demographics of resprouting in tree and shrub species of a moist tropical forest. *Journal of Ecology*. **88**(5), pp.765–777.

Pan, Y., Birdsey, R.A., Fang, J., Houghton, R., Kauppi, P.E., Kurz, W.A., Phillips, O.L., Shvidenko, A., Lewis, S.L., Canadell, J.G., Ciais, P., Jackson, R.B., Pacala, S.W., McGuire, A.D., Piao, S., Rautiainen, A., Sitch, S. and Hayes, D. 2011. A large and persistent carbon sink in the world's forests. *Science*. **333**(6045), pp.988–993.

Paneque-Gálvez, J., McCall, M.K., Napoletano, B.M., Wich, S.A. and Koh, L.P. 2014. Small drones for community-based forest monitoring: An assessment of their feasibility and potential in tropical areas. *Forests*. **5**(6), pp.1481–1507.

Parolari, A.J., Paul, K., Griffing, A., Condit, R., Perez, R., Aguilar, S. and Schnitzer, S.A. 2020. Liana abundance and diversity increase with rainfall seasonality along a precipitation gradient in Panama. *Ecography*. **43**(1), pp.25–33.

Parren, M.P.E. and Doumbia, F. 2005. Logging and lianas in West Africa *In*: F. Bongers, M. P. E. Parren and D. Traore, eds. *Forest Climbing Plants of West Africa: Diversity, Ecology and Management*. Wallingford: CABI Publishing, pp.183–201.

Parthasarathy, N., Muthuramkumar, S., Muthumperumal, C., Vivek, P., Ayyappan, N. and Sridhar Reddy, M. 2015. Liana composition and diversity among tropical forest types of peninsular India *In*: S. A. Schnitzer, F. Bongers, R. J. Burnham and F. E. Putz, eds. *Ecology of Lianas*. Chichester, UK: John Wiley & Sons, Ltd, pp.36–49.

Pasquini, S.C., Wright, S.J., Santiago, L.S. and Uriarte, M. 2015. Lianas always outperform tree seedlings regardless of soil nutrients: Results from a long-term fertilization experiment. *Ecology*. **96**(7), pp.1866–1876.

Paul, G.S. and Yavitt, J.B. 2011. Tropical Vine Growth and the Effects on Forest Succession: A Review of the Ecology and Management of Tropical Climbing Plants. *Botanical Review*. **77**(1), pp.11–30.

Peña-Claros, M., Fredericksen, T.S., Alarcón, A., Blate, G.M., Choque, U., Leaño, C., Licona, J.C., Mostacedo, B., Pariona, W., Villegas, Z. and Putz, F.E. 2008. Beyond reduced-impact logging: Silvicultural treatments to increase growth rates of tropical trees. *Forest Ecology and Management*. **256**(7), pp.1458–1467.

Penalosa, J. 1984. Basal Branching and Vegetative Spread in Two Tropical Rain Forest Lianas. *Biotropica*. **16**(1), pp.1–9.

Pérez-Salicrup, D.R. and Barker, M.G. 2000. Effect of liana cutting on water potential and growth of adult Senna multijuga (Caesalpinioideae) trees in a Bolivian tropical forest. *Oecologia*. **124**(4), pp.469–475.

Pérez-Salicrup, D.R. and De Meijere, W. 2005. Number of Lianas per Tree and Number of Trees Climbed by Lianas at Los Tuxtlas, Mexico. *Biotropica*. **37**(1), pp.153–156.

Perez-Salicrup, D.R., Sork, V.L. and Putz, F.E. 2001. Lianas and Trees in a Liana Forest of Amazonian Bolivia. *Biotropica*. **33**(1), pp.34–47.

Pflugmacher, D., Cohen, W.B. and Kennedy, R.E. 2012. Using Landsat-derived disturbance history (1972-2010) to predict current forest structure. *Remote Sensing of Environment*. **122**, pp.146–165.

Phillips, O. 1993. The potential for harvesting fruits in tropical rainforests: new data from Amazonian Peru. *Biodiversity and Conservation*. **2**(1), pp.18–38.

Phillips, O.L., Aragão, L.E.O.C., Lewis, S.L., Fisher, J.B., Lloyd, J., López-González, G., Malhi, Y., Monteagudo, A., Peacock, J., Quesada, C.A., Van Der Heijden, G., Almeida, S., Amaral, I., Arroyo, L., Aymard, G., Baker, T.R., Bánki, O., Blanc, L., Bonal, D., Brando, P., Chave, J., De Oliveira, Á.C.A., Cardozo, N.D., Czimczik, C.I., Feldpausch, T.R., Freitas, M.A., Gloor, E., Higuchi, N., Jiménez, E., Lloyd, G., Meir, P., Mendoza, C., Morel, A., Neill, D.A., Nepstad, D., Patiño, S., Peñuela, M.C., Prieto, A., Ramírez, F., Schwarz, M., Silva, J., Silveira, M., Thomas, A.S., Steege, H. Ter, Stropp, J., Vásquez, R., Zelazowski, P., Dávila, E.A., Andelman, S., Andrade, A., Chao, K.J., Erwin, T., Di Fiore, A., Honorio, E.C., Keeling, H., Killeen, T.J., Laurance, W.F., Cruz, A.P., Pitman, N.C.A., Vargas, P.N., Ramírez-Angulo, H., Rudas, A., Salamão, R., Silva, N., Terborgh, J. and Torres-Lezama, A. 2009. Drought sensitivity of the amazon rainforest. *Science*. **323**(5919), pp.1344–1347.

Phillips, O.L., Baker, T.R., Arroyo, L., Higuchi, N., Killeen, T.J., Laurance, W.F., Lewis, S.L., Lloyd, J., Malhi, Y., Monteagudo, A., Neill, D.A., Nüñez Vargas, P., Silva, J.N.M., Terborgh, J., Vásquez Martínez, R., Alexiades, M., Almeida, S., Brown, S., Chave, J., Comiskey, J.A., Czimczik, C.I., Di Fiore, A., Erwin, T., Kuebler, C., Laurance, S.G., Nascimento, H.E.M., Olivier, J., Palacios, W., Patiño, S., Pitman, N.C.A., Quesada, C.A., Saldias, M., Torres Lezama, A. and Vinceti, B. 2004. Pattern and process in Amazon tree turnover, 1976-2001. *Philosophical Transactions of the Royal Society B: Biological Sciences*. **359**(1443), pp.381–407.

Phillips, O.L. and Gentry, A.H. 1994. Increasing Turnover Through Time in Tropical Forests. *Science*. **263**(5149), pp.954–958.

Phillips, O.L., Martínez, R.V., Mendoza, A.M., Baker, T.R., Vargas, P.N., Ecology, S. and May, N. 2005. Large Lianas as Hyperdynamic Elements of the Tropical Forest Canopy. *Ecology*. **86**(5), pp.1250–1258.

Phillips, O.L., Vésquez Martínez, R., Arroyo, L., Baker, T.R., Killeen, T., Lewis, S.L., Malhi, Y., Monteagudo Mendoza, A., Neill, D., Núñez Vargas, P., Alexiades, M., Cerón, C., Di Flore, A., Erwin, T., Jardim, A., Palacios, W., Saldias, M. and Vinceti, B. 2002. Increasing dominance of large lianas in Amazonian forests. *Nature*. **418**(6899), pp.770–774.

Poorter, L., Wright, S.J., Paz, H., Ackerly, D.D., Condit, R., Ibarra-Manríquez, G., Harms, K.E., Licona, J.C., Martínez-Ramos, M., Mazer, S.J., Muller-Landau, H.C., Peña-Claros, M., Webb, C.O. and Wright, I.J. 2008. Are functional traits good predictors of demographic rates? Evidence from five neotropical forests. *Ecology*. **89**(7), pp.1908–1920.

di Porcia e Brugnera, M., Meunier, F., Longo, M., Krishna Moorthy, S.M., De Deurwaerder, H., Schnitzer, S.A., Bonal, D., Faybishenko, B. and Verbeeck, H. 2019. Modeling the impact of liana infestation on the demography and carbon cycle of tropical forests. *Global Change Biology*. **25**(11), pp.3767–3780.

Poulsen, J.R., Koerner, S.E., Miao, Z., Medjibe, V.P., Banak, L.N. and White, L.J.T. 2017. Forest structure determines the abundance and distribution of large lianas in Gabon. *Global Ecology and Biogeography*. **26**(4), pp.472–485.

Powers, J.S., Montgomery, R.A., Adair, E.C., Brearley, F.Q., Dewalt, S.J., Castanho, C.T., Chave, J., Deinert, E., Ganzhorn, J.U., Gilbert, M.E., González-Iturbe, J.A., Bunyavejchewin, S., Grau, H.R., Harms, K.E., Hiremath, A., Iriarte-Vivar, S., Manzane, E., De Oliveira, A.A., Poorter, L., Ramanamanjato, J.B., Salk, C., Varela, A., Weiblen, G.D. and Lerdau, M.T. 2009. Decomposition in tropical forests: A pan-tropical study of the effects of litter type, litter placement and mesofaunal exclusion across a precipitation gradient. *Journal of Ecology*. **97**(4), pp.801–811.

Putz, F.E. 1982. *Natural history of lianas and their influences on tropical forest dynamics. Ph.D. Dissertation*. Cornell University, New York.

Putz, F.E. 1983a. Liana biomass and leaf area of a 'tierra firme' forest in the Rio Negro Basin, Venezuela. *Biotropica*. **15**(3), pp.185–189.

Putz, F.E. 1983b. Liana biomass and leaf area of a 'tierra firme' forest in the Rio Negro Basin, Venezuela. *Biotropica*. **15**(3), pp.185–189.

Putz, F.E. 1984a. How Trees Avoid and Shed Lianas. *Biotropica*. **16**(1), pp.19–23.

Putz, F.E. 1984b. The Natural History of Lianas on Barro Colorado Island , Panama. *Ecological Society of America*. **65**(6), pp.1713–1724.

Putz, F.E. 1984c. Effects of post-felling silvicultural treatments on woody vines in Sarawak. *Malaysian Forester*. **47**(3), pp.214–226.

Putz, F.E. 1990. Liana Stem Diameter Growth and Mortality Rates on Barro Colorado Island, Panama. *Biotropica*. **22**(1), p.103.

Putz, F.E. 1995. Vines in treetops: Consequences of mechanical dependence *In*: M. D. Lowman and N. M. Nadkami, eds. *Forest Canopies*. London, UK: Academic Press Limited, pp.311–324.

Putz, F.E. and Holbrook, N.M. 1988. Further Observations on the Dissolution of Mutualism between Cecropia and Its Ants: The Malaysian Case. *Oikos*. **53**(1), p.125.

Putz, F.E. and Mooney, H.A. 1991. *The Biology of Vines*. Cambridge University Press.

Putz, F.E. and Windsor, D.M. 1987. Liana Phenology on Barro Colorado Island, Panama. *Biotropica*. **19**(4), p.334.

Quegan, S., Le Toan, T., Chave, J., Dall, J., Exbrayat, J.F., Minh, D.H.T., Lomas, M., D'Alessandro, M.M., Paillou, P., Papathanassiou, K., Rocca, F., Saatchi, S., Scipal, K., Shugart, H., Smallman, T.L., Soja, M.J., Tebaldini, S., Ulander, L., Villard, L. and Williams, M. 2019. The European Space Agency BIOMASS mission: Measuring forest above-ground biomass from space. *Remote Sensing of Environment*. **227**, pp.44–60.

R Core Team 2021. R: The R Project for Statistical Computing. [Accessed 23 August 2021]. Available from: https://www.r-project.org/.

Reiche, J., Verbesselt, J., Hoekman, D. and Herold, M. 2015. Fusing Landsat and SAR time series to detect deforestation in the tropics. *Remote Sensing of Environment*. **156**, pp.276–293.

Reichstein, M., Bahn, M., Mahecha, M.D., Kattge, J. and Baldocchi, D.D. 2014. Linking plant and ecosystem functional biogeography. *Proceedings of the National Academy of Sciences of the United States of America*. **111**(38), pp.13697–13702.

Reis, S.M., Marimon, B.S., Morandi, P.S., Elias, F., Esquivel-Muelbert, A., Marimon Junior, B.H., Fauset, S., de Oliveira, E.A., van der Heijden, G.M.F., Galbraith, D., Feldpausch, T.R. and Phillips, O.L. 2020. Causes and consequences of liana infestation in southern Amazonia. *Journal of Ecology*. **108**(6), pp.2184–2197.

Restom, T.G. and Nepstad, D.C. 2001. Contribution of vines to the evapotranspiration of a secondary forest in eastern Amazonia. *Plant and Soil*. **236**(2), pp.155–163.

Restom, T.G. and Nepstad, D.C. 2004. Seedling growth dynamics of a deeply rooting liana in a secondary forest in eastern Amazonia. *Forest Ecology and Management*. **190**(1), pp.109–118.

Ribeiro, G.H.P.M., Chambers, J.Q., Peterson, C.J., Trumbore, S.E., Magnabosco Marra, D., Wirth, C., Cannon, J.B., Négron-Juárez, R.I., Lima, A.J.N., de Paula, E.V.C.M., Santos, J. and Higuchi, N. 2016. Mechanical vulnerability and resistance to snapping and uprooting for Central Amazon tree species. *Forest Ecology and Management*. **380**, pp.1–10.

Rich, P.M., Helenurm, K., Kearns, D., Morse, S.R., Palmer, M.W. and Short, L. 1986. Height and Stem Diameter Relationships for Dicotyledonous Trees and Arborescent Palms of Costa Rican Tropical Wet Forest. *Bulletin of the Torrey Botanical Club*. **113**(3), p.241.

Richards, P.W., Frankham, R. and Walsh, R.P.D. 1996. *The tropical rain forest: An ecological study*. Cambridge, UK: Cambridge University Press.

Richardson, J.J., Monika Moskal, L. and Bakker, J.D. 2014. Terrestrial laser scanning for vegetation sampling. *Sensors (Switzerland)*. **14**(11), pp.20304–20319.

Rodríguez-Ronderos, M.E., Bohrer, G., Sanchez-Azofeifa, A., Powers, J.S. and Schnitzer, S.A. 2016. Contribution of lianas to plant area index and canopy structure in a Panamanian forest. *Ecology*. **97**(12), pp.3271–3277.

Rowe, N.P. and Speck, T. 2015. Stem biomechanics, strength of attachment, and developmental plasticity of vines and lianas *In*: S. A. Schnitzer, F. Bongers, R. J. Burnham and F. E. Putz, eds. *Ecology of Lianas*. Oxford, UK: Wiley-Blackwell, pp.323–343.

Ryu, Y., Baldocchi, D.D., Verfaillie, J., Ma, S., Falk, M., Ruiz-Mercado, I., Hehn, T. and Sonnentag, O. 2010. Testing the performance of a novel spectral reflectance sensor, built with light emitting diodes (LEDs), to monitor ecosystem metabolism, structure and function. *Agricultural and Forest Meteorology*. **150**(12), pp.1597–1606.

Saatchi, S.S., Harris, N.L., Brown, S., Lefsky, M., Mitchard, E.T.A., Salas, W., Zutta, B.R., Buermann, W., Lewis, S.L., Hagen, S., Petrova, S., White, L., Silman, M. and Morel, A. 2011. Benchmark map of forest carbon stocks in tropical regions across three continents. *Proceedings of the National Academy of Sciences of the United States of America*. **108**(24), pp.9899–9904.

Saldarriaga, J.G., West, D.C., Tharp, M.L. and Uhl, C. 1988. Long-Term Chronosequence of Forest Succession in the Upper Rio Negro of Colombia and Venezuela. *The Journal of Ecology*. **76**(4), p.938.

Saleska, S.R., Didan, K., Huete, A.R. and Da Rocha, H.R. 2007. Amazon forests green-up during 2005 drought. *Science*. **318**(5850), p.612.

Sánchez-Azofeifa, A. and Castro-Esau, K. 2006. Canopy observations on the hyperspectral properties of a community of tropical dry forest lianas and their host trees. *International Journal of Remote Sensing*. **27**(10), pp.2101–2109.

Sánchez-Azofeifa, A., Castro, K., Wright, S.J., Gamon, J., Kalacska, M., Rivard, B., Schnitzer, S.A. and Feng, J.L. 2009. Differences in leaf traits, leaf internal structure, and spectral reflectance between two communities of lianas and trees: Implications for remote sensing in tropical environments. *Remote Sensing of Environment*. **113**(10), pp.2076–2088.

Sánchez-Azofeifa, A., Rivard, B., Wright, J., Feng, J.L., Li, P., Chong, M.M. and Bohlman, S.A. 2011. Estimation of the distribution of Tabebuia guayacan (Bignoniaceae) using high-resolution remote sensing imagery. *Sensors*. **11**(4), pp.3831–3851.

van der Sande, M.T., Poorter, L., Schnitzer, S.A., Engelbrecht, B.M.J. and Markesteijn, L. 2019. The hydraulic efficiency–safety trade-off differs between lianas and trees. *Ecology*. **100**(5).

Santiago, L.S., Pasquini, S.C. and De Guzman, M.E. 2015. Physiological implications of the liana growth form *In*: S. A. Schnitzer, F. Bongers, R. J. Burnham and F. E. Putz, eds. *Ecology of Lianas*. Oxford, UK: Wiley-Blackwell, pp.288–298.

Santilli, G., Vendittozzi, C., Cappelletti, C., Battistini, S. and Gessini, P. 2018. CubeSat constellations for disaster management in remote areas. *Acta Astronautica*. **145**, pp.11–17.

Schepaschenko, D., Chave, J., Phillips, O.L., Lewis, S.L., Davies, S.J., Réjou-Méchain, M., Sist, P., Scipal, K., Perger, C., Herault, B., Labrière, N., Hofhansl, F., Affum-Baffoe, K., Aleinikov, A., Alonso, A., Amani, C., Araujo-Murakami, A., Armston, J., Arroyo, L., Ascarrunz, N., Azevedo, C., Baker, T., Bałazy, R., Bedeau, C., Berry, N., Bilous, A.M., Bilous, S.Y., Bissiengou, P., Blanc, L., Bobkova, K.S., Braslavskaya, T., Brienen, R., Burslem, D.F.R.P., Condit, R., Cuni-Sanchez, A., Danilina, D., del Castillo Torres, D., Derroire, G., Descroix, L., Sotta, E.D., d'Oliveira, M.V.N., Dresel, C., Erwin, T., Evdokimenko, M.D., Falck, J., Feldpausch, T.R., Foli, E.G., Foster, R., Fritz, S., Garcia-Abril, A.D., Gornov, A., Gornova, M., Gothard-Bassébé, E., Gourlet-Fleury, S., Guedes, M., Hamer, K.C., Susanty, F.H., Higuchi, N., Coronado, E.N.H., Hubau, W., Hubbell, S., Ilstedt, U., Ivanov, V. V., Kanashiro, M., Karlsson, A., Karminov, V.N., Killeen, T., Koffi, J.C.K., Konovalova, M., Kraxner, F., Krejza, J., Krisnawati, H., Krivobokov, L. V., Kuznetsov, M.A., Lakyda, I., Lakyda, P.I., Licona, J.C., Lucas, R.M., Lukina, N., Lussetti, D., Malhi, Y., Manzanera, J.A., Marimon, B., Junior, B.H.M., Martinez, R.V., Martynenko, O. V., Matsala, M., Matyashuk, R.K., Mazzei, L., Memiaghe, H., Mendoza, C., Mendoza, A.M., Moroziuk, O. V., Mukhortova, L., Musa, S., Nazimova, D.I., Okuda, T., Oliveira, L.C., Ontikov, P. V., Osipov, A.F., Pietsch, S., Playfair, M., Poulsen, J., Radchenko, V.G., Rodney, K., Rozak, A.H., Ruschel, A., Rutishauser, E., See, L., Shchepashchenko, M., Shevchenko, N., Shvidenko, A., Silveira, M., Singh, J., Sonké, B., Souza, C., Stereńczak, K., Stonozhenko, L., Sullivan, M.J.P., Szatniewska, J., Taedoumg, H., ter Steege, H., Tikhonova, E., Toledo, M., Trefilova, O. V., Valbuena, R., Gamarra, L.V., Vasiliev, S., Vedrova, E.F., Verhovets, S. V., Vidal, E., Vladimirova, N.A., Vleminckx, J., Vos, V.A., Vozmitel, F.K., Wanek, W., West, T.A.P., Woell, H., Woods, J.T., Wortel, V., Yamada, T., Nur Hajar, Z.S. and Zo-Bi, I.C. 2019. The Forest Observation System, building a global reference dataset for remote sensing of forest biomass. *Scientific Data*. **6**(1), pp.1–11.

Schnitzer, S.A. 2005. A mechanistic explanation for global patterns of liana abundance and distribution. *American Naturalist*. **166**(2), pp.262–276.

Schnitzer, S.A. 2018. Testing ecological theory with lianas. *New Phytologist*. **220**(2), pp.366–380.

Schnitzer, S.A. and Bongers, F. 2011. Increasing liana abundance and biomass in tropical forests: Emerging patterns and putative mechanisms. *Ecology Letters*. **14**(4), pp.397–406.

Schnitzer, S.A. and Bongers, F. 2002. The ecology of lianas and their role in forests. *Trends in Ecology and Evolution*. **17**(5), pp.223–230.

Schnitzer, S.A., Bongers, F. and Wright, S.J. 2011. Community and ecosystem ramifications of increasing lianas in neotropical forests. *Plant Signaling and Behavior*. **6**(4), pp.598–600.

Schnitzer, S.A. and Carson, W.P. 2000. Have we forgotten the forest because of the trees? . *Trends in Ecology and Evolution*. **15**(9), pp.375–376.

Schnitzer, S.A. and Carson, W.P. 2010. Lianas suppress tree regeneration and diversity in treefall gaps. *Ecology Letters*. **13**(7), pp.849–857.

Schnitzer, S.A. and Carson, W.P. 2001. Treefall gaps and the maintenance of species diversity in a tropical forest. *Ecology*. **82**(4), pp.913–919.

Schnitzer, S.A., Dalling, J.W. and Carson, W.P. 2000. The impact of lianas on tree regeneration in tropical forest canopy gaps: Evidence for an alternative pathway of gap-phase regeneration. *Journal of Ecology*. **88**(4), pp.655–666.

Schnitzer, S.A., DeWalt, S.J. and Chave, J. 2006. Censusing and Measuring Lianas: A Quantitative Comparison of the Common Methods1. *Biotropica*. **38**(5), pp.581–591.

Schnitzer, S.A., van der Heijden, G., Mascaro, J. and Carson, W.P. 2014a. Lianas in gaps reduce carbon accumulation in a tropical forest. *Ecology*. **95**(11), pp.3008–3017.

Schnitzer, S.A., van der Heijden, G., Mascaro, J. and Carson, W.P. 2014b. SSLianas in gaps reduce carbon accumulation in a tropical forest. *Ecology*. **95**(11), pp.3008–3017.

Schnitzer, S.A. and van der Heijden, G.M.F. 2019. Lianas have a seasonal growth advantage over co-occurring trees. *Ecology*. **100**(5), p.e02655.

Schnitzer, S.A., Van Der Heijden, G.M.F. and Powers, J.S. 2016. Addressing the challenges of including lianas in global vegetation models. *Proceedings of the National Academy of Sciences of the United States of America*. **113**(1), pp.E5–E6.

Schnitzer, S.A., Kuzee, M.E. and Bongers, F. 2005. Disentangling above- and below-ground competition between lianas and trees in a tropical forest. *Journal of Ecology*. **93**(6), pp.1115–1125.

Schnitzer, S.A., Mangan, S.A., Dalling, J.W., Baldeck, C.A., Hubbell, S.P., Ledo, A., Muller-Landau, H., Tobin, M.F., Aguilar, S., Brassfield, D., Hernandez, A., Lao, S., Perez, R., Valdes, O. and Yorke, S.R. 2012. Liana Abundance, Diversity, and Distribution on Barro Colorado Island, Panama. *PLoS ONE*. **7**(12), p.52114.

Schnitzer, S.A., Michel, N.L., Powers, J.S. and Robinson, W.D. 2020. Lianas maintain insectivorous bird abundance and diversity in a neotropical forest. *Ecology*. **101**(12), pp.1–10.

Schnitzer, S.A., Putz, F.E., Bongers, F. and Kroening, K. 2015b. The Past, Present, and Potential Future of Liana Ecology *In*: S. A. Schnitzer, F. Bongers, R. J. Burnham and F. E. Putz, eds. *Ecology of Lianas*. Chichester, UK: John Wiley & Sons, pp.3–10.

Schnitzer, S.A., Reich, P.B., Bergner, B. and Carson, W.P. 2002. Herbivore and pathogen damage on grassland and woodland plants: a test of the herbivore uncertainty principle. *Ecology Letters*. **5**(4), pp.531–539.

Schnitzer, S.A., Bongers, F., Burnham, R.J. and Putz, F.E. 2015a. *Ecology of Lianas* (S. A. Schnitzer, F. Bongers, R. J. Burnham, & F. E. Putz, eds.). Chichester, UK: John Wiley & Sons, Ltd.

Schnitzer, S.A. 2015. Increasing liana abundance in neotropical forests: causes and consequences *In*: S. A. Schnitzer, F. Bongers, R. J. Burnham and F. E. Putz, eds. *Ecology of Lianas*. Chichester, UK: John Wiley & Sons, Ltd, pp.451–464.

Schupp, E.W. 1986. Azteca protection of Cecropia: ant occupation benefits juvenile trees. *Oecologia*. **70**(3), pp.379–385.

Selaya, N.G. and Anten, N.P.R. 2008. Differences in biomass allocation, light interception and mechanical stability between lianas and trees in early secondary tropical forest. *Functional Ecology*. **22**(1), pp.30–39.

Selaya, N.G., Anten, N.P.R., Oomen, R.J., Matthies, M. and Werger, M.J.A. 2007. Above-ground biomass investments and light interception of tropical forest trees and lianas early in succession. *Annals of Botany*. **99**(1), pp.141–151.

Slik, J.W.F. 2004. El Niño droughts and their effects on tree species composition and diversity in tropical rain forests. *Oecologia*. **141**(1), pp.114–120.

Smith-Martin, C.M., Bastos, C.L., Lopez, O.R., Powers, J.S. and Schnitzer, S.A. 2019. Effects of dry-season irrigation on leaf physiology and biomass allocation in tropical lianas and trees. *Ecology*. **100**(11), p.e02827.

Smith-Martin, C.M., Xu, X., Medvigy, D., Schnitzer, S.A. and Powers, J.S. 2020. Allometric scaling laws linking biomass and rooting depth vary across ontogeny and functional groups in tropical dry forest lianas and trees. *New Phytologist*. **226**(3), pp.714–726.

Smith, J.R., Queenborough, S.A., Alvia, P., Romero-Saltos, H. and Valencia, R. 2017. No strong evidence for increasing liana abundance in the Myristicaceae of a Neotropical aseasonal rain forest. *Ecology*. **98**(2), pp.456–466.

Stephenson, N.L., Das, A.J., Condit, R., Russo, S.E., Baker, P.J., Beckman, N.G., Coomes, D.A., Lines, E.R., Morris, W.K., Rüger, N., Álvarez, E., Blundo, C., Bunyavejchewin, S., Chuyong, G., Davies, S.J., Duque, Á., Ewango, C.N., Flores, O., Franklin, J.F., Grau, H.R., Hao, Z., Harmon, M.E., Hubbell, S.P., Kenfack, D., Lin, Y., Makana, J.R., Malizia, A., Malizia, L.R., Pabst, R.J., Pongpattananurak, N., Su, S.H., Sun, I.F., Tan, S., Thomas, D., Van Mantgem, P.J., Wang, X., Wiser, S.K. and Zavala, M.A. 2014. Rate of tree carbon accumulation increases continuously with tree size. *Nature*. **507**(7490), pp.90–93.

Stevens, G.C. 1987. Lianas as Structural Parasites: The Bursera Simaruba Example. *Ecology*. **68**(1), pp.77–81.

Stewart, T.E. and Schnitzer, S.A. 2017. Blurred lines between competition and parasitism. *Biotropica*. **49**(4), pp.433–438.

Strahler, A.H., Jupp, D.L.B., Woodcock, C.E., Schaaf, C.B., Yao, T., Zhao, F., Yang, X., Lovell, J., Culvenor, D., Newnham, G., Ni-Miester, W. and Boykin-Morris, W. 2008. Retrieval of forest structural parameters using a ground-based lidar instrument (Echidna®). *Canadian Journal of Remote Sensing*. **34**, pp.S426–S440.

Suzuki, E. 1999. Diversity in specific gravity and water content of wood among Bornean tropical rainforest trees. *Ecological Research*. **14**(3), pp.211–224.

Swaine, M.D. and Grace, J. 2007. Lianas may be favoured by low rainfall: Evidence from Ghana. *Plant Ecology*. **192**(2), pp.271–276.

Swaine, M.D., Lieberman, D. and Putz, F.E. 1987. The dynamics of tree populations in tronical forest: A review. *Journal of Tropical Ecology*. **3**(4), pp.359–366.

Talbot, J., Lewis, S.L., Lopez-Gonzalez, G., Brienen, R.J.W., Monteagudo, A., Baker, T.R., Feldpausch, T.R., Malhi, Y., Vanderwel, M., Araujo Murakami, A., Arroyo, L.P., Chao, K.J., Erwin, T., van der Heijden, G., Keeling, H., Killeen, T., Neill, D., Núñez Vargas, P., Parada Gutierrez, G.A., Pitman, N., Quesada, C.A., Silveira, M., Stropp, J. and Phillips, O.L. 2014. Methods to estimate aboveground wood productivity from long-term forest inventory plots. *Forest Ecology and Management*. **320**, pp.30–38.

Talley, S.M., Lawton, R.O. and Setzer, W.N. 1996a. Host preferences of Rhus Radicans (Anacardiaceae) in a southern deciduous hardwood forest 1. *Ecology*. **77**(4), pp.1271–1276.

Talley, S.M., Setzer, W.N. and Jackes, B.R. 1996b. Host Associations of Two Adventitious-Root-Climbing Vines in a North Queensland Tropical Rain Forest. *Biotropica*. **28**(3), p.356.

Tang, Y., Kitching, R.L. and Cao, M. 2012. Lianas as structural parasites: A re-evaluation. *Chinese Science Bulletin*. **57**(4), pp.307–312.

Tanner, E.V.J. and Barberis, I.M. 2007. Trenching increased growth, and irrigation increased survival of tree seedlings in the understorey of a semi-evergreen rain forest in Panama. *Journal of Tropical Ecology*. **23**(3), pp.257–268.

Tobin, M.F., Wright, A.J., Mangan, S.A. and Schnitzer, S.A. 2012. Lianas have a greater competitive effect than trees of similar biomass on tropical canopy trees. *Ecosphere*. **3**(2), pp.1–11.

Toledo-Aceves, T. and Swaine, M.D. 2007. Effect of three species of climber on the performance of Ceiba pentandra seedlings in gaps in a tropical forest in Ghana. *Journal of Tropical Ecology*. **23**(1), pp.45–52.

Toledo-Aceves, T. and Swaine, M.D. 2008a. Above- and below-ground competition between the liana Acacia kamerunensis and tree seedlings in contrasting light environments. *Plant Ecology*. **196**(2), pp.233–244.

Toledo-Aceves and Swaine, M.D. 2008b. Effect of lianas on tree regeneration in gaps and forest understorey in a tropical forest in Ghana. *Journal of Vegetation Science*. **19**(5), pp.717–728.

Toledo-Aceves, T. 2015. Above- and below-ground competition between lianas and trees *In*: S. A. Schnitzer, F. Bongers, R. J. Burnham and F. E. Putz, eds. *Ecology of Lianas*. Chichester, UK: John Wiley & Sons, Ltd, pp.149–163.

Tymen, B., Réjou-Méchain, M., Dalling, J.W., Fauset, S., Feldpausch, T.R., Norden, N., Phillips, O.L., Turner, B.L., Viers, J. and Chave, J. 2016. Evidence for arrested succession in a liana-infested Amazonian forest P. Zuidema, ed. *Journal of Ecology*. **104**(1), pp.149–159.

Vane, G., Green, R.O., Chrien, T.G., Enmark, H.T., Hansen, E.G. and Porter, W.M. 1993. The airborne visible/infrared imaging spectrometer (AVIRIS). *Remote Sensing of Environment*. **44**(2–3), pp.127–143.

Verbeeck, H. and Kearsley, E. 2016. The importance of including lianas in global vegetation models. *Proceedings of the National Academy of Sciences of the United States of America*. **113**(1), p.E4.

Visser, M.D., Muller-Landau, H.C., Schnitzer, S.A., de Kroon, H., Jongejans, E. and Wright, S.J. 2018. A host-parasite model explains variation in liana infestation among co-occurring tree species D. Gibson, ed. *Journal of Ecology*. **106**(6), pp.2435–2445.

Visser, M.D., Schnitzer, S.A., Muller-Landau, H.C., Jongejans, E., de Kroon, H., Comita, L.S., Hubbell, S.P. and Wright, S.J. 2017. Tree species vary widely in their tolerance for liana infestation: A case study of differential host response to generalist parasites P. Zuidema, ed. *Journal of Ecology*. **106**(2), pp.781–794.

Wagner, E.P., Merz, J., Townsend, P.A., Wagner, E.P., Merz, J. and Townsend, P.A. 2019. EcoSIS: A Spectral Library and the Tools to Use It. *AGUFM*. **2019**, pp.B11F-2396.

Waite, C.E., van der Heijden, G.M.F., Field, R. and Boyd, D.S. 2019. A view from above: Unmanned aerial vehicles (UAVs) provide a new tool for assessing liana infestation in tropical forest canopies. *Journal of Applied Ecology*. **56**(4), pp.902–912.

Watts, A.C., Ambrosia, V.G. and Hinkley, E.A. 2012. Unmanned Aircraft Systems in Remote Sensing and Scientific Research: Classification and Considerations of Use. *Remote Sensing*. **4**(6), pp.1671–1692.

Werden, L.K., Waring, B.G., Smith-Martin, C.M. and Powers, J.S. 2018. Tropical dry forest trees and lianas differ in leaf economic spectrum traits but have overlapping water-use strategies. *Tree Physiology*. **38**(4), pp.517–530.

Whigham, D. 1984. The influence of vines on the growth of Liquidambar styraciflua L. (sweetgum). *Canadian Journal of Forest Research*. **14**(1), pp.37–39.

Wigneron, J.P., Fan, L., Ciais, P., Bastos, A., Brandt, M., Chave, J., Saatchi, S., Baccini, A. and Fensholt, R. 2020. Tropical forests did not recover from the strong 2015–2016 El Niño event. *Science Advances*. **6**(6), pp.1–10.

World Bank 2016. Forest area (% of land area). [Accessed 11 November 2019]. Available from: https://data.worldbank.org/indicator/AG.LND.FRST.ZS.

Wright, A., Tobin, M., Mangan, S. and Schnitzer, S.A. 2015. Unique competitive effects of lianas and trees in a tropical forest understory. *Oecologia*. **177**(2), pp.561–569.

Wright, S.J. 2010. The future of tropical forests. *Annals of the New York Academy of Sciences*. **1195**(1), pp.1–27.

Wright, S.J. 2005. Tropical forests in a changing environment. *Trends in Ecology and Evolution*. **20**(10), pp.553–560.

Wright, S.J. and Calderon, O. 2006. Seasonal, El Nino and longer term changes in flower and seed production in a moist tropical forest. *Ecology Letters*. **9**(1), pp.35–44.

Wright, S.J., Calderón, O., Hernandéz, A. and Paton, S. 2004. Are lianas increasing in importance in tropical forests? A 17-year record from panama. *Ecology*. **85**(2), pp.484–489.

Wright, S.J., Hernandéz, A. and Condit, R. 2007. The bushmeat harvest alters seedling banks by favoring lianas, large seeds, and seeds dispersed by bats, birds, and wind. *Biotropica*. **39**(3), pp.363–371.

Wright, S.J., Jaramillo, M.A., Pavon, J., Condit, R., Hubbell, S.P. and Foster, R.B. 2005. Reproductive size thresholds in tropical trees: Variation among individuals, species and forests. *Journal of Tropical Ecology*. **21**(3), pp.307–315.

Wright, S.J., Kitajima, K., Kraft, N.J.B., Reich, P.B., Wright, I.J., Bunker, D.E., Condit, R., Dalling, J.W., Davies, S.J., DíAz, S., Engelbrecht, B.M.J., Harms, K.E., Hubbell, S.P., Marks, C.O., Ruiz-Jaen, M.C., Salvador, C.M. and Zanne, A.E. 2010. Functional traits and the growth-mortality trade-off in tropical trees. *Ecology*. **91**(12), pp.3664–3674.

Wright, S.J. and van Schaik, C.P. 1994. Light and the phenology of tropical trees. *American Naturalist*. **143**(1), pp.192–199.

Wright, S.J., Sun, I.F., Pickering, M., Fletcher, C.D. and Chen, Y.Y. 2015. Long-term changes in liana loads and tree dynamics in a Malaysian forest. *Ecology*. **96**(10), pp.2748–2757.

Wu, J., Kobayashi, H., Stark, S.C., Meng, R., Guan, K., Tran, N.N., Gao, S., Yang, W., Restrepo-Coupe, N., Miura, T., Oliviera, R.C., Rogers, A., Dye, D.G., Nelson, B.W., Serbin, S.P., Huete, A.R. and Saleska, S.R. 2018. Biological processes dominate seasonality of remotely sensed canopy greenness in an Amazon evergreen forest. *New Phytologist*. **217**(4), pp.1507–1520.

Wu, M., Wu, C., Huang, W., Niu, Z., Wang, C., Li, W. and Hao, P. 2016. An improved high spatial and temporal data fusion approach for combining Landsat and MODIS data to generate daily synthetic Landsat imagery. *Information Fusion*. **31**, pp.14–25.

Wulder, M.A., White, J.C., Coops, N.C. and Ortlepp, S. 2009. Remote Sensing for Studies of Vegetation Condition: Theory and Application *In*: T. A. Warner, G. M. Foody and M. Nellis, eds. *The SAGE Handbook of Remote Sensing*. London: SAGE Publications Ltd, pp.355–367.

Wyka, T.P., Oleksyn, J., Karolewski, P. and Schnitzer, S.A. 2013. Phenotypic correlates of the lianescent growth form: A review. *Annals of Botany*. **112**(9), pp.1667–1681.

Yang, B., Liu, H., Kang, E.L., Shu, S., Xu, M., Wu, B., Beck, R.A., Hinkel, K.M. and Yu, B. 2021. Spatio-temporal Cokriging method for assimilating and downscaling multi-scale remote sensing data. *Remote Sensing of Environment*. **255**, p.112190.

Yanoviak, S.P. 2013. Shock value: Are lianas natural lightning rods? *In*: *Treetops at Risk: Challenges of*

Global Canopy Ecology and Conservation. Springer New York, pp.147–153.

Yanoviak, S.P. and Schnitzer, S.A. 2013. Functional roles of lianas for forest canopy animals *In*: M. Lowman, S. Devy and T. Ganesh, eds. *Treetops at risk: Challenges of global forest canopies*. New York, USA: Springer, pp.209–214.

Yorke, S.R., Schnitzer, S.A., Mascaro, J., Letcher, S.G. and Carson, W.P. 2013. Increasing Liana Abundance and Basal Area in a Tropical Forest: The Contribution of Long-distance Clonal Colonization. *Biotropica*. **45**(3), pp.317–324.

Yu, Q., Gong, P., Clinton, N., Biging, G., Kelly, M. and Schirokauer, D. 2006. Object-based detailed vegetation classification with airborne high spatial resolution remote sensing imagery. *Photogrammetric Engineering and Remote Sensing*. **72**(7), pp.799–811.

Yuan, X., Laakso, K., Marzahn, P. and Sanchez-Azofeifa, G.A. 2019. Canopy Temperature Differences between Liana-Infested and Non-Liana Infested Areas in a Neotropical Dry Forest. *Forests*. **10**(10), p.890.

Zahawi, R.A., Dandois, J.P., Holl, K.D., Nadwodny, D., Reid, J.L. and Ellis, E.C. 2015. Using lightweight unmanned aerial vehicles to monitor tropical forest recovery. *Biological Conservation*. **186**, pp.287–295.

Zanne, A.E., Lopez-Gonzalez, G., Coomes, D. a., Ilic, J., Jansen, S., Lewis, S.L.S.L., Miller, R.B.B., Swenson, N.G.G., Wiemann, M.C.C. and Chave, J. 2009. Data from: Towards a worldwide wood economics spectrum. *Ecology Letters*. **235**, p.33.

Zhang, J., Hu, J., Lian, J., Fan, Z., Ouyang, X. and Ye, W. 2016. Seeing the forest from drones: Testing the potential of lightweight drones as a tool for long-term forest monitoring. *Biological Conservation*. **198**, pp.60–69.

Zhang, Y., Fu, R., Yu, H., Dickinson, R.E., Juarez, R.N., Chin, M. and Wang, H. 2008. A regional climate model study of how biomass burning aerosol impacts land-atmosphere interactions over the Amazon. *Journal of Geophysical Research*. **113**(D14).

Zhu, S.D. and Cao, K.F. 2010. Contrasting cost-benefit strategy between lianas and trees in a tropical seasonal rain forest in southwestern China. *Oecologia*. **163**(3), pp.591–599.

Zhu, S.D. and Cao, K.F. 2009. Hydraulic properties and photosynthetic rates in co-occurring lianas and trees in a seasonal tropical rainforest in Southwestern China. *Plant Ecology*. **204**(2), pp.295–304.

Zotz, G., Cueni, N. and Korner, C. 2006. In situ growth stimulation of a temperate zone liana (Hedera helix) in elevated CO $_2$. *Functional Ecology*. **20**(5), pp.763–769.

Zou, L., Wang, Y., Giannakis, I., Tosti, F., Alani, A.M. and Sato, M. 2020. Mapping and assessment of tree roots using ground penetrating radar with low-cost GPS. *Remote Sensing*. **12**(8), p.1300.

Appendices

Appendix 1 – Summary of bootstrap tests for difference (95% Confidence Interval [CI])

Table A.1 – Summary of bootstrap tests for difference a) between treatments for net biomass change, biomass growth, biomass recruitment and biomass mortality (Mg C ha^{-1} year^{-1}) averaged over the entire eight-year census period, b) between treatments for yearly net biomass change (Mg C ha^{-1} year^{-1}) for each wood density class, and c) between treatments for yearly biomass growth (Mg C ha^{-1} year^{-1}) for each wood density class. Significant differences between treatments represented by ***.

a) 8-year average

Metric	**Treatment**	**Median**	**95% Confidence Interval**
Net Biomass Change (Mg C ha^{-1} year^{-1})			
	Control	-0.133	-0.556 – 0.754
	Removal	2.193	0.048 – 2.443
	Difference	2.112	-0.193 – 2.731
Biomass Growth (Mg C ha^{-1} year^{-1})			
	Control	1.304	1.090 – 1.579
	Removal	2.598	2.227 – 2.754
	Difference	1.271	0.897 – 1.508 ***
Biomass Recruitment (Mg C ha^{-1} year^{-1})			
	Control	0.099	0.081 – 0.136
	Removal	0.215	0.149 – 0.296
	Difference	0.117	0.047 – 0.207 ***
Biomass Mortality (Mg C ha^{-1} year^{-1})			
	Control	1.351	0.801 – 2.289
	Removal	0.731	0.491 – 2.612
	Difference	0.449	-1.431 – 1.394

b) Net biomass change per wood density class (Mg C ha^{-1} year^{-1})

Year	**Treatment**	**Median**	**95% Confidence Interval**
Low			
1	Difference	0.122	-0.590 – 0.893
2	Difference	0.633	-0.653 – 1.065
3	Difference	0.647	0.248 – 1.246 ***
4	Difference	0.559	0.212 – 1.592 ***
5	Difference	0.453	0.129 – 1.132 ***
6	Difference	0.149	-0.469 – 0.840
7	Difference	0.401	-0.602 – 1.202
8	Difference	0.906	-0.609 – 1.728
8-year average	Difference	0.357	-0.251 – 1.000
Medium			
1	Difference	0.424	-0.410 – 0.958
2	Difference	0.245	-0.369 – 1.526
3	Difference	0.916	0.368 – 2.694 ***
4	Difference	0.648	0.070 – 1.553 ***
5	Difference	0.228	-0.514 – 0.964
6	Difference	0.811	0.127 – 1.219 ***

7	Difference	0.672	0.076 – 1.383 ***
8	Difference	0.347	-0.029 – 0.707
8-year average	Difference	0.498	-0.210 – 1.114
High			
1	Difference	0.595	0.060 – 1.373 ***
2	Difference	0.485	0.286 – 1.274 ***
3	Difference	0.617	0.444 – 1.044 ***
4	Difference	0.348	0.050 – 0.739 ***
5	Difference	0.321	-0.159 – 0.518
6	Difference	0.721	0.283 – 1.157 ***
7	Difference	0.718	0.295 – 1.161 ***
8	Difference	0.638	0.178 – 1.625 ***
8-year average	Difference	0.600	-0.103 – 1.187

c) Biomass Growth per wood density class (Mg C ha^{-1} year^{-1})

Year	Treatment	Median	95% Confidence Interval
Low			
1	Difference	0.295	0.045 – 0.582 ***
2	Difference	0.622	0.290 – 0.783 ***
3	Difference	0.625	0.338 – 0.741 ***
4	Difference	0.509	0.229 – 0.657 ***
5	Difference	0.327	0.127 – 0.500 ***
6	Difference	0.411	0.184 – 0.631 ***
7	Difference	0.333	0.168 – 0.606 ***
8	Difference	0.343	0.126 – 0.520 ***
8-year average	Difference	0.421	0.199 – 0.565 ***
Medium			
1	Difference	0.141	-0.141 – 0.403
2	Difference	0.488	0.055 – 0.857 ***
3	Difference	0.597	0.325 – 0.777 ***
4	Difference	0.512	0.169 – 0.784 ***
5	Difference	0.441	0.152 – 0.684 ***
6	Difference	0.487	0.079 – 0.860 ***
7	Difference	0.503	0.046 – 0.906 ***
8	Difference	0.323	-0.008 – 0.678
8-year average	Difference	0.399	0.109 – 0.696 ***
High			
1	Difference	0.302	-0.033 – 0.583
2	Difference	0.425	0.150 – 0.922 ***
3	Difference	0.493	0.160 – 0.934 ***
4	Difference	0.378	0.074 – 0.669 ***
5	Difference	0.361	0.077 – 0.545 ***
6	Difference	0.641	0.306 – 0.854 ***
7	Difference	0.510	0.269 – 0.774 ***
8	Difference	0.554	0.240 – 0.765 ***
8-year average	Difference	0.410	0.102 – 0.793 ***

Appendix 2 – Wood Density and Tree Functional Traits

Wood density is commonly used as a proxy for functional traits related to light-tolerance and inherent growth rates (Suzuki, 1999; Muller-Landau, 2004; van der Heijden et al., 2008). In Chapter 3, tree data from the secondary forest plots was split into three broad wood density classes, low (≤0.49), medium (>0.49 - ≤0.69), and high (≥0.69) in keeping with similar studies (van der Heijden and Phillips, 2009). This was an attempt to group different tree functional groups. For example, slow-growing and shade tolerant species with lower mortality rates should predominantly fall within the high wood density class. Alternatively, fast-growing short lived pioneer species with high turnover should be represented within the low wood density class. These classes were used instead of a continuous wood density variable to broadly group pioneers and shade tolerant species on opposite sides of the slow-fast life history axis (Wright et al., 2010; Visser et al., 2017). To support these assumptions, the below plots detail the relationships between functional traits (mortality and relative growth) with opposite ends of the wood density spectrum in the dataset from Gigante, Panama (See Figures A1 and A2).

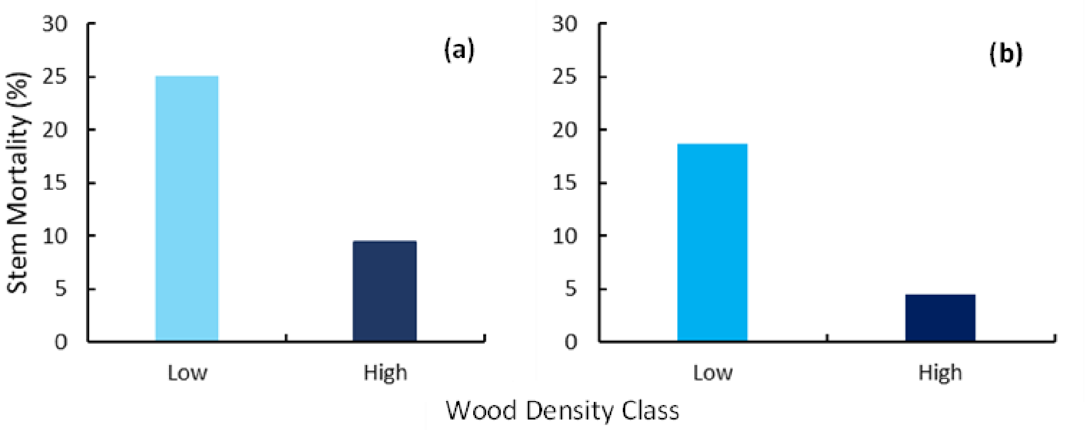

Figure A1 – Bar plot denoting percentage stem mortality within the low (≤0.49) and high (≥0.69) wood density classes for both a) control plots and b) removal plots.

In Figure A1, tree species with fast life strategies and characteristically high turnover are well represented in high stem mortality across both control and removal plots in the low wood density class. Similarly, slow-growing species across both treatments elicited lower percentage stem mortality, typical of this functional group.

Similarly, relative growth rate (%) in the low wood density class is also greater than that of individuals in the high wood density class in both control and removal plots (although this difference is more marked in removal plots), in keeping with our assumption that wood density is a suitable proxy measure for species functional traits (Figure A2). Naturally, anomalies and outliers to the rule of wood density as a proxy for tree functional traits will exist. Although for the purposes of this study, supported by relevant literature, this assumption has facilitated complex quantitative analysis between plant functional types and their response to liana removal.

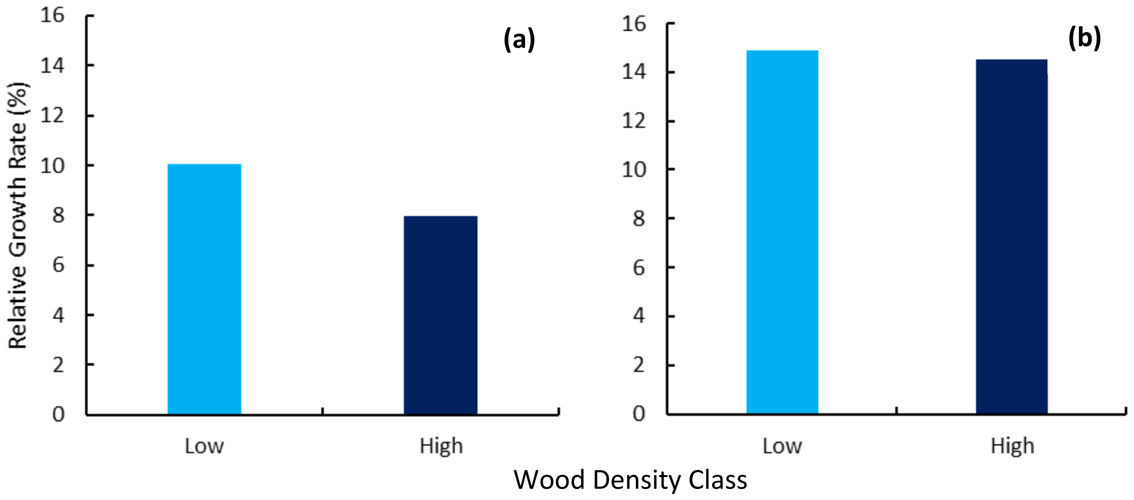

Figure A2 – Bar plot denoting relative growth rate (%) within the low (≤0.49) and high (≥0.69) wood density classes for both a) control plots and b) removal plots.