Tropical tree and liana community recovery through secondary succession

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To Mum, who was so excited to see me start this journey. I will always be grateful for the love of nature you gave me.

General abstract

Secondary forests (i.e. forests regrowing after land abandonment) are increasing in area throughout the tropics, harbouring great potential for carbon sequestration and biodiversity conservation. The rate of recovery of these forests is well understood for tree communities in early and mid-stages of tropical forest succession (< 50 years). However, studies of successional liana communities lag behind, and few late successional studies exist for either trees or lianas. Processes such as the recovery of species composition and above-ground biomass can take place over centuries, and as such they are poorly quantified by current studies. Here I investigate forest recovery over the late stages of succession for tree and liana communities. Chapters 2 and 3 study biodiversity and structural recovery in tree communities in mid-to-late-stage successional forest (aged 40 – 120 years) in Panama. I find that species and functional diversity recover by mid-succession, but species richness and rare species do not recover to old-growth levels. Species community composition can converge on old-growth communities 120-years into succession, but I also find divergent successional pathways caused by a long-lived pioneer's dominance. Leaf traits showed little variation in the mid-to-late stages of succession, but plant-stature related traits continued to change into late succession suggesting plant height as a major mechanism for competition for light in late successional stages. Chapter 4 examines the relationship between liana density and basal area across successional and climatic gradients spanning four countries in the Neotropics. I find that liana density and basal area is higher in moist/wet forests than dry forests, contrary to previous findings. Liana density is highest in early succession, and I find that liana dominance is most likely in highly seasonal tropical forests. These findings will help inform tropical forest recovery and confirm the value of old secondary forests for tree and liana communities.

Declaration of Authorship

I, Alexander David Elsy, declare that this thesis has been composed by myself and that it embodies the results of my own research. Where appropriate I have acknowledged the nature and extent of work carried out in collaboration with others.

Signed: Alex Elsy

Date: 31st March 2023

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1 Chapter 1: General Introduction

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1.1 Forests

1.1.1 The importance of forests

Forests provide key ecosystem functions and services to an estimated 1.6 billion people worldwide (Chao, 2012) and can provide direct benefits for people through food, medicine and timber (Arico et al., 2005). Forests also provide indirect benefits, such as flood control, erosion prevention, carbon storage, pollination, water quality and nutrient cycling, and have cultural and recreational value (Arico et al., 2005; Miura et al., 2015). The value of forests has been quantified in economic terms, with temperate/boreal forests worth an estimated \$3137 ha^{-1} yr^{-1} and tropical forests worth \$5382 ha^{-1} yr^{-1} in 2011 (Costanza et al., 2014). However, this valuation ignores the less tangible benefits of forests such as their importance to biodiversity; with forests holding more than 75 % of terrestrial biodiversity (FAO, 2018).

1.1.2 Tropical forests

Tropical forests are especially biodiverse, with estimates that they contain over 62 % of the world's terrestrial vertebrate species (Pillay et al., 2022) and tropical latitudes (i.e. between the Tropics of Cancer and Capricorn) in general contain 91 % of terrestrial bird species and > 75 % of the world's amphibians, freshwater fish, ants and flowering plants (Barlow et al., 2018). Tropical forests likely contain between 40,000 and 53,000 tree species and this vast biodiversity is distributed unevenly through tropical forest ecosystems, with the number of tree species in the Neotropics and Indo-Pacific vastly higher than in Africa (Slik et al., 2015).

Tropical forests are categorised by their rainfall with dry forests having < 1500 mm rainfall per year, moist forests having between 1500 and 2500 mm of rainfall per year, and wet forests with ≥ 2500 mm of rainfall per year (Rozendaal et al., 2019). Moist tropical forests can be especially biodiverse, with examples of 1200 species of coleoptera found on just 19 individual trees in Panama (Erwin, 1982) and 473 species of tree found in 1-ha of Amazonian forest in Ecuador (Valencia et al., 1994). Biodiversity hotspots of endemic species span the tropics, and associated biomes, and hotspots across Central and South America forests are estimated to contain 28,700 endemic plant species (Mittermeier et al., 2011). Tropical forests also contain much greater variety in plant growth forms than temperate forests, and lianas (woody vines) and epiphytes can comprise 27 % of plant species richness in tropical forests compared to just 3 % of species richness in temperate forests (Spicer et al., 2020)

1.1.3 Threats to tropical forests

Despite their value for people and biodiversity, tropical forests are under threat and degraded and secondary forests, i.e. forests regrowing on abandoned land (Corlett, 1994), comprise c. 50 % of remaining tropical forests (FAO, 2020). Indeed, forests in the tropics have suffered the highest rates of forest loss globally in recent years (Hansen et al., 2013) and there is evidence of ongoing primary forest loss pantropically (Turubanova et al., 2018). Myriad factors including farming, cattle ranching, plantation agriculture, fuelwood harvesting, logging, infrastructure construction and population growth all act as drivers of forest loss (Lambin and Geist, 2002; Rudel et al., 2009; DeFries et al., 2010). This land conversion from forested to non-forested land negatively impacts upon biodiversity (Fitzherbert et al., 2008; Paillet et al., 2010; Phalan et al., 2011; Philpott et al., 2008), and thus ecosystem services (Diaz et al., 2006). Often, forests are not completely converted into a new land use and are instead disturbed and degraded. An estimated 19 % of tropical forest is now within 100 m of a forest edge with potential carbon emissions (10.3 Gt) due to deleterious edge effects, comprising 31 % of estimated carbon emissions due to tropical deforestation (Brinck et al., 2017). Forest fragmentation and edge effects also cause losses in species richness, cause community divergence from intact forest communities, and degrade ecosystem functions, such as nutrient retention, pollination and productivity (Haddad et al., 2015; Laurance et al., 2007).

However, despite ongoing deforestation, many areas of the tropics are in a state of regrowth following land abandonment (Chazdon et al., 2016). Hansen et al. (2013) estimated that between 2000 and 2012 0.8 million km^2 of new forest regrowth was gained in the tropics. Secondary forests are a major carbon sink, with tropical forest regrowth found to be responsible for the uptake of 1.6 Pg C/year, versus tropical deforestation causing emissions of 2.9 Pg C/year between 1990 and 2007 (Pan et al., 2011). While these numbers are not definite, and may vary considerably by biogeographic region (Chave et al., 2020), the natural regeneration of secondary forests has the potential to sequester large amounts of CO_2 (Chazdon et al., 2016). Secondary forests also likely act as important reservoirs of old-growth forest species in human-impacted landscapes (Chazdon et al., 2009) and understanding how and when these secondary forests recover in function and species identity through successional processes has been an important question in tropical ecology for decades (Bazzaz and Pickett, 1980; Dent and Wright, 2009).

1.2 Succession

1.2.1 Primary and secondary succession

Ecological succession is the change in community composition through time after major disturbances in the local environment **(**Horn, 1974), and is split into primary and secondary succession. Primary succession occurs when habitats which have either never been exposed to an ecological community or have no trace of the previous community remaining at the site, are colonised. Classical examples include new habitat created by: wave action (Sousa, 1979a, 1979b**)**, glacial retreat (Chapin et al., 1994), sediment deposition (Kalliola et al., 1991) and lava flows (Kitayama et al., 1995) but anthropogenic impacts can also lead to primary succession e.g. in cases of mining (Wiegleb and Felinks, 2001) and dredging (El-Sheikh et al., 2012). In contrast, secondary succession occurs after a disturbance where a significant proportion of the ecological community remains at the site. Secondary succession is a continuously occurring process and large-scale examples include forest recovery after fire (Romme and Knight, 1981), logging (Bischoff et al., 2005), storm damage (Flynn et al., 2009) and land conversion (Aide et al., 1995). Many of these examples are underpinned by smaller scale processes such as tree falls, which are known to maintain biodiversity through natural disturbance processes even in established old-growth forest communities (Schnitzer and Carson, 2001).

1.2.2 Chronosequences and succession

Successional processes are often investigated through a chronosequence approach (Chazdon et al., 2006; Foster and Tilman, 2000). Chronosequences, are space-for-time substitutions, in which multiple vegetation plots of distinct known ages are sampled at a single point in time, and then inferences are made regarding temporal change through succession in the vegetation community (Chazdon et al., 2006). The major assumption of chronosequences is that any changes detected between different aged sites are due to age alone, and thus other environmental variables such as edaphic and topographic factors must be controlled for. This assumption is often violated and there are suggestions that chronosequences are often incorrectly used in successional research (Johnson and Miyanishi, 2008; Walker et al., 2010). Alternative approaches to directly track successional changes involve longitudinal monitoring of the same sites over many years (Chazdon et al., 2006; Mora et al., 2015). However, this is costly (Condit, 1995) and no long-term longitudinal studies exist for the late stages of tropical forest succession. Therefore, chronosequences often remain the most viable approach for studying succession over long timescales (Walker et al., 2010).

1.2.3 Successional theory

Succession may not be unidirectional and multiple pathways can cause the development of different plant communities at the same stage of succession (Arroyo-Rodríguez et al., 2017). A plethora of variables may influence successional pathways, from landscape-scale factors including climate, topography, land-use history, surrounding matrix characteristics and fragment size, to smaller plot-scale factors such as seed bank/seed rain availability, soil properties, inter- and intraspecific competition and dispersal/migration (Arroyo-Rodríguez et al., 2017). Despite this potential variation, a number of theories have been developed to quantify the turnover of species through succession in tropical secondary forest (summarised in Chazdon (2014)). For example, Finegan (1996) describes the general pattern of Neotropical secondary succession for forests recovering on abandoned land with three distinct phases: firstly, abandoned land is rapidly colonised by herbs, shrubs and climbing plants (< 5 years); secondly, short-lived pioneer species rapidly grow and form a canopy (10 – 30 years) and thirdly, long-lived pioneers replace short lived pioneers, and shade tolerant species subsequently begin to grow into the forest canopy. However, Finegan (1996) noted that while the early stages of succession were well characterised, uncertainty remained as to how long-lived pioneers and shade tolerant species interact and persist into later stages of succession (> 100 years).

Tropical forest succession is thus usually viewed through the lens of changing light availability driving turnover in species, from shade-intolerant, short-lived pioneers to shade-tolerant, old-growth associated species. This relates to the fast-slow continuum of plant growth strategies, where an inherent trade-off exists between the rate of resource acquisition, and thus plant growth, and the likelihood of survival (Grime et al., 1997; Reich, 2014; Salguero-Gómez et al., 2016). The fast-slow continuum has been applied to tropical forests with trees associated with higher relative growth rates also having increased mortality rates, but this trade-off may not be as evident in disturbed forests (Russo et al., 2021; Wright et al., 2010). Other factors also influence species turnover in succession, and an axis of variation relating to plant stature and recruitment, which is orthogonal to the fast-slow continuum, has been identified (Kambach et al., 2022; Rüger et al., 2018). This stature-recruitment axis has been linked to long-lived pioneer species, which are tall species with high growth and survival rates but low recruitment, and short-lived breeders, which are short-statured, with low growth and survival rates but high recruitment (Kambach et al., 2022; Rüger et al., 2020, 2018). A recent study has confirmed the importance of these demographic strategies over succession in two wet and two dry Neotropical forests (Rüger et al., 2023). Rüger et al. (2023) identified shifts in fast, slow, long-lived pioneers, short-lived breeders, and intermediate strategy species through succession. This study confirmed the pattern of succession described by Finegan (1996) for the first 50 – 100 years of succession, and built upon it finding that long-lived pioneers can continue to dominate old-growth forests in terms of basal area, even more-so than slow strategy species (Rüger et al., 2023).

1.2.4 Functional traits and succession

Functional traits, defined as any trait which influences plant fitness (Violle et al., 2007), are a common window through which to view secondary forest succession. As previously mentioned, the shift from early to late succession is partially characterised by traits changing along the fast-slow continuum (Rüger et al., 2023). One well studied aspect of the fast-slow continuum is the leaf economic spectrum, where leaves at the fast end of the spectrum acquire resources quickly, but have a short lifespan, and leaves at the slow end of the spectrum are conservative, with long lifespans (Reich, 2014; Wright et al., 2004). Short-lived pioneer species typically have fast leaf traits, and thus have high specific leaf area, leaf nitrogen content, leaf phosphorous content and low leaf toughness in comparison to conservative, shade-tolerant species (Popma et al., 1992; Rüger et al., 2012; Westoby et al., 2002; Wright et al., 2010). Wood density is another key trait which is closely linked to survival (Chave et al., 2009; Kraft et al., 2010; Larjavaara and Muller-Landau, 2010) and species with fast growth rates often haven lower wood density and increased mortality rates (King et al., 2006b). Many studies have examined these traits through succession in wet and moist tropical forest, and often find support for the shift from fast to slow strategies, with specific leaf area and leaf nitrogen content values decreasing through time and wood density and leaf toughness increasing (Boukili and Chazdon, 2017; Lohbeck et al., 2013; Muscarella et al., 2016; Poorter et al., 2019, 2021b).

1.2.5 Recovery of tree structure and diversity through succession

In recent years many large-scale syntheses examining the recovery of wet and dry Neotropical forests through succession have been conducted (Chazdon et al., 2016; Poorter et al., 2021a, 2021b, 2016; Rozendaal et al., 2019). These studies have focused on tree communities and typically found relatively rapid recovery of many forest characteristics in the early stages of succession (Poorter et al., 2021a; Rozendaal et al., 2019). For instance, soil carbon, nitrogen and bulk density recovers within the first 15 years on average, and plant functioning (wood density, specific leaf area and nitrogen fixing traits) recover within 25 years in a study across 77 sites in the Neotropics and West Africa (Poorter et al., 2021a). Species richness typically recovers slower than these function- and soil-related characteristics and is estimated to recover to old-growth levels within 54 years on average (Rozendaal et al., 2019). Species diversity recovers soon after richness (Poorter et al., 2021a), and there is similar evidence for functional diversity recovering in the mid stages of succession across multiple forests (Lohbeck et al., 2012; Warring et al., 2016; WenSheng, RunGuo and Yi, 2014; Whitfeld et al., 2014). Aspects of forest structure can recover over a similar time scale, with structural heterogeneity and maximum tree diameters usually recovering to old-growth levels within 50 years (Poorter et al., 2021a). However, tree biomass, and thus forest carbon stock, is slow to accumulate and may take 120 years or longer to reach old-growth values in secondary forests (Poorter et al., 2021a). Species community composition is typically the last aspect of tropical forests to recover in secondary forests (Poorter et al., 2021a; Rozendaal et al., 2019). Estimates range widely from 120 years (Poorter et al., 2021a) to 487 years (Rozendaal et al., 2019) for the recovery of Neotropical secondary forest to 90 % of old-growth species composition. These values are derived from chronosequence studies (Poorter et al., 2021a; Rozendaal et al., 2019), and similar rates of recovery are predicted from the palaeoecological record after forest disturbance, with median recovery times of 210 years, and mean recovery times of 503 years, to 95.5 % of pre-disturbance levels (Cole, Bhagwat and Willis, 2014).

1.2.6 Differing rates of recovery

Species richness recovers much faster than old-growth community composition as the forests in mid-succession likely contain both short-lived and long-lived pioneers as well as shade-tolerant species (van Breugel et al., 2013). Recovering to old-growth community composition on the other hand, first requires nearby old-growth seed sources and dispersal processes, which can be disrupted in fragmented tropical landscapes (Arasa-Gisbert et al., 2022; Arroyo-Rodríguez et al., 2017; Costa et al., 2012) and thus slow down the rate of secondary forest recovery. Moreover, attaining similarity to old-growth community composition also requires existing early and mid-successional trees to die and enable old-growth species to mature into the canopy, which is a process which can take centuries (Condit, 2022). Initial plot conditions in early stages of succession can also have a large impact on the rate of recovery, with remnant trees accelerating the rate of recovery towards old-growth forest (Sandor and Chazdon, 2014) and land-use history strongly affecting forest structure and species composition for decades (Jakovac et al., 2021). Furthermore, estimates of rates of recovery for processes which occur in the late stages of succession are constrained by limited late successional plots. For example, the Neotropical study by Rozendaal et al. (2019) only analysed four of 56 chronosequences which had plots ≥ 80 years old, and a pantropical meta-analysis of carbon and biodiversity recovery only included 12 of 204 plots with ages ≥ 80 years old (Martin, Newton and Bullock, 2013). This bias in the literature towards early and mid-successional forests means that it is unsurprising that estimates of late-stage successional recovery, in terms of community composition and above-ground biomass, are imprecise (Poorter et al., 2021a; Rozendaal et al., 2019). Therefore, a large knowledge gap remains in how tropical secondary forests continue to recover into the late stages of succession.

1.3 Lianas

1.3.1 Lianas through succession

Beyond trees, lianas (woody vines) are a major plant growth form (Rowe and Speck, 2005) which vary considerably through succession (Letcher, 2015). Lianas are a highly diverse guild of plants (Gianoli, 2015) which start life as terrestrial seedlings and generally rely on trees for mechanical support, although young lianas often grow independently from trees before later attaching to them (Rowe and Speck, 2005). Lianas are a major component of tropical forests, ranging from c. 10 % of woody species richness in Malaysia (Appanah, Gentry and LaFrankie, 1993), to 35 % of woody species richness and 25 % of woody stem density in Panama (Schnitzer et al., 2012) and c. 44 % of woody species richness in Amazonian Bolivia (Pérez-Salicrup, Sork and Putz, 2001).

Despite their importance in tropical forests, relatively few studies have examined how lianas change through succession (Letcher, 2015). For example, Letcher (2015) reviewed mainly studies in moist/wet Neotropical forests and found liana density and species richness to peak in the early-to-mid stages of succession. This likely relates to lianas exploiting high light and trellis availability (Putz, 1984) of young successional forests, which are conditions analogous to forest edges and treefall gaps where lianas thrive (Campbell et al., 2018; Laurance et al., 2001; Schnitzer et al., 2021; Schnitzer and Carson, 2001). Liana species composition may begin to converge towards old-growth community composition in a similar time period to tree communities, with DeWalt, Schnitzer and Denslow (2000) finding 100-year-old liana communities close in ordination space, and thus species composition, to old-growth plots in Panamanian moist forest. Functional traits of liana species also vary through succession, with liana climbing habits shifting, and lianas found to be larger seeded and more likely to have a freestanding growth form in older wet forests (Letcher and Chazdon, 2012). Late-stage successional liana studies are rare; Letcher (2015) reviewed nine studies, and only one of those chronosequences included plots over fifty years old (DeWalt, Schnitzer and Denslow, 2000). Successional liana research has progressed since 2015, and there are additional late-stage successional studies (e.g. Mumbanza et al., 2022; Lomwong et al., 2023), however there is still a dearth of studies examining lianas through succession in comparison to trees, and the few late successional plots are even more apparent.

1.3.2 Lianas and biogeography

Lianas are typically found in higher abundance in the Neotropics and Africa than in Asian tropical forests (DeWalt et al., 2015). Lianas also vary in their distribution according to combined effects of mean annual precipitation and seasonality (Schnitzer, 2005; Swaine and Grace, 2007; DeWalt et al., 2010, 2015; Parolari et al., 2020). Pantropically, liana density and basal area declines in old-growth forests with increasing precipitation, and increases with increasing dry season length (DeWalt et al., 2015, 2010; Schnitzer, 2005; Swaine and Grace, 2007). However, a separate analysis across the Neotropics found neither mean annual precipitation nor dry season length explained liana abundance (van der Heijden and Phillips, 2008) and reasons for these differences across studies were unclear (DeWalt et al., 2010; van der Heijden and Phillips, 2008). Recent research has found that mean annual precipitation may be a weak sole predictor of liana abundance along a precipitation gradient across the Isthmus of Panama, and instead an index of precipitation seasonality (Feng et al., 2013) explained a large proportion of the variation in liana abundance (Parolari et al., 2020). The increased abundance of lianas in tropical seasonal forests has been hypothesised to be due to lianas possessing a seasonal growth advantage over trees in the high light, low water conditions of the dry season (Schnitzer, 2018). Evidence for the seasonal growth advantage has been found in a seasonally dry moist tropical forest in Panama, where the liana growth rate was found to be maintained during the four-month dry season, whereas tree growth was concentrated in the wet season (Schnitzer and van der Heijden, 2019). Thus, lianas have a proven growth advantage over trees in dry seasons or drought conditions (Schnitzer and van der Heijden, 2019). This growth advantage may be due to lianas having higher water use efficiency (Cai et al., 2009; Smith-Martin et al., 2019; Willson et al., 2022) and photosynthetic rates in the dry season (Smith-Martin et al., 2019). Thus, lianas in seasonally dry forests likely have opportunities for high growth that lianas in aseasonal forests do not, leading to the differences in abundance seen among forests (DeWalt et al., 2015, 2010; Schnitzer, 2005; Swaine and Grace, 2007).

1.3.3 Liana-tree interactions

Lianas are classified as structural parasites (Stevens, 1987; Visser et al., 2018a) and have numerous negative impacts on tree communities. Recent meta-analyses examining the impact of liana removal experiments on tree performance have found that liana removal leads to strongly increased tree growth, biomass accumulation and reproductive success (Estrada-Villegas et al., 2022a; Finlayson et al., 2022). These effects may be due to a number of factors. Firstly, lianas compete strongly with trees for light (Avalos et al., 2007; Rodriquez-Ronderos et al., 2016; Schnitzer and Carson, 2010) and lianas often deploy a thin parasol of leaves above the tree canopy which shades the tree (Avalos et al., 2007). Secondly, lianas compete with trees for water and the removal of lianas from a Panamanian forest has been found to increase deeper soil moisture content by 5 – 25 % in the dry season (Reid et al., 2015). Linked to this, tree sap velocity, which is dependent on water availability, increases after liana removal (Álvarez-Cansino et al., 2015; Tobin et al., 2012). Thirdly, lianas can often cause mechanical damage to the trees they colonise (Putz, 1984; Toledo-Aceves, 2015) and may increase the risk of wind damage (Ewers et al., 2015). Moreover, lianas in high abundance can lead to arrested states of succession where tree biomass and regeneration is restricted over long time periods (Foster et al., 2008; Gerwing and Farias, 2000; Tabanez and Viana, 2000; Tymen et al., 2016).

However, lianas may have some benefits to the tree community. For instance, in early succession lianas may benefit forest recovery by causing faster canopy closure, improving connectivity between fragments and creating understorey microclimatic conditions into which shade-tolerant species are more likely to recruit (Campbell et al., 2015; Marshall et al., 2020). Lianas also cause higher mortality in fast-growing species, and so likely act as drivers of succession (Visser et al., 2018b). The benefits for animals are more certain, and a number of studies have found lianas are important food sources and structural components of forests which benefit birds, mammals and arthropods (Arroyo-Rodríguez et al., 2015; Michel, Carson and Sherry, 2015; Michel, Robinson and Sherry, 2015; Yanoviak, 2015; Schnitzer et al., 2020).

The impacts of lianas in tropical forests are likely in flux, as lianas have been found to be increasing in abundance in the Neotropics (Schnitzer, 2015; Schnitzer et al., 2011; Schnitzer and Bongers, 2011). For instance, Laurance et al. (2014) found liana abundance in central Amazonia increased by 1 % per year between 1997 and 2012. Schnitzer et al. (2021) also found that between 2007 and 2017 liana density increased by 29.2 % in the Barro Colorado Island 50-ha plot in Panama. The primary driver of this change was recruitment in canopy gaps, and Schnitzer et al. (2021) suggest that lianas may be able to act as ecosystem engineers, in that they cause and maintain canopy gaps. Increasing drought severity may also be driving increases in liana abundance (Schnitzer, 2015), given the seasonal growth advantage of lianas over trees (Schnitzer, 2018a). If this is the case, lianas are likely to continue shifting in abundance into the future with changes in precipitation and seasonality due to climate change (Caretta et al., 2022). This has large potential ramifications for trees in Neotropical forests due to the many negative impacts of lianas upon tree growth and reproduction (Estrada-Villegas et al., 2022a; Finlayson et al., 2022).

1.4 Synthesis

Secondary forests are regenerating across vast areas of the tropics and have the potential to recover in biodiversity and structure to values similar to old-growth forests. However, late-stage successional studies of tree and liana communities are rare, and large knowledge gaps remain into how secondary forests continue to recover in older secondary forests (e.g. Chazdon (2014), Finegan (1996), but see Rüger et al., 2023). Increasing understanding of late-stage successional processes is important, given that how and when biodiversity recovers needs to be understood if the world is to meet international biodiversity and ecosystem function targets (e.g. Kunming-Montreal Global Biodiversity Framework; Convention on Biological Diversity, 2022). Moreover, disentangling lianas abundance change through succession may be of major importance to help understand how and why tree carbon stocks and mortality also change, due to the multiple deleterious effects of lianas on trees (Estrada-Villegas et al., 2022a; Finlayson et al., 2022). Lianas potentially drive succession in some forests (Schnitzer et al., 2021; Tymen et al., 2016) and so both tree and liana communities need to be studied in tandem, where possible, to fully comprehend secondary successional recovery. This thesis investigates tree community compositional and functional recovery in the late stages of succession (40 - 120 years), in the Barro Colorado Nature Monument, Panama, and also examines the structural recovery of lianas across a successional and climatic gradient spanning four countries across the Neotropics.

1.5 Thesis study site: Barro Colorado Nature Monument, Panama

Three of the subsequent chapters in this study are based in the Barro Colorado Nature Monument (BCNM), central Panama. This protected area spans 5500 ha (Leigh Jr., 1999) and includes Barro Colorado Island (BCI; 9°08’60” N, -79 °50’60” W) and five mainland peninsulas whilst being centred on a section of the Panama Canal. The flooding of the Panama Canal created Lake Gatun in 1914 and isolated BCI from the mainland (Carse, 2016). BCI was first established as a protected area in 1923, although research was conducted at the site since 1916, and the field site has been run by the Smithsonian Tropical Research Institute since 1965 (Leigh Jr., 1999). Subsequently the five peninsulas were incorporated into the Barro Colorado Nature Monument in 1979 and the BCNM has been well protected from anthropogenic disturbance ever since (Wright et al., 2000).

The BCNM is comprised of tropical moist forest (Holdridge, 1947) and receives approximately 2600 mm of rainfall annually (Paton, 2020), with a distinct dry season between December and May each year with only 300 mm of rainfall within that period. Close to 50 % of BCI is comprised of intact old-growth forest (Dent and Elsy, 2023), which is estimated to have been undisturbed for between 400 and 1700 years by humans (Piperno, 2023).Old-growth forest is also present on the Gigante Peninsula and is estimated to have been undisturbed for between 650 and 1300 years (McMichael et al., 2023). The rest of the BCNM was abandoned sequentially, and as such secondary forests within the protected area are aged between 40 and > 140 years since land abandonment (Figure 1.1). Forests on Barro Colorado Island are older, due to its earlier protected status (Leigh Jr., 1999), than forests on the mainland peninsulas (Dent and Elsy, 2023). There are three main bedrock types underlying BCI, with volcanic andesite underlying the central plateau, and Bohio and Caimito formations underlying the rest of the island, with a mix of sedimentary and volcanic characteristics (Baillie et al., 2006).

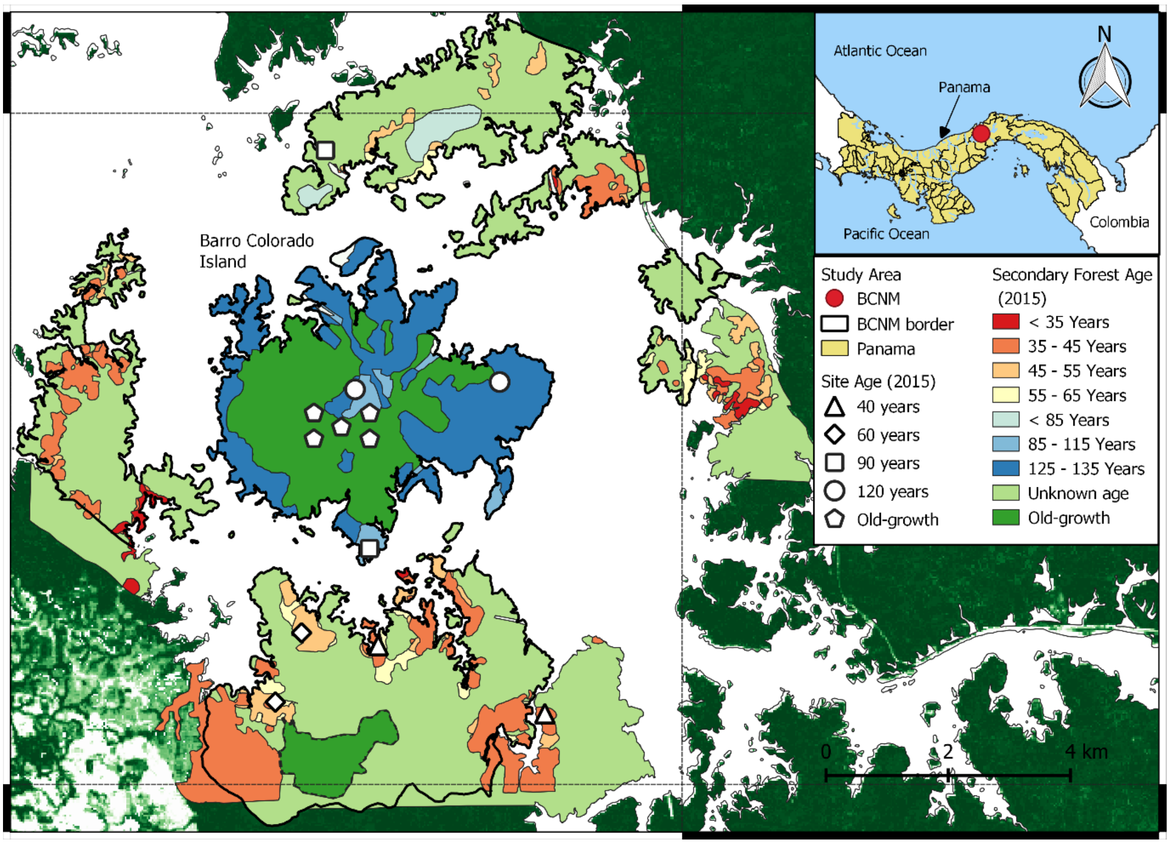

Figure 1.1. Map of the Barro Colorado Nature Monument, in central Panama with approximate forest ages in 2022 and locations of eight secondary forest plots and five old-growth plots. The map is replicated from Chapter 2 of this thesis, and it uses forest ages classified by Dent and Elsy (2023), see Chapter 6. The five old-growth plots indicated in this figure by hexagons, show the centre and corners of the long-term 50-ha forest dynamics plot on Barro Colorado Island.

The forests of BCI are highly diverse and there are an estimated 1468 vascular plant species (Garwood, 2009), 218 bird species (Robinson, 1999), and 390 butterfly species (Basset et al., 2015) found on the island itself. BCI, and the BCNM, is an immensely well studied field site in the tropics and its early establishment has enabled ecological theory to be tested over long time scales (Leigh Jr., 1999; Wright, 2020). Of particular importance to this was the establishment of the 50-ha forest dynamics plot in old-growth forest in the centre of the island in 1981 (Condit et al., 2017). A total of 423,617 individual trees over eight full censuses of the plot have been measured (Condit et al., 2017) and questions related to tree mortality, growth and recruitment (Condit et al., 2017; Wright et al., 2003), neutral theory and diversity (Condit et al., 2012; Hubbell, 2006), and functional traits (Rüger et al., 2018; Wright et al., 2010) have all been developed using these data. Moreover, the 50-ha plot censuses have recently been expanded to include lianas (Schnitzer et al., 2012), and so all woody stems are monitored within the plot.

In our analyses, we utilise the 50-ha tree data in combination with a long-term secondary forest chronosequence (Denslow and Guzman, 2000) to address questions related to forest successional recovery. The secondary forest chronosequence (see plot locations in Figure 1.1) was established in 1994, with two paired 10 x 160 m transects established in forest stands aged 20, 40, 70 and 100 years since land abandonment (Denslow and Guzman, 2000). Forest stands were accurately aged through historic literature, interviews with local landowners and the use of aerial photographs to identify stands at least 5-ha in size of a known age (Denslow and Guzman, 2000). These original transects, and subsequent recensuses in 2001 and 2011, have been used to address research questions relating to tree structural and community compositional recovery (Denslow, 2000; Denslow and Guzman, 2000; DeWalt, Maliakal and Denslow, 2003; Mascaro et al., 2012; Dent, DeWalt and Denslow, 2013) as well as seed dispersal recovery (Estrada-Villegas et al., 2022b). Moreover, the aged forest stands have been used to investigate liana (DeWalt et al., 2000), epiphyte (Woods and DeWalt, 2013) and bird community (Mayhew et al., 2019) recovery through the late stages of succession. Between 2011 and 2016 the chronosequence transects were expanded to permanent 1-ha plots and all trees ≥ 5cm DBH, and a subset of saplings 1 – 5 cm DBH, were surveyed in each plot. The secondary forest 1-ha plots were aged approximately 40, 60, 90 and 120-years since land abandonment at the time of the recensus, making this perhaps the oldest moist tropical forest chronosequence in the Neotropics (Rozendaal et al., 2019). Thus, the secondary forest chronosequence represents a unique opportunity to investigate truly late-stage succession tropical forest recovery, and while this most recent census has been utilised to investigate carbon stock recovery (Jones et al., 2019) and soil carbon in relation to functional composition (Wallwork et al., 2022), many outstanding questions remain which can be addressed by this dataset.

1.6 Thesis aims

This thesis aims to explore tropical forest successional theory in woody plants. Specifically, I will:

1. Reduce the knowledge gap concerning tropical tree community recovery in late succession by studying biodiversity (both taxonomic and functional metrics of diversity) and structural recovery in one of the oldest chronosequences in the Neotropics.
2. Improve our understanding of how functional traits recover in late succession and how this relates to both successional and functional trait theory.
3. Study liana and tree abundance through a successional and climatic gradient and disentangle the drivers of changing liana abundance across a broad range of chronosequences in the Neotropics.
4. Identify the current state of secondary succession literature and the understanding which has been gained from secondary succession research in a well-studied research site (BCNM).

1.7 Overview of chapters

Chapter 2: Incomplete recovery of tree community composition and rare species after 120 years of tropical forest succession in Panama

Secondary forests are increasingly found to be regrowing on abandoned land across the tropics, and they have high potential for biodiversity conservation (Chazdon et al., 2009). Much large-scale successional research has been carried out in recent years with findings that tree species richness and diversity can recover relatively quickly in tropical forests, but forest structural and species composition characteristics take longer to recover (Poorter et al., 2021a; Rozendaal et al., 2019). However, estimates of late-stage successional recovery for forest structure and species composition are uncertain, as very few late-stage successional plots exist in the tropics. Chapter 2 aims to address this knowledge gap, by investigating at what age tropical forests recovered in late succession to old-growth levels of species richness, diversity, forest structure and species composition. This will be completed by utilising a 40 – 120-year-old secondary forest chronosequence in central Panama, while also investigating the recovery of old-growth specialist and rare species through time.

Chapter 3: Functional recovery in leaf traits and ongoing recovery in tree stature in late-stage successional forest in Central Panama

Secondary forests have long been used to test ecological theory along successional gradients. The dominance of light-loving pioneer species in early succession, followed by the eventual accumulation of shade tolerant species in the late stages of succession links well to the fast-slow continuum of life history strategies (Rüger et al., 2023). The shift in species from acquisitive to conservative strategies in relation to light availability is often quantified using leaf functional traits. However, given the forest canopy closes within 10 – 20 years of succession, it may be that other functional traits become more important in the late stages of succession and may drive continued differences among tree communities. Chapter 3 investigates 11 functional traits in tree and sapling communities in our secondary forest chronosequence in Panama and examines the recovery of trait community weighted means over succession. The recovery of functional diversity metrics is also examined and the potential for identifying functionally distinct groupings of species at a late successional stage was explored.

Chapter 4: Moist and wet tropical secondary forests have higher liana density than dry forests across the Neotropics

Lianas have been found to be strongly influenced in their biogeographical distributions by precipitation seasonality and rainfall (DeWalt et al., 2015). However, many of the studies examining these distributions have only examined old-growth forests. Young secondary forests are hotspots of liana abundance, given they often have high trellis and light availability, but liana recovery through succession is less certain, and few studies globally have examined the relationship between lianas and succession. In this chapter, liana density and basal area relationships with tree biomass are investigated through succession, alongside climatic and disturbance related variables, across nine chronosequences in the Neotropics. Chapter 4 examines if previously identified biogeographic relationships are consistent in secondary forests and investigates the likelihood of liana dominance in seasonal and aseasonal tropical secondary forests. Lianas were examined across a range of size classes to gain a more detailed understanding of the relative importance of small, medium, and large lianas at different successional stages in wet and dry forest, as size class can be indicative of when lianas establish within a forest.

Chapter 5: General discussion

Here the implications of findings, presented in this thesis, for tropical forest successional research are summarised and synthesised. The results presented in this thesis are situated in the context of previous studies in the field. Linkages between chapters are identified, and an additional case study, surveying liana abundance in our secondary forest chronosequence is presented. Avenues for future research are identified in order to build on our evidence base for late-stage successional research. This chapter concludes with potential policy implications for the findings presented in this thesis.

[Supplementary Chapter] Chapter 6: Structure, diversity, and composition of secondary forests of the Barro Colorado Nature Monument

In this chapter, secondary forest research in the Barro Colorado Nature Monument is summarised in terms of forest structure, tree communities and bird communities. This chapter is included after the general discussion as I was second author on the manuscript. As part of this published work (Dent and Elsy, 2023) I generated a new forest age map of the Barro Colorado Nature Monument, which incorporates many previous studies and aerial photographs (see Figure 6.2, Chapter 6).

2 Chapter 2: Incomplete recovery of tree community composition and rare species after 120 years of tropical forest succession in Panama

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2.1 Abstract

Determining whether tropical forests regenerating on abandoned land fully recover characteristics of old-growth forests is increasingly important for understanding their role in conserving rare species and maintaining ecosystem services. Despite this, our understanding of forest structure and community composition recovery throughout succession is incomplete, as many tropical chronosequences do not extend beyond the first 50 years of succession. Here, we examined trajectories of forest recovery across eight 1-hectare plots in middle and later stages of forest succession (40 – 120 years) and five 1-hectare old-growth plots, in the Barro Colorado Nature Monument (BCNM), Panama. We first verified that forest age had a greater effect than edaphic or topographic variation on forest structure, diversity and composition and then corroborated results from smaller plots censused 20 years previously. Tree species diversity (Simpson's index), but not species richness, and forest structure had fully recovered to old-growth levels by 40 and 90 years, respectively. However, rare species were missing, and old-growth specialists were in low abundance, in the mid- and late secondary forests, leading to incomplete recovery of species composition even by 120 years into succession. We also found evidence that dominance early in succession by a long-lived pioneer led to altered forest structure and delayed recovery of species diversity and composition more than a century after land abandonment. Our results illustrate the critical importance of old-growth and old secondary forests for biodiversity conservation, given that recovery of community composition may take several centuries, particularly when a long-lived pioneer dominates in early succession.

Keywords: chronosequence, *Gustavia superba*, forest structure, rarity, species diversity, alternate successional pathways

2.2 Introduction

Understanding successional processes during forest recovery is increasingly important, as over 60% of the world's forests are currently regrowing following disturbance (Pugh et al., 2019). In Neotropical forests, many aspects of forest structure and diversity recover rapidly (within the first 50 years of succession), whilst attributes such as aboveground biomass and community composition recover more slowly (Guariguata and Ostertag, 2001; Poorter et al., 2021a). For instance, tree species richness can recover 80% of old-growth values in just 20 years, with complete recovery often within 50 years (Martin, Newton and Bullock, 2013; Poorter et al., 2021a; Rozendaal et al., 2019). Stem density (Kennard, 2002; Peña-Claros, 2003) and light availability (Nicotra, Chazdon and Iriarte, 1999; Denslow and Guzman, 2000; Lebrija-Trejos et al., 2011) recover to values akin to old-growth forests within the first 40 years. In contrast, aboveground biomass can take up to 120 years to recover (Poorter et al., 2021a). Community composition is typically the last characteristic of secondary forests to recover to old-growth levels, with estimates of recovery ranging from 120 years (Poorter et al., 2021a), to 210 years (Cole, Bhagwat and Willis, 2014), to several centuries (Rozendaal et al., 2019).

Chronosequences, or space-for-time substitutions, are used to study secondary succession in tropical forests (Chazdon et al., 2007). Most research in tropical forest chronosequences has focused on young forests (typically 0 – 40 years old), while old secondary forests (> 80 years old) are relatively poorly represented in the literature, in part due to difficulties in aging older secondary forest and misclassification of old secondary forests as 'undisturbed' or 'primary' forests (Brown and Lugo, 1990; Milton et al., 1994). In two recent studies of carbon and biodiversity recovery in tropical forests, only four of 56 Neotropical chronosequences (Rozendaal et al., 2019) and just 12 of 204 tropical forest plots (Martin, Newton and Bullock, 2013) included in the analyses were ≥ 80 years old. The poor representation of older plots in syntheses of secondary tropical forest recovery biases our understanding towards young forest stands. It also limits our understanding of processes that take place over long time scales, such as community compositional recovery, and may partly explain the variable recovery rates reported for biomass (Martin, Newton and Bullock, 2013; Poorter et al., 2016) and community composition (Cole, Bhagwat and Willis, 2014; Poorter et al., 2021a; Rozendaal et al., 2019). Therefore, accurately aged old secondary forest plots are critical for quantifying aspects of tropical forests that recover slowly.

Chronosequence studies often do not adequately account for biotic and abiotic differences among plots (Johnson and Miyanishi, 2008), and so it is necessary to consider environmental variables, in addition to forest age, when looking to explain rates of forest recovery. Myriad factors influence the speed and trajectory of community composition recovery throughout succession (Arroyo-Rodríguez et al., 2017). At landscape scales, old-growth forest connectivity, landscape structure and matrix composition can all influence floristic recovery (Laurance et al., 2007; Hernández-Stefanoni et al., 2011; Damschen and Brudvig, 2012; Arroyo-Rodríguez et al., 2017). At the local scale, factors such as land use history, topography, soil fertility and liana abundance may determine the tree community (Baldeck et al., 2013; Estrada-Villegas et al., 2019; Visser et al., 2018b), alter forest structure (Cushman et al., 2022; Jucker et al., 2018; Tymen et al., 2016), or even cause alternate successional pathways to develop (Arroyo-Rodríguez et al., 2017; Jakovac et al., 2021). Alternate successional pathways may result from different land use and land use intensities (Jakovac et al., 2021), disturbance regimes (Mesquita et al., 2015), arrested recovery due to liana dominance (Marshall et al., 2020), or source and disperser limitation leading to priority effects (Dent and Estrada-Villegas, 2021a; Weidlich et al., 2021), ultimately leading to taxonomically and structurally distinct tree communities within a landscape (Jakovac et al., 2015; Mesquita et al., 2015; Norden et al., 2011; Tymen et al., 2016).

The spatial scale of forest sampling also influences the interpretation of patterns in secondary forest succession; plot size, shape, and spatial extent all affect species diversity and stem density (Condit et al., 1996; Güler et al., 2016; Schnitzer et al., 2006). For instance, Chazdon et al.(2023) subsampled 1-ha tropical forest plots and found that plot sizes less than 0.5-ha may not accurately capture tree species diversity or evenness. Large plots (≥ 0.5 ha) typically encompass more heterogeneous environments and are more robust to stochastic events (e.g. treefalls; Schnitzer and Carson, 2001) than smaller plots. However, to understand variable successional pathways, study plots need to be distributed across the study landscape and must be located in single aged forest stands (Arroyo-Rodríguez et al., 2017). Thus, many secondary forest studies prioritize the number and distribution of census plots over individual plot area (see sites included in Rozendaal et al. (2019)).

Community compositional recovery in secondary forests is a complex property to capture, it is important to identify both rare species of potential conservation concern and dominant species that likely have the largest impact on ecosystem function (Cavanaugh et al., 2014; Hubbell, 2013; ter Steege et al., 2013). Moreover, examining the recovery of generalist, specialist and rare species, alongside community composition, can provide insights into why secondary forest function or composition may not converge on that of old-growth communities (Lasky et al. , 2014; Boukili and Chazdon, 2017; Norden et al., 2017). Rare species in particular are likely to recover slowly (e.g. Goosem et al., 2016), given that they often have poor dispersal ability (Gaston, 1994) and exhibit highly clustered distributions (Condit et al., 2000). Therefore, analyses which incorporate incidence-, abundance- and dominance-based community composition metrics alongside species classification techniques (e.g. Norden et al., 2017) can provide a more detailed understanding of secondary succession.

Here, we re-examine tree and palm communities across a chronosequence (40 – 120 years) in the Barro Colorado Nature Monument (BCNM), central Panama, that has previously been used to investigate recovery in forest structure, diversity, and species composition, as well as multisite comparisons (Chazdon et al., 2016; Poorter et al., 2021a, 2016; Rozendaal et al., 2019). Previous analyses have found that secondary forests in the BCNM regained old-growth species diversity and richness within 20 years, aspects of forest structure recovered within 70 years and aboveground carbon in >100 years (Denslow, 2000; Denslow and Guzman, 2000; DeWalt, Maliakal and Denslow, 2003; Mascaro et al., 2012; Dent, DeWalt and Denslow, 2013; Jones et al., 2019). They also suggest that secondary forests had not converged on old-growth species composition for trees that attain canopy or midstory stature (Dent, DeWalt and Denslow, 2013). In this study, we include a recensus c. 20 years after the original (Denslow and Guzman, 2000), with larger plots in each forest stands (1-ha vs 0.32-ha) and three additional old-growth plots, to address three main objectives: 1. Determine how quickly forest structure, species diversity and community composition (cf. rare, generalist and specialist species) recover following land abandonment; 2. Investigate whether the extended timespan and increased spatial scale of sampling within the chronosequence alters our understanding from previous studies (e.g. Dent, DeWalt and Denslow, 2013); 3. Examine the importance of topography and soil nutrients in shaping patterns of structure, diversity, and compositional recovery. This study represents one of the oldest chronosequences in the Neotropics (Buzzard et al., 2016; Rozendaal et al., 2019) and is uniquely situated to examine late-stage secondary successional forest recovery.

2.3 Methods

2.3.1 Study area

This study uses data from a secondary forest chronosequence (Denslow and Guzman, 2000) and the 50-ha ForestGEO plot (Condit, 1998; Hubbell et al., 1999) within the BCNM, central Panama. Our 13 study plots were situated on Barro Colorado Island (BCI; 9º08’60” N, -79 °50’60” W) and surrounding peninsulas (Figure S2.1). The BCNM receives ~2600 mm of rainfall annually with a distinct dry season between January and May (Paton, 2020). Vegetation in the area is classified as tropical moist forest (Holdridge, 1947); for information on the flora, geology and soils of BCI, see Croat(1978) and Baillie et al. (2006).

The BCNM secondary forest chronosequence comprises eight 1-ha plots across forest stands that were aged (in 2015) approximately 40, 60, 90 and 120 years since land-abandonment, with two independent plots per stand age (Jones et al., 2019; Figure S2.1). The chronosequence was established in 1994 with 0.32-ha plots (two paired 10 x 160 m transects); these were enlarged to 1-ha (50 x 200 m) in 2011 with plots positioned to maximise overlap with existing transects (Supplementary Material). For one 120-year-old plot (Pearson; Table S2.1), only 0.88-ha was censused due to an incomplete census in 2014. Forest stand ages were determined from aerial photographs, interviews with residents and existing literature and are accurate to within c. 10 years of land abandonment (Denslow and Guzman, 2000). All secondary forest plots were previously used for pasture, swidden or plantation farming and were undisturbed since abandonment (Denslow and Guzman, 2000); Table S2.1). The plots were a minimum distance of 1.07 km apart (mean ± SD = 4.39 ± 2.32 km). The 50-ha ForestGEO plot was predominately undisturbed old-growth forest (Condit, 1998). Five 1-ha (100 x 100 m) subplots were selected from within the 50-ha plot as old-growth forest comparisons. The 1-ha subplots were located at the corners and centre of the plot (minimum distance between subplots = 0.32 km, mean ± SD = 0.55 ± 0.25 km).

2.3.2 Data collection

2.3.2.1 Forest census

Secondary forest plots were surveyed between 2011 and 2016 (Dent et al., 2020), following ForestGEO vegetation census protocols (Condit, 2008). All trees, palms and shrubs ≥ 5 cm diameter at breast height (DBH) were measured in each plot, with trees identified to species level where possible (98.3% of individuals identified to species). Data for the old-growth 1-ha plots were obtained from the 2015 50-ha plot census (all individuals identified to species-level; (Condit et al., 2019b, 2020).

2.3.2.2 Environmental descriptions

For environmental variables we examined soil nitrogen (N), phosphorus (P) and slope. Soil inventories were obtained from Jones et al. (2019) for secondary forest plots and Wolf et al. (2015) for the old-growth 50-ha plot. Both followed ForestGEO soil sampling protocols (ForestGEO, 2010) and soil cores were sampled to 10 cm depth in regularly spaced grids, with 10 cores per secondary forest plot and 12 per old-growth plot. We averaged soil N and P per plot. For the detailed methodology, see ForestGEO (2010), Jones et al.(2019), Wolf et al., (2015). Topographic data were obtained by merging a 1 m x 1 m resolution digital elevation model (DEM) covering the BCNM and a 5 m x 5 m resolution DEM covering Central Panama (Smithsonian Tropical Research

Institute, 2020a, 2020b). The merged DEM was upscaled to 10 m x 10 m resolution using the 'aggregate' function in the *raster* R package (Hijmans, 2022), and mean values of terrain slope per plot were calculated.

2.3.3 Statistical analysis

2.3.3.1 Forest structure, species richness and diversity

Forest structural characteristics were computed as stem density and basal area per ha, including unidentified trees and multiple stems per individual tree (total number of stems = 15,281). A correction factor was applied to stem density and basal area values for the Pearson plot (0.88-ha multiplied by 1.136) to enable between-plot comparisons at 1-ha scale. Rarefied species richness (calculated on the minimum number of identified individual trees per plot, n = 807), Simpson's diversity index and Pielou's evenness index were calculated per plot using the *vegan* package (Oksanen et al., 2022) for all identified individual trees (n = 12,836). Extrapolated species richness curves were also calculated using the *iNEXT* R package and 100 bootstrapped iterations (Chao et al., 2014a; Hsieh et al., 2016). Richness values were conservatively extrapolated up to double the minimum number of trees per plot (n = 1614) and extrapolations were included to utilise all available data and allow robust comparisons between plots (Colwell et al., 2012).

We modelled changes in forest structure and diversity metrics using generalised linear models (GLMs) or beta regressions (Cribari-Neto and Zeileis, 2010), using the conditional distribution that best fit the data (see Supplementary Materials and Table S2.2) and the *DHARMa* package to examine model residuals (Hartig, 2022). We used a two-step approach, first focusing on modelling secondary forest plots solely against stand age (Tables S2.2, S2.3). Old-growth plots were excluded from these models because they could not be assigned a stand age. Secondly, we modelled all plots (including old-growth) against mean soil nitrogen, phosphorus and slope and fit full models with all three environmental variables. Model selection was carried out using the 'dredge' function (*MuMIn* package; (Bartoń, 2022) to select the model with the lowest AICc. Model averaging was conducted on models with ΔAICc ≤ 4 from the minimum AICc model (Tables S2.4, S2.5; Burnham and Anderson (2004)). Differences in forest structure and diversity between old-growth and secondary forest plots were tested using two-sample Wilcoxon tests (Table S2.6).

2.3.3.2 Species community composition

We examined species community composition recovery by calculating pairwise similarity indices comparisons between secondary forest plots and old-growth plots, following Norden et al., (2017). We followed the Hill number framework and calculated the incidence-based Sørensen similarity index (q = 0) and the abundance-based Horn (q = 1) and Morisita-Horn (q = 2) similarity indices (Chao et al., 2014b; Jost et al., 2011) using the 'SimilarityMult' function from *SpadeR* (Chao et al., 2016). Each index allowed us to examine an aspect of community recovery: the Sørensen similarity index is based on species presence-absence in a community; the Horn similarity index weights species by their relative abundance and the Morisita-Horn similarity index is heavily influenced by species dominance (Jost et al., 2011; Norden et al., 2017). We modelled pairwise similarity indices comparisons against stand age (fixed effect) using generalised linear mixed models (GLMMs) with a beta distribution (Table S2.7), and plot as a random effect (random intercept only), through the *glmmTMB* package (Brooks et al., 2017). We modelled plot as a random effect to account for non-independence of each secondary-old-growth pairwise comparison (n = 5 per eight secondary forest plots). The community composition GLMMs deviated from the expected values in residual vs. predicted plots, likely due to the influence of one 120-year-old outlier plot, Barbour. The random effect variance was not reliable, and we do not report conditional R^2 estimates derived from it. We report the overall model, however, given that the trend of community composition recovery is apparent from data visualisation (Figure 2.2).

We used non-metric multidimensional scaling (NMDS) to investigate community composition, via the ‘metaMDS’ function in *vegan* (Oksanen et al., 2022), for each similarity index with 10,000 random starts. The lowest stress run was used for each index; however, the NMDS based on the Horn similarity index had high stress (0.244), and we therefore only examined the NMDS based on Sørensen and Morisita-Horn indices (stress < 0.20).

2.3.3.3 Species specialism and rarity

We classified species as secondary forest specialists, old-growth specialists, generalists or too rare to classify, based on the multinomial model developed by Chazdon et al.(2011). This model estimates true relative species abundances in each forest type, assuming random sampling error, and takes into account potentially undetected species to calculate relative species abundances, which are compared to determine the species classification (Chazdon et al., 2011). We followed recommendations in Chazdon et al. (2011) and used a 2/3 specialisation threshold, and P = 0.00125, to conservatively classify shared species as habitat specialists (secondary forest or old-growth) or generalists through the ‘clamtest’ function in *vegan* (Oksanen et al., 2022). Those species identified as ‘too rare to classify’ were those found at too low abundance to assign to another classification, we term these species ‘rare’ species hereafter. We tested if the number of rare species differed between forest type using a Wilcoxon rank-sum test. We confirmed that differing sample areas (old-growth = 5-ha, secondary forest = 8-ha) had no effect on the results by re-running the multinomial model on all combinations of five secondary plots (n = 6,720) against the five old-growth plots (Figure S2.2).

All analyses were carried out in R (version 4.2.2; R Core Team, 2022) with data cleaning completed using the *tidyverse* (Wickham et al., 2019). Model predictions were generated using the *effects* package (Fox and Weisberg, 2019).

2.4 Results

2.4.1 Forest structure, species richness and diversity

A total of 277 species and 12,836 individual trees, palms and shrubs ≥ 5 cm DBH were surveyed across eight secondary and five old-growth 1-ha plots (Table S2.1). We found no evidence of mean N, P or slope predicting structural or diversity metrics across secondary and old-growth plots (Table S2.5), and therefore focus only on effects of forest age. Stem density was more varied among secondary than old-growth forest plots (Figure 2.1a), but there was no effect of stand age ($P = 0.886$; Table S2.3). Basal area significantly increased with stand age ($P < 0.001$, $R^2 = 0.911$) and recovered to the mean old-growth level by mid-to-late stages of succession (~90 years, Figure 2.1b). Rarefied species richness was significantly lower in secondary forest plots compared to old-growth forest (Wilcoxon test: $P = 0.002$), but no effect of stand age on richness was found (Table S2.3; Figure 2.1c). Extrapolated species richness values were also significantly lower in secondary forest plots (Wilcoxon test: $P = 0.011$), although both 60-year-old plots, and one 120-year-old plot, were approaching old-growth values (Figure S2.3). Simpson's diversity index had recovered to old-growth levels by the start of the chronosequence (Figure 2.1e). Species evenness had also recovered to old-growth levels in the youngest plots (40 years) in the chronosequence, and then declined significantly with stand age ($P = 0.028$, Figure 2.1d). One 120-year-old plot, Barbour, heavily influenced the decline in evenness over stand age (Figure 2.1d) and excluding Barbour from the evenness model removed the significant negative relationship with stand age ($P = 0.248$). Barbour was dominated by *Gustavia superba* (Lecythidaceae), which comprised 35.7% of all trees, palms and shrubs ≥ 5 cm in the plot (Table S2.8). This dominance was higher than in all other secondary forest plots (mean dominance = 12.3%), and only one old-growth plot had a similar rank-abundance relationship (Figure S2.4), due to high dominance by the understory tree *Faramea occidentalis* (Rubiaceae) (33.0%; Table S2.8).

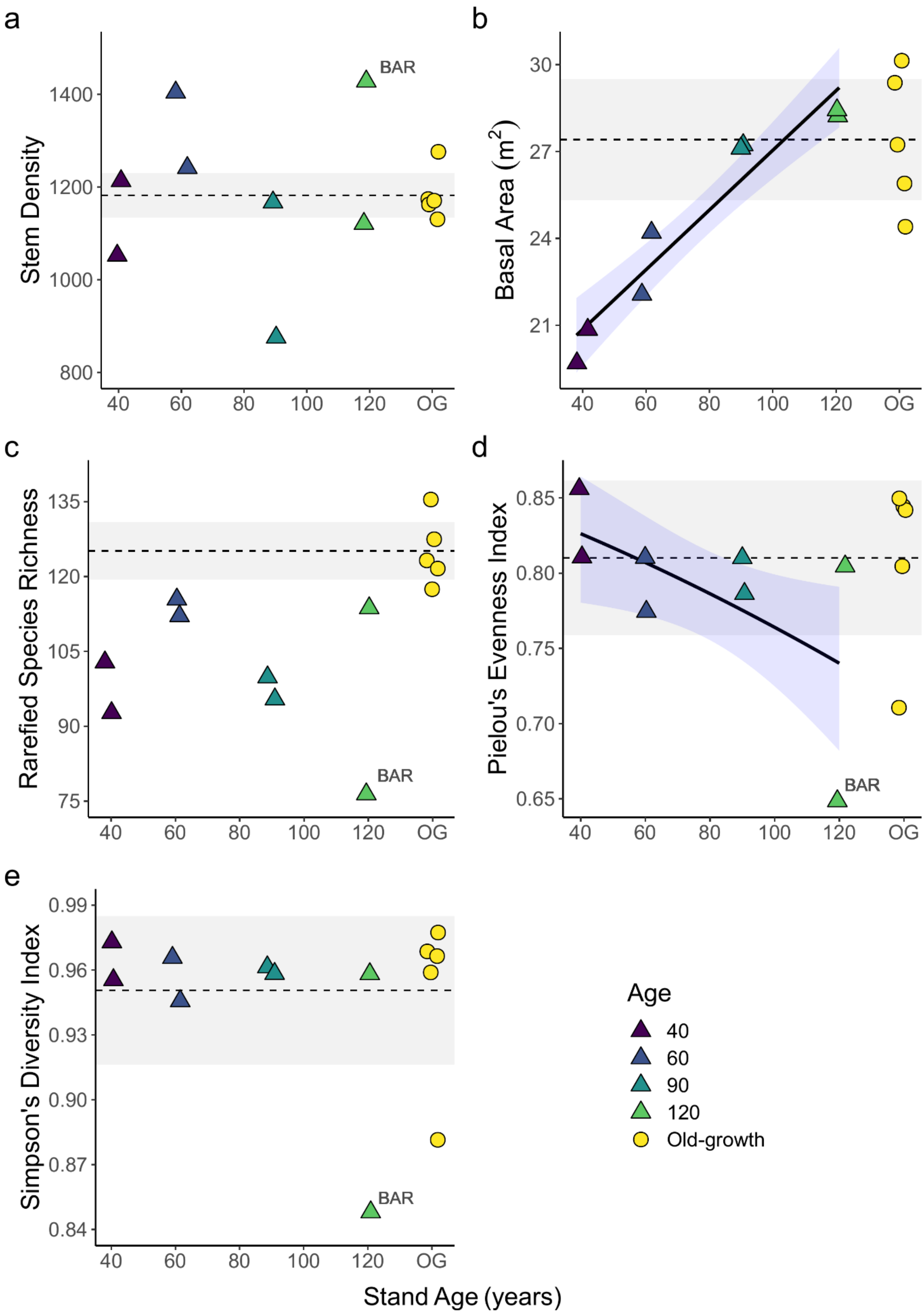

Figure 2.1. Forest structure, richness and diversity metrics plotted against stand age. **a**. Stem density; **b**. Basal area; **c**. Rarefied species richness; **d**. Pielou's evenness index and **e**. Simpson's diversity index. Mean values of old-growth plots are indicated by the dashed lines; grey shading

indicates 95% confidence intervals. Model predictions (±95% C.I.) are plotted in blue shading for models with significant age effects. The 120-year-old plot ‘Barbour’ is labelled with “BAR” in each plot because it is a frequent outlier.

2.4.2 Species community composition

The community composition of secondary forests showed evidence of convergence on old-growth composition across all pairwise similarity indices (Figure 2.2). Old-growth plots were ~80% similar to each other in species composition regardless of similarity index. Pairwise incidence-based Sørensen similarity comparisons converged fastest, with recovery within 60 years of forest regrowth, and there was no significant effect of stand age throughout the chronosequence (P = 0.144; Table S2.7). In contrast, abundance-based Horn and Morisita-Horn similarity comparisons significantly increased with stand age (P = 0.013, 0.029) and only one 120-year-old plot had converged on mean old-growth similarity (Figure 2.2b and 2.2c). This indicates that species typical of old-growth forests are present early in succession, but it takes time for the relative abundance of those species to attain patterns seen in old-growth forests. For all indices, one 120-year-old plot, Barbour, was less similar to old-growth than expected from the community composition trajectories.

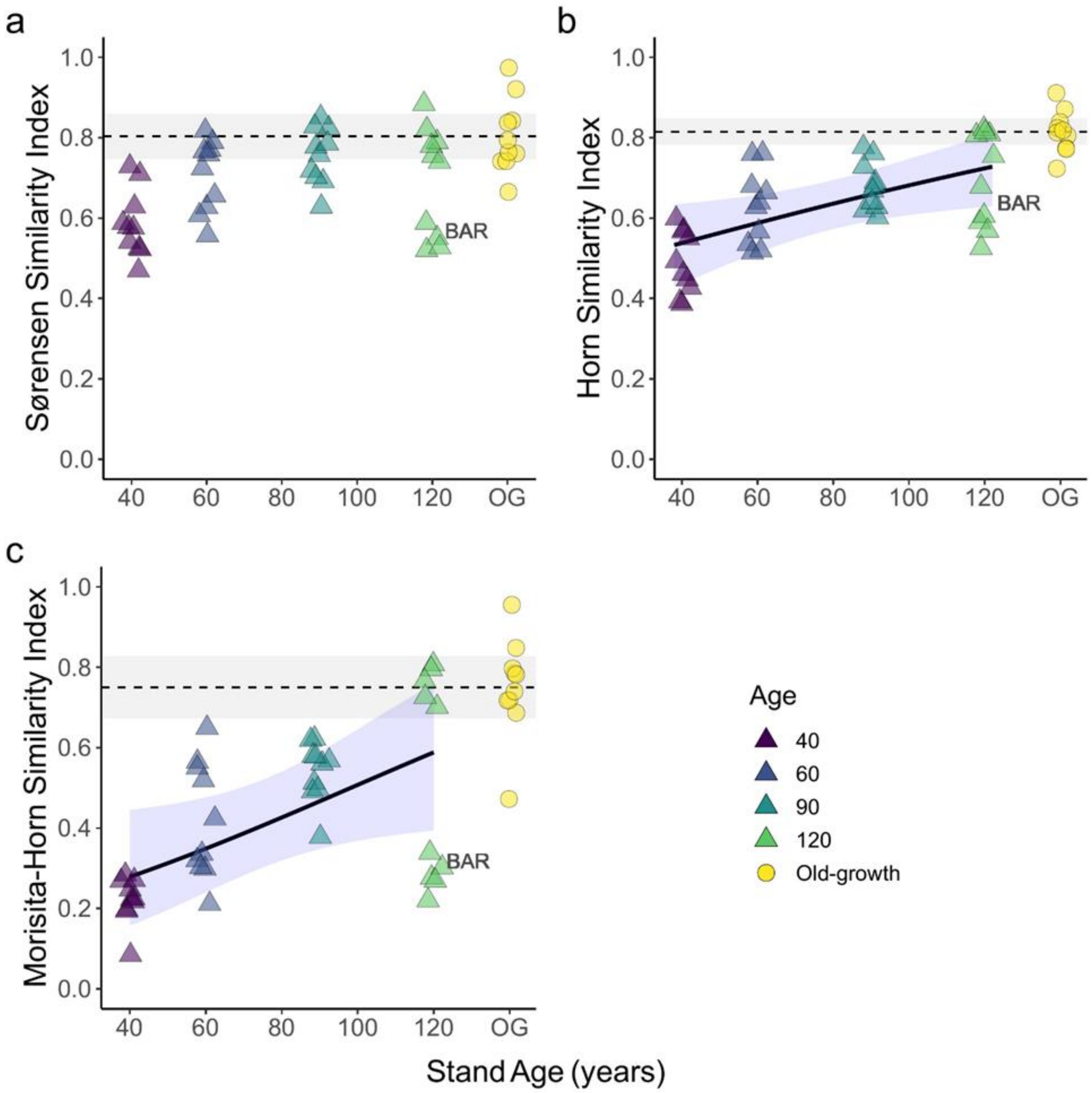

Figure 2.2. Pairwise similarity index comparisons between each secondary forest plot and old-growth plots plotted against stand age for: **a**. Sørensen similarity index; **b**. Horn similarity index and **c**. Morisita-Horn similarity index. The black line and blue 95 % confidence intervals indicate the GLMM predictions for pairwise secondary-old-growth comparisons. Old-growth pairwise comparisons are graphed for comparison but are not included in the model. Mean values of pairwise old-growth similarity comparisons are indicated by the dashed lines; grey shading indicates 95% confidence intervals. The 120-year-old plot ‘Barbour’ is labelled with “BAR” in each plot because it is a frequent outlier.

The NMDS ordinations showed these differences between incidence and abundance-based indices, with plots in the Sørensen NMDS grouped more closely together in ordination space than the Morisita-Horn NMDS (Figure 2.3). Both NMDS plots showed secondary plots became closer to old-growth plots in ordination space with increasing age, demonstrating increasing similarity to old-growth. However, none of the secondary forest plots were within the old-growth cluster (Figure 2.3).

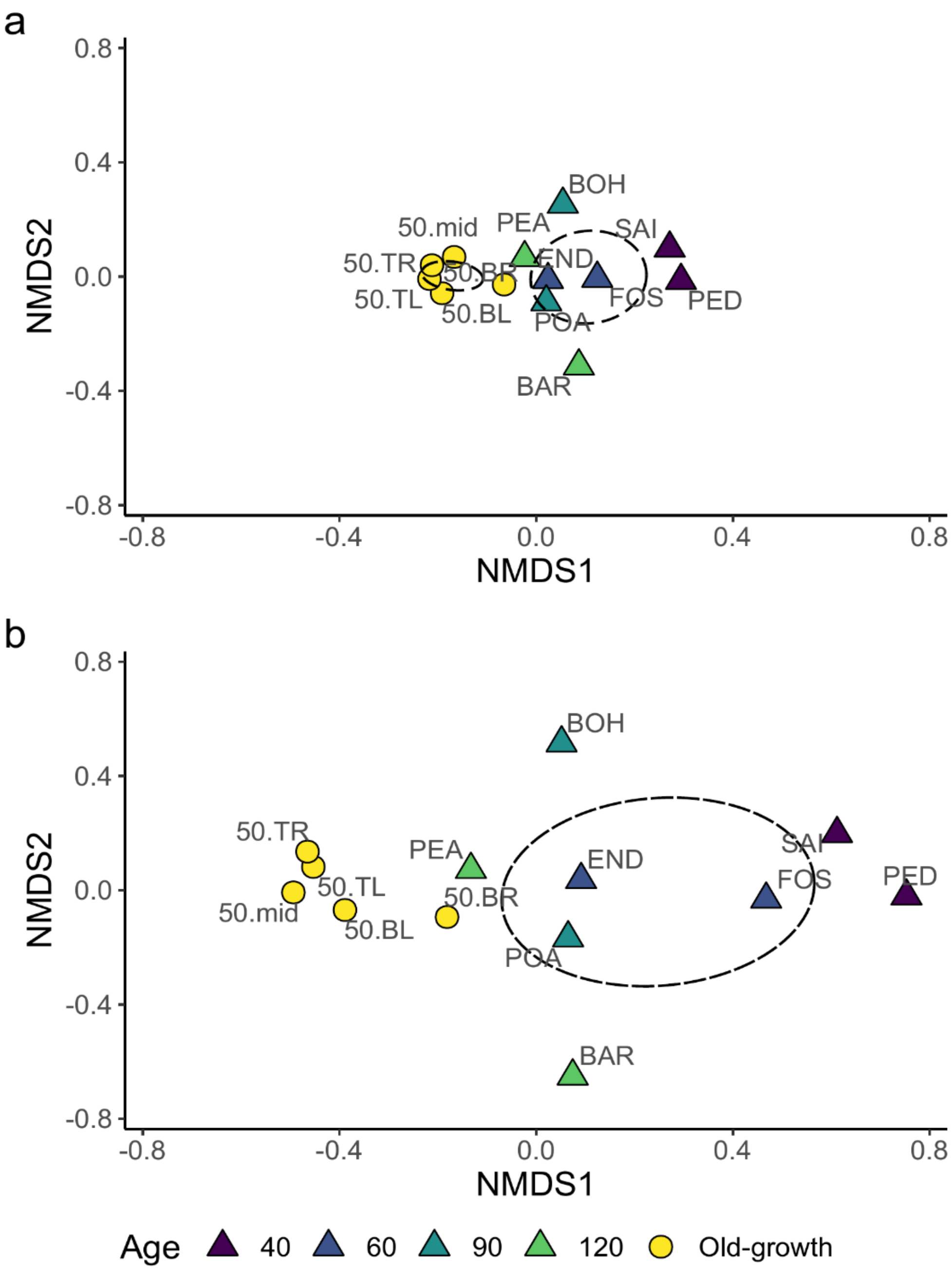

Figure 2.3 Non-metric multidimensional scaling (NMDS) graphs showing the species composition of the secondary and old-growth forest plots in two dimensions for: **a**. NMDS generated using Sorensen similarity index and **b**. NMDS generated using Morisita-Horn similarity index. Points (plots) which are closer together in ordination space are more similar and the dashed lines indicate

95% confidence ellipses for secondary and old-growth forest. Plots are labelled with their three letter abbreviations (Table S2.1).

2.4.3 Species specialism and rarity

The multinomial model classified 75 species as generalists, 29 as secondary forest specialists, 24 as old-growth specialists and 149 as too rare to classify (Figure 2.4a). As expected, generalist species were common in all plots, and rare species composed a small percentage of total tree abundance (Figure 2.4c). The proportion of old-growth specialist species increased through time in the secondary forest plots, indicating gradual floristic convergence (Figure 2.4c). The number of rare species found in secondary forest plots was significantly lower than in old-growth plots ($P = 0.008$; Figure 2.4b), and this was also found when analysed over an equal area (Figure S2.2). Secondary forest plots with low similarity to old-growth (Figure 2.2) had a larger proportion of secondary forest specialists and a smaller proportion of generalists than similarly aged secondary plots with higher similarity to old-growth (Figure 2.4c).

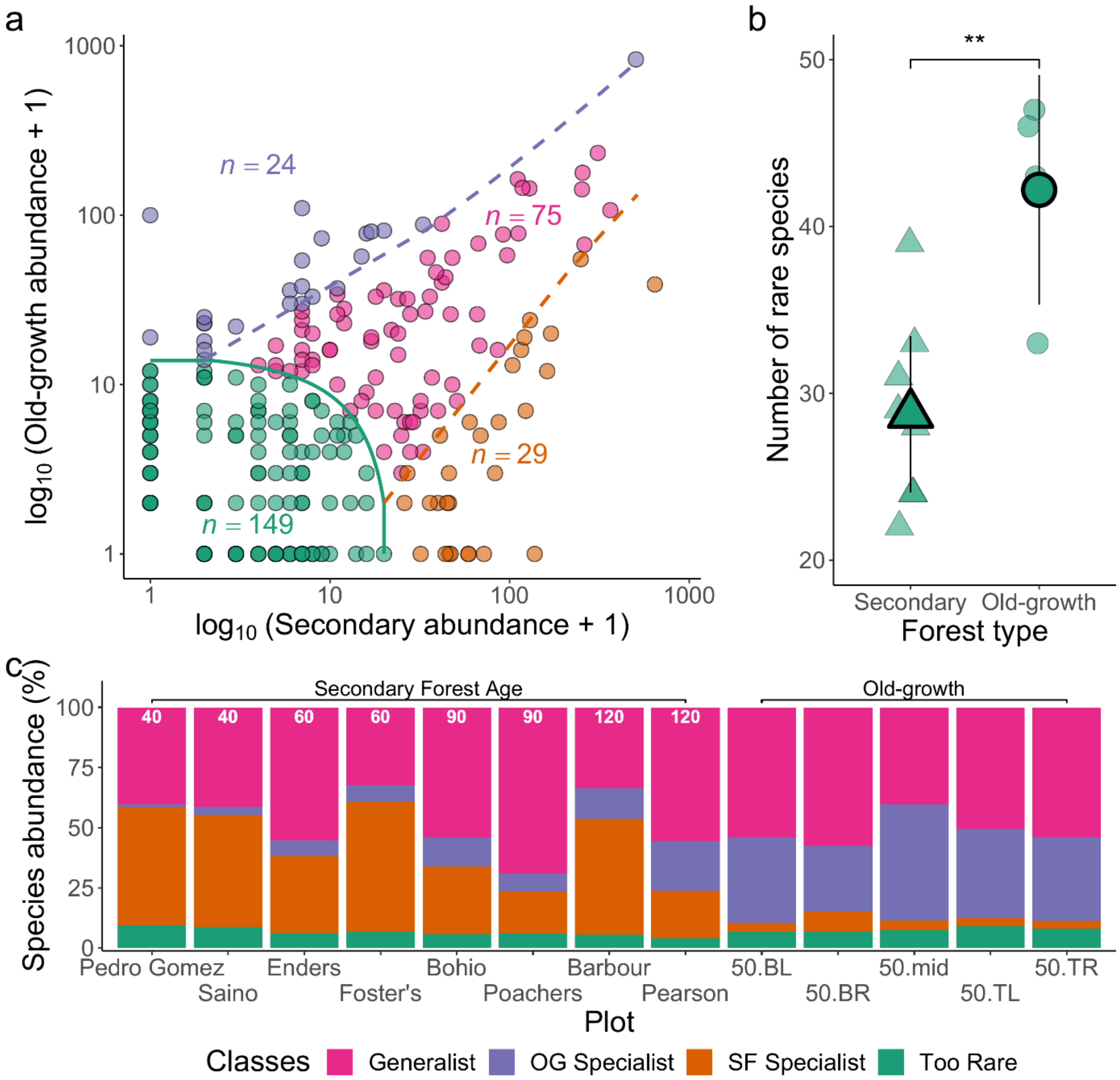

Figure 2.4. Species classifications from the multinomial model showing: **a**. the classification of each species as either a generalist, old-growth specialist, secondary forest specialist or too rare to classify, according to its abundance in both old-growth and secondary forest, **b.** the number of rare species identified per forest type and **c**. the percentage of species in each class per plot (see Table S2.1 for plot abbreviations). Black outlined shapes indicate the mean ± 95% confidence intervals and jittered points indicate individual plots in Figure 2.3b.

2.5 Discussion

The chronosequence we study in central Panama is representative of how tropical moist forests regenerate in mid-to-late succession, if left undisturbed after agricultural abandonment. Over the timescale of our chronosequence (40 – 120-year-old forests), we find that forest structure, defined as tree stem density and basal area, recovers to old-growth levels within 90 years (Figure 2.1;

Denslow, 2000; Denslow and Guzman, 2000; Mascaro et al., 2012). In addition, community composition appears to be converging on old-growth in one of the 120-year-old plots, while the other 120-year-old plot appears to be delayed in recovery or following an alternate successional pathway (Figures 2.1 – 2.3). Old-growth specialists and rare species did not recover to old-growth levels of abundance within the timespan of our secondary forest chronosequence (Figure 2.4). These long timescales for recovery highlight the need to protect secondary forests, as well as existing old-growth, to facilitate full recovery of forest structure, diversity and composition (Poorter et al., 2021a).

We found no relationship between forest structure, richness and diversity and edaphic and topographic variables (Tables S2.4, S2.5), although topography and soil nutrients are known to affect species distributions, community composition and forest structure (Clark, Clark and Read, 1998; John et al., 2007; Condit et al., 2013; Jucker et al., 2018). It could be that analysing our plots at a 1-ha scale, with only 13 plots in total, was insufficient to detect edaphic influences that may occur at more local scales (e.g. Vleminckx et al., 2015). For instance, Phillips et al. (2003a) found no edaphic effects on diversity across 10 1-ha plots but found several edaphic effects when examining 0.1-ha plots with an equal, or lower, sampling effort. Future work could examine edaphic variables at an intra-plot level but hereafter we focus the discussion on forest age.

2.5.1 Forest structure, species richness, diversity, and rarity

The results from the expanded plots corroborated previous findings along this chronosequence that forest structure and diversity of secondary forests within Panamanian moist secondary forest has fully converged on old-growth forest by ~90 years (Figure 2.1). Previous studies within the chronosequence found basal area recovery within 70 years (0.32-ha plots; Denslow and Guzman, 2000) and aboveground carbon density recovery within 85 years (20-ha plots; Mascaro et al., 2012). Other aspects of forest structure, including woody debris volume (DeWalt et al., 2003) and large tree/deadwood carbon stocks (Jones et al., 2019), also increase until the later stages of the chronosequence. Our findings are in line with other tropical secondary forests, where forest structural recovery is estimated to take between 27 and 119 years (Poorter et al., 2021a).

Species diversity (Simpson’s index) and evenness both recovered to old-growth levels by the start of the chronosequence (40-years old; Figure 2.1), with evidence of recovery just 20 years into the chronosequence (Denslow, 2000; Denslow and Guzman, 2000; Dent, DeWalt and Denslow, 2013). This is consistent with previous literature with species diversity recovering within 30 years in Neotropical forest sites in Bolivia (Peña-Claros, 2003), Colombia and Venezuela (Saldarriaga et al., 1988; Villa et al., 2018). Rapid recovery of species diversity is often linked to the recruitment of both pioneer and shade-tolerant species early in succession (Finegan, 1996; van Breugel, Bongers and Martínez-Ramos, 2007).

In contrast to forest structure and diversity, rarefied species richness in the 1-ha plots did not show evidence of convergence on old-growth forest within the timespan of the chronosequence (Figure 2.1). This conflicts with Dent, DeWalt and Denslow (2013) who found rapid species richness recovery, within 20 years, when examining midstory and canopy tree species in smaller plots in the 1994 chronosequence census. Differences between the studies remain after excluding understory trees/shrubs to match the Dent, DeWalt and Denslow (2013) methodology (Figure S2.5). The larger plot sizes of the current study may have allowed us to detect persistent differences between secondary and old-growth forests, and increased the likelihood of detecting rarer species with more aggregated distributions (Condit et al., 2000b) and species associated with a broader range of edaphic conditions (e.g. John et al., 2007). Subsampled plots less than 0.8 ha have been demonstrated to have lower rarefied species richness than 1-ha plots in tropical forest (Chazdon et al., 2023), and thus the difference between our study and Dent, DeWalt and Denslow (2013) may largely be one of spatial scale.

The observed lack of species richness recovery contrasts with evidence for median species richness recovery within 54 years across 45 Neotropical secondary forest sites (Rozendaal et al., 2019). However, only one of the 45 sites analysed included 1-ha plots and species richness values were rarefied to 25 stems in Rozendaal et al. (2019) compared to 807 stems in our study. Rarefied species richness is also highly sensitive to sample size (Chao and Jost, 2012), and small plots detect fewer rare species (Chazdon et al., 2023), so differences in recovery rates may be methodological (see Figure S2.3). These results highlight the need to consider plot size and sampling design variation when comparing across studies.

The consistently lower species richness of our secondary forest plots, compared to old-growth, may be linked to lower numbers of rare species (Figure 2.4b). On average, secondary forest plots contained 13 fewer rare species than old-growth plots (Figure 2.4b), and these species comprise over 50% of the difference in richness between forest types (Figures 2.1c). This difference could partially be explained by the higher proportion of unidentified species within some secondary compared to old-growth plots, and thus rare species may be present but not identified in secondary plots (Table S2.1). However, we still find distinctly fewer rare species in thoroughly identified secondary forest plots and suggest that ecological explanations may be more likely. The paucity of rare species in secondary forest plots is concerning given that rare species can be functionally unique and often contribute disproportionately to regional functional richness (Kearsley et al., 2019; Leitão et al., 2016; Mouillot et al., 2013a). The observed lack of rare species even 120 years into succession emphasises that the timescale for full floristic recovery of secondary forests is likely considerably longer than a century.

A portion of rare species may not have yet colonised our secondary forest sites due to dispersal limitation (Arroyo-Rodríguez et al., 2017). The BCNM is an intact mosaic of forest where we might expect rapid rates of recovery (Arroyo-Rodríguez et al., 2017). However, the majority of old-growth forest is located on Barro Colorado Island (Dent and Elsy, 2023), which is physically separated from much of the secondary forest by open water (Figure S2.1). Proximity to old-growth specialists and rare species may therefore be limited on the peninsulas where five of our secondary forest plots are located. For rare old-growth species, forests regenerating on peninsulas within the BCNM may experience both source and disperser limitation (Dent and Estrada-Villegas, 2021) as rare species in the 50-ha plot on BCI are known to be more aggregated than common species (Condit et al., 2000), and the Gatun Lake potentially acts as a barrier for faunal seed dispersion (Moore et al., 2008; Mayhew et al., 2019). Therefore, the likelihood of rare old-growth associated species establishing in the secondary forest plots on the peninsulas is likely lower than it would be in a highly connected landscape.

2.5.2 Community composition

Our finding of community composition recovery late in succession mirrors previous work in the chronosequence for lianas (DeWalt et al., 2003) and epiphytes (Woods and DeWalt, 2013), yet differs from previous work on trees which found no clear trend of community composition (Dent, DeWalt and Denslow, 2013). Dent, DeWalt and Denslow (2013) found that the dominant adult midstory and canopy tree communities (Morisita-Horn index) of secondary forests were not clearly converging on the composition of old-growth, but we found evidence of significant recovery, with one 120-year-old plot (Pearson) converging on old-growth levels (Figures 2.2, 2.3). Plot size differences between Dent, DeWalt and Denslow (2013) and our study may partially explain this difference, as larger plots are likely to be more representative of the broader forest stand and disturbances such as treefalls are less likely to influence a larger plot (see Hubbell et al., 1999).We may also be detecting changes that only occurred over the past 20 years (1994 compared to 2014) with most stands becoming more similar to old-growth forest with time, as tree species typical of old-growth forest grow into the size range to be inventoried and mid-successional species and long-lived pioneers are lost. The latter hypothesis is supported by the increasing proportion of old-growth specialist species, and decreasing secondary forest specialists, in the older secondary forest sites (Figure 2.4c). The clear exception to this pattern is the 120-year-old Barbour stand, where dominance by *Gustavia superba* appears to be exacerbating differences and leading to an alternate state.

Compositional recovery in a 120-year-old secondary forest is an important finding given the extended recovery times predicted for community composition. Median predicted recovery times have been estimated at 487 years to 90% of old-growth species composition based on chronosequence studies (Rozendaal et al., 2019) or 210 years to 95.5% forest recovery based on pollen records (Cole et al., 2014). In contrast, a large-scale analysis of tropical secondary forest sites estimated compositional recovery to take 120 years, albeit with much variation among sites (Poorter et al., 2021a). Our work, using plots older than typically found in chronosequence comparisons, partially supports the results of (Poorter et al., 2021a) as we find recovery can occur within 120 years. However, we also show that community composition recovery can be highly variable, with the Barbour 120-year-old plot far from old-growth recovery (Figures 2.2, 2.3) and showing little increase in similarity in the twenty years since the previous census (Dent, DeWalt and Denslow, 2013). Differing land use histories and initial site conditions across the chronosequence may underpin some of the variability in recovery rates (e.g. Estrada-Villegas et al., 2019; Jakovac et al., 2021), and it may be that remnant trees may have influenced succession in intermediate-aged BCNM chronosequence stands (Mascaro et al., 2012). However, given the exceptional age of the chronosequence, and the lack of baseline data from secondary forest establishment (Denslow and Guzman, 2000), we were unable to investigate this further.

2.5.3 Evidence for an alternate successional pathway

The 120-year-old plot (Barbour) consistently differed from old-growth and other old secondary forest plots (Figures 2.1 – 2.4). Barbour had high stem density, low community compositional similarity, was missing old-growth species, and was dominated by the long-lived pioneer *Gustavia superba*. This may imply the presence of divergent successional pathways; with a 'standard' pathway where structure and composition converge on nearby old-growth over time, and an 'alternate' pathway characterised by early colonisation of *G. superba* that delays recovery and alters the species composition.

Early dominance of *G. superba* has been reported in other secondary forests in central Panama (Hooper et al., 2004), and similar evidence of alternate succession can be seen in secondary forests dominated by *Vismia* species on abandoned pastures in the Brazilian Amazon (Mesquita et al., 2015). In our study we see ongoing change in the *G. superba* dominated plot, suggesting that succession is not arrested but slowed; *G. superba* dominance in midstory and canopy trees has decreased by 6% (Table S2.9) since the 1994 census, when *G. superba* comprised 53% of trees (Dent, DeWalt and Denslow, 2013). The dominance of *G. superba* could be due to multiple interacting mechanisms. Firstly, initial plot conditions may have favoured early establishment of *G. superba* post-disturbance (Estrada-Villegas et al., 2019; Hooper et al., 2004), and agouti-mediated feedback loops of seed dispersal in areas of high *G. superba* abundance (Forget, 1992) may have maintained this dominance. Secondly, *G. superba* seeds are resistant to damage and insect infestation (Dalling and Aizprua, 1997; Dalling and Harms, 1999), and *G. superba* can resprout following damage as an adult (Putz and Brokaw, 1989). Resprouting is a key trait linked to monodominance in Amazonia (ter Steege et al., 2019), and thus these traits likely maintain high *G. superba* abundance. Our finding of high species dominance throughout succession links to evidence of monodominance persistence for long time periods in many biogeographic regions (Anbarashan and Parthasarathy, 2013; Hart et al., 1989; ter Steege et al., 2019) and provides evidence that high species dominance in secondary forests (e.g. Longworth et al., 2014; Oberleitner et al., 2021) can persist past the early stages of succession.

2.5.4 Ongoing differences between old-growth and secondary forests

There were clear differences in species composition between old-growth and secondary forest plots, despite the secondary forest maturity. In the BCNM secondary forests, the number of rare species had not recovered to old-growth values, even though overall rare tree abundance was similar between plots (Figure 2.4c), and old-growth specialist species were still growing to maturity in older secondary forests, including in the 120-year-old plots (Figure 2.4c). The gradual recovery of old-growth specialists could be due to the long lifespans of many long-lived pioneers. Even relatively shade-intolerant species can live for c. 150 years in wet tropical forest (Köhl et al., 2017), and long-lived pioneers are known to persist late into succession, with some species living for up to 200 years (Vlam et al., 2017). Establishment of old-growth specialists late in succession may also be linked to more conservative resource acquisition strategies that lead to old-growth specialists being better competitors in mature forests (e.g. Boukili and Chazdon (2017), but see Letcher et al. (2015)). Further work investigating if our species classifications are associated with different functional traits would allow us to better understand how the slow recovery of old-growth specialists and rare species relates to forest function.

Ongoing differences between secondary and old-growth forests may partly be due to spatial aggregation of old-growth plots compared to the secondary forest plots. A portion of the old-growth specialists and rare species that we identified may be associated with local-scale topographic or edaphic conditions (John et al., 2007; Jucker et al., 2018; Toledo et al., 2012) within the 50-ha forest dynamics plot, rather than wider landscape of which the secondary forest plots are more representative. This is certainly possible given that we see evidence of spatial autocorrelation between plot location and environmental variables (see Supplementary materials). However, the broad spatial configuration of secondary forest plots within the study landscape likely provides more heterogeneous environmental conditions than occur within the old-growth plots, which can be related to higher species diversity (Xu et al., 2016). Despite this, we see higher numbers of rare species in old-growth compared to secondary forests (Figure 2.4b), suggesting that forest age strongly influences rare species occurrence. More generally, old-growth forests typically comprise larger forest fragments in tropical landscapes (Hansen et al., 2020) and we believe the configuration of secondary and old-growth forest plots across the BCNM is representative of fragmented forest landscapes across the Neotropics.

The analysis of our species classifications must be caveated by the fact that they are limited in scope by the small number of plots used in the study. We used the eight secondary and five old-growth plots to produce our species classifications and thus the species classifications may not be generalisable to broader Panamanian forests, as the species may be associated with local or landscape specific variables (Lindenmayer and Likens, 2011). Moreover, the classification of species into secondary or old-growth specialists is circular by definition as secondary forest plots cannot all reach old-growth levels of old-growth specialists due to the classification method (Chazdon et al., 2011). Thus, additional secondary and old growth plots in the nearby landscape would have been useful to enable us to subsample our plots and species classifications from the broader species pool and eliminate potential local habitat associations (e.g. Condit et al., 2000; John et al., 2007) and reduce the circularity of our old-growth – secondary forest specialist associations. However, other secondary forest plots nearby in Panama are either young (e.g. van Breugel et al., 2013) or imprecisely aged (e.g. Pyke et al., 2001), and the BCNM has little other old-growth forest than that surrounding the 50-ha plot (Dent and Elsy, 2023). Therefore, few other plots were available for species classification in late succession near our study site and including younger secondary forest plots would have reduced the ability to identify species associated with late-stage successional forest.

2.5.5 Conclusions

Our study in the BCNM tropical moist secondary forest chronosequence demonstrates that forest structure can recover within c. 90 years, species diversity (but not species richness) in < 40 years, and community composition by 120 years. However, divergent successional pathways are also possible, as demonstrated by one of the 120-year-plots along this chronosequence that is in an alternate state of high species dominance. Despite these recovery patterns, we find evidence that full old-growth convergence is unlikely over the timescale of our chronosequence, as rare species are missing from the secondary forest plots, and old-growth specialists are in low abundance. These findings are some of the first to accurately quantify community compositional recovery in late successional Neotropical forests (e.g. Poorter et al., 2021a; Rozendaal et al., 2019) and provide a key reference point for future studies examining late-stage successional forest. Given the long time frames involved in community composition recovery, it is imperative that existing old-growth and old secondary forests are protected to safeguard unique tree communities and contribute to global biodiversity conservation targets under the Kunming-Montreal Global Biodiversity Framework (Convention on Biological Diversity, 2022).

2.6 Acknowledgments

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2.7 Supplementary materials

2.7.1 Spanish abstract

Determinar en que medida los bosques tropicales que se regeneran en tierras abandonadas recuperan las características de los bosques primarios es cada vez más importante para comprender su papel en la conservación de especies raras y el mantenimiento de los servicios ecosistémicos. A pesar de ello, nuestro entendimiento sobre la recuperación de la estructura del bosque y la composición de la comunidad a lo largo de la sucesión es incompleta, ya que muchas cronosecuencias tropicales no van más allá de los primeros 50 años de sucesión. En este estudio, investigamos las trayectorias de recuperación del bosque en ocho parcelas de 1 hectárea en estadíos medios y tardíos de la sucesión forestal (40 - 120 años) y cinco parcelas de 1 hectárea de bosque primario, en el Monumento Natural Barro Colorado (MNBC), Panamá. En primer lugar, verificamos que la edad del bosque tenía un mayor efecto que la variación edáfica o topográfica en la estructura, diversidad y composición del bosque y luego corroboramos los resultados de parcelas más pequeñas estudiadas 20 años antes. La diversidad de especies arbóreas, pero no la riqueza de especies y la estructura forestal se habían recuperado completamente hasta alcanzar los niveles de bosque primario a los 40 y 90 años, respectivamente. Sin embargo, los bosques secundarios carecían de especies raras y presentaban una escasa abundancia de especies especialistas del bosque antiguo, lo que condujo a una recuperación incompleta de la composición de especies, incluso a 120 años de sucesión. También encontramos pruebas de que el predominio de un pionero longevo en las primeras etapas de la sucesión provocó una alteración de la estructura forestal y retrasó la recuperación de la diversidad y composición de especies más allá de un siglo después el abandono de las tierras. Nuestros resultados ilustran la importancia crítica de los bosques primarios y secundarios más antiguos para la conservación de la biodiversidad, dado que la recuperación de

la composición de la comunidad puede llevar varios siglos, especialmente cuando un pionero longevo domina en la sucesión temprana.

2.7.2 Methods

2.7.2.1 Study area

The 1-ha plots were positioned to overlap the previous 0.32-ha plots where possible and all 1-ha plots are in the same forest stands, and same aged forest, as the 0.32-ha plots. However, one 40-year-old plot (Pedro Gomez, Table S2.1) and one 60-year-old plot (Foster's, Table S2.1) do not directly overlap with the 1994 0.32-ha plots due to constraints when laying out the 1-ha plots.

2.7.2.2 Data exploration

Environmental variables (stand age, mean soil nitrogen, mean soil phosphorous and mean slope) were tested for collinearity prior to analysis and no evidence of collinearity was found (all variance inflation factors < 5). There was evidence of spatial autocorrelation between N, P and slope variables and plot location (tested using Moran's *I*). However, there was no evidence of stand age being autocorrelated with plot location, when a 500-year-old proxy age was assigned to old-growth plots. Each explanatory variable was centred and scaled by dividing by two standard deviations before analysis using the 'rescale' function (Gelman and Su, 2020; Schielzeth, 2010).

Additional data exploration was carried out with the tree census data to allow a direct comparison with Dent, DeWalt and Denslow (2013). All trees, palms and shrubs ≥ 5cm DBH were subset, in a separate analysis, to only tree or palm species which reached the midstory (maximum height = 10 – 30 m) or canopy (maximum height > 30 m) to allow the recovery of dominant species to be quantified between studies (Dent, DeWalt and Denslow, 2013; Table S2.9). Rarefied species richness (rarefied to the same number of stems as Dent, DeWalt and Denslow, (2013); n = 120), Pielou's evenness and Simpson's diversity indices were also calculated for this subset (Figure S2.5).

2.7.2.3 Model fitting

All diversity, forest structure and community composition data were modelled using either generalised linear models (GLMs) or beta regressions against plot age, mean soil nitrogen and phosphorous, and mean plot slope. The choice of model for each response variable can be seen in Table S2.2. We determined the distribution required for each model based on the underlying assumptions of each family and the residual and QQ plots, tests of normality, dispersion and outliers generated through the 'simulateResiduals' function in the *DHARMa* R package (Hartig, 2022). Negative binomial GLMs were used when count response variables were overdispersed, or residual fit improved through their usage. Rarefied richness results were rounded before analysis, to enable them to be modelled as count data. R-squared values for each model were computed using the ‘r2’ function from the *performance* R package (Lüdecke et al., 2021). Pielou’s evenness index and Simpson’s diversity index were modelled using beta regressions from the *betareg* R package (Cribari-Neto and Zeileis, 2010). These data fit the beta distribution as the values are continuous and bounded between 0 and 1 (Cribari-Neto and Zeileis, 2010). Beta regressions were run with a logit link and fixed precision parameters (with an identity link).

Table S2.1. Summary statistics for all trees, palms, and shrubs ≥ 5 cm in each 1-ha plot in the BCNM sampled between 2011 and 2016. Environmental variables were averaged per 1-ha plot with soil data obtained from Jones et al. (2019) and Wolf et al. (2015) and topographic data from the (Smithsonian Tropical Research Institute, 2020b). Land use history information was obtained from Denslow and Guzman (2000) and Baillie et al. (2006)**.** Old-growth plot codes refer to the location from which they were subsampled from in the 50-ha plot (i.e., 50.TL is the 1-ha plot from the top left of the 50-ha plot).

Plot (code)	**Age**	**Location**	**Land use history**	**Bedrock**[a]	**No. of individuals (*no. stems*)**	**Percent identified**[b]	**Species richness**	**N (%)**	**P (mg kg^{-1})**	**Slope (^{o})**
Saino (SAI)	40	Gigante	Pasture/swidden	Basalt	943 (*1214*)	95.798	96	0.517	3.174	8.800
Pedro Gomez (PED)	40	Gigante	Pasture/swidden	Basalt	933 (*1053*)	99.005	106	0.373	3.697	3.994
Foster's (FOS)	60	Gigante	Plantation	Basalt	1148 (*1404*)	99.130	125	0.689	7.276	4.613
Enders (END)	60	Gigante	Pasture/swidden	Basalt	1042 (*1242*)	98.560	126	0.428	3.958	9.371
Bohio (BOH)	90	Bohio	Pasture/swidden	Bohio	808 (875)	99.876	95	0.431	7.271	16.236
Poachers (POA)	90	BCI	Pasture	Caimito marine	1056 (*1167*)	94.883	108	0.375	7.234	8.240
Pearson (PEA)	120	BCI	Pasture	Bohio	820 (*987*)	99.878	114	0.461	7.200	7.554
Barbour (BAR)	120	BCI	Pasture	Caimito volcanic	1082 (*1427*)	99.445	84	0.369	3.783	3.321
50.TL	OG	BCI	Old-growth	Andesite	1050 (*1178*)	100.0	136	0.453	2.255	8.462
50.BL	OG	BCI	Old-growth	Andesite	1094 (*1275*)	100.0	135	0.506	2.660	8.151
50.mid	OG	BCI	Old-growth	Andesite	1024 (*1175*)	100.0	133	0.453	4.080	4.777
50.TR	OG	BCI	Old-growth	Andesite	1055 (*1170*)	100.0	148	0.400	1.826	6.875
50.BR	OG	BCI	Old-growth	Andesite	918 (*1130*)	100.0	122	0.532	2.189	4.909

[a] (Baillie et al., 2006; Denslow and Guzman, 2000), [b] Percent identified refers to the percentage of individual trees identified to a species level in each plot.

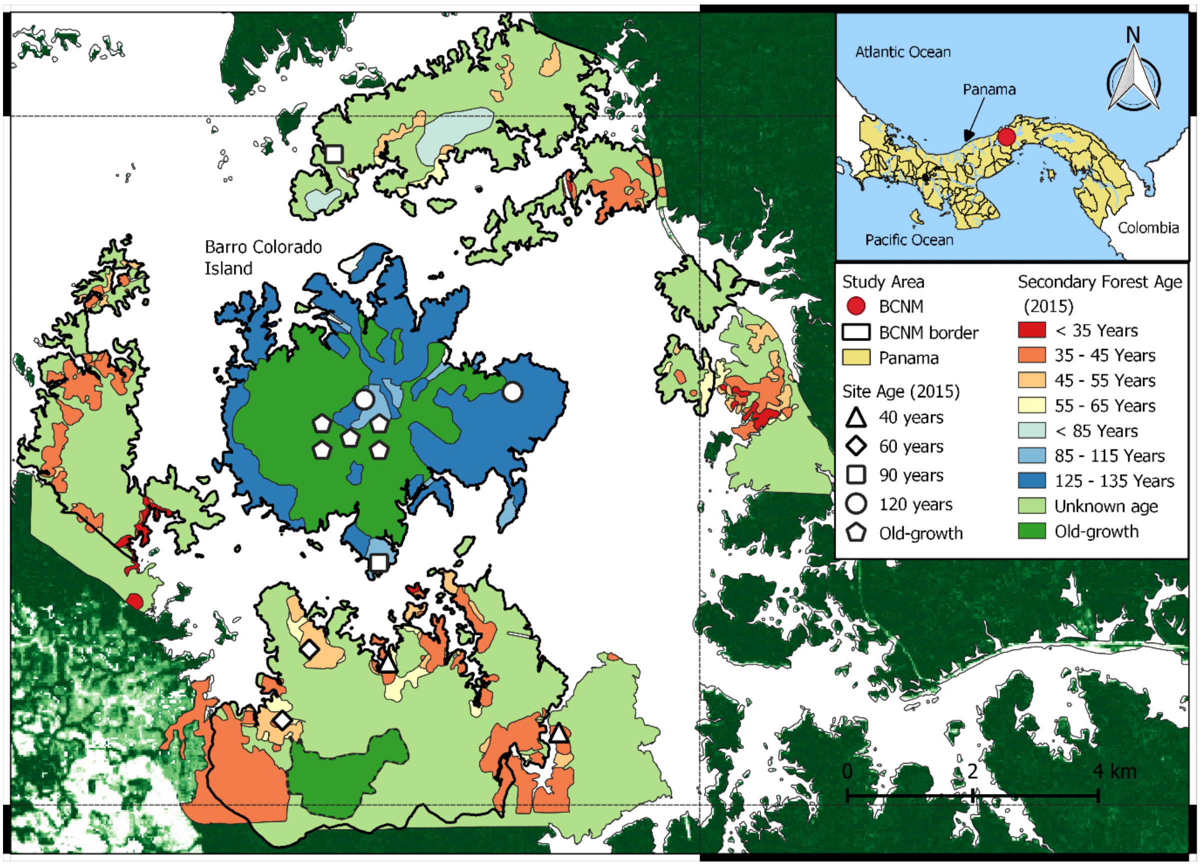

Figure S2.1. Map displaying study plots around the Barro Colorado Nature Monument (BCNM), central Panama. White shapes show 1-ha forest plots, with shape determined by stand age at time of census (2011-2016). Approximate secondary forest stand ages (as of 2015) and old growth forest extents were obtained from Dent and Elsy (2023). Forest ages were informed by Enders, (1935), Kenoyer, (1929), and aerial photographs taken by the US defence mapping agency (in 1955, 1966, 1973, 1979 and 1983). The red circle, on the country scale map, indicates the location of the BCNM within Panama. Country shapefiles were obtained from Global Administrative Areas (Hijmans et al., 2020) and the BCNM shapefiles are from (Smithsonian Tropical Research Institute, 2019). The map was made using QGIS v.3.12.3 (QGIS Development Team, 2020).

Table S2.2. Model specifications used to model both the effect of stand age on secondary forest structural and diversity metrics and to model the influence of environmental variables in all plots. Environmental variable models (mean N, mean P, and mean slope) are full models specified prior to model selection.

Secondary forest plots (*n* = 8)

Model specification	**Distribution**	**Link function**	***R* function (package)**
Stem Density ~ Stand Age	Negative binomial	log	glm.nb (MASS)
Basal Area ~ Stand Age	Gaussian	identity	glm (stats)
Rarefied Species Richness ~ Stand Age	Poisson	log	glm (stats)
Simpson's Diversity Index ~ Stand Age	Beta	logit	betareg (betareg)
Pielou's Evenness Index ~ Stand Age	Beta	logit	betareg (betareg)

All plots (*n* = 13)

Full model specification	**Distribution**	**Link function**	***R* function (package)**
Stem Density ~ P + N + Slope	Negative binomial	log	glm.nb (MASS)
Basal Area ~ P + N + Slope	Gaussian	identity	glm (stats)
Rarefied Species Richness ~ P + N + Slope	Negative binomial	log	glm.nb (MASS)
Simpson's Diversity Index ~ P + N + Slope	Beta	logit	betareg (betareg)
Pielou's Evenness Index ~ P + N + Slope	Beta	logit	betareg (betareg)

Table S2.3. Generalised Linear Model and beta regression results examining the effect of age on secondary forest structure and diversity metrics. Both the untransformed coefficients (second column) and exponentiated coefficients are reported where appropriate. Dispersion (*phi*) is the precision parameter for the beta regressions.

Stem Density

Predictors	**Log Mean (CI 95%)**	**Incidence Rate Ratios (CI 95%)**	**Statistic**	***P value***	R^2
(Intercept)	7.058 (6.787 – 7.335)	1161.984 (886.642 – 1533.426)	50.119	< 0.001	0.006
Stand age	0.000 (-0.003– 0.004)	1.000 (0.997 – 1.004)	0.169	0.886	

Basal Area

Predictors	**Estimates (CI 95%)**	**Statistic**	***P value***	R^2
(Intercept)	16.742 (14.592 – 18.892)	15.263	< 0.001	0.911
Stand age	0.103 (0.077 – 0.129)	7.815	<0.001	

Rarefied Species Richness

Predictors	**Log Mean (CI 95%)**	**Incidence Rate Ratios (CI 95%)**	**Statistic**	***P value***	R^2
(Intercept)	4.703 (4.513 – 4.889)	110.244 (91.206 – 132.789)	49.085	< 0.001	0.148
Stand age	-0.001 (-0.003 – 0.001)	0.999 (0.997 – 1.001)	-0.990	0.322	

Simpson’s Diversity Index

Predictors	**Estimate (CI 95%)**	**Exp (Estimate (CI 95 %))**	**Statistic**	***P value***	R^2

(Intercept)	3.628 (2.662 – 4.594)	37.643 (14.331 – 98.881)	7.363	< 0.001	
Stand age	-0.010 (-0.020 – 0.001)	0.991 (0.980 – 1.001)	-1.762	0.078	0.323
Dispersion (*phi*)	81.06 (0.484 - 161.636)	-	1.972	0.0486	
Pielou’s Evenness Index					
Predictors	**Estimate (CI 95%)**	**Exp (Estimate (CI 95 %))**	**Statistic**	***P value***	**R^2**
(Intercept)	1.816 (1.322 – 2.309)	6.145 (3.753 – 10.063)	7.215	< 0.001	
Stand age	-0.006 (-0.012 – -0.001)	0.994 (0.988 – 0.999)	-2.201	0.028	0.397
Dispersion (*phi*)	93.65 (2.18 – 185.12)	-	2.007	0.0448	

Table S2.4. Variables selected within Δ AICc ≤ 4 for models of structural and diversity metrics using all plots. Model weights do not sum to 1 due to the exclusion of models with Δ AICc > 4. Note R^2 values cannot currently be computed by MuMIN for beta regression model selection (Barton, 2022) and so are excluded for: Simpson's diversity index and Pielou's evenness index.

Variables included in model	**AICc**	**Δ AICc**	**Weight**	**Adjusted R^2**
STEM DENSITY:				
Intercept + mean slope	167.409	0.000	0.577	0.397
Intercept + mean N + mean slope	170.318	2.809	0.142	0.464
Intercept (only)	170.529	3.120	0.121	0.000
Intercept + mean P + mean slope	171.364	3.955	0.080	0.415
BASAL AREA:				
Intercept (only)	75.122	0.000	0.550	0.000
Intercept + mean N	77.341	2.220	0.181	0.092
Intercept + mean P	78.387	3.265	0.108	0.015
Intercept + mean slope	78.530	3.408	0.100	0.005
RAREFIED SPECIES RICHNESS:				
Intercept (only)	114.031	0.000	0.479	0.000
Intercept + mean P	115.543	1.512	0.225	0.140
Intercept + mean N	116.848	2.818	0.117	0.049
Intercept + mean slope	117.461	3.430	0.086	0.003
SIMPSON'S DIVERSITY INDEX:				
Intercept (only)	-52.191	0.000	0.500	-
Intercept + mean N	-50.660	1.530	0.232	-
Intercept + mean slope	-48.944	3.246	0.099	-
Intercept + mean P	-48.724	3.467	0.088	-
PIELOU'S EVENNESS INDEX:				
Intercept (only)	-34.812	0.000	0.488	-
Intercept + mean N	-32.935	1.877	0.191	-
Intercept + mean slope	-32.190	2.622	0.131	-
Intercept + mean P	-31.349	3.464	0.086	-

Table S2.5. Full model-averaged parameter estimates for models of structural and diversity metrics with AICc ≤ 4. Estimates are for centred and rescaled (divided by two standard deviations) explanatory variables.

Predictors	**Estimate**	**Adjusted standard error**	***z* statistic**	***P* value**
STEM DENSITY:				
Intercept	7.086	0.026	241.593	< 0.001
Mean slope	-0.139	0.073	1.795	0.073
Mean N	0.010	0.030	0.305	0.761
Mean P	0.003	0.019	0.141	0.888
BASAL AREA:				
Intercept	26.055	1.036	22.516	< 0.001
Mean N	-0.433	1.289	0.315	0.753
Mean P	0.105	0.806	0.118	0.906
Mean slope	0.053	0.744	0.064	0.949
RAREFIED SPECIES RICHNESS:				
Intercept	4.701	0.044	107.735	< 0.001
Mean P	-0.028	0.065	0.427	0.669
Mean N	0.009	0.039	0.219	0.827
Mean slope	-0.002	0.029	0.053	0.958
SIMPSON’S DIVERSITY INDEX:				
Intercept	2.896	0.183	15.823	< 0.001
Dispersion (*phi*)	58.790	27.006	2.177	0.030
Mean slope	0.135	0.301	0.449	0.654
Mean P	-0.015	0.124	0.120	0.904
Mean N	-0.000	0.112	0.003	0.997
PIELOU’S EVENNESS INDEX:				
Intercept	1.362	0.100	13.647	< 0.001
Dispersion (*phi*)	59.852	26.612	2.249	0.025
Mean slope	0.052	0.139	0.376	0.707
Mean P	-0.024	0.097	0.248	0.804
Mean N	0.001	0.066	0.015	0.988

Table S2.6. Outputs of two-sample Wilcoxon tests investigating the difference between secondary and old-growth forest for forest structure and diversity metrics.

Metric	**Comparison**	**Statistic**	***P* value**
Stem Density	Old-growth vs Secondary	20	1.000
Basal Area	Old-growth vs Secondary	30	0.171
Rarefied Species Richness	Old-growth vs Secondary	40	0.002
Extrapolated Species Richness	Old-growth vs Secondary	37	0.011
Simpson’s Diversity Index	Old-growth vs Secondary	28	0.284
Pielou’s Evenness Index	Old-growth vs Secondary	26	0.435
Number of Rare Species	Old-growth vs Secondary	38.5	0.008

Table S2.7. Generalised Linear Mixed Model results for pairwise comparisons of Sørensen, Horn and Morisita-Horn indices of similarity between secondary forest and old-growth plots. All GLMMs were run with a beta distribution and with plot as a random effect (eight levels, five replicates per level) with a random intercept. Both the untransformed coefficients (second column) and exponentiated coefficients are reported. Conditional R^2 is not reported due to the uncertainty in the random effect variance. Dispersion (*phi*) is the precision parameter for the beta distributed GLMMs.

Sørensen Similarity Index					
Predictors	**Estimate (CI 95%)**	**Exp(Estimate (CI 95%))**	**Statistic**	***P value***	***Marginal R^2***
(Intercept)	0.325 (-0.342 –1.013)	1.399 (0.711 – 2.753)	0.971	0.322	0.293
Stand age	0.006 (-0.002 – 0.014)	1.006 (0.998– 1.014)	1.461	0.144	
Dispersion (*phi*)	33.682 (20.729 – 54.725)	-	-	-	
Random effect variance = 0.101					

Horn Similarity Index					
Predictors	**Estimate (CI 95%)**	**Exp(Estimate (CI 95%))**	**Statistic**	***P value***	***Marginal R^2***
(Intercept)	-0.294 (-0.992 – 0.403)	0.745 (0.371 – 1.496)	-0.827	0.408	0.467
Stand age	0.011 (0.002 – 0.019)	1.011 (1.002 – 1.019)	2.485	0.013	
Dispersion (*phi*)	102.264 (62.783 – 166.574)	-	-	-	
Random effect variance = 0.126					

Morisita-Horn Similarity Index					
Predictors	**Estimate (CI 95%)**	**Exp(Estimate (CI 95%))**	**Statistic**	***P value***	***Marginal R^2***
(Intercept)	-1.607 (-2.826 – -0.387)	0.201 (0.059 – 0.679)	-2.582	0.010	0.389
Stand age	0.016 (0.002 – 0.031)	1.016 (1.002 – 1.031)	2.190	0.029	
Dispersion (*phi*)	41.904 (25.819 – 68.010)	-	-	-	
Random effect variance = 0.386					

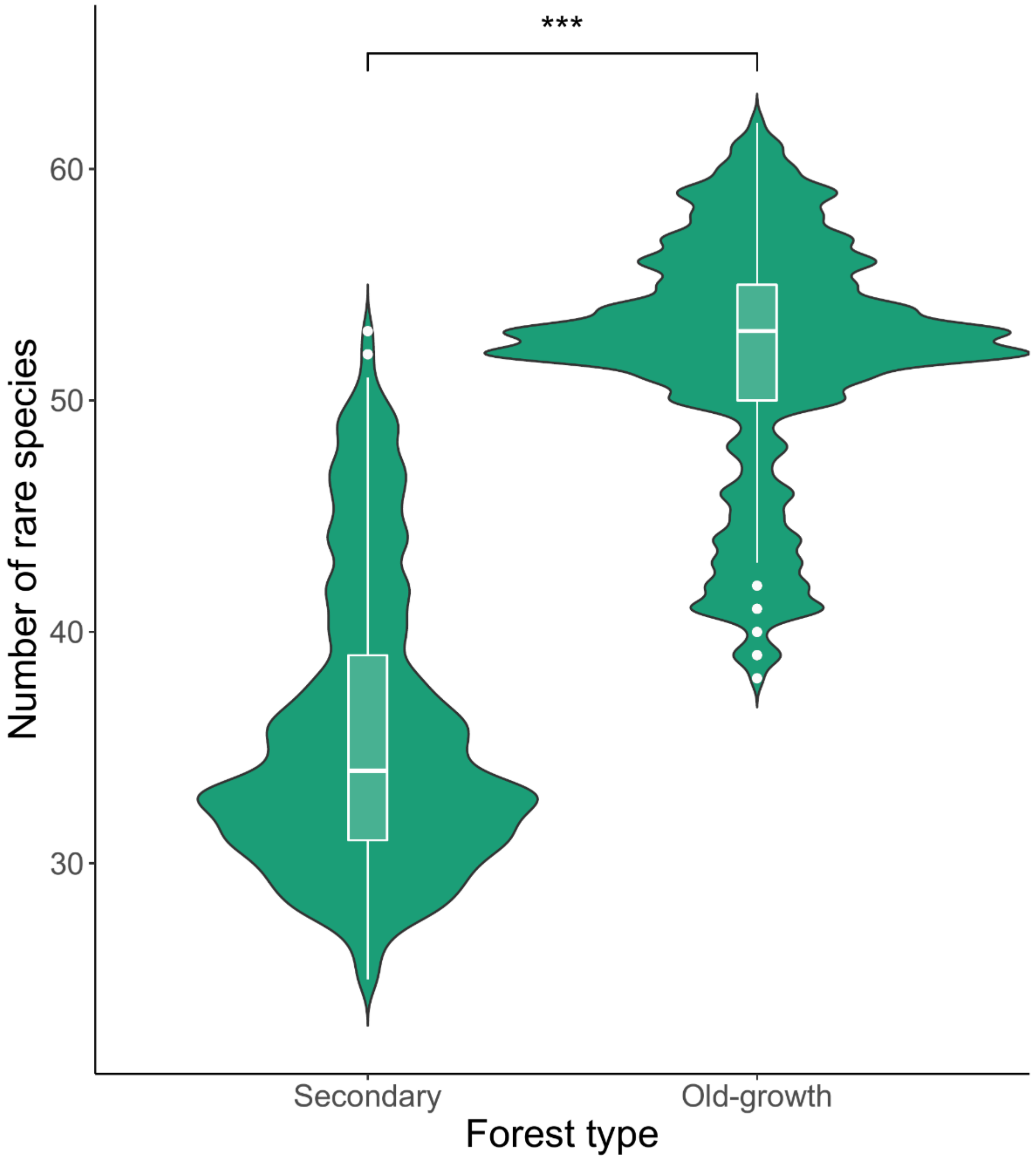

Figure S2.2. The number of locally rare species identified in either secondary or old-growth forest by the multinomial model for all possible combinations of the comparison between five 1-ha secondary forest plots (n = 6,720) and the five 1-ha old-growth plots. The asterisks indicate results of a two-tailed *t*-test between forest type ($P < 0.001$). Violin plots indicate the data distribution, and the box plots demonstrate the median, interquartile range, and outliers.

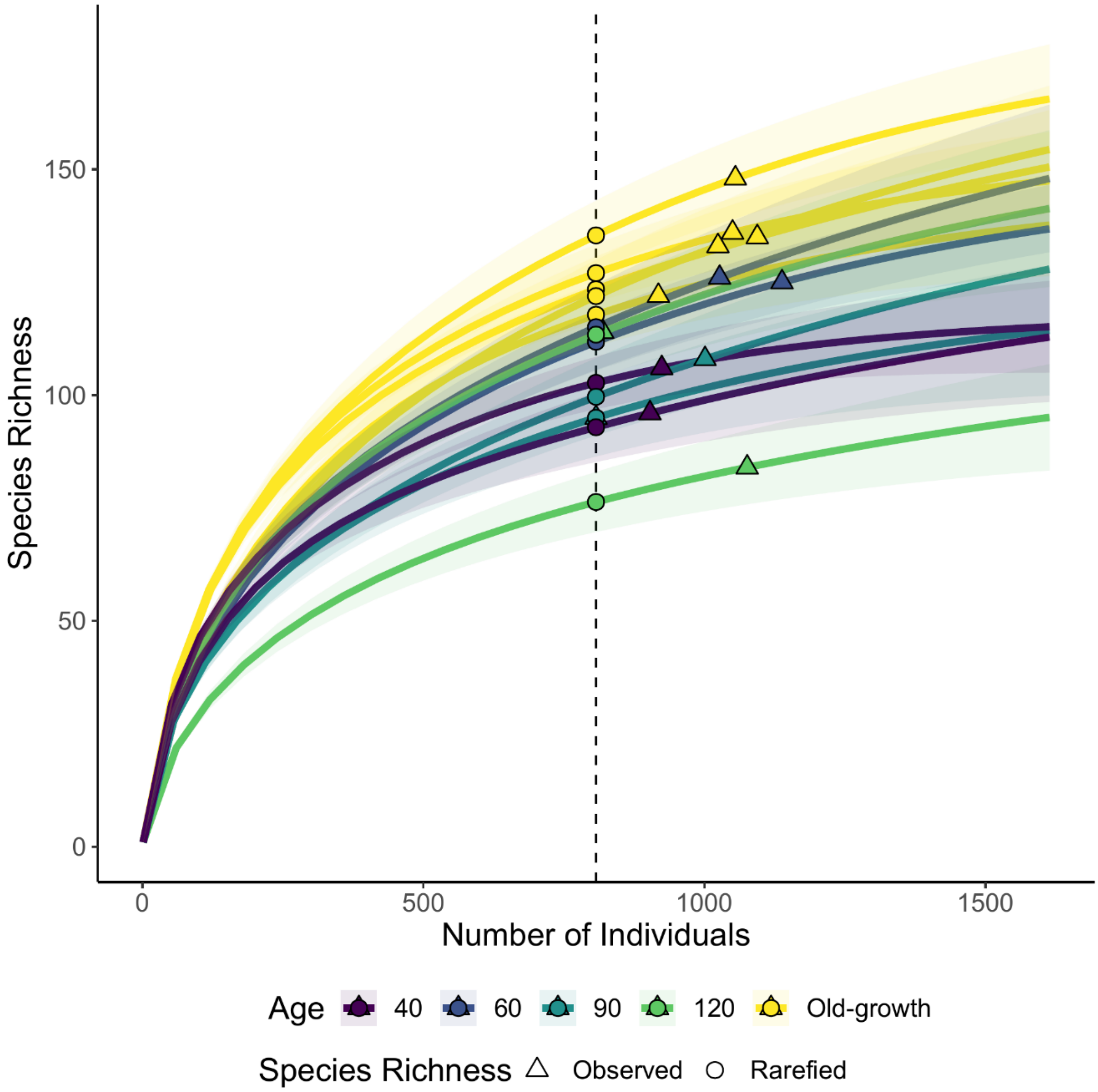

Figure S 2.3. Species rarefaction/extrapolation curves displaying observed, rarefied, and extrapolated species richness. The dashed line indicates the number of individuals to which species richness values were rarefied to, i.e. the minimum number of individual identified trees found per plot (*n* = 807). Shading either side of the line represents 95 % confidence intervals for rarefaction and extrapolation predictions.

Table S2.8. The five most abundant tree, palm or shrub species ≥ 5 cm per 1-ha plot.

Age	Plot	Species	Number of individuals	Percent of total individuals (%)
40 years	**Pedro Gomez**	*Cupania seemannii*	77	8.33
		Malouetia guatemalensis	58	6.28
		Lacistema aggregatum	41	4.44
		Xylopia frutescens	35	3.79
		Protium panamense	34	3.68
40 years	**Saino**	*Swartzia simplex*	126	13.95
		Gustavia superba	74	8.19
		Miconia argentea	56	6.20
		Inga sapindoides	55	6.09
		Spondias radlkoferi	43	4.76
60 years	**Enders**	*Oenocarpus mapora*	116	11.30
		Gustavia superba	60	5.84
		Mabea occidentalis	52	5.06
		Alseis blackiana	46	4.48
		Trichilia tuberculata	46	4.48
60 years	**Foster's**	*Coussarea curvigemma*	215	18.89
		Faramea occidentalis	67	5.89
		Inga vera	58	5.10
		Alseis blackiana	50	4.39
		Myrciaria floribunda	43	3.78
90 years	**Bohio**	*Faramea occidentalis*	78	9.67
		Cupania seemannii	58	7.19

		Gustavia superba	53	6.57
		Virola sebifera	47	5.82
		Maquira guianensis	45	5.58
90 years	**Poachers**	*Trichilia tuberculata*	106	10.59
		Protium panamense	92	9.19
		Swartzia simplex	68	6.79
		Oenocarpus mapora	55	5.49
		Xylopia macrantha	50	5.00
120 years	**Barbour**	*Gustavia superba*	384	35.69
		Faramea occidentalis	124	11.52
		Oenocarpus mapora	58	5.39
		Swartzia simplex	58	5.39
		Alseis blackiana	34	3.16
120 years	**Pearson**	*Faramea occidentalis*	110	13.43
		Trichilia tuberculata	63	7.69
		Oenocarpus mapora	48	5.86
		Astrocaryum standleyanum	43	5.25
		Swartzia simplex	43	5.25
Old-growth	**50-ha BL**	*Faramea occidentalis*	147	13.44
		Alseis blackiana	49	4.48
		Oenocarpus mapora	46	4.20
		Desmopsis panamensis	40	3.66
		Prioria copaifera	27	2.47
Old-growth	**50-ha BR**	*Faramea occidentalis*	121	13.18
		Oenocarpus mapora	72	7.84

		Drypetes standleyi	53	5.77
		Alseis blackiana	51	5.56
		Hirtella triandra	48	5.23
Old-growth	**50-ha Mid**	*Faramea occidentalis*	338	33.01
		Trichilia tuberculata	48	4.69
		Oenocarpus mapora	35	3.42
		Tetragastris panamensis	35	3.42
		Swartzia simplex	31	3.03
Old-growth	**50-ha TL**	*Faramea occidentalis*	148	14.10
		Socratea exorrhiza	57	5.43
		Alseis blackiana	50	4.76
		Oenocarpus mapora	40	3.81
		Tetragastris panamensis	26	2.48
Old-growth	**50-ha TR**	*Faramea occidentalis*	76	7.20
		Hirtella triandra	55	5.21
		Protium tenuifolium	55	5.21
		Drypetes standleyi	43	4.08
		Oenocarpus mapora	39	3.70

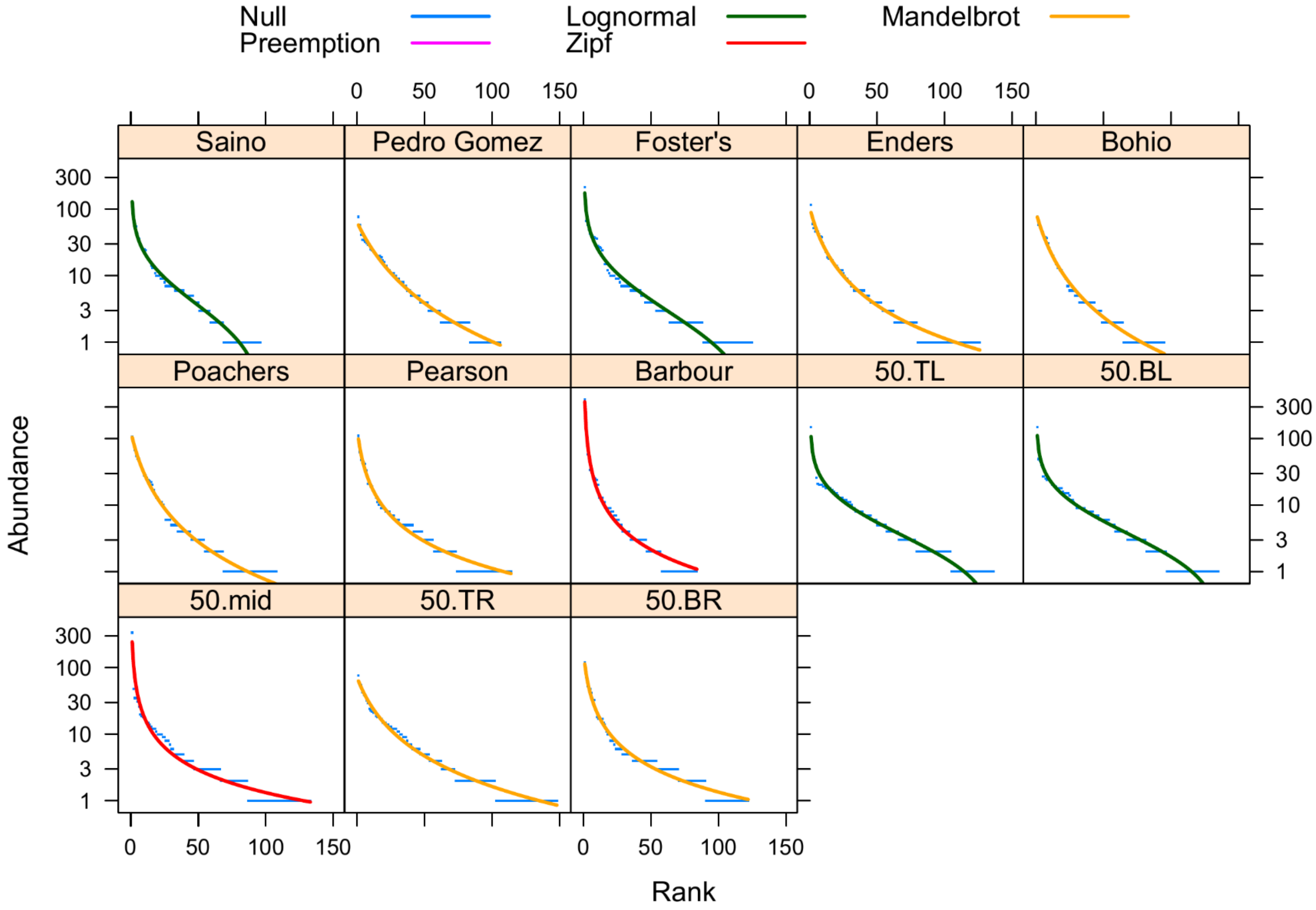

Figure S2.4. Rank abundance plot demonstrating the differences in species dominance among plots. Log species abundance is plotted against species ranked by abundance using the radfit function in ‘vegan’ (Oksanen et al., 2022). Different coloured lines correspond to the best fitting rank abundance model (all with Poisson errors) based on AIC and an automatic fitting procedure.

Table S2.9. The five most abundant midstory and canopy tree or palm species ≥ 5 cm per 1-ha plot. Midstory or canopy species were identified by their maximum height (Condit et al., 2010; Croat, 1978) and were included to allow direct comparison with Dent, DeWalt and Denslow (2013).

Age	Plot	Species	Number of individuals	Percent total individuals (%)
40 years	**Pedro Gomez**	*Malouetia guatemalensis*	58	8.68
		Xylopia frutescens	35	5.24
		Protium panamense	34	5.09
		Alseis blackiana	32	4.79
		Miconia argentea	29	4.34
40 years	**Saino**	*Gustavia superba*	74	12.63
		Miconia argentea	56	9.56
		Inga sapindoides	55	9.39
		Spondias radlkoferi	43	7.34
		Astrocaryum standleyanum	26	4.44
60 years	**Enders**	*Oenocarpus mapora*	116	15.03
		Gustavia superba	60	7.77
		Alseis blackiana	46	5.96
		Trichilia tuberculata	46	5.96
		Xylopia macrantha	46	5.96
60 years	**Foster's**	*Inga vera*	58	10.21
		Alseis blackiana	50	8.80
		Myrciaria floribunda	43	7.57
		Heisteria concinna	40	7.04
		Cordia alliodora	36	6.34
90 years	**Bohio**	*Gustavia superba*	53	8.97

		Virola sebifera	47	7.95
		Maquira guianensis	45	7.61
		Protium panamense	40	6.77
		Brosimium alicastrum	38	6.43
90 years	**Poachers**	*Trichilia tuberculata*	106	13.71
		Protium panamense	92	11.90
		Oenocarpus mapora	55	7.12
		Xylopia macrantha	50	6.47
		Tetragastris panamensis	42	5.43
120 years	**Barbour**	*Gustavia superba*	384	47.70
		Oenocarpus mapora	58	7.20
		Alseis blackiana	34	4.22
		Luehea seemannii	34	4.22
		Protium panamense	31	3.85
120 years	**Pearson**	*Trichilia tuberculata*	63	10.77
		Oenocarpus mapora	48	8.21
		Astrocaryum standleyanum	43	7.35
		Hirtella triandra	42	7.18
		Gustavia superba	33	5.64
Old-growth	**50-ha BL**	*Alseis blackiana*	49	6.23
		Oenocarpus mapora	46	5.85
		Prioria copaifera	27	3.44
		Trichilia tuberculata	27	3.44
		Protium tenuifolium	25	3.18

Old-growth	**50-ha BR**	*Oenocarpus mapora*	72	11.03
		Drypetes standleyi	53	8.12
		Alseis blackiana	51	7.81
		Hirtella triandra	48	7.35
		Tetragastris panamensis	42	6.43
Old-growth	**50-ha Mid**	*Trichilia tuberculata*	48	8.87
		Oenocarpus mapora	35	6.47
		Tetragastris panamensis	35	6.47
		Quararibea asterolepis	26	4.81
		Hirtella triandra	20	3.70
Old-growth	**50-ha TL**	*Socratea exorrhiza*	57	7.79
		Alseis blackiana	50	6.83
		Oenocarpus mapora	40	5.46
		Tetragastris panamensis	26	3.55
		Protium panamense	20	2.73
Old-growth	**50-ha TR**	*Hirtella triandra*	55	6.58
		Protium tenuifolium	55	6.58
		Drypetes standleyi	43	5.14
		Oenocarpus mapora	39	4.67
		Poulsenia armata	38	4.55

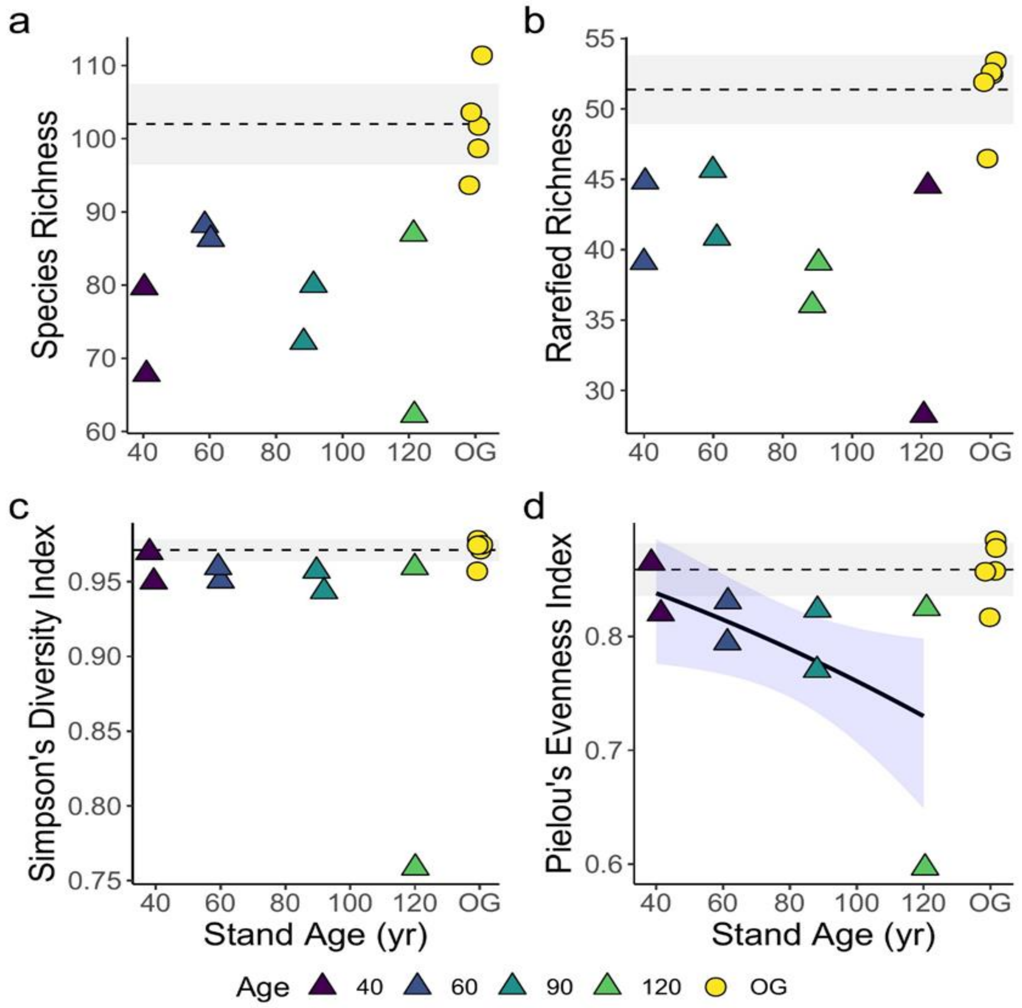

Figure S2.5. Richness and diversity metrics per plot plotted against stand age for all canopy and midstory trees and palms ≥ 5cm. **a**. Species richness; **b**. Rarefied species richness; **c**. Simpson's diversity index and **d**. Pielou's evenness index. The mean values of old-growth plots are indicated by the dashed lines; grey shading indicates 95% confidence intervals. Model predictions (+/- 95% C.I.) are plotted in blue shading for models with significant age effects (using the same model selection criteria as described above). These data use the same tree inclusion criteria as Dent, DeWalt and Denslow (2013) i.e., understory trees and shrubs were excluded prior to analysis. Rarefied richness was also rarefied to 120 stems to match Dent, DeWalt and Denslow (2013).

3 Chapter 3: Functional recovery in leaf traits and ongoing recovery in tree stature in late-stage successional forest in central Panama

Chapter authors: Alexander D. Elsy, Isabel L. Jones, Marion Pfeifer, and Daisy H. Dent.

3.1 Abstract

Functional traits are fundamental to understanding the processes and timescales involved in secondary forest recovery. Many studies have investigated how environmental filtering shapes succession across the Neotropics, in relation to tree functional traits and functional diversity. Predominately research has focused on how the fast-slow continuum of tree life history traits alters and recovers through succession. However, most of these studies encompass just the first 50 years of succession, and functional recovery beyond this time window is currently poorly understood. We addressed this knowledge gap by examining the recovery of 11 functional traits in trees, palms, and shrubs within a mid-to-late-stage secondary forest chronosequence in central Panama. We examined eight 1-ha secondary forest plots (aged 40 – 120 years since abandonment) and five old-growth plots in the Barro Colorado Nature Monument, to examine changes in trait community weighted means, functional clusters, and functional diversity through succession. We found that plant stature related traits, i.e. maximum height, maximum diameter and seed mass, continued to increase through succession. However, we found little evidence of ongoing change in leaf traits associated with the fast-slow continuum, apart from a decline in deciduous species, through succession and found no shifts in functional diversity metrics through time. Cluster analysis results identified four functional groupings, related to the fast-slow continuum and plant stature, but there were no significant changes in the abundance of these clusters through succession. These results suggest that secondary forest communities within our chronosequence have recovered to old-growth levels in relation to the fast-slow continuum, but recovery is ongoing in relation to plant stature traits, and thus likely stature-recruitment trade-offs. This evidence suggests that ongoing species community compositional differences between old-growth and secondary forest in late succession (Chapter 2) are unlikely to be linked to shifts in fast-slow continuum related traits. We propose that processes other than selection for increased shade tolerance through succession, such as dispersal limitation, are important for late-stage successional change in secondary forest.

3.2 Introduction

Functional traits are indicators of plant fitness (Violle et al., 2007) that are both directly and indirectly linked to plant growth, survival and reproduction (Grime et al., 1997; Reich, 2014). Plant functional strategies are defined by trade-offs between traits, including along the fast-slow continuum, which illustrates an inherent trade-off between acquisitive strategies, i.e. rapid resource acquisition and growth at the cost of higher mortality rates, and conservative strategies, i.e. slower resource acquisition and growth rates, but longer lifespans (Grime et al., 1997; Reich, 2014; Salguero-Gómez et al., 2016). The fast-slow continuum is well represented by the leaf economic spectrum, where at one end of the spectrum low investment leaves have rapid resource acquisition, but short lifespans, and at the other end costly, slow resource acquisition leaves have longer lifespans (Reich, 2014; Wright et al., 2004).

Evidence for the fast-slow continuum is found globally in plant communities (Díaz et al., 2016; Maynard et al., 2022; Salguero-Gómez et al., 2016) and has been applied to forest successional theory, conceptualising the shift from acquisitive pioneer species, associated with high light conditions, to conservative, shade tolerant species (Wright et al., 2010). Other axes of variation in plant communities, relating to plant stature and recruitment which are orthogonal to the fast-slow continuum, have been identified (Díaz et al., 2016; Kambach et al., 2022; Maynard et al., 2022; Rüger et al., 2018). This stature-recruitment axis is represented by plant species which reach a large stature, due to rapid growth and high survival rates, but have low recruitment rates vs those species which are short-statured, due to slow growth and low survival rates, but recruit seedlings successfully (Kambach et al., 2022; Rüger et al., 2018). Thus, by examining plant functional traits we can indirectly examine plant life history strategies and see how these strategies vary with changing environmental conditions.

Environmental filtering can select for species with functional traits that are advantageous in a given habitat, for example traits that confer drought tolerance in dry habitats. Evidence for environmental filtering has been found in relation to rainfall (e.g. Lasky et al., 2016), temperature (e.g. Bjorkman et al., 2018), soil nutrients (e.g. Andersen et al., 2012) and light intensity (e.g. Kitajima, 1994). However, the direct effects of environmental conditions on plant fitness are often difficult to disentangle from the effects of biotic interactions among species at a site (N. J. B. Kraft et al., 2015), and competitive interactions can also drive and maintain functional trait differences within plant communities (Kunstler et al., 2016; Maire et al., 2012; Uriarte et al., 2010). Thus, by examining plant functional traits within a community we examine both the abiotic and biotic conditions which may drive community assembly.

Secondary tropical forest succession has focused heavily on the role of environmental filtering in community reassembly, due to the strong changes in light availability, soil moisture and temperature that occur when open, abandoned land transitions to closed canopy forest (Bazzaz and Pickett, 1980;

Lebrija-Trejos et al., 2011; Buzzard et al., 2016; Matsuo et al., 2021). Successional theory has long focused on the shift from short-lived pioneer species, associated with high-light availability, to long-lived pioneers and then shade-tolerant species, as succession progresses (Finegan, 1996; Guariguata and Ostertag, 2001; Dent, DeWalt and Denslow, 2013). This shift along the light availability gradient is associated with forest communities changing from fast to slow resource acquisition strategies (*sensu* Grime, 1977; Reich, 2014; Wright et al., 2004), which are evidenced by changes in plant functional traits. Short-lived pioneer (fast) species typically have higher specific leaf area (SLA) and leaf nitrogen content, and lower leaf toughness, seed mass and wood density, than shade-tolerant (slow) species, which have a converse set of traits (Popma et al., 1992; Rüger et al., 2012; Westoby et al., 2002; Wright et al., 2010). The fast life history strategy is associated with higher growth and mortality rates, while slow species grow more slowly but have lower mortality (Rüger et al., 2012; Wright et al., 2010). In contrast, long-lived pioneer species are tall species with low mortality, high growth rates and poor recruitment (Rüger et al., 2018) that are abundant even 120-years into succession (Rüger et al., 2020). The traits of long-lived pioneers are better explained by the stature-recruitment axis of variation, rather than the fast-slow continuum, and thus multiple strategies shape tropical forest community assembly (Rüger et al., 2018). Examining functional trait changes through succession enables us to explore these changes in life history strategies, and the timescales over which functional recovery to old-growth communities occurs.

Recent studies have examined the recovery of functional traits through succession in both wet and dry tropical forests (Boukili and Chazdon, 2017; Craven et al., 2015; Lebrija-Trejos et al., 2010; Lohbeck et al., 2013; Muscarella et al., 2016; Poorter et al., 2021b, 2019). Rainfall, seasonality and temperature are key factors determining plant functional traits, and wet and dry tropical forests follow distinct successional pathways, due to differences in resource availability over succession (Lohbeck et al., 2015, 2013; Poorter et al., 2021b, 2019). Tropical dry forests are a stressful environment for plant growth in early succession, characterised by low water availability and high temperatures (Lebrija-Trejos et al., 2011; Pineda-García, Paz and Meinzer, 2013). This environment becomes less stressful through time, as the forest canopy closes (Lebrija-Trejos et al., 2011; Pineda-García, Paz and Meinzer, 2013), and thus, tropical dry forests tend to change from drought tolerant, conservative resource acquisition strategies in early succession to more acquisitive strategies in late succession (Lohbeck et al., 2013; Paz et al., 2015; Poorter et al., 2021b, 2019). In contrast, wet tropical forests are not often constrained by water availability, and shifts in light availability through succession drive plant life history strategies (Bazzaz and Pickett, 1980). Therefore, wet tropical forest succession typically progresses from fast resource acquisitive strategies in early succession, to slow, conservative strategies in late succession when light becomes limited (Lohbeck et al., 2013; Poorter et al., 2021b). These changes in wet tropical forests are characterised by shifts in plant functional traits with values of SLA, leaf nitrogen content and deciduousness declining through succession, whilst wood density, leaf toughness, tree size and seed mass increase (Boukili and Chazdon, 2017; Lohbeck et al., 2013; Muscarella et al., 2016; Poorter et al., 2021b, 2019). However, these patterns have generally been described in early-to-mid stages of succession (0 – 50 years), where light availability changes most drastically (Lebrija-Trejos et al., 2011), and few studies examine how functional traits continue to change in the late stages of succession, where shade intolerant species have been excluded and the forest understory and canopy begins to resemble old-growth communities (Chazdon, 2014). For example, in a recent analysis of functional recovery in secondary forests only three of the 30 chronosequences analysed included plots over 80 years old (Poorter, et al., 2021b). As a result, there is a knowledge gap regarding how plant functional traits continue to change in late successional tropical forests and at what age functional similarity to old-growth occurs (but see Buzzard et al., 2016; Marcilio-Silva et al., 2016).

In addition to individual traits, metrics of functional diversity can help to explain changes in ecosystem function and successional recovery. Functional diversity is multidimensional and consists of multiple metrics that relate to the relative abundance, and variation, of species traits in functional trait space (Mouillot et al., 2013b; Villéger et al., 2008). Many studies have found that functional diversity explains ecosystem functioning better than species diversity metrics (Cadotte et al., 2011; Díaz and Cabido, 2001; Gross et al., 2017; Mouillot et al., 2011; Tilman et al., 1997). For example, in a grassland experiment, species functional identity and functional divergence metrics explained primary productivity and decomposition variation better than species diversity (Mouillot et al., 2011). Alternatively, the dominant species in a community may have the largest impact on ecosystem function (i.e. the `mass-ratio hypothesis` Grime, (1998); Mokany, Ash and Roxburgh, (2008)). For instance, a recent global study of grassland communities found that dominant species best explained variation in productivity, and there was no relationship between functional diversity and productivity (Engel et al., 2023). On the other hand, a study from 72 sites across eight biomes in China found that community weighted means and ecosystem traits, and thus dominant species, explained up to 59 % of variation in ecosystem function (Yan et al., 2023). In this study, functional diversity was still an important predictor, explaining more variation in ecosystem function than species richness or phylogenetic diversity (Yan et al., 2023). Thus, both functional diversity and measures of dominant species' traits, i.e., functional trait community weighted means, can give insights into how changing plant communities may influence ecosystem function.

Functional traits, and functional diversity, are expected to be constrained in the early stages of tropical forest succession due to strong environmental filtering effects (i.e. high light and temperatures; Lebrija-Trejos et al., 2011) selecting for a subset of plant functional traits and few viable ecological strategies. In later stages of succession, functional diversity is likely to increase, as environmental filters decrease in importance and, instead, functional composition is driven by competitive and facilitative interactions among species (Letcher et al., 2012; Purschke et al., 2013; Valiente-Banuet and Verdú, 2013), and stochastic colonisation events (Li et al., 2015). This “functional divergence” hypothesis (Boersma et al., 2016) has found support in moist tropical forest succession; multiple studies find functional diversity increases over early succession (Lohbeck et al., 2012; Warring et al., 2016; WenSheng et al., 2014; Whitfeld et al., 2014). On the other hand, Craven et al. (2018) found functional diversity to saturate just 10 years into succession, and found evidence of functional convergence as succession progressed (up to 30 years since land abandonment). Similarly, Muscarella et al. (2016) found evidence of functional convergence in the maximum height of adult trees, but found no pattern for three other traits, over 90 years of succession in subtropical Puerto Rico. Thus, changes in functional diversity through succession can be uncertain and because most studies focus on forests aged 0 – 50 years, we have a limited understanding of how functional diversity continues to change in late successional tropical forests. Understanding ongoing changes in functional diversity is important because higher functional diversity can improve tropical forest resilience to disturbance (Schmitt et al., 2020) and may enable forests to adapt to changing climatic patterns (Sakschewski et al., 2016).

Here, we study a chronosequence in the Barro Colorado Nature Monument (BCNM), central Panama, to address the current knowledge gap in functional trait research in late successional tropical forests. Our chronosequence, aged 40 – 120 years, is one of the oldest in the Neotropics (Poorter, et al., 2021b; Rozendaal et al., 2019 but see Buzzard et al., 2016), and we have previously used it to examine questions related to recovery of tree community composition, forest structure and carbon (Denslow, 2000; Denslow and Guzman, 2000; Dent, DeWalt and Denslow, 2013; DeWalt, Maliakal and Denslow, 2003; Jones et al., 2019; Mascaro et al., 2012 and see Chapter 2). Recent work has also examined the relationship between soil carbon and tree functional groups associated with shade tolerance (Wallwork et al., 2022). However, questions of functional composition and diversity recovery, across a wide range of functional traits, have not yet been investigated. We aim to address the following questions and hypotheses:

1. Can we identify clusters of species that relate to distinct life-history strategies (i.e., species associated with fast or slow life history strategies or long-lived pioneers)? We predict that we will find evidence of both fast and slow strategies, but also strategies associated with the stature-recruitment axis i.e. large, long-lived species with low recruitment and small, short-lived species with high recruitment rates (Kambach et al., 2022; Rüger et al., 2018).
2. Do community weighted means of plant functional traits shift along the fast-slow continuum from mid to late stages of succession? We predict that traits associated with “fast” life history strategies will decline through the late stages of succession (e.g. Lohbeck et al., 2013; Poorter et al., 2021b).
3. Does functional diversity increase from mid to late stages of succession? We predict that we will find functional diversity increases through the mid-to-late stages of succession (Lohbeck

et al., 2012; Warring et al., 2016; WenShen, RunGuo and Yi, 2014; Whitfeld et al., 2014; however see Craven et al., 2018; Muscarella et al., 2016).

4. Are the specialist and generalist species classifications, generated in Chapter 2 of this thesis, relevant in terms of functional traits? Are there underlying differences in functional traits for plots that follow divergent successional pathways (see Chapter 2)?

To address these questions, we analyse 12 functional traits: leaf lamina toughness, leaf area, leaf nitrogen content, leaf phosphorous content, leaf thickness, specific leaf area (SLA), seed dry mass, maximum height, maximum diameter, wood density, leaf compoundness and leaf deciduousness (see Table 3.1 for trait functions and predictions for changes through succession). Traits were selected due to their association with the fast-slow continuum and leaf economic spectrum and the stature-recruitment axis (Díaz et al., 2016; Kambach et al., 2022; Maynard et al., 2022; Reich, 2014; Rüger et al., 2018; Wright et al., 2004). We examine functional relationships for both trees (≥ 5 cm DBH) and saplings (1-5 cm DBH) as evidence of environmental filtering may differ among size classes.

Table 3.1. The functional traits included in this study and their relationship with plant function and expected changes through tropical forest succession.

Functional Trait	Units	Function and correlates	Prediction
Leaf Lamina Toughness	J m^{-2}	Increased leaf toughness is related to lower herbivory (Choong, 1996; Coley, 1983) and longer leaf lifespans (Onoda et al., 2011; Reich et al., 1991).	Increase through succession (e.g. Craven et al., 2015) as competition for light decreases and species become more shade tolerant.
Leaf Area	mm^2	Higher leaf areas are linked to thicker boundary layers and slower heat loss (Westoby et al., 2002) and small leaves are expected in high temperature, high light environments (Parkhurst and Loucks, 1972) i.e. early succession.	Increases through succession as the environment becomes darker (Poorter et al., 2021b).
Leaf Nitrogen Content	mg g^{-1}	High leaf nitrogen content is directly related to high rates of photosynthesis (Evans, 1989; Reich et al., 1998) and associated with shorter leaf lifespans (Reich et al.,	Declines through succession (Boukili and Chazdon, 2017).

		1991) and increased herbivory (Coley and Barone, 1996).	
Leaf Phosphorous Content	mg g^{-1}	High leaf phosphorous content is related to high rates of photosynthesis, and can be more important than leaf nitrogen content (Raaimakers et al., 1995). Pioneer species have higher leaf phosphorous content than late successional species (Raaimakers et al., 1995).	Declines through succession (Raaimakers et al., 1995).
Leaf Thickness	mm	Leaf thickness is important for photosynthesis (Agustí et al., 1994) and higher leaf thickness is linked to lower growth rates (Nielsen et al., 1996). Leaf thickness is strongly related to SLA and leaf dry matter content (Vile et al., 2005).	Increases, or is neutral, through succession (Lohbeck et al., 2013; Boukili and Chazdon, 2017).
Specific Leaf Area (SLA)	mm^{2} mg^{-1}	High SLA is related to short leaf lifespan, higher leaf nitrogen content, higher photosynthetic rates, increased relative growth rates and pioneer strategies (Reich, 2014; Reich et al., 1998, 1997; Westoby et al., 2002).	Declines through succession (Boukili and Chazdon, 2017; Lohbeck et al., 2013; Poorter et al., 2021b).
Seed Dry Mass	mg	Increased seed mass linked to higher seedling survival (King et al., 2006c; Moles and Westoby, 2004). Small seeds are more fecund, less resistant to stress (Muller-Landau, 2010) and disperse shorter distances than large seeds, although plant height explains dispersal better (Thomson et al., 2011).	Increase in seed dry mass through succession as light availability declines (Muscarella et al., 2016).
Maximum Height	m	Trees which are taller than their neighbours have access to more light and thus photosynthetic potential	Increase through succession (Falster and Westoby, 2005; Muscarella et al., 2016).

		(Westoby et al., 2002), but there is are construction costs and hydraulic safety trade-offs (Liu et al., 2019; Ryan and Yoder, 1997). Tree height is related to biomass (Chave et al., 2014) and decreased wood density (Liu et al., 2019). Increased height is also related to increased seed dispersal distances (Thomson et al., 2011).	
Maximum Stem Diameter	m	Related to tree growth rate (Hérault et al., 2011; King et al., 2006a), tree height (King et al., 2006a) and biomass (Chave et al., 2014)	Increases through succession (Craven et al., 2015).
Wood Density	**-**	Related to water transport, structural support and higher wood density is related to lower growth rates and mortality (Chave et al., 2009).	Increases through succession (Poorter et al., 2021b).
Leaf Compoundness	**-**	Species with compound leaves are more associated with dry (Lohbeck et al., 2013; Poorter and Markesteijn, 2008) and seasonally dry forests (Malhado et al., 2010). Species with compound leaves tend to be fast growing, but not more associated with pioneer species than simple-leafed species (Malhado et al., 2010; Popma et al., 1992), and compound leaves may act as disposable branches (Warman et al. (2011) and references therein).	Either decrease or be neutral through succession (Lohbeck et al., 2013).
Deciduousness	**-**	Deciduous trees generally have lower leaf toughness, high leaf nitrogen content, and higher SLA than evergreen trees and they avoid drought by dropping their leaves	Decrease through succession, following the expected shift from acquisitive to conservative strategies (Lohbeck et al., 2015).

	(Eamus, 1999; Poorter and Markesteijn, 2008; Pringle et al., 2011). Deciduous trees are more likely to be pioneer species (Popma et al., 1992).	

3.3 Methods

3.3.1 Study area

Here we use a secondary forest chronosequence in the Barro Colorado Nature Monument (BCNM), initially established by Denslow and Guzman (2000), and data from the 50-ha forest dynamics plot on Barro Colorado Island (BCI; Condit, 1998; Hubbell et al., 1999) to investigate forest functional recovery. The BCNM chronosequence comprises eight 1-ha secondary forest plots (50 x 200 m), distributed across BCI and the surrounding peninsulas, that were located in secondary forest stands aged approximately 40, 60, 90 and 120 years since land-abandonment. The chronosequence has two independent plots per forest stand age and plots were 1.07 km apart at a minimum (mean ± SD = 4.39 ± 2.32 km). The 50-ha forest dynamics plot was used as an old-growth forest comparison to the secondary forest chronosequence. Five 1-ha (100 x 100 m) subplots were subsampled from the 50-ha plot, with these plots located at the corners and centre of the 50-ha plot. For further information on the study area please see Chapter 2 and Figure S2.1 therein.

3.3.2 Data collection

3.3.2.1 Forest census

All trees, palms and shrubs ≥ 5 cm diameter at breast height (DBH) were measured in each 1-ha plot (Condit et al., 2019b; Dent, DeWalt and Lopez, 2020), following ForestGEO vegetation census protocols (Condit, 2008). Tree, palm, and shrub saplings (1 – 5 cm DBH) were also measured in each plot to a subsampled area of 0.5-ha, composed of five parallel transects (5 x 200 m) per plot. One 120-year-old plot, Barbour, only had saplings 2.5 – 5 cm measured and one 90-year-old plot, Bohio, had no saplings measured. Trees and saplings were identified to species level where possible (99.3 % identified for the secondary forest chronosequence individuals (n = 20,875), all species identified for the old-growth plots (n = 15,723). Unidentified individuals (n = 246) were removed from the dataset prior to analysis, as it was not possible to relate these to functional trait data, and a total of 36,598 individuals and 318 species were analysed.

3.3.2.2 Functional traits

Functional trait data for all trees and saplings were primarily obtained from the TRY plant trait database (Kattge et al., 2020). All trees and saplings had their nomenclature standardised to match the TRY database prior to the data request, using the *Taxonstand* R package (Cayuela et al., 2021). We chose to examine the following continuous traits: leaf nitrogen content, leaf phosphorous content, leaf area, leaf thickness, specific leaf area, leaf lamina toughness, seed dry mass, wood density, maximum plant height and maximum plant diameter (Table 3.1). These functional traits were chosen to span the leaf economic spectrum and plant size axes (Díaz et al., 2016; Wright et al., 2004) and also functional clusters distinct from the two main axes of variation (Maynard et al., 2022). We chose functional traits representing each distinct cluster identified by Maynard et al. (2022), apart from root depth due to the lack of data available in TRY for our species, to encompass the variation of life-history strategies found in the species included in our plots. The categorical traits, leaf compoundness and leaf phenology, were also examined and obtained from Kattge et al. (2011, 2012), as these traits may be related to species success at different successional stages (Poorter et al., 2021b).

The trait values obtained from the TRY plant trait database (Zheng, 1983; Baruch and Goldstein, 1999; Carswell et al., 2000; Niinemets, 2001; Pillar and Sosinski Jr., 2003; Moles et al., 2004; Wright et al., 2004, 2007, 2010, 2017; Kirkup et al., 2005; Scweingruber and Landolt, 2005; Kerkhoff et al., 2006; Poorter and Bongers, 2006; Sack and Frole, 2006; Domingues, Martinelli and Ehleringer, 2007; Müller et al., 2007; Cornwell et al., 2008; Kraft, Valencia and Ackerly, 2008; Reich et al., 2008; Royal Botanic Gardens (Kew), 2008; Chave et al., 2009; Craine et al., 2009; Fyllas et al., 2009; Kattge et al., 2009; Poorter, 2009; Poorter et al., 2009; Reich, Oleksyn and Wright, 2009; Wirth and Lichstein, 2009; Zanne et al., 2009; Baraloto et al., 2010; Messier, McGill and Lechowicz, 2010; Powers and Tiffin, 2010; Onoda et al., 2011, 2017; Swenson, Anglada-Cordero and Barone, 2011; Blonder et al., 2012; Choat et al., 2012; De Araujo et al., 2012; Gallagher and Leishman, 2012; Higuchi et al., 2012; Vergutz et al., 2012; Martínez-Garza, Bongers and Poorter, 2013; Adler et al., 2014; Slot et al., 2014; Atkin et al., 2015; Falster et al., 2015; Forgiarini et al., 2015; Maire et al., 2015, 2016; Paine et al., 2015; Neuschulz et al., 2016; Bahar et al., 2017; Hietz et al., 2017; Iversen et al., 2017; Kearsley et al., 2017; Chacón-Madrigal et al., 2018; Rodrigues et al., 2018; USDA, 2009) were supplemented with additional values obtained from the Botanical Information and Ecology Network (BIEN) trait database (Han et al., 2005; Kraft and Ackerly, 2010; Westbrook et al., 2011a, 2011b; Mayor, Wright and Turner, 2014a, 2014b; Price et al., 2014, 2015; Letcher et al., 2015, 2016; T. S. Kraft et al., 2015; Balzotti et al., 2016a, 2016b; Kraft et al., 2016) which were used to fill in missing values in the TRY dataset where possible. Trait data from the BIEN database were obtained using the *BIEN* R package (Maitner, 2022; Maitner et al., 2018). Additional functional trait values were obtained from a tropical tree dataset gathered from the BCNM (S. J. Wright, personal communication). A number of unpublished datasets were also the source of trait values and were publicly accessible through the TRY and BIEN databases. Missing values for maximum height, leaf compoundness and leaf phenology, which were not found in the TRY or BIEN database, were obtained from plant floras accessed through World Flora Online (WFO, 2023) and the Smithsonian Tropical Research Institute Portal (STRI, 2023). We used additional datasets with information on tree diameters, i.e. data from our secondary forest chronosequence census (Dent, DeWalt and Lopez, 2020), the 50-ha forest dynamics plot (Condit et al., 2019b) and 65 plots across the isthmus of Panama (Condit et al., 2013; Condit et al., 2019a), to replace TRY and BIEN maximum diameter values when the database values were lower than the Panamanian datasets, as these locally measured values were not included in the pantropical databases.

3.3.2.3 Species classifications

All trees, palms and shrubs ≥ 5 cm DBH were classified as either generalists, secondary forest specialists, old-growth specialists or too rare to classify according to a multinomial model (Chazdon et al., 2011) in Chapter 2. These classifications were used in further analyses here to test if the abundance-derived classifications also have a functional basis.

3.3.2.4 Phylogeny

A phylogeny was constructed for all 318 species censused in the secondary forest chronosequence and subsampled old-growth plots using the *V.PhyloMaker* R package (Jin and Qian, 2019). We built the phylogeny using the mega-tree `GBOTB.extended.tre` provided by Jin and Qian (2019) which combined, and updated, trees created by Smith and Brown (2018) and Zanne et al. (2014). All species nomenclature was standardised according to The Plant List (TPL, 2013) to match the nomenclature used in the mega-tree. We used the `*phylo.maker*` function and scenario `*S3*` to generate our phylogenetic tree (Figure S3.1). Three species (*Lindackeria laurina*, *Trichospermum galeottii*, *Stylogyne turbacensis*; 132 individuals) were unable to be bound to the tree, as they were not included in the mega-tree and had no close relatives (at the genera level) within our dataset. This phylogeny was constructed to allow missing trait data imputation in subsequent stages of the analysis.

3.3.3 Data cleaning

The data obtained from the TRY and BIEN databases (Kattge et al., 2020; Maitner et al., 2018) were cleaned prior to analysis, following Díaz et al. (2016). Duplicate trait values (i.e., identical values from the same source) were first removed from the dataset. Next, trait values which were derived from senesced leaves or from non-dry seeds and diaspores for the seed dry mass trait were also removed, as these values would likely add uncertainty into the dataset. Leaf lamina toughness values were simplified to only include those measured as the “work to shear the leaf/leaf thickness (J/m^2)” in the dataset, to allow consistency among measurement techniques. Trait values > 4 standard deviations from their taxonomic group mean were removed (following Díaz et al. (2016)) for all traits, except for maximum height and diameter, as these values were deemed likely to be incorrect measurements or data transcription errors rather than extreme true values. Maximum height and diameter values were checked separately by plotting the values against each other. The height-diameter relationship was assumed to be close to linear before saturating near the maximum canopy height for the region (Feldpausch et al., 2011). Height-diameter points which did not fit this relationship were examined, with outliers excluded or corrected after cross referencing with maximum height values recorded in plant floras (STRI, 2023; WFO, 2023).

Subsequently, The 10 highest and lowest values for each trait were examined and excluded if deemed erroneous, after cross checking the data with the original data sources and methodology and examining intraspecific trait distributions (following Díaz et al. (2016)). Bivariate relationships between traits were then plotted and any outliers identified were examined for plausibility, and again excluded if necessary. The leaf phenology trait was simplified from "deciduous", "deciduous/evergreen" and "evergreen" categories to "deciduous" and "evergreen" after preliminary investigations revealed "deciduous" and "deciduous/evergreen" species to be functionally similar.

Mean functional trait values were calculated for each species, using all data sources, after cleaning. The cleaned dataset resulted in 88.3 % of species (n = 265) missing < 4 traits per species (Figure S3.2) and most traits had values for > 81 % of species and > 92 % of individuals, the notable exception being leaf phosphorous for which we were missing trait values for > 53 % species and > 43 % individuals (Figure S3.3). Maximum plant height, maximum diameter, leaf compoundness and leaf phenology had no missing values for any species.

3.3.4 Data imputation

Missing trait values were imputed using the *Rphylopars* R package (Goolsby et al., 2017) as it is deemed a robust approach for imputing missing data (Johnson et al., 2021). We used the `*phylopars*` function with the phylogeny constructed through *V.PhyloMaker* to impute missing functional trait values for all species included in the phylogeny. The three species which could not bind to the phylogenetic tree were then combined with the phylogenetically imputed dataset. This combined dataset was then imputed using the *mice* R package (van Buuren and Groothuis-Oudshoorn, 2011) and the random forest approach, as recommended in Johnson et al. (2021), to fill in missing leaf area values for the three species not bound to the phylogenetic tree. After trait imputation, and due to high degrees of missing data, leaf phosphorous content was excluded from further analyses, as imputation with high proportions of missing data is often inaccurate (Johnson et al., 2021). Pearson's correlation coefficient values were calculated between all functional traits, after imputation (Figure S3.4).

3.3.5 Statistical analysis

Firstly, we examined if our trees and saplings differed in trait space by conducting a principal component analysis (PCA) on the functional traits. Traits were log-transformed and standardised by their mean and variance prior to the PCA. The PCA was then used to group similar species into clusters using the hierarchical clustering on principal components method through the 'HCPC' function in the *factoextra* R Package (Kassambara and Mundt, 2020). The optimal number of clusters to divide species into was identified as being four, through using the 'fviz_nbclust' function and the 'silhouette' method (Kassambara and Mundt, 2020). Changes in the abundance of species within each cluster were analysed by modelling binomial generalised linear mixed models (logit-link) against plot basal area (i.e., summed tree basal areas per plot), with plot as a random effect to account for unmeasured environmental variables (random intercept only; Table S3.1). Plot basal area was used as a predictor variable instead of stand age, as stand age is highly correlated with plot basal area (r^2 = 0.967, $P < 0.001$) and using plot basal area allowed inclusion of old-growth plots in analyses (as old-growth plots cannot be aged accurately). Thus, plot basal area can be seen as being analogous to stand age. Plot basal area was multiplied by a correction factor for one 120-year-old plot, Pearson, as only 0.88-ha was surveyed for this plot. Plot biomass was considered as an alternative to plot basal area, with biomass values calculated using the *BIOMASS* R package (Réjou-Méchain et al., 2017). We used the 'summaryByPlot' function (Réjou-Méchain et al., 2017) and a generic height-diameter model (through providing individual plot coordinates via the 'coord' argument (equation 7 in Chave et al., 2014)) to calculate per plot biomass values. Plot biomass and plot basal area were strongly linked and were found to have a significant quadratic relationship (Figure S3.5; $P = 0.006$). Due to the strong relationship between basal area and biomass (Figure S3.5), we chose to conservatively continue analysing basal area alone (see Chazdon et al., 2007) to avoid propagating uncertainty into our subsequent models due to the use of Pantropical allometric equations (Chave et al., 2014).

We then calculated community weighted mean (CWM) functional trait values for all plots using mean species trait values. We weighted CWMs by both species' abundance (CWM_{sp}) and basal area (CWM_{BA}) and calculated these for trees (DBH ≥ 5 cm) and saplings (1 – 5 cm DBH) separately. Sapling CWM_{BA} were not analysed further, as the size class cut off made the basal area weighting a poor indicator of plant performance as there was an upper bound to individual sapling basal areas. Each functional traits' CWM values were analysed separately against plot basal area. We used a mixture of linear regressions, gamma-distributed generalised linear models (GLMs) and weighted least squares regressions to examine the effect of plot basal area and size class on the CWMs (Tables S3.2, S3.3). The choice of model was made after examining model residuals (using the *DHARMa* package (Hartig, 2022)), checking modelling assumptions and finding the best fitting model using an AICc approach (Burnham and Anderson, 2004). We considered a model with AICc ≤ 2 lower than competing models to have considerably more support (Burnham and Anderson, 2004). CWMs weighted by species abundance were analysed for both saplings and trees, and so these models included a size class interaction term with plot basal area (Table S3.3). Post-hoc analyses of the models were conducted using the *emmeans* R package (Lenth, 2023) when significant trends were found in the predictor variables (Table S3.4). The impact of trait imputation on CWMs was tested by analysing only the data with complete cases for $\mathrm{CWM_{SP}}$, and no significant differences in relationships were found between the imputed and complete case results (results not shown). Thus, all subsequent analyses are conducted solely on the imputed dataset.

Leaf compoundness and leaf phenology are categorical traits, and thus they were converted into proportions prior to analysis, i.e. the proportion of compound-leaved species per plot and the proportion of deciduous species per plot. Leaf compoundness and leaf phenology were modelled against plot basal area, interacting with size class (Table S3.5, S3.6), using beta regressions from the *betareg* R package (Cribari-Neto and Zeileis, 2010) as the proportions were bounded between 0 and 1. Understorey trees/shrubs (n = 1098; maximum height < 10 m) were removed from the leaf phenology data before modelling, as understory trees and shrubs are unlikely to be deciduous (100 % were evergreen in our data) due to understory species typically investing highly in shade-tolerant, long-lived leaves (Poorter and Bongers, 2006). Differences between deciduous and evergreen species traits were examined using pairwise Wilcoxon tests, with P values adjusted for multiple comparisons by controlling for the false discovery rate to reduce type I and type II errors (Verhoeven et al., 2005). Differences in CWMs between secondary and old-growth plots were also examined using pairwise Wilcoxon tests with adjusted P values.

Mean species trait values were also examined in terms of species classifications, i.e. generalist, secondary forest specialist, old-growth specialist, or ‘too rare to classify’ species (Chapter 2, Chazdon et al., 2011). We again used a standardised PCA to examine if different species classifications differed across trait space. We also analysed differences in functional trait values between species classifications using one-way ANOVAs (Table S3.7) and Tukey post-hoc tests when significant differences were found (Table S3.8). Leaf area and seed dry mass were log transformed prior to analysis. Species classification analyses were only conducted on trees ≥ 5 cm DBH as the multinomial classification, which separated trees into classes, was conducted on this subset of the data in Chapter 2.

Functional diversity metrics were computed using the *mFD* R package (Magneville et al., 2022). We used the ‘alpha.fd.multidim’ function to extract six functional diversity metrics (functional dispersion, functional richness, functional divergence, functional evenness, functional specialisation and functional originality – see Villéger et al. (2008), Mouillot et al. (2013b) and Table S3.9 for definitions) based on the multidimensional functional trait space generated from our trait matrix, and weighted by species abundance (Magneville et al., 2022). Seed dry mass and leaf area were log transformed prior to generating the diversity metrics. These metrics were extracted for each size class (trees/saplings) and analysed against the interaction of plot basal area and size class using beta regressions (logit-link) and the *betareg* package (Cribari-Neto and Zeileis, 2010). Differences between old-growth and secondary forest functional diversity metric values were analysed using pairwise Wilcoxon tests with adjusted *P* values.

All analyses were conducted in R version 4.2.2 (R Core Team, 2022) with data cleaning completed using the *tidyverse* collection of packages (Wickham et al., 2019). Mixed models were fitted using *glmmTMB* (Brooks et al., 2017).

3.4 Results

12,910 individual trees (≥ 5cm) and 16,484 individual saplings (1 – 5 cm) were included in our analysis; with 227 species found in both the tree and sapling size class, 41 species found only in the sapling size class and 50 species found only in the tree size class.

PCA axes 1 and 2 encompassed 51.0 % of the variation in species trait values (Figure 3.1). The first axis is mainly characterised by a shift in species with high SLA and low lamina toughness on the left-hand side, to taller, larger diameter species with tougher leaves on the right-hand side (Figures 3.1, S3.6, S3.7). The second axis is also characterised by maximum plant height and leaf lamina toughness (Figure S3.7), but leaf nitrogen content is the most well represented by the axis (Figure S3.6), and high leaf nitrogen content species can be found at the top of the graph (Figure 3.1). The third PCA axis, which encompasses 15.4 % of variation, is primarily defined by a trade-off between high wood density and high leaf area (Figures S3.6, S3.8). We do not see clear distinctions between size related plant traits and leaf economic spectrum related traits as they interact on the same axes (Figure 3.1).

Hierarchical clustering divided tree and sapling species into four clusters based upon their functional traits (Figure 3.1, Table S3.10). Cluster 1 is characterised by small stature, small leaved species, with high SLA, small seeds, and low lamina toughness (Figure 3.1, Table S3.10). Cluster 2 also contains high SLA species, but these species predominately have high nitrogen content leaves, and they are larger stature, with large seeds and low lamina toughness, leaf area and leaf thickness (Figure 3.1, Table S3.10). In contrast, species in Cluster 3 are not related to tree size traits but instead are species with high lamina toughness, wood density and leaf thickness but low leaf nitrogen content and SLA (Figure 3.1, Table S3.10). Cluster 4 species are also associated with low SLA and leaf nitrogen content, but they also have larger maximum height, DBH and leaf area and lower wood density (Figure 3.1, Table S3.10). Despite these differences in functional traits, and thus life history strategies between species, we see no significant changes in the abundance of species belonging to any cluster with plot basal area (Figure S3.8; Table S3.1) and thus no changes through succession (as plot basal area is used as a proxy for stand age; r^2= 0.967). There are trends of species associated with Clusters 3 and 4 increasing in abundance with plot basal area, whereas Clusters 1 and 2 decline slightly, which is in line with successional theory, however, this trend is not significant (Figure S3.9; Table S3.1).

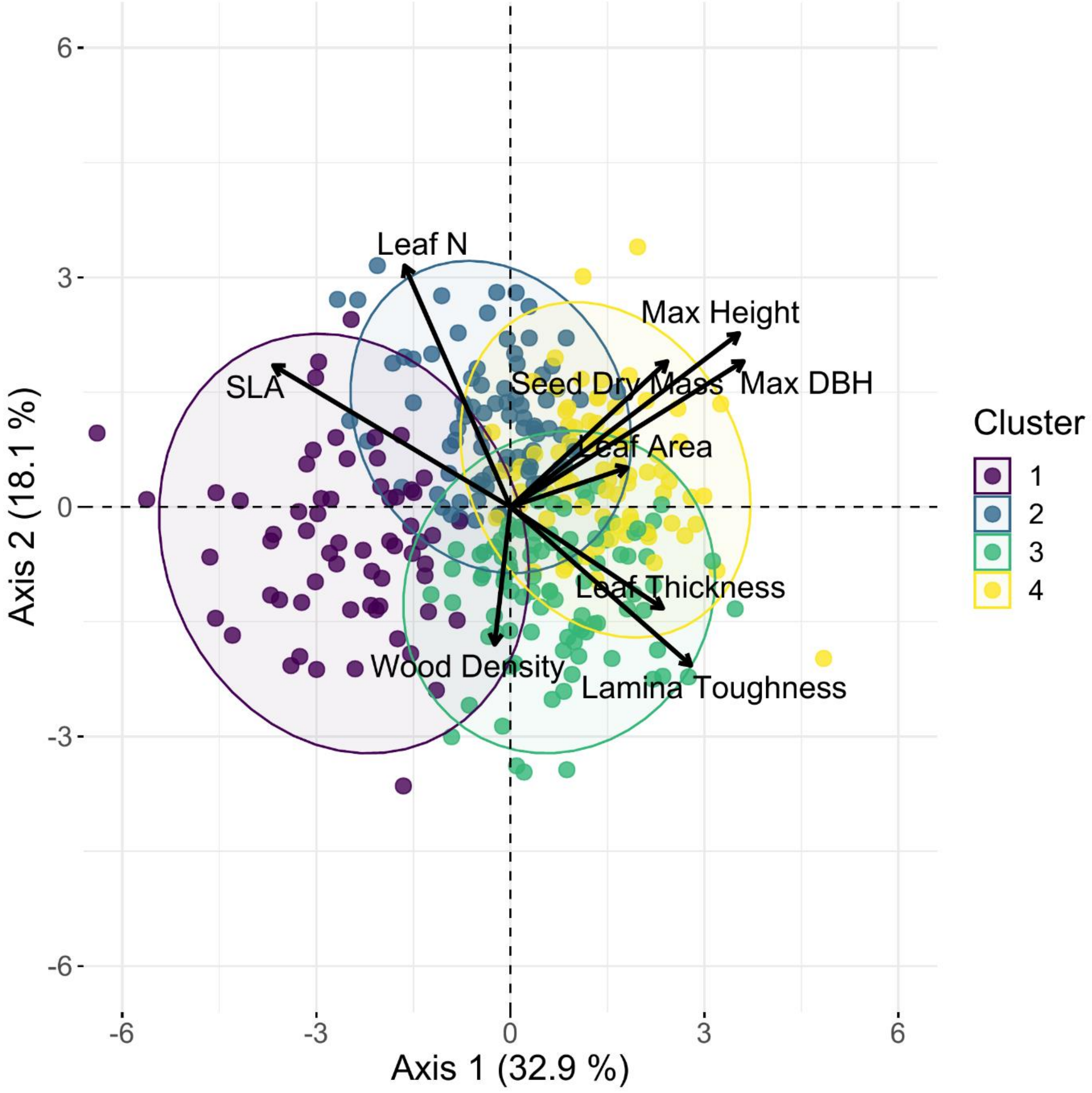

Figure 3.1. Principal Component Analysis results showing species classified by their functional traits into distinct clusters.

3.4.1 Community Weighted Means

Basal area weighted CWMs showed significant shifts with plot basal area, and thus throughout succession, for three of the nine continuous functional traits investigated (Figure 3.2, Table S3.2). Large-statured species with high maximum height and diameter ($P < 0.001$ and $P = 0.001$, respectively) increased in basal area with increasing plot basal area, and thus stand age (Figure 3.2G, 3.2H). Old-growth plots also contained species with significantly greater maximum height than secondary forest plots (*Wilcoxon rank sum test* (*df* = 5, 8): *P* = 0.019), although high basal area secondary forest plots were often similar (Figure 3.2G). Mean seed dry mass increased with plot basal area (*P* = 0.037, Figure 3.2F), suggesting that the basal area of late-successional animal dispersed tree species increased over succession. No leaf trait showed any significant relationship with increasing plot basal area (Figure 3.2, Table S3.2). However, a trend of decreasing SLA with increasing plot basal area was apparent (Figure 3.2), and old-growth plots had significantly lower SLA than secondary forests (*Wilcoxon rank sum test* (*df* = 5, 8): *P* = 0.002). Moreover, leaf thickness was significantly higher in old-growth plots (*Wilcoxon rank sum test* (*df* = 5, 8): *P* = 0.019).

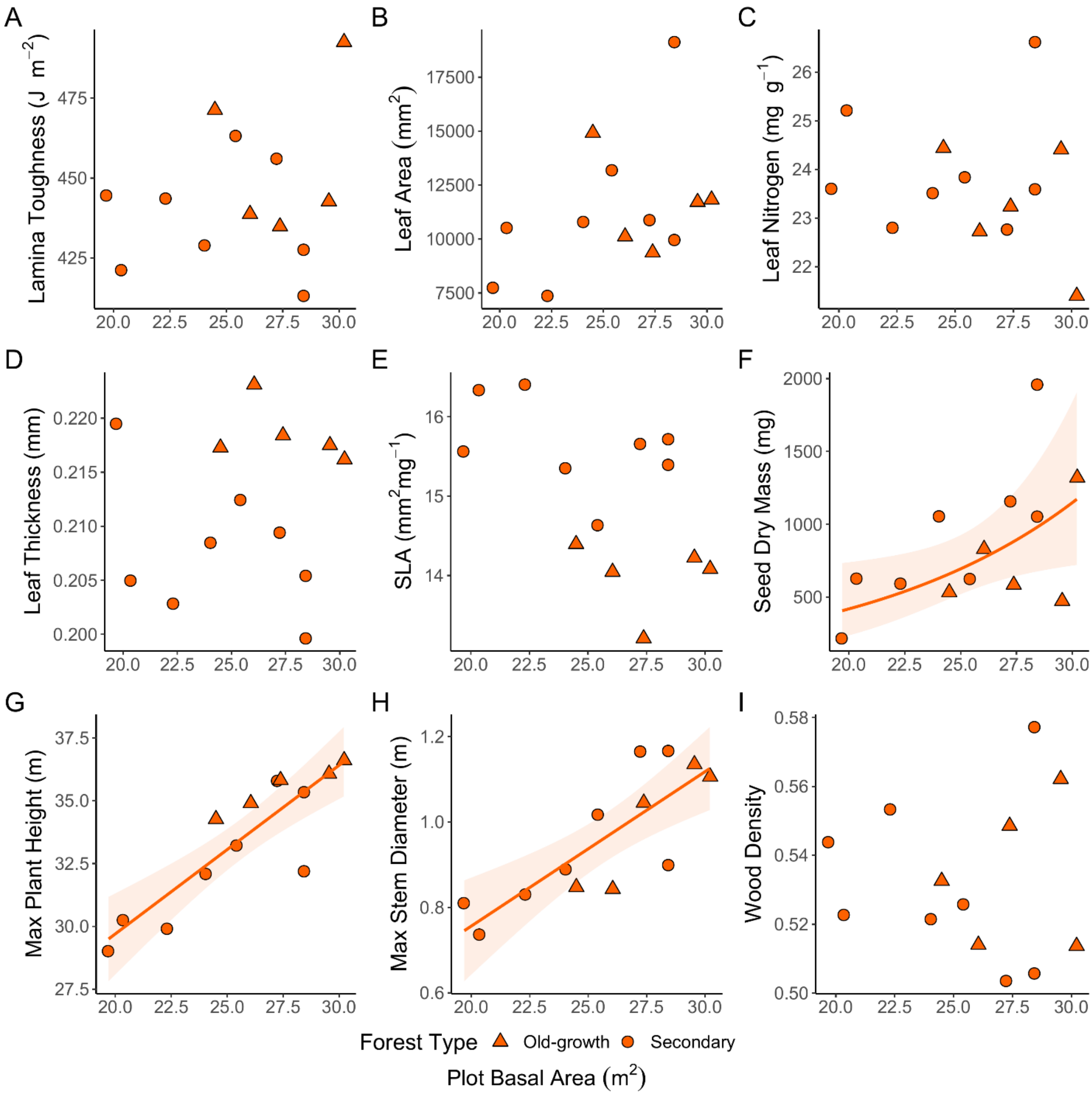

Figure 3.2. Basal area community weighted mean values per functional trait plotted against plot basal area. Only trees, palms or shrubs ≥ 5 cm DBH are included. Significant relationships are indicated by the solid lines, with orange shading indicating 95% confidence intervals.

Fewer relationships were found for CWMs weighted by species abundance and some relationships were distinct between sapling and tree communities (Table S3.3, Figure 3.3). Maximum plant height (P = 0.042) and maximum stem diameter (P = 0.030) CWMs again increased with plot basal area, and thus increased through succession (Figures 3.2 and 3.3, Table S3.3). There was no significant interaction between maximum plant height/maximum stem diameter and size class (Table S3.3), but post-hoc tests revealed that increases in sapling mean functional trait values mainly drove the significant relationships with plot basal area for maximum plant height and stem diameter (Table S3.4, Figure 3.2G, 3.2H). Seed dry mass showed no relationship with plot basal area, when CWMs were weighted by species abundance (*P* = 0.415), and no leaf traits showed any relationship with basal area, and thus stand age, for either trees or saplings (Figure 3.3). However, leaf nitrogen content was significantly lower in old-growth compared to secondary forest plots (*Wilcoxon rank sum test* (*df* = 5, 8): *P* = 0.006) and leaf thickness was significantly higher in old-growth plots (*Wilcoxon rank sum test* (*df* = 5, 8): *P* = 0.019). Wood density showed no relationship with plot basal area for either CWM measurement (Figure 3.2I, Figure 3.3I).

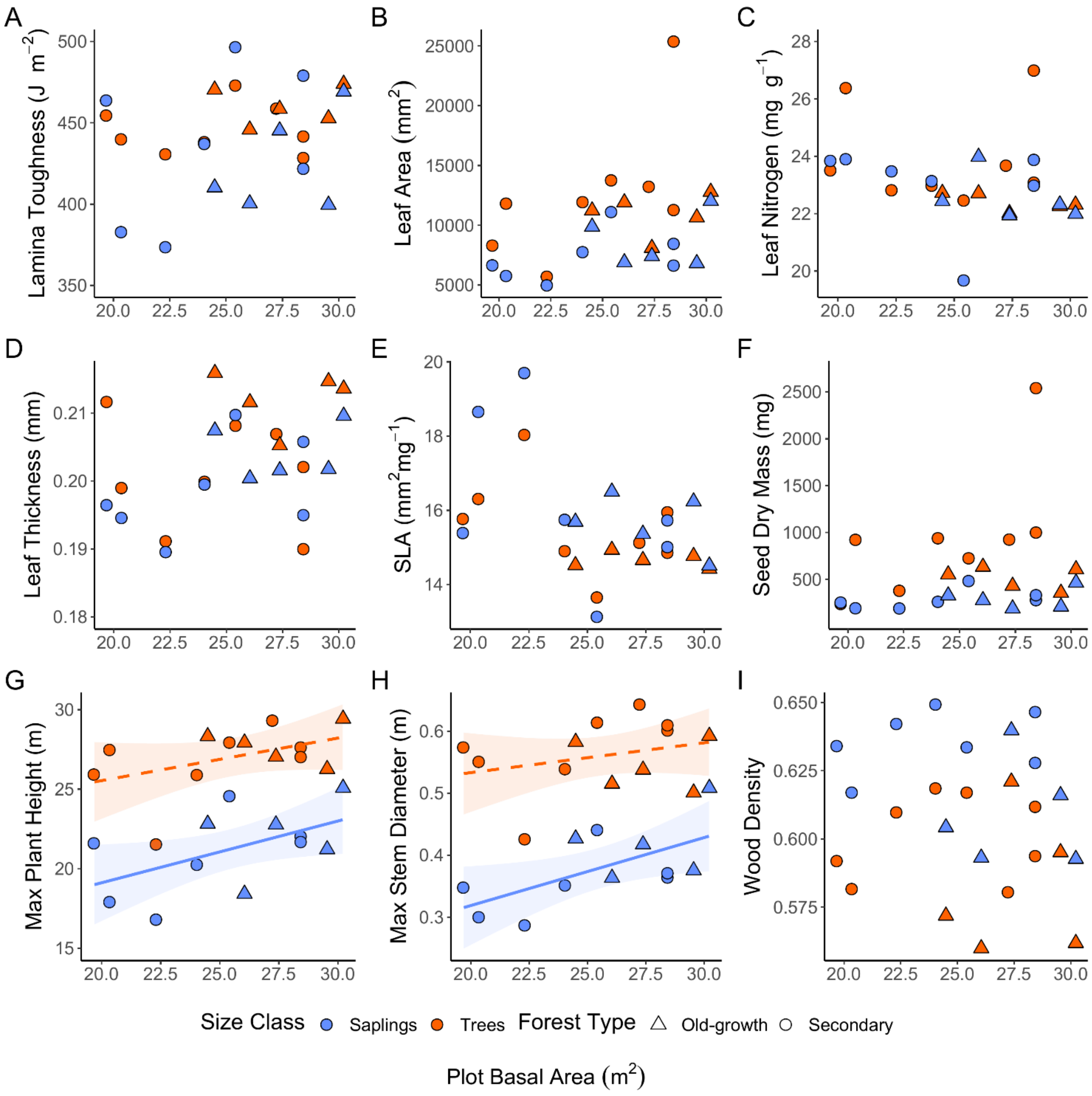

Figure 3.3. Species abundance weighted community weighted mean values per functional trait plotted against plot basal area. Trees, palms or shrubs (≥ 5 cm DBH) are indicated in orange and saplings/shrubs (1-5cm) are indicated in blue. Significant relationships are indicated by the solid lines, with shading indicating the 95% confidence intervals. Non-significant trends are indicated by dashed lines.

3.4.2 Categorical Functional Traits

Deciduousness varied significantly with plot basal area (Figure 3.4). The proportion of deciduous species did not vary overall with plot basal area (Table S3.5; *P* = 0.260) but plot basal area significantly interacted with size class (Table S3.5; *P* = 0.002) and trees were more likely to be deciduous than saplings (Table S3.5; *P* < 0.001). The proportion of deciduous trees declined from almost 15% of all tree species, to just 5.6 – 8.7 % of trees in the highest basal area plots (Figure 3.4, Table S3.6; *P* < 0.001) but there was no significant relationship for saplings (Figure 3.4, Table S3.6; *P* = 0.257). Deciduous tree species were associated with higher mean leaf nitrogen content (*P* < 0.01, Figure S3.9), specific leaf area (*P* < 0.001, Figure S3.10), maximum diameter (*P* < 0.001, Figure S3.10) and maximum height (*P* < 0.001, Figure S3.10), and lower lamina toughness (*P* < 0.05, Figure S3.10), than evergreen tree species. The proportion of species with compound leaves showed no relationship with plot basal area for trees or saplings (Table S3.3, Figure 3.4).

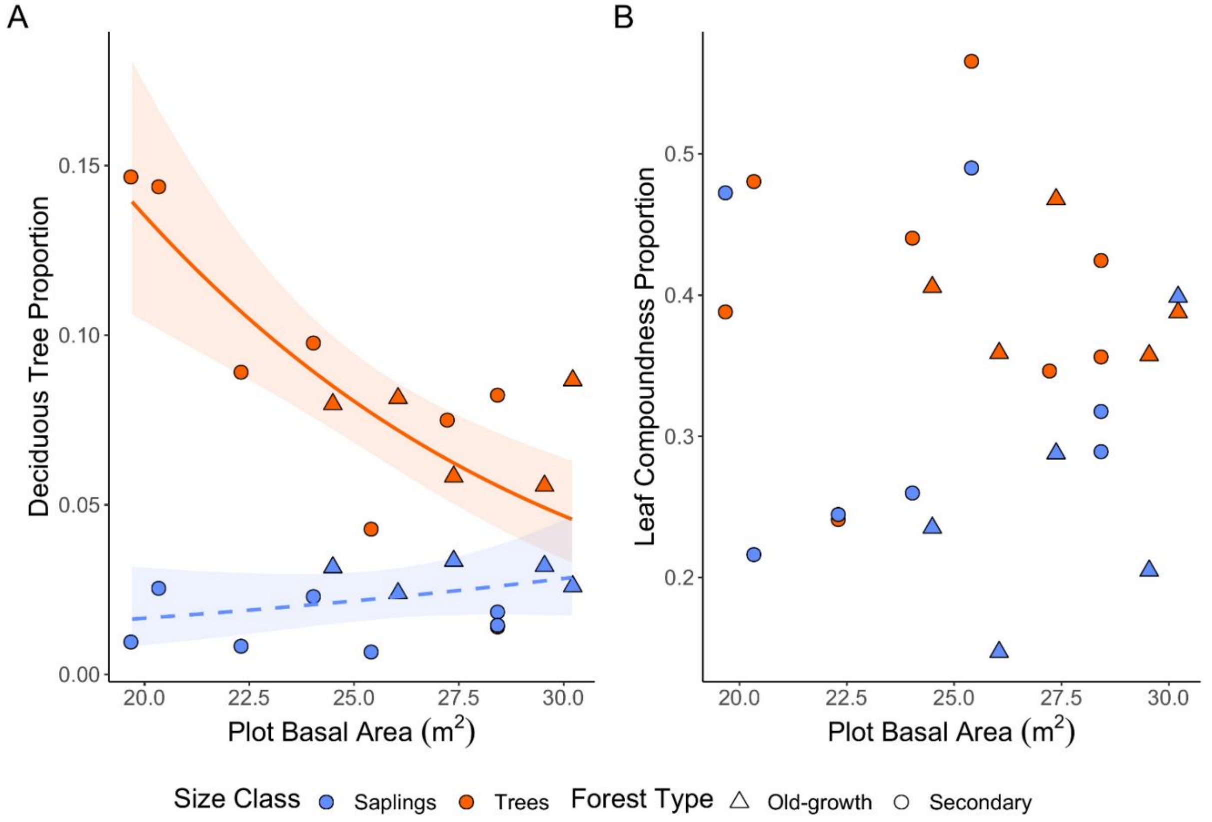

Figure 3.4. Leaf categorical traits, as a proportion of individuals within each site, plotted against plot basal area. Only trees with a maximum height > 10 m are plotted and modelled for deciduous trees (A). Significant effects are indicated by solid lines, with 95 % confidence intervals indicated by the shading. Non-significant trends are indicated by dashed lines.

3.4.3 Functional diversity

No metric of functional diversity showed any relationship with plot basal area, and thus with successional recovery (Figure S3.11, Table S3.11). We also found no difference between functional diversity metric values for saplings or trees (Table S3.11) and there were no significant interactions between size class and plot basal area (Table S3.11). When we compared secondary to old-growth forests, only functional richness was significantly lower in secondary forest plots (*P* < 0.001, Figure 3.6), which is likely linked to the lower species richness of secondary forest plots compared to old-growth forest (see Chapter 2). In support of this we find significant correlations between functional richness and species richness for both trees (*P* < 0.001, r^2= 0.820) and saplings (*P* < 0.001, r^2= 0.827). The lack of trends in functional diversity suggests that most metrics of functional diversity have likely recovered early in succession, and so we no longer see patterns of recovery beyond 40-years after land abandonment.

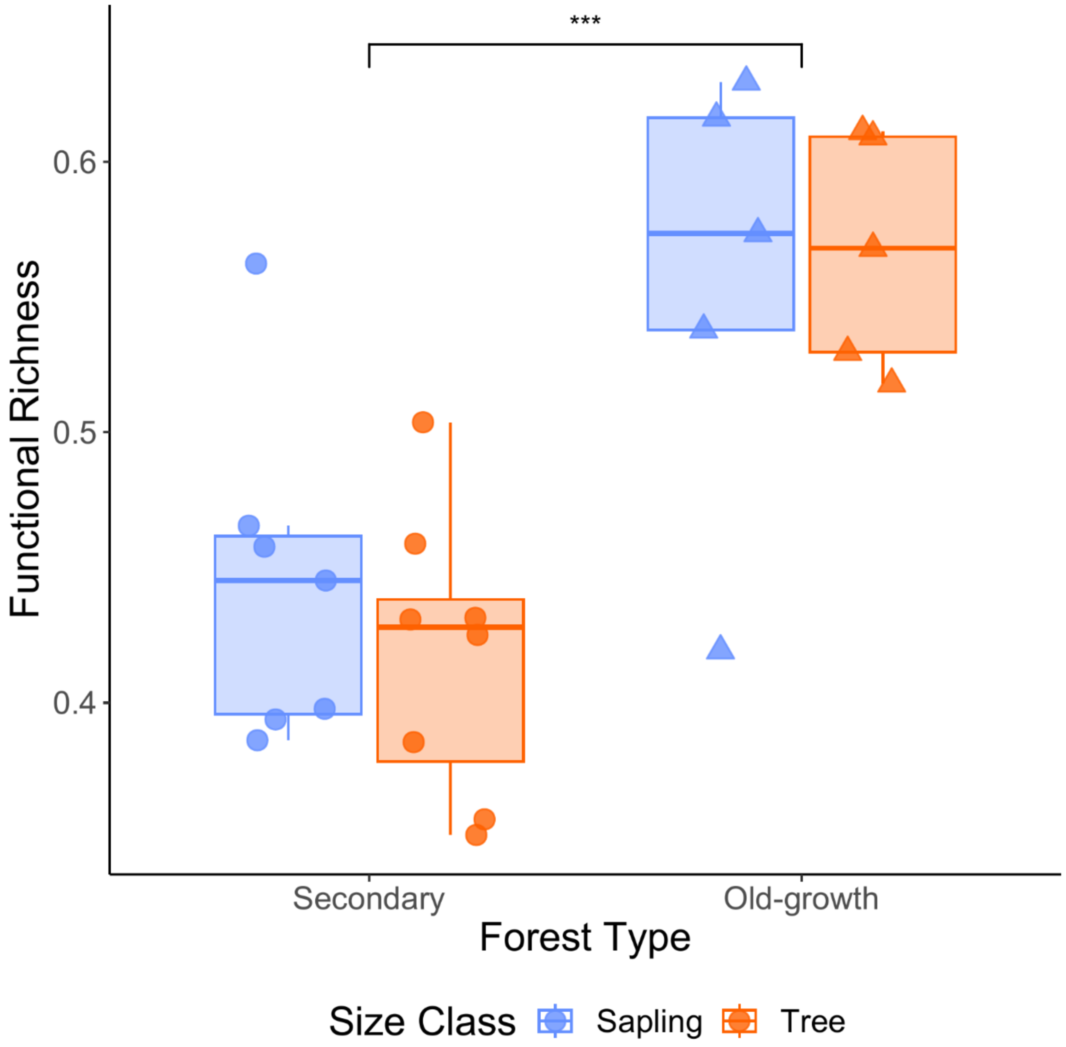

Figure 3.5. Boxplot showing the difference in median functional richness values between secondary and old-growth forest for sapling and tree communities. The asterisks indicate a significant difference between old-growth and secondary forest, irrespective of size class (*P* < 0.001).

3.4.4 Species classifications and outliers

The four species classifications (generalist, old-growth specialist, secondary forest specialist and too rare to classify; Chapter 2) were very similar in terms of trait space occupied in the PCA (Figure

3.6A). However, some trends were still evident: old-growth specialists tended to be larger stature species, with thick leaves and low wood density, which is mostly confirmed by the ANOVA analyses (Tables S3.7, S3.8; Figure S3.12). Secondary forest specialists did not tend to differ from generalists in their functional traits (Figure 3.6A), and no significant differences were found when comparing functional trait species means (Table S3.8, Figure S3.12). Rare species were found to have lower maximum heights than generalist and old-growth specialist species, and lower maximum diameters and wood density than generalist species (Table S3.8, Figure S3.12). The PCA suggests that rare species are also more associated with high SLA (Figure 3.6A), and this trend is supported by the higher proportion of rare species within Cluster 1, which was characterised by high SLA species (Figure 3.6B; Table S3.9). Cluster 1 also has low proportions of generalist and specialist species (Figure 3.6B) which suggests that species within this cluster are in low abundance throughout the chronosequence and are perhaps pioneer species. The highest proportion of old-growth specialists are found in Cluster 4 (Figure 3.6B), which was associated with species with conservative leaf traits and large stature individuals. No differences were found among species-level leaf trait means for any species classification (Figure S3.11).

In Chapter 2, we showed that one 120-year-old plot, Barbour, had much lower diversity, species richness and similarity to old-growth than expected. Functionally however, this taxonomic separation is less evident. Although Barbour can still be seen as an outlier in terms of leaf area, leaf nitrogen content and seed dry mass (the outlier with high functional trait values and high basal area; Figures 3.2 and 3.3), all other traits were very similar to other plots with similar basal areas. These outlier traits are likely because *Gustavia superba* (Figure S3.13), the species which dominates Barbour, has higher leaf nitrogen content (> 93.4 % of species), leaf area (> 97.2 % of species) and dry seed mass (> 98.4 % of species) than the majority of species censused. However, Barbour shows no evidence of deviating from the other plots in any functional diversity metrics (Figure S3.11).

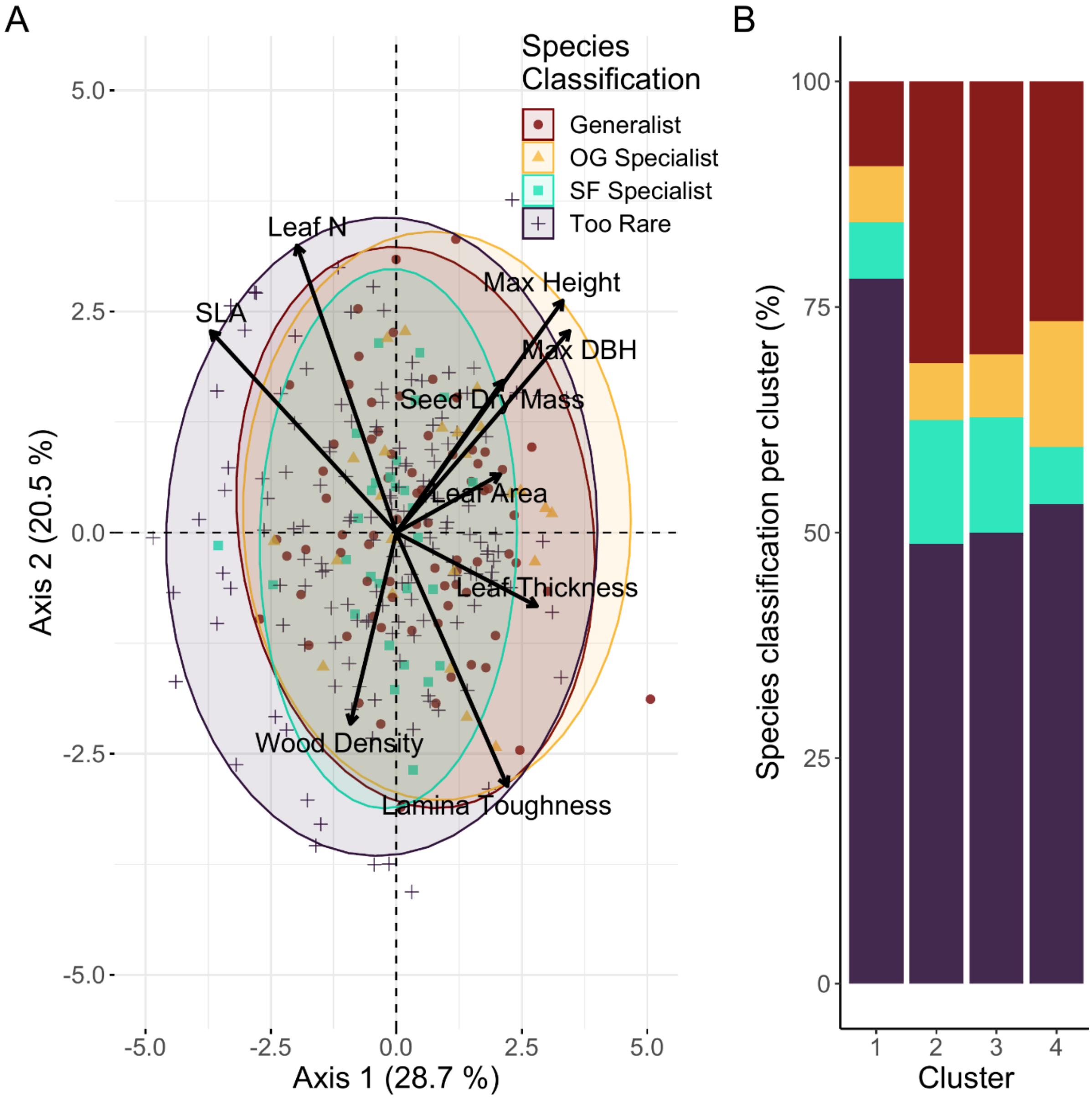

Figure 3.6. Graphs of the relationships between the multinomial model abundance-based classifications and functional traits. **A**: Principal Component Analysis results showing species grouped by the multinomial species classification. **B**: Proportion of species within each cluster assigned to each multinomial model-based classification. Only individuals ≥ 5cm are included in this analysis, to match the classifications exactly from Chapter 2. The abundance-based classifications used here are generalist (red), old-growth specialist (yellow), secondary forest specialist (turquoise) and too rare to classify (purple).

3.5 Discussion

Contrary to our hypotheses, we found little change in functional traits associated with the fast-slow continuum (Reich, 2014; Wright et al., 2004) over mid-to-late succession, apart from the decline in deciduous trees (Figure 3.4), and many of our leaf traits and wood density had recovered to old-growth levels by the midpoint of the chronosequence (Figures 3.2 and 3.3). However, SLA (for $\mathrm{CWM}_{\mathrm{BA}}$), leaf nitrogen content (for $\mathrm{CWM}_{\mathrm{SP}}$) and leaf thickness (for both CWM) values still differed between old-growth and secondary forest, indicating an incomplete recovery of leaf functional traits (Figures 3.2 and 3.3). Stature related plant traits (i.e., maximum height, maximum diameter, and seed mass) differed from leaf traits and continued to increase into late succession (Figures 3.2 and 3.3). We identified functional trait clusters relating to the fast-slow continuum and the plant stature axis (Figure 3.1) but found no significant trends in the representation of these groups over succession (Figure S3.9). We found no relationships between functional diversity and increasing plot basal area (Figure S3.11), but functional richness was higher in old-growth compared to secondary forests (Figure 3.5). Our results suggest that moist tropical forests can rapidly recover in terms of function, and that functional traits appear to recover more quickly than species identity; in Chapter 2 as we found that community composition was still recovering 120 years into succession.

3.5.1 Functional strategies and key traits

There were no significant relationships between plot basal area and any leaf trait associated with the fast-slow continuum (SLA, leaf nitrogen content, leaf area, leaf thickness, leaf lamina toughness) for community means weighted by basal area or species abundance, and for both tree and sapling communities (Figures 3.2 and 3.3). Previous studies have found support for leaf traits shifting from acquisitive to conservative strategies over succession in wet tropical forests (Boukili and Chazdon, 2017; Lohbeck et al., 2013; Muscarella et al., 2016; Poorter et al., 2021b) but we did not find this pattern. However, we did see turnover in certain species associated with pioneer strategies as the proportion of adult deciduous trees declined with forest age (Figure 3.4). Deciduous trees are often pioneer species (Ouédraogo et al., 2013; Popma et al., 1992) with higher leaf nitrogen content and SLA, and lower leaf toughness than evergreen trees (Eamus, 1999; Poorter and Markesteijn, 2008; Pringle et al., 2011). We saw a decline in abundance of adult deciduous trees but not saplings, which could be an indication of pioneer species dying out in the 40- and 60-year-old plots. Short-lived pioneers typically die out within the first 30-years of succession (Finegan, 1996) but the deciduous trees in our plots may also be associated with long-lived pioneer strategies. We found that deciduous tree species had higher leaf nitrogen content and SLA and lower lamina toughness than evergreen species (Figure S3.10), confirming the association between the deciduous life history strategy and rapid resource acquisitive leaf traits (Eamus, 1999; Poorter and Markesteijn, 2008; Pringle et al., 2011). We also found a positive relationship between large plant stature and deciduousness (Figure

S3.10), which was previously reported in tropical dry forest in Puerto Rico (Lasky et al., 2016) and seasonal moist forest in the Congo basin (Loubota Panzou et al., 2018; Réjou-Méchain and Cheptou, 2015). Deciduous trees may be larger, on average, than evergreen trees in our study system because they invest more carbon into stem growth, as they are photosynthetically more efficient than evergreen trees (Reich et al., 1992), and do not invest as much carbon into deep root systems (Hasselquist et al., 2010), due to higher water use efficiency and the avoidance of water loss during the dry season. The higher size related traits could also indicate that some deciduous species are long-lived pioneers, that typically persist later into succession and often have high growth and survival rates, but low recruitment success (Rüger et al., 2018). Thus, the lens of leaf phenology gives us an insight into ongoing change in species groups in the later stages of succession.

Changes in the light environment over tropical forest succession may explain the lack of a relationship between leaf traits and plot basal area. During the first 10 years of succession available light reaching the forest understory decreases over seven-fold (Lebrija-Trejos et al., 2011), and soon after 15-years, the forest canopy closes and, whilst light availability is heterogeneous, ongoing changes in light availability are minimal (Nicotra, Chazdon and Iriarte, 1999; Denslow and Guzman, 2000; Montgomery and Chazdon, 2001; Lebrija-Trejos et al., 2011). Thus, low light availability becomes a strict environmental filter which acts from 10 – 20 years into succession and affects new seedling, sapling, and small tree establishment. The 40 – 120-year-old forests in our chronosequence likely have low light availability in the understory, and as a result most species recruiting into the canopy are likely light-limited, and will have slow, conservative resource acquisition strategies (*sensu* Reich, 2014; Wright et al., 2004). The exceptions are species growing in canopy gaps, which are known to maintain short-lived pioneer species abundance (Schnitzer and Carson, 2001) and are found throughout succession, but in low densities (Mascaro et al., 2012). In support of this, we found that the rare species, from our classification in Chapter 2, were disproportionately represented by species with fast resource acquisition related traits. By mid-succession the majority of short-lived pioneer have died out (Finegan, 1996), and so other environmental or biotic filters are potentially more important than shifting light availability as succession progresses beyond 40 years. The low abundance of short-lived pioneers within our plots also explains the lack of a relationship between wood density and plot basal area in our chronosequence. Wood density tends to increase over succession in wet and moist tropical forests (Poorter et al., 2019; Poorter, Rozendaal, et al., 2021) but appears to saturate after 40-50 years (Poorter et al., 2021). This coincides with when low wood density pioneer species die off and are replaced by long lived species, which tend to have higher wood density (Muller-Landau, 2004). We have likely missed this period of species and wood density turnover in our chronosequence, due to our youngest plots (40 years since land abandonment) already approaching the mid-stages of succession.

Despite the lack of significant relationships between plot basal area and stand age, differences remain between old-growth and secondary forest plots for some leaf traits (Figures 3.2. and 3.3). We found a negative trend in $\mathrm{CWM}_{\mathrm{BA}}$ SLA with plot basal area (Table S3.2; $P = 0.053$) and old-growth plots had significantly lower SLA than secondary forest plots. Leaf thickness was also significantly higher in old growth plots for both $\mathrm{CWM}_{\mathrm{BA}}$ and $\mathrm{CWM}_{\mathrm{SP}}$, although mean differences were only 0.01 mm, and leaf nitrogen content was significantly lower in old-growth plots (Figures 3.2 and 3.3). This suggests that successional recovery may still be ongoing for some leaf traits during the chronosequence, and that full recovery of leaf traits is unlikely within the first 40 years of succession. The different results between CWMs weighted by basal area and those weighted by species abundance also highlights the importance of utilising multiple approaches to capture functional trait changes over time. For instance, there is no significant difference between old-growth and secondary forest SLA when examining $\mathrm{CWM}_{\mathrm{SP}}$ ($P = 0.065$), which may indicate that low SLA species have increased in abundance through succession but are not yet dominant in terms of basal area in the secondary forest plots. This might be expected, as even shade-intolerant species can persist for c. 150 years in wet tropical forest (Köhl et al., 2017) and thus $\mathrm{CWM}_{\mathrm{BA}}$ values will likely turnover more slowly through succession than $\mathrm{CWM}_{\mathrm{SP}}$.

Plant stature appears to increase over the chronosequence; maximum plant height and maximum plant diameter increase with plot basal area, and thus with successional age (Figures 3.2 and 3.3). Maximum height and diameter increase in tandem, because these traits are highly correlated ($r = 0.77$ in our study; Figure S3.4), and tall trees require large diameters to be physically stable (see Poorter, Bongers and Bongers, (2006)). Other successional studies have reported similar patterns (Craven et al., 2015; Muscarella et al., 2016). For example, in plots aged 0 to c.50 years old in Panama, CWMs of maximum diameter increased with plot basal area, and thus succession (Craven et al., 2015) and in Puerto Rico, CWM maximum height increases over 90 years of wet tropical forest succession (Muscarella et al., 2016), but only for trees 1 – 10 cm DBH, potentially because ongoing hurricane disturbance prevents similar stratification in height for adult trees (DBH > 10 cm). We also found that saplings drove increases in maximum height and maximum diameter over time for $\mathrm{CWM}_{\mathrm{SP}}$ (Table S3.4), indicating that the tree species found in the sapling community, that have the potential to reach the canopy, are increasingly comprised of large stature species. Our sapling classification (DBH 1 – 5 cm) also included understory trees and shrubs which will never reach the forest canopy, so changes in the maximum height of this size class could also be indicative of shifts in the abundance of understory species, perhaps in relation to increased light heterogeneity in the later stages of succession (Chazdon, 2014). Our findings suggest that the plant stature axis (Díaz et al., 2016; Kambach et al., 2022; Maynard et al., 2022; Rüger et al., 2018) is of key importance in mid-to-late successional and old-growth forests where it appears to explain species turnover better than fast-slow continuum related traits. Plant height may be the primary mechanism by which canopy species compete for light in late succession, rather than adaptive leaf strategies, since the vast majority of individuals establish in low light conditions (e.g. Poorter et al., 2005). Taller tree species intercept more light than small tree species (Poorter et al., 2005), and often have higher relative growth rates, and lower mortality rates (Poorter et al., 2008). Thus, these patterns may indicate shifts in demography, as well as canopy height, as succession progresses. Tree height has been linked to changes in ecosystem function, with increasing tree height associated with increases in proxies of ecosystem productivity, energy use and carbon nutrient cycling in temperate forests across the USA (LaRue et al., 2019), as well driving increases in above-ground biomass (Ali et al., 2019). Thus, with evidence for increasing maximum height and diameter into late succession, we are likely seeing ongoing shifts in ecosystem function. We see evidence for this within our chronosequence, as above-ground carbon stocks, and large diameter necromass, increase up to 120 years into succession (Jones et al., 2019)

Seed dry mass (CWM_{BA}) increased with plot basal area (Figure 3.2), indicating a delayed impact of increasing light limitation as succession progresses. Large seeds are more stress tolerant than small seeds and higher seed mass is linked to increased seedling survival due to increased carbon and nutrient stores (King et al., 2006c; Moles et al., 2004; Muller-Landau, 2010). Larger seeds are also related to increased dispersal distances, primarily due to increased plant height (Thomson et al., 2011), which suggests that patterns of dispersal are also changing through succession in our plots, in tandem with the successional changes for height and seed mass. Increased availability of larger seeds suggests that animal seed dispersal increases in importance through succession, and larger bodied species are likely to become more important dispersal agents (e.g. due to potential gape-size limitation Rehling et al. (2021)). Estrada-Villegas et al. (2022b) confirmed this relationship in earlier censuses of the BCNM chronosequence (aged 20 – 100 years); flightless mammals and large birds dispersed a greater proportion of tree species' seeds as succession progressed. The BCNM has a relatively intact mammal population (Wright et al., 2000), as it is protected from poaching, but 50 % of the world's tropical forests are estimated to be partially mammal defaunated (Benítez-López et al., 2019). As such, our finding that seed mass increases into the late stages of succession, may not occur in many regenerating forests due to local species extirpation (Markl et al., 2012).

3.5.2 Species Clusters and Classifications

We identified four distinct functional clusters (Figure 3.1), which were associated with different aspects of the fast-slow continuum and stature-recruitment axes. Cluster 1 was associated with fast leaf traits, low seed mass, and small stature, perhaps indicating short-lived pioneer species, which may still be present in our late-stage successional forest in canopy gaps. Cluster 3 was associated with slow, conservative leaf traits and high wood density. Therefore, Clusters 1 and 3 likely represent species along the fast-slow continuum in our chronosequence, represented by the leaf-economic spectrum (Reich, 2014; Wright et al., 2004) and the wood economic spectrum (Chave et al., 2009). Cluster 2 appears likely related to long lived pioneers or deciduous species strategies, as the associated traits are all fast leaf traits combined with high maximum height and diameters (Pringle et al., 2011; Rüger et al., 2018). Cluster 4 is associated with large stature species, with conservative leaf traits, and is likely indicative of large, shade tolerant old-growth specialists. However, there were no significant changes in the representation of these clusters through succession (Figure S3.9), suggesting functional recovery early on in our chronosequence. Many of our clusters include both stature and fast-slow continuum related traits suggesting that we do not see a clear separation between stature and resource acquisition related traits, unlike Maynard et al. (2022). The species clusters are not clearly delineated along the fast-slow axis and all but one cluster are defined by stature, which suggests that importance of fast-slow continuum in shaping tree communities declines into late succession while plant stature increases in importance.

In Chapter 2, we found differences among species classifications through succession with a greater number of rare species in old growth forest, and ongoing recovery of old-growth specialists in older secondary forest plots. However, there were minimal differences in functional traits between these classifications, with no differences in leaf traits but some variation in wood density between old-growth and secondary forest specialists (Figure S3.12). This results contrasts with Boukili and Chazdon (2017), who found that old growth specialists had lower leaf nitrogen and leaf phosphorous content and higher wood specific gravity than both generalist and secondary forest specialist species in a lowland wet forest in Costa Rica. However, these Costa Rican forests were aged 10 – 42 years (Boukili and Chazdon, 2017) and so captured earlier stages of succession than our plots (aged > 40 years). The rare species classification had lower stature than generalist and old-growth specialist species (Figure S3.12), and were more associated with cluster 1 (i.e., short-lived pioneers; Figure 3.6), while cluster 4 was more associated with old-growth species (i.e., species that are both large-stature and associated with slow leaf traits). Thus some rare species tended to be short-lived pioneers that occupy the infrequent gaps found in old secondary forest (Mascaro et al., 2012; Schnitzer and Carson, 2001), and the old-growth specialists are more likely to be tall, conservative species. More generally, the lack of differences in functional traits associated with the fast-slow continuum between classifications further suggests that light availability does not continue to drive differences in community composition between old-growth and old secondary forests (see Chapter 2). The lack of functional differences among the species classifications may be due to low sampling area and it might be informative to explore whether expanding the plots used to inform the multinomial species classification model, e.g. to nearby old-growth forests (Ibáñez et al., 2002), increases the functional separation among species classifications (Chazdon et al., 2011). Moreover, the relatively low sampling area may mean that not all the rare species identified in Chapter 2 are truly rare species, i.e. species found at low abundance across the entire BCNM. Instead, some of the species classified as ‘too rare to classify’ will likely be secondary or old-growth specialists or generalists which were found in low abundance, by chance, in our plots, as 1-ha plots sampled at a single time point can miss

> 20 % of the entire species assemblage (Chazdon et al., 2023). Thus, expanding the sampling area may help to elucidate differences among our species classifications, especially for rare species.

3.5.3 Functional diversity

Functional diversity metric values showed no relationship with basal area, suggesting that forest functional diversity has recovered, and saturated prior to the start of the chronosequence (Figure S3.11). This result appears to differ from several successional studies: Warring et al. (2016) found functional richness and functional dispersion, but not functional evenness, to increase through succession in the Atlantic Forest, Brazil; Whitfeld et al., (2014) found functional richness increases throughout succession in Papua New Guinea, but no pattern in functional evenness or divergence; WenSheng, RunGuo and Yi, (2014) found functional richness to increase from the early stages to the late stages of succession in Chinese tropical forest; and Lasky et al. (2014) found lower functional diversity in mid-aged successional stands compared to old-growth in wet tropical forest, Costa Rica. However, many of these changes occur in early succession, and if we look only at the mid stages of succession (40 – 60 years) reported in these same studies, many functional diversity metrics have stabilised to values comparable to old-growth (Lasky et al., 2014; Warring et al., 2016; WenSheng, RunGuo and Yi, 2014; Whitfeld et al., 2014). Therefore, it seems likely that functional diversity commonly reaches old-growth values by the mid stages of succession, or even earlier (Craven et al., 2018).

Our functional diversity results mirror early recovery of species diversity in the chronosequence (See Chapter 2). This is likely because there is a strong positive relationship between functional diversity and species richness/diversity (Biswas and Mallik, 2011; Lohbeck et al., 2012; Petchey and Gaston, 2002). Indeed only functional richness was significantly higher in old-growth than secondary forest (Figure 3.5) reflecting the higher species richness of old-growth forests (Cornwell, Schwilk and Ackerly, 2006; Biswas and Mallik, 2011; see Chapter 2). The early recovery of functional diversity suggests that older tropical forests may have functional redundancy, which can increases resilience of ecosystem processes to perturbation (e.g. Pillar et al., 2013), but further work would be necessary to confirm this.

3.5.4 Caveats

There are several caveats associated with this analysis. First, the relatively few changes in community weighted means we find over succession could also be partially related to data limitations. We used data from global databases (for leaf traits, seed mass and wood density), rather than data measured *in situ* (Kattge et al., 2020, 2011; Maitner et al., 2018). This may mean that the averaged traits included in the study are not fully representative of the growing conditions in the chronosequence. However, previous studies have found that traits from the global databases are tightly correlated with *in situ* trait measurements. For example, a study examining herbaceous species in Mediterranean fields found only one of nine functional traits studied differed in mean value between the TRY dataset and locally collected trait values (Kazakou et al., 2014). Furthermore, the Barro Colorado Nature Monument is incredibly well studied, and many of the studies included in the global databases collected data from our study region of Panama (e.g. Sack and Frole, 2006; Craven et al., 2007; Wright et al., 2010; Westbrook et al., 2011; Mayor, Wright and Turner, 2014b; Slot et al., 2014; Kraft et al., 2016; Hietz et al., 2017). Therefore, it is likely that the trait data from the global databases are accurate for our study species.

Second, the use of global databases to obtain functional trait data limited us to interspecific analyses, and we could not investigate intraspecific trait variation through succession. Intraspecific phenotypic plasticity in leaf traits can be high, for example between high-light and shade conditions some leaf traits vary considerably (e.g. SLA, leaf nitrogen content) while others do not (e.g. leaf toughness and leaf size), and shade-tolerant species tend to have higher plasticity in their response to light than pioneer species (Rozendaal et al., 2006). However, our functional trait estimates are likely robust given that interspecific variation in functional traits explains the majority of trait variance (Siefert et al., 2015) and increasing species richness within a community lowers the importance of intraspecific variation relative to interspecific variation (Siefert et al., 2015).

Throughout our analysis we use a chronosequence approach, as a space-for-time substitution, to examine changes in plant functional traits through succession. Chronosequence approaches have been questioned because the assumption that all plots within a chronosequence experience the same environmental conditions, apart from age, is often violated (Johnson and Miyanishi, 2008; Walker et al., 2010). Indeed, Poorter et al., (2021b) found no trends in 60 – 70 % of 190 chronosequences they examined for plant functional trait recovery through succession and suggested this may be caused by initial founder effects varying among chronosequences, and some chronosequences retaining remnant old-growth species in early succession. Ideally, to examine functional recovery through succession we would examine longitudinal data to eliminate the effect of different environmental variables and land-use histories. However, longitudinal data are rarely available for late successional plots, and long-term monitoring of permanent plots is costly (Condit, 1995). Our chronosequence is likely robust to differences among plots, given that it has been undisturbed since land abandonment, and was accurately aged using a mix of aerial photography and local interviews (Denslow and Guzman, 2000).

A further caveat to our analysis is our choice to use plot basal area over stand age to model functional trait changes through succession. Plot basal area is commonly used over stand age to analyse successional change (e.g. Boukili and Chazdon, 2017; Lohbeck et al., 2014) and it often varies very predictably through succession (e.g. Chazdon et al., 2007; Chapter 2). We made the choice to use plot basal area as it allowed us to analyse our secondary and old-growth plots in one model, rather than just using old-growth plots as a comparison, as in Chapter 2. This choice was made as old-growth plots cannot be accurately aged (old-growth forest on BCI is between 400 and 1700 years old (Piperno, 2023)) and we wanted to ameliorate the low sample size of our secondary forest plots (*n* = 8) by including our five old-growth plots. Preliminary investigations into using stand age over plot basal area showed similar results for CWM weighted by basal area. However, due to basal area recovering to old-growth levels in approximately 90 years (see Chapter 2), it could be argued that the late stages of succession would be better represented by models of stand age. Future work building on this chapter will involve investigating how the choice of stand age, basal area or tree biomass affects our models of functional trait recovery through sensitivity analyses.

3.5.5 Implications and conclusions

Our forests in the BCNM, in some ways represent a best-case scenario for forest regeneration in the Neotropics. The BCNM has seen no anthropogenic disturbance since its establishment as a protected area in 1979 (Leigh Jr., 1999; Wright et al., 2000) and therefore, functional trait recovery rates within our plots are likely quicker than in more disturbed landscapes. On the other hand, although there are old-growth seed sources close to our older secondary forest plots, the matrix of water surrounding Barro Colorado Island likely inhibits long distance seed dispersal to the peninsulas (Moore et al., 2008; Mayhew et al., 2019), where old-growth forests are missing (Dent and Elsy, 2023). This lack of seed dispersal may impact the arrival of rare species (See Chapter 2) but appears to have little impact on forest function. Thus, the results from this study should be taken in the context of an undisturbed, but partially fragmented forest landscape.

In conclusion, our results indicate that functional traits associated with the fast-slow continuum have mostly recovered by the beginning of our chronosequence and show little evidence of ongoing shifts with forest age. We also find no change in functional diversity through time. In contrast, we find plant stature related traits, and the correlated seed mass trait, to still be in a process of recovery in our mid-to-late successional secondary forests (aged 40 – 120 years). Rapid recovery in the majority of functional traits is likely important for the recovery of ecosystem function (Funk et al., 2017), but ongoing shifts in stature related traits, and differences between some leaf traits in old-growth and secondary forest, still indicate that our late-stage secondary forests are not fully recovered to old-growth levels, even after 120 years of succession (see Jones et al., 2019). Thus, protection of existing old-secondary forest is imperative in order to enable the plant community to fully recover in terms of ecosystem function.

3.6 Acknowledgements:

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3.7 Supplementary Material

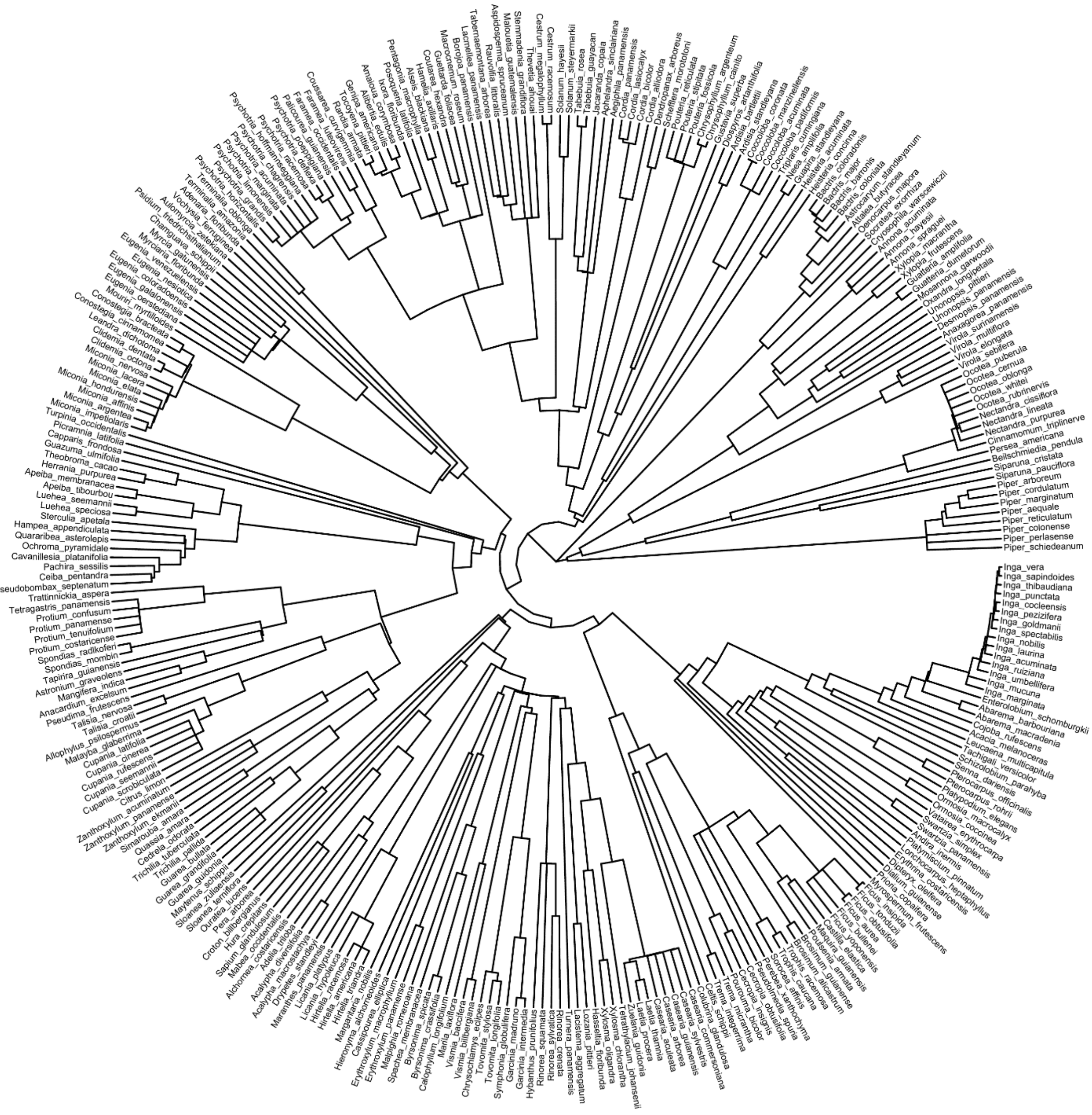


Figure S3.1. Phylogenetic tree of all the tree and sapling species censused in the study. Note three species were not bound to the tree (*Lindackeria laurina*, *Trichospermum galeottii*, *Stylogyne turbacensis*) as they were not included in the mega-tree and had no close relatives.

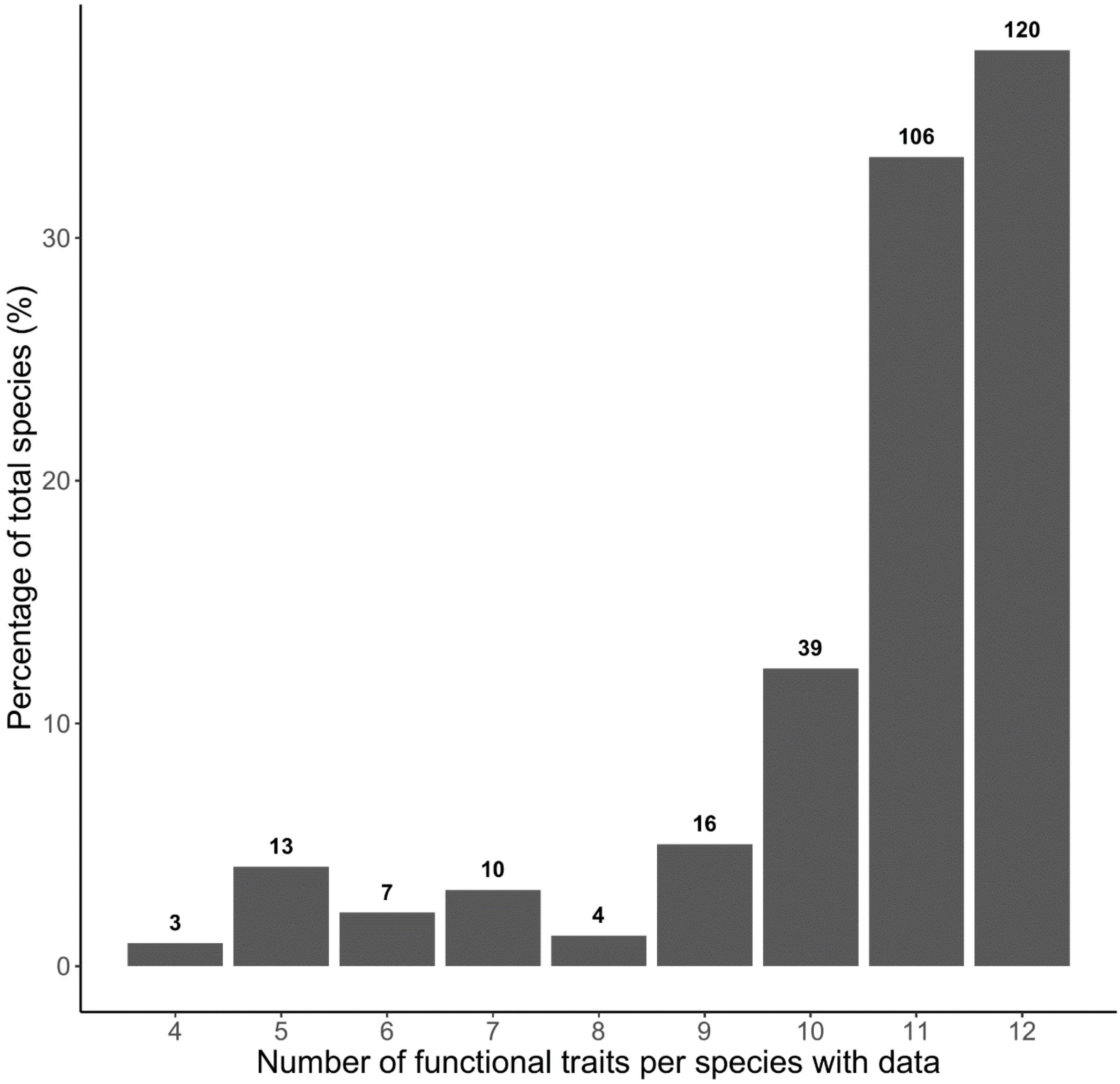


Figure S3.2. The number of functional traits we have values for per species plotted against the percentage of species with that number of traits. The number in bold above each column is the number of species within each column. There are 12 functional traits in the dataset, so those species with 12 functional traits have no missing values.

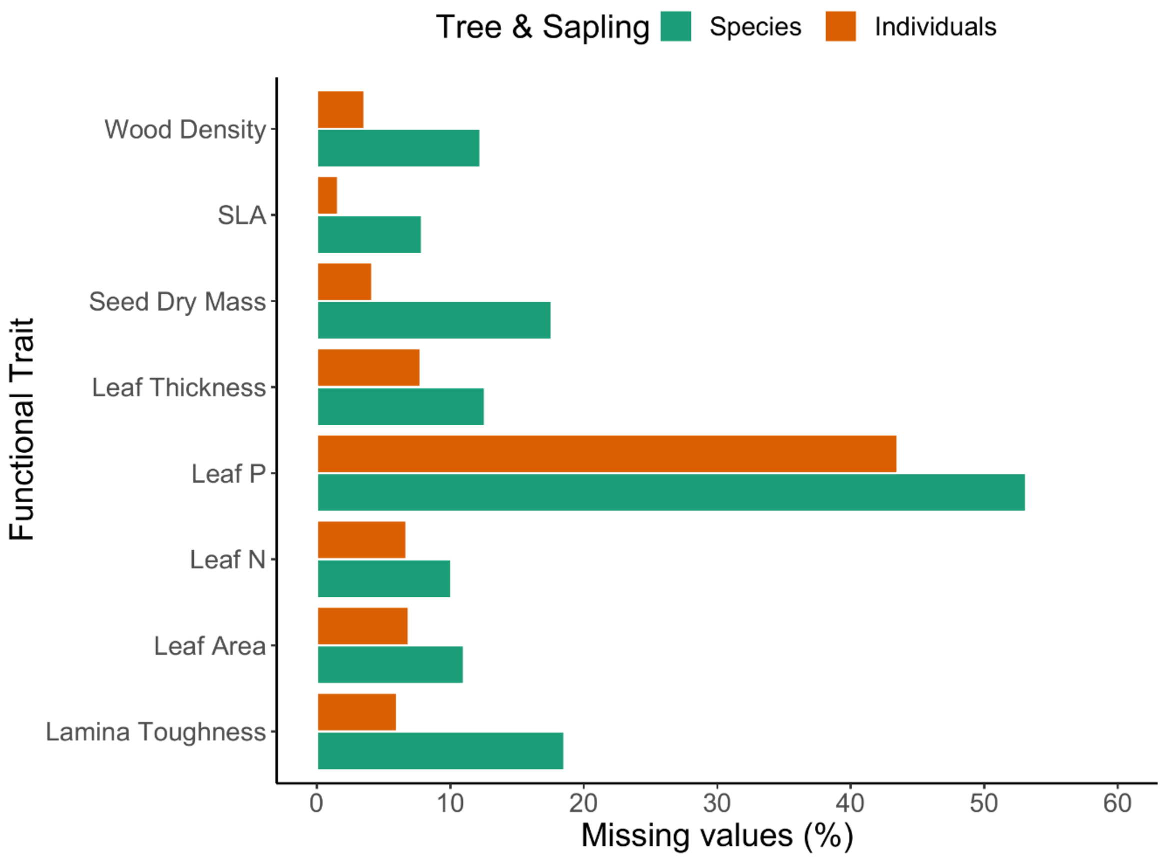
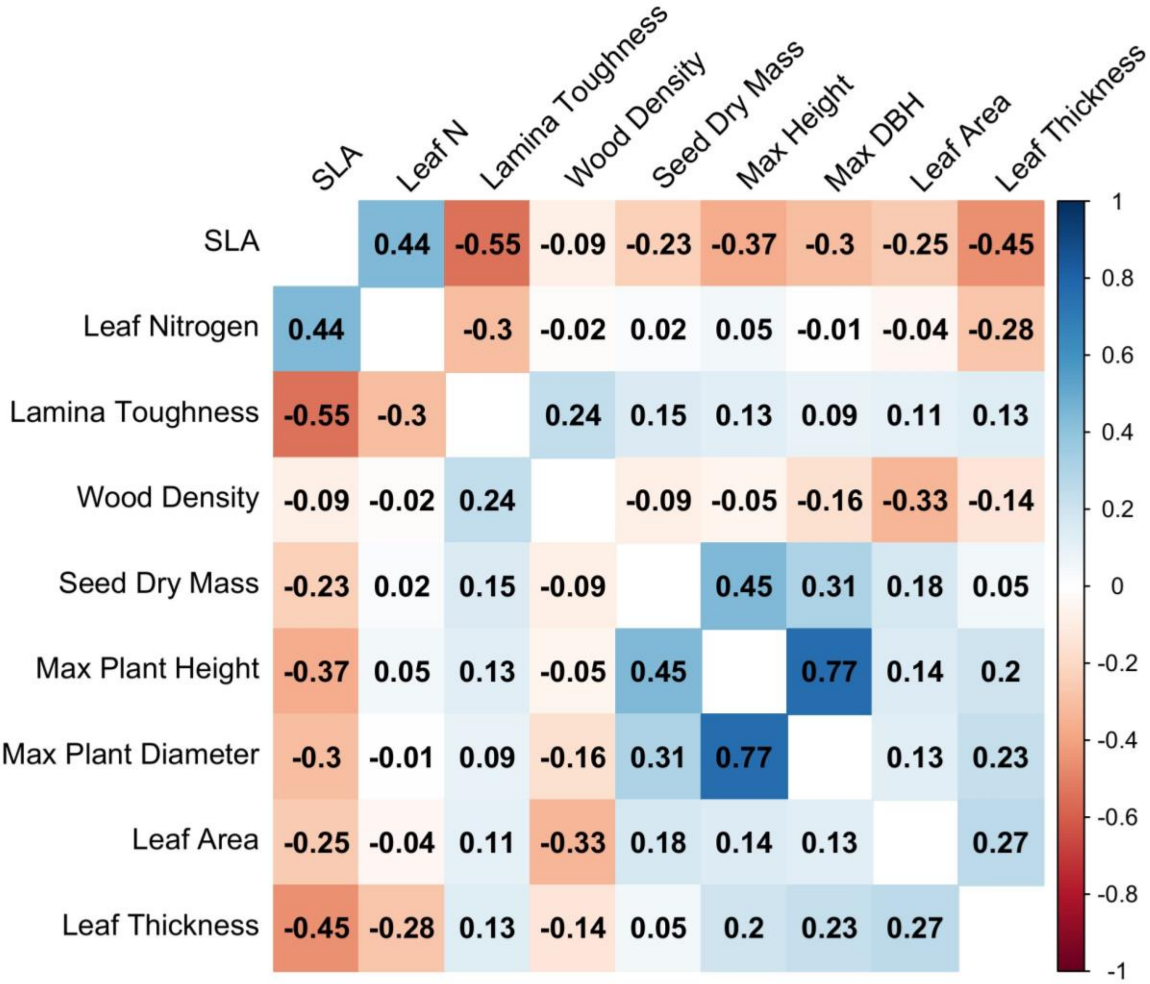


Figure S3.3. The percentage of missing value per functional trait by species and the total number of individuals included in the dataset. The maximum height, maximum diameter, leaf compoundness and leaf phenology traits are not included as they have no missing values.



	SLA	Leaf N	Lamina Toughness	Wood Density	Seed Dry Mass	Max Height	Max DBH	Leaf Area	Leaf Thickness
SLA		0.44	-0.55	-0.09	-0.23	-0.37	-0.3	-0.25	-0.45
Leaf Nitrogen	0.44		-0.3	-0.02	0.02	0.05	-0.01	-0.04	-0.28
Lamina Toughness	-0.55	-0.3		0.24	0.15	0.13	0.09	0.11	0.13
Wood Density	-0.09	-0.02	0.24		-0.09	-0.05	-0.16	-0.33	-0.14
Seed Dry Mass	-0.23	0.02	0.15	-0.09		0.45	0.31	0.18	0.05
Max Plant Height	-0.37	0.05	0.13	-0.05	0.45		0.77	0.14	0.2
Max Plant Diameter	-0.3	-0.01	0.09	-0.16	0.31	0.77		0.13	0.23
Leaf Area	-0.25	-0.04	0.11	-0.33	0.18	0.14	0.13		0.27
Leaf Thickness	-0.45	-0.28	0.13	-0.14	0.05	0.2	0.23	0.27	

Figure S3.4. Pearson correlation coefficient values between pairs of plant functional traits. Positive correlations are indicated in blue and negative correlations are indicated in red.

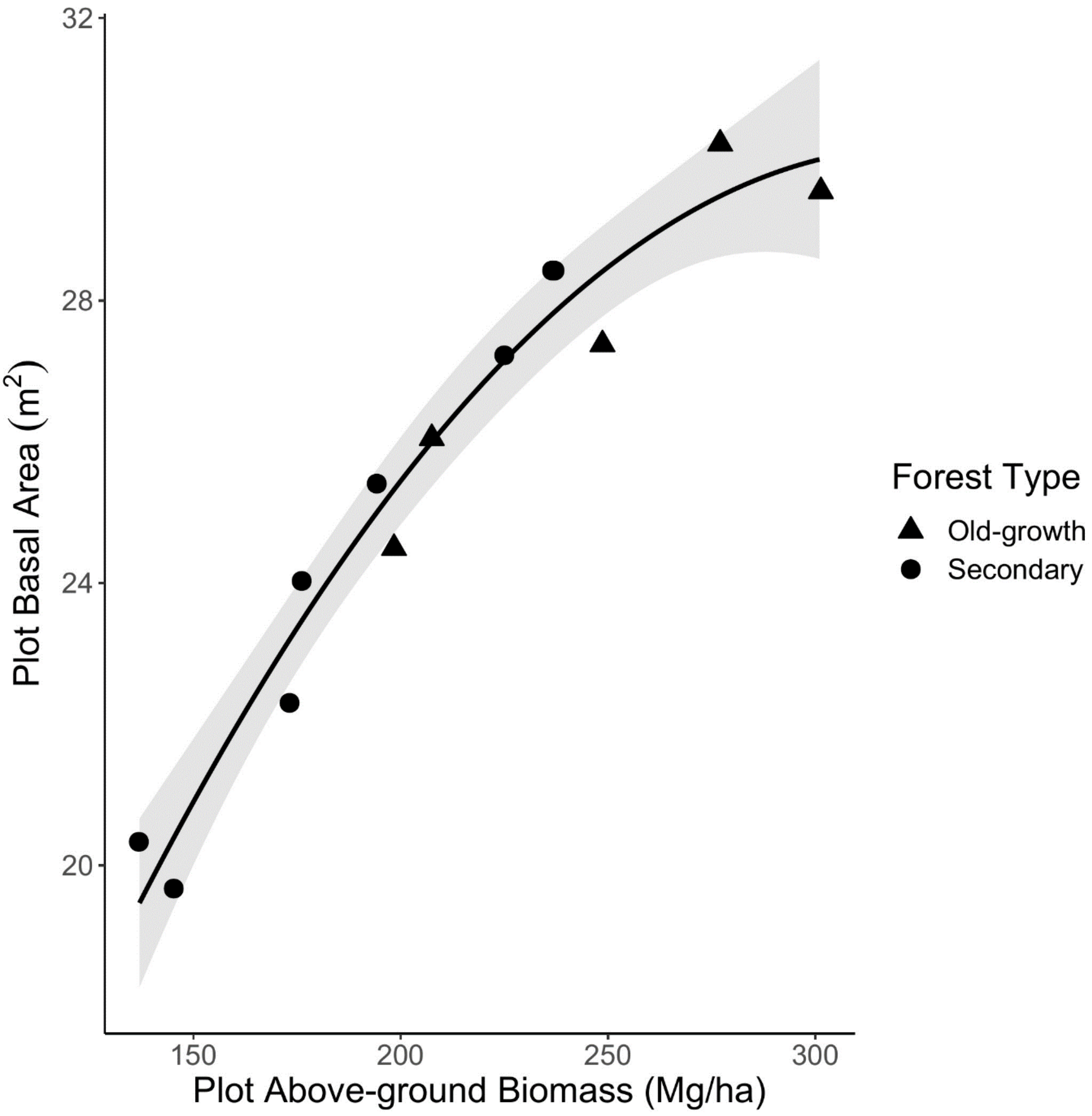


Figure S3.5. Relationship between plot above-ground biomass and plot basal area for all secondary and old-growth forest plots. A significant relationship between biomass and basal area (polynomial regression: Plot Basal Area ~ Plot AGB + (Plot AGB)^2) is indicated by the black line with grey shading indicating 95% confidence intervals on the model prediction. The relationship between basal area and above-ground biomass is polynomial with significant values for AGB ($P < 0.001$) and AGB^2 ($P = 0.006$).

Table S3.1. Model outputs for binomial generalised linear mixed models looking at the effect of plot basal area on the abundance of species in each cluster. *P* values are adjusted for multiple comparisons using the ‘fdr’ method from the ‘p.adjust’ function.

Cluster	**Predictor**	**Estimate**	**Standard error**	***z* statistic**	***P* value**
Cluster 1	(Intercept)	1.462	2.219	0.659	0.680
	Plot Basal Area	-0.133	0.086	-1.551	0.161
	(1|Plot) SD	1.000			
Cluster 2	(Intercept)	0.140	1.032	0.136	0.892
	Plot Basal Area	-0.046	0.039	-1.156	0.247
	(1|Plot) SD	0.464			
Cluster 3	(Intercept)	-1.686	0.805	-2.093	0.073
	Plot Basal Area	0.049	0.031	1.587	0.161
	(1|Plot) SD	0.362			
Cluster 4	(Intercept)	-4.416	1.252	-3.527	0.002
	Plot Basal Area	0.104	0.048	2.149	0.126
	(1|Plot) SD	0.562			

Table S3.2. Linear regressions and generalised linear models (GLM) examining the effect of plot basal area on basal area weighted community weighted mean values for all functional traits. Only individuals ≥ 5 cm were modelled here. Nagelkerke pseudo- R^2 was calculated for the Leaf Area GLM.

Leaf Lamina Toughness (Linear Regression)

Predictors	**Estimates (CI 95%)**	**Statistic**	***P* value**	R^2
(Intercept)	407.972 (299.843 – 516.100)	8.304	< 0.001	0.049
Plot basal area	1.424 (-2.758 – 5.605)	0.749	0.469	

Leaf Area (GLM – Gamma Distribution (log-link))

Predictors	**Estimates (CI 95%)**	**Statistic**	***P* value**	R^2
(Intercept)	4428.128 (1293.286 – 15161.628)	15.014	< 0.001	0.217
Plot basal area	1.037 (0.989 – 1.088)	1.684	0.120	

Leaf Nitrogen Content (Linear Regression)

Predictors	**Estimates (CI 95%)**	**Statistic**	***P* value**	R^2
(Intercept)	25.141 (18.626 – 31.656)	8.494	< 0.001	0.021
Plot basal area	-0.056 (-0.308 – 0.196)	-0.490	0.634	

Leaf Thickness (Linear Regression)

Predictors	**Estimates (CI 95%)**	**Statistic**	***P* value**	R^2
(Intercept)	0.208 (0.171 – 0.245)	12.275	< 0.001	0.006
Plot basal area	0.000 (-0.001 – 0.0012)	0.249	0.808	

Specific Leaf Area (Linear Regression)

Predictors	**Estimates (CI 95%)**	**Statistic**	***P* value**	R^2
(Intercept)	19.052 (14.903 – 23.201)	10.107	< 0.001	0.299
Plot basal area	-0.158 (-0.318 – 0.003)	-2.166	0.053	

Log (Seed Dry Mass) (Linear Regression)

Predictors	**Estimates (CI 95%)**	**Statistic**	***P* value**	R^2

(Intercept)	4.026 (1.780 – 6.273)	3.945	0.002	0.372
Plot basal area	0.101 (0.014 – 0.188)	2.551	0.037	
Maximum Plant Height (Linear Regression)				
Predictors	**Estimates (CI 95%)**	**Statistic**	***P* value**	***R^2***
(Intercept)	16.270 (9.886 – 22.654)	5.609	< 0.001	0.765
Plot basal area	0.672 (0.425 – 0.918)	5.987	< 0.001	
Maximum Plant DBH (Linear Regression)				
Predictors	**Estimates (CI 95%)**	**Statistic**	***P* value**	***R^2***
(Intercept)	0.034 (-0.415 – 0.483)	0.165	0.872	0.656
Plot basal area	0.036 (0.019 – 0.054)	4.579	0.001	
Wood Density (Linear Regression)				
Predictors	**Estimates (CI 95%)**	**Statistic**	***P* value**	***R^2***
(Intercept)	0.535 (0.419 – 0.651)	10.158	< 0.001	0.000
Plot basal area	-0.000 (-0.005 – 0.004)	-0.043	0.967	

Table S3.3. Linear regressions and generalised linear models (GLM) examining the effect of plot basal area and size class on species abundance weighted community weighted mean values for all functional traits. Nagelkerke pseudo- R^2 was calculated for the GLM.

Leaf Lamina Toughness (Weighted Least Squares Regression)

Predictors	Estimates (CI 95%)	Statistic	*P* value	R^2
(Intercept)	347.728 (154.637– 540.820)	3.745	0.001	0.172
Plot basal area	3.284 (-3.781 – 10.349)	0.967	0.345	
Size class (Tree)	73.003 (-142.294 – 288.300)	0.705	0.488	
Plot basal area * Size class (Tree)	-2.096 (-10.001 – 5.808)	-0.552	0.587	

Leaf Area (GLM – Gamma Distribution (log-link))

Predictors	Estimates (CI 95%)	Statistic	*P* value	R^2
(Intercept)	3023.802 (740.305 – 12350.830)	11.844	< 0.001	0.486
Plot basal area	1.038 (0.983 – 1.096)	1.414	0.172	
Size class (Tree)	1.165 (0.160 – 8.482)	0.160	0.874	
Plot basal area * Size class (Tree)	1.010 (0.935 – 1.091)	0.275	0.786	

Leaf Nitrogen Content (Linear Regression)

Predictors	Estimates (CI 95%)	Statistic	*P* value	R^2
(Intercept)	26.004 (19.470 – 32.539)	8.276	< 0.001	0.125
Plot basal area	-0.126 (-0.380 – 0.128)	-1.030	0.315	
Size class (Tree)	0.268 (-8.948 – 9.485)	0.061	0.952	
Plot basal area * Size class (Tree)	0.013 (-0.344 – 0.370)	0.075	0.941	

Leaf Thickness (Linear Regression)

Predictors	Estimates (CI 95%)	Statistic	*P* value	R^2
(Intercept)	0.176 (0.143 – 0.210)	10.626	< 0.001	0.198
Plot basal area	0.001 (-0.000 – 0.002)	1.538	0.139	
Size class (Tree)	0.017 (-0.031 – 0.066)	0.731	0.473	

Plot basal area * Size class (Tree)	-0.000 (-0.002 – 0.001)	-0.549	0.588	
Specific Leaf Area (GLM – Gamma Distribution (log-link))				
Predictors	**Estimates (CI 95%)**	**Statistic**	***P* value**	***R*^{2}**
(Intercept)	23.179 (15.876 – 33.841)	17.273	< 0.001	0.296
Plot basal area	0.985 (0.971 – 1.000)	-2.071	0.051	
Size class (Tree)	0.861 (0.505 – 1.468)	-0.583	0.566	
Plot basal area * Size class (Tree)	1.004 (0.984 – 1.025)	0.408	0.687	
Log (Seed Dry Mass) (Linear Regression)				
Predictors	**Estimates (CI 95%)**	**Statistic**	***P* value**	***R*^{2}**
(Intercept)	4.730 (2.502 – 6.958)	4.415	< 0.001	0.526
Plot basal area	0.035 (-0.052 – 0.121)	0.831	0.415	
Size class (Tree)	0.309 (-2.833 – 3.452)	0.205	0.840	
Plot basal area * Size class (Tree)	0.022 (-0.100 – 0.144)	0.374	0.712	
Max Plant Height (Linear Regression)				
Predictors	**Estimates (CI 95%)**	**Statistic**	***P* value**	***R*^{2}**
(Intercept)	11.360 (1.797 – 20.924)	2.470	0.022	0.727
Plot basal area	0.388 (0.016 – 0.760)	2.172	0.041	
Size class (Tree)	8.837 (-4.651 – 22.326)	1.362	0.187	
Plot basal area * Size class (Tree)	-0.121 (-0.644 – 0.402)	-0.481	0.636	
Max Plant DBH (Linear Regression)				
Predictors	**Estimates (CI 95%)**	**Statistic**	***P* value**	***R*^{2}**
(Intercept)	0.099 (-0.153 – 0.352)	0.820	0.422	0.782
Plot basal area	0.011 (0.002 – 0.020)	2.326	0.030	
Size class (Tree)	0.337 (-0.019 – 0.693)	1.971	0.062	
Plot basal area * Size class (Tree)	-0.006 (-0.020 – 0.008)	-0.927	0.364	

Wood Density (Linear Regression)				
Predictors	**Estimates (CI 95%)**	**Statistic**	***P* value**	***R^2***
(Intercept)	0.661 (0.562 – 0.759)	13.947	< 0.001	0.403
Plot basal area	-0.001 (-0.005 – 0.002)	-0.769	0.451	
Size class (Tree)	-0.053 (-0.192– 0.086)	-0.793	0.437	
Plot basal area * Size class (Tree)	0.001 (-0.005 – 0.006)	0.330	0.745	

Table S3.4. Post-hoc results investigating the estimated marginal means of each size class, and their relationship with plot basal area, for functional traits which were found to have significant plot basal area relationships for the Community Weighted Means (weighted by species abundance). Estimated marginal means were calculated via the *emmeans* R package (Lenth, 2023).

Maximum Plant Height			
Size Class	**Plot basal area trend (CI 95%)**	***t*-ratio**	***P* value**
Tree	0.267 (-0.101 – 0.635)	1.510	0.146
Sapling	0.388 (0.017 – 0.760)	2.172	0.042
Maximum Plant Diameter (DBH)			
Size Class	**Plot basal area trend (CI 95%)**	***t*-ratio**	***P* value**
Tree	0.005 (-0.005 – 0.015)	1.031	0.314
Sapling	0.011 (0.001 – 0.021)	2.326	0.030

Table S3.5. Beta regressions examining the effect of plot basal area and size class on the categorical functional traits, leaf compoundness and leaf deciduousness, as a proportion of the total number of individuals. Dispersion (phi) is the precision parameter for beta regressions.

Proportional Leaf Deciduousness				
Predictors	**Estimates (CI 95%)**	**Statistic**	***P* value**	R^2
(Intercept)	0.006 (0.000 – 0.068)	-4.073	< 0.001	
Plot basal area	1.056 (0.960 – 1.161)	1.125	0.260	
Size class (Tree)	279.034 (16.917 – 4602.386)	3.938	< 0.001	0.699
Plot basal area * Size class (Tree)	0.843 (0.757 – 0.940)	-3.089	0.002	
Dispersion (phi)	129.540 (56.550 – 202.530)	3.479	< 0.001	

Proportional Leaf Compoundness				
Predictors	**Estimates (CI 95%)**	**Statistic**	***P* value**	R^2
(Intercept)	0.514 (0.088 – 3.007)	-0.738	0.460	
Plot basal area	0.992 (0.926 – 1.063)	-0.230	0.818	
Size class (Tree)	1.446 (0.129 – 16.172)	0.299	0.765	0.269
Plot basal area * Size class (Tree)	1.004 (0.914 – 1.103)	0.088	0.930	
Dispersion (phi)	27.745 (12.608 – 42.882)	3.593	< 0.001	

Table S3.6. Post-hoc results investigating the estimated marginal means of each size class, and their relationship with plot basal area, for categorical functional traits which were found to have significant plot basal area relationships. Estimated marginal means were calculated via the *emmeans* R package (Lenth, 2023).

Proportional Leaf Deciduousness			
Size Class	**Plot basal area trend (CI 95%)**	***z*-ratio**	***P* value**
Tree	-0.008 (-0.012 - -0.005)	-4.557	< 0.001
Sapling	0.001 (-0.001 – 0.003)	1.133	0.257

Table S3.7. ANOVAs of mean species' functional trait values against multinomial species classifications. Dependent variables were transformed, and model specifications altered to fit ANOVA assumptions of normality of residuals and homogeneity of variance. Species classifications refer to old-growth specialists, secondary forest specialists, generalists and species too rare to classify.

Functional Trait	**Model specification**	**Effect (*df*)**	***F* statistic**	***P* value**
Leaf Lamina Toughness	Linear Regression	Classification(3, 273)	0.882	0.451
Leaf Area (log-transformed)	Linear Regression	Classification(3, 273)	2.542	0.057
Leaf Nitrogen Content	Linear Regression	Classification(3, 273)	0.938	0.423
Leaf Thickness	Linear Regression	Classification(3, 273)	1.321	0.268
Maximum DBH (log-transformed)	Weighted Least Squares Regression	Classification(3, 273)	6.167	< 0.001
Maximum Height	Weighted Least Squares Regression	Classification(3, 273)	8.940	< 0.001
Seed Dry Mass (log-transformed)	Linear Regression	Classification(3, 273)	1.044	0.374
SLA (square-root-transformed)	Weighted Least Squares Regression	Classification(3, 273)	1.933	0.125
Wood Density	Linear Regression	Classification(3, 273)	5.115	0.002

Table S3.8. Tukey multiple comparison post-hoc tests examining differences between multinomial species classifications means for functional traits which had significant ANOVA results.

Functional Trait	Classification comparison	Difference (95 % CI)	*P* value
Maximum DBH	OG Specialist – Generalist	-0.142 (-0.632 – 0.348)	0.877
	Secondary Specialist – Generalist	-0.126 (-0.582 – 0.331)	0.893
	Too Rare – Generalist	-0.443 (-0.738 – -0.147)	0.001
	Secondary Specialist – OG Specialist	0.017 (-0.560 – 0.593)	0.999
	Too Rare – OG Specialist	-0.300 (-0.760 – 0.159)	0.330
	Too Rare – Secondary Specialist	-0.317 (-0.741 – 0.107)	0.216
Maximum Height	OG Specialist – Generalist	1.362 (-4.977 – 7.702)	0.945
	Secondary Specialist – Generalist	-4.157 (-10.067 – 1.754)	0.267
	Too Rare – Generalist	-6.405 (-10.232 – -2.578)	< 0.001
	Secondary Specialist – OG Specialist	-5.519 (-12.978 – 1.940)	0.225
	Too Rare – OG Specialist	-7.767 (-13.713 – -1.822)	0.005
	Too Rare – Secondary Specialist	-2.249 (-7.735 – 3.238)	0.714
Wood Density	OG Specialist – Generalist	-0.104 (-0.188 – -0.019)	0.009
	Secondary Specialist – Generalist	0.001 (-0.078 – 0.080)	0.999
	Too Rare – Generalist	-0.055 (-0.106 – -0.004)	0.029
	Secondary Specialist – OG Specialist	0.104 (0.005 – 0.204)	0.035
	Too Rare – OG Specialist	0.049 (-0.031 – 0.128)	0.387
	Too Rare – Secondary Specialist	-0.056 (-0.129 – 0.017)	0.201

Table S3.9. Functional diversity metric definitions and associated references.

Functional Diversity Metric	Definition	Reference
Functional Evenness	The uniformness of the abundance distribution of species in functional trait space. This is examined through calculations of the minimum spanning tree, which links all species in *n*-dimensional space by the smallest number of branch lengths.	(Mouillot et al., 2013b; Villéger et al., 2008)
Functional Dispersion	The mean distance of species trait values examined in the subgroup from the centre of functional trait space for the total species assemblage.	(Mouillot et al., 2013b)
Functional Divergence	The spread of the most abundant species in a community from the centre of functional trait space (identified via the vertices of the convex hull volume). If the most abundant species are central in trait space, then functional divergence is low i.e. close to 0.	(Mouillot et al., 2013b; Villéger et al., 2008)
Functional Originality	The average functional uniqueness of species within a community, with the most functionally distinct species having the least common combinations of functional trait values.	(Mouillot et al., 2013b, 2008)
Functional Richness	The proportion of functional trait space, derived from minimum convex hull volume for all species included in the study, occupied by the examined grouping of species communities.	(Cornwell et al., 2006; Mouillot et al., 2013b; Villéger et al., 2008)
Functional Specialisation	The average specialisation of species within a community i.e. how far species are from the centre of functional trait space. Increased distance from the centre indicates increased functional specialisation.	(Mouillot et al., 2013b; Villéger et al., 2010)

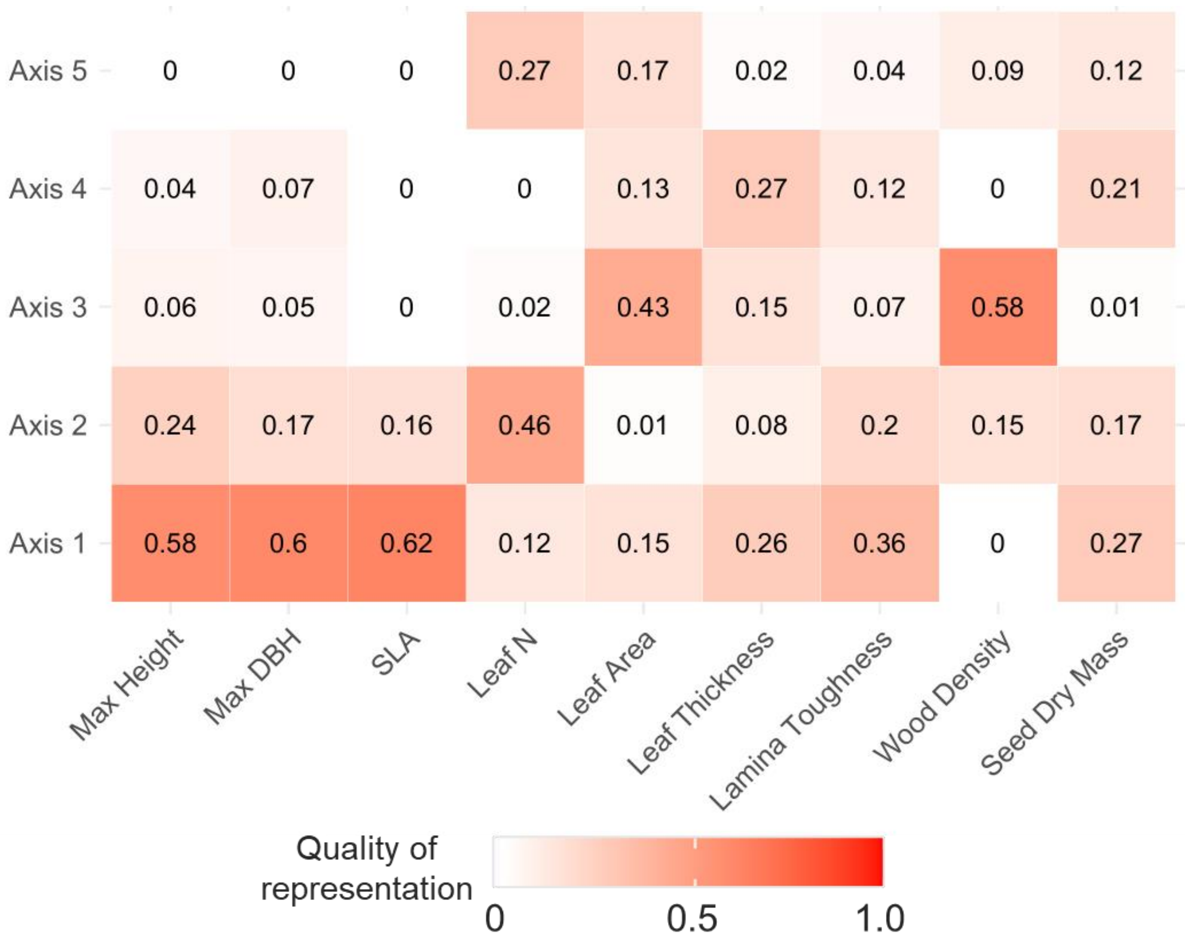


Figure S3.6. The quality of representation of each functional trait with the first five axes from the Principal Component Analysis. Functional traits were log-transformed and scaled and centred prior to analysis.

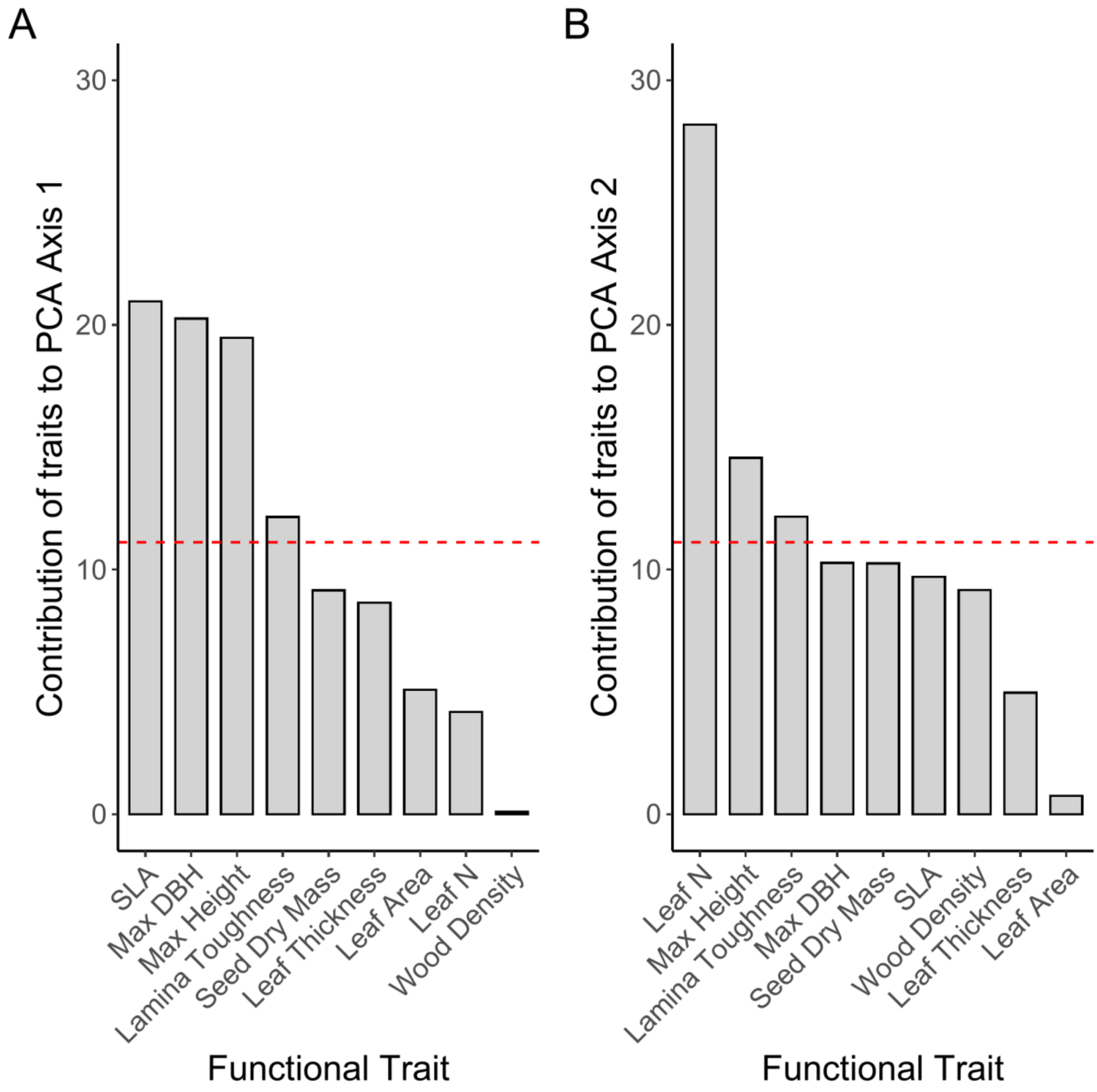


Figure S3.7. Relative contribution of each functional trait to: **A** PCA Axis 1 and **B** PCA Axis 2. The red dotted line indicates the contribution each trait would provide if they all contributed equally to each axis.

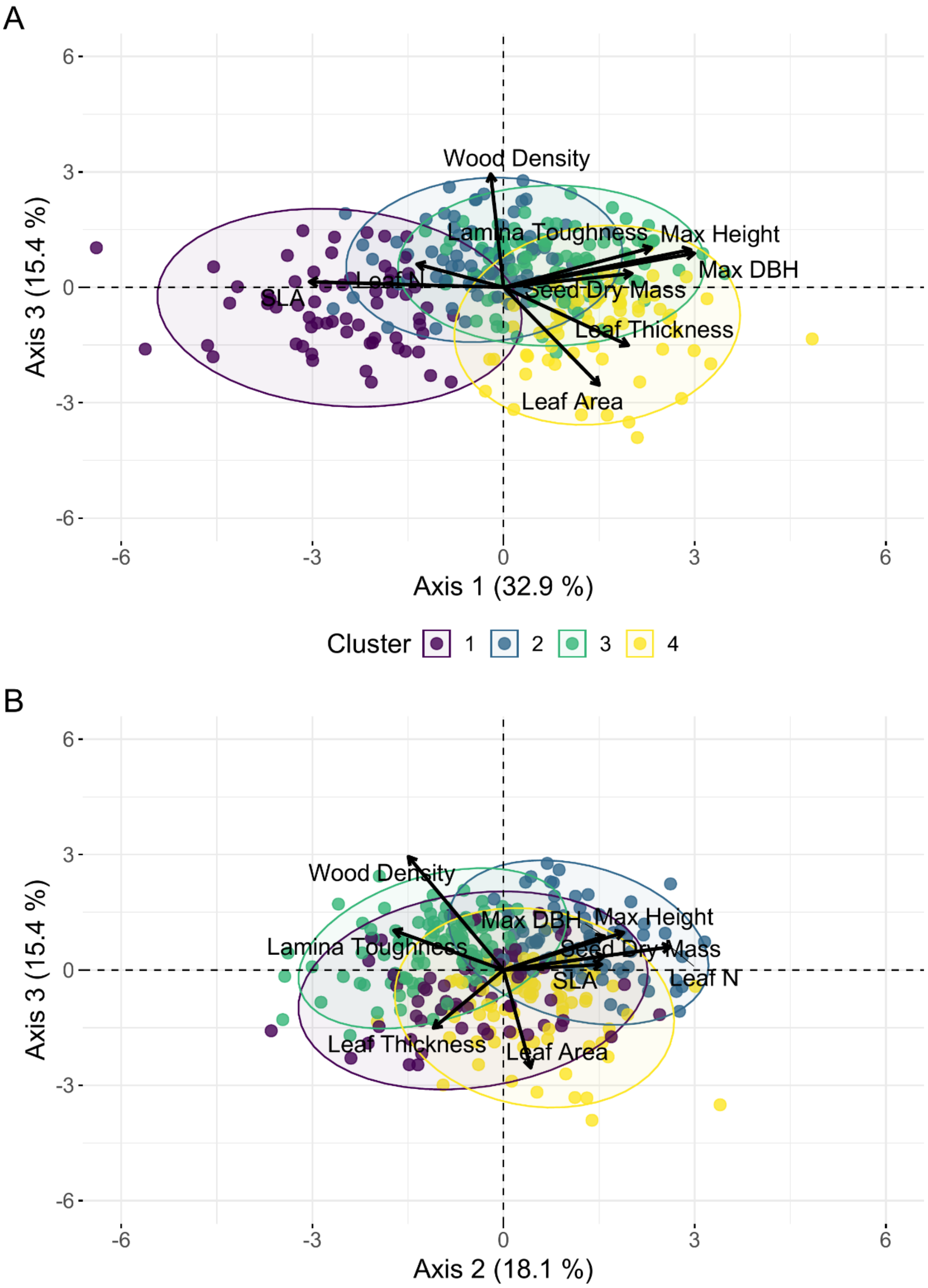


Figure S3.8. Principal Component Analysis results showing species classified by their functional traits into distinct clusters. This graph shows PCA axis 3 and its relationship with PCA axis 1 and PCA axis 2.

Table S3.10. Functional trait associations with each of the four clusters identified by the hierarchical clustering method on the PCA. Note that all cluster mean values are for functional trait values which were log transformed, centred, and scaled prior to analysis and they are compared to overall means equal to zero and standard deviations of one.

Cluster	Functional Trait	Kuiper test	Cluster Mean (SD)	*P* value
Cluster 1	Specific Leaf Area	8.931	1.008 (0.723)	< 0.001
	Leaf Area	-3.559	-0.402 (0.920)	< 0.001
	Leaf Thickness	-4.374	-0.494 (1.108)	< 0.001
	Lamina Toughness	-7.586	-0.856 (0.857)	< 0.001
	Seed Dry Mass	-7.962	-0.898 (0.752)	< 0.001
	Maximum DBH	-12.461	-1.406 (0.819)	< 0.001
	Maximum Height	-12.979	-1.464 (0.756)	< 0.001
Cluster 2	Leaf Nitrogen Content	9.164	0.872 (0.747)	< 0.001
	Specific Leaf Area	5.789	0.551 (0.690)	< 0.001
	Maximum Height	4.698	0.447 (0.529)	< 0.001
	Seed Dry Mass	3.915	0.372 (0.714)	< 0.001
	Maximum DBH	3.452	0.328 (0.592)	< 0.001
	Wood Density	2.011	0.191 (0.857)	0.043
	Leaf Area	-2.809	-0.267 (0.813)	0.005
	Lamina Toughness	-3.055	-0.291 (0.820)	0.002
	Leaf Thickness	-5.799	-5.799 (0.792)	<0.001
Cluster 3	Lamina Toughness	9.343	0.809 (0.750)	< 0.001
	Wood Density	8.247	0.714 (0.507)	< 0.001

	Leaf Thickness	2.404	0.208 (0.794)	0.016
	Leaf Nitrogen Content	-7.289	-0.631 (0.807)	<0.001
	Specific Leaf Area	-8.125	-0.703 (0.675)	<0.001
Cluster 4	Leaf Area	7.867	0.767 (1.052)	< 0.001
	Leaf Thickness	7.367	0.719 (0.744)	< 0.001
	Maximum DBH	7.282	0.710 (0.615)	< 0.001
	Maximum Height	6.817	0.665 (0.495)	< 0.001
	Seed Dry Mass	4.534	0.442 (0.841)	< 0.001
	Leaf Nitrogen Content	-2.753	-0.268 (0.733)	0.006
	Specific Leaf Area	-5.518	-0.538 (0.746)	< 0.001
	Wood Density	-9.244	-0.902 (0.963)	< 0.001

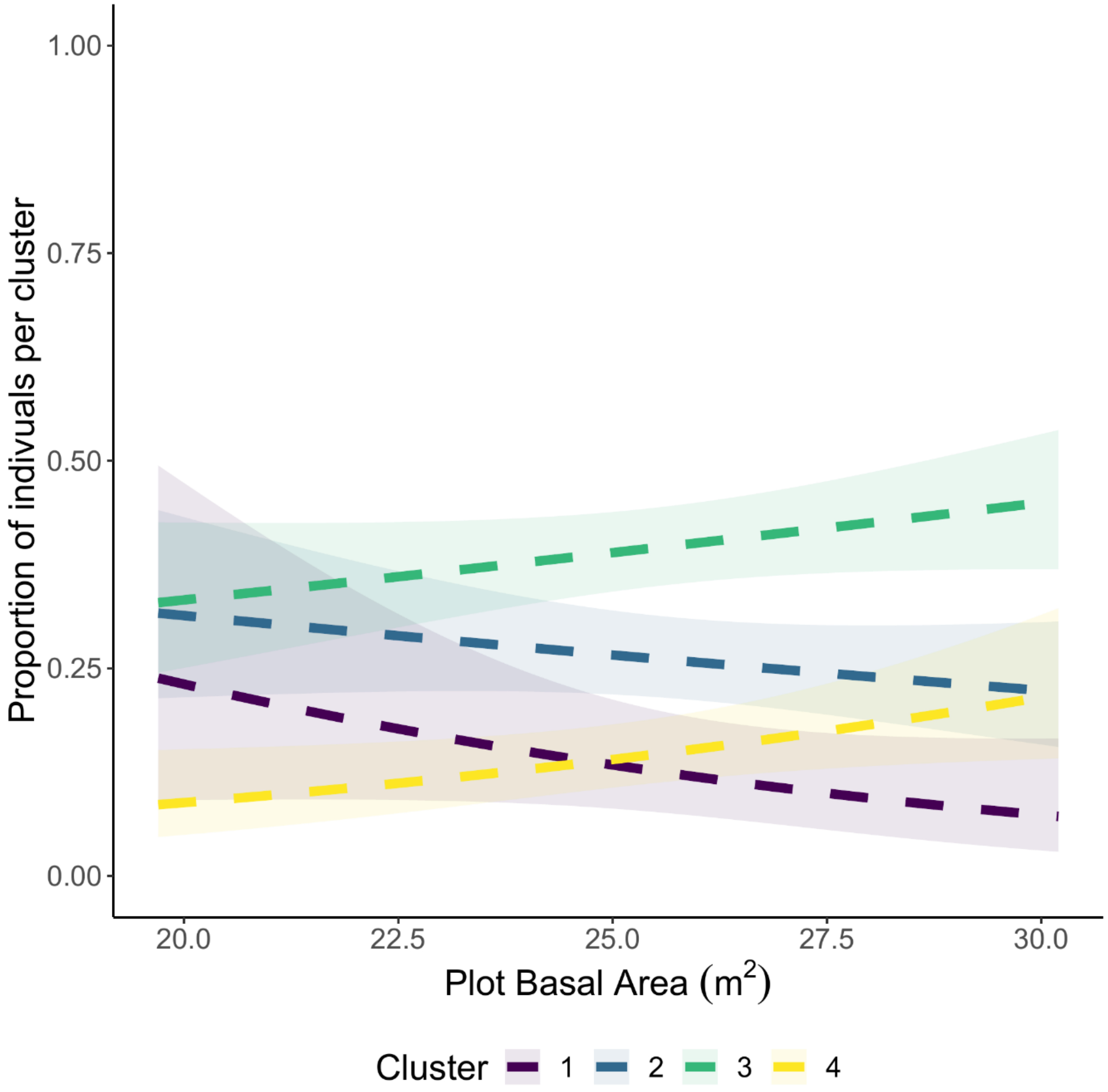


Figure S3.9. Modelling results from binomial generalised linear mixed models examining the effect of plot basal area on the abundance of individuals per cluster. Dashed lines indicate trends which are not statistically significant. Shaded areas either side of the dashed lines indicate 95 % confidence intervals.

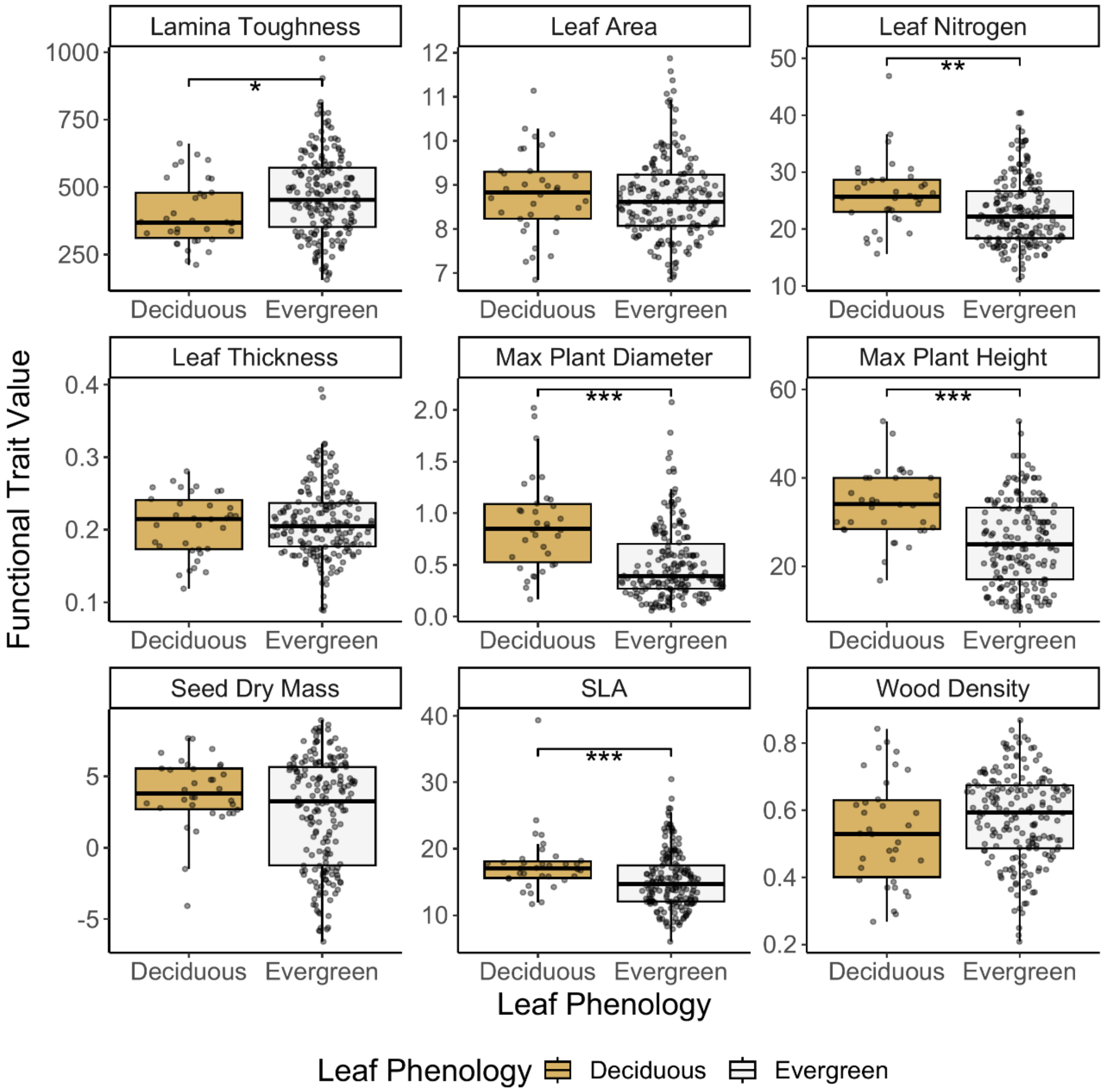


Figure S3.10. Differences in functional trait values between deciduous and evergreen tree species (≥ 5 cm DBH, excluding understory species). Boxplots depict the median species value per category, and the interquartile range of values. Both seed dry mass and leaf area are log transformed on this plot, and were log transformed prior to analysis. Significant differences between categories are indicated by the asterisks (* = *P* < 0.05, ** = *P* < 0.01, *** = *P* < 0.001).

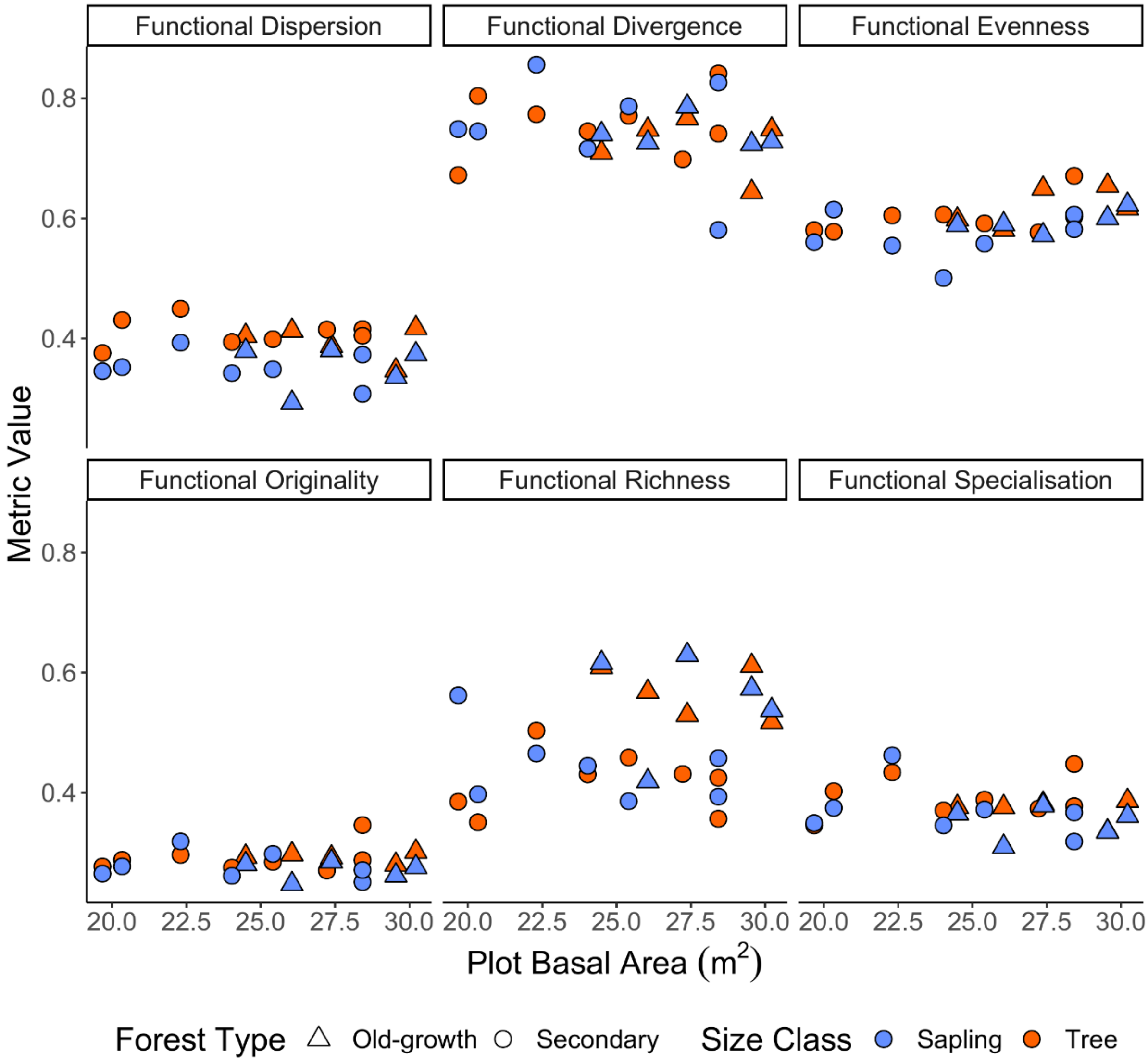


Figure S3.11. Functional diversity metrics plotted against plot basal area. Size class is indicated by the colour, with blue for saplings and orange for trees. Forest type is indicated by the shape, with triangles for old-growth and circles for secondary forest plots.

Table S3.11. Beta regression model outputs (logit link) for all functional diversity metrics. The relationship between the functional diversity metric and plot basal area interacting with size class was examined for all metrics. Dispersion (phi) is the precision parameter for beta regressions.

Metric	**Predictor**	**Estimate**	**Standard error**	***z* statistic**	***P* value**
Functional Dispersion	(Intercept)	-0.508	0.255	-1.994	0.046
	Plot basal area	-0.004	0.099	-0.405	0.685
	Size class (Tree)	0.311	0.354	0.876	0.381
	Plot basal area * Size class (Tree)	-0.003	0.014	-0.250	0.803
	Dispersion (phi)	333.523	94.200	3.541	< 0.001
Functional Evenness	(Intercept)	-0.054	0.246	-0.218	0.828
	Plot basal area	0.015	0.096	1.527	0.127
	Size class (Tree)	-0.095	0.349	-0.272	0.785
	Plot basal area * Size class (Tree)	0.008	0.014	0.618	0.536
	Dispersion (phi)	333.070	94.069	3.541	< 0.001
Functional Richness	(Intercept)	-0.409	0.723	-0.566	0.571
	Plot basal area	0.015	0.028	0.519	0.604
	Size class (Tree)	-0.685	1.023	-0.670	0.503
	Plot basal area * Size class (Tree)	0.024	0.039	0.612	0.540

	Dispersion (phi)	37.009	10.329	3.583	< 0.001
Functional Diversity	(Intercept)	1.736	0.672	2.581	0.001
	Plot basal area	-0.025	0.026	-0.977	0.328
	Size class (Tree)	-0.606	0.940	-0.645	0.519
	Plot basal area * Size class (Tree)	0.023	0.036	0.623	0.533
	Dispersion (phi)	58.065	16.316	3.559	< 0.001
Functional Originality	(Intercept)	-0.777	0.194	-4.006	< 0.001
	Plot basal area	-0.008	0.008	-1.004	0.316
	Size class (Tree)	-0.309	0.272	-1.136	0.256
	Plot basal area * Size class (Tree)	0.015	0.011	1.456	0.145
	Dispersion (phi)	655.966	185.416	3.538	< 0.001
Functional Specialism	(Intercept)	-0.153	0.303	-0.507	0.612
	Plot basal area	-0.016	0.012	-1.377	0.169
	Size class (Tree)	-0.277	0.425	-0.653	0.514
	Plot basal area * Size class (Tree)	0.015	0.016	0.892	0.373
	Dispersion (phi)	231.653	65.387	3.543	< 0.001

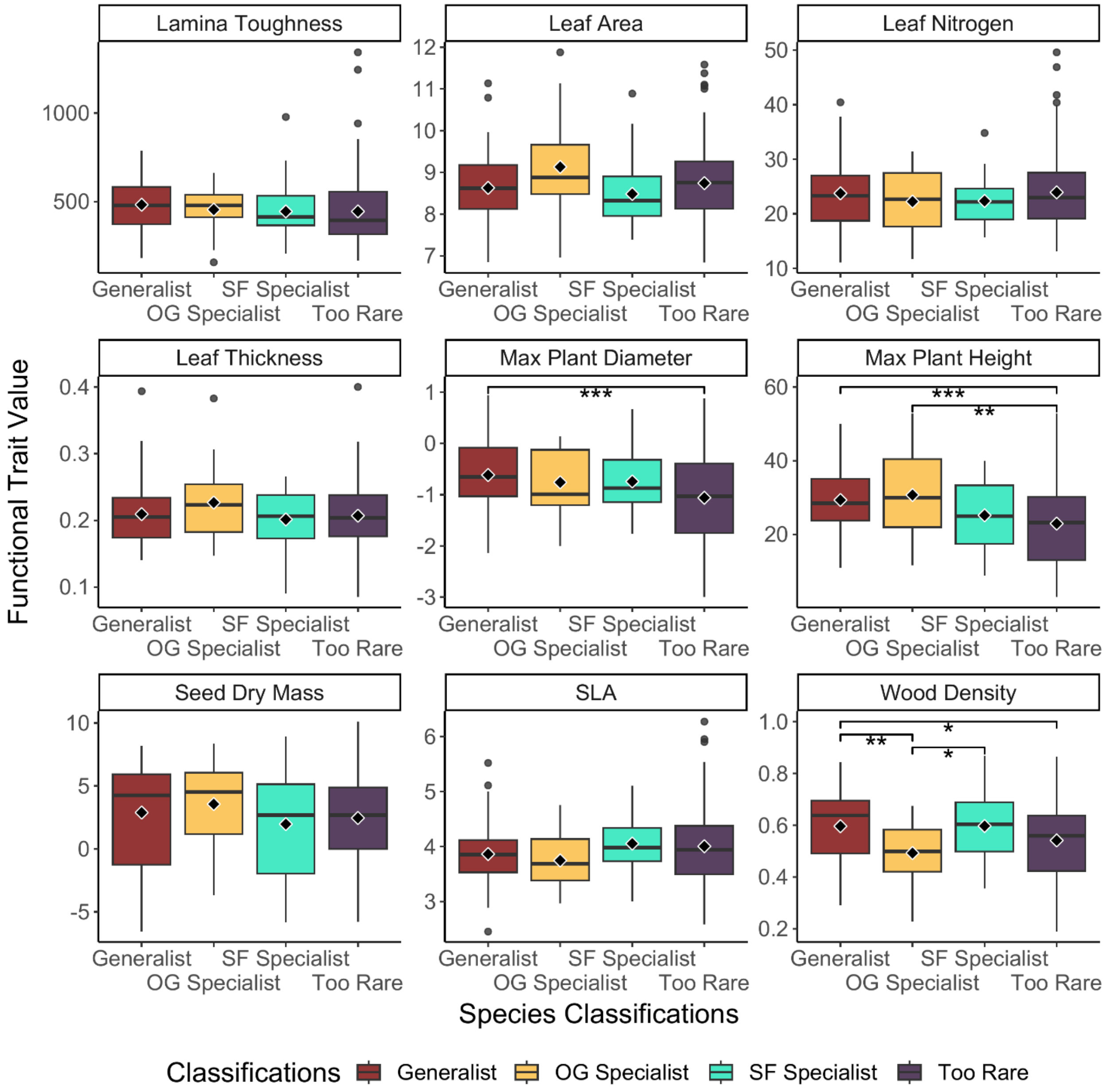


Figure S3.12. Differences in functional trait values between tree species (≥ 5 cm) separated by their multinomial model species classifications. Boxplots depict the median species value per classification, and the interquartile range of values. Black diamonds indicate mean species value per classification. Leaf area, maximum plant diameter, and seed dry mass are log transformed on this plot, and were log transformed prior to analysis. Similarly, SLA is square root transformed and was transformed prior to analysis. Significant differences between classifications are indicated by asterisks (* = P < 0.05, ** = P < 0.01, *** = P < 0.001).

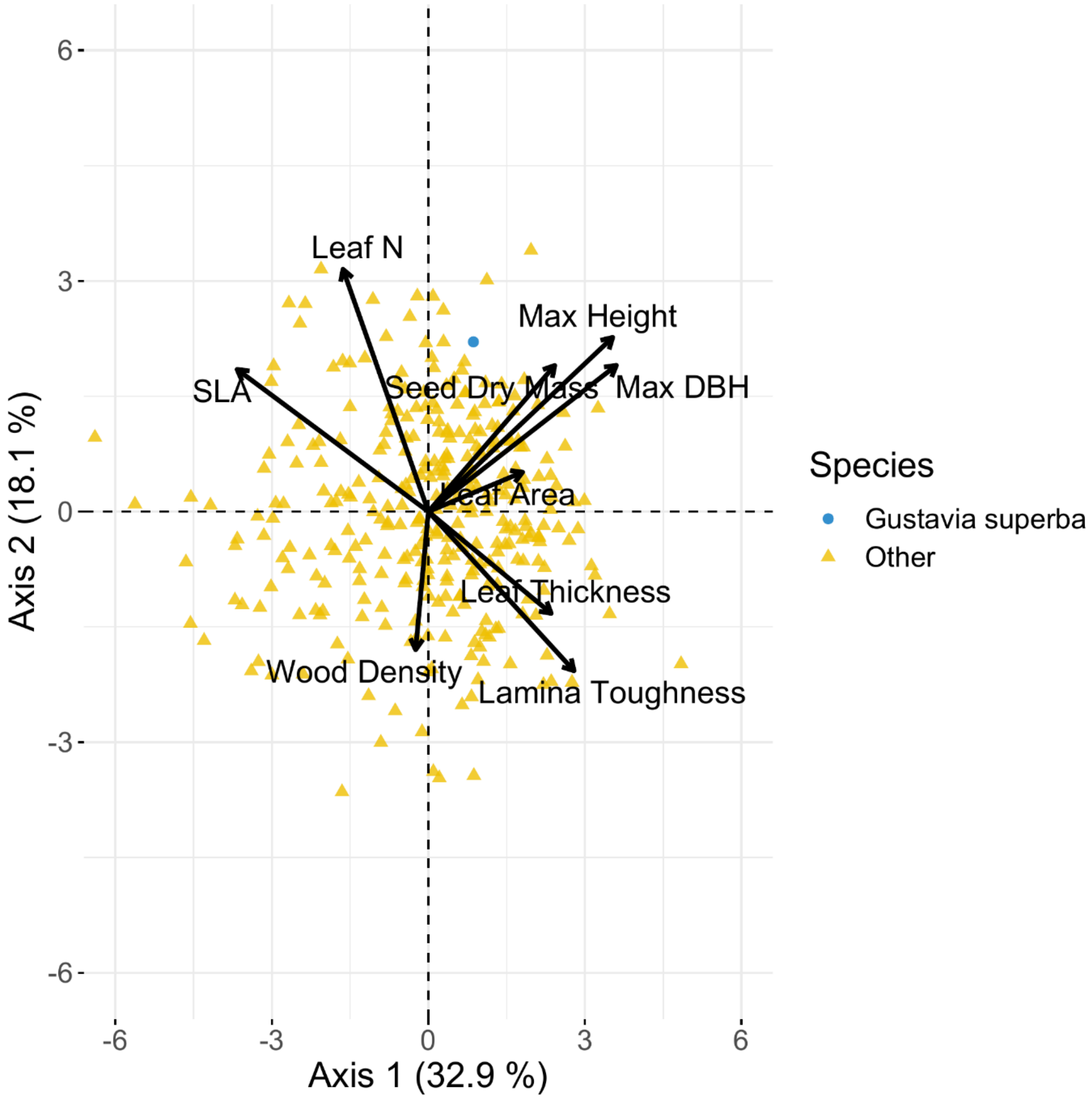


Figure S3.13. Principal Component Analysis results showing the location of *Gustavia superba* in the functional trait space compared to all other species. *Gustavia superba* is the dominant species in Barbour, one of the 120-year-old plots (see Chapter 2).

4 Chapter 4: Moist and wet tropical secondary forests have higher liana density and basal area than dry forests across the Neotropics

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Data contributors have not commented on this Chapter but all data contributors and members of the 2ndFOR research group (2ndFOR, 2020) will be involved as co-authors when we prepare the chapter for submission.

4.1 Abstract

Lianas are structural parasites with strong negative impacts on tree growth, fecundity, and survival in tropical forests. Lianas are increasing in abundance throughout the Neotropics, potentially increasing the effects of lianas on trees. Previous pantropical biogeographical comparisons of liana distributions suggest that liana density is higher in low rainfall, highly seasonal forests. However, these studies have primarily focused on lianas within old-growth forests and no large-scale studies have examined how liana abundance in successional forests changes along precipitation and seasonality gradients. Here we examine 12 Neotropical secondary forest chronosequences along an annual precipitation gradient ranging from 800 – 3900 mm per year to describe patterns of liana abundance through succession. We use a wet/dry forest dichotomy and examine liana density and basal area changes across liana size classes in the first 100 years of tropical forest succession. We found that moist/wet tropical forests had higher liana densities than dry tropical forests, contrary to expectations, and that liana densities were highest in early successional, low biomass forests. Interactions between tree biomass, forest classification and liana density and basal area revealed that moist/wet forests contained significantly higher densities of large lianas than dry forest in high biomass forests, suggesting that liana size is limited in dry forests. Liana dominance was found to be most likely in highly seasonal forests. These results suggest that liana density varies considerably through succession and between wet and dry forests. However, the relationship between mean annual precipitation, seasonality and forest age is complex and all play a role in defining liana abundance. This study is the first to integrate climatic factors across successional gradients in the Neotropics and lays key groundwork for investigating liana distributions across secondary forests. This is important given that changing climate cycles and increases in forest perturbations may drive increases in liana abundance in the future, with high potential for negative effects on tree carbon uptake and sequestration.

4.2 Introduction

Degraded and secondary forests make up c. 50% of remaining tropical forests globally (FAO, 2020). Evidence suggests that secondary tropical forests have real potential to mitigate the loss of ecosystem services that accompanies primary forest loss and rapidly uptake atmospheric CO_2 and bind carbon into above-ground biomass (Poorter et al., 2016). However, lianas (woody vines) can infest secondary forests and may prevent biomass accumulation (van der Heijden et al., 2015) and suppress forest development (Tymen et al., 2016). Lianas are a key component of tropical forests commonly comprising up to 25% of woody plant stems and 35% of woody species (Schnitzer and Bongers, 2002; Schnitzer et al., 2015). Lianas are often classified as structural parasites (Stevens, 1987; Visser et al., 2018a) which exploit trees as trellises to access the forest canopy (Putz, 1984) and compete with trees for light and below-ground resources (Avalos and Mulkey, 1999; Rodriquez-Ronderos et al., 2016). The negative impacts of lianas on trees range from reducing tree growth, fecundity and carbon accumulation to increasing tree mortality (Estrada-Villegas et al., 2022a; Finlayson et al., 2022; Ingwell et al., 2010; Kainer et al., 2014; Marshall et al., 2017; Schnitzer and Carson, 2010; van der Heijden et al., 2015; van der Heijden and Phillips, 2009; Wright et al., 2015). Several studies have estimated liana impacts on the carbon balance of tropical forests (see van der Heijden and Phillips, 2009; Durán and Gianoli, 2013; van der Heijden et al., 2013; Schnitzer et al., 2014; van der Heijden, Powers and Schnitzer, 2015, 2019; Estrada-Villegas et al., 2022a; Finlayson et al., 2022). For example, results from a liana removal experiment in Panama suggest that six years after liana removal, tree biomass accumulation was 46.9 % lower in the dry season, and 48.5 % lower in the wet season, in plots where lianas were present compared to liana-free plots (van der Heijden et al., 2019). Furthermore, a meta-analysis of 26 tropical studies investigating the effects of climber (lianas and non-woody vines) removal on trees, found tree growth to increase 1.5 fold and tree biomass to increase 2.09 fold following climber removal (Finlayson et al., 2022). Therefore, lianas have critical impacts on forest ecosystem processes, and should be considered a key influence on secondary forest regeneration in terms of biomass recovery and forest structure.

At a local scale, liana abundance is tightly linked to forest disturbance and liana densities tend to be higher in treefall gaps (Schnitzer and Carson, 2001), forest edges (Laurance et al., 2001) and in young secondary or degraded forest (Barry et al., 2015; DeWalt et al., 2000; Jones et al., 2017; Letcher and Chazdon, 2009). A number of factors may enable lianas to proliferate in disturbed environments: 1. lianas can resprout readily following disturbance and displacement from the canopy (Rocha et al., 2020; Yorke et al., 2013); 2. Lianas tend to be limited by light availability in old-growth forests but the higher light availability of canopy gaps and young secondary forest may drive increased liana abundance (Dalling et al., 2012; DeWalt et al., 2000); 3. Lianas have access to more trellises (small diameter trunks and branches) in disturbed/early successional environments and so have more routes to reach the forest canopy (Putz, 1984; Balfour and Bond, 1993). However, field studies highlight considerable variation in liana density over succession; some tropical secondary forest studies show that lianas peak in stem density in early-to-mid succession (summarised in Letcher (2015)), while others show peaks in liana density at 60 or even 100 years into succession (Lomwong et al., 2023; Mumbanza et al., 2022). Liana biomass and basal area may follow different successional trajectories to stem density (Letcher, 2015). For example, DeWalt, Schnitzer and Denslow (2000) found that liana basal area was relatively constant throughout succession, while stem density declined. In contrast, Mumbanza et al. (2022) found a linear increase in liana basal area, up to 100-years into succession, with liana density instead peaking in 60-year-old forest. Lianas compete with trees and can strongly affect tree biomass accumulation, even in early succession (Estrada-Villegas et al., 2020; Lai et al., 2017). Lai et al., (2017) found that just 5 years into succession, in a tropical moist forest, lianas reduced tree biomass growth by 19 %, which increased to a 32 % reduction in 30-year-old forests. However, the impacts of lianas through succession may not be uniform across climatic gradients. A liana removal experiment in early and late successional dry forests in western Panama found no effect of lianas on tree biomass accumulation (Estrada-Villegas et al., 2021), in direct contrast to the effects of a liana removal experiment in early successional moist forest in central Panama (Estrada-Villegas et al., 2020).

The relationship between water availability and liana density has been a focus of ecological theory for the past two decades (Schnitzer, 2005, 2018). At a regional scale, liana density in old-growth forest increases with dry season length and decreases with increased mean annual precipitation (MAP; Schnitzer, 2005; Swaine and Grace, 2007; DeWalt et al., 2010, 2015). Tree density may have a converse relationship with MAP, with evidence that tree density increases with increasing MAP (Schnitzer, 2005). Relationships between MAP and liana density can be weak (e.g. $R^2 = 0.11$ in Schnitzer (2005)), especially in the Neotropics (van der Heijden and Phillips, 2008), and other measures which better capture temporal trends in water availability and plant water stress may better explain liana distributions (Manzané-Pinzón et al., 2018; Parolari et al., 2020). For example, Parolari et al. (2020) examined liana density across a Panamanian rainfall gradient and found that a normalised seasonality index, combining MAP and a measure of inter-month rainfall variation (Feng et al., 2013), explained 38 % of the variance in liana density compared to just 9 % for MAP. This finding relates to the growing body of evidence that lianas have a seasonal growth advantage over trees (Schnitzer, 2018; Schnitzer and van der Heijden, 2019). Therefore, including other methods of quantifying rainfall variability (e.g. Schwartz et al., 2020) may improve our understanding of liana distributions. This is especially important given changing patterns of seasonality and rainfall in some tropical regions (Boisier et al., 2015; Feng et al., 2013; Fu et al., 2013), and the potential for future forest loss to further impact the hydrological cycle (Smith et al., 2023), which could potentially lead to shifting patterns of liana abundance (Schnitzer, 2018).

Studies of liana abundance in wet versus dry forests have focused primarily on old-growth forests (Schnitzer, 2005; van der Heijden and Phillips, 2008; DeWalt et al., 2010, 2015), which has enabled standardisation across sites, and eliminated potential confounding effects of secondary forest age and disturbance (e.g. DeWalt, Schnitzer and Denslow, (2000); Barry et al., (2015)). However, this approach also means there is a knowledge gap in how liana density in secondary forests changes along precipitation and seasonality gradients.

Water is not the only resource which differs between wet and dry tropical forests, light and nutrient availability can also vary; dry forests tend to have higher light availability (Ceccon et al., 2006; Coomes and Grubb, 2000) and differ in soil nutrient availability (Austin and Vitousek, 1998; Quinto-Mosquera and Moreno-Hurtado, 2016; Santiago et al., 2005) compared to wet forests. The availability of abiotic resources over succession also differs between dry and wet forests (Powers and Marín-Spiotta, 2017; van der Sande et al., 2022; Werden et al., 2020), and abiotic differences have been linked to alternate functional strategies in tree communities in the early stages of succession (Lohbeck et al., 2013; Poorter et al., 2021b). Trees in early dry forest succession may often follow more conservative growth and resource acquisition strategies than trees in early wet forest succession (Lohbeck et al., 2013; Poorter et al., 2021b). This is linked to young dry forests being more stressful environments, with lower water availability, higher light availability and higher temperatures than wet forests (Lebrija-Trejos et al., 2011). Thus, lianas may also have different responses and strategies between early successional dry and wet forests. Generally, there is evidence that lianas have more acquisitive leaf traits but similar water use strategies to trees in seasonally dry forest (Medina-Vega et al., 2021; Werden et al., 2018), whereas, wet forest trees and lianas have similar leaf traits (Medina-Vega et al., 2021). However, the consequences of these different liana strategies in early succession are uncertain, due to the bias of liana studies towards moist/wet secondary forest (da Cunha Vargas et al., 2021; Letcher, 2015).

Lianas colonise and impact trees from the earliest stages of succession (Lai et al., 2017; Marshall et al., 2020). Even the smallest size classes of lianas, i.e. < 1 cm diameter, can colonise understory trees and climb to the canopy (Putz, 1984; Putz and Chai, 1987; Kurzel, Schnitzer and Carson, 2006), and once lianas colonise a tree, the likelihood of subsequent liana colonisation increases (Putz, 1984; Pinard and Putz, 1994; Pérez-Salicrup, Sork and Putz, 2001). Kurzel, Schnitzer and Carson (2006) found that between 10 and 40 % of lianas 1 cm in diameter reach the forest canopy, depending on the study site, and this increases rapidly to > 80 % of lianas 2.5 cm in diameter and all lianas 5 cm in diameter. Thus, lianas of all size classes may access the canopy and compete with trees for light (Toledo-Aceves, 2015). Large lianas may become key components of liana biomass as succession progresses as liana density declines but liana basal area remains constant (DeWalt et al., 2000). Moreover, as lianas increase in size it is likely that the mechanical stresses they place on their host trees also increases, with implications for tree damage (Putz, 1984; Visser et al., 2018b) and changing tree allometries (Dias et al., 2017). As a result, investigating lianas across a wide range of size classes is key to cover the breadth of potential interactions with the tree community.

Multiple interacting factors of light availability, precipitation, seasonality, and forest age may thus drive differences in liana abundance, especially over forest succession (Letcher, 2015; Schnitzer, 2018). The effects of each of these variables are therefore important to quantify, given the continued loss of old-growth forest and regrowth of secondary tropical forest (Pugh et al., 2019; Rosa et al., 2021; Turubanova et al., 2018), and the potential changes in seasonality and rainfall under changing climatic patterns (Caretta et al., 2022). These changes, in tandem with the recent increases in liana abundance in the Neotropics (Laurance et al., 2014; Schnitzer et al., 2021; Schnitzer and Bongers, 2011), suggest that liana-forest interactions are altering and may continue to do so into the future. Thus, the current relationship between liana abundance in secondary forests and rainfall and seasonality is of key importance to understand how tropical forests, and the impacts of lianas on trees, may develop in a changing world.

Here we aim to further our understanding of how liana density and tree biomass recover through secondary succession across the Neotropics. A number of high profile recent syntheses describe tree structural and biodiversity recovery through secondary succession across the Neotropics (Poorter et al., 2021a; Rozendaal et al., 2019). However, little comparable research exists for lianas, at a similar regional scale. We use data from 12 Neotropical sites, spanning four countries and a MAP gradient of 800 – 3900 mm, to describe patterns of liana recovery across a forest age gradient, which will be used alongside seasonality (Schwartz et al., 2020) and disturbance (Grantham et al., 2020; Hansen et al., 2013) metrics, combined with tree biomass and density, to investigate the relative importance of each of these factors. We aim to address the following key questions:

1. Do wet and dry secondary forests differ in liana density and basal area?
2. Are there distinct successional patterns for small versus large lianas?
3. Do patterns of liana density and basal area through succession vary between wet and dry forests?
4. Does the relative density of lianas versus trees vary between wet and dry forests?

We hypothesise that seasonal, dry forests will have higher liana densities than wet, aseasonal forests, due to the seasonal growth advantage of lianas (Schnitzer, 2018), and that liana densities will peak in the early stages of succession (Letcher, 2015). We also propose that large lianas will peak in abundance in late succession and that dry forests will have higher liana densities than wet forests (Schnitzer, 2005).

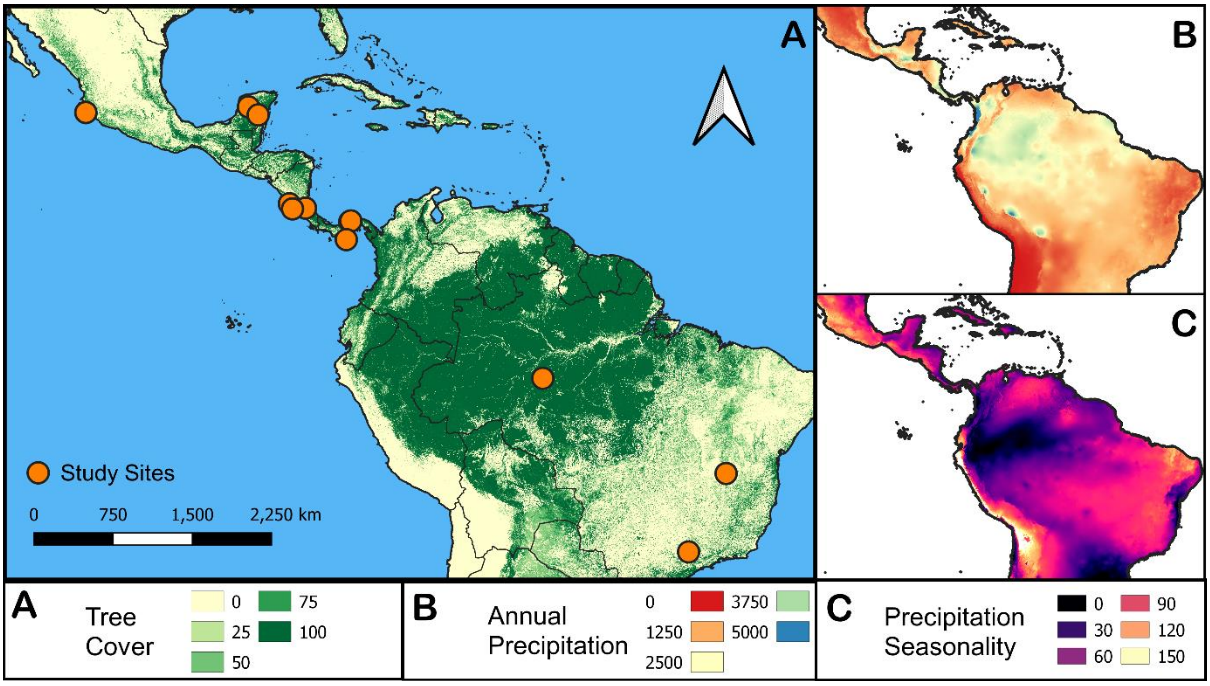

Figure 4.1. Map depicting our 12 study sites across the Neotropics. Sites are situated in secondary forests (**A**) along precipitation (**B**) and precipitation seasonality (**C**) gradients. See Table S4.1 for site details and descriptions.

4.3 Methods

4.3.1 Study sites and census methods

We obtained data from 12 Neotropical chronosequences (space-for-time substitutions including 672 plots) which spanned a c. 3000 mm annual precipitation gradient across dry, moist, and wet tropical forests with varied seasonality (Figure 4.1, Table S4.1). Chronosequence plots were typically located on land which had previously been used as pasture, or for shifting cultivation, prior to land abandonment and forest regeneration. Plots spanned early, mid, and late stages of secondary forest succession and ranged in age from 0 – 120 years since land abandonment (mean age = 31.7 years, Table S4.1).

Lianas and trees were surveyed within each site according to widely varying site designs and censusing methodologies (Figure S4.1, Table S4.1). Plots ranged in shape, from circular sampling designs, to transect designs and rectangular plots. Plots also differed in size (minimum plot size = 0.02-ha, maximum plot size= 0.2-ha). Trees were generally surveyed with a minimum diameter of 5 cm DBH, although plots in Santa Rosa and Palo Verde were surveyed with a minimum diameter of 7 cm DBH (Figure S4.1). Liana survey methods were more variable and minimum diameters censused ranged from 0.5 cm for plots in the Barro Colorado Nature Monument (BCNM) and Sarapiqui chronosequences to 5 cm in the Rio Madeira plots (Figure S4.1). The point of measurement for liana diameters also varied between sites: five sites followed recommendations by Gerwing et al., (2006) and Schnitzer, Rutishauser and Aguilar (2008) and measured lianas 130 cm from the base; another five sites measured liana diameters at breast height (130 cm from the ground); one site (BCNM) measured the diameter at the largest point and one site (Piracicaba) measured the density of liana stems along a transect, with no diameter measurement (Table S4.1). Ramets and genets were measured for all sites apart from for the BCNM chronosequence, which only measured genets, and Piracicaba, which did not distinguish between stem types.

4.3.2 Data cleaning

All data cleaning was carried out using the *tidyverse* library of packages (Wickham et al., 2019) in R version 4.2.1 (R Core Team, 2022). Firstly, each site had family, genera and species names validated and corrected according to The Plant List (2013), which was accessed through the `TPL` function in the *Taxonstand* R package (Cayuela et al., 2021). Species growth forms were subset to just liana and trees when additional growth forms were censused. Subsequently, non-woody climbers were removed from the data, following DeWalt et al. (2015), by filtering out individuals in the Arecaceae, Marcgraviaceae, Araceae, Poaceae families. After taxonomic standardisation, the percentage of trees identified to a species level ranged from 97. 32 % - 100 % (mean = 99.55 %; Table S4.1), and lianas identified to a species level ranged from 67.78 % - 100 % (mean = 93.0 %; Table S4.1). Due to the differences in liana identification, compared to trees, we did not further analyse taxonomic data.

Liana densities were initially incomparable, due to different sampling designs, and required standardisation to enable comparisons to be made. Firstly, both liana and tree individual diameters were converted from circumference at breast height (CBH) to diameter at breast height (DBH) for one site (Mata Seca). Secondly, one of our sites, Kiuic, had a clustered plot design, with 12 plots per `landscape`, which was dissimilar to all other sites (Figure S4.2). Unfortunately, we did not have plot coordinates for all other sites, and thus could not take this clustering into account by modelling spatial autocorrelation (Figure S4.2). Thus, plots in Kiuic were aggregated per landscape (276 plots to 23), with liana and tree abundance summed per landscape, and forest age averaged.

Different liana sampling methodologies per site (Table S4.1) were accounted for by using equations in Schnitzer, DeWalt and Chave (2006) to convert all liana diameters to values as if they were measured at 130 cm from their rooting position. Due to the differences in sampling methodology between sites for lianas, lianas were analysed in different size classes, to enable as many sites' data to be utilised as possible. Lianas were split into three classes: $1 \leq$ diameter < 2.5 cm (small) lianas, $2.5 \leq$ diameter < 5 cm (medium) lianas and lianas ≥ 5 cm (large). These size classes are also functionally distinct, given that 10 – 40 % of 1 cm diameter lianas, ≥ 80 % of 2.5 cm diameter lianas and 100 % of 5 cm lianas have been found to be present in the forest canopy (Kurzel et al., 2006). Liana densities were then calculated per plot/subplot for each size class and then standardised to liana stem density per 0.1-ha, to allow comparison between sites. Liana basal area was also calculated on a size class basis per 0.1-ha.

Tree densities were calculated per plot for all trees ≥ 5 cm DBH and then transformed to tree density values per 0.1-ha. Trees in plots in Santa Rosa and Palo Verde were only measured to a minimum of 7 cm DBH, and not 5 cm DBH. Density values in those plots were corrected to a 5-cm equivalent density value by multiplying up by a correction factor i.e., the median proportion of stems found at the other plots, which were 5 – 7 cm in diameter (36.28 %). Above-ground biomass (AGB) values were also calculated for each site, for all trees ≥ 5 cm DBH, using the *BIOMASS* R package (Réjou-Méchain et al., 2017). Firstly, tree wood density values were obtained for all tree species which did not have values present in the dataset, using both the BIEN trait database (Maitner, 2022; Maitner et al., 2018) and the *BIOMASS* package (Chave et al., 2009; Réjou-Méchain et al., 2017; Zanne et al., 2009). In cases where no species-specific wood density value was found, genera values were assigned to the species where possible, or a site-based average wood density was used. Our datasets contained no tree height measurements, and so these were estimated using the `retrieveH` function from the *BIOMASS* package (Feldpausch et al., 2012; Réjou-Méchain et al., 2017). AGB values were then calculated per plot, using the wood density, height and diameter values, using the `summaryByPlot` function (Réjou-Méchain et al., 2017) which utilises the pantropical allometric equation from Chave et al. (2014) . Biomass values for Santa Rosa and Palo Verde were similarly extrapolated for the missing trees between 5 and 7 cm DBH. 29 plots in early succession had only trees and no lianas surveyed and so were excluded from analysis. Often these plots were small e.g., 1 – 2.5 cm lianas in a 0.005 ha subplot in Quintana Roo, and thus the option of entering these missing liana values as 0 when extrapolated to 0.1-ha seemed inaccurate, and it was deemed more accurate to remove the plots from the analysis. Tree basal area values per 0.1-ha were also calculated.

Gini coefficients of the liana and tree diameters were calculated per site to investigate the size range of lianas and trees for early and late successional plots, using the *ineq* R package (Zeileis, 2014). The Gini coefficient is a measure of inequality, bounded between 0 and 1, and low values in our use case would indicate a more equal distribution of diameters, whereas higher values would indicate that trees or lianas were very variable in size.

4.3.3 Environmental data

Each site provided information on the forest ages of all their plots, which were derived from a mixture of interviews, satellite imagery and aerial photography. Prior land use history was also available for many plots, with the predominant prior land use before abandonment being pasture or shifting cultivation. However, there was a lack of clarity on land-use for many of the plots (e.g. classed broadly as pasture/shifting cultivation) and several plots would not fit neat land use categories, and so land use classifications were not used further.

In addition to these data, we obtained monthly precipitation and potential evapotranspiration data from the TerraClimate dataset for all years between 1958 and 2015 (Abatzoglou et al., 2018). These precipitation data were at a 4 km^2 resolution (Abatzoglou et al., 2018), and so there was precipitation variability within sites at a plot level. Monthly precipitation and potential evapotranspiration values were used to calculate mean annual precipitation (MAP), dry season length (in months), dry season rainfall, maximum climatological water deficit and a precipitation seasonality index, at a plot level, following code available in Schwartz et al. (2020). Dry season length was defined as those months in which precipitation was lower than potential evapotranspiration and maximum climatological water deficit was defined as the largest negative difference between precipitation and potential evapotranspiration over a 12-month period (Schwartz et al., 2020). We calculated a seasonality index derived from Feng, Porporato and Rodriguez-Iturbe (2013), which is a dimensionless metric which quantifies the distribution of precipitation throughout the year in relation to the mean annual precipitation of a plot, and the maximum annual precipitation within the entire dataset (i.e. all precipitation across all 12 chronosequences). High seasonality index values, thus indicate that precipitation is highly varied throughout the year whereas, low seasonality index values can indicate uniform precipitation throughout the year or low total precipitation (Feng, Porporato and Rodriguez-Iturbe, 2013). Sites were also classified as either dry forest (MAP < 1500 mm year^{-1}) or moist/wet forests (MAP ≥ 1500 mm year^{-1}) following Rozendaal et al. (2019). We did not have enough wet forest sites to distinguish between moist/wet forest in this classification.

Furthermore, we obtained tree cover (Hansen et al., 2013) and forest landscape integrity data (Grantham et al., 2020) as proxies for landscape disturbance. Global tree cover rasters, with a 30 m x 30 m resolution (Hansen et al., 2013), showing the percentage of tree canopy cover per pixel during the peak growth season in 2010, for all trees ≥ 5m tall, were obtained from the Global Land Analysis and Discovery (2010) website. Tree cover per pixel was converted to percent forest cover in a circular 5-km buffer surrounding each plot based upon a 30 % tree cover threshold to classify each pixel as forest/non-forest and then the percentage of forest pixels/total pixels was calculated, following Rozendaal et al. (2019). Similarly, median forest landscape integrity index values were extracted for 5-km buffers surrounding each plot. The forest landscape integrity index data has a 300 x 300 m resolution and was calculated for forest extents in 2019 (Grantham et al., 2020). The forest landscape integrity index is derived from: forest extent data; observed human pressures on the landscape (i.e. nearby infrastructure, crop intensity and the past 18 years of deforestation); inferred human pressures (i.e. modelled edge effects over 5-km into the forest, human impacts such as hunting, grazing and pollution events) and finally, the loss of forest connectivity within a 80-km area (Grantham et al., 2020). High values of forest integrity are indicative of undisturbed, naturally regenerating forests with little human influence, and low values of forest integrity indicate highly fragmented landscapes, under strong anthropogenic pressures (Grantham et al., 2020). Thus, the landscape forest integrity index may be a useful proxy to assess disturbance, and thus potential impacts on liana abundance, as lianas are known to be found in higher abundance at forest edges, and in fragmented landscapes (Campbell et al., 2018; Laurance et al., 2001). For the two sites which only had site-based coordinates available (Figure S4.2), percent forest cover and forest landscape integrity index were only calculated for 5-km buffers surrounding those points.

4.3.4 Data analysis

Potential collinearity among environmental variables (forest age and all precipitation and disturbance related metrics) was examined using the `vifstep` function in the *usdm* R package (Naimi et al., 2014) and a variance inflation factor cut-off of 10. Dry season length, dry season rainfall and MAP/ maximum climatological water deficit were all found to be collinear and so only MAP was retained for further analyses, due to the use of MAP across previous biogeographical liana studies (e.g. DeWalt et al., 2010; Parolari et al., 2019; Schnitzer, 2005; van der Heijden and Phillips, 2008). Percent forest cover and the median landscape forest integrity index were also strongly correlated (Figure S4.3) and so only one of these variables was fit in subsequent models.

We modelled liana density per 0.1 ha, for all liana genets and ramets in secondary forest, according to Equation 4.1 using a generalised linear mixed model (GLMM), with a zero inflated negative binomial distribution (log-link function) through the *glmmTMB* R package (Brooks et al., 2017). The zero inflated negative binomial distribution was chosen as we were modelling count data which had evidence of overdispersion (P = 0.024), and simple negative binomial and Poisson distribution models had poor residual fit. Thus, a zero inflated term was added with tree AGB as the variable used to explain excess zeros in the model. Tree AGB was used because: 1. The very earliest successional plots may not have been colonised by lianas yet, particularly in stressful, dry forest sites; 2. It was a proxy which accounted for the fact that many early successional sites had smaller plot sizes, and thus a higher chance of encountering zero lianas in a plot (Table S4.1, Figure S4.1). The three-way interaction was included in the model (Equation 4.1) as it allowed us to directly test how different sized lianas varied through succession in both dry and moist/wet forest. Moreover, models excluding this interaction were not viable as experimental design constraints meant that different size cut-offs for liana measurements were used across sites (Table S4.1, Figure S4.1). Thus, including the liana size class term allowed us to compare similarly measured liana stems across each site, irrespective of the original size cut-off used. The Forest Integrity Index was included in the model (Equation 4.1) as a proxy for disturbance and Seasonality Index was included to explore changes in precipitation throughout the year, over absolute precipitation (the wet-dry classification).

Equation 4.1:

$$\begin{aligned} Liana\ Density\ per\ 0.1\ ha \sim\ & poly(Tree\ AGB\ per\ 0.1\ ha, 2) * Liana\ Size\ Class * Wet \\ & - Dry\ Classification + Seasonality\ index + Forest\ Integrity\ Index \\ & + (1|Site), \qquad Family = nbinom2(link = "log"), \\ & ziformula\ =\ \sim Tree\ AGB\ per\ 0.1\ ha \end{aligned}$$

Similarly, we modelled liana basal area per 0.1-ha, according to Equation 4.2, using a GLMM with a zero inflated gamma distribution through the *glmmTMB* R package (Brooks et al., 2017). A gamma distribution was chosen for the model due to the liana basal area data being strongly right skewed. Zero inflated gamma distributions are a type of hurdle model, as gamma distributions cannot contain zero values, and thus non-zero and zeros in the liana basal area model were modelled as if separate. Tree biomass was included to explain the zero-inflated data values for the same reason as above. However, we also included an interaction term with the moist/wet and dry forest classification as liana basal area was more likely to be zero in small plots which were predominately located in dry forest sites.

Equation 4.2:

$$\begin{aligned} Liana\ Basal\ Area\ per\ 0.1\ ha \sim\ & poly(Tree\ AGB\ per\ 0.1\ ha, 2) * Liana\ Size\ Class * Wet \\ & - Dry\ Classification + Seasonality\ index + Forest\ Integrity\ Index \\ & + (1|Site), \qquad Family = ziGamma(link = "log"), \\ & ziformula\ =\ \sim Tree\ AGB\ per\ 0.1\ ha\ *\ Wet - Dry\ Classification \end{aligned}$$

Site was included as a random intercept in both models, to account for potential spatial autocorrelation among plots within a site, as we did not have coordinate data for all sites to include a spatial autocorrelation term in the model. One site, Piracicaba, was excluded from all analysis, as it did not have individual liana diameter measurements, and another site, Kiuic, was excluded due to its different site structure negatively impacting model residuals. Rio Madeira was also not examined in these models, as it only included lianas > 5 cm in diameter.

We initially tried models with MAP as a continuous variable instead of the dry – moist/wet forest classification dichotomy. However, model residuals and assumptions of normality were violated when MAP was used, in both Equation 4.1 and Equation 4.2, and so we used the dry and moist/wet forest classification in the model and model fit improved. Model assumptions were checked through use of the *DHARMa* R package (Hartig, 2022) to examine model residuals (Figure S4.4, S4.5), and AIC values were used to select the best fitting model, with models ≥ 2 AIC lower than other models deemed to have considerably more support (Burnham and Anderson, 2004). Both liana density and basal area models displayed variation in their residual vs predicted plots (Figure S4.4, S4.5), but no modelling assumptions were violated. Tree AGB was used instead of forest age as an explanatory variable, as the two are significantly correlated (*Pearson's correlation* = 0.581, $P < 0.001$) and the inclusion of tree AGB rather than forest age improved the model fits. The use of AGB over forest age is also beneficial as it potentially incorporates ongoing disturbance and removes some of the uncertainty which is associated with the estimates of older forest stand ages. AGB values were truncated to 35 Mg ha^{-1} for both equation 4.1 and 4.2 to exclude outliers, and to avoid extrapolating model predictions for dry and moist/wet tropical forest. Only five values in the dataset had AGB values > 35 Mg ha^{-1} (values ranged between 49 and 51 Mg ha^{-1}) and inclusion of these values in analyses caused significant outliers (e.g. Equation 1: *DHARMa outlier test;* $P = 0.028$) which negatively influenced model predictions. Whilst the values may be accurate, the five identified outlier AGB values were excluded as their inclusion led to model predictions being extrapolated over the 35-50 Mg ha^{-1} section of tree biomass, as we had no other data spanning this biomass range. Neither tree basal area, nor tree density improved model fit and so only tree aboveground biomass was included in the models.

Post-hoc model comparisons were conducted using the *emmeans* R package (Lenth, 2023) to extract estimated marginal means and to compare them for each combination of categorical variables (forest type and size class) when the GLMM indicated significant differences between categories. Estimated marginal means were conducted for the three-way interaction, in both the density and basal area models, by comparing the liana size class and forest type interaction against tree aboveground biomass at six separate contrasts (AGB = 5, 10, 15, 20, 25, 30 Mg per 0.1-ha) spanning the range of our tree biomass data, and thus the range of model predictions (Table S4.3, S4.5). Multiple pairwise comparisons were adjusted for using the Tukey adjustment (Lenth, 2023). Model predictions were visualised using the *sjPlot* R package (Lüdecke, 2022).

Further investigations into liana-tree relationships were carried out by first examining how Gini coefficients of liana and tree diameter varied between sites in early-to-mid succession (defined as 0 – 50 years) and late succession/old growth forest (forest > 50 years old). Comparisons between diameter Gini coefficients were done at a site level, due to the differing plot sizes between sites, and non-parametric Kruskal Wallis tests were used to examine differences between growth form and successional stage.

We also examined the probability of liana density being greater than tree density per 0.1-ha scaled plot using a binomial GLMM with a logit link function (see Equation 4.3) via the *glmmTMB* R package (Brooks et al., 2017). In this model we subset the data to the nine sites which measured lianas ≥ 1 cm in diameter, and included liana genets and ramets, and compared liana density (for all stems ≥ 1 cm per 0.1-ha) to tree density (all stems ≥ 5 cm per 0.1-ha). Thus, this liana dominance measure does not indicate that liana density is definitively greater than tree density *per se*, as we do not have the data to compare liana density to similar size trees saplings (≥ 1 cm), but it does indicate plots where lianas are particularly high abundance. Liana density > tree density was coded as 1, and liana density < tree density coded as 0, for the binomial GLMM. Model selection procedures and checks of model fit were carried out as above.

Equation 4.3:

$$Liana\ Density > Tree\ Density\ Binomial \sim Seasonality\ Index + Tree\ AGB + (1|Site),$$
$$Family = binomial(link = "logit")$$

4.4 Results

We analysed data for 27,964 liana stems and 93,042 tree stems across nine Neotropical chronosequences, after sites were excluded due to data limitations, to investigate liana density and basal area changes through succession. Individual sites were highly variable in liana density, due to both local and regional environmental characteristics and site survey methods (Figure S4.6).

4.4.1 Liana Density

Liana density per 0.1-ha was 3.07 times higher in moist/wet forest than in dry forest (Figure 4.2A, Table S4.2), and our model explained a high proportion of the variability in liana density (Table S4.2; Marginal R^2 = 0.656, Conditional R^2 = 0.709). Small liana density was three times higher than medium liana density and 40 times higher than large lianas (Table S4.2, Figure S4.7D). When analysed by size-class, the density of small, medium, and large lianas did not significantly differ between moist/wet and dry forests (Table S4.2).

Liana density declined linearly with increasing above-ground biomass (Figure S4.7A, Table S4.2), and thus with increasing forest age as the two are strongly correlated. Seasonality had no apparent effect on liana density, but liana density increased marginally with increasing forest landscape integrity (Figure S4.7C, S4.7D, Table S4.2). The number of plots containing zero lianas decreased significantly with increasing above-ground biomass (Table S4.2).

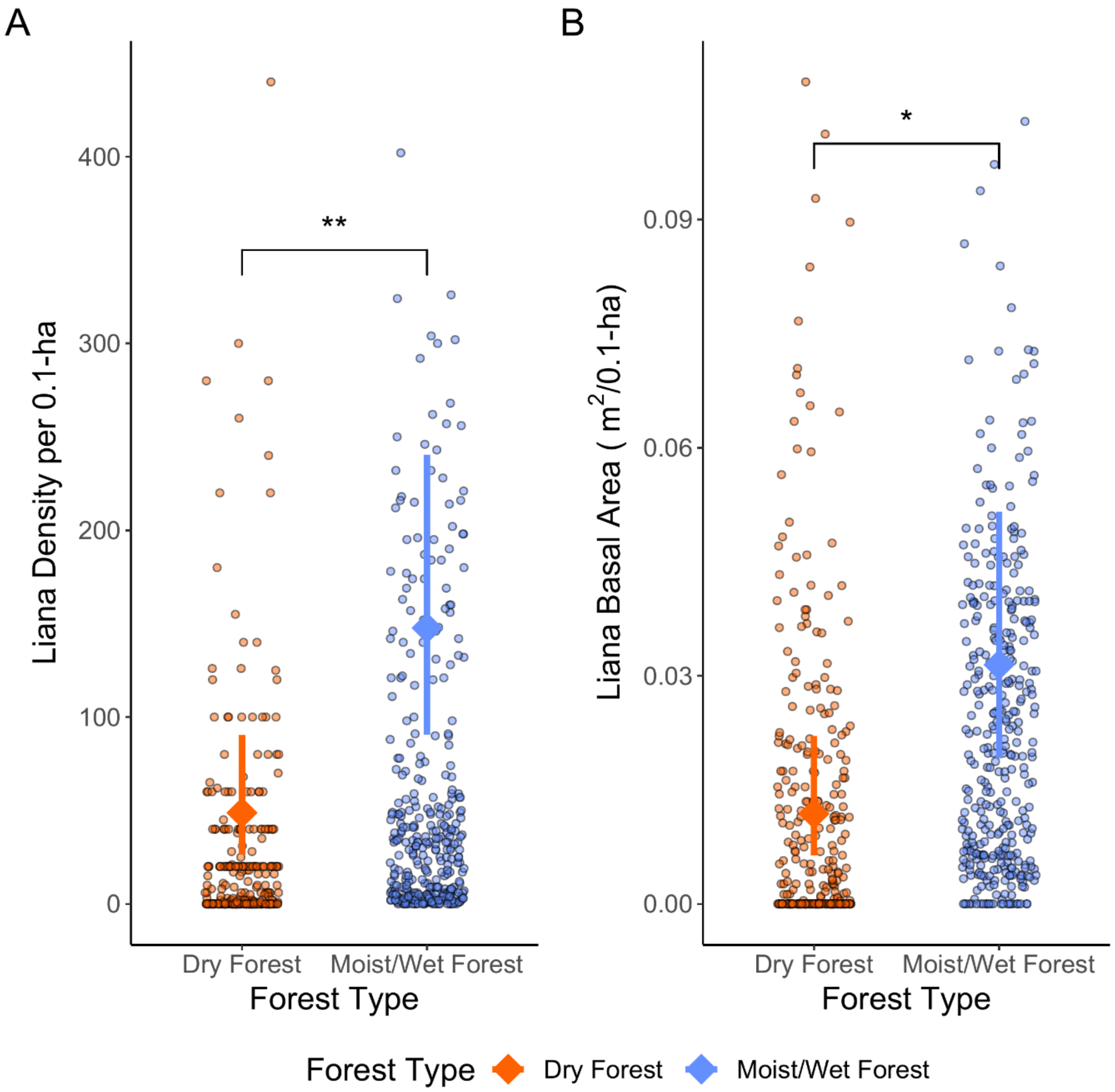

Figure 4.2. Predicted values of liana density (**A**) and liana basal area (**B**) for dry and moist/wet tropical forests. Diamond shapes and lines indicate the mean predicted value and the associated 95 % confidence interval. Jittered points indicate the raw data upon which models are based. Significant differences between categories are indicated by the asterisks (* = P < 0.05, ** = P < 0.01).

Significant three-way interactions were found for liana density when investigating the effect of size class, forest type and above-ground biomass (Figure 4.3, Table S4.2, S4.3). First, small lianas exhibit a more linear relationship with aboveground tree biomass than medium and large lianas; small liana density peaks early in succession and declines with increasing forest biomass (Figure 4.3). Thus, in low biomass forests, small lianas make up a larger component of liana stem density than medium and large lianas, but this difference disappears as forests age and accumulate biomass (Figure 4.3, Table S4.3). Second, small lianas in moist/wet forest appear to have a higher peak density, and a more rapid decline, than small lianas in dry forests, but differences between the two were not significant (Figure 4.3, Table S4.3). Third, medium lianas have intermediate peaks in density in both moist/wet forests and dry forests, although the peak appears to be in lower biomass forests for lianas in dry forests (Figure 4.3). Finally, large lianas are in low abundance throughout succession for both moist/wet and dry forests (Figure 4.3). However, in high biomass forests (AGB > 15Mg / 0.1ha) large lianas have significantly higher densities in moist/wet forests compared to dry forests (Table S4.3).

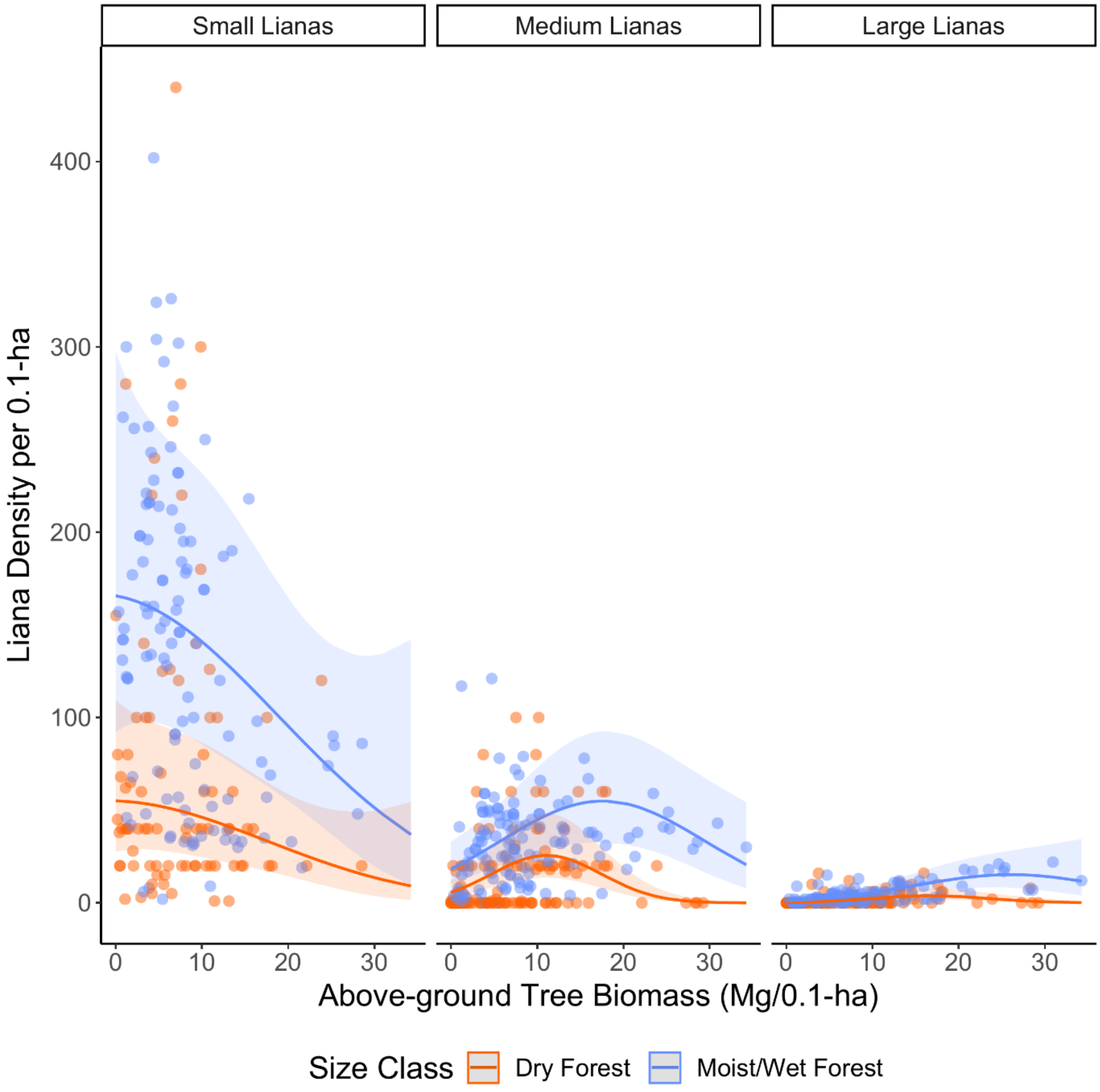

Figure 4.3. Plot depicting the interaction between liana density and above-ground tree biomass, liana size class and forest type. Small lianas were defined as stems 1 cm ≤ diameter < 2.5 cm; medium lianas were defined as stems 2.5 cm ≤ diameter < 5 cm and large lianas were ≥ 5 cm in diameter. Above-ground tree biomass was calculated for all tree stems ≥ 5 cm DBH. Model predictions are indicated by the solid lines and shaded areas indicate ±95% confidence intervals.

4.4.2 Liana Basal Area

The basal area model explained a lower proportion of variation than the liana density model (Table S4.4; Marginal $R^2 = 0.286$, Conditional $R^2 = 0.507$). Overall, moist/wet forest liana basal area was significantly higher than dry forest liana basal area (Figure 4.2B, Table S4.4), and medium size class lianas had higher basal area than both small and large lianas (Figure S4.8, Table S4.4). Small and medium moist/wet forest lianas had higher basal area than large moist/wet forest lianas but there were no differences in basal area among dry forest liana size classes or between dry and wet forest liana size classes (Figure S4.9). No relationship was found between liana basal area and aboveground tree biomass or seasonality index, but again there was a marginal increase in basal area with increasing forest integrity index values (Figure S4.8, Table S4.4). The number of plots with zero liana basal area was strongly related to the forest classification, and dry forests had significantly more plots with zero lianas (Table S4.4). This pattern is likely because of dry forest sites generally having smaller plot sizes, prior to standardisation, and fewer medium and large lianas. Increasing aboveground biomass was associated with a decreased likelihood of finding zero lianas within a plot, as was the interaction of increasing aboveground biomass and plot location in moist/wet forest (Table S4.4).

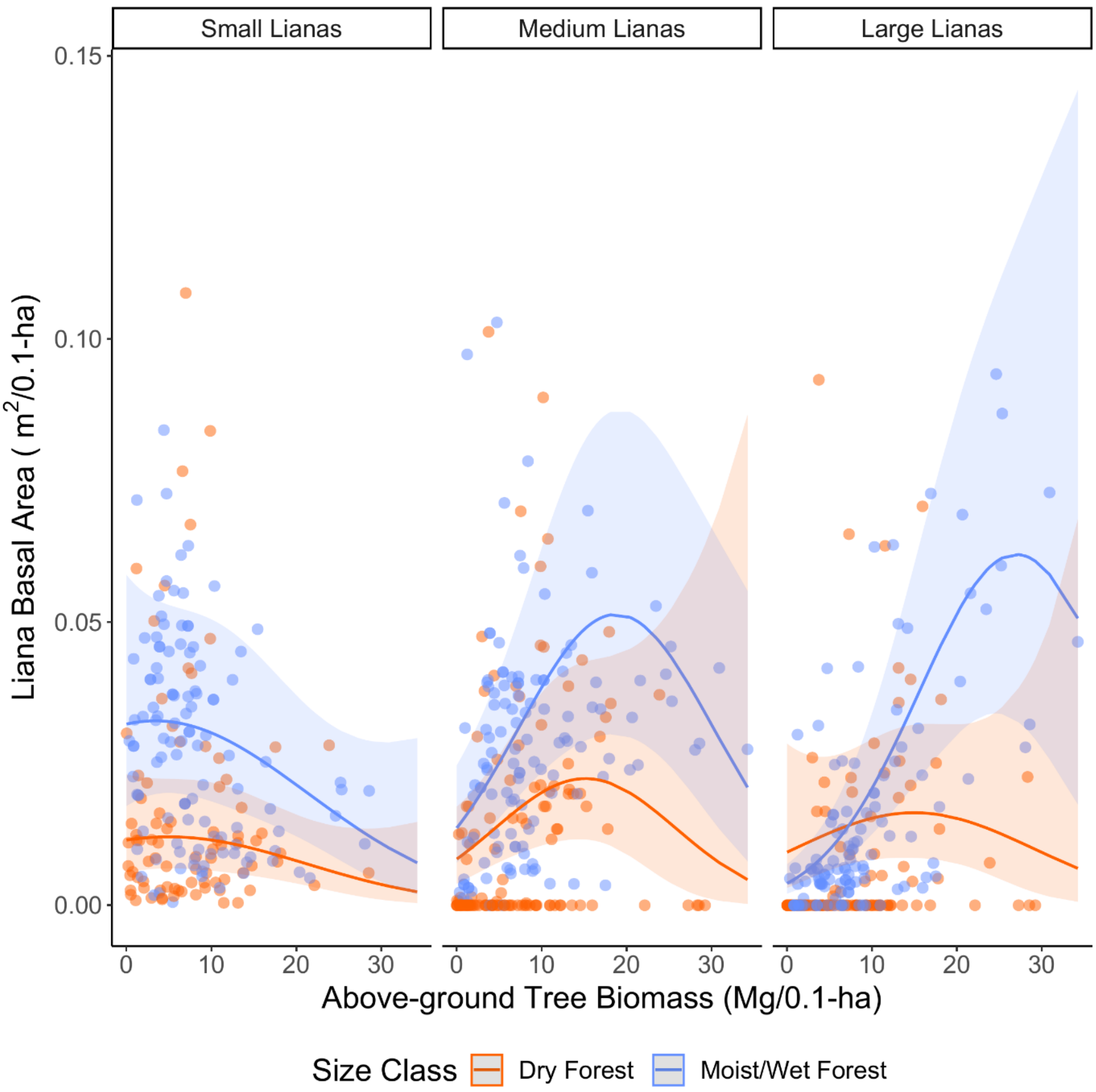

Figure 4.4. Interaction between liana basal area and above-ground tree biomass, liana size class and forest type. Small lianas were defined as stems 1 cm ≤ diameter < 2.5 cm; medium lianas were defined as stems 2.5 cm ≤ diameter < 5 cm and large lianas were ≥ 5 cm in diameter. Note that zeros present in the liana basal area model were modelled separately in a hurdle model process, and so do not influence the relationships shown here. Model predictions are indicated by the solid lines and shaded areas indicate ±95% confidence intervals.

Liana basal area significantly interacted with size class, tree biomass and forest type when examining three-way interactions, but differences between same-size class lianas in moist/wet and dry forest were limited (Figure 4.4, Table S4.4, S4.5). The basal area of small and medium lianas was consistently higher in moist/wet forest than dry forest, but not significantly so, and this relationship did not significantly differ with increasing aboveground tree biomass (Figure S4.4, Table S4.5). In contrast, large lianas in moist/wet forest had significantly higher basal area than large dry forest lianas at higher values of aboveground biomass values between 15 and 20 Mg 0.1 ha (Figure 4.4, Table S4.5). Large and medium lianas follow intermediate peaks in basal area, which appear to differ in magnitude between forest type (Figure 4.4). Conversely, small liana basal area peaks in low biomass forests for both moist/wet and dry forest lianas (Figure 4.4).

4.4.3 Liana-tree relationships

In dry forest sites, lianas were more constrained in size than trees (Figure 4.5). Gini coefficient values were consistently low for dry forest lianas, indicating that liana stems in dry forest are more equal in diameter than tree stems in the same forests (Figure 4.5). This pattern holds for both early and late successional dry forests ($P = 0.011$ for early and mid-successional stages and $P = 0.018$ for late succession and old-growth sites), but no equivalent significant relationship was found for lianas and trees in moist/wet forest (Figure 4.5; $P = 0.117$ and $P = 0.078$ for early and late successional sites respectively). However, the trends between trees and lianas were similar (Figure 4.5), and it may be that with a larger sample size a similar relationship between lianas and trees in moist/wet forests may emerge. Gini coefficients for lianas did not differ significantly with forest type (i.e. dry forest compared to moist/wet forest; $P = 0.361$), although moist/wet forest sites generally had higher Gini coefficient values in both early and late succession, indicating a greater range of liana diameters (Figure 4.5).

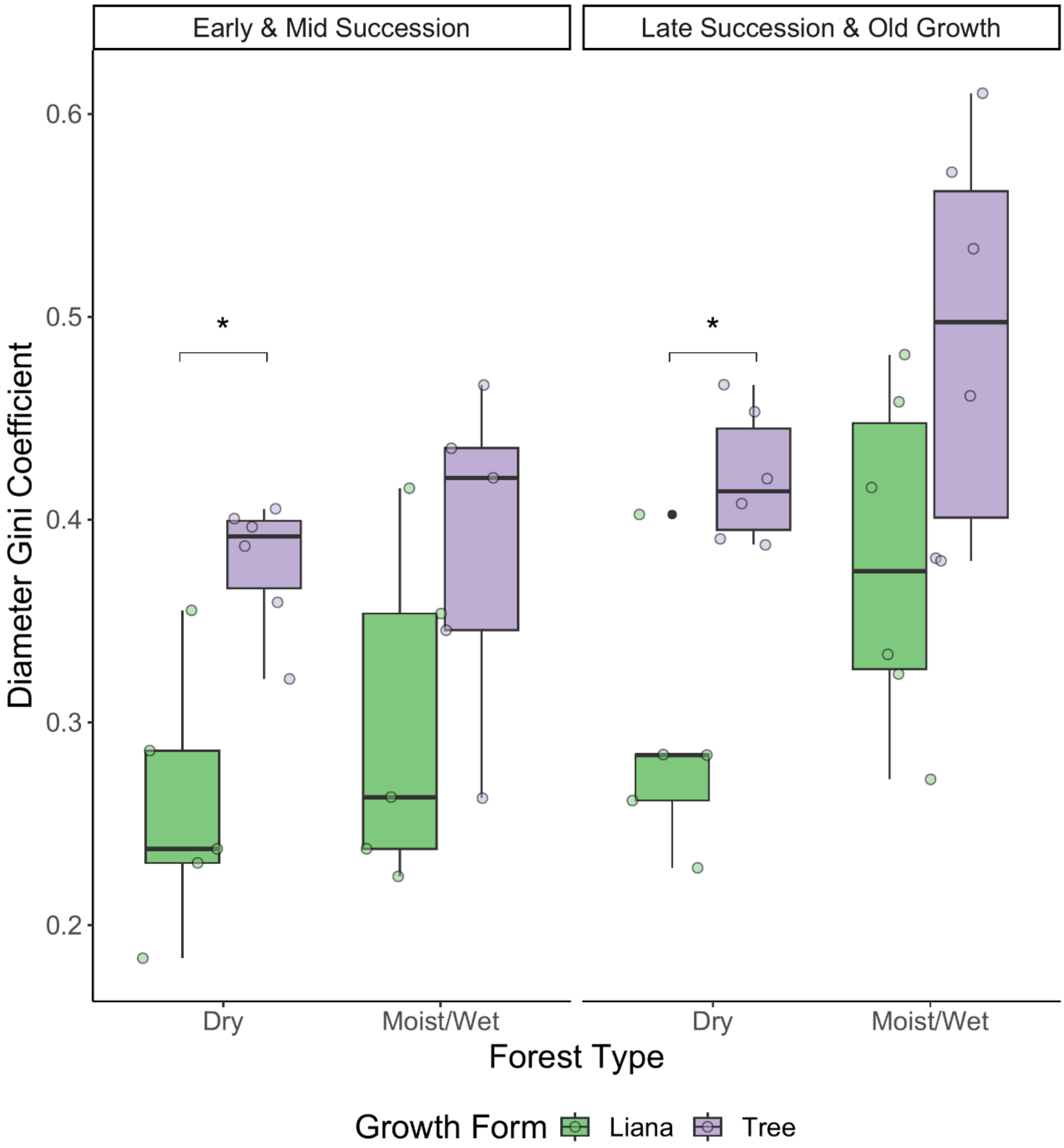

Figure 4.5. Gini coefficient of trees and liana diameters grouped by site, forest type and successional stage. Early and mid-succession (forests aged 0 – 50 years) and late succession and old growth were grouped to allow categorical analyses.

Liana dominance (i.e. liana density > tree density per 0.1-ha plot) did not significantly differ with above-ground biomass, yet there is a trend of decreasing liana dominance with increasing tree biomass, and thus forest age(Figure 4.6, Table S4.6, *P* = 0.137). Liana dominance is low in aseasonal plots and increases significantly with increasing seasonality, with up to ~80% of plots predicted to be dominated by lianas in the most seasonal plots (Figure S4.6, Table S4.6, *P* = 0.014). These results may suggest evidence of the seasonal growth advantage hypothesis (Schnitzer, 2018b). However, they must be caveated with the fact that only nine chronosequences are included in this analysis, and these sites do not span the full breadth of MAP, seasonality, and biomass values across the region (Figure S4.10). Specifically, we lack late successional (high biomass) sites with high rainfall and our low seasonality sites are biased towards dry forest (Figure S4.10), hence the large confidence intervals in our predictions.

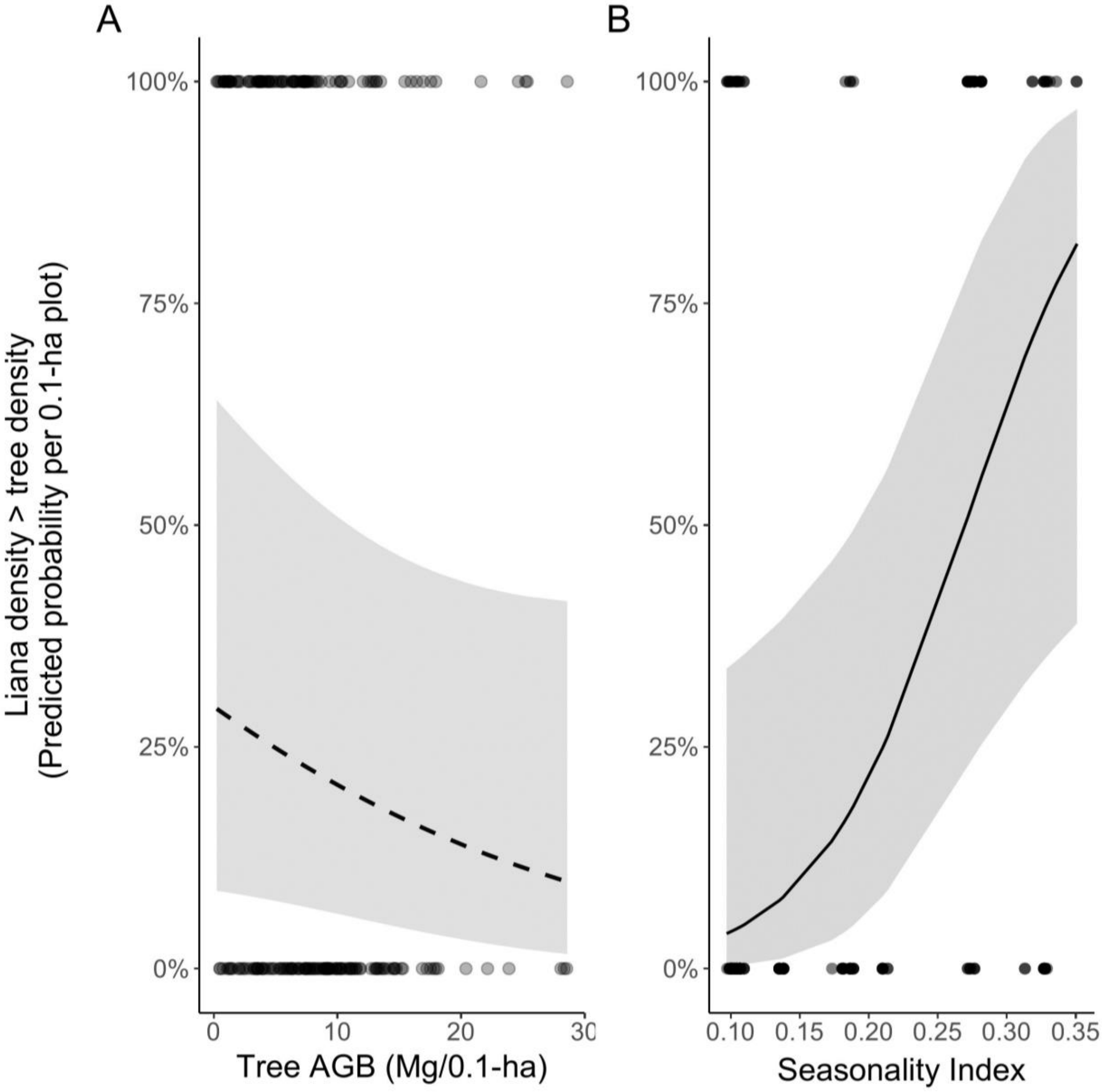

Figure 4.6. Probability of liana density (all stems ≥ 1 cm) being greater than tree density (all stems ≥ 5 cm). Panel **A** examines the non-significant relationship with tree AGB; **B** examines the relationship with seasonality. The shading associated with each line represents the 95 % confidence intervals.

4.5 Discussion

Contrary to expectations, we found that liana density and basal area were higher in moist/wet tropical forest than dry tropical forest (Figure 4.2). Small lianas had the highest density, but medium lianas made up the largest proportion of liana basal area across our sites (Figures 4.3 and 4.4). We found no significant differences between moist/wet and dry forest liana density or basal area when purely examining interactions with liana size class. However, interactions between tree biomass, forest classification and liana density and basal area revealed that most/wet forests contained significantly higher densities of large lianas than dry forest in high biomass forests (Figures 4.3 and 4.4). Moreover, we found evidence that liana dominance i.e., plots where liana density > tree density, is most likely in highly seasonal forests (Figure 4.6). Thus, we find that liana density in secondary forests may have a different relationship with MAP to the established paradigm in old-growth plots (DeWalt et al., 2015, 2010; Schnitzer, 2005) and also find evidence supporting the seasonal growth advantage hypothesis (Schnitzer, 2018b).

4.5.1 Liana density and basal area in wet and dry forests

Our finding, that moist/wet tropical forests have higher liana density and basal area than dry forest (Figure 4.2), contrasts with many previous studies that have found the converse relationship (DeWalt et al., 2015, 2010; Schnitzer, 2005; Swaine and Grace, 2007), or no relationship with MAP (van der Heijden and Phillips, 2008; Poulsen et al., 2017). There are several differences between our study and previous studies, which may explain the contrasting results. We analysed only secondary forests, whereas most other studies primarily examined old-growth forests (Schnitzer, 2005; van der Heijden and Phillips, 2008; DeWalt et al., 2010, 2015). Therefore, it may be that the relationship between liana density and MAP differs between secondary forests and intact old-growth forests. One mechanism which may promote this difference is that shifts in light availability differ in importance through succession between wet and dry tropical forests (Ceccon et al., 2006; Lohbeck et al., 2013). Tropical dry forests have lower canopy heights than moist and wet tropical forests (Klein et al., 2015; Lefsky, 2010), and therefore forest light availability in the understory may be less limited in dry than wet old-growth forests. Moreover, tropical dry forests are more deciduous than wet tropical forests (Poorter et al., 2021b), and thus the understory of tropical dry forests receives more light during the dry season. Dry forests in the early stages of succession are initially stressful, high temperature and low water availability environments, but these conditions are ameliorated by canopy closure as succession progresses (Lebrija-Trejos et al., 2011). Therefore, it may be that the initial highly stressful environments of young dry forests, are not conducive for typically acquisitive liana species (Mello et al., 2020) to survive in high densities (e.g. Carvalho et al., (2016)), in comparison to young moist/wet forest, as earlier successional trees in dry forests are often conservative in strategy (Poorter et al., 2021b). However, the increased light availability in dry forests in old growth-forest, compared to wet forests, could mean increased opportunity for liana colonisation in dry forests, whereas lianas in moist/wet forests typically rely on canopy gaps to reach the canopy (Schnitzer et al., 2021). Thus, inherent light and water availability differences between wet and dry forest through succession could play a key role in determining liana abundance.

Alternatively, our moist/wet and dry forest classification may be masking changes in seasonality between sites, which are known to drive differences in liana abundance (DeWalt et al., 2015, 2010;

Parolari et al., 2020). We found no effect of precipitation seasonality on liana density or basal area in our study (Tables S4.2 and S4.4). However, many of the forests included in our moist/wet forest category have higher seasonality than forests in the dry forest category (Figure S4.10). Increased seasonality is thought to drive liana abundance due to the seasonal growth advantage of lianas in dry conditions (Schnitzer, 2018b; Schnitzer and van der Heijden, 2019). This seasonal growth advantage may be due to lianas utilising water more efficiently than trees (Cai et al., 2009; Smith-Martin et al., 2019; Willson et al., 2022), being more plastic in leaf water usage (Maréchaux et al., 2017), having higher photosynthetic rates (Smith-Martin et al., 2019) or potentially accessing deeper water sources (Chen et al., (2015); but see Smith-Martin et al. (2019) and Willson et al. (2022)). Therefore, it may be that the difference in liana densities we find between moist/wet and dry forests could be partially explained by precipitation seasonality, and not MAP *per se*. In support of this idea, are the generally weak effects of MAP on liana densities found by other studies (Schnitzer, 2005; van der Heijden and Phillips, 2008; Poulsen et al., 2017; Parolari et al., 2020). However, our highest seasonality site, Chamela, is found in tropical dry forest, and has lower liana densities than many less seasonal forests sites (Figure S4.6). Moreover, one site, Mata Seca, has very low MAP of approximately 800 mm per year, and very low liana density (Figure S4.6) and lianas are known to be limited in abundance in the driest tropical forests (Carvalho et al., 2016). Therefore, we suggest that multiple factors, including light availability, MAP, seasonality, and site history, likely interact to drive the observed differences in liana density between sites.

4.5.2 Liana density and basal area relationships with tree biomass

We found declines in liana density with increasing tree biomass, but no relationship between liana basal area and tree biomass overall (Figure S4.7, Figure S4.8). This general pattern of liana density peaking in early-to-mid succession i.e., low tree biomass, mirrors findings from single site chronosequences in tropical secondary forests (DeWalt, Schnitzer and Denslow, 2000; Kuzee and Bongers, 2005; Letcher and Chazdon, 2009; Madeira et al., 2009; Mumbanza et al., 2022; but see Lomwong et al., 2023). This finding is likely because lianas are highly abundant in high-light conditions, such as treefall gaps and forest edges (Laurance et al., 2001; Schnitzer et al., 2021; Schnitzer and Carson, 2001), and the understory of young tropical forests receives more light than in late successional forests, releasing lianas from light limitation (Lebrija-Trejos et al., 2011). We use datasets from a number of studies that found high liana abundance early in succession (e.g. DeWalt, Schnitzer and Denslow, 2000; Letcher and Chazdon, 2009; Madeira et al., 2009), and we have extended these studies to investigate patterns across liana size classes. Different liana size classes peak in density and basal area, and thus ecological importance, at different successional stages; low tree biomass forests, i.e. early successional forests, have the highest density of small lianas in wet and dry forest, whereas medium and large lianas peak in density in the mid and late stages of succession (Figure 4.3). This difference among size classes is important because it suggests that if studies only include medium or large lianas, and they are examining successional gradients, they may miss major differences in density through time and thus underestimate the importance of lianas in secondary forests. The suppression of tree biomass accumulation by lianas (e.g. van der Heijden, Powers and Schnitzer, 2019; Estrada-Villegas et al., 2022a; Finlayson et al., 2022), may mean that the association between high liana density and low tree biomass is partially causal, and not solely related to deterministic successional processes.

We found that liana basal area was unrelated to tree biomass (Figure S4.8). DeWalt, Schnitzer and Denslow (2000), similarly found no relationship with liana basal area and successional stage, as liana declines in density through time were compensated by remaining lianas having larger basal areas, on average. In contrast, Letcher and Chazdon (2009) found liana biomass, which is related to liana basal area, to continually increase through succession, although differences between old-growth liana biomass and mid-stage successional plots were non-significant. Mumbanza et al. (2022) and Lomwong et al. (2023) also found liana basal area to increase into the late stages of succession. The lack of a general trend between liana basal area and tree biomass in our study may be due to the inclusion of sites that span precipitation and seasonality gradients, meaning that differences among sites could hide individual site relationships.

We found that small lianas had the highest density in early succession (Figure 4.3), which suggests that liana interactions with pioneer tree species are also high, despite pioneer tree adaptations, e.g. large leaves and few branches, to reduce infestation rates (Putz, 1984). These liana-tree interactions in early succession are often negative to tree growth, given the high mortality of liana infested pioneer tree species (Visser et al., 2018b) and the ability of lianas to stall succession (Tymen et al., 2016). However, lianas in early succession may also have a beneficial effect on forest recovery, and Marshall et al. (2020) proposed that lianas may enable faster forest regeneration by improving understorey microclimatic conditions for seedling regeneration in some tropical forests. Medium and large lianas increase in relative importance in the later stages of succession (Figure 4.3), likely due to the time taken for liana growth and accumulation of carbon, and low abundance of larger lianas in early succession has previously been found (Estrada-Villegas et al., 2019). Large lianas are known to be associated with higher tree biomass (Poulsen et al., 2017) and we confirm findings by Phillips et al. (2005) that large lianas can comprise the majority of liana biomass/basal area, at least in our late stage successional plots (Figure 4.4). Thus, the presence of large lianas may be indicative of mature, high biomass forests (Jones et al., 2017; Poulsen et al., 2017).

Only large lianas differed significantly in density and basal area between high biomass moist/wet and dry forests in our plots (Figures 4.3 and 4.4). Moreover, liana basal area peaks for medium lianas in dry forests, unlike in moist/wet forests where liana basal area is highest in large lianas in high biomass plots. This suggests that lianas in dry forests are more constrained in size than lianas in moist/wet forest and have a lower upper size limit than lianas in wet forests. We see evidence for this in our analysis of diameter Gini coefficients among sites, where late-successional lianas in moist forest are qualitatively less similar in diameter than lianas in dry forests (Figure 4.5). Moreover, lianas are more constrained in size than trees are in dry forest, but the same significant relationship is not found in moist/wet forests (Figure 4.5). This diameter constraint, and the lower abundance of large lianas in dry forest, may be because lianas generally operate with less hydraulic safety than trees (De Guzman et al., 2017) and since xylem diameter and embolism risk scales with plant size (Rosell et al., 2017), large lianas in dry forest may constrained by the risk of embolism due to low water availability in drought periods.

4.5.3 Liana dominance in tropical forests

Lianas were more likely to dominate (i.e. liana density (1 cm min) > tree density (5 cm min)) in highly seasonal forests than aseasonal forests (Figure 4.6). This result provides evidence for the seasonal growth advantage hypothesis (Schnitzer, 2018; Schnitzer and van der Heijden, 2019) which our analyses on liana density and liana basal area struggles to detect. This suggests that the complexity of our liana density and basal area analyses, i.e. the inclusion of liana size classes and the wet-dry forest classification, may have made it difficult to detect seasonality effects (as mentioned above).We found no effect of tree biomass on liana dominance (Figure 4.6), which is surprising given that one would predict liana dominance to be highest in low biomass forests, i.e. early successional forests (e.g. Barry et al., 2015; DeWalt, Schnitzer and Denslow, 2000). It may be that site specific environmental and landscape factors such as differing land use histories, temperatures, connectivity, edge effects etc. (e.g. Arroyo-Rodríguez et al., 2017) increased the variance in our liana dominance results and so no significant tree biomass relationship was found, although a trend can be seen (Figure 4.6). These results may indicate the bioclimatic conditions under which liana dominated forests, which can arrest succession, are more likely to develop (Foster et al., 2008; Pérez-Salicrup et al., 2001; Tymen et al., 2016).

4.5.4 Liana census methodologies remain unstandardised

An incidental finding from our study is that standardised survey methodologies are still underused in liana research; across the 12 study sites plots varied in size from 0.02 ha to 0.2 ha with minimum liana census diameters varying from 0.5 to 10 cm in some subplots (Table S4.1; Figure S4.1). Gerwing et al. (2006) and Schnitzer, Rutishauser and Aguilar (2008) developed a standardised method to census lianas over 15 years ago, however only five out of 12 of our examined chronosequences explicitly followed this methodology. This may be because some of our data were collected prior to these developments in census methodology, however, data remain difficult to compare among sites. The plot sizes, shapes and diameter cut-offs used to survey lianas within our study differed considerably, and only two pairs of sites had directly equivalent methodologies (Figure S4.1). This is important, as plot shape has been found to influence the abundance of liana genets encountered, and same-area transects can encounter > 50 % more genets than square plots (Schnitzer, DeWalt and Chave, 2006). Schnitzer, DeWalt and Chave (2006) found that liana measurement location can significantly change liana density calculations, and so we used the equation derived by Schnitzer, DeWalt and Chave (2006) to standardise our liana diameters prior to calculating stem density and creating liana size classes. However, this equation was developed for lianas in the wet forests of French Guiana, which has a two-month dry season (Schnitzer, DeWalt and Chave., 2006). It is therefore feasible that errors may be propagated into liana diameters, when this conversion is used, as it may be that seasonal dry forest lianas of Central America do not follow the same allometric relationships. Understanding liana distributions is increasingly important given the increases in liana abundance in the Neotropics may have implications for patterns of secondary forest regeneration and carbon accumulation (Schnitzer, 2015; Schnitzer and Bongers, 2011). It is therefore imperative that we standardise liana survey methods in the future, to enable accurate comparisons in the secondary forests where lianas are likely most abundant.

4.5.5 Future work

We believe our study is an important baseline study for secondary forest liana comparisons in the Neotropics. Future work to improve the study would primarily begin with obtaining data from sites that span the full precipitation gradient, from 800 – 3900 mm (MAP). We have only one true wet forest site in the dataset (Sarapiqui, 3900 mm MAP; Figure 4.1, Table S4.1), and thus our generalisations of patterns in liana basal area and density are limited for wetter tropical forest sites. For instance, Schnitzer (2005) uses Alwyn Gentry's pantropical plant transect data that includes nine sites with MAP over 4000 mm. Including wetter sites is important, as they may reveal stronger relationships between MAP, seasonality and liana density. Moreover, additional sites may increase the number of high biomass plots within the dataset, and thus the uncertainty associated with many of our predictions in late succession may be better quantified (Figures 4.3, 4.4).

Future analyses to examine the role of disturbance within our plots could also aid interpretation of the results. Our chosen metric of disturbance, the landscape forest integrity index (Grantham et al., 2020), showed a slight positive relationship between forest integrity and increasing liana density, contrary to expectations (Figure S4.7). Lianas are typically found in high densities in highly disturbed environments (Campbell et al., 2018; Jones et al., 2017; Schnitzer and Carson, 2001). Therefore, it may be that, due to the relatively low number of independent sites in our study, landscape integrity was confounded with rainfall or seasonality metrics, as tropical dry forests are likely more threatened by human activity than wet forests (Miles et al., 2006). Alternatively, it may be that many of the broad spectrum of variables condensed into the landscape forest integrity index are simply not as relevant to liana abundance as a more direct measure may be (Grantham et al., 2020). To address this, we could first analyse forest integrity in a range of buffer zones surrounding each plot to see if smaller buffers, than the 5-km radius we used, are more indicative of actual disturbance conditions within each plot which may affect liana abundance. Other metrics of disturbance, e.g. the rate of local deforestation at the time of the chronosequence census could also be derived from the Hansen et al. (2013) forest change dataset as it is continually updated.

Additionally, future studies that examine how liana plot sizes influence genet and ramet densities would be of great value to the field. Such studies, could utilise long term forest dynamics plots with liana censuses, e.g. the 50-ha plot on Barro Colorado Island, Panama (Schnitzer et al., 2012) or in Pasoh, Malaysia (Wright et al., 2015), to examine how different plot sizes may impact the number of lianas encountered and to estimate optimum plot shapes and areas for liana censuses. Using consistent plot sizes, or methodologies to standardise plot size reliably, and census methodologies would increase the accuracy of liana censuses and enable reliable comparisons among liana studies in the future.

4.5.6 Conclusions

Our study is the first, large scale analysis of the relationship between liana density in dry and moist/wet successional forests. We find evidence suggesting that in secondary forests liana density may be higher in moist/wet forests than dry forests, contrary to previous findings from old-growth forests (DeWalt et al., 2015, 2010; Schnitzer, 2005). We also find evidence that seasonality increases the probability of liana dominance in secondary forests, and thus find direct support for the seasonal growth advantage hypothesis for lianas (Schnitzer, 2018). Our dataset also highlights the need for improved consistency across liana censuses as we show a diverse range of methodologies are still used for liana censuses. Our results are important tests of ecological theories in secondary forests given the increasing abundance of secondary forest worldwide (FAO, 2020) and suggest that liana abundance in secondary forests are influenced by forest age and tree biomass, in addition to precipitation and seasonality.

4.6 Acknowledgments:

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4.7 Supplementary Material

Table S4.1. Summary information for the chronosequences included in the study. Percentages of individuals identified to a species level are after data cleaning. Stand ages reported are in years and are approximate, as they were derived from a mix of interviews and satellite imagery/aerial photography.

Study Site	Country	MAP (mm)	No. of dry months	No. of plots	Mean Age (Range)	Liana diameter measurement location	No. of liana stems	% Liana individuals identified	No. of tree stems	% Tree individuals identified
Chamela/ Reserbos[a]	Mexico	800	7.9	12/30	13.7 (0 – 42)	130 cm from ground/ 10 cm from base	701/337	90.20 /100	6632/10742	99.86/99.75
Mata Seca	Brazil	825	9.4	18	18.5 (11 – 23)	130 cm from ground	254	85.43	2804	100
Kiuic	Mexico	1100	8.5	276	24.0 (6 – 60)	130 cm from ground	1567	100	33746	99.91
Quintana Roo	Mexico	1250	8.4	159	42.9 (2 – 100)	130 cm from ground	472	99.15	14823	99.91
Piracicaba	Brazil	1367	6.7	51	28.5 (11 – 48.5)	0.5 – 2m from ground	1367	0[b]	6597	97.32
Palo Verde	Costa Rica	1444	6.1	6	36 (18 – 71)	130 cm from base	742	98.38	356	100
Playa Venado	Panama	1550	5.3	13	24.3 (7 – 76)	130 cm from base	5585	99.64	10222	99.97
Santa Rosa	Costa Rica	1765	6.5	12	34.1 (16 – 71)	130 cm from base	708	98.44	919	100
Rio Madeira	Brazil	2507	3.3	75	45.4 (5 – 120)	130 cm from ground	90	67.78	8483	98.56
BCNM	Panama	2600	4.4	10	57.5 (20 – 100)	Largest point[c]	1895	84.22	3560	98.88
Agua Salud	Panama	2700	3.9	52	21.1 (6 – 56)	130 cm from base	23491	99.68	47360	99.99
Sarapiqui	Costa Rica	3900	1.9	30	38.5 (26 – 60)	130 cm from base	3771	99.89	7020	100

[a] Chamela and Reserbos were surveyed differently but are located in the same landscape; [b] Only liana density measured; [c] Only genets were surveyed

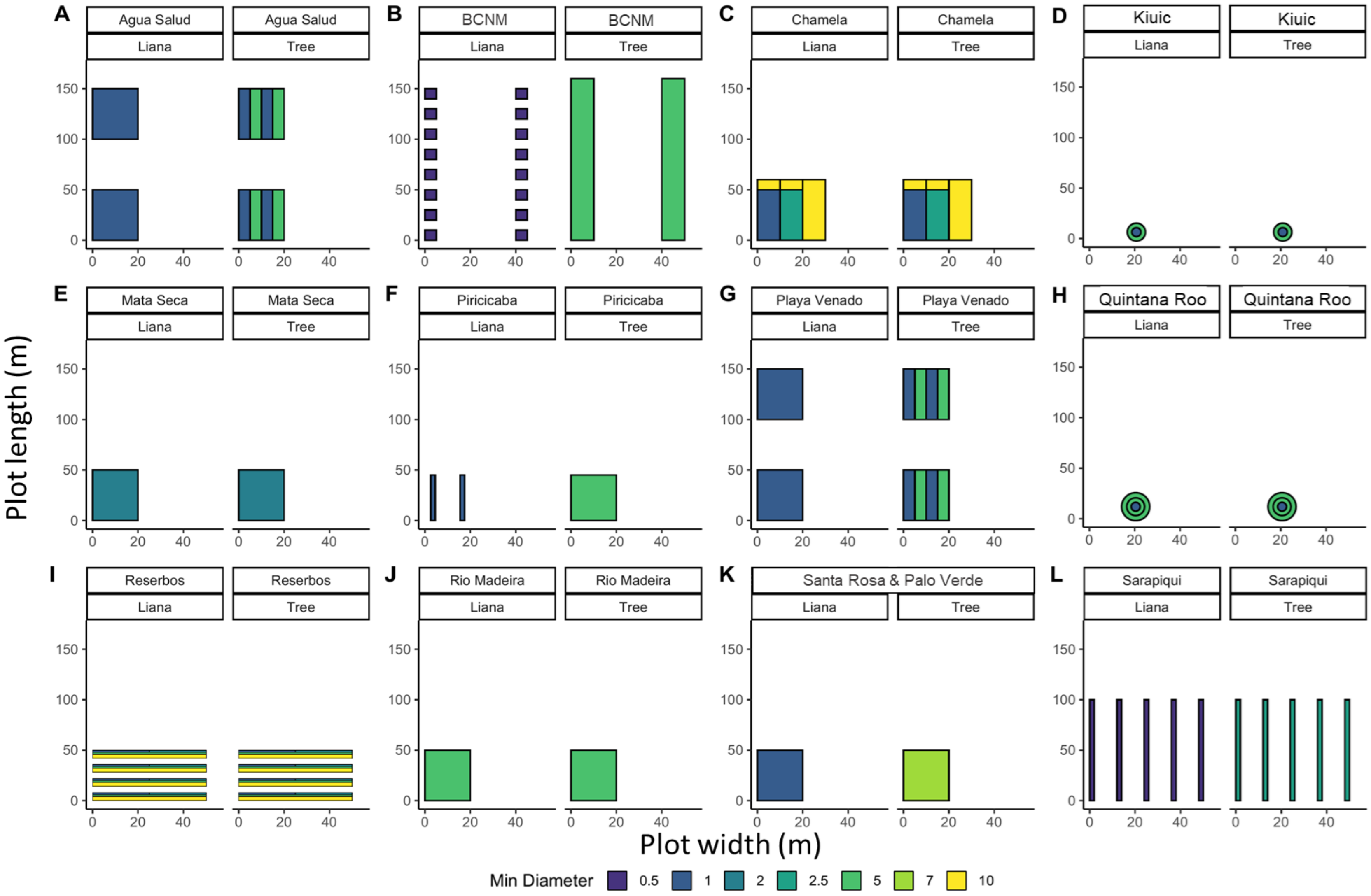

Figure S4.1. Plot layouts and census methods split by liana and tree per site/chronosequence. All subplots, and the minimum diameter that plants are surveyed to, are noted per site.

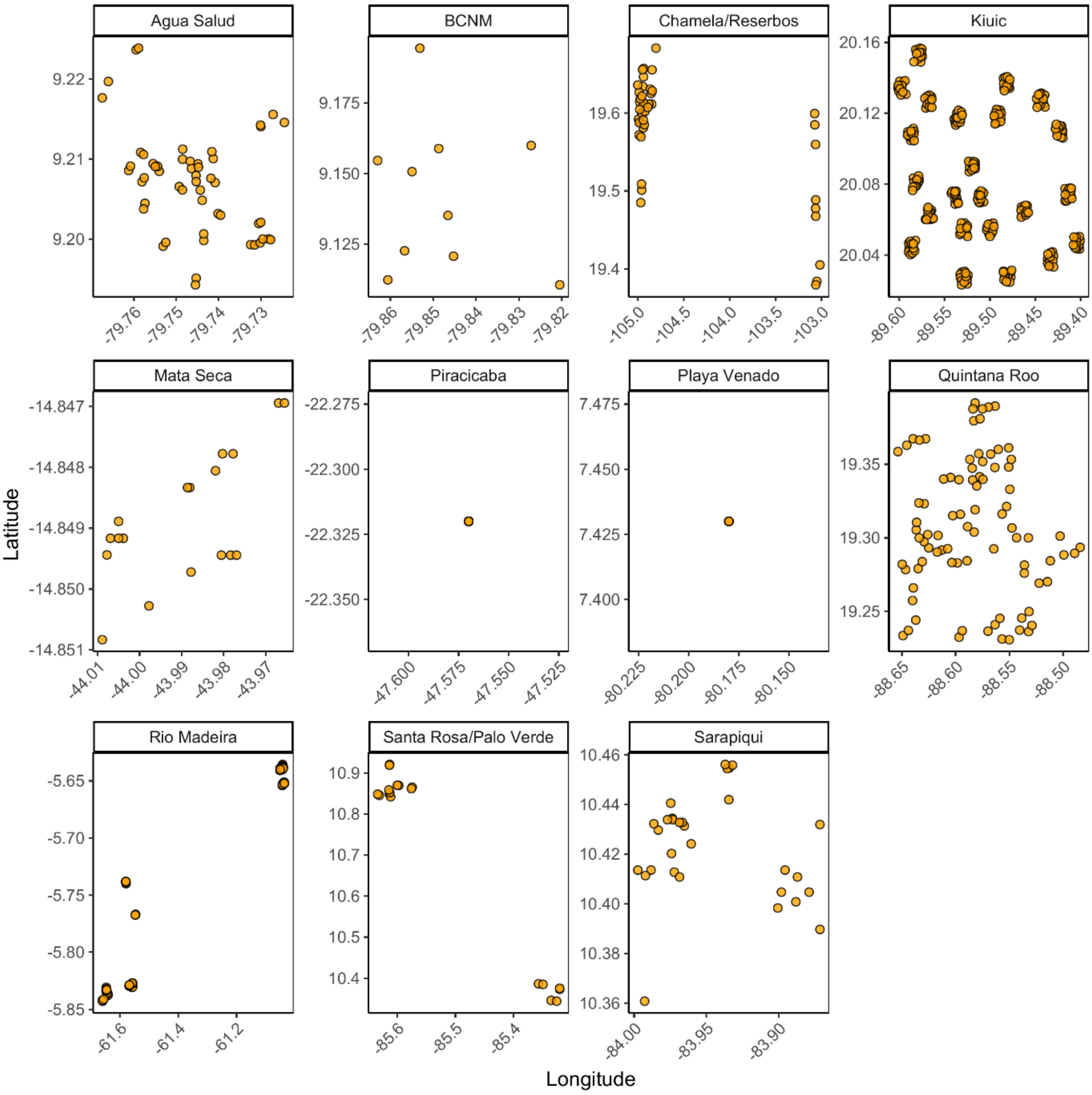

Figure S4.2. The spatial locations of each of the plots within our study sites. Note that Piracicaba and Playa Venado did not have GPS locations avaiable for the plots and so are indicated by a central lat-long value. In the Santa Rosa/ Palo Verde panel, Palo Verde is the subset of plots to the bottom right.

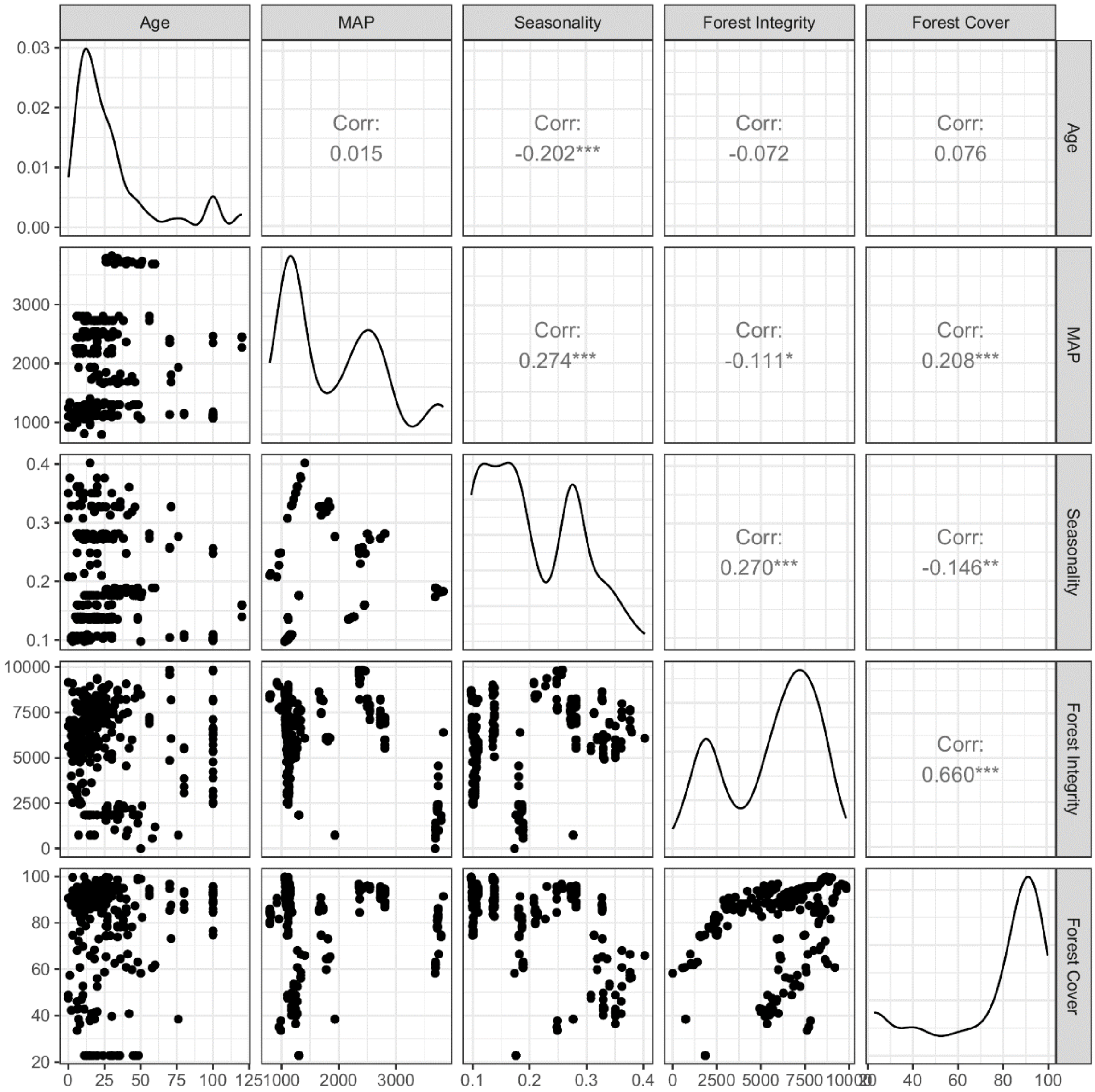

Figure S4.3. Correlations between environmental variables which are used to model changes in liana density and liana basal area. Potentially collinear variables were removed before plotting.

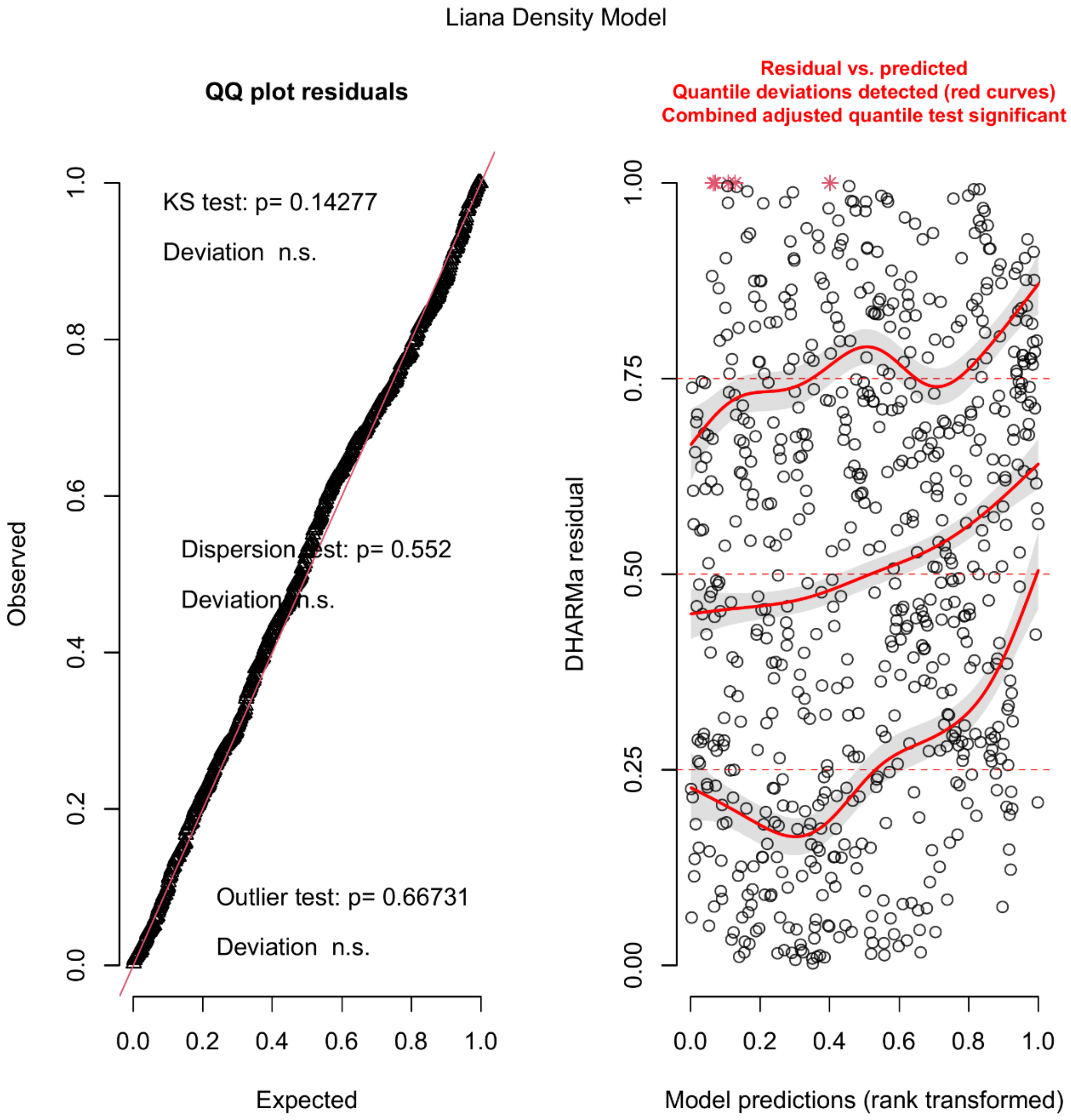

Figure S4.4. Model residuals for the Generalised Linear Mixed Model examining liana density against aboveground biomass, forest type and size class.

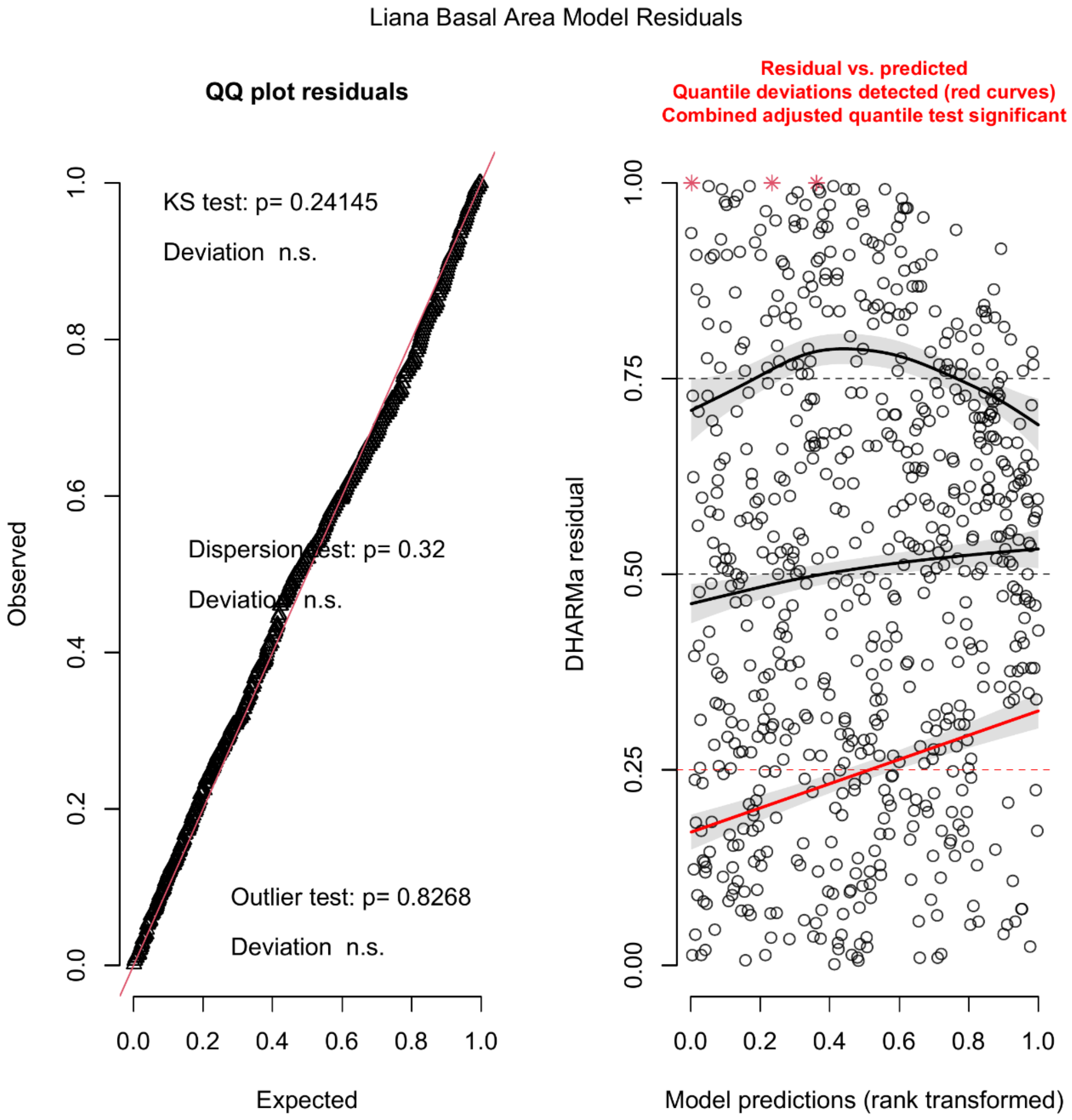

Figure S4.5. Model residuals for the Generalised Linear Mixed Model examining liana basal area against aboveground biomass, forest type and size class.

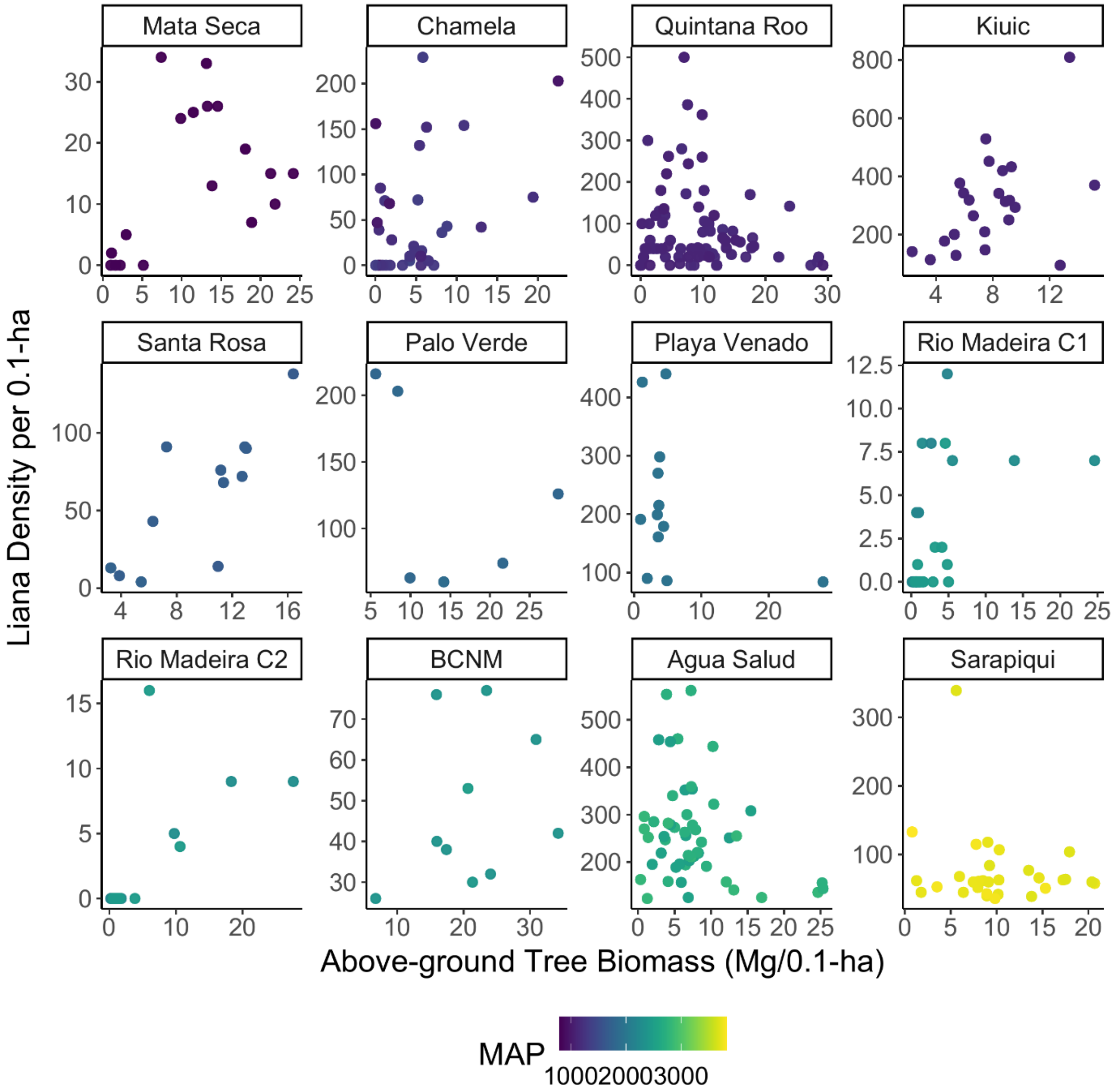

Figure S4.6. Liana density plotted per site against above-ground tree biomass. All plots were scaled to 0.1-ha prior to plotting. Different sites had different liana size cutoffs (ranging from 1 – 5 cm). Kiuic and both Rio Madeira chronsoequence sites are included for comparison but were not analysed in the final liana density or basal area model.

Table S4.2. Model output for the liana density generalised linear mixed model. Model estimates were transformed into incidence rate ratios using the *sjPlot* `tab_model` function (Lüdecke, 2022). Wet/Dry refers to the classification of forests according to mean annual precipitation. AGB refers to Above-Ground Tree Biomass for all trees ≥ 5 cm DBH.

Predictors	***Incidence Rate Ratios***	***95 % CI***	***Statistic***	***P value***
Count Model				
(Intercept)	60.866	19.546 – 189.538	7.089	**<0.001**
AGB [1st degree]	0.001	0.000 – 0.176	-2.645	**0.008**
AGB [2nd degree]	0.097	0.001 – 16.180	-0.894	0.371
Size Class [Medium]	0.297	0.229 – 0.385	-9.158	**<0.001**
Size Class [Large]	0.025	0.018 – 0.034	-21.930	**<0.001**
Wet/Dry [Moist/Wet]	3.070	1.413 – 6.667	2.834	**0.005**
Seasonality Index	0.035	0.001 – 1.450	-1.764	0.078
Forest Integrity	1.000	1.000 – 1.000	2.221	**0.026**
AGB [1st degree] * Size Class [Medium]	1.922	0.001 – 2510.590	0.178	0.858
AGB [2nd degree] * Size Class [Medium]	0.000	0.000 – 0.000	-4.376	**<0.001**
AGB [1st degree] * Size Class [Large]	$2.584 * 10^9$	$8.930 \text{ x } 10^5$ – $7.482 \text{ x } 10^{12}$	5.329	**<0.001**
AGB [2nd degree] * Size Class [Large]	0.000	0.000 – 0.002	-3.440	**0.001**
AGB [1st degree] * Wet/Dry [Moist/Wet]	2.754	0.005 – 1554.664	0.313	0.754

AGB [2nd degree] * Wet/Dry [Moist/Wet]	1.631	0.002 – 1372.203	0.142	0.887
Size Class [Medium] * Wet/Dry [Moist/Wet]	0.823	0.596 – 1.137	-1.180	0.238
Size Class [Large] * Wet/Dry [Moist/Wet]	1.067	0.715 – 1.592	0.316	0.752
AGB [1st degree] * Size Class [Medium] *Wet/Dry [Moist/Wet]	72471.135	8.964 – 5.859 x 10^{8}	2.438	**0.015**
AGB [2nd degree] * Size Class [Medium] *Wet/Dry [Moist/Wet]	793459.012	58.404 – 1.078 x 10^{10}	2.798	**0.005**
AGB [1st degree] * Size Class [Large] * Wet/Dry [Moist/Wet]	7.244	0.000 – 150900.881	0.390	0.696
AGB [2nd degree] * Size Class [Large] * Wet/Dry [Moist/Wet]	30069.464	1.034 – 8.746 x 10^{8}	1.966	**0.049**
(Intercept)	6.912	5.202 – 9.646		
Zero-Inflated Model				
(Intercept)	0.269	0.159 – 0.456	-4.890	**<0.001**
AGB	0.916	0.855 – 0.981	-2.509	**0.012**
Random Effects				
σ^2	1.33			
$\tau_{00\ \mathrm{Site3}}$	0.25			
ICC	0.16			
N_{Site3}	9			
Observations	680			
Marginal R^2 / Conditional R^2	0.656 / 0.709			

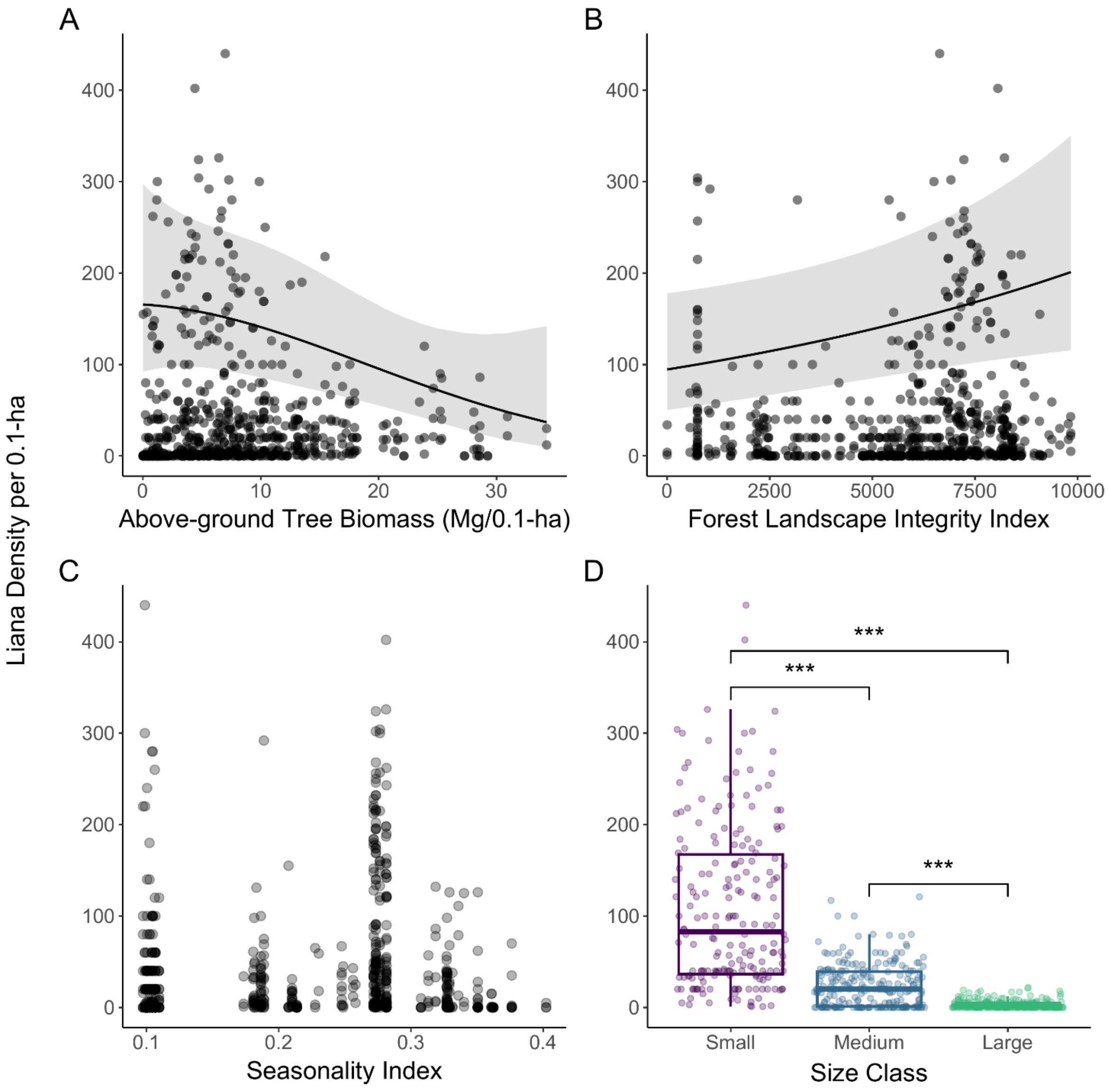

Figure S4.7. Relationship between liana density and above-ground tree biomass (**A**), forest landscape integrity index (**B**), seasonality index (**C**) and among liana size classes (**D**). Black lines and the shaded 95 % confidence intervals are present when a significant relationship was found. Relationships between size classes were determined by post-hoc tests using the *emmeans* R package (Lenth, 2023).

Table S4.3. Post-hoc test results from the three-way liana density interactions examining the effect of size class and forest type on liana density at set tree AGB values. Small, medium, and large in the table refer to liana size classes. Only significant differences between three-way interactions are recorded here due to table size constraints.

Contrast	*Estimate*	*SE*	*df*	*t ratio*	*P value*	*AGB*
Small Dry Forest - Medium Dry Forest	-0.166	0.038	656	-4.381	0.000	5
Small Dry Forest - Large Dry Forest	-0.264	0.047	656	-5.615	0.000	5
Small Dry Forest - (Medium Moist/Wet Forest)	-0.107	0.034	656	-3.125	0.023	5
Small Dry Forest - (Large Moist/Wet Forest)	-0.181	0.039	656	-4.672	0.000	5
Medium Dry Forest - (Small Moist/Wet Forest)	0.165	0.038	656	4.331	0.000	5
Large Dry Forest - (Small Moist/Wet Forest)	0.262	0.047	656	5.601	0.000	5
Large Dry Forest - (Medium Moist/Wet Forest)	0.157	0.047	656	3.373	0.010	5
(Small Moist/Wet Forest) - (Medium Moist/Wet Forest)	-0.105	0.032	656	-3.278	0.014	5
(Small Moist/Wet Forest) - (Large Moist/Wet Forest)	-0.179	0.037	656	-4.853	0.000	5
Small Dry Forest - (Medium Moist/Wet Forest)	-0.085	0.022	654	-3.948	0.001	10
Small Dry Forest - (Large Moist/Wet Forest)	-0.148	0.022	654	-6.688	0.000	10
Medium Dry Forest - (Small Moist/Wet Forest)	0.066	0.023	654	2.870	0.048	10
Medium Dry Forest - (Large Moist/Wet Forest)	-0.084	0.024	654	-3.501	0.007	10
Large Dry Forest - (Large Moist/Wet Forest)	-0.105	0.033	654	-3.144	0.021	10

(Small Moist/Wet Forest) - (Medium Moist/Wet Forest)	-0.086	0.020	654	-4.345	0.000	10
(Small Moist/Wet Forest) - (Large Moist/Wet Forest)	-0.150	0.021	654	-7.285	0.000	10
(Medium Moist/Wet Forest) - (Large Moist/Wet Forest)	-0.064	0.020	654	-3.170	0.020	10
Small Dry Forest - (Medium Moist/Wet Forest)	-0.066	0.022	654	-2.975	0.036	15
Small Dry Forest - (Large Moist/Wet Forest)	-0.129	0.023	654	-5.744	0.000	15
Large Dry Forest - (Large Moist/Wet Forest)	-0.091	0.027	654	-3.430	0.008	15
(Small Moist/Wet Forest) - (Medium Moist/Wet Forest)	-0.064	0.018	654	-3.636	0.004	15
(Small Moist/Wet Forest) - (Large Moist/Wet Forest)	-0.127	0.018	654	-7.074	0.000	15
(Medium Moist/Wet Forest) - (Large Moist/Wet Forest)	-0.063	0.015	654	-4.335	0.000	15
Small Dry Forest - (Large Moist/Wet Forest)	-0.110	0.037	654	-2.986	0.035	20
(Small Moist/Wet Forest) - (Large Moist/Wet Forest)	-0.104	0.030	654	-3.519	0.006	20

Table S4.4. Model output for the liana basal area generalised linear mixed model. Model estimates were transformed using the *sjPlot* `tab_model` function (Lüdecke, 2022). Wet/Dry refers to the classification of forests according to mean annual precipitation. AGB refers to Above-Ground Tree Biomass for all trees ≥ 5 cm DBH.

Predictors	***Estimates***	***95 % CI***	***Statistic***	***P value***
Count Model				
(Intercept)	0.011	0.004 – 0.037	-7.464	**<0.001**
AGB [1st degree]	0.008	0.000 – 1.182	-1.895	0.058
AGB [2nd degree]	0.046	0.000 – 9.054	-1.142	0.254
Size Class [Medium]	1.368	1.053 – 1.776	2.347	**0.019**
Size Class [Large]	1.199	0.823 – 1.748	0.944	0.345
Wet/Dry [Moist/Wet]	2.694	1.230 – 5.901	2.478	**0.013**
Seasonality Index	0.070	0.002 – 3.244	-1.359	0.174
Forest Integrity	1.000	1.000 – 1.000	2.407	**0.016**
AGB [1st degree] * Size Class [Medium]	7009.200	1.156 – 4.249 x 10^7	1.993	**0.046**
AGB [2nd degree] * Size Class [Medium]	0.018	0.000 – 244.446	-0.827	0.408
AGB [1st degree] * Size Class [Large]	1062.658	0.117 – 9.618 x 10^6	1.499	0.134
AGB [2nd degree] * Size Class [Large]	0.397	0.000 – 7738.906	-0.183	0.855
AGB [1st degree] * Wet/Dry [Moist/Wet]	1.083	0.002 – 698.257	0.024	0.981
AGB [2nd degree] * Wet/Dry [Moist/Wet]	1.786	0.002 – 1827.052	0.164	0.870

Size Class [Medium] * Wet/Dry [Moist/Wet]	0.711	0.512 – 0.986	-2.044	**0.041**
Size Class [Large] * Wet/Dry [Moist/Wet]	0.386	0.251 – 0.595	-4.313	**<0.001**
AGB [1st degree] * Size Class [Medium] *Wet/Dry [Moist/Wet]	54.138	0.002 – 1.730 x 10^{6}	0.754	0.451
AGB [2nd degree] * Size Class [Medium] *Wet/Dry [Moist/Wet]	1.535	0.000 – 93751.109	0.076	0.939
AGB [1st degree] * Size Class [Large] * Wet/Dry [Moist/Wet]	1.767 x 10^{7}	360.468 – 8.658 x 10^{11}	3.028	**0.002**
AGB [2nd degree] * Size Class [Large] * Wet/Dry [Moist/Wet]	0.065	0.000 – 5950.002	-0.470	0.639
Zero-Inflated Model				
(Intercept)	1.187	0.837 – 1.682	0.961	0.337
AGB	0.945	0.910 – 0.981	-2.971	**0.003**
Wet/Dry [Moist/Wet]	0.250	0.110 – 0.569	-3.310	**0.001**
AGB * Wet/Dry [Moist/Wet]	0.836	0.725 – 0.963	-2.479	**0.013**
Random Effects				
σ^2	0.56			
$\tau_{00\ \text{Site3}}$	0.25			
ICC	0.31			
N_{Site3}	9			
Observations	680			
Marginal R^2 / Conditional R^2	0.286 / 0.507			

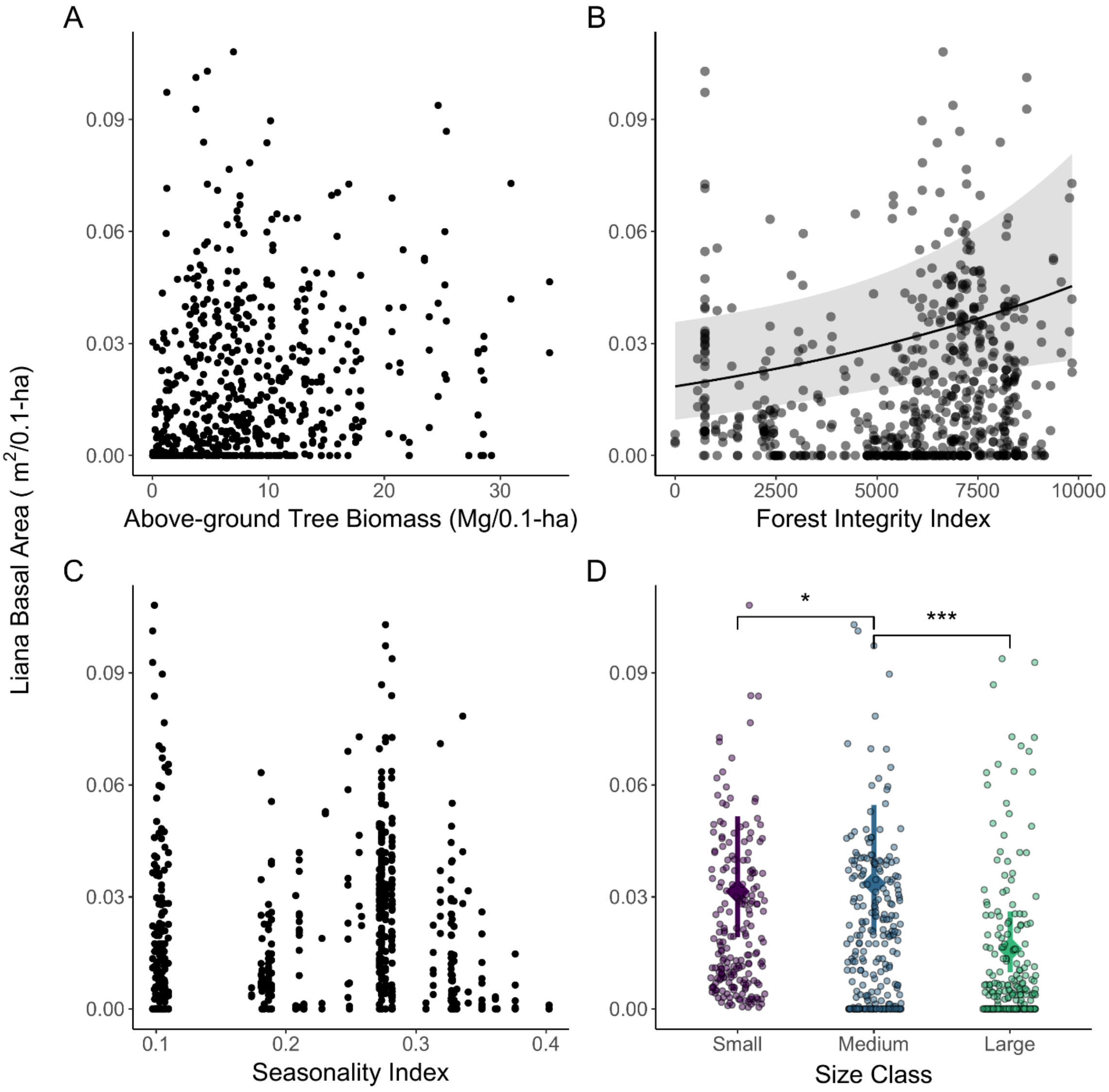

Figure S4.8. Relationship between liana basal area and above-ground tree biomass (**A**), forest landscape integrity index (**B**), seasonality index (**C**) and among liana size classes (**D**). Black lines and the shaded 95 % confidence intervals are present when a significant relationship was found. Relationships between size classes were determined by post-hoc tests of marginal means using the emmeans R package (Lenth, 2023).

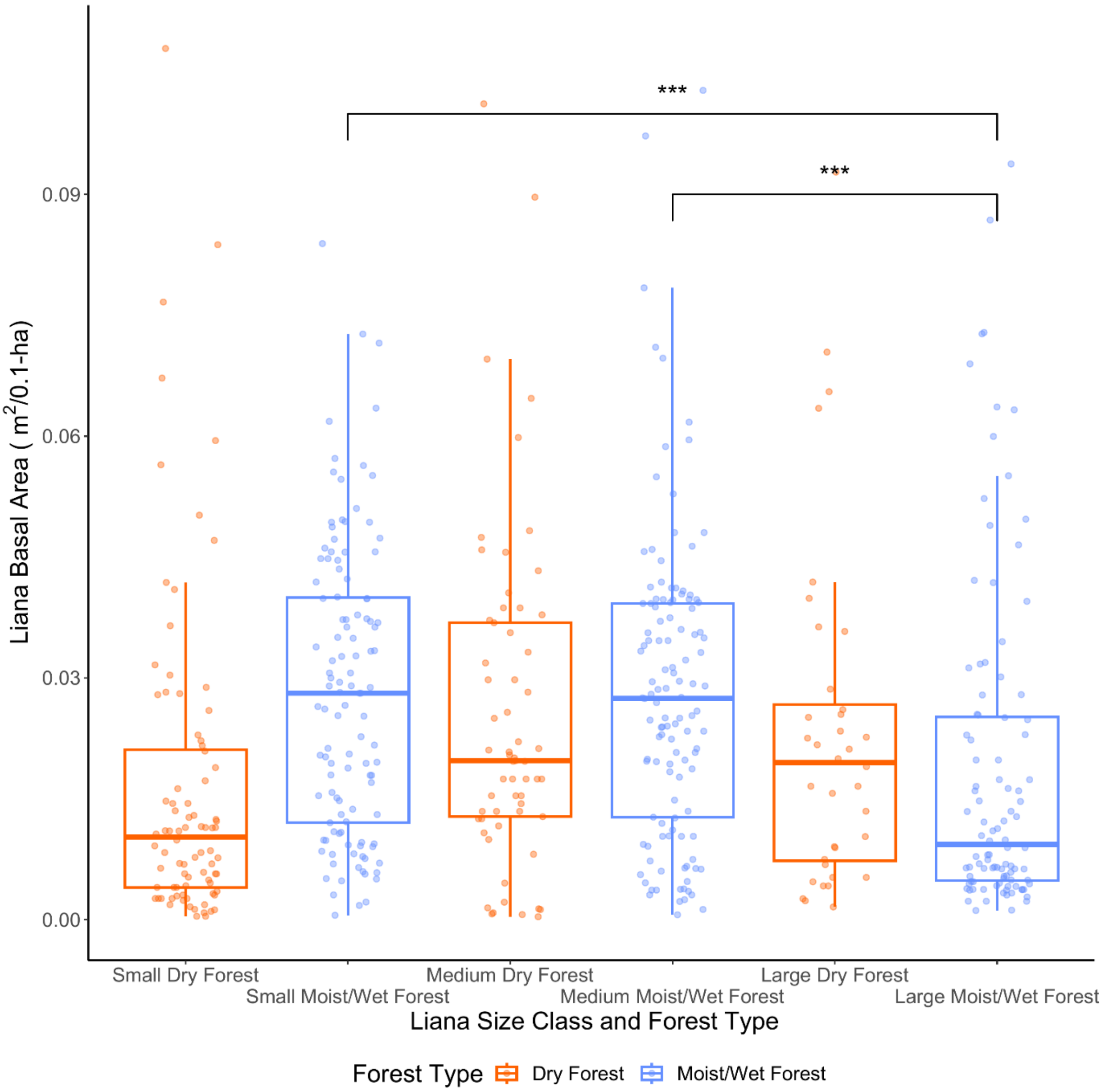

Figure S4.9. Box plots displaying liana basal area between different size class lianas and between dry and moist/wet forest types. Significant differences between categories are indicated by the asterisks and were determined by post-hoc marginal means tests. Zeros are not included in this plot as they were modelled in a separate hurdle model process.

Table S4.5. Post-hoc test results from the three-way liana basal area interactions examining the effect of size class and forest type on liana basal area at set tree AGB values. Small, medium, and large in the table refer to liana size classes. Only significant differences between three-way interactions are recorded here due to table size constraints.

Contrast	*Estimate*	*SE*	*df*	*t ratio*	*P value*	*AGB*
Small Dry Forest - (Medium Moist/ Wet Forest)	-0.104	0.035	654	-2.959	0.037	5
Small Dry Forest - (Large Moist/Wet Forest)	-0.168	0.036	654	-4.612	0.000	5
(Small Moist/Wet Forest) - (Medium Moist/Wet Forest)	-0.109	0.033	654	-3.284	0.014	5
(Small Moist/Wet Forest) - (Large Moist/Wet Forest)	-0.173	0.034	654	-5.020	0.000	5
Small Dry Forest - (Medium Moist/Wet Forest)	-0.085	0.022	654	-3.948	0.001	10
Small Dry Forest - (Large Moist/Wet Forest)	-0.148	0.022	654	-6.688	0.000	10
Medium Dry Forest - (Small Moist/Wet Forest)	0.066	0.023	654	2.870	0.048	10
Medium Dry Forest - (Large Moist/Wet Forest)	-0.084	0.024	654	-3.501	0.007	10
Large Dry Forest - (Large Moist/Wet Forest)	-0.105	0.033	654	-3.144	0.021	10
(Small Moist/Wet Forest) - (Medium Moist/Wet Forest)	-0.086	0.020	654	-4.345	0.000	10
(Small Moist/Wet Forest) - (Large Moist/Wet Forest)	-0.150	0.021	654	-7.285	0.000	10
(Medium Moist/Wet Forest) - (Large Moist/Wet Forest)	-0.064	0.020	654	-3.170	0.020	10

Small Dry Forest - (Medium Moist/Wet Forest)	-0.066	0.022	654	-2.975	0.036	15
Small Dry Forest - (Large Moist/Wet Forest)	-0.129	0.023	654	-5.744	0.000	15
Large Dry Forest - (Large Moist/Wet Forest)	-0.091	0.027	654	-3.430	0.008	15
(Small Moist/Wet Forest) - (Medium Moist/Wet Forest)	-0.064	0.018	654	-3.636	0.004	15
(Small Moist/Wet Forest) - (Large Moist/Wet Forest)	-0.127	0.018	654	-7.074	0.000	15
(Medium Moist/Wet Forest) - (Large Moist/Wet Forest)	-0.063	0.015	654	-4.335	0.000	15
Small Dry Forest - (Large Moist/Wet Forest)	-0.110	0.037	654	-2.986	0.035	20
(Small Moist/Wet Forest) - (Large Moist/Wet Forest)	-0.104	0.030	654	-3.519	0.006	20

Table S4.6. Binomial GLM output investigating the relationship between plots with higher liana density than tree density and seasonality and above-ground biomass.

Predictors	***Log-Odds***	***95 % CI***	***Statistic***	***P* value**
(Intercept)	-4.590	-8.451 – -0.729	-2.330	**0.020**
Seasonality Index	18.458	3.688 – 33.229	2.449	**0.014**
AGB	-0.047	-0.109 – 0.015	-1.486	0.137
Random Effects				
σ^2	3.29			
$\tau_{00\ \mathrm{Site3}}$	2.45			
ICC	0.43			
N_{Site3}	9			
Observations	219			
Marginal R^2 / Conditional R^2	0.310 / 0.605			

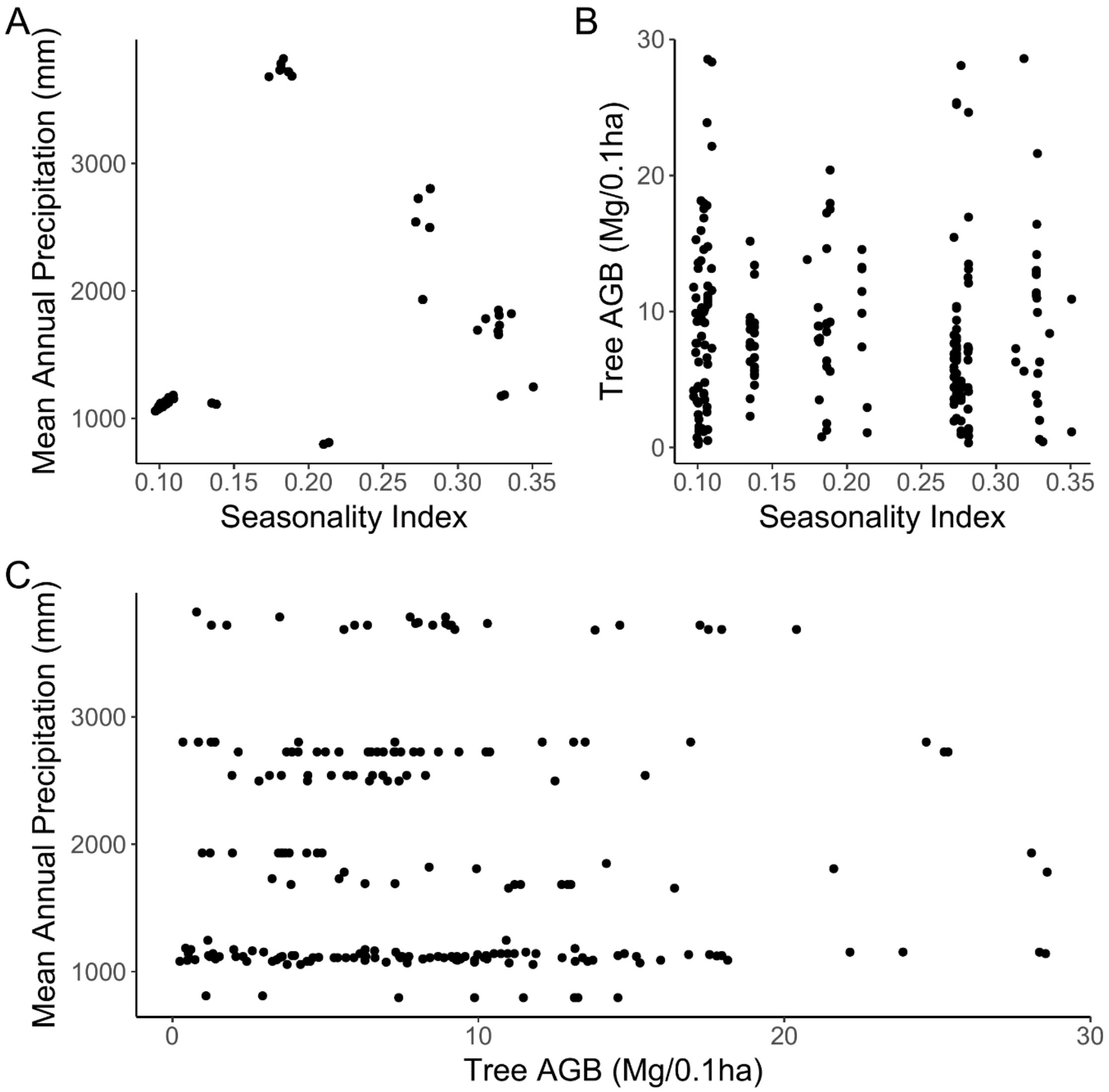

Figure S4.10. Graphs depicting the environmental variables behind the binomial GLMM model investigating liana density dominance. Panel **A** shows the relationship between mean annual precipitation and seasonality; **B** shows the relationship between tree aboveground biomass (per 0.1-ha) and seasonality and **C** shows the relationship between mean annual precipitation (MAP) and tree aboveground biomass. Each point represents one plot within a site. MAP was not included in the analysis due to the patchy relationship between MAP and seasonality.

5 Chapter 5: General discussion

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5.1 Background

The world's tropical forests are increasingly under anthropogenic pressure, and approximately 50 % of remaining tropical forests are now degraded or secondary forests (FAO, 2020). Tropical forest deforestation is still prevalent (Hansen et al., 2013; Turubanova et al., 2018), despite recent global commitments to halt deforestation and reverse land degradation by 2030 (COP26, 2021). However, secondary forests are also increasingly regenerating on abandoned agricultural land (Hansen et al., 2013), with great potential for biodiversity conservation (Chazdon et al., 2009; Dent and Wright, 2009) and carbon sequestration (Chazdon et al., 2016) if they are allowed to recover. Recent syntheses of data from sites across the Neotropics have shown that processes of secondary forest recovery which occur within the early to mid-stages of succession (< 50 years) are well quantified for tree communities (Poorter et al., 2021a, 2021b; Rozendaal et al., 2019) and generally successional theory is well understood over this period (Finegan, 1996). However, the later stages of tropical forest succession are much more uncertain and understanding of patterns of recovery in above-ground biomass and species composition for tree communities is limited by a lack of late-stage successional forest plots > 75 years old (e.g. Martin, Bullock and Newton, 2013; Rozendaal et al., 2019; Poorter et al., 2021a). A lack of data, in combination with myriad potential biotic and abiotic factors which influence succession (Arroyo-Rodríguez et al., 2017), make accurately-aged late successional chronosequences essential for quantifying how and when tropical secondary forests recover in structure, function and diversity to old-growth levels.

The lack of late stage successional data for liana communities is even more apparent than it is for trees (Letcher, 2015). Very few studies have examined the later stages of liana succession (but see DeWalt, Schnitzer and Denslow, 2000; Mumbanza et al., 2022; Lomwong et al., 2023) despite an exponential increase in liana research in recent years (Marshall et al., 2020). Lianas are more abundant in tropical than temperate regions (Schnitzer and Bongers, 2002) and have been found to be most abundant in low rainfall, highly seasonal forests (DeWalt et al., 2015, 2010; Schnitzer, 2005). Studies of liana biogeographic relationships have primarily focused on old-growth forests (DeWalt et al., 2015, 2010; Schnitzer, 2005) and uncertainty remains as to how liana communities in secondary forests vary with rainfall and seasonality.

In this thesis, I aimed to fill the knowledge gap in late successional research for trees and improve our understanding of changes in liana density and abundance through succession in the Neotropics. In Chapters 2 and 3 I focused on tree recovery to old-growth levels through late succession by looking at species, functional, and structural recovery within a secondary forest chronosequence in Panama. In Chapter 4, I examined liana density and basal area through a unique dataset of paired liana and tree censuses across successional and climatic gradients in the Neotropics.

5.2 Tropical secondary forests and recovery through succession

5.2.1 Most aspects of diversity and structure recover within 90 years

In Chapter 2 and Chapter 3 I found that species diversity and functional diversity had recovered 40-years into our chronosequence. This result is in line with other Neotropical studies for species diversity recovery (Peña-Claros, 2003; Poorter et al., 2021a; Saldarriaga et al., 1988; Villa et al., 2018b) and for functional diversity recovery (Lasky et al., 2014; Warring et al., 2016; WenSheng, RunGuo and Yi, 2014; Whitfeld et al., 2014). Functional traits related to the fast-slow continuum (specific leaf area, wood density, leaf nitrogen content, leaf toughness and leaf thickness; Chapter 3) had also mostly recovered by the midpoint of the chronosequence and I found recovery in deciduousness, between 60 to 90 years into succession, which is also associated with fast resource acquisition strategies (Ouédraogo et al., 2013; Popma et al., 1992). I found that forest structure, indicated by tree basal area and density, had recovered 90 years into succession (Chapter 2) and I found ongoing recovery in plant stature related traits, with 120-year-old forests similar in maximum tree height and diameter to old-growth forest (Chapter 3). This is likely linked to continued changes in ecosystem function through succession, in particular ongoing above-ground and deadwood carbon accumulation within the chronosequence (Jones et al., 2019). These forest structure-related results for trees link to our analysis of lianas through succession (Chapter 4), where we found liana density of all stems peaked in early succession, but medium and large lianas peaked in density in the later stages of succession. Surprisingly, species richness showed no evidence of recovery over succession in secondary forest plots, even though recovery is often expected within 50 to 60 years (Martin, Bullock and Newton, 2013; Rozendaal et al., 2019) and this likely links to higher numbers of rare species (Chapter 2) and functional richness (Chapter 3) in old-growth plots. We quantified species community compositional recovery and found that recovery can occur within 120 years (Chapter 2), which is an important validation of large scale syntheses which are otherwise extrapolations of existing data (e.g. Rozendaal et al., 2019; Poorter et al., 2021a). However, we also see evidence of an alternate successional pathway in one of our 120-year-old plots, where dominance of a long-lived pioneer, *Gustavia superba*, appears to delay successional recovery to old-growth (Chapter 2). This pathway could potentially persist for centuries, given the persistence of long-lived pioneers in old-growth forests in wet and dry tropical forests (Rüger et al., 2023).

5.2.2 Drivers of ongoing differences between secondary and old-growth forest in the BCNM

A key finding of Chapters 2 and 3 is while many metrics of diversity and structure recover in the mid-stages of succession, several processes appear to take at least a century to converge on old-growth values, and others appear to be ongoing. Differences in species richness and functional richness among old-growth and secondary forests are surprising, given that the BCNM has been fully protected for decades (Leigh Jr., 1999) and has been subjected to limited anthropogenic perturbations as it is well protected by rangers (Wright et al., 2000). It may be that dispersal limitation is a major factor in preventing full recovery of species richness. For instance, Mayhew et al. (2019) surveyed bird communities within the chronosequence and found that the 120-year-old forest stands had the lowest species richness and density for all birds, including forest specialists, of all secondary and old-growth forests examined. This study concluded that the 120-year-old plots and old-growth forest on Barro Colorado Island (BCI) are isolated from the mainland forest landscape by the Panama Canal and so bird movement between the mainland and BCI may be limited (Mayhew et al., 2019). There is evidence from Panama that many forest bird species will not traverse even 100-m over open water (Moore et al., 2008) and Mayhew et al. (2019) found that the old-growth forest on BCI contained 15 species which were missing from old-growth forest on the mainland, and was in turn missing 44 species from mainland old-growth forest. Thus, it is feasible that faunal seed dispersal from the old-growth forest on Barro Colorado Island to the 40- and 60-year-old forests on the mainland is limited, and so old-growth species may take much longer than expected to reach those forest sites.

However, this cannot be the sole explanation for different species and functional richness among secondary and old-growth, as if it were, we might expect the 120-year-old plots to have recovered in species richness as they are near the old-growth plots on Barro Colorado Island. Another piece to the puzzle is that old-growth forests were found to contain more rare species than the secondary forest plots (Chapter 2). A portion of these rare species are likely pioneer species recruiting in canopy gaps (Chapter 3) and so they are likely aggregated in distribution to areas of forest where canopy gaps exist. Given that Mascaro et al. (2012) found that canopy gaps were lowest in abundance in the 90-year-old forest stands (which were 85-years-old at the time of survey), another major difference may counterintuitively be that pioneer species are in higher abundance in old-growth plots compared to some of the secondary forest plots. This may be quite likely given that we found recovery in fast-slow continuum related traits at the start of the chronosequence (Chapter 3) and short-lived pioneer species often die out within the first 30 years of successional recovery (Finegan, 1996). Moreover, rare species are generally more aggregated than common species in tropical rainforests (Condit et al., 2000), and many tropical tree species show habitat preferences relating to different soil conditions (Phillips et al., 2003b). Therefore, there could be an element of stochasticity in the time taken for rare species to disperse into the right habitat, and establish, within our secondary forest plots which may explain the continued lower species richness and functional richness values.

5.2.3 Implications

Our work in Chapters 2 and 3 shows that many aspects of tropical forest diversity and structure recover rapidly under natural regeneration without human assistance. This is an important finding for global conservation aims as restoring terrestrial ecosystems and halting biodiversity loss is a key part of goal 15 of the UN Sustainable Development Goals (UN, 2023) and we are now two years into the UN Decade of Ecosystem Restoration. Previous rapid recovery rates of soil, functional, structural and diversity related attributes have been reported in the Neotropical secondary forests, with soil and function recovered to old-growth levels after just 20 years of succession (Poorter et al., 2021a). Ecosystem services are also expected to recover quickly in tandem with these attributes. However, there is evidence that important characteristics such as forest biomass, carbon stocks and community composition can take over 100 years to recover to old-growth levels (Jones et al., 2019; Poorter et al., 2021a; Rozendaal et al., 2019). In this thesis, we quantify the slow recovery of community composition, with only one of two 120-year-old sites recovered to old-growth levels and find that plant-stature related traits continue to recover into the late stages of succession. This means that it is imperative that secondary forests gain long term protection, as otherwise unique old-growth forest assemblages will never fully establish within them, and biodiversity will be lost. This goal will require more than just unenforced protected areas (Bonham et al., 2008) and schemes such as REDD+ may be one way to fund long-term forest protection through involving the private sector (Pauly and Tosteson, 2022).

Although, we see most aspects of secondary and old-growth forest recover within the timespan of our chronosequence, we also see likely evidence of dispersal limitation slowing species richness, rare species, and old-growth forest specialist recovery (Chapter 2). This emphasises that landscape structure and connectivity is incredibly important to seed dispersal and tropical forest regeneration (Holl, 1999; Damschen and Brudvig, 2012; Arroyo-Rodríguez et al., 2017; Dent and Estrada-Villegas, 2021). Thus, methods to speed up succession within even relatively undisturbed forest landscapes could focus on increasing connectivity between forest patches, e.g. through corridors joining patches together, to enable higher seed dispersal and thus higher likely establishment success (Jesus et al., 2012; Levey et al., 2005). In the BCNM, these processes would not work due to the barrier of the Panama Canal. Instead, active restoration could be considered, and perhaps the recovery of rare species with high stature related traits

(Chapters 2 and 3) could be assisted. Active restoration is increasingly common in tropical forests and is often used to accelerate successional processes (Banin et al., 2022). However, planted trees often have high mortality rates, and actively restored plots may not significantly differ in terms of above-ground carbon, basal area, or species richness from natural regeneration (Banin et al., 2022). A targeted direct seeding approach could still potentially benefit the BCNM though (Cole et al., 2011), as we have a robust knowledge of the species which are not recovering in our secondary forest plots.

5.3 The knowledge gap of late succession

The lack of old secondary forest plots to inform successional recovery of liana and tree communities is a theme throughout Chapters 2, 3 and 4. This lack of knowledge of processes past 100-years of succession has long been noted (Finegan, 1996). However, few new late-stage successional plots have been identified and utilised in recent studies (Martin, Bullock and Newton, et al., 2013; Poorter et al., 2021a; Rozendaal et al., 2019). Our secondary forest plots are part of one of the oldest secondary forest chronosequences in the Neotropics, alongside a similar chronosequence described by Buzzard et al. (2016), and therefore our results are unique in their importance to quantifying the late stages of succession. However, they do not have to be unique, tropical forests can be aged from aerial photography, satellite imagery and interviews with landowners, as Denslow and Guzman (2000) originally did when establishing the BCNM chronosequence. If sources of aerial photography are identified (e.g. Lertlum and Moore, 2005), they can be cross referenced with modern satellite imagery and boundaries for different aged forest stands can be established. Moreover, techniques to extract forest change information from Landsat satellite imagery have existed since at least 1980 (Malila, 1980). Therefore, chronosequences up to at least 40 years in age should be able to be established with readily accessible data. The establishment of additional late stage successional chronosequences is important to increase the generality of our results from Chapters 2 and 3. Moreover, even fewer late-stage successional liana data exist, with one of the few late-stage successional liana studies from within our chronosequence in the BCNM (DeWalt, Schnitzer and Denslow, 2000). In the subsequent case study section of this Chapter, I discuss results investigating liana structural changes through succession within the BCNM chronosequence 20 years post the original DeWalt, Schnitzer and Denslow (2000) paper.

5.4 Case study: Lianas in the late stages of succession

Prior to the Covid-19 pandemic, I intended to focus on collecting and analysing new liana census data from the BCNM chronosequence. Thus, in 2019 I conducted a three-month field season that generated a small, but insightful, dataset of liana densities and distributions, which I have summarised below. However, due to the pandemic, subsequent data were not collected, and we could not assign species identifications by trained botanists to the data collected in 2019. This lack of species identification precluded any analysis of community composition shifts through succession. I therefore present a short summary of these data here to illustrate structural composition changes of lianas through succession, but this case study does not form a complete data chapter in my thesis.

5.4.1 Overview

The late stages of tropical secondary forest succession are understudied for both trees (Martin, Bullock and Newton, 2013; Rozendaal et al., 2019) and lianas (Letcher, 2015). Indeed, relatively few studies have examined patterns of liana recovery through any successional stage (Letcher, 2015), despite the high abundance of lianas in environments analogous to early successional conditions, i.e., canopy gaps and forest edges (Campbell et al., 2018; Laurance et al., 2001; Schnitzer et al., 2021; Schnitzer and Carson, 2001), and the myriad negative impacts they may have on tree communities (Estrada-Villegas et al., 2022a; Finlayson et al., 2022; Schnitzer and Bongers, 2002). Letcher's (2015) narrative review of successional liana studies in the tropics includes nine successional studies, of which five investigate only the early stages of succession (1 – 30 years), three investigate up until the mid-stages of succession (< 50 years) and only one study (DeWalt, Schnitzer and Denslow, 2000) examines the later stages of succession with plots aged 20 – 100 years.

Recent liana studies in the late stages of tropical forest succession have been conducted in seasonal, moist forests of Thailand (Lomwong et al., 2023) and semi-deciduous forests in the Congo Basin (Mumbanza et al., 2022). Findings differ among late successional liana studies: DeWalt, Schnitzer and Denslow (2000) found a linear decline in liana density from 20-year-old forest to old-growth in Panama, and no trend in liana basal area. Lomwong et al. (2023) found a continual increase in liana density, even 100 years into succession, and found that basal area concurrently increased with density. In contrast, Mumbanza et al. (2022) found an intermediate peak in liana density in mid succession (60-year-old forest) and also a linear increase in liana basal area. Differences between these studies could be explained by biogeographical and climatic differences (DeWalt et al., 2015), as well as differences in land use history, disturbance or forest fragmentation (Arroyo-Rodríguez et al., 2017). However, our understanding of late-stage succession is limited by a lack of old secondary forest plots. For example, in Chapter 4 only three of nine chronosequences contained plots over 75 years old. Thus, further studies are necessary to accurately characterise how liana density and abundance changes into the late stages of succession.

In this case study, we censused lianas across seven of eight secondary forest plots within the secondary forest chronosequence in the Barro Colorado Nature Monument (aged 40 – 120 years). We aimed to help fill the gap in late successional liana studies and investigate fundamental structural metrics of lianas in late succession. We examined the following questions:

1. How does liana density and basal area recover over succession?
2. Does the relative importance of liana stems decline through succession, in comparison to tree stems?
3. Do we find evidence of shifting patterns of liana clonality through succession?

We hypothesised that we would find a decline in liana density and no trend in basal area through succession mirroring the results of DeWalt, Schnitzer and Denslow (2000), as they conducted research in the same forest stands 20 years prior. We also hypothesised that we would see declines in the relative abundance of liana stems in relation to tree density, as the number of small lianas decline, and large lianas increase in abundance over succession (see Chapter 4). Finally, we predicted that liana clonality would increase through succession, as canopy gaps open, and lianas clonally reproduce to exploit the high light areas (Schnitzer et al., 2021).

5.4.2 Methods

In this case study we censused lianas in a secondary forest chronosequence within the Barro Colorado Nature Monument, central Panama. Forest plots were aged 41 – 121 years since land abandonment (Denslow and Guzman, 2000) and have been undisturbed since establishment. For a full description of the study site see Chapters 1 and 2.

5.4.2.1 Liana census:

The liana census was conducted between February and May 2019 in the central 10 x 200 m (0.2-ha) of the 1-ha plots. All 61-, 91- and 121-year-old plots were fully censused, but only half of one 41-year-old plot (10 x 100 m) was surveyed, and due to fieldwork time constraints and Covid-19 travel restrictions we were unable to complete the censuses in the 41-year-old plots.

All liana stems ≥ 1 cm in diameter were measured (Figure 5.1), following the standardised liana protocols developed by Gerwing et al. (2006) and Schnitzer, Rutishauser and Aguilar (2008), by two expert field assistants. Stems were measured at 130 cm from the rooting point, with stems <

5 cm in diameter measured at the largest point using callipers, and larger stems measured using diameter tape. Main liana stems (the largest independently rooted stem of a liana), clonal stems (separately rooted liana stems still attached to the principal stem), and branches within 130 cm of the rooting point were all included in the census (following Schnitzer et al. (2012)). Liana rooting locations were mapped, and stems tagged, to allow future censuses to be carried out. Each liana rooting location was checked, and corrected if necessary, and a subsample of liana stems were remeasured to check the accuracy of the census. Species were identified where possible following Pérez et al. (2015), however species identities could not be confirmed by a botanist, and so were excluded from analysis.

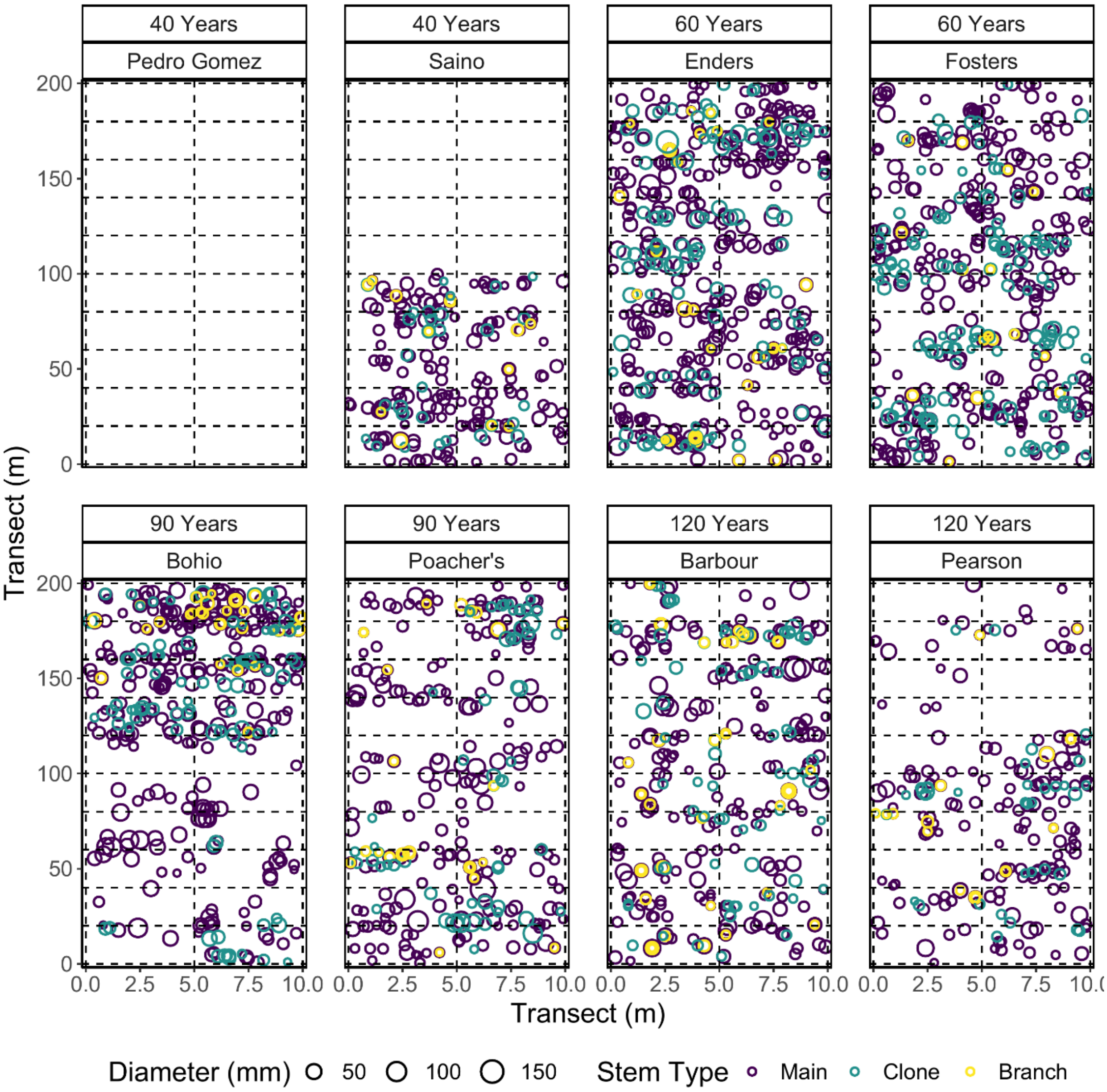

Figure 5.1. Map of lianas stems ≥ 1 cm in diameter censused in central transects within the 1-ha plots of the BCNM secondary forest chronosequence.

5.4.2.2 Tree census

Data from the tree censuses carried out between 2011 and 2016 were used to compare to the liana censuses. We subsampled the data to all saplings and trees ≥ 1 cm DBH in the central transect of the 1-ha plots. Bohio, a 91-year-old plot, was not surveyed for saplings and so is not included in liana-tree comparisons. Barbour also only had saplings surveyed to ≥ 2.5 cm DBH and so estimates relating to Barbour tree density will be underestimates. For a full description of the tree census see Chapters 2 and 3.

5.4.2.3 Analyses

Liana and tree density and basal area were calculated per 0.2-ha transect. Only main and clonal stems were included in the density calculation to match, and enable comparisons with, the Barro Colorado Island 50-ha plot data (Schnitzer et al., 2012). One 41-year-old transect, Saino, was only surveyed for half the area for lianas and so density and basal calculations were doubled to match the other transects. Liana stem density and basal area as a proportion of total stem density (tree + liana density) and total basal area (tree + liana basal area) were calculated per transect. The proportion of independently rooted clonal stems were also calculated per transect (branches were excluded from this analysis). We also calculated diameter Gini coefficient values, using the *ineq* R package (Zeileis, 2014), for all liana and tree stems, to investigate if the distribution of liana or tree diameters changed through succession.

All metrics were modelled solely against stand age. Liana density was modelled using a GLM with a negative binomial distribution, due to count data being overdispersed. Liana basal area was modelled using a gaussian GLM. All other metrics were analysed using beta regressions, due to values being bounded between 0 and 1. Appropriate model distributions were chosen after examining model residuals and assumptions using the *DHARMa* R package (Hartig, 2022).

5.4.3 Results and discussion

We censused a total of 2390 lianas stems, comprised of 1632 main stems, 541 clonal stems and 217 branched stems across our transects. This compares to 3722 tree stems across the same area, comprised of 2893 main stems and 829 branched stems, which is certainly an underestimate considering saplings were only surveyed to 2.5 cm DBH in Barbour, and were not surveyed in Bohio.

Similar to DeWalt, Schnitzer and Denslow (2000), we found a significant decline in liana density through the mid-to-late stages of succession (Figure 5.2A, $P = 0.003$). This is likely because our plots miss the early stages of succession where liana density is highest in Neotropical forests and the plot ages likely coincide with an intermediate peak in liana density in medium sized lianas (see Chapter 4). Recovery to similar liana densities as those seen in old-growth forest appears to occur in our secondary forests aged between 100 and 120 years (Schnitzer et al., 2012). This demonstrates the importance of long timespan chronosequences, as much previous secondary forest research in the Neotropics has focused on the early stages of succession (e.g. Letcher, 2015) and thus not quantified precisely when liana density recovers to old-growth levels.

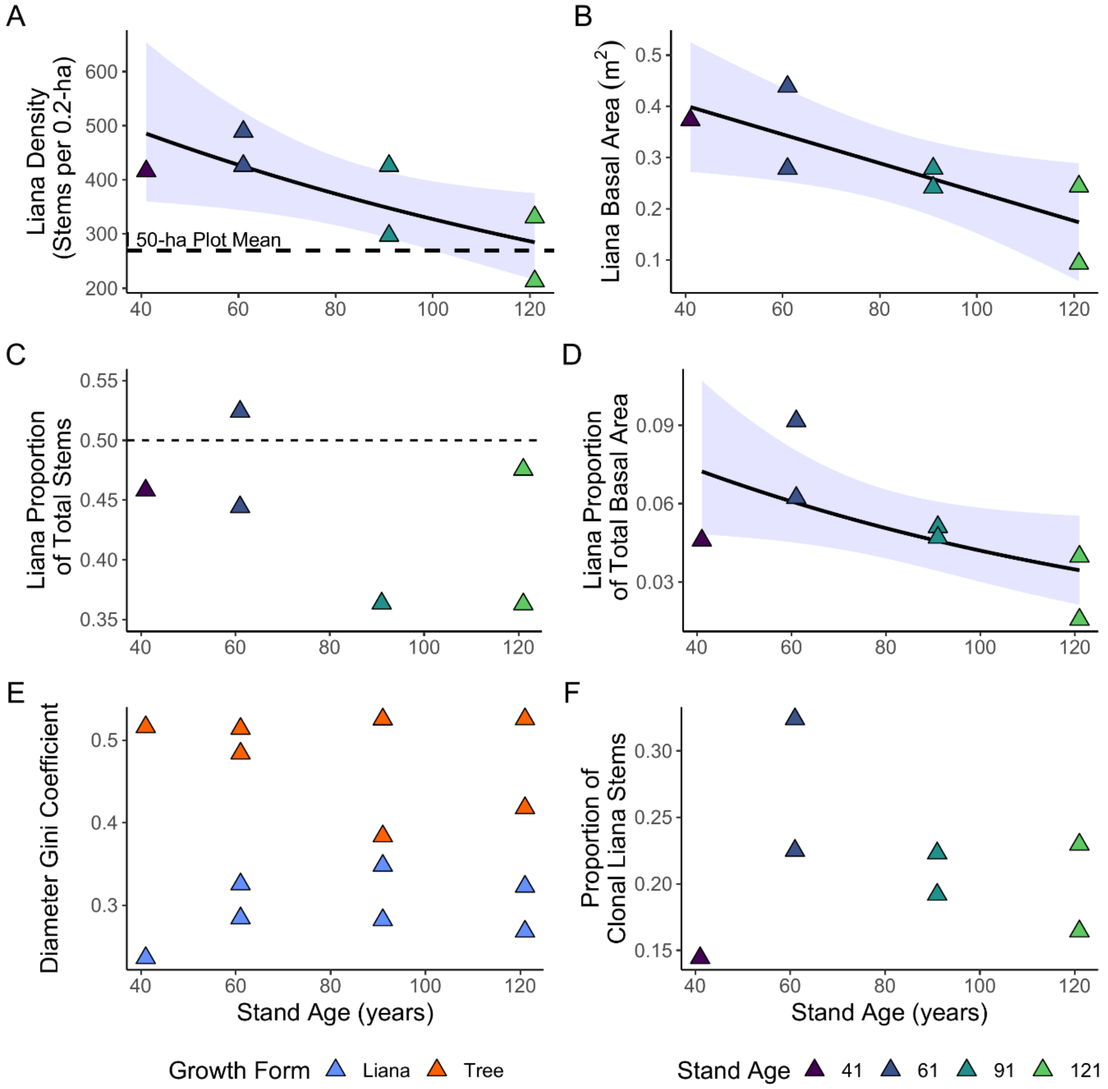

Figure 5.2. Liana structural characteristics plotted against stand age: **A** relationship between liana density and stand age, with the 50-ha old-growth plot mean liana density plotted as a dashed line for comparison; **B** relationship between liana basal area and stand age; **C** proportion of liana stems comprising the total woody stem density per transect; **D** liana basal area as a proportion of total basal area; **E** liana and tree diameter Gini coefficients and **F** the proportion of independently rooted clonal liana stems.

Unlike the previous census within these forest stands (DeWalt et al., 2000), we found a significant decline in liana basal area through time (Figure 5.2B, *P* = 0.032). Differences between our study and DeWalt, Schnitzer and Denslow (2000), may simply be due to sampling variation, as although we surveyed in the same forest stands we did not survey within the same transects and lianas are highly clustered in distribution, especially in disturbed areas of forest (Ledo and Schnitzer, 2014; Schnitzer et al., 2012). Alternatively, the 20-year time difference between the two censuses may have resulted in the loss of large lianas from the transects and thus a decline in basal area, given that large lianas (> 10 cm) are dynamic elements of tropical forests (Phillips et al., 2005). For example, a study in Amazonia found that large lianas have a residence time of just 13.8 years in the largest size class (Phillips et al., 2005). We do not see any definitive patterns in the contributions of each liana size class towards the total basal area and large lianas contributions are variable in the 61-, 91- and 121-year-old plots (Figure 5.3). Thus, we do not see a loss of large lianas within our own dataset. However, it would be possible that a turnover in larger lianas happened in between the two censuses, given the short residence time of the largest lianas in tropical forests (Phillips et al., 2005). Plots would need to be studied longitudinally, e.g. like liana censuses in the 50-ha forest dynamics plot (Schnitzer et al., 2012), to fully explore large liana dynamics through succession.

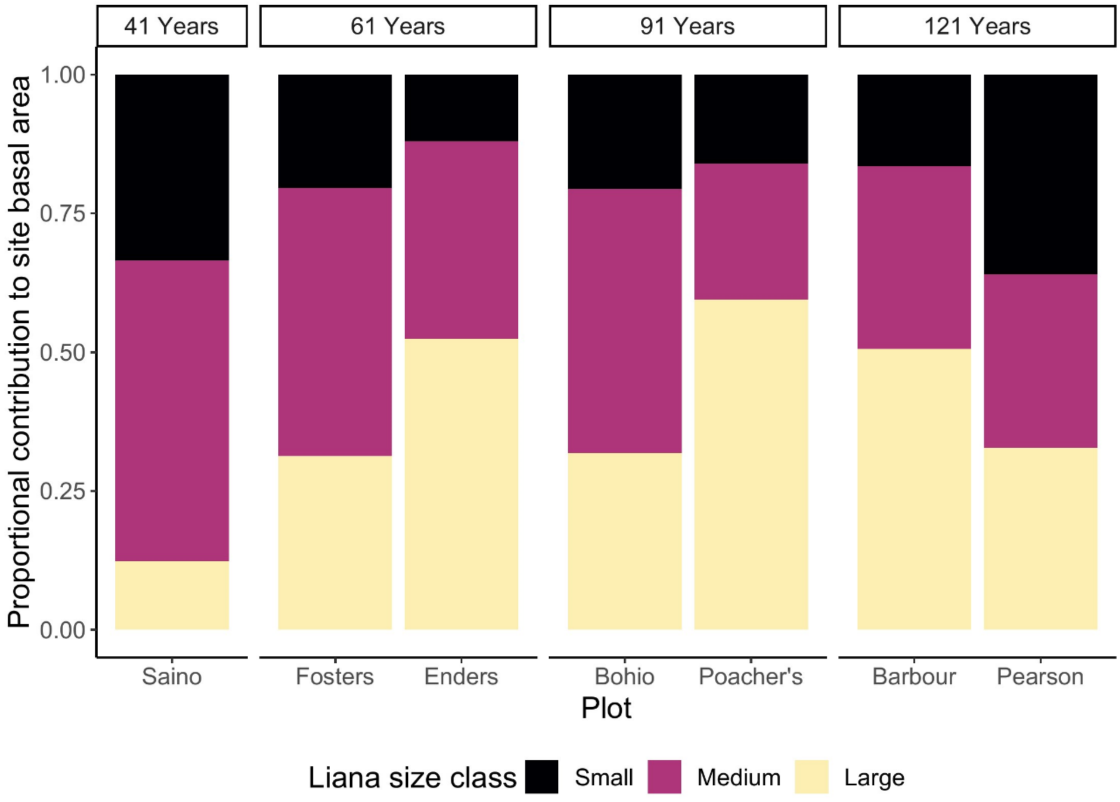

Figure 5.3. Liana size class contribution to total site basal area. Small lianas were defined as stems 1 cm ≤ diameter < 2.5 cm; medium lianas were defined as stems 2.5 cm ≤ diameter < 5

cm and large lianas were ≥ 5 cm in diameter. Plots are plotted in age order (41 – 121 years since land abandonment).

The contribution of liana basal area to total woody stem basal area significantly declined through time (Figure 5.2D, $P = 0.041$), from a predicted 7 % of basal area in 40-year-old forest to 4 % of basal area in 120-year-old forest. This is linked to the increasing basal area of the tree community (previously found in Chapter 2) and shows that liana basal areas are approaching similarity to old-growth, given that Schnitzer et al. (2012) found rooted liana individuals to comprise 2.9 % of total woody basal area in the BCI 50-ha plot. This low proportion of woody basal area is due to lianas maintaining smaller diameters than trees on average (Schnitzer et al., 2012) as they use trees as trellises (Putz, 1984) instead of investing in woody structural support to reach the canopy.

Despite their low relative basal area, lianas are still a key component of overall woody stem density in Panamanian forests, ranging from 36 to 53 % of woody stem density in our transects (Figure 2C). We find no significant trend in the proportion of total stems represented by lianas through succession (Figure 5.2C, $P = 0.207$). Proportional woody stem density within our secondary forest transects was still greater than that found in old-growth forest on BCI (mean = 24. 5 %; Schnitzer et al. (2012)). This result illustrates the importance of lianas in secondary forest structure and connectivity. A number of recent studies highlight that lianas have influences on bird, mammal and arthropod communities and connect forest canopies (Kilgore et al., 2010; Michel et al., 2015a; Michel et al., 2015b; Schnitzer et al., 2020; Yanoviak, 2015).

The Gini coefficient of lianas and trees did not change over succession (Figure 5.2E, $P = 0.430$), which suggests that the size distributions of both trees and lianas are relatively constant through succession, or that they shift consistently i.e. towards equally larger stems. Trees have a consistently higher Gini coefficient value than lianas (Figure 5.2E, $P < 0.001$), likely because the potential size range of tree diameters is an order of magnitude different than that of lianas (Schnitzer et al., 2012). We found no relationship between the proportion of clonal stems and stand age (Figure 5.2F, $P = 0.903$), mirroring results from the early-to-mid stages of succession when compared with old-growth in Costa Rican wet forest (Letcher and Chazdon, 2009). This may be because clonal reproduction is an essential life history strategy by which lianas maintain abundance in closed-canopy forest, as it enables rapid colonisation of canopy gaps (Schnitzer et al., 2021). Furthermore, when lianas suffer falls from the canopy, e.g. due to associated tree falls, clonality may be a key strategy driving survival, recruitment and dispersal (Yorke et al., 2013).

In summary, we furthered late-stage successional liana research in this case study and illustrate that in central Panama secondary forest liana density converges on old-growth levels after 100 to 120 years of forest recovery. Consistent declines in basal area and proportional basal area over late-stage secondary forest succession support previous studies. We suggest that future work encompassing old secondary forests is key to understanding the generality of our findings.

5.5 Lianas across Neotropical climatic and successional gradients

5.5.1 Key results

In Chapter 4, I investigated changes in liana density and basal area across combined successional, mean annual precipitation and seasonality gradients in Neotropical forests. Contrary to prior hypotheses, we found that liana density and basal area was higher in moist/wet tropical forests than in dry tropical forests. Previous research has found the opposite trend (DeWalt et al., 2015, 2010; Schnitzer, 2005), or no trend (van der Heijden and Phillips, 2008), with annual rainfall. I found no effect of precipitation seasonality on liana density or basal area *per se* but speculate that seasonality effects may be partially linked to the wet/dry forest classification used in analyses. Liana density was highest in the lowest tree biomass plots, analogous to early succession, which confirms previous research in early successional Neotropical forests (Barry et al., 2015; DeWalt et al., 2000; Letcher, 2015). I also found significant interactions for liana density and basal area between liana size class, tree biomass and the wet/dry forest classification, and large lianas were found to have higher basal area and density in late successional wet forest plots than in dry forest. This, and other results, suggests that lianas in dry tropical forest may be more restricted in size than in wet tropical forest. Finally, I found that liana dominance was highest in highly seasonal forests. This provides support for the seasonal growth advantage of lianas hypothesised by Schnitzer (2018). In summary, we find that mean annual precipitation, precipitation seasonality and tree biomass all impact liana density and basal area but the complexities of the data make different drivers difficult to disentangle.

5.5.2 Implications

My primary finding that liana density and basal area were higher in moist/wet forest than dry forest is surprising as it appears to contradict several pantropical studies (DeWalt et al., 2015, 2010; Schnitzer, 2005). However, these studies were carried out in old-growth forests (DeWalt et al., 2015, 2010; Schnitzer, 2005), and, as I suggest in Chapter 4, it may be that the different abiotic conditions of early stages of succession versus old-growth forest in dry and wet forests are behind these differences in results. Furthermore, there is evidence that lianas in the Neotropics may be less strongly influenced by mean annual precipitation than elsewhere (van der Heijden and Phillips, 2008), and so previous patterns in precipitation found in old-growth forests may be masked by the stronger influence of succession on liana density. This finding has fundamental implications for our understanding of liana distributions in the tropics and may be indicative of a central difference between how lianas organise in old-growth and secondary forests. Our other key finding, that liana dominance is higher in forests with high seasonality provides support for lianas having a seasonal growth advantage over trees (Schnitzer, 2018). This may mean that under changing climatic conditions in the tropics (Caretta et al., 2022), and potentially longer dry seasons in some regions (Boisier et al., 2015; Fu et al., 2013), lianas may increase disproportionately in seasonal forests in the future. Given that lianas in the Neotropics are currently increasing in abundance (Schnitzer, 2015), liana-tree interactions are likely to change into the future with potentially negative impacts for biomass accumulation and carbon sequestration (Estrada-Villegas et al., 2022a; Finlayson et al., 2022). Further work is needed to expand the generality of our findings across older secondary forest plots and additional seasonal and aseasonal forests.

5.6 Future work

Chapter 2 and Chapter 3 described patterns of recovery across the BCNM chronosequence well. However, due to the limited sample size of only eight secondary and five old-growth forest plots, inferences around the potential impact of edaphic and topographic variables on metrics of diversity, structure and function were restricted. The next steps in this analysis would first involve digitising the coordinate data for all 29,394 trees and saplings in the eight secondary forest plots. Spatial point pattern analyses could then be carried out to quantify tree species interactions, examine habitat preferences among species (e.g. edaphic/topographic) and look into species distributions (e.g. Lin et al., 2011; Velázquez et al., 2016; Harvey et al., 2020). This would enable us to make the best use of the large amount of census data that we have collected. Moreover, if I managed to complete the liana census in the BCNM chronosequence, liana and tree spatial patterns could be examined. Knowledge of how liana communities change through succession, in terms of functional traits, is limited (Letcher and Chazdon, 2012) and liana traits have currently not been included in models of liana infestation (Visser et al., 2018a). Thus, there is an opportunity to use the BCNM chronosequence to examine both questions in tandem, and to look into if there is evidence for certain tree traits providing protection from liana infestation, which has been little investigated (Muller-Landau and Pacala, 2020). The BCNM chronosequence is a unique opportunity for analyses such as these due to the long timescale of the chronosequence. Moreover, future analyses will benefit from additional 20-year-old plots, which are located just outside the BCNM and have recently been incorporated into the chronosequence (Daisy Dent, personal communication). These will improve our understanding of successional processes within the chronosequence as we will be more likely to capture early successional processes, such as short-lived pioneer abundance and subsequent die-off, in our analyses.

To develop Chapter 4 further, I would first begin with trying to obtain data from a wider range of rainfall gradients in the Neotropics. Our data, were slightly limited in scope compared to the Gentry dataset originally used by Schnitzer (2005), a 3100 mm gradient vs a c. 4500 mm rainfall gradient, and a larger gradient may enable me to better disentangle the effects of mean annual precipitation and seasonality. I would also look into including additional variables which may explain differences in liana abundance. Namely, I think that including liana clonality explicitly in the models, rather than grouping genets and ramets together, might give me an insight into disturbance regimes at the site, as clonality is known to maintain liana abundance in canopy gaps (Schnitzer et al., 2021; Yorke et al., 2013). Finally, as mentioned in Chapter 4, I think it is important to address standardising liana survey methodologies where possible and I would look into utilising 50-ha plot data to quantify the impacts of different plot sizes and plot shapes upon my model, furthering work by Schnitzer, DeWalt and Chave (2006).

Beyond potential improvements to the chapters within this study, I would carry out further work within the BCNM chronosequence to try and elucidate firmer answers regarding the relationship between trees, lianas, and edaphic conditions through succession. We have recently mapped out the forest stands within the chronosequence (Chapter 6; Dent and Elsy, 2023) and thus have delineated accurately aged forest stands into which we could establish additional forest transects. If funding were no object, a new field campaign would expand the replication within our chronosequence and focus on establishing a large number of small transects (e.g. 0.1-ha) per aged-forest stand (each mapping all woody stems ≥ 1 cm DBH). I would focus on smaller transects as they are significantly lower effort to establish than 1-ha plots, and they allow a broader range of edaphic conditions to be encountered within the forest (Phillips et al., 2003a). Additional transects would likely cover more heterogeneous habitats within each forest stand and thus may allow me to determine how common the alternate successional pathway characterised by *Gustavia superba* dominance (see Chapter 2) is within the study landscape. Furthermore, increasing the sample size would allow weaker edaphic and topographic effects on biodiversity to potentially be investigated (Phillips et al., 2003a) and more advanced statistical models (e.g. mixed effects models) could be used. I would also aim to sample within the old-growth forest on the mainland Gigante peninsula (Figure 6.2) so that the potential effects of island isolation (e.g. Moore et al., 2008; Mayhew et al., 2019) could be accounted for and modelled appropriately. Moreover, this would prevent all the old-growth reference plots being associated with one bedrock type (Baillie et al., 2006) and being situated on a relatively flat plateau (Harms et al., 2001). Tree and liana communities could be simultaneously sampled, and the associated dataset would be unique in late successional forest. Furthermore, the additional small transects would make a dataset more comparable to many other sites in the

Neotropics (see studies in Rozendaal et al., 2019) and thus would have broad use in syntheses in the future.

5.7 Synthesis

Secondary forests are increasingly being recognised as key reservoirs of biodiversity and ecosystem services in a changing world. Tropical forests remain under threat, and important processes relating to carbon storage and liana-tree interactions may shift under future climate conditions. As such, it is essential to quantify how and when secondary forests recover in terms of biodiversity, forest structure and function to better understand the role that secondary forests play in human modified landscapes. In this thesis I provided a unique late-stage successional examination of species and functional recovery in tree communities which found evidence of convergence in most metrics by mid succession, but rare species recovery, community composition and plant stature traits may take at least a century to recover. I also provided the first large-scale synthesis examining the interacting effects of successional age and climatic factors on Neotropical lianas. I found that liana density in successional forests is higher in moist/wet forests than dry forests, contrary to previous findings in old-growth forest, and liana dominance is highest in seasonal forests. These findings warrant further investigation in the late stages of succession. Old secondary forests (> 100 years) are likely to be similar to in structure and composition to old-growth forests and thus need further protection to safeguard community assemblages which can take centuries to develop.

6 Chapter 6: Structure, diversity and composition of secondary forests of the Barro Colorado Nature Monument

Chapter authors: Daisy H. Dent and Alexander D. Elsy

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It has been formatted for the thesis but otherwise remains identical to the published work. Daisy H. Dent wrote the text of the book chapter, and I conducted the geospatial analysis and made suggestions to the draft.

6.1 Abstract

Secondary forests are increasingly important for biodiversity conservation and carbon sequestration. The Barro Colorado Nature Monument is composed of approximately 1015 ha younger secondary forest (40 – 80 years), 929 ha older secondary forest (> 80 years old), 909 ha old-growth forest, and 3276 ha of mature forest that cannot be accurately aged. Secondary forests in the BCNM represent the longest known trajectory of secondary forest regeneration in the Neotropics (45 – 125 years) enabling us to study biodiversity and carbon recovery over long time scales. Secondary forest studies in the BCNM span almost a century and indicate rapid recovery of tree and liana species diversity (< 40 years) as well as many structural characteristics (< 70 years). In contrast, plant species composition and above-ground carbon stocks recover more slowly (> 100 years), while soil carbon is less predictable and often does not track stand age. The diversity and composition of bird species increased with forest age but were also significantly affected by isolation across the BCNM chronosequence. The effects of isolation are particularly severe for understory bird species. These results reflect broader patterns reported for secondary forests across the Neotropics. However, most other studies are from younger forests (< 40 years old) and so the BCNM's older secondary forests are key to better understanding those forest characteristics that recover slowly, such as above-ground biomass and species composition.

Keywords: Biodiversity; Carbon storage; Regeneration; Succession

6.2 Introduction

Secondary forests comprise over 50 % of remaining tropical forests (FAO, 2020) and have immense potential for carbon sequestration and biodiversity conservation (Poorter et al., 2016; Rozendaal et al., 2019). The value of secondary forests depends on the rate of recovery of forest structure, diversity, composition, and function, and these characteristics recover at different rates (Poorter et al., 2021a). Many aspects of forest structure, including stem density, light availability, plant and animal species richness and mean plant trait values, recover to old-growth levels in under 50 years (Kennard, 2002; Peña-Claros, 2003; Lebrija-Trejos et al., 2011; Martin, Newton and Bullock, 2013; Rozendaal et al., 2019; Poorter et al., 2021a). In contrast, recovery of aboveground biomass generally takes 100 years or more (e.g. Poorter et al., 2016; Poorter et al., 2021a), and community composition of plant and animal taxa tends to recover most slowly and is highly variable (Acevedo-Charry and Aide, 2019; Guariguata and Ostertag, 2001; Poorter et al., 2021a), with tree species composition attaining similarity to old-growth at 120 years to several centuries (Poorter et al., 2021a; Rozendaal et al., 2019). Outlined above are general trends in secondary forest recovery, but site-specific rates and trajectories of succession can be highly variable and are determined by availability of abiotic resources, site and landscape characteristics and ongoing disturbance (Arroyo-Rodríguez et al., 2017; Dent and Estrada-Villegas, 2021).

6.3 Theories of secondary forest succession

Current theories of secondary succession focus on trade-offs in plant functional strategies, and how these relate to changes in abiotic resources (Coomes and Grubb, 2003; Muller-Landau, 2010; Rüger et al., 2020). In moist tropical forests, light availability tends to decline over succession driving changes in community composition. A trade-off between growth and survival can be seen over succession, where light-demanding species that recruit early in succession tend to have traits that maximize resource acquisition and growth (e.g., high specific leaf area (SLA), low wood density; fast species), while shade-tolerant species that recruit later in succession tend to have conservative traits (e.g., low SLA, high wood density) that allow survival in low-resource environments (slow species; Reich, 2014; Rüger et al., 2020). Recently, an orthogonal stature–recruitment trade-off has been shown to contribute to succession, with species that grow to a large size, live long, and recruit early in succession (long-lived pioneers; Rüger et al., 2018, 2020)and species that attain modest maximum sizes, produce large numbers of offspring and recruit after canopy closure (short-lived breeders; Rüger et al., 2018, 2020). Changes in light availability largely explain changes in the relative abundance of these four strategies (fast, slow, long-lived pioneers, and short-lived breeders) over succession (Chazdon, 2014; Rüger et al., 2020).

Although changes in abiotic resources such as increasing shade in the understory contribute to predictable shifts in community composition over succession, the abundance and turnover of individual species depends on species-specific reproduction events and effective seed dispersal (Norden et al., 2009; Dent, DeWalt and Denslow, 2013; Rozendaal et al., 2019). The availability and dispersal of seeds depends strongly on processes at the landscape scale, such as connectivity and distance to seed sources, and at more local scales, such as previous land-use (Dent and Estrada-Villegas, 2021). Thus, landscape and site properties strongly affect the rate and trajectories of succession. Sites located closer to mature forest, with an intact frugivore community and a history of low impact land-use will have more rapid and more predictable recovery than sites with a converse set of traits (Arroyo-Rodríguez et al., 2017).

6.4 Patterns of tropical secondary forest succession in the Neotropics and Panama

In the Neotropics, secondary forest succession typically occurs on abandoned pasture or agricultural land (Figure 6.1A; Chazdon et al., 2016). Seeds of early-successional trees and shrubs are blown to the site or carried in the faeces of small bats and birds, and, in the absence of grazing and fires, these small seeds germinate, establish and initiate forest succession (Carlo and Morales, 2016; Martínez-Garza et al., 2013; Piotto et al., 2019). Early successional, pioneer species grow rapidly creating forest structure and changing the microclimate of the site (Figure 6.1B, 6.1C; Guariguata and Ostertag, 2001; Lohbeck et al., 2014). Over the initial 20 years of succession, moist tropical forests develop increased structural complexity, improved nutrient cycling, and a cooler, darker understory, which provides suitable conditions for other plants and animals to recruit (Fig 6.1D; Denslow and Guzman, 2000; Guariguata and Ostertag, 2001; Dent and Wright, 2009).

Figure 6.1. Photographs of (**A**) forest regenerating in a recently abandoned pasture (< 10 years old), (**B** and **C**) young secondary forest (20 – 30 years old) and (**D**) mature secondary forest (> 50 years old) in central Panama. Credit: Christian Ziegler.

In central Panama, young forests (< 20 years old) are often dominated by small-statured tree and shrub species with fleshy fruits from the genera *Conostegia*, *Miconia*, *Vismia* and *Xylopia* (Figure 6.1A - C; van Breugel et al., 2013), which provide food resources for small birds and bats further encouraging successional development. Early successional tree species are then gradually replaced by more shade-tolerant species, as individuals that recruited at the start of succession die and create canopy gaps that are filled by more shade-tolerant seedlings and saplings from the young forest understory. In central Panama, we see large seeded species, such as *Gustavia superba* and *Protium panamense,* recruit into the understory of young forests and peak in abundance in 20- to 70-year-old forests (Figure 6.1D; Knight, 1975; Dent, DeWalt and Denslow, 2013). Other species with variable seed sizes continue to increase and are most abundant in forests > 100 years old, including the tree species *Alseis blackiana*, *Tetragastris panamensis* and *Trichilia tuberculata* and the palm *Oenocarpus mapora* (Dent, DeWalt and

Denslow, 2013). As the forest ages, increased structural complexity and increased abundance of large-seeded, fleshy-fruited tree species provides habitat and food resources for animal species that are forest specialists (Acevedo-Charry and Aide, 2019; Estrada-Villegas et al. 2022b). Thus, over time species and functional composition of secondary forest tends to converge on that of undisturbed forest (Finegan, 1996; Chazdon et al., 2010).

6.5 Land-use history of the Barro Colorado Nature Monument

Much of the Barro Colorado Nature Monument (BCNM) is secondary forest that currently ranges in age from about 40 to over 200 years old (Chapman, 1938; Knight, 1975; Denslow and Guzman, 2000). In Figure 6.2 we present a complete forest age map of the BCNM combining descriptions of BCI secondary forests in Kenoyer (1929), the vegetation maps of BCI presented in Enders (1935) and aerial photographs of the canal zone taken from 1927 to 1983 (US Defense Mapping Agency; Denslow and Guzman, 2000). Central Panama has a long history of human settlement and people lived on Barro Colorado Island (BCI) in pre-Columbian times (Piperno, 1990). Approximately, 754 ha of BCI is old-growth forest and the remaining 840 ha is old secondary (90 – 140 years old; Fig 6.2; Kenoyer, 1929; Enders, 1935; Chapman, 1938). We now know that the old-growth forest on BCI and the Gigante Peninsula likely varies in age from 400 to several thousand years old (McMichael et al., 2023; Piperno, 2023). Archaeological data suggest that prehistoric people lived within the BCI 50-ha plot approximately 1700 to 1300 years ago and indigenous Panamanians occupied these areas until 700 to 400 years ago. In areas with high human activity the forests that grew back are likely ca. 400 - 500 years old today, whereas in areas with little to no history of disturbance forests are likely to be thousands of years older (Piperno, 2023).

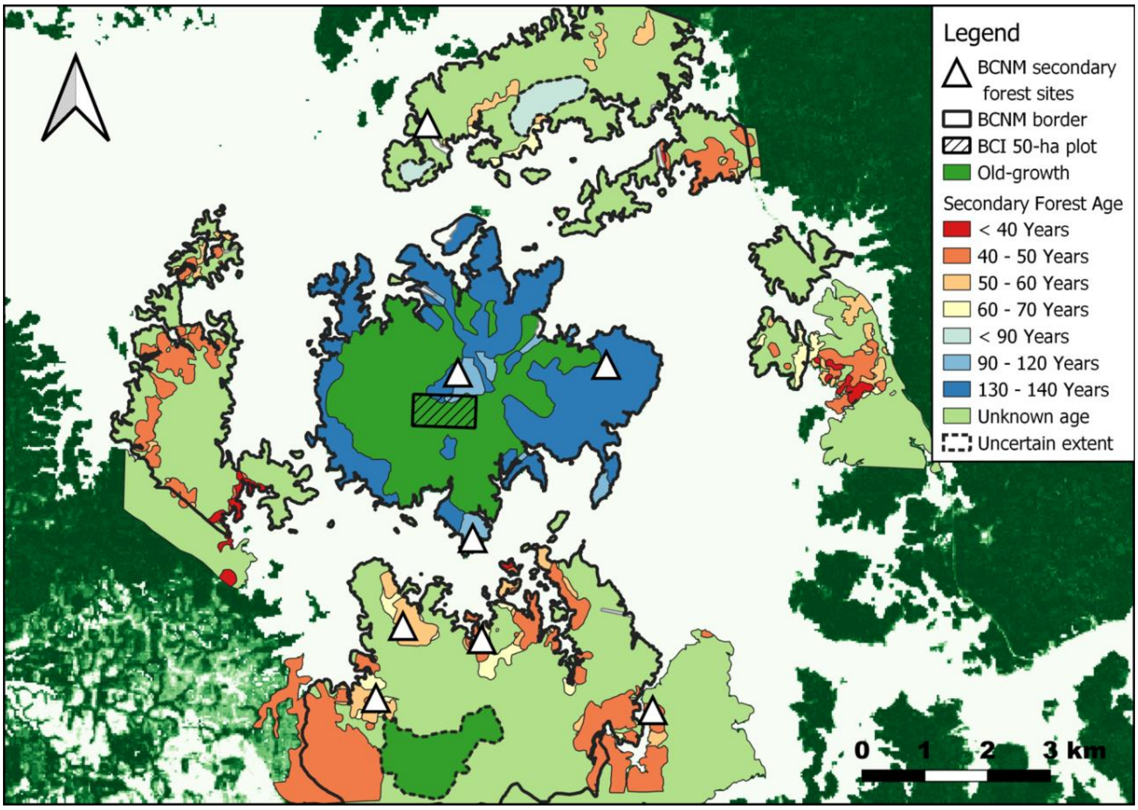

Figure 6.2. Map of the Barro Colorado Nature Monument with approximate forest ages in 2022 and locations of eight secondary forest plots. Forest ages were derived from Kenoyer (1929) and Enders (1935) for Barro Colorado Island. Surrounding peninsula ages were derived from aerial photographs taken by the US defence mapping agency in 1955, 1966, 1973, 1979 and 1983. Photographs were digitised and forests were classified as old-growth, secondary forest, and non-forest. Forest ages were then calculated when forest type was seen to transition between photographs e.g. non-forest in 1955 to secondary forest in 1966. Secondary forests which could not be aged are displayed in pale green (minimum age c. 80 years).

In 1923, BCI was designated as a reserve and the only remaining farm on the island was purchased and closed (the distal third of Poacher's Point; Leigh Jr., 1996). At this time, the forest covering the north-eastern half of the island was estimated to be about 50 years old, regenerating on land that had been previously used for agriculture (including, sugarcane, bananas, and cacao; Kenoyer, 1929; Chapman, 1938). In 1979, the five surrounding mainland peninsulas were incorporated to create the BCNM (Fig. 6.2). The forests on these peninsulas are more difficult to age as we lack historical maps such as those created by Enders (1935) for BCI. The Gigante Peninsula contains old-growth forest of uncertain extent (McMichael et al., 2023), approximately 3276 ha are mature forests of unknown age, and 1104 ha are secondary forests (< 80 years old; Fig. 6.2). These younger secondary forests have regenerated on land that was used for human settlements and farming, including slash-and-burn, pasture, and small banana plantations, before the BCNM was created (Denslow and Guzman, 2000). Secondary forests have now regenerated on abandoned farmland across the entire reserve, such that today the BCNM is a forested landscape.

Most tropical secondary forest studies focus on the initial 20 to 30 years post land abandonment and the later stages of succession are not so well studied, this is largely due to the difficulty of accurately aging older forests (Martin, Newton and Bullock, 2013; Rozendaal et al., 2019). The secondary forests of the BCNM are an exception. The long history of research in the BCNM, its strict protection, and a catalogue of aerial photographs dating from 1927, have enabled us to accurately age older secondary forests (see Fig 6.2). The first secondary forest studies from the BCNM largely describe forest structure and composition in the older secondary forests on BCI (Kenoyer, 1929; Knight, 1975; Lang and Knight, 1983). The land-use history of the broader BCNM was derived from aerial photographs taken from 1927 to 1983 (US Defense Mapping Agency) and interviews with local landowners (Fig 6.2; Denslow and Guzman, 2000). In the late 1980s, STRI funded Brian Bock to compile aerial photographs of the BCNM. In 1994, Julie Denslow used these photographs to produce a historical sequence of vegetation maps and establish a chronosequence of secondary forest plots aged from 20 to 100 years old (Fig. 6.2). The 1.5-ha plot of older secondary forest established by Lang and Knight (1983) and the chronosequence plots (Fig. 6.1; Denslow and Guzman, 2000) continue to be studied today, generating valuable forest dynamics data.

6.6 Secondary forest research in the BCNM

6.6.1 Early studies (1928 – 1990)

Early botanical and ecological studies from BCI describe shifting composition over secondary succession, and report reduced complexity and canopy height in secondary compared to old-growth forests (Bennet, 1963; Kenoyer, 1929; Standley, 1928). Standley (1928) reported fallow fields near BCI rapidly becoming overgrown with herbs (such as, *Heliconia* and *Calathea*) and fast-growing *Cecropia* species, followed by shrubs and trees from the genera *Conostegia*, *Ochroma*, *Piper* and *Trema*. In 1929, Kenoyer characterized four phases of succession: 1. Rough grasses, herbs, and large monocots, such as *Heliconia sp.* (0 – 3 years after land abandonment), 2. Dominance by short-live pioneers from the genera *Cecropia*, *Miconia*, *Ochroma* and *Trema* (3 – 15 years), 3. Mixed secondary forest with long-lived pioneers from the genera *Ficus*, *Gustavia* and *Protium* (15 – 50 years), 4. Climax forest (> 50 years). These early descriptive studies include no quantitative analysis and do not distinguish among later stages of succession.

From 1975 to 1990, quantitative studies of secondary forests on BCI describe differences in species composition and forest structure of accurately aged secondary compared to old-growth forests (Foster and Brokaw, 1982; Knight, 1975; Lang and Knight, 1983). In 1975, Knight studied 13 forest stands on BCI including a small area of 15-year-old forest adjacent to the lab clearing, seven stands aged 50 – 80 years and five aged 100 – 200 years. Knight reported consistent differences in large tree communities in relation to forest age and concluded that species diversity increased rapidly in the first 15 years of succession but continued to increase subsequently and that succession continued beyond 100 years (Knight, 1975). Subsequent studies focused on forest structure and found that older secondary forest (> 80 years) had greater tree density, lower basal area, and lower canopy height than old-growth forest on BCI (Foster and Brokaw, 1982; Lang and Knight, 1983). In addition, canopy gaps tended to be smaller and less frequent in secondary compared with old-growth (Foster and Brokaw, 1982) and, in secondary forests, gaps became more common with age (Knight, 1975; Lang and Knight, 1983). These initial studies from BCI, identify two key patterns that are supported by a number of recent studies that span the Neotropics: 1. Changes in community composition persist beyond one hundred years (Norden et al., 2009; Rozendaal et al., 2019; Poorter et al., 2021a), and 2. Forest structure recovers more quickly but some properties, such as basal area and above-ground carbon sequestration, recover very slowly (Martin, Newton and Bullock, 2013; Poorter et al., 2016, Poorter et al., 2021a).

6.6.2 BCNM chronosequence (1994 – present) - forest structure

The BCNM chronosequence has been studied since 1994 and the age range of the plots is currently c. 45 – 125 years old (Denslow and Guzman, 2000). Since 1994, various aspects of forest structure have been studied, as well as diversity and composition of a range of taxa, including trees, lianas, epiphytes, and birds (Dent, DeWalt and Denslow, 2013; DeWalt, Schnitzer and Denslow, 2000; Mayhew et al., 2019; Woods and DeWalt, 2013). Structural characteristics of secondary forests, such as available light, seedling density, large living tree (>65 cm diameter) density and coarse-woody debris volume, attained equivalent values to old-growth within 70 – 100 years (Denslow and Guzman, 2000; DeWalt, Maliakal and Denslow, 2003; Jones et al., 2019). Above-ground biomass and carbon storage increased with stand age, but the most recent data indicate that aboveground carbon of 120-year-old secondary forests was c. 73% of nearby old-growth forest, indicating that biomass recovery continues beyond 120 years (Mascaro et al., 2012; Jones et al., 2019). Soil carbon was unrelated to forest age across the chronosequence and instead was correlated with soil nutrient status (Jones et al., 2019). These studies reflect general patterns from across the tropics with rapid recovery of many structural characteristics while above ground carbon stocks increase with forest age and reach old-growth levels from 100 years onwards (Poorter et al., 2016, Poorter et al., 2021a), and in contrast soil carbon is less predictable and often does not track stand age (Powers and Marín-Spiotta, 2017).

6.6.3 BCNM chronosequence – plant communities

Species richness and diversity recovered rapidly across all plant groups studied in the chronosequence, including trees and shrubs, lianas, and epiphytes. By 20 years, tree species richness and diversity were equivalent in secondary compared to old-growth forest (DeWalt, Maliakal and Denslow, 2003; Dent, DeWalt and Denslow, 2013). Diversity tended to be lower and species dominance higher for seedlings than saplings or adult trees (Dent, DeWalt and Denslow, 2013). Lianas were more diverse and approximately twice as abundant in younger forests (< 40 years) than in older secondary forests and old-growth (DeWalt, Schnitzer and Denslow, 2000). In contrast, epiphyte species richness recovered more slowly with 55-year-old forests containing 65% of old-growth species richness, although both richness and abundance increased with forest age (Woods and DeWalt, 2013).

Tree species composition tends to recover more slowly than other metrics of forest structure and diversity (Poorter et al., 2021a). In the BCNM chronosequence, similarity between old secondary forest (100 years old) and old-growth tree communities was 40%, compared to 81% similarity between old-growth communities forest (DeWalt, Maliakal and Denslow, 2003; Dent, DeWalt and Denslow, 2013). Although there were some trends of increasing similarity to old growth over time, species composition largely reflected site-specific variation in abundance of individual species (Dent, DeWalt and Denslow, 2013). For example, the palm *Oenocarpus mapora* was the most abundant species in the old-growth sites (almost 20% of individuals), while the most abundant species in secondary forests varied from site to site. In contrast, functional patterns were more predictable; light-demanding tree species became less common and shade-tolerant species more common with stand age, suggesting that the functional composition of older secondary forests converged on that of old growth (Dent, DeWalt and Denslow, 2013). Liana species composition differed between younger and older forests; with *Clitoria javitensis* and *Phryganocydia corymbosa* indicative of younger forest and *Cydista aequinoctalis* indicative of older forest (DeWalt, Schnitzer and Denslow, 2000). Epiphyte similarity to old-growth forests increased with age, with 75% similarity to old-growth at 115 years (Woods and DeWalt, 2013).

Rapid recovery of tree species richness, diversity and functional composition and delayed recovery of tree species composition are representative of the broader secondary forest literature (Poorter et al., 2021a). Studies that investigate other plant forms in secondary forests agree with results from the BCNM that liana density peaks early in succession and can show distinct successional patterns (Barry et al., 2015; Letcher and Chazdon, 2009), while epiphytes tend to track tree recovery (Benavides et al., 2006; Cascante-Marín et al., 2006).

6.6.4 BCNM chronosequence – bird communities

In contrast to plant communities, the richness, diversity, and composition of bird species were affected by both forest age and isolation across the BCNM chronosequence, and it is difficult to disentangle these two effects. Forests on BCI and isolated peninsulas (not connected to larger areas of mature forest) had reduced species diversity and distinct composition compared to mainland sites connected to other areas of forest, irrespective of forest age (Bradfer-Lawrence, Gardner and Dent, 2018; Mayhew et al., 2019). To assess the effects of isolation, we compared bird communities of the BCNM chronosequence plots to island old-growth, mainland old-growth and mainland secondary forest sites (Mayhew et al., 2019). Isolated secondary forest sites slowly converged on old-growth over time, whereas secondary forest connected to areas of old-growth rapidly converged on old-growth community composition (Mayhew et al., 2019), and even very young forests (20 years old) had high densities of forest species if they were adjacent to old-growth forest.

The successful dispersal of birds into regenerating secondary forests appears to be strongly dependent on nearby mature habitat and a lack of barriers to colonization (Dunn, 2004; Lees and Peres, 2010, 2009). Canopy bird species tend to be mobile and potentially less inhibited by isolation than understory species (Bradfer-Lawrence, Gardner and Dent, 2018). Understory bird communities were particularly affected by isolation in the BCNM, where isolation has potentially interrupted the recovery of understory bird communities over succession (Robinson, 2001; Moore et al., 2008; Lees and Peres, 2010). Many understory bird species are highly dispersal limited and unable to fly even short distances (< 100 m) between habitat fragments (Moore et al., 2008). Species-specific variation in dispersal ability correlates strongly with extinction and persistence of individual bird species across the BCNM (Moore et al., 2008), and so understory bird assemblages in the BCNM secondary forests may be determined by local extirpations and dispersal limitation as well as successional processes. In contrast, more mobile, canopy species tend to recover rapidly during tropical forest succession (Bradfer-Lawrence, Gardner and Dent, 2018; Dent and Wright, 2009).

Thus, although young forests can provide food and habitat resources for many forest species (DeWalt, Maliakal and Denslow, 2003), recolonization of regenerating forests may be inhibited for dispersal limited species in sites isolated from larger tracts of mature forest (Chazdon et al., 2009; Acevedo-Charry and Aide, 2019).

6.7 Conclusions

Secondary forest research within the BCNM spans almost a century and results are in line with broader patterns reported from secondary forests elsewhere, although sites may be more affected by isolation and less by ongoing disturbance than at other Neotropical secondary forests. The BCNM sites are largely representative of forest regeneration throughout Central America, where forests regenerate on abandoned agricultural land within a broader mosaic of farmland, old-growth and secondary forest patches (Asner et al., 2009), however there may be a greater impact of isolation in the BCNM where water, as well as forest, can separate regeneration sites (Figure 6.2). In contrast, the BCNM differs from many Neotropical secondary forests as it is strictly protected with no ongoing disturbance, hunting or timber extraction. Therefore, the BCNM provides a valuable comparison to secondary forest sites that experience ongoing disturbance, and where seed sources and animal seed dispersers are rare, and forest clearance can interrupt succession (van Breugel et al., 2013; Chazdon, 2014).

Finally, the BCNM chronosequence spans the longest documented trajectory of secondary forest regeneration in the Neotropics (45 – 125 years) and provides the oldest accurately dated secondary forests in the 2ndFOR network (see Poorter et al., 2021a, 2016; Rozendaal et al., 2019). Data from the chronosequence have been included in several meta-analyses that provide broader scale understanding of tropical forest recovery across climatic gradients (Gei et al., 2018; Poorter et al., 2021a, 2016; Rozendaal et al., 2019). In these contexts, the forests from BCNM are valuable older forest data points enabling us to more accurately model forest properties that recover slowly, such as species composition and above-ground biomass (Poorter et al., 2021a).

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"The mountains are calling and I must go, and I will work on while I can, studying incessantly." – John Muir, 1873.