Plant biodiversity effects on aboveground carbon storage in second-growth and old-growth tropical forests

by

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Abstract

Tropical forests are experience structural changes that may reduce carbon storage potential. These changes include increases in liana density, turnover rates of species, and increments in temperature and seasonality. Much research on aboveground carbon storage (AGC), however, has focused on the role of climate, with little understanding of the role of other biotic components. I examined the effects of plant biodiversity in its broad sense (e.g, functional types, abundance, functional traits) for aboveground carbon storage (AGC) in tropical forests. At global scales, I evaluated the relative importance of lianas, stand variables (e.g., basal area, wood density, tree size) and climate on AGC in old-growth forests. I found that stand variables are stronger predictors of carbon storage across tropical forest types, and explained more variation than climate at global scales. Climate effects on AGC were mainly driven by direct effects of climate on stand variables than by direct effects of climate on AGC, which emphasizes the importance of simultaneously evaluating direct and indirect effects of abiotic variables on AGC. I also found negative effects of liana abundance on AGC in moist forests, which harbor the greatest carbon stocks in tropical regions. My research is one of the first studies showing the impacts of lianas on carbon stocks, and the differential effect of lianas on biomass carbon across tropical forests. At regional scales I evaluated how species richness and functional diversity change along succession, and how these changes influence carbon stocks in second-growth forests in dry areas. At local scales, I used temporal data (6 years) to examine the effect of climate, stand age and functional traits in tree dynamics in dry forests. Results at regional and local scales indicate that both climate and land use changes influence stored and accumulation of AGC, but stand age was one of the most important drivers determining the recovery rate of diversity and AGC in dry forests. Species richness rather than functional diversity appears to explain more variation of AGC in secondary dry forests. The increase of tree-species richness along succession, which reflects an increase in AGC, has important implications for managing secondary forests, as carbon sinks could be maximized in higher mixed-species stands. Overall, my results indicate that different components of plant biodiversity influence carbon storage, and the relative importance of each component varies across forest types. Incorporating plant biodiversity in its broad increase the amount of variance explained by models of carbon stocks in tropical forests.

Preface

Some of the results from this research are the result of collaborative work, thus it contains journal articles co-authored by researchers from other universities different than University of Alberta:

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The future belongs to those who believe in the beauty of their dreams
(E. Roosevelt).

for my mom

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1. Introduction[1]

Tropical forests hold at least two-thirds of the world terrestrial biodiversity and contribute more than 30% of terrestrial carbon stocks (Gardner *et al*., 2009; Keith *et al*., 2009). Nonetheless, there is high uncertainty about the future of tropical forests due to anthropogenic changes that have the potential to alter the global carbon cycle and the forest area (Phillips & Lewis, 2014). These changes include increases rates in deforestation in tropical regions, land degradation due to intensive management practices (e.g., overgrazing), and increments in carbon dioxide emissions associate with land clearing, forest fires and the use of fossil fuels (Laurance, 2010). The reduction in forest area not only contributes to the accumulation of carbon dioxide, but also reduces the amount of biological resources, and accelerates biodiversity loss (Gardner *et al*., 2009; Strassburg *et al*., 2010).

Assessments of the human impacts on forests ecosystems have demonstrated that climate change can have significant repercussions on biodiversity (Appendix 1.1) through changes in habitat, species range and number (MEA 2005; Díaz *et al*., 2006). Moreover, it has been found that changes in biodiversity can also affect human wellbeing through indirect effects on ecosystem processes and services (Appendix 1.1, Fig. 1.1, MEA 2005). As a result, in the last decade there has been an increasing interest in identifying synergies between carbon storage and biodiversity conservation in an attempt to develop strategies that allow preservation of biodiversity and mitigation of climate change (Strassburg *et al*., 2010). Nonetheless, current initiatives in tropical regions continue to consider biodiversity mainly as an ancillary benefit, with most efforts attempting to protect areas in regions identified as having high value for carbon sequestration (Díaz *et al*., 2006; Strassburg *et al*., 2010), rather than attempting to understand whether changes in biodiversity are likely to have consequences for the accumulation of biomass carbon in tropical forests.

Growing evidence suggests that tropical forests are experiencing dramatic changes in composition, structure, and dynamics of woody plants, but there is a limited understanding of how these structural and compositional changes might impact carbon sequestration (Stegen *et al*., 2011; Baraloto *et al*., 2011). Changes in species composition and forest structure can have

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[1] *The research in Chapters 2-6 is the result of collaborative work, so I used the pronoum "we" throughout those chapters.*

inevitable consequences for carbon stocks in tropical forests, because plant species vary in their ability to sequester and store carbon (Phillips & Lewis, 2014). Nonetheless, current models that attempt to project the future of carbon sinks in tropical forests continue focusing mostly on the role of abiotic drivers, and particularly in the effect of climate (IPCC, 2007). To reduce uncertainty about the future of forest carbon sinks, it is necessary to comprehend the role of both: abiotic and biotic drivers of change for carbon storage and sequestration in tropical forests.

1.1 Abiotic drivers of carbon stocks in tropical forests

The role of climate

To date, much research evaluating variation in aboveground carbon storage (AGC) in tropical forests has focused in the role of climate. This research has provided evidence that some parameters such as mean annual precipitation (Sankaran *et al*., 2005), mean annual temperature (Raich *et al*., 2006), seasonal temperature variation (Larjavaara & Muller-Landau, 2011), precipitation of the driest quarter (Saatchi *et al*., 2007), or the combination of mean annual temperature and precipitation (Keith *et al*., 2009) may limit biomass and carbon in forested ecosystems. The effect of these climatic variables on forest biomass across studies, however, has not been consistent. For instance, Raich *et al*. (2006) found a positive relationship of forest biomass with mean annual temperature in moist forests; while Stegen *et al*. (2011) found a very weak relationship, and temperature only explained 2% of forest biomass within the same forest type. The precipitation of the driest quarter has been positively correlated with forest biomass in wet and moist tropical forests in some studies (Saatchi *et al*., 2007), but not in others (Stegen *et al*., 2011). Lack of consistency across studies is problematic since increases uncertainty to make predictions. Moreover, regional and global studies within tropical forests have found that climate explained only a small proportion of the variation in AGC, while other structural parameters such as basal area, wood density, and maximum individual biomass accounted for greater variation (Malhi *et al*., 2006, Slik *et al*., 2010, Baraloto *et al*., 2011; Stegen *et al*., 2009; 2011). Models that capture the contribution of both climatic variables and forest structural parameters could improve our knowledge of how forest biomass and carbon stocks will response under current global changes.

Soil effects on carbon stocks

Another important factor influencing carbon stocks is soil fertility and the effects of physical and chemical soil factors (Baraloto *et al*., 2011). There exists, however, less consensus on the effect of soils on AGC in tropical forests. For example, some studies have found increases in AGC associated with soil fertility, suggesting that biomass carbon could be limited by nutrient availability (Laurance *et al*., 1999; DeWalt & Chave, 2004; Slik *et al*., 2010). In contrast, studies in the Amazon have found the highest AGC on relatively poor soils (Malhi *et al*., 2006; Saatchi *et al*., 2007). Contrasting results among studies appear related with spatial variation in soil factors or variation in tree species composition across sites (Paoli *et al*., 2008; Baraloto *et al*., 2011). Baraloto *et al*. (2011) assessed the role of soil, climate and forest stand variables (e.g., basal area, tree size) on AGC in Amazonian forests and they found that stand variables explained more variation in AGC than climate and soil combined. Nonetheless, it is still unknown whether this pattern holds for other tropical forests, and whether the role of soil in AGC is undermined after accounting for the effect of forest stand variables. More research where the combined effects of soil, climate and stand variables on AGC are evaluated is necessary to disentangle the abiotic correlates of AGC.

Land-use and land-cover changes

Land conversion is the second largest source of human-induced climate change, and accounts for approximately 17–20% of anthropogenic greenhouse gas emissions (Gullison *et al*., 2007). Estimating resulting carbon emissions from land conversion is it therefore of high priority in order to provide accurate assessments of the carbon budget and the global carbon cycle (Houghton, 2005). Land clearing in tropical forests is very high with reductions in forest cover by up to 130 000 km2 per year due to burning, grazing or cultivation (Laurance, 2010). These high rates of transformation have led to decreases in the extent of old-growth forests with subsequent replacement of areas for agriculture or cattle ranching (Houghton, 2005). Despite land conversion, significant steps have been made to restore and recover degraded lands by preventing fire and grazing and allowing natural regeneration, specifically in some protected areas (Janzen, 2002). As a result, current landscape in tropical regions is becoming dominated by patches of secondary forest succession (Houghton, 2005). Secondary succession is the long-term directional change in community composition following a disturbance event (Chazdon, 2014).

Currently, secondary or second-growth forests occupy more area than old-growth forests within tropical regions (Laurance, 2010). Thus, tropical forest succession constitutes a central topic in forest ecology.

The recovery of aboveground carbon storage (AGC) in secondary forests depends on many factors such as soil fertility, precipitation and seasonality, the frequency and intensity of previous land uses, temperature, the initial species colonization, functional traits of the species present (Appendix 1.1) and site productivity (Read & Lawrence, 2003; Quesada *et al*., 2009; Chazdon *et al*., 2007). During succession vegetation structure, species diversity, composition, and biomass carbon change in synchrony, thus increases in diversity are extremely linked to accumulation of biomass (Chazdon, 2014). Nonetheless, little is known about how changes in species diversity and composition influence the accumulation of ecosystem processes such as AGC. Few studies have attempted to establish linkages between species richness, functional composition and carbon stocks in secondary forests (Becknell & Powers, 2014; Bu *et al*., 2014; Lohbeck *et al*., 2015). These studies, however, have focused mainly in wet forests (Bu *et al*., 2014; Lohbeck *et al*., 2015), with limited information in tropical dry forests (Becknell & Powers, 2012); despite the fact the dry forests represent 42% of all tropical forests (Miles *et al*., 2006) and have experienced greater rates of transformation than wet and moist forests, with subsequent biodiversity loss (Quesada *et al*., 2009).

Tropical dry forests (TDFs) are broadly defined as a vegetation type dominated by deciduous trees, with an annual average temperature of at least 25°C or higher, annual precipitation of 700-2000 mm per year, and a dry season (precipitation less than 100 mm) of three or more months (Sánchez-Azofeifa *et al*. 2005). TDFs support a larger diversity of life forms than other tropical forests and a high number of endemic species (Mooney *et al*., 1995, Trejo & Dirzo 2002). TDFs, in contrast to wet forests, show a lower number of plant species, fewer canopy strata, basal area, and plant species are predominantly wind dispersed in early successional stages (Mooney *et al*. 1995, Vieira & Scariot 2006). These differences are likely to affect rates of change in vegetation structure and composition after disturbance in TDFs (Vieira & Scariot, 2006, Chazdon *et al*., 2007). Consequently, more studies are needed to identify which biotic and abiotic factors influence the recovery of carbon stocks in secondary TDFs to understand how TDFs recover after disturbance and propose management strategies for forest remnants.

1.2 Plant biodiversity components and their influence on carbon stocks

Biodiversity in its broad sense is defined as the number, abundance, composition, spatial distribution, and interactions of genotypes, populations, species richness, functional types and traits, and landscape units in a given system (Díaz *et al*., 2006). Cumulative evidence in the last two decades has demonstrated that different components of biodiversity influence ecosystem processes such as primary production, nutrient cycling and carbon sequestration (Hooper *et al*., 2005, MEA, 2005), which contribute to the provision of ecosystem services and human wellbeing (Fig. 1). In tropical regions, different studies have indicated that plant diversity components such as the abundance, species richness, functional types and functional traits have an influence aboveground carbon storage (AGC) and the amount of AGC accumulation in old-growth tropical forests (Slik *et al*., 2010; Baraloto *et al*., 2011). The effect of some of these components on AGC has already been evaluated in tropical forests, while the effect of others still remains elusive.

Abundance, size and functional traits

In the last decade several studies have assessed the role of stand variables for aboveground carbon storage (AGC) in tropical forests in order to identify which forest structural parameters are positive correlates of AGC. Among these parameters, it is known that basal area (Malhi *et al*., 2006; Slik *et al*., 2010), tree size (Baraloto *et al*., 2011), maximum individual biomass (Stegen *et al*., 2011) and the density of large trees (≥ 70 cm diameter) (Slik *et al*., 2013) are strong predictors and positive correlates of AGC. There is growing recognition that classifying plant species in terms of their functional traits has a strong predictive power to address ecological questions about species response to environmental changes (Cornelissen *et al*., 2003). Functional traits are attributes of an organism (e.g., morphological or ecophysiological) considered to reflect adaptations or responses to the environment (Hooper *et al*., 2005).

A functional trait that has captured great attention in studies on variation in AGC is wood density. Wood density is the oven-dry mass of a section of the main stem of a plant divided by its fresh volume (Cornelissen *et al*., 2003), and it is generally associated with life history strategies, mechanical support and diameter growth rates (Chave *et al*., 2009). Numerous studies have claimed that declines in wood density could cause a decline in AGC in tropical forests and thus in overall terrestrial carbon pools (Bunker *et al*., 2005; van der Heijden *et al*., 2013; Phillips & Lewis, 2014). However, it has been found that wood density does not always increase AGC in tropical forests (Stegen *et al*., 2009). In contrast, the AGC-wood density relationship varies from negative to null to positive depending of the forest community and forest identity (Baker *et al*., 2004; Stegen *et al*., 2009). Regardless whether stand variables have positive or negative effects on AGC, there appears to be a consensus in that incorporating forest stand variables increase the amount of variation explained in AGC, since they have explained more variation than other abiotic factors such as climate at regional and global level (Chave *et al*., 2009; Slik *et al*., 2010; Stegen *et al*., 2011).

Functional traits related with plant performance are also useful to establish linkages with ecosystem processes such as primary production or AGC (Tilman, 1997; Hooper *et al*., 2005). For example, leaf traits such as specific leaf area (SLA, i.e., the ratio of leaf area to dry mass) or the concentration of nutrients in the leaf such as nitrogen and phosphorus are expected to influence rates of carbon dynamics because these traits are related with leaf longevity, carbon investment in secondary compounds, nutrition quality, growth rates, and resource use efficienty (Cornelissen *et al*., 2003).

Functional types: the role of lianas

Functional type is a set of species or organisms that have similar responses to environmental conditions (Hooper *et al*., 2005). Similar responses by a group of species are related to similar morphological or physiological attributes. For example, lianas or woody vines represent a conspicuous component in tropical forests, characterized to climb other plants to reach the forest canopy and to have high canopy: stem ratio, which results in a higher proportion of photosynthetic biomass compared to the biomass present in wood plants (Gentry, 1991; Putz, 1991; Schnitzer & Bongers, 2002).

Lianas are an important component of tropical forests, where they account for 25 to 40% of the woody stems and more than 25% of the woody species (Schnitzer & Bongers, 2011). They are a polyphyletic group, with at least 133 plant families including woody climbers (Gentry, 1991). Seedlings and seedling-sized plants of many woody vines are initially self-supporting, and usually achieve 30-40 cm of vertical growth, although some species can reach 1-2 m height, before requiring mechanical support (Putz, 1991). Lianas increase their likelihood of finding a suitable support by actively searching, waiting, and being able to climb a variety of support sizes (Putz, 1991; Schnitzer & Bongers, 2002). Lianas have different adaptations for attaching themselves to their hosts such as thorns, spines, clasping tendrils that arise from stem, adhesive hairs, and adventitious roots (Hegarty, 1991; Putz, 1991; DeWalt *et al*., 2000). The mechanism for climbing determines the maximum diameter support a liana can use as well as the required distribution of hosts (the trellis structure) (Putz, 1991).

Due to their dependency of trees for structural support, lianas compete intensely with trees for above- and below-ground resources such as light, water and nutrients (Schnitzer & Bongers, 2002; 2011). Moreover, lianas are able to reduce tree growth and reproductive output, increase the risk of tree mortality and inhibit tree regeneration (Wright, 2005; Ingwell *et al*., 2010; Schnitzer & Bongers, 2011). Lianas might also induce changes in forests composition because they show higher infestation rates in slow-growing and shade-tolerant trees than fast-growing or light-tolerant species (van der Heijden *et al*., 2013). A removal experimental study in Panama assessed tree composition in areas with and without lianas and found an increased in the density, growth and diversity of shade-tolerant tree species after 8 years of liana removal (Schnitzer & Carson, 2010). These detrimental impacts of lianas, which affect tree dynamics, have also the potential to reduce biomass carbon and the accumulation of carbon over time in tropical forests.

Compelling evidence indicated that liana density and biomass are increasing in old-growth tropical forests (Phillips *et al*., 2002; Schnitzer & Bongers, 2011), and this increase has been considered as one of the structural changes that could reduce carbon storage potential (Phillips & Lewis, 2014). Nevertheless, lianas continue to be neglected in studies about variation in carbon stocks in tropical regions. Increases of lianas in tropical forests appear to be associated with higher temperature and evapotranspirative demand, reductions in mean annual rainfall and increasing seasonality (DeWalt *et al*., 2010; Schnitzer & Bongers, 2011). With current models predicting higher temperatures and seasonality in tropical regions (IPCC, 2007), it is fundamental to comprehend whether lianas could impact current carbon sinks, and if so what is their relative importance compared to other environmental factors such as climate or forest stand variables. This information will enhance our understanding of how forests will respond to further increments in liana abundance related with climate changes.

Species richness and functional diversity effects on carbon pools

With the emergence of research on the effects of biodiversity on ecosystem processes, major advances have been made in the role of species and the effects of biodiversity loss for ecosystem processes (Cardinale *et al*., 2012; Hooper *et al*., 2012). Ecosystem processes (Appendix 1.1) refers to stocks of energy and materials, and includes processes such as primary production, nutrient cycling, and decomposition (Hooper *et al*., 2005). Cumulative research demonstrated that biodiversity affects ecosystem processes and the provision of ecosystem services (Appendix 1.1, Cardinale *et al*., 2012; Hooper *et al*., 2012). This research has shown that diversity increases ecosystem processes such as primary production (Tilman, 1997), nutrient retention (Finlay *et al*., 1997), and biomass (Hooper *et al*., 2005). Most of this evidence, however, has focused on small-scale and highly controlled experiments under conditions that differ markedly form those of natural systems in real landscapes (e.g., microcosms) (Hooper *et al*., 2005; Srivastava & Vellend, 2005) and have been mostly restricted to plant communities in temperate or grassland ecosystems (Cardinale *et al*., 2012; Hooper *et al*., 2012).

Empirical studies in forests ecosystems are rather limited. Research in temperate forests confirms that species-rich forests generally show higher productivity than species poor forest (Caspersen & Pacala, 2001; Thompson *et al*., 2009; Vilà *et al*., 2013). Others have found that rather than the number of species the traits of some dominant species may play a more important role for primary production (Jacob *et al*., 2010). In tropical forests, a handful of studies have evaluated the role of biodiversity on aboveground carbon storage (AGC) focusing on simulations, comparisons between plantations and natural forests and few empirical studies. For example, Balvanera *et al*., (2005) simulated the removal of of functionally important species (e.g., commercially valuable trees) in a conserved forest, and found tht 13% species contributed to 90% of AGC, and the removal could diminish AGC by up to 60%. Another study simulated 18 possible extinction scenarios and its effect on AGC, and it found that tree species composition was the main factor influencing changes in AGC (Bunker *et al*., 2005). Comparisons between a natural forest and a tree plantation have found that AGC is influenced by different components of diversity. For example, in a tree plantation a positive association between AGC and species richness has been found, while in the contiguous natural forests AGC was mostly affected by the dominance of tallest trees (e.g., most abundant canopy trees) (Ruíz-Jaen & Potvin, 2011). More recent studies have found that changes in AGC are positively related to the functional diversity rather than the number of species (Conti & Díaz, 2013, Finegan *et al*., 2015). Functional diversity is the kind, range, value and relative abundance of organismal traits present in a community (Díaz & Cabido, 2001). Initial studies in grasslands emphasized the effect of species richness (Tilman, 1997; Srivastava & Vellend, 2005), while in the last decade recent evidence has indicated that functional diversity is the most important component of biodiversity in its broad sense and ecosystem processes (Díaz & Cabido, 2001; Díaz *et al*., 2007). In tropical forests, however, little is known about which diversity component (e.g., functional traits, species richness) has stronger influences on AGC.

Different diversity components are related with different mechanisms to explain how changes in biodiversity influence ecosystem processes (Mokany *et al*., 2008). For example, functional composition or identity is more related with the mass-ratio hypothesis, while the heterogeneity or variance in the functional traits in the community is more related with niche complementarity (Appendix 1.1). The mass-ratio hypothesis, states that ecosystem processes are mainly determined by the functional traits of the dominant species (Grime, 1998), while the niche-complementarity establishes that a more diverse community has a greater heterogeneity of functional traits than a less diverse community, which facilitate a better utilization of resources and as result increases total ecosystem process (Tilman, 1997). Understanding which component has a stronger effect on ecosystem processes, and in particular on AGC, it is essential for managing forest ecosystems in a way that AGC can be maximized by retaining species diversity or by conserving dominant species with particular traits (Caspersen & Pacala, 2001). Moreover, identifying the tree species and their attributes that allow them to maximize AGC in tropical forests has great potential for restoration of degraded lands.

1.3 Thesis overview

The overall objective of my dissertation is to assess the role of plant biodiversity, in a broad sense, to explain variation in aboveground carbon storage in tropical forests. To this end, I examined the effect of different diversity components on carbon storage at different scales in old-growth and second-growth forests (Fig. 1.2). For the purpose of this study I used the definition of secondary forests by Brown & Lugo (1990), which specifies that second-growth forests are those formed as a consequence of human disturbance with the last 80 years old, since secondary forests older than 80 years become indistinguishable from old-growth or mature forests (Richards, 1995).

Chapter 2. Liana impacts on carbon cycling in tropical old-growth and second-growth forests. In this chapter I reviewed the available evidence of liana effects on carbon cycling in tropical forests. I compiled published literature to examine the effects of liana abundance on aboveground carbon storage, aboveground woody productivity (e.g., tree growth), and primary productivity (e.g., litterfall production) in old-growth and second-growth forests.

Chapter 3. Carbon stocks in tropical forests decrease with liana density. Using a standardized data set of old-growth forests worldwide, I assessed the role of liana abundance, mean annual temperature and dry season length on AGC. In old-growth forests it has been found that few species may account for approximately 80 percent of AGC (Balvanera *et al*., 2005). Thus, I used the tree composition data to evaluate the effect of liana abundance on the dominance of the tree community. Dominance in each plot was calculated as the proportion of the most common tree species (e.g., Simpson index) weighted by tree density (No. trees ha^{-1}) and basal area (m^2 ha^{-1}).

Chapter 4. Climate, stand variables and lianas control forest carbon in old-growth tropical forests. Following results from Chapter 3, I found that lianas have negative effects on AGC, which could jeopardize the capacity of tropical forests to sequester carbon in the future. Nonetheless, patterns of abundance distribution of lianas in tropical forests suggest that lianas may have differential effects on AGC across forest types. For instance, lianas are more abundant in dry forests than wet and moist forests. Moreover, it is unclear what the relative importance of lianas is for AGC compared to stand variables and climate, and whether this importance change across forest types. Thus, in this chapter I developed an integrative framework to determine the relative importance of lianas, stand variables, and climatic conditions on AGC across forest types.

Chapter 5. A multi-site analysis of the impact of tree diversity on carbon storage in secondary tropical dry forests. To assess the role of plant biodiversity in AGC, I worked at regional level with forest inventory data in secondary tropical dry forests (TDFs). Although, changes in plant biodiversity and accumulation of carbon biomass are strongly linked during succession, there is limited knowledge of how changes in plant biodiversity in secondary succession influence AGC. Here I conducted a multi-site analysis using standardized forest inventory data to disentangle the effects of climate, stand age (time since land abandonment) and different diversity components on AGC.

Chapter 6. What drives the rates of carbon accumulation in secondary tropical dry forests? To better understand the role of plant biodiversity on AGC, it is necessary to examine whether diversity drives changes in AGC. To this end, I used forest inventory data collected during 6 years to assess whether changes in AGC were influenced by species richness, functional diversity or were mostly related to stand age. I related these factors to three different carbon pools related with carbon gain: AGC accumulation, AGC increment and aboveground primary productivity in secondary tropical dry forests. AGC accumulation is the net amount of AGC obtained from tree recruitment plus tree growth minus tree mortality. AGC increments are estimated based on recruitment and growth only, and primary productivity is based on litterfall production along 3 years.

1.4 References

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

Balvanera P, Kremen C, Martinez-Ramos M. (2005) Applying community structure analysis to ecosystem function: Examples from pollination and carbon storage. *Ecological Applications* **15**, 360-375.

Baraloto, C., Rabaud, S., Molto, Q., Blanc, L., Fortunel, C., Herault, B., Davila, N., Mesones, I., Rios, M., Valderrama, E. & Fine, P.V.A. (2011) Disentangling stand and environmental correlates of aboveground biomass in Amazonian forests. *Global Change Biology*, **17**, 2677-2688.

Becknell, J. & Powers, J. (2014) Stand age and soils as drivers of plant functional traits and aboveground biomass in secondary tropical dry forest. *Canadian Journal of Forest Research*, **613**, 604–613.

Brown, S., & Lugo, A. E. (1990) Tropical secondary forests. Journal of Tropical Ecology **6**, 1–32.

Bu, W., Zang, R. & Ding, Y. (2014) Field observed relationships between biodiversity and ecosystem functioning during secondary succession in a tropical lowland rainforest. *Acta Oecologica*, **55**, 1–7.

Bunker, D., DeClerck, F. & Bradford, J. (2005) Species loss and aboveground carbon storage in a tropical forest. *Science*, **310**, 1029–1031.

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace, G.M., Tilman, D., Wardle, D. a, Kinzig, A.P., Daily, G.C., Loreau, M., Grace, J.B., Larigauderie, A., Srivastava, D.S. & Naeem, S. (2012) Biodiversity loss and its impact on humanity. *Nature*, **486**, 59–67.

Caspersen, J. P. &Pacala, S. W. (2001) Successional diversity and forest ecosystem function. *Ecological Research,* **16**, 895-903.

Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G. & Zanne, A.E. (2009) Towards a worldwide wood economics spectrum. *Ecology letters*, **12**, 351–66.

Chazdon, R. L. (2014). *Second growth*: The promise of tropical forest regeneration in an age of deforestation. University of Chicago Press.

Conti, G. & Díaz, S. (2013) Plant functional diversity and carbon storage–an empirical test in semi-arid forest ecosystems. *Journal of Ecology* **101**, 18-28.

Cornelissen, J. H. C., Lavorel, S., Garnier, E., Díaz, S., Buchmann, N., Gurvich, D.E., Reich, P.B., ter Steege, H., Morgan, H.D., van der Heijden M.G. A., Pausas, J. P. & Poorter, H. 2003. A handbook of protocols for standardise and easy measurement of plant functional traits worldwide. *Australian Journal of Botany* **51**, 335-380.

DeWalt, S.J. & Chave, J. (2004) Structure and biomass of four lowland Neotropical forests. *Biotropica*, **36**, 7-19.

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

DeWalt, S., Schnitzer, S. & Chave, J. (2010) Annual rainfall and seasonality predict pan-tropical patterns of liana density and basal area. *Biotropica*, **42**, 309–317.

Díaz, S., & Cabido, M. 2001. Vive la différence: plant functional diversity matters to ecosystem processes. *Trends in Ecology and Evolution*, **16,** 464–655.

Díaz, S., Fargione, J., Chapin III, F. S., & Tilman, D. (2006). Biodiversity loss threatens human well-being. *PLoS biology*, **4,** e277.

Díaz, S. & Lavorel, S. (2007) Incorporating plant functional diversity effects in ecosystem service assessments. *Proceedings of the National Academy of Sciences*, **104**, 20684-20689.

Finegan, B., Peña-Claros, M., Oliveira, A., Ascarrunz, N., Bret-Harte, M. S., Carreño-Rocabado, G., & Poorter, L. (2015). Does functional trait diversity predict above-ground biomass and productivity of tropical forests? Testing three alternative hypotheses. *Journal of Ecology*, **103**, 191-201.

Finlay, B. J., Maberly, S. C. & Cooper, J. I. (1997) Microbial diversity and ecosystem function. *Oikos,* **80**, 209-213.

Gardner, T. A., Barlow, J., Chazdon, R., Ewers, R. M., Harvey, C. A., Peres, C. A., & Sodhi, N. S. (2009). Prospects for tropical forest biodiversity in a human-modified world. *Ecology Letters,* 12, 561-582.

Gentry A. (1991). The distribution and evolution of climbing plants. *The biology of vines* (ed. By F.Putz, H. Mooney), pp. 3–49. Cambridge: Cambridge University Press.

Grime, J. P. (1998). Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology,* **86**, 902–910.

Gullison, R.E., Frumhoff P.C., Canadell J.G., Field, C. B., Nepstad, D.C., Hayhoe, K., Avissar, R., Curran, L. M., Friedlingstein, P., Jones, C. D. & Nobre, J. (2007). Environment. Tropical forests and climate policy. *Science* **316**, 985–986.

Hegarty, E. E. (1991) Leaf litter production by lianas and trees in a sub-tropical Australian rainforest. *Journal of Tropical Ecology*, **7**, 201-214.

van der Heijden, G.M., Schnitzer, S.A., Powers, J.S. & Phillips, O.L. (2013) Liana impacts on carbon cycling, storage and sequestration in tropical forests. *Biotropica*, **45**, 682-692

Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J., Vandermeer, J. & Wardle, D.A. (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs*, **75**, 3–35

Hooper, D. U., Adair, E. C., Cardinale, B. J., Byrnes, J. E., Hungate, B. A., Matulich, K. L. & O'Connor, M. I. (2012) A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature*, **486**, 105-108.

Houghton, R. A. (2005). Aboveground forest biomass and the global carbon balance. *Global Change Biology*, **11**, 945-958.

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

IPCC (2007) Climate change 2007: the physical science basis. Cambridge University Press, Cambridge, UK.

Jacob, M., Leuschner, C., & Thomas, F. M. (2010) Productivity of temperate broad-leaved forest stands differing in tree species diversity. *Annals of Forest Science*, **67**, 503.

Janzen, D.H. (2002). Tropical dry forest: Area de Conservacıón Guanacaste, northwestern Costa Rica. In: Perrow, M.R., Davy, A.J. (Eds.), Handbook of Ecological Restoration, vol. 2. Cambridge University Press, Cambridge, pp. 559–583.

Keith, H., Mackey, B.G. & Lindenmayer, D.B. (2009) Re-evaluation of forest biomass carbon stocks and lessons from the world's most carbon-dense forests. *Proceedings of the National Academy of Sciences*, **106**, 11635-11640.

Laurance, W. F., Fearnside, P. M., Laurance, S. G., Delamonica, P., Lovejoy, T. E., Rankin-de Merona, J. M., Chamber, J. Q. & Gascon, C. (1999) Relationship between soils and Amazon forest biomass: a landscape-scale study. *Forest Ecology and Management*, **118**, 127–138.

Larjavaara, M. & Muller-Landau, H.C. (2012) Temperature explains global variation in biomass among humid old-growth forests. *Global Ecology and Biogeography*, **21**, 998-1006.

Lohbeck, M., Poorter, L., Martínez-Ramos, M. & Bongers, F. (2015) Biomass is the main driver of changes in ecosystem process rates during tropical forest succession. *Ecology*, 96, 1242-1252

Malhi, Y., Wood, D., Baker, T.R., Wright, J., Phillips, O.L., Cochrane, T., Meir, P., Chave, J., Almeida, S., Arroyo, L., Higuchi, N., Killeen, T.J., Laurance, S.G., Laurance, W.F., Lewis, S.L., Monteagudo, A., Neill, D.A., Vargas, P.N., Pitman, N.C.A., Quesada, C.A., Salomao, R., Silva, J.N.M., Lezama, A.T., Terborgh, J., Martinez, R.V. & Vinceti, B.

(2006) The regional variation of aboveground live biomass in old-growth Amazonian forests. *Global Change Biology*, **12**, 1107-1138.

MEA. (2005) *Ecosystems and human well-being: current state and trends, Volume 1*. Island Press, New York.

Miles, L., Newton, A.C., DeFries, R.S., Ravilious, C., May, I., Blyth, S., Kapos, V. &Gordon, J.E. (2006) A global overview of the conservation status of tropical dry forests. *Journal of Biogeography*, **33**, 491–505.

Mokany, K., Ash, J. & Roxburgh, S. (2008) Functional identity is more important than diversity in influencing ecosystem processes in a temperate native grassland. *Journal of Ecology*, **96**, 884–893.

Mooney, H.A., Bullock, S.H. & Medina, E. (1995) *Seasonally Dry Tropical Forests*. Cambridge, Cambridge University Press.

Paoli, G.D., Curran, L. M. & Slik, J. W. F. (2008) Soil nutrients affect spatial patterns of aboveground biomass and emergent tree density in southwestern Borneo. *Oecologia*, **155**, 287–299.

Paquette, A. & Messier, C. (2011) The effect of biodiversity on tree productivity: from temperate to boreal forests. *Global Ecology and Biogeography*, **20**, 170–180.

Phillips, O. & Lewis, S. (2014) Recent changes in tropical forest biomass and dynamics. *Forests and Global Change*, **4**, 77-108.

Phillips, O.L., Martinez, R.V., Arroyo, L., Baker, T.R., Killeen, T., Lewis, S.L., Malhi, Y., Mendoza, A.M., Neill, D., Vargas,P.N., Alexiades, M., Cerón, C., Di Fiore, A., Erwin, T., Jardim, A., Palacios, W., Saldias, M. & Vinceti, B. (2002) Increasing dominance of large lianas in Amazonian forests. *Nature*, **418**, 770–774.

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

Raich, J.W., Russell, A.E., Kitayama, K., Parton,W.J. & Vitousek, P.M. (2006) Temperature influences carbon accumulation in moist tropical forests. *Ecology*, **87**, 76–87.

Richards, P. W. 1955. The secondary succession in the tropical rain forest. *Science Progress London* **43**, 45-57.

Read, L. & Lawrence, D. (2003) Litter Nutrient Dynamics During Succession in Dry Tropical Forests of the Yucatan: Regional and Seasonal Effects. *Ecosystems*, **6**, 747–761.

Ruíz-Jaen, M. C. & Potvin C. 2011. Can we predict carbon stocks in tropical ecosystems from tree diversity? Comparing species and functional diversity in a plantation and a natural forest. New Phytologist, 189, 978-987.

Saatchi, S.S., Houghton, R.A., Dos Santos Alvalá, R.C., Soares, J.V. & Yu, Y. (2007) Distribution of aboveground live biomass in the Amazon basin. *Global Change Biology*, **13**, 816–837.

Sánchez-Azofeifa, G. A., Quesada, M., Rodríguez, J. P., Nassar, J. M., Stoner, K. E., Castillo, A., & Cuevas-Reyes, P. (2005) Research Priorities for Neotropical Dry Forests. *Biotropica*, **37**, 477-485

Sankaran, M. & McNaughton, S. J. (1999) Determinants of biodiversity regulate compositional stability of communities. *Nature*, **401**, 691-693.

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

Schnitzer, S.A. & Bongers, F. (2011) Increasing liana abundance and biomass in tropical forests: emerging patterns and putative mechanisms. *Ecology letters*, **14**, 397-406.

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

Slik, J.W.F., Aiba, S.I., Brearley, F.Q., Cannon, C.H., Forshed, O., Kitayama, K., Nagamasu, H., Nilus, R., Payne, J., Paoli, G., Poulsen, A.D., Raes, N., Sheil, D., Sidiyasa, K., Suzuki, E. & Valkenburg, J.L.C.H. (2010) Environmental correlates of tree biomass, basal area, wood specific gravity and stem density gradients in Borneo's tropical forests. *Global Ecology and Biogeography*, **19**,50–60. 73

Slik, J.W.F., Paoli, G., McGuire, K., Amaral, I., Barroso, J., Bastian, M., Blanc, L., Bongers, F., Boundja, P., Clark, C., Collins, M., Dauby, G., Ding, Y., Doucet, J.-L., Eler, E., Ferreira, L., Forshed, O., Fredriksson, G., Gillet, J.-F., Harris, D., Leal, M., Laumonier, Y., Malhi, Y., Mansor, A., Martin, E. et al. (2013) Large trees drive forest aboveground biomass variation in moist lowland forests across the tropics. *Global Ecology and Biogeography*, **22**, 1261-1271.

Srivastava D. S. and M. Vellend. 2005. Biodiversity–ecosystem function research: is it relevant to conservation? *Annual Review of Ecology, Evolution and Systematics*, **36**, 267–94.

Stegen, J.C., Swenson, N.G., Valencia, R., Enquist, B.J. & Thompson, J. (2009) Above-ground forest biomass is not consistently related to wood density in tropical forests. *Global Ecology and Biogeography*, **18**, 617–625.

Stegen, J.C., Swenson, N.G., Enquist, B.J., White, E.P., Phillips, O.L., Jørgensen, P.M., Weiser, M.D., Monteagudo Mendoza, A. & Núñez Vargas, P. (2011) Variation in above-ground forest biomass across broad climatic gradients. *Global Ecology and Biogeography*, **20**, 744-754.

Strassburg, B. B., Kelly, A., Balmford, A., Davies, R. G., Gibbs, H. K., Lovett, A. & Rodrigues, A. S. (2010). Global congruence of carbon storage and biodiversity in terrestrial ecosystems. *Conservation Letters*, **3**, 98-105.

Tilman, D. (1997) Distinguishing between the effects of species diversity and species composition. *Oikos*, **80**, 185.

Trejo, I. & Dirzo, R. (2000) Deforestation of seasonally dry tropical forest: a national and local analysis in Mexico. *Biological Conservation*, **94**, 133–142.

Vieira, D.L.M. & Scariot, A. (2006) Principles of natural regeneration of tropical dry forests for restoration. *Restoration Ecology*, **14**, 11–20.

Vilà, M., A. Carrillo-Gavilán, J. Vayreda, H. Bugmann, J. Fridman, W. Grodzki, J. Haase, G. Kunstler, M. Schelhaas, and A. Trasobares. (2013). Disentangling biodiversity and climatic determinants of wood production. *PLoS ONE*, **8**, e53530

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

1.5 Figures

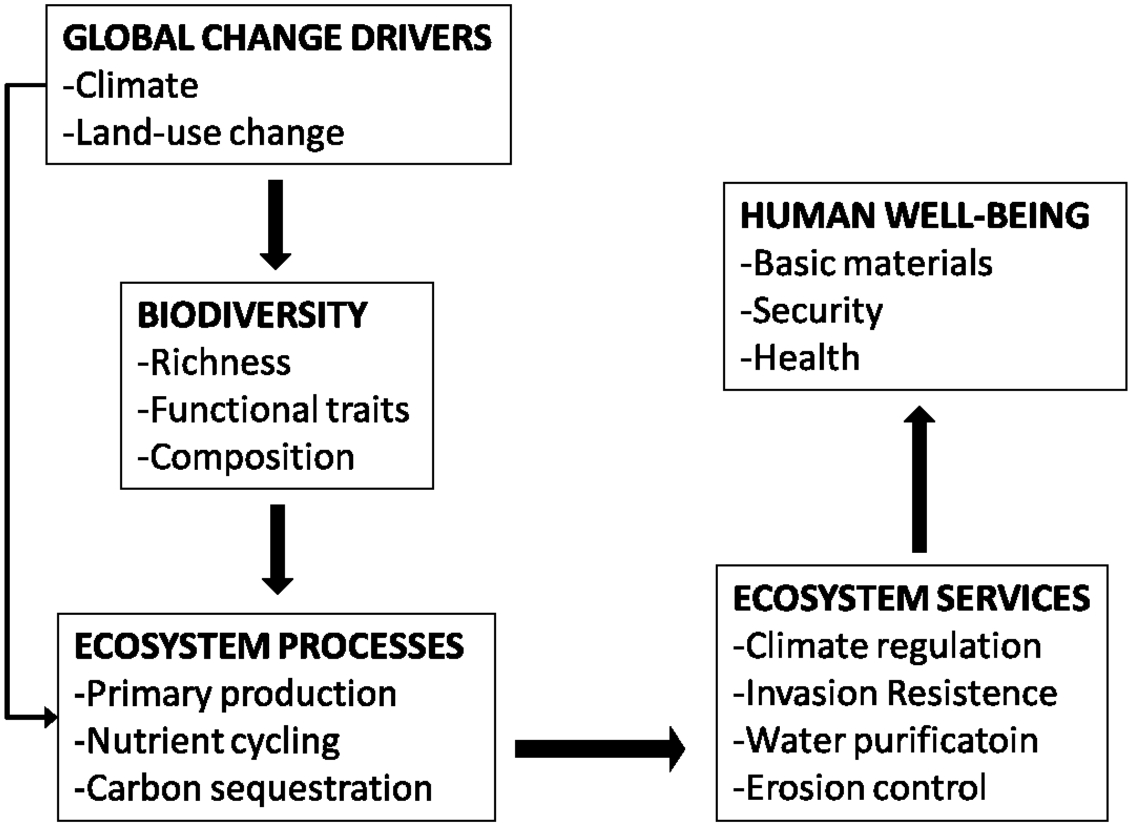

Figure 1.1. Conceptual framework of the role of biodiversity in ecosystem processes and services. Biodiversity is both a response variable affected by global change drivers and a factor that can affect human wellbeing through indirect effects on ecosystem services. Biodiversity is defined in its broad sense including species richness, composition, biotic interactions, and functional traits. Adapted from the Millennium Ecosystem Assessment (MEA 2005).

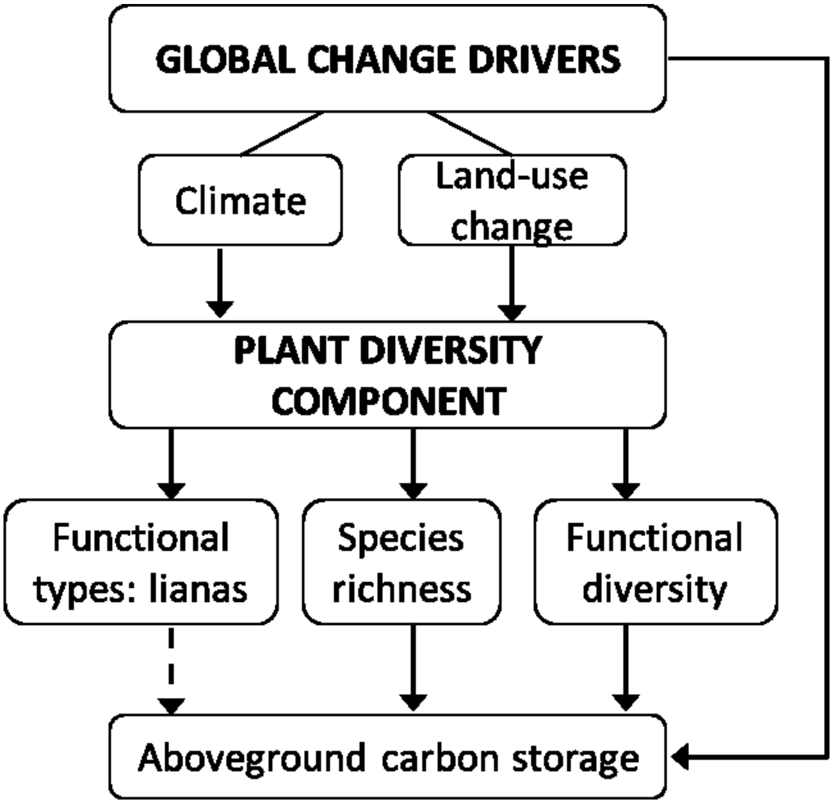

Figure 1.2. Schematic conceptual framework to this research to evaluate the role of climate and land-use change (age since last disturbance) on diversity and aboveground carbon storage (AGC) in second-growth and old-growth forests (modified from MEA, 2005). The framework indicates that global change drivers such as climate and land-use change influence plant biodiversity and AGC. At the same time different diversity components such as functional types, species richness or functional diversity can influence AGC. Solid arrows represent hypothesised positive effects of diversity on AGC (second-growth forests), while dashed arrows represent hypothesised negative effects (old-growth forests).

Appendix 1.1. Glossary.

- **Biodiversity**: Biodiversity in the broad sense is the number, abundance, composition, spatial distribution, and interactions of genotypes, populations, species, functional types and traits, and landscape units in a given system (Díaz *et al*., 2006).
- **Ecosystem processes**: Ecosystem processes refers to stocks of energy and materials, as well as the complex interactions and flow of energy and materials among biotic and abiotic elements of ecosystems (Díaz & Cabido, 2001).
- **Ecosystem services**: are the benefits that ecosystems provide to humanity either directly or indirectly (Díaz *et al*., 2006). The Millenium Ecosystem Assessment classify the ecosystem services in supporing (e.g., primary production, nutrient cycling, regulating (e.g., climate regulation, pest control), provisioning (e.g., food, wood, fresh water), and cultural services (e.g., recreation and aesthetic values) (MEA, 2005).
- **Functional traits**: the characteristics or attributes of an organism that are considered relevant to its response to the environment or its effect on ecosystem process. For example, leaf size, longevity, seed size and dispersal mode (Díaz & Cabido, 2001; Hooper *et al*., 2005).
- **Functional diversity**: the value, range and abundance of functional traits of the organisms present in a given community (Díaz & Cabido, 2001).
- **Functional type**: is a set of species that have similar effects on a specific ecosystem process or similar responses to environmental conditions (Hooper *et al*., 2005).
- **Lianas**: are woody vines or woody climbers that use tree stems as treellises to reach the forest canopy. They are a poliphyletic group with different adaptations for attaching themselves to their hosts (Putz, 1991).
- **The mass-ratio hypothesis**: this hypothesis proposes that species influence ecosystem processes according to their functional traits and in direct proportion to their relative abundance (Grime, 1998).
- **The niche complementarity**: this hypothesis is based on the idea that diversity of both the organisms in a community and their functional traits influences ecosystem processes through mechanisms such as complementary resource use (Tilman, 1997).

2. Liana impacts on carbon cycling in tropical old-growth and second-growth forests[2]

2.1 Introduction

Tropical forests store over 30 % of the global carbon budget in forest ecosystems and account for 32 % of the global primary productivity (Malhi, 2012). Thus, any alteration in tropical forests can have strong impacts on the global carbon cycle and ultimately in the global climate. Growing evidence suggests that tropical forests are experiencing major structural changes as a consequence of forest fragmentation and logging (Schnitzer & Bongers, 2011). Some of these changes include increases in rainfall seasonality, air temperature, atmospheric CO_2 and liana abundance and biomass (Lewis *et al*., 2009). Liana density, their relative dominance and the size of individual lianas have increased in tropical forests in the last two decades (Phillips *et al*., 2002; Schnitzer & Bongers, 2011). Nonetheless, lianas continue to be disregarded in studies assessing variation in carbon stocks in tropical forests (Stegen *et al*., 2011; Slik *et al*., 2013).

Lianas are a key structural component of tropical forests, they represent on average 20 to 45 % of the woody biomass in old-growth tropical forests and 25 % of all woody species (Schnitzer & Bongers, 2002). Lianas depend on trees for physical support in order to reach the forest canopy and can be detrimental for host trees by creating mechanical stresses (Pérez-Salicrup & Barker, 2000), competing for above and belowground resources (Chen *et al*., 2008), reducing tree growth (Schnitzer, 2005; van der Heijden & Phillips, 2009), fecundity (Wright *et al*., 2005), survival, and recruitment (Schnitzer & Carson, 2010).

Lianas considered light-loving plants, because they respond positively to disturbance and are more prevalent in areas of secondary forest succession (Paul & Yavitt, 2011). Nonetheless, liana communities have been described primarily in disturbed areas or old-growth forests, with little research of lianas during secondary forest succession (Kalácska, 2005; Letcher & Chazdon, 2009). Secondary forest succession is defined as the woody vegetation that re-grows after complete forest clearance for pasture, agriculture or other human activities such as clear-cutting or timber extraction (Chazdon *et al*., 2007). Secondary or second-growth forests increasingly

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[2] *A version of this chapter has been published. Durán SM, Sánchez-Azofeifa GA. 2015. Liana effects on carbon storage and uptake in mature and secondary tropical forests. In Biodiversity of Lianas (eds. N. Parthasarathy). Springer-Verlag, Dordrecht.*

dominate tropical regions, and currently occupy more area than old-growth forests (Laurance, 2010). Thus, tropical forest succession constitutes a central topic in forest ecology (Chazdon *et al.*, 2007). Expansion of second-growth forests, however, may contribute to liana proliferation, since they provide an optimal balance of tree host availability and high light (Schnitzer & Bongers, 2011). How liana may impact carbon stocks in second-growth forests, however, is not yet understood.

Here we review current evidence on the effects of lianas on carbon cycling in old-growth and second-growth forests in the tropics, specifically on aboveground carbon storage and net primary productivity. For second-growth forests, we focused specifically studies conducted in forests formed as a consequence of human impact rather than forests resulting from natural disturbances such as hurricanes or landslides (Brown & Lugo 1990). This includes studies using the chronosequence approach, which identifies forest stands that differ in age, and infer long-term vegetation changes by assuming space-for-time substitution (Chazdon *et al.*, 2007). Most data found provided values of forest carbon as plant biomass, thus we converted these values to carbon pools by assuming that carbon accounts for 47 % of woody biomass (Hughes *et al.*, 1999). Although, net primary productivity includes both annual changes in plant growth and litterfall production, we discuss them separately as lianas have an important contribution to litterfall production; though can cause reductions in woody productivity (e.g. tree growth). Throughout the review, we provide information on the contribution of lianas to carbon cycling in order to illustrate whether liana proliferation in tropical forests could compensate for reduction in carbon pools. Furthermore, we identify research needs required to improve predictions of how tropical carbon sinks will respond to liana increases.

2.2 Liana effects on carbon cycling in old-growth forests

Aboveground carbon storage

Estimations of the total carbon sink in tropical areas are still under debate. Current estimates indicate that tropical forests sequester 1.1 ± 0.8 Pg C year^{-1} (Pan *et al.*, 2011), but some argue that this estimation could be biased by the choice of the allometric equation used for estimating aboveground biomass (Wright, 2013). Moreover, carbon sinks in tropical forests have already undergone a decline from 1.5 Pg C year^{-1} to 1.1 Pg C year^{-1} from 1990 to 2007, and future projections still hold 10 to 20 % uncertainty (Pan *et al*., 2011). This uncertainty is due to the few sets of long-term studies that provide data on climate, stand variables and forest dynamics for both tree and liana species (Phillips *et al*. 2002). In addition, most studies on tropical forest carbon storage have emphasized the role of climate, but growing evidence indicates that stand variables (e.g., basal area, wood density) rather than climate explain more of the variation in carbon storage by tropical forests (Baraloto *et al*., 2011; Stegen *et al*., 2011, Slik *et al.,* 2013). Moreover, increases in tree growth, mortality and turnover rates in tropical forests have been associated with greater concentrations of CO_2 and liana proliferation (Phillips *et al*., 2004; Schnitzer & Bongers, 2011), but the overall effects of lianas on net carbon balance are not yet understood (van der Heijden *et al*., 2013).

To date only two reports have provided confirmation of the negative effect of liana density on biomass carbon in old-growth tropical forests. One of them examined the relationship between the number of lianas (≥ 2.5 cm diameter) and tree carbon storage (> 10 cm diameter) in 145 locations worldwide, and estimated that lianas could reduce aboveground carbon storage by up to 50 percent (Chapter 3). A more recent study in 36 sites in the Amazon, also found a negative effect of liana (≥ 2 cm diameter) density on biomass carbon, with lianas explaining 18 % of the variation in biomass of trees > 10 cm diameter (Laurance *et al*., 2014). The loss in tree biomass, however, may not necessarily be compensated by a buildup in liana biomass. Liana stems generally constitute less than 10 % of the aboveground carbon storage in old-growth tropical forests (DeWalt & Chave 2004) due to their relatively slender stems and low wood density (Laurance *et al*., 1997; DeWalt & Chave 2004). In the central Amazon, total aboveground biomass of trees declined after forest fragmentation by 36.1 Mg ha^{-1}, while liana biomass increased by only 0.46 Mg ha^{-1} (Laurance *et al*., 1997).

Reductions in aboveground carbon storage due to liana density may be due in part to greater rates of tree mortality. The probability of mortality for trees infested by lianas is two to three times greater than for liana-free trees (Ingwell *et al*., 2010). Moreover, the susceptibility of trees to be infested by lianas is higher in shade-tolerant and slow-growing trees, which in general show higher basal areas and high wood density (van der Heijden *et al*., 2008). Thus, lianas may be promoting directional changes in species composition toward more fast-growing species with low wood density that store less carbon (van der Heijden *et al.,* 2013). A simulation analysis of the effects of different biodiversity scenarios on carbon storage in Barro Colorado Island found that liana-induced shifts in species composition toward fast-growing trees could lead to reductions in the carbon storage capacity by 34 percent (Bunker *et al.*, 2005). Nonetheless, the assumptions of this analysis are invalid, as the authors assumed that forest biomass and stand basal area increase with community wood density, but two empirical studies have demonstrated that forest biomass and total basal area in Barro Colorado followed an opposite pattern and decline with wood density (Chave *et al.*, 2004; Stegen *et al.*, 2009). Thus, it is still unknown whether liana could promote shifts in species composition and the potential consequences for carbon sequestration.

Censuses from permanent plots in Amazonian forests have indicated a growth in tree carbon storage of 0.46 Mg C ha^{-1} year^{-1} due to an incremental change in recruitment rates (Baker *et al.*, 2004). Nonetheless, it is still unknown whether this gain in carbon is accompanied by changes in tree community composition, which could cutback the carbon storage of tropical forests in the long term (Phillips *et al.*, 2002). Baker et al. (2004) found an increase of 0.6 ± 0.5 Mg C ha^{-1} year^{-1} year across five plots in Tambopata Peru from 1983−2001. In the same location, significant decreases (−2 percent) in mean wood density of tree species were also registered from 1983 to 2011, indicating an overall greater number of fast-growing tree species (van der Heijden *et al.*, 2013). Whether these changes are influenced by liana infestation has not been determined yet.

To understand to what extent lianas can drive changes in carbon stocks over time, we could assess whether rates of change in carbon stocks are driven by rates of change in liana density. To answer this question, we obtained data from two different studies where rates of change in biomass carbon and liana density (> 10 cm diameter) have been estimated from permanent plots censused every 2−5 years during 25 years in 26 old-growth forest plots in the Amazon region (Phillips *et al.*, 2002; Baker *et al.*, 2004). We then conducted a regression analysis and found that changes in aboveground carbon storage per year decreased with annual increments in liana density per hectare (Fig. 2.1). Although, it is unknown whether extrinsic mortality events such as droughts have influenced reductions in carbon stocks (Laurance *et al.*, 2014), this result clearly suggests that rates of change in liana density have the potential to diminish rates of change in carbon stocks, especially if lianas further increase in the future (Schnitzer & Bongers, 2011). Future studies should incorporate the role of climate in these relationships to examine the relative importance of lianas against other environmental correlates of carbon stocks in old-growth forests such as precipitation, seasonality and temperature.

Aboveground woody productivity

It is well established that liana infestation reduces tree growth rates in tropical forests (Clark & Clark, 1990; Ingwell *et al*., 2010; van der Heijden & Phillips, 2009; van der Heijden *et al*., 2013). Competition for below and aboveground resources appears as an important mechanism explaining these reductions. In wet forests, lianas deploy leaves on the canopy competing intensely with trees for above and belowground resources. Aboveground, high liana loads in the canopy reduce light availability and incoming solar radiation, which can lower photosynthetic rates and carbon uptake (Graham *et al*., 2003). Reductions in light availability can also provide cover for seed and seedling predators decreasing the reproductive output of tree species (Schnitzer *et al*., 2000). Belowground, lianas and trees can compete for nutrients or soil resources (Chen *et al*., 2008).

In seasonal forests, lianas appear to have a competitive advantage over trees due to their efficient vascular system, which allow lianas to tap water during seasonal drought while their tree competitors are dormant (Schnitzer, 2005). The broad overlap of life history strategies of lianas and trees as seedlings constitutes another example of their competitive interactions (Gilbert *et al*., 2006). Despite the cumulative knowledge of liana impacts on tree growth, there is limited information on how tree growth reductions translate into declines in forest carbon storage. A study in the Peruvian Amazon used data on tree growth rates, local environmental conditions, and liana competition for aboveground resources to quantify changes in carbon uptake (van der Heijden & Phillips, 2009). The results indicated that liana-induced reductions of tree growth rates diminish tree carbon uptake by 0.25 Mg C ha^{-1} year^{-1}, which correspond to 10 % reduction in tree carbon increment in this old-growth forest (van der Heijden & Phillips, 2009). Tree growth rates in these forests averaged 2.70 Mg C ha^{-1} year^{-1}, while liana biomass growth was only 0.09 Mg C ha^{-1} year^{-1}, which represents 3.3 % of total stem production (van der Heijden *et al*., 2013). Thus, carbon uptake by lianas is not able to compensate for reductions in tree carbon uptake.

Understanding liana-tree interactions may provide a more accurate assessment of the effects of lianas on carbon uptake (Ingwell *et al*., 2010). Turnover rates of both lianas and trees are increasing in tropical forests (Phillips *et al.*, 2004; 2005). Permanent-plots in the Amazon region showed that tree turnover rates have changed on average by 2 % per year in a period of 25 years (Phillips *et al.*, 2004), with steeper turnover rates for lianas (Phillips *et al.*, 2002). Greater turnover rates are presumably the result of greater concentration of CO_2 in the atmosphere (Phillips *et al.*, 2004). Carbon dioxide enrichment may intensify photosynthesis and accelerate forest productivity and plant growth (Körner, 2004). Nonetheless, greater forest productivity does not necessarily translate in greater carbon sinks in the long term. Accelerated growth intensifies plant competition, which can lead to rapid tree mortality and recruitment as well as faster tree senescence (Laurance *et al*., 2014). Moreover, enrichment of carbon dioxide might fertilize lianas to a greater extent than trees leading to further liana increases (Körner, 2004). Recruitment and mortality rates of lianas appear to be three times greater than those reported by trees (Ingwell *et al.*, 2010). In addition, turnover rates of lianas are positively associated with high tree turnover rates (Phillips *et al.*, 2005). Thus, lianas may be increasing their own abundance and biomass through positive feedback, which could raise stand productivity and rapid carbon accumulation but reduce overall carbon storage capacity over time (Schnitzer & Bongers, 2011). Long-term data on liana and tree dynamics are imperative to provide more accurate calculations of the net losses and gain of forest carbon.

Primary productivity: litterfall production

Liana contribution to litterfall production is predicted to be high since lianas allocate few resources to a self-supporting system, and rather assign more resources to leaf productivity in the canopy (Schnitzer & Bongers, 2002). Most research in litterfall production provided estimation of leaf and total litterfall, but few attempts exist to discriminate litterfall contributions by different functional types (e.g., trees and lianas). Information about the contribution of lianas to aboveground net primary productivity (ANPP) is quite limited as well, as most detailed measurements are provided for trees and their components (e.g., branch, stem, and leafs). In a lowland forest, liana contribution to aboveground primary productivity averaged 1.32 Mg C ha^{-1} $year^{-1}$, which corresponds to 14.8 % of the total ANPP (van der Heijden *et al*., 2013).

Aboveground primary productivity across six tropical forests worldwide showed that leaf litterfall production of lianas averaged 2.15 Mg C ha^{-1} (from 0.8 to 3.1 Mg C ha^{-1}), which represents 23.5 % (11–38 %) of total litterfall in old-growth tropical forests (Hladik, 1974;

Burghouts *et al*., 1994; Wright *et al*., 2004; Pragasan & Parthasarathy, 2005; Chave *et al*., 2008; Da hora *et al.*, 2008). Since liana density and biomass are becoming higher in old-growth tropical forest, the overall contribution of lianas to ANPP is probably greater as well. Therefore, total contribution of trees to forest canopy productivity may be diminished as well, but overall effects of lianas on ANPP are still unknown (van der Heijden *et al*., 2013).

2.3 Liana effects on carbon cycling in second-growth forests

Research on carbon dynamics in second-growth forests has traditionally focused on evaluating recovery rates of structural characteristics (e.g., basal area, stem density, plant growth), and carbon pools (above and belowground), and estimating the time it would take for second-growth forests to reach similar values to those found in old-growth forests (Hughes *et al*., 1999; Chazdon *et al*., 2007). In general, this research has revealed that second-growth forests have the potential to accumulate carbon pools similar to those in old-growth forests, with the rate and pattern of this recovery extremely affected by the severity and duration of previous land uses (Read & Lawrence, 2003; Susan & Letcher, 2009). Little is still known about what other factors besides land use have the potential to accelerate or slow down recovery rates in these regenerating forests.

Lianas may in turn dominate in disturbed vegetation or following forest fragmentation (Gehring *et al*., 2004). Second-growth stands favored liana abundance by providing both high light availability and abundant small trees that act as trellises (Schnitzer & Bongers, 2002). In treefall gaps the high dominance of lianas inhibits tree growth, regeneration, and suppresses the density of shade-tolerant trees by obstructing light penetration (Schnitzer *et al*., 2000). Early in the successional recovery of forest after disturbance in old-growth and second-growth forests, lianas can form dense stands, often referred as tangles, which can persist for long periods and alter the pathway of forest recovery to one stalled by liana abundance (Uhl *et al*., 1988; Buschbacher *et al*., 1988; Hegarty, 1991; Schnitzer *et al*., 2000; Paul & Yavitt, 2011). Thus, lianas are able to arrest forest succession, negatively affect the development of tree species (Schnitzer *et al*., 2000) and even change the rate of carbon accumulation in regenerating forests (Schnitzer *et al*., 2014).

It is unknown how long lianas can persist with dominance strong enough to change the regeneration process (Paul & Yavitt, 2011). Some have found liana density to increase up until

20 years after disturbance, and then decline (DeWalt *et al*., 2000; Letcher & Chazdon, 2009). The decline in liana density appears to be associated with increases in canopy height, and declines in tree-host availability during succession (Putz, 1984; Letcher & Chazdon, 2009). Lianas that fail to reach the canopy early in succession have lower chances of doing so later on (Letcher & Chazdon, 2009). As the canopy closes, light availability is reduced and tree diameter is increased, thus it becomes difficult for lianas to gain the vertical growth necessary to compete with other plants (Letcher &Chazdon, 2009; Paul &Yavitt, 2011). Several studies have demonstrated that lianas are more abundant in second-growth than old-growth forests in tropical regions, but few have examined changes of liana abundance and biomass during succession (DeWalt *et al*., 2000; Letcher & Chazdon, 2009; Madeira *et al*., 2009). Thus, the role of lianas in second-growth forests remains elusive.

Aboveground carbon storage

Liana impacts on carbon storage in second-growth forests are still unknown. Evidence on the recovery of carbon pools provides some insights in the relative contribution of lianas to forest carbon. The overall contribution of lianas (> 10 cm diameter) to carbon stocks in second-growth forests is less than 10 %, while tree contribution varies from 60 to 94 % (Table 1). Comparisons of liana biomass across stand ages are mixed, with one study displaying significant increases during succession (Letcher & Chazdon, 2009), with others showing no variation in liana biomass with forest age (DeWalt *et al*., 2000; Feldpaush *et al*., 2005). Tree carbon storage (> 10 cm diameter) in second-growth forests accounted for 60–95 % of total carbon pools depending on land use history (Table 1). Tree carbon storage and basal area in second-growth forests accumulates with age, with older stands showing greater values and sometimes attaining similar values to old-growth forests after the first 35 years of regeneration (Cifuentes-Jara, 2008). Conversely, the relative contribution of lianas to total carbon stocks is much lower than trees and could vary from 4 percent (> 40 years) in old stands up to 8 percent in young stands (< 20 years) (Read and Lawrence 2003; Feldpaush *et al*., 2005; Cifuentes-Jara, 2008). It is still undetermined whether these changes in liana biomass have an impact on tree dynamics, and if so the potential consequences for carbon dynamics.

Aboveground carbon accumulation

In general, accumulation of tree biomass during succession occurs very rapidly (Chazdon *et al*., 2007), while lianas show relatively slow recovery of biomass during succession due to slower growth rates (Letcher & Chazdon, 2009). Information on the role of lianas in carbon accumulation in second-growth forests comes entirely from small-scale disturbances such as treefall gaps (Dupuy & Chazdon, 2006; Schnitzer & Carson, 2010). Dupuy & Chazdon (2006) evaluated the effect of removal of vegetation in second-growth forests on the recruitment, mortality and density of seedlings of lianas and trees over 2.5 years. They found that recruitment of tree saplings was positively affected by light availability, but was unrelated to recruitment of liana saplings, which have lower numbers in advance regeneration. Tree seedlings experienced high mortality, probably related to greater competition by herbaceous species rather than lianas. Similar to what has been found for adult lianas, the density of liana saplings also declined in advance regeneration, and was lower than that of tree saplings (Dupuy & Chazdon, 2006).

Schnitzer *et al*. (2014) conducted an experiment to evaluate the effects of lianas on carbon accumulation in treefall gaps with and without lianas in second-growth moist forests. Within these gaps, they quantified rates of tree growth and mortality during 8 years in treefall gaps and found that lianas substantially decreased tree carbon accumulation by 4.2–8.4 % through reductions mainly in tree growth. Liana growth only contributed 24 % of the tree biomass accumulation they displaced. An important finding of this study was that reductions of biomass carbon increment in treefall gaps depended on initial tree biomass, and that lower declines of biomass accumulation were found in gaps with low initial tree biomass (Schnitzer *et al*., 2014). Consequently, understanding the recovery of biomass in early stages of regeneration, where lianas tend to be more abundant remains essential to determine whether carbon accumulation can be reduced or enhanced during the successional process.

Although, canopy gaps provide an essential mechanism for regeneration of lianas and fast-growing trees (Schnitzer & Carson, 2010); they are relatively small and infrequent in second-growth tropical forests compared to old-growth forests (Chazdon *et al*., 2007). In addition, gap closure and dynamics may occur at a faster rate in old-growth forests, since gap size and canopy height are smaller, and woody growth and plant density are higher (Paul & Yavitt, 2011). Therefore, more comparable studies at larger spatial scales in second-growth forests are needed to improve our knowledge about tree-liana dynamics along succession and their consequences for the recovery of biomass carbon.

Litterfall production

Lianas devote a large proportion of their energy to leaf production, and have a higher ratio of leaf mass to basal area (Paul & Yavitt, 2011). Moreover, lianas have shorter leaf life-spans than trees (Hegarty, 1991); hence the proportion of leaf litter of lianas in second-growth forests may be higher than in old-growth forests (DeWalt *et al*., 2000). Unfortunately, assessments of litterfall production in second-growth forests are scarce. To our knowledge only two studies have compared litterfall production of lianas across stands of different ages. Buschbacher *et al*. (1988) evaluated litterfall production in abandoned pastures in the Amazon and found that liana leaf litterfall production varied from 0.1 to 0.5 Mg C ha^{-1}, with lower values in abandoned pastures that were grazed for less than 5 years, while greater values found in pastures previously grazed by more than 10 years. More recent data in a deciduous second-growth forest showed that contribution to lianas to litterfall were greater in intermediate stages of regeneration (25−35 years) compared to younger or older stands (> 50 years) (Kalacska *et al*., 2005). Together these two studies also support previous findings of densities of lianas declining with the advance of secondary succession.

2.4 Conclusions

This review provides evidence that lianas can have negative effects on carbon stocks and sequestration in tropical forests. Although some mechanisms by which lianas could impact carbon pools are well known (e.g., reduction of tree growth and increases in tree mortality), more research is needed to determine whether the negative effects of lianas are consistent across tropical areas. Liana density increases with rainfall seasonality and evapotranspirative demand (Schnitzer & Bongers, 2011), with greater abundance of lianas in seasonal than unseasonal forests (Schnitzer, 2005). Thus, the role of lianas for carbon sequestration may be more important in seasonal forests rather than wet forests where most research is currently being carried out. It is also essential to estimate liana litterfall production and liana growth rates in order to assess whether reductions of carbon stocks and accumulation due to lianas can be compensated by carbon gain and uptake through litterfall production and increases in liana biomass. This is particularly important in second-growth forests, where lianas' contribution to primary productivity could be even greater to what it has been reported for old-growth forests, since lianas are more abundant in second-growth forests, and have shorter leaf life span and higher turnover rates. Priorities for future research in old-growth forests include determining whether increases in tree turnover rates and reductions in wood density are caused by increases in liana density. In second-growth forests, examining long-term changes of tree and lianas are urgently required for a general understanding of the contribution of this ecosystem to global carbon cycling. Ultimately, estimates of liana-induced changes in tropical forests need to be incorporated to current global circulation models to predict whether tropical forests in the future will act as carbon sinks (e.g. greater carbon stocks over time) or carbon sources (e.g. lower carbon stocks over time).

2.5 References

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

Baraloto, C., Rabaud, S., Molto, Q., Blanc, L., Fortunel, C., Herault, B., Davila, N., Mesones, I., Rios, M., Valderrama, E. & Fine, P.V.A. (2011) Disentangling stand and environmental correlates of aboveground biomass in Amazonian forests. *Global Change Biology*, **17**, 2677-2688.

Brown, S. & Lugo, A. (1990) Tropical secondary forests. Journal of Tropical Ecology, **6**, 1–32.

Bunker, D., DeClerck, F. & Bradford, J. (2005) Species loss and aboveground carbon storage in a tropical forest. *Science*, **310**, 1029–1031.

Burghouts, T.B.A., Campbell, E.J.F. & Kolderman, P.J. (1994) Effects of tree species heterogeneity on leaf fall in primary and logged dipterocarp forest in the Ulu Segama Forest Reserve, Sabah, Malaysia. *Journal of Tropical Ecology*, **10**, 1.

Buschbacher, R., Uhl, C. & Serrao, E. (1988) Abandoned pastures in eastern Amazonia. II. Nutrient stocks in the soil and vegetation. *Journal of Ecology*, **76**, 682–699.

Chave, J., Condit, R., Aguilar, S., Hernandez, A., Lao, S. & Perez, R. (2004) Error propagation and scaling for tropical forest biomass estimates. *Philosophical Transactions of the Royal Society Series B-Biological Sciences*, **359**, 409–420

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

Chazdon, R.L., Letcher, S.G., van Breugel, M., Martínez-Ramos, M., Bongers, F. & Finegan, B. (2007) Rates of change in tree communities of secondary Neotropical forests following major disturbances. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, **362**, 273–89.

Chen, Y.J., Bongers, F., Cao, K.F., Cai, Z.Q. (2008) Above-and below-ground competition in high and low irradiance: tree seedling responses to a competing liana *Byttneria grandifolia*. *Journal of Tropical Ecology*, **24**, 517-524.

Cifuentes-Jara, M. (2008) Aboveground Biomass and Ecosystem Carbon Pools in Tropical Secondary Forests Growing in Six Life Zones of Costa Rica. Dissertation. Oregon State University, Corvallis, Oregon, USA.

Clark, D. & Clark, D. (1990) Distribution and effects on tree growth of lianas and woody hemiepiphytes in a Costa Rican tropical wet forest. *Journal of Tropical Ecology*, **6**, 321–331.

Da Hora, R. C., Primavesi, O., & Soares, J. J. (2009). Contribuição das folhas de lianas na produção de serapilheira em um fragmento de floresta estacional semidecidual em São Carlos, SP. *Embrapa Pecuária Sudeste-Artigo em periódico indexado (ALICE)*.

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

DeWalt, S.J. & Chave, J. (2004) Structure and biomass of four lowland Neotropical forests. *Biotropica*, **36**, 7-19.

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

Dupuy, J.M. & Chazdon, R.L. (2006) Effects of vegetation cover on seedling and sapling dynamics in secondary tropical wet forests in Costa Rica. *Journal of Tropical Ecology*,

22, 65–76.

Feldpausch, T.R., Riha, S.J., Fernandes, E.C.M. & Wandelli, E. V. (2005) Development of Forest Structure and Leaf Area in Secondary Forests Regenerating on Abandoned Pastures in Central Amazônia. *Earth Interactions*, **9**, 1–22.

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

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

Graham, E.A., Mulkey, S.S., Kitajima, K., Phillips, N.G. & J. Wright. 2003. Cloud cover limits net CO_2 uptake and growth of a rainforest tree during tropical rainy seasons. *Proceedings of the National Academy of Sciences*, **100**, 572-576.

Hegarty, E.E. (1991) Leaf litter production by lianas and trees in a sub-tropical Australian rain forest. *Journal of Tropical Ecology*, **7**, 201–214.

Hladik, A. (1978). Phenology of leaf production in rainforest of Gabon: distribution and composition of food for folivores. *The ecology of arboreal folivores*, **278**, 51–71.

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

van Der Heijden, G.M.F. & Phillips, O. (2009) Liana infestation impacts tree growth in a lowland tropical moist forest. *Biogeosciences*, **6,** 2217–2226

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

Hughes, R.F., Kauffman, J.B. & Jaramillo, V.J. (1999) Biomass, carbon, and nutrient dynamics of secondary forests in a humid tropical region of Mexico. *Ecology*, **80**, 1892-1907.

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

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

Körner, C. (2004) Through enhanced tree dynamics carbon dioxide enrichment may cause tropical forests to lose carbon. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, **359**, 493–8.

Laurance, W. (2010) Habitat destruction: death by a thousand cuts. *Conservation Biology for All* (ed. Sodhi, N.S., & P.R. Ehrlich), pp. 73–87. New York: Oxford University Press.

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

Laurance, W., Andrade, A. & Magrach, A. (2014) Long-term changes in liana abundance and forest dynamics in undisturbed Amazonian forests. *Ecology*, **95**, 1604–1611.

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

Lewis, S.L., Lloyd, J., Sitch, S., Mitchard, E.T. a. & Laurance, W.F. (2009) Changing Ecology of Tropical Forests: Evidence and Drivers. *Annual Review of Ecology, Evolution, and Systematics*, **40**, 529–549.

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

Malhi, Y. (2012) The productivity, metabolism and carbon cycle of tropical forest vegetation. *Journal of Ecology*, **100**, 65–75.

Pan, Y., Birdsey, R. a, Fang, J., Houghton, R., Kauppi, P.E., Kurz, W. A, Phillips, O.L., Shvidenko, A., Lewis, S.L., Canadell, J.G., Ciais, P., Jackson, R.B., Pacala, S.W., McGuire, a D., Piao, S., Rautiainen, A., Sitch, S. & Hayes, D. (2011) A large and persistent carbon sink in the world's forests. *Science (New York, N.Y.)*, **333**, 988–93.

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

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

Phillips, O.L., Martinez, R.V., Arroyo, L., Baker, T.R., Killeen, T., Lewis, S.L., Malhi, Y., Mendoza, A.M., Neill, D., Vargas, P.N., Alexiades, M., Cerón, C., Di Fiore, A., Erwin, T., JardIm, A., Palacios, W., Saldias, M. & Vinceti, B. (2002) Increasing dominance of large lianas in Amazonian forests. *Nature*, **418**, 770–774.

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

Phillips, O.L., Vásquez Martínez, R., Monteagudo Mendoza, A., Baker, T.R. & Núñez Vargas, P. (2005) Large lianas as hyperdynamic elements of the tropical forest canopy. *Ecology*, **86**, 1250–1258.

Pragasan, L. A., & Parthasarathy, N. (2005). Litter production in tropical dry evergreen forests of south India in relation to season, plant life-forms and physiognomic groups. *Current science*, **88**, 125-126.

Putz, F.E. (1984) The Natural History of Lianas on Barro Colorado Island, Panama. *Ecology*, **65**, 1713.

Read, L., Lawrence, D. (2003) Recovery of biomass following shifting cultivation in dry tropical forests of the Yucatan. *Ecological Applications*, **13,** 85–97.

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

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

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

Schnitzer, S.A. & Bongers, F. (2011) Increasing liana abundance and biomass in tropical forests: emerging patterns and putative mechanisms. *Ecology letters*, **14**, 397-406.

Schnitzer, S. A & Carson, W.P. (2010) Lianas suppress tree regeneration and diversity in treefall gaps. *Ecology letters*, **13**, 849–57.

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

Schnitzer, S. A., van der Heijden, G.M.F., Mascaro, J. & Carson, W.P. (2014) Lianas in Gaps Reduce Carbon Accumulation in a Tropical Forest. *Ecology*, **95**,3008–3017.

Sierra, C. a., del Valle, J.I., Orrego, S. a., Moreno, F.H., Harmon, M.E., Zapata, M., Colorado, G.J., Herrera, M. a., Lara, W., Restrepo, D.E., Berrouet, L.M., Loaiza, L.M. & Benjumea, J.F. (2007) Total carbon stocks in a tropical forest landscape of the Porce region, Colombia. *Forest Ecology and Management*, **243**, 299–309.

Slik, J.W.F., Paoli, G., McGuire, K., Amaral, I., Barroso, J., Bastian, M., Blanc, L., Bongers, F., Boundja, P., Clark, C., Collins, M., Dauby, G., Ding, Y., Doucet, J.-L., Eler, E., Ferreira, L., Forshed, O., Fredriksson, G., Gillet, J.-F., Harris, D., Leal, M., Laumonier, Y., Malhi, Y., Mansor, A., Martin, E., et al. (2013) Large trees drive forest aboveground biomass variation in moist lowland forests across the tropics. *Global Ecology and Biogeography*, **22**, 1261–1271.

Stegen, J.C., Swenson, N.G., Valencia, R., Enquist, B.J. & Thompson, J. (2009) Above-ground forest biomass is not consistently related to wood density in tropical forests. *Global Ecology and Biogeography*, **18**, 617–625.

Stegen, J.C., Swenson, N.G., Enquist, B.J., White, E.P., Phillips, O.L., Jørgensen, P.M., Weiser, M.D., Monteagudo Mendoza, A. & Núñez Vargas, P. (2011) Variation in above-ground forest biomass across broad climatic gradients. *Global Ecology and Biogeography*, **20**, 744-754.

Uhl, C., Buschbacher, R. & Serrao, E. (1988) Abandoned pastures in eastern Amazonia. I. Patterns of plant succession. *The Journal of Ecology*, **76**, 663–681.

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

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

Wright, S.J. (2013) The carbon sink in intact tropical forests. *Global change biology*, **19**, 337–9.

2.6 Tables and Figures

Table 2.1 Contribution of trees and lianas to aboveground carbon storage in secondary tropical forests. Rate of recovery refers to the time it would take for carbon stocks to reach old-growth levels.

Forest type*	Stand age	Trees		Lianas		Previous land use	Recovery rate	
	(years)	Mg C ha^{-1}	%	Mg C ha^{-1}	%		(years)	Source
Moist	0.5–50	105.9	75–85	1.6	1	Grazing, crops	73 years	Hughes et al. (1999)
Moist	20–70	–	–	3.3	–	Grazing, crops	–	DeWalt et al. (2000)
Dry	7–13	12.3	94	1.4	6	Logging, burning	–	Restom and Nepstad (2001)
Dry	2–25	16.1	92	1.3	5	Logging, crops, development	65–120	Read and Lawrence (2003)
Moist	0–14	23.2	90	1.8	2	Grazing	–	Feldpausch et al. (2005)
Moist	4–22	20.6	92	0.6	3	Grazing, crops, mining	> 60	Sierra et al. (2007)
Dry	9–82	34.4	61	1.6	5	Grazing	35	Cifuentes-Jara (2008)
Moist	0.4–40	23.4	65	2.5	7	Grazing	80	
Wet	0.5–60	40.2	71	1.9	3	Grazing	108–124	
Dry	9–50	25.5	85	2.1	6	Grazing, crops	–	Madeira et al. (2009)

* Forest type followed Chave et al. (2005).

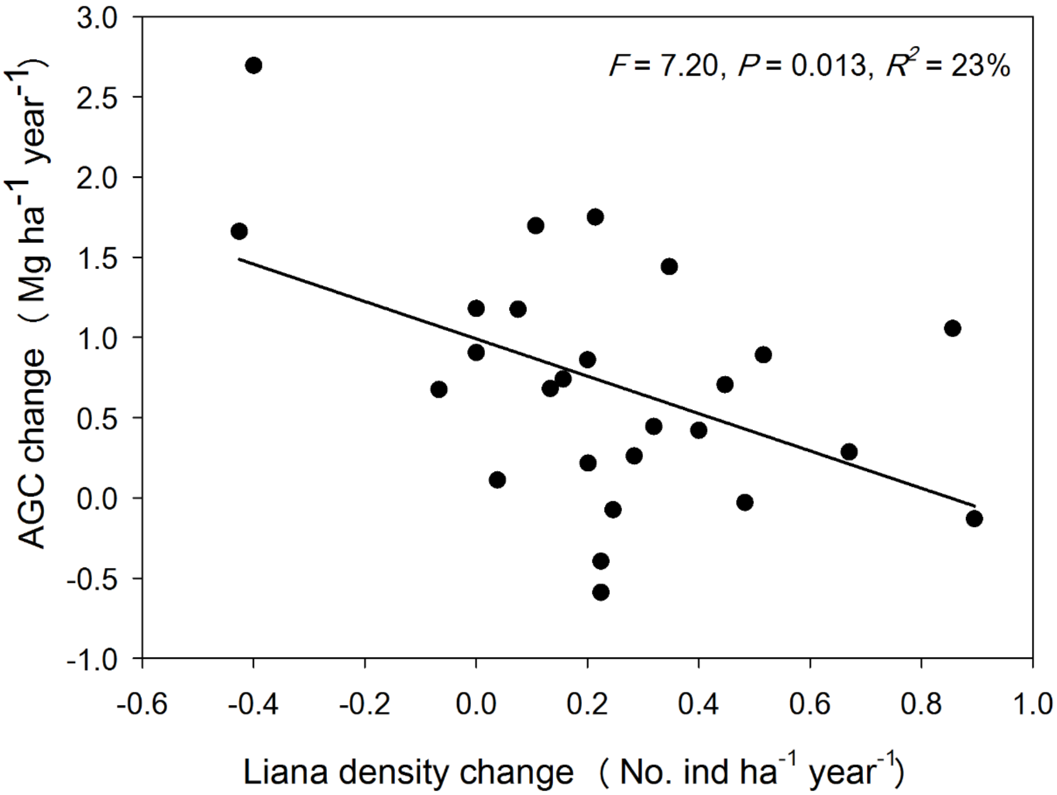

Figure 2.1 Relationship between changes in liana density and changes in aboveground carbon (AGC) storage in 26 old-growth forests in the Amazon region. Data source: Phillips *et al*. (2002) and Baker *et al*. (2004).

3. Carbon stocks in tropical forests decrease with liana density[3]

3.1 Introduction

Lianas are a key structural component of forests around the world, especially in the tropics, where they make important contributions to the productivity and species richness of forests (Putz 1984, Schnitzer & Bongers, 2002). Lianas typically constitute approximately 25% of woody plant species in tropical forests, and can represent up to 40% of the woody species in some Amazonian wet forest (Schnitzer & Bongers, 2011). Lianas are important for ecosystem processes such as forest transpiration and primary productivity, since they contribute up to 40% of forest leaf area and leaf production (Hegarty, 1991).

Lianas depend on trees for physical support in order to reach the forest canopy and, as a result can be detrimental for host trees by creating mechanical stresses (Pérez-Salicrup & Barker, 2000), competing for above and belowground resources (Schnitzer, 2005; van der Heijden *et al*., 2013, reducing tree growth (Clark & Clark, 1990, van der Heijden & Phillips, 2009), and reproduction (Kainer *et al*., 2006). Many lianas are light-loving species and respond positively to forest disturbance (Putz, 1984, Schnitzer & Bongers, 2002). In tropical forests, treefall gaps are one of the most common disturbances that favored liana abundance providing both increased light and abundant small trees that provide supports for climbing plants (Laurence *et al.,* 2001). In treefall gaps, the high dominance of lianas inhibit tree regeneration and suppress the density of shade-tolerant trees by obstructing light penetration, imposing mechanical interference and possibly causing strong belowground competition (Schnitzer *et al*., 2000, Schnitzer & Carson, 2010). In old-growth forests, lianas reduce tree fecundity and increase tree mortality (Wright *et al*., 2005, Ingwell *et al*., 2010). By increasing tree mortality and diminishing tree regeneration, lianas may have a major impact on forest dynamics and may reduce the amount of carbon that is sequestered in plant biomass (Schnitzer & Bongers, 2002).

Recent evidence indicates that lianas are increasing in dominance in old-growth tropical forests (Schnitzer & Bongers, 2011), probably related to changes in CO_2 levels and high turnover of tree species (Phillips & Gentry 1994, Granados & Korner, 2002). An increase in liana density could have serious consequences for tree species diversity and may jeopardize capacity of

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[3] *A version of this chapter has been published. Durán SM, Gianoli E. 2013. Carbon stocks decrease with liana density. Biology Letters 9 (4): 20130301*

tropical forests to store carbon (Schnitzer & Bongers, 2011). For example, in the tropical forests of French Guiana, forest plots dominated by lianas support less aboveground biomass (less than 100 Mg ha^{-1}) than the rest of the plots (more than 284 Mg ha^{-1}) (Chave *et al*., 2001). The loss in tree biomass, however, may not necessarily be compensated by an increase of liana biomass. Liana stems generally constitute less than 10% of the aboveground biomass in old-growth tropical forests due to their relatively slender stems and low wood density (van der Heijden *et al*., 2013).

The role of lianas in forest carbon sequestration has been discussed earlier (Schnitzer & Bongers, 2002; 2011). Nonetheless, lianas have been neglected in studies evaluating variation in aboveground carbon stocks in tropical forests (Keith *et al*., 2009; Stegen *et al*., 2011). We examined the relationship between aboveground carbon storage (AGC) and liana abundance for small (≤ 10 cm diameter) and large trees (> 10 cm diameter) across 145 tropical forests worldwide. We hypothesised that AGC would be lower in plots with higher abundance of lianas, and that lianas would have a stronger effect on AGC of large trees. We also assessed the influence of climate on carbon storage to weight their importance against lianas. Furthermore, we evaluated whether the dominance of the tree community varies with liana abundance given that a few species may account for ~80% of total carbon stocks in old-growth tropical forests (Balvanera *et al*., 2005).

3.2 Methods

Study sites

We use a subset of the Alwyn H. Gentry Forest Transect Data Set (Phillips *et al*., 2002). Gentry sampled a total of 226 forest plots across the globe with a standardized sampling design of 10 separate transects, each measuring 2 x 50 m. The plots were distributed across a homogeneous old-growth forest, avoiding anthropogenic edges and successional habitats (Phillips *et al*., 2002). Within these plots, Gentry measured all trees, lianas, hemi-epiphytes and shrubs with stems ≥ 2.5 cm at diameter at breast height (DBH) in 0.1 ha samples. We selected the whole pan-tropical dataset and obtained climate data for each site. We then obtained mean annual temperature (MAT), mean annual precipitation (MAP) and dry of season length from the WorldClim dataset

(Hijmans *et al*., 2005); http://worldclim.org/bioclim.htm). The final dataset included 145 plots for which reliable climate data were obtained (Fig. 3.1).

Some sites had more than one plot, but they were located on contrasting soil types, thus they were assumed to represent independent sampling units (Phillips & Miller, 2002). Dry season length was defined as the number of consecutive months of rainfall averaging < 100 mm month^{-1}. We classified each plot as wet, moist or dry forests based on the climatic data for each location and by using the criteria used by Chave *et al*. (2005). Forests where evapotranspiration exceeds rainfall during less than a month were classified as wet forests. This corresponds to high-rainfall lowland forests, where rainfall is usually greater than 3500 mm year^{-1} and has no seasonality. Dry forests, in contrast, were defined as those where evapotranspiration exceeds rainfall in 5 or more months. This coincides with forests where plants suffer serious water stress, sometimes with a deciduous canopy, and precipitation levels usually lower than 1500 mm year^{-1} (Chave *et al*., 2005). This comprises 54 plots in wet forests, 48 in moist and 43 in dry forests spanning a precipitation gradient from 528 to 7426 mm year^{-1} and an elevation gradient from 10 to 2660 m.a.s.l (Appendix 3.1).

Carbon stocks

To evaluate the contribution to the aboveground carbon stocks of trees ≥ 2.5 cm in DBH, we calculated the aboveground biomass (AGB) for individual trees distinguishing between small trees of 2.5-10 cm DBH and large trees ≥ 10 cm DBH for each forest type. Trees and shrubs between 1 and 10 cm represent trellises available for lianas, and may be positively associated with liana density (Nabe-Nielsen, 2001). In addition, allometric equations have been usually generated for trees with diameters greater than 10 cm DBH (Baker *et al*., 2004). To estimate the contribution of trees and shrubs ≤ 10 cm DBH to AGB at plot level, we employed an allometric equation that requires only DBH as an input (Hughes *et al*., 1999; appendix 3.2). To estimate contribution of trees > 10 cm DBH to AGB, we used a pantropical equation for wet and dry forests that requires data on wood density and DBH (Chave *et al*., 2005; appendix 3.2). Wood density data for each species in each study site were derived from the literature (Baker *et al*., 2004, Chave *et al*., 2009; Zanne *et al*., 2009). When wood densities were not available at species level, we used a genus-level (for 36% of the species), family-level (for 9% of the species) or an overall species mean of 0.6 g cm^{-3} (1% of the species). Palms were grouped with trees for biomass estimates, and a mean specific wood density of 0.31 g cm^{-3} was used. This value was also allocated for Cyatheaceae and Strelitziaceae (1% of the species) (Baker *et al*., 2004). We excluded all hemi-epiphytes and non-woody monocots before AGB estimations. For individuals with multiple stems, we calculated AGB of each stem and summed them (Chave *et al*., 2005). We estimated aboveground carbon storage (AGC) per plot as: C (Mg C ha^{-1}) = AGB x 0.47/plot area (Hughes *et al*., 1999). Since liana infestation may covary with wood density (van der Heijden & Phillips, 2009), we also estimated AGC for large trees using an allometric equation based on DBH only (Brown, 1997; appendix 3.2).

Statistical analyses

To evaluate the effect of lianas on carbon stocks we used simple and multiple regressions. First, we conducted simple linear regressions to evaluate the independent effects of lianas and each climatic factor on AGC. We then conducted a multiple regression including only those variables that had significant effects in simple regressions. To examine the relative importance of each parameter in the full model, we partitioned the total variation in the response variable. We evaluated the effect of lianas on the dominance of the tree community with simple linear regression using the Simpson's dominance index, which was calculated using abundance as tree density (No. trees ha^{-1}) and basal area (m^{2} ha^{-1}).Variables were square-root transformed to meet regression assumptions. We tested normality of residuals using the Shapiro-Wilk test and plotted fitted values against residuals to test for non-constant variance and non-linear patterns.

3.3 Results

The 145 pantropical sites spanned a considerable range in MAP (494-5175 mm), MAT (12-28 °C) and dry season length (0-10 months) (appendix 3.1). Small trees accounted for less than 10% of carbon stocks, while large trees stored over 90% of total forest carbon (Table 3.1). Neither liana abundance nor climate variables were related to carbon stocks of small trees. However, carbon stocks of large trees were negatively associated with liana abundance at the plot level (Fig. 3.2). The linear fit showed that stored carbon in forest plots where lianas were highly abundant was less than one-half of that stored in plots with low liana density (Fig. 3.2). Liana abundance alone explained as much variation in carbon stocks as MAT (R^2=0.11, Table 3.2). After controlling for variation in climate variables across sites, this effect was still significant, and liana abundance explained more variation in carbon stocks (R^2=0.10) than MAT and MAP together (R^2=0.06 and R^2=0.03, respectively, table 2). Lianas contributed 5% of forest AGC (Table 3.1, appendix 3.1). Analyses for large trees using equations with and without wood density provided similar results (appendix 3.2 and 3.3). Liana abundance did not affect dominance of the tree community as indicated by the Simpson index using tree density ($t = -0.31$, $p = 0.75$) or tree basal area ($t = -1.35$, $p = 0.17$).

3.4 Discussion

This is the first comprehensive evaluation of the relationship between liana abundance and aboveground carbon stocks (AGC) across tropical forests. Results indicate that lianas could reduce AGC by up to 50% in large trees, which account for 90% of total carbon stored in tropical forests. A study in an Amazonian forest reported that liana-free trees contained 25% less carbon per unit basal area than liana-infested trees (van der Heijden & Phillips, 2009), thus suggesting a positive association between lianas and carbon. However, this one-site study included areas with regular disturbance (seasonal flooding), thus it cannot be considered representative of tropical old-growth forests. We found that dominance of the tree community did not vary with liana abundance across forest plots. Although we lack data on individual tree infestation, this suggests that lianas may be reducing carbon stocks via increased proportion of infested trees and/or more severe infestations rather than having high infestation rates on high-biomass, dominant trees. The proportion of infested trees per hectare may be as high as 50% in some tropical forests (van der Heijden & Phillips, 2009, Ingwell *et al*., 2010). Reduced C stocks in trees were not driven by changes in wood density as a consequence of compositional shifts. This was verified by the fact that results were the same when we estimated aboveground biomass with and without considering wood density, thus suggesting that the negative relationship between lianas and C stocks is mainly explained by lianas' impact on tree diameter.

Empirical studies provide possible mechanisms underlying the negative effects of lianas on carbon stocks. The high leaf-stem ratio allows lianas to aggressively compete with trees by deploying leaves on the canopy and covering tree crowns. By competing with trees, lianas are able to reduce annual increments of tree biomass by 10%, equivalent to 0.25 Mg C $ha^{-1}year^{-1}$[4], and may reduce tree growth and reproduction even at low abundance (van der Heijden & Phillips, 2009; Wright *et al*., 2005). Large lianas, which represent approximately 6% of woody stems ≥ 10 cm, are able to remove 30% of tree basal area in old-growth forests (Phillips *et al*., 2005). Moreover, the probability of mortality for liana-infested trees is two to three times greater than for liana-free trees (Phillips *et al*., 2005, Ingwell *et al*., 2010). Over time, this liana-driven reduction in tree biomass may affect the ability of tropical forests to store carbon and might alter global climate by releasing some of the carbon currently stored (Keith *et al*., 2009).

Notwithstanding the compelling arguments and evidence presented here, alternative explanations for the liana-carbon relationship may be explored. Liana abundance is correlated negatively with rainfall and positively with seasonality across the tropics (Schnitzer, 2005; DeWalt *et al*., 2010). Low-carbon forests in this study include seasonal and deciduous forests with long dry seasons. Lianas may be particularly successful in these forests due to their efficient vascular system and their extended leaf longevity (Schnitzer, 2005; Schnitzer & Bongers, 2011). Future research should address these alternative explanations quantitatively. This will lead to a better understanding of the impact of lianas on carbon stocks, thus improving predictions of global changes in tropical forests.

3.5 References

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

Brown, S. (997) *Estimating biomass and biomass change of tropical forests*: a primer. FAO Forestry Paper No. 143, Rome.

Chave, J., Riéra, B., & Dubois, M. A. (2001). Estimation of biomass in a Neotropical forest of French Guiana: spatial and temporal variability. *Journal of Tropical Ecology*, ***17***, 79-96.

Chave, J., Andalo, C., Brown, S., Cairns, M.A., Chambers, J.Q., Eamus, D., Folster, H., Fromard, F., Higuchi, N., Kira, T., Lescure, J.P., Nelson, B.W., Ogawa, H., Puig, H., Riera, B. & Yamakura, T. (2005) Tree allometry and improved estimation of carbon stocks and balance in tropical forests. *Oecologia*, **145**, 87-99.

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

Clark, D. & Clark, D. (1990) Distribution and effects on tree growth of lianas and woody hemiepiphytes in a Costa Rican tropical wet forest. *Journal of Tropical Ecology*, **6**, 321–331.

DeWalt, S., Schnitzer, S. & Chave, J. (2010) Annual rainfall and seasonality predict pan-tropical patterns of liana density and basal area. *Biotropica*, **42**, 309–317.

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

Hegarty, E.E. (1991) Leaf litter production by lianas and trees in a sub-tropical Australian rain forest. *Journal of Tropical Ecology*, **7**, 201–214.

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

van der Heijden, G.M., Schnitzer, S.A., Powers, J.S. & Phillips, O.L. (2013) Liana impacts on carbon cycling, storage and sequestration in tropical forests. *Biotropica*, **45**, 682-692

Hughes, R.F., Kauffman, J.B. & Jaramillo, V.J. (1999) Biomass, carbon, and nutrient dynamics of secondary forests in a humid tropical region of Mexico. *Ecology*, **80**, 1892-1907.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International journal of climatology*, **25**, 1965-1978.

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

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

Keith, H., Mackey, B.G. & Lindenmayer, D.B. (2009) Re-evaluation of forest biomass carbon stocks and lessons from the world's most carbon-dense forests. *Proceedings of the National Academy of Sciences*, **106**, 11635-11640.

Laurance, W. & Pérez-Salicrup, D. (2001) Rainforest fragmentation and the structure of Amazonian liana communities. *Ecology*, **85**, 2630–2637.

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

124, 469–475.

Phillips, O.L. & Gentry, A.H. (1994) Increasing turnover through time in tropical forests. *Science*, **263**, 954–958.

Phillips, O., Miller, J.S. & Hollowell, V.C. (2002) *Global patterns of plant diversity: Alwyn H. Gentry's forest transect data set*. Missouri Botanical Press Louis, MO.

Phillips, O.L., Vásquez Martínez, R., Monteagudo Mendoza, A., Baker, T.R. & Núñez Vargas, P. (2005) Large lianas as hyperdynamic elements of the tropical forest canopy. *Ecology*, **86**, 1250–1258. Putz, F.E. (1984) The Natural History of Lianas on Barro Colorado Island, Panama. *Ecology*, **65**, 1713.

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

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

Schnitzer, S.A. & Bongers, F. (2011) Increasing liana abundance and biomass in tropical forests: emerging patterns and putative mechanisms. *Ecology letters*, **14**, 397-406.

Schnitzer, S. & Carson, W.P. (2010) Lianas suppress tree regeneration and diversity in treefall gaps. *Ecology letters*, **13**, 849–57.

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

Stegen, J.C., Swenson, N.G., Enquist, B.J., White, E.P., Phillips, O.L., Jørgensen, P.M., Weiser, M.D., Monteagudo Mendoza, A. & Núñez Vargas, P. (2011) Variation in above-ground forest biomass across broad climatic gradients. *Global Ecology and Biogeography*, **20**, 744-754.

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

Zanne, A., Lopez-Gonzalez, G., Coomes, D.A., Ilic, J., Jansen, S., Lewis, S.L., Miller, R.B., Swenson, N.G., Wiemann, M.C. & Chave, J. (2009) Global Wood Density Database. Dryad Identifier: http://hdl.handle.net/10255/dryad.235.

3.6 Tables and Figures

Table 3.1. Aboveground carbon storage (Mg ha^{-1}) of small (≤ 10 cm diameter) and large trees (> 10 cm), and tree and liana density (no. individuals per 0.1 ha) in tropical forests (*n*=145). SE: standard error; CI: confidence interval.

	mean	SE	95% CI
aboveground carbon storage			
small trees	4.90	0.13	4.65−5.16
large trees	146.50	6.04	134.5−158.4
total	151.37	6.03	139.4−163.3
density			
small trees	202.47	5.40	191.7−213.2
large trees	92.70	3.45	85.8−99.5
lianas	62.60	2.72	57.3−68.0

Table 3.2 Simple and multiple regressions evaluating the effect of liana abundance and climate on aboveground carbon storage (AGC, Mg ha^{-1}) in tropical forests (n=145). β denotes the standardized regression coefficients, and SE their standard error.

	AGC Trees ≤ 10 cm					AGC Trees > 10 cm				
simple regression	β	SE	*t*-value	*p*-value	R^2	β	SE	*t*-value	*p*-value	R^2
liana abundance	-0.02	0.01	-1.19	0.235	-	-0.16	0.03	-4.22	<0.001	0.11
MAP	0.002	0.003	0.81	0.418	-	0.05	0.02	2.26	0.02	0.03
MAT	0.12	0.08	1.38	0.17	-	-2.65	0.63	-4.19	<0.001	0.11
DSL	-0.006	0.03	-0.18	0.850	-	-0.27	0.27	-0.99	0.32	-
multiple regression										
liana abundance						-0.10	0.03	-2.58	0.01	0.10
MAP						0.05	0.02	2.36	0.02	0.03
MAT						-2.20	0.65	-3.37	<0.001	0.06
full model							$F_{3,141}$ = 11.43		<0.001	0.19

MAP = mean annual precipitation, MAT = mean annual temperature, DSL = dry season length.

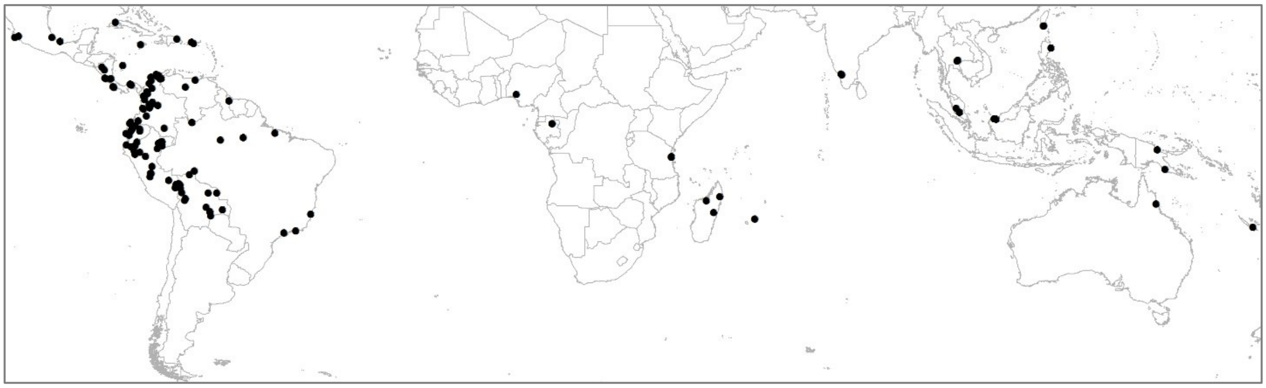

Figure 3.1 Spatial distribution of Gentry's forest plots (0.1 ha) used in the current study (n = 145).

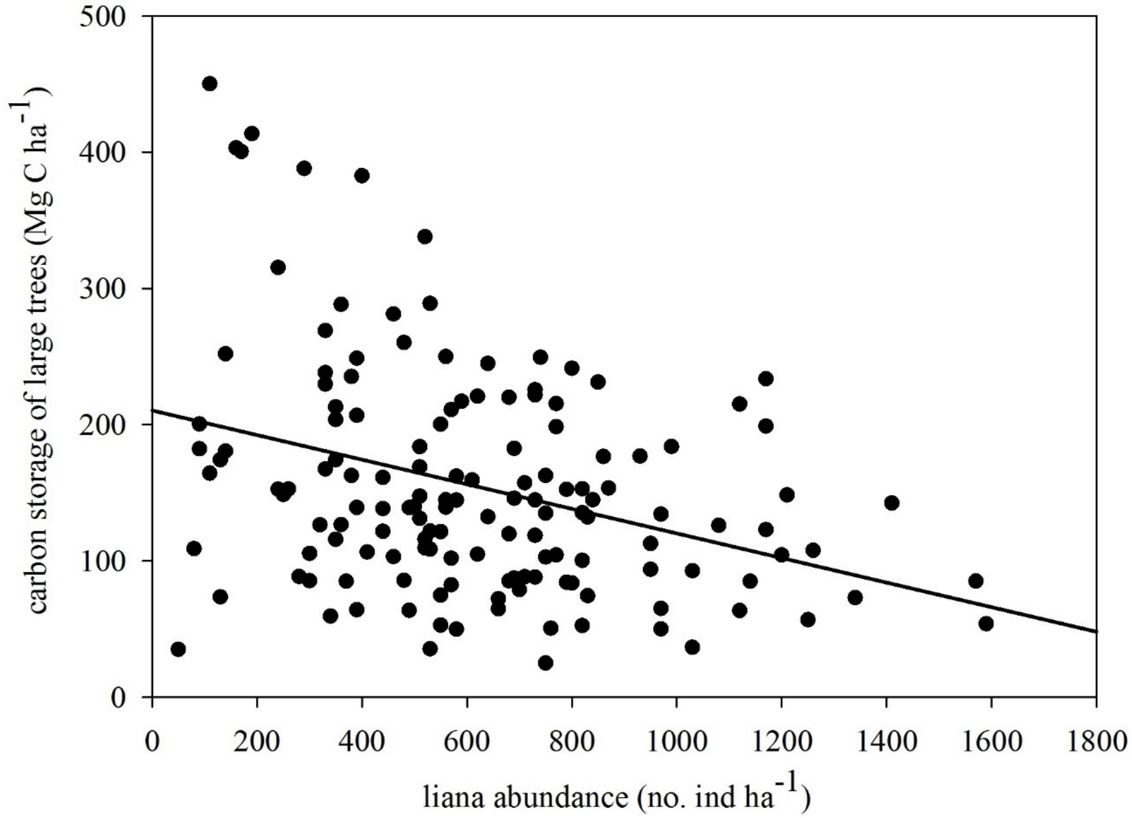

Figure 3.2 Relationship between liana abundance on aboveground carbon storage of large trees (> 10 cm diameter at breast height) in tropical forests (*n*=145). Carbon storage decreases with liana abundance (p-value <0.001; $R^2 = 0.11$). Carbon stocks were estimated using allometric equations based on DBH and wood density for each forest type following Chave et al. (2005).

3.7 Supplementary Material Chapter 3

Appendix 3.1. Aboveground carbon storage (AGC), basal area (BA), climate data (MAT, MAP, DSL), and liana abundance for the 145 sample units. Site names follow the Gentry dataset. MAP = mean annual precipitation, MAT = mean annual temperature, DSL = dry season length.

site	site name	location			climate data			trees ≤ 10 cm		trees > 10 cm		lianas ≥ 2.5 cm	
no.		country	latitude	longitude	MAP	MAT	DSL	BA (m^2/ha)	AGC (Mg /ha)	BA (m^2/ha)	AGC (Mg /ha)	no. ind/ha	AGC (Mg /ha)
1	Davies River State Forest	Australia	-17.08	145.57	1739	19.8	6	3.94	4.65	52.46	288.28	360	2.24
2	Alto Madidi	Bolivia	-13.58	-68.77	2293	25.1	3	4.97	5.87	39.30	118.71	730	7.34
3	Alto Madidi ridge top	Bolivia	-13.58	-68.77	2293	25.1	3	4.59	5.35	37.66	135.38	820	4.94
4	Chaquimayo	Bolivia	-14.57	-68.47	1627	21.7	5	1.20	2.54	39.25	148.38	1210	8.04
5	Curuyuqui	Bolivia	-18.77	-62.23	585	24.8	12	6.33	8.06	26.67	72.24	660	2.65
6	Curuyuqui Riverine	Bolivia	-18.75	-62.30	584	24.8	12	4.81	6.44	53.35	198.89	1170	4.88
7	El Encanto	Bolivia	-14.63	-60.70	1451	23.5	5	0.61	2.12	34.66	92.73	1030	10.22
8	Incahuara	Bolivia	-15.92	-67.58	1404	21	6	6.91	8.11	22.24	88.57	280	1.05
9	Nuevo Mundo	Bolivia	-10.65	-66.77	1781	26.2	5	1.10	4.30	35.88	104.93	620	8.56
10	Perserverancia	Bolivia	-14.63	-62.62	1295	24.9	7	2.97	5.37	22.41	53.86	1590	14.49
11	Quiapaca	Bolivia	-18.33	-59.50	1111	25	7	2.86	5.00	25.63	104.35	1200	8.80
12	Río Negro	Bolivia	-9.83	-65.67	1609	26.4	5	2.02	6.09	22.95	64.85	660	20.89
13	Sacramento	Bolivia	-16.30	-67.80	843	14.5	8	6.15	7.25	26.22	78.91	700	1.87
14	Santa Cruz	Bolivia	-17.77	-63.07	1094	24.4	9	0.66	1.69	34.51	102.76	750	6.81
15	Yanaígua	Bolivia	-19.70	-62.10	494	24.6	12	5.24	6.21	28.99	73.57	130	1.31
16	Alter de Chao	Brazil	-2.50	-54.97	1977	26.1	5	3.38	4.05	12.84	35.08	50	0.23
17	Belém Mocambo	Brazil	-1.50	-47.98	2380	26.8	3	3.42	4.03	37.98	260.28	480	4.97
18	Boraceia	Brazil	-23.38	-46.00	1368	18.6	4	5.29	6.28	49.75	238.20	330	3.55
19	Camorin-Jacarepaguá	Brazil	-22.93	-43.37	1205	23.3	6	3.90	4.58	45.20	250.05	560	5.44
20	Ducke Reserve	Brazil	-3.00	-59.97	2179	27.1	3	5.30	6.22	42.29	248.76	390	2.43
21	Linhares	Brazil	-19.30	-40.07	1207	24.1	6	0.48	5.30	46.37	153.46	870	14.52
22	Alto de Cuevas	Colombia	6.67	-76.50	3675	24	0	3.14	3.79	43.88	121.92	530	12.15

site	site name	location			climate data			trees ≤ 10 cm		trees > 10 cm		lianas ≥ 2.5 cm	
no.		country	latitude	longitude	MAP	MAT	DSL	BA (m^2/ha)	AGC (Mg /ha)	BA (m^2/ha)	AGC (Mg /ha)	no. ind/ha	AGC (Mg /ha)
23	Alto de Mirador	Colombia	10.92	-73.83	2445	12	3	4.70	5.66	45.92	180.52	140	0.63
24	Alto de Sapa	Colombia	7.17	-75.90	2877	14.5	1	4.90	5.32	52.85	220.76	620	4.02
25	Anchicayá	Colombia	3.75	-76.83	1486	22.4	3	5.72	6.78	41.26	206.87	390	1.74
26	Antado	Colombia	7.25	-75.92	2798	15.5	1	3.97	4.69	42.16	144.75	730	26.60
27	Araracuara	Colombia	-0.42	-72.32	2915	26.7	1	5.29	6.17	43.04	176.61	860	9.78
28	Bajo Calima	Colombia	3.92	-77.00	6987	26.2	0	6.49	7.61	26.36	84.97	370	1.92
29	Bosque de la Cueva	Colombia	11.08	-73.47	1828	23.2	3	2.68	3.10	38.25	162.21	580	5.41
30	Carpanta	Colombia	4.58	-73.67	2184	13.2	2	2.95	3.81	36.11	174.16	350	18.12
31	Carpanta Siete Cuerales	Colombia	4.58	-73.67	2184	13.2	2	3.29	3.51	31.98	126.56	320	2.36
32	Cedral	Colombia	4.75	-75.55	2099	14.3	1	5.55	6.46	47.61	139.27	390	2.27
33	Cerro Kennedy	Colombia	11.08	-74.02	2661	19.5	3	2.71	3.21	46.80	174.15	130	0.62
34	Colosó	Colombia	9.40	-75.58	1139	27.6	4	0.95	3.30	28.01	65.16	970	18.63
35	Finca Mehrenberg	Colombia	2.27	-76.20	1899	14.4	0	3.99	4.68	47.22	161.18	440	1.67
36	Galerazamba	Colombia	10.77	-75.24	884	27.6	7	1.43	2.41	15.26	36.56	1030	7.89
37	La Planada	Colombia	1.13	-77.97	1599	17.6	4	5.72	6.81	37.38	182.30	90	1.39
38	La Raya	Colombia	8.33	-74.92	3103	28	3	5.16	6.10	40.66	221.73	730	9.72
39	Loma de Los Colorados	Colombia	9.97	-75.17	1547	27.3	4	3.05	6.22	25.46	73.05	1340	9.42
40	Lomas de Santo Tomás	Colombia	4.92	-74.83	1592	26.5	4	2.45	3.95	27.55	74.38	830	3.24
41	Manaure	Colombia	10.37	-73.13	1300	26.9	4	3.84	1.79	43.18	162.62	750	49.95
42	Mariquita	Colombia	5.25	-74.83	2104	26.5	1	4.14	4.79	48.05	315.40	240	1.35
43	Murrí	Colombia	6.58	-76.83	5175	27.3	0	3.55	4.16	39.02	115.86	350	2.73
44	Providencia Island	Colombia	13.35	-81.37	1584	27.6	5	3.80	6.50	23.32	52.87	550	4.36
45	Río Manso	Colombia	7.50	-76.08	2736	24.5	3	5.23	6.16	36.95	215.44	770	6.16
46	Sabana Rubia	Colombia	10.50	-72.92	2231	14.5	3	3.93	4.59	75.62	413.63	190	0.79
47	Tayrona National Park	Colombia	11.33	-74.03	1082	27.4	8	2.56	4.17	29.97	93.77	950	3.79
48	Tutunendo	Colombia	5.77	-76.58	7426	26.5	0	6.76	7.89	27.92	82.51	570	3.03
49	Ucumarí	Colombia	4.00	-75.50	2020	17.2	1	6.24	7.33	46.29	144.83	560	3.32

site	site name	location			climate data			trees ≤ 10 cm		trees > 10 cm		lianas ≥ 2.5 cm	
no.		country	latitude	longitude	MAP	MAT	DSL	BA (m^2/ha)	AGC (Mg /ha)	BA (m^2/ha)	AGC (Mg /ha)	no. ind/ha	AGC (Mg /ha)
50	Guanacaste gallery forest	Costa Rica	10.50	-85.17	1578	26.6	4	1.43	5.88	39.96	152.61	240	0.94
51	Guanacaste upland	Costa Rica	10.53	-85.30	1601	26.2	4	3.32	6.72	16.57	50.01	970	3.18
52	La Selva	Costa Rica	10.43	-84.02	3990	26	0	4.18	4.90	43.05	168.94	510	6.61
53	Magsaysay	Costa Rica	10.40	-84.05	4127	25.5	0	4.10	4.80	34.86	139.09	490	9.87
54	Osa Sirena	Costa Rica	8.46	-83.38	3768	25.5	3	2.69	3.16	59.90	337.96	520	4.46
55	Rancho Quemado	Costa Rica	8.70	-83.55	3423	24.8	3	3.26	3.84	58.09	387.97	290	4.40
56	Sierra Rosario	Cuba	22.83	-83.00	1617	23.3	4	2.36	2.78	36.91	167.50	330	2.55
57	Los Haitaises National Park	Dominican Republic	19.08	-69.50	2061	25.7	1	1.45	5.70	40.22	68.32	950	4.96
58	Capeira	Ecuador	-2.00	-79.97	731	25.5	8	1.59	3.24	52.90	101.96	570	4.55
59	Centinela	Ecuador	-0.58	-79.33	2683	24	5	3.41	3.99	42.07	217.11	590	2.41
60	Cuangos	Ecuador	-3.48	-78.23	3102	20.7	0	4.43	5.24	42.08	138.31	440	2.59
61	Esmeraldas Tropical Garden	Ecuador	0.90	-79.62	939	25.6	8	1.32	3.05	46.07	144.85	840	6.72
62	Fila de Bilsa	Ecuador	0.62	-79.85	1666	24.9	6	3.62	4.27	36.63	203.67	350	1.73
63	Huamaní	Ecuador	-0.67	-77.67	4186	18.8	0	4.16	4.92	46.07	159.41	610	3.59
64	Jatun Sacha	Ecuador	-1.07	-77.60	3663	23.9	0	5.57	6.56	37.80	132.22	830	8.82
65	Jauneche	Ecuador	-1.10	-79.63	1833	25.5	6	2.18	4.41	23.36	56.87	1250	6.10
66	Maquipucuna	Ecuador	0.12	-78.62	1745	18.1	6	4.94	5.79	54.39	269.05	330	1.63
67	Miazi	Ecuador	-4.30	-78.67	2307	21.8	0	4.13	4.84	44.37	147.52	510	5.13
68	Perro Muerto	Ecuador	-1.60	-80.70	613	21.6	8	0.98	2.46	28.75	85.74	480	2.97
69	Río Nangaritza	Ecuador	-4.30	-78.67	2307	21.8	0	3.21	8.31	55.19	220.06	680	8.26
70	Río Palenque1	Ecuador	-0.57	-79.33	2681	24.3	5	3.83	4.55	20.77	106.42	410	2.18
71	Río Palenque2	Ecuador	-0.57	-79.33	2681	24.3	5	4.17	4.93	34.59	213.07	350	2.61
72	San Sebastián	Ecuador	-1.60	-80.70	613	21.6	8	1.55	4.30	37.27	85.28	680	3.84
73	Makokou1	Gabon	0.57	12.87	1646	24	3	2.39	2.76	31.99	183.91	990	13.93
74	Makokou2	Gabon	0.57	12.87	1646	24	3	2.65	3.08	31.92	198.45	770	5.36
75	Berbice River	Guyana	5.50	-58.08	2341	26.7	0	3.03	3.71	54.30	281.22	460	7.17

site	site name	location			climate data			trees ≤ 10 cm		trees > 10 cm		lianas ≥ 2.5 cm	
no.		country	latitude	longitude	MAP	MAT	DSL	BA (m^2/ha)	AGC (Mg /ha)	BA (m^2/ha)	AGC (Mg /ha)	no. ind/ha	AGC (Mg /ha)
76	Avalanche	India	11.30	76.58	2095	14.5	3	6.07	7.08	75.18	400.41	170	1.12
77	Nadugani	India	11.45	76.38	2936	23.8	4	2.07	2.41	36.16	162.59	380	4.83
78	Round Hill (Top)	Jamaica	17.90	-77.50	1872	21.9	3	5.74	6.84	31.00	108.97	80	0.20
79	Ankarafantsika	Madagascar	-16.32	46.82	1491	26.3	7	3.03	5.26	32.45	107.71	1260	7.73
80	Nosy Mangabe	Madagascar	-15.50	49.77	3000	23.4	1	7.17	8.41	67.54	233.59	1170	5.73
81	Perinet Forestry Station	Madagascar	-18.92	48.42	1839	19.3	6	9.53	11.25	42.33	215.13	1120	3.46
82	Bako National Park	Malaysia	1.56	110.38	4053	27.1	0	3.92	4.61	35.37	121.77	440	3.88
83	Genting Highlands	Malaysia	3.97	101.63	2826	24.8	0	4.52	5.30	47.42	182.59	690	5.12
84	Pasoh 30	Malaysia	3.00	102.33	2012	25.8	0	4.35	5.10	22.43	85.00	1140	7.42
85	Pasoh 40	Malaysia	3.00	102.33	2012	25.8	0	3.75	4.36	35.89	126.15	1080	6.35
86	Semengoh Forest Preserve	Malaysia	1.60	110.00	4026	26.7	0	6.16	7.23	39.34	148.61	250	2.38
87	Brise Fer	Mauritius	-20.38	57.43	1839	21	4	11.20	13.29	69.81	403.18	160	0.90
88	Bosque de Guadalupe	Mexico	19.50	-96.95	1650	18.5	4	2.68	3.11	69.37	200.28	550	3.89
89	Chamela Arroyos	Mexico	19.50	-105.05	782	26.2	6	2.44	4.69	48.70	142.53	1410	14.12
90	Chamela Upland 1	Mexico	19.50	-105.05	782	26.2	6	3.11	6.53	18.96	64.16	390	2.58
91	Chamela Upland 2	Mexico	19.50	-105.05	782	26.2	6	6.21	9.55	11.78	35.49	530	3.50
92	Chamela 4	Mexico	19.50	-105.05	782	26.2	6	4.57	2.67	22.97	87.43	690	2.49
93	Los Tuxtlas	Mexico	18.58	-95.13	2693	21.6	4	4.28	5.02	34.96	183.77	510	4.43
94	Quince Ocotes	Mexico	19.73	-104.25	868	22.9	5	2.15	2.52	72.09	200.51	90	0.63
95	Rivière de Pirogues	New Caledonia	-22.17	166.83	2059	21.9	2	9.17	10.83	35.41	103.14	460	4.57
96	Baitete	New Guinea	-5.17	145.80	3423	26.7	0	3.03	3.57	36.36	119.92	680	5.85
97	Varirata National Park	New Guinea	-9.50	147.50	2807	23.9	1	5.12	5.97	36.51	121.47	550	4.55
98	Cerro El Picacho	Nicaragua	13.00	-85.92	1710	18.8	5	2.35	2.76	80.57	450.18	110	0.42
99	Cerro Olumo	Nicaragua	12.30	-85.40	1579	23	4	1.21	2.83	46.95	126.62	360	1.61
100	Omo Forest Reserve	Nigeria	7.00	5.00	1592	26.1	2	2.55	2.94	35.47	225.55	730	2.84
101	Curundu	Panama	8.98	-79.55	1830	27.1	4	1.07	3.17	20.20	49.88	580	2.06
102	Madden Forest	Panama	9.10	-79.60	2156	26.2	4	5.36	6.39	29.22	104.39	770	4.12

site	site name	location			climate data			trees ≤ 10 cm		trees > 10 cm		lianas ≥ 2.5 cm	
no.		country	latitude	longitude	MAP	MAT	DSL	BA (m^2/ha)	AGC (Mg /ha)	BA (m^2/ha)	AGC (Mg /ha)	no. ind/ha	AGC (Mg /ha)
103	Pipeline Road	Panama	9.17	-79.75	2553	26	4	4.90	5.76	21.20	88.35	710	4.29
104	Allpahuayo	Peru	-3.95	-73.42	2764	26.4	0	4.05	4.71	55.34	231.17	850	8.83
105	Bosque von Humboldt	Peru	-8.83	-75.00	2574	26.1	2	3.65	4.25	22.64	60.80	730	4.42
106	Cabeza de mono	Peru	-10.33	-75.30	2536	23.4	3	4.32	5.10	17.93	63.72	490	4.60
107	Cerro Aypate	Peru	-4.58	-79.53	982	19.5	8	4.96	5.86	53.76	235.36	380	1.94
108	Cerros de Amotape	Peru	-4.15	-80.62	784	20	8	4.27	6.30	27.71	59.49	340	3.03
109	Chirinos	Peru	-5.42	-78.88	1032	22.5	8	5.04	5.95	68.76	382.72	400	2.22
110	Cocha Cashu	Peru	-11.85	-71.32	2489	25	2	3.70	4.34	36.27	135.05	750	4.26
111	Constancia	Peru	-4.25	-72.75	2671	26	0	5.28	6.24	33.98	116.13	520	20.21
112	Cuterva National Park	Peru	-6.17	-78.67	730	19.9	9	4.71	5.50	58.67	288.95	530	3.33
113	Cuzco Amazonico	Peru	-12.58	-69.15	2195	25.5	4	3.74	4.39	46.81	211.03	570	6.54
114	Indiana	Peru	-3.52	-73.07	2808	26.4	0	3.48	4.07	50.01	176.85	930	7.85
115	Jenaro Herrera	Peru	-4.92	-73.75	2601	26.9	0	5.28	6.18	31.92	132.46	640	11.16
116	La Genoa	Peru	-11.08	-75.42	1383	17.6	5	4.48	5.14	30.48	131.20	510	6.91
117	Mishana Old Floodplain	Peru	-3.78	-73.50	2832	26.3	0	6.20	7.28	25.76	84.36	790	4.94
118	Mishana Tahuampa	Peru	-3.78	-73.50	2832	26.3	0	5.41	6.33	30.08	134.29	970	11.14
119	Mishana White Sand	Peru	-3.78	-73.50	2832	26.3	0	4.57	5.36	20.42	74.93	550	2.95
120	Pampas del Heath	Peru	-12.83	-68.83	2166	25.5	4	3.58	4.14	30.04	157.24	710	7.39
121	Río Candamo	Peru	-13.50	-69.83	3669	24.4	0	5.00	5.87	44.38	139.84	500	5.07
122	Río Távara	Peru	-13.35	-69.67	3363	24.7	0	5.03	5.97	40.77	152.88	820	6.32
123	Shiringamazú	Peru	-10.33	-75.17	2661	23.6	2	4.06	4.77	24.12	83.75	800	8.18
124	Tambopata Alluvial	Peru	-12.83	-69.28	2498	25.4	3	3.43	4.07	35.96	100.42	820	7.66
125	Tambopata Lateritic	Peru	-12.78	-69.28	2456	25.4	3	3.48	4.07	38.73	241.35	800	4.11
126	Tambopata Swamp Trail	Peru	-12.78	-69.28	2456	25.4	3	3.26	3.78	43.65	249.42	740	5.85
127	Tambopata Upland Sandy	Peru	-12.82	-69.72	3097	25	0	2.82	3.31	42.63	152.51	790	6.45
128	Tarapoto	Peru	-6.58	-76.42	1083	25.4	5	3.25	6.94	18.28	52.55	820	4.86
129	Venceremos	Peru	-5.75	-77.67	1117	18.4	5	5.83	6.85	50.46	229.73	330	3.33

site	site name	location			climate data			trees ≤ 10 cm		trees > 10 cm		lianas ≥ 2.5 cm	
no.		country	latitude	longitude	MAP	MAT	DSL	BA (m^2/ha)	AGC (Mg /ha)	BA (m^2/ha)	AGC (Mg /ha)	no. ind/ha	AGC (Mg /ha)
130	Yanamono 1	Peru	-3.43	-72.85	2805	26.3	0	3.14	3.67	38.52	144.61	580	3.57
131	Yanamono 2	Peru	-3.43	-72.85	2805	26.3	0	3.25	3.79	38.77	139.34	560	5.81
132	Yanamono Tahuampo	Peru	-3.47	-72.83	2814	26.4	0	3.71	4.35	62.89	244.86	640	4.93
133	Palanan	Philippines	17.13	122.52	2664	26.7	1	3.72	4.41	75.48	252.01	140	1.38
134	Luquillo	Puerto Rico	18.18	-65.83	2433	24.1	2	1.72	2.03	42.65	164.34	110	0.80
135	Mogotes de Nevárez	Puerto Rico	18.42	-66.25	1796	25.6	2	2.76	3.24	33.64	105.51	300	1.08
136	Kenting National Park	Taiwan	22.00	120.75	2273	24.8	4	2.12	2.97	39.33	146.05	690	4.56
137	Nanjen Shan Ecological Area	Taiwan	22.00	120.83	2522	24.4	4	11.03	13.00	31.71	108.60	530	2.14
138	Pande Forest Reserve	Tanzania	-6.67	39.08	981	25.8	5	1.14	0.94	17.34	63.56	1120	8.19
139	Pugu Forest Reserve	Tanzania	-6.83	39.08	1025	25	5	1.77	2.65	27.77	85.19	1570	14.78
140	Khao Yai National Park	Thailand	14.33	101.83	1370	25.2	4	0.19	2.61	43.29	122.99	1170	9.35
141	Sakaerat 1	Thailand	14.50	102.00	1386	26.5	4	3.32	5.56	34.47	109.58	520	5.06
142	Blohm Ranch	Venezuela	8.57	-67.58	1378	27.4	4	1.32	3.19	22.44	50.60	760	4.63
143	Boca de Uchire	Venezuela	10.09	-65.45	757	27	7	1.64	3.16	9.58	25.05	750	3.72
144	Cerro de la Neblina1	Venezuela	0.83	-66.18	3125	26.7	0	3.49	4.06	22.91	85.44	300	3.58
145	Cerro de la Neblina2	Venezuela	0.83	-66.18	3125	26.7	0	3.95	4.59	33.08	152.78	260	4.66

Appendix 3.2. Equations to estimate aboveground biomass of tropical forests based on diameter at breast height (DBH), wood density (WD) or basal area (BA), using Gentry's data sites. All biomass values are expresses as dry mass (Mg).

parameter	equation[a]	R^2
trees ≤ 10 cm DBH[b]	$(\mathrm{EXP}\ (4.9375 + 1.0583\ \ln\ (\mathrm{DBH})^2)\ 1.14\ /10^6$	0.93
trees > 10 cm DBH[c]		
wet forest	$\mathrm{WD} \times \mathrm{EXP}\ (-1.239 + 1.980\ \ln\ (\mathrm{DBH}) + 0.207\ (\ln\ (\mathrm{DBH}))^2 - 0.0281\ \ln(\mathrm{DBH}))^3)$	0.97
moist forest	$\mathrm{WD} \times \mathrm{EXP}\ (-1.499 + 2.148\ \ln\ (\mathrm{DBH}) + 0.207\ (\ln\ (\mathrm{DBH}))^2 - 0.0281\ \ln(\mathrm{DBH}))^3)$	0.97
dry forest	$\mathrm{WD} \times \mathrm{EXP}\ (-0.667 + 1.784\ \ln\ (\mathrm{DBH}) + 0.207\ (\ln\ (\mathrm{DBH}))^2 - 0.0281\ \ln(\mathrm{DBH}))^3)$	0.97
trees > 10 cm DBH[d]		
wet forest	$(21.297 - 6.953\ (\mathrm{DBH}) + 0.740\ (\mathrm{DBH}^2))\ /10^3$	0.92
moist forest	$(\mathrm{EXP}\ (-2.134 + 2.530\ \ln\ (\mathrm{DBH}))\ /10^3$	0.97
dry forest	$10\text{^}\ (-0.535 + \log_{10}\ (\mathrm{BA}))\ /10^3$	0.94
lianas[e]	$10\text{^}\ (-0.12 + 0.91\ \log_{10}\ (\mathrm{BA}))\ /10^3$	0.82

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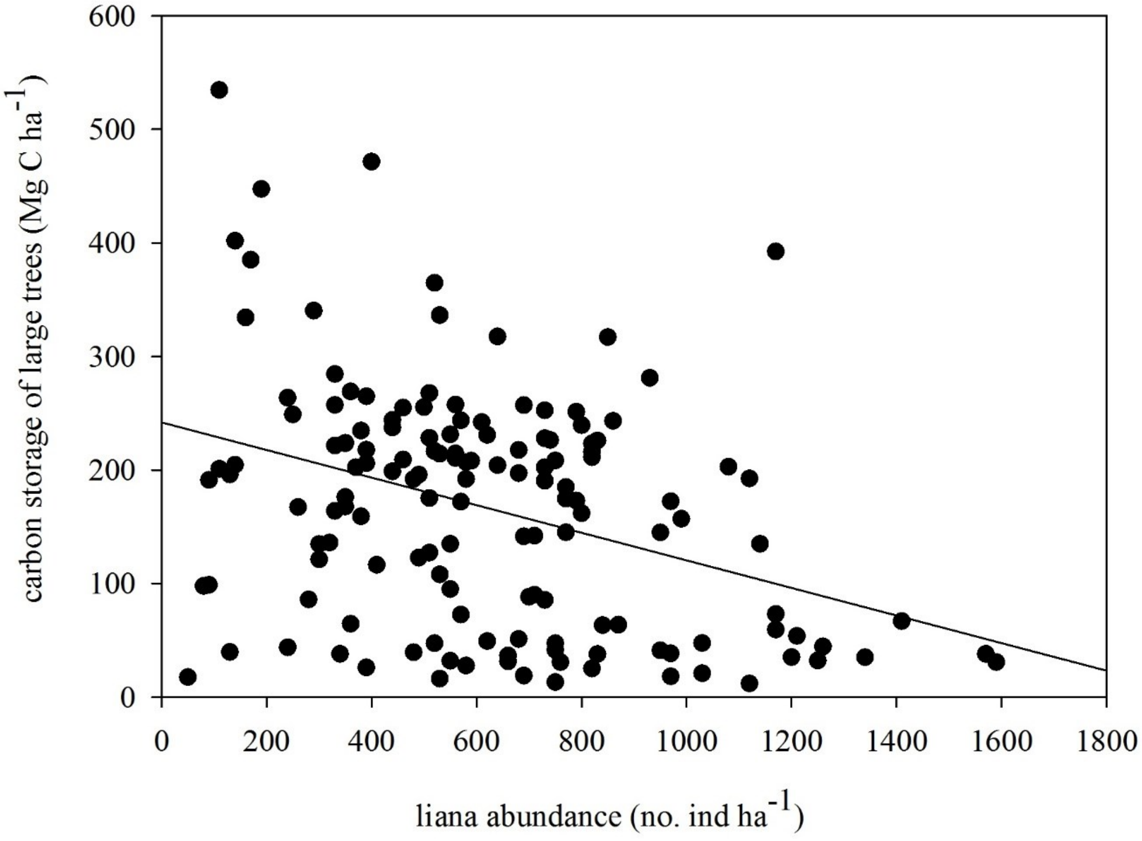
[a] EXP indicates the natural logarithm ($e = 2.71828$) is raised to the power indicated in the formula (e.g. $\mathrm{EXP}(-1.239) = e^{-1.239}$), whereas 10^ indicates that the base-10 logarithm is used (e.g. $\mathrm{base10}(0.5) = 10^{0.5}$). DBH is in cm, WD in g/cm^3, and BA in cm^2.

[b] Hughes et al. 1999 [16].

[c] Chave et al. 2005 [15].

[d] Brown 1997 [19].

[e] Putz 1983 [18]



Appendix 3.3. Relationship between liana abundance on aboveground carbon storage of large trees (> 10 cm diameter) in tropical forests (*n*=145). Carbon storage decreased with liana abundance ($t = -4.32$, *p*-value < 0.001; $R^2 = 0.11$). Carbon stocks were estimated using allometric equations based only on DBH for wet, moist, and dry forests following Brown (1997). See appendix 3.2 for full equations.

4. Climate, stand variables and lianas control forest carbon in old-growth tropical forests [4]

4.1 Introduction

Tropical forests are considered carbon sinks; they sequester 1.2 Pg C per year and process 41 Pg C annually through photosynthesis and respiration (Malhi, 2012). There is considerable concern regarding the future of these carbon sinks because current environmental drivers are restructuring tropical forests, thus influencing forest biomass and carbon uptake (Phillips & Lewis, 2014). Drivers include increases in atmospheric carbon dioxide, air temperatures, changes in rainfall, and changes in forest structural parameters such as increases in liana abundance and biomass (Phillips & Lewis, 2014). Although the magnitude and trend of some of these drivers have been acknowledged (Schnitzer & Bongers, 2011), there is little information about how the combined effects of all these drivers influence aboveground carbon storage (AGC) across tropical forests.

Most research evaluating variation in AGC in tropical forests has been related to changes in climatic conditions, but results across studies have provided little consensus. For example, AGC does not generally increase with precipitation, as the highest carbon stocks are found in moist tropical forests rather than wet forests (Keith *et al*., 2009; Stegen *et al*., 2011). Similarly, AGC does not consistently increase with temperature. In moist forests, AGC has been positively related to mean annual temperature (Raich *et al*., 2006), while in wet forests a negative association has been found (Stegen *et al*., 2011). Moreover, forest stand variables (e.g., density of large trees) are strong predictors of AGC (Chave *et al*., 2005; Baraloto *et al*. 2011; Slik *et al*., 2013) and have explained more variation in AGC than climate in regional and global studies (Slik *et al*., 2010; Baraloto *et al*., 2011; Stegen *et al*., 2011). Nonetheless, other stand variables such as liana abundance have been disregarded despite the impact that lianas have on the tropical forest carbon cycle (van der Heijden *et al*., 2013). Lianas reduce tree growth (van der Heijden & Phillips, 2009), fecundity (Wright *et al*. 2005) and survival (van der Heijden *et al*., 2013). Thus, they can reduce carbon sequestration in tree biomass. A recent study across tropical forests showed that liana abundance may reduce tree carbon storage by up to 50% (Durán & Gianoli,

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[4] *A version of this chapter has been published. Durán SM, Sánchez-Azofeifa GA, Rios RS, Gianoli E. The relative importance of climate, stand variables, and liana abundance for carbon storage in tropical forests. 2015. Global Ecology and Biogeography. doi: 10.1111/geb.12304*

2013). Therefore, it is essential to incorporate lianas in studies addressing variation in AGC, and evaluate their importance relative to other stand variables and environmental drivers.

Carbon stocks in tropical forests may be the result of complex interactions among climate, stand variables and liana abundance. Across tropical regions, AGC declines in forests with greater seasonality (Stegen *et al*., 2009). This pattern has been attributed to increases in tree mortality, declines in tree growth rates, and reductions in stand basal area and tree density associated with long periods of moisture stress (Slik *et al*., 2010; Phillips & Lewis, 2014). Rising temperatures in tropical forests also reduce tree diameter growth due to higher respiration costs (Clark *et al*., 2010). Lianas could also be responsible for declines in AGC. Across the tropics liana density was found to increase with dry season length and decreased with mean annual precipitation (DeWalt et al., 2010), and greater liana abundance was found in seasonal forests (Schnitzer, 2005). Lianas in tropical forests can decrease the increment in tree biomass by 0.25 Mg C ha^{-1} per year, (van der Heijden & Phillips, 2009), reduce tree diameter and basal area (van der Heijden *et al*., 2013), and increase tree mortality risks by two- to three-fold (Ingwell *et al*., 2010). Moreover, liana infestation rates are higher on shade-tolerant, slow-growing tree species with high wood density, which generally store more carbon than fast-growing species (van der Heijden *et al*., 2013). To date, our knowledge of AGC in tropical forests is far from complete. For instance, the concomitant effects of climate, stand variables and lianas on AGC (and their interactions) have not been evaluated. To fully understand how AGC is controlled in tropical forests, it is necessary to account for the network of interactions among climate, stand variables and lianas, and quantify the relative strengths of direct versus indirect drivers of AGC.

Our first aim in this study was to evaluate the relative importance of climate, stand variables and liana abundance in explaining variation in AGC. Our second aim was to disentangle the interactions among these components by testing their direct and indirect effects on AGC using a multivariate framework by means of structural equation modeling (SEM). To this end, we proposed an *a priori* model (Fig. 4.1a) that posits direct and positive effects of stand variables on AGC as established earlier (Malhi *et al*., 2006; Slik *et al*., 2010; Baraloto *et al*., 2011). Stand variables, specifically basal area, tree diameter, and –to a lesser extent– wood density, are strong positive correlates of forest carbon, and may explain more variation in AGC than climate at regional scales (Baker *et al*., 2004, Malhi *et al*., 2006; Silk *et al*., 2010; Baraloto *et al*., 2011). Moreover, it has been suggested that stand variables should be the first level of analysis of variation in AGC (Baraloto *et al*., 2011). Our model assumed that basal area, tree diameter, and wood density have a direct effect on AGC (Fig. 4.1a). We further assumed that the effects of liana abundance on AGC are mainly indirect, through the direct –and negative– effects of lianas on stand variables. Climate effects on AGC are considered to be both direct and indirect via effects on liana abundance and stand variables (Baraloto *et al*., 2011; Schnitzer & Bongers, 2011; Stegen *et al*., 2011). Finally, to test the generality of our model, we evaluated whether relationships among parameters are consistent across tropical forest types in different geographic regions (dry, moist, and wet forests).

4.2 Methods

Climate data

We selected three variables to describe climatic conditions: mean annual temperature (MAT, °C), mean annual precipitation (MAP, mm), and evapotranspirative demand. MAT and MAP are important explanatory factors for AGC and liana abundance in tropical forests (Stegen *et al*., 2011; DeWalt *et al*., 2010). MAT and MAP were obtained for each plot from the WorldClim dataset (Hijmans *et al*., 2005) at a resolution of 30 arcsec (~ 1 km^2 at the equator). Evapotranspirative demand was estimated as potential evapotranspiration (PET, mm) according to the Penman-Monteith equation, which was obtained from a global dataset of monthly potential evapotranspiration (CRU CL 1.0 Global Climate dataset; 30 arcsec) (Allen *et al*., 1998). We then estimated the ratio of PET to MAP to obtain the dryness index (DI) (Maass & Burgos, 2011). The DI represents the water balance and plant growth conditions for a specific location and has been widely used to evaluate vegetation responses to climate (Maass & Burgos, 2011). With these data we classified each location as dry, moist or wet forest following Chave *et al*. (2005).

Forest variables and carbon stocks

We used a forest inventory database that spans a broad climatic gradient across the tropics (Fig. 4.2, Appendix 4.1) based on a standardized sampling of 0.1-ha plots of old-growth forests (Gentry's dataset, see Phillips *et al*., 2002). Within each plot, all trees, palms, shrubs, and lianas with stems ≥ 2.5 cm diameter at breast height (DBH) were identified at the species level. We analyzed 145 plots for which standardized climatic data were available, which included forests ranging from 10 to 3000 m in elevation (Appendix 4.1). We updated the species identification and nomenclature using the vouchers provided for each individual in the Gentry dataset, and derived current classification from the Tropicos database and the Plant List (2013). We only updated nomenclature when all vouchers for a record had the same species determination.

To estimate carbon stocks, we first calculated aboveground biomass (AGB) of each plot using the pan-tropical regression equations for wet, moist, and dry forests that include wood density and DBH data (Chave *et al*., 2005). Wood density data were obtained from the literature (Chave *et al*., 2009; Zanne *et al*., 2009). When we lacked data on wood density at the species level, a genus-level (for 52% of the species), family-level (for 12% of the species), or a pantropical mean (0.6 g cm^{-3} for <1% of the species) was used. For multiple-stemmed individuals we calculated AGB of each stem and summed them (Chave *et al*., 2005). We estimated AGC per plot using the following equation: C (Mg C ha^{-1}) = AGB x 0.47/plot area (Hughes *et al*., 1999). AGC was estimated for all woody plants with a dbh > 10 cm because lianas do not have an effect on carbon stocks of trees ≤ 10 cm DBH (Durán & Gianoli, 2013), and more than 90 % AGC of old-growth forests is stored in plants > 10 cm dbh (DeWalt & Chave, 2004; Durán & Gianoli, 2013). Total AGC represents carbon stocks of shrubs, palms and trees. We did not include the AGC of lianas to avoid any circularity in our models when linking carbon stocks with liana abundance. Lianas' AGC accounts for ~5% AGC in our forest plots (Durán & Gianoli, 2013). We selected three stand variables that are strong predictors of AGC in tropical forests (Baraloto *et al*., 2011): stand basal area (BA) summed across all individuals, mean wood density (WD), and mean tree diameter (DBH). Liana abundance and stand variables were estimated on a per-plot basis (0.1 ha) for each location.

Data analysis

Comparisons of climate, stand variables, liana abundance and AGC across forest types (dry, moist, and wet) were conducted with ANOVA and Tukey post-hoc tests to compare group means. To assess the relative contribution of climate, stand variables, and liana abundance to AGC, we used structural equation modeling (SEM). SEM is a powerful tool to unravel the structure linking variables that are correlated in a multivariate way, allowing the disentanglement of direct and indirect effects of a predictor variable (Shipley, 2004). SEM assess the fitting of the model by comparing the covariance matrix of the hypothesised model against the covariance matrix obtained from the data using a chi-square (χ^2) statistic with good-fitting models showing a *P*-value > 0.05 (Shipley, 2004). Variables were log-transformed when needed to meet the assumptions of ANOVA and SEM. After these transformations, our data were not always adjusted to the multivariate normal distribution required for SEM analysis. Therefore, a comparison between covariance matrices was conducted using the maximum likelihood (ML) and the goodness of fit based on the Satorra-Bentler test statistics (Satorra & Bentler 1994). These tests provide more robust χ^2 and standard errors than conventional ML techniques and are used when data fail to meet the multivariate normality assumption (Shipley, 2004). We also used the comparative fit index (CFI), with good-fitting models indicated by CFI > 0.95 and RMSEA (root mean square error of approximation) ≤ 0.05.

Our model assumed that BA, DBH, and WD have direct effects on AGC; these are shown by single-headed arrows (Fig. 4.1a). These components are not necessarily independent, as they are used to estimate AGC. BA is a function of tree diameter and tree density (Chave *et al*., 2005, Slik *et al*. 2010), and variation in tree BA depends in part on initial tree diameter (Brown *et al*., 1989). WD correlates negatively with tree diameter because large trees tend to have lower wood density (Chave *et al*., 2004; Iida *et al*., 2011). Thus, we expected a positive correlation between BA and DBH, and a negative correlation between WD and DBH (Fig. 4.1a). Failing to account for these covariances may lead to incorrect inferences. Bunker *et al*. (2005) simulated the effects of biodiversity loss on carbon storage in Barro Colorado Island (BCI), and estimated that liana-induced shifts in tree species composition from slow-growing toward fast-growing species could lead to a 34% reduction in AGC in tropical forests. This result, however, may be questioned because they assumed that forest carbon increases with wood density, but empirical studies in BCI indicate that AGC and BA decrease with WD (Chave *et al*., 2004; Stegen *et al*., 2009). Consequently, it is still unclear whether such a shift in tree species composition would lead to an overall decrease in AGC in tropical forests. The effects of WD on forest carbon are partly determined by the BA-WD correlation. Thus, the greater the biomass dominance of low WD species, the weaker the relationship between BA and WD. If this relationship is significant, AGC will also decrease with WD (Stegen *et al*., 2009). This has been found in BCI and other tropical forests (Chave *et al*., 2004; Iida *et al*., 2011). To avoid making causal assumptions (e.g., increases in AGC with WD) we allowed stand variables to freely covary (Shipley, 2004). These covariances are indicated by doubled-headed arrows in our model (Fig. 4.1a).

We hypothesised that liana abundance would reduce AGC indirectly, through direct negative effects on BA, DBH, and WD. Several studies in tropical forests have shown that lianas can reduce tree diameter and BA (van der Heijden & Phillips, 2009; Ingwell *et al*., 2010; van der Heijden *et al*., 2013). Liana infestation rates are higher on shade-tolerant species with high wood density (van der Heijden & Phillips, 2009). Therefore, lianas could reduce AGC by promoting directional changes in tree species composition towards fast-growing species with low WD, which in general store less AGC (van der Heijden *et al*., 2013). We also expected a positive association between liana abundance and DI. Overall, liana abundance in the tropics increases with decreasing rainfall, increasing temperature, and evapotranspirative demand (Schnitzer 2005; Schnitzer & Bongers, 2011). It has been proposed that lianas have a competitive advantage over trees in dry forests due to their efficient vascular systems, which enhance water uptake -and hence growth- during the dry season while trees are dormant (Schnitzer, 2005).

We hypothesised that increments in DI will reduce AGC both directly and indirectly. Direct effects of DI on AGC may result from declines in tree growth, lower photosynthetic rates and increases in tree mortality due to stressful conditions for plant growth (high evapotranspirative demand and temperature) (Slik *et al*., 2010; Phillips & Lewis, 2014). Indirect effects of DI on AGC may arise from direct negative effects of lianas on stand variables, due to the greater abundance of lianas in sites with high DI values.

We used exploratory SEM and thus began with a full model that included all hypothesised connections between variables (Fig. 4.1a). To assess fit of our model to the data, we iteratively removed non-significant connections between variables one at a time and assessed whether including those paths in the model reduced or increased model fit using the χ^2, the CFI and RMSEA statistics. Upon finding a good-fitting model (Fig.4.1b), we evaluated the degree to which the three forest types fit a common model by using multigroup SEM, a multivariate tool that tested whether the model paths differ statistically among dry, moist, and wet tropical forests. To fit a multigroup model we started with the most constrained structure across groups (across forest types in our case), in which all path coefficients, covariances, and variances are forced to be equal (Shipley, 2004). This fully constrained model was rejected ($\chi^2 = 75.4$, d.f. = 53, $P = 0.02$), indicating that at least one path varied across groups (Shipley, 2004). The next step consisted in fitting a series of nested models to identify which paths significantly differed among groups; for this, we removed each path of the model one at a time. The difference in the maximum likelihood χ^2 statistics between models was then used to test for differences in the parameters across forest types after Bonferroni correction (Shipley, 2004). The final model for multigroup comparison was then fitted by relaxing the constraints for those parameters that rejected the null hypothesis of equality across groups. All statistical analyses were done using the R platform and the lavaan package version 0.5−15 (Rosseel, 2012).

4.3 Results

Carbon stocks varied across forest types, with the greatest AGC found in moist forests, followed by wet and dry forests (Table 4.1). MAT did not differ among forest types, while the DI was higher in dry forests compared to moist and wet forests (Table 4.1). All stand variables showed differences across forest types, except for DBH. WD was higher in dry forests, while BA was greater in moist and wet forests. Dry forests had the greatest abundance of lianas (Table 4.1).

Fit of the data to the initial model ($\chi^2 = 3.1$, d.f. = 2, $P = 0.22$) excluded the hypothesised connections between MAT and DBH, and the WD-BA covariance ($P > 0.05$, Fig. 4.1b). This model explained 81% of variation in AGC, and indicated that stand variables were strong predictors of AGC, which increased with WD, DBH, and BA (Fig. 4.1b). Changes in DBH appear to be more affected by DI than MAT. The effects of MAT on AGC were indirect (–0.17) rather than direct, while the opposite was found for DI, with direct effects being stronger (–0.23) than indirect ones (–0.15). Liana abundance did not affect stand variables significantly, but the removal of these paths affected the overall model fit (Fig. 4.1b).

The multigroup analysis revealed variation in path coefficients across forest types, as the hypothesis of total equality of pathways was rejected. Goodness of fit of the multigroup model improved significantly ($\chi^2 = 41.7$, d.f. = 43, $P = 0.53$) when five paths were released from the constraint of being equal across groups. These paths include the negative impact of lianas on BA and DBH, the influence of DI on AGC, the effect of MAT on WD, and the error variance of WD (Table 4.2). Three interesting patterns arose from this multigroup model. First, the predictor variables included in the model accounted for over 85% variation in AGC consistently in dry, moist and wet tropical forests. BA, DBH and WD showed a positive and significant association with AGC in all forest types (Fig. 4.3). Second, climate effects were mainly indirect rather than direct (Fig. 4.3, Appendix 4.2). Total indirect effects of MAT on AGC were –0.21, –0.38, –0.14 in dry, moist, and wet forests, respectively (appendix 4.3), with no significant direct effects across forest types (Fig. 4.3). Direct effects of DI on AGC were significant only in dry forests, with direct effects (–0.17) stronger than indirect effects (–0.11, appendix S3; Fig. 4.3b-c). Finally, effects of liana abundance on AGC varied across forest types, with reductions in DBH and BA in moist forests only (Fig. 4.3, Appendix 4.2), and no significant effects on WD across forest types. Contrary to our expectations, DI did not have a significant effect on lianas, but removing this path from the initial model (Fig. 4.1a) reduced the goodness of fit.

4.4 Discussion

Tropical forests are among the greatest carbon pools worldwide (Keith *et al*., 2009), but they are experiencing structural changes that may reduce carbon storage potential (Phillips & Lewis, 2014). It is necessary to improve our understanding of how carbon pools will respond to current global changes. Our approach differed from other studies in that it assessed the indirect and direct effects of all predictors in an integrative framework, rather than modeling each predictor separately. It also included the effect of lianas, which have not been included in studies of AGC variation in tropical forests (Malhi *et al*., 2006; Keith *et al*., 2009: Baraloto *et al*., 2011; Stegen *et al*., 2011, Slik *et al*., 2013). We found that climate effects on AGC were mainly indirect through direct effects of climate on stand variables, including liana abundance. This may explain why previous studies in tropical forests evaluating direct effects of temperature and precipitation on AGC have found that climate explained little variation in AGC at regional and global scales (Malhi *et al*., 2006; Keith *et al*., 2009; Stegen *et al*., 2011, Slik *et al*., 2013).

Our model explained over 85% of variation in AGC in tropical forests at global scales, and it was consistent across forest types in different geographic regions, thus showing general relationships between both biotic and environmental predictors and AGC. This highlights the usefulness of an integrative approach to improve predictions of the effects of global change drivers on tropical carbon sinks. Effects of stand variables on AGC were similar across forest types, but the relative importance of climate and liana abundance changed with forest type. Thus, AGC in dry forests appears to be limited by evapotranspirative demand, rainfall and temperature, which overrides the negative effects of liana density. In contrast, in moist forests, climate -in particular, temperature- is as important as liana abundance in explaining changes in AGC. In wet forests, temperature -and its effect on stand variables- is a stronger driver of AGC variation compared to liana abundance and dryness index (DI). In agreement with other global studies, we found the greatest carbon stocks in moist forests (Keith *et al*., 2009; Stegen *et al*., 2011), and the greatest liana abundance in dry forests (Schnitzer, 2005; Schnitzer & Bongers, 2011).

We found a consistent negative effect of temperature on AGC across forest types, with stronger total effects in dry and moist forests. These effects were mainly indirect via negative effects on basal area (BA). In tropical forests carbon uptake may be limited at high temperatures as primary production generally peaks at 25°C, declining at higher temperatures due to greater costs of plant maintenance (Larjavaara & Muller-Landau, 2012). Increases in temperature seasonality may also reduce the density of trees > 70 cm diameter, which store large amounts of biomass carbon (Slik *et al*., 2013). This has important implications for the global carbon budget, since it is predicted that temperature in the tropics will increase between 1 and 6 °C, with potential detrimental effects on carbon sinks (IPCC, 2007; Slik *et al*., 2013).

Increased DI was associated with reduced AGC in dry forests. In forests where evapotranspirative demand is not met by available water, maximum individual biomass -and therefore total biomass carbon in the forest- is constrained by water deficit (Stegen *et al*., 2011). With moisture stress, declines in forest biomass can be related to reduced photosynthesis due to prolonged stomatal closure (Phillips & Lewis, 2014), reductions in wood production (Clark *et al*., 2010) and greater tree mortality due to extended drought periods (Phillips *et al*., 2010; Phillips & Lewis, 2014). Nonetheless, we did not find negative indirect effects of DI on AGC through reductions in stand variables. Thus, the observed reductions in AGC may be related to increments in tree mortality rather than reductions in growth (e.g., lower DBH and BA). Studies assessing drought impacts in tropical forests have indicated that tree mortality may be more significant than growth processes in reducing forest biomass, because mortality of large trees (> 10 cm DBH) increased remarkably at higher levels of moisture stress (Nepstad *et al*., 2007; Phillips *et al*., 2010). Our results suggest that dry forests are more vulnerable to water deficit, as no negative effects of DI on AGC were found in moist and wet forests. Moisture depletion could have the greatest impact in dry forests, where for many tree species there is a high risk of crossing a biome threshold to savanna with increased temperature and decreased rainfall (Phillips *et al*., 2010; Phillips & Lewis, 2014).

Wood density (WD) and mean tree diameter (DBH) increased with DI across forest types, with stronger effects in wet forests. The DI represents the balance between water and energy since it is the ratio of potential evapotranspiration to precipitation. Woody species tend to have higher wood densities in environments where water and energy are limited (Poorter *et al*., 2008), such as those in dry and wet forests, respectively. High WD in dry forests may be of functional value during water shortage as it increases resistance to xylem cavitation (Hacke *et al*., 2006) and is associated with wider tree crowns, which could explain the increase in trunk diameter (Iida *et al*., 2011). In wet forests, where water is not a limiting factor (Stegen *et al*., 2011), plant growth is mainly limited by energy (Poorter *et al*., 2008). DI increments in wet forests indicate energy increments (e.g., high irradiance), which could favor carbon uptake and photosynthesis, and may explain the positive association between DI and both DBH and WD (Dong *et al*., 2012).

As shown in previous studies, we found that stand variables are strong predictors of AGC in dry, moist, and wet tropical forests: increased AGC was associated with increments in forest stand variables (Baker *et al*., 2004; Chave *et al*., 2005; Malhi *et al*., 2006; Slik *et al*., 2010, Baraloto *et al*., 2011). Other studies where BA did not covary with WD also reported a positive and significant effect of WD on AGC (Baker *et al*., 2004; Stegen *et al*., 2009). We found a strong relationship between BA and AGC across forest types, which confirms the major role of large trees for AGC shown in other studies in the tropics (DeWalt & Chave, 2004; Slik *et al*., 2013).

Liana abundance increased with temperature across tropical forests. This result may be influenced by the inclusion of montane forests (> 1000 m a.s.l.) in our dataset since liana abundance decreases sharply at high altitudes (van der Heijden & Phillips, 2008). Such a relationship was not found when only lowland forests (≤ 1000 m a.s.l.) were included ($r = 0.13$, $P = 0.15$). Another pantropical study based on Gentry's dataset found similar patterns, with no effects of temperature on lianas when montane forests were excluded from the analysis (van der Heijden & Phillips, 2008). Contrary to our expectations, liana abundance was not positively related to DI. Effects of precipitation on lianas across the tropics are not consistent, with some studies showing a negative association (Schnitzer, 2005; DeWalt *et al*., 2010) and others finding no relationship (van der Heijden & Phillips, 2008; Durán & Gianoli, 2013). Studies at the global level suggest that forest stand variables may be more important in explaining liana distribution across the tropics than climate (van der Heijden & Phillips, 2008). The greatest liana abundance in dry forests may be related to the higher incoming solar radiation (Kalácska *et al*., 2005) and/or the greater light availability throughout the year (DeWalt *et al*., 2010), which may provide more favorable conditions for liana proliferation (Schnitzer and Bongers, 2011).

Following the hypothesis that lianas have a dry-season growth advantage over trees (Schnitzer, 2005), we expected that liana abundance would exert stronger negative effects on carbon stocks in dry forests. However, we found stronger negative effects of lianas on AGC in moist forests, despite the greater absolute abundance of lianas in dry forests. It may be conceived that lianas thrive in dry forests due to the greater light availability given by shorter forest stature, deciduousness, and lower leaf area index when compared to moist forests (Kalácska *et al*., 2005). The higher growth and abundance of lianas relative to trees in dry forests may reflect differential strategies to cope with harsh environments, rather than competitive effects. Most tree species are geared toward resource conservation, survival, and stress avoidance, which are facilitated by low growth rates, leaf shedding during the dry season to reduce transpiration rates, and stem water storage (Kalácska *et al*., 2005; Hacke *et al*., 2006). Lianas generally aim at resource acquisition, with higher photosynthetic and growth rates, which is facilitated by lower construction costs of wood and leaves (low WD, high specific leaf area), and higher water use efficiency than trees (Cai *et al*. 2009; Schnitzer, 2005). The differences in ecophysiological traits between lianas and trees suggest a large potential for resource partitioning between trees and lianas in dry forests (Sánchez-Azofeifa *et al*., 2009). Our results suggest that tree-liana competition is more intense in moist forests, and thus aboveground competition for light would be more important than belowground competition for water. Moist forests have greater canopy height and larger basal area, and the lower light availability may promote competition for light between trees and lianas (van der Heijden *et al*., 2013; Tobin *et al*., 2012) that ultimately can reduce AGC. In moist forests, liana infestation on tree crowns reduces tree carbon uptake, sap flow, growth rate, and reproductive success, and increases tree mortality (Wright *et al*., 2005; van der Heijden & Phillips, 2009; Ingwell *et al*., 2010; Tobin *et al*., 2012).

Towards a general framework of aboveground carbon storage

Numerous studies have addressed the drivers of variation in carbon stocks in tropical forests (e.g., Baker *et al*., 2004; DeWalt & Chave, 2004, Malhi *et al*., 2006; Keith *et al*., 2009; Slik *et al*., 2010; Stegen *et al*., 2011), but little consensus has been reached across studies on climate effects on AGC (Stegen *et al*., 2011; Slik *et al*., 2013). We argue that these discrepancies are partly due to the limited number of drivers evaluated in conjunction with other factors (Slik *et al*., 2010; Baraloto *et al*., 2011; Stegen *et al*., 2011), the exclusive focus on direct effects overlooking indirect effects, and the lack of studies incorporating liana abundance. Outcomes of our model were generally consistent across dry, moist and wet tropical forests, and indicated that indirect effects are important to understand the relative importance of drivers of AGC in tropical forests. Our results also indicated that lianas have stronger effects in moist forests, which harbor the greatest carbon stocks in the tropics (Keith *et al*., 2009; Stegen *et al*., 2011). It is therefore necessary to undertake an integrative approach that evaluates the interplay between the main drivers of AGC, including liana abundance, since it is now clear that lianas are increasing in abundance and biomass across the tropics (Schnitzer & Bongers, 2011).

We propose a general framework for evaluating the variation in AGC in tropical forests, based on our analysis and current evidence (Fig. 4.4). Forest stand variables should constitute the first-proximal- level of analysis as it has been indicated in previous studies (Baraloto *et al*., 2011). In this study we focused on three stand variables (wood density, tree diameter, basal area), but other variables such as maximum individual biomass and density of large trees, which are important predictors of AGC (Stegen *et al*., 2011; Slik *et al*., 2013), can be incorporated. Liana abundance should be the second level of analysis, and the final -distal- level would include abiotic conditions, specifically climate components and soil characteristics. Soil fertility has been hypothesised to increase AGC, but current evidence is mixed (Slik *et al*., 2010; Baraloto *et al*., 2011). Research on liana-soil interactions is scarce, but some studies have found greater liana abundance on more fertile soils (DeWalt *et al*., 2006). Moreover, lianas could also have positive effects on soil given the leaf litterfall quantity they contribute in tropical forests (Hegarty, 1991), which could have disproportionate effects on nutrient cycling (Powers, 2014). Future studies should be conducted to disentangle the environmental correlations of AGC, in particular the relative importance of lianas and soils on AGC, and the indirect effects of soil on AGC via stand variables and liana abundance.

4.5 References

Allen, R.G., Pereira, L.S., Raes, D. & Smith, M. (1998) Crop evapotranspiration-Guidelines for computing crop water requirements-FAO Irrigation and drainage paper 56. *FAO, Rome*, **300**, 6541.

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

Baraloto, C., Rabaud, S., Molto, Q., Blanc, L., Fortunel, C., Herault, B., Davila, N., Mesones, I., Rios, M., Valderrama, E. & Fine, P.V.A. (2011) Disentangling stand and environmental correlates of aboveground biomass in Amazonian forests. *Global Change Biology*, **17**, 2677-2688.

Brown, S., Gillespie, A. & Lugo, A. (1989) Biomass estimation methods for tropical forests with applications to forest inventory data. *Forest Science*, **35**, 881–902.

Bunker, D., DeClerck, F. & Bradford, J. (2005) Species loss and aboveground carbon storage in a tropical forest. *Science*, **310,** 1029–1031.

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

Chave, J., Condit, R., Aguilar, S., Hernandez, A., Lao, S. & Perez, R. (2004) Error propagation and scaling for tropical forest biomass estimates. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, **359**, 409–20.

Chave, J., Andalo, C., Brown, S., Cairns, M.A., Chambers, J.Q., Eamus, D., Folster, H., Fromard, F., Higuchi, N., Kira, T., Lescure, J.P., Nelson, B.W., Ogawa, H., Puig, H., Riera, B. & Yamakura, T. (2005) Tree allometry and improved estimation of carbon stocks and balance in tropical forests. *Oecologia*, **145**, 87-99.

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

Clark, D.B., Clark, D. a. & Oberbauer, S.F. (2010) Annual wood production in a tropical rain forest in NE Costa Rica linked to climatic variation but not to increasing CO_2. *Global Change Biology*, **16**, 747–759.

DeWalt, S.J. & Chave, J. (2004) Structure and biomass of four lowland Neotropical forests. *Biotropica*, **36**, 7-19.

DeWalt, S.J., Ickes, K., Nilus, R., Harms, K.E. & Burslem, D.F.R.P. (2006) Liana habitat associations and community structure in a Bornean lowland tropical forest. *Plant Ecology*, **186**, 203–216.

DeWalt, S., Schnitzer, S. & Chave, J. (2010) Annual rainfall and seasonality predict pan-tropical patterns of liana density and basal area. *Biotropica*, **42**, 309–317.

Dong, S.X., Davies, S.J., Ashton, P.S., Bunyavejchewin, S., Supardi, M.N.N., Kassim, A.R., Tan, S. & Moorcroft, P.R. (2012) Variability in solar radiation and temperature explains observed patterns and trends in tree growth rates across four tropical forests. *Proceedings of the Royal Society B-Biological Sciences*, **279**, 3923-3931.

Durán, S.M. & Gianoli, E. (2013) Carbon stocks in tropical forests decrease with liana density. *Biology letters*, **9**, 20130301.

Hacke, U.G., Sperry, J.S., Wheeler, J.K. & Castro, L. (2006) Scaling of angiosperm xylem structure with safety and efficiency. *Tree Physiology*, **26**, 689-701.

Hegarty, E. E. (1991) Leaf litter production by lianas and trees in a sub-tropical Australian rainforest. *Journal of Tropical Ecology*, **7**, 201-214.

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

van der Heijden, G. & Phillips, O. (2009) Liana infestation impacts tree growth in a lowland tropical moist forest. *Biogeosciences*, **6**, 2217-226.

van der Heijden, G.M., Schnitzer, S.A., Powers, J.S. & Phillips, O.L. (2013) Liana impacts on carbon cycling, storage and sequestration in tropical forests. *Biotropica*, **45**, 682-692.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**, 1965-1978.

Hughes, R.F., Kauffman, J.B. & Jaramillo, V.J. (1999) Biomass, carbon, and nutrient dynamics of secondary forests in a humid tropical region of Mexico. *Ecology*, **80**, 1892-1907.

Iida, Y., Kohyama, T.S., Kubo, T., Kassim, A.R., Poorter, L., Sterck, F. & Potts, M.D. (2011) Tree architecture and life-history strategies across 200 co-occurring tropical tree species. *Functional Ecology*, **25**, 1260-1268.

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

IPCC (2007) *Climate change 2007: the physical science basis*. Cambridge University Press, Cambridge, UK.

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

Keith, H., Mackey, B.G. & Lindenmayer, D.B. (2009) Re-evaluation of forest biomass carbon stocks and lessons from the world's most carbon-dense forests. *Proceedings of the National Academy of Sciences*, **106**, 11635-11640.

Larjavaara, M. & Muller-Landau, H.C. (2012) Temperature explains global variation in biomass among humid old-growth forests. *Global Ecology and Biogeography*, **21**, 998-1006.

Maass, M. & Burgos, A. (2011) Water dynamics at the ecosystem level in seasonally dry tropical forests. *Seasonally Dry Tropical Forests*, pp. 141-156. Island Press, Washington, USA.

Malhi Y. 2012.The productivity, metabolism and carbon cycle of tropical forest vegetation. *Journal of Ecology*, **100,** 65–75

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

Nepstad, D.C., Tohver, I.M., Ray, D., Moutinho, P. & Cardinot, G. (2007) Mortality of large trees and lianas following experimental drought in an amazon forest. *Ecology*, **88**, 2259–2269.

Phillips, O., Miller, J.S. & Hollowell, V.C. (2002) *Global patterns of plant diversity: Alwyn H. Gentry's forest transect data set*. Missouri Botanical Press Louis, MO.

Phillips, O. & Lewis, S. (2013) *Recent changes in tropical forest biomass and dynamics*. *Forests and Global Change*, **4**, 77-108

Phillips, O.L., Heijden, G. Van Der, Lewis, S.L., Lo, G., Lloyd, J., Malhi, Y., Monteagudo, A., Almeida, S., Da, E.A., Andelman, S., Andrade, A., Arroyo, L., Aymard, G., Baker, T.R., Costa, L., Feldpausch, T.R., Fisher, J.B., Fyllas, N.M., Freitas, M.A., Jime, E., Keeling, H., Tim, J., Gloor, E., Higuchi, N., Lovett, J.C., Meir, P., Mendoza, C., Morel, A., Nu, P., Prieto, A., Quesada, C.A., Peh, K.S., Pen, A., Schwarz, M. & Silva, J. (2010) Drought – mortality relationships for tropical forests. *New Phytologist*, **187**, 631–646.

Poorter, L., Wright, S.J., Paz, H., Ackerly, D.D., Condit, R., Ibarra-Manriques, G., Harms, K.E., Licona, J.C., Martinez-Ramos, M., Mazer, S.J., Muller-Landau, H.C., Pena-Claros, M., Webb, C.O. & Wright, I.J. (2008) Are functional traits good predictors of demographic rates? Evidence from five Neotropical forests. *Ecology*, **89**, 1908-1920.

Powers, J.S. 2014. Reciprocal interactions between lianas and soils. *Ecology of Lianas* (ed. by S.Schnitzer, F. Bongers, R. Burnham, and F. Putz), Wiley Press. USA.

Raich, J.W., Russell, A.E., Kitayama, K., Parton, W.J. & Vitousek, P.M. (2006) Temperature influences carbon accumulation in moist tropical forests. *Ecology*, **87**, 76-87.

Rosseel, Y. (2012) lavaan: An R package for structural equation modeling. *Journal of Statistical Software*, **48**, 1-36.

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

Satorra, A. & Bentler, P.M. (1994) Corrections to test statistics and standard errors in covariance structure analysis. *Latent variable analysis: applications to developmental research*, (e.d. von Eye, A., & Clifford, C.C.), pp. 399-419. Sage Publications, Inc. Thousand Oaks, CA.

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

Schnitzer, S.A. & Bongers, F. (2011) Increasing liana abundance and biomass in tropical forests: emerging patterns and putative mechanisms. *Ecology letters*, **14**, 397-406.

Shipley, B. (2002) *Cause and correlation in biology: a user's guide to path analysis, structural equations and causal inference*. Cambridge University Press.

Slik, J.W.F., Aiba, S.I., Brearley, F.Q., Cannon, C.H., Forshed, O., Kitayama, K., Nagamasu, H., Nilus, R., Payne, J., Paoli, G., Poulsen, A.D., Raes, N., Sheil, D., Sidiyasa, K., Suzuki, E. & Valkenburg, J.L.C.H. (2010) Environmental correlates of tree biomass, basal area, wood specific gravity and stem density gradients in Borneo's tropical forests. *Global Ecology and Biogeography*, **19**,50–60.

Slik, J.W.F., Paoli, G., McGuire, K., Amaral, I., Barroso, J., Bastian, M., Blanc, L., Bongers, F., Boundja, P., Clark, C., Collins, M., Dauby, G., Ding, Y., Doucet, J.-L., Eler, E., Ferreira, L., Forshed, O., Fredriksson, G., Gillet, J.-F., Harris, D., Leal, M., Laumonier, Y., Malhi, Y., Mansor, A., Martin, E. et al. (2013) Large trees drive forest aboveground biomass variation in moist lowland forests across the tropics. *Global Ecology and Biogeography*, **22**, 1261-1271.

Stegen, J.C., Swenson, N.G., Valencia, R., Enquist, B.J. & Thompson, J. (2009) Above-ground forest biomass is not consistently related to wood density in tropical forests. *Global Ecology and Biogeography*, **18**, 617–625.

Stegen, J.C., Swenson, N.G., Enquist, B.J., White, E.P., Phillips, O.L., Jørgensen, P.M., Weiser, M.D., Monteagudo Mendoza, A. & Núñez Vargas, P. (2011) Variation in above-ground forest biomass across broad climatic gradients. *Global Ecology and Biogeography*, **20**, 744-754.

The Plant List (2013). Version 1.1. Published on the Internet; http://www.theplantlist.org/ (accessed September 15, 2014).

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

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

Zanne, A., Lopez-Gonzalez, G., Coomes, D.A., Ilic, J., Jansen, S., Lewis, S.L., Miller, R.B., Swenson, N.G., Wiemann, M.C. & Chave, J. (2009) Global Wood Density Database. Dryad Identifier: http://hdl.handle.net/10255/dryad.235.

4.6 Tables and Figures

Table 4.1 Differences in climate, stand variables, liana abundance and aboveground carbon storage (AGC) among dry, moist, and wet tropical forests (per 0.1-ha plot).

	Forest type													
	Dry (*n* = 47)				Moist (*n* = 52)				Wet (*n* = 46)					
Variable	mean	SE	min	max	mean	SE	min	max	mean	SE	min	max	F	*P*-value
BA (m^2 ha^{-1})	30.5a	2.1	8.0	70.7	41.1b	2.0	17.6	79.6	38.8b	1.4	20.2	65.2	8.4	<0.001
DBH (cm ha^{-1})	25.7a	0.7	17.8	37.3	26.1a	0.5	19.5	37.0	24.7a	0.5	18.5	34.7	0.4	0.672
WD (g cm^{-3})	0.63a	0.01	0.5	0.8	0.57b	0.01	0.4	0.7	0.58b	0.01	0.4	0.6	15.6	<0.001
AGC (Mg ha^{-1})	106.0a	7.8	22.1	242.8	230.0b	14.4	201.1	258.9	145.4c	6.0	133.3	157.4	41.6	<0.001
No. lianas (ha^{-1})	771.5a	57.6	50	1590	506.5b	29.5	110	990	594.3b	38.8	90	1170	6.6	0.002
DI	1.6a	0.09	0.7	3.7	0.77b	0.04	0.5	2.1	0.54c	0.02	0.2	0.9	79.2	<0.001
MAT (°C)	24.3a	0.43	14.5	27.6	23.2a	0.50	13.2	28.0	23.6a	0.61	12.0	28.0	1.2	0.294

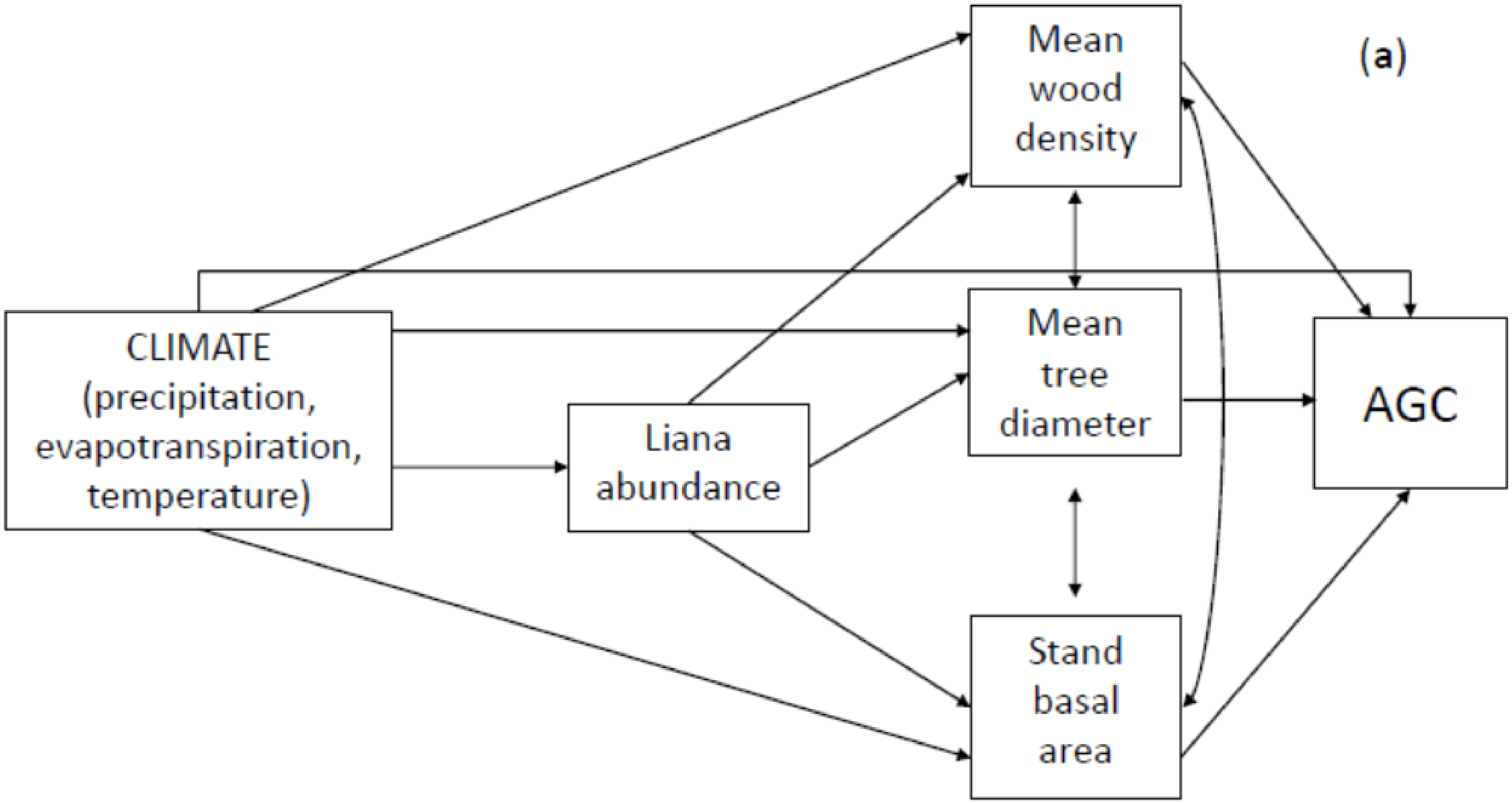
F and *P*-values correspond to ANOVA analyses, d.f. = 2. Means followed by different letters are significantly different at $P < 0.05$ (Tukey test). BA, stand basal area, WD, mean wood density; DBH, tree diameter at breast height (1.3 m from the ground), MAT, mean annual temperature. DI, dryness index (unitless) is the mean value of the ratio of potential evapotranspiration to mean annual rainfall.

Table 4.2 Multigroup comparison of path coefficients among dry, moist, and wet tropical forests.

Free parameter whose between-group equality constraint was released	MLχ^2	Δ ML χ^2	P-value
None	72.9		
Path from Basal area to AGC	70.8	2.1	0.349
Path from tree diameter to AGC	72.6	0.3	0.860
Path from Wood density to AGC	67.9	5.0	0.082
Path from Liana abundance to Basal area	59.8	13.1	**0.001**
Path from Liana abundance to tree diameter	60.4	12.5	**0.002**
Path from Liana abundance to Wood density	70.9	2.0	0.367
Path from Dryness index to AGC	56.9	15.9	**<0.001**
Path from Dryness index to Basal area	70.1	2.8	0.250
Path from Dryness index to Wood density	69.0	3.9	0.142
Path from Dryness index to tree diameter	71.7	1.2	0.548
Path from Dryness index to liana abundance	69.3	3.6	0.165
Path from MAT to AGC	70.2	2.7	0.260
Path from MAT to Basal area	71.4	1.5	0.472
Path from MAT to Wood density	58.8	14.1	**<0.001**
Path from MAT to tree diameter	71.5	1.4	0.496
Path from MAT to liana abundance	70.4	2.5	0.286
Covariance Basal area and tree diameter	67.3	5.6	0.060
Covariance Wood density and tree diameter	68.8	4.1	0.128
Error variance Basal area	71.9	1.0	0.606
Error variance tree diameter	72.5	0.4	0.818
Error variance Wood density	59.5	13.4	**0.001**
Error variance liana abundance	71.6	1.3	0.522
Error variance AGC	68.3	4.6	0.100

The first row shows the maximum likelihood χ^2 estimates (MLχ^2) after constraining all free parameters to the same value. Below is the effect on MLχ^2 by relaxing one constraint at a time.

The difference between the constrained model and the rest is given as $\Delta ML\chi^2$, and the *P*-value indicates the probability that the release of that parameter improves the model significantly. MAT, mean annual temperature. Bonferroni-corrected *P*-value threshold, 0.05/23=0.0021.


(a)
Mean wood density
CLIMATE (precipitation, evapotranspiration, temperature)
Liana abundance
Mean tree diameter
AGC
Stand basal area

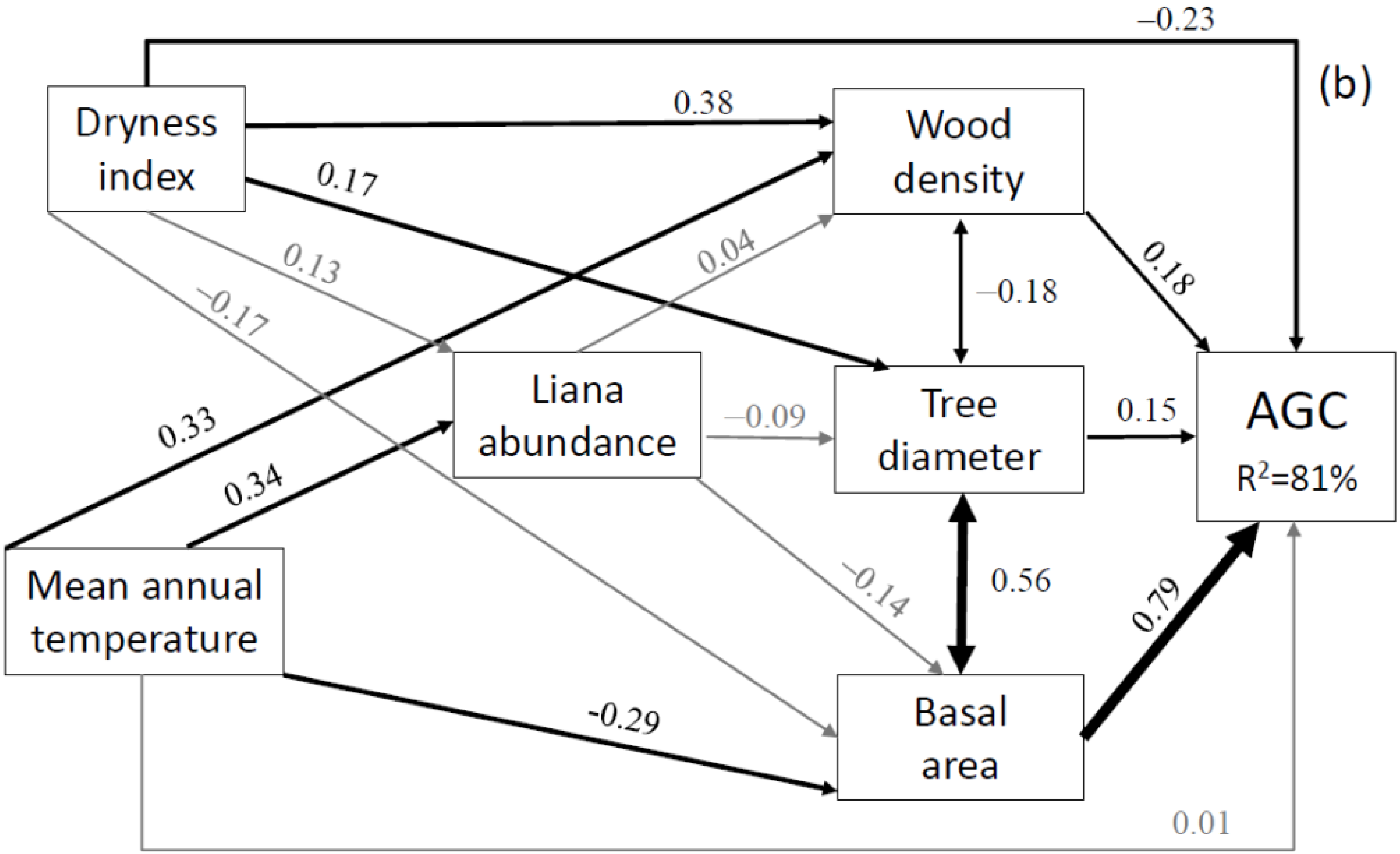
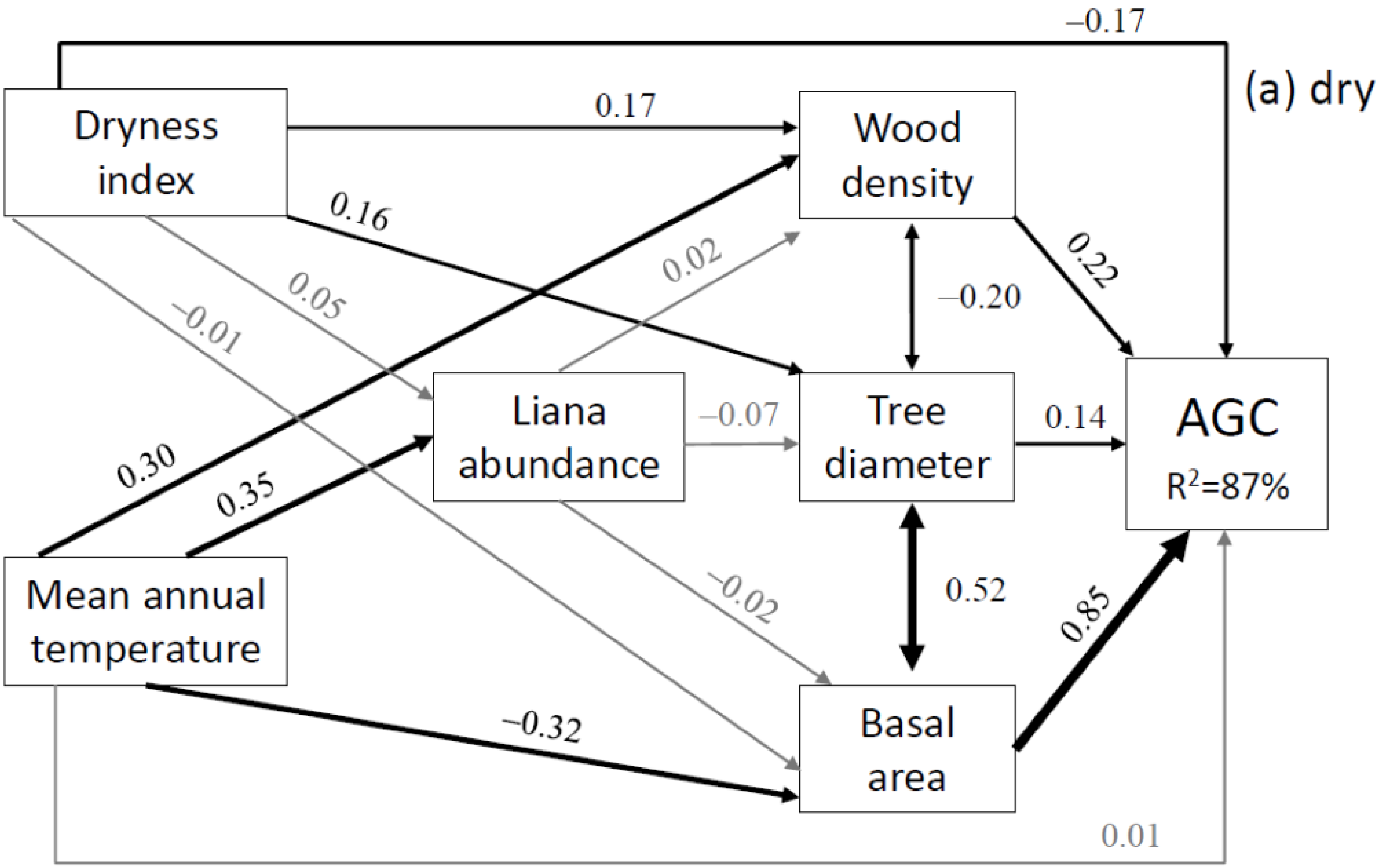
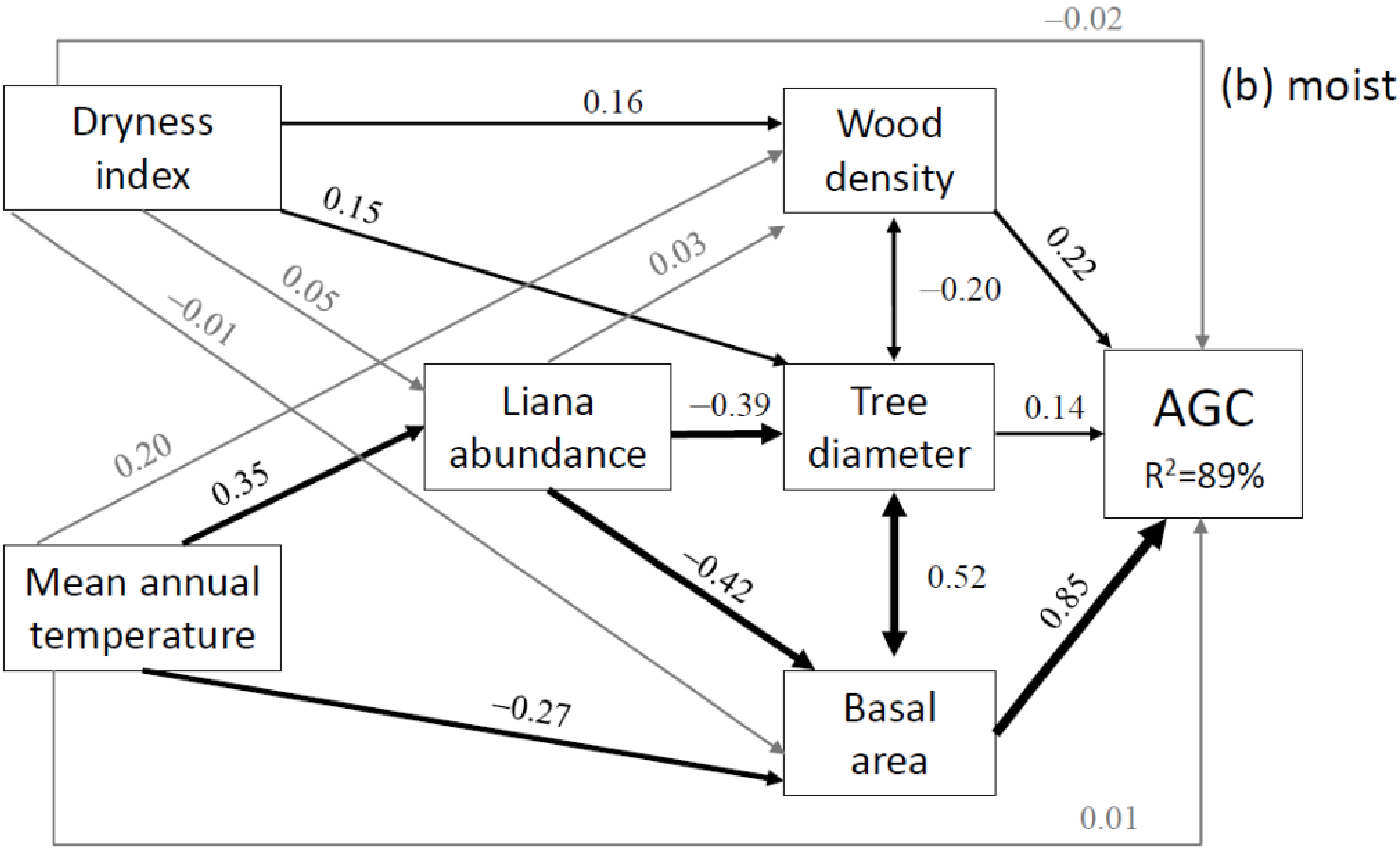

(b)
Dryness index
Wood density
Liana abundance
Tree diameter
AGC
R²=81%
Mean annual temperature
Basal area
–0.23
0.38
0.17
0.13
–0.17
0.04
–0.18
0.18
0.33
0.34
–0.09
0.15
–0.14
0.56
0.79
-0.29
0.01

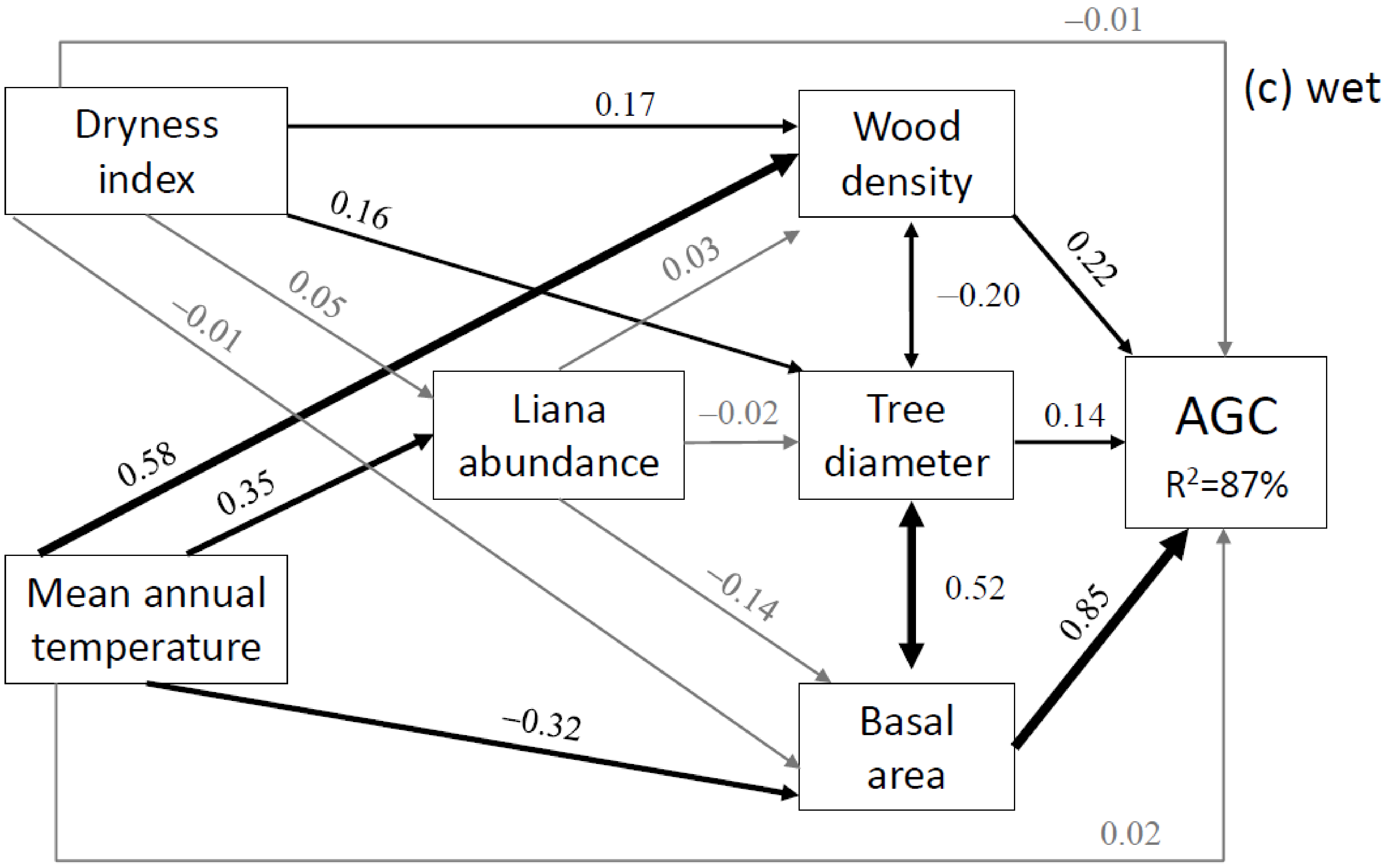
Figure 4.1 (a) An *a priori* model of the causal relationships among climate, stand variables, lianas and aboveground carbon storage (AGC) in tropical forests. Stand variables include mean wood density, tree diameter at breast height, and stand basal area. The model hypothesizes that stand variables increase AGC, while abundance of lianas decrease AGC indirectly through negative effects on stand variables. Single-headed arrows represent causal relationships; double-headed arrows are free correlations. (b) Fitting of model (a) to the data for all forest types. Model statistics indicate a good fit ($\chi^2 = 3.1$, d.f. = 2, $P = 0.22$) with CFI (comparative fit index) = 0.99, and RMSEA (root mean square error of approximation) = 0.04. Solid black arrows indicate significant effects ($P < 0.05$), while gray arrows denote non-significant effects. The path coefficients are standardized regression weights (black: significant; gray: non-significant). The arrow thickness is proportional to the path coefficient. The amount of variance explained (R^2) for AGC in the model is shown as percentage.

Figure 4.2 Spatial distribution of the study sites. Due to the size of the dots they can encompass more than one location. The total number of sites is: dry 47, moist 52, and wet 46. Forests were classified according to Chave *et al*. (2005).


(a) dry
Dryness index
Wood density
Liana abundance
Tree diameter
Mean annual temperature
Basal area
AGC
R^2=87%
–0.17
0.17
0.16
0.05
–0.01
0.02
–0.20
0.22
0.30
0.35
–0.07
0.14
–0.02
0.52
0.85
–0.32
0.01



(b) moist
Dryness index
Wood density
Liana abundance
Tree diameter
AGC
R²=89%
Mean annual temperature
Basal area
–0.02
0.16
0.15
0.05
–0.01
0.03
0.22
–0.20
–0.39
0.14
0.20
0.35
–0.42
0.52
0.85
–0.27
0.01



(c) wet
–0.01
Dryness index
0.17
Wood density
0.16
0.05
–0.01
0.03
0.22
–0.20
Liana abundance
–0.02
Tree diameter
0.14
AGC
R²=87%
0.58
0.35
Mean annual temperature
–0.14
0.52
0.85
Basal area
–0.32
0.02

Figure 4.3 Fitted multigroup model showing the influence of climate, stand variables, and liana abundance on aboveground carbon storage (AGC) in (a) dry (*n* = 47), (b) moist (*n* = 52), and (c) wet (*n* = 46) tropical forests. Model fit to the data was good ($\chi^2 = 41.7$, d.f. = 43, $P = 0.53$). The model's robust indices were CFI = 1.0, and RMSEA < 0.001. Single-headed arrows indicate causal relationships, while double-headed arrows represent free correlations. Black arrows indicate significant paths ($P < 0.05$), while gray arrows are non-significant. Printed coefficients are standardized regression weights (black: significant; gray: non-significant). Arrow thickness corresponds to standardized path strength. The amount of explained variance (R^2) in each forest type is shown as percentage.

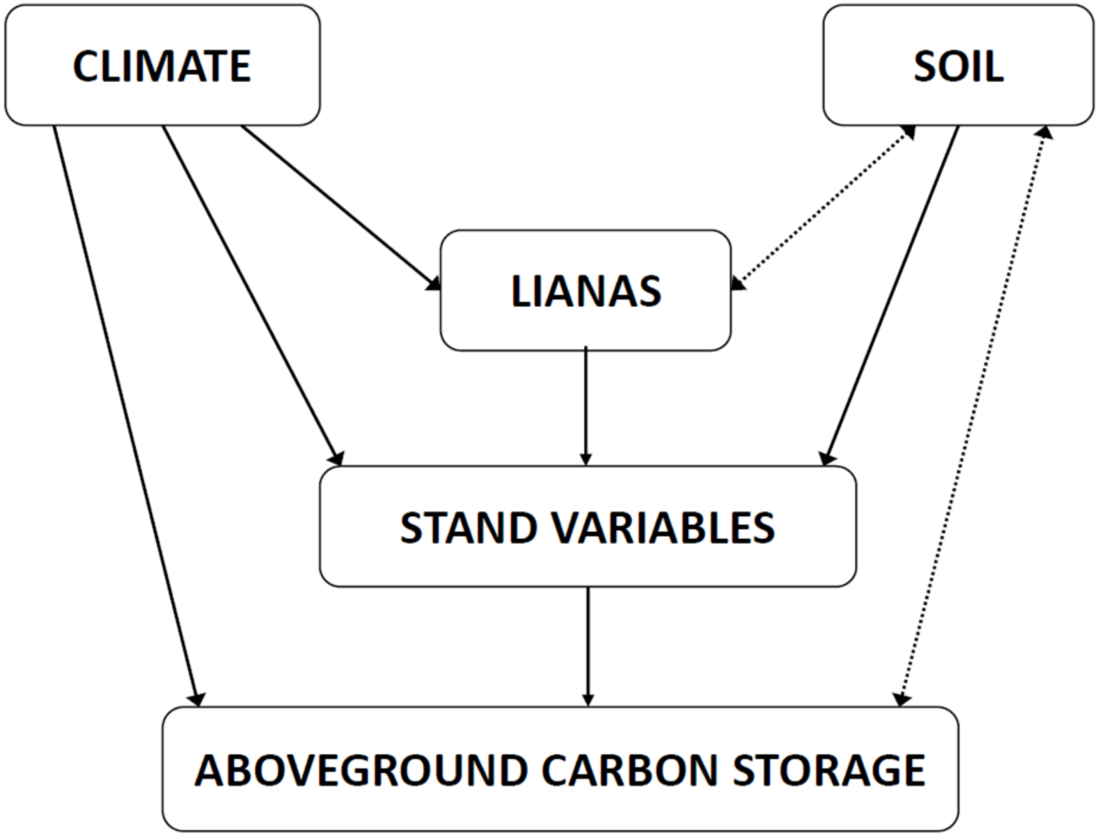


Figure 4.4 A general framework to evaluate aboveground carbon storage (AGC) variation in tropical forests. Single arrows represent causal paths, while dotted lines indicate pathways where more research is needed to establish causality, as current evidence is mixed. The effects of lianas on AGC are assumed to be negative, while stand variables effects are positive based on current evidence.

4.7 Supplementary Material Chapter 4

Appendix 4. 1. Climate, stand variables, liana abundance and aboveground carbon storage for the 145 study locations in tropical forests. Stand variable and the number of lianas are shown for each location. MAP = mean annual precipitation, MAT = mean annual temperature, PET = potential evapotranspiration, DI=Dryness index (PET/MAP ratio). BA=stand basal area, DBH=mean diameter, WD=mean wood density

					Climate data					Stand variables			
Site No.	Country	Site name	Latitud	Longitud	MAT (°C)	MAP (mm)	PET (mm)	DI	No. Lianas (ha)	BA (m^2/ha)	dbh (cm/ha)	WD (g/cm^3)	AGC (Mg/ha)
1	Australia	Davies River State Forest	-17.08	145.57	19.8	1739	1443	0.83	360	51.94	25.70	0.64	292.18
2	Bolivia	Alto Madidi	-13.58	-68.77	25.1	2293	1661	0.72	730	38.75	23.33	0.55	194.81
3	Bolivia	Alto Madidi ridge top	-13.58	-68.77	25.1	2293	1661	0.72	820	36.60	23.65	0.65	189.13
4	Bolivia	Chaquimayo	-14.57	-68.47	21.7	1627	1425	0.88	1210	37.98	28.42	0.72	171.68
5	Bolivia	Curuyuqui	-18.77	-62.23	24.8	584	1828	3.13	660	24.54	23.24	0.69	73.42
6	Bolivia	Curuyuqui Riverine	-18.75	-62.30	24.8	585	1826	3.12	1170	50.88	35.29	0.74	228.29
7	Bolivia	El Encanto	-14.63	-60.70	23.5	1451	1805	1.24	1030	33.66	25.68	0.64	111.43
8	Bolivia	Incahuara	-15.92	-67.58	21.0	1404	1570	1.12	280	21.41	18.40	0.59	63.67
9	Bolivia	Nuevo Mundo	-10.65	-66.77	26.2	1781	1765	0.99	620	35.68	26.37	0.57	126.62
10	Bolivia	Perserverancia	-14.63	-62.62	24.9	1295	1820	1.41	1590	21.71	23.42	0.51	60.80
11	Bolivia	Quiapaca	-18.33	-59.50	25.0	1111	1824	1.64	1200	24.05	25.11	0.83	115.20
12	Bolivia	Río Negro	-9.83	-65.67	26.4	1609	1758	1.09	660	22.80	25.07	0.57	77.18
13	Bolivia	Sacramento	-16.30	-67.80	14.5	843	1460	1.73	700	23.14	19.98	0.52	59.07
14	Bolivia	Santa Cruz	-17.77	-63.07	24.4	1094	1657	1.51	750	34.01	31.16	0.65	119.18
15	Bolivia	Yanaígua	-19.70	-62.10	24.6	494	1824	3.69	130	28.63	33.85	0.69	85.79
16	Brazil	Alter de Chao	-2.50	-54.97	26.1	1977	1652	0.84	50	12.84	18.40	0.65	40.16
17	Brazil	Belém Mocambo	-1.50	-47.98	26.8	2380	1688	0.71	480	37.56	25.90	0.66	268.46
18	Brazil	Boraceia	-23.38	-46.00	18.6	1368	1290	0.94	330	48.06	23.24	0.59	156.75
19	Brazil	Camorin-Jacarepaguá	-22.93	-43.37	23.3	1205	1375	1.14	560	43.86	24.48	0.64	160.01
20	Brazil	Ducke Reserve	-3.00	-59.97	27.1	2179	1603	0.74	390	42.05	23.53	0.65	262.11

21	Brazil	Linhares	-19.30	-40.07	24.1	1207	1501	1.24	870	45.80	25.38	0.66	181.45
22	Colombia	Alto de Cuevas	6.67	-76.50	24.0	3675	1648	0.45	530	43.09	28.11	0.43	135.68
23	Colombia	Alto de Mirador	10.92	-73.83	12.0	2445	1127	0.46	140	43.89	23.75	0.46	143.85
24	Colombia	Alto de Sapa	7.17	-75.90	14.5	2877	1262	0.44	620	50.91	34.76	0.52	222.64
25	Colombia	Anchicayá	3.75	-76.83	22.4	1486	1583	1.07	390	39.91	23.30	0.53	223.33
26	Colombia	Antado	7.25	-75.92	15.5	2798	1297	0.46	730	41.44	22.90	0.53	145.26
27	Colombia	Araracuara	-0.42	-72.32	26.7	2915	1619	0.56	860	42.51	24.26	0.65	180.83
28	Colombia	Bajo Calima	3.92	-77.00	26.2	6987	1484	0.21	370	26.16	18.56	0.58	90.87
29	Colombia	Bosque de la Cueva	11.08	-73.47	23.2	1828	1620	0.89	580	38.05	28.01	0.47	172.57
30	Colombia	Carpanta	4.58	-73.67	13.2	2184	1183	0.54	350	35.20	24.29	0.52	171.66
31	Colombia	Carpanta Siete Cuerales	4.58	-73.67	13.2	2184	1183	0.54	320	30.74	23.50	0.52	135.04
32	Colombia	Cedral	4.75	-75.55	14.3	2099	1170	0.56	390	43.73	22.99	0.51	151.59
33	Colombia	Cerro Kennedy	11.08	-74.02	19.5	2661	1432	0.54	130	45.30	26.12	0.50	135.83
34	Colombia	Colosó	9.40	-75.58	27.6	1139	1697	1.49	970	27.55	25.57	0.61	84.97
35	Colombia	Finca Mehrenberg	2.27	-76.20	14.4	1899	1296	0.68	440	46.27	27.59	0.50	162.51
36	Colombia	Galerazamba	10.77	-75.24	27.6	884	1492	1.69	1030	14.66	26.38	0.52	43.13
37	Colombia	La Planada	1.13	-77.97	17.6	1599	1393	0.87	90	36.51	23.40	0.55	131.23
38	Colombia	La Raya	8.33	-74.92	28.0	3103	1778	0.57	730	40.47	23.11	0.58	225.90
39	Colombia	Loma de Los Colorados	9.97	-75.17	27.3	1547	1816	1.17	1340	24.79	24.47	0.59	80.73
40	Colombia	Lomas de Santo Tomás	4.92	-74.83	26.5	1592	1788	1.12	830	24.05	22.74	0.63	87.86
41	Colombia	Manaure	10.37	-73.13	26.9	1300	1851	1.42	750	29.64	26.56	0.61	160.44
42	Colombia	Mariquita	5.25	-74.83	26.5	2104	1707	0.81	240	47.84	34.90	0.55	347.76
43	Colombia	Murrí	6.58	-76.83	27.3	5175	1709	0.33	350	38.79	24.75	0.53	121.22
44	Colombia	Providencia Island	13.35	-81.37	26.1	1584	1462	0.92	550	20.72	19.90	0.58	84.94
45	Colombia	Río Manso	7.50	-76.08	24.5	2736	1655	0.60	770	36.30	23.96	0.63	229.96
46	Colombia	Sabana Rubia	10.50	-72.92	14.5	2231	1264	0.57	190	74.25	33.57	0.57	441.72
47	Colombia	Tayrona National Park	11.33	-74.03	27.4	1082	1719	1.59	950	28.41	25.48	0.68	105.79
48	Colombia	Tutunendo	5.77	-76.58	26.5	7426	1713	0.23	570	27.44	22.09	0.55	96.44
49	Colombia	Ucumarí	4.00	-75.50	17.2	2020	1292	0.64	560	44.14	24.23	0.54	147.48
50	Costa Rica	Guanacaste gallery forest	10.50	-85.17	26.6	1578	1739	1.10	240	31.72	36.46	0.65	137.26

51	Costa Rica	Guanacaste upland	10.53	-85.30	26.2	1601	1745	1.09	970	12.14	25.59	0.57	47.34
52	Costa Rica	La Selva	10.43	-84.02	26.0	3990	1587	0.40	510	42.72	26.86	0.49	164.42
53	Costa Rica	Magsaysay	10.40	-84.05	25.5	4127	1572	0.38	490	34.41	25.12	0.58	127.24
54	Costa Rica	Osa Sirena	8.46	-83.38	25.5	3768	1736	0.46	520	59.24	27.80	0.51	319.02
55	Costa Rica	Rancho Quemado	8.70	-83.55	24.8	3423	1749	0.51	290	57.77	29.49	0.59	351.75
56	Cuba	Sierra Rosario	22.83	-83.00	23.3	1617	1475	0.91	330	35.42	27.79	0.57	185.90
57	Dominican Republic	Los Haitaises National Park	19.08	-69.50	25.7	2061	1588	0.77	950	31.17	32.82	0.51	115.05
58	Ecuador	Capeira	-2.00	-79.97	25.5	731	1676	2.29	570	51.00	27.30	0.57	159.33
59	Ecuador	Centinela	-0.58	-79.33	24.0	2683	1527	0.57	590	38.11	21.11	0.54	191.05
60	Ecuador	Cuangos	-3.48	-78.23	20.7	3102	1566	0.50	440	40.97	24.22	0.53	148.70
61	Ecuador	Esmeraldas Tropical Garden	0.90	-79.62	25.6	939	1391	1.48	840	45.16	27.17	0.62	174.08
62	Ecuador	Fila de Bilsa	0.62	-79.85	24.9	1666	1324	0.79	350	36.11	25.37	0.54	209.14
63	Ecuador	Huamaní	-0.67	-77.67	18.8	4186	1510	0.36	610	45.11	26.38	0.52	160.53
64	Ecuador	Jatun Sacha	-1.07	-77.60	23.9	3663	1624	0.44	830	37.43	23.34	0.55	134.10
65	Ecuador	Jauneche	-1.10	-79.63	25.5	1833	1608	0.88	1250	22.15	22.53	0.56	64.29
66	Ecuador	Maquipucuna	0.12	-78.62	18.1	1745	1452	0.83	330	54.00	28.09	0.51	286.38
67	Ecuador	Miazi	-4.30	-78.67	21.8	2307	1640	0.71	510	43.79	23.28	0.55	148.78
68	Ecuador	Perro Muerto	-1.60	-80.70	21.6	613	1374	2.24	480	27.14	31.77	0.64	101.29
69	Ecuador	Río Nangaritza	-4.30	-78.67	21.8	2307	1640	0.71	680	38.40	24.96	0.57	220.94
70	Ecuador	Río Palenque1	-0.57	-79.33	24.3	2681	1541	0.57	410	20.63	28.06	0.51	116.21
71	Ecuador	Río Palenque2	-0.57	-79.33	24.3	2681	1541	0.57	350	34.03	28.15	0.51	220.82
72	Ecuador	San Sebastián	-1.60	-80.70	21.6	613	1374	2.24	680	36.12	25.92	0.51	106.86
73	Gabon	Makokou1	0.57	12.87	24.0	1646	1553	0.94	990	31.71	28.25	0.63	188.60
74	Gabon	Makokou2	0.57	12.87	24.0	1646	1553	0.94	770	31.76	29.09	0.63	206.01
75	Guyana	Berbice River	5.50	-58.08	26.7	2341	1615	0.69	460	53.86	31.96	0.66	471.76
76	India	Avalanche	11.30	76.58	14.5	2095	1188	0.57	170	72.98	30.06	0.57	402.61
77	India	Nadugani	11.45	76.38	23.8	2936	1474	0.50	380	35.93	25.62	0.55	174.65
78	Jamaica	Round Hill (Top)	17.90	-77.50	21.9	1872	1275	0.68	80	22.17	17.79	0.64	76.45
79	Madagascar	Ankarafantsika	-16.32	46.82	26.3	1491	1869	1.25	1260	31.18	27.40	0.63	122.58

80	Madagascar	Nosy Mangabe	-15.50	49.77	23.4	3000	1423	0.47	1170	65.20	22.80	0.63	252.74
81	Madagascar	Perinet Forestry Station	-18.92	48.42	19.3	1839	1454	0.79	1120	40.95	21.27	0.58	133.32
82	Malaysia	Bako National Park	1.56	110.38	27.1	4053	1621	0.40	440	34.68	24.97	0.57	125.54
83	Malaysia	Genting Highlands	3.97	101.63	24.8	2826	1702	0.60	690	47.25	27.10	0.59	183.61
84	Malaysia	Pasoh 30	3.00	102.33	25.8	2012	1661	0.83	1140	22.37	23.00	0.60	83.15
85	Malaysia	Pasoh 40	3.00	102.33	25.8	2012	1661	0.83	1080	35.65	23.78	0.62	142.44
86	Malaysia	Semengoh Forest Preserve	1.60	110.00	26.7	4026	1589	0.39	250	39.05	21.60	0.63	147.72
87	Mauritius	Brise Fer	-20.38	57.43	21.0	1839	1220	0.66	160	65.56	26.35	0.67	473.84
88	Mexico	Bosque de Guadalupe	19.50	-96.95	18.5	1650	1338	0.81	550	67.96	37.31	0.57	226.28
89	Mexico	Chamela 4	19.50	-105.05	26.2	782	1824	2.33	690	12.49	21.53	0.69	79.24
90	Mexico	Chamela Arroyos	19.50	-105.05	26.2	782	1824	2.33	1410	46.49	26.73	0.69	167.61
91	Mexico	Chamela Upland 1	19.50	-105.05	26.2	782	1824	2.33	390	16.60	20.21	0.73	68.50
92	Mexico	Chamela Upland 2	19.50	-105.05	26.2	782	1824	2.33	530	9.60	18.37	0.73	34.92
93	Mexico	Los Tuxtlas	18.58	-95.13	21.6	2693	1366	0.51	510	34.52	29.14	0.60	185.47
94	Mexico	Quince Ocotes	19.73	-104.25	22.9	868	1813	2.09	90	70.69	36.36	0.55	242.81
95	New Caledonia	Rivière de Pirogues	-22.17	166.83	21.9	2059	1227	0.60	460	33.27	21.34	0.56	161.90
96	New Guinea	Baitete	-5.17	145.80	26.7	3423	1491	0.44	680	36.09	25.30	0.53	114.05
97	New Guinea	Varirata National Park	-9.50	147.50	23.9	2807	1578	0.56	550	35.74	21.26	0.55	117.59
98	Nicaragua	Cerro El Picacho	13.00	-85.92	18.8	1710	1381	0.81	110	79.62	37.07	0.55	485.99
99	Nicaragua	Cerro Olumo	12.30	-85.40	23.0	1579	1518	0.96	360	45.23	28.02	0.54	263.46
100	Nigeria	Omo Forest Reserve	7.00	5.00	26.1	1592	1613	1.01	730	34.70	26.83	0.61	247.98
101	Panama	Curundu	8.98	-79.55	27.1	1830	1535	0.84	580	19.69	24.78	0.50	83.60
102	Panama	Madden Forest	9.10	-79.60	26.2	2156	1470	0.68	770	28.79	26.58	0.49	102.97
103	Panama	Pipeline Road	9.17	-79.75	26.0	2553	1413	0.55	710	20.52	25.41	0.51	90.86
104	Peru	Allpahuayo	-3.95	-73.42	26.4	2764	1692	0.61	850	55.20	24.25	0.60	238.73
105	Peru	Bosque von Humboldt	-8.83	-75.00	26.1	2574	1837	0.71	730	22.37	20.83	0.58	83.19
106	Peru	Cabeza de mono	-10.33	-75.30	23.4	2536	1728	0.68	490	17.64	20.33	0.62	86.94
107	Peru	Cerro Aypate	-4.58	-79.53	19.5	982	1660	1.69	380	50.23	28.83	0.54	160.47
108	Peru	Cerros de Amotape	-4.15	-80.62	20.0	784	1613	2.06	340	27.03	25.41	0.59	78.67

109	Peru	Chirinos	-5.42	-78.88	22.5	1032	1678	1.63	400	67.80	29.55	0.53	376.16
110	Peru	Cocha Cashu	-11.85	-71.32	25.0	2489	1739	0.70	750	36.00	23.92	0.56	202.30
111	Peru	Constancia	-4.25	-72.75	26.0	2671	1677	0.63	520	33.76	21.84	0.58	130.41
112	Peru	Cuterva National Park	-6.17	-78.67	19.9	730	1594	2.18	530	56.82	29.42	0.54	296.18
113	Peru	Cuzco Amazonico	-12.58	-69.15	25.5	2195	1752	0.80	570	45.86	26.16	0.51	231.79
114	Peru	Indiana	-3.52	-73.07	26.4	2808	1711	0.61	930	49.62	24.78	0.58	185.08
115	Peru	Jenaro Herrera	-4.92	-73.75	26.9	2601	1760	0.68	640	31.70	21.95	0.65	133.89
116	Peru	La Genoa	-11.08	-75.42	17.6	1383	1623	1.17	510	30.28	24.64	0.56	148.93
117	Peru	Mishana Old Floodplain	-3.78	-73.50	26.3	2832	1707	0.60	790	25.41	20.80	0.57	95.67
118	Peru	Mishana Tahuampa	-3.78	-73.50	26.3	2832	1707	0.60	970	29.57	24.41	0.65	135.20
119	Peru	Mishana White Sand	-3.78	-73.50	26.3	2832	1707	0.60	550	20.24	21.25	0.61	79.94
120	Peru	Pampas del Heath	-12.83	-68.83	25.5	2166	1730	0.80	710	29.48	22.15	0.57	166.51
121	Peru	Río Candamo	-13.50	-69.83	24.4	3669	1600	0.44	500	43.48	23.51	0.58	144.07
122	Peru	Río Távara	-13.35	-69.67	24.7	3363	1630	0.48	820	40.38	27.25	0.58	164.82
123	Peru	Shiringamazú	-10.33	-75.17	23.6	2661	1738	0.65	800	23.83	20.37	0.61	127.67
124	Peru	Tambopata Alluvial	-12.83	-69.28	25.4	2498	1723	0.69	820	35.38	23.84	0.50	141.38
125	Peru	Tambopata Lateritic	-12.78	-69.28	25.4	2456	1730	0.70	800	38.48	27.77	0.52	261.29
126	Peru	Tambopata Swamp Trail	-12.78	-69.28	25.4	2456	1730	0.70	740	43.24	26.44	0.56	230.68
127	Peru	Tambopata Upland Sandy	-12.82	-69.72	25.0	3097	1682	0.54	790	42.01	22.01	0.56	171.12
128	Peru	Tarapoto	-6.58	-76.42	25.4	1083	1916	1.77	820	16.60	18.78	0.67	58.57
129	Peru	Venceremos	-5.75	-77.67	18.4	1117	1435	1.28	330	49.80	23.38	0.54	241.06
130	Peru	Yanamono 1	-3.43	-72.85	26.3	2805	1689	0.60	580	38.34	26.08	0.56	145.65
131	Peru	Yanamono 2	-3.43	-72.85	26.3	2805	1689	0.60	560	38.71	25.89	0.56	145.89
132	Peru	Yanamono Tahuampo	-3.47	-72.83	26.4	2814	1688	0.60	640	62.53	29.55	0.55	256.03
133	Philippines	Palanan	17.13	122.52	26.7	2664	1560	0.59	140	74.30	26.19	0.56	362.54
134	Puerto Rico	Luquillo	18.18	-65.83	24.1	2433	1525	0.63	110	41.26	30.13	0.55	161.34
135	Puerto Rico	Mogotes de Nevárez	18.42	-66.25	25.6	1796	1521	0.85	300	30.73	27.33	0.64	137.48
136	Taiwan	Kenting National Park	22.00	120.75	24.8	2273	1298	0.57	690	35.31	24.70	0.56	165.50
137	Taiwan	Nanjen Shan Ecological Area	22.00	120.83	24.4	2522	1288	0.51	530	28.90	19.58	0.57	125.64

138	Tanzania	Pande Forest Reserve	-6.67	39.08	25.8	981	1647	1.68	1120	8.07	22.44	0.75	64.21
139	Tanzania	Pugu Forest Reserve	-6.83	39.08	25.0	1025	1600	1.56	1570	27.15	28.54	0.66	96.28
140	Thailand	Khao Yai National Park	14.33	101.83	25.2	1370	1669	1.22	1170	42.93	28.17	0.58	132.95
141	Thailand	Sakaerat 1	14.50	102.00	26.5	1386	1734	1.25	520	32.10	25.20	0.64	116.18
142	Venezuela	Blohm Ranch	8.57	-67.58	27.4	1378	1756	1.27	760	20.69	27.31	0.54	65.17
143	Venezuela	Boca de Uchire	10.09	-65.45	27.0	757	1734	2.29	750	8.55	21.88	0.61	22.16
144	Venezuela	Cerro de la Neblina1	0.83	-66.18	26.7	3125	1739	0.56	300	21.39	22.90	0.67	93.40
145	Venezuela	Cerro de la Neblina2	0.83	-66.18	26.7	3125	1739	0.56	260	32.19	27.47	0.68	159.67

Appendix 4.2. Standardized path coefficients in a fitted multigroup structural equation model depicting the effects climate, stand variables and liana abundance on aboveground carbon storage (AGC). The proportion of variance explained (R^2) by each multiple regression model is shown for each dependent variable in each forest type

Dependent variable	Independent variable	Dry forest (*n* = 47)			Moist forest (*n* = 52)			Wet forest (*n* = 46)		
		β	*P*-value	R^2	β	*P*-value	R^2	β	*P*-value	R^2
AGC (Mg C ha^{-1})	Dryness index	−0.17	< 0.01	0.87	−0.02	0.76	0.89	−0.01	0.92	0.87
	MAT	0.01	0.70		0.01	0.70		0.02	0.70	
	Basal area	0.85	< 0.01		0.85	< 0.01		0.85	< 0.01	
	Mean DBH	0.14	< 0.01		0.14	< 0.01		0.14	< 0.01	
	Wood density	0.22	< 0.01		0.22	< 0.01		0.22	< 0.01	
Wood density (g cm^{-3})	Dryness index	0.17	0.02	0.13	0.16	0.01	0.06	0.17	0.01	0.38
	MAT	0.30	0.02		0.20	0.13		0.58	< 0.01	
	Liana abundance	0.02	0.74		0.03	0.74		0.03	0.74	
Mean dbh (cm ha^{-1})	Dryness index	0.16	0.04	0.03	0.15	0.04	0.18	0.16	0.04	0.03
	Liana abundance	−0.07	0.62		−0.39	< 0.01		−0.02	0.87	
Basal área (m^2 ha^{-1})	MAT	−0.32	< 0.01	0.09	−0.27	< 0.01	0.31	−0.32	< 0.01	0.08
	Dryness index	−0.01	0.95		−0.01	0.95		−0.01	0.96	
	Liana abundance	−0.02	0.88		−0.42	< 0.01		0.14	0.34	
Liana abundance	Dryness index	0.05	0.50	0.13	0.05	0.50	0.13	0.05	0.50	0.13
(No.ind ha^{-1})	MAT	0.35	< 0.01		0.35	< 0.01		0.35	< 0.01	

Dryness index (unitless) is the mean value of the ratio of potential evapotranspiration to mean annual rainfall. MAT, mean annual temperature (°C).

Appendix 4.3. Direct, indirect and total effects of dryness index, mean annual temperature (MAT), and liana abundance on aboveground carbon storage (AGC) in dry, moist and wet forest types based on standardized values of statistically significant paths ($P < 0.05$). Only significant paths originating with independent variables and terminating with AGC are included, and effects due to free correlations are excluded.

Independent variable	Effect	Dry	Moist	Wet
Dryness index (DI)	Direct	DI, AGC (–0.17)	–	–
	Indirect	DI, WD, AGC (0.04)	DI, WD, AGC (0.04)	DI, WD, AGC (0.04)
		DI, DBH, AGC (0.02)	DI, DBH, AGC (0.02)	DI, DBH, AGC (0.02)
	Total	–0.11	0.06	0.06
MAT (°C)	Direct	–	–	–
	Indirect	MAT, WD (0.06)	MAT, lianas, DBH, AGC (–0.02)	MAT, WD, AGC (0.13)
		MAT, BA (–0.25)	MAT, lianas, BA, AGC (–0.13)	MAT, BA, AGC (–0.27)
			MAT, BA, AGC (–0.23)	
	Total	–0.28	–0.38	–0.40
Lianas (No.ind ha^{-1})	Indirect	–	–	–
		–	Lianas, DBH, AGC (–0.05)	–
		–	Lianas, BA, AGC (–0.36)	–
	Total	–	–0.41	

BA, basal area, DBH, diameter at breast height, WD, wood density.

5. A multi-site analysis of the impact of tree diversity on carbon storage in secondary tropical dry forests[5]

5.1 Introduction

Human activities have modified more than 40% of natural ecosystems for agricultural and urban uses (Chazdon, 2014). Forest ecosystems, for instance, have been drastically converted by half of their historical extent, with a high transformation rate up to 13 million hectares per year (Laurance, 2010). Resulting habitat loss and transformation have raised concern due to the potential consequences of biodiversity loss for ecosystem processes and the provision of ecosystem services (Hooper *et al.*, 2005; Naeem *et al.*, 2009).

Ecosystem processes refers to stocks of energy and materials, as well as the complex interactions and flow of energy and materials among biotic and abiotic elements of ecosystems, including processes such as primary production, nutrient cycling, decomposition (Díaz and Cabido 2001). Ecosystem services are those processes that benefit human wellbeing either directly or indirectly, which include food, timber, and climate regulation, among others (MEA, 2005).

Compelling evidence now shows that species loss affects ecosystem processes and services that are useful to humans (Naeem *et al.*, 2009; Cardinale *et al.*, 2012). This evidence suggests increases in biomass, productivity and nutrient retention and other ecosystem processes with higher species richness (Hooper *et al.*, 2005; Díaz *et al.*, 2007, Paquette & Messier, 2011). A positive relationship between species richness and ecosystem processes, however, is neither simple nor universal (Díaz & Cabido, 2001). Some studies have found that this relationship is variable through time and space (Rusch & Oesterheld, 1997), negative (Hooper & Vitousek, 1997), or nonexistent (Lohbeck *et al.*, 2015). More recent studies, however, have found that functional diversity rather than species number *per se* is a stronger predictor of ecosystem processes such as biomass and primary productivity (Rusch & Oesterheld, 1997; Grime, 1998, Díaz & Cabido, 2001). This has raised the question whether species richness or functional diversity are more important to ecosystem processes. Functional diversity is the kind, range, and

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relative abundance of functional traits in a given biological community (Díaz & Cabido 2001, Díaz *et al*., 2007).

Much controversy still remains over which diversity component matters to ecosystem processes (Cardinale *et al*., 2012). Increases in ecosystem processes with increasing diversity (species richness or functional diversity) may originate from two main mechanisms: the niche complementarity effects and the mass-ratio hypotheses (Hooper *et al*., 2005). The first one states that a community with higher number of species has a greater variety of organisms and functional traits than a community with less species richness, which allow better utilization of a pool of resources, thus increasing total ecosystem process (Tilman, 1997). The mass-ratio hypothesis, by contrast, states that ecosystem processes are influenced by the functional traits of the dominant species in the community, with negligible effect of species richness or less abundant species (Grime, 1998). Although the niche-complementarity effects and the mass-ratio hypothesis are not mutually exclusive, and both mechanisms can be important for ecosystem processes in different situations (Potvin & Gotelli, 2008; Mouillot *et al*., 2011), little work has simultaneously assessed the effects of both mechanisms in natural systems (Thompson *et al*., 2005; Mokany *et al*., 2008).

Moreover, most research has been conducted in synthetically assembled communities, under conditions that differ markedly from those of natural systems (Srivastava & Vellend, 2005) or have been mostly restricted to plant communities in temperate grassland ecosystems (Hooper *et al*., 2005). Little empirical research has been conducted in forest ecosystems. Earlier studies in forests have focused on temperate ecosystems, and the relationship between tree species richness and productivity (Jacob *et al*., 2010; Paquette & Messier, 2011; Seidel *et al*., 2013; Vilà *et al*., 2013). These studies have shown mixed support, with some studies showing positive relationships (Paquette & Messier, 2011; Vilà *et al*., 2013), while others have found no effects (Jacob *et al*., 2010; Seidel *et al*., 2013). In tropical old-growth forests, some studies have found that few dominant species contributed disproportionately to other ecosystem processes such as aboveground carbon storage (Balvanera *et al*., 2005; Ruiz-Jaen & Potvin, 2011), supporting the mass-ratio hypothesis. In secondary forests, recent studies on aboveground carbon storage suggest that tree species richness played a minor role on biomass carbon (Becknell & Powers, 2014) or that its effect can be weaker or stronger depending on the stand age (Bu *et al*., 2014).

Tropical dry forests (TDFs) have been rarely included in the diversity debate, despite that they are considered among the most threatened ecosystem in the tropics due to habitat transformation and subsequent biodiversity loss (Janzen, 1988; Sanchez-Azofeifa *et al*., 2005). Due to this transformation, the current extent of TDFs is represented by a landscape consisting of a matrix of agricultural fields and patches of secondary forest succession (Sanchez-Azofeifa *et al*., 2005). During secondary succession, ecosystem development occurs, and biomass carbon is expected to increase leading to a maximal biomass stage, a process that implies sequential changes in species richness, composition and diversity over time (Quesada *et al*., 2009, Martin *et al*., 2013). The time required for secondary TDFs to recover diversity and ecosystem processes after disturbance, however, vary upon a number of factors such as climatic conditions, soil properties, and functional traits of the species present (Becknell & Powers, 2014).

In general, species replacement during succession is characterized by species with high resource acquisition rates in early stages of succession to species with conservative resource use in late succession (Chazdon, 2014). Acquisitive species are characterized by traits that maximize resource acquisition, such as high specific leaf area (SLA) and high leaf nutrients, which allow them to be successful in high resource habitats, since they can have high growth rates reducing construction costs (Sterck *et al*., 2011). On the other hand, conservative species are characterized by low SLA, and leaf nutrients to maximize resource conservation; thus these species generally show slow growth rates, greater tolerance to stressful conditions, and are successful in low resource habitats (Wright *et al*., 2004). The acquisitive-conservative continuum has been widely documented in wet forests, since light, which is the main limiting resource, decreases with stand age (Sterck *et al*., 2011). In contrast, in TDFs, water is the major limiting resource, thus functional traits may vary from conservative to acquisitive strategies, since species in early succession experience higher stressful conditions due to hotter and drier conditions than species in late succession (Lebrija-Trejos *et al*., 2011). The limited number of studies evaluating changes in functional traits in TDFs have yielded mixed results, with some studies showing increases in functional traits (e.g., SLA) with stand age (Alvarez-Añorve *et al*., 2012; Becknell & Powers, 2014), while others showing decreases during succession (Lebrija-Trejos *et al*., 2011; Lohbeck *et al*., 2013). Acquisitive strategies should increase the rates of ecosystem processes (e.g., higher carbon fluxes and higher productivity), while conservative strategies should lead to a decreases in such rates (Wright *et al*., 2004). How changes in functional traits during succession influence ecosystem processes in TDFs, however, remains unclear.

In this study we evaluate the effect of stand age, climate and different diversity components on aboveground carbon storage (AGC) in secondary TDFs. To this end, we used a standardized experimental design at five study sites in three different countries. These sites differed in climate, stand age, and species richness which enable us to test the robustness of the diversity-AGC linkages in a wide range of conditions. We addressed three questions: 1) how do species richness, functional traits and functional diversity changes during secondary succession? 2) How do these changes in diversity influence aboveground carbon storage? 3) What are the mechanisms driving the relationship between tree diversity and carbon storage in secondary forests? Ours is one of the first observational studies assessing large gradients of species richness (across stand ages within locations and among sites), and their contribution to AGC in secondary TDFs. We used confirmatory path analysis in a multilevel context to assess whether changes in AGC are explained by the mass-ratio hypothesis, the niche complementarity effect or both.

5.2 Methods

Study sites

Our analysis used data from published literature and field studies in five secondary forests in three different countries (Fig. 5.1): Chamela (Mexico), Santa Rosa (Costa Rica), Serra do Cipo, Patos and Mata Seca (Brazil). The data from Mexico and Costa Rica come from previously published studies (Quesada *et al*., 2014; Hilje *et al*., 2015), while the data from Brazil come from field work. The study sites are classified as seasonally tropical dry forests with a precipitation ranging from 700 to 2000 mm yr^{-1} and a minimum of 4 months of dry season (Sánchez-Azofeifa *et al*., 2005). Previous land uses in the study sites were dominated by agriculture and cattle ranching, with most vegetation removed and few (Mexico) or nonexistent fragments of old-growth forest (Madeira *et al*., 2009; Cabral *et al*., 2013; Quesada *et al*., 2014, Hilje *et al*., 2015). Each site followed a consistent experimental design and methods where a set of plots was established in pastures of different ages since land abandonment for natural regeneration (Nassar *et al*., 2005). Time since land abandonment in each study site was made by using a combination of forest structure data (e.g., number of vertical strata), land use history, and remote sensing data (e.g., reflectance signatures of forest stands with known age) following previous approaches for seasonally dry forests (Arroyo-Mora *et al*., 2005).

Vegetation characteristics, data on structure and composition, and mean values of functional traits per species in Chamela (Mexico) were obtained from three different studies (Alvarez-Añorve *et al*. 2012; Quesada *et al*., 2014; Hesketh, 2014). Similar data for Santa Rosa (Costa Rica) were obtained from two different publications (Powers & Tiffin, 2010; Hilje *et al*., 2015). Structure and composition data for Santa Rosa were taken in the wet season of 2012 (Hilje *et al*., 2015), in Chamela were taken in the wet season of 2013 (Quesada *et al*., 2014), and in the Brazilian sites we collected field data in the wet season of 2012. Detailed descriptions for the Brazilian sites have been published elsewhere (Cabral *et al*., 2013; Madeira *et al*., 2009). Main characteristics of environmental conditions, tree diversity, and carbon storage of all study sties are summarized in Table 5.1. We used the geographic coordinates of each study site to obtain climatic conditions for each plot from a global gridded layer at 2.5 arc-second resolution (~ 5 km at the equator, available at chave.ups-tlse.fr/pantropical_allometry.htm) (Chave *et al.,* 2014). Specifically, we selected two variables to describe climate: the long-term climatological water deficit (CWD) and the environmental stress (E). The CWD is determined by the number of months where evapotranspiration exceeds precipitation, measured in mm per year (Chave *et al*., 2014). The E (unitless) is a combined variable that depends on temperature seasonality, the CWD and rainfall seasonality, and is an important environmental factor on the diameter-height allometry of trees (Chave *et al*., 2014). E varies from 0 to 1 with values closer to 1 indicating higher environmental stress related to increases in temperature and decreases in water availability.

Forest inventory data and functional traits

The forest inventory data used in this study included 60 plots of 50 x 20 m (0.1 ha each). The data from Chamela and Santa Rosa, which were obtained from published studies included 18 plots, while the data collected in the field included 42 plots (Table 5.1). Each site followed the same experimental design and methods to estimate structure and composition, with plots separated by at least 200 m and established under similar topographic, soil and microclimatic characteristics to reduce variation in physical condition (Nassar *et al*., 2008). Within each plot, all individual trees with diameter at breast height (DBH at 1.30 m) ≥ 5 cm were measured and identified. We used the structure and composition data in each study site to estimate the number of species, the relative abundance of each species, and the basal area (BA) per plot. BA is the cross-sectional area at breast height (1.3 m from the ground) expressed in m^2, and calculated as $(DBH/2)^{2}*\pi$ (Chave *et al.*, 2005). We used the BA estimations to select the most abundant species as those that together represent at least 75% of the total BA in each study site. To estimate functional diversity for the most abundant species we selected four functional traits that are known to affect ecosystem processes associated with carbon cycling and storage. The traits were specific leaf area (SLA), calculated as the one area of a fresh leaf divided by its oven-dry mass (expressed in cm^2 g^{-1}), leaf nitrogen (LNC, % mass), leaf phosphorus concentration (LPC, % mass), and wood density (WD, g cm^{-3}). SLA is a positive correlate of photosynthetic and growth rates, with lower values generally associated with high investment in leaf defenses and long leaf lifespan (Poorter & Bongers, 2006). LNC and LPC are the total amounts of nitrogen and phosphorus per unit of dry leaf mass (mg g^{-1}). LNC and LPC are generally associated with high nutritional quality (Wright *et al.*, 2004). WD is the oven-dried mass over fresh volume of a section of the main stem of a plant (Cornelissen *et al.*, 2003). WD is related with mechanical support, water storage and the growth-survival tradeoff (Chave *et al.*, 2009). Functional traits for Chamela and Santa Rosa were obtained from previous studies in the same geographic locations (Powers and Tiffin 2010; Alvarez-Añorve *et al.* 2012; Hesketh 2014). For the Brazilian sites, we measured the four functional traits following standard protocols and collecting leafs from 5-10 individuals per species in each site (Cornelissen *et al.*, 2003). We used the WD data to calculate aboveground biomass (AGB) of each plot using an allometric equation for secondary forests based on WD and DBH (van Breugel *et al.*, 2011). We then estimated aboveground carbon storage (AGC) per plot as C (Mg C ha^{-1}) = AGB x 0.47/plot area (Hughes *et al.*, 1999).

Diversity indices

To evaluate the effect of tree diversity on aboveground carbon storage (AGC), we selected different diversity components, since each component is related to a different hypothesis (Table 5.2, Fig. 5.2). To address niche complementarity, we estimated a variety of diversity indices. Diversity was described as (1) the total number of species per plot (species richness), (2) the number of species rarefied to the lowest number of individuals in a plot (Smin), and to the (3) mean number of individuals per plot across sites, which correspond to 17 and 100 individuals respectively. We also estimated (3) the Shannon diversity index (H’) based on Jost (2006), and (4) the functional richness (FRic), which do not include species abundance. FRic represents the trait space filled by the community and incorporates trait data (Mason *et al*., 2005). For the variety of trait values, we used the functional trait divergence index (FDvar), which represents the variance in trait values, weighted by the abundance (basal area) of each species (Mason *et al*., 2005). FDvar was calculated for (5) specific leaf area, (6) leaf nitrogen concentration and (7) leaf phosphorus concentration. We also calculated (8) the functional divergence (FDiv), which quantifies how species diverge in their distances (weighted by their abundance) from the center of gravity in the multi-trait functional space (Villéger *et al*., 2008). FDiv is largest when functionally different species with large trait differences reach similar high abundances (Mouchet *et al*., 2010). Finally, we estimated (9) the functional evenness (FEve), which measures the regularity of spacing between species in the community weighted mean (CWM), calculated as the averaged trait value in the community, weighted by the species abundance (basal area) (Garnier *et al*., 2004) for (10) specific leaf area, (11) leaf nitrogen and (12) and leaf phosphorus concentration. We did not include WD in the calculations of the functional diversity indices to avoid any circularity linking AGC with functional diversity, since WD is included in the allometric equation to estimate AGC.

Statistical analyses

Given the hierarchical structure of our data, with plots within stand ages, and stand ages within study sites, we used linear mixed models (LMMs) to assess how the diversity components and AGC vary with stand age. Preliminary analyses indicate that AGC and species richness increases with stand age, but the rate of increase varies across study sites (appendix 5.1). Thus, we used a random-intercept and slope model (Zuur *et al*., 2009), with site (intercept) and stand age (slope) as random effects. To evaluate which predictors were the most important for AGC, analyses were carried out in two main steps. First, we evaluated changes in AGC by contrasting the performance of competing models including all possible combinations of climate, stand age and the diversity components. Upon finding the best model explaining AGC, we selected the independent variables included in that model to examine the network of interactions among variables using path analysis. We related AGC to CWD and E, the natural log of stand age (to account for nonlinear relationships (appendix 5.1), and the whole array of diversity indices (Table 5.2) using LMMs with random intercept and slope. This produced more than 30 different models that could explain variation in AGC in secondary TDFs. We then used a model-selection approach to compare all possible models of predictors using the second order Akaike's Information Criterion (AICc) to select the best-fitting of the models (Anderson, 2008). Using AICc is recommended when $n/K < 40$, where n is sample size and K is the number of parameters. We compared models using ΔAICc values, which were calculated by subtracting the AICc value for the model with the lowest AICc from the AICc value for each model. All models with ΔAICc < 2 were considered competitive in explaining the variable response (Anderson, 2008).

We used the results of the best-subsets LMMs models to narrow down the wide array of possible variables to use for the path analysis, which led us to include the community-weighted means of SLA, LNC, and LPC, as well as species richness, stand age, and environmental stress (E). Path analysis requires *a priori* elaboration of hypothesised relationships between independent and dependent variables (Shipley, 2004). Our conceptual model hypothesised that AGC will increase along succession. Changes in the diversity components will impact AGC, with positive increases in AGC with species richness or FRic (e.g., niche complementarity) or positive increases of AGC with mean trait values (e.g., mass-ratio hypothesis, Fig. 5.2). These relationships are expected to be significant after controlling for variation across sites and the effect of climatic conditions. Climate effects on AGC are expected to be negative, as the chosen variables are indicators of environmental stress (Chave *et al*., 2014).

We run different path models including all combinations of the diversity components, which generated 7 different possible models for AGC. The hierarchical structure in our data prevents multivariate normality, which impedes the use of the maximum likelihood chi-square of classical structural equation models (Shipley, 2004). Therefore, we test our path models using d-separation tests (Shipley, 2009; 2013) to test the conditional independences given the hierarchical data. For example, a d-sep test in our causal path diagrams will test the conditional independence of AGC and climate after statistically holding constant stand age, or the conditional independence between AGC and climate after controlling for the effect of functional traits (Fig. 5.2). To assess fit of the model to data, it is then necessary to estimate the null probability (p_i) of each independence claim in the path model. We estimated these p_i using LMMs with randomly varying slopes and intercepts (Bates *et al*., 2014). Finally, we combined these null probabilities to estimate the Fisher's C statistic as $C = -2 \Sigma \ln (p_i)$. This statistic follows a chi-squared distribution with degrees of freedom equal to $2c$, with c corresponding to the number of independence claims. Fit of the data to the model is finally assessed by estimating the probability of the *C* value with 2*c* degrees of freedom, with good-fitting models showing a *P*-value > 0.05 (Shipley, 2004; 2009). When more than one model was competitive, best model was chosen using AICc model selection applied to path models (Shipley, 2013), with best models indicated by ΔAICc < 2 (Anderson, 2008). The amount of variance explained (R^2) by the best models using LMMs and path analysis was calculated using the equations developed by Nakagawa & Schielzeth (2013). We also estimated the percent variation of each diversity component by calculating the reductions in the residual variance due to the addition of the fixed effects, after accounting for variation due to random effects and environmental variables (E, and stand age). Analyses were conducted using the lme4 (Bates *et al.*, 2014) and the ggm (Marchetti, 2014) packages in the R platform.

5.3 Results

Aboveground carbon storage (AGC) ranged from 25.4 to 80.7 Mg C ha^{-1} with the lowest AGC in Patos, Brazil, and the highest value in Santa Rosa, Costa Rica. Average number of species per plot varied from 3 to 41 species with the low number of species in Patos, Brazil and the highest in Chamela, Mexico (Table 5.1). The total number of species, the rarefied species richness, the FRic, and Shannon's diversity (H') increased with stand age, as well as AGC, SLA and the functional divergence of SLA (FDvarSLA) (Table 5.3), while none of the multi-trait diversity indices (FDiv, FEve) change along succession. Although, the relationship of AGC and species richness with stand age varied across sites, the rates of change of AGC appear to be steeper than those of species richness along stand age (appendix 5.1). Stand age explained 53% variation in AGC, while it accounted for 23% of the variation in species richness (Table 5.3). Stand age also explained little variation in other diversity components such as SLA (11%) and functional richness (28%).

Bivariate relationships between AGC and the diversity components indicated that AGC increases with species richness ($\beta = 0.49$, $P < 0.01$, $R^2 = 0.30$), FRic ($\beta = 0.15$, $P = 0.07$, $R^2 = 0.03$), and H' ($\beta = 0.28$, $P < 0.01$, $R^2 = 0.15$). Effects of species richness were still significant after normalization by the lowest ($\beta = 0.33$, $P < 0.01$, $R^2 = 0.13$) and the average number of individuals per plot ($\beta = 0.45$, $P < 0.01$, $R^2 = 0.25$). Nonetheless, the total number of species per plot explained more variation than any other diversity index ($R^2 = 0.30$), thus was retained in subsequent models (Table 5.3). Results from LMMs of the effect of stand age, climate and diversity components of AGC indicated that the best models included species richness, stand age, and LPC (Table 5.3, appendix 5.2). Models that exclude any of these variables in general have a poor fit (ΔAICc > 7). Among the diversity components, species richness and the mean trait values of SLA, LNC, and LPC were retained in final models to explain variation in AGC (Table 5.4). Overall the selected models using LMMs explained more than 70% variation in AGC (Table 5.4), with species richness explaining more variation (25%) than mean trait values (~ 10%) after accounting for random effects and the effect of environmental stress (E) and stand age (Table 5.4). Our best path model indicated that AGC declines with E, and increased with stand age. Total effects (direct and indirect) of stand age and E on AGC were 0.79 and 0.24 respectively (Fig. 5.3). Species richness and mean trait values of LPC increased AGC (Fig. 5.3). This model explained 80% of the variation in AGC, and agreed with previous LMMs with species richness having a stronger effect (standardized coefficient = 0.46) than the mean trait value of LPC (standardized coefficient = 0.26).

5.4 Discussion

While old-growth forests continue to be lost due to high deforestation rates, secondary forests are becoming increasingly dominant in tropical regions (Laurance, 2010). Nevertheless, our knowledge of the mechanisms governing carbon storage in these ecosystems is quite limited (Quesada *et al*., 2009). We evaluated the effect of stand age, climate and diversity components to identify the main factors explaining variation in AGC in secondary tropical dry forests (TDFs). Ours is one of the first multi-site analyses to empirically evaluate the linkages between diversity and AGC in TDFs. Although we did not include manipulative experiments, our dataset from multiple locations provide enough variation in species richness and plant functional diversity, which allow us to make generalizations about the relationship between diversity and AGC in TDFs. Our consistent experimental design and field methods across secondary TDFs, along with our statistical approach, enable us to assess the relative importance of different diversity components for AGC, while controlling for the different environmental correlates of AGC along succession in different locations.

Changes in AGC and diversity components with stand age

We found that AGC and species richness increased along succession across study sites with stand age explaining much of the variation in AGC. This is consistent with previous studies reporting that time since land abandonment is the main factor controlling AGC recovery in secondary tropical forests (Martin *et al*., 2013; Becknell & Powers, 2014). Although there was some variation in the rates of change of AGC and species richness across sites in our data set, the rates of change of species richness with stand age appear slower and more gradual than the rates of AGC accumulation with succession. A recent meta-analysis of biomass carbon stocks and species richness recovery in secondary tropical forests found that species richness showed higher recovery rates (~ 50 years) than AGC (~ 80 years) (Martin *et al*., 2013). Our different patterns may be related with the lack of old-growth forests around our study sites. Most of our study sites are surrounded by a landscape mosaic of pastures and agriculture, rather than patches of old-growth forests, which can serve as a propagules source to facilitate colonization of species limited by dispersion. Among our sites, only Chamela has some patches of old-growth forests, which may contribute to the high species richness found in this site (Quesada *et al*., 2009). Previous land uses in TDFs may also be responsible for the slow recovery of species richness. The use of fire for forest clearing to cultivate has been a common practice in TDFs, which may jeopardize the seed bank available for forest recovery during succession (Janzen, 1988; Barlow & Peres, 2004).

Variation in carbon storage in our study sites was also influenced by climatic conditions. For example, the lowest AGC was found in Patos, the site with the lowest annual rainfall and the greatest AGC was found in Santa Rosa, the site with the highest annual precipitation (Santa Rosa). This coincides with previous studies indicating that regenerating TDFs at the end of the precipitation spectrum (1500-2000 mm year^{-1}, 1720 mm in Santa Rosa) can attain greater biomass carbon than TDFs with lower annual rainfall (Becknell *et al*., 2012). We found declines in AGC with environmental stress, which includes changes in temperature, and the number of months were potential evapotranspiration is higher than precipitation (Chave *et al*., 2014). Thus, the amount of water available during the dry season also plays an important role. In our study sites a high percent of species drop their leaves during dry periods (40–95%, ~ 70% on average), which reduces the rate of AGC accumulation, since carbon capture and vegetation dynamics are confined to the wet season. Increases in temperature can also reduce photosynthetic rates of tree species in TDFs, because when temperature exceeds 25°C, there is a high cost of plant maintenance to capture CO_2 even in ecosystems that are not limited by water (Larjavaara & Muller-Landau, 2012).

Functional richness and SLA increased with stand age and had positive effects on AGC, but were not retained in the final best models. Studies in ecological succession in general predict a decrease in functional traits such as SLA, LNC and LPC with stand age (Chazdon, 2014). Previous studies have suggested that in TDFs, an increase in these functional traits could be expected due to the harsh environmental conditions in early succession in TDFs (e.g., hot and dry) (Lohbeck *et al*., 2013). Our greater values of SLA support this hypothesis. The increase in functional richness with stand age also suggests a conservative strategy in late succession, since lower functional richness in early succession indicates that some of the resources potentially available to the community are unused (Mason *et al*., 2005). Higher resource acquisition rates with stand age contribute to higher carbon gain rates, since acquisitive species are characterized by higher levels of photosynthetic proteins (such as Rubisco) than conservative species (Sterck *et al*., 2011).

Effects of diversity components on AGC

Our final models showed positive increases in AGC with species richness and mean trait values of leaf phosphorus concentration (LPC). These effects were important after controlling for changes in environmental conditions and stand age across sites. Our results indicated that both mechanisms: the mass-ratio and the niche complementarity hypothesis explain the relationship between diversity and AGC in secondary tropical dry forests. These mechanisms are not mutually exclusive, but it is unlikely that both the mechanisms are equal on their influence on AGC (Mokany *et al*., 2008). We found that species richness explained two times more variation in AGC than LPC.

It is possible that the relative importance of each diversity component changes with stand age, with mean trait values exerting stronger effects in early succession, while species richness and functional diversity contributing to greater AGC values in late succession. Environmental harshness in early succession could limit species composition to a relatively narrow set of functional traits that allow species to cope with environmental stress (Alvarez-Añorve *et al.*, 2012), which limits the possibility for strong effects of functional diversity on AGC (Hooper *et* *al*., 2005). As forest develops, the environment becomes moister and cooler (Lebrija-Trejos *et al.* 2011), which favor the establishment of a greater number of species. Therefore, competing species are able to coexist if they show differences in their functional traits (Sterck *et al*., 2011). Differences in functional traits along gradients in water availability are considered to cause functional divergence and niche differentiation of tree species in tropical forests (Balvanera *et al*., 2011). Our results show an increase in the functional divergence of SLA and greater FRic richness with succession, suggesting that different functional strategies are present in later stages of succession, which could lead to a fuller resource exploitation by the plant community and lead to enhanced AGC (Scherer-Lorenzen *et al*., 2007). Other studies have also found that the spatio-temporal heterogeneity of water availability in the soil increased resource partitioning in TDFs as a result of functional shifts in water use (Balvanera *et al*., 2011; Sterck *et al*., 2011).

Our best models indicated that AGC increased with LPC, although we did not find changes in foliar phosphorus with stand age. In TDFs phosphorus is presumed to be limited because water limitation influences the release and mineralization of nutrients due to slower decomposition (Chazdon, 2014). Nevertheless, plants in TDFs show a high phosphorus use efficiency (PUE), among the highest reported for tropical forests (Vitousek, 1984; Lugo & Murphy, 1986; Read & Lawrence, 2003), which suggest that phosphorus indeed is a limiting resource in TDFs (Read & Lawrence, 2003). PUE in TDFs tend to increase with rainfall seasonality (Read & Lawrence, 2003), which may explain the positive association of LPC with our climatic variable of environmental stress. Some studies have found that phosphorus cycling also can vary with succession in TDFs, with greater concentration of phosphorus in litterfall of late stages than early stages (Valdespino *et al*., 2009). Therefore, it has been hypothesised that changes in tree diversity may influence the amount of nutrients, including phosphorus in the soil (Scherer-Lorenzen *et al*., 2007; Zeugin *et al*., 2010). Zeugin *et al*. (2010) assessed the effect of tree diversity on phosphorus and nitrogen pools, and found that tree diversity had a positive effect on phosphorus pools of tree stems in some species mixtures, but not in others. They also showed that species richness had a significant effect on PUE, which is related to a greater niche complementarity between species in the mixture (Zeugin *et al*., 2010). Some studies in wet tropical forests, however, have found that the opposite pattern can also be true, and phosphorus enrichment may reduce species diversity (Siddique *et al*., 2010). Future studies should quantify above- and below ground nutrients during succession to provide deeper insights of the mechanisms governing the positive increases in AGC with species richness and LPC in secondary TDFs.

In conclusion, the results from our multi-site analysis suggest that stand age is one of the main determinants for recovery of AGC in TDFs. Among the diversity components, the number of species is also of main importance in determining the effect of diversity on AGC in secondary TDFs. Although, most studies have focused on assessing the mass-ratio hypothesis and this appears to govern diversity-function linkages in old-growth forests (Balvanera *et al*., 2005; Ruíz & Potvin, 2011), increasing research has shown that changes in species accumulation, vegetation structure and biomass accumulation with stand age are tightly linked (Chazdon, 2014). Consequently, a positive relationship between species richness and AGC along succession can be expected. The increase of tree-species richness with succession, which reflects an increase of carbon storage, has important implications for managing secondary forests, as carbon sinks could be maximized in higher mixed-species stands.

Empirical studies assessing the role of biodiversity on AGC in natural forests are usually limited to local scales, because there is a high concern that many co-varying factors (e.g., climate, local environmental conditions) are not accounted for, which may mask the crucial relationships (Scherer-Lorenzen *et al*., 2007). Although, experimental studies offer a great advantage of isolating cause and effect in their analysis, they are rather simplistic and preclude the possibility to determine trends of how biodiversity loss can influence ecosystem processes of high-diverse systems such as tropical forests. In this study, we employed a multi-site analysis to attempt to make generalizations on the diversity effects on AGC in TDFs. We minimized variation in environmental factors by using consistent experimental design and methods across locations. Ideally, it would be better to have the same sample size in each study site, but using appropriate statistical approaches such as mixed models, can be useful to work with heterogeneity in sample sizes or related with different environmental conditions (Zuur *et al*., 2009). Furthermore, using analysis such as confirmatory path analysis in a multilevel context, such as our approach, it is possible to disentangle the different co-varying factors that could mask any relationship among variables. We stress the need to conduct more studies in natural systems, and particularly in secondary forests, since a better understanding of the effects of biodiversity on ecosystem processes during secondary succession will facilitate the management and restoration of degraded ecosystems in tropical regions.

5.5 References

Alvarez-Añorve, M.Y., Quesada, M., Sánchez-Azofeifa, G.A., Avila-Cabadilla, L.D. & Gamon, J. (2012) Functional regeneration and spectral reflectance of trees during succession in a highly diverse tropical dry forest ecosystem. *American journal of botany*, **99**, 816–26.

Anderson, D. R. (2008) *Model based inference in the life sciences: a primer on evidence* (p. 184). New York: Springer.

Arroyo-Mora, J. (2005) Secondary forest detection in a Neotropical dry forest landscape using Landsat 7 ETM+ and IKONOS Imagery. Biotropica, 37, 497–507.

Balvanera, P., Kremen, C., Martinez-Ramos, M. (2005). Applying community structure analysis to ecosystem function: examples from pollination and carbon storage. *Ecological Applications* **15**, 360–375.

Balvanera, P., Quijas, S. & Pérez-Jiménez, A. (2011) Distribution Patterns of Tropical Dry Forest Trees Along a Mesoscale Water Availability Gradient. *Biotropica*, **43**, 414–422.

Barlow, J., & Peres, C. A. (2004) Fire-mediated dieback and compositional cascade in an Amazonian forest. *Philosophical Transactions of the Royal Society B*, 363, 1787–94.

Bates, D., Maech, M., Bolker, B., Walker, S., Christensen, R. H. B., Singmann, H. & Dai, B. (2014) Package "lme4."

Becknell, J.M., Kissing Kucek, L. & Powers, J.S. (2012) Aboveground biomass in old-growth and secondary seasonally dry tropical forests: A literature review and global synthesis. *Forest Ecology and Management*, **276**, 88–95.

Becknell, J. & Powers, J. (2014) Stand age and soils as drivers of plant functional traits and aboveground biomass in secondary tropical dry forest. *Canadian Journal of Forest Research*, **613**, 604–613.

Bu, W., Zang, R. & Ding, Y. (2014) Field observed relationships between biodiversity and ecosystem functioning during secondary succession in a tropical lowland rainforest. *Acta Oecologica*, **55**, 1–7.

Cabral, G.A.L., de Sá Barreto-Sampaio, E.V., & J. S., de Almeida-Cortez. (2013) Estrutura espacial e biomassa da parte aérea em diferentes estádios successionais de caatinga, em Santa Terezinha, Paraíba. *Revista Brasileira de Geografía Física,* **6**, 566-574.

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace, G.M., Tilman, D., Wardle, D. a, Kinzig, A.P., Daily, G.C., Loreau, M., Grace, J.B., Larigauderie, A., Srivastava, D.S. & Naeem, S. (2012) Biodiversity loss and its impact on humanity. *Nature*, **486**, 59–67.

Chave, J., Andalo, C., Brown, S., Cairns, M.A., Chambers, J.Q., Eamus, D., Fölster, H., Fromard, F., Higuchi, N., Kira, T., Lescure, J.-P., Nelson, B.W., Ogawa, H., Puig, H., Riéra, B. & Yamakura, T. (2005) Tree allometry and improved estimation of carbon stocks and balance in tropical forests. *Oecologia*, **145**, 87–99.

Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G. & Zanne, A.E. (2009) Towards a worldwide wood economics spectrum. *Ecology letters*, **12**, 351–66.

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

Chazdon, R. L. (2014). *Second growth: The promise of tropical forest regeneration in an age of deforestation*. University of Chicago Press.

Cornelissen, J. H. C., Lavorel, S., Garnier, E., Díaz, S., Buchmann, N., Gurvich, D.E., Reich, P.B., ter Steege, H., Morgan, H.D., van der Heijden M.G. A., Pausas, J. P. & Poorter, H. 2003. A handbook of protocols for standardise and easy measurement of plant functional traits worldwide. *Australian Journal of Botany* **51**, 335-380.

Díaz, S. & Cabido, M. (2001) Vive la difference: plant functional diversity matters to ecosystem processes. *Trends in Ecology & Evolution*, **16**, 646–655.

Díaz, S, Lavorel, S., de Bello, F., Quétier, F., Grigulis, K. & Robson, M. (2007) Incorporating plant functional diversity effects in ecosystem service assessments. *Proceedings of the National Academy of Sciences*, **104**, 20684-20689.

Garnier, E., Cortez, J., Billès, G., Navas, M.-L., Roumet, C., Debussche, M., Laurent, G., Blanchard, A., Aubry, D., Bellmann, A., Neill, C. & J. P., Toussaint, J.-P. (2004) Plant functional markers capture ecosystem properties during secondary succession. *Ecology*, **85**, 2630–263

Grime, J. P. (1998). Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology,* **86**, 902–910.

Hesketh, M.S. (2014) Temporal dynamics and leaf trait variability in Neotropical dry forests by Doctor of Philosophy Department of Earth and Atmospheric Sciences. University of Alberta.

Hilje, B., Calvo-Alvarado, J., Jimenez-Rodriguez, C. & G.A. Sánchez-Azofeifa. (2015). Tree species composition, breeding systems, pollination and dispersal syndromes in three forest successional stages in a tropical dry forest in Mesoamerica. *Tropical Conservation Science*.

Hooper, D.U. & Vitousek, P. (1997) The Effects of Plant Composition and Diversity on Ecosystem Processes. *Science*, **277**, 1302–1305.

Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J., Vandermeer, J. & Wardle, D.A. (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs*, **75**, 3–35.

Hughes, R.F., Kauffman, J.B. & Jaramillo, V.J. (1999) Biomass, Carbon, and Nutrient Dynamics of Secondary Forests in a Humid Tropical Region of Mexico. *Ecology*, **80**, 1892.

Jacob, M., Leuschner, C., & Thomas, F. M. (2010) Productivity of temperate broad-leaved forest stands differing in tree species diversity. *Annals of Forest Science*, **67**, 503.

Janzen, D., 1988. Tropical dry forests: the most endangered major tropical ecosystems. In: Wilson, E.O. (Ed.), Biodiversity. National Academy Press, pp. 130–137

Jost, L. (2006) Entropy and diversity. *Oikos*, **113**, 363-375.

Larjavaara, M. & Muller-Landau, H.C. (2012) Temperature explains global variation in biomass among humid old-growth forests. *Global Ecology and Biogeography*, **21**, 998-1006.

Laurance, W. (2010) Habitat destruction: death by a thousand cuts. *Conservation Biology for All* (ed. Sodhi, N.S., & P.R. Ehrlich), pp. 73–87. New York: Oxford University Press.

Lebrija-Trejos, E., Pérez-García, E.A., Meave, J.A., Poorter, L. & Bongers, F. (2011) Environmental changes during secondary succession in a tropical dry forest in Mexico. *Journal of Tropical Ecology*, **27**, 477–489.

Lohbeck, M., Poorter, L., Lebrija-Trejos, E., Martínez-Ramos, M., Meave, J.A., Paz, H., Pérez-García, E.A., Romero-Pérez, I.E., Tauro, A. & Bongers, F. (2013) Successional changes in functional composition contrast for dry and wet tropical forest. *Ecology*, **94**, 1211–216.

Lohbeck, M., Poorter, L., Martínez-Ramos, M. & Bongers, F. (2015) Biomass is the main driver of changes in ecosystem process rates during tropical forest succession. *Ecology*, **96**, 1242-1252

Lugo A. E., Murphy, P. G. 1986. Nutrient dynamics of a Puerto Rican subtropical dry forest. *Journal of Tropical Ecology*, **2**, 55–72.

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

Marchetti, A.G.M., Drton, M., Sadeghi, K. & Marchetti, M.G.M. (2014) Package " ggm ."

Martin, P.A., Newton, A.C. & Bullock, J.M. (2014) Carbon pools recover more quickly than plant biodiversity in tropical secondary forests. *Proceedings of the Royal Society B: Biological Sciences*, **281**, 20140303–20140303.

Mason, N.W.H., Mouillot, D., Lee, W.G., Wilson, J.B. & Functional, J.B. (2005) Functional richness, functional evenness and functional divergence : the primary components of functional diversity. **1**, 112–118.

MEA. (2005) *Ecosystems and human well-being: current state and trends, Volume 1*. Island Press, New York.

Mokany, K., Ash, J. & Roxburgh, S. (2008) Functional identity is more important than diversity in influencing ecosystem processes in a temperate native grassland. *Journal of Ecology*, **96**, 884–893.

Mouchet, M.A., Villéger, S., Mason, N.W.H. & Mouillot, D. (2010) Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. *Functional Ecology*, **24**, 867–876.

Mouillot, D., Villéger, S., Scherer-Lorenzen, M. & Mason, N.W.H. (2011) Functional Structure of biological communities predicts ecosystem multifunctionality. *PLoS ONE*, **6**, e17476.

Naeem, S., Bunker, D. E., Hector, A., Loreau, M., & Perrings, C. (2009). *Biodiversity, ecosystem functioning, and human wellbeing. An ecological and economic perspective*. Oxford University Press, Oxford, UK.

Nakagawa, S., Schielzeth, H. (2013) A general and simplemethod for obtaining R^2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution* **4**, 133-142.

Nassar, J.M., Rodriguez, J.P., Sanchez-Azofeifa, A., Garvin, T.D. & M. Quesada. (2008).

Human, Ecological and Biophysical Dimensions of Tropical Dry Forests Ediciones IVIC. 135 Pp.

Paquette, A. & Messier, C. (2011) The effect of biodiversity on tree productivity: from temperate to boreal forests. *Global Ecology and Biogeography*, **20**, 170–180.

Poorter, L. & Bongers, F. (2006) Leaf traits are good predictors of plant performance across 53 rainforest species. *Ecology*, **87**, 1733–1743.

Powers, J.S. & Tiffin, P. (2010) Plant functional type classifications in tropical dry forests in Costa Rica: leaf habit versus taxonomic approaches. Functional Ecology, 24, 927–936.

Portillo-Quintero, C. A. & Sánchez-Azofeifa. G.A. 2010. Extent and conservation of tropical dry forests in the Americas. *Biological Conservation* **143**, 144-155.

Potvin, C. & Gotelli, N.J. (2008) Biodiversity enhances individual performance but does not affect survivorship in tropical trees. *Ecology Letters*, **11**, 217–223.

Quesada, M., Sanchez-Azofeifa, G.A., Alvarez-Añorve, M., Stoner, K.E., Avila-Cabadilla, L., Calvo-Alvarado, J., Castillo, A., Espírito-Santo, M.M., Fagundes, M., Fernandes, G.W., Gamon, J., Lopezaraiza-Mikel, M., Lawrence, D., Morellato, L.P.C., Powers, J.S., Neves, F.D.S., Rosas-Guerrero, V., Sayago, R. & Sanchez-Montoya, G. (2009) Succession and management of tropical dry forests in the Americas: Review and new perspectives. *Forest Ecology and Management*, **258**, 1014–1024.

Quesada, M., Alvarez-Añorve, M., Ávila-Cabadilla, L., Castillo, A., Lopezaraiza-Mikel M., Martén-Rodríguez, S., Rosas-Guerrero, V., Sáyago, R. Sánchez-Montoya, G., Contreras-Sánchez, J. M., Balvino-Olvera, F., Olvera-García, S.R., Lopez-Valencia, S. & N. Valdespino-Vázquez. (2014) Tropical Dry Forest Ecological Succession in Mexico: Synthesis of a Long-Term Study. *Tropical dry forests of the Americas: ecology, conservation and management* (ed. by J.S. Powers, G. Sánchez-Azofeifa, G.W. Fernandes and M. Quesada), pp. 237-248. CRC Press, New York, USA.

Read, L. & Lawrence, D. (2003) Litter Nutrient Dynamics During Succession in Dry Tropical Forests of the Yucatan: Regional and Seasonal Effects. *Ecosystems*, **6**, 747–761.

Ruiz-Jaen, M.C. & Potvin, C. (2011) Can we predict carbon stocks in tropical ecosystems from tree diversity? Comparing species and functional diversity in a plantation and a natural forest. *The New Phytologist*, **189**, 978–987.

Rusch G. M. & M. Oesterheld. (1997). Relationship between productivity, and species and functional group diversity in grazed and non-grazed pampas grassland. *Oikos,* **78, 5**19–526

Sánchez-Azofeifa, G. A., Quesada, M., Rodríguez, J. P., Nassar, J. M., Stoner, K. E., Castillo, A., & Cuevas-Reyes, P. (2005) Research Priorities for Neotropical Dry Forests., *Biotropica*, **37**, 477-485.

Scherer-Lorenzen, M., Bonilla, J.L. & Potvin, C. (2007) Tree species richness affects litter production and decomposition rates in a tropical biodiversity experiment. *Oikos*, **116**, 2108–2124.

Seidel, D., Leuschner, C., Scherber, C., Beyer, F., Wommelsdorf, T., Cashman, M. J., & Fehrmann, L. (2013) The relationship between tree species richness, canopy space exploration and productivity in a temperate broad-leaf mixed forest. *Forest Ecology and Management*, **310**, 366-374.

Shipley, B. (2004) *Cause and correlation in biology: a user's guide to path analysis, structural equations and causal inference*. Cambridge University Press.

Shipley, B. (2009) Confirmatory path analysis in a generalized multilevel context. *Ecology*, **90**, 363–368.

Shipley, B. (2013) The AIC model selection method applied to path analytic models compared using a d-separation test. *Ecology*, **94**, 560–4.

Siddique, I., Vieira, I. & Schmidt, S. (2010) Nitrogen and phosphorus additions negatively affect tree species diversity in tropical forest regrowth trajectories. *Ecology*, **91**, 2121–2131.

Srivastava, D.S. & Vellend, M. (2005) Biodiversity-ecosystem function research: Is it Relevant to Conservation? *Annual Review of Ecology, Evolution, and Systematics*, **36**, 267–294.

Sterck, F., Markesteijn, L., Schieving, F. & Poorter, L. (2011) Functional traits determine trade-offs and niches in a tropical forest community. *Proceedings of the National Academy of Sciences of the United States of America*, **108**, 20627–32.

Thompson, K., Askew, A.P., Grime, J.P., Dunnett, N.P. & Willis, A.J. (2005) Biodiversity, ecosystem function and plant traits in old-growth and imold-growth plant communities. *Functional Ecology*, **19**, 355–358.

Tilman, D. (1997) Distinguishing between the effects of species diversity and species composition. *Oikos*, **80**, 185.

Valdespino, P., Romualdo, R., Cadenazzi, L. & Campo, J. (2009) Phosphorus cycling in primary and secondary seasonally dry tropical forests in Mexico. *Annals of Forest Science*, **66**, 107–107.

van Breugel, M., Ransijn, J., Craven, D., Bongers, F. & Hall, J.S. (2011) Estimating carbon stock in secondary forests: Decisions and uncertainties associated with allometric biomass models. *Forest Ecology and Management*, **262**, 1648–1657.

Vilà, M., A. Carrillo-Gavilán, J. Vayreda, H. Bugmann, J. Fridman, W. Grodzki, J. Haase, G. Kunstler, M. Schelhaas, and A. Trasobares. (2013) Disentangling biodiversity and climatic determinants of wood production. PLoS ONE 8:e53530

Villéger, S., Mason, N.W.H. & Mouillot, D. (2008) New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology*, **89**, 2290–2301

Vitousek P. (1984) Litterfall, nutrient cycling, and nutrient limitation in tropical forests. *Ecology* **65**, 285–98.

Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-bares, J., Chapin, T., Cornelissen, J.H.C., Diemer, M., Flexas, J., Garnier, E., Groom, P.K. & Gulias, J. (2004) The worldwide leaf economics spectrum. *Nature*, **12**, 821–827.

Zeugin, F., Potvin, C., Jansa, J. & Scherer-Lorenzen, M. (2010) Is tree diversity an important driver for phosphorus and nitrogen acquisition of a young tropical plantation? *Forest Ecology and Management*, **260**, 1424–1433.

Zuur, A. F, Ieno, E. N., Walker, N., Saveliev, A. A. & Smith, G.M. (2009) *Mixed Effects Models and Extensions in Ecology with R*. Springer. New York.

5.6 Tables and Figures

Table 5.1. Main environmental and forest structural characteristics of the study sites.

Country	Mexico	Costa Rica	Brazil		
Site	Chamela	Santa Rosa	Serra do Cipo	Patos	Mata Seca
Latitud	19° 18' N	10° 48' N	19° 20' S	7° 1' S	14° 51' S
Longitud	105° 1' W	85° 36' W	43° 37' W	37° 15' W	43° 59' W
MAT (°C)	26.2	25	20.3	25.3	24.3
MAP (mm)	839	1720	1519	755	825
Dry season length (No.months < 100 mm rainfall)	8	6	6	8	6
Climatological water deficit (mm year^{-1})	875	632	335	1267	904
Environmental stress (E)	0.4	0.1	0.1	0.6	0.5
Mean number of species (per plot)	27	25	18	8	19
Range of species richness (per plot)	5 – 41	14 –37	8 – 37	3 – 15	11 – 26
Average number of individuals (ha^{-1})	128	108	97	85	92
Basal area (m^2 ha^{-1})	15.3	21	14	8	15.5
Stand age (years)	12 – 62	20 – 55	8 – 50	22 – 64	14 – 58
AGC (Mg C ha^{-1})	55.7	80.7	51.3	25.4	59.1
Deciduousness species (%)	80	40-60	50	95	90-95

MAT, mean annual temperature, MAP, mean annual precipitation, AGC, aboveground carbon storage. The percent of deciduous species is calculated as the percent of species dropping their leaves in the dry season.

Table 5.2. Descriptive statistics for the diversity components, their abbreviation, units and the hypothesis to which each index is relevant.

Index	Acronym	Mean	SE	Min	Max	Relevant hypothesis
Species richness	SR	18.0	1.29	3	41.0	Niche complementarity
SR rarefied to lowest No.Ind per plot	Smin	8.5	0.5	2	14	Niche complementarity
SR rarefied to mean No.Ind per plot)	Smean	17	1.1	3	36	Niche complementarity
Shannon diversity (H’)	H’	9.3	0.8	1.2	25.7	Niche complementarity
Functional group richness	FRic	0.5	0.03	0.05	1.0	Niche complementarity
Functional evenness	FEve	0.5	0.02	0.05	0.8	Niche complementarity
Functional divergence	FDiv	0.8	0.02	0.42	1.0	Niche complementarity
Community weighted means	CWM					
CWM Specific leaf area	SLA	137.5	4.00	87.6	224.0	Mass-ratio hypothesis
CWM Leaf nitrogen concentration	LNC	2.4	0.04	1.7	3.0	Mass-ratio hypothesis
CWM Leaf phosphorus concentration	LPC	0.2	0.01	0.08	0.4	Mass-ratio hypothesis

Table 5.3. Results of the linear mixed models evaluating changes in diversity components and aboveground carbon storage (AGC) with stand age. Standardized coefficients (Beta), standard errors (SE) are indicated, and explained variation (R^2) is shown for significant relations.

Variable	Beta	SE	P	R^2
AGC	0.82	0.18	< 0.01	0.53
SR	0.55	0.11	< 0.01	0.23
Smin	0.48	0.11	< 0.01	0.17
Smean	0.52	0.08	< 0.01	0.19
Shannon	0.47	0.11	< 0.01	0.18
FRic	0.62	0.13	< 0.01	0.28
FEve	0.11	0.21	0.61	
FDiv	–0.12	0.34	0.73	
CWM SLA	0.40	0.10	< 0.01	0.11
CWM LNC	–0.19	0.37	0.60	
CWM LPC	–0.31	0.39	0.42	
CWM WD	–0.31	0.16	0.07	

For abbreviations of the variable names refer to Table 5.2

Table 5.4. Model selection results for the effect of the diversity components, stand age and environmental stress (E) on aboveground carbon storage (AGC). For each model the degrees of freedom (df), the second order Akaike's Information Criterion (AICc), and the differential AICc (ΔAICc) are shown. Best models (ΔAICc < 2) are indicated in bold.

Model	Species richness	Stand age (years)	SLA (cm^2 g^{-1})	LNC (% mass)	LPC (% mass)	E	df	AICc	ΔAICc	R^2
1	+	+	+		+	−	50	60.5	**0.0**	0.79
2	+	+			+	−	51	61.3	**0.8**	0.80
3	+	+	+	−	+		50	62.4	**1.9**	0.71
4	+	+		−	+	−	50	63.7	3.2	
5	+	+	+		+		51	65.1	4.6	
6	+	+		−	+		51	65.6	5.1	

Confidence intervals of all variables in the best models did not include zero (see Table A1).

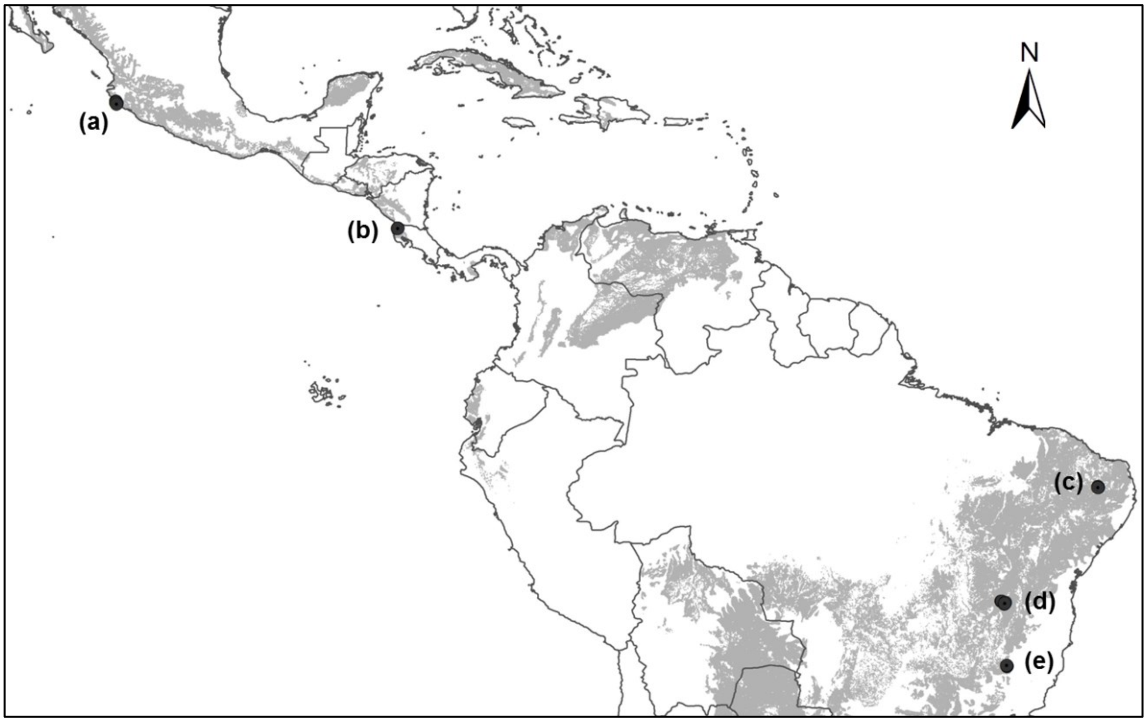


Figure 5.1. Locations of the five study sites used to assess the effects of tree diversity on aboveground carbon storage in tropical dry forests: (a) Chamela, Mexico, (b) Santa Rosa, Costa Rica, (c)Patos, Brazil, (d) Mata Seca, Brazil, (e) Serra do Cipo, Brazil. The shaded gray area indicates the extent and geographical distribution of Neotropical dry forests (from Portillo-Quintero & Sanchez-Azofeifa, 2010).

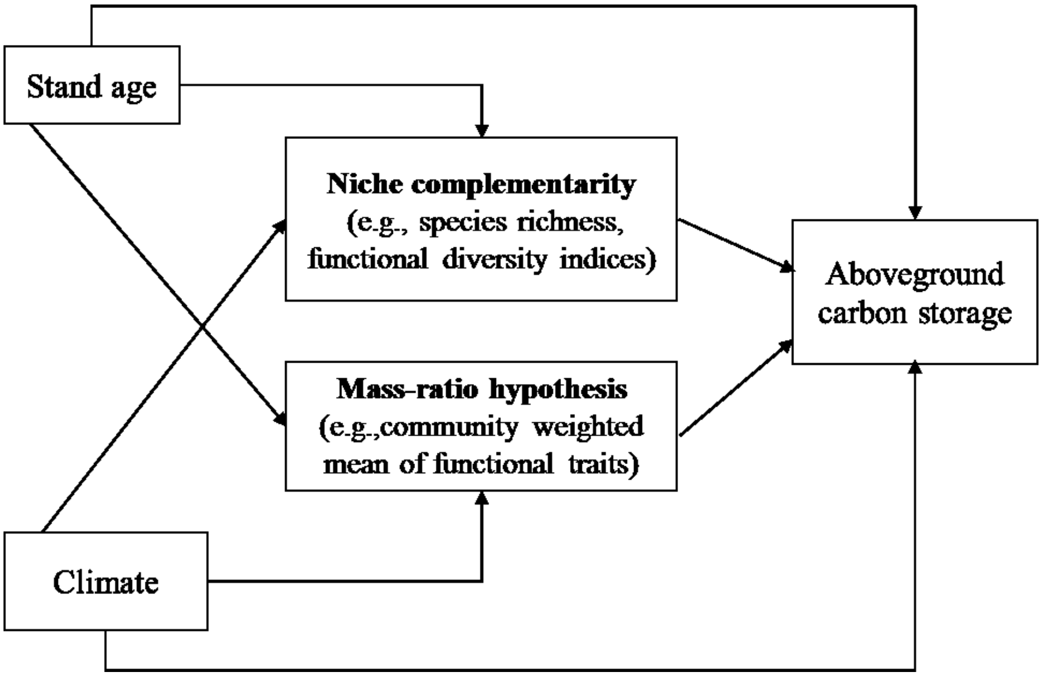


Figure 5.2. Conceptual model to evaluate the direct and indirect effects of stand age, climate and the diversity components on aboveground carbon storage (AGC) in tropical dry forests. The model hypothesizes that aboveground carbon storage increases along succession, and it is positively affected by diversity, either by species richness, the mean trait values or the functional diversity indices. Stand age is also hypothesised to influence the diversity components, with positive increases on species richness.

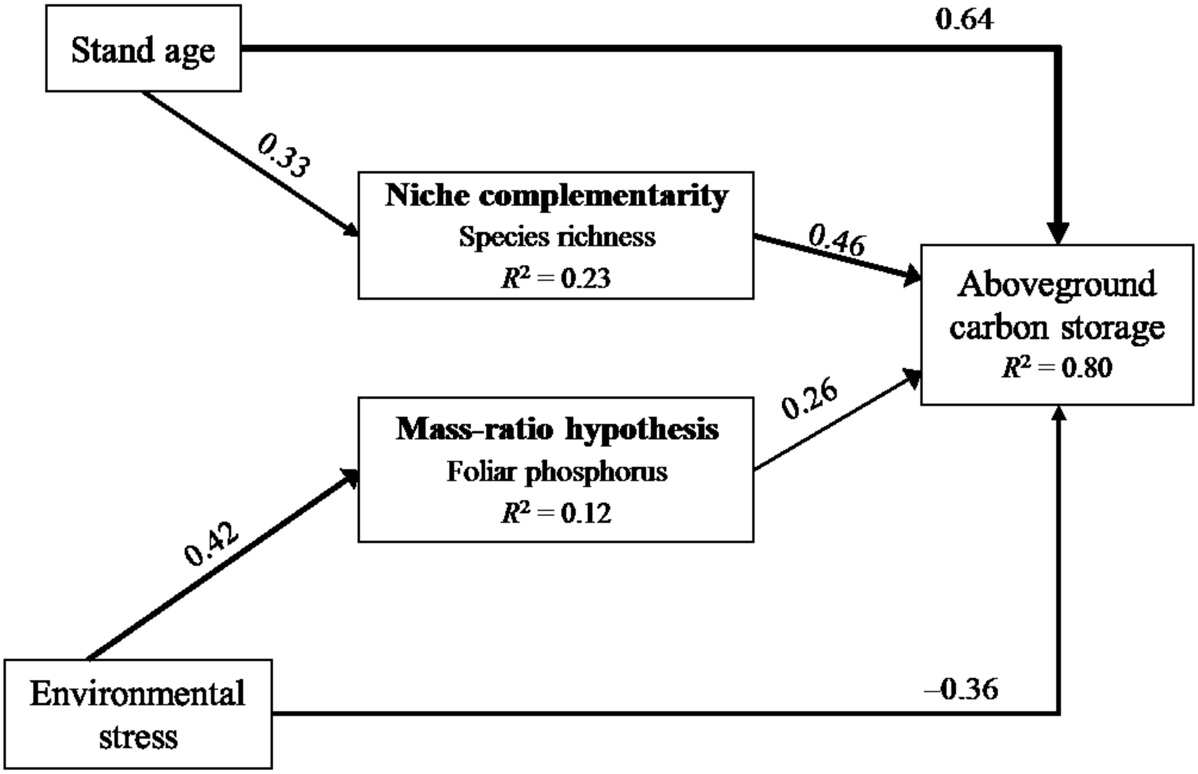
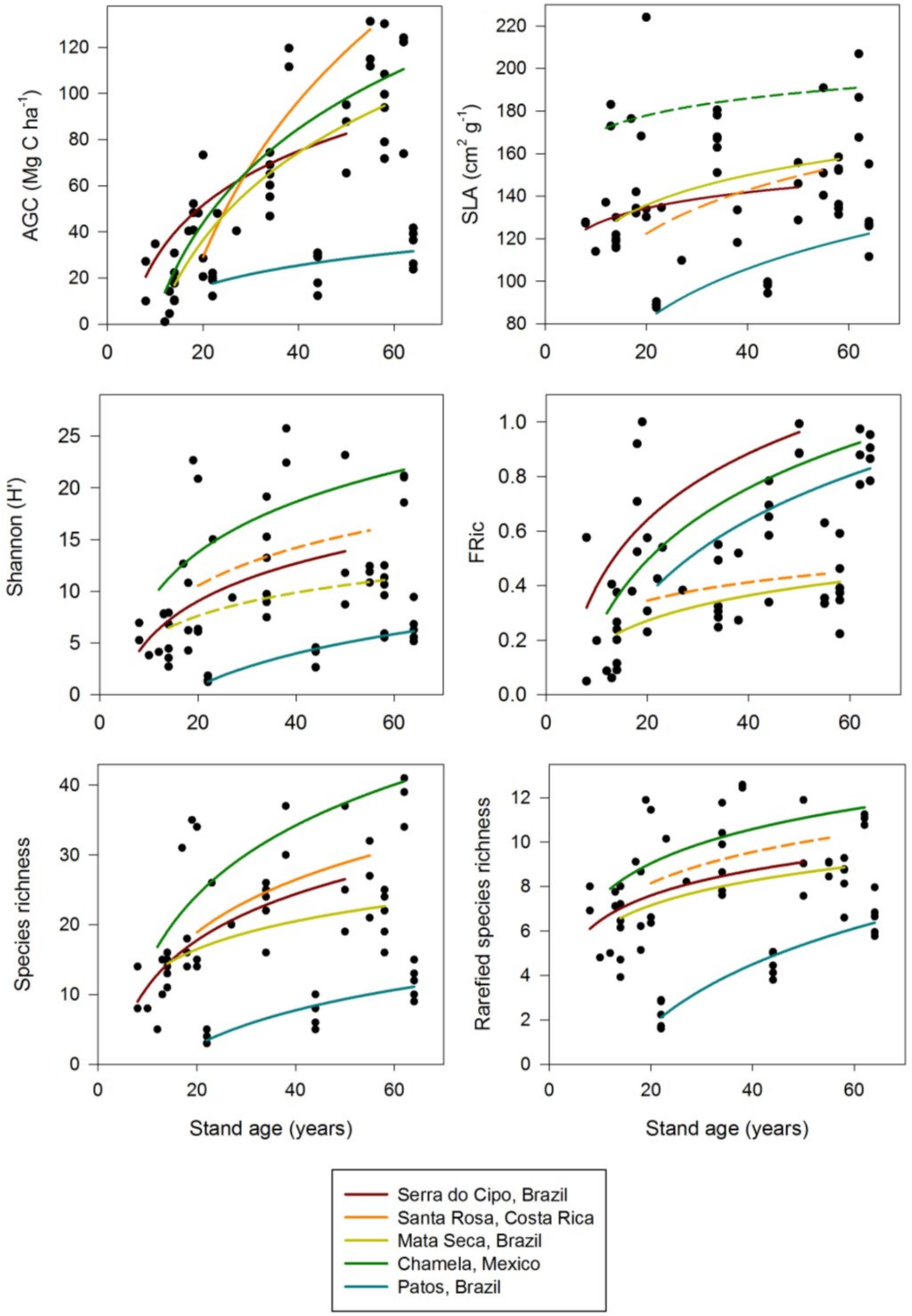


Figure 5.3. Fitting of the conceptual model (Fig. 5.2) showing the effects of species richness, mean traits, stand age and environmental stress on aboveground carbon storage (AGC) in tropical dry forests. Model fit to the data was good ($C = 7.25$, df = 8, $P = 0.5$). Model selection results indicated this as the best model (AICc = 73.56) with alternative models showing ΔAICc values > 10. Single-headed arrows represent causal relationships. Solid black arrows indicate significant effects ($P < 0.05$). The path coefficients are standardized regression weights resulting from LMMs. The arrow thickness is proportional to the path coefficient. The amount of variance explained (R^2) for the dependent variable is indicated.

5.7 Supplementary Material Chapter 5



Appendix 5.1. Variation in aboveground carbon storage (AGC) and the diversity components with stand age in secondary tropical dry forests. Each line represents a study site. Linear fits are shown for significant relationships with the natural log of stand age in each study site. Non-significant fits are indicated by dashed lines. FRic, functional richness. The rarefied plot correspond to the rarefied species richness to the lowest number of individuals per plot (Smin).

Appendix 5.2. Linear mixed model with ΔAICc < 2 for the effect of diversity, stand age and environmental stress on aboveground carbon storage. Standardized coefficients (Beta), standard errors (SE), Lower (L) and Upper (U) limit of 95% confidence intervals are shown for each variable.

Model	Variables	Beta	SE	L	U
1	Richness (No.sps/plot)	0.43	0.08	0.28	0.59
	stand age (years)	0.63	0.11	0.40	0.85
	SLA (cm2 g-1)	0.16	0.07	0.02	0.30
	LPC (% mass)	0.31	0.07	0.18	0.44
	E	-0.38	0.14	-0.66	-0.10
2	Richness (No.sps/plot)	0.47	0.08	0.32	0.62
	stand age (years)	0.65	0.12	0.41	0.89
	LPC (% mass)	0.26	0.06	0.13	0.39
	E	-0.36	0.11	-0.58	-0.13
3	Richness (No.sps/plot)	0.50	0.08	0.35	0.65
	stand age (years)	0.52	0.17	0.19	0.85
	SLA (cm2 g-1)	0.19	0.07	0.05	0.33
	LPC (% mass)	0.27	0.07	0.13	0.40
	LNC (% mass)	-0.19	0.07	-0.33	-0.05

6. What drives the rates of carbon accumulation in secondary tropical dry forests?

6.1 Introduction

Old-growth forests in tropical regions are disappearing due to deforestation and agriculture expansion (Gibbs *et al*., 2010). This transformation constitutes one of the main sources of carbon dioxide to the atmosphere at global level (Houghton, 2005). One way to mitigate the impact of land use change in tropical areas is through reforestation or recuperation of degraded areas. In tropical regions, many areas have been recovered by allowing natural regeneration after cultivation, specifically within or in areas surrounding protected areas (Janzen, 2002; FAO, 2010; Griscom & Ashton, 2011). As a result, many regions in the tropics are represented by patches of forest succession. Secondary succession is the long-term directional change in community composition following a disturbance event (Chazdon *et al*., 2007). Secondary forests may play an important role in the carbon cycling in tropical regions, since they have fast rates of aboveground biomass production, and can sequester up to 1.4 Pg C year^{-1}, ameliorating raising levels of atmospheric CO_2 (Hughes *et al*., 1999; Houghton, 2005). Currently, secondary forests represent 57% of the world's forest and occupy more area than old-growth forests in tropical regions (FAO, 2010; Gibbs *et al*., 2010). Thus, assessing their role as potential carbon sinks is important to improve estimations of global carbon emissions (Houghton, 2005).

Several studies have indicated that recovery rates of biomass carbon during succession depend on land use history, soil fertility, rainfall seasonality, temperature and initial species colonization (Hughes *et al*., 1999; Read & Lawrence, 2003; Chazdon, 2014). Among these, forest age (e.g., time since disturbance) and land use history appear to be very important, as the recovery rate of carbon accumulation can be severely affected by the intensity and duration of previous land uses (Read & Lawrence, 2003). For example, the number of cultivation-fallow cycles, as well as the use of fire for forest clearance, may have a huge impact in the recovery of biomass carbon due to reductions in the amount of nutrients available for plant growth (Guariguata & Ostertag, 2001; Chazdon *et al*., 2007). Biotic factors such as the number of tree species or species composition (e.g., the presence of nitrogen fixers) may also influence accumulation of carbon biomass during succession (Powers & Tiffin, 2010; Batterman *et al*., 2013). More recent research has also indicated that functional traits also play an important role in carbon accumulation, as they underlie differences in growth rates among species, and rates of nutrient acquisition and leaf decomposition during succession (Bu *et al*., 2014).

Secondary forest succession has been extensively studied in the Neotropics (Chazdon *et al*., 2007; Quesada *et al*., 2009; Sánchez-Azofeifa *et al*., 2014). Most knowledge in tropical succession however, has been obtained from wet forests (Sánchez-Azofeifa *et al*., 2005); despite the fact that TDFs represent 42% of all tropical forests, while wet forests represent 25% (Murphy & Lugo, 1986). TDFs are broadly defined as a vegetation type dominated by deciduous trees, with an annual average temperature of at least 25°C or higher, annual precipitation of 700-2000 mm per year, and a dry season (precipitation less than 100 mm) of three or more months (Sánchez-Azofeifa *et al*., 2005). TDFs, in contrast to wet forests, show a lower number of plant species, fewer canopy strata, basal area, and more frequent vegetative reproduction (Murphy & Lugo, 1986; Quesada *et al*., 2009). These differences are likely to affect rates of change of biomass accumulation and forest recovery after disturbance in TDFs. In wet forests, changes in functional traits during succession generally run from short-lived, fast-growth leafs with high resource acquisition rates to resistant, slow-growth and long-lived leafs in later stages of succession (Lohbeck *et al*., 2013). In TDFs, however, variation in functional traits change from conservative traits to cope with hot, sunny and dry environments early in succession to those that enhance light acquisition and water use in late successional stages (Lebrija-Trejos *et al*., 2010; Alvarez-Añorve *et al*., 2012). Consequently, results from wet forests cannot be extrapolated to TDFs; hence more studies are needed to identify the main mechanisms of succession in TDFs to understand how carbon pools recover in TDFs disturbance.

Accumulation of species diversity and biomass carbon during succession are tightly linked. Nonetheless, our understanding of how changes in diversity components affect the rates of changes of ecosystem processes in TDFs is very limited (Becknell & Powers, 2014). Studies in old-growth forests have indicated that average ecosystem processes (e.g., primary productivity) may increase with higher species richness (niche complementarity hypothesis) (Vilà *et al*., 2013), or conversely can increase due to the functional traits of the dominant species (the mass-ratio hypothesis) (Ruiz-Jaen & Potvin, 2011). Alternatively, diversity may have no effects on ecosystem processes and in the particular case of secondary forests, land use history, initial biomass and proximity to nearby old-growth forests may play a more important role (Becknell & Powers, 2014; Lohbeck *et al*., 2015). It is still unclear what underlies the rates of changes in ecosystem processes in TDFs, and the factors that may enhance the capacity of these ecosystems to accumulate biomass carbon overtime.

In this study we assess the rates of changes of different carbon pools during secondary succession in TDFs. We quantified the rate of carbon accumulation, carbon gain and primary productivity to identify the main drivers of carbon pools in secondary TDFs. Specifically, we address three questions: 1) what is the effect of stand age on rates of carbon accumulation (recruitment + growth – mortality), carbon gain (due to growth and recruitment only), and litterfall production. We predict that the rate of carbon gain and accumulation will decrease with forest age, as higher productivity is generally found in early stages of succession related to faster and higher turnover rates of growth and mortality (Chazdon *et al*., 2007). 2) Do species richness, mean functional traits or functional diversity influence the rates of carbon pools in secondary TDFs? We hypothesize that stands with acquisitive traits (e.g., high values of specific leaf area, leaf nitrogen concentration, and leaf phosphorus concentration) will have faster rates of change in carbon accumulation. 3) What is the effect of initial aboveground biomass in rates of carbon accumulation? We included initial aboverground biomass, because variation in aboveground biomass during succession may be driven by density-dependent effects (Finegan *et al*., 2015). Moreover, stands with higher initial biomass may have stronger effects in the rate of carbon uptake and accumulation compared to stands with lower initial biomass (Guariguata & Ostertag, 2001). Finally, we assess our hypothesis in two TDFs with similar temperature and dry season length, but different annual precipitation (825 mm year^{-1} vs. 1720 mm year^{-1}) and land use history. We expect a faster rate of carbon accumulation and gain in the site with the highest precipitation.

6.2 Methods

Study sites

Our analysis used data from forest inventories conducted during 6 years in two TDFs: Santa Rosa National Park (SRNP) in Costa Rica (10° 48' 53" N, 85° 36' 54" W) and Parque Estadual da Mata Seca (PEMS) in Brazil (14° 48' 36" N, 43° 55' 12" W) (Fig.1). The SRNP site, with an area of 50,000 ha, suffered intense deforestation due to the expansion of pasture lands since the early 1700s. Today and after the creation of SRNP, the uplands of the park are a mosaic of secondary forest in various stages, of succession and with different land use histories related to anthropogenic fires (Kalácska *et al*., 2004). The early stage constitutes a very open and patchy canopy, with a thick herbaceous understory; the intermediate state is a forest with a range of canopy openness, and the late stage constitutes a canopy with two layers of vegetation: dominant canopy trees and shade tolerant species (Castillo *et al*., 2012). This site receives 1720 mm of annual rainfall, has a mean annual temperature of 25°C and a 6-month dry season (Dec−May), with 40−60% of deciduous species (Kalácska *et al*., 2004).

The Brazilian site covers an extent of 10,281 ha and is located in the valley of the São Francisco River in the State of Minas Gerais in Brazil. The region has flat and nutrient rich soils in a semiarid climate, with a mean annual temperature of 24.3 °C and mean annual precipitation of 825 mm (IEF, 2000). Deciduous trees dominate this forest, with almost 90−95% leaf loss during the dry season (May−October) (Madeira *et al*., 2009). Approximately 15% of the PEMS consists of abandoned pastures and agricultural fields in different stages of natural regeneration, while the remaining area is composed of secondary and old-growth forest. The early stage is composed of a heterogeneous canopy with an herbaceous and shrubby understory; the intermediate stage comprises up to two strata with canopy gaps in some areas, and the late stage represents old-growth forest with the highest number of species, stem density and basal area (Madeira *et al*., 2009).

Estimation of carbon pools

In 2006, permanent plots of 0.1 ha (50 x 20 m) were established in each study area in stands of different ages. Nine plots were established in SRNP in stands from 20 to 55 years old, while 18 plots were established in PEMS in stands from 14 to 58 years old. The plots followed standardized research protocols, where all trees with diameter at breast height (DBH, measured at 1.3 m from the ground) ≥ 5.0 cm were tagged and identified yearly to estimate growth (e.g., increment in tree diameter), recruitment and mortality (Nassar *et al*., 2008). Experienced field assistants identified trees and vouchers were collected regularly for new or unknown species, which were identified in local botanical collections. Annual census were conducted in each study site for 6 years (2006−2012). Recruits into the 5-cm diameter class were tagged and measured at each census. Mortality was defined as death or disappearance of individual trees during this period. With these data we estimated annual rates of growth, mortality and recruitment per individual tree.

To estimate changes in carbon pools, we calculated aboveground biomass (AGB) using an allometric equation for secondary forests (van Breugel *et al*. 2011) based on DBH and wood density. Wood density was obtained for each species in each study site from literature (Chave *et al*., 2009; Powers & Tiffin, 2010) or in the field following standard protocols in 5 individuals per species (Chapter 5, Cornelissen *et al*., 2003). We used this equation to estimate AGB per tree in each plot. For individual trees with multiple stems, we calculated AGB of each stem and summed them. Aboveground carbon storage per plot was estimated by using C (Mg C ha-1) = AGB x 0.47/plot area (Hughes *et al*., 1999). We then estimated AGC accumulation (ΔAGCcum) in Mg C ha^{-1} $year^{-1}$ mm per plot in each study site as the net changes in AGC due to increases in growth plus recruitment (e.g., new trees recruiting to the 5-cm DBH each year) minus mortality. The rate of aboveground carbon increment (ΔAGCin) in Mg C ha^{-1} $year^{-1}$ per plot was calculated as the annual increment of biomass obtained from tree growth and recruitment only. Values of initial AGC (AGCi) were estimated using total AGC in 2006 for each study site.

To estimate rates of aboveground primary productivity (AGPP), we estimated litterfall production in the two study sites. Litterfall represents the most common measure of primary production in secondary dry forests (Jaramillo *et al*., 2011). Moreover, litterfall constitute an important flux of carbon and nutrients from the canopy to the forest floor (Clark *et al*., 2001). We measured litterfall production by placing eight 0.5 x 1.0 m litter traps within each plot in each study site. In SRNP, all nine plots were sampled, while in PEMS, only 12 plots contained litter traps. Litter was collected monthly in SRNP from May 2007 through April 2010, and in PEMS from April 2008 through March 2010. This gave us three complete years of litterfall data for each study site. The litter collected from each trap was dried at ~60°C for 72 hours and weighted to estimate dry biomass. Total litterfall per plot was calculated by taking the average monthly litterfall mass from the 8 litter traps in each plot and dividing it by the total area of the traps, and is expressed as megagrams of dry biomass per hectare (Mg ha^{-1}).

Diversity components

We used the structure and composition data in each study site to estimate the number of species in each year from 2006 to 2012. To estimate functional traits and the functional diversity indices, we selected the most common species in each study site, which were those that account for at least 75% of total basal area. Basal area is defined as the cross-sectional area at breast height (in m^2), estimated as $(DBH/2)^2 * \pi$ (Chave *et al*., 2005), where DBH is diameter at breasth height. Once the most common species were identified in each study site, we obtained information on three functional traits related with carbon accumulation, higher photosynthetic rates, plant growth and survival (Poorter *et al*., 2008). These trait were specific leaf area (SLA), leaf concentration of nitrogen (LNC, % mass), and leaf phosphorus concentration (LPC, % mass). Functional traits for the common species in SRNP were obtained from previous studies in the same region (Powers & Tiffin, 2010). In PEMS, we estimated functional traits by collecting leafs on 5-10 individuals per species during the wet season of 2012 following standard protocols (Cornelissen *et al*., 2003).

To evaluate the effect of diversity on the different carbon pools, we calculated different indices related with two main mechanisms: the niche complementarity and the mass-ratio hypothesis (Table 6.1): (1) the initial number of species richness (SRi), (2) the community-weighted mean (CWM) of each functional trait: SLA, foliar nitrogen and foliar phosphorus. The CWM is the mean trait value in the community weighted by the abundance of the species, and it is related to the mass-ratio hypothesis (Garnier *et al*., 2004). We also estimated (3) the functional regularity index (FRO), which uses the relative abundance of species and captures the heterogeneity or evenness of a single functional trait in the community (Mouillot *et al*., 2005). We also calculated two multi-trait indices combining the values of the three functional traits. These indices include: (4) the functional divergence (FDiv), which quantifies how the trait values are spread along the range of a trait space, and it varies from 0 to 1 (Mouchet *et al*., 2010) and (5) the functional richness (FRic), which represent the trait space filled by the community. Low values of FRic indicate that some of the resources potentially available to the community are unused (Mason *et al*., 2005). All functional diversity indices were weighted by basal area, except for the FRic, which do not consider species abundance.

Data analysis

To determine the main drivers of carbon pools in TDFs, a series of simple linear regressions were conducted to evaluate the effect of stand age and diversity components on AGC_i, $\Delta AGCcum$, $\Delta AGCin$, and AGPP for each study site. We also conducted t-tests to compare whether rates of AGCcum, AGCin, and AGPP were higher in SRNP compared to PEMS. We related each carbon parameter to stand age and the whole array of diversity indices (Table 6.1) using linear regressions. These regressions started with 11 potential predictor variables (AGC_i, the number of species richness, six single-trait indices, and three multi-trait indices) for each study site, yielding a total of 88 possible models. Thus, we employed model selection and compare all possible models using the second order Akaike Information Criterion (AICc) for small sample sizes. Best models were chosen as $\Delta AICc \leq 2$, with ΔAICc calculated as the difference between the lowest AICc and the AICc value for each model (Anderson, 2008). All analyses were conducted using the R-software and the AICcmodavg package (R Development Core Team, 2012).

6.3 Results

In SRNP the rate of AGC accumulation was relatively low with 0.5 ± 5.4 Mg ha^{-1} $year^{-1}$ (from −6.0 to 11.0). The rate of AGCin was 6.4 ± 4.1 Mg ha^{-1} $year^{-1}$ (2.9−15.6), and the average of AGPP was 6.6 ± 2.4 Mg ha^{-1} $year^{-1}$ (3.1−10.1). Initial AGC was higher in Santa Rosa than PEMS with an average of 42.4 ± 26.5 Mg ha^{-1} $year^{-1}$ (9.1−73.1), and a mean value of 30.7 ± 26.0 Mg ha^{-1} $year^{-1}$ (0.7–82.4) in Mata Seca. The initial biomass carbon in PEMS averaged 30.73 Mg ha^{-1}. The rate of AGCcum per year in PEMS has high variation across years, with a mean rate of 1.53 ± 6.4 Mg ha^{-1} $year^{-1}$ (from −10.7 to 12.5). The rate of AGCin and AGPP were 6.25 ± 4.6 (0.9−16.3) and 4.6 ± 0.8 Mg ha^{-1} $year^{-1}$ (3.7–6.0) respectively. Comparison between sites indicated that AGCcum ($t = 1.08$, $P = 0.31$) and AGCin ($t = 0.2$, $P = 0.64$) were similar.

The diversity components followed different trajectories along succession between sites. Species richness in SRNP increased up to mid-succession (~ 40 years) and declined in late stages (> 50 years), while there was a continuous increase in PEMS (Fig. 6.2). In SRNP, the site with the highest precipitation, we found that AGC_i was positively affected by initial species richness (SRi), stand age, and negatively affected by the variety of functional traits in the community (FDiv) (Table 6.2). The FDiv had a negative effect on AGC_i in this site (Table 6.3). This suggests that increases in AGC are more related with the time since disturbance required for species establishment than the variety of functional traits in the community (Fig. 6.3). ΔAGCcum was not explained by any of our selected models, but AGCin (growth and recruitment) was best explained by functional richness, which explained 67% variation in carbon gain (Table 6.3). AGPP was mainly dependent of time since disturbance and increases in the community-weighted mean of specific leaf area (SLA), which indicates that later stages in SRNP are characterized by soft, fast-growth leafs cheap leaves (Fig. 6.3), which generally have higher turnover rates (Table 6.2).

In PEMS, the community-weighted mean (CWM) of foliar nitrogen, and the functional regularity of leaf nitrogen concentration (LNC) decreased with stand age, while the CWM of SLA increased along succession. SRNP showed an opposite pattern than PEMS, with higher mean trait values of foliar nitrogen and foliar phosphorus in late stages of succession (Fig. 6.2). In PEMS, the site with the lowest precipitation, AGC_i was positively related with stand age, SRi, and FDiv (Fig. 6.3), and negatively related to the mean trait values of foliar nitrogen and the functional regularity (FRO) of LNC (Table 6.2). This suggest that higher AGC is associated with higher number of species that differ in their functional traits, and specifically species with conservative leaf traits such as low values of LNC. Initial AGC also had a negative effect in ΔAGCcum and ΔAGCin. ΔAGCin was also negatively related to CWM SLA. Aboveground primary productivity (AGPP) was negatively affected by FRO LNC. Together, these results suggest higher growth and recruitment rates, and high turnover of leaf production of species. Results from model selection indicated that ΔAGCcum in PEMS were mainly dependent of time since land abandonment, while the rate of AGCin (growth and recruitment) depended strongly in the variety of functional traits in the community for resource acquisition (Table 6.3, Fig. 6.3).

6.4 Discussion

Secondary forests are increasingly dominating tropical regions (Gibbs *et al*., 2010), but their role in carbon cycling and the factors controlling carbon pools in these ecosystems are still unclear (Houghton, 2005). Furthermore, there is still little understanding of how changes of tree diversity influence ecosystem processes in secondary forests, despite that rapid change in both species composition and ecosystem processes occur during succession (Becknell & Powers, 2014). We evaluated the effect of stand age and diversity components on net carbon accumulation (growth+recruitment−mortality), carbon gain (growth+recruitment only) and primary productivity in two secondary tropical dry forests (TDFs) to examine whether stand age or diversity components explained better the rates of change in carbon pools.

We expected that dry forests would show a change from conservative to acquisitive traits during succession, since early successional species are required to cope with hot, dry, and sunny microclimate, while late in succession conditions become moister and cooler allowing species for higher resource acquisition. We found partial support for this pattern in SRNP, with higher values of foliar nitrogen and phosphorus late in sucession. In PEMS, we found an increase of the community-weighted mean of SLA with stand age, while foliar nitrogen decreased. During succession, changes in functional traits may be explained by the niche hypothesis, which states that species segregate along a trade-off axis between competitive ability and rapid growth when resources are abundant, in contrast to low growth and high mortality when resources are limiting (Pacala & Rees, 1998). The positive increases in foliar nitrogen and phosphorus in SRNP, and SLA in PEMS suggest high resource conditions in late stages of succession. The positive increase in FRic in PEMS also suggest less resource use early in succession, as lower values of FRic indicates that some resources potentially available are not utilized (Mason *et al*., 2005), probably due to buffering of species against harsh environmental conditions (Tilman, 1996). The reductions in foliar nitrogen in PEMS may be related to changes in species composition along succession in PEMS, in particular a reduction in the species number of legumes which generally have high foliar nitrogen and tend to be more abundant in early stages of succession (Nunes *et al*., 2014).

The initial amount of aboveground carbon (AGCi) was tightly correlated with stand age, and was slightly higher in SRNP than PEMS. Nonetheless, AGCi had a strong effect in the rates of carbon accumulation (ΔAGCcum) and the rates of carbon increment (ΔAGCin) in PEMS, but it did not affect changes of carbon pools in SRNP. In PEMS, the rates of carbon accumulation and gain were also negatively related to the variety of functional traits in the community. This suggests that rates of change of carbon pools in PEMS are mainly driven by the amount of vegetation, with negative density dependence in this case, rather than by diversity components. Interspecific competition between pioneer and late successional species and consequent reductions of tree growth rates and survivals along succession due to competitive interactions may be the mechanisms associated with density-dependent effects (Guariguata & Ostertag, 2001). In PEMS, in fact, higher rates of growth, recruitment and mortality have been found in early stages of succession (Calvo-Rodríguez, 2012), which may be the result of strong competitive interactions in early succession. In PEMS there is a high dominance of the heliophile trees *Myracrodruon urundeuva, Handroanthus ochraceus* and *Mimosa hostilis*, which show the highest density and the highest growth rates of all species in the study area, with increments of

7–13 mm per year, while most species do not grow more than 5 mm year^{-1} in PEMS (Calvo-Rodríguez, 2012) or in other TDFs (Murphy & Lugo, 1986). The high success of these species in early succession appear related with a high leaf concentration of phenols, which allow them to reduce herbivory rates increasing the amount of carbon allocated to growth (Silva *et al*., 2011). Another factor that can explain higher turnover rates is the greater soil moisture and low acidity of plots in early succession, which suggest higher soil fertility compared to plots in late succession (Nunes *et al*., 2014).

We expected to find faster rates of AGC accumulation in SRNP, since this site has higher annual rainfall. Nonetheless, rates of AGC accumulation were similar to PEMS, although there is a lot of variation in carbon accumulation and gain in SRNP plots. Soils in PEMS have higher clay concentration and lower stone content, which suggest higher soil moisture (Nunes *et al*., 2014), which may be contributing to fast recovery of species in PEMS and could explain similar values to those presented in SRNP. We did not find any model explaining variation in AGC accumulation (growth plus recruitment minus mortality); neither stand age nor initial AGC influenced AGC accumulation over time. Estimates of recovery rates in TDFs have found that increases in biomass during succession could occur rapidly when remnants of old-growth forests were present in the region, because these forests can act as propagules source and facilitate the colonization of tree species that can be limited by dispersion (Read & Lawrence, 2003). In SRNP, however, there are no fragments of old-growth forests, which may reduce biomass accumulation rates and delay forest recovery. Human disturbance, including cultivation history and fire activity, may be important factors constraining the recovery of biomass carbon in this study site (Kalacska *et al*., 2004). Some studies in the same region have shown that tree growth rates as well as turnover of species distribution, which may influence changes in aboveground biomass, have been associated with soil properties and the duration and intensity of grazing (Powers *et al*., 2009; Carvajal-Vanegas & Calvo-Alvarado, 2014).

The lack of significant effects of stand age on AGC accumulation may be explained by differences in turnover rates of growth, recruitment and mortality with succession. Carvajal-Vanegas & Calvo-Alvarado (2014) found that recruitment rates tend to be highest early in succession (< 20 years of time since disturbance), while mortality and growth rates tend to be highest in intermediate stages (30-40 years) of succession. Thus, there is not a consistent decrease in carbon gain along succession, as carbon can accumulate early in succession due to increases in tree density, and can decrease in intermediate stages due to higher mortality rates. This mortality is associated with changes in species composition from pioneer species to more shade-tolerant and slow-growth trees, which tend to dominate in late succession (Carvajal-Vanegas & Calvo-Alvaado, 2014).

In contrast to what we found at the PEMS, diversity affected the rate of AGC increment (growth and recruitment only) in SRNP, specifically AGCin was mainly determined by functional richness, which explained 67% of the variation in carbon gain. This suggests that at the SRNP the main mechanism explaining diversity effects on AGC gain are related to niche complementarity rather than the mass-ratio hypothesis. In SRNP, the positive association between AGCin and FRic indicate that carbon capture may be enhanced in the community by differences in resource allocation (e.g., nutrients, light), resource efficiency, and the difference in functional traits among species (Hooper *et al*., 2005; Mason *et al*., 2005).

Primary productivity in PEMS was negatively affected by the functional regularity of foliar nitrogen and the community-weighted mean of leaf nitrogen concentration ($P = 0.06$), which decreased with stand age. This suggests that the heterogeneity in foliar nutrient is a factor than influence turnover rates, with greater leaf production in species with low evenness in foliar nitrogen or with low nitrogen concentration. Although, this result is against our expectations of high production rates in stands with high resource acquisition (e.g., high foliar nitrogen), perhaps other factors such as changes in species composition or herbivory rates may also influence primary production. Herbivores tend to prefer leafs with higher nutrient content (Silva *et al*., 2011), hence stands with a high heterogeneity of foliar nutrients, and high nutrient contents (e.g., nitrogen) may have higher herbivory rates. The increase in herbivory can be responsible for increases in leaf turnover rates by promoting leaf production, which could result in higher primary productivity in those stands. Overall patterns of ecosystems processes in PEMS suggest a recovery strongly dependent of stand age and initial biomass, with diversity components playing a minor role in accumulation of biomass carbon. Similar patterns have been found in other forest ecosystems where the direct effect of basal area on productivity is much larger than the effects of diversity in temperate forests in North America (Paquette & Messier, 2011) and Europe (Vilà *et al*., 2013).

The AGPP rate was positively associated with stand age and higher values of hetereogeneity in specific leaf area in SRNP. This result also supports the niche complementarity hypothesis for the positive increases in AGPP with variation in SLA along succession. The CWM of LNC and LPC also increased with stand age in this study site, which suggest a change from conservative to acquisitive strategies at SRNP, rather than the acquisitive-conservative continuum generally found in wet forests (Lohbeck *et al*., 2013). This result in SRNP was expected with stands with acquisitive traits (e.g., high values of SLA, LNC, and LPC) showing greater rates of primary productivity. In wet forests in general, primary production decreases with succession (Chazdon *et al*., 2007), but in TDFs the opposite pattern can be expected as functional traits in species may run from conservative to acquisitive strategies. In TDFs during succession, the environment changes from dry and hot to relatively moister and cooler (Lebrija-Trejos *et al*., 2011). Thus, early successional species have better drought-coping strategies and enhanced water use efficiency compared to late successional species (Alvarez-Añorve *et al*., 2012). In late stages then, species are geared toward high resource acquisition rates and high growth, which could enhance AGPP and AGC increment.

Understanding the factors driving the recovery of biomass carbon in secondary forests is critical to manage regenerating forests, and can be useful for restoration purposes. Our results indicate that the initial biomass and the time allowed for forest recovery are the main constraints for forest development in areas with low precipitation and high seasonality. Furthermore, our results highlight the role of different diversity components, and emphasize that depending of the ecosystem process (e.g., primary productivity, tree growth) some components may be more important than others. Thus, it is necessary to establish linkages in diversity as well as in biomass carbon to fully understand the factors controlling carbon accumulation rates after disturbance in regenerating forests.

6.5 References

Alvarez-Añorve, M.Y., Quesada, M., Sánchez-Azofeifa, G.A., Avila-Cabadilla, L.D. & Gamon, J. (2012) Functional regeneration and spectral reflectance of trees during succession in a highly diverse tropical dry forest ecosystem. *American journal of botany*, **99**, 816–26.

Anderson, D. R. (2008) *Model based inference in the life sciences: a primer on evidence* (p. 184). New York: Springer.

Batterman, S. A., Hedin, L. O., van Breugel, M., Ransijn, J., Craven, D. J., & Hall, J. S. (2013). Key role of symbiotic dinitrogen fixation in tropical forest secondary succession. *Nature*,

507, 90-101.

Becknell, J. & Powers, J. (2014) Stand age and soils as drivers of plant functional traits and aboveground biomass in secondary tropical dry forest. *Canadian Journal of Forest Research*, **613**, 604–613.

Bu, W., Zang, R. & Ding, Y. (2014) Field observed relationships between biodiversity and ecosystem functioning during secondary succession in a tropical lowland rainforest. *Acta Oecologica*, **55**, 1–7.

Calvo Rodríguez, S. C. (2012). Crecimiento diamétrico del bosque seco tropical en tres estadios sucesionales, Parque Estadual da Mata Seca, Estado de Minas Gerais, Brasil. Instituto Tecnológico de Costa Rica. Escuela de Forestal.

Carvajal-Vanegas, D. & Calvo-Alvarado, J. (2014) Tree diameter growth of three successional stages of tropical dry forest, Santa Rosa National Park, Costa Rica. *Tropical dry forests of the Americas: ecology,conservation and management* (ed. by J.S. Powers, G. Sánchez-Azofeifa, G.W. Fernandes and M. Quesada), pp. 351–364. CRC Press, New York, USA.

Castillo, M., Rivard, B., Sanchez-Azofeifa, A., Calvo-Alvarado, J., & Dubayah, R. 2012. LIDAR remote sensing for secondary Tropical Dry Forest identification. *Remote Sensing of Environment,* **121,** 132-143.

Chave, J., Andalo, C., Brown, S., Cairns, M.A., Chambers, J.Q., Eamus, D., Fölster, H., Fromard, F., Higuchi, N., Kira, T., Lescure, J.-P., Nelson, B.W., Ogawa, H., Puig, H., Riéra, B. & Yamakura, T. (2005) Tree allometry and improved estimation of carbon stocks and balance in tropical forests. *Oecologia*, **145**, 87–99.

Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G. & Zanne, A.E. (2009) Towards a worldwide wood economics spectrum. *Ecology letters*, **12**, 351–66.

Chazdon, R. L. (2014). *Second growth: The promise of tropical forest regeneration in an age of deforestation*. University of Chicago Press.

Chazdon, R.L., Letcher, S.G., van Breugel, M., Martínez-Ramos, M., Bongers, F. & Finegan, B. (2007) Rates of change in tree communities of secondary Neotropical forests following major disturbances. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, **362**, 273–89.

Clark, D., S. Brown, D. Kicklighter, J. Chambers, Thomlinson, J., & Ni, J. 2001. Measuring net primary production in forests: concepts and field methods. *Ecological Applications*

11, 356–370.

Cornelissen, J. H. C., Lavorel, S., Garnier, E., Díaz, S., Buchmann, N., Gurvich, D.E., Reich, P.B., ter Steege, H., Morgan, H.D., van der Heijden M.G. A., Pausas, J. P. & Poorter, H. 2003. A handbook of protocols for standardise and easy measurement of plant functional traits worldwide. *Australian Journal of Botany* **51**, 335-380.

FAO (2010) *Global Forest Resources Assessment* 2010. FAO Forestry, Rome.

Finegan, B., Peña‐Claros, M., Oliveira, A., Ascarrunz, N., Bret‐Harte, M. S., Carreño‐Rocabado, G., & Poorter, L. (2015). Does functional trait diversity predict above‐ground biomass and productivity of tropical forests? Testing three alternative hypotheses. *Journal of Ecology*, **103**, 191-201.

Garnier, E., Cortez, J., Billès, G., Navas, M.-L., Roumet, C., Debussche, M., Laurent, G., Blanchard, A., Aubry, D., Bellmann, A., Neill, C. & J. P., Toussaint, J.-P. (2004) Plant functional markers capture ecosystem properties during secondary succession. *Ecology*, **85**, 2630–263

Gibbs, H. K., Ruesch, A. S., Achard, F., Clayton, M. K., Holmgren, P., Ramankutty, N., & Foley, J. A. (2010) Tropical forests were the primary sources of new agricultural land in the 1980s and 1990s." *Proceedings of the National Academy of Sciences* **107**, 16732-16737.

Griscom, H. P., & Ashton, M. S. 2011. Restoration of dry tropical forests in Central America: A review of pattern and process. *Forest Ecology and Management* **261**, 1564–1579.

Guariguata, M. R., & Ostertag, R. (2001). Neotropical secondary forest succession: changes in structural and functional characteristics. *Forest ecology and management*, **148**, 185-206.

Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J., Vandermeer, J. & Wardle, D.A. (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs*, **75**, 3–35.

Houghton, R. A. (2005). Aboveground forest biomass and the global carbon balance. *Global Change Biology*, **11**, 945-958.

Hughes, R.F., Kauffman, J.B. & Jaramillo, V.J. (1999) Biomass, Carbon, and Nutrient Dynamics of Secondary Forests in a Humid Tropical Region of Mexico. *Ecology*, **80**, 1892.

IEF—Instituto Estadual de Florestas (2000) Parecer técnico para a criação do Parque Estadual da Mata Seca. Instituto Estadual de Florestas, Belo Horizonte.

Janzen, D.H. (2002) Tropical dry forest: Area de Conservacıón Guanacaste, northwestern Costa Rica. In: Perrow, M.R., Davy, A.J. (Eds.), *Handbook of Ecological Restoration*, vol. 2. Cambridge University Press, Cambridge, pp. 559–583.

Jaramillo, V., Martínez-Yrízar, A., & Sanford, R. 2011. Primary productivity and biogeochemistry of seasonally dry tropical forests. In: Young, H., Mooney, A., & Ceballos, G. (Eds.), *Seasonally dry tropical forests: ecology and conservation*, Island Press, USA, pp. 109–128

Kalacska, M., Sanchez-Azofeifa, G. a., Calvo-Alvarado, J.C., Quesada, M., Rivard, B. & Janzen, D.H. (2004) Species composition, similarity and diversity in three successional stages of a seasonally dry tropical forest. *Forest Ecology and Management*, **200**, 227–247.

Lebrija-Trejos, E., E. A. Pe´rez-Garcı´a, J. A. Meave, F. Bongers, and L. Poorter. (2010) Functional traits and environmental filtering drive community assembly in a species-rich tropical system. *Ecology,* **91**,386–398.

Lebrija-Trejos, E., Pérez-García, E.A., Meave, J.A., Poorter, L. & Bongers, F. (2011) Environmental changes during secondary succession in a tropical dry forest in Mexico. *Journal of Tropical Ecology*, **27**, 477–489.

Lohbeck, M., Poorter, L., Lebrija-Trejos, E., Martínez-Ramos, M., Meave, J.A., Paz, H., Pérez-García, E.A., Romero-Pérez, I.E., Tauro, A. & Bongers, F. (2013) Successional changes in functional composition contrast for dry and wet tropical forest. *Ecology*, **94**, 1211–1216.

Lohbeck, M., Poorter, L., Martínez-Ramos, M. & Bongers, F. (2015) Biomass is the main driver of changes in ecosystem process rates during tropical forest succession. *Ecology*, **96**, 1242-1252.

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

Mason, N.W.H., Mouillot, D., Lee, W.G., Wilson, J.B. & Functional, J.B. (2005) Functional richness, functional evenness and functional divergence : the primary components of functional diversity. **1**, 112–118.

Mouchet, M.A., Villéger, S., Mason, N.W.H. & Mouillot, D. (2010) Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. *Functional Ecology*, **24**, 867–876.

Mouillot, D., Mason, N.W.H., Dumay, O. & Wilson, J.B. (2005) Functional regularity: a neglected aspect of functional diversity. *Oecologia*, **142**, 353–359.

Murphy, P.G. & Lugo, A.E. (1986). Ecology of tropical dry forest. *Annual Review of Ecology and Systematics,* **17**, 67–88.

Nassar, J.M., Rodriguez, J.P., Sanchez-Azofeifa, A., Garvin, T.D. & M. Quesada. (2008). *Human, Ecological and Biophysical Dimensions of Tropical Dry Forests* Ediciones IVIC. 135 Pp.

Nunes, Y.R.F., Rodrigues da Luz, G., de Souza, S.R., da Silva, D. L., Veloso, M.D.M., Espírito-Santo, M.M. & dos Santos R.M. (2014) Floristic, structural, and functional group variations in tree assemblages in a Brazilian tropical dry forest: effects of successional stage and soil properties. Tropical Dry Forest Ecological Succession in Mexico: Synthesis of a Long-Term Study. *Tropical dry forests of the Americas: ecology, conservation and management* (ed. by J.S. Powers, G. Sánchez-Azofeifa, G.W. Fernandes and M. Quesada), pp. 325−346. CRC Press, New York, USA.

Pacala, S.W. & Rees, M. (1998) Models suggesting field experiments to test two hypotheses explaining successional diversity. *American Naturalist*, **152**, 729–737.

Paquette, A. & Messier, C. (2011) The effect of biodiversity on tree productivity: from temperate to boreal forests. *Global Ecology and Biogeography*, **20**, 170–180.

Poorter, L., Wright, S.J., Paz, H., Ackerly, D.D., Condit, R., Ibarra-Manriques, G., Harms, K.E., Licona, J.C., Martinez-Ramos, M., Mazer, S.J., Muller-Landau, H.C., Pena-Claros, M., Webb, C.O. & Wright, I.J. (2008) Are functional traits good predictors of demographic rates? Evidence from five Neotropical forests. *Ecology*, **89**, 1908-1920.

Powers, Jennifer S., Becknell, J. M., Irvin, J. & Perez-Aviles, D. (2009) Diversity and structure of regenerating tropical dry forests in Costa Rica: geographic patterns and environmental drivers. *Forest Ecology and Management* **258**, 959-970.

Powers, J.S. & Tiffin, P. (2010) Plant functional type classifications in tropical dry forests in Costa Rica: leaf habit versus taxonomic approaches. *Functional Ecology*, **24**, 927–936.

Quesada, M., Sanchez-Azofeifa, G.A., Alvarez-Añorve, M., Stoner, K.E., Avila-Cabadilla, L., Calvo-Alvarado, J., Castillo, A., Espírito-Santo, M.M., Fagundes, M., Fernandes, G.W., Gamon, J., Lopezaraiza-Mikel, M., Lawrence, D., Morellato, L.P.C., Powers, J.S., Neves, F.D.S., Rosas-Guerrero, V., Sayago, R. & Sanchez-Montoya, G. (2009) Succession and management of tropical dry forests in the Americas: Review and new perspectives. *Forest Ecology and Management*, **258**, 1014–1024.

R Development Core Team. 2012. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0.

Read, L., Lawrence, D. (2003) Recovery of biomass following shifting cultivation in dry tropical forests of the Yucatan. *Ecological Applications*, **13,** 85–97.

Ruiz-Jaen, M.C. & Potvin, C. (2011) Can we predict carbon stocks in tropical ecosystems from tree diversity? Comparing species and functional diversity in a plantation and a natural forest. *The New Phytologist*, **189**, 978–987.

Sánchez-Azofeifa, G. A., Quesada, M., Rodríguez, J. P., Nassar, J. M., Stoner, K. E., Castillo, A., & Cuevas-Reyes, P. (2005) Research Priorities for Neotropical dry forests. *Biotropica*, **37**, 477-485.

Sánchez-Azofeifa, G. A., Powers, J. S., Fernandes, G. W. & Quesada, M. 2014. *Tropical Dry forests of the Americas: Ecology, Conservation, and Management*. CRC Press, New York.

Silva, J. O., Espírito-Santo, M. M., & Melo, G. A. (2011). Herbivory on Handroanthus ochraceus (Bignoniaceae) along a successional gradient in a tropical dry forest. *Arthropod-Plant Interactions*, **6**, 45-57.

Tilman, D. 1996. Biodiversity: population versus ecosystem stability. *Ecology* **77**, 350-363.

van Breugel, M., Ransijn, J., Craven, D., Bongers, F. & Hall, J.S. (2011) Estimating carbon stock in secondary forests: Decisions and uncertainties associated with allometric biomass models. *Forest Ecology and Management*, **262**, 1648–1657.

Vilà, M., Carrillo-Gavilán, A., Vayreda, J., Bugmann, H., Fridman, J., Grodzki, W., & Trasobares, A. (2013). Disentangling biodiversity and climatic determinants of wood production. *PloS one*, **8**, e53530.

6.6 Tables and Figures

Table 6.1. Definitions, abbreviations and units of variables used to evaluate the main drivers of aboveground carbon storage (AGC in Mg C ha^{-1} year^{-1}) in secondary dry forests.

Abbreviation	Definition	Relevant hypothesis
ΔAGCcum	AGC accumulation = growth + recruitment - mortality	
ΔAGCin	AGC increment = growth + recruitment	
AGPP (Mg ha^{-1} year^{-1})	Aboveground primary productivity	
AGCi (Mg C ha^{-1})	Initial aboveground carbon storage	Density-dependent effects
SRi	Number of species in the first census	Niche complementarity
FRic	Functional group richness	Niche complementarity
FDiv	Multi-trait functional divergence	Niche complementarity
FRO SLA (cm^2 g^{-1})	FRO Specific leaf area	Niche complementarity
FRO LNC (% mass)	FRO Leaf nitrogen concentration	Niche complementarity
FRO LPC (% mass)	FRO leaf phosphorus concentration	Niche complementarity
CWM	Community-weighted mean	
CWM SLA (cm^2 g^{-1})	CWM Specific leaf area	Mass-ratio hypothesis
CWM LNC (% mass)	CWM Leaf nitrogen concentration	Mass-ratio hypothesis
CWM LPC (% mass)	CWM leaf phosphorus concentration	Mass-ratio hypothesis

Table 6.2. Bivariate relationship between carbon pools, stand age, and diversity components for two tropical dry forests. Regression coefficients (β) and significance levels (*P*-values) are shown; significant levels are in bold.

	Santa Rosa National Park								Parque Estadual da Mata Seca							
	AGCi		ΔAGCcum		ΔAGCin		AGPP		AGCi		ΔAGCcum		ΔAGCin		AGPP	
Variable	β	*P*	β	*P*	β	*P*	β	*P*	β	*P*	β	*P*	β	*P*	β	*P*
AGCi	–	–	0.0	0.54	0.1	0.26	0.1	0.06	–	–	−0.2	**<0.01**	−0.1	**0.01**	0.4	0.06
Stand age	1.5	**<0.01**	0.1	0.37	0.1	0.14	0.1	**<0.01**	1.3	**<0.01**	−0.2	**<0.01**	−0.1	**0.02**	0.6	0.15
SRi	2.1	**0.03**	−0.1	0.57	0.2	0.16	0.1	0.14	2.8	**<0.01**	-0.7	0.01	−0.5	**0.01**	0.5	0.42
FRic	31.5	0.68	7.5	0.63	24.8	**<0.01**	9.1	0.16	56.2	0.23	−12.9	0.27	−15.6	0.05	0.7	0.68
FDiv	−244.9	**<0.01**	2.4	9.31	−20.6	0.31	−16.9	0.14	138.8	**<0.01**	-32.3	**<0.01**	−22.8	**<0.01**	0.6	0.72
FRO SLA	196.7	0.07	3.9	0.87	18.4	0.32	20.8	**0.02**	16.9	0.74	−9.7	0.44	-9.8	0.27	−3.0	0.2
FRO LNC	59.2	0.65	−12.9	0.63	−36.6	0.04	1.3	0.91	−183.9	**<0.01**	25.6	0.14	13.2	0.3	**−6.7**	**<0.01**
FRO LPC	156.9	0.13	−4.6	0.84	18.2	0.27	9.5	0.33	−68.6	0.37	0.5	0.98	10.7	0.43	0.6	0.83
CWM SLA	0.4	0.3	2.7	0.84	0.0	0.75	0.1	0.05	0.3	0.42	−0.1	0.11	−0.1	**0.02**	0.0	0.9
CWM LNC	73.7	0.03	−6.8	0.4	2.8	0.65	5.7	0.08	−85.7	**<0.01**	11.0	0.13	2.8	0.6	−2.8	0.06
CWM LPC	145.9	9.01	−104.8	0.46	45.5	0.68	97.1	0.09	33.4	0.76	24.1	0.37	38.3	**0.03**	0.0	0.9

Table 6.3. Model selection results for the effect of stand age and diversity components on carbon pools in two tropical dry forests. The second order Akaike's Information Criterion (AICc), and the differential AICc (ΔAICc) are shown. Best models (ΔAICc < 2) are indicated in bold.

	Santa Rosa National Park								Parque Estadual da Mata Seca							
	AGCi		ΔAGCc		ΔAGCin		AGPP		AGCi		ΔAGCc		ΔAGCin		AGPP	
Variable	AICc	ΔAICc	AICc	ΔAICc	AICc	ΔAICc	AICc	ΔAICc	AICc	ΔAICc	AICc	ΔAICc	AICc	ΔAICc	AICc	ΔAICc
AGCi			65.2	4.3	59.1	8.2	46.2	7.2	–	–	116.5	2.6	105.5	2.8	32.1	4.2
Stand age	80.5	**0.0**	64.7	3.7	57.9	7.0	39.0	**0.0**	142.0	**0.0**	113.9	**0.0**	105.9	3.2	34.4	6.5
SRi	88.1	7.6	65.3	4.4	58.2	7.3	48.0	9.0	166.8	24.8	117.5	3.6	105.6	2.8	36.1	8.2
FRic	94.0	13.5	65.4	4.5	50.9	**0.0**	48.3	9.3	173.3	31.3	123.4	9.5	108.1	5.4	36.7	8.9
FDiv	82.1	**1.6**	65.7	4.8	59.4	8.5	48.0	9.0	163.1	21.1	116.1	2.2	102.7	**0.0**	36.8	8.9
Functional regularity																
SLA	89.8	9.3	65.7	4.8	59.5	8.6	44.1	5.1	174.9	32.9	124.1	10.2	111.2	8.4	34.9	7.1
LNC	94.0	13.5	65.4	4.5	55.2	4.3	51.0	12.0	165.7	23.7	122.4	8.5	111.3	8.6	–27.9	**0.0**
LPC	91.1	10.5	65.7	4.8	59.2	8.3	49.7	10.7	174.1	32.1	124.8	10.9	111.9	9.1	36.9	9.0
Community-weighted mean																
SLA	92.8	12.3	65.7	4.8	60.7	9.8	45.7	6.7	174.3	32.2	121.9	8.0	106.1	3.3	36.9	9.1
LNC	87.8	7.2	64.8	3.8	60.6	9.7	46.9	7.9	162.0	20.0	122.1	8.2	112.3	9.5	32.6	4.8
LPC	85.7	5.2	65.0	4.1	60.6	9.7	47.2	8.2	174.9	32.9	123.9	10.0	107.5	4.8	36.9	9.1

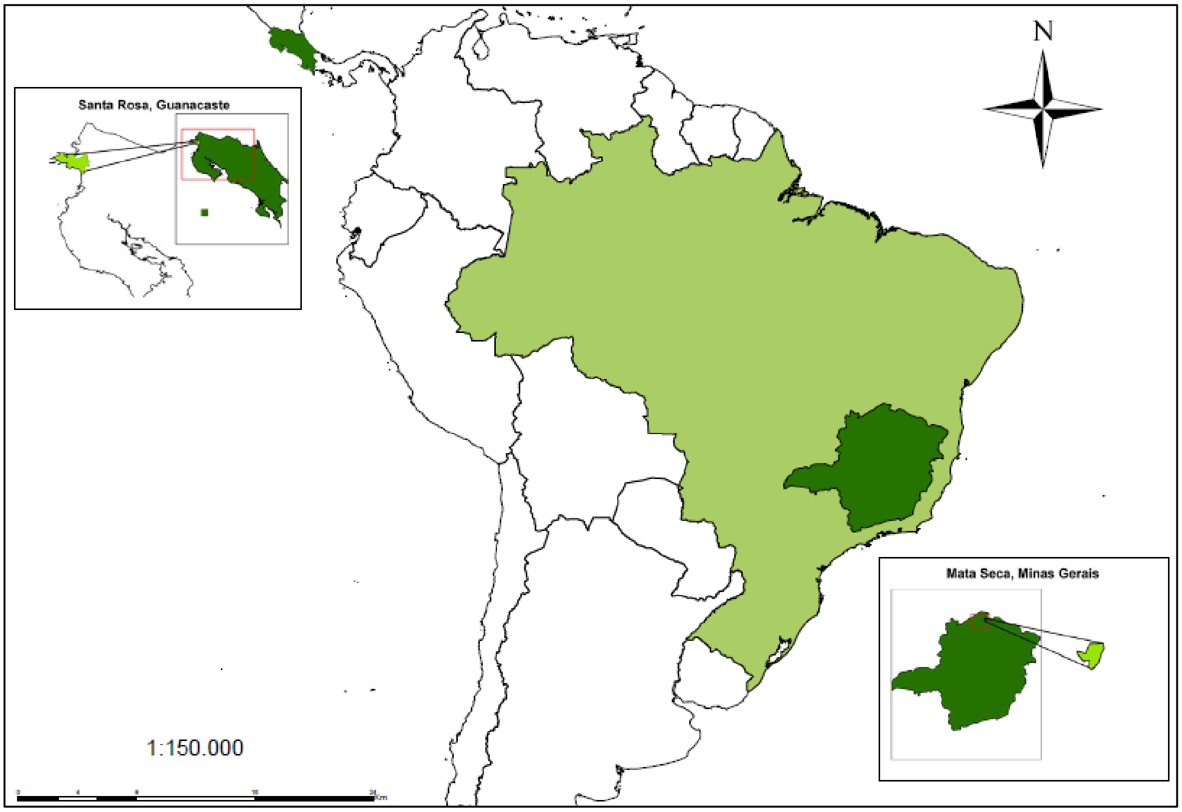


Figure 6.1. Location of the study areas: Santa Rosa National Park (SRNP) in Costa Rica, and Parque Estadual da Mata Seca (PEMS) in Brazil.

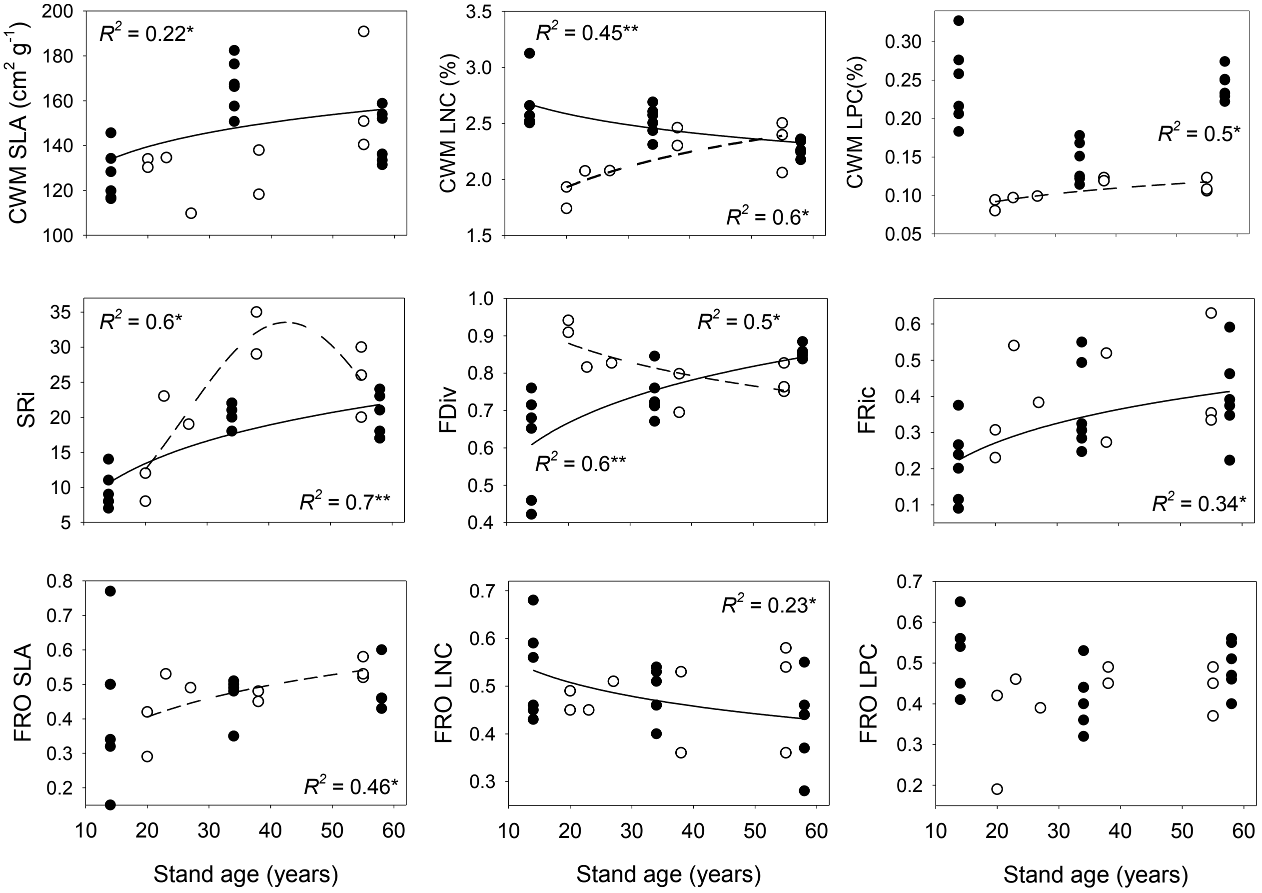


Figure 6.2. Changes in diversity components along succession in Parque Estadual da Mata Seca (PEMS, solid circles, *n* = 18 plots) and Santa Rosa National Park (SRNP, open circles, *n* = 9 plots). Regression lines (continuous in PEMS, dashed in SRNP) and coefficients of determination (R^2) are shown for significant relationships with the natural log of stand age. For abbreviations refer to Table 6.1. *$P < 0.05$; ** $P < 0.01$.

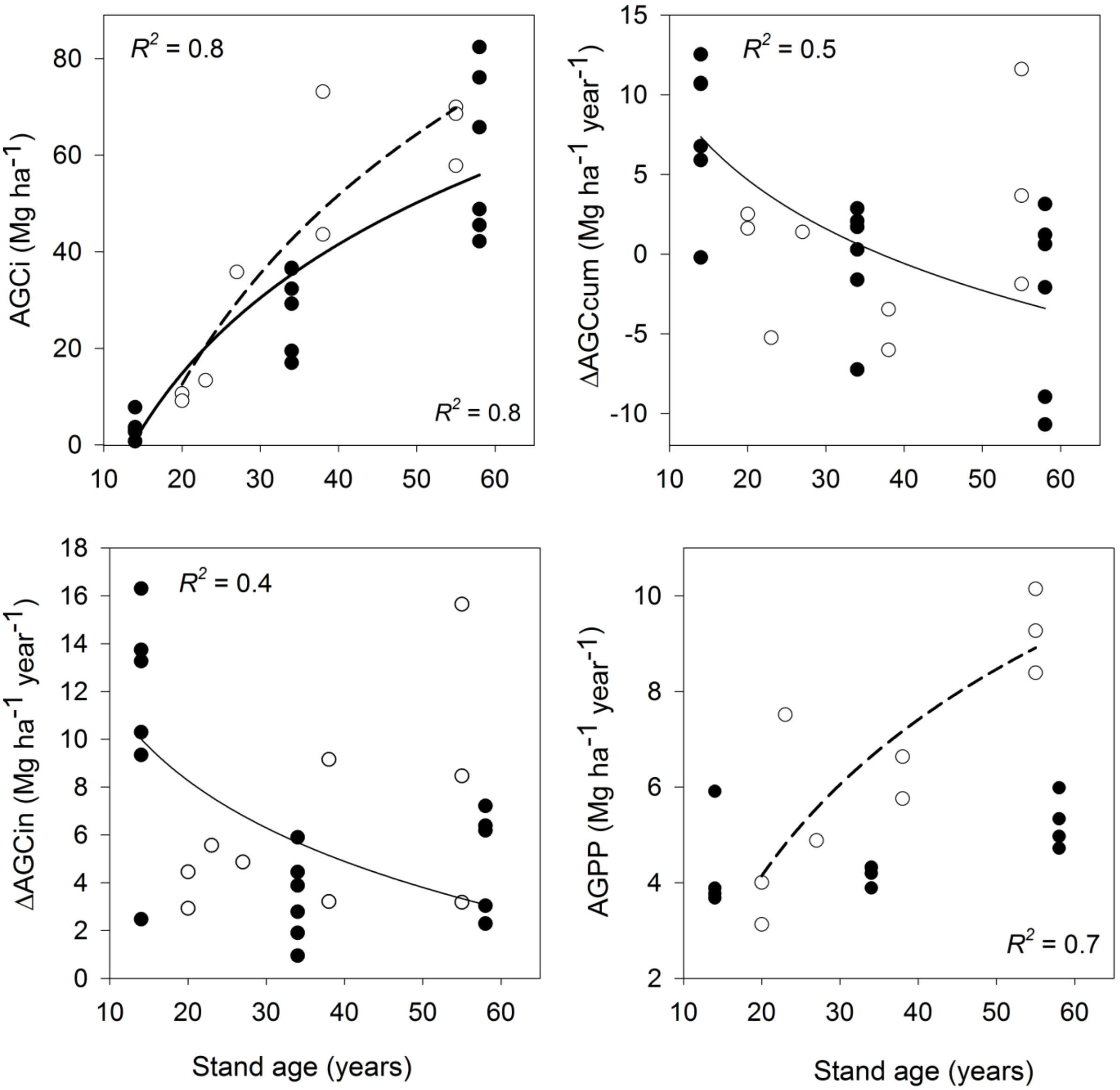


Figure 6.3. Effects of stand age on initial aboveground carbon storage (AGCi), aboveground carbon accumulation (ΔAGCcum), aboveground carbon increment (ΔAGCin), and aboveground primary productivity (AGPP) in two tropical dry forests. Symbols represent sites: circles, Parque Mata Seca in Brazil; triangles, Santa Rosa National Park in Costa Rica. Regression lines (continuous in PEMS, dashed in SRNP) and coefficients of determination (*R^2*) are shown for significant relationships with the natural log of stand age.

7. Synthesis

7.1 Conclusions

The objective of my dissertation was to evaluate the effect of plant biodiversity on aboveground carbon storage (AGC) in old-growth and second-growth tropical forests. Studies assessing variation in aboveground carbon storage (AGC) in old-growth forests have mainly focused on the role of climate (Stegen *et al*., 2011; Keith *et al*., 2009), while studies on AGC in second-growth forests have been limited to assess recovery rates of biomass after disturbance (Chazdon, 2014), but there has been a limited knowledge about the effect of different components of plant diversity, the evaluation of the relative importance of abiotic factors compared to diversity components, and the assessment of direct and indirect effects of both biotic and abiotic effects to disentangle the interactions among these components.

Much of the research described here is geared toward identifying the main predictors of AGC in old-growth and second-growth tropical forests, specifically focusing on the role of plant biodiversity in its broad sense. Tropical forests are important carbon sinks and hotspots of biodiversity, thus there is an increasing interest in identifying synergies that allow biodiversity preservation and ecosystem processes such as AGC (Strassburg *et al*., 2010). Nonetheless, there is still limited knowledge about the role of plant biodiversity or the effect of different components of plant diversity on AGC in tropical forests ecosystems because much research on AGC has focused on the role of climate. The overall results in this dissertation confirmed that plant biodiversity is a factor that has direct effects on ecosystem processes such as AGC, therefore can have indirect effects on human wellbeing (Fig. 1.1, MEA, 2005). Plant biodiversity can have positive and negative effects on AGC in tropical forests, depending of the component of plant diversity under assessment (Chapter 3-6). Specifically, plant functional types such as lianas could reduce AGC in moist forests, which harbor the greatest carbon stocks in tropical forests (Chapter 4). In second-growth dry forests, carbon stocks could be maximized by mixed-species stands, which have important implications for restoration and management of the remaining vegetation in dry regions (Chapter 5). Accumulation in AGC in secondary dry forests was mostly determined by land-use change, but diversity components such as functional traits, related with resource acquisition, also contributed to explain temporal changes in carbon capture and uptake (Chapter 6).

7.2 Contributions and significance

The literature review in Chapter 2 summarizes research on the effect of lianas in AGC, carbon capture and uptake in tropical old-growth and second-growth forests. This chapter synthesizes the literature into specific research needs to understand the role of lianas for carbon sequestration in tropical forests. Tropical forests are experiencing structural changes such as increases in temperature, seasonality, tree turnover rates, and liana abundance (Phillips & Lewis, 2014). The role of functional types such as lianas in carbon sequestration had been continuously emphasized, but to date no studies have evaluated their role for carbon storage using a comprehensive data set at global scales. At global scales I found that the abundance of lianas may reduce aboveground carbon storage (AGC) in tropical forests. Depending of the forest type different diversity components gain or lose importance for carbon storage. For example, in old-growth forests functional traits such as tree wood density and stand variables such as basal area and tree size appear to enhance AGC in wet and dry forests. In moist forests, however, the abundance of functional types such as woody climbers (lianas) could reduce AGC. Lianas have shown increases in abundance and biomass in tropical regions, but we still know little about the role of lianas for carbon cycling in secondary forests despite that lianas tend to proliferate in disturbed habitats (Chapter 2). My research is one of the first studies identifying lianas as a driver of change in AGC, enumerating the potential effects of lianas on AGC in secondary forests, illustrating the differential effect of lianas on AGC across forest types, and incorporating lianas in a conceptual framework to future assessments of AGC in tropical forests (Chapter 2-4).

Secondary succession remain as a central topic in ecology because second-growth forests currently occupy more area than old-growth forests, and might be the dominant ecosystem in the future in tropical regions (Wright, 2005). Nevertheless, our understanding of secondary succession in tropical dry forests (TDFs) has lagged behind the knowledge of successional processes in wet forests (Chazdon, 2014). TDFs, in contrast to wet forests, show a lower plant species richness, fewer canopy strata, high percentage of deciduous tree species (40–95%) during the dry periods and plant species mostly dispersed by wind dispersed in early successional stages (Mooney *et al*., 1995, Vieira & Scariot, 2006). These differences are likely to affect rates of change in vegetation structure and composition after disturbance in TDFs (Vieira & Scariot, 2006; Chazdon *et al*., 2007). Furthermore, most attempts to related plant diversity components in secondary forets have been conducted at local scales (Bu *et al*., 2014; Lohbeck *et al*., 2015, with limited knowledge in dry forests (Becknell & Powers, 2014), and to my knowledge there are not studies yet examining the main drivers of AGC accumulation in TDFs.

My research is one of the first multi-site analyses of the effect of species richness and functional diversity in seasonally dry forests (Chapter 5), and of the first studies identifying drivers of change of carbon capture and uptake in TDFs (Chapter 6). At regional and local scales I evaluated the role of plant biodiversity on AGC in secondary forests. Secondary forests are becoming increasingly dominant in tropical regions, and may likely become the dominant ecosystem in the future (Wright, 2005). Thus understanding the factors that control AGC in these ecosystems is essential. I focused on tropical dry forests and evaluated the role of stand age, climate, species richness and functional diversity on AGC at regional scales to attempt to make generalizations about the relative importance of each of these factors on AGC. I found that stand age was the most important driver of AGC in secondary forests, as it could be expected, but among the diversity components, I found that species richness and the community weighted mean of foliar phosphorus also contributed to explain variation in AGC across sites. Thus, both mechanisms the mass-ratio hypothesis and the niche complementarity effects are likely to explain the linkages between AGC and plant diversity (Chapter 5). This contributes to the long lasting debate about which element of biodiversity matters the most for ecosystem processes. The increase of tree-species richness along succession in the study areas, which reflects an increase of carbon storage, has important implications for management and restoration of degraded lands as carbon sinks can be maximized in higher mixed-species stands.

Finally, to ultimately understand whether biodiversity can be a driver of change in AGC in tropical forests, it is necessary to assess whether changes in AGC over time are positively or negatively influenced by any diversity component. To address this question, I took advantage of long-term data taken in two locations using a standardized experimental design, and evaluated changes in different carbon gain in two secondary dry forests. I found that the most important parameter controlling increases in AGC is the stand age (or age since land abandonment), and that in some cases biodiversity can be important for some ecosystem processes such as primary production, while in other cases the initial amount of plant biomass may be the most important factor to determine recovery of AGC in dry forets (Chapter 6).

7.3 Avenues for future research

This dissertation examined large data sets at global and regional level, which allowed making some inferences and generalizations at broad scales. Although my results highlighted the different patterns of the diversity-carbon storage relationship in different systems, little is still known about the mechanisms underlying the significant relationships found here. For example, in the first component about the role of lianas, it is unknown why lianas appear to have stronger effects on moist forests, despite their higher abundance in seasonally dry forests. This contradicts current literature that states that lianas have a competitive advantage over trees in tropical dry forests (TDFs), and that lianas may have deeper roots than trees in TDFs in order to continue growing in dry periods (Schnitzer, 2005; Schnitzer & Bongers, 2011; Tobin *et al*., 2012). Future studies should evaluate tree-liana competition in forests in broader gradients of precipitation, and specifically incorporate sites with extreme seasonality to determine whether lianas indeed have deeper roots than trees in TDFs or whether the water use strategies of both groups do not overlap and allow for niche differentiation rather than competition. Moreover, it is also necessary to incorporate infestation rates in studies evaluating tree-liana interactions in order to determine whether lianas reduce AGC due to a high proportion of infested trees or by removing high-biomass trees.

Research of patterns of distribution of lianas in second-growth forests are scarce, and current evidence of successional changes of liana abundance are mixed. For instance, one study found increases of liana biomass with forest age (Letcher & Chazdon, 2009), while others howed no variation (DeWalt *et al*., 2000; Feldpausch *et al*., 2005). Two studies found that liana density appears to increase with stand age up to 20 years of land abandonment, and then decrease (DeWalt *et al*., 2000; Letcher & Chazdon, 2009). In secondary dry forests, higher liana density has been found in stand ages of more than 30 years, but lower density in stands younger than 20 years, and older than 50 years (Kalacska *et al*., 2005). Consequently, what the main attributes that contribute to higher abundance of lianas in secondary forests are, and whether liana density decline consistently in secondary forests in dry and wet environments.

In treefall gaps, lianas can arrest forest succession by forming dense tangles early in succession, and are able to change the rate of biomass accumulation in regeneraging forests (Schnitzer *et al*., 2000; 2014). Nonetheless, it is still unknown whether lianas could arrest secondary succession in tropical forests as they do in forest gaps (Schnitzer *et al*., 2000), and if so whether this effect is generalized across dry, moist or wet forests. It is unknown whether lianas in secondary forests follow the similar distributional patterns as those found in old-growth forests, which showed that lianas have higher abundance in dry than moist and wet forests (Chapter 4).

My results from the effects of diversity on tropical dry forests highlighted the role of species richness. Due to the strong debate in previous years about whether species richness or functional diversity drives ecosystem processes, most studies have focused mainly on the latter, leaving species richness out and replacing it for indices of functional diversity (Díaz & Cabido, 2001; Díaz *et al*., 2007; Finegan *et al*., 2015). All indices should be evaluated simultaneously whenever the information is available, as the indices are related with different hypothesis, and each index also has different assumptions (Chapter 5, 6). With current statistical packages such as R, estimation of diversity indices is a fast process and including more variables could reduce the bias in interpretations. For example, several studies have tested the mass-ratio hypothesis with results supporting this mechanism (Garnier *et al*., 2004; Finegan *et al*., 2015). Nonethelesss, these studies did not test simultaneously niche complementarity, although previous studies indicate that these two mechanisms are not mutually exclusive (Thompson *et al*., 2005; Mokany *et al*., 2008). In the specific case of secondary forests, it is also fundamental to identify which species could enhance carbon storage, as these species can be used for restoration programs. By including functional diversity parameters alone, it is difficult to provide practical solutions for forest managers, although identifying the traits that maximize carbon capture in a community offers some potential (Laughlin, 2014).

My results also indicated that successional pathways in TDFs do not conform to the expected trajectories proposed for secondary succession in the literature. There is an enormous gap in this field, with most research focusing on secondary succession in wet forests even in the most recent compendium (Chazdon, 2014). In general, most successional models have been developed assuming that light is the strong limiting factor in regenerating forests, but in TDFs, water availability appears as the main constraint for forest development. Future studies should incorporate other factors not evaluated here such as the number of cycles of slash and burning, grazing intensity, and fire frequency to understand how land use history affects forest recovery in secondary forests. Incorporation of other landscape parameters such as fragment size, distance to nearest old-growth forests, and composition of the matrix surrounding TDF is also needed to assess other factors that may act at larger spatial scales.

A key unanswered question for tropical forests is how forests may change with current declines in biodiversity, and increases in turnover rates of woody species. Using modelling or simulation studies it is possible to run scenarios for the future of tropical forests that include: 1) potential changes of carbon storage under different species loss scenarios, 2) potential changes in carbon uptake in tropical forests related with increases in temperature and seasonality, 3) potential increases in forest productivity due to increases in atmospheric CO_2, and increases in liana abundance and biomass; and 4) a combination of all the different models to understand the relative importance of each scenario for the future or carbon sinks.

Finally, the belowground component, which was completely ignored in this study, also needs to be incorporated to fully understand how changes in water availability and nutrient resources in the soil may impact the accumulation of carbon storage in tropical forests. This is particular important in TDFs, since belowground carbon pools are very important for the maintenance of the aboveground component in water-constrained ecosystems (Pregitzer & Euskirchen, 2004).

7.3 References

Becknell, J. & Powers, J. (2014) Stand age and soils as drivers of plant functional traits and aboveground biomass in secondary tropical dry forest. *Canadian Journal of Forest Research*, **613**, 604–613.

Bu, W., Zang, R. & Ding, Y. (2014) Field observed relationships between biodiversity and ecosystem functioning during secondary succession in a tropical lowland rainforest. *Acta Oecologica*, **55**, 1–7.

Chazdon, R. L. (2014). *Second growth: The promise of tropical forest regeneration in an age of deforestation*. University of Chicago Press.

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

Díaz, S., & Cabido, M. 2001. Vive la différence: plant functional diversity matters to ecosystem processes. *Trends in Ecology and Evolution*, **16,** 464–655.

Díaz, S. & Lavorel, S. (2007) Incorporating plant functional diversity effects in ecosystem service assessments. *Proceedings of the National Academy of Sciences*, **104**, 20684-20689.

Feldpausch, T.R., Riha, S.J., Fernandes, E.C.M. & Wandelli, E. V. (2005) Development of Forest Structure and Leaf Area in Secondary Forests Regenerating on Abandoned Pastures in Central Amazônia. *Earth Interactions*, **9**, 1–22.

Finegan, B., Peña-Claros, M., Oliveira, A., Ascarrunz, N., Bret-Harte, M. S., Carreño-Rocabado, G., & Poorter, L. (2015). Does functional trait diversity predict above-ground biomass and productivity of tropical forests? Testing three alternative hypotheses. *Journal of Ecology*, **103**, 191-201.

Garnier, E., Cortez, J., Billès, G., Navas, M.-L., Roumet, C., Debussche, M., Laurent, G., Blanchard, A., Aubry, D., Bellmann, A., Neill, C. & J. P., Toussaint, J.-P. (2004) Plant functional markers capture ecosystem properties during secondary succession. *Ecology*, **85**, 2630–263

Keith, H., Mackey, B.G. & Lindenmayer, D.B. (2009) Re-evaluation of forest biomass carbon stocks and lessons from the world's most carbon-dense forests. *Proceedings of the National Academy of Sciences*, **106**, 11635-11640.

Laughlin, D. C. (2014). Applying trait-based models to achieve functional targets for theory-driven ecological restoration. *Ecology letters*, **17**, 771.784.

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

Lohbeck, M., Poorter, L., Martínez-Ramos, M. & Bongers, F. (2015) Biomass is the main driver of changes in ecosystem process rates during tropical forest succession. *Ecology*, **96**, 1242-1252.

MEA. (2005) *Ecosystems and human well-being: current state and trends, Volume 1*. Island Press, New York.

Mokany, K., Ash, J. & Roxburgh, S. (2008) Functional identity is more important than diversity in influencing ecosystem processes in a temperate native grassland. *Journal of Ecology*, **96**, 884–893.

Mooney, H.A., Bullock, S.H. & Medina, E. (1995) *Seasonally Dry Tropical Forests*. Cambridge, Cambridge University Press.

Phillips, O. & Lewis, S. (2014) Recent changes in tropical forest biomass and dynamics. *Forests and Global Change*, **4**, 77-108

Pregitzer, K. S. & Euskirchen, E. S. (2004). Carbon cycling and storage in world forests: biome patterns related to forest age. *Global Change Biology*, **10**, 2052-2077.

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

Schnitzer, S.A. & Bongers, F. (2011) Increasing liana abundance and biomass in tropical forests: emerging patterns and putative mechanisms. *Ecology letters*, **14**, 397-406.

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

Schnitzer, S. A., van der Heijden, G.M.F., Mascaro, J. & Carson, W.P. (2014) Lianas in Gaps Reduce Carbon Accumulation in a Tropical Forest. *Ecology*, **95**,3008–3017.

Stegen, J.C., Swenson, N.G., Enquist, B.J., White, E.P., Phillips, O.L., Jørgensen, P.M., Weiser, M.D., Monteagudo Mendoza, A. & Núñez Vargas, P. (2011) Variation in above-ground forest biomass across broad climatic gradients. *Global Ecology and Biogeography*, **20**, 744–754.

Strassburg, B. B., Kelly, A., Balmford, A., Davies, R. G., Gibbs, H. K., Lovett, A. & Rodrigues, A. S. (2010). Global congruence of carbon storage and biodiversity in terrestrial ecosystems. Conservation Letters, 3, 98-105.

Thompson, K., Askew, A.P., Grime, J.P., Dunnett, N.P. & Willis, A.J. (2005) Biodiversity, ecosystem function and plant traits in old-growth and imold-growth plant communities. *Functional Ecology*, **19**, 355–358.

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

Vieira, D.L.M. & Scariot, A. (2006) Principles of natural regeneration of tropical dry forests for restoration. *Restoration Ecology*, **14**, 11–20.

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